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ALUN RHUN HUGHES
on his 75th birthday,
to mark a lifetime of dedicated service to palaeoanthropology

Alun Hughes at Sterkfontein, where he has meticulously conducted an excavation programme since December, 1966.

Palaeont. afr., **28**, 1-8 (1991)

ALUN RHUN HUGHES: A TRIBUTE AFTER FORTY FOUR YEARS OF COMPANIONSHIP IN ANATOMY AND ANTHROPOLOGY

by

Phillip V. Tobias

Director, Palaeo-Anthropology Research Unit; Head, Department of Anatomy and Human Biology (1959 - 1990)
University of the Witwatersrand, Johannesburg

The Anatomy Department at the Wits Medical School has been blessed by many fine and long-serving staff members during the 72 years that have elapsed since its inception. A number of these true and faithful servants have given thirty or more years of service to the Anatomy Department. As far as I can trace only two people have served this Department for forty or more years: one is Alun Rhun Hughes and the other, myself, a fact commemorated in the title of this tribute.

By the time this *Festschrift* is scheduled to appear, at the celebration of Alun Hughes's 75th birthday on 16 July 1991, it will be a shade over forty-four years and two months since he started working under Professor R.A. Dart, in the Department of Anatomy. In this respect, too, Hughes has been one of a very small group of record holders: for I know of no other staff member who has remained on the payroll of the University up to so advanced an age, save for the late Dr. A.O.D. ("Bertie") Mogg in our Department of Botany, the late Professor H.H. Paine in the Department of Physics, and Mr. E.L. ("Eddie") Huddle, of the University's senior administrative staff.

What manner of man is this, who can serve with such perseverance, such loyalty, such patience, for so long a span of time?

EARLY LIFE AND CAREER

In the midst of World War I, Alun Hughes was born at Anglesey, North Wales, on 16 July 1916. He received his senior schooling at Lancing College, Sussex, where he passed the Oxford and Cambridge Schools Examination Certificate with five credits and London Matriculation Exemption. He early showed sterling qualities when, at school, he was Head of his House, a Prefect, Secretary of Athletics and recipient of an *A* Certificate in the Officers' Training Corps. After commencing university studies towards the B.Sc. degree, at the University College of Southampton in 1936, he emigrated to South Africa in 1937.

Afflicted from an early age with chest trouble, he was drawn to the dry, healthy climate of the eastern Orange Free State. There he spent a year as a teacher under the Society of the Sacred Mission at Modderpoort. He taught English and Mathematics to high school pupils and to black learner-teachers. In 1938, he registered as a first year medical student at the University of the Witwatersrand. A year later, as a second year medical student, he first set foot in the Department of Anatomy, which was to be his spiritual home for over half of his life to date. Joining the South African Medical Corps in 1940, he was discharged as medically unfit in 1941. (His asthma and a tendency to severe chest infections have been lifelong ailments.)

Over the period from 1942 to 1946, while serving as a special constable with the Civic Guard, Hughes registered as a Science student at the University of the Witwatersrand. He completed courses in Botany and Geology, but did not write the final examinations owing to illness and lack of funds. In 1945, he assisted Dr. T.D. Hall and Dr. D. Meredith in their botanical research programme at the University Field Research Station, Frankenwald, under the aegis of Professor John F.V. Phillips, head of the Department of Botany.

Early in 1947, Hughes joined the administrative staff of the University, when he completed a stocktaking and costing of the various maintenance workshops with Mr. Robin Moore, at that time the University Maintenance Architect.

HUGHES IN THE ANATOMY DEPARTMENT

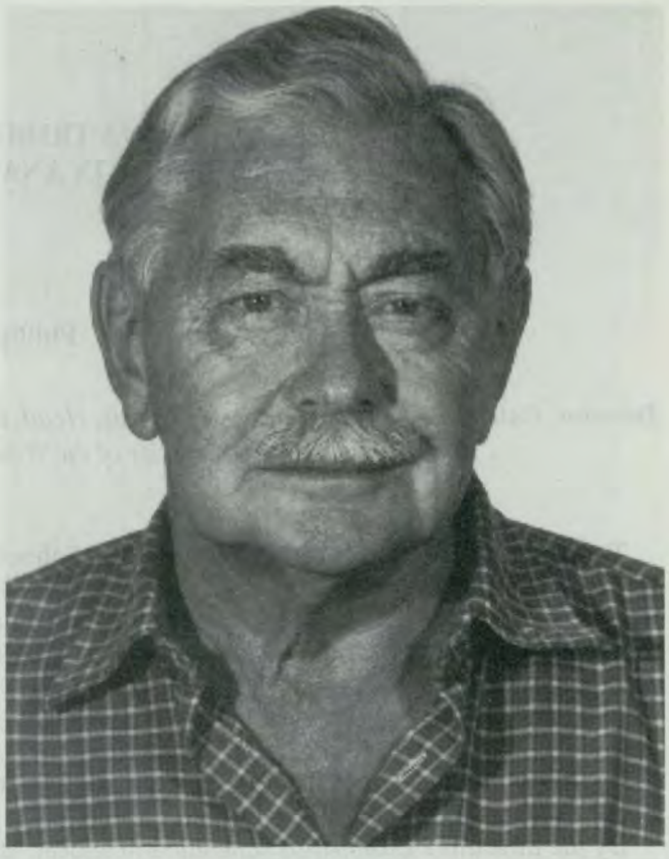
In May 1947, when he was thirty years of age, Alun Hughes became a Grade III Laboratory Assistant in the Anatomy Department under Professor R.A. Dart. Thereafter, he served continuously on a full-time basis in the same Department, for nearly twelve years under Professor Dart and for 26 years with myself. He rose through the ranks, becoming Senior Technician in April 1953 in succession to Eric E. Williams. In recognition of his personal technical skills, he was promoted to the post of Special Grade Technician in January 1963 and in July 1975 he became the Anatomy Department's first Chief Technician.

During those decades he mastered many skills. In the field these comprised survey work, retrieval of specimens and excavation techniques. In the Department, he ultimately had overall charge of the entire technical team of sixteen or more persons. He provided the head of the department with invaluable help in the allocation of tasks to individual technicians, the deployment of staff on specific assignments, the supervision and training of staff, the hiring, confirmation and promotion of technical officers, the investigation and determining of the technical needs of the Department, the budget and many other managerial responsibilities. Technically, he was a brilliant photographer; he displayed consummate artistry in making drawings, graphs and other illustrations for books, research articles and chapters. He became proficient at developing fossils from their matrix, and at restoring and reconstructing hominid skulls and other skeletal parts. In his heyday, there were few around the world who could hold a candle to him in these pursuits.

Not only did he master the niceties of these difficult techniques, but he shared them willingly with all who wished to learn. He imparted his experience and his ideas freely to the numerous visitors who, from 1959 onwards, came to the Anatomy Department in ever-increasing numbers, from both the New World and the Old World. His views were considered authoritative and were quoted in many publications.

In 1948, Dart placed Hughes in charge of the Hunterian Museum. He began recataloguing and reorganising the collections, including the dissected specimens and the human skeletal collections which were then housed in the basement of the Old Medical School in Hospital Hill. Along with the late Dr. A.G. Oettlé, then a brilliant research student and staff member of the Anatomy Department, he evolved a new method for the cataloguing and storing of the Department's collections. Hughes began to acquire and build up a hoard of extant animal skeletons, essential materials for the study and identification of the Plio-Pleistocene fossils that were accumulating in the Department from the early hominid and other sites. Similarly, along with myself, he gathered, catalogued and curated casts of fossil hominids from many parts, with the result that, when these are added to those assembled by Professor Dart, the Department holds today one of the largest such collections in the world.

Alun Hughes may be regarded as a foiled academic: had circumstances – especially medical and economic – been otherwise, there is no doubt in my mind that he would have made an outstanding professor. With his logical mind, his clear and flowing writing, his teaching of generations of B.Sc. and Honours students, his ability to turn a polished memorandum, and his long list of publications and reports, Hughes went a long way towards breaking down the formerly rigid barriers between academics and technicians and he spearheaded a new phase when such distinctions are rapidly becoming obsolete.



Alun Rhun Hughes

At the end of 1984, he retired from the full-time service of the University, as he had passed his 68th birthday on 16th July 1984. Despite his legal superannuation, the Foundation for Research and Development (Scientia, Pretoria) provided my Palaeo-anthropology Research Unit with funds sufficient to retain Alun Hughes's services as a part-time Senior Research Officer in charge of Field and Laboratory Operations, for each year from 1985 to 1990, while similar funding by the Wits Research Committee has permitted an extension of this arrangement to 1991.

HUGHES IN THE UNIVERSITY

Mr Hughes's outstanding administrative and organisational skills were recognised by his peers when, in 1954, he was elected as the Medical School representative on the Executive Committee of the Technicians and Maintenance Staff Association of the University. He served for an unprecedented 21 years (1960-1981) as the Chairman of that Association. His competency as spokesman and his ability to produce a carefully worded, persuasive and logical memorandum stood him in excellent stead in overtures to the University authorities – sometimes grievances complained of, more often constructive proposals for the amelioration of conditions. I am able to testify to his impeccable and somewhat "laid-back" manner when he presided over the annual banquet of the

Association, at one time when I was the guest speaker. He did the honours of the occasion with style!

HUGHES AND MAKAPANSGAT

Alun Hughes's interest in digging up the past started when he was only 18 years old: at that time he helped excavate burials in the chalk of the Sussex Downs in England. Soon after his arrival in South Africa, he assisted J. Eddols in collecting artefacts and in locating rock paintings at Modderpoort, Orange Free State, as well as at Maseru and Leribe in Lesotho. These specimens later became part of the type collection of what came to be called for a time the "Modderpoort Culture", at the hands of Mr. B.D. ("Berry") Malan, the successor to Professor C. van Riet Lowe as Director of the South African Archaeological Survey.

In 1948, Professor R.A. Dart placed Hughes in charge of field operations at the Makapansgat Limeworks in the northern Transvaal. From that time, for more than a dozen years, Hughes spent periods at Makapansgat ranging from several weeks up to six months at a time. With the generous help of the University, the C.S.I.R. and the Leighton Wilkie Foundation of Des Plaines, Illinois, Dart made it possible for Hughes to hire workers from the local populace. At some periods, Hughes had up to 40 assistants in the field. His systematic sorting of the limeworks dumps over the years 1948 to 1960 was a monumental labour. During this time he completed the first survey of the Limeworks, the quarry excavations and the surrounding area. He personally discovered eleven of the fossil hominids entombed in the calcified cave earth of the Makapansgat Formation: these were called by Dart *Australopithecus prometheus*, but today they are assigned to *Australopithecus africanus transvaalensis*. Moreover, Hughes recognised the first coprolites in the deposit and made a study of them (1964). Apart from the hominid specimens, he recovered many tens of thousands of fossil bones of animals that lived at the same time as *A. africanus*.

It later became known that the hominids emanated from what Professor T.C. Partridge (1979) recognised as Members 3 and 4 of the Makapansgat Formation, of late Pliocene derivation. Member 3 was dated to some 3 million years before the present. As this dating is older than any of the datings claimed for Sterkfontein, Swartkrans, Kromdraai or Taung, the Member 3 hominids found by Hughes at Makapansgat are, thus far, the oldest hominids found in southern Africa. Though these Makapansgat hominids are contemporary with some of those found at Hadar in Ethiopia, and slightly older than the famous australopithecine partial skeleton of "Lucy", East Africa has yielded some more ancient hominids, such as those from the oldest deposits at Hadar, from Laetoli in Tanzania and from Maca in Ethiopia.

Not only did Hughes show his skill in the field; in the laboratory he carried out numerous reconstructions of the australopithecines and of other fossil hominids. He played an important role in the research programme of Professor Dart, making drawings, superimpositions, reconstructions and restorations, photographs, measurements and calculations. Hughes likewise helped with the survey and excavation of the Cave of Hearths near the Makapansgat Limeworks. He developed and photographed the probably late Middle Pleistocene hominid mandible recovered there by Ben Kitching in September 1947. Hughes assisted Dart in his preliminary study (1948) and myself in the later more detailed study (1968, 1971) of that jawbone, which I assigned provisionally to *Homo sapiens rhodesiensis*, an ascription supported by F.C. Howell (1978)

HUGHES AND HYAENAS

Hughes's concern with the habits of hyaenas dates back to 1948.

World-wide interest, indignation and controversy were aroused by R.A. Dart's claims that *Australopithecus* at Makapansgat used tools of bone, tooth and horn, the basis of his "Osteodontokeratic Culture". The polemic and the counter-claims that hyaenas had damaged and amassed the enormous quantities of bones, led Dart (1956) to question "the myth of the bone-accumulating hyaena". So Hughes started to study the habits of carnivores especially of hyaenas. He excavated hyaena lairs in the Kalahari Gemsbok National Park in the northern Cape Province, at Mala Mala near the Kruger National Park, on the farm *Uitkomst* north-east of Swartkrans in the Transvaal, at Klerksdorp in the south-western Transvaal and in East Africa.

When the University of the Witwatersrand agreed in 1957 to studies on the habits of Carnivora and porcupines in the Kalahari Gemsbok National Park, Hughes became a member of the National Parks Board of Trustees Committee on Scientific Research in the Gemsbok Park. This gave him the opportunity to pursue his personal project – on the habits of Carnivora in the Gemsbok Park. It became a "pet project" when, from 1958 to 1962 Alun Hughes kept his own brown hyaena at the Johannesburg Zoo, where he meticulously recorded its habits.

By 1960, it had begun to seem to Dart and Hughes that the large-jawed spotted hyaenas in South Africa chewed bones up so thoroughly that relatively little accumulation of bones occurred in hyaena lair deposits. Thus, Dart claimed that the habits of these kinds of hyaenas could not have been responsible for the accumulation of the hundreds of thousands of largely broken bones entombed in the cave deposit of Makapansgat.

In 1957 I had begun working with Dr. L.S.B. Leakey and Dr. Mary Leakey and, after 1959, when he and she had invited me to undertake the definitive study of Olduvai hominid 5 (the type specimen of *Australopithecus (Zinjanthropus) boisei*), I had enjoyed a close working association with them which was to last up to Louis Leakey's death in 1972. On one of my frequent visits to Nairobi, I raised with Leakey the question of the habits of hyaenas in relation to the accumulation of bones. He pointed out that the small-jawed East African striped hyaena did not masticate bones as vigorously as Hughes had found the larger-jawed spotted hyaena did. He took me to a known striped hyaena lair in a cave just below the Kinankop Plateau, on the flank of the Eastern Rift Valley. There I saw masses of bones, many of which, on superficial inspection, showed similar damage to that seen in the fossil deposit at Makapansgat. This was so important a turn in the argument that the Leighton Wilkie Foundation gave Hughes a grant in 1961 to proceed to East Africa to study the habits of striped hyaenas.

On this visit Hughes visited the Queen Elizabeth Park and the Kisoro Gorilla Sanctuary. [At Kisoro, some years previously Dart and I had set up a Witwatersrand University Uganda Gorilla Research Unit, under the local charge of Mr. W. Baumgartel and the more remote supervision of Professor Alexander Galloway at Kampala, and of Dr. Louis Leakey at Nairobi. Jill Donisthorpe was our first field-worker and she studied the habits of the mountain gorilla on the Virunga volcanoes in south-western Uganda of which she published an account in the *South African Journal of Science* in 1958.] Whilst in East Africa Hughes excavated a Middle Stone Age site and a porcupine lair at Olorgesaillie.

As a result of his field studies, Hughes produced a number of publications including an important paper in the *American Journal of Physical Anthropology* in 1954. It now seems clear that spotted hyaenas do on occasion accumulate bones in their lairs, though the picture may be complicated by the use of the same den by porcupines or by brown hyaenas. His work constituted a significant early essay in the new discipline of taphonomy. Hughes's findings are reviewed in detail in C.K. Brain's monumental "The Hunters or the Hunted?" (1981).

HUGHES AND STERKFONTEIN

During the 1960's, after the departure of Dr. J.T. Robinson from the Transvaal Museum for the University of Wisconsin, I was repeatedly urged to begin a new excavation at Sterkfontein. As a third year "Medical B.Sc." student, I had organised and led an all-student expedition to excavate there under the aegis of Dr. Robert Broom, in April 1945. Moreover, I had taken parties of medical, dental, therapy, nursing and science students to visit and learn about Sterkfontein, in 1946 (when I and my colleagues organised a Prehistory Week at the Wits Medical School) and annually since 1951. So I was naturally drawn to the famous Sterkfontein site, from which, in August 1936, Broom had recovered the first adult australopithecine which he had made the holotype of a new genus and species, *Plesianthropus transvaalensis*. Later, at the hands of Robinson (1954), it had come to be assigned to *Australopithecus africanus transvaalensis*.

A number of reconnaissance visits were organised to the site in the middle 1960's: I was accompanied and advised by Alun Hughes, R.A. Dart, H.B.S. Cooke, A.S. Brink and, above all, R.J. Mason. Of all those who were coercing me to open a new "dig" at Sterkfontein, none was more insistent than Hughes. Our excavation at Makapansgat, which I had "inherited" from Dart in 1959, had ground to a halt and Hughes, confined for a time to the departmental laboratories, was chafing to get back to systematic field work. In 1966, having succeeded in raising generous subvention from the University and from the Council for Scientific and Industrial Research, I decided to recommence excavation at Sterkfontein. Field-work started about the centenary of the birth of R. Broom (30 November 1866). Naturally, I placed Alun Hughes in charge of operations and his delight and enthusiasm at the resumption of field work were infectious.

From December 1966 until the present – an unbroken 24 years by the end of 1990 – he has run the field excavation, five days a week, for some 48 weeks a year, with a field team of 8 to 10 persons under his direction. This makes the Sterkfontein "dig", which he has meticulously conducted, the most intensive and prolonged unbroken excavation of a single site ever undertaken. In that time, he has assisted Professor I. Watt in the topographical survey of the site, Professor T. C. Partridge (1978) in the stratigraphic and geomorphological study of the Sterkfontein Caves and Formation, the late Dr. A.O.D. Mogg in the botanical survey of the area, undertaken the fencing of the site and of dangerous sinkholes in its vicinity, run the entire field operation, and caringly looked to the welfare of the field staff. He and the field-aides have recovered masses of valuable fossils, including over 550 hominid fossils, about 4 335 baboon and monkey specimens, about 116 000 non-primate fossils, over 45 000 microfaunal fossils and some 6 000 foreign stone specimens and implements, specimens of wood and of ostrich eggshell.

Among the more spectacular finds he has made at Sterkfontein are the first skull of a member of the genus *Homo*, probably *Homo habilis*, from Member 5 (1976), the first fossil wood from the site (1982), an admirable partial skeleton of an australopithecine (1987) and an excellent, nearly complete cranium of *A. africanus* (1989).

The University of the Witwatersrand has made it possible for the excavation to be continued in 1991 and it is our hope that it will be maintained until the end of 1993, when, with my retirement from the full-time staff of the University, it is expected that the Palaeo-anthropology Research Unit will cease to operate.

With 13 years of work at Makapansgat and 24 years at Sterkfontein, Hughes is the most experienced excavator of consolidated deposits in dolomitic limestone caves in the world. Small wonder that his advice and help are often sought.

All of his studies on the sites and the fossils recovered from them were thorough, painstaking and thoughtful and they went far beyond mere technical exercises. His knowledge of, and views on, the australopithecine fossils and sites have come to be widely respected. For over thirty-five years he has conducted countless visitors from all parts of the world, including numerous specialists, and parties of students around Makapansgat and Sterkfontein, and in his own right has become an authority on these sites.

HUGHES AND TAUNG

In 1951 Alun Hughes, along with James Kitching and myself, excavated a prehistoric cave deposit, into which the Buxton limeworkers at Taung had blasted. From this site Later Stone Age tools, a San-like calvaria and numerous, isolated, deciduous and permanent human teeth were recovered. Some 30 years later, when I began exploring the possibility of resuming excavation at or close to the site of the discovery of the type specimen of *Australopithecus africanus* in November 1924, the counsel and help of Hughes were invaluable during several reconnaissance visits to the Buxton Limeworks. When the new preliminary excavations started in 1983-1984, and the definitive programme in 1988, once again Alun Hughes's advice and assistance were made freely available to myself and to the two officers to whom the conducting of the field operations was entrusted, namely Dr. M. Toussaint (in 1988) and Dr. J.K. McKee (in 1989-1991). His help was especially valuable in our planning of the excavation at Hrdlicka's Pinnacle and he assisted McKee in positioning the extended grid over the excavation.

In September 1984, at the end of the Ancestors' Exhibition at the American Museum of Natural History in New York City, Hughes paid his first visit to the New World, expressly to bring the Taung child safely back to Johannesburg. On the same trip, he visited the Anthropology Department of the University of California at Berkeley, at the invitation of the Dr. F.C. Howell.

HUGHES AND 'SPRINGBOK FLATS MAN'

The name 'Springbok Flats Man' or, as R. Broom (1929) called him, 'Bushveld Man', was applied to the fossilised human skeleton that had been found by a road-making party under Bishop-Brown in 1929, on the farm Tuinplaas (formerly Tuinplaats), near the village of Settlers on the Springbok Flats about 130km north of Pretoria. The site was examined by C. J. Swierstra, curator of the Transvaal Museum, and H. Lang (1929) and, soon afterwards, by C. van Riet Lowe (1929), who excavated and close by recovered implements ascribed to the Middle Stone Age. Then the site was to all intents and purposes 'lost' for over twenty years. Hughes and I visited the area in 1952 in an endeavour to re-locate the discovery-site – in which persuit we found reason to believe we were successful and we made a thorough examination of the site.

For forty years Alun Hughes has retained an almost obsessional love affair with the specimen, which comprised a fragmentary cranium, mandible and a nearly complete postcranial skeleton. L.H Wells (1969) would have inclined to include it in the hypodigm of *H. sapiens afer*, though F.C. Howell (1978) did not allocate the Tuinplaas skeleton to this taxon because of uncertainty about either its relative or absolute age. P. V. Tobias (1972, 1974) concluded that it may well represent an Upper Pleistocene population ancestral to both the sub-Saharan African Negro and Khoisan populations. The only indirect pointers to the age of the skeleton are the presence of (1) the extinct long-horned buffalo, *Homoioceras [Bubalus] baini*, now lumped into *Pelorovis antiquus*, close to, and at the same level as, the human skeleton; (2) an extinct large horse, named *Equus capensis* by Broom (1909), supported by Churcher (1970) and Churcher and Richardson (1978), who rejected the earlier views of L.H. Wells that *E. capensis* was inderterminable and of H.B.S. Cooke that it fell within *E. helmei*, and of which we found an isolated molar *in situ* on our 1952 excursion; and (3) Middle Stone Age implements identified by Van Riet Lowe (1929) from the locality.

Aside from Broom's original announcement of the discovery in *Nature* in 1929, and G.W.H. Schepers' description of the mandible in 1941, little work had been carried out on this interesting fossilised skeleton.

In 1950 Hughes made a reconstruction of the skull and postcranial bones and, in 1955, he and the late Dr. M.J. Toerien (then a lecturer in the Anatomy Department) published the first account of the limb bones of Springbok Flats Man. Hughes presented his new reconstruction of the Tuinplaas skeleton to the Annual Congress of the South African Association for the Advancement of Science (Cape Town, 1952) and a later revised version to the Anatomical Society of Southern Africa (Durban, 1969) and a note was published on it in the *S.A. Medical Journal* in 1970.

In 1990, once again, Hughes came back to the Tuinplaas skeleton. This has now become even more important and relevant in the light of claims that the human skeletal remains from Border Cave, near the village of Ingwavuma, Kwazulu, and from Klasies River Mouth Caves, some 120 km west of Port Elizabeth, are the earliest remains of anatomically modern *H.sapiens*. The dates of both of these sets of remains, claimed to be over 100 000 years, have been questioned. Tuinplaas (whose cranium resembles the adult skull of Border Cave) would seem to be a third South African site from which an early, anatomically modern *H. sapiens* has been recovered, though how early seems to be at present indeterminate. This background adds point to Hughes's latest comprehensive assessment of the Tuinplaas skeleton, published in G. Sperber's new book, "*From Apes to Angels*" (1990). In this study Hughes publishes a new reconstruction of the Tuinplaas skull and a careful, comprehensive re-appraisal of the entire skeleton. Although he acknowledges that the dating still remains uncertain, he concludes that, if the skeleton is not less than 15 000 years old (as suggested by the evidence of associated finds), "it seems reasonable to infer that Tuinplaas man represents one of the protonegriform populations from which Negro and Khoisan ethnic groups later diverged." Perhaps it is time to attempt to apply some of the newer methods of dating to the Tuinplaas skeleton, as a quarter of a century has elapsed since K.P. Oakley obtained a tentative relative dating of the specimen.

OTHER FIELD VENTURES AND NATURAL HISTORY

Many other field surveys and excavations were conducted by Hughes, such as those to the Iron Age skeletons and artefacts collected by Mr. J. Fichardt on his farm Wellington Estate near Settlers, Central Transvaal (1951); the Anatomy Department expedition to Lake Chrissie to study the last-surviving San (Bushman) population in the Union of South Africa (1954); dolomitic cave breccia deposits at Rustenburg, Transvaal (1956); the expedition to "Vegkoppie" in the valley of the Lulu Mountains, Sekukuniland, eastern Transvaal (1956); and a visit, with J.W. Kitching, to the Zaka district of Zimbabwe to recover skeletons of elephant, buffalo and other animals (1957).

In 1958 he was invited to join Dr. D. Marais on his first Transafrican Waterways Expedition and to accompany Dr. F. Zumpt on his entomological expedition to northern Botswana. Two years later Hughes was inspecting a fossil site at Colenso in Natal and, in 1962, a fossil conifer site in the Senekal district of the Orange Free State. In 1963, the Barberton Municipality chanced upon pottery during the excavation of a new sewage disposal works: Hughes inspected and reported on this protohistoric occurrence. Later that year he recovered the skeletons of five white rhinoceroses in the Umfolozi Game Reserve, Natal. In the following year he represented Professor H.P.A. de Boom and myself at a meeting in that Reserve to discuss the proposed complete investigation of the white rhinoceros, a proposal greatly stimulated by the German engineer, industrialist and rhino-lover, Dr. W.T. Schaurte (who for a number of years made the Anatomy Department his "headquarters" for his natural history endeavours in southern Africa). A year later saw Alun Hughes participating, by invitation, in a meeting of the Rhinoceros Group of the Survival Service Commission of the International Union for the Conservation of Nature.

To his many interests Hughes added ornithology. He was a member of the S.A. Wild Life Protection Society from 1951 to 1970 and of the S.A. Ornithological Society from 1958 to 1970. Following on the earlier (unpublished) list compiled by A.C. Allison in 1945, Hughes between 1955 and 1962 prepared a list of the birds of the Makapansgat area in the Potgietersrus District, Transvaal. In 1960 he became a Founder Member of the Zoological Society of Southern Africa.

In all of these ventures he revealed his love of the African veld, its animals, its trees and other flora, its scenery and its rocks, and its people, past and present. During long, lonely months, spent in the research house that he and James Kitching built, in the Makapansgat valley, his Austin Roberts' *Birds of South Africa* (1940) and his binoculars were constant companions. He was a critical and enquiring observer.

HUGHES AND HUMAN BIOLOGY

Reference has already been made to some of Alun Hughes's physical anthropological and palaeoanthropological interests and activities. A few remain to be mentioned. During excavations on the site of the old Witwatersrand Deep Mine, human skeletons were encountered. Hughes and I together inspected the site in 1951: it turned out to be an old cemetery in which departed Chinese indentured mineworkers had been buried. Hughes exhumed some 36 skeletons from the site. It was never quite certain whether the cemetery had been for the exclusive use of Chinese persons: an assumption to this effect led to R.A. Dart's oddly entitled and oddly compounded paper, "A Hottentot from Hongkong" (1952).

In 1959, Hughes joined forces with P. Beaumont, then of the Archaeological Survey of the Union of South Africa, in excavating a burial at Brotherton near Cathedral Peak in Natal.

An interesting venture into human genetics was a study by Hughes and Dr. J.K.G. Grieves, also of the staff of the Anatomy Department, and members of the National Institute for Personnel Research, of a black family at *Singlewood* on the Springbok Flats, a number of whose members showed medium-grade microcephaly. The Hughes-Grieves article on this family was published in 1953.

ARTISTRY, PHOTOGRAPHY, MODELLING, EXHIBITING, MUSEOLOGY

A man of many talents, painstaking, methodical, artistic, Hughes became an accomplished photographer, displaying his camera craft in the field and the laboratory. For a dozen years he helped Professor Dart's research by making drawings, superimpositions, reconstructions, photographs, restorations and models. His photographs were published in *Life* magazine and the *Illustrated London News*, among many other periodicals, and in numerous articles and texts. After I assumed the headship of the Anatomy Department in 1959, he rendered similar valuable help in my research undertakings, especially in my studies on *A. boisei*, *H. habilis* and *H. erectus* from Olduvai and other East African sites.

He was most proficient in preparing and mounting exhibits. Outstanding examples were the displays he erected at the Rhodes Centenary Exhibition in Bulawayo, Rhodesia (now Zimbabwe) in 1953; at the Witwatersrand University Exhibitions in 1955, 1964 and 1974; at I.S.M.A. (Institute for the Study of Man in Africa) functions in Johannesburg in 1959, 1960, 1962 and in the great I.S.M.A. Exhibition in the Johannesburg City Hall in 1963. Hughes aided in the building up of the Museum of Man in Johannesburg by helping me pack and transport the Juan Fichardt Collection from the Springbok Flats, the Guy Atwater Gardner Collection from Nottingham Road, the Konrad White Collection from Klerksdorp, the Paul Lowenstein Collection from Ladybrand and the

Heinz Geldmacher Collection from the Krugersdorp district.

His innumerable contributions (excluding routine duties) have included the devising, with the late Dr. A.G. Oettlé, of a new method of cataloguing and storing the Anatomy Department's collections; the building up of the Anatomy Department's large collection of animal skeletons; the making, mounting and displaying of life-masks of human faces; the provision of photographic assistance to the Departments of Geology and Archaeology and to the Bernard Price Institute for Palaeontological Research.

CONCLUSION

Alun Hughes's contributions to the advancement of anatomical, physical anthropological and palaeoanthropological sciences have been unusual, indeed unique. They have unquestionably redounded to the credit and advantage of the University and of South African science at large. His qualities were recognised when he was awarded a Certificate of Merit by the South African Association for the Advancement of Science (1967) for "service to the advancement of knowledge in the field of Physical and Palaeo-anthropology". They were acknowledged also when he was made an Honorary Senior Field Research Officer of the Bernard Price Institute for Palaeontological Research (1976), an Associate Member of the Transvaal Museum, Pretoria, for his services rendered to that great institution (1981) and a Master of Science *honoris causa* of the University of the Witwatersrand (1985). His single-minded devotion to his researches, to the interests of the University and of a number of its departments, his unselfish willingness at all times to help the work of others, his patient, back-breaking, often unrewarding, protracted fieldwork – all these and many more traits mark him as one who richly deserves the accolade of this 75th Birthday Festschrift.

As I look back on the 44 years in which our paths have crossed and criss-crossed in a fruitful and productive interaction, I am conscious of a sense of profound gratitude to him. After the dozen years of dedicated service he had given to that veritable father-figure, Professor Dart, it could not have been easy for him to fall suddenly under a man over nine years his junior, when I assumed the stewardship of the Anatomy Department in 1959. Yet he gave me unstinting support, backing, encouragement and guidance – and has continued to do so these last 32 $^1/_2$ years. Thank you Alun: may you be blessed with reasonable health, with peace of mind and with a sense of satisfaction at a job superbly done.

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REFERENCE LIST

BRAIN, C.K. 1981. *The Hunters or the Hunted? An Introduction to African Cave Taphonomy*, pp. 1-365. Chicago, Univ. of Chicago Press.

BROOM, R. 1909. On evidence of a large horse recently extinct in South Africa. *Ann. S. Afr. Mus.*, **7**, 281-282.

BROOM, R1929. The Transvaal fossil human skeleton. *Nature*, **123**, 415-416.

BROOM, R 1936. A new fossil anthropoid skull from South Africa. *Nature*, **138**, 486-8.

CHURCHER, C.S. 1970. The fossil Equidae from the Krugersdorp caves. *Ann. Transvaal. Mus.*, **26**(6), 145-168

CHURCHER, C.S and Richardson, M.L. (1978). Equidae. **In:** Maglio, V.J., Cooke, H.B.S., Eds., *Evolution of African Mammals*, 379-422. Cambridge, Cambridge University Press.

DART, R.A. 1948. The first human mandible from the Cave of Hearths, Makapansgat. *S. Afr. archaeol. Bull.*, **3**, 96-98.

DART, R.A. 1952. A Hottentot from Hong-Kong: pre-Bantu population exchanges between Africa and Asia. *S. Afr. J. med. Sci.*, **17**, 117-142

DART, R.A. 1956. The myth of bone-accumulating hyena. *Amer. Anthrop.*, **58**, 40-62.

DONISTHORPE, J. 1958. A pilot study of the mountain gorilla (*Gorilla gorilla beringei*) in South West Uganda, February to September, 1957. *S. Afr. J. Sci.*, **54**, 195-217.

HOWELL, F.C. 1978. Hominidae. **In:** Maglio, V.J., Cooke, H.B.S., Eds., *Evolution of African Mammals*, 70-156. Cambridge, Cambridge University Press.

HUGHES, A.R. 1954. Habits of hyaenas. *S. Afr. J. Sci.*, **18**, 19-30.

HUGHES, A.R. 1964. Report on coprolites from Late Stone Age cave Site (Scotts Cave) in the Gamtoos Valley. Unpublished Report, Department of Anatomy, University of the Witwatersrand.

HUGHES, A.R. 1970. The Springbok Flats skull. *S.A. Med. J.*, 2 May, 536.

HUGHES, A.R.1990. The Tuinplaas human skeleton from the Springbok Flats, Transvaal. **In:** Sperber, G.H., Ed., *From Apes to Angels: Essays in Anthropology in Honor of Phillip V. Tobias*, 197-214. New York, Wiley-Liss, Inc.

HUGHES, A.R. & GRIEVES, K.J.G. 1953. Medium grade microcephaly in a Bantu family. *S. Afr. J. Med. Sci.*, **18**, 19-30.

LANG, H. 1929. The discovery of the Springbok man. *Illustrated London News*, 16 March, 427-428.

LOWE, C. VAN RIET 1929. Notes on some stone implements from Tuinplaats, Springbok Flats. *S. Afr. J. Sci.*, **26**, 623-630.

PARTRIDGE, T.C. 1979. Re-appraisal of lithostratigraphy of Makapansgat Limeworks hominid site. *Nature*, **279**, 484-488.

ROBINSON, J.T. 1954. The genera and species of the Australopithecinae. *Am. J. Phys. Anthropol.*, **12**, 181-200.

SCHEPERS, G.W.H. 1941. The mandible of the Transvaal fossil human skeleton from Springbok Flats. *Ann. Transvaal Mus.*, **20**, 253-271.

SPERBER, G.H. 1990. (Ed.). *From Apes to Angels: Essays in Anthropology in Honor of Phillip V. Tobias* New York, Wiley-Liss, Inc.

TOERIEN, M.J. & HUGHES, A.R. 1955. The limb bones of Springbok Flats Man. *S. Afr. J. Sci.*, **53**(5), 125-128.

TOBIAS, P.V. 1968. Middle and early Upper Pleistocene members of the genus *Homo* in Africa. **In:** Kurth, G. Ed., *Evolution und Hominisation* (2nd Ed), 176-194. Stuttgart, Gustav Fischer Verlag.

TOBIAS, P.V. 1971. Human skeletal remains from the Cave of Hearths, Makapansgat, Northern Transvaal. *Am. J. Phys. Anthropol.*, **34**, 335-367.

TOBIAS, P.V.1972. Recent human biological studies in Southern Africa, with special reference to Negroes and Khoisans. *Trans. Roy. Soc. S.Afr.*, **40**(3), 109-133.

TOBIAS, P.V. 1974a. Springbok Flats man. **In:** *Standard Encyclopaedia of Southern Africa*, **10,** 232. Cape Town, Nasou Ltd.

TOBIAS, P.V. 1974b. Tuinplaas. **In:** *Standard Encyclopaedia of Southern Africa*, **10,** 652-653. Cape Town, Nasou Ltd.

WELLS, L.H. (1969). *Homo sapiens afer Linn.* Content and earliest representatives. *S. Afr. Archaeol. Bull.*, **24,** 172-173.

Palaeont. afr., **28**, 9-21 (1991)

DINOFELIS BARLOWI (MAMMALIA, CARNIVORA, FELIDAE) CRANIAL MATERIAL FROM BOLT'S FARM, COLLECTED BY THE UNIVERSITY OF CALIFORNIA AFRICAN EXPEDITION

by

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ABSTRACT

The collections made by the University of California African Expedition in 1947-48 at Bolt's Farm, near Sterkfontein, included some fine cranial and postcranial material of *Dinofelis barlowi*, associated with baboon skeletons and crania suggestive of a natural trap situation. The *Dinofelis* crania are described and compared with other species of this genus, generally lending support to Hemmer's view of a lineage *D. diastemata, D. barlowi, D. piveteaui*. The age of the deposit is estimated to be in the vicinity of 2 Ma.

INTRODUCTION

Bolt's farm lies due south of the celebrated ape-man site of Swartkrans and 3 km southwest of the Sterkfontein locality (fig. 1). Chance finds of fossils were made during small-scale lime quarrying operations by the farm owner, Mr W. Bolt, and by Dr Robert Broom in his reconnaissance of the area in 1936; several interesting specimens have been described, notably by Broom (1937, 1939, 1948) and Shaw (1938). In 1947 and 1948, the area was studied systematically by the Southern Section of the University of California African Expedition, under the leadership of Dr Charles Camp. A number of small patches of breccia were located and a considerable amount of fossil material was recovered by Dr Frank Peabody and, after crude preparation in the field, it was shipped back to the University of California at Berkeley for curation. At the invitation of the Director of the Museum of Paleontology, Dr R.A. Stirton, the present writer spent the period October 1957 to June 1958 at Berkeley for the purpose of developing and identifying the material but the resulting Report was not published. Peabody (1954) had completed a valuable account of the geology of the Taung deposits, including a list of the fossils then identified, but his untimely death in 1958 occurred before he had prepared any account of the material from the Transvaal deposits. However, the present writer was fortunate in having useful discussions with Dr Peabody and access to his field notes, as well as a subsequent opportunity to examine the deposits in the field . The collections were re-examined in 1975 during a lengthy stay in Berkeley and again updated in 1983 during a shorter visit. A new mustelid from Pit 10 has already been described (Cooke, 1985) and accounts of other "highlights" from the collections are in preparation, but the bulk of the material remains largely unpublished.

THE BOLT'S FARM DEPOSITS

The geological setting of the australopithecine breccias in the Sterkfontein area has been well described by Brain (1958), whose masterly analysis of the mechanisms of formation of the deposits and the characteristics imposed on the sediments by their genesis is still probably the best model available. Bolt's Farm was not specifically included in Brain's account. The cavities in which the breccias were deposited were formed in the dolomite limestones of the Chuniespoort Group of the Transvaal Sequence and have a generally northerly to northwesterly dip, varying locally as a result of minor folding. On Bolt's Farm the inclination is around 15° towards the northwest. The solution fissures on the farm are related to a joint or fracture system orientated at approximately 065° east of north, and there is a secondary fracture system at about 160°, solution having taken place most readily at the intersections of these two fracture systems.

Dr Peabody carried out a plane table survey of the Bolt's Farm area and assigned numbers to the individual collecting localities. Figure 1 is redrawn directly from his map and the names assigned to the localities are given in Appendix "A", together with the University of California Museum of Paleontology locality numbers. Topographically this area consists of the greater part of a rounded hill the crest of which is formed by a chert-rich zone in the limestones and rose some 50m above a small seasonal creek that runs northwards on the east side of the hill. Most of Peabody's sites have been destroyed in recent years by extensive quarrying and reliance must be placed on Peabody's field notes and on notes made in 1958 by the present writer.

The individual sites at Bolt's Farm were not comparable in scale to those of Swartkrans or Sterkfontein and in general consisted of residual pockets of material, the

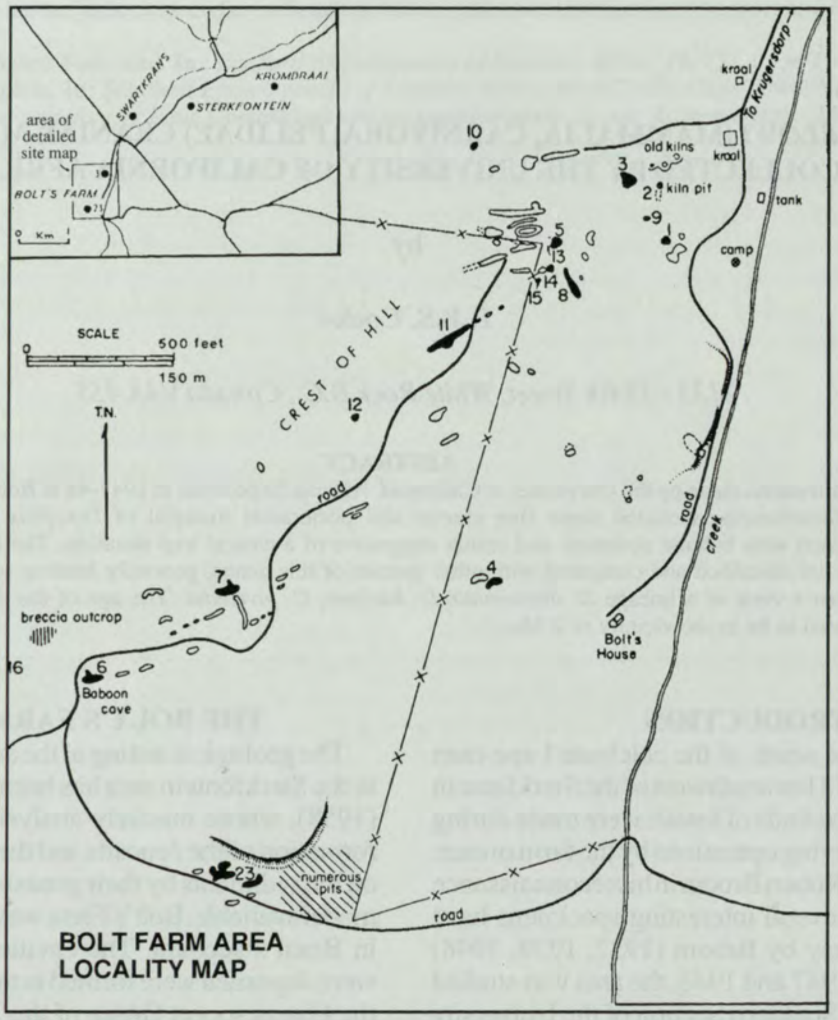

Figure 1. Plan of a portion of Bolt's Farm showing the localities worked by the University of California African Expedition in 1947-48 (from a plane-table survey by Dr. F.E. Peabody). The names and University of California locality numbers are given in Appendix A. The *Dinofelis* came from the southernmost site, Pit 23 (UCMP Loc. V-4888). Inset shows the relationship to the well-known australopithecine cave breccia localities.

relationship of which to the former walls and floors of the original cavities could not be determined. Few of the sites were rich in fossils but in the aggregate they have furnished very substantial collections of fossils and it is probable that they differ somewhat in age. The matrix in which the bones occur is usually a little darker than the typical so-called "pink" breccia from Sterkfontein and resembles rather the material from Swartkrans and Kromdraai. The colour is nearest to the "moderate brown" (5 YR 4/4) of the Rock Colour Chart of the Geological Society of America but some samples may trend in the direction of moderate or pale reddish brown (10R 4/6 and 10R 5/4). Mineralogical analyses confirm the general resemblance to the Swartkrans and Kromdraai deposits, as indicated by Brain's data (1958). In a number of cases the consolidated breccia is overlain by a "loose fill" of dark uncemented debris, often containing identifiable bones of living species and sometimes stone flakes or artefacts. Occasionally parts of the breccia have been decalcified and may resemble the "loose fill". For the record, the various sites and taxa identified from the breccias are given briefly in Appendix "A", The most interesting deposit, from which the fine *Dinofelis* material came, is Pit 23, and it is described below.

"TIT HILL PIT", NO. 23

Peabody's Pit 23 (UCMP Locality V-4888) was nicknamed "Tit Hill Pit" and is of particular interest as the breccia is unusually rich in bone, representing the remains of a relatively small number of individuals whose cranial and postcranial skeletons are preserved, although not generally in articulation. The vast amount of postcranial material was only partially developed for display purposes and not all the cercopithecoid cranial remains were extracted by the present writer in 1957/58. Cercopithecids are dominant and from the cranial remains it would appear that not fewer than 8 and not more than 15 individuals left their skeletons in the deposit. Surprisingly, they belong to three distinct genera, the two baboons *Parapapio broomi* and *Papio robinsoni*, together with the colobine *Cercopithecoides williamsi*. The best cranial material was sent to Dr Leonard Freedman, who described it in 1965, then including a fourth species *Parapapio whitei* now synonymized with *P. broomi*. Subsequently all the cercopithecoid material was studied by Dr Eric Delson at the American Museum of Natural History, further developed and reassessed. The co-occurrence of these three primates would, according to the criteria discussed by Delson (1984), suggest an age for the deposit very close to 2.0 Myr. The other major element comprises three felid crania referred to *Dinofelis barlowi*, as well as a large number of postcranial bones, including some limb segments in partial articulation. Only the cranial elements will be considered here as the postcranial material is at present being extracted and studied by Dr Curtis W. Marean, who will describe it in due course, adding immensely to our knowledge of the genus and its functional anatomy. He has already (Marean, 1989) given an interesting discussion of the probable habits of the African sabre-toothed cats. According to Dr Marean (in litteris) there is one large carnivore astragalus that is distinct from those assigned to *Dinofelis* and similar in some respects to material referred to *Homotherium*.

The unique character of this association clearly demands some abnormal mode of occurrence. The felids are an adult male and female and a younger individual, probably male, so that it is likely that they represent a single family. Their presence is suggestive of some sort of trap into which they fell and from which they could not escape – a natural game-pit in fact. Such a trap could also account for the presence of the baboons, which include at least two infants that might have been riding on their mothers' backs. Both cat and baboon coprolites occur, showing that some animals were alive for a time at least, and yet the deposit is quite unlike a den or lair. The only other identifiable fossils are passerine bird skull and limb bone, a few fragmentary bones of a canid (probably a jackal), and an assortment of bits of small insectivores, rodents and lizards in the typical "rodent" breccia derived from owl pellets. The absence of any bovid or equine remains is in striking contrast to their normal abundance in the cave breccias and this may suggest that the opening of the inferred trap was in a rather inaccessible location such that only agile animals could be trapped. An opening within an elevated rocky outcrop might meet these requirements, but it must be admitted that these inferences are speculative.

DESCRIPTION

Dinofelis barlowi (Broom, 1937)

Meganthereon barlowi Broom, 1937, 1939
Machaerodus transvaalensis (Pars) Broom, 1939
Therailurus barlowi Ewer, 1955
Machaerodus darti Toerien, 1955
Dinofelis barlowi Hemmer, 1965

A damaged skull (Transvaal Museum 1541) and an upper canine (TM 1542) from the Sterkfontein Type Site were described by Broom in 1937 as a new species, placed in the genus *Meganthereon* as *M. barlowi*, primarily because of the size and form of the upper canine. A brief description of the upper carnassial was added two years later (Broom 1939) and in this paper another new species was described as *Machaerodus transvaalensis* on the basis of a canine from Sterkfontein, together with a left upper carnassial (TM 1579).

In 1955, Ewer described a new species, on the basis of a good cranium from Kromdraai (TM Ka 61) with the cheek teeth, basicranium and zygomatic arches almost perfectly preserved but lacking most of the frontals and the saggital crest; there were also two mandibular fragments (TM Ka 62, 63). Ewer referred this material to the European Pliocene genus *Therailurus* and named the Kromdraai form *T.piveteaui* in honour of the founder of that genus. At the same time she described a much crushed and broken skull with some associated mandibular fragments (TM STS 131) and the tip of an upper canine (TM STS 132) found at the Sterkfontein Type site, assigning it to Broom's species *barlowi* but placing this in the genus *Therailurus*. She also withdrew from *Machaerodus transvaalensis* the upper carnassial Broom had included with the type canine and referred this tooth to *Therailurus barlowi*. While Ewer's paper was still in the press, Toerien (1955) described a mandibular ramus and the anterior portions of a snout and mandible from the Makapansgat Limeworks, naming it *Machaerodus darti*, although mentioning the similarity of the canine to that of *"Meganthereon barlowi"*. In 1956 Ewer indicated that *darti* should be regarded as a synonym of *Therailurus barlowi*.

A decade later Hemmer (1965) reviewed the genotypical species of *Therailurus*, *T. diastemata* and concluded that it belonged to the same genus as the northern Chinese *Dinofelis abeli* Zdansky 1924, which genus therefore had priority. Hemmer suggested that *Dinofelis diastemata*, *D. barlowi* and *D. piveteaui* formed a connected succession while *D. abeli* was more isolated morphologically. Subsequently he proposed (Hemmer 1973) that "*Felis*" *cristata* Falconer and Cautley 1836 from the Pinjor stage of the Siwaliks in India and "*Panthera*" *palaeoonca* from the Blancan of Texas should also be regarded as species of *Dinofelis* and he endeavoured to show some degree of temporal relationship in the relative increase in lengths of the carnassials as expressed in the ratios P^4/P^3 and M_1/P_4.

Material: Bolt's Farm, Pit 23 (UCMP Loc. V-4888): Cranium and mandible, TM BF 55-22, 23 (cast UC 113720); smaller, damaged cranium, UC 69506, and associated mandibular rami; crushed remains of cranium and mandible, UC 64443; numerous associated postcranial bones, UC 69525-69530, 80286-80288, 80309-80310, 88754-88802.

The best cranium and its associated mandible have been given to the Transvaal Museum, Pretoria (TM BF 55-22,23) and casts are retained at the Museum of Paleontology in Berkeley. It is convenient to designate this skull as "A" and it is believed to have been an adult male. The second skull, "B", is also well preserved, but smaller and is considered to have been an adult female (UC 69506); the two halves of its mandible are incomplete. The third skull, "C", is extremely crushed and distorted, the lower jaw having been driven partly into the cranium and twisted sideways (UC 64443). It is thought that this skull belonged to a full-grown, but still youthful, male animal as it appears to be almost as large as skull "A"; exact measurements are not possible.

The Cranium: Skull "A" is very well preserved, the main damage being corrosion of the right side of the braincase in the frontal region, damage to the jugal, to the squamosal and to the tympanic areas. There is no obvious distortion or crushing and it has been possible to restore the missing parts with considerable accuracy. The zygomatic arches are lost and their original contour is a little uncertain. The extreme tip of the premaxilla is missing and the incisors are broken or lost, except for RI^3. Both canines are present, although the tip of the right one is damaged. On the left side P^3, P^{4}and M^1 are reasonably well preserved, but on the right side all are damaged, P^4 only slightly so. The cranium is shown in lateral aspect in Figure 2A and a palatal view is given in Figure 2B. Measurements are set out in Table 1.

TABLE 1
Measurements on crania of Transvaal *Dinofelis*

	BOLT'S FARM PIT 23			
	'A'	'B'	Type	Ratio
	TM/BF 55-22	UC 69506	TM/Ka61	Piv/'B'
Skull height (sagittal crestabove foramen magnum)	60 e	58 e	71	1,22
Occiput height	54 e	52 e	61 e	1,17
Condylobasal length	246	230 e	223 e	0,97
Basilar length	227	206 e	198 e	0,96
Bizygomatic breadth	184 e	168	186 e	1,10
Length of zygomatic opening	55	49	44	0,90
Cranial width	82	-	-	-
Width of nasal opening	39	-	39 e	-
Width of nasal bones at anterior end	41 e	-	40 e	-
Bulla length/breadth	42/26,5	44/27	42/26	0,95/0,96
Palate length (I-P^4/P^4 line)	105	96	96 e	1,00
Width across incisor row (I^3-I^3)	43,5	39,5	45	1,14
Width of palate behind canines	69	61	66	1,08
Width of palate across outside P^4-P^4.	116	104	117	1,13

e= estimated measurement

Skull "B" is 8-9% smaller than skull "A", as will be noted from the comparable palatal views in Figure 2c and the measurements in Table 1. The left zygomatic arch is broken but that on the right side is intact. The tip of the premaxilla is broken away and only the socket of the RI^3 is preserved. Both canines are marked by matrix-filled alveoli but a pair of detached canines was found in the block and it is possible that they belong to the skull. The first molars are lost. LP^3 and LP^4 are intact but those of the right side are damaged. The nasal and frontal areas are well preserved but the back of the parietal and the lambdoidal ridge are broken.

Skull "C" is badly crushed, although the back of the palate and the basicranial region, including the auditory bullae and occipital condyles, are moderately intact. The mandible is apparently complete but was driven obliquely upwards and the left ramus, from canine to M$_1$, can be seen against the maxilla while, on the other side, the right P^3 and P^4 are exposed against the middle of the right ramus.

It seems reasonable to regard any differences between "A" and "B" as due to sexual dimorphism but, as size alone tends to be deceptive, Figure 3A has been prepared to compare the palatal aspects by enlarging "B" to the same condylobasal length as "A". The fit is surprisingly close, with only minor differences in the sutures which are probably within the range of individual variation. "A" does seem to be slightly broader and the restoration of the zygoma in "A" may well be an underestimate. "A" appears to have the cheek teeth slightly farther forward and they lie a little closer to the wall of the maxilla. There are some differences in the auditory bullae, that in 'A' being antero-posteriorly more compressed, somewhat like that of the tiger. The bullae are not greatly inflated and are largely hidden in profile view by the large mastoid processes and paraoccipital process. Both processes are relatively smaller in "B" than in "A".

The charcteristics of the skull in *Dinofelis piveteaui* have been well described by Ewer (1955) and major features of four species were compared in tabular form by Hemmer (1965). However, the cranium of *D. barlowi* has been known hitherto only by very poorly preserved material and it seems useful to comment on features shown by the Bolt's Farm crania. The braincase is inflated and the interorbital constriction may be slightly narrower than the postorbital constriction, whereas in the living large cats the converse is usually true. The postorbital process is short and blunt with the tip curving downwards. The occiput is narrow and resembles that of the leopard more than that of either lion or tiger. The mastoid process is large and lies closer to the post-glenoid than to the large paraoccipital process; the latter wraps around the bulla to about the same extent as in the lion. The enlarged mastoid process extends forwards under the external auditory meatus. The styliform process is weakly developed. The stylomastoid process is fairly well back and is unusually large and well separated from the medial vertical wall of the mastoid process. The bullae are relatively short and the glenoid process has the appearance of being "pushed back" towards the mastoid process, giving a sharp curvature to the root of the zygoma, unlike the gentle sweep in the leopard. The glenoid fossae are almost perpendicular to the axis of the skull and lie well above the occlusal plane. The articular surfaces of the glenoid are short and the zygoma curves forward rather abruptly (see Figure 2B). The anterior border of the premaxilla is wide and broadly rounded, being less rounded than in the leopard and not as

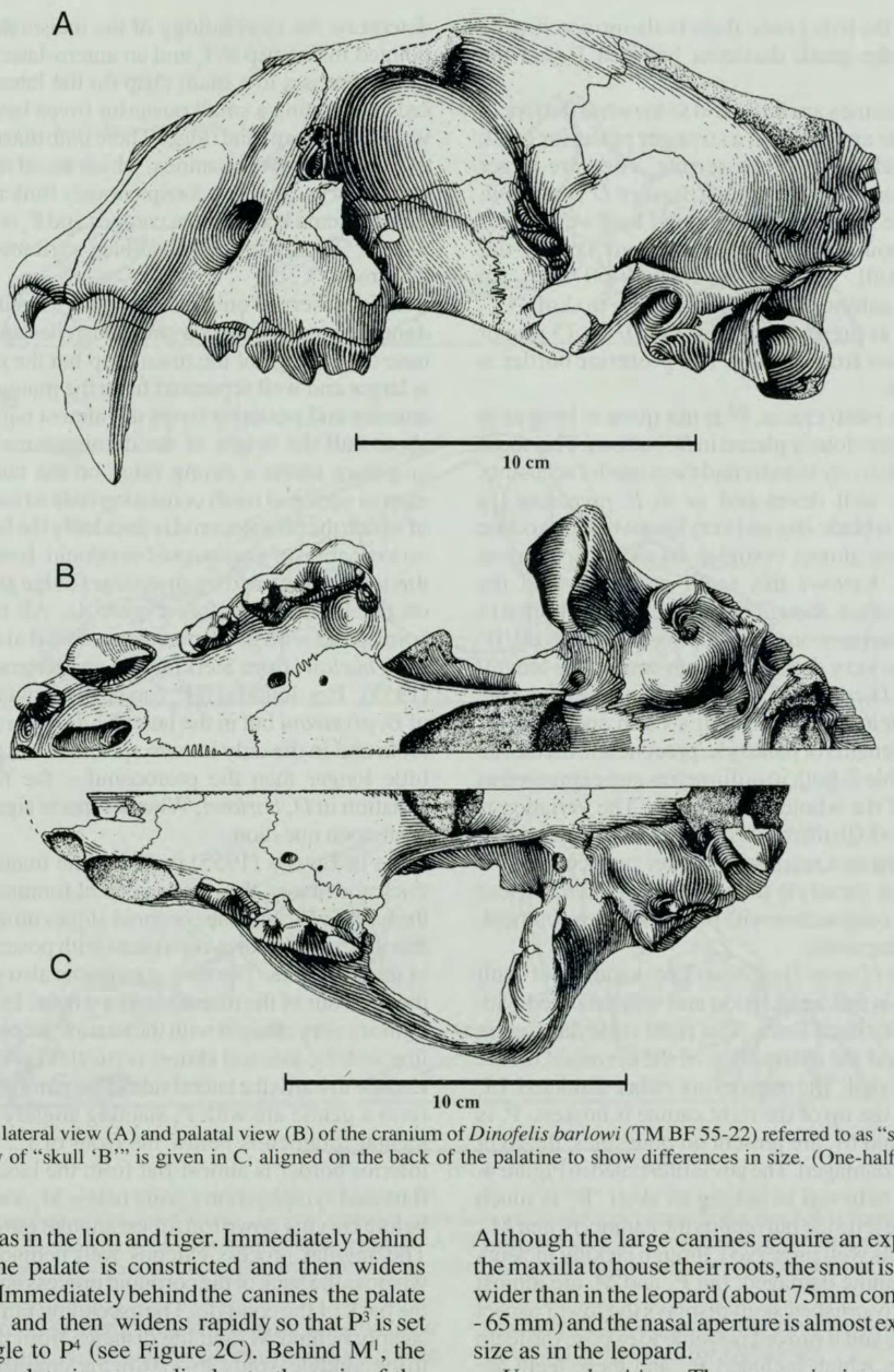

Figure 2. Left lateral view (A) and palatal view (B) of the cranium of *Dinofelis barlowi* (TM BF 55-22) referred to as "skull 'A'". Palatal view of "skull 'B'" is given in C, aligned on the back of the palatine to show differences in size. (One-half natural size)

"squared off" as in the lion and tiger. Immediately behind the canines the palate is constricted and then widens lion and tiger. Immediately behind the canines the palate is constricted and then widens rapidly so that P^3 is set at a slight angle to P^4 (see Figure 2C). Behind M^1, the border of the palate is perpendicular to the axis of the skull, then curves abruptly towards the back to flank a rather wide palatine notch. This notch is rounded in a single smooth curve, unlike the rather rectangular shape seen in lion and tiger or the double curve usually found in the leopard. The mid-line of the palatine extends only a little way behind the back of the maxilla at M^1 - M^1, unlike the prolonged palatine found in leopard, lion and tiger. Both the precanine and postcanine diastemas are short. Although the large canines require an expanded area of the maxilla to house their roots, the snout is not very much wider than in the leopard (about 75mm compared with 60 - 65 mm) and the nasal aperture is almost exactly the same size as in the leopard.

Upper dentition: The upper incisors are all badly damaged, with the exception of the left I^3 in skull "A". This has a simple pointed main cusp with a moderately well developed posterior wear fossette; the tooth is gently curved. It is slightly longer and narrower than in *D. piveteaui* (see Table 2). The width across the incisors is 43.5 mm. The central incisors were clearly smaller than I^3. As in the true sabre-toothed cats, the incisors were set in a very gentle curve, unlike the almost straight arrangement in the living cats; there is also no notch in the premaxilla in the small diastema between I^3 and the canine.

The upper canines are large and somewhat flattened, with a moderate anterior and a stronger posterior crest, neither of which seems to be serrate. They are larger antero-posteriorly and wider than those of *D. piveteaui*. In the latter the canine was estimated by Ewer (1955) to be only about 40-45 mm long from jaw to tip, whereas in skull "A" it measures 59-60 mm. An isolated upper canine, possibly belonging to skull "C", is 40 mm long as preserved but lacks at least 15 mm or probably 20 mm from the tip. The posterior border is almost straight.

In the Bolt's Farm crania, P^3 is not quite as long as in the specimens previously placed in *D. barlowi*. This tooth in skull 'B' is relatively broader and the posterior accessory cusp is not as well developed as in *D. piveteaui*. In *D. piveteaui* P^4 is blade-like and very long with a protocone so weak as to be almost vestigial. In all the specimens referred to *D. barlowi* this tooth is shorter and the protocone is distinct, though not large, and it is joined to the summit of the paracone by a sloping ridge. In skull 'B' the protocone is very distinct, though small. The length/breadth ratio in *D. piveteaui* is about 3.1 and in *D. barlowi* from Sterkfontein and in the Bolt's Farm specimens is about 2.2. The lengths of parastyle, pracone and metacone are given in Table 3, both in millimetres and expressed as a percentage of the whole length of P^4. The variation is fairly large, although there does seem to be a tendency for *D. barlowi* to have a relatively shorter metacone and a relatively larger parastyle than in *D. piveteaui*. These trends, taken in conjunction with protocone development, are probably diagnostic.

Mandible and Lower Dentition: The mandible of skull 'A' was found in full articulation and was detached with great skill by Richard Estes. The right condylar region was missing, and the extreme tip of the coronoid on the left side is corroded. The incisors are rather damaged, LI_1 being lost, and the tip of the right canine is broken. P_3 is broken but P_4 and M_1 are present on both sides, the right ones somewhat damaged. The jaw is illustrated in Figure 4. The mandible believed to belong to skull 'B' is much damaged on the left side but retains the canine, P_4 and M_1; the right ramus is well preserved, though lacking incisors and with the canine damaged, but P_4 and M_1 are almost intact. The badly crushed skull displays the lower aspect of the mandible and it proved possible to expose the teeth of the left side, which included P_3, and these teeth are illustrated in Figure 4C. The dimensions are given in Table 4.

The size and general form of the jaw resemble a large leopard but the symphysis is wider, shorter and flatter, tending towards the form of the tiger symphysis. The incisors are about the same size as those of the lion and are also arranged in a similar very gentle curve – almost a straight line. They are placed well above the occlusal plane of the cheek teeth. Damage makes it difficult to determine the morphology of the incisors, but there is a pointed main cusp in I_3 and an antero-lateral wear facet. In I_2 there is a low main cusp on the lateral side of the crown, creating a small posterior fovea between it and a weak postero-medial ridge. There is no diastema between the incisors and the canines, which are of moderate size, gently curved and not conspicuously flattened or ridged. The diastema between the canines and P_3 is about 25 mm in "A", 22 mm in the mandibles attributed to "B" and 21 mm in "C".

P_3 is preserved only in "C" and is a small tooth with a dominant central cusp; a small cusp lies anteriorly at the base of the ridge of the main cusp but the posterior cusp is larger and well separated from the main one. In P_4 the anterior and posterior cusps are almost equal in size and about half the height of the dominant main cusp. The cingulum forms a strong ridge on the talonid. M_1 is a narrow sectorial tooth consisting only of two main cusps of which the prototoconid is decidedly the larger. There is no indication of a metaconid or talonid. In mandible "A", this tooth is widened by an outward bulge at the cingulum on the lingual side (see Figure 4). All these features correspond with those noted in material already referred to *D. barlowi* from Sterkfontein and Kromdraai by Ewer (1955). It is doubtful if P_4 can be distinguished from that of *D. piveteaui* but in the latter M_1 is apparently a stouter tooth and in the only known specimen the paraconid is a little longer than the protoconid – the reverse of the situation in *D. barlowi*. Whether this is significant or not is an open question.

As in Ewer's (1955) material, the mandible is rather thick and heavy, the inferior dental foramen lies close to the back of M_1, and the coronoid slopes up sharply behind this tooth, all features consistent with posterior reduction in the mandible. The new specimens also serve to show the controur of the mandible as a whole. In plan view the rami are very straight with the narrow ascending ramus in line with the axis and almost vertical (Fig. 4A). The cheek teeth lie towards the lateral side of the ramus but themselves form a gentle arc with P_3 slanting slightly inwards. The mental foramen is below the front of P_3. In profile the inferior border is almost flat from the base of the rather flattened symphysis to a point below M_1, then rises gently before curving down to a robust angular process (Fig. 4B). The angular process extends well behind the condyle, whereas the back of the coronoid process is directly above the back of the condyle. The ascending ramus rises fairly steeply behind M_1 and the distance from the back of M_1 to the condyle is only 36-37% of the length of the jaw from the front of the incisor sockets to the condyle, which is shorter than in the leopard or lion and more like the tiger. The coronoid process is also relatively short.

Ewer's (1955) reconstruction of the back of the ramus in the left mandible Ka 63 from Kromdraai, referred to *D. piveteaui*, shows a very small angular process lying in front of the condyle and this may well be incorrect, unless there is a significant departure from the situation in *D. barlowi*.

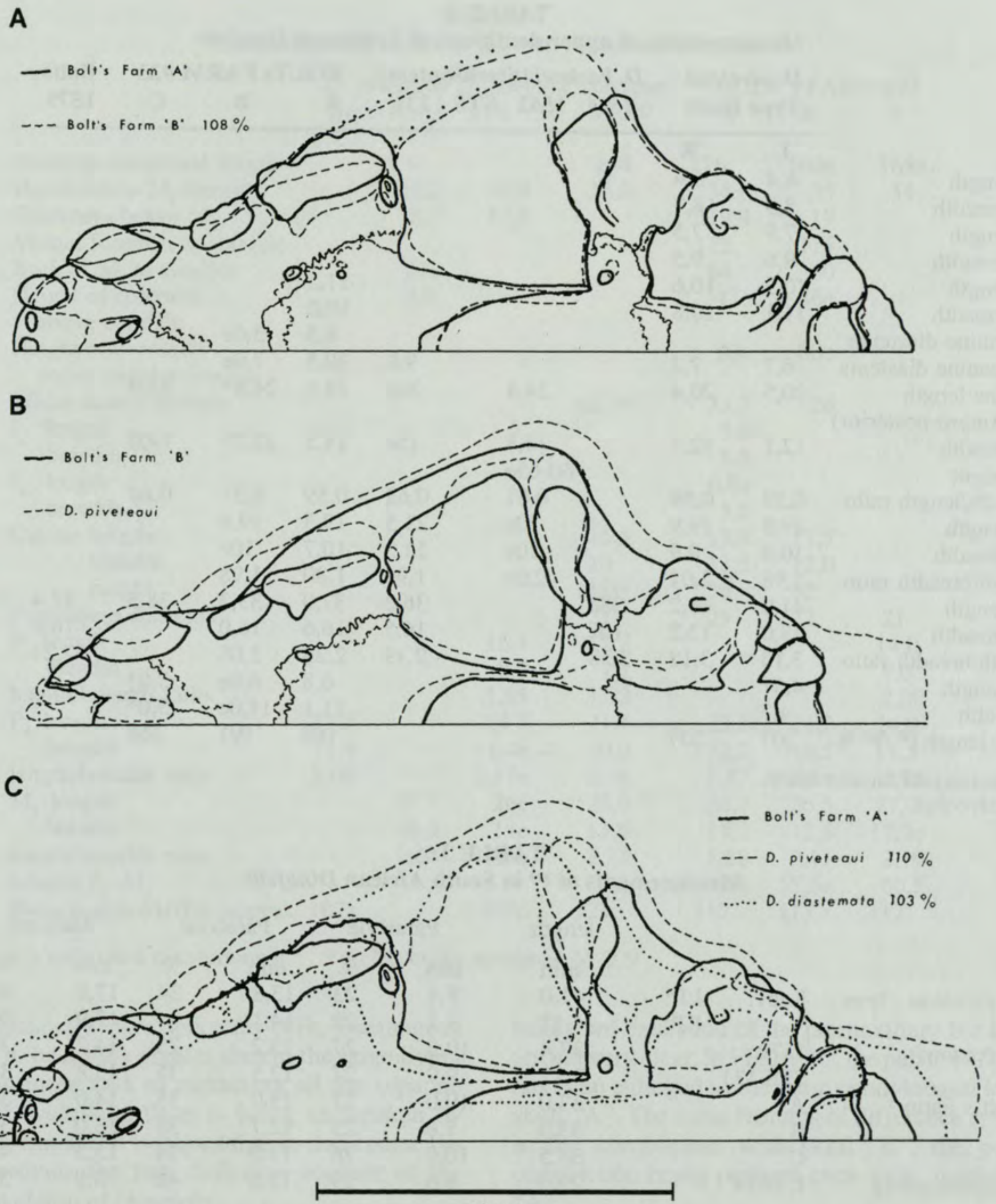

Figure 3. Comparative outlines of palatal aspect of different specimens of *Dinofelis*. A compares the two Bolt's Farm skulls 'A' and 'B' with 'B' enlarged to the same condylobasal length as 'A'. B compares skull 'B' with the similar-sized type cranium of *Dinofelis piveteau* and with a specimen of the European *D. diastemata*, both enlarged to the same condylobasilar length as 'A'.

Ewer (1955), in her consideration of *D. piveteaui* attempted to estimate the height of the coronoid above the condyle of the lower jaw by assuming that it followed the normal feline pattern of being 70 - 80% of the zygomatic opening. In skull "A" the zygomatic opening is 55 mm, 80% of which would be 44 mm. However the height of the coronoid as preserved is 42 mm and it is reliably estimated to have been close to 47 mm (or 85% of the opening). For skull "B" the zygomatic opening is 49 mm, yet restoration indicates that the height of the coronoid was close to 46 mm, or more than 90% of the size of the zygomatic opening. This suggests that Ewer's interesting formula does not work well for *Dinofelis*.

Wear on the teeth: Although the canines in skull "A" are damaged, they show signs of wear on the antero-lingual surface, which is matched by very weak facets on the lower canines. However, the main wear on the lower canines, both in "A" and in "B ", is on the lingual face, away from any possible interaction with the upper teeth. This is presumably the result of rasping bones. There is also a wear facet on the antero-internal face resulting from the contact with I^3. P^3 shows no wear on the external face

TABLE 2
Measurements of upper dentitions of Transvaal *Dinofelis*

	***D. piveteau* Type Ka61**		***D. barlowi* (Sterkfontein)**			**BOLTs FARM #23**			**Bolts**
			1541	**1542**	**STS 131**	**A**	**B**	**C**	**1579**
	L	**R**							
1^1 length	6,4	6,4							
breadth	8,5	8,7							
1^2 length	7,9	7,5							
breadth	9,6	9,5							
1^3 length	10,3	10,6				11,5			
breadth	11,1	10,8				10,0			
Precanine diastema						8,5	5,0e		
Postcanine diastema	6,7	7,2			9,0	10,5	7,0e		
Canine length (Antero-posterior)	20,5	20,4		24,4	24e	24,5	24,8*	23,0	
breadth	12,1	12,1		14,8	15e	14,5	12,7*	14,0	
height				60-65e					
breadth/length ratio	0,59	0,59		0,61	0,62	0,59	0,51	0,64	
P^3 length	19,8	19,9		20e	21,5	19,3	19,8		
breadth	10,0	9,9		10e	11,3	10,7	10e		
length/breadth ratio	1,98	2,01		2,0e	1,90	1,80	1,98		
P length	41,0	41,2	38e		36,2	37,0	33,3	38,5	37,4
breadth	13,0	13,2	16e		16,5	16,6	16,0		16,8
length/breadth ratio	3,15	3,12	2,38		2,19	2,23	2,08		2,23
M^1 length	4,5*					6,8	6,0e	3,0*	
breadth	4,7					11,1	11,0e	5,0*	
ratio length P^4 /P^3 %	207	207				168	191	168	

e = estimated measurement
* = alveolus

TABLE 3
Measurements of P^4 in South African *Dinofelis*

			length	Parastyle		Paracone		Metcone	
			mm	mm	%	mm	%	mm	%
D. piveteau type	Ka61	LP^4	41,0	9,4	23	13,8	34	17,8	43
		RP^4	4,12	9,2	22	14,1	34	17,9	44
D. barlowi	1579		37,4	10,0	27	13,2	25	14,2	38
	STS 131		36,2	9,9	27	12,5	35	13,8	38
Bolt's Farm	A		37,0	10,0	27	13,0	35	14,0	38
	B		33,3	7,6	23	12,7	38	13,0	39
	C		38,5	10,0	26	13,0	34	15,5	40
Langebaanweg	L 2674		29,0	8,6	29	11,5	40	8,9	31

but there is wear on most of the lingual side and the tips of the main and anterior cones are flattened obliquely. Relatively slight wear is apparent on the external surface of P$_4$, the tip of which just touches the heel of P$_3$, leaving a faint groove. P^4 has a facet or shallow groove truncating the back part of the ridge from the small protocone to the paracone, with matching wear on the antero-internal corner of paraconid of M$_1$. The whole of the back part of P^4 is polished on its lingual side, as is the outer surface of M$_1$ but there are no extra facets like those described by Ewer (1955A) in *D. piveteaui*. M$_1$ has dentine exposed at its tip, although it does not occlude with M$_1$.

Postcranial skeleton: Most of the individual skeletal elements are represented in the collections and included several blocks with articulated or partially-articulated bones. One large block (UC 88774) shows the distal end of the right femur and also the damaged remains of the lower half of the left tibia and fibula, in articulation with the astragalus and calcaneum. Another block (UC 88773) contains an almost complete left front foot with the carpal bones and metacarpals articulated but the phalanges somewhat scattered. A third large block (UC 88775) exposes much of the left scapula with the articular half hidden beneath a right hip bone, while the proximal ends of a right tibia and fibula emerge from beneath the scapula. The lower half of a baboon pelvis lies across the feline pelvis. Many additional blocks contain other parts so that the total collection includes most of the elements of the skeleton. There appear to be three size groups, the largest representing an animal not fully adult, as is shown by the state of the epiphyses. The second individual is only marginally smaller but fully grown and the third is

TABLE 4

Measurements on lower jaws of Transvaal *Dinofelis*

	D. piveteaui		*D. barlowi*	Makapan	BOLT's FARM #23		
	Ka62	Ka63	STS 131	M 607	A	B	C
Condylo-symphsial length				154	176	160e	165e
Depth below M_1 (inner)		35,2	32,0	33,0	36	35	34
Thickness below M_1		18,7	17,5		19,4	17	
Mental foramen to condyle					122	115	
Back of M_1 to condyle		61e			64	60	
Height of coronoid above condyle		43e			47e	46e	
Height of coronoid above angular process					90e	83e	
Width across incisors				(27)*	33,7	26	
I_2 length					5,0		
breadth					5,5		
I_3 length					6,8e		
breadth					5,5		
Canine length				16,5	18,9	17,5	
breadth				10	13,5	12,0	
height				(35)*	30	32	
Postcanine diastema				21	25	22	21
P_3 length			16,1	12,2			14,0
breadth			8,7	7,1			7,0
length/breadth ratio			1,85	1,72			2,00
P_4 length	23,7		24,7	21,4	22,8	22,5	24,0
breadth	11,4		11,4e	10,0	12,2	10,5	11,5
length/breadth ratio	2,08		2,17e	2,14	1,87	2,14	2,08
M_1 length		27,7	26e	25,9	26,7	26,5	27,0
breadth		16,9	14e	11,6	14,2	12,5	12,3e
length/breadth ratio		1,64	1,85e	2,23	1,88	2,11	2,19
Length P_3-M_1				57,5	60e	57,5e	60,5
Ratio length M1/P4 (approx. 107)			105e	121	117	117	112

e = estimated measurement   *on Makapan specimen M 209

an adult but distinctly more delicately built. The range in size appears to be a little greater than in the large living cats. The enormous task of extracting all the separate bones and of evaluating them is being undertaken by Dr Curtis Marean and it is hoped that in due course his report will provide the first definitive account of the postcranial skeleton of *Dinofelis*.

DISCUSSION

The type specimen of *D. piveteaui* is very similar in size to skull "B" and the palatal aspects are very alike, as will be seen in Figure 3B. The zygomatic breadth is a little greater in *D. piveteaui*, the ratio of zygomatic width to basilar length being 94% in *D. piveteaui* compared with 82% in both the Bolt's Farm crania. The mandibular fossa is longer in *D. piveteaui* and extends to the edge of the zygomatic opening. The palate itself is wider in *D. piveteaui* and not much constricted at the postcanine diastema, as it is in skull 'B'. The back of the palatine lies a little farther forward in *D. piveteaui*, level with M^1 but otherwise the palatine bones are very similar in shape. It is suspected that the left and right maxillae do not meet on the mid-line of the palate but are separated by a narrow backward extension of the premaxillary but the sutures are not very clear. In Figure 3C, the palate of *D. piveteaui* has been enlarged to the same condylobasal length as in skull "A". The same features of difference are shown as in the comparison with skull "B", the post-canine constriction being perhaps even more marked in skull "A".

As Ewer (1955) and Hemmer (1965) have noted, the frontal and occipital regions in *Dinofelis* lie at about the same height above the palatal plane, unlike the situation in most other large cats. The braincase is large and inflated, with a distinct post orbital constriction. The height of the braincase at the frontal/parietal border relative to the condylobasal length is about the same in both the type of *D.piveteaui* and in skull 'A' but the profiles are rather different (Figure 5), especially in the occipital and tympanic regions. The occiput is actually higher in *D. piveteaui* than it is in the physically larger skull "A" and the braincase thus has a relatively longer and flatter, more leopard-like profile. *D. piveteaui* displays a considerable backward extension of the lambdoid crest which overhangs the condyles by about 3 cm, compared with about half this amount in skull 'A', even if a generous

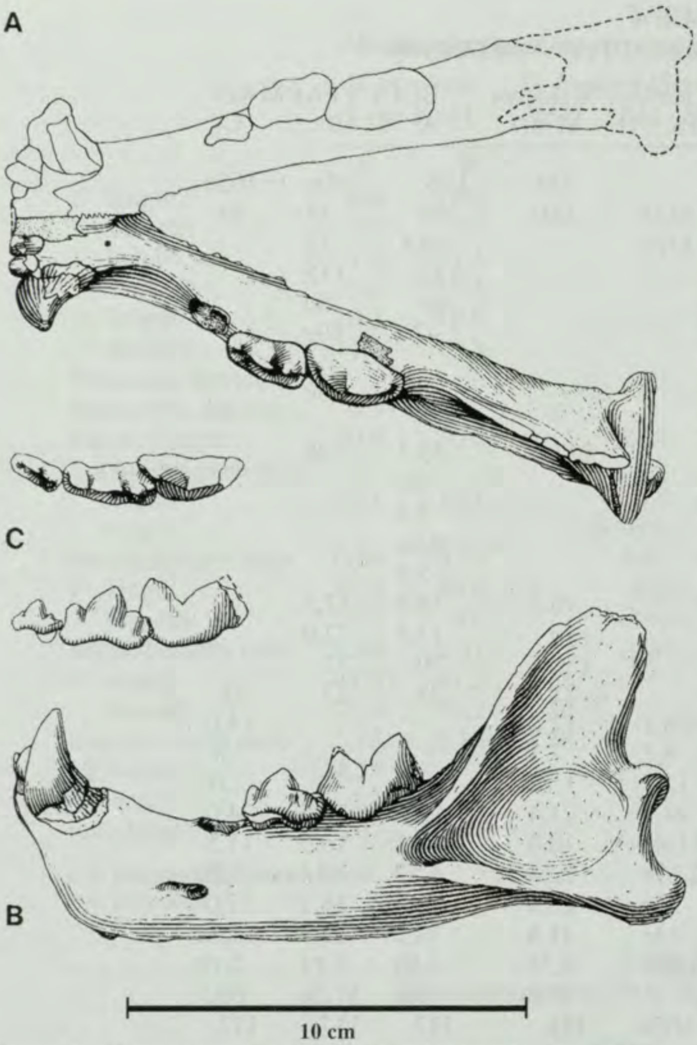

Figure 4. Dorsal view (A) and left lateral view (B) of mandible of Bolt's Farm 'A'. C shows occlusal and outer lateral views of left cheek teeth of specimen 'C'. (One half natural size).

allowance is made for possible losses in the fossil. In all three of the Bolt's Farm crania the auditory bullae are less inflated than in *D. piveteaui* and are antero-posteriorly compressed, more like the tiger than the lion or leopard. The mastoid process is large and in profile the bullae are almost hidden, whereas in *D. piveteaui* the bullae project well below the mastoid process and paraoccipital process (Figure 5). With reference to a theoretical plane from the tips of the premaxillae to the base of the occipital condyles (which might loosely be called the "basal plane") the bases of the crowns of P^3 and P^4 in the Bolt's Farm crania lie effectively *on* the plane (as in the leopard, for example) whereas in *D. piveteaui* they tilt forwards at an angle of about 8 - 9°, bringing P^3 well below the reference plane. Thus the front of the palate appears to be elevated above the "basal plane" and the canine is slightly tilted forwards rather than lying vertical. By comparison, the front of P^3 in *D. diastemata* is only slightly below the reference plane but P^4 is well below it so that the bases of the P^3 and P^4 in *D. diastemata* have a backward tilt of almost 10° from the reference plane (Figure 5). If confirmed by other material, this could be a useful diagnostic feature and is consistent with Hemmer's (1965, 1973) concept of a lineage from *D. diastemata* through *D. barlowi* to *D. piveteaui*. In the true sabre-toothed cats, the cheek teeth lie well below this reference plane.

Hitherto, the mandible has been poorly known. *D. piveteau* is represented only be a piece of the left mandible broken in front of M_1 and again through the ascenind ramus so that the back part was missing (Ka63). It was illustrated by Ewer (1955), Figure 6) with a reconstruction that does not agree very well with the mandibles of "A" or "B" from Bolt's Farm, probably underestimating the unusual enlargement of the angular process. There is also part of a right mandible from Swartkraans (SK335) which Ewer (1955) declined to identify specifically but which probably belongs to *D. piveteaui* as the rather damaged P_4 and M_1 are very similar to Ka63 and Ka64. The only other mandible is that from Makapansgat (M607) described by Toerien (1955) as *Machaerodus darti* but regarded as referable to *Dinofelis barlowi* by Ewer (1956), partly on the grounds of its general resemblance to the lower jaw of the European *D. diastemata*. In size the Makapansgat jaw is closely comparable with that of the specimen "B" from Bolt's Farm and the profiles of the two are compared in Figure 6B, aligned approximately along the bases of the cheek teeth and the condylar process. The angular process is damaged and its original size cannot be determined but it was probably not as large as in 'B'. The height of the corpus below M_1 is less in the Makapansgat jaw than in "B" but the contour of the inferior border is otherwise similar. The symphsis is not flattened, nor as high, so the base of the canine appears to be roughly on the same plane as the cheek teeth, instead of well above it as in the Bolt's Farm specimens and in European *D. diastemata*. There may be some damage or distortion of the symphsial area but this is not obvious. A rather damaged snout (M 209) figured by Toerien (1955) has a canine a little higher than in the Bolt's Farm specimens but is otherwise very similar. The portion of the symphysis resembles that of the mandible but is distorted and cannot be used to determine the original form. The Makapansgat partial premaxilla and maxilla retain almost half of each of the upper canines, which are indistinguishable from those of the Sterkfontein and Bolt's Farm specimens, leaving little doubt that it belongs to a *Dinofelis*. The incisors are smaller than in other specimens but damage makes exact measurements difficult. The lower cheek teeth are marginally smaller than in material from Bolt's Farm and Sterkfontein but the M_1 has the typical elongation of the protoconid as compared with the paraconid; there is a vestigial talonid in M_1 not seen in the other material but regarded as unimportant by Ewer (1956). The apparent difference in the symphysis makes assignment to *D. barlowi* a little uncertain, although not unreasonable.

Langebaanweg, in the southwestern Cape Province has furnished some material from "E" quarry, including several fragments and a few loose teeth, but also the two halves of a well preserved mandible (L20284) with the canines and cheek teeth on both sides, although the backs

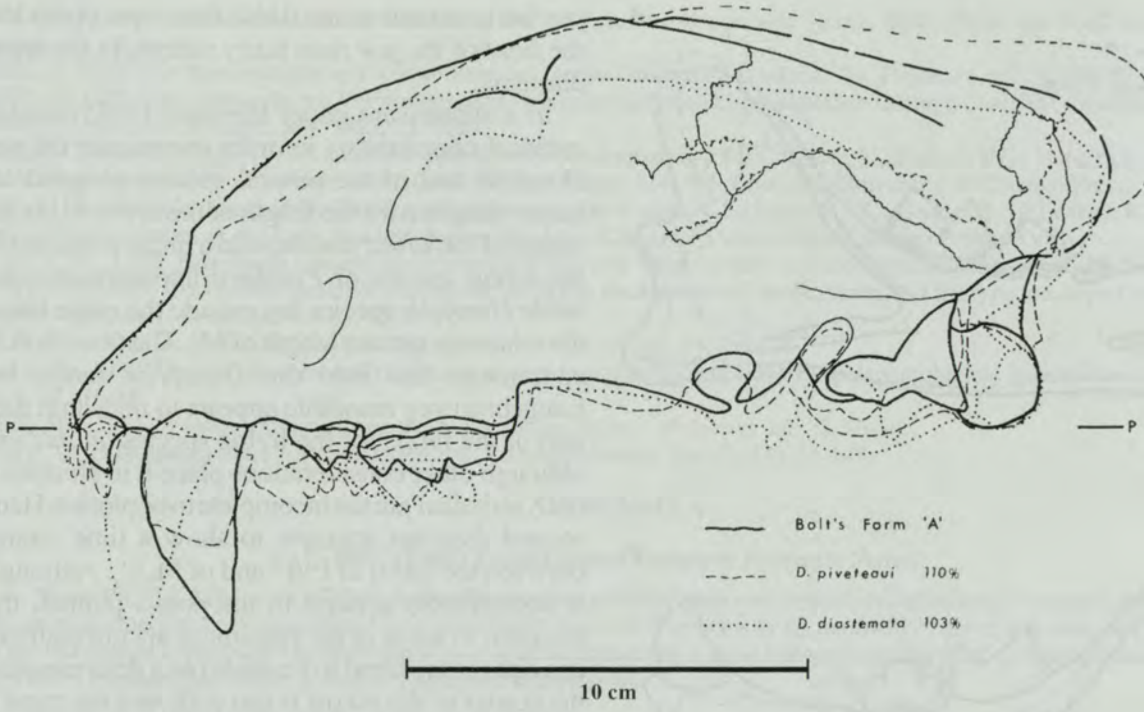

Figure 5 Comparative outlines of crania of *Dinofelis* specimens orientated on a plane (P-P) from the tip of the prexmaxilla to the base of the occipital condyle, enlarged to the same condylobasal length. (Bolt's Farm specimen 'A' is one half natural size).

of the ascending rami are lost. It was described by Hendey (1974) who placed it in *Dinofelis* and regarded it as not separable from the European *D. diastemata*. The upper canines are very similar both in size and morphology to those of *D. barlowi* and *D. piveteaui*. The only known P^3 is narrower than in the Transvaal material and the well worn P^4 is smaller, with the paracone significantly longer than the metacone (see Table 3); there are much abraded remains of what was originally a fairly prominent protocone lying between the parastyle and paracone, apparently better developed than in *D. barlowi*. The lower cheek teeth are morphologically very similar to those of *D. barlowi* but P_4 is a little narrower and M_1 is shorter as well as slightly narrower with the paraconid blade little more than half of the length of the protoconid (6,5 and 12,3 mm); there is a vestigial talonid, as in the Makapansgat jaw. The profile of the jaw is shown in Figure 6A in comparison with Bolt's Farm mandibles. The similarity is clear but the differences appear to warrant the specific separation of the Langebaanweg material from *D.barlowi*, for which it nevertheless provides a very reasonable ancestor. The reference of this material to the European *D. diastemata*, however, is less certain as the European species has a shallower corpus. the incisors carried on a slightly protruding shelf, and the M^1 with the paraconid not as small compared with the protoconid as it is in the Langebaanweg material.

Dinofelis is now also known from East Africa, although only preliminary accounts have been published. M.G. Leakey (1976) records a good mandible (KNM-ER 1549) from below the KBS tuff which matches very well with the South African material of *D. barlowi*, although the postcanine diastema is a little shorter; this may possibly be due to age as the canines are not yet fully erupted. There is also an undescribed, somewhat damaged cranium (KNM-ER 2612) from Koobi Fora which matches quite well with skull "B" from Bolt's Farm (Leakey *in litteris*). The Ileret beds, higher in the sequence have provided a partial mandible (KMN-ER 666) with the teeth damaged but the reduction in size of the incisors and of P_3, together with the short diastema suggest affinity with *D. piveteaui* (Leakey 1976). An expedition from Yale University, led by David Pilbeam, recovered a good cranium at Kanam East (KNM-KE 21), together with some postcranial material and this is referred by M.G. Leakey (*in litteris*) to *D. piveteaui* but is slightly smaller than the Kromdraai type cranium. The Omo area has also yielded material from the Usno Formation and from various levels in the Shungura Formation which appear to belong to *Dinofelis*, some of it resembling *D. barlowi* (Howell and Petter 1976). Thus the range of the genus in Africa is fairly extensive and detailed accounts of the East African material are awaited with interest.

In 1965, Hemmer listed the major characteristics for four species of *Dinofelis* – *D. abeli*, *D. diastemata*, *D. piveteaui* and *D. barlowi*. The Bolt's Farm material serves to confirm the comments made by Hemmer, but also allows some additions to the following items for which data were not available for *D. barlowi*: The nasals are similar to those of *piveteaui*. In both *D. abeli* and *D. diastemata* the mastoid process is nearer to the paraoccipital process than to the post-glenoid process whereas both in *D. piveteaui* and *D. barlowi* the reverse is the case; in all four the mastoid is large, possibly larger

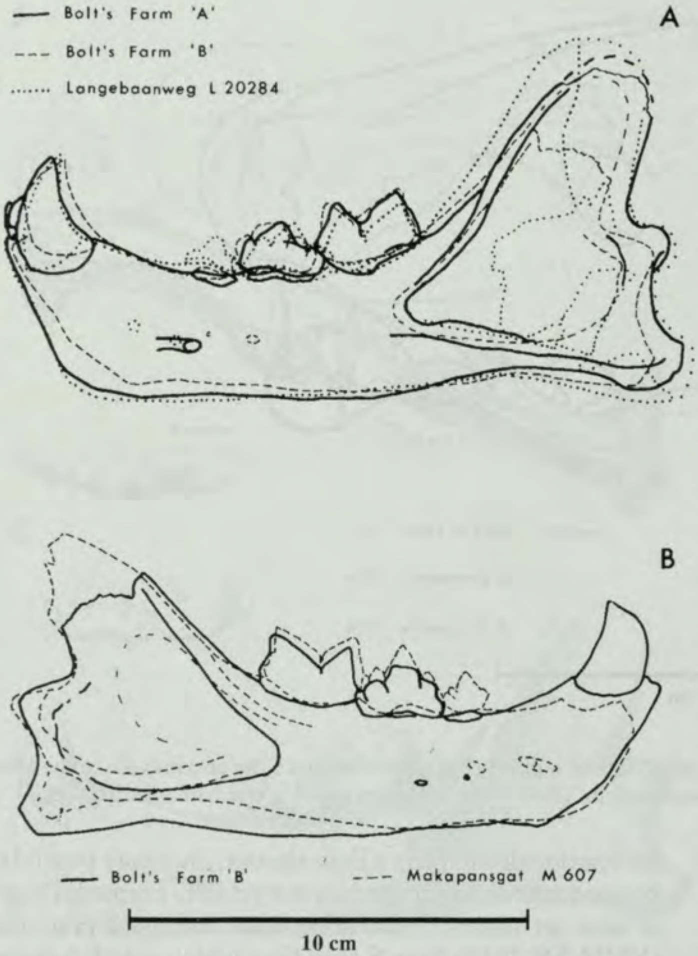

Figure 6 Comparative outlines of (A) of mandibles of Bolt's Farm 'A', Bolt's Farm 'B' and Langebaanweg L 20284 (A); and (B) of Bolt's Farm 'B' and Makapansgat M607 to show similarites and differences. (All one half natural size).

in *D. barlowi* than in *D. piveteaui*. The palatine notch is broad and rounded at the front, as in *D. piveteaui* and *D. diastemata* whereas in *D. abeli* it is a little less rounded and narrower. The upper incisor row is gently rounded, as in the other species. Otherwise Hemmer's diagnoses are fully supported by the new material although one might add the strong development of the angular process in the lower jaw of *D. barlowi*. Hemmer states that the mandibular border in the diastema does not rise particularly; this is apparently the case in the Makapansgat jaw but is not true of the Bolt's Farm specimens in which the front of the jaw rises fairly sharply in the area of the diastema.

In a subsequent paper Hemmer (1975) made some metrical comparisons in order to evaluate the status of *Dinofelis* and of the several species assigned to it. A scatter diagram for the length of the lower M_1 against the length of the lower jaw showed a linear relationship with the living species of *Panthera* appropriately clustered while *Dinofelis* species lay outside the range because of the relatively greater length of M_1. The three Bolt's Farm specimens fall into the *Dinofelis* range but the Langebaanweg mandible appears to lie within the upper part of the range for the living species *on this criterion* although other considerations place it in *Dinofelis*. Data of *D. piveteaui* are too incomplete to be plotted. Hemmer's second diagram attempts to show a time relationship between the ratios of P^4/P^3 and of M_3/P_4. Although there is undoubtedly a trend in the points plotted, the ages assigned to some of the specimens are not really reliable enough for the trend to be useful as a determinative tool; the scatter of the points is too wide and the trend for the lower jaw is too flat to be useful for discrimination. Nevertheless, this comparison endorses Hemmer's earlier (1965) inference on morphological grounds for an evolutionary sequence from *D. diastemata* through *D. barlowi* to *D. piveteaui*. Hendey's (1974) tentative phylogeny invoking phylogeny invoking a separation between the European and African *D. diastemata* seems to fit the data very well.

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REFERENCES

BRAIN, C.K. 1958. The Transvaal Ape-Man-Bearing cave deposits. *Mem. Transv. Mus.*, **11,** 1-131.

BROOM, R. 1937. On some new Pleistocene mammals from limestone caves of the Transvaal. *S. Afr. J. Sci.,* **33,** 760-768.

BROOM, R. 1939. A preliminary account of the Pleistocene carnivores of the Transvaal caves. *Ann. Transv. Mus.,* **19,** 331-338.

BROOM, R., 1948. Some South African Pliocene and Pleistocene mammals. *Ann. S. Afr. Mus.,* **31**(1), 1-38.

COOKE, H.B.S. 1985. *Ictonyx bolti*, a new mustelid from cave breccias at Bolt's Farm, Sterkfontein area, South Africa. *S. Afr. J. Sci.,* **81,** 618-619.

DELSON, E. 1984. Cercopithecoid biochronology of the African Plio-Pleistocene: correlation among eastern and southern hominid-bearing localities. *Courier Forsch. Inst. Senckenberg*, **69,** 199-218.

EWER, R.F. 1955. The fossil carnivores of the Transvaal caves. Machairodontinae. *Proc. Zool. Soc. Lond.,* **125,** 587-615.

EWER, R.F. 1956. Some fossil carnivores of the Makapansgat valley. *Palaeont. afr.* **4,** 57-67.

FREEDMAN, L. 1965. Fossil and subfossil Primates from the limestone deposits at Taung, Bolt’s Farm and Witkrans, South Africa. Palaeont. afr., **9,** 19-48.

HEMMER, H. 1965. Zur Nomenklatur und Verbreitung des Genus *Dinofelis* Zdansky, 1924. *Palaeont. afr.,* **9,** 785-89.

HEMMER, H. 1973. Neue Befunde zur Verbreitung und Evolution der pliozän-pleistozänen Gattung *Dinofelis* (Mammalia, Carnivora, Felidae). *N. Jb. Geol. Paläont. Mh.* **1973,** 157-169.

HOWELL, F.C. & G. PETTER, 1976. Carnivora from Omo Group formations. **In:** Coppens, Y., Howell, F.C., Isaac, G.L. & Leakey, R.F. Eds, *Earliest Man and Environments in the Lake Rudolph Basin,* 314-331. Chicago, University of Chicago Press.

LEAKEY, M.G., 1976. Carnivora of the East Rudolf succession. **In:** Coppens, Y., Howell, F.C., Isaac, G.L. & Leakey, R.F. Eds, *Earliest Man and Environments in the Lake Rudolph Basin,* 302-313. Chicago, University of Chicago Press.

MAREAN, C.W., 1989. Sabertooth cats and their relevance for early hominid diet and evolution. *J. Hum. Evol.,* **18,** 559-582.

PEABODY, F.E. 1954. Travertines and cave deposits of the Kaap Escarpment of South Africa and the type locality of *Australopithecus africanus* Dart. *Bull. Geol. Soc. Amer.,* **65,** 671-706.

PIVETEAU, J., 1948. Un Felidé du Pliocène duRousillon. *Ann. Paléont.,* **34,** 99-124.

SHAW, J.C.M., 1938. Growth changes and variations in wart-hog third molars and their palaeontological importance. *Trans. Roy. Soc. S. Afr.,* **27,** 51-94.

TOERIEN, M.J. 1955. A sabre tooth cat from the Makapansgat valley. *Palaeont. afr.,* **3,** 43-46.

ZDANSKY, O. 1924. Jungtertiäre Carnivoren Chinas. *Palaeont. Sinica, Ser. C,* **2** (1), 1-149.

APPENDIX A

Bolt’s Farm Localities and Principal Elements Found

Pit 1 “Kraal Pit” (UCMP Loc. V-67256). Loose fill containing several jaws and teeth of springbuck and bontebok, many bovid bones and teeth, an equine hoof bone, a mandible of long eared fox (*Otocyon*), fragments of the aardwolf *Proteles* and some bird and lagomorph bones. This is a typical assemblage. Modest quantity of breccia containing a good baboon foot and other skeletal elements, some feline phalanges and a damaged left femur tentatively assigned to *Dinofelis.*

Pit 2 Kiln (Loc V-67257) “Rodent” brecia” only.

Pit 3 “Kaffir Beer Cave” (Loc. V-67258) Loose fill with various living taxa, two crude stone-age cores in chert and quartzite. Breccia with much “rodent” breccia and seventy other specimens including a good, though crushed, cranium of *Procavia transvaalensis,* an almost complete, laterally compressed, skull of *Phacochoerus modestus* (= *antiquus,* to be described elsewhere) and several specimens of *Antidorcas recki.*

Pit 4. “Garage Ravine Cave” (Loc. V-67259). Scanty breccia but including a partial cranium of a large felid and the crushed mandible of a large extinct horse, probably *Equus capensis.*

Pit 5 “Smith Cave” (Loc. V-67260). Very little material.

Pit 6 “Baboon Cave” (Loc. V-67261). Thirty specimens, including a good partial skull of *Procavia transvaalensis,* a crushed cranium of *Antidorcas recki* and good partial crania of *Papio robinsoni* and *Cercopithecoides williamsi* (the latter included by Freedman, 1965). There is also a right proximal femur probably of *Dinofelis.*

Pit 7. “Elephant Cave” (Loc. V-67262). Modest amount of “rodent” breccia and the only macrofossil is a damaged proboscidean molar (to be described elsewhere).

Pit 8 Two fragmentary fossils and some “rodent” breccia.

Pit 9 No specimens.

Pit 10 “Grey Bird Pit” (Loc. V-67263). Abnormal deposit of reddish brown to dark brown breccia containing magnanous lime and dull grey bones of birds and lizards, as well as a few teeth and bones of bovids, and two baboon fragments. The best specimen is a skull of a mustelid, described (Cooke, 1985) as a new species.

Pits 11, 12, 13 Very scanty and scrappy material.

Pit 14 “Bench Mark Pit” (Loc. V-67264). Plentiful “rodent” breccia and some cranial and dental fragments of a suid resembling *Potamochoeroides shawi* but differing in some respects from the type material.

Pit 15 Very scrappy material.

Pit 16 “Equine Pit” (Loc. V-67265). Somewhat dark manganous breccia yielding 20 equine teeth and bones and rather more bovid fragments, as well as one bird skull.

Pit numbers 17 to 22 were not mapped as they yielded no worthwhile material.

Pit 23 - see text

Pits 24 and 25 lay just to the southwest of the mapped area on the property of the S.A. Mining Trust. Pit 24 yielded some rodent breccia, a fragment of an indeterminate baboon cranium and a piece of a small carnivore.

Pit 25 “Gazelle Pit” (Loc. V-67267) furnished an antelopine mandible and part of a humerus, a tooth referred to *Equus* cf *capensis* and a partial mandible and other fragments referred to a variant of *Canis mesomelas.*

Old Dumps (Loc. V-67270) near the kilns yielded twenty scrappy specimens but the exception is a good right upper first molar of *Hipparion libycum.*

Palaeont. afr., **28**, 23-28 (1991)

MIOCENE FAUNAL REMAINS FROM THE BURJI-SOYAMA AREA, AMARO HORST, SOUTHERN SECTOR OF THE MAIN ETHIOPIAN RIFT

by

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ABSTRACT

The Palaeoanthropological Inventory of Ethiopia is dedicated to the discovery and documentation of palaeoanthropologically significant study areas in the Main Ethiopian Rift and Afar Depression. Fieldwork in the area at the southern end of the Amaro Horst during the 1989 field season was focused on a fossiliferous sedimentary succession with intercalated volcanic horizons. Potassium-argon dating sets a minimum age of 11.1 my for sediments bearing vertebrate remains. The partial skeleton of a fossil proboscidean recovered at Burji is described, illustrated and assessed comparatively. The remains are those of a primitive species of choerolophodont mastodon. Biochronological considerations place this specimen in the time range of 15-17 my. The presence of fossiliferous sediments in the Burji area suggest that a rift-related basin had developed in this part of Ethiopia by Middle or Early Miocene times.

Palaeoanthropologists have, over the past six decades, established Africa as a continent with much fossil and contextual evidence elucidating human origins and evolution. Discoveries in the last thirty years have shown that the human family, genus and species all seem to have arisen in Africa. It is also in Africa that the earliest cultural evidence has been recovered. The substantial palaeontological data that anchor this knowledge have been acquired through the efforts of a very small group of fieldworkers, first in the southern, and subsequently in both the southern and eastern parts of the continent.

Among eastern African states, Ethiopia has contributed much to the growing knowledge of human origins and evolution. Field research has concentrated on a few key sites: the Omo, Melka Kontoure, Gadeb, the Middle Awash and Hadar. However, despite the length of the Ethiopian Rift and its relatively broad lake basins, only a small number of Ethiopian palaeoanthropological sites have yet been discovered, often by accident rather than by systematic survey. In a comparative sense, the Ethiopian Rift has not been investigated as thoroughly for palaeoanthropological resources as the rift in Kenya or Tanzania. As a result, it is currently impossible to accurately gauge the full extent of Ethiopian palaeoanthropological resources in quantity, spatial distribution or time depth.

Since the early 1980's, the development of Ethiopian manpower and facilities in palaeoanthropology has proceeded rapidly, and a strong infrastructure for intensified research is now in place. In 1988, the Ethiopian Ministry of Culture began a project designed to inventory the palaeoanthropological resources of the Ethiopian rift and Afar Depression. This project enables a closer monitoring of Ethiopia's antiquities and sets priorities for the scientific investigation of these resources.

Over 60 years ago the late Raymond Dart captured the attention of the palaeoanthropological world with his recognition of the Taung hominid. Now, as then, what is needed most in palaeoanthropology is the discovery of new fossils and contextual evidence. Although evidence will continue to come from sites that are already known, evidence from undiscovered sites may hold even more potential for advancing knowledge about our origins. We report here on the palaeontological content and potential of one of the areas visited by the inventory project in 1989. This is Burji, a Miocene palaeontological resource in the Amaro Horst region of the Main Ethiopian Rift (MER) of southern Ethiopia.

GEOGRAPHY

The southern terminus of the Main Ethiopian Rift is bifurcated into the Ganjuli and Galana grabens on either side of an uplifted and faulted block known as the Amaro Horst. The Burji palaeontological area lies at the southern tip of the Amaro Horst, above the headwaters of the Segen

River. It is approximately 40 km southwest of Agere Mariam, at an elevation of approximately 1650 m, in the Sidamo administrative region (Figure 1). Mapping in the Burji area by Ethiopian Institute of Geological Survey geologists resulted in the identification of terrestrial sediments interbedded with volcanics of unknown age (Seyid and HabteGiorgis 1987). Some vertebrate postcranial fossils had been collected from one locality by the geologists and brought to Addis Ababa. The inventory team went to Burji to establish the age of the sediments and to assess their palaeoanthropological potential.

GEOLOGY AND GEOCHRONOLOGY

Figure 1 Map of Ethiopia, showing four new palaeoanthropological study areas established in 1988 and 1989 by the Ethiopian Ministry of Culture's Palaeoanthropological Inventory of Ethiopia. The Burji area yielded the Miocene proboscidean remains which constitute the subject of this paper.

The Amaro Horst is a 90 km long and 25 km wide block that was uplifted about 1.5 km above the surrounding graben floors sometime in the Late Miocene (Levitte *et al.*, 1974). The block comprises crystalline basement rocks (Precambrian) overlain 5-30 m of sedimentary grits, and by widespread Tertiary volcanic flows and intercalated sedimentary strata of >150m in thickness (Mohr and Gouin 1968; Levitte et al. 1974; WoldeGabriel *et al.* in press). The vertebrate fossils and silicified wood described below come from a volcaniclastic deposit intercalated with mafic lavas southwest of Burji-Kilicho Village. The fossiliferous unit ranges in thickness from 10 - 20 m within the mapped area and consists of altered crystal and lithic tuff, finely bedded dark-brown silt and clay horizons with fossil wood and leaves, a thick reddish sandstone unit which yielded the vertebrate remains, and a yellow crystal tuff. This sedimentary unit is capped by 20-30 m thick, fresh, and sparsely porphyritic basalt flows. The flow above the fossil vertebrate site, BUR1, is a porphyritic olivine basalt that yielded a minimum K/Ar age for the vertebrate remains of 11,1 my (a correlative flow from the nearby Gembo Mountains yielded an age of 11,9 my; WoldeGabriel *et al.* in press).

PALAEOBOTANY

The fossiliferous volcaniclastic unit, with its reworked tephra, silt, and clayey beds, was probably primarily deposited in a lacustrine environment characterised by a swampy zone with abundant vegetation. Our survey team noted large (1-50 cm) pieces of petrified wood at the BUR1 locality. Where similar sediments crop out in the general area of Burji, fossil wood was found to be locally abundant, with tree trunk sections up to 70 cm diameter being fairly common. Associated sediments were not sampled for pollen and no identification of the macrobotanical specimens was attempted. These Burji palaeobotanical remains are, however, diverse and important, particularly in light of the poor but growing knowledge of Neogene eastern African palaeoflora from 3,6-18 my (Jacobs and Kabuye 1987).

VERTEBRATE PALAEONTOLOGY

The Early to Middle Miocene vertebrate faunas of Eastern Africa are very well known due to the recovery of abundant and diverse remains from a large number of localities in Kenya and Uganda. The assemblages from these localities are perhaps best known for their primate faunas, but proboscideans, in particular, have been valuable elements in the resolution of regional biochronological relationships, with the best-known Early Miocene remains known from Rusinga (17,8 my; Drake *et al.* 1988), Buluk (>17,2 my; McDougall and Watkins 1985), and Kalodirr (16-18 my; Leakey and Leakey 1987). Middle Miocene sites with biochronologically significant proboscidean remains include Maboko (15-16 my; Andrews *et al.* 1981), Fort Ternan (14 my; Shipman *et al.* 1981), Ngorora (c. 10 - 12,7 my; Hill and Ward (1988), and Nakali (9 my; Pickford 1987).

Previous to the discovery of the Burji area, there were only two reported Miocene vertebrate occurrences in Ethiopia. These occurrences comprised a deinothere molar from Miocene lignites at Adi Ugri (Eritrea; Vialli 1966), and a small Upper Miocene vertebrate collection from Chorora, including *Stegotetrabelodon*, dated to c. 10 my (Sickenberg and Schonfeld 1975; Tiercelin et al. 1979). Due to the paucity of the Ethiopian record, the geographic placement of Ethiopia between the East African Miocene localities and others in Eurasia, the Burji BUR1 vertebrate fossil locality takes on particular significance.

The vertebrate remains from the BUR1 locality are all derived from a thin red sandstone bed located below the dated basalt horizon (11,1 my). The remains themselves are extremely well preserved, with complete fossilization and limited crushing of the postcranial elements. All of

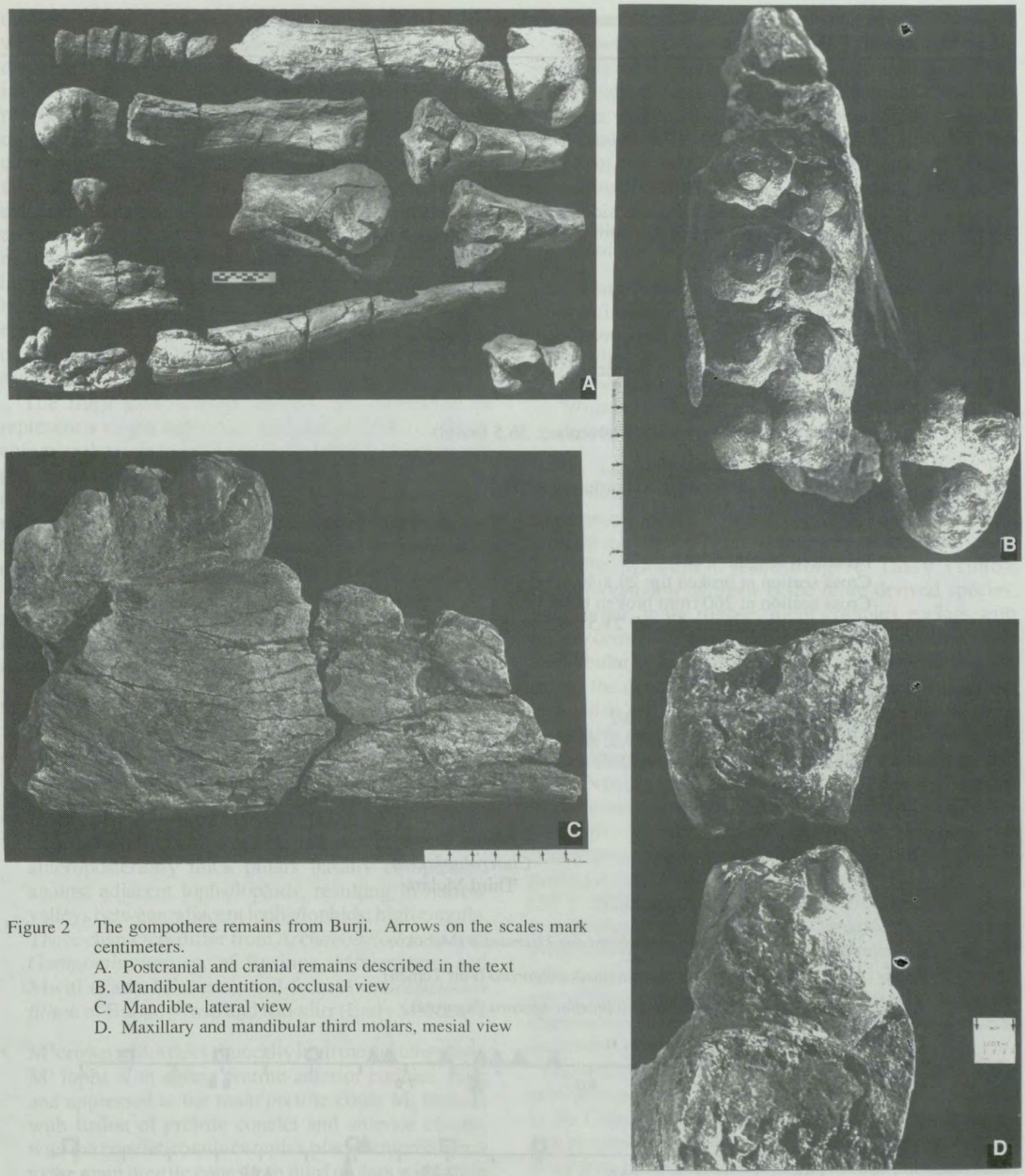


Figure 2 The gompothere remains from Burji. Arrows on the scales mark centimeters.

A. Postcranial and cranial remains described in the text
B. Mandibular dentition, occlusal view
C. Mandible, lateral view
D. Maxillary and mandibular third molars, mesial view

TABLE 1. Measurements on BUR1-1 (in millimeters)

Element at Pillar Number	1	2	3	4	5
RM^3					
Maximum breadth	66	66,2	-	-	-
Basal breadth	c,59	59,3	-	-	-
Lingual pillar height	55(w)	58	-	-	-
Buccal pillar height	47,5(w)	53,1	-	-	-
RM_3					
Basal length: 115+30 (from lt, side) = 145					
Maximum length 122,5+33 (from lt, side) = 155,5					
Maximum breadth	59,5	57,5	54	53,5	c,43
Basal breadth	56	-	-	51	-
Lingual pillar height	50(w)	52	-	53	-
Buccal pillar height	50(w)	57,5	59,5	56,5	49(lt)

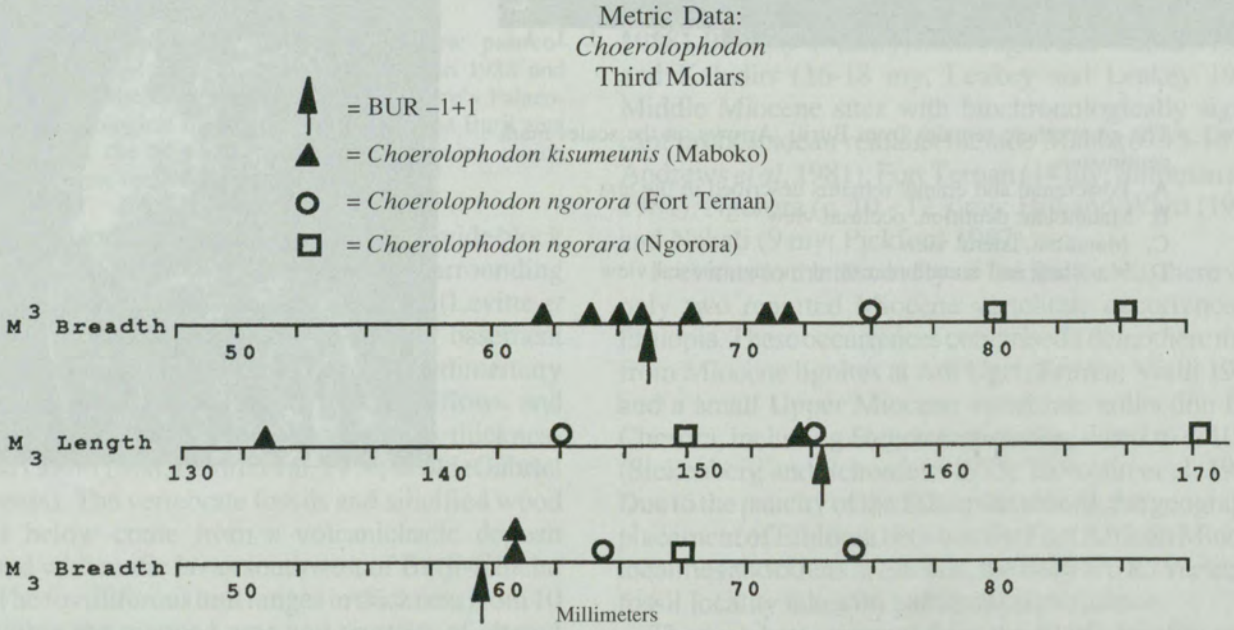
Mandible:
Height below mesial M_3:132 (medial); 109 (lateral)
Height below mesial M_2:87,5
Breadth at mid M_3:82
Breadth at mesial M_2 root: 43 (alveolar): 36,5 (basal)

M_2-M_3 alveolar length: 220
Center of mental foramen to corpus base: 57,5
Mental foramen diameter: 15

Lower tusk:
Preserved length: 630
Cross section at broken tip: 29 x 40,5, no pulp chamber
Cross section at 260 from broken base: 64,5 x 76, no pulp chamber
Cross section at base: 55x94; 21,5x39,5 pulp chamber

Upper tusk:
Preserved length: 120
Enamel band width: c,45
Enamel band thickness: 0,6-0,7
Larger cross section: 65,8x95,3, no pulp chamber
Smaller cross section: 61,0x85,5, no pulp chamber

(w)=worn tooth



Measurements of the third molar teeth. Data from Tassy, 1986

Figure 3 Comparison between measurements of the third molar teeth of various *Choerolophodon* fossils. The Burji specimen is indicated by the vertical arrows below each scale.

the vertebrate remains at the BUR1 locality were found within a radius of 50 m in adjacent, minor, north-to-south drainages. Fossilization and matrix of all specimens is identical. All but one element represent a large proboscidean, with no duplication of body parts, with compatibility of sizes of all elements, and with compatibility of all ontogenetic ages (young adult with third molars erupting, major vertebral, tibial, femoral and calcaneal epiphyses attached, with epiphyseal lines apparent). A second individual of indeterminate mammalian taxon is represented by a rhinoceros-sized humeral midshaft found in the eastern drainage, separated by 30 m from the closest other vertebrate fossil. No other remains were found in the limited 2-day reconnaissance of this locality and nearby exposures of contemporary sediments.

The Burji proboscidean remains are considered to represent a single individual designated BUR1-1. They comprise the right mandibular body with M_2 alveolus and root, and most of the M_3, the mesial right M^3, a lower tusk of 630 mm preserved length; fragments of upper tusk; right and left proximal tibiae; a right distal femur; the left femur lacking the proximal end; most of the ?left humerus; the right calcaneus; and five vertebral bodies.

The gnathic elements of this individual allow diagnosis as a choerolophodont mastodont. Our diagnosis is as follows (Figure 2; metric data in Table 1; comparative statements based in Tassy 1986 and Tobien 1973):

- M_3 with 4 lophids, 1 terminal pillar, no pillar alternation; M_2 with 3 lophids (judged from root). These characters exclude attribution as *Stegotetrabelodon*, *Tetralophodon* and *Anancus*.

- Both third molar crowns relatively narrow buccolingually, with steep buccal and lingual walls; anteroposteriorly thick pillars basally compressed against adjacent lophs/lophids, resulting in narrow valleys between adjacent lophs/lophids; high cingula. These characters differ from *Archaeobelodon* sp. and *Gomphotherium* sp. of Rusinga, Mfwangano, and Mwiti (Early Miocene); and from *Archaeobelodon filholi* of Buluk, Mwiti and Kalodirr (Early Miocene).

- M^3 crown with a thick, buccally high mesial cingulum; M^3 lophs with strong pretrite anterior conules, high and appressed to the main pretrite cone; M_3 lophids with fusion of pretrite conelet and anterior conule, with the conelet/conule complex placed anterolingual to the main pretrite cone; both third molars with a thin cementum cover. These traits conform to the *Choerolophodon* pattern.

- Our interpretation is that the BUR1-1 individual had an upper tusk with an enamel band, and a lower tusk. This is because the 630 mm long tusk piece, with portions of the pulp chamber preserved, has no enamel band, but another tusk fragment with larger cross-section dimensions has no pulp chamber and bears an enamel band. Possession of a lower tusk is the primitive condition for gomphotheres in general, and does not by itself contradict a *Choerolophodon* attribution. The lower tusk is oval in cross section. This character excludes *Archaeobelodon* of Buluk, Kalodirr and Mwiti and *Protanancus* of Maboko and Fort Ternan because both of these taxa have flattened lower tusks.

- Mandible slender. *Anancus* and *Archaeobelodon* mandibles are more robust.

- Calcaneus with same basic morphology as Fort Ternan specimens attributed by Tassy (1986) to *Choerolophodon*. Femur with same basic morphology but slightly smaller than largest Fort Ternan femora. Tassy (1986) refers the two Fort Ternan femora to ?*Protanancus*, but the BUR1-1 remains suggest a reconsideration of femoral variation.

The pattern described here is characteristic of *Choerolophodon*, but the features are shared with both *Choerolophodon kisumuensis* of Maboko and *Choerolophodon ngorora* of Fort Ternan, Ngorora, and Nakali (Middle Miocene). According to Tassy (1986), *Choerolophodon ngorora* is the more derived species, with larger, more rugose, more complex molars with thicker cementum cover, strong inferior inclination of the mandibular symphysis and deepening of the corpus anterior to the dental arcade, lack of an enamel band of the upper tusk, and inferred lack of a lower tusk. The last four characters are, however, unknown for *C. kisumuensis*.

The Burji specimen lacks the molar complexity seen in some Ngorora and Nakali specimens. Some Ngorora, Fort Ternan and Maboko specimens are fairly simple, but not to the degree seen in Burji, with the M_3 post-trite conelet present only on lophid 1 and the lack of discernible posterior conules on pretrite lophids 2-4 (M_3) or loph 2 (M^3). BUR1-1 is thus unique, but most closely approximated by Maboko counterparts in metrics and morphology of the third molar. Enamel rugosity and cementum cover is not extreme in BUR1-1, as opposed to some Ngorora/Nakali specimens. On the other hand, the expression of these traits is similar to the condition seen on other Ngorora and Fort Ternan specimens.

In summary, the Burji specimen appears to represent a primitive species of *Choerolophodon*, with molar features at the *Choerolophodon kisumuensis* stage of evolution. The extreme occlusal pattern simplicity exhibited by the Burji specimen is not a primitive pattern of gomphotheres in general, and must be either a uniquely derived condition, or a variation of the basal *Choerolophodon* pattern.

Characteristics of the tusks of *Choerolophodon kisumuensis* are unknown, and if this taxon is shown to lack lower tusks or lack enamel bands in upper tusks, the BUR1-1 specimen would be a different species.

The biochronological placement of a primitive *Choerolophodon* species like that described here for Burji would be in the time range of 15-20 my. However, the lack of *Choerolophodon* in the Early Miocene of eastern Africa, particularly at the Kenyan site of Buluk, approximately 200 km to the southwest of Burji and with abundant proboscidean remains, would suggest a most likely age of the Burji specimen as 15 - 17 my.

SIGNIFICANCE OF THE BURJI AREA

The radiometric dating and biochronological information derived from our preliminary work in the Burji area have already led to a better understanding of volcanism and rifting in the southern section of the Main Ethiopian Rift (WoldeGabriel *et al.* in press). The discovery of vertebrate palaeontological remains at Burji holds out the promise that other localities, perhaps with primates, will be found nearby. It is clear that further investigation of the Burji locality's macrobotanical and vertebrate palaeontological potential is warranted. The Burji fossils are roughly contemporary with those from Pasalar, Turkey (Bernor and Tobien 1990). This part of the Middle Miocene is rapidly becoming better calibrated and understood (Steininger, Bernor and Fahlbusch 1990), allowing palaeontologists to model Old World Miocene faunal evolution as related to multiple, eustatically regulated intercontinental migration events (Bernor and Tobien 1990). Further investigation of the Burji locality, Ethiopia's first of this age, promises to contribute significant data to our understanding of Middle Miocene African floral and faunal evolution.

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We are pleased to be able to dedicate this contribution to Alun Hughes. We share great admiration and respect for the remarkable innovation and dedication which Alun has brought to his quest for knowledge about human origins. He will continue to inspire us wherever we engage in fieldwork.

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REFERENCES

ANDREWS, P., MEYER, G.E., PILBEAM, D.R., VAN COUVERING, J.A., & VAN COUVERING, J.A. 1981. The Miocene fossil beds of Maboko Island, Kenya: Geology, age, taphonomy and palaeontology. *Journal of Human Evolution*, **10,** 35-48

BERNOR, R.L. & TOBIEN, H. 1990. The mammalian geochronology and biogeography of Pasalar (Middle Miocene, Turkey). *Journal of Human Evolution*, **19,** 551-568.

DRAKE, R.L., VAN COUVERING, J.A., PICKFORD, M., CURTIS, G.H. & HARRIS, J.A. 1988. New chronology for the Early Miocene mammalian faunas of Kisingiri, Western Kenya. *Journal of the Geological Society of London*, **145,** 479-491.

HILL, A. & WARD, S. 1988. Origin of the Hominidae: The record of African large hominoid evolution between 14 my and 4 my. *Yearbook of Physical Anthropology*. **31,** 49-83.

JACOBS, B.F. & KABUYE, C.H.S. 1987. A middle Miocene (12.2 my old) forest in the East African Rift Valley, Kenya. *Journal of Human Evolution*, **16,** 147-155.

LEVITTE, D., COLUMBA, J., & MOHR, P.A. 1974. Reconnaissance geology of the Amaro Horst, southern Ethiopia. *Geological Society of America Bulletin*, **85,** 417-422.

LEAKEY, R.E. & LEAKEY, M.G. 1987. A new Miocene small-bodied ape from Kenya. *Journal of Human Evolution*, **16,** 369-387.

MCDOUGALL, I. & WATKINS, R. 1985. Age of hominoid-bearing sequence at Buluk, northern Kenya. *Nature*, **318,** 175-178.

MOHR, P.A. & GOUIN, P. 1968. Gravity traverses in Ethiopia (Third Interim Report). *Bulletin of the Geophysical Observatory, Addis Ababa*, **10,** 15-52.

PICKFORD, M. 1978. The chronology of the Cercopithecoidea of East Africa. *Human Evolution*, **2** (1),1-17.

SHIPMAN, P., WALKER, A.C., VAN COUVERING, J.A., HOOKER, P.J., & MILLER, J.A. 1981. The Fort Ternan hominoid site, Kenya: Geology, age, taphonomy and paleoecology. *Journal of Human Evolution*, **10,** 49-72.

SEYID, G. & HABTEGIORGIS, A. 1987. Preliminary report on the geology of Subsheets N and O, Agere Mariam Sheet (NB 37-10). Ethiopian Institute of Geological Surveys, Regional Geology Department (unpublished report).

SICKENBERG, O. & SCHONFELD, M., 1975. The Chorora Formation-Lower Pliocene limnical sediments in the southern Afar (Ethiopia). **In:** A Pilger and A. Rosler (Eds.), *Afar Depression of Ethiopia, Volume 1*. Stuttgart: E. Schweizerbartsche Verlagsbuchhandlung. p. 377-284.

STEININGER, F.F., BERNOR, R.L. & FAHLBUSCH, V. 1990. European Neogene marine/continental chronologic correlations. **In:** E.H. Lindsay, V. Fahlbusch, and P. Mein (Eds) *Topics on European Mammalian Geochronology*. New York: Plenum.

TASSY, P. 1986. *Nouveaux Elephantoidea (Mammalia) dans le Miocene du Kenya*. Paris, Cahiers de Paleontologie.

TIERCELIN, J.-J., MICHAUX, J. & BANDET, Y. 1979. Le Miocene superieur du Sud de la Depression de l'Afar, Ethiopie: Sediments, faunes, ages isotopiques. *Bulletin Societe Geologique Francais*, **7,** 255-258.

VIALLI, V. 1966 Sul rivenimento di Dinoterio (*Deinotherium* cf. *hobleyi* Andrews) nelle ligniti di Adi Ugri (Eritrea). *Giron. Geol., Ser.* **2,** (33) 447-458.

WOLDEGABRIEL, G. YEMANE, T., SUWA, G., WHITE, T., & ASFAW, B. in press. Age of volcanism and rifting in the Burji-Soyoma area, Amaro Horst, southern Main Ethiopian Rift: Geo and biochronologic data. *Journal of African Earth Sciences*.

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THE PALAEONTOLOGY OF HAASGAT A PRELIMINARY ACCOUNT

by

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ABSTRACT

Haasgat is a cave on the steep western slope of the upper reach of the Witwatersrand Spruit, on the farm Leeuwenkloof 480 JQ, in the Brits District. It was heavily mined for flowstone (calcite). The cave contains a deposit of fossiliferous cave silt and breccia that was partially removed by the miners and dumped on the steep slopes of the valley.

The original entrance was probably a shallow inclined pit, leading into an upper chamber and then into the preserved depository.

Both porcupines and carnivores served as accumulating agents for the bones.

Fossils of the primates *Parapapio* and *Cercopithecoides*, hyaena (*Chasmaporthetes*), fox, porcupines, several species of bovids and two species of Hyrax have been recovered. An insufficient number of fossils have been prepared to determine the age of the deposit with certainty. The deposit was provisionally thought to be of *Pliocene* age because of the occurrence of *Parapapio*. At this stage it would be unwise to correlate this occurrence with any other caves in this age range.

It is concluded that the cave silts were deposited by flash floods, under a wetter climatic regime than that of the present.

MAIN FEATURES AND ORIGIN OF THE DEPOSIT

Haasgat is the remains of what once was a more extensive cave on the farm Leeuwenkloof 48 JQ in the Brits District. It is situated on the steep western slope at the uppermost end of the Witwatersrand Spruit Valley (Figure 1). The cave was mined for calcite flowstone early in the present century, and is so damaged that it is impossible to ascertain the original conformation of the cave at the time of discovery by the limeworkers.

Occurrences of basal collapse breccia outside the cave prove that it was once a much larger cave than is presently preserved.

The cave originated as a phreatic chamber along a joint or small fault, in dolomite of the Eccles Formation of the Malmani Subgroup (Chunniespoort Group). The oldest sediment in the cave is a basal collapse breccia that must have formed shortly after the cave was drained of its phreatic water by the downcutting of the Witwatersrand Spruit Valley. This was followed by the deposition of a thick basal flowstone that cemented the basal collapse breccia. At this stage the cave was intersected by the formation of the valley, and developed an opening to the surface through which external clastic material and animals could enter the cave. From this stage onward the cave was filled with fossiliferous cave silt and breccia. These sediments were cemented by calcite deposited from percolating vadose water. Further cutting down of the valley led to the removal of the upper parts of the cave and the excavation of a smaller cave or Makondo (Brink and

Figure 1. View of Haasgat from the opposite side of the valley of the Witwatersrandspruit. The arrow indicates the position of the large opening in the roof of the cave. Note the extensive dumps on the steep slope below the cave entrance

Partridge 1980) within the sediment of the original cave fill. This cave was in turn also filled with fossiliferous rubble that became partially cemented. Later on much of the roof of the cave was removed by weathering.

Presently the cave consists of an elongate irregular passage with a large opening in the roof near the entrance (Figure 1). A bridge of cemented cave sediment is formed between the entrance and the collapse opening in the roof. Over much of the length of the cave the ceiling consists of fossiliferous cave sediment. Mining caused part of this ceiling to collapse, leaving a large heap of fossiliferous blocks in the middle section of the cave. This collapse probably occurred after the miners had abandoned the operation. The material from this collapse has not been studied yet.

During operations the limeworkers entirely removed the basal flowstone from the cave, and caused the collapse of a large part of the cave fill. They dumped this material downslope, below the cave entrance (See Figure 1). The fauna described here was retrieved by mechanical preparation of blocks from this dump. The fossil deposit was discovered by Dr. J.E.J. Martini, and was surveyed and studied by Dr Martini and the author (Keyser and Martini 1991). The purpose of this paper is to give a preliminary overview of the fauna.

PALAEONTOLOGY

The cave silts preserved in Haasgat are fossiliferous but do not anywhere contain the great concentration of bone seen in some other caves like Sterkfontein and Makapansgat.

As yet, only material from the dumps has been prepared and studied. This material probably came mostly from the siltstone beds immediately above the floor flowstone and is not highly fossiliferous. It is possible that the cave opening was relatively much smaller when the lower siltstone beds were deposited, and it is possible that the siltstone rubble from the roof collapse in the limeworks would be more productive.

SOME TAPHONOMIC CONSIDERATIONS

Virtually all the fossil specimens from the sediment blocks on the dumps were badly broken and weathered prior to fossilization. Bones in all stages of weathering, according to the scale of Behrensmeyer (1981), are encountered. A very large number have, however, weathered to stage 5. The weathering and other destruction could have happened on the surface, but bones in all stages of weathering are encountered in other caves in the vicinity. In another cave in the area, Hyaena Cave (Martini and Keyser, 1989), bones associated with hyaena droppings can be seen at all stages of weathering. This weathering is obviously taking place in the cave because many cracked and weathered bones have all their fragments lying in association. This exfoliation and fragmentation are often due to the crystallization of brushite, forming shiny needles which resemble frost. This phenomenon is very common in caves in the area (Martini and Kavalieris 1978). It is therefore possible that most of the weathered bone and bone fragments found in the cave silts of Haasgat weathered on a debris-cone below an opening in the cave, and were broken when they were transported down the slopes of the debris cone together with boulders and other clasts by gravity, and later transported by floods and deposited in the cave slits. Weathering would have stopped immediately after deposition. The possibility that the bones were weathered in an upper chamber connecting the cave entrance (which could have been either a sinkhole or a passage) with the lower cave, also deserves serious consideration. No definite decision can be reached on the available evidence.

There can be no doubt that porcupines and carnivores were important accumulators of bones in the cave sediment. In Figure 2 a fragment of a large bone that was first chewed by a porcupine, then broken and afterwards transported to be deposited in the cave silts, is shown. This can be deduced from the fact that the fracture cuts across the porcupine-type gnawing marks (Maguire and Pemberton 1980), and that some matrix still adheres to the fracture surface. In Figures 3 and 4 puncture marks of carnivore teeth on an antelope sacrum are illustrated. Figure 4 is an enlarged photograph of the puncture marks in Figure 3.

Since the whole of the eastern end of the cave that included the opening to the surface has been weathered away, thereby exposing the ancient cave sediments, a more exact model for bone accumulation may never be found.

THE FOSSIL FAUNA

Primates

A nearly complete *Parapapio* (baboon) female skull, without the occiput and its canines (Figure 5), was found. It was a fairly young female with the second molars starting to erupt. A palate with some teeth of another juvenile individual was also recovered. According to Simons and Delson (1978), it would be unwise to attempt a definite identification on such an inadequate sample.

Figure 2. Bone gnawed by a porcupine

Figure 3. Anterior view of antelope sacrum with a puncture mark caused by the teeth of a carnivore.

Figure 5. Skull of a young female *Parapapio*

The specimen does resemble a specimen of *Parapapio broomi* illustrated by Maier (1970).

Several skulls of the colobine monkey, *Cercopithecoides williamsi*, (Figure 6) were also recovered. A piece of jaw with two very worn large molars could possibly be a Simonpithecus; the material, however, is too inadequate to be sure.

No remains of hominids have been recovered to date.

Carnivora

A left maxilla of a hyaenid, possibly *Chasmapoorthetes nitidula* (Ewer) (Figure 7), was recovered from the dumps. The present specimen has a slightly larger pm^3 than most of the material from Kromdraai. This tooth is again smaller than that of *Hyaena brunnea* Thunberg. Both the above taxa are known from Sterkfontein Member 4 (Turner 1987). The left jaw of a fox was also found. Unfortunately all the teeth of this jaw have been lost, and a definite identification is not possible. It is comparable in size with that of *Canis mesomelas*.

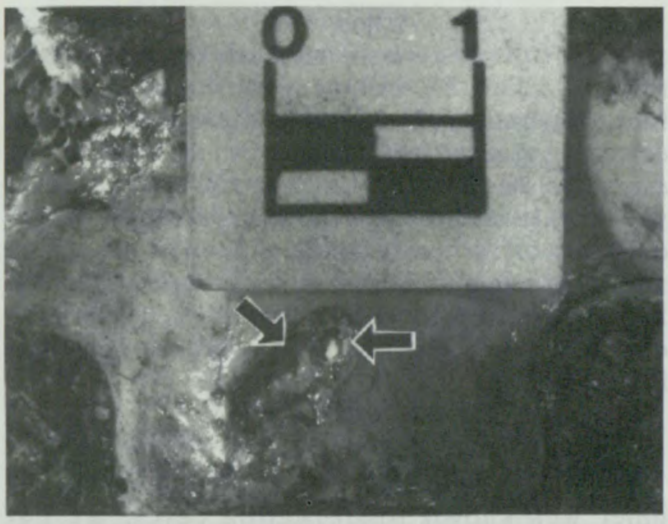

Figure 4. Enlargement of the puncture marks seen in Figure 3, showing smaller puncture marks within the larger puncture.

Figure 6. Partial skull of *Cercopithecoides williamsi*.

Hyracoidea

Two species of hyracoids were recovered. The large one appears to be *Procavia transvaalensis* Shaw (Figure 8), while the smaller species is *Procavia antiqua* Broom (Figure 9), as is evidenced by its more brachydont dentition when compared with recent *Procavia capensis*. Only one juvenile lower jaw of the smaller species has been recovered to date.

Artiodactyla

Teeth of several species of Artiodactyla were recovered from the dumps. Most of the material is, however, so badly damaged that identification is doubtful. A badly-distorted palate and lower jaw (Figure 10) of *Pelea capreolus*, the living grey rhebok, could be identified with confidence. A ramus of the lower jaw with complete dentition was also found. A large molar of an alcelaphine and one of an *Antidorcas*-like antelope were also found. Many fragments of bones of large bovids were seen in the dumps, but no teeth have been recovered. As yet no suids have come to light.

Rodentia

Large concentrations of rodent bones, common in the other well-known fossil-bearing caves, are not encountered in the dumps of the roof collapse in Haasgat. A possible explanation is that the preserved sediments were deposited very far from the cave entrance where owls did not roost (Maguire *et al.* 1985). The only identifiable rodent material is a lower jaw with two post-canine teeth, and some isolated incisors and molars of a hystricoid that can not be distinguished from recent *Hystrix africae-australis*.

Age of the Fauna

All the taxa recovered from Haasgat are known from all the other fossil-bearing caves in the Krugersdorp area, i.e. Sterkfontein, Swartkrans and Kromdraai, as well as from Makapansgat Limeworks near Potgietersrus. The presence of *Parapapio* and *Chasmaporthetes* leaves no doubt that the Haasgat deposit is of similar age to the other cave deposits and is therefore near the Plio-Pleistocene boundary – probably upper Pliocene. It is however, impossible to correlate it unequivocally with any one of the other known deposits at present, because an insufficient number of identifiable fossils have been recovered to date. If hominids

Figure 8. Teeth of *Procavia transvaalensi* Shaw (above) compared with a lower jaw of a large individual of *Procavia capensis*

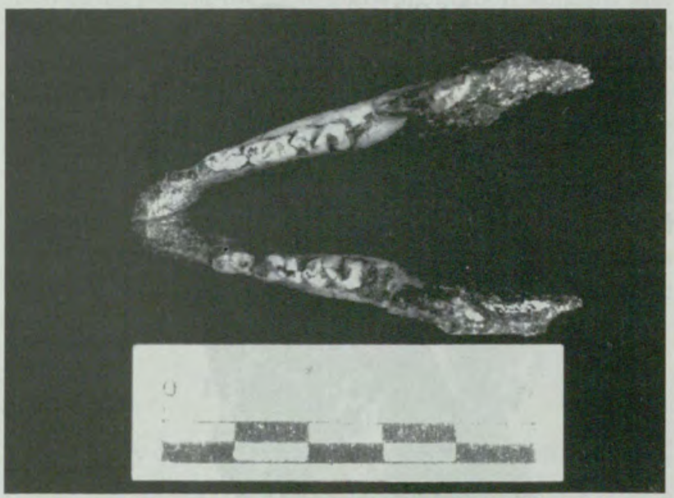

Figure 9. Lower jaw of a juvenile *Procavia antiqua* Broom.

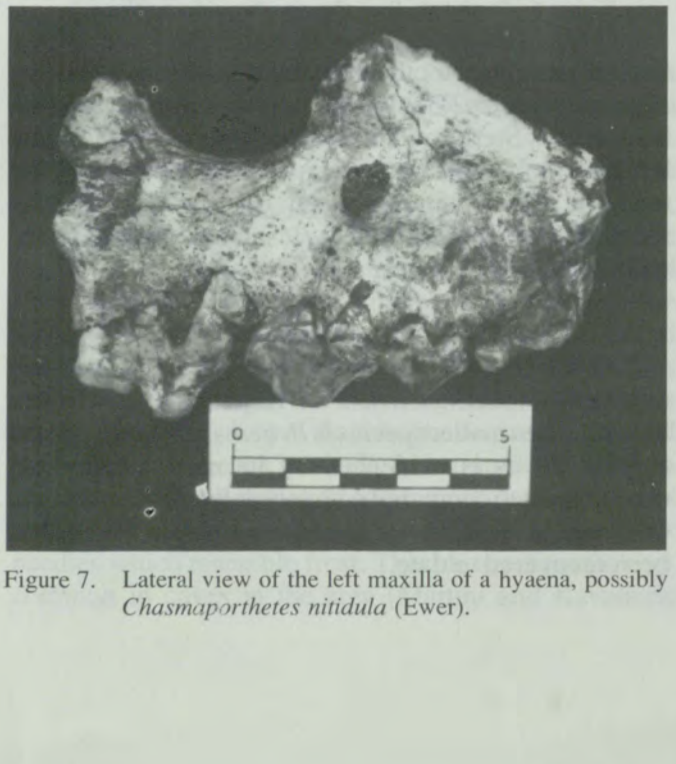

Figure 7. Lateral view of the left maxilla of a hyaena, possibly *Chasmaporthetes nitidula* (Ewer).

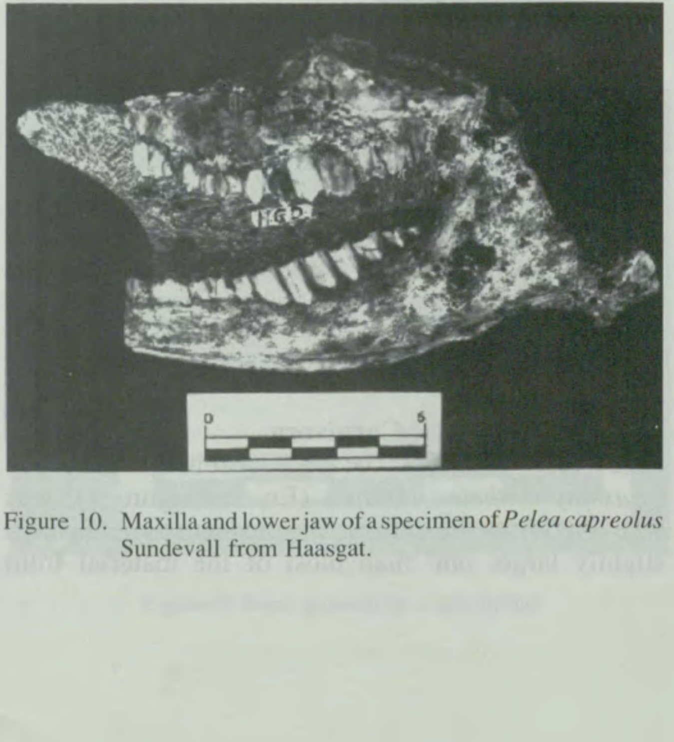

Figure 10. Maxilla and lower jaw of a specimen of *Pelea capreolus* Sundevall from Haasgat.

and/or suids could be found, a better correlation will be possible.

Palaeoclimatic considerations

The most abundant ruminant in the collection of fossils from Haasgat is *Pelea capreolus*, the grey rhebok. The fossil material does not appear to differ from the recent species in any way. Grey rhebok tend to frequent grassy plateaux and can be regarded as an upland animal.

Their presence in Haasgat suggests that the African surface was a grassy upland at the time when the Haasgat deposit was being formed. Carcasses were probably brought into the cave by scavenging carnivores.

Of all taxa, *Cercopithecoides williamsi*, a colobine monkey, is the most abundant (seven individuals). Colobines tend to be specialized leaf-eaters, as is clearly displayed by the high cusps on the molars (Brain 1981). It is possible that *Cercopithecoides williamsi* occupied the same ecological niche as recent *Cercopithecus aethiops* (Brain 1981). The long, sharp cusps on the molariform teeth of *Cercopithecoides* do, however, indicate that it was a forest rather than a savannah dweller. These facts support the conclusion that the then much shallower Witwatersrandspruit Valley contained a dense forest. Colobine monkeys normally sleep in trees and do not shelter in caves. It therefore appears likely that the *Cercopithecoides* material found in Haasgat was scavenged from the forest.

The presence of a fairly dense forest in the Witwatersrandspruit Valley is indicative of a higher annual rainfall than is presently encountered in the Haasgat area. Because of its high elevation and the fact that most of the original proximal deposits have been weathered away, there is still reason to believe that Haasgat can be older than the lower members of Sterkfontein and Makapansgat, which are generally thought to be the oldest cave deposits. It is therefore intended to have more material prepared in order to establish a better biostratigraphic correlation with the other, better-known deposits.

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REFERENCES

BRAIN, C.K. 1981. *The Hunters or the Hunted?* Chicago, University of Chicago Press.

BRINK, A.B.A. & PARTRIDGE, T.C. 1980. The nature and genesis of solution-cavities (Makondos) in Transvaal cave breccias. *Palaeont. afr.* **23,** 47-49.

KEYSER, A.W. & MARTINI, J.E.J. 1990. Haasgat, a new Plio-Pleistocene fossil locality. *Palaeoec. Afr.* **21,** 119-129.

MAGUIRE, J.M. & PEMBERTON, D. 1980. The Makapansgat Limeworks grey breccia. Hominids, hyaenas, hystricids or hillwash? *Palaeont. afr.* **23,** 75-98.

MAGUIRE, J.M., SCHRENK, F. & STANISTREET, I.G. 1985. The lithostratigraphy of the Makapansgat Limeworks Australopithecine site. Some matters arising. *Ann. geol. Surv. S. Afr.* **19,** 37 - 51.

MAIER, W. 1970. New fossil Cercopithecoidea from the Lower Pleistocene cave deposits of the Makapansgat Limeworks, South Africa *Palaeont. afr.* **13,** 69 - 107.

MARTINI, J.E.J. & KAVALIERIS 1978. Mineralogy of the Transvaal caves. *Trans. geol. Soc. S. Afr.* **81,** 47 -54.

MARTINI, J.E.J. & KEYSER, A.W. 1989. The caves of the John Nash Game Reserve. *Bull. S. Afr. Spel. Ass.* **30,** 39 - 46.

PARTRIDGE, T.C. 1978. Re-appraisal of the lithostratigraphy of Sterkfontein hominid site. *Nature* **275,** 282 - 287.

SIMONS, E.L. & DELSON, E. 1978. Cercopithecidae and Parapithecidae **In:** Maglio, V. and Cooke, H.B.S. Eds., *Evolution of African Mammals*. Cambridge, Harvard University Press.

TURNER, A. 1987. New fossil carnivore remains from the Sterkfontein hominid site. *Ann. Tvl. Mus.*, **34**, 319-347.

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THE STRATIGRAPHY OF THE STERKFONTEIN HOMINID DEPOSIT AND ITS RELATIONSHIP TO THE UNDERGROUND CAVE SYSTEM

by

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ABSTRACT

A programme of orientated core drilling was carried out during 1989 to elucidate stratigraphic relationships within the Sterkfontein Formation and to obtain a representative suite of samples for palaeomagnetic analysis. The cores have revealed that the hominid-bearing cave deposits occur as a continuous succession comprising 6 Members and extending to a maximum depth of about 30 m below present surface. Of these Member 1 (comprising a sterile, residual fill) and Member 3 are the most extensive. This sequence has been displaced vertically downwards within a zone of decalcification coinciding with the central part of the deposit. This zone has been the focus of recent deep excavations at the site.

The results of the drilling, in conjunction with recent surveys of the underground cave system, confirm that a dolomite floor existed at an average depth of about 20 m at the time of first cave filling. Subsequent cavern development down to depths in excess of 50 m caused the local collapse of some lower units of the Sterkfontein Formation and, as new openings developed to the surface, permitted the ingress of younger fills below the base of the hominid-bearing succession.

INTRODUCTION

The three-dimensional stratigraphy of the Sterkfontein hominid deposit has, until recently, been largely a matter of speculation owing to poor exposure, particularly of its lower units. During May and June 1989 five cored boreholes were sunk through the deposit into underlying dolomite bedrock under the direction of T.C. Partridge. The drilling sites were positioned so as to provide maximum information on stratigraphic relationships; orientation of the cores has also permitted their use in a new programme of palaeomagnetic analysis, the results of which will be reported elsewhere.

PREVIOUS INTERPRETATIONS OF THE STERKFONTEIN STRATIGRAPHY

The Sterkfontein deposit has become world-famous as a result of the discovery, from 1936 onwards, of hominid remains in excavations carried out near the summuit of a hill underlain by dolomite of the Monte Christo Formation (Transvaal Sequence). Since that time more than 600 hominid specimens and several hundreds of thousands of faunal remains have been recovered from the calcified filling of an ancient cave system which has become deroofed and exposed at the surface by erosion. Until the commencement of the current programme of excavation of the University of the Witwatersrand in 1966, an appreciation of the stratigraphy of these hominid-bearing deposits was based largely on the exposures provided by the surface excavations initiated during lime quarrying operations and subsequently extended by Drs. Robert Broom and John Robinson of the Transvaal Museum (Brain 1958; Robinson 1962). In the early 1970's the possibility was raised that calcified cave fills exposed at depths of 20 m and more below surface in the cave system beneath the Sterkfontein hill were continuous with those of the surface excavations (Wilkinson 1973). Surveys carried out by I.B. Watt confirmed the superposition of the two sets of deposits and indicated a minimum vertical separation of some 7,5 m between the relevant exposures. On the assumption that continuity did, in fact, exist and using the data from *in situ* observations and sedimentological analyses carried out on a large suite of samples, Partridge (1978) subsumed the hominid-bearing deposits within a Sterkfontein Formation comprising 6 members. The vertical extent and distribution of these members was further elucidated in Stiles and Partridge (1979).

In subsequent papers on the morphology of the Sterkfontein cave system Wilkinson (1983, 1985) claimed that the fossiliferous deposits have a continuous vertical extent of more than 50 m and are likely to span a period of some six million years. These claims contradicted the earlier findings of Partridge (1978) that the base of the Sterkfontein Formation was nowhere located more than about 30 m below present ground surface.

In order to resolve these differences and to provide definitive information on the three-dimensional stratigraphy of the Sterkfontein Formation, as well as to recover samples for palaeomagnetic analysis, a programme of orientated core drilling was carried out at the site during

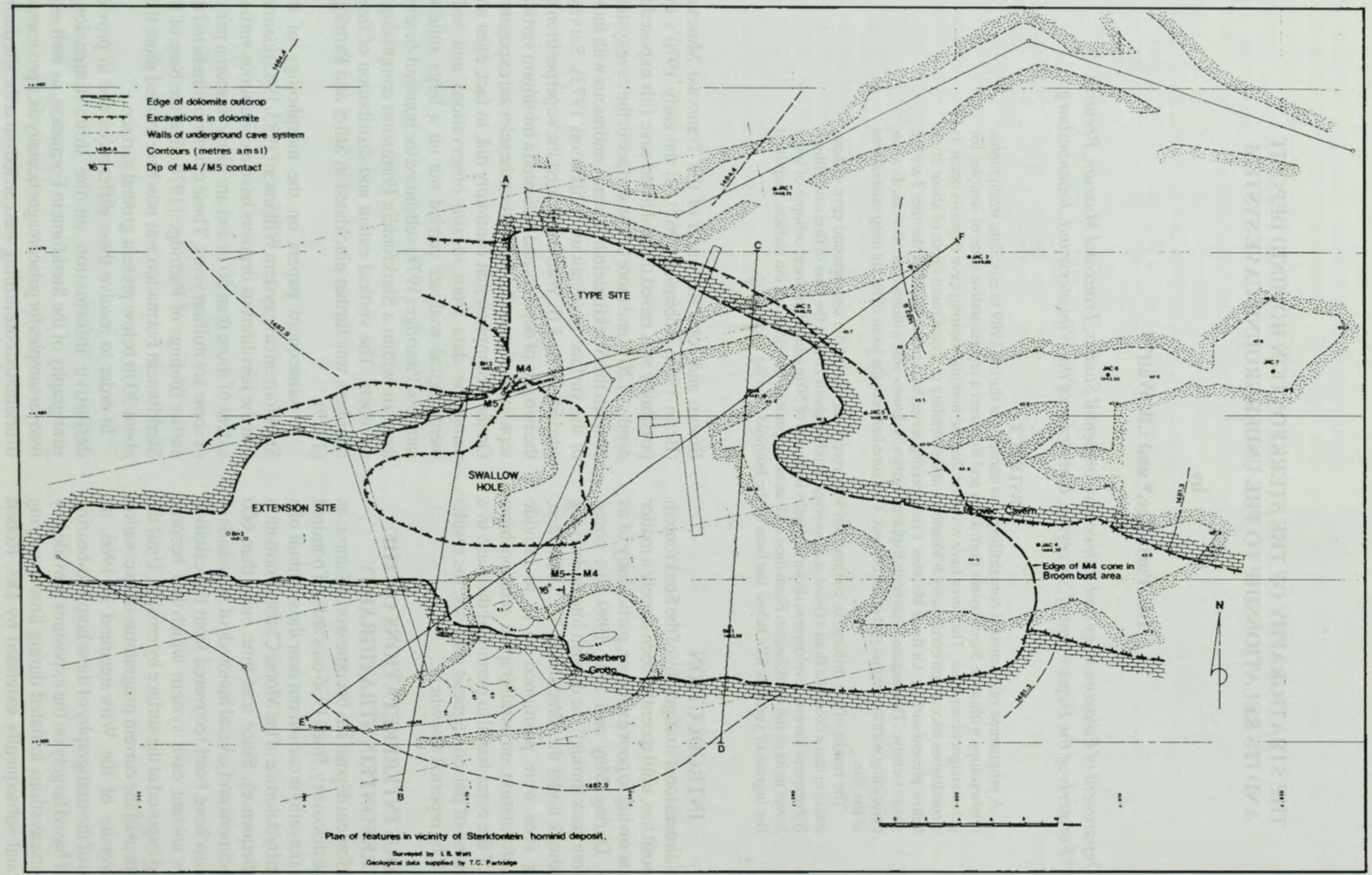

Figure 1: Plan showing surface extent of the calcified cave fill comprising the Sterkfontein Formation and underlying portions of the underground cave system.

May and June 1989. This programme involved the sinking of 5 cored boreholes using diamond-crowned bits with an internal diameter of 58,7mm. A total of 139,45m of core was recovered, and orientation with respect to true north was achieved over more than 90% of the core length using the impression method. The findings of this programme are discussed below.

RESULTS OF THE 1989 CORE DRILLING PROGRAMME

The positions of the 5 cored boreholes are shown in Figure 1; this figure, which is based on surveys carried out by I.B. Watt, also shows the extent of the surface outcrop of the Sterkfontein Formation and key elements of the underground cave system. Within the cores the vertical thickness of the Sterkfontein Formation ranges from 12,0m to 29,75m, averaging approximately 20m. Where possible (i.e. where the borehole did not terminate in a large cavity) each hole was continued at least 5m into the dolomite floor to confirm that the base of the deposit had been reached.

The vertical extent of the Sterkfontein Formation is thus in accord with the earlier estimates of Partridge (Partridge 1978; Stiles and Partridge 1979). The six-member subdivision of the Sterkfontein Formation proposed in these papers is likewise confirmed. The drilling results have, in addition, been used, in conjunction with the underground survey data, to construct a number of stratigraphic sections, which are presented in Figures 2 - 4. These sections demonstrate that, over substantial areas, the base of the Sterkfontein Formation is formed by a dolomite floor which, *contra* Wilkinson (1983, 1985), separates this older depository from deeper, but more recent chambers which extend down to the water table at depths of up to 55m below surface. Over part of its area the Sterkfontein Formation terminates above a cavern formed by the subsidence of this floor into lower-lying cavities belonging to the younger cave system. These lower-lying caverns contain both collapsed debris derived from lower members of the Sterkfontein Formation and younger debris cones which have accumulated beneath avens (or slots) to the surface, through which colluvium from the hillside has been washed. In several instances roof drip has calcified the upper layers of these debris accumulations to form hard carapaces; where further subsidence has occurred, remnants of such younger carapaces have been left as hanging remnants adhering to the dolomite walls and roofs of these deep chambers. Our recent drilling and surveying programmes have demonstrated a clear separation between the Sterkfontein Formation and these deeper (but younger) fills.

As has been pointed out previously (Partridge 1978) the surface excavations carried out to date have sampled only the upper members of the Sterkfontein Formation, despite the fact that excavations carried out by Alun Hughes in the area between the Type and Extension sites since 1983 have now reached a depth in excess of 12 m below the original surface of the cave fill. These new excavations have been restricted almost exclusively to a partially decalcified zone within the deposit in which progress is considerably more rapid than in adjacent well cemented fills, whose consistency approaches that of concrete. In the course of these excavations it became apparent that an almost vertical contact separates the older Member 4 deposits to the east from the younger Member 5 deposits to the west; this contact has previously been claimed to form a dividing line between the occurrence of australopithecine remains and that of specimens of *Homo habilis* in association with an Early Acheulian stone industry (Clarke 1985, 1988; Partridge *et al.* 1991). Since the westward declivity of this contact, as revealed over a much wider area sampled by the borehole cores, does not exceed 20°, its extreme steepness within the decalcified zone is clearly a local phenomenon. In fact, all evidence points to the occurrence in this area, some time after deposition, of vertical movements totalling about 5 m. Although some disturbance and mixing inevitably take place during such movements, the general stratigraphic sequence is commonly preserved; this has resulted in Member 5 within the swallow hole zone being brought into juxtaposition with Member 4 in the unaffected cave fill along an almost vertical plane of separation. Swallow hole translocations of this type are common in partically cemented cave fills, either as a result of ongoing solutional activity below poorly calcified materials or as a result of early deroofing and decalcification in zones underlain at depth by cavities. The latter seems more probable in the present instance. The associated vertical movements account for the failure of the deep excavations carried out to date to penetrate Member 3, which occurs at shallower depth on either side of the decalcified zone. This interpretation, made possible by the results of the drilling programme, is contrary to earlier views that the steepness of the M4/M5 contact in the excavation zone is the result of substantial erosion of the flank of the debris cone of Member 4 prior to the accumulation of Member 5.

The implications of the existence of this swallow hole zone within the Sterkfontein cave fill for the correlation of its lithostratigraphic units with hominid remains are considerable. As was the case in analogous fills in the Cave of Hearths (Partridge 1982), the movements associated with the development of the swallow hole do not appear to have disrupted completely the overall stratigraphic sequence within the displaced block; however, within the swallow hole zone the general positions of the contacts between members, particularly between M4 and M5, remain to be determined before the extent of the vertical displacement can be better estimated. There are thus reasonable prospects that it will be possible to relate most hominid specimens from this zone to individual stratigraphic units, as has been possible elsewhere in the deposit. It seems worthwhile, also, to emphasise the distinction between swallow hole development and the formation of *makondos* or solution pits (Brink and Partridge 1980). The latter are common within the eroded surfaces of Members 4 and 5, and one

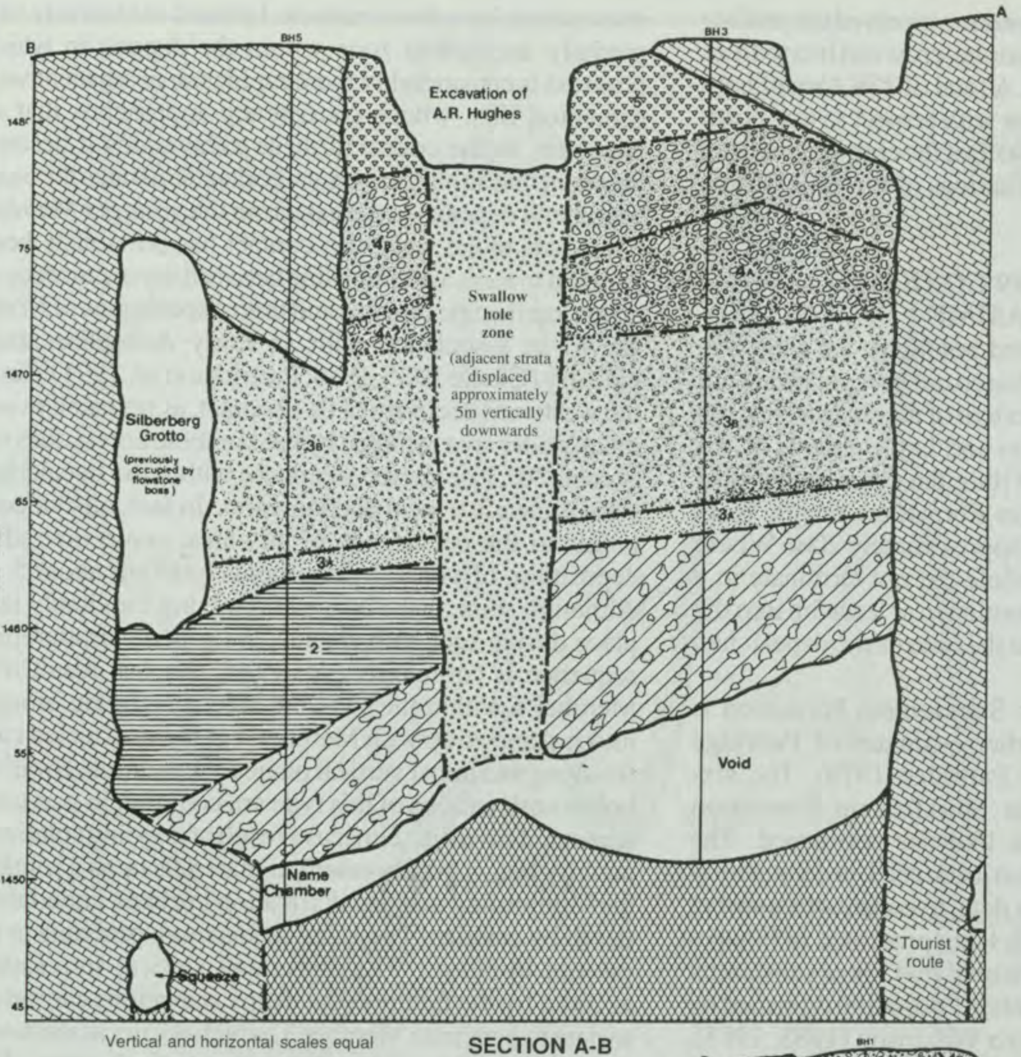

Figure 2

SUMMARY DESCRIPTION OF UNITS OF THE STERKFONTEIN FORMATION

Member 6: (Absent in sections). Basal calcite flowstone followed by dark reddish brown, moderately calcified, clastic fill. Middle Pleistocene fauna.

Member 5: Reddish brown, generally well calcified, clastic fill with abundant rock debris. *Homo habilis*, Early Pleistocene fauna and Early Acheulian stone industry.

Member 4: Bed D - localised banded calcite (pool deposits)
Bed C - Reddish brown, generally well calcified clastic fill with scattered large dolomite/chert blocks.
Bed B - Reddish brown, well calcified, clastic fill with abundant rock debris.
Bed A - Dolomite/chert roof-fall debris cemented by calcite.
All beds contain *Australopithecus africanus* and a Late Pliocene fauna, but no stone artefacts.

Member 3: Bed B - Reddish brown clastic fill with sparse rock debris and some bone.
Bed A - Basal calcite flowstone.

Member 2: Pale brown and red, well bedded, clastic fill with sparse rock debris and locally abundant bone.

Member 1: Dark brown, manganiferous, residual clastic fill with clay pellets, large dolomite/chert blocks and interbedded calcite layers.

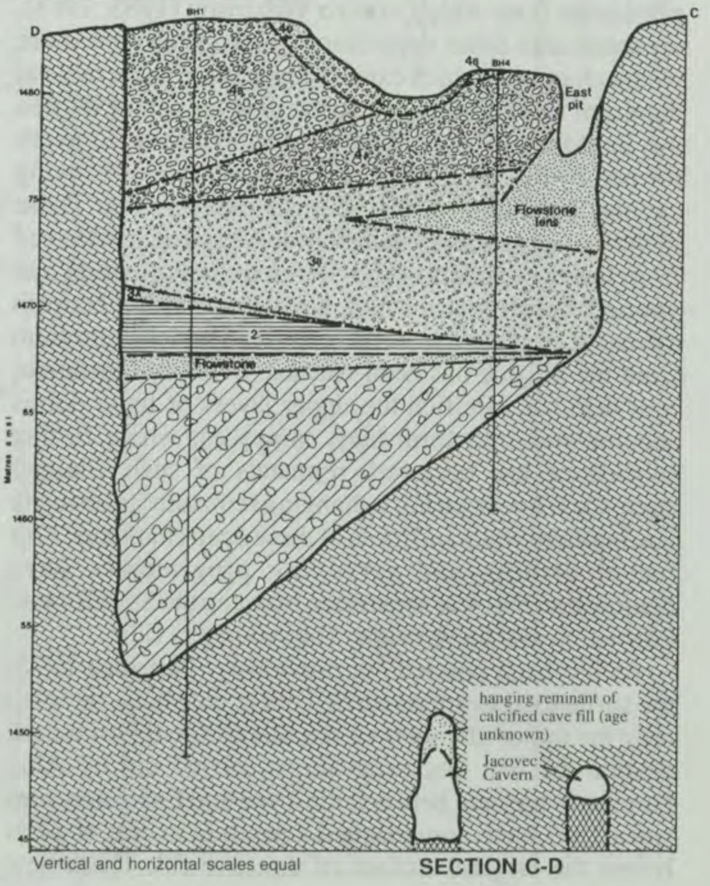

Figure 3

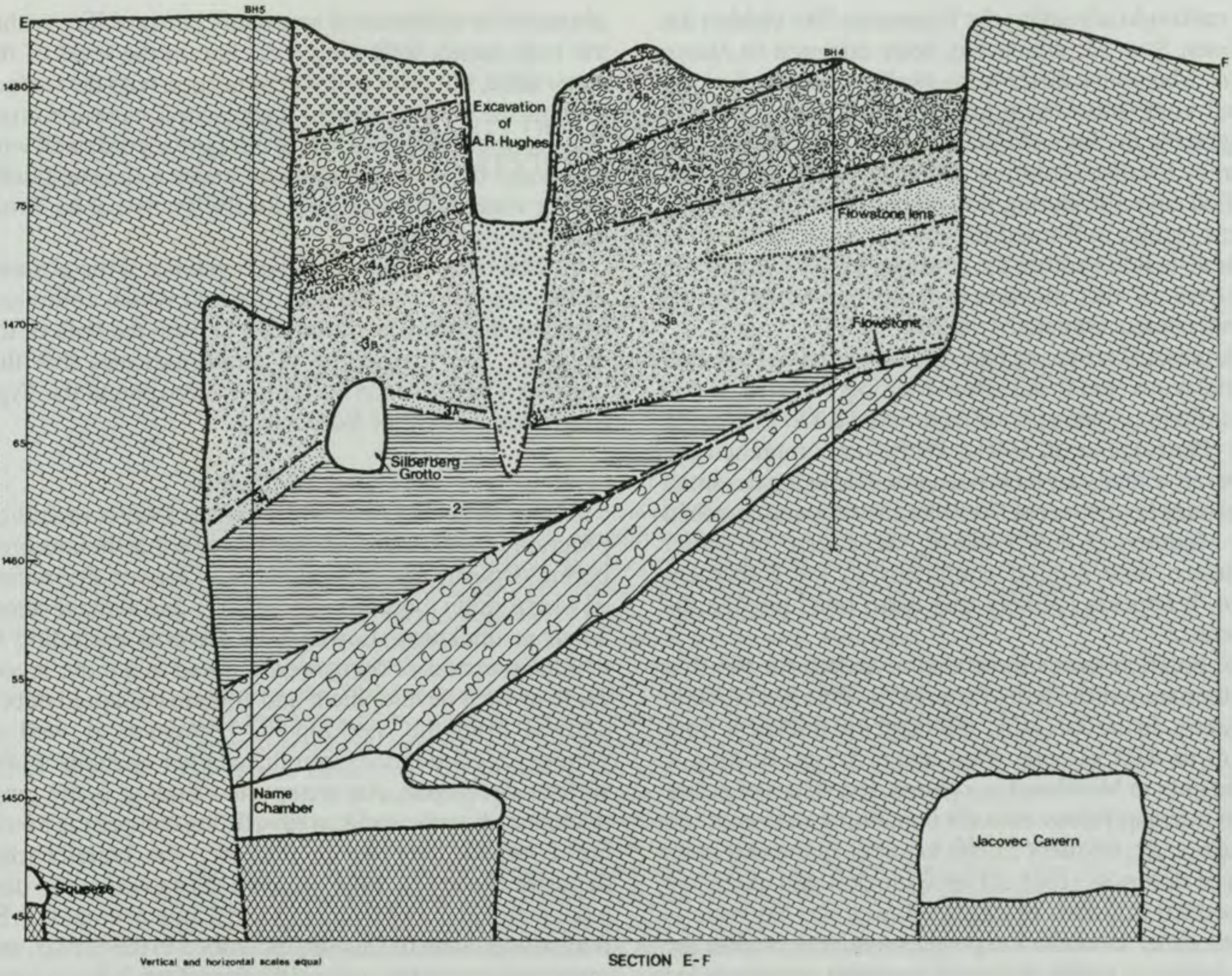

Figure 4

LEGEND

STERKFONTEIN FORMATION

5	**Member 5**	
4D	**Bed D (flowstone)**	**Member 4**
4C	**Bed C**	
4B	**Bed B**	
4A	**Bed A**	
3B	**Bed B**	**Member 3**
3A	**Bed A (flowstone)**	
2	**Member 2**	
1	**Member 1**	
⁘	**Swallow hole filling**	
▩	**Collapse debris**	
▧	**Dolomite (Monte Christo Formation, Transvaal Sequence)**	

Figures 2 - 4: Sections through the Sterkfontein Formation drawn up from borehole data and surface and underground exposures. Positions of the section lines are shown in Figure 1. Legend and summary description of lithostratigraphic units accompanies Figure 2.

Note: although no stratigraphy is shown within the swallow hole zone, there is evidence that the general stratigraphic sequence was maintained within the slumped block.

such makondo adjoining the Extension Site yielded the specimen Stw 53, which has been assigned to *Homo habilis*. Makondos differ from swallow holes in lacking a basal void, subsidence into which displaces the full stratigraphic thickness of the deposits. They are formed, rather, by localised solution within the upper zone of the calcified cave fill; during this process loss of carbonate cement results in limited downward movement of the insoluble residue within the confines of the solution pit, the extent of this movement being governed by the original cement content of the fill.

The present consensus, based on the faunal and hominid material recovered to date from Members 4 and 5, is that these units may span a period from about 2,8 to 1,5 million years (Partridge *et al.* 1991). While no comprehensive comparative analyses have been possible using the small faunal samples recovered from blocks of deposit detached from Members 2 and 3 during the course of earlier subsurface lime mining operations in the Silberberg Grotto, it appears unlikely that these units predate the Pliocene.

The borehole cores have also revealed, for the first time, the nature and extent of Member 1 of the Sterkfontein Formation. In the cores this unit ranges in thickness from 2,51 m to 8,03 m, averaging about 5,5 m, making it second only to Member 3 in volume. It consists of a dark brown manganiferous clay-silt containing pellets of red unctuous clay, frequent calcite veinlets, numerous large clasts of dolomite (roof collapse blocks) and extensive interbedded horizons of calcite flowstone. No bone is evident either in limited exposures available within the cave system or within the cores, but bone fragments are cemented into its uppermost few centimetres in the Silberberg Grotto. The bulk of this member thus appears to have accumulated within deep phreatic chambers of the cave system subsequent to their drainage and aeration (through the existence of secondary permeability within the rock mass), following a decline in the level of the water table, but prior to their connection with the surface through the development of macroscopic cave openings. The occurrence of basal fills of this type accords well with the model of cave development under a spasmodically falling water table proposed for the Transvaal by Brink and Partridge (1965).

A final issue resolved by the boreholes is the position of the original cave opening through which colluvium from the hillside was introduced to form the bulk of the cave fill. The disposition of strata indicates that this opening was located in the north-eastern part of the Type Site in the vicinity of Borehole 4.

CONCLUSIONS

The evidence now available from the 1989 core drilling programme at Sterkfontein has revealed that the hominid-bering deposits comprising the Sterkfontein Formation nowhere attain more than about 30 m and average about 20 m in thickness. Lower-lying caverns extending to depths in excess of 50 m were formed in a more recent cycle of cave development and contain collapsed debris derived from the Sterkfontein Formation as well as younger accumulations introduced after openings to the surface developed. An unexpected finding is the great thickness of sterile, residual cave filling comprising Member 1, which everywhere underlies the bone-bearing deposits. Since scientific excavations carried out to date have sampled only Members 4 and 5, much remains to be done to elucidate the history entombed in the earlier, and even more extensive, units of the Sterkfontein Formation. For the progress already achieved towards this goal the scientific world is greatly indebted to Alun Hughes, who has dedicated much of his life to the excavation of this uniquely important hominid deposit.

REFERENCES

BRAIN, C.K. 1958 The Transvaal Ape-man-bearing Cave Deposits. *Memoir No. 11, Transvaal Museum,* Pretoria.

BRINK, A.B.A. & PARTRIDGE, T.C. 1965. Transvaal karst: some considerations of development and morphology. *S. Afr.Geog. J.*, **47,** 11-34.

BRINK, A.B.A. & PARTRIDGE, T.C. 1980. The nature and genesis of solution cavities (makondos) in Transvaal cave breccias. *Palaeont. afr.*, **23,** 47-49.

CLARKE, R.J. 1985. Early Acheulean with *Homo habilis* at Sterkfontein. **In:** Tobias, P.V., Ed., *Hominid Evolution: Past, Present and Future*. Alan R. Liss Inc., New York, 287-298.

CLARKE, R.J. 1988. Habiline handaxes and paranthropine pedigree at Sterkfontein. *World Archaeology*, **20,** 1-12.

PARTRIDGE, T.C. 1978. Re-appraisal of lithostratigraphy of Sterkfontein hominid site. *Nature*, **275,** 283-287.

PARTRIDGE, T.C. 1982. The chronological positions of the fossil hominids of southern Africa. *Proc. 1st Intnl. Cong. Human Palaeont.*, Nice, **2,** 617-675.

PARTRIDGE, T.C., TOBIAS, P.V. & HUGHES, A.R. 1991. Paléoécologie et affinités entre les australopithécinés d'Afrique du Sud: nouvelles données de Sterkfontein et Taung. *L'Anthropologie* (Paris), **95,** 363-378.

ROBINSON, J.T. 1962. Australopithecines and artefacts at Sterkfontein, Part 1. Sterkfontein stratigraphy and the significance of the extension site. *South African Archaeological Bulletin*, **17,** 87-107.

STILES, D.N. & PARTRIDGE, T.C. 1979. Results of recent archaeological and palaeoenvironmental studies at the Sterkfontein Extension Site. *South African Journal of Science*, **75,** 346-352.

WILKINSON, M.J. 1973. *Sterkfontein Cave System: Evolution of a Karst Form.* Unpublished M.A. thesis, University of the Witwatersrand, Johannesburg.

WILKINSON, M.J. 1983. Geomorphic perspectives on the Sterkfontein Australopithecine breccias. *J. Archaeol. Sci.*, **10,** 515-529.

WILKINSON, M.J. 1985. Lower-lying and possibly older fossiliferous deposits at Sterkfontein. **In:** Tobias, P.V., Ed., *Hominid Evolution: Past, Present and Future*, Alan R. Liss, Inc., New York, 165-170.

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PALAEO-ECOLOGY OF THE STERKFONTEIN HOMINIDS: A REVIEW AND SYNTHESIS

by

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Abstract

Excavations at the Sterkfontein hominid fossil site have yielded a rich and revealing faunal assemblage. Evolutionary transitions are evident in early hominids and associated fauna between the times represented by Members 4 and 5. Member 4 has yielded a large and variable sample of *Australopithecus africanus* as well as evidence of considerable species diversity among the artiodactyls, carnivores and primates. The appearance of early *Homo* along with stone and bone tools in Member 5 coincides with a reduction of species representation in the orders of larger mammals as well as with the occurrence of new derived species and apparent extinctions.

Three hypotheses have been suggested to account for the trends seen in the hominid-bearing members of the Sterkfontein Formation. The 'Climatic Change Hypothesis' accounts for the evolutionary trends by the causal factors of global and local cooling and aridification with evidence of savanna-grasslands supplanting an earlier environment with a denser cover of vegetation. The 'Taphonomic Hypothesis' explains changes in relative species representation at Sterkfontein in terms of the bone-accumulating agents; in Member 4 primary carnivores were largely responsible for the deposition of large mammalian fauna, whereas the scavenging activities of early *Homo* would have accounted for much of the bone and all of the artefacts found in Member 5. A third proposition is the 'Species Interaction Hypothesis', a derivative of the 'Red-Queen Hypothesis'; here the dynamics of species interaction, including competition and commensalism among hominids, carnivores and cercopithecids, propel the evolutionary changes and cause the extinctions.

These hypotheses are not mutually exclusive, but the relative effects of the factors involved must be verified or refuted with better chronological controls and further analyses of the African fossil sites. The Sterkfontein Formation represents a microcosm in which various scenarios of African mammalian evolution can be tested.

INTRODUCTION

Since Robert Broom revealed the first adult specimen of *Australopithecus* in 1936, the Sterkfontein fossil site has been recognized globally as a vital source of information on hominid evolution. Excavations by Broom and J.T. Robinson yielded a wealth of Plio-Pleistocene fauna along with the hominids (Brain 1981). Later work by P.V. Tobias and A.R. Hughes, still in progress today, has significantly multiplied the fossil data base from Sterkfontein (Tobias and Hughes 1969; Tobias 1973; Tobias *et al*. 1990). The time depth and fossil richness of the Sterkfontein Formation thus provide a valuable basis for testing hypotheses concerning the evolution of hominids and other African fauna.

Palaeontological description of the Sterkfontein fossils has focused on hominid morphology, anatomical adaptations and phylogenetic positions. The complete framework of evolution, however, requires a careful analysis of the adaptive milieu in which the early hominids were living. Such ecological analyses are among the stated goals of the current excavation (Tobias & Hughes 1969; Tobias 1973). In this review I address issues of palaeo-ecology from a faunal perspective, updating Brain's (1981) comprehensive analysis with recently published research that has yielded new perspectives on the Plio-Pleistocene environments sampled in the Sterkfontein deposits.

Ecological reconstructions of the ancient Sterkfontein habitats are far from complete. The tasks remain to (1) differentiate climatic from taphonomic effects in fossil representation, (2) identify and assess the total fossil sample within a geological and chronological framework, and (3) apply the data in a holistic manner to hypotheses of current evolutionary theory. Recent work has made significant inroads into these tasks, and here my aim is to review the palaeo-ecological research and construct a framework of testable hypotheses for further analyses.

CONTEXT OF THE STERKFONTEIN HOMINIDS

Contextual information of the Sterkfontein hominids comes from the ancient caves in which they were deposited. The Sterkfontein fossil site formed as one of a number of dolomitic caves in the Blaaubank river valley of the South

African Transvaal. Three other sites in the immediate vicinity have yielded early hominid remains, namely Swartkrans, Kromdraai and Cooper's. The fossils were discovered in cave-fill matrix exposed by lime quarry operations, natural erosion and palaeontological excavation.

In a sedimentological and stratigraphical analysis, Partridge (1978) defined the Sterkfontein Formation as a series of six successive deposits or "members". Of concern here are Members 4 and 5, both of which have yielded hominid remains. Although Member 4 has been further subdivided into Beds A-D, very few of the fossils have been assigned to a specific bed.

Excavations of Sterkfontein Member 4 have produced a large and valuable sample of *Australopithecus africanus* fossils. Within this member it is apparent that the hominid fossils come from different beds of this cone-shaped deposit (Partridge 1978), but the time span represented by this depositional sequence is not yet known. The hominids are so variable that Clarke (1985, 1988a, 1988b) and Kimbel and Rak (1991) have suggested the possibility of two hominid species being represented in different parts of Member 4; this notion requires further substantiation.

Sterkfontein Member 5 is differentiated from Member 4 by the fossils as well as by the artefactual content of Early Acheulian stone tools (Stiles and Partridge 1979; Clarke 1985, 1988b; Mason 1985; but see Leakey 1970) and at least two bone tools (Robinson 1959; Brain 1981) in Member 5. Clarke (1985) was able to discern a distinct, nearly vertical division between the two members along a single transect separating the *Australopithecus* fossils of Member 4 from the artefacts in Member 5. Along with the artefacts were the fossil remains, some of which have been identified as *Homo habilis* (Hughes and Tobias 1977).

Analyses of the stone tool distribution and skeletal remains of Member 5 have led Stiles and Partridge (1979) and Brain (1985) to suggest that it is likely that the entrance to the Sterkfontein cave was occupied by early *Homo*. Thus Member 5 could represent not only a different time period from Member 4, but a distinct part of the cave. In his analysis of the rich microfaunal component of Member 5, Pocock (1987) stated that the fossils were primarily of owl pellet origin, implying accumulation near the outer reaches of the cave (Andrews 1990). Member 4 could have accumulated through a different entrance, consistent with the paucity of microfauna (Brain 1981; Pocock 1987) and the inferred talus-cone shape of the formation.

Differences in the pattern of bone accumulation in Members 4 and 5 are discussed in greater detail in the following sections, but a cautionary note is necessary concerning the possibility of collecting biases toward cranial material among the early fossil collectors. Brain (1981) attributed the paucity of post-cranial material in Member 4 to a loss of the bones before fossilization, implying that the cave was not a death trap for animals (which would result in more complete representation of the body). The continuing excavations have revealed considerably more post-cranial material of all species in Member 4 (Alun Hughes personal communication), including a remarkably complete partial hominid skeleton (Tobias *et al.* 1987). Thus a collecting bias on the part of the earlier investigators may have significantly affected the apparent relative frequencies of skeletal body parts. One cannot exclude the possibility that Member 4 material accumulated in a death trap or place for animals to die, for the total body representation is consistent with such a notion.

Accurate geological dating of the fossil site has proved problematic (Partridge 1982; Jones *et al.* 1986), for the results of the palaeomagnetic assessments have not been definitive. Faunal dating is also somewhat tenuous. Primarily on the basis of the bovid fossils, Vrba (1982, 1985) estimates that Sterkfontein Member 4 was deposited between 2,3 and 2,8 mya. Member 5 is dated to around 1,5 mya (Vrba 1982), but there is a suggestion that a component of Member 5 may be closer to 2 mya (Vrba 1985). Delson's (1984, 1988) cercopithecid chronology places Member 4 just after 2,5 mya; the weak cercopithecid evidence from Member 5 suggests a date between 1,5 and 2,0 mya. Further work is necessary to refine these dates, for an ecological assessment of the hominid adaptive process depends on an accurate chronological correlation of the faunal sites.

Palaeo-ecological studies of the Sterkfontein Formation require an interdisciplinary approach, but have been difficult due to the nature of the cave sites. Palynological data that could reveal the environment surrounding the Sterkfontein caves during periods of deposition have been difficult to find. Although initial pollen analyses by Horowitz (1975) suggested the possibility of an open grassland and drier environment in Member 4 than that present during deposition of Member 5, the presence of *Pinus* pollen revealed that the sample had been contaminated by modern pollen (Scott and Bonnefille 1986). The geological evidence for climatic changes at Sterkfontein, summarized by Partridge (1982), is ambiguous at best. The most revealing clues to the palaeoenvironments have come from the fauna preserved in the deposits.

The earlier faunal analyses relate fossils to Robinson's (1962) original stratigraphic sequence or to parts of the excavation site, and some clarification is necessary to correlate the literature. Partridge (1978) equates Member 4 with Robinson's 'lower breccia', encompassing the 'Type Site' in which the *Australopithecus* remains were recovered, and the base of the 'Extension Site' where Robinson worked in 1957 and 1958. Member 5 then corresponds to the 'Middle Breccia', including much of the Extension Site and the uppermost portion of the Type Site. (The 'Upper Breccia' of the Extension Site comprises Member 6.) As will be discussed below, it is important to note that Members 4 and 5 do not necessarily correspond directly to the Type and Extension Sites respectively, thus not all of the fauna of the earlier excavations can be assigned confidently to a specific member or time period.

FAUNAL CHANGES AT STERKFONTEIN AND MAN'S ADAPTIVE ENVIRONMENT

Any environmental changes apparently associated with hominid evolution are revealed in part by the animals that changed, or did not change, within the same local context. Faunal analyses can either corroborate or challenge ecological hypotheses, and provide an important context for the appearance of the genus *Homo* and associated artefacts within a biotic community.

The currently identified fossil species represented among the Sterkfontein large fauna are listed in Table 1. Although an environmental reconstruction can be gleaned from the fossil remains, it must be remembered that the fossil record represents only a portion of the animals living at the time of deposition (Thackeray 1980; Turner 1983b) and that the samples of some taxa are currently too small to be of much value in palaeoecological studies. The taxa discussed below are those that have been assessed in the literature and which have direct relevance to the adaptive environment of early man. The ecological significance of the fauna is subject to varied interpretations.

Bovidae

It is apparent from the list of bovid species in Table 1 that Sterkfontein Members 4 and 5 differ both in number and types of species represented. An extensive analysis of the Sterkfontein fossil bovids is provided in a remarkable series of publications by Elisabeth Vrba stemming from her doctoral thesis work (Vrba 1976). The resulting palaeo-ecological interpretations exemplify the potential as well as the pitfalls of such analyses.

One of the main differences between bovid representations in Members 4 and 5 is the number of *Makapania broomi* and cf. *Hippotragus cookei* (formerly *?Hippotragus*), increasing the Member 4 percentage of buck assumed to be adapted to dense vegetation (Vrba 1976, 1980). Member 4 has the latest representation of these two species (Vrba 1988), suggesting subsequent extinction. A comparison of Sterkfontein Members 4 and 5 also shows a distinct shift in the proportions of bovid types represented. Member 5 contains significantly greater relative frequencies of alcelaphines and antilopines (Vrba 1974, 1975, 1976). Other evolutionary changes among the bovids are indicated by differences in the dental morphology of the dominant species in Member 5 (and Swartkrans Member 1) that suggest a change in the adaptive environment (Vrba 1980, 1988).

Natural habitat preferences of modern bovids provide a model for environmental reconstructions which suggest that changes may have taken place between the times of Members 4 and 5. The basic assumptions of Vrba's palaeo-ecological model are that bovids are adapted to specific environments and thus are sensitive to changes in their habitat (Vrba 1976). Furthermore, this should be reflected in the relative proportions of fossil accumulations at southern African cave sites (Vrba 1980). In particular, abundant representation of the alcelaphini and antilopini tribes are thought to be indicative of open plains and grasslands (Vrba 1975, 1980). Vrba's inference is that the relative frequencies of bovids at Sterkfontein indicate a drier climate with more open grassland in Member 5 times, supplanting the earlier, bush loving forms of Member 4.

Support for the notion of a regional climatic change comes from observations of Kromdraai A and Swartkrans Member 1, close in time to Sterkfontein Member 5, where there are comparably high proportions of alcelaphines and antilopines (Vrba 1976, 1980), consistent with a regional shift to a more grassland environment by 1.5 mya. But an important consideration in the climatic interpretation is that at no site studied in the Blaaubank river valley is the proportion of alcelaphini and antilopini below 51% (Vrba 1975).

Certainly the open grassland area preferred by the alcelaphines and antilopines was at least nearby throughout the depositional sequence. A mosaic of local environments is quite common in southern Africa today, and a predator need not travel far to find a variety of prey in open grassland. Furthermore, Wells (1967) noted that the alcelaphini would have been adapted to a great variety of ecological conditions. He adds: "It is very tempting to interpret these observations in relation to climatic fluctuations. However, it appears wise to be very cautious in this matter." (Wells 1967: 104).

A change in climate is not the only way by which one can account for changes in the relative frequencies of bovid types. Thackeray (1980) noted three factors that could affect ungulate representation in archaeological faunal assemblages: environmental factors including rainfall and temperature, a preservational bias against smaller fauna, and predation by hunters and scavengers.

Under a changing regime of taphonomic agents leading to bovid death and deposition, the frequencies of bovid types would be expected to change. This is suggested by the differences in representation of predators at Sterkfontein, possibly including the genus *Homo*. Member 4 accumulations have been attributed to primary kills of carnivores, whereas the lower percentage of juvenile bovids in Member 5 seems to indicate scavenged remains and indeed could be attributed to the activities of the hominids (Vrba 1975, 1976, 1980). Bovids requiring a mesic or woodland environment could have been in the area, but their representation in the fossil record depends in part on the habits of the predators and scavengers. As Vrba (1980: 258) put it, "As bovids do not live in caves, the vast majority of their remains must have been carried there by other animals".

Some caution is necessary in the interpretation of the bovid assemblages, for Vrba initially did her counts on fossils assigned to the Sterkfontein Type Site and the Sterkfontein Extension Site. Partridge (1978, 1982) warns of the possible mixing during earlier collecting phases of Member 4 and Member 6 fossils into the supposedly Member 5 sample. Vrba (1982) addresses this problem and reassigns some individuals (notably those of

TABLE 1.

List of Large Mammal Species from Sterkfontein Members 4 & 5.

Member 4

Order	Family	Genus	Species
Primates	Hominidae	*Australopithecus*	*africanus*
			sp.?
	Cercopithecidae	*Parapapio*	*jonesi*
			broomi
			whitei
		Papio	*hamadryas robinsoni*
			izodi
		Cercopithecoides	*williamsi*
Carnivora	Felidae	*Panthera*	*pardus*
			leo
		Dinofelis	*barlowi*
		Megantereon	*cultridens*
		Homotherium	*crenatidens*
	Hyaenidae	*Chasmaporthetes*	*silberbergi*
			nitidula
		Crocuta	*crocuta*
		Hyaena	*brunnea*
		Pachycrocuta	*brevirostris*
	Canidae	*Canis*	*mesomelas*
Artiodactyla	Bovidae	*Damaliscus*	sp.1
		or *Parmularius*	sp.
		Connocheates	sp.
		cf. *Megalotragus*	sp.
		Hippotragus	cf. *equinus*
		cf. *Hippotragus*	*cookei*
		Redunca	*darti*
		Antidorcas	cf. *recki*
			cf. *bondi*
		Oreotragus	*major*
		Gazella?	sp.
		Syncerus	sp.
		Tragelaphus	sp. aff. *angasi*
		Makapania	cf. *broomi*
	Suidae	*Metridiochoerus*	sp.
Perissodactyla	Equidae	*Equus*	*capensis*
Proboscidea	Elephantidae	*Elephas*	*recki*

Member 5

Order	Family	*Genus*	Species
Primates	Hominidae	*Homo*	*habilis*
	Cercopithecidae	*Papio*	sp.
Carnivora	Felidae	*Homotherium*	*crenatidens*
		Megantereon	*cultridens*
	Hyaenidae	*Chasmaporthetes*	*silberbergi*
			nitidula
		Crocuta	*crocuta*
		Pachycrocuta	*brevirostris*
	Canidae	*Canis*	cf. *mesomelas*
Artiodactyla	Bovidae	*Damaliscus*	sp. 1
		or *Parmularius*	sp.
		Damaliscus	sp. 2
		cf. *Connochaetes*	sp.
		cf. *Megalotragus*	sp.
		Antidorcas	*recki*
		Oreotragus	*major*
		Taurotragus	cf. *oryx*
	Suidae	gen. indet.	
Perissodactyla	Equidae	*Equus*	*burchelli*
Proboscidea	Elephantidae	*Elephas*	*recki*

Notes: Compiled from Brain (1981), Churcher (1970), Delson (1984), Eisenhart (1974), Turner (1986a, 1987), Vrba (1976, 1982, 1988). Bovids not yet identified to genus are not included. Vrba (1982) questions the presence of *Equus capenis* in Member 4, suggesting that the specimen may have originated from Member 5. For additional information on the mammalian orders not discussed in this paper, see Brain (1981), Churcher (1970), Pocock (1987), Vrba (1982).

Makapania) from Member 5 to Member 4. Although the remaining fossils that could have an incorrect provenance may be insignificant in number, the mixing problem must be acknowledged for it could alter the relative frequencies of species and thus affect the resulting climatic interpretation.

Environmental reconstructions based on the bovid samples are also subject to possible errors due to inherent sample size problems. Vrba's Member 4 sample of bovids is significantly larger than that obtained from Member 5. The continuing excavation at Sterkfontein has uncovered a much larger sample from both deposits and future analysis may reveal a greater number of species present in the deposits.

Differences among the bovids represented in the hominid bearing deposits at Sterkfontein do indicate a change in the adaptive environment. Vrba's model, albeit the most constructive one proposed to date, is limited by problems of deposition, taphonomy, and fossil recovery. Certainly it is clear that local environmental changes occurred between the times represented by Members 4 and 5: there are new derived species and apparent extinctions of other species. To what degree these can be interpreted in terms of the broader contexts of climatic or taphonomic effects remains debatable. Some clues, however, can be found in corroborating evidence from the other faunae represented at Sterkfontein.

Carnivora

Although carnivores appear in low frequencies at Sterkfontein, as is expected of animals at higher trophic levels (Walker 1984), they comprise an important component for ecological analyses. Of the carnivore taxa that have been identified (Table 1), as with the bovids, there are fewer species represented in Member 5 than in Member 4. This complicates notions concerning the environmental implications of the carnivores with considerations of the taphonomy and sampling of the two deposits.

Since Brain (1981) realigned the relationships of hunters to hunted in the minds of palaeontologists, most investigators tend to think of carnivores as the agents of bone deposition in cave deposits. There is only minimal evidence in Sterkfontein Member 4 of carnivore activity as recorded by tooth marks on the bone, but poor preservation possibly obscured further evidence of carnivore damage (Brain 1981). As noted above, the high percentage of juvenile bovids (Vrba 1975, 1976) is suggestive of primary carnivore involvement in Member 4. Brain (1981) also noted an exceptionally high ratio of carnivores to ungulates in the deposit.

Herbivorous animals are almost certainly deposited in the caves by the hunting and scavenging carnivores. One must also consider the forces that led to the deposition of the carnivores themselves. They account for nearly 8,1% of individual animals represented in Member 4 (by the earlier account of Brain (1981)), many of which are primary carnivores. Turner (1984) noted that the small number of scavenging hyaenas and hyaena-damaged bones in southern African cave sites suggested the hyaenas were not using the sites as dens or even consuming much prey near the sites. At least in Member 4 one may envisage a primary carnivore based model of accumulation along the lines of Brain (1981).

It appears that hominids may have been among the accumulating agents in Member 5 as either predators or scavengers. A low ratio of carnivores to ungulates is represented (Brain 1981), and the bovid composition including a greater number of adult specimens suggests scavenged remains (Vrba 1975, 1976, 1980), implying possible hominid scavenging. It is worth noting that some of the bones in Member 5 show signs of having been chewed by carnivores or gnawed by porcupines. These observations indicate at least minimal carnivore involvement in bone accumulation (Brain 1981), but it is also likely that the large carnivores could have been responsible for the carrion scavenged by the hominids.

Fossil carnivore remains give few clues to the prehistoric climatic environment unless considered as a group. Ewer (1967: 120) stated that the diversity of scavenging hyaenids and canids, such as that seen in Sterkfontein Member 4, "presupposes the existence of a rich primary predator fauna: this, in turn, implies an abundance of herbivores as prey". The large number of species represented in Member 4 (Table 1) fit her model well. The apparent pruning of the number of predators and prey represented in Member 5 may suggest some evolutionary changes in the local biotic community that are consistent with Vrba's model of climatic change. On the other hand, the modern carnivore species represented in Member 4 (see below) all prefer drier savanna environments today (Skinner and Smithers 1990). Furthermore, the inclusion of a presumably scavenging form of hominid in Member 5 precludes a confirmation of the climatic model, for it is clear that the hominids probably changed the pattern of bone accumulation in the cave.

There are intriguing clues as to the early relationship between man and the carnivores. Walker (1981) proposed that early hominids were in competition with the guild of carnivores, and not with other hominid species. The evidence is found in the correlations between hominid and carnivore evolution. On the basis of the same evidence, Turner (1986b) opts for an alternative approach, stating that such competition need not be invoked into a model of hominid evolution. He argues for climatic shifts as the agent responsible for coincident speciations in hominids, carnivores and bovids (Turner 1983a).

Inferences drawn from the Sterkfontein carnivore sample do not necessarily support Turner's view. Sterkfontein is especially intriguing for the number of modern carnivore species repersented in Member 4, before the speciation of the hominids. For example, a large *Panthera leo* first appears in the southern African fossil record in this deposit (Turner 1986a). Furthermore, Turner (1984) notes that *Crocuta* fossils from all of the Blaaubank valley sites do not differ from *Crocuta crocuta* at even a subspecies level. These examples, along with those of *Panthera pardus*, *Hyaena brunnea* and *Canis mesomelas*, demonstrate a distinct lack of speciation 'events' in some key carnivores during a number of hominid 'speciations' in Africa since the time of Member 4 deposition. Whereas some carnivore extinctions may correlate with the evolution of hominids (Ewer 1967; Klein 1977; Walker 1984), it is difficult to account for the carnivore stasis as well as the hominid evolution in a palaeo-ecological model. As discussed below, hominid scavengers may have had a commensal relationship with the surviving primary carnivores.

Cercopithecidae

Numerous taxonomic schemes to categorize the Sterkfontein cercopithecid fossils have been proposed over the years. Ecological assessments of the Sterkfontein cercopithecids have been superseded by years of indecision in systematics, as well as by the lack of analysis of post-cranial material and of Member 5 fossils. The many permutations of species designations for individual fossils from Member 4 cannot be resolved here. Yet the number of cercopithecid species and genera proposed have implications for palaeo-ecological models of the Sterkfontein environment and may bear directly on the competitive forces encountered by early hominids.

The taxonomic assessment of Eisenhart (1974) is adopted here for purposes of this discussion, with the exception that his division of *Parapapio broomi* fossils into two species (small and large) seems to be unjustified. Member 4 then has as many as six approximately coeval species of cercopithecids (Table 1). Any palaeo-ecological model must thus accommodate all of these species as well as *Australopithecus africanus*, all filling an apparently similar niche.

High relative frequencies of cercopithecids are known from Sterkfontein Member 4, with *Parapapio* being the most common found (Brain 1981). *Parapapio* species represent the more primitive form of papionins (Szalay and Delson, 1979; Simons and Delson 1978). The three putative species of *Parapapio* are distinguished largely on the basis of tooth size, as articulated by Freedman (1957). Freedman (1976) and Freedman and Stenhouse (1972) detected a trimodal curve of tooth size, with *P. jonesi*, *P. broomi*, and *P. whitei* in increasing size order. Eisenhart (1974) redesignated some of these individuals to other species on the basis of facial morphology, and saw less distinction among the taxa in tooth size. In particular, *P. broomi* and *P. whitei* are very similar in tooth indices (Maier 1971), with the only significant difference in tooth measurements being in the distal breadth of the M2 (Eisenhart 1974).

Evidence from the stratigraphic relations of the fossils suggests relative contemporaneity of the three species of *Parapapio*. Although Sterkfontein Member 4 could have been deposited over a long period of time, there is no evidence that these three species are separated stratigraphically. Likewise, in Makapansgat Members 2, 3 and 4 there is no evidence of a size change through the deposits in which all three occur (Freedman 1957; Freedman and Stenhouse 1972; Eisenhart 1974; Delson 1984). Thus it is unlikely that the three *Parapapio* species represent chronospecies.

Examination of the morphological data suggests an alternative hypothesis that *Parapapio* fossils could all belong to one highly variable species. In this case it would be no coincidence that the mid-range species (*P. broomi*) is the most common, as would be expected in a normal distribution of size. Furthermore, the mid-range baboons may have been preferred by the collecting agents; there is evidence of carnivore tooth marks on a *P. broomi* mandible (Brain 1981).

Characteristics of the *Parapapio* species suggest that they could have inhabited a range of habitats in the savanna and open woodlands (Eisenhart 1974; Szalay and Delson 1979), with a possibility of greater arboreality than that seen in modern *Papio* (Simons and Delson 1978). Eisenhart (1974) speculates further that *P. jonesi* was adapted to gallery forest and savanna, whereas the elongated muzzle of the smaller specimens of *P. broomi* suggest a terrestrial adaptation. The general implication is that *Parapapio* varieties are most consistent with an interpretation of a local mesic woodland environment during Member 4 deposition.

Other papionin fossils, with a distinctive facial morphology as compared to that of *Parapapio*, fall into two species of *Papio*. *Papio hamadryas robinsoni* (formerly *Papio robinsoni*) is seen as a temporal subspecies of the modern form of baboon found in East Africa (Simons and Delson 1978; Delson 1984). One juvenile specimen of *Papio* is morphologically indistinguishable from *Papio izodi* of Taung (Eisenhart 1974; McKee 1991), but remains the sole representative of this second species of the genus at Sterkfontein.

Living species of *Papio* have a wide range of adaptations, but are primarily terrestrial quadrupeds with a significant degree of arboreal adaptations. Studies of modern baboons have focused on their savanna adaptations (eg. DeVore and Hall 1965), but Rowell (1979) demonstrates the ability of *Papio* to adapt effectively to a forest environment. Jolly (1972) suggested that early *Papio* were forest-fringe dwellers whereas *Theropithecus* species (not found at Sterkfontein) were more common in open savanna. Carbon isotope studies of tooth enamel lend support to this conclusion, showing *Theropithecus* to be more graminivorous, and hold promise for further studies of the cercopithecid diets (Lee-Thorp *et al.* 1989).

Observations on the remaining Member 4 cercopithecoid, *Cercopithecoides williamsi*, suggest that it was a relatively large colobine monkey. The presence of this form may seem to indicate moist forest habitats as with modern African colobines (Tappen 1968), yet the relatively large size of *C. williamsi* suggests that it was probably the most terrestrially adapted colobine ever (Szalay and Delson 1979; Delson 1984). As with *Parapapio* and *Papio*, post-cranial material will be crucial for the determination of their relative reliance on arboreality as opposed to terrestriality.

Generalizations concerning the climatic and environmental implications of the cercopithecid fossils require a consideration of the primates as a group. The net result of this survey is that we have six cercopithecoids as well as the hominid(s) all living in the same local environment. Most would agree that this is a most remarkable situation (Freedman 1976; Eisenhart 1974), for the available niches appear to be somewhat saturated with primate species. All were adapted or adaptable to both savanna and open woodland, and perhaps even forest, making the environmental implications unclear. Tappen (1968) observed that there are strong factors producing speciations among forest monkeys, thus the large number of cercopithecoid species at Makapansgat and Sterkfontein Member 4 could indicate a relatively rich forest environment. This is at least consistent with Vrba's reconstruction of the Member 4 environment, but confirmation of the environmental implications of the cercopithecids can come only with the analysis of the post-cranial material and clarification of the taxonomic problems.

Inevitably one must consider the enigmatic connotations of the negative evidence, but with due caution. Member 4 has yielded none of the very large terrestrial baboons. *Theropithecus* in particular occurs at Makapansgat, before Sterkfontein Member 4 times, and afterwards at Swartkrans. Whereas their absence at Sterkfontein could indicate an environment in which the large graminivores could not adapt or compete, *Theropithecus* existed in association with nearly all of the Sterkfontein types at Makapansgat (where there are as many as seven cercopithecoid species (Eisenhart 1974)).

Cercopithecid remains in Sterkfontein Member 5 are scarce. So far only *Papio* sp. has been identified. Nevertheless, there is a clear lack of *Parapapio* and *Cercopithecoides*. It is tempting to account for this decreased representation with a model of competitive exclusion in an environment saturated with primates, especially in the light of the decreased number of species at other southern African fossil sites through time. Further analyses may verify or refute the inference that Member 5 contains fewer species within the primates as within other orders of mammals. Fortunately, recent work is yielding a larger sample from which various ecological models can be tested further (Tobias *et al.* 1990).

DISCUSSION

Analyses of the Sterkfontein fauna and their context reveal a changing local environment for the evolving hominids. The later deposited Member 5 can be differentiated from Member 4 on the basis of at least four key features: 1) the presence of stone and bone artefacts; 2) fewer number of species represented in mammalian families for which there are adequate samples; 3) the presence of new derived species, including a representative of the genus *Homo*; 4) a change in the proportional representations of species within families. Each of these features may have implications for reconstructions of the early hominid adaptive environment.

Local changes seen in faunal representation between Sterkfontein Members 4 and 5 can be interpreted in a number of ways. From this review it is clear that there are three primary hypotheses to explain the changes in the Sterkfontein fossil record: (1) climatic changes of cooling and aridification in the region caused or propelled evolutionary events among the fauna; (2) changes in the bone accumulating agencies resulted in different proportions of species representation; and (3) interactions of the evolving faunal species caused shifts in the adaptive patterns of members in the biotic community. Although these notions are not mutually exclusive, they are treated individually below.

Climatic Change Hypothesis

Biotic turnover among many African faunal taxa in the Plio-Pleistocene seem to correlate with climatic change. The fossil evidence, and in particular the bovid sample, has led Vrba (1985) and Turner (1983a) to suggest that changes in global climate *caused* the evolution of African mammals in the Plio-Pleistocene. Variations in relative frequencies of bovid species that are thought to be sensitive to the climatic and vegetational environment at Sterkfontein are consistent with such a climatic change hypothesis. Additional supportive evidence comes from the greater species diversity of carnivores and cercopithecids that suggests a richer, wooded local environment during Sterkfontein Member 4 times than the drier, more grassland environment inferred for Member 5.

Analyses of global trends in temperature confirm that the hypothesis is at least tenable. It is evident that sometime between 2.5 and 2.3 mya there occurred considerable cooling and aridification that could have affected southern Africa (Boaz and Burckle 1983; Shackelton *et al.* 1984; Partridge 1986; Van Zinderen Bakker and Mercer 1986; Prentice and Denton 1988). Faunal dates place Sterkfontein Member 4 just before or within this climatic episode, and Member 5 after successive global temperature fluctuations.

Legitimate reasons to question the climatic hypothesis must be raised from the same data used in its support. It is not clear that the inferred climatic changes would have been enough to cause speciation events or even accentuate them. Behrensmeyer and Cooke (1985) remind us that vegetation is under strong local control, and that there would have been a mosaic of local vegetational types. Thus a change in temperature could result in nothing more than local changes in geographic distribution of faunal species as they seek out their preferred habitat.

An alternative model to adaptive evolution in response to climatic change is thus that of species 'distribution drift'. Vrba (1988) acknowledges this possibility, but notes the parsimonious changes among fossil fauna witnessed in both eastern and southern Africa that coincide with changes in African climate. The problem is that her argument for biotic turnover with continental climatic change is tautologous. The faunal dating of southern African sites is based on eastern African fauna, so it is no coincidence that the continental faunal changes correlate to the same putative event of climatic change.

New fossil evidence has contradicted the notion that the divergence of the 'gracile' and 'robust' hominid lineages corresponded to the putative climatic 'event' at 2.5 mya. The perceived coincidence of biotic turnover with hominid divergence had to be rejected with the discovery of an early hyper-robust form (the 'Black skull') in eastern Africa that predates the 2.5 mya climatic change (Walker *et al.* 1986; Vrba 1988). Vrba (1988:415) sums up the status of the hypothesis by stating that "the problem of hominid-associated environmental change in South Africa is badly in need of additional approaches".

Conclusions on the tenability of the climatic change hypothesis for mammalian evolution in the African Plio-Pleistocene are not possible at this stage. Further corroborating evidence is needed from analyses of Sterkfontein and other African faunal sites. In addition, accurate dating of the sites is essential before one can correlate faunal changes with the global climatic models.

Taphonomic Agent Hypothesis

Evidence from detailed taphonomic analyses of the Sterkfontein deposits support the notion that changes in the bone accumulating agents contributed to the different proportions of species represented in Members 4 and 5. As discussed above, the scavenging activities of early man may have been a primary source of the bones deposited in Member 5. The appearance of *Homo* along with stone tools, patterns of cut marks on the bones (Brain 1981, 1985), and the lower percentage of juvenile bovids (Vrba 1975, 1976, 1980), all point to the likelihood that early man left his scavenged food remains in the later deposit at Sterkfontein.

An assessment of the negative evidence reveals intriguing but tenuous clues. There is a distinct lack of primates in Member 5; not only cercopithecids but also other hominids are missing. Tobias *et al.* (1987) commented on the expectation that *Australopithecus robustus* would be found in Member 5, but to date no such discovery has been made. This could be interpreted in terms of the local dominance of early *Homo* over his competitors, at least at the cave entrance if not over a larger area, for many of these primate species did exist in Africa at the time. As Huxley (1894: 89) stated in a similar context, "I know of no more striking evidence than these facts afford, of the caution which should be used in drawing the conclusion from the absence of organic remains in a deposit, that animals or plants did not exist at the time it was formed".

Numerical changes in proportions of species between Members 4 and 5 are as consistent with the taphonomic hypothesis as they are with the climatic hypothesis. The evidence for changes in the taphonomic processes between the successive Sterkfontein deposits does not preclude the possibility of climatic change. However, it does inhibit any firm inferences of climatic change based on species representations, for it is not yet possible to differentiate the relative effects of environmental and of taphonomic changes.

Despite the tenability of the taphonomic hypothesis, it deals only with changes in bone accumulation patterns at Sterkfontein. Additional hypotheses must be sought to explain the evolution of derived species that are also apparent at the site.

Species Interaction Hypothesis

The dynamics of species interactions within a changing biotic community may be sufficient to account for the evolutionary changes evident at Sterkfontein and other sites. One thing that is indisputable is that a number of mammalian species evolved in Africa between the times represented by Sterkfontein Members 4 and 5. Apparent extinctions and derived morphological states among numerous taxa are evident at southern African sites and are consistent with evolutionary models of species interactions (Klein 1984), comprising elements of competition, commensalism and mutualism.

Habitats of the australopithecines can be reconstructed most effectively with a consideration of all the roughly coeval species preserved in Sterkfontein Member 4, representing a significant proportion of the local faunal community. There was considerable species diversity in primary carnivores and scavengers, including forms that have remained relatively static in morphology to today. There was also a wide variety of primates, including *Australopithecus*. In line with Vrba's reconstruction, it appears that a rich mesic environment was present at the time allowing for such species diversity.

Environmental constraints on early hominid adaptations were imposed by the coeval species. Because of the number of potential scavengers represented, it is likely that *Australopithecus* fed at low trophic level and remained a non-scavenging omnivore. This ecological consequence is consistent with the dental morphology and clues from the masticatory apparatus suggesting a primary reliance of *Australopithecus* on a vegetarian diet (eg. Robinson 1954; 1963; Grine 1981; McKee 1989). This early hominid was too slow, too small, and ill-equipped to be a scavenger or a predator in competition with the diverse carnivores in the Sterkfontein environment. However, this put *Australopithecus* into potential competition with the other primates filling foraging niches in the same geographic area.

Novel hominid adaptations may have profoundly affected the competitive environment and depositional process by the time of Member 5 deposition. Somewhere in Africa, the early hominid had evolved into a scavenger and was ultimately responsible for accumulating much of the bone and all of the stone tools at Sterkfontein. The development of stone tool technology may have equipped early *Homo* with the competitive edge necessary for entry into a scavenging niche, although perhaps only to a limited extent (Shipman and Walker 1989).

Competitive exclusion models are not sufficient to explain the fewer number of carnivore species represented in Sterkfontein Member 5; too many forms appear before and after at other nearby sites. Indeed, the primary carnivores were necessary to provide scavenging opportunities for the hominids and other scavenging species. The adaptable hominids persisted; *Homo* and the robust australopithecines had diverged by the time of Member 5 deposition, presumably occupying separate niches. Scavenging opportunities would have been more limited if all the carnivores had survived in this environment with early *Homo*. If one thinks of hunters as impatient scavengers (Colinvaux 1978), then early *Homo* in this environment of reduced opportunity was a prime candidate for an incipient hunter. The diversity of scavengers and large carnivores was eventually reduced due to competition with *Homo* (Klein 1984), except perhaps in the earliest member at Swartkrans.

Local reduction in the number of primates by the time of Member 5 deposition seems to be well substantiated. *Parapapio* species had been excluded from all of the later Transvaal sites, including Sterkfontein Member 5, and *Papio* was reduced in variability. It is entirely plausible that they had been out- competed by a hominid during the *Australopithecus* to *Homo* transition. Some cercopithecids, not represented at Sterkfontein, did persist, as witnessed at Swartkrans and Kromdraai. These were the larger and more graminivorous forms such as *Theropithecus*, that probably were not in direct competition with the omnivorous hominids.

In the above model, the taphonomic hypothesis may be a necessary corollary. The observed reduction in total faunal diversity and altered proportional representation of bovid species at Sterkfontein is not clearly explicable by the species interaction hypothesis alone. But if early *Homo* had indeed become an opportunistic scavenger, then the bone accumulations in Member 5 would have been affected by his scavenging preferences and opportunities.

Mammalian species interactions, including competition among the primates and commensalism of hominids with the primary carnivores, are sufficient to account for the evolutionary and representational processes. Ostensibly, the Red-Queen hypothesis (Van Valen 1973; Foley 1984) of perpetual changes in some species affecting the adaptations of others is indicated. In this model climatic change is not necessary as a driving force.

As with the climatic and taphonomic hypotheses, many aspects remain to be tested and verified. Turner (1983a, 1986b) insists that it is not necessary to propose inter-specific or inter-order competition models, for the coincident changes in species may have been due to climatic shifts. Likewise, Grine (1986) states that it is not necessary to invoke the Red-Queen hypothesis for hominid divergence when climatic changes can account for species differentiation and extinction. But one should not equate correlation of climate and evolution with causality (Boaz and Burckle 1983; Tobias 1985). Even with climatic changes, species interactions must change in order to propel adaptive evolutionary changes. In other words, to adapt to a new vegetational environment caused by putative climatic change, species must compete for altered or diminished food sources at all trophic levels.

CONCLUSIONS

The sequence of fossils represented at Sterkfontein provides a data base for the testing of hypotheses concerning the early hominid role in the biotic community. Man's dual role as a scavenger and forager necessitated interactions with other species in similar niches, with a net result of evolutionary changes in many species. Whether or not one can conclude that this was propelled by climatic changes depends on an accurate assessment of climatic effects on local environments and better chronological controls. Ecological effects on bone deposition and preservation are also inextricably intertwined with taphonomic processes.

Environmental reconstructions of the early hominid habitats must utilize data from the total biotic community; species taken individually reveal very little. Holistic approaches to hominid palaeo-ecology are possible with the abundance of clues exposed at sites such as Sterkfontein. The analyses reviewed here demonstrate the potential value of fossil data, as well as the methodological problems that must be overcome with innovative techniques. It is still true that "there is an urgent need to intensify studies on the comparative fauna" (Tobias and Hughes 1969: 167), for more species from Sterkfontein remain to be identified and analyzed. Alternative hypotheses may then be tested in the fossil 'laboratories' in which the hominid past is preserved.

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REFERENCES

ANDREWS,P. 1990. *Owls, Caves and Fossils*. Chicago, University of Chicago Press.

BEHRENSMEYER,A.K., & COOKE,H.B.S. 1985. Paleoenvironments, stratigraphy, and taphonomy in the African Pliocene and Early Pleistocene. **In:**Delson,E.,Ed., *Ancestors: The Hard Evidence*, 60-62. New York, Alan R. Liss.

BOAZ,N.T., & BURCKLE,L.H. 1983. Paleoclimatic framework for African hominid evolution. **In:** Vogel,J.C.,Ed., *Late Cainozoic: Palaeoclimates of the Southern Hemisphere*, 483-490. Rotterdam, A.A. Balkema.

BRAIN,C.K. 1981. *The Hunters or the Hunted*? Chicago, University of Chicago Press.

---------- 1985. Cultural and taphonomic comparisons of hominids from Swartkrans and Sterkfontein. **In:** Delson,E.,Ed., *Ancestors: The Hard Evidence*, 72-75.New York, Alan R. Liss.

CHURCHER,C.S. 1970. The fossil equidae from the Krugersdorp caves. *Ann. Transvaal Mus.*, **26**(6), 146-168.

CLARKE,R.J. 1985. Early acheulian with *Homo habilis* at Sterkfontein. **In:**Tobias,P.V.,Ed., *Hominid Evolution: Past, Present and Future*, 287-298. New York, Alan R. Liss.

---------- 1988a. A new *Australopithecus* cranium from Sterkfontein and its bearing on the ancestry of *Paranthropus*. **In:**Grine,F.E., Ed., *Evolutionary History of the "Robust" Australopithecines*, 285-292. New York, Aldine de Gruyter.

---------- 1988b. Habiline handaxes and Paranthropine pedigree at Sterkfontein. *World Archaeology*, **20**(1), 1-12.

COLINVAUX,P. 1978. *Why Big Fierce Animals are Rare*. Princeton, Princeton University Press.

DELSON,E. 1984. Cercopithecid biochronology of the African Plio-Pleistocene: Correlation among eastern and southern hominid-bearing localities. *Cour. Forsch. Inst. Senckenberg*, **69**, 199-218.

---------- 1988. Chronology of South African australopith site units. **In**:Grine,F.E.,Ed., *Evolutionary History of the "Robust" Australopithecines*, 317-324. New York, Aldine de Gruyter.

DEVORE,I., & HALL,K.R.L. 1965. Baboon ecology. **In:**DeVore,I.,Ed., *Primate Behavior – Field Studies of Monkeys and Apes*, 20-52. New York, Holt, Rinehart and Winston.

EISENHART,W.L. 1974. *Fossil Cercopithecoids of Makapansgat and Sterkfontein*. Unpublished BA thesis, Harvard University.

EWER,R.F. 1967. The fossil hyaenids of Africa – A reappraisal. **In:**Bishop,W.W., & Clark,J.D.,Eds., *Background to Evolution in Africa*, 109-123. Chicago, University of Chicago Press.

FOLEY,R. 1984. Early man and the Red Queen: Tropical African community evolution and hominid adaptation. **In:**Foley,R.,Ed., *Hominid Evolution and Community Ecology*, 86-110. London, Academic Press.

FREEDMAN,L. 1957. The fossil cercopithecoidea of South Africa. *Ann. Transvaal Mus.*, **23**(2), 122-262.

---------- 1976. South African fossil cercopithecoidea: A reassessment including description of new material from Makapansgat, Sterkfontein and Taung. *J. Hum. Evol.*, **5**, 297-315.

---------- & STENHOUSE,N.S. 1972. The *Parapapio* species of Sterkfontein, Transvaal, South Africa. *Palaeont. afr.*, **14**, 93-111.

GRINE,F.E. 1981. Trophic differences between 'gracile' and 'robust' australopithecines: a scanning electron microscope analysis of occlusal events. *S. Afr. J. Sci.*, **77**, 203-230.

---------- 1986. Ecological causality and the pattern of Plio- Pleistocene hominid evolution in Africa. *S. Afr. J. Sci.*, **82**, 87-89.

HOROWITZ,A. 1975. Preliminary palaeoenvironmental implications of pollen analysis of Middle Breccia from Sterkfontein. *Nature*, **258**, 417-418.

HUGHES,A.R., & TOBIAS,P.V. 1977. A fossil skull probably of the genus *Homo* from Sterkfontein, Transvaal. *Nature*, **265**, 310-312.

HUXLEY,T.H. 1894. *Science and Hebrew Tradition* – Collect*ed Essays Vol 4*. New York, D. Appleton and Company.

JOLLY,C.J. 1972. The classification and natural history of *Theropithecus (Simopithecus)* (Andrews, 1916), baboons of the African Plio-Pleistocene. *Bull. Brit. Mus. (Nat. Hist.), Geol.*, **22**, 1-22.

JONES,D.L.,BROCK,A., & MCFADDEN,P.L. 1986. Palaeomagnetic results from the Kromdraai and Sterkfontein hominid sites. *S. Afr. J. Sci.*, **82**, 160-163.

KIMBEL,W.H., & RAK,Y. 1991. Phylogenetic species and the taxonomic diversity of South African early hominids (abstract). *Am. J. Phys. Anthrop.*, Supplement 12, 105.

KLEIN,R.G. 1977. The ecology of early man in southern Africa. *Science* **197**, 115-126.

---------- 1984. The large mammals of southern Africa: Late Pliocene to recent. **In**:Klein,R.G.,Ed., *Southern African Prehistory and Paleoenvironments*, 107-146. Rotterdam, A.A. Blakema.

LEAKEY,M.D. 1970. Stone artefacts from Swartkrans. *Nature*, **225**, 1222-1225.

LEE-THORP,J.A.,VAN DER MERWE,N.J., & BRAIN,C.K. 1989. Isotopic evidence for dietary differences between two extinct baboon species from Swartkrans. *J. Hum. Evol.*, **18**, 183-190.

MASON,R.J. 1985. Sterkfontein Member 5 stone artefact identification and the Klipplaatdrif gravels. **In:**Tobias,P.V., Ed., *Hominid Evolution: Past, Present and Future*, 299-301. New York, Alan R. Liss.

MAIER,W. 1971. Two new skulls of *Parapapio antiquus* from Taung and a suggested phylogenetic arrangement of the genus *Parapapio*. *Ann. S. Afr. Mus.*, **71**(1), 1-16.

MCKEE,J.K. 1989. Australopithecine anterior pillars: A reassessment of the functional morphology and phylogenetic relevance. *Am. J. Phys. Anthrop.*, **80**(1), 1-9.

---------- 1991. Evolutionary affinities of *Papio izodi* fossils from Taung and Sterkfontein (abstract). *ASSA Newsletter* in press.

PARTRIDGE,T.C. 1978. Re-appraisal of lithostratigraphy of Sterkfontein hominid site. *Nature*, **275**, 282-287.

---------- 1982. The chronological positions of the fossil hominids of southern Africa. **In:**de Lumley,H.,& de Lumley,M.A.,Eds., *Proc. Congres Internationale de Paleontologie Humaine*, 2, 617-675. Nice, Union Internationale des Sciences Prehistoriques et Protohistorique.

---------- 1986. Palaeoecology of the Pliocene and Lower Pleistocene hominids of southern Africa: how good is the chronological and palaeoenvironmental evidence? *S. Afr. J. Sci.*, **82**(2), 80-83.

POCOCK,T.N. 1987. Plio-Pleistocene fossil mammalian microfauna of southern Africa – A preliminary report including description of two new fossil muroid genera. *Palaeont. afr.*, **26**(7), 69-91.

PRENTICE,M.L.,DENTON,G.H. 1988. The deep-sea oxygen isotope record, the global ice sheet system and hominid evolution. **In:** Grine, F.E.,Ed., *Evolutionary History of the "Robust" Australopithecines*, 383-403. New York, Aldine de Gruyter.

ROBINSON,J.T. 1954. Prehominid dentition and hominid evolution. *Evolution*, **8**, 324-334.

---------- 1959. A bone implement from Sterkfontein. *Nature*, **184**, 583-585.

---------- 1962. Sterkfontein stratigraphy and the significance of the extension site. *S. Afr. Archaeol. Bull.*, **17**, 87-107.

---------- 1963. Adaptive radiation in the australopithecines and the origin of man. **In:**Howell,F.C., & Bourliere,F.,Eds., *African Ecology and Human Evolution*. Viking Fund Publication in Anthropology **36**, 385-416.

SCOTT,L.,BONNEFILLE,R. 1986. Search for pollen from the hominid deposits of Kromdraai, Sterkfontein and Swartkrans: some problems and preliminary results. *S. Afr. J. Sci.*, **82**, 380-382.

SHACKELTON,N.J., BACKMAN,J., ZIMMERMAN,H., KENT,D.V., HALL,M.A., ROBERTS,D.G., SCHNITKER,D., BALDAUF,J.G., DESPRAIRIES,A., HOMRIGHAUSEN,R., HUDDLESTUN,P., KEENE,J.B., KALTENBACK,A.J., KRUMSIEK,K.A.O., MORTON,A.C.,

MURRAY,J.W., & WESTBERG-SMITH,J. 1984. Oxygen isotope calibration of the onset of ice-rafting and history of glaciation in the North Atlantic region. *Nature*, **307,** 620-623.

SHIPMAN,P., & WALKER,A. 1989. The costs of becoming a predator. *J. Hum. Evol.*, **18**(4), 373-392.

SIMONS,E.L., & DELSON,E. 1978. Cercopithecidae and Parapithecidae. **In:**Maglio,V.J., & Cooke,H.B.S.,Eds., *Evolution of African Mammals*, 100-119. Cambridge, Harvard University Press.

SKINNER,J.D. & SMITHERS,R.H.N. 1990. *The Mammals of the Southern African Subregion*. Pretoria, University of Pretoria.

STILES,D.N. & PARTRIDGE,T.C. 1979. Results of recent archaeological and palaeoenvironmental studies at the Sterkfontein Extension site. *S. Afr. J. Sci.*, **75:** 346-352.

SZALAY,F.S. & ELSON,E. 1979. *Evolutionary History of the Primates*. New York, Academic Press.

TAPPEN,N.C. 1968. Problems of distribution and adaptation of the African monkeys. **In**:Chiarelli,B.,Ed., *Taxonomy and Phylogeny of Old World Primates with Reference to the Origin of Man*, 197-270. Turin, Rosenberg and Sellier.

THACKERAY,J.F. 1980. New approaches in interpreting archaeological faunal assemblages with examples from southern Africa. *S. Afr. J. Sci.*, **76**(5), 216-223.

TOBIAS,P.V. 1973. A new chapter in the history of the Sterkfontein early hominid site. *J. S. Afr. Biol. Soc.* **14,** 30-44.

---------- 1985. Ten climacteric events in hominid evolution. *S. Afr. J. Sci.* **81,** 271.

---------- & HUGHES,A.R. 1969. The new Witwatersrand University excavation at Sterkfontein. *S. Afr. Archaeol. Bull.* **24,** 158-169.

---------- HUGHES,A.R., & STRONG,V.E. 1987. *21st Annual Report of PARU and its Precursors*. Johannesburg, Wits Anatomy Department.

---------- 1990. *24th Annual Report of PARU*. Johannesburg, Wits Anatomy Department.

TURNER,A. 1983a. Biogeography of Miocene-Recent larger carnivores in Africa. **In**:Vogel,J.C.,Ed., Late Cainozoic: Palaeoclimates of the Southern Hemisphere, 499-506. Rotterdam, A.A. Balkema.

---------- 1983b. The quantification of relative abundances in fossil and subfossil bone assemblages. *Ann. Transvaal Mus.*, **33**(20), 311-321.

---------- 1984. The interpretation of variation in fossil specimens of spotted hyaena (*Crocuta crocuta* Erxleben, 1777) from Sterkfontein valley sites. *Ann. Transvaal Mus.*, **33**(27), 399-418.

---------- 1986a. Miscellaneous carnivore remains from Plio-Pleistocene deposits in the Sterkfontein valley (Mammalia: Carnivora). *Ann. Transvaal Mus.*, **34**(8), 203-226.

---------- 1986b. Correlation and causation in some carnivore and hominid evolutionary events. *S. Afr. J. Sci.*, **82**(2), 75-76.

---------- 1987. New fossil carnivore remains from the Sterkfontein hominid site (Mammalia: Carnivora). *Ann. Transvaal Mus.*, **34**(15), 319-347.

VAN VALEN,L. 1973. A new evolutionary law. *Evol. Theory* **,1,** 1-30.

VAN ZINDEREN BAKKER,E.M., & MERCER,J.H. 1986. Major late Cainozoic climatic events and palaeoenvironmental changes in Africa viewed in a world wide context. *Palaeogeog., Palaeoclim., Palaeoeco.*, **56,** 217-235.

VRBA,E.S. 1974. Chronological and ecological implications of the fossil bovidae at the Sterkfontein australopithecine site. *Nature* **250,** 19-23.

---------- 1975. Some evidence of chronology and palaeoecology of Sterkfontein, Swartkrans and Kromdraai from the fossil bovidae. *Nature*, **254,** 301-304.

---------- 1976. The fossil bovidae of Sterkfontein, Swartkrans and Kromdraai. *Transvaal Mus. Memoir*, **21.**

---------- 1980. The significance of bovid remains as indicators of environment and predation patterns. **In:**Behrensmeyer,A.K., & Hill,A.P.,Eds., *Fossils in the Making*, 247-271. Chicago, University of Chicago Press.

---------- 1982. Biostratigraphy and chronology, based particularly on bovidae, of southern hominid-associated assemblages: Makapansgat, Sterkfontein, Taung, Kromdraai, Swartkrans; also Elandsfontein (Saldanha), Broken Hill (now Kabwe) and Cave of Hearths. **In:**de Lumley,H., & de Lumley,M.A.,Eds., *Proc. Congres Internationale de Paleontologie Humaine*, **2,** 707-752. Nice, Union Internationale des Sciences Prehistoriques et Protohistorique.

---------- 1985. Early hominids in southern Africa: Updated observations on chronological and ecological background. **In:** Tobias,P.V.,Ed., *Hominid Evolution: Past, Present and Future*, 195-200. New York, Alan R. Liss.

---------- 1988. Late Pliocene climatic events and hominid evolution. **In**:Grine,F.E.,Ed., *Evolutionary History of the "Robust" Australopithecines*, 405-426.

WALKER,A. 1984. Extinction in hominid evolution. **In:**Nitecki,M.H., Ed., *Extinctions*, 119-152. Chicago, University of Chicago Press.

---------- LEAKEY,R.E.,HARRIS,J.M., & BROWN,F.H. 1986. 2.5-Myr *Australopithecus boisei* from west of Lake Turkana, Kenya. *Nature*, **322,** 517-522.

WELLS,L.H. 1967. Antelopes in the Pleistocene of southern Africa. **In:**Bishop,W.W., & Clark,J.D.,Eds., *Background to Evolution in Africa*, 99-107. Chicago, University of Chicago Press.

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ENAMEL THICKNESS IN SOUTH AFRICAN AUSTRALOPITHECINES: NONINVASIVE EVALUATION BY COMPUTED TOMOGRAPHY

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ABSTRACT

Until recently, it has not been possible to systematically study enamel thickness in fossil hominids except by physically sectioning the teeth. Because sectioning studies destroy original specimens, sample sizes will always be low. For this reason, anthropologists have had to devise other methods for acquiring these data such as by measuring enamel in naturally fractured teeth or where it is exposed in worn teeth. It is clearly important to develop and apply non-invasive techniques to augment and expand the data base of early hominid enamel thickness. This is a first attempt to provide such data for a sample of South African australopithecines by utilizing high-resolution computed tomography (CT). This study is based on over 130 CT scans taken at 1 mm slice thickness on a sample of 22 original *Australopithecus africanus* and *A. robustus* lower molars from Sterkfontein, Kromdraai, Makapansgat, Swartkrans and Taung.

Mean values of absolute and relative enamel thickness between *A. africanus* and *A. robustus* are significantly different, confirming that robust australopithecines have thicker enamel than their gracile counterparts. CT sections were taken in the buccolingual plane through the mesial cusps (protoconid, metaconid). While the mean value of enamel thickness at the buccal cusp (protoconid) is greater in *A. robustus* than in *A. africanus*, the difference is not statistically significant. The difference in enamel thickness at the lingual cusp (metaconid) is statistically significant, however.

This study represents an important, albeit preliminary, first step in establishing a methodology for the non-invasive evaluation of enamel thickness in fossil hominids by computed tomography. It demonstrates the viability of the technique and the type of problem oriented approach that can be tackled using computed tomography in modern anthropological research. Measurements derived from CT cannot, of course, be expected to have the same degree of precision as those taken directly from sectioned teeth; nevertheless, important insights into the functional morphology of early hominid teeth are still easily decipherable from the CT data. Given that the alternative to CT is the physical destruction of original hominid fossils, the slight loss in mensurational accuracy seems well worth the price.

INTRODUCTION

> "The most useful measurement of the amount of enamel on a tooth would be the volume of the tissue. This could be expressed as a thickness by dividing the volume of enamel by the surface area of the enamel/dentine junction over which the enamel formed; this area is proportional to the number of ameloblasts which formed the enamel"
> (L. Martin, 1985:260).

Until recently, it has not been feasible to meet this goal in paleoanthropological studies. Determination of total enamel volume in fossil hominid teeth would require a complete set of sequential thin sections to be taken of original specimens, a procedure not enthusiastically endorsed by many museum curators. For this reason anthropologists have had to devise other methods for measuring enamel thickness, for example by utilizing naturally fractured teeth or by using teeth in which the enamel was exposed through wear (Beynon and Wood 1986; Gantt 1985; Kay 1981).

Due to its destructive nature, studies dependent upon sectioning techniques are only able to muster limited sample sizes for both extant and extinct primates (Molnar and Gantt 1977; Martin 1985; Grine and Martin 1988). For example, dental sections are available for only two *Australopithecus africanus* teeth (Stw 284, Stw 402), one *Paranthropus robustus*[1] tooth (KB 5223), and one *P. crassidens* tooth (SKX 21841) (Grine and Martin 1988). Thus it is important to develop and apply non-invasive, non-destructive imaging techniques to augment and expand the data base of early hominid enamel thickness. This contribution describes the feasability of providing such data through high-resolution computed tomography (CT).

Although Robinson (1956) was the first to specifically

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[1] Grine and Martin (1988) place all species of "robust" australopithecines in the genus *Paranthropus*.

comment on enamel thickness in australopithecines, it was not until Jolly's (1970) classic paper on the "seed-eating hypothesis" that attention was focused on enamel thickness as an important functional adaptation of early hominid teeth. This theme was later reinforced by several other studies that related enamel thickness to occlusal wear patterns (Pilbeam 1972; Simons and Pilbeam 1972). By the end of the 1970's it had become anthropological dogma that australopithecine teeth were characterized by "hyper-thick" enamel even though actual measurements of enamel thickness remained few and far between. The limited number of direct enamel thickness measures available were based solely on naturally broken tooth fragments (Robinson 1956; Gantt 1983).

More recently, Beynon and Wood (1986) completed a study of enamel thickness in 47 East African australopithecine and early *Homo* teeth using naturally broken tooth fragments. They concluded that absolute enamel thicknesses at cusp tips and occlusal surfaces were significantly greater in robust australopithecines compared to early *Homo* even after correcting for overall tooth-size differences.

In a more controlled study using finely polished sections, Grine and Martin (1988) were able to measure enamel thickness on four South African australopithecine molars by carefully sectioning each tooth buccolingually through the mesial two cusps (protoconid and metaconid). They also sectioned two australopithecine specimens from Omo, one buccolingually through the entoconid and hypoconid and the other mesiodistally through the protoconid and hypoconid. Although sample sizes were necessarily small given the destructive nature of such procedures, they concluded that relative enamel thickness values in *A. africanus* fell within the 99% confidence limits for the means of their combined upper and lower molar sample of modern *Homo sapiens*, whereas the *Paranthropus robustus*, *P. crassidens*, and *P. boisei* values fell well above those same limits.

Conventional radiographic techniques have also been used to assess enamel thickness in australopithecines but their limitations are well recognized because of relatively low contrast and geometric errors due to inherent magnification errors and/or X-ray beam angulation variations (Sperber 1985). Computed tomography does not have such inherent geometric distortions because of the fixed geometry thinly collimated X-ray beam (typically 1-2mm) and has great potential for non-invasive studies of dental structures (Zonneveld and Wind 1985; Conroy 1987; Conroy and Vannier 1987, 199la,b; but see Grine 1991).

METHODS

This study of enamel thickness is based upon approximately 130 high-resolution CT scans of specimens listed in Table 1. All scans were taken at slice thicknesses of 1 mm. Pixel edge length in the plane of section varied between 0,1 – 0,3 mm. CT sections were taken in the buccolingual plane through the mesial cusps (protoconid and metaconid) in order to be as comparable as possible to the data reported by Martin (1985) and Grine and Martin (1988).

Each specimen was properly aligned in the CT scanner by first producing a topogram (digital radiograph) of the specimen from which the desired CT slice could be automatically selected by using the built-in light-pen integrated into the CT console. In selected cases, contiguous sequences of 1 mm thin CT sections were taken through the entire tooth in order to determine: 1) total enamel volume; and 2) total dentine/enamel surface area over which the enamel formed (see below).

All scans were taken on a Siemens Somatom DR3 CT Scanner in the Radiology Department, Hillbrow Hospital, Johannesburg (operating at 125 KVP and 160 to 520 mAs; with a scan file diameter of 552 mm). The Somatom DR3 can scan objects with density values from air (-1000 Hounsfield Units or H.U.) to cortical bone (+1000 H.U. typically). By definition, water is 0 H.U. The maximum range of X-ray attenuation measured by the DR3 is ordinarily +3072 H.U., and under softward control, we can extend this to approximately +7000 H.U. Extended bone range window settings were used since the density of the fossils was well beyond +1000 Hounsfield units, the upper limit of cortical bone in normal CT viewing. The CT scans (512^2 or 256^2 matrices) and digital scan projection radiographs used for localization of CT sections (topograms) were stored on 8" floppy disks (DEC RX01 format, 0,5 byte/disk) and carried back to the Mallinckrodt Institute of Radiology, Washington University Medical School, St. Louis. There they were copied from the floppy disks onto magnetic tape using a Siemens Evaluscope-DR reviewing console and transferred from the tape to a DEC MicroVax 3600. The images were sent from the Vax to a Macintosh IIfx workstation via a thin-wire Ethernet network with a DECNET/PACER protocol. There they were automatically converted into an image (PICT format) which could be stored, scaled, and displayed in an image analysis program (IMAGE) developed by Wayne Rasband at the National Institutes of Health (NIH).

Original australopithecine specimens from Sterkfontein (N=10), Swartkrans (n=9), Kromdraai (n=1), Makapansgat (n=1), and Taung (n=1) were examined utilizing the methods described above (Table 1). These specimens represent both gracile (n=12) and robust (n=10) australopithecines and are currently housed in the Department of Anatomy, University of the Witwatersrand, Johannesburg, and the Transvaal Museum, Pretoria. The specimens from Swartkrans and Kromdraai are referred to *A. robustus* and those from Sterkfontein, Makapansgat and Taung to *A. africanus*. Only lower molars exhibiting little, if any, occlusal wear were used in this study.

A number of measures of enamel thickness have been defined over the past several years and from these a number of indices of relative enamel thickness have been calculated (see Fig. 1.8 in Grine and Martin 1988). I have followed Martin (1985) and Grine and Martin (1988) in

TABLE 1 (all measurements are in millimeters)

Specimen	tooth	taxon	enamel area (c)	EDJ length (e)	c/e	buc. cusp ht	ling.cusp ht
Taung 1	LM1	*A. africanus*	23,25	17,17	1,35	2,17	2.17
MLD 2	LM2	*A. africanus*	45,52	20,06	2,27	3,10	2.91
TM 1536	RM1	*A. africanus*	14,63	14,40	1,02	1,90	1.67
STW 14	RM3	*A. africanus*	35,11	20,64	1,70	2,39	1.74
STW 269	RM3	*A. africanus*	33,61	17,89	1,88	2,20	2.20
STW 278	RM3	*A. africanus*	38,94	20,35	1,91	2,56	3.02
STW 308	RM2	*A. africanus*	33,84	17,95	1,89	2,62	2.62
STW 309	RM1	*A. africanus*	32,18	19,13	1,68	2,22	2.50
STW 364	RM1	*A. africanus*	25,48	14,62	1,74	2,67	2.22
STW 412	RM2	*A. africanus*	19,52	16,28	1,20	1.96	1.74
STW 419	LM2	*A. africanus*	25,43	15,34	1,66	2.17	1.96
SK 6	RM2	*A. robustus*	52,22	21,47	2,43	3.48	3.26
SK 6	RM3	*A. robustus*	48,20	23,55	2,05	3,04	3.26
SK 19	RM2	*A. robustus*	23,32	13,86	1,68	2,86	2.71
SK 25	RM1	*A. robustus*	34,59	16,24	2,13	2,54	3.05
SK 25	RM2	*A. robustus*	44,70	21,42	2,09	3,45	3.17
SK 37	LM2	*A. robustus*	46,88	19,75	2,37	3,33	3.33
SK 61	RM1	*A. robustus*	45,89	22,17	2,07	2,56	2.82
SK 63	LM1	*A. robustus*	36,59	17,64	2,07	2,59	3.10
SK 1587	LM2	*A. robustus*	30,86	16,50	1,87	2,50	2.50
KB 5223	LM1	*A. robustus*	31,24	30,07	1,56	1,52	1.74

defining relative (or average) enamel thickness as the ratio of enamel cap area in the plane of section (c) divided by the length of the enamel/dentine junction (EDJ) of the same section (e). The vertical thickness of enamel of the buccal and lingual cusps are measured from the cuspal tips perpendicular to a line drawn tangent to the apices of the dentine horns (measurements f and g in Fig. 1 of Grine and Martin 1988) (Figure 1).

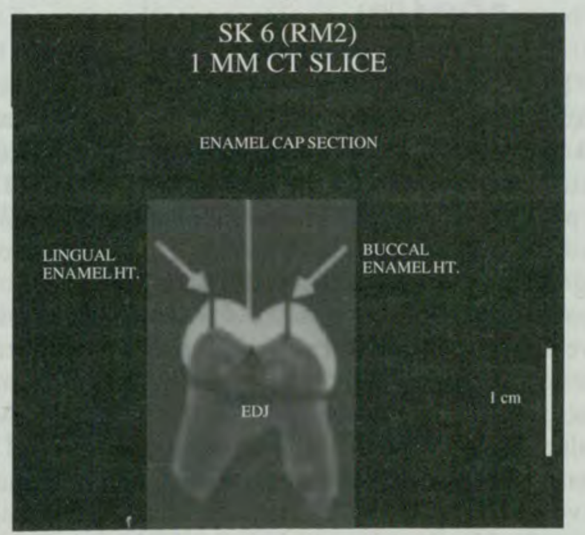

Figure 1 1mm thin CT slice of SK 6 (RM$_2$) showing measurements used in this study: CT sectioned enamel cap area (in white), enamel height at buccal and lingual mesial cusps (protoconid and metaconid) (white arrows), length of enamel/dentine junction (EDJ) (black arrow).

As each scaled CT section was brought up into the IMAGE program on the workstation, the area of the sectioned enamel cap was determined by thresholding (level slicing) the image so that the gray scale levels of all pixels comprising the enamel were highlighted. The area of the highlighted pixels could then be automatically calculated by the IMAGE program. The length of the EDJ could also be calculated by manually tracing its contour on the computer screen with a built-in cursor. Determination of enamel thickness of buccal and lingual cusps was a straightforward procedure using the built-in ruler command of the IMAGE program. The CT scan data are associated with a header record that contains calibration information, most importantly the field of view, matrix size (256 or 512), magnification factor, and number of pixels per 10 cm. All measurements were recorded (in millimeters) and entered into a statistical program (Statview II) for analysis.

The precision of any measurement calculated from a CT scan is of course, limited by the size of the pixels that make up the image (i.e. pixel edge length). The overall reliability of the measurements derived from the australopithecine CT's was cross-checked in two independent ways. Two specimens, Sts 14 and Sts 96, were CT scanned at right angles to their naturally fractured enamel caps. Enamel thicknesses calculated by the IMAGE program were consistently within 0,2 – 0,3 mm of the true values measured directly on the original specimens (i.e., within the pixel edge length values of the CT images). It is worth emphasizing that since this small mensurational imprecision is essentially random with respect to membership in either *A. africanus* or *A. robustus*, it does not significantly influence the results of comparative differences in absolute or relative enamel thicknesses observed between these two fossil species. Indeed, random measurement error would actually make it **more difficult** to obtain the statistically significant results reported below.

The second cross-check on the reliability of the CT methods was quite fortuitous. One of the South African specimens actually sectioned through the mesial cusps by Grine and Martin (1988) was KB 5223, a slightly damaged unworn RM$_1$ from Member 3, Kromdraai (Grine 1982). Direct measurements of enamel cap area (c) and EDJ length (e) gave values of 31,71 and 19,56 respectively for a c/e ratio 1,62 (corrected values for the slightly damaged enamel cap were 36,39, 18,00

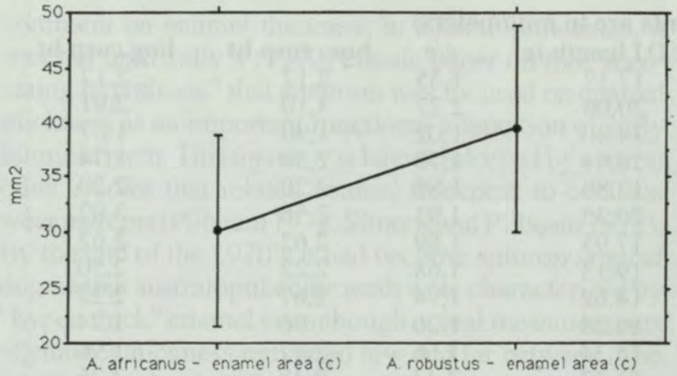

Figure 2. Mean and one standard deviation bar for enamel area

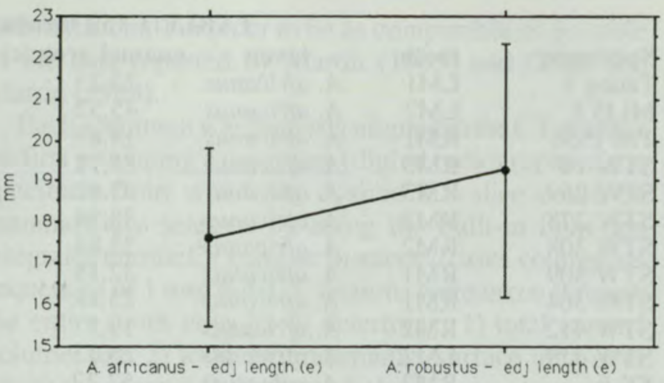

Figure 3. Mean and one standard deviation bar for EDJ Length

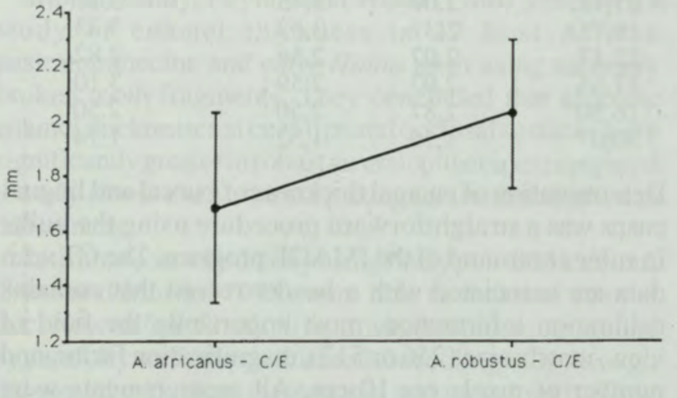

Figure 4. Mean and one standard deviation bar for relative enamel thickness (C/E)

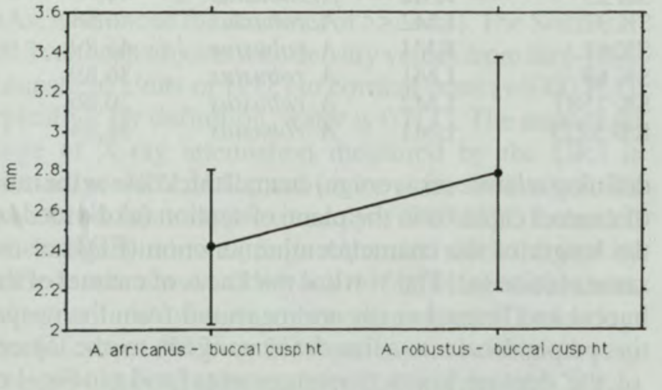

Figure 5. Mean and one standard deviation bar for enamel thickness at Buccal cusp

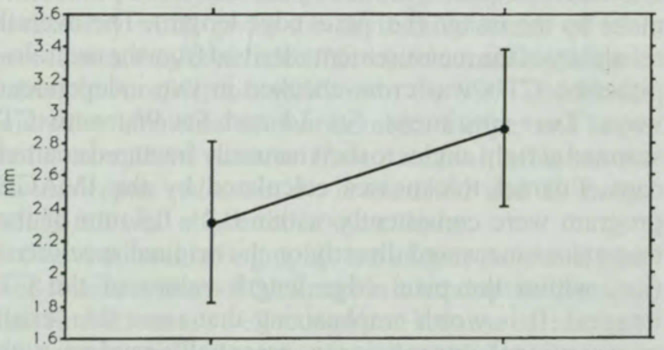

Figure6. Mean and one standard deviation bar for enamel thickness at Lingual Cusp

and 1,02 respectively) (Grine and Martin 1988). Evaluation of a CT section through the mesial cusps of the unworn LM$_1$ from the same individual gave reasonably similar results (31,24 and 20,07 for a c/e ratio of 1,56; Table 1).

RESULTS AND DISCUSSION

The raw data for enamel thickness measurements are presented in Table 1 and basic statistical data in Tables 2 – 6. Sample means and one standard deviation bars for each of the measurements are illustrated in Figures 2 - 6.

The mean value of enamel cap area in CT sections taken through the mesial cusps of the lower molars is 30.15 mm^2 in *A. africanus* and 39.45 mm^2 in *A. robustus*, a statistically significant difference at the 5% level (Table 2; p=,026). However, the mean EDJ lengths of 17,63 mm in *A. africanus* and 19.27 mm in *A. robustus* are not significantly different (Table 3; p=,160).

As discussed above, relative enamel thickness (or average enamel thickness) is measured as the ratio of the sectioned enamel cap area to the EDJ length from the buccal to the lingual cervix of the same section. Mean values for this ratio of 1,69 mm in *A. africanus* and 2,03 mm in *A. robustus* are significantly different at the 5% level (Table 4; p=,019), confirming that robust australopithecines have relatively thicker enamel than their gracile counterparts.

While the mean value of enamel thickness at the buccal cusp is greater in *A. robustus* (2,79 mm) than in *A. africanus* (2,42 mm), this difference approaches, but is not, statistically significant at the 5% level (Table 5; p=,092). However, the difference in enamel thickness at the lingual cusp between *A. robustus* (2,89 mm) and *A. africanus* (2,32 mm) is statistically significant (Table 6; p=,013). (Undoubtedly, differences between the two species would be even greater if the extremely small, rather thin enamelled specimen KB 5223 were not included in the *A. robustus* sample).

TABLE 2: Enamel area (mm²) in South African australopithecines

	Mean	SD	95% lower	95% upper	Prob. (2-tail)
A. africanus	30,15	8,69	24,63	35,67	,258*
A, robustus	39,45	9,41	32,72	46,19	
combined sample	34,38	10,00	29,95	38,81	

TABLE 3: EDJ length (mm) in South African australopithecines

A. africanus	17,63	2,17	16,25	19,01	,160
A. robustus	19,27	3,09	17,06	21,48	
combined sample	18,37	2,69	17,18	19,57	

TABLE 4: Relative enamel thickness (c/e) in South African australopithecines

A. africanus	1,69	,35	1,47	1,91	,0188*
A. robustus	2,03	,27	1,84	2, 23	
combined sample	1,84	,36	1,69	2,00	

TABLE 5: Enamel thickness at buccal cusp (mm) in South African australopithecines

A. africanus	2,42	,39	2,17	2,66	,0924
A. robustus	2,79	,59	2,37	3,21	
combined sample	2,59	,51	2,36	2,81	

TABLE 6: Enamel thickness at lingual cusp (mm) in South African australopithecines

A. africanus	2,32	,50	2,00	2,63	,0129*
A. robustus	2,89	,49	2,55	3,24	
combined sample	2,59	,513	2,36	2,81	

* indicates significane at $P<0.05$ level

The results reported here can be compared and contrasted to similar data for small samples of australopithecines and larger samples of extant hominoids provided by Grine and Martin (1988). Mean values for enamel cap areas in sectioned lower molars were 11,52 in *Pan* (n=8), 23,81 in *Gorilla* (n=8), 20,04 in *Pongo* (n=9), and 20,07 in *Homo* (n=6). Mean values for EDJ length were 17,83 in Pan (n=8), 26,03 in *Gorilla* (n=8), 19,46 in *Pongo* (n=9), and 15,22 in *Homo* (n=6). Average enamel thickness (c/e) of lower molars was 0,63 in *Pan*, 0,92 in *Gorilla*, 1,05 in *Pongo*, and 1,32 in *Homo*.

Grine and Martin (1988) were only able to section 4 australopithecine teeth through the mesial two cusps (Stw 184, Stw 402, KB 5223, SKX 21841). They report values for c, e and c/e for each specimen as follows:

Stw 284:	46,30	25,59	1,81
Stw 402:	38,67	21,69	1,78
KB 5223:	31,71	19,56	1,62
SKX 21841:	62,01	23,64	2,62

The relative enamel thickness values of 1, 81 and 1,78 for the two *A. africanus* specimens from Sterkfontein (Stw 284, Stw, 402) fall within the 95% confidence limits of the *A. africanus* sample reported here and beyond the 95% confidence limits of the *A. robustus* sample (Table 4); the value of 1.62 for the Kromdraai *A. robustus* specimen (KB 5223) is almost identical to the mean value for *A. africanus* reported here and lies outside the 95% confidence interval for *A. robustus;* and the value of 2,62 for the Swartkrans specimen (SKX 21841) is beyond the 95% confidence interval for *A. robustus* reported here.

These data also make it clear that relative enamel thickness is greater in both gracile and robust australopithecines than in any extant hominoid, including *Homo*.

As noted by the quotation cited at the beginning of this paper, a most useful measure of the amount of enamel on a tooth would be the total volume of the tissue expressed as a relative thickness by dividing the enamel volume by the surface area of the enamel/dentine junction over which it formed (Martin 1985). I have done this experiment

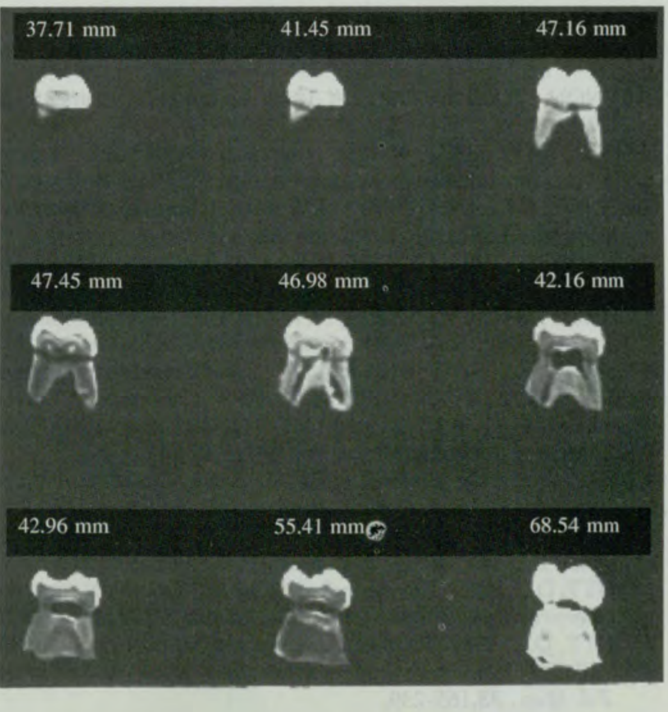

Figure 7. A sample of 9 contiguous 1mm CT scans of (out of a total of 20) SK 6 taken in the buccolingual plaine. Enamel cap area (mm²) of each section is given.

on one specimen, the RM_2 of SK 6. Contiguous 1 mm thin CT slices were taken through the entire tooth in the buccolingual plane (Figure 7). The total enamel cap volume was calculated by summing the individual enamel cap section volumes (area of section x slice thickness). The total surface area of the enamel/dentine junction over which the enamel cap formed was calculated by summing the individual EDJ areas (EDJ length x slice thickness). The ratio of total enamel cap volume to enamel-dentine junction area for this specimen turns out to be 2,23 mm. The fact that the c/e ratio for a single CT section of this tooth is somewhat similar (2,43 mm; Table 1) gives us some hope that single CT slices (or sections) through the mesial cusps of hominid teeth may be reasonable first approximations of relative (or average) enamel thickness over the entire tooth.

CONCLUSIONS

Ultimately, a complete assessment of enamel thickness in early hominids will require further investigations and larger sample sizes. It is imperative to CT scan and archive as large a sample of gracile and robust australopithecines as possible in order to examine intra- and interspecific variation in enamel thickness of early hominids. CT scanning of relevant material, using methods described herein, can contribute to the resolution of these issues by making the previously hidden enamel dimensions more "visible" to investigators.

This study represents an important, albeit preliminary, first step in establishing a methodology for the non-invasive determination of enamel thickness in fossil hominids by computer tomography. It demonstrates the viability of the technique and the type of problem oriented approach that can be tackled using computed tomography in modern anthropological research (Conroy 1987; Conroy and Vannier 1984, 1985, 1986, 1987, 1988, 1991 a,b; Conroy *et al.* 1990).

Measurements derived from CT cannot, of course, be expected to have the same degree of precision as those taken directly from sectioned teeth; nevertheless, important insights into the functional morphology of early hominid teeth are still easily decipherable from the CT data. Given that the alternative to CT is the physical destruction of original hominid fossils, the slight loss in mensurational accuracy seems well worth the price.

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REFERENCES

BEYNON, A.D. & WOOD, B.A. 1986. Variations in enamel thickness and structure in East African hominids. *Amer. J. Phys. Anthrop.*, **70,** 177-194.

CONROY, G.C. 1987. Alleged synapomorphy of I1/M1 eruption patterns in robust australopithecines and *Homo*: Evidence from high-resolution computed tomography. *Amer. J. Phys. Anthrop.*, **75,** 487-492.

CONROY, G.C. & VANNIER, M.W. 1984. Noninvasive three dimensional computer imaging of matrix filled fossil skulls by high resolution computed tomography. *Science*, **26,** 456-458.

CONROY, G.C. & VANNIER, M.W. 1985. Endocranial volume determination of matrix filled fossil skulls using high resolution computed tomography. **In:** Tobias, P. Ed., *Hominid Evolution: Past, Present and Future*, 419-426. New York, Alan Liss Co.

CONROY, G.C. & VANNIER, M.W. 1986. Three dimensional computer imaging: some anthropological applications. **In:** Else, J. and Lee, P. Eds., Proc. *10th International Primat. Cong., Nairobi*, 211-222. Cambridge, Cambridge Univ. Press.

CONROY, G.C. & VANNIER, M.W. 1987. Dental maturation of the Taung skull by computed tomography. *Nature* **329,** 625-627.

CONROY, G.C. & VANNIER,M.W. 1988. The nature of Taung dental maturation continued. *Nature*, **303,** 808.

CONROY, G.C., VANNIER, M.W., TOBIAS, P.V. 1990. Endocranial features of *Australopithecus africanus* revealed by 2 and 3-D computed tomography. *Science*, **247,** 838-841.

CONROY, G.C. & VANNIER, M.W. 1991a. Dental development in South African australopithecines Part I: Problems of pattern and chronology. *Amer. J. Phys., Anthrop.* (in press).

CONROY, G.C. AND VANNIER, M.W. 1991b. Dental development in South African australopithecines Part II: Dental stage assessment. *Amer. J. Phys. Anthrop.*, (in press).

GANTT, D.G. 1983. The enamel of Neogene hominoids: structural and phyletic implications. **In:** Ciochon, R. and Corruccini, R. Eds., *New Interpretations of Ape and Human Ancestry*. 249-298. New York, Plenum.

GANTT, D.G. 1985. Enamel thickness and human evolution. *Amer. J. Phys. Anthrop.*, **66,**171.

GRINE, F.E. 1982. A new juvenile hominid (Mammalia: Primates) from member 3, Kromdraai Formation, Transvaal, South Africa. *Ann. Tvl. Mus.*, **33,**165-239.

GRINE, F.E. 1991. Use of computed tomography to measure tooth enamel thickness. *Amer. J. Phys. Anthrop.* Suppl. 12, 84.

GRINE, F.E. & MARTIN, L.B. 1988. Enamel thickness and development in *Australopithecus* and *Paranthropus*. **In:** Grine, F.E. Ed., *Evolutionary History of the "Robust" Australopithecines*, 3-42. New York, Aldine de Gruyter.

JOLLY, C.J. 1970. The seed-eaters: a new model of hominid differentiation based on a baboon analogy. *Man*, **5**:5 - 26.

KAY, R.F. 1981. The nut-crackers – A new theory of the adaptations of the Ramapithecinae. *Amer. J. Phys. Anthrop*. **55,** 141-152.

MARTIN, L. 1985. Significance of enamel thickness in hominoid evolution. *Nature*, **314,** 206-263.

MOLNAR, S. & GANTT, D.G. 1977. Functional implications of primate enamel thickness. *Amer. J. Phys. Anthrop*. **46,** 447-454.

PILBEAM, D.R. 1972. *The Ascent of Man*. New York, MacMillan.

ROBINSON, J.T. 1956. The dentition of the Australopithecinae. *Transv. Mus. Mem*., **9,** 1-179.

SIMONS, E.L. & PILBEAM, D.R. 1972. Hominoid paleoprimatology. **In:** Tuttle, R. Ed., *The Functional and Evolutionary Biology of Primates*, 36-63. Chicago, Aldine.

SPERBER, G.H. 1985. Comparative primate dental enamel thickness: a radiodontological study. **In:** Tobias, P. Ed., *Hominid Evolution: Past, Present and Future*, 443-454. New York, Alan Liss co.

ZONNEVELD, F.W. & WIND, J. 1985. High-resolution computed tomography of fossil hominid skulls: a new method and some results. **In:** Tobias, P. Ed., *Hominid Evolution: Past, Present and Future*, 427-436. New York, Alan Liss Co.

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COMPUTED TOMOGRAPHY AND THE MEASUREMENT OF ENAMEL THICKNESS IN EXTANT HOMINOIDS: IMPLICATIONS FOR ITS PALAEONTOLOGICAL APPLICATION

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ABSTRACT

Isolated permanent lower molars of *Homo sapiens*, *Pan troglodytes* and *Gorilla gorilla* were imaged by computed tomography (CT) using a 1,5 mm thick section through the mesial cusps. The teeth were examined dry and immersed in water. Measurements of enamel thickness were made on enlargements of hard copy images. Following CT examination, the crowns were sectioned in the same plane, and the cut faces with maximum dentine content were micrographed for measurement using a scanning electron microscope (SEM). Enamel thickness measurements from the CT images were noticeably exaggerated compared to the ideal (sectioned) values, and the CT values for dry specimen images were even larger than those for wet specimen images. These results indicate that CT cannot be employed to measure enamel thickness with any degree of reliability in modern specimens. There is no close correspondence between the SEM and CT values; therefore, the latter cannot even be used to predict the actual values. Thus, the application of CT in the measurement of enamel thickness in fossils is rather dubious.

INTRODUCTION

Anthropologists have long recognized the importance of tooth enamel thickness in the analysis of Miocene hominoid fossils (e.g., Jolly 1970; Simons and Pilbeam 1972; Kay 1981; Martin 1985; Gantt 1986), and several recent studies have pointed to its significance in the interpretation of the early hominid fossil record (Beynon and Wood 1986, 1987; Grine and Martin 1988). Robinson (1956), who was the first and, until quite recently, the only worker to have published measurements of early hominid tooth enamel thickness, recorded maximum and minimum measurements for six naturally fractured *Paranthropus* molars from Swartkrans. He also claimed (1956: 21) that "*Australopithecus* does not appear to differ markedly in this respect," although no data was provided for that taxon. Based upon measurements of several broken teeth, Gantt (1986: 466) has claimed that both *Australopithecus* and *Paranthropus* possess "significantly" thicker enamel than any other hominoid, including modern humans. As noted by Grine and Martin (1988), however, the sources of Gantt's data are unclear, and Beynon and Wood (1986) have noted inconsistencies in his published values.

The first comparative analysis of enamel thickness in fossil hominid taxa was undertaken by Beynon and Wood (1986), who employed linear measurements of occlusal, cusp tip and lateral enamel in naturally fractured cheek-teeth attributed to *P. boisei* and "early" *Homo* (*H. habilis* and *H. erectus*) from eastern Africa. That study also represents the first attempt to obtain relative enamel thickness measurements from estimates of tooth size. They recorded that the size-corrected values for cusp tip and occlusal enamel in *P. boisei* were significantly larger than the corresponding values in their *Homo* sample. Beynon and Wood (1986), however, noted that their techniques of size correction were rather crude, and that measurements of naturally fractured enamel should be related to more accurate measures obtained from sectioned specimens. Grine and Martin (1988) obtained measurements of enamel thickness for sectioned permanent molars of *P. boisei*, *P. robustus* and *A. africanus*. As a result, they were able to provide the first reliable size-corrected (i.e., relative) thickness values for these taxa. Grine and Martin (1988) found that *A. africanus* has enamel of the same relative thickness as modern humans, while *Paranthropus* specimens possess relatively thicker enamel. That study, however, was constrained by very small fossil samples (two molars each of *A. africanus*, *P. robustus*, and *P. boisei*). Despite the fact that the technique employed by Grine and Martin (1988) resulted in the loss of only a 70μm thick section of tooth crown, it is unlikely that statistically adequate samples of Plio-Pleistocene hominid teeth will be available for sectioning until the numbers of available fossils that can be sampled have been increased substantially.

As one approach to increase sample size, Sperber (1985) used lateral radiographs to measure enamel thickness in unworn fossil hominid molars. Gantt (1977), however, had previously noted that measurements from x-rays cannot be considered accurate because they may vary by up to 50% from the true values obtained from thin sections of the same teeth. While Sperber (1985) recognized some of the limitations on accuracy imposed by this indirect method of measurement, he nevertheless concluded that *Paranthropus* molar enamel was generally thicker than that of *A. africanus*, which, in turn, exceeded modern human enamel thickness.

Within the last few years, computed tomography (CT) has become increasingly utilized as a noninvasive tool by which to investigate the internal structure of hominid fossils (Wind 1984; Wind and Zonneveld 1984; Conroy and Vannier 1985, 1987, 1991; Zonneveld and Wind 1985; Daegling 1989; Grine *et al.* 1989; Zonneveld *et al.* 1989; Daegling and Grine 1990, 1991; Floch-Prigent 1989; Conroy *et al.* 1990). Zonneveld and Wind (1985) recorded a maximum occlusal enamel thickness of 3,3 mm from a CT scan of a worn *P. robustus* M^2 from Kromdraai, and Zonneveld *et al.* (1989) recorded a maximum thickness of 2,6 mm from a parasaggital CT section through the M^2 of a *P. robustus* specimen from Swartkrans. Conroy and Vannier (1991) have recently used CT scanning to measure maximum enamel thickness in sections through the mesial cusps of lower molars from Sterkfontein and Swartkrans; they also have reconstructed enamel volume for some teeth.

Although CT has been employed successfully for the measurement of cortical bone thickness and area in modern and fossil specimens (Jungers and Minns 1979; Ruff and Leo 1986; Daegling 1989; Daegling and Grine 1990, 1991), its accuracy depends on a variety of factors such as specimen density, size and shape. To date, the precision with which tooth enamel thickness can be measured by CT has not been established for recent materials, let alone fossils. In view of the potential problems that can be encountered in the use of CT for quantification (Brooks and DiChiro 1976; McCullough 1977; Joseph 1981; Pullan *et al.* 1981; Ruff and Leo 1986; Daegling 1989), the present study was undertaken to investigate the efficacy of CT for the measurement of enamel thickness in modern hominoids as a guide to its possible palaeontological application.

MATERIALS AND METHODS

Isolated permanent lower molars of modern humans and African apes were chosen to compare enamel thickness measurements obtained from CT and mechanical sectioning. These samples were selected, not only because they display significant differences in enamel thickness (Martin 1985; Grine and Martin 1988), but also because they approximate the overall sizes of fossil hominid teeth. Ten unworn teeth of *Homo sapiens* (M$_1$=1, M$_2$=3, M$_3$=6), three unworn or slightly worn specimens of *Pan troglodytes* (M$_1$=1, M$_2$=2), and three unworn or slightly worn molars of *Gorilla gorilla* (M$_1$=3) were chosen for examination. The inclusion of worn teeth presents no difficulty, since the object of this study was to establish the correspondence between measurements obtained from CT and mechanical sectioning, rather than to provide pristine enamel thickness values for these taxa. Each crown was imaged first by CT, using an x-ray slice through the tips of the mesial cusps, and then after mechanical sectioning in the same plane. An unworn M^3 of *Homo sapiens* that was mechanically sectioned prior to CT examination was employed as a "standard" by which to establish the optimum window level and width settings for CT imaging.

The tips of the protoconid and metaconid on each tooth were marked in ink to facilitate alignment for CT and mechanical sectioning. For CT examination, the tooth roots were pushed firmly into a length of 3M strip caulking that was stuck to the base of a large plastic container (21 x 16,5 x 7 cm; Omega Barfel 2L.A346/2). This permitted each crown to be properly positioned with reference to the coronal and horizontal planes, and it enabled the teeth to be examined both in air (dry) and immersed in water (wet).

Specimens were examined immersed in water in order to minimize beam-hardening artifacts that result from the differential attenuation of heterogeneous x-ray beams (Brooks and DiChiro 1976; Sumner *et al.* 1985; Daegling 1989). Beam hardening in dense materials, such as dentine and enamel, results in beam attenuation that may not be strictly proportional to the thickness of the object being traversed. Its effect is accentuated when the difference between the attenuation coefficients of adjacent media is increased (Rao and Alfidi 1981). Modern CT scanners are calibrated so that the attenuation coefficient of air is -1,000 and that of water is zero; bone values vary from +500 to +2,000 (Ruff and Leo 1986). Although a clearer image of the outer margins of a tooth crown may be obtained through its immersion in water, specimens were also examined dry, since it may not be advisable to place fossils in water.

Specimens were examined in a GE model 9800 scanner, and each tooth was aligned independently in the gantry so that the laser alignment light passed across the ink spots on the cusp tips. The calibration of the the laser alignment system of the scanner used in this study is checked monthly so as to ensure that the CT section plane and the light beams are precisely aligned. Each CT image was generated using a 1,5 mm thick slice with a 4 second exposure at 170 MA and 120 kV; the bone reconstruction algorithm was used. A 13 cm field of view and a 2,75x magnification factor were employed. The teeth were examined dry, and then wet. The previously sectioned "standard" was used to determine the most precise window level and width settings by measuring the total buccolingual (BL) diameter of the image as well as the linear diameter of the enamel cap from the tips of the dentine horns to the tips of the cusps on the CRT display. Width and level settings may substantially effect the reliability of an image when objects approach the extremes of the Hounsfield scale, and high density objects are especially sensitive to window level variation because of the "point spread effect" (Joseph 1981; Ruff and Leo 1986). Thus, as has been aptly noted by Ruff and Leo

TABLE 1.

Buccolingual (BL) crown diameters recorded from wet CT images and SEM micrographs.

	N	$\bar{X}$	SD	SE	CV%	Obs. Range
Human sample						
CT	10	10,20	0,53	0,17	5,20	9,51-11,14
SEM	10	10,13	0,52	0,16	5,13	9,54-10,95
Ape sample						
CT	6	12,33	1,62	0,66	13,14	9,91-14,50
SEM	6	12,42	1,99	0,81	16,02	9,59-14,97

(1986) and Daegling (1989), the cleanest ("prettiest") CT image does not necessarily equate to the most accurate image. Window settings of 1500L and 4000W for wet specimens, and 1000L and 4000W for dry specimens* were determined to be the most reliable for accurate imaging by means of the previously sectioned "standard."

Hard copy images consisting of a 512^2 pixel matrix were obtained for each section at an enlargement of 2,75x to enable the image contours to be traced precisely in ink on a clear acetate sheet. Following Daegling (1989), each hard copy sheet included scale grids along the vertical and horizontal axes to control for possible hard copy image distortion, or "flattening." Each tracing was enlarged to a final magnification of 5,5x for measurement.

Following examination by CT, each crown was coated with a thin layer of epoxy (to prevent enamel spalling during sectioning), and sectioned using a Buehler Isomet with a 0,15 mm diamond wafering blade. The edge of the blade was positioned immediately distal to the ink marks on the cusp tips so that the mesial crown section would include the dentine horns. The mesial cut face was then ground and polished with 6 μm, 1μm and 0,25 μm diamond paste on a Buehler Microcloth to obtain the ideal, topography-free section with maximum dentine content (i.e., a section including the very tips of both dentine horns). The polished surface was lightly etched with 0,5% H_3PO_4 for 15 seconds to remove any smeared enamel, ultrasonicated in distilled water, air dried, mounted on an aluminum stub and coated with silver. These surfaces were micrographed at magnifications of between 7,5x and 11,5x using an AMRAY 1810D scanning electron microscope (SEM) at 10 or 20 kV in the secondary electron mode, and at 20 kV for the detection of backscattered electrons. Micrographs were recorded using Polaroid type 55 P/N film, and the positive contacts were employed for measurement.

Linear and area measurements on the CT tracings and micrographs were made using Bioquant System IV software interfaced with a SummaSketch II tablet. All values were recorded to the nearest 0,01 mm or 0,01 mm^2. As an additional means of control to ensure that the CT tracings were scaled accurately, the maximum BL crown diameter on the tracing was compared to the same diameter on the micrograph. These values were very similar for both the human and ape samples (Table 1), indicating that at least for this parameter, the CT images could be considered reliable indicators of crown size.

The BL diameter of each trigonid was also measured with vernier calipers prior to being sectioned; for the human sample this mean was 10,29 mm and for the ape sample it was 12,58 mm. In both instances, the mean obtained by direct crown measurement exceeds the BL average recorded from the micrographs (in the human sample the SEM value ranged from being 9,4% smaller to 2,0% larger than the direct measurement, and in the ape sample the SEM value ranged from being 5,6% smaller to 6,4% larger than the direct measurement). While the direct measurement of BL crown diameter might provide a reasonable rough guide by which to gauge the accuracy of a CT image, it cannot be considered wholly reliable or accurate, since the points that define the maximum breadth of the crown (or even part of the crown) may not lie in the plane that bisects the cusp tips.

Six measurements of enamel thickness were recorded on each tracing and micrograph (Figure 1). These measurements are as defined by Grine and Martin (1988). Measurement "a" is the total area of the crown section, measurement "b" is the area enclosed by the enamel-dentine junction (EDJ), measurement "c" is the area of the sectioned enamel cap, and measurement "e" is the perimeter length of the EDJ from the buccal to the lingual cervix. Measurement "k" is the linear thickness of enamel on the buccal side of the protoconid measured perpendicular to the EDJ from a point at which a line drawn parallel to one between the tips of the dentine horns and tangent to the lowest point of the EDJ between the cusps intersects the EDJ at the side of the crown. Measurement "l" is the linear thickness of the enamel on the lingual side of the metaconid as defined by the same method.

The proportional contribution of the enamel cap to the entire crown section may be expressed by (c/a) x 100. Overall relative enamel thickness may be expressed by the formula $[(c/e)/\sqrt{b}]$ x 100, and relative buccal and lingual enamel thicknesses may be expressed by (k/e) and (l/e) respectively (Grine and Martin 1988).

RESULTS

The proportional enamel cap areas determined from wet and dry CT images, and SEM micrographs are recorded in Table 2. The human values from SEM are similar to those recorded by Grine and Martin (1988) for a separate sample of six human lower molars ($\bar{X}$ = 42,92, SD = 5,68, Range = 34,0-48,8). The values derived from CT images are noticeably greater, and the wet CT image values are closer to the ideal sectioned values than the dry CT values. The wet CT values are, on average, about 34% larger than the true values, while the dry CT values are, on average, nearly 7% larger again. Individual values from wet CT images overestimated proportional enamel thickness by anywhere from about 16% to 47%, while individual dry CT image values were exaggerated by about 24% to 55%. The same pattern applies to the

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* The window level values for dry and water immersed specimens reported in Grine (1991) were inadvertently transposed.

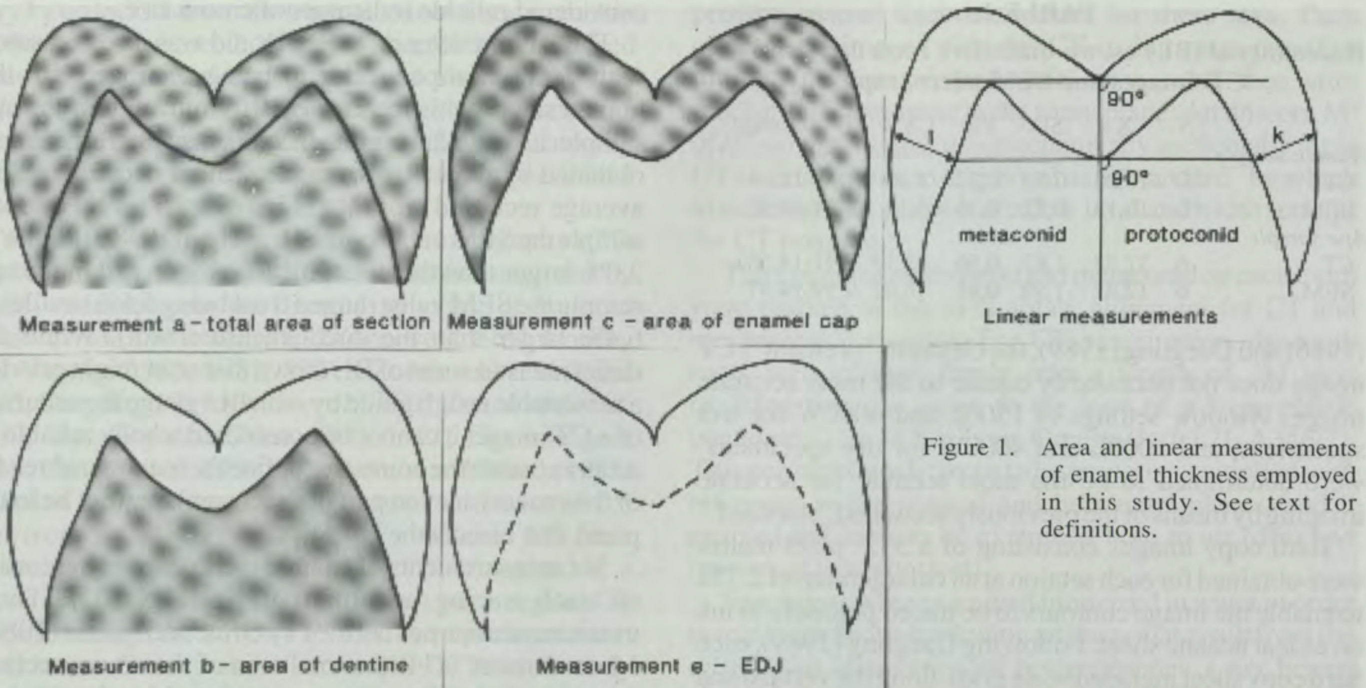

Figure 1. Area and linear measurements of enamel thickness employed in this study. See text for definitions.

TABLE 2.

Proportional enamel thickness [(c/a) x 100] values recorded from wet and dry CT images and SEM micrographs.

	N	$\bar{X}$	SD	SE	CV%	Obs. Range
Human sample						
CT wet	10	52,91	3,77	1,19	7,13	47,48- 59,97
CT dry	10	55,81	4,58	1,45	8,21	50,13- 61,62
SEM	10	39,77	3,63	1,15	9,13	32,47- 44,62
% Diff. CTw-SEM	10	133,70	11,28	3,57	33,47	115,76-146,55
% Diff. CTd-SEM	10	141,37	12,00	3,79	8,49	123,47-155,16
Ape sample						
CT wet	6	34,49	4,39	1,79	12,73	27,20- 39,74
CT dry	6	38,05	4,45	1,82	11,70	32,98- 43,22
SEM	6	24,61	4,37	1,78	17,76	18,85- 30,59
% Diff. CTw-SEM	6	141,53	13,67	5,58	32,92	124,81-163,69
% Diff. CTd-SEM	6	163,92	17,47	7,13	10,66	141,71-183,08

TABLE 3.

Relative enamel thickness [(c/e)/ √b x 100] values recorded from wet and dry CT images and SEM micrographs.

	N	$\bar{X}$	SD	SE	CV%	Obs. Range
Human sample						
CT wet	10	38,49	5,90	1,87	15,33	31,28- 50,37
CT dry	10	45,31	8,22	2,60	18,14	35,75- 54,31
SEM	10	21,10	3,08	0,97	14,60	15,20- 24,49
% Diff. CTw-SEM	10	185,79	32,61	10,31	17,55	139,39-238,38
% Diff. CTd-SEM	10	216,13	33,12	10,47	15,32	161,23-268,86
Ape sample						
CT wet	6	17,94	3,14	1,28	17,50	13,26- 22,60
CT dry	6	21,56	3,63	1,62	16,84	17,30- 26,07
SEM	6	10,83	2,30	0,94	21,24	7,94- 13,87
% Diff. CTw-SEM	6	167,51	19,37	7,91	11,56	146,48-202,88
% Diff. CTw-SEM	6	213,72	33,04	13,49	15,46	166,34-253,42

combined *Pan* and *Gorilla* sample, although here the discrepancy is even larger. In this sample, wet CT images resulted in proportional enamel thickness being overestimated by 25% to 64%, and dry CT images were exagerated by 42% to 83%.

The "standard" specimen provided a proportional enamel thickness value of 37,00 from the SEM micrograph; the corresponding wet and dry CT values were 42,96 and 45,92 respectively based on the most reliable settings. The wet CT value is 16% larger than the true SEM value, and the dry CT value is 7% greater than the wet CT value. Thus, despite the fact that the total BL diameter of the section and the linear enamel measurements were very nearly the same for the SEM and CT images, the latter still yielded noticeably greater values for proportional enamel thickness.

Relative enamel thickness values from SEM micrographs as well as wet and dry CT images are recorded in Table 3. The human sample values from SEM are comparable to those recorded by Grine and Martin (1988) for a different human sample ($\bar{X}$= 25,90, SD = 5,66, Range = 17,4-32,3). The CT images, however, yield gross overestimates of the ideal values for both thin and thickly enamelled teeth. Here too, the wet CT values are somewhat more accurate than those from dry CT images. Within the human sample, the wet CT values are, on average, 85% larger than the ideal values, while the dry CT values are about 21% greater again. In the ape sample, wet CT values are exaggerated by an average of 68%; dry CT values are 27% larger than the wet CT values.

The unpredictable nature of CT exaggeration is revealed by correlation analysis of individual relative enamel thickness [(c/e)/√b x 100] values obtained from wet CT images and SEM micrographs. In the combined ape+human sample R^2 = 0,39, for the human sample alone R^2 =0,03, and for the ape sample alone R^2 = 0,39.

TABLE 4.

Total section area (a), dentine area (b), enamel cap area (c), and enamel-dentine junction length (e) recorded from wet CT images and SEM micrographs.

	N	$\overline{X}$	SD	SE	CV%	Obs. Range
Total Section Area (a)						
Human sample						
CT Wet	10	55,90	8,22	2,60	14,70	39,0- 68,6
SEM	10	59,98	7,10	2,25	11,84	51,5- 73,0
% Diff.	10	93,24	9,57	3,03	10,26	74,1-102,6
Ape sample						
CT Wet	6	70,29	19,89	8,12	28,30	46,0- 90,5
SEM	6	76,78	25,75	10,51	33,54	48,3-108,4
% Diff.	6	92,93	8,21	3,35	8,83	84,8-105,2
Dentine Area (b)						
Human sample						
CT Wet	10	26,44	5,14	1,63	19,44	17,1- 35,7
SEM	10	36,15	4,93	1,56	13,64	28,5- 43,8
% Diff.	10	73,25	11,08	3,51	15,13	53,4- 88,5
Ape sample						
CT Wet	6	46,66	15,72	6,42	33,69	27,7- 65,9
SEM	6	58,55	21,99	8,98	37,56	33,5- 88,0
% Diff.	6	80,67	6,31	2,58	7,82	77,8- 91,2
Enamel Cap Area (c)						
Human sample						
CT Wet	10	29,46	4,12	1,30	13,99	21,9- 37,2
SEM	10	23,83	3,45	1,09	14,48	19,7- 29,9
% Diff.	10	124,27	13,26	4,19	10,67	106,3-145,6
Ape sample						
CT Wet	6	23,63	4,75	1,94	20,10	18,3- 30,7
SEM	6	18,23	4,49	1,83	24,63	13,1- 25,8
% Diff.	6	131,78	19,76	8,07	14,99	119,1-160,0
Enamel-Dentine Junction Length (e)						
Human sample						
CT Wet	10	15,11	1,54	0,49	10,19	12,0- 17,6
SEM	10	18,94	1,46	0,46	7,71	16,9- 21,5
% Diff.	10	79,96	7,48	2,37	9,35	66,3- 89,2
Ape sample						
CT Wet	6	19,93	3,23	1,32	16,21	15,4- 23,0
SEM	6	22,77	3,44	1,40	15,11	18,4- 27,4
% Diff.	6	87,44	11,02	4,50	12,60	83,4- 94,2

TABLE 5.

Linear enamel thickness recorded from wet CT images and SEM micrographs for lingual (l) and buccal (k) sides.

	N	$\overline{X}$	SD	SE	CV%	Obs. Range
Lingual (l)						
Human sample						
CT wet	10	1,58	0,20	0,06	12,66	1,20- 1,84
SEM	10	1,15	0,18	0,06	15,65	0,83- 1,40
% Diff.	10	138,51	16,97	5,37	12,25	109,02-162,50
Ape sample						
CT wet	6	1,40	0,08	0,03	5,71	1,25- 1,49
SEM	6	1,00	0,09	0,04	9,00	0,88- 1,13
% Diff.	6	141,42	16,14	6,59	11,41	116,82-159,09
Buccal (k)						
Human sample						
CT wet	10	2,02	0,29	0,09	14,36	1,55- 2,39
SEM	10	1,61	0,23	0,07	14,29	1,30- 2,00
% Diff.	10	125,99	13,26	4,19	10,52	113,95-157,45
Ape sample						
CT wet	6	1,40	0,26	0,11	18,57	1,03- 1,69
SEM	6	1,05	0,21	0,09	20,00	0,77- 1,29
% Diff.	6	133,40	6,68	2,72	5,01	126,80-144,94

TABLE 6.

Relative enamel thickness values recorded from wet CT images and SEM micrographs for buccal enamel (k/e) and lingual enamel (l/e).

	N	$\overline{X}$	SD	SE	CV%	Obs. Range
Relative Buccal (k/e)						
Human sample						
CT Wet	10	13,48	2,24	0,71	16,62	10,0- 16,7
SEM	10	8,48	0,87	0,28	10,26	6,9- 9,8
% Diff.	10	159,02	23,00	7,27	14,46	127,0-192,0
Ape sample						
CT Wet	6	7,05	0,83	0,34	11,77	5,5- 8,0
SEM	6	4,62	0,56	0,23	12,12	3,7- 5,3
% Diff.	6	152,83	8,60	3,51	5,63	144,0-169,3
Relative Lingual (l/e)						
Human sample						
CT Wet	10	10,62	2,39	0,76	22,50	8,0- 15,4
SEM	10	6,09	0,93	0,29	15,27	4,4- 7,3
% Diff.	10	175,18	31,04	9,82	17,72	124,1-237,1
Ape sample						
CT Wet	6	7,19	1,37	0,56	19,05	5,4- 9,3
SEM	6	4,42	0,50	0,20	11,31	4,1- 5,4
% Diff.	6	159,99	20,54	8,39	12,84	130,8-185,6

Thus, on the basis of the data for the combined ape and human sample, one could predict a CT value from an ideal value with only about 38% greater accuracy than if there was absolutely no relationship betwen these values.

The "standard" specimen yielded relative enamel thickness values of 20,09 for SEM, 24,23 for wet CT, and 28,42 for dry CT. While its CT values are closer to the ideal value than in the other specimens comprising the sample, the wet CT value is still 16% larger than the SEM value, and the dry CT value is some 7% larger still.

The individual area and linear measurements from which the proportional and relative thickness values were calculated are recorded in Table 4. The SEM and CT images yielded similar total section areas. The latter are slightly smaller on average in both the ape and human samples, being from about 74% to about 105% of the SEM values. Dentine area also tends to be smaller when measured from CT images, and in this instance the difference is somewhat greater than with the total section area. In the ape and human samples, CT image values are some 53% to 91% of the SEM image values for dentine area. Similarly, the length of the EDJ tends to be somewhat shorter on CT than on SEM images. While total section area measurements tend to be smaller on CT images, the dentine area and EDJ length values tend to be even smaller still, resulting in enamel cap areas that are exaggerated when compared to the true SEM measurements.

Linear enamel thickness measurements for the buccal and lingual sides of the crown as determined from CT images and SEM micrographs are recorded in Table 5. For these diameters, the human sample values are comparable to those recorded by Grine and Martin (1988) for a different human sample. The values determined from wet CT images are, on average, about 40% larger than the SEM values for the lingual side of the crown, and

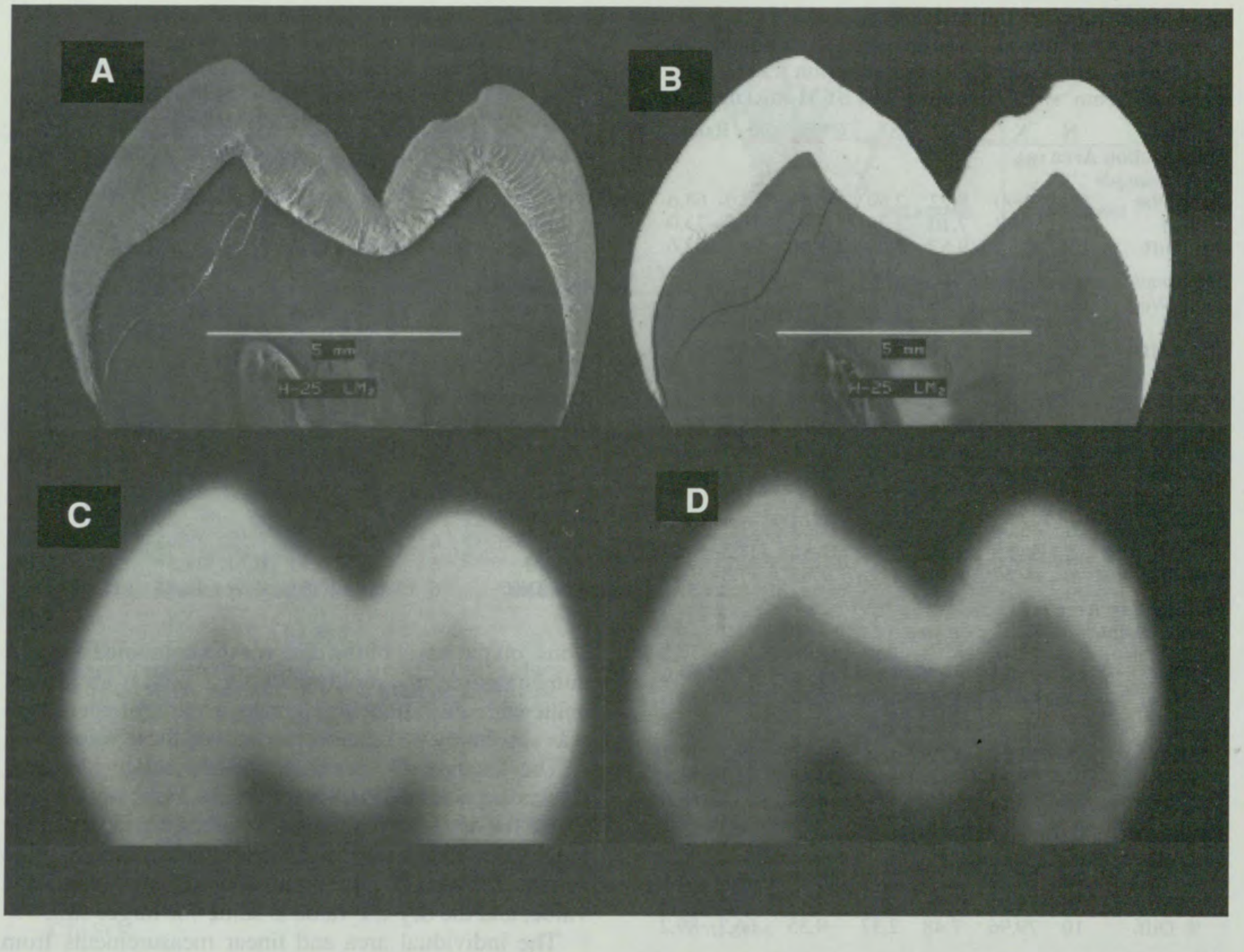

Figure 2. Comparison of scanning electron micrographs (A,B) of sectioned faces and CT images (C,D) through the mesial cusps of a LM$_2$ of *Homo sapiens*. Micrograph (A) is a secondary electron image at 20kV, (B) is a back scattered electron image at 20kV that highlights the enamel cap by atomic number contrast. The CT images are of a water immersed tooth; for image (C) L=900, W=4000; for image (D) L=1500, W=4000. Note the loss of the cervical margins in the CT images, and the difference in enamel thickness at different window level settings. In this instance, the shapes of the dentine horns are similar in the SEM and CT images.

about 30% larger for the buccal enamel. These percentage differences correspond roughly to the differences between wet CT image and ideal values for proportional enamel thickness (Table 2). The CT values range from being some 9% larger to about 62% larger than the real diameters. Here too, it is evident that there is not a close correspodence between CT and real values for individual specimens.

The relative thickness values for buccal and lingual enamel, as determined from the linear measurements are recorded in Table 6. As would be expected from the fact that the linear enamel thickness measurements tend to be exaggerated in CT images, while the EDJ length tends to be under-represented in these same images, the CT values for relative buccal and lingual enamel thickness are noticeably exaggerated. These values are on the order of 56% too large for buccal enamel, and 68% too large for lingual enamel. In both the ape and human samples, the discrepancy is greater with regard to the lingual side of the crown, where the enamel is thinner (Table 6; see also Grine and Martin 1988).

DISCUSSION AND CONCLUSIONS

Enamel thickness measurements by CT are noticeably exaggerated compared to the true values recorded from images that were obtained by mechanical sectioning. The values from CT sections that were recorded for water immersed teeth are somewhat closer to the ideal values than are those for CT images of crowns surrounded by air. This suggests that beam hardening artifacts (Brooks and DiChiro 1976; McCullough 1977; Rao and Alfidi 1981) have affected the dry specimen images more than those obtained for water-immersed teeth.

Beam hardening may also be a factor in the exaggeration of the CT images of water immersed teeth, although the similarity in the total BL diameters of the wet CT and SEM sections indicates that other factors may be primarily

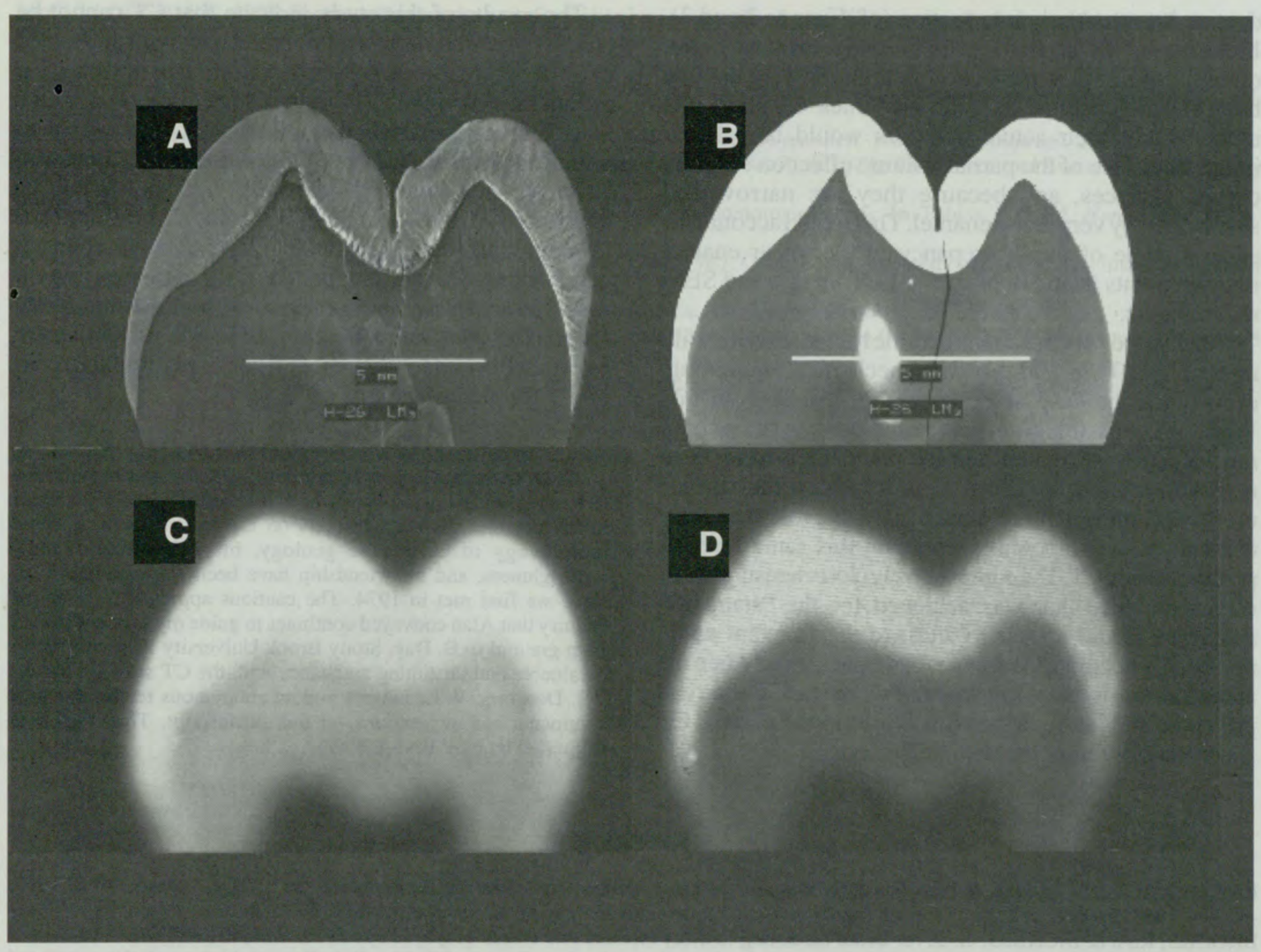

Figure 3. Comparison of scanning electron micrographs (A,B) of sectioned faces and CT images (C,D, through the mesial cusps of a LM$_3$ of *Homo sapiens*. Micrograph (A) is a secondary electron image at 20kV, (B) is a back scattered electron image at 20kV that highlights the enamel cap by atomic number contrast. The CT images are of a water immersed tooth; for image (C) L=900, W=4000; for image (D) L=1500, W=4000. Note the loss of the cervical margins in the CT images, and the difference in enamel thickness at different window level settings. Note also that in this specimen the dentine horns (especially the protoconid) have been blunted in the CT images because the CT section missed the tips of the horns.

responsible for the inaccuracies of the CT images. Partial volume effect would seem to be a likely factor, although the reconstruction algorithm may be at least partially responsible, since they tend to artificially enhance lucency near object borders (Joseph 1981).

The comparatively small size of the tooth crown and the density of enamel, coupled with the narrow apices of the dentine horns and the thin cervical enamel margins probably account for much of the distortion perceived in CT images (Figure 2 and 3).

The CT image is a planar (two dimensional) representation of a three dimensional (1,5 mm thick) slice. Thus, the pixels actually represent three dimensional voxels. Although the algorithm that is employed to produce the image assumes that each voxel uniformly attenuates the x-ray beam, this is almost certainly not the case where thin cervical margins and finely tapered dentine horns are concerned. This partial volume effect may be especially acute at object borders (Pullan *et al.* 1981). On CT scans, the thin, finely tapered cervical margins of the enamel cap, which are clearly seen in mechanically sectioned specimens, are not visualized. Rather, they take the form of blunt borders that are situated to the inside, rather than the outside of the level of the root margin as it approaches the crown (Figures 2 and 3). This has a rather profound effect on the measurement of relative enamel thickness – not only might the thickness of the enamel be exaggerated near the cervix, but the apparent inability to resolve the very thin enamel near the extremity of the margin also reduces the length of the EDJ and the total enclosed area, with a disporoprtionate loss of area under the EDJ.

The dentine horns in apes and humans are generally rather finely tapered at their apices, and they display a rather tight radius of curvature in the horizontal plane close to their tips. It is very possible to miss the tips of the dentine horns entirely in a section (cf. Figures 2 and 3). Indeed, most CT sections through cusp tips reveal blunt, obtusely angled dentine horn outlines. Even if the dentine horn tips are captured by a 1,5 mm thick CT slice, it is unlikely that their actual contours would be reliably imaged because of the partial volume effect on strongly curved surfaces, and because they are narrow and surrounded by very dense enamel. This would account for at least some of the discrepancy in the linear enamel measurements (k and l) taken from CT images and SEM micrographs.

Finally, the very tips of the dentine horns can be readily missed by 100 to 200 µm with mechanical sectioning, even when the cusp apices have been marked in ink. While it is possible to visualize the dentine horns on a mechanically sectioned surface when they have been narrowly missed, and then to polish/grind the surface until maximum dentine content is achieved, it is very difficult, if not impossible, to attain this same level of precision using CT. The comparatively close mensurational correspondence that was achieved for the "standard" specimen would appear to attest to the fact that while reasonably accurate CT images can be achieved when the actual dimensions are known (and when the CT slice can pass precisely along a previously sectioned plane), CT slices variably miss the dentine horn tips.

The results of this study indicate that CT cannot be employed to determine enamel thickness with the degree of reliability and accuracy that is required for comparative purposes. Although CT images may provide a rough visual impression of whether a tooth has thin enamel (e.g., a modern African ape) or thick enamel (e.g., a modern human), measurements of these images cannot be considered reliable. Certainly the use of such measurements in a comparative statistical analysis would lead to spurious conclusions. The employment of CT in palaeontology is potentially even more problematical because diagenetic factors that may affect the mineralization of fossil teeth can only but add to the factors that can confound the use of CT for quantification.

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REFERENCE

BEYNON, A.D. & WOOD, B.A. 1986. Variation in enamel thickness and structure in East African hominids. *Am. J. Phys. Anthrop.*, **70**, 177-193.

---------- 1987. Patterns and rates of enamel growth in the molar teeth of early hominids. *Nature*, **326**, 493-496.

BROOKS, R.A. & DiCHIRO, G. 1976. Beam hardening in x-ray reconstructive tomography. *Phys. Med. Biol.*, **21**, 390-398.

CONROY, G.C. & VANNIER, M.W. 1985. Endocranial volume determination of matrix filled fossil skulls using high resolution computed tomography. **In:** Tobias, P.V., Ed., *Hominid Evolution: Past, Present and Future*, 419-426. New York, Alan R. Liss.

---------- 1987. Dental maturation of the Taung skull by computed tomography. *Nature*, **329**, 625-627.

---------- 1991. Noninvasive evaluation of enamel thickness and volume in South African australopithecines by computed tomography. *Am. J. Phys. Anthop.*, **suppl. 12**, 60.

---------- & TOBIAS, P.V. 1990. Endocranial features of *Australopithecus africanus* revealed by 2 and 3-D computed tomography. *Science*, **247**, 838-841.

DAEGLING, D.J. 1989. Biomechanics of cross-sectional size and shape in the hominoid mandibular corpus. *Am. J. Phys. Anthrop.*, **80**, 91-106.

---------- & GRINE, F.E. 1990. Biomechanics of australopithecine mandibles from computed tomography. *Am. J. Phys. Anthrop.*, **81**, 211.

---------- 1991. Compact bone distribution and biomechanics of early hominid mandibles. *Am. J. Phys. Anthrop.*, **86**, in press.

FLOCH-PRIGENT, P. 1989. Scannographie du crâne de Pétralona: coupes systématiques dans les trois plans; première partie: résultats morphologiques. *C.R. Acad. Sci. Paris*, **309**, 1855-1862.

GANTT, D.G. 1977. *Enamel of primate teeth: its thickness and structure with reference to functional and phyletic implications*. Unpublished PhD Thesis, Washington University, St. Louis.

---------- 1986. Enamel thickness and ultrastructure in hominoids with reference to form, function and phylogeny. **In:** Swindler, D.R. & Erwin, J., Eds, *Comparative Primate Biology*, Vol. 1: *Systematics, Evolution and Anatomy*, 453-475. New York, Alan R. Liss.

GRINE, F.E. 1991. Use of computed tomography to measure tootH enamel thickness. *Am. J. Phys. Anthrop.*, **suppl. 12**, 84.

—————— & MARTIN, L.B. 1988. Enamel thickness and development in *Australopithecus* and *Paranthropus*. **In**: Grine, F.E., Ed., *Evolutionary History of the "Robust" Australopithecines*, 3-42. New York, Aldine de Gruyter

——————, COLFLESH, D.E., DAEGLING, D.J., KRAUSE, D.W., DEWEY, M.M., CAMERON, R.H. & BRAIN, C.K. 1989. Electron probe x-ray microanalysis of internal structures in a fossil hominid mandible and its implication for biomechanical modelling. *S. Afr. J. Sci.*, **85**, 509-514.

JOLLY, C.J. 1970. The seed-eaters: a new model of hominid differentiation based on a baboon analogy. *Man*, **5**, 5-26.

JOSEPH, P.M. 1981. Artifacts in computed tomogrphy. **In:** Newton, T. H. & Potts, D.G., Eds, *Radiology of the Skull and Brain*, vol. 5: *Technical Aspects of Computed Tomography*, 3956-3992. St. Louis, Mosby.

JUNGERS, W.L. & MINNS, R.J. 1979. Computed tomography and biomechanical analysis of fossil long bones. *Am. J. Phys Anthrop.*, **50**, 2855-290.

KAY, R.F. 1981. The nut-crackers: a new theory of the adaptations of the Ramapithecinae. *Am. J. Phys. Anthrop.*, **55**, 141-152.

MARTIN, L.B. 1985. Significance of enamel thickness in hominoid evolution. *Nature*, **314**, 260-263.

McCULLOUGH, E.C. 1977. Factors affecting the use of quantitative information from a CT scanner. *Radiology*, **124**, 99-107.

PULLAN, B.R., RITCHINGS, R.T. & ISHERWOD, I. 1981. Accuracy and meaning of CT attenutation values. **In**: Newton, T.H. & Potts, D.G., Eds, *Radiology of the Skull and Brain*, vol. 5: *Technical Aspects of Computed Tomography*, 3904-3917. St Louis, Mosby

RAO, P.S & ALFIDI, R.J. 1981. The environmental density artifact: a beam hardening effect in computed tomography. *Radiology*, **141**, 223-227.

RUFF, C.B. & LEO, F.P. 1986. Use of computed tomography in skeletal structure research. *Yrbk. Phys. Anthrop.*, **29**, 181-196.

SIMONS, E.L. & PILBEAM, D.R. 1972. Hominoid paleoprimatology. **In**: Tuttle, R., Ed., *The Functional and Evolutionary Biology of Primates*, 36-62. Chicago, Aldine.

SPERBER, G.H. 1985. Comparative primate dental enamel thickness: a radiodontological study. **In**: Tobias, P.V., Ed., *Hominid Evolution: Past, Present and Future*, 443-454. New York, Alan R. Liss.

SUMNER, D.R., MOCKBEE, B., MORSE, K., CRAM, T. & PITT, M. 1985. Computed tomography and automated image analysis of prehistoric femora. *Am. J. Phys. Anthrop.*, **68**, 225-232.

WIND, J. 1984. Computerized x-ray tomography of fossil hominid skulls. *Am. J. Phys. Anthrop.*, **63**, 265-282.

——— & ZONNEVELD, F.W. 1984. Computed tomography: a new technique to describe fossil hominid skulls. A study of the Sts 5 skull (Mrs. Ples). *Naturwiss* **76**, 325-327.

ZONNEVELD, F.W. & WIND, J. 1985. High resolution computed tomography of fossil hominid skulls: a new method and some results. **In:** Tobias, P.V., Ed., *Hominid Evolution: Past, Present and Future*, 427-436. New York, Alan R. Liss.

———, SPOOR, C.F. & WIND, J. 1989. The use of CT in the study of the internal morphology of hominid fossils *Medicamundi*, **34**, 117-128.

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A PALAEONTOLOGICAL MODEL FOR DETERMINING THE LIMITS OF EARLY HOMINID TAXONOMIC VARIABILITY

by

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ABSTRACT

This paper has examined the utility and implications of using *Australopithecus boisei* as a model for assessing the limits of intraspecific variation in early hominid species. When compared to variation in a sample of lowland gorilla, the coefficient of variation values of the 25 cranial and mandibular, and 44 dental measurements taken on the *A. boisei* hypodigm were not excessive; the main difference between the two samples was the higher levels of canine variability within *gorilla*.

Levels of variability in *A. boisei* were compared with those in the hypodigms of *A. robustus* and *A. africanus*. In neither case did comparisons demonstrate that those hypodigms were excessively variable. This suggests that if more than one taxon is present within these collections, then any differential diagnosis needs to be based on excessive variation in shape and not size.

INTRODUCTION

The problem of deciding the point at which phenotypic variation exceeds that which can be tolerated within a single species is one that is widely recognised in both palaeontology in general (Mayr, Linsley and Usinger 1953; Sylvester-Bradley 1956; Simpson 1961), and in hominid palaeontology in particular (e.g. Weidenreich 1946; Campbell 1962; Zwell and Pilbeam 1972; Pilbeam 1978; Wolpoff 1978). Some have linked these difficulties with attempts to equate fossil species with neontological ones. Resolutions proposed in the past have included redefining the meaning that is conveyed when a fossil species is erected. For example, the 'palaeospecies' and 'chronospecies' concepts of Cain (1954) and George (1956), respectively, are deliberately intended to invoke a wider concept, i.e. the whole (George 1956), or part (Pilbeam 1972), of an evolutionary lineage. Campbell (1972) is the latest to espouse an alternative solution, which suggests that dating information should supplant morphological evidence as a means of defining species, but it is a view that has attracted few supporters. A third approach leaves the classificatory categories untouched, but suggests that Bayesian probability theory might offer a formal scheme for determining whether fossil site samples are likely to be derived from one, or more, early hominid species (Pilbeam and Vaisnys 1975; Pilbeam 1978).

One strategy for making judgements about the boundaries of palaeontological species has been to base criteria for species variability on variation observed within living taxa. The extent of variation within one, or more, variables in a reference sample is usually compared with that in the fossil sample, and a recent study has proposed that the 'degree' and the 'pattern' of variation should be given separate consideration (Wood, Li and Willoughby 1991). The same study used an 'outgroup' approach, and investigated the pattern of variation in modern humans and the African higher primates. Molecular, and other, evidence have consistently shown these to be the extant taxa most closely related to modern humans, and thus to fossil hominids (Sibley and Ahlquist 1984, 1987; Miyamoto, Slightom and Goodman 1987; Miyamoto *et al*. 1988; Caccone and Powell 1989; Saitou 1991). Univariate and multivariate methods were employed to compare patterns of variation, and the results suggest that the most appropriate extant analogue for assessing the pattern of dental variation is modern *Homo sapiens*, whereas, apparently, both *Homo* and *Pan* provide suitable pattern analogues for assessing cranial and mandibular variation.

Extant reference taxa which can usefully serve as analogues for the degree of variation are more difficult to identify. Several authors have pointed out that no neontological species provides an apt model because the time spanned by palaeontological samples introduces an additional, unquantifiable, source of variation (Pilbeam 1978; Lieberman, Pilbeam and Wood 1988; Wood and Xu 1991). Within the higher primates the degree of intraspecific variation is lowest in *Homo sapiens* and *Pan*. Although these two taxa are judged to be the forms most closely related to early hominids (e.g. Caccone and Powell 1989) many workers have erred on the side of caution and selected a more dimorphic ape, usually *Gorilla*, with the intention of trying to allow for the extra, temporal, influence on variation that is implicit in a fossil sample (e.g. Lieberman *et al*. 1988; Wood *et al*. 1991).

An alternative to using extant analogues is to compare the variation within the test sample with that observed within another hominid species. This strategy has the advantage that both reference and test samples would include the elusive temporal element which is lacking in extant analogues, as well as ensuring that the reference sample provides a type which is genetically closely-related to the test sample. Any fossil taxon used as a reference sample should preferably be defined by autapomorphies (Table 1), so that disagreement about the nature of the reference hypodigm is reduced to a minimum. The fossil taxon should also have a similar, or equivalent, geographical range to the material being evaluated. This serves to eliminate yet another confounding factor, namely the influence of geographical variation.

In the light of these criteria, it was decided to investigate *Australopithecus boisei* as a possible early hominid reference taxon. This paper reports an investigation which sought to explore whether the diagnostic criteria for *A. boisei* could be utilised to identify samples large enough to estimate population parameters. The latter were then computed, as were equivalent parameters generated from extant analogues and the two sets were compared. The results of the investigation were then reviewed to see if they have implications for the assessment of variation within material which has been assigned to other fossil hominid taxa.

TABLE 1

Probable Autapomorphies of *Australopithecus Boisei*

1. **Overall size, shape and form of the cranium.**
   - i. Massive, but orthognathic viscerocranium, with a mean cranial capacity of around 500 ml.
   - ii. Substantial overlap at the parietotemporal suture, with *striae parietalis*.
   - iii. Glabella located on a rounded projection.
2. **Face**
   - iv. Great absolute and relative width of the midface, combined with modest alveolar and midfacial prognathism.
   - v. Nasal bones broader superiorly than inferiorly, combined with well-defined nasal margins.
3. **Cranial base**
   - vi. 'Heart-shaped' foramen magnum.
   - vii. Narrow cranial base, combined with coronally-orientated petrous bones with vertically-inclined posterior faces.
   - viii. Laterally-expanded mandibular fossa, combined with a deep glenoid fossa, short postglenoid process, articular eminence with a steep face and bounded laterally by a substantial articular tubercle and a posteriorly-situated entoglenoid process.
4. **Mandible**
   - ix. Large, robust, corpus, with marked lateral prominence, wide, extramolar sulcus, vertical inner wall and "bulging" lateral wall.
   - x. Long alveolar planum, with both a superior, and a relatively larger inferior, transverse tori.
5. **Dentition**
   - xi. Modest sized incisors and canines combined with massive premolar and molar crowns.
   - xii. Absolutely large-crowned, but relatively buccolingually-narrowed, P_4s.
   - xiii. Absolutely and relatively large premolar and molar talonids.
   - xiv. Molariform P_3 roots.
   - xv. Mesial to distal gradient of increasing root size and robusticity from P_3 - M_3.
   - xvi. Retention in the adult premolars and molars of the deciduous mode of enamel formation.

MATERIALS AND METHODS

The data used in this investigation were gathered by the author as part of a larger study of Plio-Pleistocene hominid evolution (Wood, 1991). The main sample included all the Plio-Pleistocene remains from the East African sites of Koobi Fora, Omo, Olduvai, Peninj, Chesowanja and West Turkana which had been assigned to, or likened to, *A. boisei* (Table 2). The *A. africanus* and *A. robustus* samples include some of the more recently reported additions to the respective hypodigms (Clarke 1988; Grine 1988a). Details of the provenance of the *Gorilla* sample are given in Wood *et al.* (1991).

Metrical data form the core of the evidence, but several non-metrical observations were also included. The cranial and mandibular measurements included in this study are listed in Table 3, and maxillary and mandibular dental measurements are set out in Tables 4 and 5; detailed

TABLE 2

Probable Autapomorphies of *Australopithecus Boisei*

1.	*KOOBI FORA* (KNM-ER)			N=51	
	403	404	405	406	407
	725	726	727	728	729
	732	733	801	802	805
	810	812	814	818	1170
	1171	1467	1468	1469	1477
	1479	1509	1803	1804	1806
	1816	1819	1820	3229	3230
	3729	3737	3885	3886	3890
	3954	5429	5679	5887	6082
	13750	15930	15940	15950	16841
	17760				
2.	*WEST TURKANA* (KNM-WT)			N=2	
	17396	17400			
3.	*PENINJ*			N=1	
	Mandible				
4.	*CHESOWANJA* (KNM-CH)			N=3	
	1	302		304	
5.	*OLDUVAI* (OH)			N=3	
	5	26		30	
6.	*OMO*			N=14	
	F203-1	L64-2	L74A-21	L338y-6	
	L427-7	L628-1	L628-2	L628-5	
	L704-2	L726-11	Omo 47-46	Omo76-37	
	Omo141-2	Omo323-896			

Total Number of Specimens = 74

definitions are to be found in Wood (1991). With the exception of OH5, the remains from West Turkana and a few specimens from the Omo Shungura Formation, all measurements were made on original specimens.

Parameters of taxon hypodigms were calculated using standard formulae except that Coefficient of Variation (CV) calculations for samples of less than ten were based on a formula for small samples (Sokal and Rohlf 1987). Methods are available for assessing the statistical significance of differences in variability (e.g. Sokal and Braumann 1980; Schultz 1985), but the small sample sizes do reduce confidence in any conclusions based on these tests, and in this study no attempt has been made to assess the statistical significance of any CV differences.

RESULTS

The process of assembling a hypodigm of *A. boisei* began by reviewing the characteristics of the type specimen, OH5, employing suitable casts as well as information contained in Tobias (1967). Specimens showing clear resemblances to OH5 were evident in the site collections from Koobi Fora (eg KNM-ER 406 and 733), Chesowanja and the Omo. This expansion of the cranial hypodigm enabled both qualitative and quantitative estimates to be made of the likelihood that smaller crania (eg KNM-ER 407 and 732) may be smaller-bodied, presumably female, representatives of *A. boisei* (Wood 1991).

The absence of a mandible from the type specimen (OH5) means that the mandibular morphology of *A. boisei* has to be inferred. The tooth dimensions of *A. boisei* crania and maxillary/mandibular tooth area ratios of extant higher primates provide a suitable starting point, for the null hypothesis would suggest that the dental dimensions of the mandibles of *A. boisei* should be within the range of mandibular tooth size predicted from the maxillary dentition of *A. boisei*. Such a calculation does indicate that mandibles such as that from Peninj and several from Koobi Fora (eg KNM-ER 729, 3230 etc) most likely belong to *A. boisei*. Likewise, studies of tooth crown and root morphology (Wood and Abbott 1983; Wood, Abbott and Graham 1983; Wood and Uytterschaut 1987; Wood Abbott and Uytterschaut 1988; Wood and Engleman 1988) and of the enamel micro-structure (Beynon and Wood 1986, 1987) of teeth associated with cranial and mandibular remains diagnostic of *A. boisei*, have provided criteria for allocating partial dentitions, and even single, isolated, tooth crowns, to the

TABLE 3

Parameters of Selected Cranial and Mandibular Dimensions for *Australopithecus boisei* compared with the CVs of *Gorilla gorilla* and the Hypodigms of *Australopithecus africanus* and *Australopithecus robustus*.

		Australopithecus boisei					*Gorilla* (N=64)	*Australopithecus africanus*		*Australopithecus robustus*	
		N	X	RANGE	CV	95%CL	CV	N	CV	N	CV
Glabella-opisthocranion	(1)	4	158	130-173	12,7	-	11,8	-	-	-	-
Posterior cranial length	(3)	3	47	46-48	2,3	-	17,9	3	7,3	-	-
Minimum frontal breadth	(8)	6	66	60-74	8,2	2,1-14,3	6,2	-	-	3	6,0
Maximum parietal breadth	(9)	6	98	90-110	8,0	2,0-14,0	4,7	-	-	-	-
Biporionic breadth	(11)	5	119	103-134	10,9	1,2-20,6	10,5	4	2,4	-	-
Bimastoid breadth	(13)	4	128	110-144	14,3	-	11,1	-	-	-	-
Biorbital breadth	(50)	3	93	82-100	11,0	-	8,7	3	5,3	3	14,6
Bijugal breadth	(51)	3	124	107-135	13,0	-	10,5	-	-	3	7,0
Interorbital breadth	(55)	4	24	23-27	8,8	-	21,7	4	7,4	-	-
Alveolar breadth (outer)	(54)	3	73	62-81	14,8	-	7,3	-	-	4	5,1
Orbital breath	(56)	3	37	30-38	12,3	-	7,1	3	1,8	-	-
Orbital height	(57)	3	33	30-36	10,2	-	6,9	-	-	-	-
Nasal width	(68)	4	31	28-34	10,3	-	10,2	7	13,6	-	-
Palate length	(90)	3	61	52-71	16,8	-	12,7	3	4,7	3	6,7
Intercanine distance (U)	(98)	3	29	28-31	5,6	-	10,8	8	5,5	10	7,4
Palate height	(103)	3	20	19-20	3,2	-	13,9	6	20,7	8	22,0
Alveolar breadth (inner)	(93)	3	32	31-34	5,1	-	9,2	-	-	4	8,1
Cranial capacity	(-)	6^2	501	427-530	7,9	3,4-12,4	14,1	6^3	11,7	1^4	-
Symphyseal height	(141)	11	47	40-57	15,0	7,7-22,3	13,4	-	-	-	-
Symphseal depth	(-)	11	28	24-32,5	9,5	5,0-14,1	13,1	-	-	-	-
Corpus height (M_1)	(150)	25	42	34-50	9,9	7,0-12,8	11,8	6	11,7	5	7,9
Corpus width (M_1)	(151)	25	29	24-37	11,8	8,3-15,3	9,8	5	10,2	5	14,5
Corpus area (M_1)	(152)	25	960	660-1414	21,3	14,8-27,8	18,7	5	11,6	5	21,5
Robusticity (M_1)	(-)	25	69	57-80	7,5	5,3-9,7	10,0	5	16,9	5	10,6
Intercanine distance (L)	(166)	5	21	20-22,5	5,0	0,6-9,4	14,3	-	-	-	-

NB:

(1) Numbers in parentheses refer to the measurement number in Wood (1991).

(2) Specimens included in *A. boisei* cranial capacity sample = KNM-ER 406,407, 732, 13750; 0h5; Omo L338y-b.

(3) Specimens included in *A. africanus* cranial capacity sample = Sts 5, 19, 60, 71; MLD 37/38; Taung.

(4) Specimen included in *A. robustus* cranial sample = SK 1585.

TABLE 4

Parameters of Maxillary Tooth Crown Dimensions for *Australopithecus boisei* compared with the CVs of *Gorilla gorilla* and of the Hypodigms of *Australopithecus africanus* and *Australopithecus robustus.*

		Australopithecus boisei					*Gorilla* (N=64)	*Australopithecus africanus*		*Australopithecus robustus*	
		N	X	RANGE	CV	95%CL	CV	N	CV	N	CV
I^1	LL	-	-	-	-	-	8,8	3	2,4	13	5,4
	MD	-	-	-	-	-	12,5	3	15,1	15	7,6
I^2	LL	5	6,4	5,6-7,5	13,1	1,4-24,8	11,5	5	10,6	8	10,4
	MD	5	6,5	6,2-6,9	6,5	0,8-12,2	12,9	5	8,8	9	14,5
C	LL	6	8,9	7,6-9,9	10,5	2,6-18,4	20,4	6	5,2	19	7,4
	MD	7	8,8	8,2-10,7	10,6	3,6-17,6	20,9	7	4,2	19	5,9
	CA	6	75,5	63,0-87,0	13,6	3,3-23,9	39,0	6	9,1	19	11,9
P^3	BL	8	15,4	13,9-17,0	8,0	3,2-12,8	8,3	14	6,4	16	5,0
	MD	8	10,9	10,2-12,0	5,7	2,3-9,1	9,1	14	2,2	17	4,0
	CA	8	168,0	142,0-185,5	9,6	3,9-15,3	15,5	14	7,8	16	8,5
P^4	BL	7	16,3	14,3-18,0	8,3	2,8-13,8	7,6	9	5,3	18	5,2
	MD	7	11,7	10,6-12,1	4,5	1,6-7,5	8,4	9	5,1	18	5,6
	CA	7	191,0	151,5-212,5	12,0	4,0-20,0	13,9	9	9,0	18	10,0
M^1	BL	8	16,3	14,9-17,7	6,9	2,8-11,0	7,2	12	5,1	20	4,7
	MD	8	14,8	13,5-15,7	5,6	2,3-8,9	7,1	12	3,9	20	3,0
	CA	8	241,0	212,0-269,0	11,0	4,4-17,6	13,3	12	7,7	20	6,4
M^2	BL	8	18,2	16,4-21,0	10,2	4,1-16,3	7,6	15	6,5	17	5,6
	MD	8	16,1	14,7-17,3	7,0	2,8-11,2	8,3	15	6,5	17	5,6
	CA	8	295,0	242,5-361,0	16,1	6,3-25,9	14,3	15	13,1	17	9,1
M^3	BL	4	18,9	16,2-21,5	14,0	-	9,8	14	8,4	19	4,1
	MD	4	15,7	14,2-16,6	7,4	-	10,2	14	9,5	19	6,0
	CA	4	298,0	230,0-366,0	17,7	-	19,4	14	17,2	19	9,2

NB: LL = Labiolingual diameter; MD = Mesiodistal diameter; CA = Computed crown area: BL = Buccolingual diameter,

TABLE 5

Parameters of Maxillary Tooth Crown Dimensions for *Australopithecus boisei* compared with the CVs of *Gorilla gorilla* and of the Hypodigms of *Australopithecus africanus* and *Australopithecus robustus*

		Australopithecus boisei					*Gorilla* (N=64)	*Australopithecus africanus*		*Australopithecus robustus*	
		N	X	RANGE	CV	95%CL	CV	N	CV	N	CV
I_1	LL	7	6,8	6,1-8,0	12,3	4,1-20,5	8,8	3	10,6	11	9,8
	MD	7	5,4	4,5-5,9	9,7	3,3-16,1	12,5	3	14,0	10	3,6
I_2	LL	4	6,9	6,4-8,1	12,3	-	11,5	3	9,1	8	5,7
	MD	5	6,4	6,1-6,6	3,3	0,4-6,2	12,9	4	13,0	8	6,5
C	LL	9	8,8	7,5-9,7	9,4	4,3-14,6	20,4	7	9,8	12	7,6
	MD	8	8,0	7,3-9,3	9,1	3,7-14,5	20,9	7	6,5	12	7,9
	CA	8	69,0	57,0-83,5	14,2	5,6-22,8	39,0	7	16,5	12	14,2
P_3	BL	7	12,9	11,6-13,9	7,3	2,5-12,1	8,3	6	6,2	7	7,7
	MD	7	10,9	9,6-12,1	7,6	2,6-12,6	9,1	6	6,3	17	4,0
	CA	7	140,5	119,0-165,0	12,8	4,3-21,3	15,5	6	9,7	17	9,7
P_4	BL	14	14,7	12,7-16,5	7,7	4,5-10,9	7,6	6	4,2	16	7,8
	MD	14	13,9	12,2-15,7	7,3	4,3-10,3	8,4	6	7,9	17	4,4
	CA	14	205,0	170,0-240,0	13,1	7,7-18,5	13,9	6	11,7	16	11,2
M_1	BL	11	14,7	12,8-16,0	6,9	3,6-10,2	7,2	11	7,6	26	6,5
	MD	11	16,1	14,6-17,0	5,1	2,7-7,5	7,1	11	5,8	26	5,3
	CA	11	238,5	187,0-262,0	10,3	5,4-15,2	13,3	11	11,2	26	10,9
M_2	BL	14	17,0	14,5-19,0	7,8	4,6-11,0	7,6	10	5,6	22	6,7
	MD	14	18,6	16,0-20,8	8,8	5,2-12,4	8,3	13	4,5	21	5,5
	CA	14	317,5	232,0-384,0	16,4	9,5-23,3	14,3	11	9,5	21	11,9
M_3	BL	18	16,7	15,0-20,0	8,5	5,5-11,5	9,8	11	5,0	20	6,8
	MD	18	19,5	17,2-23,5	8,8	5,7-11,9	10,2	12	8,4	21	5,2
	CA	18	327,0	273,0-470,0	17,2	11,0-23,4	19,4	10	13,5	20	11,1

A. boisei hypodigm (e.g. KNM-ER 802, 1479, 2607). By proceeding in this manner, from what is known to what is unknown, probable autapomorphies of *A. boisei* have been assembled. These are summarised in Table 1, and further details are provided in Wood (1991). These presumed auta-pomorphies, together with apparently unique combinations of characters possessed by *A. boisei*, have allowed the specimen listed in Table 2 to be identified as the hypodigm of *A. boisei*. This relatively restricted hypodigm of *A. boisei* does not include material others have assigned to *Australopithecus aethiopicus* or *Australopithecus aff. aethiopicus* (Howell, Haesaerts and de Heinzelin 1987; Suwa 1988, 1990). The sample size, mean value, range and coefficient of variation for each of the cranial, mandibular, maxillary dental and mandibular dental variables are given in Tables 3-5.

The overall level of variability of cranial and mandibular variables in the *A. boisei* hypodigm matches that in the *Gorilla* sample (Table 3). Alveolar breadth is one of the few variables that show substantially higher levels in the fossil taxon, but the sample size, three specimens only, is small. Despite the major differences in facial and mandibular form between *Gorilla* and *A. boisei*, generally there is remarkable similarity in variability between the two samples. Turning to the dental data, with one exception, variability in *A. boisei* and the *Gorilla* sample is well-matched. The exception is canine size, for while *Gorilla* exhibits high levels of canine variability, reflecting the strong sexual dimorphism in canine size, in the *A. boisei* hypodigm the samples of between six and nine in number have CV values which are half, or less, those of the *Gorilla* sample.

DISCUSSION

Attempts to apply phylogenetic analytical techniques to early hominid taxa have demonstrated that *A. boisei* is the most distinctive of the early hominid taxa (Skelton, McHenry and Drawhorn 1986; Chamberlain and Wood 1987; Wood 1991). This distinctiveness has, however, not been sufficient to insulate it from controversy about its taxonomic status. Such problems relate to judgements about the 'degree' of variation which is admissable within the taxon, and one also impinges on a more general discussion about the meaning of palaeontological species (Bown and Rose 1987). The latter debate, concerning the extent to which the *A. boisei* hypodigm should be expanded to embrace all hyper-megadont East African hominids (Walker *et al.* 1986) will not be reviewed here. Nonetheless, it is relevant to comment on the proposals that the main *A. boisei* hypodigm may subsume two species which differ mainly in size. The basis for these proposals are, firstly, the extent of the multivariate mahalanobis D^2 morphological distance between crania included in the *A. boisei* hypodigm, namely KNM-ER 406 and 732 (Bilsborough and Wood 1988), and, secondly, the extent of variation in mandibular corpus size of juvenile (e.g. KNM-ER 1477 and 1820) and adult (e.g. KNM-ER 729 and 1469) mandibles assigned to *A. boisei* (Dean 1988). However, the evidence from the data in table 3 suggests that neither cranial variables, nor dimensions of the adult mandibular corpus, show levels of variability that obviously exceed those in an extant *Gorilla* sample.

The parameters of the *A. boisei* sample given in tables 3-5 can be usefully compared with parameters for *A. africanus* and *A. robustus*. Such comparisons are justified, for while differences in body size is one of the factors known to be correlated with levels of intraspecific variability (Leutenegger and Cheverud 1985), the most recent estimates suggest that the body sizes of the three taxa are similar, with mean values restricted to between 45-50 kg (Jungers 1988; McHenry 1988). When the parameters of the two 'robust' australopithecines are compared, with the exception of the mesiodistal diameter of the I^2, the CV values of *A. robustus* are similar to those of *A. boisei*. These data thus underscore the taxonomic integrity of the *A. robustus* hypodigm, despite the complexities of deposition at the main Swartkrans site of the hypodigm (Brain 1988). These data do not support the claim that *A. robustus* shows unusually low levels of intraspecific, specifically sexually dimorphic, variation (Robinson 1956). Nor do they suggest that the 'degree' of variability within the *A. robustus* hypodigm provides evidence that the taxon subsumes two taxa, *A. robustus* sensu stricto and *A. crassidens* (Grine 1988b). Such claims will need to demonstrate significant morphological distinctions between the two subsets of *A. robustus*.

It has recently also been suggested that the hypodigm of *A. africanus* from Member 4 at Sterkfontein may comprise not one, but two, taxa (Clarke 1988; Kimbel and White 1988). With the exception of some of the diameters of the mandibular incisor teeth (Table 5), there is, however, no evidence that the Sterkfontein Member 4 hypodigm considered in this study is excessively variable, as judged by either fossil, *A. boisei*, or extant, *Gorilla*, reference samples.

CONCLUSIONS

These results suggest that a hypodigm of *A. boisei* cranial, mandibular and dental remains, assembled using morphological criteria, is not excessively variable when compared to a sample of extant *Gorilla* crania. It is proposed that this fossil taxon has greater utility as a comparator for assessing variation within putative early hominid taxa because its orthognathic face and relatively small canines are among the important shared-derived features which distinguish hominids from pongids.

Proposals that what we presently assume to be 'good' palaeontological species samples, *A. africanus* and *A. robustus*, may instead be an amalgam of several species must rest on evidence that the hypodigms in question are excessively variable in either, or both, the 'pattern' and the 'degree' of their variability. When the 'degree' of variability in the two hypodigms is compared with that in *A. boisei*, there is apparently no evidence that the variability they subsume is excessive.

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REFERENCES

BEYNON, A.D. & WOOD, B.A. 1986. Variations in enamel thickness and structure in East African hominids. *Am. J. Phys. Anthropol.*, **70,** 177-193.

---------- 1987. Patterns and rates of enamel growth in the molar teeth of early hominids. *Nature* **326,** 493-496.

BILSBOROUGH, A. & WOOD, B.A. 1988. Cranial morphometry of early hominids I. Facial region. *Am. J. Phys. Anthropol.*, **76,** 61-86.

BOWN, T.M. & ROSE, K.D. 1987. Patterns of dental evolution in early Eocene Anaptomorphine primates (Omomyidae) from the Bighorn Basin, Wyoming. *J. Paleont.*, **61** (2), 1-162.

BRAIN, C.K. 1988. New information from the Swartkrans cave of relevance to "robust" australopithecines. **In:** Grine, F.E., Ed., *Evolutionary history of the "robust" australopithecines,* 311-316, New York, Aldine de Gruyter.

CACCONE, A. & POWELL, J.R. 1989. DNA divergence among hominoids. *Evolution*, **43,** 925-942.

CAIN, A.J. 1954. Animal species and their evolution. London, Hutchinson.

CAMPBELL, B. 1962. The systematics of man. *Nature*, **194,** 225-232.

CAMPBELL, B.G. 1972. Conceptual progress in physical anthropology: fossil man. *Ann. Rev. Anthropol.*, **1,** 27-54.

CHAMBERLAIN, A.T. & WOOD, B.A. 1987. Early hominid phylogeny. *J. Hum. Evol.*, **16,** 119-133.

CLARKE, R.J. 1988. A new *Australopithecus* cranium from Sterkfontein and its bearing on the ancestry of *Paranthropus*. **In:** Grine, F.E., Ed., *Evolutionary history of the "robust" australopithecines,* 285-292, New York, Aldine de Gruyter.

DEAN, M.C. 1988. Growth of teeth and development of the dentition in *Paranthropus*. **In:** Grine, F.E., Ed., *Evolutionary history of the "robust" australpithecines,* 285-292, New York, Aldine de Gruyter.

GEORGE, T.N. 1956. Biospecies, chronospecies, and morphospecies. **In:** Sylvester-Bradley, P.C., Ed., *The species concept in paleontology,* 123-137. London, The Systematics Association.

GRINE, F.E. 1988a. New craniodental fossils of *Paranthropus* from the Swartkrans Formation and their significance in "robust" australopithecine evolution. **In:** Grine, F.E., Ed., *Evolutionary history of the "robust" australopithecines*, 223-243. New York, Aldine de Gruyter.

---------- 1988b. Evolutionary history of the "robust" australopithecines: a summary and historical perspective. **In:** Grine, F.E., Ed., *Evolutionary history of the "robust" australopithecines*, 509-520. New York, Aldine de Gruyter.

HOWELL, F.C., HAESAERTS, P. & DE HEINZELIN, J. 1987 Depositional environments, archaeological occurrences and hominids from Members E and F of the Shungura Formation (Omo Basin, Ethiopia). *J. Hum. Evol.*, **16,** 665-700.

JUNGERS, W.L. 1988. New estimates of body size in australopithecines. **In:** Grine, F.E., Ed., *Evolutionary history of the "robust" australopithecines*, 115-125. New York, Aldine de Gruyter.

KIMBEL, W.H. & WHITE, T.D. 1988. Variation, sexual dimorphism and the taxonomy of *Australopithecus*. **In:** Grine, F.E., Ed., *Evolutionary history of the "robust" australopithecines*, 175-192. New York, Aldine de Gruyter.

LEUTENEGGER, W. & CHEVERUD, J.M. 1985. Sexual dimorphism in primates: the effects of size. **In:** Jungers, W., Ed., *Size and scaling in primate biology*, 33-50. New York, Plenum.

LIEBERMAN, D.E., PILBEAM, D.R. & WOOD, B.A. 1988. A probabilistic approach to the problem of sexual dimorphism in *Homo habilis:* a comparison of KNM-ER 1470 and KNM-ER 1813. *J. Hum. Evol.*, **17,** 503-511.

MCHENRY, H.M. 1988. New estimates of body weight in early hominids and their significance to encephalization and megadontia in "robust" australopithecines. **In:** Grine, F.E., Ed., *Evolutionary history of the "robust" australopithecines,* 133-148. New York, Aldine de Gruyter.

MAYR, E., LINSLEY, E.G. & USINGER, R.L. 1953. *Methods and Principles of Systematic Zoology*, 1-328. New York, McGraw-Hill.

MIYAMOTO, M.M., SLIGHTOM, J.L. & GOODMAN, M. 1987. Phylogenetic relations of humans and African apes from DNA sequences in the un-globin gene. *Science*, **238,** 369-373.

MIYAMOTO, M.M., KOOP, B.F., SLIGHTOM, J.L., GOODMAN, M. & TENNANTS, M.R. 1988. Molecular systematics of higher primates: geneological relationships and classification. *Proc. Nat. Acad. Sci.*, **85,** 7627-7631.

PILBEAM, D. 1972. T*he ascent of man. An introduction to human evolution*. London, Collier Macmillan.

---------- 1978. Recognising specific diversity in heterogeneous fossil samples. **In:** Jolly, C., Ed., *Early hominids of Africa*, 505-515. London, Duckworth.

PILBEAM, D. & VAISNYS, J.R. 1975. Hypothesis testing in paleoanthropology. **In:** Tuttle, R.H., Ed., *Paleoanthropology. Morphology and Paleoecology*, 3-13. The Hague, Mouton.

ROBINSON, J.T. 1956. The dentition of the australopithecinae. *Mem. Trans. Mus.*, **9.**

SAITOU, N. 1991. Reconstruction of molecular phylogeny of extant hominoids from DNA sequence data. *Am. J. Phys. Anthropol.*, **84,** 74-85.

SCHULTZ, B.B. 1985. Levene's test for relative variation. *Syst. Zool.*, **34,** 449-456.

SIBLEY, C.G. & AHLQUIST, J.E. 1984. The phylogeny of the hominoid primates, as indicated by DNA-DNA hybridization. *J. Mol. Evol.*, **20,** 2-15.

---------- 1987. DNA hybridization evidence of hominoid phylogeny: results from an expanded data set. *J. Mol. Evol.*, **26,**99-121.

SIMPSON, G.G. 1961. *Principles of Animal taxonomy*, 1-247. New York, Columbia University Press.

SKELTON, R.R., MCHENRY, H.M. & DRAWHORN, G.M. 1986. Phylogenetic analysis of early hominids. *Curr. Anthropol.*, **27,** 21-43.

SOKAL, R.R. & BRAUMANN, C.A. 1980. Significance tests for coefficients of variation and variability profiles. *Syst. Zool.*, **29,** 50-66.

SOKAL, R.R. & ROHLF, F.J. 1987. *Introduction to biostatistics* (2nd Ed), 1-363. New York, Freeman.

SUWA, G. 1988. Evolutiion of the "robust" australopithecines in the Omo succession: evidence from mandibular premolar morphology. **In:** Grine, F.E., Ed., *Evolutionary history of the "robust" australopithecines*, 199-222. New York, Aldine de Gruyter.

--------- 1990. *A comparative analysis of hominid dental remains from the Shungura and Usno Formations, Omo Valley, Ethiopia.* Unpublished PhD thesis, University of California, Berkeley.

SYLVESTER-BRADLEY, P.C. 1956. *The species concept in palaeontology*, 1-145. London, The Systematics Association.

TOBIAS, P.V. 1967. *Olduvai Gorge, Volume 2. The cranium and maxillary dentition of Australopithecus (Zinjanthropus) boisei.* Cambridge, Cambridge University Press.

WALKER, A., LEAKEY, R.E., HARRIS, J.M. & BROWN, F.H. 1986. 2.5 Myr *Australopithecus boisei* from west of Lake Turkana, Kenya. *Nature*, **322,** 517-522.

WEIDENREICH, F. 1946. Generic, specific and subspecific characters in human evolution. *Am. J. Phys. Anthropol.*, **4,** 413-431.

WOLPOFF, M.H. 1978. Analogies and interpretation in palaeonanthropology. **In:** Jolly, C.J., Ed., *Early hominids of Africa*, 461-503. London, Duckworth.

WOOD, B.A. 1991. *Koobi Fora research project. Volume 4: Hominid cranial remains.* Oxford, Clarendon Press.

WOOD, B.A. & ABBOTT, S.A. 1983. Analysis of the dental morphology of Plio-Pleistocene hominids. I. Mandibular molars – crown area measurements and morphological traits. *J. Anat.*, **136,** 197-219.

WOOD, B.A., ABBOTT, S.A. & GRAHAM, S.H. 1983. Analysis of the dental morphology of Plio-Pleistocene hominids. II. Mandibular molars – study of cusp areas, fissure pattern and cross-sectional shape of the crown. *J. Anat*, **137**, 287-314.

WOOD, B.A., ABBOTT, S.A. & UYTTERSCHAUT, H. 1988. Analysis of the dental morphology of Plio-Pleistocene hominids. IV. Mandibular postcanine tooth morphology. *J. Anat.*, **156,** 107-139.

WOOD, B.A. & ENGLEMAN, C.A. 1988. Analysis of the dental morphology of Plio-Pleistocene hominids. III. Mandibular premolar crowns. *J. Anat.* **161,** 1-35.

WOOD, B.A. & XU, Q. 1991. Variation in the Lufeng dental remains. *J. Hum. Evol.*, **20,** 291-311.

WOOD, B.A., YU, L. & WILLOUGHBY, C. 1991. Intraspecific variation and sexual dimorphism in cranial and dental variables among higher primates and their bearing on the hominid fossil record. *J. Anat.*, **174,** 185-205.

ZWELL, M. & PILBEAM, D.R. 1972. The single species hypothesis, sexual dimorphism, and variability in early hominids. *Yb. Phys. Anthropol.*, **16,** 69-79.

Palaeont. afr., **28**, 79-81 (1991)

THE CONTRIBUTION OF ALUN R. HUGHES TO THE EARLY DEVELOPMENT OF CAVE TAPHONOMY: A TRIBUTE

by

C.K. Brain

Transvaal Museum, Pretoria

As a new direction in science crystallises into a recognised discipline, it is easy to overlook early seminal contributions, innovative and pioneering at their time, on which accepted conceptual structures were later built. More than 30 years ago, Alun Hughes made significant contributions of this kind to the field now known as cave taphonomy. The purpose of this brief tribute is to ensure that Hughes' part in the launching of the now fashionable field of taphonomy is not overlooked.

It was Raymond Dart's preoccupation with the bone rich grey breccia at Makapansgat Limeworks, and the dramatic conclusions he drew from the study of the contained fossil assemblage, that precipitated two decades of animated debate on the behaviour of australopithecines. From 1948 onwards, Dart produced a stream of highly provocative papers on the predatory nature of early hominids, claiming that australopithecines in southern Africa had not only been highly effective hunters but also murderous cannibals (Dart 1948, 1949a, b, 1953, 1956, 1957). He further argued that this instinctive behaviour was crucial to the understanding of aggressive tendencies in contemporary humans. As was clearly Dart's intention, these assertions provoked a spirited response from many people, including myself, and promoted the emergence of taphonomy as a discipline, based securely on observation and experimentation.

The acquisition of a fossil bone assemblage from the Makapansgat Limeworks breccia, running to over 7 000 specimens, was made possible by the systematic sorting of the Limeworks dumps by Hughes and his colleagues over a nine year period, starting in 1948. Fossiliferous blocks of breccia were then subjected to mechanical preparation in a major palaeontological operation supervised by Hughes. This project demonstrated Hughes' competence both in the field and the laboratory, – a dual ability abundantly confirmed in subsequent years.

The Makapansgat Limeworks collection represented the first complete fossil assemblage ever to have been extracted from an African early hominid site and the interpretation of the assemblage was a pioneering and unprecedented effort by Dart. Guidelines in fossil assemblage interpretation were few at that time and Dart came to the firm conclusion that most, if not all, of the very numerous fossil bones in the lower levels of the Limeworks cave had been collected there by hominids, who selected them for their potential usefulness as tools.

For more than a century it had been customary to attribute large bone accumulations in caves to spotted hyaenas (*Crocuta crocuta*), following an excavation conducted in 1921 by William Buckland (1823) at Kirkdale cave in Yorkshire which revealed vast numbers of hyaena remains, together with teeth of hippopotamus and other animals. He concluded that the cave had served as a hyaena lair during antediluvian times and that the layer of mud that covered the remains had been laid down in the cave by waters of the biblical deluge.

The concept of the bone-accumulating hyaena was vigorously challenged by Hughes (1954a, b) who solicited opinions from wildlife authorities and undertook a study of modern spotted hyaena lairs. He visited the farm Mala Mala, close to the Kruger National Park where he thoroughly investigated two lairs. One consisted of a series of nine antbear holes, the vicinity of which had been virtually cleared of vegetation by the trampling of hyaenas. Hughes excavated one of the tunnel systems and found that it covered a surface area of 13 m by 5 m, descending to a depth of almost 2 m. Although the tunnels had clearly been used as a hyaena breeding lair, they were empty except for a single tortoise carapace. Outside the entrance to the lair were four chewed bones and one set of hyaena droppings.

The second lair at Mala Mala consisted of a low shelter under an outcrop of granite. It too was empty, although a few broken bones, a tortoise shell and some droppings were found outside it.

In his search for additional evidence, Hughes (1958) also investigated four spotted hyaena lairs in the Kalahari Gemsbok National Park. These consisted of two hyaena resting places beneath calcrete outcrops along the Auob River, both of which were devoid of bones or droppings, and two similar breeding lairs. No bones were found inside either lair, although two chewed springbok horns lay outside the first and 18 bones and horns outside the second.

On the basis of his observations, Hughes was able to conclude that, in normal circumstances, spotted hyaenas do not accumulate impressive collections of bones in their cave lairs, although it has been found subsequently that some items are occasionally brought back (Brain 1981). It now appears likely that the striking bone accumulations in British caves, such as Kirkdale and Tornewton, may have resulted from the fact that hyaenas were forced to take refuge in such places during severe winters and that many died and were eaten by their fellows on such occasions (Sutcliffe 1969).

The fossil assemblage that Hughes and his colleagues extracted from the Makapansgat Limeworks breccia contained the remains of many *Hyaena hyaena* individuals, living representatives of which still survive further north in Africa and Asia Minor as the striped hyaena. As early as 1961 Hughes recognised the need to study the habits of striped hyaenas and to establish whether these included bone-accumulating tendencies. With a grant from the Wilke Foundation he therefore visited East Africa in 1961 with the purpose of locating and examining the contents of striped hyaena lairs (Hughes 1961). The project was logistically difficult however and Hughes wrote: "if it is to be proved that striped hyaenas carry bones to and accumulate them in their lairs, then it is necessary for further investigations to be conducted into the habits of striped hyaenas". Following Hughes' advice, such studies have, in fact, been carried out, particularly in Israel (Skinner, Davis and Illani 1980).

It has been positively established that *Hyaena hyaena* is a highly significant collector of bones in its feeding and breeding lairs and that the Makapansgat Limeworks cave may very well have served as such a lair three million years or so ago.

The investigation made by Hughes of spotted hyaena lairs in the Kalahari Gemsbok National Park had an unexpected and highly significant by-product: it showed that porcupines are perhaps the most important of all bone-collecting agents in African caves. Unlike hyaenas, porcupines are not carnivores, but they have the habit of collecting dry bones and other objects in their lairs, and of gnawing them at their leisure. The habit appears to have a dual purpose: that of wearing back the constantly growing incisors and of providing a phosphate supplement to their diets.

In 1956 Hughes located two porcupine lairs in the calcrete banks of the Auob River, from which he recovered 90 and 57 bones respectively, noting that over 70% of each assemblage had been porcupine-gnawed. He also made a collection of 1420 bones and other objects from a porcupine lair in the calcrete bank of the Nossob River, in the south of the Kalahari Gemsbok National Park and kindly made this collection available to me for further study. I was able to return to the site 12 years after it had been cleared of bones by Hughes and recovered a further 380 objects (including an empty gin bottle with porcupine tooth marks on its screw-top!), establishing that the rate of bone collecting was about 32 bones per year at this particular locality. Other conclusions drawn from these Kalahari porcupine-collected assemblages suggested that the bones hoarded in the lairs mirror, in a crude way, the natural abundance of animal species in the area; that the porcupines select larger bones as favoured gnawing objects and that they have a very decided preference for dry and naturally defatted bones (Brain 1981). These and other well established conclusions about porcupine bone-collecting are now part of the source-literature on cave taphonomy and they owe their origin to the early insights of Alun Hughes.

For the last 25 years or so, Hughes has been preoccupied with the excavation of the Sterkfontein site under the general direction of Professor P.V. Tobias. This undertaking, carried out in the meticulous Hughes tradition, has provided a wealth of significant hominid and other fossils (e.g. Hughes and Tobias 1977), together with highly significant insights into the nature of the cavern itself and its contents. For me, one of the particular pleasures and privileges of my palaeontological sojourn at Swartkrans, over the same period and just across the valley from Sterkfontein, has been my regular weekly contacts with Alun Hughes, who I have come to respect and admire as the unfailing and unassuming gentleman of palaeo-anthropology.

ACKNOWLEDGEMENT

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REFERENCES

BRAIN, C.K. 1981. *The Hunters or the Hunted? An Introduction to African Cave Taphonomy*. Chicago, University of Chicago Press.

BUCKLAND, W. 1823. *Reliquae Diluvianae; or Observations on the organic remains contained in cave fissures, and other diluvial gravel and on other geological phenomena attesting to the action of a universal deluge*. (2nd Ed.), London, Murray.

DART, R.A. 1948. An adolescent promethian australopithecine mandible from Makapansgat. *S. Afr. J. Sci.*, **45,** 73-75.

---------- 1949a. The predatory implemental technique of *Australopithecus. Am. J. Phys. Anthrop.* n.s. **7,** 1-38.

---------- 1949b. The bone-bludgeon hunting technique of *Australopithecus. S. Afr. J. Sci.*, 2: 150-152.

---------- 1953. The predatory transition from ape to man. *Int. Antrop. Ling. Rev.* , **1**(4), 201-218.

---------- 1956. Cultural status of the South African man-apes. *Smithsonian Report* No. 4240, 317-318.

---------- 1958. The Osteodontokeratic Culture of *Australopithecus prometheus.Transvaal Museum Memoir*, **10.**

HUGHES, A.R. 1954a. Habits of hyaenas. *S. Afr. J. of Sci.*, **51,** 1456-158.

---------- 1954b. Hyaenas versus australopithecines as agents of bone accumulations. *Am. J. Phys. Anthrop.* **12**(4), 467-486.

---------- 1958. Some ancient and recent observations on hyaenas. *Koedoe* **1,** 105-114.

---------- 1961. Further notes on the habits of hyaenas and bone gathering by porcupines. *Zoological Society of Southern African* News Bulletin, **3**(1), 35-37.

HUGHES, A.R. & TOBIAS, P.V. 1977. A fossil skull probably of the genus *Homo* from Sterkfontein, Transvaal. *Nature*, **265** (5592), 310-312.

SKINNER, J.D., DAVIS, S. & ILLANI, G. 1980. Bone collecting by Striped Hyaenas, *Hyaena hyaena*, in Israel. *Pal. afr.*, **23**, 99-104.

SUTCLIFFE, A.J. 1969. Adaptations of spotted hyaenas to living in the British Isles. *Mammalogy Society Bulletin* **31,** 1-4.

Palaeont. afr., **28**, 83-85 (1991)

ALUN R. HUGHES : PUBLICATIONS AND REPORTS

1946	A.R. Hughes	Report on a comparison of inorganic fertilizers and compost on natural pastures in South Africa. Department of Botany, University of the Witwatersrand, Johannesburg.
1949	R. Broom and A.R. Hughes	Notes on the fossil baboons of Makapan Caves. *S. Afr. Sci.,* 2 (9), 194-196.
1952	A.R. Hughes	A new reconstruction of the Springbok Flats skeleton. (Read at Town Congress of the South African Association for the Advancement of Science.)
1953	A.R. Hughes and J.K.G. Grieves	Medium grade microcephaly in a Bantu family. *S. Afr. J. Med. Sci.,* 18, 19-30.
1954.	A.R. Hughes	Habits of hyaenas. *S. Afr. J. Sci.*, 51(5), 156-158. (Read at Bloemfontein Congress of the South African Association for the Advancement of Science).
1954.	A.R. Hughes	Hyaenas versus australopithecines, as agents of bone accumulation. *Am. J. Phys. Anthropol.*, 12(5), 467-486.
1955.	M.J. Toerien and A.R. Hughes	The limb bones of Springbok Flats Man. *S.Afr. J. Sci.,* 53(5), 125-128.
1957	A.R. Hughes	Rock slides, burials and ancestral worship in the Transvaal. *S. Afr. Arch. Bull.*, 12(47), 102-107.
1958	A.R. Hughes	Some ancient and recent observations on hyaenas. *Koedoe*, Journal of Scientific Research in National Parks, South Africa, No. 1.
1961	A.R. Hughes	Further notes on the habits of hyaenas and bone gathering by porcupines. *Zoological Society of Southern Africa News Bulletin,* 3(1), 35-37.
1961	A.R. Hughes	Report on visit to East Africa in January 1962, for the purpose of studying the habits of striped hyaenas.
1963	A.R. Hughes	Report on a visit to the Town Lands of Barberton from 31 March to 1 April 1963.
1964	A.R. Hughes	Report on a visit to the Makapansgat Limeworks from 22 to 25 July 1964, accompanied by the Inspector of Mines, Pretoria.
1964	A.R. Hughes	Report of a meeting held at the Umfolozi Game Reserve on 4 March 1964 to discuss the proposed complete investigation of the White Rhinoceros.
1964	A.R. Hughes	Report on four visits to the Makapansgat Limeworks during April, June and July 1964, for the purpose of removing the loose material in decalcified pockets in the Upper Phase I Breccia at the Limeworks.
1964	A.R. Hughes	Report on coprolites from Late Stone Age cave site (Scotts Cave) in the Gamtoos Valley.
1965	A.R. Hughes	Some observations on hyaenas and porcupines. (Presented to Anatomy Colloquium, University of the Witwatersrand, Johannesburg.)

1966	A.R. Hughes	Progress report on preparation for excavations at Sterkfontein, 31 December 1966 to 17 August 1977.
1967	A.R. Hughes and P.V. Tobias	Report on new excavations at Sterkfontein. Detailed progress report for period July 1966 to August 1967.
1968	A.R. Hughes	Report on coprolites from Later Stone Age Site Melkhoutboom in the Zuurberg.
1968	P.V. Tobias and A.R. Hughes	Some problems connected with the Sterkfontein Site.
		Progress report on activities from 1966-1968.
1968-1970	A.R. Hughes	Various reports on purchase and to sub-division of the farm Swartkrans. Also on the fencing at Makapansgat Limeworks and the Cave of Hearths.
1968-1991	P.V. Tobias and A.R. Hughes	Annual Reports on the Palaeo-anthropology Research Unit and its predecessors, Palaeon-anthropology Research Unit and Department of Anatomy, University of the Witwatersrand, Johannesburg.
1969	A.R. Hughes	Confidential report on meeting of Mineral Baths Board of Trustees of the Transvaal Provincial Administration held on farm Makapansgat, Potgietersrus district.
1969	A.R. Hughes and P.V. Tobias	The new Witwatersrand excavation at Sterkfontein. Progress report, some problems and first results. Presented to meeting of Quaternarists, convened by the Royal Society of South Africa and the Council for Scientific and Industrial Research, Cape Town, February 1969.
1969	A.R. Hughes	The Springbok Flats Skull. (Read at Durban meeting of Anatomical Society of South Africa.)
1969	P.V. Tobias and A.R. Hughes	The new Witwatersrand University excavation at Sterkfontein. *S. Afr. Arch. Bull.*, 24(3 & 4), 153-169.
1970	A.R. Hughes	The Springbok Flats Skull. *S.A. Med. J.*, 1 May 1970, p. 536.
1975	P.V. Tobias and A.R. Hughes	Report to the Bernard Price Institute for Palaeontological Research on Work at Sterkfontein and Makapansgat and related studies, August 1974 to August 1975.
1975	A.R. Hughes	The mode of accumulation of the bones in the Makapansgat Limeworks grey breccia. *Nyame Akuma*, 7, p. 43.
1976	P.V. Tobias and A.R. Hughes	Report to the National Monuments Council on the progress of the work at Sterkfontein and Makapansgat during 1975.
1977	A.R. Hughes and P.V. Tobias	A fossil skull probably of the genus *Homo* from Sterkfontein, Transvaal. *Nature*, 265 (5592), 310-312.
1977-1990	A.R. Hughes	Various reports to National Monuments Council, C.S.I.R. and University Council Research Committee.
1979	A.R. Hughes	SASQUA Meeting – read paper on comparison of recent bones damaged by porcupines and fossil bones recovered from Member 3, Makapansgat Limeworks.

1985	A.R. Hughes and P.V. Tobias	Wits Anatomy Department and Hunterian Museum. **In:** Maguire, J., Ed., *Taung Diamond Jubilee International Symposium: Excursions Handbook*, 6 - 7. Johannesburg, University of the Witwatersrand.
1985	P.V. Tobias and A.R. Hughes	Sterkfontein. **In:** Maguire, J., Ed., *Taung Diamond Jubilee International Symposium: Excursions Handbook*, 8-14. Johannesburg, University of the Witwatersrand.
1990	A.R. Hughes	The Tuinplaas human skeleton from the Springbok Flats, Transvaal. **In:** Sperber, G.H., Ed., *From Apes to Angels: Essays in Anthropology in Honor of Phillip V. Tobias*, 197-214. New York, Wiley-Liss, Inc.
1991	T.C. Partridge, P.V. Tobias and A.R. Hughes	Paléoécologie et affinités entre les australopithécines d'Afrique du Sud: nouvelles données de Sterkfontein et Taung. *L'Anthropologie*, Paris 95:363-378.

IN PRESS

T.C. Partridge, A.R. Hughes	The Sterkfontein formation: new perspectives on distribution and stratigraphy with special reference to the provenance and age of the hominid remains and the affinities of some recent hominid specimens. *Proceedings of IInd International Congress of Human Palaeontology*, Turin, Italy. September 28 to October 3 1987.

PENDING

A.R. Hughes	A method of cataloguing an extensive anatomy teaching and research museum collection.
A.R. Hughes	A list of birds of the Makapansgat Valley.
A.R. Hughes	A porcupine lair in the Nossop River.
A.R. Hughes	An Amazizi burial near Cathedral Peak.
A.R. Hughes	A comparison between bones damaged by porcupines and the damaged bones recovered from the Makapansgat grey breccia.
M. Toussaint, G.A. Macho, A.R. Hughes and P.V. Tobias	A new Plio-Pleistocene partial human skeleton from Sterkfontein, Transvaal.

(Compiled by P.V. Tobias, H. White and V.E. Strong, 1991)

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Examples of reference citations

ANDERSON, H.M. 1976. *A revision of the genus* Dicroidium *from the Molteno Formation*. Unpublished PhD thesis, University of the Witwatersrand, Johannesburg.

------ & ANDERSON, J.M. 1970. A preliminary review of the biostratigraphy of the uppermost Permian, Triassic and lowermost Jurassic of Gondwanaland. *Palaeont. afr.*, **13**, 1-22.

VAN DER MERWE, N.J., LEE-THORP, J.A., THACKERAY, J.F., HALL-MARTIN, A., KRUGER, F.J., COETZEE, H., BELL, R.H.V., & LINDEQUE, M. 1990. Source-area determination of elephant ivory by isotopic analysis. *Nature* **346**, 744-746.

CROMPTON, A.W. 1962. On the dentition and tooth replacement in two bauriamorph reptiles. *Ann. S. Afr. Mus.*, **46**(9), 231-255.

ROMER, A.S. 1966. *Vertebrate Palaeontology* (3rd Ed.). Chicago, University of Chicago Press.

------ 1973. Permian reptiles. **In:** Hallam, A., Ed., *Atlas of Palaeobiogeography*, 159-168. Amsterdam, Elsevier.

HOPSON, J.A. & BARGHUSEN, H.R. 1986. An analysis of therapsid relationships. **In:** Hotton, N., P.D. MacLean, Roth, J.J. & Roth, E.C., Eds, *The ecology and biology of mammal-like reptiles*, 159-168. Washington, Smithsonian Institution Press.

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When referring to them in the text the word Table should be spelled out in full and given a capital initial letter, e.g. Table 2.

Illustrations

All illustrations are termed Figures, (the word is to be spelled out in full with a capital initial letter and they are numbered consecutively with arabic numerals. Each illustration should bear in pencil on the reverse side the author's name, a key word(s) from the title, the figure number and the word "top" in the appropriate position to indicate orientation. Authors should mark the position of figures by pencil notation in the margin of the text.

When referring to Figures in the text the word is spelled out in full with a capital initial letter, e.g. Figure 3.

All artwork should be submitted ready for the camera. The use of dry transfer lettering is preferred and stencil or hand lettering is to be avoided. Graphic scale indicators are preferred in all artwork where a scale is appropriate.

Drawings, maps and diagrams should be in black drawing ink on translucent drawing film, high quality tracing paper or good quality white card. They should be designed for same-size printing or slight reduction (by no more than 1/3) in the final form. The maximum acceptable size for illustrations on the printed page is 245 mm x 175 mm. Tip-ins and fold-outs are not accepted except under very special circumstances.

Photographs should be high quality glossy prints of good contrast made from critically focused negatives, and similar constraints on size apply as in the case of drawings.

Authors should submit the original of each figure plus 2 xerox copies.

Numerical data

The metric system (SI units) is to be used throughout for all numerical data. If for some good reason units other than metric are used, the SI metric equivalents should also be given in parentheses. Authors should familiarise themselves with the correct abbreviation of SI metric units.

ACCEPTANCE OF PAPERS

All manuscripts offered to the Editor are submitted to two or more referees for critical appraisal, and the substance of the referees' comments are forwarded to the author in the event that the manuscript is rejected or requires revision. The Editor will advise the author whether or not the manuscript is accepted for publication.

If the manuscript is accepted, galley proofs will be submitted to the author for careful checking and these must be returned as soon as possible. The cost of any additions or major alterations to the text at proof stage may be charged to the author. Further proofs may be submitted to the author if the Editor judges it to be necessary or desirable.

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Papers presented in honour of
ALUN RHUN HUGHES
on his 75th birthday,
to mark a lifetime of dedicated service to palaeoanthropology