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ANNALS OF THE BERNARD PRICE INSTITUTE FOR
PALAEONTOLOGICAL RESEARCH
UNIVERSITY OF THE WITWATERSRAND
JOHANNESBURG

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PREFACE

On 26 October 1995 the Bernard Price Institute for Palaeontological Research celebrated 50 years of palaeontological endeavour. To celebrate this important milestone, the Institute hosted a 1-day symposium. Fourteen speakers, all leaders in their field of palaeontological endeavour, were invited to give review papers on aspects of palaeontology in which the Institute has played an important developmental role. A feature of the symposium was that each of these palaeontologists has had a close association with the BPI, as a student, member of staff, or member of the Board of Control.

AFTERNOON

DR DICK RAYNER	Cretaceous fossils from the Gaps Diamond Mine
PROF PHILLIP TOBIAS	Some little known fossils from the Karoo
PROF JAMES KITCHING	Assessing the biology of fossil vertebrates
DR BOB BRAIN	The contribution of the Karoo to palaeontology
DR ANDRÉ KEYSER	The role of fossils in palaeontology

Symposium Programme

MORNING

PROF FRIEDEL SELLSCHOP
OPENING ADDRESS

DR BRUCE RUBIDGE
The BPI – 50 years of palaeontological activity

PROF JAMES KITCHING
What was known about Karoo stratigraphy in 1945?

DR ROGER SMITH
Interpreting Karoo palaeoenvironments from sediments and bones

DRS HEIDI & JOHN ANDERSON
Karoo palaeobotanical advances in the last 50 years

DR CHRIS GOW
The quest for the origin of mammals

DR ANUSUYA CHINSAMY
Physiological implications of fossil bone microstructure

DR COLIN MACRAE
Answers blowing in the wind – contributions of palynology to Karoo geology

DR ROSEMARY FALCON
From fossils to fire – the BPI's role in the development of coal research

MR JOHN HANCOX
The role of fossils in interpreting development of the Karoo basin

AFTERNOON

DR DICK RAYNER
Cretaceous fossils from the Orapa Diamond Mine

PROF PHILLIP TOBIAS
Early chapters in the history of the Makapansgat fossil hominid site

PROF JAMES KITCHING
Reminiscences of excavations at Makapansgat

DR BOB BRAIN
The contribution of Raymond Dart to the development of cave taphonomy

DR ANDRÉ KEYSER
From Makapansgat to Drimolen – new discoveries in palaeo-anthropology

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Figure 1: Dr Bernard Price – benefactor of the Institute.

the Department of Zoology. This led to the "Bernard Price Institute for Palaeontological Research" in 1946, and ultimately in February 1949, the Bernard Price Institute for Palaeontological Research, which was administered by a Board of Control with Professor van der Horst as both Chairman and Honorary Director of the Institute. After the death of Bernard Price in 1942 his son Bernard (Robbie) was elected a member of the Board of Control and still serves in that capacity to this day. On the sudden death of Professor van der Horst he was succeeded as chairman by the Head of the Department of Zoology, Professor T.W. Orver, and Dr S.H. Houghton is member of the Board since 1947) became the Honorary Scientific Director. Dr Basil Cooke, who is a palaeontologist of international repute, was also involved in the initial setting up of the Institute, now heading as Chairman of the Board of Control.

Brain not only planned the road that led to the establishment of the BPI, but also staffed it with one of

THE BPI – 50 YEARS OF PALAEOONTOLOGICAL ACTIVITY

by

Bruce S. Rubidge

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ABSTRACT

The Bernard Price Institute for Palaeontological Research at the University of the Witwatersrand was established from an endowment made by Bernard Price in 1945. Now, a mere 50 years later, the Institute ranks as a prominent palaeontological research centre in Africa. It curates large collections of fossils including Karoo reptiles, mammals from the Makapansgat valley and other Plio-Pleistocene sites, invertebrates from the Bokkeveld and Zululand, and has a large palaeobotany herbarium. The Institute produces the journal *Palaeontologia africana*, the only journal in Africa dedicated to the publication of palaeontological papers. The BPI is closely affiliated to the Department of Palaeontology and Palaeoenvironmental Studies, the only department of palaeontology at a South African University. During the 50 years of its existence the BPI has played an important role in the advancement and dissemination of palaeontological knowledge in southern Africa.

KEYWORDS: Bernard Price Institute, University of the Witwatersrand

INTRODUCTION

On 26 October 1995 the Bernard Price Institute celebrated 50 years of palaeontological endeavour, a milestone that owes its origins to the infectious enthusiasm of one of South Africa's greatest scientists combined with the foresight of a generous Johannesburg philanthropist. *"In 1897 there arrived in Cape Town the man who was to change the face of South African palaeontology. Robert Broom, a*

medical doctor intensely interested in fossil mammal-like-reptiles, had come to South Africa" (Cluver & Barry 1977 p325). Broom changed the face of South African palaeontology in many ways. In 1945, while employed at the Transvaal Museum, he presented a lecture at the University of the Witwatersrand stressing the need for the collection and preservation of Karoo fossils. Fortuitously, Bernard Price, at that time Managing Director of the Victoria Falls Power Company, was present and responded to Broom's plea by agreeing to provide £2000 annually, on condition that the fossil material collected be curated by the University of the Witwatersrand. Immediately a small "Committee of Palaeontology" was established under the chairmanship of Professor C.J. van der Horst, Head of the Department of Zoology. This led to the "Bernard Price Foundation for Palaeontological Research" in 1946, and ultimately in February 1949, the Bernard Price Institute for Palaeontological Research, which was administered by a Board of Control with Professor van der Horst as both Chairman and Honorary Director of the Institute. After the death of Bernard Price in 1948 his son Bernard (Bobby) was elected a member of the Board of Control and still serves in that capacity to this day. On the sudden death of Professor van der Horst he was succeeded as chairman by the Head of the Department of Geology, Professor T.W. Gevers, and Dr S.H. Haughton (a member of the Board since 1947) became the Honorary Scientific Director. Dr Basil Cooke, now a geologist and palaeontologist of international repute, was also involved in the initial setting up of the Institute, later serving as Chairman of the Board of Control.

Broom not only planted the seed that led to the establishment of the BPI, but also staffed it with one of

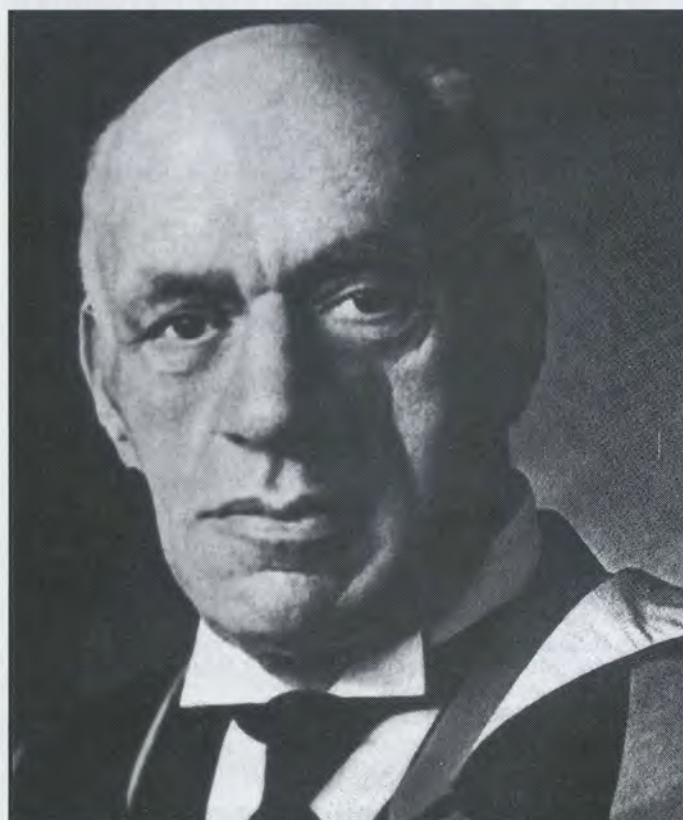


Figure 1: Dr Bernard Price – benefactor of the Institute.

his protégés. In 1912 he had met up with Croonie Kitching, an overseer of road construction in the Graaff-Reinet and Nieu Bethesda districts, and together they collected fossils in that area. Croonie in turn encouraged three of his sons (James, Ben and Scheepers) in this skill. Following Broom's advice, on 26 October 1945 the young James Kitching, recently returned from military service in Italy, was appointed as the first member of staff of the BPI in the joint capacity of Field Officer and Laboratory Technician. Such was the drive and enthusiasm of Kitching to collect fossils that five days later, on 1 November, he set off by train to the Graaff-Reinet district where he had grown up and which he

knew intimately. Despite being rationed to only 45 litres of petrol per month and having to use his mother's car, Kitching succeeded in collecting more than 200 well-preserved fossils during the first trip. Since then the BPI and James Kitching have been synonymous and he has undertaken many more field trips to the Karoo. From records at the BPI it is evident that James has spent some 216 months in the field in the Karoo alone, a cumulative period of more than 18 years (Table 1). In addition James Kitching spent many months at Makapansgat excavating the Cave of Hearths, and collecting fossil mammals from the Limeworks site.

Until the early 1940s the most important

TABLE 1.
Some collecting trips of J W Kitching (from 1952 to 1989 he was accompanied by R Huma)

Nov 1945 - March 1946	Graaff-Reinet with B J Kitching. 200 therapsid skulls.
Oct 1946 - Feb 1947	Karoo with B J, S C Kitching. 474 therapsid skulls.
Nov 1948 - Feb 1949	Murraysburg, Graaff-Reinet.
March 1949	Bethulie, Burgersdorp, Murraysburg, Beaufort West with D M S Watson (London University).
1950 - 1958	Regular trips of 3-4 months to Beaufort Group.
1954	Harrismith and eastern Free State. Dinosaurs collected.
1955 (3.5 months)	Burgersdorp, Murraysburg, Graaff-Reinet, Beaufort West, Aberdeen, Victoria West. 300 specimens.
July 1956	Bergville, Estcourt. <i>Lystrosaurus</i> , <i>Thrinaxodon</i> specimens.
Oct - Nov 1956	Burgersdorp, Cathcart, Leeu-Gamka, Beaufort West, Victoria West, Murraysburg, Aberdeen, Morgan Bay, Bulwer and Impendhle. 360 specimens.
1957	Harrismith, Oliviershoek, Golden Gate.
Sept - Oct 1958	Impendhle, Bulwer, Dordrecht, Burgersdorp, Murraysburg with Manten (geologist from Utrecht, Holland). On one farm in the Murraysburg district a slab containing 40 amphibian skulls and skeletons was unearthed.
June 1958	Oliviershoek Pass, Bergville, Harrismith.
Jan - Feb 1959	Murraysburg with A S Brink, Stebbins (University of California). 50 amphibian skulls.
July - Oct 1963	Upper Luangwa Valley Zambia with A R Drysdall.
1961 (3 months)	Throughout Karoo with N. Hotton III (Smithsonian Institute, Washington). 200 skulls.
1961 (4 months)	Luangwa Valley Zambia with A R Drysdall.
1962 (1 month)	Lesotho (Elliot & Clarens Formations) with E Jarvik (Sweden), K A Kermack (University College, London).
1962 (2 months)	Beaufort Group with E Jarvik (Sweden), D Sigogneau (Institut de Paléontologie, Paris). 98 specimens.
1962	Traverse through Karoo with E H Colbert (American Museum of Natural History, New York). 100 specimens.
June - Aug 1963	Upper Luangwa Valley Zambia. Combined expedition of the Natural History Museum and University of London (J Attridge, A Charig, B Cox).
Sept 1963	Bergville with E P Plumstead, Haas (Jerusalem).
1964 (2 months)	Karoo excursion with R Parrington (Cambridge University), N Hotton III, (Smithsonian Institute, Washington).
May 1964	Graaff-Reinet, Middelburg with N Hotton III (Smithsonian).
1964	Springfontein.
Aug - Oct 1965:	Gariep Dam. 410 Karoo vertebrates, 800 mammals from archaeological excavations. Material placed in National Museum, Bloemfontein.
1966 (2 months):	Van der Kloof Dam. 553 specimens.
1967	Victoria West, Richmond, Gariep Dam with C S Churcher.
1970 (6 months)	Antarctica.
1971	Harrismith, Clarens, Thaba N'chu.
1972	Graaff-Reinet, Aliwal North, Rouxville. 20 specimens.
1973	Graaff-Reinet, Pearston with R Carroll (Redpath Museum, Canada). 28 skulls.
Oct 1973	Harrismith, Bergville with 4 Japanese geologists.
1974 (2 weeks)	Etjo Mountain & Otjiwarongo, Namibia with A R I Cruickshank, A W Keyser. 30 well preserved therapsids and archosaur fragments.
1974 (Sept - Oct)	Victoria West, Pearston, Graaff-Reinet, Rouxville with M Kitching. 180 specimens.
1975 (May)	Harrismith, Oliviershoek Pass with A R I Cruickshank, J Cosgriff (Wayne State University)
1975 (Nov)	Pearston with J Brown, B Turner.
1978	Bethlehem, Fouriesburg with J A Hopson, A Busbey (University of Chicago), J W A van Heerden, M J Nyaphuli (National Museum, Bloemfontein).
1980	Ficksburg, Clocolan.
1982	Prince Albert with B Rubidge, M J Nyaphuli (National Museum, Bloemfontein).
1983	Clocolan, Ladybrand with M A Raath & B S Rubidge (National Museum, Bloemfontein).
1984 (2 months)	Barkly East, Lady Grey with C E Gow, F Durand.
1990	Kestel, Paul Roux, Senekal with J P Welman (National Museum, Bloemfontein), G Groenewald (Golden Gate National Park).
1990	Maclear with M A Raath (Port Elizabeth Museum), R Shone, G Rossouw (University of Port Elizabeth).
1991	Laingsburg with B S Rubidge & M J Nyaphuli (National Museum, Bloemfontein), M A Raath (Port Elizabeth Museum), R M H Smith, A Crean, P October (S A Museum, Cape Town).
1992 (1 week)	Aliwal North, Burgersdorp, Sterkstroom with P J Hancox, B S Rubidge.
1992 (8 weeks)	Laingsburg.
1993 (4 weeks)	Laingsburg, part of the time with L Freeman, E Latimer, R Lewis, P Mukanela, J Nyaphuli, B Rubidge.
1993 (6 weeks)	Murraysburg, Aberdeen
1994	Senekal, Zastron, Aliwal North, Burgersdorp with M Shishkin, (Palaeontological Institute, Moscow), B S Rubidge, P J Hancox.

palaeontological collections in South Africa were housed at the South African Museum in Cape Town, the Albany Museum in Grahamstown, the National Museum in Bloemfontein and the Transvaal Museum in Pretoria. Today however the BPI is also an important palaeontological centre in South Africa. From initial accommodation in a small army hut, the Institute has continued to expand and has outgrown three different buildings through the years. Today the BPI houses a large collection of fossils including Karoo reptiles and amphibians, invertebrates from the Bokkeveld, Zululand and the Sundays River Valley, and mammals from Kalkbank and the Makapansgat Limeworks and Cave of Hearths sites. It also has the largest palaeobotany herbarium in Africa, and a comparative collection of modern vertebrates.

Plio-Pleistocene Research

Price was so impressed by the large number of fossils collected by James Kitching during the first six months of operation that, with the prompting of Professor Raymond Dart, he doubled the fund of £2000 to broaden the scope of research to include the Plio-Pleistocene fossils from the Makapansgat caves near Potgietersrus.



Figure 2: Raymond Dart preparing fossils. Photo: A.R. Hughes

As this operation required more manpower, James' brothers, Ben and Scheepers, were appointed initially to assist with the excavation of the Cave of Hearths archaeological site and later to undertake the huge task of sorting through dumps of fossiliferous breccia left by the limeworkers. From discoveries at the Limeworks site, Dart pioneered taphonomic studies in South Africa and developed his famous theory of the "osteodontokeratic (O.D.K) culture" of the australopithecines, an idea that was to play an important part in the development of modern ideas of cave taphonomy (see Brain this volume). Since 1945 the BPI has been involved with research on the various cave sites on the farm "Makapansgat". Members of staff such as Brian and Judy Maguire have made important scientific contributions in the development of this site.



Figure 3: Sorting through limeworker's dumps at Makapansgat in search of fossils in 1949.

Archaeological sites were also researched by the Institute. In 1946 James and Ben Kitching assisted B D Malan with excavations at the Stone Age site of Rose Cottage Cave at Ladybrand, and in 1957 more than 3200 bone specimens (associated with Middle Stone Age lithic artefacts) from an open site at Kalkbank near Pietersburg were prepared and studied by Dart and Kitching. Bone breakage patterns from this Middle Stone Age site and the Makapansgat Limeworks osteodontokeratic material were compared. At one time the Kalkbank accumulation was considered to confirm Dart's osteodontokeratic hypothesis.

During 1947 it became necessary to establish a collection of modern vertebrate skulls and skeletons which could be used as a framework of comparison for the study of fossils. Although numerous specimens had been added to this collection in the formative years, largely through the efforts of Kitching while on his extended field excursions, the first serious attempt to build up this collection was undertaken in 1957 by Kitching and Alun Hughes of the Medical School when they paid a visit to the Zaka district of Zimbabwe. Here they collected skeletons of crocodiles, waterbuck, kudu, buffalo and elephant which were being culled under government authority. At a later stage a large collection of leopard, hyena, baboon and rhebok skulls and other material was collected through the efforts of Brian and Judy Maguire, with the co-operation of the Morea Estates, a private nature reserve near Klaserie in the



Figure 4: Initiation of the building of the research house at Makapansgat, November 1947.



Figure 5: Stalwarts of Makapan, Alun Hughes (left), Gordon Peppercorn (centre), James Kitching (right), reminiscing at the retirement function for James Kitching in 1990.

eastern Transvaal. Today this collection, which includes skeletal material of numerous rare mammals and reptiles, is a most useful asset and is used extensively by archaeologists, palaeontologists, palaeo-anthropologists and zoologists for a variety of research projects.

SIDNEY H HAUGHTON – DIRECTOR 1949-1974

In 1949, Sidney Haughton, the recently retired Director of the Geological Survey of South Africa and member of the Board of Control of the Institute, was appointed honorary director. During the latter half of the same year A S (Ian) Brink, who had recently obtained his doctorate at London University, was appointed as the



Figure 6: Sidney Haughton – first director of the Institute.

Institute's first scientific officer. He published extensively on the morphology and taxonomy of Karoo fossils.

Because of the ever-expanding fossil collections gathered from both the Karoo and various sites at Makapansgat, storage space became an increasing problem in the little wooden military hut on the corner of Yale and Jorissen Streets. In 1952 the Institute moved into two larger huts which had previously been occupied by the Oral and Dental Hospital of the University. The BPI was again later to outgrow its premises and accommodation problems were overcome in 1963 when the University offered Douglas Smit House, which had formerly been a student residence. The Institute now had ample space for the storage of growing collections, a library, laboratories, lecture rooms, and the nucleus of a museum which served the dual interests of students and the public.

One of the most time-consuming and important tasks in palaeontology is the careful preparation of fossil material from the surrounding rock so that it can be researched. Initially this was undertaken largely by the Kitching brothers themselves. In 1946 Piet Huma, who had previously prepared fossils for Broom, was appointed as the first full time preparator at the BPI. The following year he was joined by his son Regent (Lukas) who later accompanied James Kitching on all his collecting expeditions to the Karoo, loyally serving the Institute in this capacity for 42 years until his retirement in 1989. As the amount of fossil material in the collections increased, swelled in particular with fossils



Figure 7: Brian Maguire photographed at the Makapansgat research house in 1960. *Photo: A.R. Hughes*



Figure 8: The old "milk van", the first field vehicle of the BPI with James Kitching "rebooting" behind.

from the Makapansgat Limeworks, a growing need for even more assistance with fossil preparation arose. In the early 1950s Dart obtained money from the Wilkie Foundation and the CSIR and employed up to ten preparators to extract fossil bones from the growing collection of Limeworks material. The increased number of preparators eased the bottleneck of unprepared material and allowed for speedier access to fossils by researchers.

Dart retired from the Chair of Anatomy at the Medical School in 1957 and was offered rooms and a laboratory at the BPI to continue his work. Later, during 1965, Drs Edna P Plumstead, a palaeobotanist of international repute, and George F Hart, a micropalaeontologist, transferred from the Geology Department to the BPI, and so the research interests of the Institute were broadened to include: Karoo vertebrates (A S Brink), palaeobotany (E P Plumstead), micro-palaeontology (G F Hart), and Quaternary research (R A Dart).

Until this stage, palaeobotanical research had not been undertaken by the BPI, but with Plumstead and the large palaeobotanical collection from the Geology Department, this field of research became an important function, and Brink's dream of uniting all branches of palaeontology under one roof were realised.

The fossil plant collections inherited from the Geology Department included a large collection donated by the late Dr T L Leslie, and the much larger Le Roux collection from the rocks of the Ecca Group near Vereeniging. At the BPI this collection was maintained and extended by Plumstead and her students Ann Anderson, John Anderson and Heidi Anderson (nee Schwyzer), Anna Malleeson (nee Beneke), Judy Maguire, Shirley Smithies, and Rosemary Falcon. From 1975-1977 the herbarium was curated by Dr J T Brown, a graduate from the University of Montana, who was the palaeobotanist. During the 1980s this task was undertaken by Dr R J Rayner, with the assistance of his students Marion Bamford, Ian McKay and Saskia Waters. During this time extensive collections of fossil plants and insects from Cretaceous crater lake deposits at Orapa, Botswana were made.

Plumstead was invited to study the first plant fossils collected in Antarctica by members of the British Trans-

Antarctic expeditions of 1955-1958: she demonstrated that identical plant fossils were found in Antarctica, South America, South Africa, India and Australia, and so convinced a still-sceptical scientific community that the ancient continent of Gondwana had indeed once existed.

Hart resigned in 1966 to take up a post at the University of Louisiana in the USA, and was succeeded by Dr R J Davey of Nottingham and Sheffield Universities, who was appointed as a CSIR Fellow. After Ian Brink resigned to assume the Directorship of the Museums of Man and Science in Johannesburg in 1965, Arthur Cruickshank, a graduate of Cambridge University, was appointed deputy director in 1967. In the same year John Anderson joined the staff as a palynologist to examine borehole cores for SOEKOR, who were then involved in petroleum exploration in the Karoo. Judy Maguire was appointed part time lecturer and undertook taphonomic research at Makapansgat. Soon afterwards Chris Gow was appointed research officer, and undertook research initially on *Milleretta* and later on early diapsids. Brian Turner became the sedimentologist on the staff, and pioneered modern sedimentological techniques on the rocks of the Karoo.

In 1970 South Africa hosted the second meeting of the I.U.G.S. Sub-commission on Gondwana Stratigraphy and Palaeontology, and the BPI staff played a prominent role in the organisation of this event. Many international scientists took part and participants from all over the world still recall the unique week-long geological and palaeontological excursion across the Karoo attended by 150 delegates.

Kitching's reputation as a fossil hunter spread far and wide. One of the highlights of his illustrious career was being invited in 1970 to accompany the United States Antarctic Research Group. Here he discovered numerous fossils of *Lystrosaurus* Zone age – thus providing corroborative palaeontological evidence for the close correlation between Antarctica and South Africa during Gondwanan times. At this stage James Kitching was still very active with fieldwork in the Karoo, and his son Matthew, who was also gifted with the talent of spotting fossils in the field, joined the



Figure 9. James Kitching (left) and Ian Brink sharing famous Kitching field cuisine on Hoeksplaas, Murraysburg, in 1952.

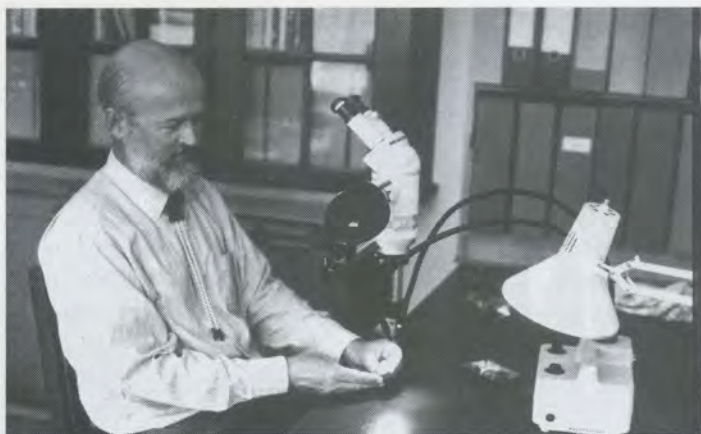


Figure 10: Chris Gow examining the second *Megazostrodon* specimen discovered near Clocolan.

Institute in 1974 as a field assistant to his father, a position he filled with distinction until he transferred to the Geology Department in 1976.

With growing numbers of staff and students in the late 1960s and resultant increased research activity, the collections grew rapidly and accommodation once again became a problem. In 1971 building extensions to Douglas Smit House commenced to include a laboratory for SOEKOR researchers, and stores for Karoo fossil reptiles, Makapansgat material, and a palaeobotanical herbarium.

STANLEY P JACKSON – DIRECTOR 1974-1978

Sidney Haughton retired as director in 1974, and was succeeded by Stanley Jackson as the first full-time director. Professor Jackson, who had retired as Deputy Vice-Chancellor the previous year, and had previously been head of the Geography Department, was thoroughly familiar with the innermost workings of the University. He established a formal teaching and research structure at the Institute, and integrated the activities of the BPI with those of other departments on campus.

During Jackson's directorship the Institute joined the University interdepartmental programme on coal research, and Dr Rosemary Falcon was appointed to establish a coal petrography laboratory. The palaeontology section of SOEKOR moved into the ground floor of the Douglas Smit Building in 1974, thus providing yet another area of expertise. This mutually beneficial arrangement lasted until 1986 when SOEKOR moved its headquarters to Cape Town.

During 1977 the Institute hosted a two day symposium on Karoo Palaeontology, attended by delegates from South Africa and Zimbabwe. At this gathering, one of the few palaeontological meetings organised in South Africa up until that stage, the idea of establishing a Palaeontological Society of Southern Africa took root. The idea had been conceived by Dr Jacques van Heerden of the National Museum, Bloemfontein, and the 1977 symposium gave it the impetus needed to become a reality. The PSSA has since gone from strength to strength and over the years various members of the BPI staff have played leading roles in it.

MICHAEL A RAATH – DIRECTOR 1978 - 1987.

In 1978 Mike Raath was appointed Director and at the same time Head of the newly established Department of Palaeontology and Palaeoenvironmental Studies, the only Department of this type at a South African University.

Up to that time most Karoo research done by the BPI had centred on mammal-like-reptiles and plants. The arrival of Raath, whose primary research interest was dinosaurs, stimulated research on these creatures and a field programme to collect fossils from the "Stormberg" rocks in the Free State and Eastern Cape was launched and maintained by Kitching.

Under Raath's guidance the BPI emerged as an important teaching department at the University. He was also involved in establishing a unified School of Earth Sciences, of which he was the first chairman. Raath brought out from Paris Professor Armand de Ricqlès, a palaeo-bone histologist of international repute, in order to set up a bone histology laboratory.

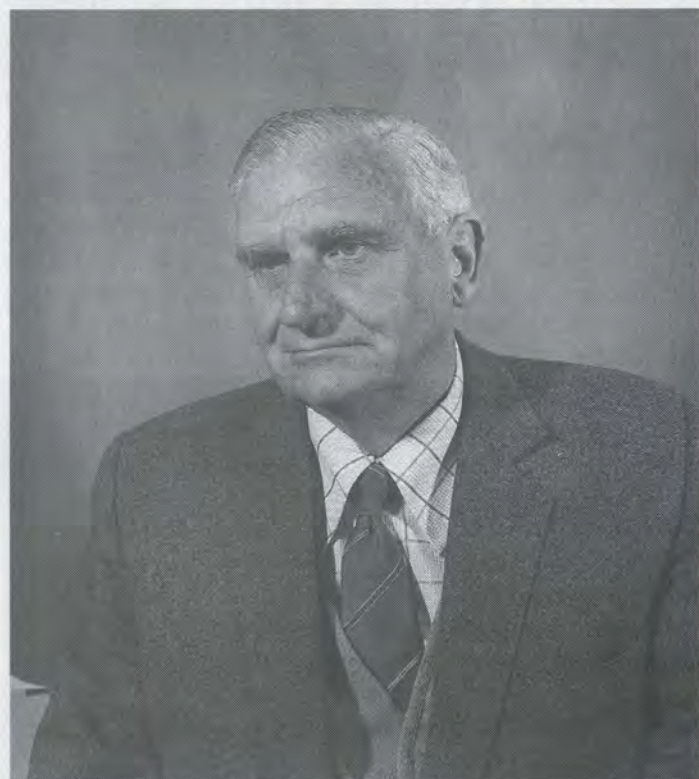


Figure 11: Stanley Jackson, second director of the Institute

In 1983 Dr R J (Dick) Rayner, a graduate of the University College of Cardiff, was appointed palaeobotanist to curate the large and important palaeobotanical herbarium. Soon afterwards the BPI was approached by the Orapa Mine in Botswana to study the rich fossil flora from the Cretaceous crater-lake deposits at the mine. Rayner encouraged several students to research the remarkable fossil flora and arthropod fauna from this locality.

Early in the 1980s the University acquired the Showgrounds of the Witwatersrand Agricultural Society when they moved premises to NASREC in Johannesburg. This solved some major accommodation



Figure 12: James Kitching (left), Edna Plumstead, Raymond Dart and Mike Raath at the combined celebration of Dart's 90th birthday and the 60th anniversary of his announcement of the discovery of *Australopithecus*.

problems on the old "East Campus" as many of the exhibition halls could now be occupied by University departments. The building vacated by the Maintenance Department on the East Campus was allocated to be shared by the Archaeology Department and the Bernard Price Institute (Palaeontology). The task of planning for this move landed on Raath's shoulders while he was on sabbatical leave, forcing him to return to duty. With the assistance of James Kitching the plans were put into effect and the move successfully carried out with almost no damage to any of the thousands of fossils in the huge collections.

The building into which the Institute moved in 1985, since named the van Riet Lowe Building, was co-incidentally situated on the site of the original army hut where the BPI Palaeontology had started four decades earlier. The Institute had gone full circle, but now it returned with more staff and a large collection of priceless fossils. Because of the large size and the sheer weight of the fossil collections, let alone their delicate nature, this move was extremely disruptive to research and teaching activities. Although the Institute now had less space for its various activities, the new location on the East Campus next to the BPI Geophysics building ensured that it was more centrally positioned and accessible to students.

JAMES W KITCHING – DIRECTOR 1987-1990.

Professor James Kitching, who had been Deputy Director since 1979, became Acting Director when Mike Raath resigned to take up the directorship of the Port Elizabeth Museum and Oceanarium in 1987. Kitching was able to consolidate the BPI in its new premises in the van Riet Lowe Building because, although the Institute had been physically moved by the time Raath left, there was still a great deal of sorting out

of the collections to do. The re-establishment of these collections was a priority and occupied much of Kitching's time. Even so, he was able to fulfil his teaching obligations and undertake some fieldwork. During this period he and Johann Welman of the National Museum in Bloemfontein established that the *Cynognathus* Zone, the youngest biozone of the Beaufort Group, was present in the northern part of the Karoo Basin, and not restricted only to the south. This discovery had important implications for interpreting the depositional history of the rocks of the upper Beaufort Group (Hancox & Rubidge, this volume).

During the directorship of Kitching several projects were completed. Anusuya Chinsamy, now a palaeo-bone histologist, completed her PhD study initiated under Raath to study the bone histology of the South African dinosaurs *Massospondylus* and *Syntarsus*. This was the first time that histological studies had been carried out on dinosaur bone in South Africa.

BRUCE S RUBIDGE – DIRECTOR 1990-

James Kitching retired in May 1990 after 45 years of dedicated service to the University. Bruce Rubidge, previously Head of the Palaeontology Department of the National Museum in Bloemfontein, was appointed his successor as Director of the Institute and at the same time Head of the Department of Palaeontology and Palaeoenvironmental Studies. Kitching was allocated working space at the BPI and appointed Honorary Research Professorial Fellow. Retirement to Kitching made no difference to his great palaeontological productivity and in the five years that he has been retired he still diligently works in his office and on the collections every day.

Since 1990, South Africa has emerged from political isolation, making it possible once more to set up

collaborative programmes with palaeontologists from other countries and so increase the research productivity of the Institute. In 1993 and 1994 Dr David Dilkes, recently graduated from the University of Toronto, spent 18 months at the Institute as a postdoctoral fellow researching fossil rhynchosaur from the Beaufort Group. Dr Michael Shishkin from the Palaeontological Institute in Moscow spent five months at the BPI as a W D Wilson travel Fellow researching fossil amphibians from the *Lystrosaurus* and *Cynognathus* Zones of the Beaufort Group.

Dr Anusuya Chinsamy was appointed to a contract lecturing position in the Department of Palaeontology and Palaeoenvironmental studies for two years. Because of the demand for contract research work to be undertaken for industry, Drs Marion Bamford (palaeobotanist) and Ann Cadman (palynologist) also joined the staff. The number of postgraduate students has increased, and so too the number of research projects the Institute has been able to undertake.

Two facilities which were present in the Douglas Smit building were set up in the van Riet Lowe Building. The re-establishment of the palynology laboratory in 1991 has proved its worth in the number of contract research projects undertaken from this laboratory, as well as a training facility for postgraduate students. In 1993 the Palaeontology Museum was re-established under the guidance of principal technician Richard Lewis and artist Imogen Berry, recently retired from the Transvaal Museum. This facility has been a great asset in creating an awareness of, and interesting students in, the palaeontological wealth of South Africa.

During 1992 the BPI hosted the 8th Biennial Conference of the Palaeontological Society of Southern Africa. Despite the important involvement of the Institute in the establishment of this Society, largely through the efforts of Raath and Kitching, this was the first meeting of the Society to be hosted by the Institute. More than 70 delegates attended, making this the largest gathering of the PSSA to be held to date.

Apart from its research and teaching legacy, "the strengths of the Institute lie in the fields in which it has worked since its inception. Its collections are known and respected in palaeontological circles around the world; they undoubtedly provide an international scientific resource of considerable standing and significance" (Raath 1986, p18). The steady stream of visiting scientists since 1949 to undertake research on

specimens in the various collections bears testimony to their international importance. Recently, with the assistance of student helpers Grigor Aitken, Heidi Fourie, John Hancox, Elizabeth Latimer and Michael Raum, much attention has been given to the curation of, the remarkable collections, and great progress has been made in transcribing the catalogues onto computer database.

The BPI has now reached its half century; apart from its research activities, it has become a valuable teaching department in the University, and curates a fine collection of fossils. It has also distributed high quality casts of important specimens to institutions worldwide. In addition it produces the only African journal dedicated to the publication of palaeontological papers. *Palaeontologia africana* first appeared in 1953 under the editorship of Sidney Haughton and continued under Mike Raath. More recently produced under the guidance of an editorial panel with Bruce Rubidge as editor and Chris Gow and Dick Rayner as associate editors and a panel of international consulting editors, it is now into its 32nd volume.

CONCLUSION

This brief summary of activities of the BPI highlights the important role that the staff and students of the Institute have played in the advancement and dissemination of palaeontological knowledge in southern Africa. This is illustrated by the fact that four scientists who have been employed by the Institute; Sidney Haughton, Edna Plumstead, James Kitching and Rosemary Falcon, have been awarded the Draper Memorial Medal of the Geological Society of S.A. - The highest award of this society for contributions to the development of Earth Sciences in South Africa.

During its 50 years of existence the Bernard Price Institute for Palaeontological Research has achieved international standing as an important centre of active palaeontological teaching and research. It is also the custodian of a large part of the palaeontological heritage of South Africa.

ACKNOWLEDGEMENTS

The author, a relative newcomer to the BPI, is indebted to numerous people for endless discussions on the past history of the BPI, and for reading the numerous previous drafts of this manuscript. In particular I wish to thank John and Heidi Anderson, Chris Gow, James Kitching, Colin MacRae and Mike Raath. Basil Cooke and Judy Maguire are thanked for the effort they put into critically reading the manuscript.

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INTRODUCTION

Three distinct phases in the 170-year history of head-plate collecting and research in South Africa can be discerned. Each lasted close on 50 years. The second history here described is drawn from Anderson & Anderson (1983), as a part of the floral and faunal data collected for the Middle Tertiary and Tertiary Formations. The purpose of that earlier work, besides continuing the history of palaeontological collecting in South Africa, was to provide a full systematic revision and documentation of all pre- and Cenozoic fossil plants in the country. Most of the botanical and plant data from those of the Middle Tertiary were collected by us and plant were further worked. All available collections from the country were studied and re-examined. The work on the Middle Tertiary and Tertiary formations, and relatively little has been added on the Tertiary and Cenozoic floras.

Recognition phase (1845-1945)

The first period of activity may be traced to Charles Lyell's *Principles of Geology* (1830-33), generally regarded as the most influential text in the history of geology. With the denunciation of catastrophism and

the popularisation of Hutton's uniformitarianism, it opened the way for a great flowering of geology and palaeontology not only in Britain but throughout the colonies and overseas. Andrew Geddes Burt, who was building frontier roads in the south-eastern Cape, started to read a copy of the book in 1837 and became through all the years of South Africa's geology and palaeontology.

It is Richard Nathaniel Rubidge (nephew of Bruce Rubidge, current director of the Bernard Price Institute), through, who takes credit for making the earliest collection (in 1845) of fossil plants in the country. These came from the Early Cretaceous Doodfontein locality in the Alphen Basin near Port Elizabeth. Further collections of this period, including William Albertson, George Saw, Alfred 'Gloag' Fraser and Thomas Lewis, amongst others, were nearly all British, often being well-known doctors, all were self-taught amateurs in natural history. They were gentlemen with much remarkably diverse scientific interests and were not only well-read but also well-informed in the history of the South African continent. Their collections were small, and the part that was described was not regarded for the purpose.

TOWARDS NEW PARADIGMS IN PERMO-TRIASSIC KAROO PALAEOBOTANY (AND ASSOCIATED FAUNAS) THROUGH THE PAST 50 YEARS

by

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ABSTRACT

Advances through the past 50 years (1945 to 1995) have shown, indisputably, that the Permo-Triassic Karoo flora (with associated insect faunas) is as important globally as is the famous tetrapod fauna. We justify this in regard to the three most productive horizons: the Middle Ecca (Early to Middle Permian), Estcourt Formation (Late Permian) and the Molteno Formation (Late Triassic).

The Middle Ecca gained international prominence through the collections of Le Roux from 1946 to 1955 and the publications of Plumstead from 1952 to 1962, which demonstrated for the first time a wide suite of fructifications found attached to *Glossopteris* leaves. Similar finds have subsequently been made throughout the rest of the Gondwana Permian. The Glossopteridales remain unique among fossil gymnosperm orders in yielding such a diverse range of articulated (organically attached) foliage/fruit material.

The Estcourt Formation offers an unparalleled opportunity to study ecosystems of the Late Permian prior to the extinction event terminating the period. The formation is singular in that it yields an excellent, well known flora and insect fauna (sampled primarily by van Dijk from 1957 to 1984 and Benceke, Anderson and Anderson from 1969 to 1971) in conjunction with a diverse tetrapod fauna.

The Molteno Formation provides a window onto Late Triassic plant and insect communities, at around the time of origin of the mammals, dinosaurs and birds, perhaps unrivalled elsewhere in the world. The extensive/intensive collections of the Molteno (made by Anderson and Anderson over nearly 30 years from 1967 to the present) allow the application of a statistical projection hinting at the extraordinary possibility of biodiversities akin to those of today. The gymnosperms of the Late Triassic may well have been as rich in species and orders as are the extant angiosperms (flowering plants).

KEYWORDS: Karoo, Permo-Triassic, megaf flora, insects, tetrapods, biodiversity.

INTRODUCTION

Three distinct phases in the 150-year history of fossil-plant collecting and research in South Africa can be discerned. Each lasted close on 50 years. The skeletal history here sketched is drawn from Anderson & Anderson (1985), as is most of the floral and faunal data outlined for the Middle Ecca and Estcourt Formations. The purpose of that earlier work, besides outlining the history of palaeobotanical collecting in South Africa, was to provide a full taxonomic revision and documentation of all pre mid-Cretaceous fossil floras in the country. Most traceable localities, aside from those of the Molteno, were revisited by us and many were further sampled. All available collections around the country were studied and incorporated. Our work on the Molteno has advanced considerably since, but relatively little has been added on the Ecca and Estcourt floras.

Reconnaissance phase (1845-1895)

This first period of activity may be traced to Charles Lyell's *Principles of Geology* (1830-33), generally regarded as the most influential text in the history of geology. With the denunciation of catastrophism and

the popularisation of Hutton's uniformitarianism, it opened the way for a great flowering of geology and palaeontology not only in Britain but throughout the colonies and elsewhere. Andrew Geddes Bain, who was building frontier roads in the south-eastern Cape, chanced to read a copy of the book in 1837 and became (at age 40) the father of South African geology and palaeontology.

It is Richard Nathaniel Rubidge (ancestor of Bruce Rubidge, current director of the Bernard Price Institute), though, who takes credit for making the earliest collection (in 1845) of fossil plants in the country. These came from the Early Cretaceous Dunbrody locality in the Algoa Basin near Port Elizabeth. Further collectors of this period, including William Atherstone, George Stow, Alfred 'Gogga' Brown and Thomas Leslie, amongst others, were nearly all British, often they were medical doctors, all were self-taught amateurs in natural history. They were Renaissance men with remarkably diverse interests who flourished in and fostered the intellectual climate of the frontier towns. Collections remained small, and the part that was described was sent overseas for the purpose.

Transitional phase (1895-1945)

The Geological Commission of the Cape of Good Hope was instituted in 1895 to 'organise, control and direct the work of geological exploration and survey...'; and it ushered in a new era of palaeontology with a new character. The period is marked by the efforts of six men in particular: William Anderson, A.W. Rogers, E.H.L. Schwarz, A.L. Du Toit, S.H. Haughton and E.D. Mountain. All six were British or British trained and in marked contrast to the amateur enthusiasts of the earlier period, all were fully-trained professional geologists, though none were specialist palaeobotanists. They were the pioneers of systematic geological mapping in the country and their palaeobotanical collecting was mostly incidental.

Palaeobotanical research in the first half of the century was very largely taxonomic and still based on relatively small collections from few localities. Aside from Alexander Du Toit, who delved systematically into the fossil plants of the Karoo, most of this descriptive work was completed by overseas specialist palaeobotanists such as Sir Albert Charles Seward and Hugh Hamshaw Thomas, both of Cambridge, and Ove Arbo Høeg of Oslo, Norway.

Post-war phase (1945-1995)

This third phase of palaeobotanical research coincides precisely with the fifty-year history of the Bernard Price Institute (BPI) and, in large measure, is directly linked to the Institute. Dr Edna Plumstead, of international renown, was the key figure and inspiration during the first half of this phase, whilst her post-graduate students, most enduringly Heidi and John Anderson, and a subsequent generation at BPI, Dick Rayner and Marion Bamford, took over in the later quarter century. The roles of researchers from other institutes, such as van Dijk (University of Natal, Pietermaritzburg) and Kovács-Endrödy (Geological Survey, Pretoria); from overseas, notably Kräusel (Senckenberg Museum, Germany), Townrow (Reading University, England and later Tasmania); and of independents, most importantly Le Roux of Vereeniging, are however significant.

A marked growth and widening of palaeobotanical activity is witnessed. Intensive collecting from many clearly-defined localities or taphocoenoses (TCs) plays an increasingly significant role. Whilst taxonomic studies still, by necessity, form the foundation of research, far more interest is given to palaeoecology, palaeogeography, palaeobiology, evolutionary theory and biodiversity trends. Interdisciplinary research and co-operative projects with an international flavour become more and more the pattern.

Though the emphasis in this paper is palaeobotanical, we summarise current knowledge on the major faunal groups, the insects and tetrapods, for the three formations discussed. This is in line with the rapidly increasing interest in evolutionary palaeoecology both in Karoo studies and globally. Evolution is a process based on the synergy between all plants and animals

and their ever-changing physical environment. Our previously independent disciplines can no longer stand alone.

THE MIDDLE ECCA (E. – M. PERMIAN)

Significance

The Glossopteridales, by far the most prominent group of plants through the Gondwana Permian, invariably play a significant role in the cladistic analysis of the gymnosperms and the origin of the angiosperms (Crane 1985, 1988). They remain unique among fossil gymnosperm orders in yielding a morphologically diverse range of fruit borne directly on foliage. It was in the Middle Eccla beds of the northern Karoo Basin that this major discovery was first made and publicised: through the collections of Le Roux (1946-1955) and the papers of Plumstead (1952-1962). A wide suite of taxa within the order, showing similarly attached material, has since been unearthed through all the Gondwana continents.

Stratigraphy

With the melting of the Dwyka ice and for the duration of deposition of the Eccla Group, there developed an extensive, essentially non-marine epicontinental sea across the greater part of South Africa. Deltas and coal swamps characterised the northern margin of the sea, in the former northern Orange Free State (OFS), southern Transvaal and northern Natal, during the regressive Middle Eccla phase of deposition. The Middle Eccla (Vryheid Formation) attains its fullest development of 425m in the Vryheid area where it comprises a clear regressive cycle: delta front to delta with coal swamps to delta front. This arenaceous formation wedges out southwards into the typical carbonaceous siltstones of the Lower and Upper Eccla.

History of collecting

The earliest plant collections from the Middle Eccla – some 200 slabs in total – were made by George William Stow in 1878, David Draper from c.1890 to 1895 and Thomas Nicolas Leslie from c.1892 to 1904. It was Stow who first discovered the coalfields (Vereeniging included) in the northern Orange Free State and adjoining Transvaal and correctly interpreted their regional setting. A long interval followed before Le Roux initiated his extensive collecting from various sites in the Vereeniging district in 1941.

The Vereeniging Brick & Tile Company carried out large-scale quarrying of refractory shales (2 quarries) on the farm Leeukuil, 4 km south west of Vereeniging, between 1946 and 1952. Le Roux frequently visited these two quarries, and a third earlier one in the near vicinity, during this interval and made comprehensive systematic collections (Le Roux & Anderson 1977). He made the seminal discovery at these quarries in 1949/50 of the now famous fructifications found attached to the midrib of *Glossopteris* leaves. The recognition of their significance persuaded Plumstead to shift her research interests from coal petrology to palaeobotany.

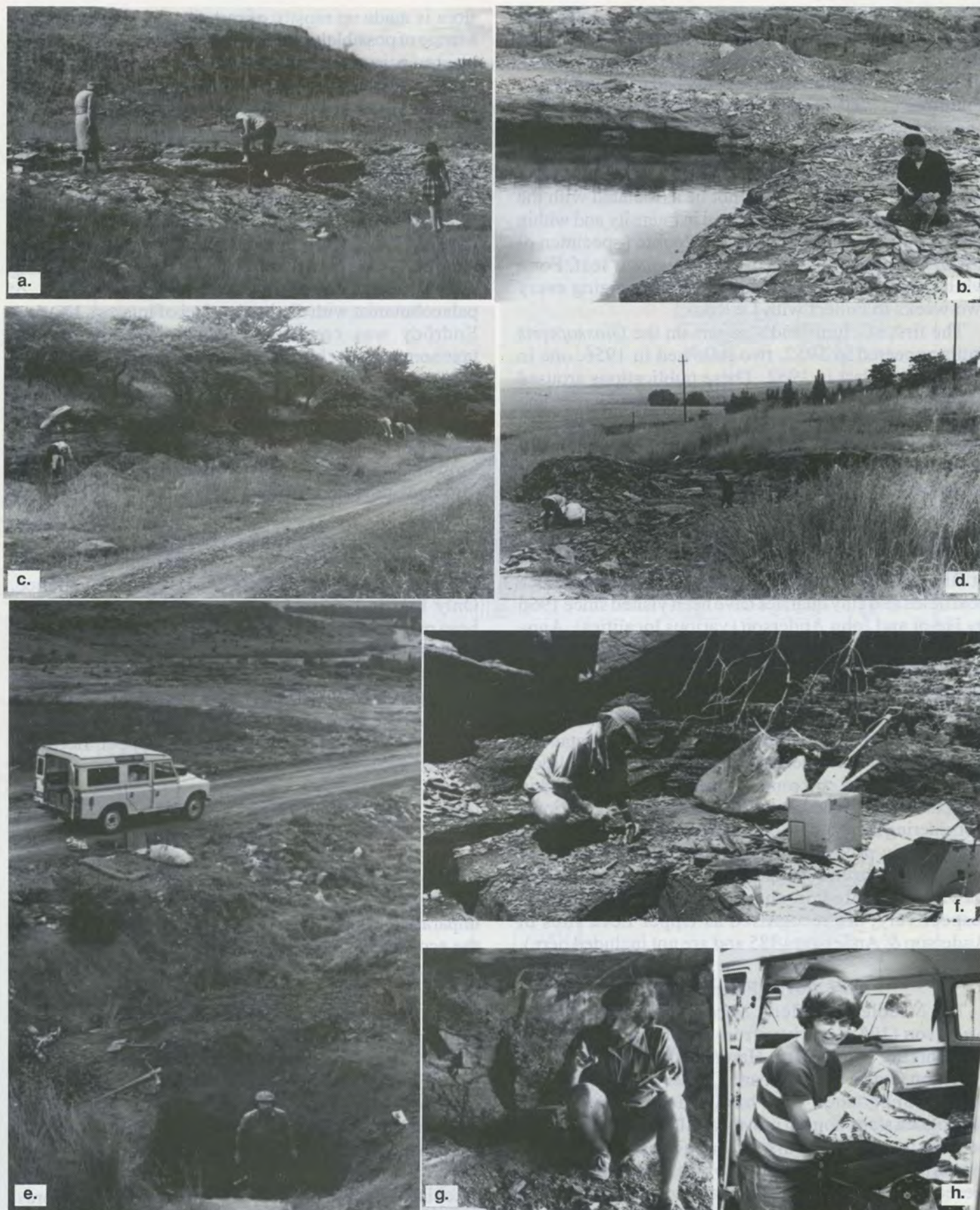


Figure 1 a-h. Collecting Karoo plants. **a.** Middle Ecra, E/M. Permian; Vereeniging (Ver 111), at Leeukuil Quarry. Left to right: Edna Plumstead, Anna Benecke, Shirley Dickinson. Photo by HMA, 30/4/1969. **b.** Middle Ecra, E/M. Permian; Hammanskraal (Ham 111), N. of Pretoria. Eva Kovács-Endrödy cleaving slabs. Photo by HMA, July 1973. **c.** Estcourt Formation, L. Permian; Rondedraai, near Estcourt (Est 211). Left to right: Ann Anderson, Anna Benecke, John Anderson, Mr Green. Photo by HMA, 15/12/1969. **d.** Estcourt Formation, L. Permian; Bergville (Ber 111). Left to right: Judy Roets, Brian Maguire, Brian Turner. Photo by HMA, 19/4/1969. **e.** Molteno Formation, L. Triassic; Matatiele (Mat 111). John Anderson excavating. Photo by HMA, 31/7/1982. **f.** Molteno Formation, L. Triassic; "Waterfall locality", Upper Umkomaas (Umk 111). John Anderson cleaving slabs. Photo by HMA, 24/1/1979. **g.** Molteno Formation, L. Triassic; Little Switzerland (Lit 111). John Anderson examining specimens. Photo by HMA, 13/10/1980. **h.** Kombi and 6 metal trunks; our standard procedure for transporting plant fossils. Heidi Anderson unpacking. Photo by JMA, 30/1/1979.

Plumstead first met Le Roux and saw the collection at his Vereeniging home in c.1949. The meeting had been arranged by Mr Leach, a mining engineering student at Witwatersrand University. Le Roux had in his collection a number of well-preserved detached fruits, as well as one specimen of the foliage *Glossopteris retifera* which appeared to have a narrow fruit-like body attached to its midrib. It was mooted whether *Glossopteris*, being dominant in the beds, might not be associated with the fruits. Le Roux's collecting gained in intensity and within a month he discovered the first undoubted specimen of a fruit (*Scutum*) attached to a *Glossopteris* leaf. For a while after that, Plumstead visited Vereeniging every two weeks to collect with Le Roux.

The first of Plumstead's papers on the *Glossopteris* fruits appeared in 1952, two followed in 1956, one in 1958 and the last in 1962. These publications aroused much controversy over morphological interpretation and suggestions on the origin of angiosperms, and established Plumstead's international reputation. It seems a pity that Le Roux did not publish jointly on some of the material, thereby sharing in the world acclaim.

Le Roux, together with Plumstead and her post-graduate students, continued collecting from Vereeniging till 1974: by which date some 2500 slabs, mostly housed at BPI, were available for study. Other Middle Ecca coalfields and clay quarries have been visited since 1966 by Heidi and John Anderson (various localities), Anna Benecke (Vereeniging), Shirley Smithies (Hammanskraal), Eva Kovács-Endrödy (Hammanskraal and other localities), Colin MacRae (Ermelo) and Dick Rayner (various sites). These have yielded a further 2000 slabs. Many additional specimens of attached and detached glossopterid fruits were unearthed at these new localities. The Middle Ecca still remains clearly undersampled in comparison with the Estcourt and Molteno formations. Considering the extent of coal mining and other quarrying currently in progress, there exists almost unlimited potential for further systematic collecting. (Cedara and Lawley, sampled in the early 1970s and 1980s respectively, are recognised as Upper Ecca sites in Anderson & Anderson 1985 and are not included here).

The flora (Figures 2-7)

The Middle Ecca flora, as revised in Anderson & Anderson (1985), derives from five broad localities – Vereeniging (Figure 1a), Hammanskraal (Figure 1b), Libernon Gold Mine, Hlobane Colliery, and Ermelo, in order of importance – and has yielded a total of 4,500 catalogued slabs housed mostly at BPI. The flora cannot be discussed in terms of taphocoenoses (TCs, assemblages) as the bulk of the material from Vereeniging and Hammanskraal was not originally provenanced to sufficient resolution. It includes 23 genera with 42 species, about twice as rich as the later Permian Estcourt Formation, but far less so than the Triassic Molteno Formation. The glossopterids (Figures 2-6) heavily dominate the flora in abundance and diversity, though lycopods (Figure 7) and conifers are also common. Horsetails are rare and lacking in diversity. The remaining

flora is made up mostly of rare ferns (in 3 genera) and a range of possible ginkgophytes (4 genera). Two primary plant associations can be defined: glossopterid-dominated, medium-diversity forest and woodland along river banks (levees) and other elevated ground; and dense monospecific lycopod stands fringing intertributary pans and swamps – the niche later filled by the sphenophytes.

Further papers since our 1985 review include Rayner (1985, 1986, 1988) on lycopods and Kovács-Endrödy (1987, 1990, 1991) on glossopterid foliage. In a very tangible sense these two researchers, though publishing concurrently, represent successive generations of palaeobotanist with distinctive foci of interest. Kovács-Endrödy was concerned almost exclusively with taxonomy and the historical intricacies of nomenclature, whilst Rayner's attention was drawn to the overall plant and its palaeobiology. Through a study of leaf characteristics most sensitive to climate, Rayner (1995) concluded that extremely favourable conditions for plant growth, comparable to tropical regions today, prevailed during Middle Ecca times.

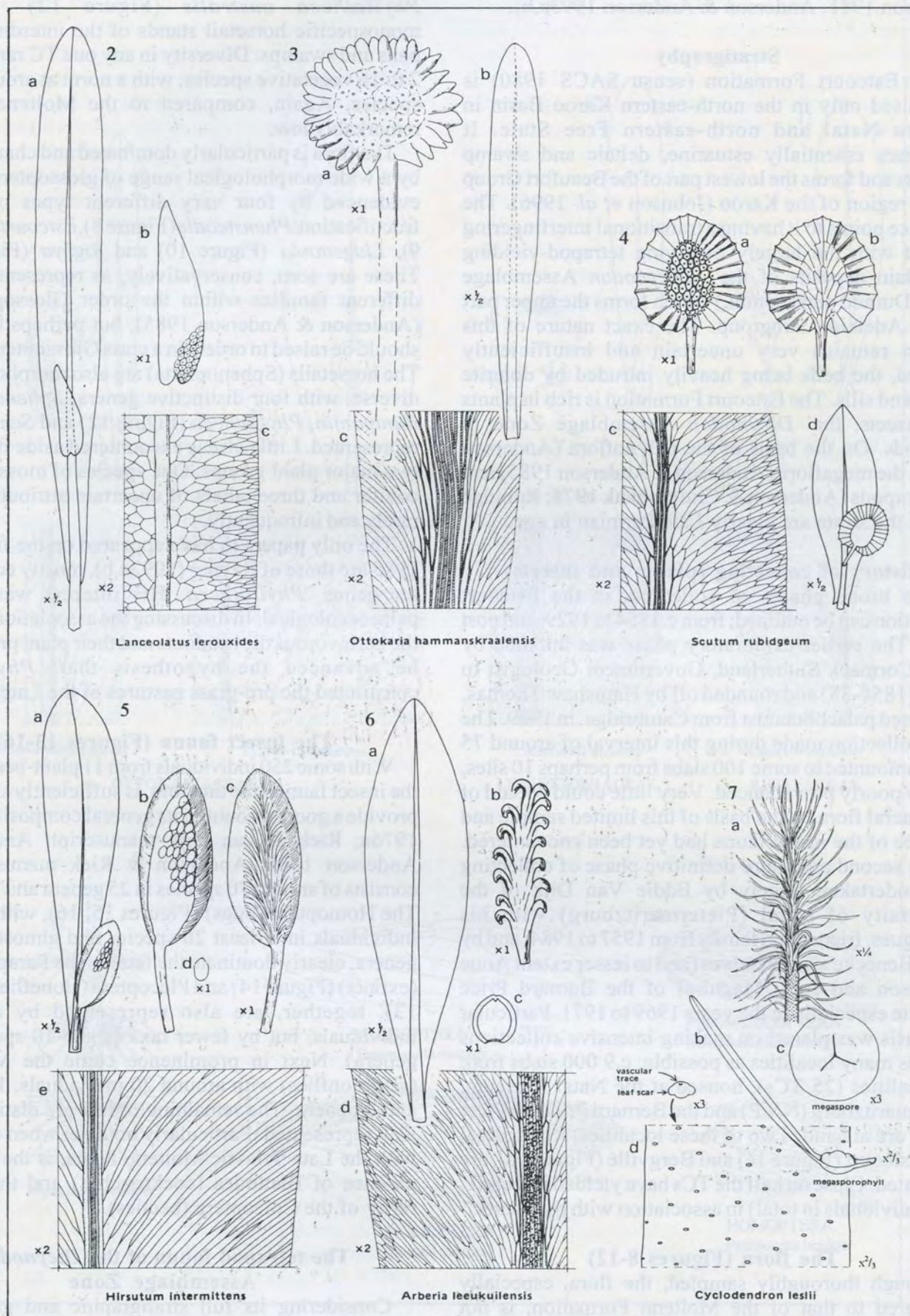
The insect fauna

Unlike in the later Estcourt and Molteno formations, the insect fauna of the Middle Ecca is extremely limited. Only four individual specimens (Riek 1976c,d) have been recovered from the Hammanskraal locality (Figure 1b) – by Kovács-Endrödy in the years 1973-75. It is difficult to explain why the other Middle Ecca localities are apparently barren of insect remains and yet show evidence of insect activity on the leaves (Plumstead 1963). (The Lawley locality of the Upper Ecca has yielded a few specimens.)

THE ESTCOURT FORMATION (L. PERMIAN)

Significance

The combined Estcourt Formation/*Dicynodon* Assemblage Zone of the Natal midlands provides an unparalleled opportunity, at least for Gondwana, to study the ecosystems of the Late Permian prior to the global extinction terminating the Palaeozoic. This uniqueness stems from the co-occurrence of abundant plants, insects and tetrapods. Whilst Late Permian floras are well-developed in all the Gondwana continents, they are largely inadequately documented in regard to frequency and abundance of taxa, the composition of taphocoenoses (TCs), the delineation of associations and palaeoecology. Taxonomic revision and palaeoecological analysis on a supracontinental basis would prove invaluable. Good insect faunas are probably associated with many of these Gondwana-wide floras, but very little is yet known of them. The Belmont fauna, from the Sydney Basin of Australia, is the only other well-sampled and described fauna to compare with that of the Estcourt Formation. It includes some 450 individuals with around 140 described species in 100 genera, but much of the taxonomic work goes back to the 1920s and 30s and needs updating. Late Permian



Figures 2–7. Middle Ecca Flora

2–6 Portrayal of five of the six genera of glossopterids characterising the Middle Ecca; the plant group heavily dominated the flora in abundance and diversity. 7. *Cyclo dendron leslii*, one of two lycopod taxa interpreted as forming monospecific stands fringing interdistributary pans and swamps.

tetrapod faunas from elsewhere in Gondwana remain very poorly known (Anderson & Cruickshank 1978; Anderson 1981; Anderson & Anderson 1993a,b).

Stratigraphy

The Estcourt Formation (sensu SACS 1980) is recognised only in the north-eastern Karoo Basin in western Natal and north-eastern Free State. It comprises essentially estuarine, deltaic and swamp deposits and forms the lowest part of the Beaufort Group in this region of the Karoo (Johnson *et al.* 1996). The evidence points to it having a transitional interfingering contact with the largely overlying tetrapod-yielding floodplain deposits of the *Dicynodon* Assemblage Zone (Durand pers. comm.) which forms the upper part of the Adelaide Subgroup. The exact nature of this contact remains very uncertain and insufficiently mapped, the beds being heavily intruded by dolerite dykes and sills. The Estcourt Formation is rich in plants and insects, the *Dicynodon* Assemblage Zone in tetrapods. On the basis of the palynoflora (Anderson 1977), the megaf flora (Anderson & Anderson 1985) and the tetrapods (Anderson & Cruickshank 1978; Rubidge 1995), the strata are clearly Late Permian in age.

History of collecting (plants and insects)

Two broad phases of collecting in the Estcourt Formation can be outlined; from c. 1854 to 1929, and post 1957. The earlier exploratory phase was initiated by Peter Cormack Sutherland, Government Geologist to Natal (1854-56) and rounded off by Hamshaw Thomas, the famed palaeobotanist from Cambridge, in 1929. The total collection made during this interval of around 75 years amounted to some 100 slabs from perhaps 10 sites, mostly poorly provenanced. Very little could be said of the general flora on the basis of this limited sample and no trace of the insect fauna had yet been encountered.

The second and more definitive phase of collecting was undertaken largely by Eddie Van Dijk of the University of Natal (Pietermaritzburg) with his colleagues, friends and family from 1957 to 1984; and by Anna Benecke and ourselves (and to lesser extent Anne Anderson and Judy Maguire) of the Bernard Price Institute especially in the years 1969 to 1971. Particular emphasis was placed on making intensive collections from as many localities as possible: c. 9 000 slabs from 21 localities (25 TCs), housed at the Natal Museum, Pietermaritzburg (NMP) and the Bernard Price Institute (BPI), are at hand. Two of these localities, Rondedraai near Estcourt (Figure 1c) and Bergville (Figure 1d), are illustrated. Close on half the TCs have yielded insects (c. 250 individuals in total) in association with the plants.

The flora (Figures 8-12)

Though thoroughly sampled, the flora, especially compared to that of the Molteno Formation, is not diverse. As revised in Anderson & Anderson (1985) it includes just 24 vegetative species (in 14 genera). Only two basic floral associations can be recognised: *Lidgettonia* (Figure 10) (and other glossopterid genera)

– medium diversity forest and woodland along river banks (levees) and other elevated ground; and *Phyllothea australis* (Figure 12) – dense monospecific horsetail stands of the intertributary pans and swamps. Diversity in any one TC ranges from 2 to 16 vegetative species, with a norm at around 5 or 6 species. Again, compared to the Molteno, this is remarkably low.

The flora is particularly dominated and characterised by a wide morphological range of glossopterid taxa as evidenced by four very different types of female fructification: *Plumsteadia* (Figure 8), *Estcourtia* (Figure 9), *Lidgettonia* (Figure 10) and *Rigbya* (Figure 11). These are seen, conservatively, as representing three different families within the order Glossopteridales (Anderson & Anderson 1985); but perhaps their rank should be raised to orders in a class Glossopteridopsida. The horsetails (Sphenophyta) are also morphologically diverse, with four distinctive genera, *Sphenophyllum*, *Raniganjia*, *Phyllothea* (Figure 12) and *Schizoneura*, represented. Little else is encountered aside from these two major plant groups. One species of moss, one of a conifer and three others of uncertain attribution occur rarely and infrequently.

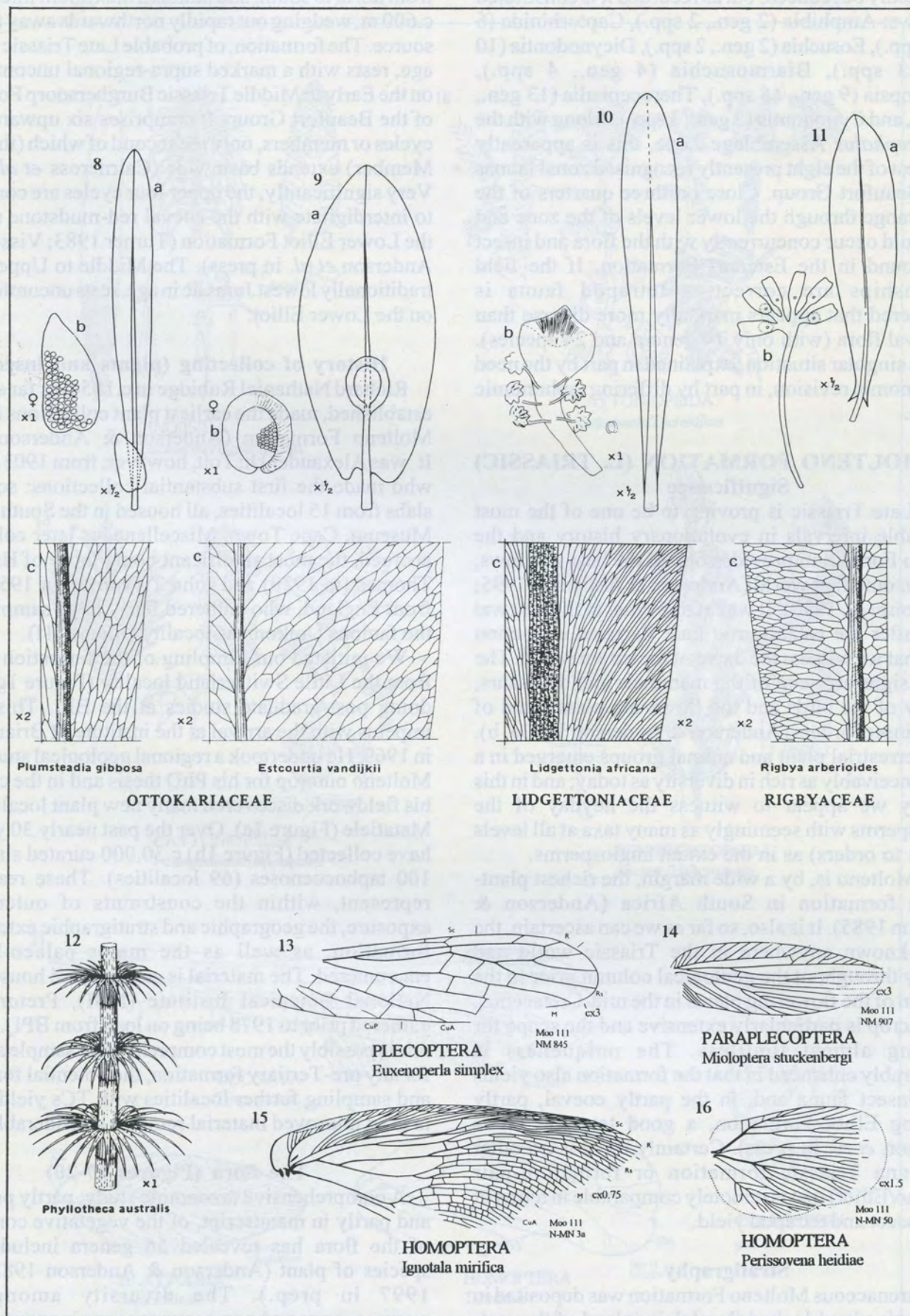
The only papers to have appeared on the flora since 1985 are those of Rayner (1992a,b), mostly concerning the genus *Phyllothea*. His interest was largely palaeoecological. In discussing the association between the herbivorous dicynodonts and their plant preferences he advanced the hypothesis that *Phyllothea* constituted the pre-grass pastures of the Late Permian.

The insect fauna (Figures 13-16)

With some 250 individuals from 11 plant-bearing TCs, the insect fauna, like the flora, is sufficiently sampled to provide a good account of its general composition (Riek 1976a; Riek & van Dijk manuscript; Anderson & Anderson 1985; Anderson & Riek manuscript). It consists of around 70 species in 25 genera and 14 orders. The Homoptera (bugs) (Figures 15, 16), with some 80 individuals in at least 20 species and almost as many genera, clearly dominate the fauna. The Paraplecoptera (extinct) (Figure 14) and Plecoptera (stoneflies) (Figure 13), together, are also represented by about 80 individuals, but by fewer taxa (some 10 species in 8 genera). Next in prominence come the Mecoptera (scorpionflies) with around 20 individuals, 13 species and 7 genera. The remaining orders are distinctly less well represented. Particularly notable, when compared with the Late Triassic Molteno fauna, is the complete absence of Blattodea (cockroaches) and the distinct rarity of the Coleoptera (beetles).

The tetrapod fauna of the *Dicynodon* Assemblage Zone

Considering its full stratigraphic and geographic extent through the main Karoo Basin and into the north-eastern outcrop area in Natal, the tetrapod fauna of the *Dicynodon* Assemblage Zone, as currently known, includes 49 genera with 73 species (Rubidge 1995). With



Figures 8–16. Estcourt Formation Flora and Insects

8–11. Foliage and fruit of the four genera of glossopterids identified in the Estcourt flora; as earlier in the Permian, this plant group still dominates in abundance and diversity. 12. *Phyllothea australis*, the dominant horsetail taxon found widely through the formation that may have formed the pastures of the Late Permian. 13–16. Representative wings of the three most prominent insect orders found directly associated with the Estcourt plants.

modern taxonomic revision this large tally of taxa will undoubtedly be reduced, but as recorded it is constituted as follows: Amphibia (2 gen., 2 spp.), Captorhinida (6 gen., 6 spp.), Eosuchia (2 gen., 2 spp.), Dicynodontia (10 gen., 23 spp.), Biarmosuchia (4 gen., 4 spp.), Gorgonopsia (9 gen., 18 spp.), Therocephalia (13 gen., 14 spp.), and Cynodontia (3 gen., 3 spp.). Along with the *Tapinocephalus* Assemblage Zone, this is apparently the richest of the eight presently recognised zonal faunas of the Beaufort Group. Close on three quarters of the genera range through the lower levels of the zone and thus would occur concurrently with the flora and insect fauna found in the Estcourt Formation. If the field relationships are correct, a tetrapod fauna is encountered that appears markedly more diverse than the coeval flora (with only 14 genera and 24 species). This is a singular situation, explained in part by the need for taxonomic revision, in part by differing taphonomic controls.

THE MOLTENO FORMATION (L. TRIASSIC)

Significance

The Late Triassic is proving to be one of the most remarkable intervals in evolutionary history and the Molteno Formation provides one of the best windows, globally, onto that world (Anderson & Anderson 1995; Anderson *et al.* 1996). It was at this time, in the renewal of life after the cataclysmic Late Permian extinction event, that we witness the dawn of the extant world. The earliest signs are seen of the mammals and dinosaurs, possibly of the birds and the flowering plants, and of several insect orders (Anderson & Anderson 1993a, b). These terrestrial plant and animal groups emerged in a biota conceivably as rich in diversity as today; and in this diversity we appear to witness the heyday of the gymnosperms with seemingly as many taxa at all levels (species to orders) as in the extant angiosperms.

The Molteno is, by a wide margin, the richest plant-bearing formation in South Africa (Anderson & Anderson 1985). It is also, so far as we can ascertain, the richest known anywhere in the Triassic world and possibly throughout the geological column prior to the radiation of the flowering plants in the mid-Cretaceous. The outcrop is particularly extensive and the scope for sampling almost limitless. The uniqueness is considerably enhanced in that the formation also yields a rich insect fauna and, in the partly coeval, partly overlying Elliot Formation, a good tetrapod fauna (Anderson *et al.* in press). Certainly there is no other Gondwana Triassic formation or formation-pair (Molteno/Elliot) that is remotely comparable in terms of plant, insect and tetrapod yield.

Stratigraphy

The arenaceous Molteno Formation was deposited in an extensive land-locked floodplain inland of the east-west fold-belt zone which formed the southern periphery of Pangaea. The erosional remnant of the Molteno

stretches some 200 km from west to east and 400 km from north to south, and attains a maximum thickness of c.600 m, wedging out rapidly northwards away from the source. The formation, of probable Late Triassic Carnian age, rests with a marked supra-regional unconformity on the Early to Middle Triassic Burghersdorp Formation of the Beaufort Group. It comprises six upward-fining cycles or members, only the second of which (the Indwe Member) extends basinwide (Cairncross *et al.* 1995). Very significantly, the upper four cycles are considered to interdigitate with the coeval red-mudstone strata of the Lower Elliot Formation (Turner 1983; Visser 1984; Anderson *et al.* in press). The Middle to Upper Elliot, traditionally lowest Jurassic in age, rests unconformably on the Lower Elliot.

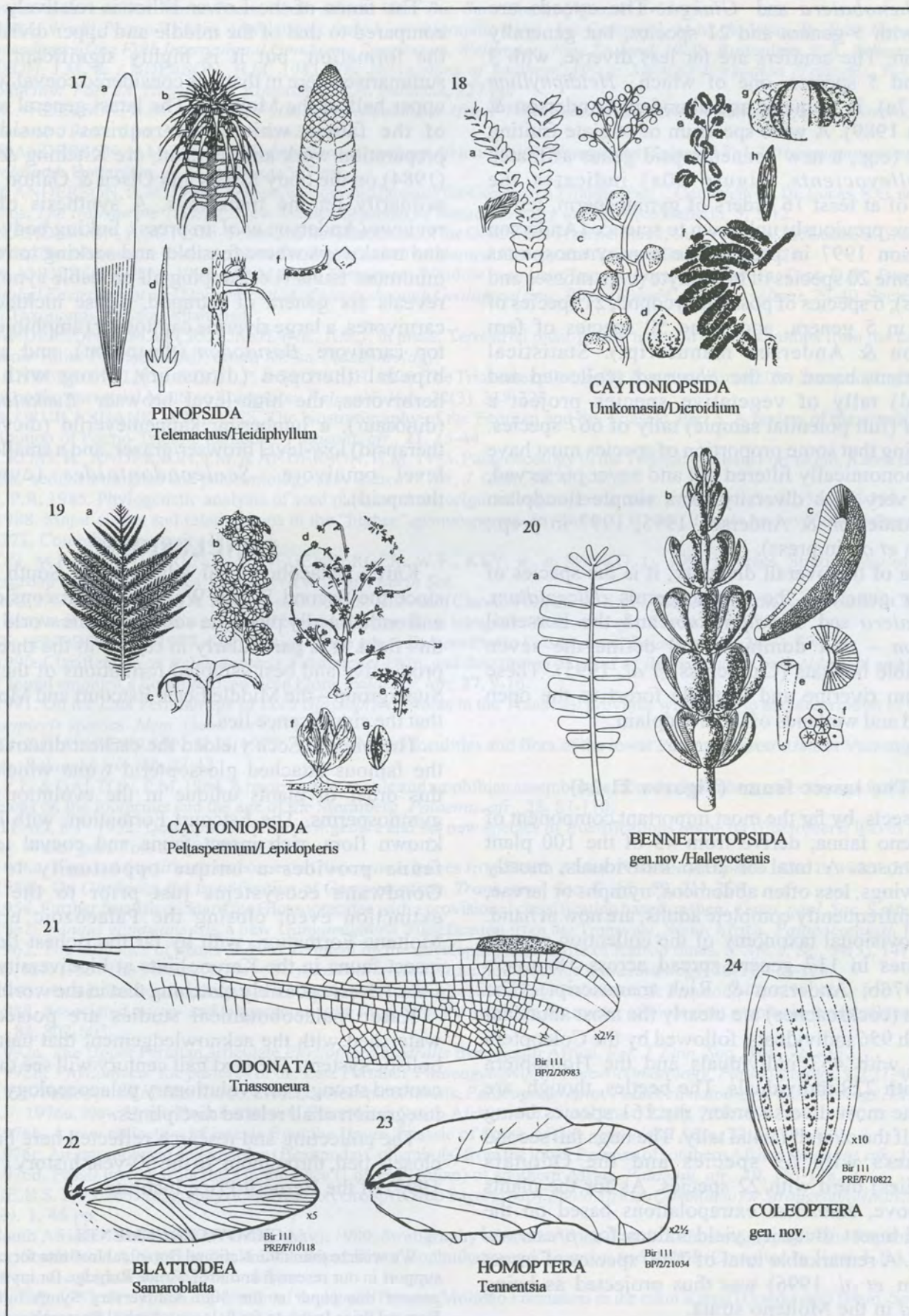
History of collecting (plants and insects)

Richard Nathaniel Rubidge in c.1850, as far as can be established, made the earliest plant collections from the Molteno Formation (Anderson & Anderson 1985). It was Alexander Du Toit, however, from 1903 to 1913, who made the first substantial collections: some 500 slabs from 15 localities, all housed in the South African Museum, Cape Town. Miscellaneous later collections accrued, the most significant being those of Hamshaw Thomas (in 1929) and John Townrow (in 1956), both from England, who gathered fairly large samples from the famous Umkomaas locality (Figure 1f).

We initiated our sampling of the formation in 1967 from the Little Switzerland locality (Figure 1g) whilst doing post-graduate studies at the BPI. This gained impetus with the arrival at the institute of Brian Turner in 1969. He undertook a regional geological study of the Molteno outcrop for his PhD thesis and in the course of his fieldwork discovered many new plant localities, eg. Matatiele (Figure 1e). Over the past nearly 30 years we have collected (Figure 1h) c.30,000 curated slabs from 100 taphocoenoses (69 localities). These reasonably represent, within the constraints of outcrop and exposure, the geographic and stratigraphic extent of the formation, as well as the major palaeo-habitats encountered. The material is currently all housed at the National Botanical Institute (NBI), Pretoria (that gathered prior to 1978 being on loan from BPI). Though this is possibly the most comprehensive sample available for any pre-Tertiary formation, the potential for finding and sampling further localities with TCs yielding new taxa or improved material remains considerable.

The flora (Figures 17-20)

A comprehensive taxonomic study, partly published and partly in manuscript, of the vegetative component of the flora has revealed 56 genera including 204 species of plant (Anderson & Anderson 1983, 1989, 1997 in prep.). The diversity amongst the gymnosperms and non-gymnosperms is approximately equal. The seed-fern *Dicroidium* (Figure 18a), which strongly characterises the Gondwana Triassic, is



Figures 17–24. Molteno Formation Flora and Insects

17–20. Selected foliage and fruit of four of the 16 orders of gymnosperm recognised in the Molteno suggesting the great diversity in the formation; the bennettitopsid is one of 10 of these orders that are new to science. 21–24. Representative wings of the four most prominent insect orders found in intimate association with the Molteno flora.

represented in the Molteno by 19 species. Other prominent seed ferns include *Lepidopteris* (Figure 19a), *Sphenobaiera* and *Ginkgo*. The cycads are diverse, with 5 genera and 21 species, but generally uncommon. The conifers are far less diverse, with 3 genera and 5 species, one of which, *Heidiphyllum* (Figure 17a), is frequent and abundant (Anderson & Anderson 1989). A wide spectrum of ovulate fruiting structures (e.g., a new bennettitopsid genus affiliated with *Halleyoctenis*, Figure 20a) indicates the presence of at least 16 orders of gymnosperm, ten of which were previously unknown to science (Anderson & Anderson 1997 in prep.). The non-gymnosperms include some 20 species of bryophyte (e.g., mosses and liverworts), 6 species of possible lycopod, 21 species of horsetail in 5 genera, and some 50 species of fern (Anderson & Anderson manuscript). Statistical extrapolations based on the *observed* (collected and described) tally of vegetative species project a *preserved* (full potential sample) tally of 667 species. Considering that some proportion of species must have been taphonomically filtered out and never preserved, this is a very high diversity for a simple floodplain biome (Anderson & Anderson 1995, 1997 in prep.; Anderson *et al.* in press).

In spite of the overall diversity, it is the species of only four genera – the gymnosperms *Dicroidium*, *Sphenobaiera* and *Heidiphyllum* and the horsetail *Equisetum* – that dominate and define the seven recognisable habitats (Cairncross *et al.* 1995). These range from riverine and lakeside forest to the open woodland and wetlands of the floodplain.

The insect fauna (Figures 21–24)

The insects, by far the most important component of the Molteno fauna, derive from 43 of the 100 plant taphocoenoses. A total of 2056 individuals, mostly isolated wings, less often abdomens, nymphs or larvae, and very infrequently complete adults, are now at hand. A full provisional taxonomy of the collection reveals 333 species in 117 genera spread across 18 orders (Riek 1976b; Anderson & Riek manuscript). The Blattodea (cockroaches) are clearly the most abundant order with 956 individuals, followed by the Coleoptera (beetles) with 453 individuals and the Homoptera (bugs) with 229 individuals. The beetles, though, are clearly the most diverse order, the 161 species being nearly half the overall faunal tally. The bugs fall second in richness with 69 species and the Odonata (dragonflies) third with 22 species. As for the plants noted above, statistical extrapolations based on the *observed* insect diversity yield values for *preserved* diversity. A remarkable total of 7740 species of insect (Anderson *et al.* 1996) was thus projected as being *preserved* in the Molteno strata.

The tetrapod fauna of the Lower Elliot Formation (coeval with the Upper Molteno)

The fauna of the Lower Elliot is relatively sparse compared to that of the middle and upper divisions of the formation, but it is highly significant and is summarised here in that it is considered coeval with the upper half of the Molteno. The latest general reviews of the fauna, which still requires considerable preparation work and revision, are Kitching & Raath (1984) on the body fossils and Olsen & Galton (1984) primarily on the trackways. A synthesis of these reviews (Anderson *et al.* in press), linking body fossils and trackways where feasible, and seeking to record a minimum fauna (i.e. lumping all probable synonyms), reveals six genera of tetrapod. These include three carnivores, a large riverine capitosaur (amphibian), the top carnivore *Basutodon* (thecodont), and a small bipedal theropod (dinosaur); along with three herbivores, the high-level browser *Euskelosaurus* (dinosaur), a lumbering kannemeyeriid (dicynodont therapsid) low-level browser/grazer, and a smaller low-level omnivore *Scalenodontoides* (cynodont therapsid).

CONCLUSIONS

Karoo palaeobotanical advances in South Africa since the Second World War have been considerable and undoubtedly place the country on the world map in this field. It is particularly in regard to the three most productive and best sampled formations of the Karoo Supergroup – the Middle Ecce, Estcourt and Molteno – that the significance lies.

The Middle Ecce yielded the earliest discoveries of the famous attached glossopterid fruits which make this order of plants unique in the evolution of the gymnosperms. The Estcourt Formation, with its well known flora, rich insect fauna and coeval tetrapod fauna provides a unique opportunity to study Gondwana ecosystems just prior to the global extinction event closing the Palaeozoic era. The Molteno Formation, with by far the richest flora and insect fauna in the Karoo, hints at biodiversity in the Late Triassic possibly matching that in the world today.

Karoo palaeobotanical studies are poised on a watershed with the acknowledgement that nature is a holistic system. The next half century will see the focus centred strongly on evolutionary palaeoecology and the integration of all related disciplines.

The collecting and research reflected here has been closely tied, throughout, to the 50-year history (1945 to 1995) of the Bernard Price Institute.

ACKNOWLEDGEMENTS

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THE IMPORTANCE OF KAROO FOSSILS IN THE SEARCH FOR MAMMAL ORIGINS.

by

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ABSTRACT

It has long been known that mammals belong to the group Synapsida (more familiar to most in South Africa by the now discredited term Mammal-like Reptiles), a group with a long fossil history, much of which was first established from the Karoo. In palaeontology mammals are traditionally defined by the possession of a squamosal/dentary jaw joint, as opposed to the quadrate/articular jaw joint of non-mammalian tetrapods. This paper recounts some of the advances in our knowledge of the therapsids (advanced synapsids) over the past 50 years, including the discovery of a sequence of forms leading to those which possess both pre-mammalian and mammalian jaw hinges, transitional forms which thus by definition qualify as mammals. Brief mention is made of some historical aspects of phylogenetic interpretation, pointing out that some early workers following Darwin, were as aware of the central role of species in phylogenetics as are the disciples of Hennig and Eldredge and Gould. Brief reference is made to the crown group definition of mammals proposed by Rowe (1988), as it contrasts with the traditional character-based definition. Finally, it is encouraging that modern workers are not only as aware of the problems of distinguishing homology and homoplasy as were earlier workers, but are starting to acknowledge the importance of missing information. In this way, just as the double jaw joint was first predicted and then found, we can actively seek to fill some of the many remaining gaps in our knowledge.

KEYWORDS: Synapsids, Mammal Origins.

"The animals which are dealt with in this story are not in fact members of a single line of descent leading up to mammals. Nonetheless, our now very extensive knowledge of these reptiles makes it evident that the phenomenon of parallel evolution is so widely displayed among them that so long as we pick the members of our series from not too remote groups, and of the right time, we shall not be seriously in error."

D. M. S. Watson 1953.

THERAPSIDES

It has been known since the late 19th century that some of the fossils of the Karoo are extraordinarily mammal-like, primarily through the efforts of Broom, but also Olson, Owen, Seeley and Watson. Broom was able to show that the therapsids became increasingly mammal-like with time, and were unquestionably ancestral to mammals.

There was disagreement as to which of the theriodont groups was the most probable source of the mammals. Broom (1932, 1938) always favoured derivation from bauriamorph therocephalians. Others favoured cynodonts, and this unsettled situation was still evident in the 1950s. Romer (1956) stated guardedly "...the phyletic relationship of cynodonts to mammals is debatable."

Also in 1956, A. S. Brink, a student of Watson's and the first scientific officer of the Bernard Price Institute, published a much cited paper, entitled "Speculations on some advanced mammalian characteristics in the higher mammal-like reptiles." Brink accepted Crompton's

(1955) opinion that mammals were derived from therocephalians, but went on to consider only cynodonts, this approach being validated by the extraordinary number of advanced characters shared by therocephalians and cynodonts.

It is instructive at this time to examine some of Brink's (1956) speculations and to see how they have been scientifically tested in the intervening years.

Brink's speculations.

1. In his paper Brink was preoccupied with the possibility that cynodont therapsids may have possessed a diaphragm. Jenkins (1971) in a major study of the cynodont skeleton concluded that there is no evidence for the presence of a diaphragm, and that is the position as it remains today.
2. Brink suggested that the improved dentition of cynodonts (the postcanine teeth have several additional cusps which would have enabled them to break up food into smaller pieces before swallowing) indicated improved mastication and hence more rapid digestion. No-one would dispute that, and a considerable literature on tooth morphology and replacement has built up since that time.
3. The secondary palate was also involved with improved mastication. By separating nasal and oral passages the animal could chew and breathe at the same time, a necessary "preadaptation" for the

suckling behaviour of mammals. It is also involved in the next point.

4. It raises the possibility that mammal-like scroll bones (turbinals) could have been present in the nasal passages of therapsids. Watson as early as 1913 had suggested that attachment ridges for these delicate structures (themselves never preserved) were present in therapsids. This question has recently been investigated by Hillenius (1992, 1994). By careful experimental work with living animals, he has shown that of the three types of turbinals (nasal, ethmoidal and maxillary) it is only the maxilloturbinals of mammals that are exclusively respiratory – they reduce desiccation associated with rapid, continuous breathing, which is a characteristic of endothermic animals. The other turbinal bones are related to the more primitive olfactory function. Hillenius (1992, 1994) thus claims that attachment ridges for maxilloturbinals would be the first reliable indication of endothermy in this lineage that can be used in the fossil record. Like several other advanced mammalian characters, ridges for attachment of maxilloturbinals are present in therocephalians and cynodonts.

Starting in the Late Permian, “full endothermy” may, according to Hillenius, have taken 50Ma to develop: whether this was a gradual or punctuated progression we would still like to know. Hillenius’ use of the term endothermy is significant: an endotherm is an animal which, because it generates metabolic heat, is “warm blooded”. Thus sharks, tuna and sea turtles for example are all endothermic. Most birds and mammals are homeotherms, that is endotherms capable of maintaining constant body temperature. Crompton, Taylor and Jagger (1978) presented an elegant argument as to why homeothermy should be linked to the appearance of the first mammals – in effect it opened up the niche of nocturnal insectivore for the first time.

5. Not mentioned by Brink, but not unrelated to the diaphragm question, is the matter of gait. Primitive amniotes deploy their limbs out sideways – they are termed sprawlers. Most extant mammals bring the limbs in under the body to give themselves an erect stance and parasagittal gait. Lizards can run just as fast as mammals of the same size, with no difference in the energy cost of running, but, in the process, lizards incur an oxygen debt so cannot *sustain* these speeds. This difference was investigated by Carrier (1987), whose work can be summarised as follows. Ectothermic tetrapods have a sprawling gait and short-burst anaerobic exercise metabolism. Endothermic tetrapods have erect posture and parasagittal gait and sustained aerobic metabolism. Sprawlers flex the body laterally during rapid locomotion, thus compressing the lungs alternately and effectively preventing breathing. (Carrier has done the experiments necessary to demonstrate this

with live lizards and dogs.) In upright tetrapods body flexure is in the vertical plane and rapid movement actually enhances ventilation of the lungs.

Of living animals a muscular diaphragm is present only in mammals, birds, crocodiles and turtles (these latter of course being a special case). In this context it is noteworthy that early (terrestrial) crocodiles had a fully erect posture and were thus in all likelihood endothermic (bone histological studies are needed to confirm this).

THE SEARCH FOR THE DOUBLE JAW HINGE

One of the great triumphs of 19th century anatomists was the establishment, from embryological studies, of the homology between the non-mammalian articular and quadrate and the mammalian malleus and incus; this became known as Reichert’s Theory. The therapsids exhibit a steady increase in the size of the dentary and reduction of the post-dentary bones. As Parrington (1949) pointed out, Reichert’s theory implied that at some stage the original tetrapod quadrate/articular and the mammalian squamosal/dentary jaw articulations must have existed together, as it is hardly conceivable that there could be a stage with no bony jaw hinge. Thereafter the hunt was on to find a fossil that would bear out this prediction.

Some pertinent fossils had already been found. The very mammal-like South African cynodont *Diarthrognathus* was first mentioned by Broom (1925); the British putative mammal *Morganucodon* was first described (as *Eozostrodon*) by Parrington (1941), but it was some time before the skull was pieced together.

Kermack and Mussett (1958) demonstrated the presence of both articulations in *Morganucodon*, and in the same year Crompton claimed the same for *Diarthrognathus*, but later (1972) retracted, stating that although *Diarthrognathus* had a dentary “condyle”, there was no squamosal glenoid. However, one may visualise this part of the dentary being restrained and guided by aponeuroses and fasciae, and it was eventually possible to show (Gow 1981) that Crompton had misidentified the quadrate and articular.

Romer (1956) described two very exciting advanced cynodonts from South America, *Probelesodon* and *Probainognathus* (Romer 1969 a, b). In the former there seemed to be a facet on the squamosal with which the surangular of the lower jaw made contact, while in the latter a more convincing squamosal facet could have articulated with both the surangular and the dentary. Here are two animals achieving a similar result to *Diarthrognathus* but doing it rather differently – yet another instance of parallelism in cynodonts. What all three seem to be doing, is bracing the articular region of the lower jaw from the *side*, presumably against muscle forces tending to splay the jaw rami. The quadrate/articular joint was still functional in *Probelesodon* and *Probainognathus*, as indeed it still was in *Morganucodon*. It is easy to conceive of a

Probainognathus-like condition leading to a form with a more transverse squamosal glenoid to accommodate a true dentary condyle which would, in time, free the quadrate and articular from their traditional role.

THE FATE OF THE POST-DENTARY BONES

The quadrate=incus, articular=malleus homologies have been secure since the 19th century. The position of the eardrum (tympanum) is very different in reptiles and mammals, and for a long time the position of the tympanum in non-mammalian synapsids was unsure. This problem was resolved by Allin (1975). Non-synapsid reptiles have the tympanum behind the quadrate, whereas Allin showed that in synapsids the tympanum lay in front of the quadrate, supported by the reflected lamina of the articular bone, which is thus the homologue of the mammalian tympanic bone.

THE SEARCH FOR THE FIRST TRUE MAMMALS

Several groups of mammals are known from the Late Triassic/ Early Jurassic, but I will consider here only morganucodonts as they are the only adequately known group. Others are too poorly known (for a review see Lucas and Luo 1993), though their presence suggests that mammals must have appeared even earlier.

Walter G. Kuhne moved to England from Germany just before the outbreak of World War II, knowing from previous fossil finds that there was a good possibility of finding early mammal fossils in fissure fills in the Triassic palaeokarst of Wales. He found the tritylodontid *Oligokyphus* in 1939, and penned its description during internment on the Isle of Man. Also in 1939, Kuhne found two tiny mammalian molar teeth which he sold to Cambridge University and which Parrington (1941) described as *Eozostrodon* (*E. parvus* and *E. problematicus*). Kuhne discovered in 1947 what he was to call *Morganucodon*. He published his description in 1949 on the basis of a single molar tooth, explicitly recognising that *Eozostrodon* could be part of the same dentition. *Morganucodon* was clearly a mammal and at the time the earliest known, with an age of 190-200 Ma.

By this time it was known that another tritylodont, *Bienotherium* (Young 1947), occurred in the Lufeng Beds in China, and in 1948 a Catholic priest, Father Oehler, found the skull of a mammal in these beds. This specimen was to be described by Father Rigney who had instigated the search, but he only received it in 1956, after a series of misfortunes which included being imprisoned by the Chinese for four years. Rigney (1963) finally described the specimen as *Morganucodon oehleri*. Subsequently the work on *Morganucodon* became the preserve of K.A. Kermack at University College, London. He and co-workers have published superb, detailed accounts of the skull and jaws of *Morganucodon* based mainly on fissure fill material of Early Jurassic age (Kermack, Mussett & Rigney 1973, 1981).

Both *Tritylodon* (Owen 1884) and of course

Diarthrognathus were already known from the Stormberg (Elliot and Clarens Formations) of southern Africa, and it was not long before Crompton initiated a field programme with one of its primary objectives the search for Triassic mammals. The first (*Erythrotherium*, Crompton 1964) was found by pure chance in the laboratory in the matrix surrounding a small fabrosaurid dinosaur skeleton. Not long afterward, *Megazostrodon* (Crompton and Jenkins 1968) was found. Incredibly, both these tiny specimens turned out to be almost complete articulated skeletons. Kitching subsequently found a second skull of *Megazostrodon* that was described by Gow (1986).

At present the oldest known mammal is *Adelobasileus* (Lucas & Hunt 1990) from the Dockum beds of Texas, dated at 225Ma. This little skull is remarkable as it shows unmistakable signs of having passed through the gut of a predator (Lucas & Hunt 1990).

This brief historical overview has been necessarily selective: enormous strides have also been made in our knowledge of early mammal dentitions, muscle systems, jaw mechanics and braincase structure, to list just a few aspects. These things have been made possible through increasing technical sophistication in the study of living as well as fossil animals.

PHYLETIC EVOLUTION

As evolutionary biologists we are interested in the relationships of the animals we study. The basic premise is that the more similar two animals are the more likely they are to be closely related. But of course this is not necessarily true, and also their characters may be similar for different reasons, not all phylogenetically useful. The closer two evolving groups are to each other, the more likely they are to evolve similar (homoplastic) characters in parallel. Despite considerable progress in the theory of phylogenetic interpretation during the past thirty years these problems have not gone away, nor are they likely to. There has been speculation particularly about the origin of major new groups: was it poly- or monophyletic? That is, were there several crossings of the grade boundary, or just one? Some of the early workers were quite clearly concerned about this question. Haeckel (1897) said, "We are compelled if we in any way acknowledge the Theory of Evolution, to assume the monophyletic hypothesis, that all Mammals, including Man, must be traced from a single mammalian parent form". Broom stated (1932, p.69.): "one small form in the upper Triassic gave rise to a mammal." And Simpson (1959) explained, "Evolutionary or so-called phylogenetic classification does not express phylogeny but is based on phylogenetic interpretation of the observational data. It is always necessary in a formal classification (so unlike an actual phylogeny) to compromise sooner or later between horizontal and vertical separation of taxa. *That each taxon sometime included only one species in its ancestry should be true*, but it is a completely impractical requirement that each taxon be so delimited and defined as to include and

begin with that species." So much for any lack of understanding on Simpson's part. He then goes on to say "In practice it is a sufficient principle for evolutionary taxonomy that each taxon arose wholly from one of lower categorical level, as Class Mammalia from Order Therapsida." It is for this view that Simpson is remembered and it has resulted in much confusion.

These old insights were explicitly rearticulated by Hennig in 1966, followed in 1972 by the *Punctuated Equilibrium* theory of Eldredge and Gould, which was a logical extension of Hennig's ideas. The following quotes state the case: As Hennig (1966) remarked, "A monophyletic group is a group of species descended from a single species, and which includes all species descended from this species." And Eldredge (1979) accordingly infers, "It is species that do the evolving. A genus or family cannot give rise to another genus or family."

In view of the above, it is interesting to see what palaeontologists have had to say about the origin of mammals. The first recent explicit proposal for the "monophyletic" derivation of Mammalia from Cynodontia is that of Hopson and Crompton (1969). They quote Simpson (1961 p.124), who defined monophyly as "the derivation of a taxon through one or more lineages from one immediately ancestral taxon of the same or lower rank." They rightly consider this polyphyletic and state, "Our criterion for the monophyletic origin of... the Class Mammalia would be derivation from an ancestral taxon (through one or possibly more lineages) of much lower rank, on the level of Family or perhaps even lower." Clearly the difference is one of degree only, and this is also polyphyly.

Hopson (1967, p.33): "I suggest that the ancestors of all the early mammals were very advanced Late Triassic cynodonts...", preceded (p.32) by this profound insight: "we must hypothesise the existence in the later part of the Triassic of a line of persistently small and dentally conservative cynodonts which were acquiring in parallel many of the mammalian features seen in their larger more specialised relatives."

I stated much the same thing in concluding my study of the braincases of cynodonts (Gow 1991): "What

seems most probable is that Tritylodontoidea are the sister clade of another middle Triassic to lower Jurassic cynodont clade, which includes Mammalia, but several key members of which are not represented in the fossil record."

Hennig's influence led to the cladistic method of phylogenetic analysis, a method tailor-made for the computer age. The result is that relationships are nowadays presented as computer-generated cladograms.

Hopson (1994) continues to define Mammalia by the possession of a dentary-squamosal jaw articulation, in the traditional manner. Rowe (1988), following Hennig, defines Mammalia as the monophyletic group comprising Monotremata plus Theria, their most recent common ancestor, and all its descendants. This is the cladistic view, i.e. that one can only define taxa by genealogy, not defining characters. This is a theoretically excellent definition, but one can appreciate that the practicality issue remains a real concern.

Hopson (1994 p. 212) concludes a recent exhaustive cladistic analysis of the synapsids as follows "With our greatly improved knowledge of the phylogeny of non-mammalian synapsids, it has become clear that mammals arose from Triassic cynodonts, *in my view from animals similar to Probainognathus but with cheek teeth more like those of Thrinaxodon*" (my emphasis). Compare that with Crompton's (1972) view of the relationships of ictidosaur "These forms appear to have arisen from a primitive cynodont, perhaps even more primitive than *Thrinaxodon*." These intuitive views appear to suggest a conviction that key players have so far not been found in the fossil record and that the best cladograms currently available provide sister groupings which speak of relationships too distant to be intellectually satisfying.

These are encouraging signs and hopefully cladistics will in future be seen as part of the solution to phylogenetic studies in palaeontology, and not an end in itself as has tended to be the case.

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ASSESSING THE BIOLOGY OF FOSSIL VERTEBRATES THROUGH BONE HISTOLOGY

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ABSTRACT

Soon after death and burial of an animal, the organic components of bone generally decay. The closely associated inorganic components (mainly apatite) are more resilient and even after millions of years of burial, preserve the spatial organisation of the collagen fibres and hence the structure of the bone. In the past fossil bone histology has been the subject of substantial research. Such studies have included a wide array of extinct vertebrates including fishes, amphibians, pelycosaurs, therapsids, ichthyosaurs, pterosaurs, and dinosaurs.

The relative rate of bone formation is indicated by the texture of the fibrillar matrix, while the overall nature of the primary compact bone provides a direct assessment of whether bone deposition was continuous or interrupted. The amount of secondary bone formation depicts the extent of primary bone resorption and subsequent redeposition. In addition, the internal organisation of bone indicates remodelling and relocation processes of growth, including functional adaptations of the bone morphology. Thus, osteohistology reflects ontogeny, growth dynamics, biomechanical adaptations, as well as various events that punctuate the life history of an animal.

KEYWORDS: Bone histology, bone microstructure, osteohistology, vertebrates, fossils.

INTRODUCTION

Fossilization subjects a bone to a variety of diagenetic processes resulting in substantial changes in the composition of the bone. Notable among these are an increase in apatite crystallinity, loss of organic matter, and the uptake or loss of minor elements. The amount of diagenesis that occurs is variable and depends on a variety of factors including biological and chemical ones. Occasionally the microscopic structure of a fossil bone is affected by microbial action, but it is more usual for the integrity of the histology to be preserved. Even after millions of years of burial some of the earliest vertebrates have the histological structure of their bones intact.

Early studies in fossil bone microstructure (e.g. Hasse 1878; Quekett 1849; Seitz 1907), laid the foundation for further research into comparative osteohistology. As early as 1923, Moodie reported pathologies in fossil bones and in 1933, Nopsca & Heidsieck used bone microstructure to distinguish ontogenetic status of half grown and immature trachodont dinosaurs. Further research (e.g. Enlow 1969; Enlow & Brown 1956, 1957, 1958; Gross 1934; Peabody 1961) provided a better understanding of histological patterns among major vertebrate groups, from fishes to mammals, including both fossil and recent samples. More recently workers such as Ricqlès (e.g. 1974, 1976, 1980) and Reid (e.g. 1984a, 1984b, 1987, 1990) advanced the field of palaeo-osteohistology substantially by documenting bone structure among a variety of tetrapods, and particularly provided more insight into the nature of dinosaurian bone. My own work has dealt with the histological changes through ontogeny among various species of

dinosaurs (Chinsamy 1990, 1993, 1995b). I have also considered both modern and fossil reptiles (Chinsamy 1991; 1994; Chinsamy & Rubidge 1993) and birds (Chinsamy 1995a; Chinsamy *et al.* 1994, 1995).

The physiological meaning of dinosaur bone has been the subject of much debate (e.g. Bakker 1986; Reid 1987; Ricqlès 1980). In this short paper, I present some of the characteristics of bone microstructure and an interpretation of their implications. It was presented to a general audience at the 50th Anniversary Celebrations of the Bernard Price Institute for Palaeontological Research, Johannesburg. For a more comprehensive analysis of bone microstructure, the referenced papers should be consulted.

WHAT DOES BONE MICROSTRUCTURE ACTUALLY REVEAL?

Macroscopic examination of a section of bone immediately reveals the amount of compact bone making up the bone wall, the size and shape of the medullary cavity (if present), and whether or not cancellous bone is present. When a thin section is prepared (Chinsamy & Raath 1992) and examined under a light microscope, microstructural details are revealed. Several aspects of the biology and overall growth of an animal can be deduced on the basis of histological characteristics present in the bone. Notable among these are the following:

Rate of osteogenesis

By examining a thin section of fossil bone under crossed polarisers, the organisation of the fibrillar matrix can be assessed. When bone formation is rapid, the

matrix is random and disorganised, resulting in woven bone tissue. When this tissue is formed numerous blood vessels are typically enclosed. Lamellar bone is later deposited around the vessels to form primary osteons, and the tissue is then termed fibro-lamellar bone (Figure 1). When bone deposition is slow, the matrix is more organised and lamellar bone tissue results (Amprino 1947) (Figure 2). Both these tissue types, and variants thereof, can be observed in a single section of bone. Thus, the rate at which an animal grows is directly reflected by the rate at which bone is deposited and the nature of the fibrillar matrix (Amprino 1947).

Cyclical versus non-cyclical growth

The overall structure of the primary compact bone provides a direct assessment of whether bone deposition was continuous or interrupted. A cyclical rate of bone deposition is evident when the compacta is stratified into

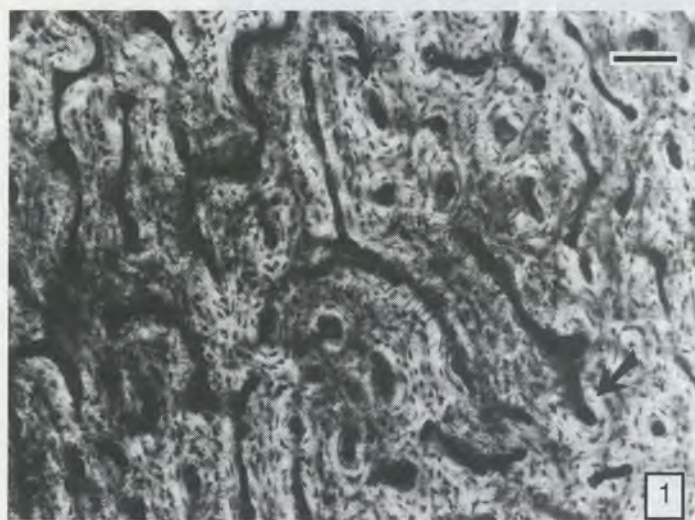


Figure 1: Cross section of a juvenile *Massospondylus* femur (BP/1/ 5253) from the Early Jurassic of South Africa, showing fibro-lamellar bone with numerous primary osteons (arrows) embedded in the woven bone matrix. Scale bar = 76 microns.

distinct growth rings or alternating bands of tissue types. This type of tissue is termed lamellar-zonal and the resulting bands of tissue are the zones and annuli. The zones tend to be more vascularised and represent periods of fast growth, while the poorly vascularised annuli signal periods of slower growth. Pauses in osteogenesis are marked by distinct lines of arrested growth (LAGs).

Among extant reptiles, it is generally found that a single zone and annulus are formed per year. Experiments with fluorochrome dyes have verified that this pattern of bone deposition is seasonally related, with zones formed during the warmer months and annuli resulting during unfavourable periods. Thus, the stratification of the compacta into zones and annuli allows an animal to be aged on the basis of its bones. This study is termed skeletochronology (Castanet & Smirina 1990; Patnaik & Behera 1981). Double or accessory lines can sometimes occur: e.g., Caetano (1990) has demonstrated bi-annual cycles of activity in *Triturus marmoratus* living at high altitudes. These are readily

discernible and are known to be linked to bi-annual cycles of activity. It should be noted that there are no reports of only one LAG formed every two years, which supports the deductions that LAGs in fossil vertebrates are more than likely annual (e.g., Chinsamy 1990, 1993; Sander 1990; Varricchio 1993).

In a study of nine mammalian orders Klevezal & Kleinenberg (1969) reported growth lines occurring in the bones of animals from cold regions, and marine habitats, as well as in mandibles of small lagomorphs and rodents. More recently Leahy (1991) reported growth lines in the bones of a kangaroo, while Chinsamy has found growth lines in a polar bear (Chinsamy & Dodson 1995). It is therefore apparent that growth lines are not restricted to reptiles. More research is required to ascertain what triggers the switch from uninterrupted fibro-lamellar bone to an interrupted type (Farlow *et al.* 1995).

Sustained, uninterrupted bone formation results in the lack of zonation in the compacta. The tissue comprising the compacta can be wholly of fibro-lamellar bone or can grade into a pseudo-lamellar or lamellar type of tissue.

Fibro-lamellar bone is common among mammals and birds, and is known to be formed by rapid osteogenesis (e.g. Amprino 1947; Reid 1990) (Figure 1). The frequent occurrence of this tissue in the bones of dinosaurs has led to assertions that dinosaurs were endotherms (e.g. Bakker 1986). However, fibro-lamellar bone is known from bones of juvenile crocodiles (Buffr  nil 1980), pelycosaur (Enlow & Brown 1957), captorhinids (Enlow & Brown 1957), gorgonopsians (Ricql  s 1976) and dicynodonts (Chinsamy & Rubidge 1993; Gross 1934; Ricql  s 1972). Thus the occurrence of fibro-lamellar bone in these reptiles, which are generally considered to be ectotherms, fails to support a correlation between fibro-lamellar bone and endothermy. It therefore appears that a sustained rate of fibro-lamellar bone formation indicates that bone deposition was rapid. However, exactly how fast deposition has to be to form fibro-lamellar type of tissue is uncertain, and requires further research.

Several dinosaur species appear to have an interrupted pattern of bone deposition (Chinsamy 1994; Reid 1990). This usually takes the form of alternating fibro-lamellar bone and LAGs, with or without annuli, thus switching from rapid to slow deposition periodically, and possibly annually (Figure 3). The trigger for this alternating rate of bone deposition is unknown, but could be seasonal as in modern reptiles. This ability to vary the rate and trajectory of growth is possibly a result of variable metabolic rates, which would have enabled the animal to survive periodically stressful periods.

Extent of vascularisation

The amount and type of vascularisation is revealed by microscopic examination of thin sections of the bone. Depending on the rate of bone formation different forms of vascularisation can result. The orientation of the vascular canals depends on the form of the spaces that were initially enclosed. Ricql  s (1974; 1976) used the



Figure 2: Transverse section of a recent lizard femur showing lamellar-zonal bone tissue. Note the periodic LAGs indicated by the arrows. Simple, radially arranged blood vessels occur in the compacta. Scale bar = 192 microns.

arrangement of the vascular canals to define topological categories of tissues within the fibro-lamellar complex: e.g., reticular, plexiform, laminar etc.

Vascularity can be sparse or dense. Simple blood vessels, primary osteons and secondary osteons can be easily recognised in a bone section (Figures 1, 2, 3, 4). Simple blood vessels show no alteration in the bone around the vascular channel (Figure 2), while primary osteons show a lamellar type of tissue around the blood vessels (Figure 1, 3). Primary osteons are formed during rapid bone deposition, whereas secondary osteons (Figure 4) do not reflect rate of bone formation, but are produced by a process termed Haversian reconstruction. This involves the removal of bone around a primary vascular canal, followed by subsequent redeposition of bone in the erosion cavity. Primary and secondary cylindrical osteons usually contain single vascular canals whereas the irregular, circumferential and radial types commonly contain multiple canals.

Secondary osteons are easily identified due to the occurrence of a cement line or reversal line which marks the furthest extent of bone removal. Successive generations of secondary osteons can form in the same location, resulting in dense Haversian tissue, where even the interstitial bone between the secondary osteons is secondary in nature.

The time taken to form a secondary osteon can be assessed by addition of the time taken for resorption and



Figure 3: Cross section of a metatarsal of the Late Cretaceous *Archaeornithomimus* from the Iren Dabasu Formation of the Peoples Republic of China, showing LAGs (arrowheads) interrupting the deposition of fibro-lamellar bone in the compacta. Scale bar = 192 microns.

that for redeposition (Lacroix 1971). I have used this formula to estimate the minimum age of a juvenile *Dryosaurus* which had just begun to undergo Haversian reconstruction in its bone (Chinsamy 1995b). It is also possible to multiply the number of generations of osteons by the number of days it takes to form a single osteon in order to estimate the minimum age of an animal. However, caution needs to be exercised when doing this since Haversian reconstruction can occur at different stages of ontogeny (e.g. Currey 1960), and also since



Figure 4: Secondary osteons in a sauropod bone fragment from the Early Cretaceous of Niger, Africa. Scale bar = 192 microns.

secondary osteons are not formed continuously, there is no way of determining the time lapse between each generation of osteons.

Numerous suggestions have been proposed regarding the biological significance of secondary osteon formation. These have included metabolic starvation resulting in damage to the vascular system (Currey 1960), physical necrosis of osteocytes (Enlow 1962), and biomechanical adaptation to physical strain. One of the arguments that has received the most support is that secondary osteons are the result of phosphocalcic metabolism (Amprino 1967). This argument was utilised by Bakker (e.g., 1986) to propose that the dense Haversian bone in dinosaur bone implies high metabolic rates, and hence endothermy in dinosaurs. It has however, now become increasingly clear that secondary osteons are not reliable indicators of metabolic rates. They are known to occur in bones of turtles (Enlow & Brown 1957), crocodiles (Chinsamy 1990) and tortoises (Reid 1987), but are absent in small mammals such as rodents and bats, as well as in passerine birds which are highly active (Bouvier 1977).

Ontogenetic Status

Generally, surface texture and articular surfaces of a fossil bone can indicate ontogenetic status of the animal. However, occasionally one is faced with a specimen that cannot be readily distinguished as adult or juvenile purely on morphological grounds. An examination of the animal's bone microstructure will reveal its ontogenetic status since juvenile and adult bone have distinctive microscopic structure (e.g. Nopsca & Heidsieck 1933).

The bone tissue of juveniles appears more porous in structure. Rapid bone formation results in a woven bone matrix with osteocytes haphazardly arranged (Figure 5). With increasing development the porous spaces become infilled by lamellar bone tissue, and primary osteons result (Figure 6). (In more slowly growing animals, e.g., lizards, the juvenile tissue can consist of a parallel fibred or pseudo-lamellar tissue with simple blood vessels). With maturity, the animal may switch from an earlier more rapidly formed type of bone tissue, to a more slowly formed tissue. For example, an earlier fibro-lamellar bone tissue pattern may change to a lamellar, pseudo-lamellar or lamellated type.

Microscopic changes in bone structure have been documented by the examination of growth series of specific skeletal elements of individual dinosaur species. For example, Chinsamy has documented the histological changes in growth series of femora of *Syntarsus* (Chinsamy 1990), *Massospondylus* (Chinsamy 1993) and *Dryosaurus* (Chinsamy 1995b), while Varricchio (1993) reported on the bone microstructure of three metatarsals and two tibiae of different sized *Troodon formosus*.

Bone formed late in life typically shows a slow rate of accretion. Depending on the nature of the tissue deposited during late ontogeny, it is possible to deduce whether an animal experienced indeterminate or determinate growth. Lamellated late bone or a series of closely spaced

peripheral rest lines have been reported in mammals and birds that experience terminal growth. Such lines have also been recorded in *Brachiosaurus* (Gross 1934) which has an earlier non-zonal pattern, while *Syntarsus* (Chinsamy 1990), an unidentified theropod (Reid 1993; probably *Sauronitholestes*, personal communication 1996), and *Rhabdodon* (Reid 1990) record rest lines

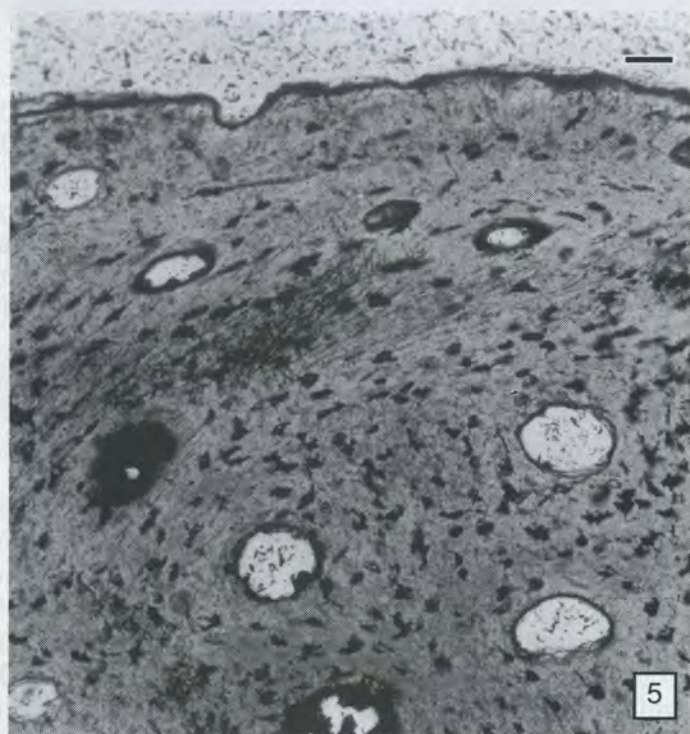


Figure 5: Juvenile bone tissues. A. Transverse section of a juvenile hadrosaur from the Late Cretaceous of Alberta showing rapid bone formation with several longitudinally orientated vascular channels. Scale bar = 46 microns.

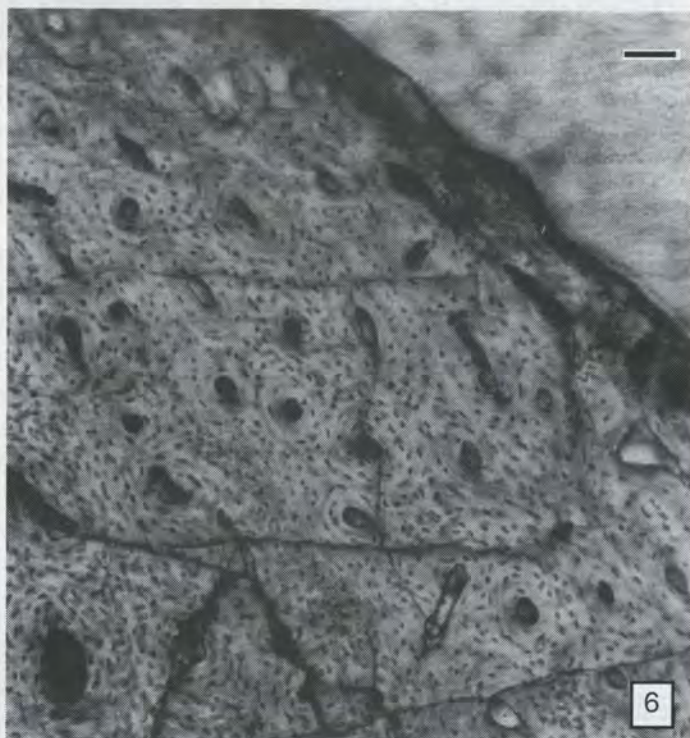


Figure 6: A juvenile *Dryosaurus* from the Late Jurassic Tendaguru beds of Tanzania showing distinct primary osteons in the woven bone matrix of the fibro-lamellar bone tissue. Scale bar = 50 microns

after a zonal pattern of bone deposition. Indeterminate growth is indicated by the absence of such lines, and the continuous formation of bone in the peripheral region e.g. in *Massospondylus* (Chinsamy 1993) and in *Dryosaurus* (Chinsamy 1995b).

Remodelling and Relocation

The internal microscopic texture of a bone bears testimony to the reshaping (remodelling) of the bone during its growth through ontogeny. As a bone grows in length and in diameter, various regions are relocated to new positions (Enlow 1969). Growth in length is attained by endochondral formation of bone, while growth in diameter occurs by subperiosteal or subendosteal deposits. The occurrence of different tissues signifies the occurrence of different events; e.g., the presence of compacted coarse cancellous bone tissue indicates that endosteal deposits of bone resulted in the compaction of a region that previously consisted of spongy bone (Figure 7). Reversal in the direction of growth from inward to outward (or vice versa) is indicated by the occurrence of reversal lines as well as differing tissue types. Thus, the stratified compacta of a bone represents the different types of tissue produced by different growth and remodeling activities that the bone experienced (Enlow 1969).

Biomechanical adaptations

It is generally accepted that the architecture of a bone is adapted to the weight of the animal, and to the mechanical properties of the bone itself (e.g. Rogers & Labarbera 1993). Various tensile and fatigue tests have shown that the different tissue types in the compacta exhibit different strengths. Thus, the tissue type, as well as its porosity and composition, results in a variation of the mechanical properties throughout the cortical thickness.

Bone is recognised as an adaptive tissue and remodels in response to changes in its mechanical environment. In a recent study, Heinrich *et al.* (1994) found that in a growth series of *Dryosaurus lettowvorbecki*, a



Figure 7: Compacted coarse cancellous bone in the compacta of an adult *Dryosaurus* (GPIT 1713/103 distal) from the Tendaguru beds of Tanzania. Scale bar = 76 microns.

distinctive change in the relative amount and distribution of the cortical bone occurred through ontogeny. They ascribed these changes in the cross sectional properties of the femora to increasing mechanical loads, and a caudal shift in the animals' centre of gravity as a result of a change in its preferred mode of locomotion (i.e., a shift from quadrupedality to bipedality).

Bone wall thickness

A functional relationship exists between bone wall thickness, the habitat of the animal (Bühler 1986; Wall 1983) and the forces that act on the bone. It appears that long bones of animals are structures that have minimum mass which enables them to perform locomotory functions at minimum energy cost (Currey & Alexander 1985).

Examination of cross sectional architecture of femora of different species reveals distinct differences in bone wall thickness which appear to be related to the lifestyles of the animal. Some bones have thick walls and a small medullary cavity or sometimes none, whilst others have thin walls and large medullary cavities. Much research has been directed to quantify and ascertain why these differences occur (Bühler 1986; Currey & Alexander

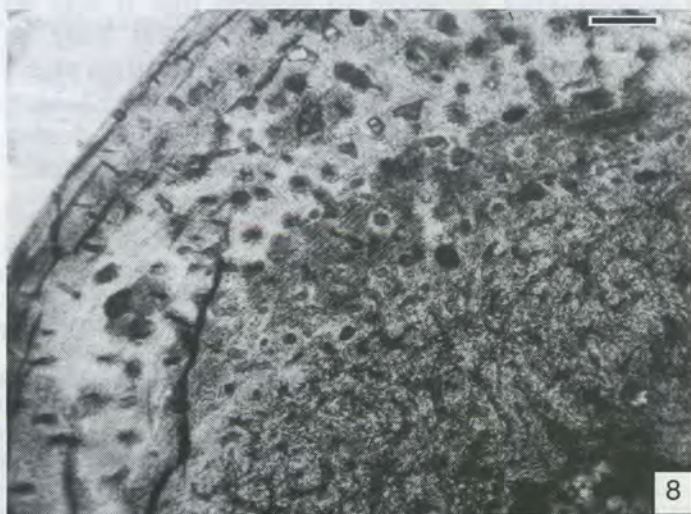


Figure 8: Note the pachyostotic character of the bone of *Claudiosaurus* from the Late Permian of Madagascar. Scale bar = 285 microns.

1985; Wall 1983). Bühler (1986) quantified the observable differences in bone wall thickness by using a value termed the relative bone wall thickness (RBT) which is a ratio of the cross sectional bone wall thickness to the cross sectional diameter. Bühler (1986) calculated the RBT for a variety of birds, and deduced that long bones of birds are highly developed light weight structures, with large flying birds having much thinner bone walls than small to medium sized species.

Wall (1983) measured the volume and weight of limb bones of terrestrial and aquatic mammals. He found that the limb bones of aquatic animals exhibited higher densities than terrestrial ones. Wall suggested that aquatic animals use an increase in compact bone mass to attain buoyancy in water, i.e. to counteract the buoyancy of the lungs.

Upon examination of the relative bone wall thickness (RBT) of adult *Syntarsus*, *Massospondylus*, *Crocodylus niloticus* and two species of birds (*Sagittarius serpentarius* and *Struthio camelus*) I found that the amphibious crocodile exhibited the highest bone wall thickness, while both birds had much lower RBT values than the dinosaurs, with *Sagittarius* having the lowest RBT (Chinsamy 1991). These findings correlate well with those of Wall (1983) and Bühler (1986).

Bone Microstructure of aquatic vertebrates

Besides the gross morphological adaptations that are evident in the skeletons of aquatic tetrapods, the internal organisation of the bone is also subjected to modifications. Depending on the particular type of adaptation of the animal, a very compacted, dense structure can result, termed pachyostosis, as in nothosaurs and sirenians (Buffrénil & Schoevaert 1989; Nopsca & Heidsieck 1933) or extreme cancellousness as in ichthyosaurs (Buffrénil & Mazin 1989), cetaceans (Buffrénil & Schoevaert 1988) and marine turtles (Rhodin *et al.* 1981) can occur. Buffrénil & Mazin (1989) used the pachyostotic nature of the compacta of *Claudiosaurus germaini* to suggest that it was an aquatic reptile (e.g. Figure 8). In a recent study on mosasaur rib microstructure, Sheldon & Bell (in press) deduced that *Clidastes* and *Tylosaurus*, which exhibited a reduced bone density inhabited deeper waters than *Platecarpus* which showed pachyostosis.

CONCLUSION

A fossilised skeleton of an animal provides a tremendous amount of information regarding its overall size and shape. Study of the microstructure of the bones provides an analysis of aspects of the biology and growth of the animal. In addition to phylogeny, bone tissue structure reflects ontogeny, and biomechanical function, as well as various other events that punctuate the life history of an individual.

The field of fossil bone microstructure is continually evolving. New research, particularly comparative and experimental studies of modern vertebrates, will allow deeper insight into the factors that influence bone deposition and bone biology as a whole. The outcome of such research, applied to fossil bone microstructure, will enhance our understanding of the biology and growth of extinct vertebrates.

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CONTRIBUTIONS IN THE FIELD OF PALAEOPALYNOLOGY AT THE BERNARD PRICE INSTITUTE, PAST, PRESENT AND FUTURE

by

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ABSTRACT

A brief chronological summary of the palynological research carried out by students and past members of the staff at the Bernard Price Institute for Palaeontological Research is presented. The contribution that each of these studies has made to the understanding of stratigraphic relationships in the southern African region is highlighted. A correlation chart of palynological biozones documented from South African localities is presented (Table 1).

KEYWORDS: Palaeopalynology, biostratigraphy, spores, pollen, acritarchs, Karoo Basin.

INTRODUCTION

Over the past 40 years palaeopalynological research has provided a powerful means of correlating sediments in southern Africa. Earlier studies employing this methodology in our country focused on the major coal-bearing beds of Permian age. Here the Karoo Basin, rich in its fossil floras, faunas and mineral deposits, provided an ideal setting for palaeopalynological research. More recently attention has shifted to the younger Cretaceous and Tertiary-aged sediments.

Many of the pioneering individuals who dedicated themselves to southern African palynology have, at one time or another, had links with the Bernard Price Institute for Palaeontological Research. It is through their efforts that future students have a solid foundation on which to build.

HISTORICAL REVIEW

Edna Plumstead was the first person associated with the BPI to become involved in palynological research. She documented the fossil floras of the southern African coal measures by illustrating certain spore genera typical of the coal-bearing strata of the Eccia Group (1957, 1966a, 1966b). Palynological endeavour, however, began in earnest at the BPI with the appointment of George Hart in 1965. A graduate of Sheffield University in the United Kingdom, he had already initiated research on the palynofloras of the Ketewaka-Mchuchuma Coalfield in Tanzania and was able to subdivide the coal-bearing strata there into one transitional and two major florizonas. (Hart 1960, 1965a). He later used this scheme to correlate strata and the Songwe-Kiwiri Coalfield of that country (Hart 1965b) and clearly demonstrated the value of palynology in defining equivalent rock strata over a wide geographical area. His first publication on South African material (Hart 1963) documented an assemblage from a borehole in the Orange Free State and he concluded that

it contained both Carboniferous and Permian species. His first subdivision of the South African Lower Karoo strata (Hart 1967) resulted in the definition of four zones, with subsequent papers (Hart 1969a, 1969b, 1971) enlarging the stratigraphic subdivision of the Lower Karoo and its equivalents in southern and central Africa. He produced various taxonomic papers (Hart 1964a, 1964b, 1966), but the most ambitious was a systematic revision and account of the distribution of Permian miospores (Hart 1965c).

The appointment of Roger Davey in November 1967 led to research on hystrichospheres of the Cretaceous sediments of Zululand. He demonstrated that stages in evolutionary development in three genera could be used to correlate sections of these strata. Two papers followed (Davey, 1969a, 1969b) documenting dinoflagellate cysts and hystrichospheres from the Upper Cretaceous of Zululand, but his stratigraphic results were not published due to the confidential nature of the project. Richard Pienaar, a student of the BPI at that time, documented the calcareous nannoplankton of these rocks (Pienaar 1969).

John Anderson was appointed in 1968 as a palynologist on the BPI staff, with financial support from SOEKOR (Southern Oil Exploration Corporation). His research on the miospores of the northern Karoo Basin in South Africa led him to propose eight zones and 21 subzones, ranging from the Permo-Carboniferous Dwyka to the *Daptocephalus* Zone (now *Dicynodon* Assemblage Zone) of the Beaufort Group in the Late Permian (Anderson 1977). He also provided a detailed correlation of these units.

Registration of Rosemary Falcon for a masters degree in 1970 led to the production of a thesis documenting the palyno-stratigraphy of the Mid-Zambesi Basin in Rhodesia (now Zimbabwe) (Falcon 1972, see also Falcon 1973, 1975). Continued research for a higher degree extended this correlation scheme to

CHRONOSTRATIGRAPHIC UNITS <i>vide Harland et al. 1982</i>				SOUTH AFRICA													
				N. Karoo Basin	Waterberg/ Pafuri	Main Basin	Main Karoo Basin	North Main									
	EPOCH	AGE	CHRON	Aitken 1998	MacRae 1988	Hart 1967	Anderson 1977	Falcon 1978									
TRIASSIC	EARLY TRIASSIC	Scythian		X	F												
				IX													
	LATE PERMIAN	Tatarian		VIII					Striatiti Zone	ZONE 7							
				VII								ZONE 6					
				VI									ZONE 5				
				V													
				Kazanian			IVB	Zonati Zone					d	h'			
												IVA			c		
		PERMIAN	Kungurian	Irenian	III	D	Cingulati Zone	ZONE 3 b	IV								
										Filpovian	II	a	III				
Artinskian	Baigendzinian					d	II										
								Aktaskian			d						
													Sterlitamakian			ZONE 2 c	
Asselian								I									
									Krumaian	Uskalikian	a						
		Surenan															
CARBONIFEROUS	GZELIAN	Noginskian		Dwyka	A		ZONE 1	a									
									Klazminskian								
	KASIMOVIAN	Dorogomilovskian															

TABLE 1.

Correlation chart of zones defined with international chronostratigraphic units and assemblages or biozones documented from South African localities (shaded areas = no information).

include sediments on both sides of the Rhodesian watershed (Falcon 1978). Correlation of these assemblages with similar material from many Gondwanan localities confirmed the Early Permian age of the coal-bearing strata equivalent to our Karoo. Falcon, in collaboration with other researchers, provided a palynological framework for the South African Witbank Basin coal measures and associated sediments, and related this to the Zimbabwe sections (Falcon, Pinheiro and Shepherd, 1984).

Also in 1970, Ian McLachlan registered for a higher degree (part-time) at the BPI. During this time he was still an employee of SOEKOR. He studied the problematic microfossils termed *Anellotubulata*, found in Lower Karoo beds. The term *Anellotubulata* was given to these microfossils as similar forms had been described from the Lias of Germany. Tests using X-ray diffraction and electron microprobe work showed that these microfossils were comprised mainly of iron, phosphorus and a small amount of calcium. Unfortunately they were of limited biostratigraphic use due to their long range. McLachlan (1973) reported similar forms from Cretaceous sediments in Eastern Australia. The nature of their depositional environment was questioned and conclusions indicated that Karoo anellotubulates flourished in fresh rather than marine waters. However, the presence of glauconite bands, spinose acritarchs and sponge spicules suggested that conditions were more saline at times, but the lack of recognisable marine faunas indicated that a connection with the sea was unlikely. In 1977 McLachlan published a palynological assessment of petroleum source rocks of the Mesozoic and Cenozoic on the coastal margin of South Africa.

Research for a masters degree by Colin MacRae, on the coal-bearing Karoo strata near Francistown, Botswana, resulted in the definition of three palynological biozones (MacRae 1978). He correlated these biozones with palynological schemes established for other African and Gondwanan localities. This highlighted the presence of coal seams in strata equivalent to the Lower Ecca Group: previously it was thought that coal seams were restricted to the Middle Ecca. MacRae extended his palynological research to the Waterberg, Pafuri and Springbok Flats Basins of South Africa for his doctorate. Six palynostratigraphic zones were defined and their distribution over a considerable distance correlated (MacRae 1988). These biozones were also compared with similarly defined units Gondwana-wide and an attempt was made to date the sections. His results challenged the generally accepted Early Permian age of the middle Ecca (Vryheid Formation equivalent horizons), favouring a slightly younger age. Broad palaeoenvironmental conclusions were drawn for the various units and some economic aspects and implications for future mining highlighted. Carboniferous sediments in South Africa

were documented, and the location of the Carboniferous/Permian boundary in the Waterberg Basin was also identified (MacRae 1991).

Grigor Aitken recently completed palynological studies of the No. 4 and 5 seams (Vryheid Formation, Ecca Group) in the Witbank and Highveld Coalfields (Aitken, 1992, 1994). He included this work as part of a doctoral thesis and extended his research to include Beaufort Group sediments in the northern Karoo Basin. Ten biozones were presented and compared with the work of Hart, Anderson, Falcon and MacRae. A composite biostratigraphic section was proposed for the northern Karoo Basin extending from the Dwyka of Late Carboniferous age to the Beaufort of Late Permian/Triassic age.

Ann Cadman, a staff member of the BPI and Sue de Villiers, a PhD student presently registered at the Institute, are presently studying the Late Cretaceous/Early Tertiary spore and pollen assemblages from the west coast and adjacent Namaqualand interior. These studies will provide valuable information about climatic and plant regimes during this time. So far, assemblages from the Koiningnaas site in Namaqualand indicate a Palaeogene age and show that the climate was humid and subtropical. The vegetation was predominantly ancient rain forest which included gymnospermous elements of araucarian and podocarp affinity, with abundant angiosperm trees, shrubs and herbs (De Villiers 1994). Looking at assemblages from various sites on – and offshore, Ann Cadman was able to conclude that the diverse fern representatives and many angiosperm forms indicated conditions vastly different from present on the west coast of southern Africa (Cadman 1994).

CONCLUSIONS

The scope of palynological work still to be done in southern Africa remains unlimited. It is hoped that future research will continue to focus on the creation and refinement of biozonation schemes and that collaborative work will continue between the palaeontological and geological disciplines. A clearer understanding of the past can only be achieved by applying and integrating the research emanating from the various palaeontological subdivisions. Students and past staff members of the BPI have without doubt significantly contributed to the quest of unraveling the historical development of the earth's crust in southern Africa. It is sincerely hoped that the BPI will continue to foster palynological research and that in time many useful answers will be found in studying the fossil spores and pollen that were 'blowing in the wind' many millions of years ago.

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THE ROLE OF FOSSILS IN INTERPRETING THE DEVELOPMENT OF THE KAROO BASIN

by

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ABSTRACT

The Permo-Carboniferous to Jurassic aged rocks of the main Karoo Basin of South Africa are world renowned for the wealth of synapsid reptile and early dinosaur fossils, which have allowed a ten-fold biostratigraphic subdivision of the Karoo Supergroup to be erected. The role of fossils in interpreting the development of the Karoo Basin is not, however, restricted to biostratigraphic studies. Recent integrated sedimentological and palaeontological studies have helped in more precisely defining a number of problematical formational contacts within the Karoo Supergroup, as well as enhancing palaeoenvironmental reconstructions, and basin development models.

KEYWORDS: Karoo Basin, Biostratigraphy, Palaeoenvironment, Basin Development.

INTRODUCTION

The main Karoo Basin of South Africa preserves a retro-arc foreland basin fill (Cole 1992) deposited in front of the actively rising Cape Fold Belt (CFB) in southwestern Gondwana. It is the deepest and stratigraphically most complete of several depositories of Permo-Carboniferous to Jurassic age in southern Africa and reflects changing depositional environments from glacial to deep marine, deltaic, fluvial and aeolian (Smith *et al.* 1993).

The sedimentary rocks of the Karoo Basin have yielded a diverse and important fossil biota including macro- and micro-palaeobotanical remains, vertebrate and invertebrate body fossils and traces. These fossils preserve a picture of the evolution of life during the Permo-Triassic and early Jurassic, and are also of interest for the information they supply in unravelling the geological development of the Karoo Basin.

The role of palaeobotanical megaplant fossils is reviewed by Anderson and Anderson (this volume) and will not be covered here. Research on fossil wood is becoming an important aid, both for its biostratigraphic potential, and for the elucidation of palaeoclimatic and palaeoenvironmental variables (Bamford *pers. comm.*). Palynological studies are increasingly proving important for biostratigraphic applications (MacRae 1988; Aitken 1995), age refinements and for the palaeoenvironmental information they supply.

Invertebrate fossils are rare in Karoo strata, except for the Estcourt and Molteno Formations, where insects are fairly common (van Dijk 1978; Rieck 1973, 1974, 1976 a,b,c,d; Cairncross *et al.* 1995; Anderson & Anderson, this volume). The Ecca Group and the Molteno, Elliot and Clarens Formations of the "Stormberg Group" also preserve a limited shelled invertebrate fauna (Du Toit 1936; Rilett 1951, 1963; Le Roux 1960; Teichert & Rilett 1974; Tasch 1984; Cairncross *et al.* 1995).

Invertebrate remains are important as indicators of facies genesis, including water temperature and salinity, as age indicators, and for their biostratigraphic potential.

Fossil fish are relatively rare in the Karoo Supergroup, but where present are useful indicators of gross palaeoenvironments (e.g. Keyser 1966) and also have biostratigraphic potential (Jubb 1973; Bender *et al.* 1991). Current research on the fish of the Eccca Group (Evans *pers. comm.*), the Beaufort Group (Bender *pers. comm.*) and the Molteno Formation (Sytychevskaya *et al. in prep.*) of the "Stormberg Group", may show them to be valuable aids in further delineating biostratigraphic associations, palaeoenvironments and as an aid to understanding the infilling of the Karoo Basin.

Despite their relative abundance in the rocks of the Karoo Supergroup, ichnofossils have received only cursory attention in the literature, with most work being of a purely descriptive nature (e.g. Anderson 1975 a,b,c, 1981; Visser & Loock 1978; Shone 1978). Ichnofossils also have vast potential for palaeoenvironmental reconstructions in the Karoo (e.g. Hobday & Taverner-Smith 1975; Stanistreet *et al.* 1980; Smith, 1993) in that they provide for estimates of water depth, sedimentation rates and possibly even biostratigraphic studies (Ellenberger 1970; Olsen & Galton 1984; Raath *et al.* 1990). In addition their potential for aiding in the recognition of deltaic subenvironments has implications for coal exploration and exploitation.

Palaeosols (fossil soils) are also useful, in that they reflect the prevailing groundwater conditions and palaeoclimate in the basin, and also delineate times of non-deposition. Research into palaeosols has proved useful for palaeoenvironmental and basin fill interpretations of the Karoo (Smith 1990b; Smith & Kitching 1997). A recent study of the taphonomy and areal extent of the *Tritylodon* Acme Zone, a

CLARENS F.	BEDS	ZONES				ASSEMBLAGE ZONES			
	Broom (1906)	Watson (1914a, modified 1914b)	Watson (1942)	Kitching (1970, 1977)	Cooper 1982	Keyser & Smith (1977–78)	Keyser (1979) SACS (1980)	Rubidge SACS (1996)	Kitching & Raath (1984)
ELLIOT F.									Massospondylus
									Euskelosaurus
MOLTENO F.									
BEAUFORT GROUP	Cynognathus	Cynognathus	B	Cynognathus	Tetragonias	Kannemeyeria	Kannemeyeria–Diademodon	Cynognathus	
		Cynognathus	A		Kannemeyeria				
	Procolophon	Procolophon		Lystrosaurus	Lystrosaurus	Lystrosaurus	Lystrosaurus–Thrinaxodon	Lystrosaurus	
	Lystrosaurus	Lystrosaurus							
	Kistecephalus	Cistecephalus	B	Daptocephalus	Dicynodon	Dicynodon lacerticeps	Dicynodon lacerticeps–Whaitsia	Dicynodon	
			A	Cistecephalus	Cistecephalus	Aulacephalodon–baini	Aulacephalodon–Cistecephalus	Cistecephalus	
	Endothiodon	Endothiodon	B			Tropidostoma microtrema	Tropidostoma–Endothiodon	Tropidostoma	
			A						
	Pareiasaurus	Tapinocephalus		Tapinocephalus	Robertia	Pristerognathus/Diictodon	Pristerognathus/Diictodon	Pristerognathus	
						Dinocephalian	Dinocephalian	Tapinocephalus	
								Eodicynodon	

Figure 1: Past and present biostratigraphic subdivisions of the Karoo Supergroup (modified after Rubidge, 1995).

fossiliferous palaeosol horizon, shows it to be important in understanding basinal development during upper Elliot (*Massospondylus* Assemblage Zone) times (Smith & Kitching 1997).

Although numerous different fossil types aid in our overall understanding of the Karoo Basin, this paper concentrates mainly on the role tetrapod body fossils have played in the biostratigraphic zonation, contact definitions and tectono-sedimentary development of the main Karoo Basin.

Because of their abundance in the Beaufort Group and the paucity of basin-wide lithostratigraphic marker horizons, synapsid tetrapod fossils (particularly therapsids) have long been used for the biostratigraphic subdivision and stratigraphic correlation of the Group (Broom 1906, 1907, 1909; Haughton 1924a, 1963, 1969; Kitching 1970, 1972, 1977, 1984; Keyser & Smith 1977-1978; Keyser 1979; Rubidge 1995; SACS 1980) (Figure 1). Different genera of the infra-order Dicynodontia are the most abundant fossil tetrapod taxa in the Beaufort Group and for this reason they are used as index fossils for five of the eight assemblage zones (Rubidge 1995). Although all of the eight biozones are based on therapsids, temnospondyl amphibians also form an important component of the tetrapod fauna of the Beaufort Group (Kitching 1978), and have recently been utilised in subdividing the upper Beaufort *Cynognathus* Assemblage Zone into three subzones (Hancox *et al.* 1995; Shishkin *et al.* 1995; Hancox & Rubidge 1995; Shishkin *et al.* 1996; Hancox 1998). Tetrapod fossils are relatively common in the "Stormberg Group" (Haughton 1924b) and have also been used for the biostratigraphic subdivision of the Elliot and Clarens Formations (Kitching & Raath 1984).

The biostratigraphic scheme erected for the Karoo Supergroup is used as the international standard for global correlation of Permian-Jurassic nonmarine deposits (Anderson 1973, 1977, 1980; Anderson & Anderson 1970, 1993 a,b; Anderson & Cruickshank 1978; Ochev *et al.* 1979; Ochev & Shishkin 1988; Battail 1993) and the world-wide distribution of Karoo fossils makes them ideal candidates for defining global biochrons (Cooper 1982; Lucas 1993; DeFauw 1993). In turn this allows for the relative ages of the biozones to be established, based on faunal contemporaneity with better dated European, Russian and South American sequences.

BIOSTRATIGRAPHY OF THE KAROO SUPERGROUP

Although the rocks of the Dwyka and Eccca Groups contain a variety of fossils, no formal biostratigraphic subdivision of these strata has yet been accepted. Informal biostratigraphies have, however, been proposed for the rocks of the Eccca Group, based on palynomorphs, invertebrates, fish and tetrapods.

The rocks of the Whitehill Formation (lower Eccca) are restricted to the southern Karoo Basin and contain fossils of *Mesosaurus*, the oldest tetrapod taxon known from the Karoo Supergroup. These strata also host a

number of other fossils including palaeoniscid fish and the crustacean *Notocaris tapscottii* (Oelofsen 1981). Based on the presence of these forms, Oelofsen (1987) established an informal biostratigraphy for the Whitehill Formation, which he correlated with the Irati Shale Formation of Brazil. On the basis of their palynological signatures, the Whitehill Formation (southern Eccca Facies) has more recently also been correlated with the Vryheid Formation of the coal bearing northern Eccca Facies (Cairncross, 1989; Aitken & MacRae *pers. comm.*). MacRae (1988) proposed a biostratigraphic subdivision of the rocks of the Eccca Group in the Waterberg Basin based on the ranges of Permian palynomorphs and Aitken (1995) applied this scheme to the Vryheid Formation in Gauteng and Mpumalanga.

The vertebrate biostratigraphic subdivisions of the overlying Beaufort Group are better established and have become the global biostratigraphic standard for the nonmarine Permo-Triassic. The most widely followed early work was that of Broom (1906), which was accepted for some 60 years, until revised by Kitching (1970, 1972, 1977). Keyser & Smith (1977-78) proposed a new vertebrate biozonation for the Beaufort Group west of 26°E, and linked these zones to the lithostratigraphy. This work was revised by Keyser (1979) and accepted by S.A.C.S. (1980). Since this time the biostratigraphy has been further refined and expanded to include the new basal *Eodicynodon* Assemblage Zone (Rubidge 1990), in strata which were previously held to be of the Eccca Group (Barry 1970, 1974).

These new additions and revisions have culminated in the present eight-fold biostratigraphy of the Beaufort Group (Rubidge 1995) (Figure 1). At present no subdivisions of the various biozones are accepted, although recent research suggests that this may be possible for the *Tapinocephalus* Assemblage Zone (Boonstra 1969; Looock *et al.* 1995) and *Cynognathus* Assemblage Zone (Hancox *et al.* 1995).

Boonstra (1969) first suggested a threefold subdivision for the *Tapinocephalus* Assemblage Zone, based on the relative abundance of dinocephalians and dicynodonts. He proposed a lower subzone, in which dinocephalians were the most abundant form, a middle subzone in which dicynodonts were most abundant and dinocephalians were rare, and an upper subzone in which dinocephalians were absent. Boonstra's (1969) upper subzone may be equated to the *Pristerognathus* Assemblage Zone (Keyser & Smith 1978). Boonstra (1969) was, however, unable to tie the ranges and abundances to the lithostratigraphy. Looock *et al.* (1995), in a combined litho- and biostratigraphic project, were able to correlate the contact of the lower and middle subzones of Boonstra (1969) with the contact between the Wilgerbos and Koornplaats Members of the Abrahamskraal Formation. This finding has economic implications in that it allows for the stratigraphic delineation of the DR-3 Uranium anomaly near Laingsburg.

Although the *Cynognathus* Assemblage Zone is not presently biostratigraphically subdivided, previous workers (Watson 1942; Kitching 1977; Keyser & Smith 1977-78; Cooper 1982) have documented various biostratigraphic trends and Hancox *et al.* (1995) have proposed a threefold subdivision for the biozone. This subdivision is based primarily on the spatial (Figure 2) and temporal ranges (Figure 3) of three key temnospondyl amphibian genera, and their associated faunas. These workers proposed a lower subzone (A), based on the first appearance datum (FAD) of the amphibian *Kestrosaurus*, a middle subzone based on the FAD of *Parotosuchus africanus* and an upper subzone based on the FAD of new, large capitosauroid amphibians similar to *Parotosuchus megarhinus* from East Africa.

Further collecting and research has allowed for the refinement of this subdivision and of the biostratigraphic ranges of the component faunas. *Kestrosaurus*, the index genus for subzone A is restricted in its range to the subzone, and the subzone may be further delineated by: the presence of the trematosuchid amphibian *Trematosuchus* (Shishkin & Welman 1995); primitive brachyopid amphibians (Shishkin *pers. comm.*); primitive archosaurs, similar to the Russian genus *Gaijania* (Welman *pers. comm.*);

and the cynodont *Trirachodon kannemeyeri* (Welman *pers. comm.*). To date no dicynodonts are known from subzone A. The base of the overlying subzone B is further characterised by: the FAD of the dicynodont *Kannemeyeria*; the presence of the brachyopid amphibian *Batrachosuchus*; the archosauriforms *Erythrosuchus* and *Euparkeria*; the rhynchosaurs *Howesia* and *Mesosuchus*; and the cynodont *Trirachodon berryi* (Welman *pers. comm.*). The uppermost subzone (C) is further defined by the presence of stahleckerioid and shansiodontid dicynodonts (Hancox & Rubidge 1994, 1996; Hancox 1998) (Figure 3).

The biostratigraphy of the overlying "Stormberg Group" is not as well constrained and although the Molteno Formation preserves one of the richest assemblages of Triassic megaplant and insect fossils, it is presently not biostratigraphically subdivided. Ellenberger (1970) proposed a biostratigraphic subdivision for the Molteno, Elliot and Clarens Formations based on vertebrate trackways. This division has however failed to find general scientific acceptance. Recent discoveries by Raath *et al.* (1990) of dinosaur trackways in the upper Molteno Formation may shed new light on the biostratigraphic potential of trackways in the upper part of the Molteno Formation. Anderson & Anderson (*pers. comm.*) propose a five-fold subdivision for the Molteno Formation based on the association of various plant and insect genera.

Kitching & Raath (1984) proposed a two-fold subdivision of the Elliot and Clarens Formations, based on the ranges of the prosauropod dinosaurs, *Euskelosaurus* and *Massospondylus*. Within the *Massospondylus* Assemblage Zone is

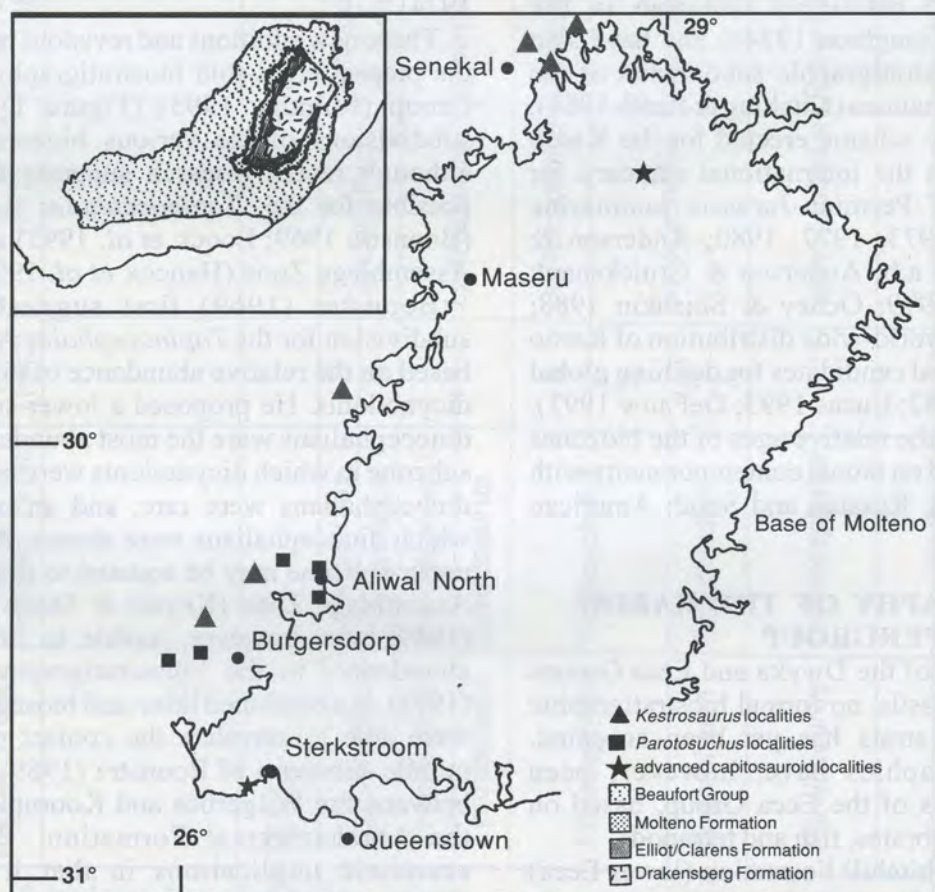


Figure 2: Spatial distribution of the three key capitosauroid amphibian genera from the *Cynognathus* Assemblage Zone.

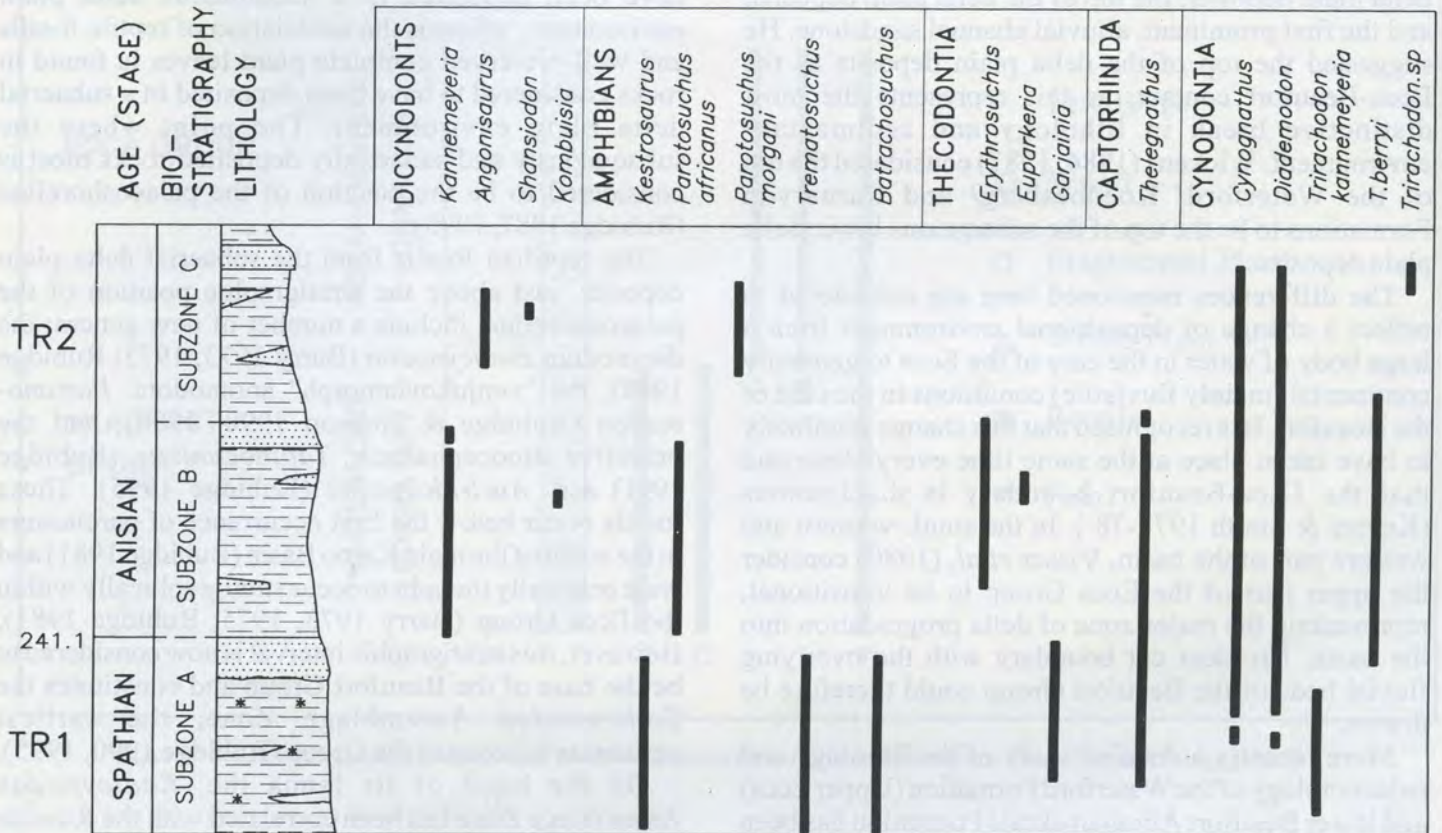


Figure 3: Temporal ranges of the key amphibian genera and associated tetrapod faunas of the *Cynognathus* Assemblage Zone (from Hancox, 1998).

a thin reworked palaeosol unit (Smith & Kitching, 1997), designated the *Tritylodon* Acme Zone based on the abundance of the cynodont *Tritylodon longaevus* (Kitching & Raath 1984).

THE USE OF FOSSILS IN AIDING IN THE DEFINITION OF FORMATIONAL CONTACTS.

Apart from their biological and biostratigraphic significance, fossils have also been utilised in defining formational contacts in the Karoo Supergroup (e.g. Rubidge 1987, 1988; Turner 1975; Christie 1981; Hancox 1998). The following section documents two case studies, the first for the basal Beaufort-Ecca Group contact, and the second for the upper Beaufort "Stormberg Group" contact.

The Ecca-Beaufort Contact

The exact stratigraphic position of the Ecca-Beaufort boundary in the southern Karoo Basin has long been a contentious issue and various parameters have in the past been used to define the boundary. This has resulted in confusion amongst workers, as the criteria previously used to define the boundary represent variations of lithostratigraphic, biostratigraphic, and palaeo-environmental characteristics.

Initially the boundary between the Ecca and Beaufort Groups was defined biostratigraphically as the FAD of pareiasaurian remains (Hatch & Corstophine 1909; Rogers 1905; Rogers & du Toit 1909; Schwarz 1912). Researchers later defined the contact lithologically, on

the occurrence of the first purple mudstones (Haughton *et al.* 1953; Mountain 1946; Rossouw 1961; Rossouw & De Villiers 1952). This boundary is no longer regarded as satisfactory because the first appearance of purple mudstones varies stratigraphically on a regional scale (Johnson 1976, 1979). Chert beds have also been considered as a useful lithostratigraphic criterion in defining the boundary as lenses of cherty rock occur at various horizons in typically Beaufort beds, but are absent below the purple shale except for one well-defined chert horizon not far below the first purple shale (Haughton 1969; Haughton *et al.* 1953; Rossouw *et al.* 1964). Another lithostratigraphic character previously used is the base of the first massive sandstone above the argillaceous Fort Brown Formation (Venter 1969; Woodward 1964).

More recently a lithostratigraphic boundary based on the change in lithology from thick accumulations of dark fines, to interbedded lenticular sandstones and fines has been used. This contact is further thought to reflect a change from deposition in a deep-water marine and deltaic environment in the case of the Ecca, to continental fluvial conditions in the Beaufort Group (Johnson 1976, 1979; Looock *et al.* 1979; S.A.C.S. 1980; Visser & Looock 1974). Jordaan (1981) identified four sedimentary associations in the Ecca-Beaufort transition in the Western Karoo which reflect deposition in the prodelta, delta front, delta plain, and flood plain environments. He considered four options for the Ecca-Beaufort contact in this area: the base of the Upper Ecca (Waterford Formation); the base of the

delta plain deposits; the top of the delta plain deposits; and the first prominent, alluvial channel sandstone. He suggested the top of the delta plain deposits as the Ecce-Beaufort contact, as this represents the most distinctive break in lithology and sedimentary environment. Wickens (1984, 1987) considered the top of the Waterford/ Koedoesberg/ and Carnarvon Formations to be the top of the subaqueous lower delta plain deposits.

The differences mentioned here are considered to reflect a change of depositional environment from a large body of water in the case of the Ecce to generally continental (mainly fluvial) conditions in the case of the Beaufort. It is recognised that this change is unlikely to have taken place at the same time everywhere and that the Ecce-Beaufort boundary is diachronous (Keyser & Smith 1977-78). In the south-western and western part of the basin, Visser *et al.* (1980) consider the upper part of the Ecce Group to be transitional, representing the major zone of delta progradation into the basin. No clear cut boundary with the overlying fluvial beds of the Beaufort Group could therefore be drawn.

More recently a detailed study of the lithology and palaeontology of the Waterford Formation (Upper Ecce) and lower Beaufort Abrahamskraal Formation has been undertaken in the southern Karoo (Rubidge 1987, 1988). At all localities studied, therapsid fossils were found only in the upper part of the stratigraphic sequence, together with the remains of complete well-preserved leaves and stems of the plants *Glossopteris* and *Schizoneura*. Some of the latter were found in their position of growth (Rubidge 1987; 1988). Raindrop impressions, wrinkle marks, and rare sand-filled mudcracks have been found on the upper surface of mudrocks and suggest subaerial exposure. Furthermore, calcareous nodular horizons, of possible palaeosol origin (Smith 1990), are frequently present in the argillaceous sediments. The association of fossil reptiles and well-preserved fossil plants, some even in their growth position, in the upper part of the stratigraphic interval, supports the concept of a subaerial depositional environment for these rocks, which are considered to have been deposited in a subaerial delta plain environment (Loock *et al.* 1979; Stear 1980 a,b; Rubidge 1988).

The fossils that characterise the lower part of the stratigraphic interval are fragments of silicified wood and fossil tree stumps, as well as numerous small plant fragments similar to those often referred to as 'coffee grounds' in the Mississippi delta. The fragmentary nature of the plant material probably reflects the fact that they had been transported, and not preserved close to their growth positions. The wood probably drifted in (Visser & Loock 1978), became waterlogged and sank, and, as driftwood is hard and resistant, the fragments could have been transported a long way (Rubidge 1987). It is considered that the rocks of this interval were deposited in a subaqueous delta plain environment.

Two biological associations are thus evident (Figure 4): waterlogged wood and finely ground-up plant remains tend to be confined to the rocks considered to

have been deposited in a subaqueous delta plain environment, whereas the association of reptile fossils and well-preserved complete plant leaves is found in rocks considered to have been deposited in a subaerial delta plain environment. The point where the subaqueously and subaerially deposited rocks meet is considered to be the position of the palaeoshoreline (Rubidge 1987, 1995).

The reptilian fossils from the subaerial delta plain deposits, just above the stratigraphic position of the palaeoshoreline, include a number of new genera; the dicynodont *Eodicynodon* (Barry 1973, 1975; Rubidge 1988), the "venjukoviamorph" anomodont *Patranomodon* (Rubidge & Hopson 1990, 1996), and the primitive dinocephalians *Tapinocaninus* (Rubidge 1991) and *Australosyodon* (Rubidge 1995). These fossils occur below the first occurrence of pareiasaurs in the south of the main Karoo Basin (Rubidge 1981) and were originally thought to occur stratigraphically within the Ecce Group (Barry 1973, 1975; Rubidge 1981). However, this stratigraphic interval is now considered to be the base of the Beaufort Group and constitutes the *Eodicynodon* Assemblage Zone, the earliest vertebrate biozone of the Group (Rubidge 1990, 1995).

On the basis of its fauna the *Eodicynodon* Assemblage Zone has been correlated with the Russian Ocher and Ishevo complexes (Rubidge 1995), and the Xidagou Formation at Yumen in the Gansu Province of China (Li & Cheng 1995; Li *et al.* 1996). Correlation of the primitive anomodont and dinocephalian fauna of this zone with a similar fauna from the Russian complexes suggests a Kazanian age (Rubidge 1987, 1995).

The recognition of a new fauna at the base of the Beaufort has important implications for the placement of the Ecce-Beaufort contact on the palaeoshoreline and the recognition of the palaeoenvironment of the Upper Ecce and Lower Beaufort (Figure 5). Lowering the stratigraphic position of the Ecce-Beaufort contact has increased the thickness of the Lower Beaufort by some 300-650m, dependant on the locality (Rubidge 1990) and has given new insight for interpretation on the basinal development of the earliest terrestrial deposits of the Karoo. Because the oldest biozone of the Beaufort is found only in the southwestern part of the basin, it is evident that the oldest terrestrial deposits of the Karoo are limited to that part of the basin. This feature has important implications for defining the diachronous nature of the Ecce-Beaufort contact, as progressively younger fossils are found along this contact farther north in the Karoo Basin (Ryan & Whitfield 1979). Because reptilian fossils have now been found immediately above the stratigraphic position of the palaeoshoreline, it is unlikely that remains of older terrestrial reptiles will be found in the Karoo Supergroup of South Africa, unless their remains were washed into the Ecce "sea" (Rubidge 1995a).

The Beaufort-Molteno Contact

The nature and stratigraphic position of the contact between the Beaufort and "Stormberg" Groups has also been the subject of much debate (e.g. Du Toit 1954;

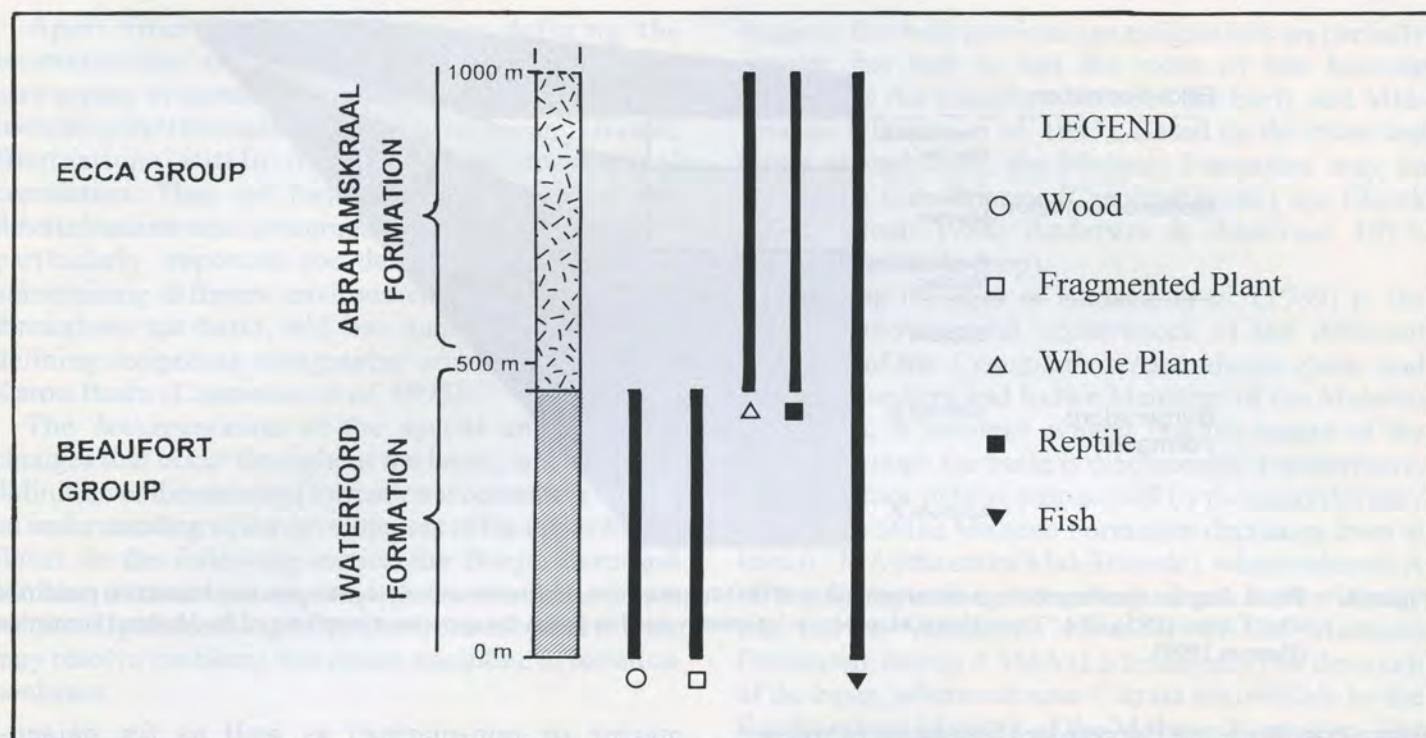


Figure 4: Biostratigraphy of the rocks of the Eccca-Beaufort transition in the southern Karoo (From Rubidge, 1988).

Turner 1975; Christie 1981; Visser 1991). This contact has in the past been defined as the base of the first coarse glittering sandstone of the Molteno Formation (Du Toit 1954); on the change in the predominant type and colour of the strata (Rust 1959, 1962; Kitching 1977); by the occurrence of well rounded pebbles in the sandstones (Kitching 1977); by its dominantly arenaceous nature (Turner 1975; Christie 1981); by the presence of coal (Du Toit 1954); and as a $\pm 100\text{m}$ thick, conformable transitional zone (Johnson & Hiller 1990). Presently the lower contact of the Molteno Formation in the south of the basin is placed at the boundary between the Burgersdorp Formation and the Bamboesberg Member of the Molteno Formation, whereas in the northern part of the basin the boundary is between the

Burgersdorp Formation and the Indwe Sandstone Member of the Molteno Formation (Figure 6).

The lower boundary of the Molteno Formation has therefore been the subject of several attempts at definition, with much debate centred around the definition and placement of the basal contact. Most of the criteria previously used are untenable and of the previous lithological criteria, only the inclusion of quartz pebbles and the presence of coal are valid at present (Hancox 1998).

Rust (1959, 1962) proposed that a better contact might be established palaeontologically and Turner (1975) noted that the lower boundary of the Molteno Formation recorded an important palaeontological break, in that the vertebrate fossils so prolific in the Elliot

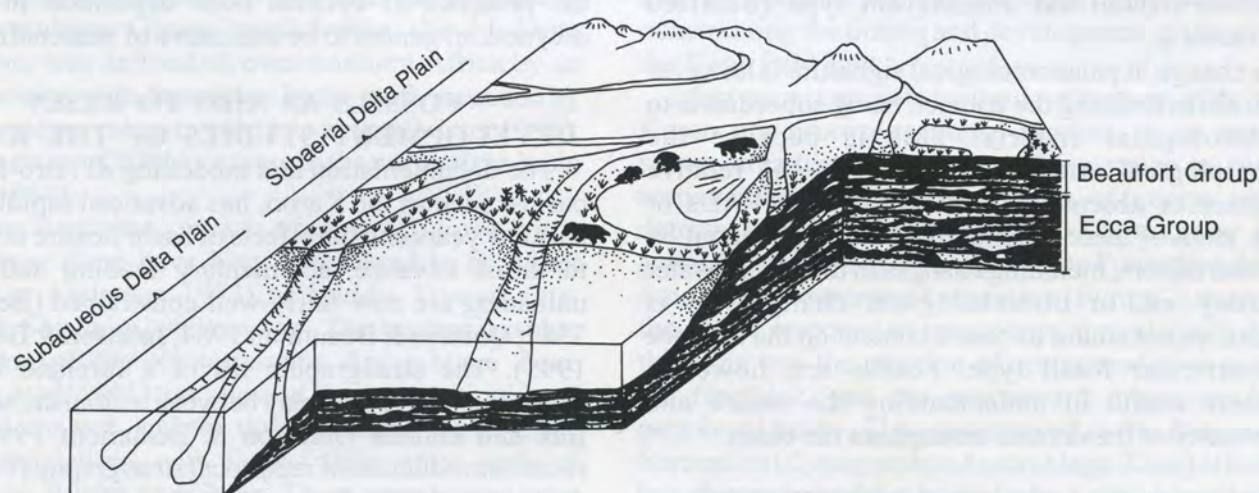


Figure 5: Palaeoenvironmental interpretation of the rocks of the Eccca-Beaufort contact in the southern Karoo. Note the relationship between the palaeoenvironment and the lithofacies associations (from Rubidge 1988, 1995).

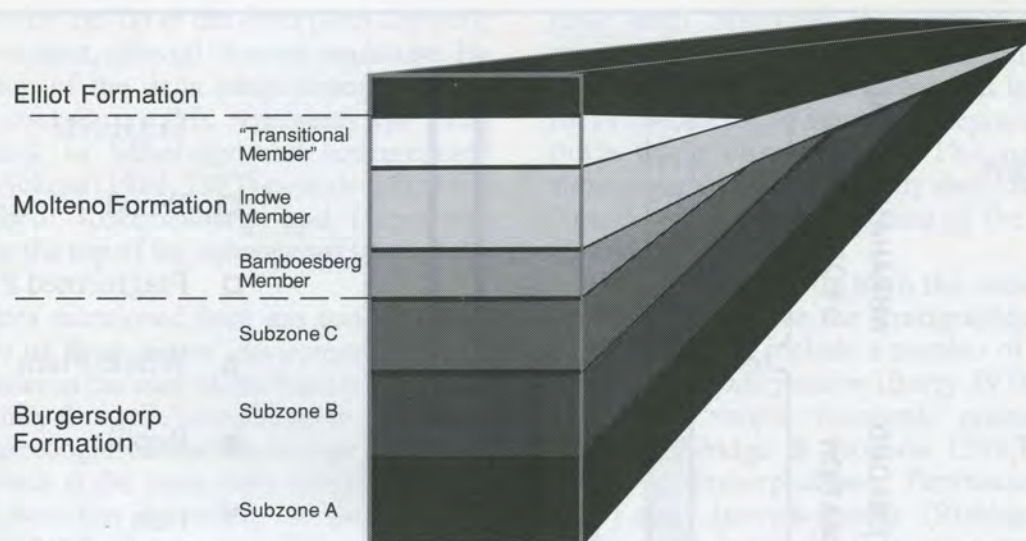


Figure 6: Block diagram showing the regional relationship of the Molteno Formation to the underlying Burgersdorp Formation (modified after Turner 1975). The 'Transitional Member' is informally used to group the uppermost members of the Molteno Formation (Hancox 1998).

Formation above and Burgersdorp Formation below, are absent in the Molteno Formation (Turner, 1972). The abrupt palaeontological break as noted by Turner (1975) has been verified by numerous authors including Anderson & Anderson (1993), Cairncross *et al.* (1995) and Hancox (1998).

Recent application of integrated stratigraphic, sedimentological and palaeontological studies has allowed for a more detailed description of the nature of this contact and the contact has now been defined sedimentologically (Hancox 1998) in terms of the differences in the gross sandstone geometries, architectural elements and facies associations between the Burgersdorp and Molteno Formations. These changes occur concomitantly with a sharp palaeontological break as documented by Turner (1975). Palaeontological criteria used to aid in defining the contact are: that tetrapod fossils are absent in the Molteno Formation; the presence of an abundant flora and insect fauna (Cairncross *et al.* 1995); and the change in wood from podocarp type to *Auricarioxylon* and *Rhexoxylon* type (Bamford *pers. comm.*).

The change in palaeontological signature is however used to aid in defining the contact, being subordinate to the lithological criteria. This is because the palaeontological criteria are based on the relative abundance or absence of taxa and not on FADs or ranges. Both of these criteria may be brought about by numerous factors, including changes in the groundwater chemistry and/or climatological changes. It is furthermore not sound to base a contact on the absence of a particular fossil type. Fossils are, however, extremely useful in understanding the nature and diachroneity of the contact throughout the basin.

FOSSILS AS AIDS TO INTERPRETING PALAEOENVIRONMENTS OF THE KAROO

Fossils have been used in interpreting the broad-scale palaeoenvironmental setting of depositional facies (i.e.

marine or non-marine) as well as for palaeoenvironmental reconstructions within the Karoo Supergroup (e.g. Hutton 1967; Boonstra 1969), including palaeoclimatic models (Visser 1991; Rayner 1995). More recently, detailed studies of the fossil assemblages have been employed to enhance earlier palaeoenvironmental interpretations (Kitching 1977; Kitching & Raath 1984) and high resolution taphonomic studies of vertebrate fossil assemblages have played an important role in recognising and delineating the spatial aspects of floodplain sub-environments within the Lower Beaufort (Smith 1978, 1980, 1981, 1989), and regional base level changes in the Elliot Formation (Smith & Kitching 1997). Rubidge (1988) used palaeontological criteria for documenting terrestrial versus subaqueous facies, as well as for delineating the palaeoshoreline of the Beaufort Group.

The presence of growth rings in fossil wood has been used to infer seasonality (Anderson 1976) and more recently Chinsamy & Rubidge (1993) have suggested the presence of cyclical bone deposition in certain dicynodont genera to be indicative of seasonality.

FOSSILS AS AIDS TO BASIN DEVELOPMENT STUDIES OF THE KAROO

The documentation and modelling of retro-foreland basins, such as the Karoo, has advanced rapidly in the past few years and the effects of basin flexure in relation to thrust advance, sedimentary loading and source unloading are now fairly well constrained (Beaumont 1981; Quinlan & Beaumont 1984; Johnson & Beaumont 1995). The stratigraphic fill of a foreland basin is controlled by the interplay between tectonism, sediment flux and climate (Johnson & Beaumont 1995). The recent introduction of reciprocal stratigraphy (Flemings & Jordan 1989; Etensohn 1994; Cataneanu 1997; Cataneanu *et al.* 1998) has meant that there is a strong need to recognise synchronous shallow and deep water settings.

Apart from their usefulness in defining the biostratigraphy and formational contacts, fossils may also supply evidence for a number of these parameters including: the timing and duration of tectonism; climatic fluctuations within the basin; and intrabasinal correlation. They are further of use in relative age determinations and for intrabasinal correlation. This is particularly important for defining time lines and constraining different environments of the same age throughout the basin, and has major applications in defining reciprocal stratigraphic architectures for the Karoo Basin (Cataneanu *et al.* 1998).

The documentation of the spatial and temporal changes that occur throughout the basin, and a concise definition of the nature of formational contacts is vital to an understanding of the development of the upper Karoo Basin. In the following section the Burgersdorp and Molteno Formations are used as an example of how combined palaeontological and sedimentological studies may resolve problems that either discipline in isolation could not.

Basin development of the upper Karoo during the Triassic

Prior to the combined use of palaeontological and sedimentological data, the controls on facies genesis for the Burgersdorp and Molteno Formations were not well understood. The proposed palaeoclimate for the Molteno Formation deviated dramatically from the global standard (Frakes 1979) and the ages of the two formations were poorly interpreted. This meant that the time represented by the contact between the Beaufort and "Stormberg" groups was not constrained and the timing of events that controlled their sedimentary fill was not well understood.

Because of the lack of direct palaeontological correlatives between the Burgersdorp and Molteno Formations, Turner (1975) found the time represented by the unconformity at the base of the Formation difficult to evaluate, but thought that the disconformity suggested a considerably greater timespan than the physical evidence indicated. Visser (1984) felt that the base of the "Stormberg Group" and hence the Molteno Formation, was defined all over southern Africa by an unconformity, with deposition in the south preceded by an erosional period up to 10MA in extent (Visser 1991), but in the order of 50MA or more in the north of the basin (Visser 1984).

In the past the rocks of the *Cynognathus* Assemblage Zone have been considered to be either Early (e.g. Anderson 1973) or Middle Triassic (e.g. Ochev & Shishkin 1989) in age. The biostratigraphic subdivision of the *Cynognathus* Assemblage Zone (Hancox *et al.* 1995) has allowed for the partitioning of its faunal content, and the direct comparison of these faunal associations with faunas from other parts of Gondwana, Russia and China. These correlations have shown that subzone A is late Early Triassic (Scythian) in age, whereas subzones B and C encompass most of the early Middle Triassic (Anisian). This partitioning

suggests that both previous age assignments are partially correct, but that in fact the rocks of this biozone encompass the boundary between the Early and Mid-Triassic (Hancox *et al.* 1995). Based on the plant and insect assemblages, the Molteno Formation may be assigned a Late Triassic (Carnian/Norian) age (Rieck 1974; Falcon 1986; Anderson & Anderson 1993; Anderson *et al.* in prep).

Applying the ages of Harland *et al.* (1989) to the spatial and temporal occurrences of the different subzones of the *Cynognathus* Assemblage Zone, and the Bamboesberg and Indwe Members of the Molteno Formation, it becomes evident that the nature of the contact through the basin is diachronous. Furthermore, the magnitude of time represented by the unconformity at the base of the Molteno Formation decreases from at least 6.1MA (the entire Mid-Triassic), where subzone A of the *Cynognathus* Assemblage Zone is overlain by the Indwe Sandstone Member of the Molteno Formation, to only 4.5MA (Ladinian only) for the south of the basin, where subzone C strata are overlain by the Bamboesberg Member of the Molteno Formation. The palaeontological signatures of the two formations therefore show that the time break between the two is of far less magnitude than suggested by previous authors (e.g. Visser 1991) and that the Mid-Triassic Lacuna proposed by Cole (1992) probably only spans the upper Anisian and parts of the Ladinian in the south of the basin.

The spatial and temporal distribution of the *Cynognathus* Assemblage Zone faunas also shows that the aerial extent of the Burgersdorp Formation decreased and shifted sourceward through time (Hancox 1998) (Figure 7). In foreland basins, such sourceward facies migrations are controlled by the flexural response to source area loading. Tectonism in the thrust belt brings about downward flexure of the lithospheric plate and the creation of accommodation space proximal to the thrust belt (Beaumont 1981; Quinlan & Beaumont 1984). This flexure also brings about the sourceward migration of the peripheral bulge and its uplift. This has important implications for constraining the timing and development of thrusting in the Cape Fold Belt.

Most current models for the development of the upper Karoo are process-response models, in as much as source area tectonism (process) is seen to be directly responsible for the progradation of coarse grained detritus into the basin (response). The decrease in the aerial distribution of the Burgersdorp Formation through time and its sourceward migration (Figure 7) shows that the actual response to source area thrusting (P) during this time was the creation of accommodation space in the forethick, and the sourceward migration of the peripheral bulge. The ages applied to the Burgersdorp Formation (*Cynognathus* Assemblage Zone) allows for this deepening of the basin to be tightly correlated to source area activity at ± 239 Ma (Gresse *et al.* 1992).

These findings, especially the timing of events based on biostratigraphic data, have allowed for previous

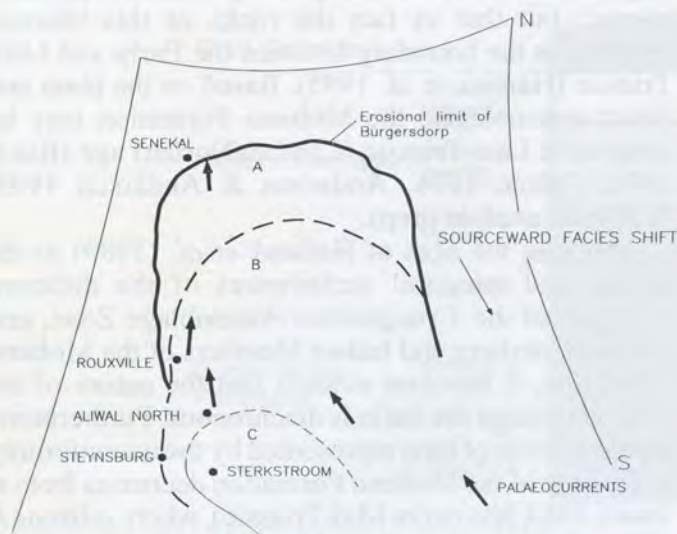


Figure 7: Spatial distribution of the Burgersdorp Formation through time, showing a retrogradational sourceward facies shift.

models for the development of the fill of the upper Karoo (Rust 1959, 1962; Cole 1991; Smith *et al.* 1993; Hancox & Rubidge 1995; Groenewald 1996) to be revised. Based on these ideas, the progradation of coarse grained detritus into the basin (such as the basal part of the Molteno Formation) represent a period of quiescence (Q) following source area thrusting, where sediment supply exceeds thrust induced subsidence. Such pulse-quiescence cycles may be more accurately modelled using the current literature on foreland basin development (Beaumont 1981; Quinlan & Beaumont 1984; Flemings & Jordan 1989; Beaumont *et al.* 1993; Ettensohn 1994; Cataneanu 1997).

In the upper Karoo Supergroup, fossils have therefore played an important role in re-evaluating the fill of the basin (Hancox *et al.* 1995; Hancox 1998; Cataneanu *et al.* 1998) by allowing for the recognition of synchronous, spatially separate depositional settings and by the delineation of chronostratigraphically significant surfaces.

DISCUSSION AND CONCLUSIONS

Fossils from the Karoo Supergroup have provided not only important data about the evolutionary history of life through the Permo-Triassic and early Jurassic, but also provide the basis for the biostratigraphic subdivision of the sequence, aid in defining formational contacts and considerably enhance palaeoenvironmental reconstructions. New finds over the past two decades have allowed for the refinement of the biostratigraphy of the Karoo Supergroup and improved correlation with faunas from other parts of southern Gondwana, Russia and China. This in turn has allowed for the refinement of the relative ages of various parts of the Karoo. The application of these relative ages to the stratigraphy has allowed for the definition of diachronous contacts within the basin (Rubidge 1988; Hancox *et al.* 1995) and the generation

of chronostratigraphically significant timelines. This represents a significant step forward in the definition of sequence based stratigraphy. Relative dating based on faunal contemporaneity is also critical for the information it supplies regarding the timing of events within the basin, and the correlation of these events to dated periods of tectonic activity in the source area (Hälbich 1983, 1992; Gresse *et al.* 1992).

It is becoming clear that biostratigraphy and lithostratigraphy have a complex inter-relationship in the Karoo Basin and although biostratigraphic subdivisions may cross lithological contacts, they are often fairly similarly constrained (Keyser & Smith 1977-8; Groenewald 1990; Loock *et al.* 1995). The combined use of biostratigraphy and lithostratigraphy has allowed for the delineation of economically important ore bodies, including the DR3 Uranium anomaly (Loock *et al.* 1995) and palaeontological parameters are also useful in defining the spatial aspects of coal deposits (Stanistreet *et al.* 1980).

Fossils have recently proved useful in the development and refinement of basin models for the deposition of the rocks of the Karoo Supergroup (Rubidge 1988; Hancox *et al.* 1995; Cataneanu *et al.* 1998) and have solved problems that lithological studies alone could not.

Fossil data, including vertebrate and invertebrate body fossils, micro and macrofloral remains, palaeosols and traces have helped to define the stratigraphy, facies genesis and palaeoclimate prevailing during the deposition of the Burgersdorp and Molteno Formations. Fossils have also played a pivotal role in defining the timespan represented by the hiatal surface between the Burgersdorp and Molteno Formations. Megafloral remains, in particular silicified wood, have also been useful in dispelling the myth of the anomalous cold, wet Molteno.

Numerous authors have previously correlated tectonic events in the Cape Fold Belt (Hälbich *et al.* 1983) with their sedimentary responses. Recent holistic studies based on combined sedimentological and palaeontological evidence have, however, added more refined time constraints to the sedimentary responses.

Combined sedimentological, stratigraphic and palaeontological studies have therefore allowed for greater stratigraphic resolution than could isolated studies on their own. Such holistic studies have allowed for the Karoo basin's long and complex developmental history to be better understood and constrained, largely due to the wealth of information provided by the fossil record.

ACKNOWLEDGEMENTS

This review paper is based on the work of numerous earth scientists whose work during the past century and a half has brought our knowledge of the Karoo Basin to its present level. The few highlighted workers are but a small number of the many upon whose work the current state of knowledge was dependant, the authors' own contributions being but a very small part of the accumulated knowledge.

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CRETACEOUS FOSSILS FROM THE ORAPA DIAMOND MINE

by

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ABSTRACT

The Orapa kimberlite pipe, situated in north-central Botswana, is well-known for its rich reserves of diamonds. It is indeed one of the largest and richest diamond mines in the world. The kimberlite magma transporting the diamonds from the upper mantle erupted through a sequence of Karoo-aged rocks before the deposition of the Kalahari Sands. This eruption has been radiometrically dated at early Late Cretaceous (Cenomanian-Coniacian). When volcanism ceased, a succession of epiclastic crater lake sediments was deposited above the kimberlite plug. Analysis of these sediments, which mostly comprise the results of mudflows and debris flows and finer sediments during quiescent times, suggests that most of the sediments within the crater were deposited rapidly as mass flows, and were therefore mobilised soon after the volcanic eruption. Buried within the fine-grained sediments is a unique assemblage of fossils including flowering plants and many whole-bodied insects. The fossils are commonly exquisitely preserved in extremely fine-grained mudstone. Interpretation of the sedimentary facies and fossils is that the mid-Cretaceous climate of central Botswana was temperate, seasonal and wet, and the area surrounding the crater was forested. The fossils represent the recovery of the biota of the area after the violent eruptions of Orapa and other nearby kimberlite fissures and pipes. The fossils have contributed considerably to our understanding of mid-Cretaceous insects and flowering plants and suggest intimate relationships between the two at an early stage in the radiation of flowering plants. It seems that southern Gondwana (including southern Africa) was a centre of diversification for both insects and angiosperms in the mid-Cretaceous.

KEYWORDS: Fossil angiosperms, Fossil insects, Fossil spider, Lagerstätten, Orapa.

INTRODUCTION

Unusually rich and well-preserved fossil assemblages have contributed considerably to our knowledge of the history of life (Whittington & Conway Morris 1985). Indeed, Sepkoski (1981) found that 20% of the clades he used in his factor analysis of Phanerozoic marine diversity were known exclusively from three such Palaeozoic localities (Hunsrückschiefer, Burgess Shale and Mazon Creek). The classic Eocene beds from Germany gave a name for these exceptional fossil localities – they are called fossil *Lagerstätten*. The information that outstanding fossil assemblages yield provides us not only with details of extinct animals and plants, and thus an indication of differing levels of diversity in the past, but, more importantly, they produce insights into palaeoecological and evolutionary relationships – since entire communities are often preserved. Such details are often lacking or incomplete in more scattered fossil assemblages. The contribution that these fossil *Lagerstätten* have made is, therefore, as remarkable as their preservation (Rayner 1993).

These exceptional *Lagerstätten* localities have almost all been found in the Northern Hemisphere, where most palaeontological activity is centred.

Recently, however, some fossiliferous sediments, which lay claim to this status, have been discovered in Southern Africa. These sediments form the infill of a volcanic crater and have been exposed by diamond mining operations. The mining activities have centred on a

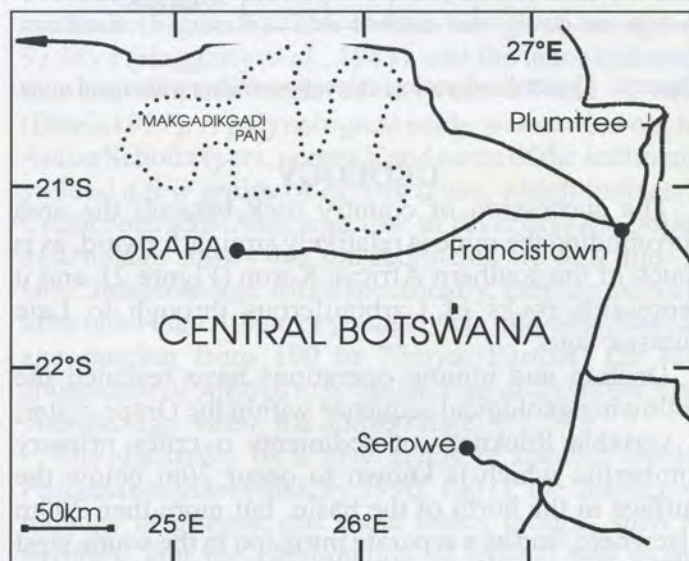


Figure 1. Map showing the locality of Orapa diamond mine.

diatreme of a large diamondiferous kimberlite pipe, located c.220 km west of Francistown in North-Central Botswana (Figure 1). The Director of the National Museum of Botswana, Alec Campbell, invited members of the BPI Palaeontology to visit the diamond mine in 1983. Professor Raath, then director of the BPI, handed the invitation on to Drs Maguire and Rayner. Subsequent excursions have produced many thousands of fossil specimens.

Kimberlites are fairly common in this part of Botswana, Orapa being the largest of a swarm of 29 kimberlite diatremes in the area. Indeed, its lobed appearance at the surface suggests it may be composite, consisting of two or even three individual kimberlite pipes (Figure 3). Recent examination by one of us (RJR) of cores taken from the central area of the mine confirms that the diatreme divides with depth.

The area surrounding the mine is extremely flat, with only a few low hills and ridges, and an average surface elevation of 960m above sea-level. The Makgadikgadi pans lie to the north, and the area is mapped as part of the Kalahari Desert. The climate today is arid to semi-arid, with an average rainfall of approximately 500mm per year. This figure is typically variable, and the rains fall almost exclusively in the summer months. The dominant vegetation is mopane bush (*Colophospermum mopane*).



Figure 2. Generalised geological section of Orapa diamond mine.

GEOLOGY

The succession of country rock beneath the area surrounding the mine is relatively straightforward, as is much of the southern African Karoo (Figure 2), and it represents rocks of Carboniferous through to Late Jurassic age.

Drilling and mining operations have revealed the following geological sequence within the Orapa crater: a variable thickness of sediments overlies primary kimberlite which is known to occur 30m below the surface in the north of the basin, but more than 200m elsewhere, and as a separate intrusion in the south-west sector. Such sediments which overlie primary kimberlite from which they were derived are termed epiclastic

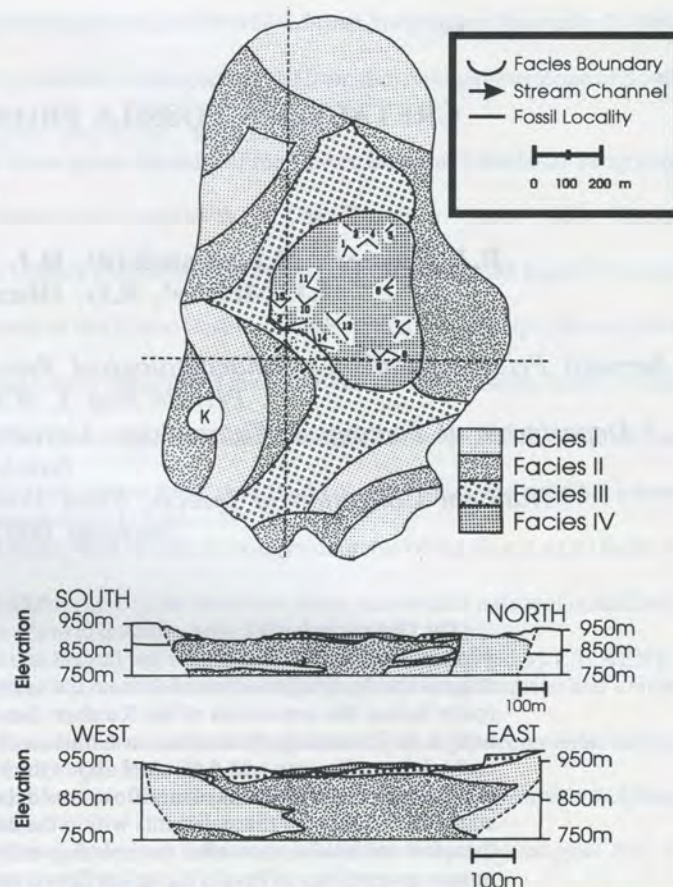


Figure 3: Facies plan and cross sections of Orapa diamond mine. The lobed outline of the crater sediments suggests that they are underlain by up to three kimberlite pipes.

kimberlite (Hawthorne 1975). An important characteristic of the petrology of kimberlite, which in this case assisted fossil preservation, is its great susceptibility to chemical and mechanical weathering and alteration. The fine-grained nature of the Orapa kimberlite matrix is particularly unstable, and would have rapidly supplied large quantities of clay-sized particles during decomposition. Further, the instability of the crater wall slopes and the subsidence as the diatreme cooled, de-gassed and contracted has produced a complex mixture of different facies. The sediments have been classified on the basis of grain size, depositional dip, nature of the matrix, sedimentary structures and genesis into four facies (Figure 3) (Rayner *et al.* 1991).

Facies I – Volcanogenic and Talus Slope Deposits

These are coarse sediments containing clasts of country rock up to 10m across. Their dips are generally greater than 20° and they are poorly sorted. At least some of these are pyroclastics (detrital volcanic material explosively ejected from the kimberlite vent). They form the outer and basal crater facies, and were formed as the diatreme grew, or just after.

Facies II Debris Flow Deposits

These have well-defined flow boundaries, and shallower dips (5-15°), and they are situated closer to the centre of the crater, and are often interbedded with finer material. Flow boundaries consist of layers of shale and

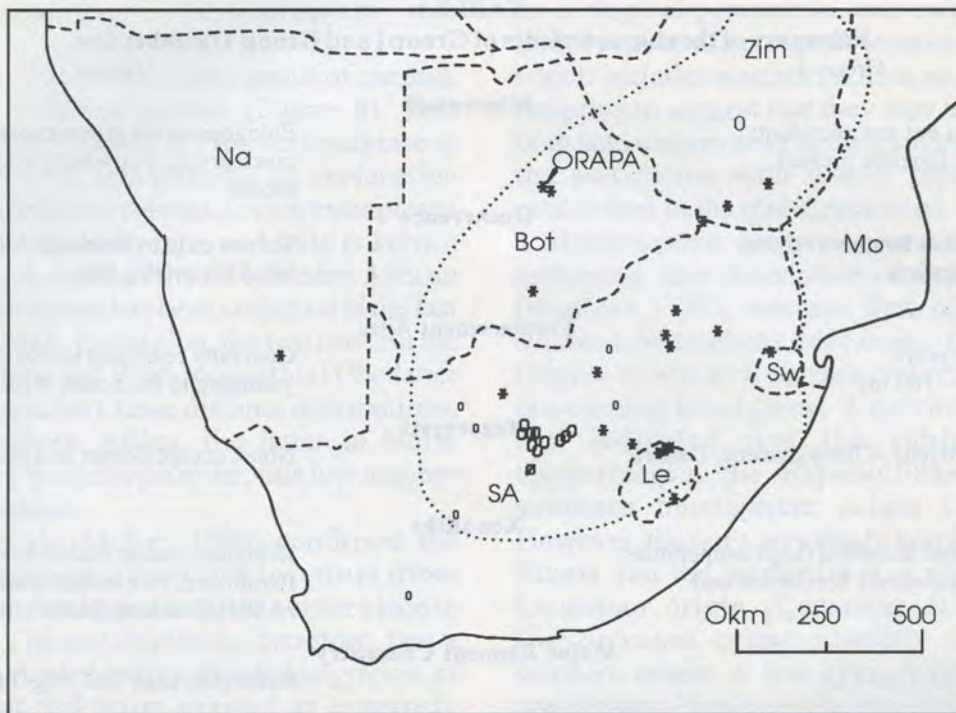


Figure 4: Localities of the Southern African Group I (*) and Group II (o) kimberlites that have been reliably dated (dates in Figure 5). Bot = Botswana; Mo = Mozambique; Na = Namibia; SA = South Africa; Sw = Swaziland; Zim = Zimbabwe. The extent of the Transvaal Craton is shown by a dotted line.

sandstone, which may be destroyed by the loading of boulders from overlying flows.

Facies III Granular Mass Flows (Mudflows)

These are finer-grained than either I or II, and are interbedded with the finest grained sediments close to the centre of the crater. They vary in thickness from over a metre to less than a centimetre, but are poorly sorted. They are persistent over many metres and dip at around 5°.

Facies IV Fine-Grained Sediments

These are the fossiliferous sediments. They occupy an oval area, 500m x 750m, to the east of the crater centre. They are well-bedded, fine mudstones, interbedded with the mud and debris flows, and vary in colour from grey-green, red, brown, to cream.

AGE OF THE SEDIMENTS AND FOSSILS

The conclusion from the nature of Facies I, II and III (Figure 3) is that they were deposited in a very short time. Indeed the deposition of the pyroclastics would have been part of the kimberlite emplacement process. Further, mud and debris flows are deposited instantaneously, commonly taking only minutes from initiation to completion (Beatty 1970; Smith 1986). These sediments comprise most of the sedimentary infill, and indicate that much of the crater was filled very rapidly. The halo of diamond-bearing soils and gravels (initially tuff and air-fall agglomerates of the ash cone) surrounding the crater indicates that, not only were the crater walls washed outwards as well as into the crater, but between 50m and 100m of sediments have been removed by erosion (Rayner *et al.* 1991). The original crater may, therefore, have had a depth of 300m. The

fine-grained fossiliferous beds are interpreted as turbidites. Each lamination represents either an individual rain storm, or several pulses within a single storm event. This tends to reinforce the suggestion of rapid infill.

A number of kimberlite pipes in southern Africa, including Orapa, have been dated radiometrically (Figures 4, 5). The pipes can be divided into two groups, mainly on the basis of mineralogy and isotope and major element chemistry (Table 1).

The indication is that the two groups have different origins. Indeed, Orapa is a group I kimberlite and almost all of these range in age from 85-110 million years ago (Figure 5).

The Orapa kimberlite has been dated by both the low-contamination hydrothermal U/Pb, and the fission track methods (Figure 6). The former has given an age of 93 Mya (Haggerty *et al.*, 1983), and the latter indicates that the eruption occurred between 87 and 92 mya (Davis 1977). A palynological study was carried out by Anton Scholtz (pers. comm.), and some of the sediments yielded a few grains of *Ephedripites*, which indicate a Cretaceous age. Although low in diversity, the pollen assemblage shows that the sediments are of a mid- to late Cretaceous age. More specifically, they are unlikely to be older than Albian or younger than mid-Senonian, an age ranging from 100 to 75mya. Further, the low abundance of species may indicate an older rather than younger age within the above range.

The discovery of a new genus of carabid beetle, *Palaeoaxinidium* (McKay 1990, 1991), the absence of remains of grasses and some insect groups, such as termites, and the combination of extinct and extant genera, are all consistent with a Cretaceous age for both the eruption and the subsequent deposition of the

TABLE 1.
Summary of the characteristics of Group I and Group II kimberlites.

Group I		Group II
Mineralogy		
Phlogopite present but not abundant; Perovskite Zircon Ilmenite present		Phlogopite-rich groundmass ± phlogopite macrocrysts, Perovskite-poor; Zircon Ilmenite absent
Occurrence		
Widely distributed in Southern Africa; Known on most cratons		Known only in Southern Africa, generally in NE-SW trending belt
Emplacement Ages		
1 600 - 50 million years; Most between 85 - 100 my		Generally restricted to 200-110 million years, younging to the South West
Megacrysts		
Olivine, Orthopyroxene, Clinopyroxene, Garnet, Ilmenite, Zircon		None, except Garnet in a few occurrences
Xenoliths		
Eclogites, coarse and deformed (high temperature) Peridotites, metasomatized Peridotites and MARIDS		Eclogites, coarse Peridotites, rare deformed Peridotites, rare metasomatized Peridotites, MARIDS lacking Rutile ± Ilmenite
Major Element Chemistry		
Relatively high TiO ₂ CaO CO ₂		Relatively high SiO ₂ MgO K ₂ O Al ₂ O ₃
Trace Element Chemistry		
Relatively high V Nb U P/Ce OIB		Relatively high Rb Ba Pb LREE/HREE, low P/Ce
Isotopic Compositions		
$^{206}\text{Pb}/^{204}\text{Pb}_0 = 18.3-20.0$ $^{87}\text{Sr}/^{86}\text{Sr} = 0.703-0.705$ $^{87}\text{Sr}/^{86}$ $^{143}\text{Nd}/^{144}\text{Nd}_0 = 0.51268-0.51276$ $^{13}\text{C} = -6.4 \pm 0.8 \text{ ‰}$		$^{206}\text{Pb}/^{204}\text{Pb}_0 = 17.2-17.7$ $\text{Sr} = 0.7075-0.710$ $^{143}\text{Nd}/^{144}\text{Nd}_0 = 0.51206-0.51227$ $^{13}\text{C} = -7.2 \pm 0.3 \text{ ‰}$

sediments. This leads us to conclude that the Orapa fossiliferous sediments (which were deposited immediately after eruption) are Cenomanian (c.95 Mya) in age.

PALAEONTOLOGY

The fossils are compressed along bedding planes, and commonly organic matter is preserved. This type of preservation is commonly referred to as coalified compression (*sensu* Schopf 1975). Specimens collected in the upper parts of the succession, however, are mere compressions, the organic matter having been

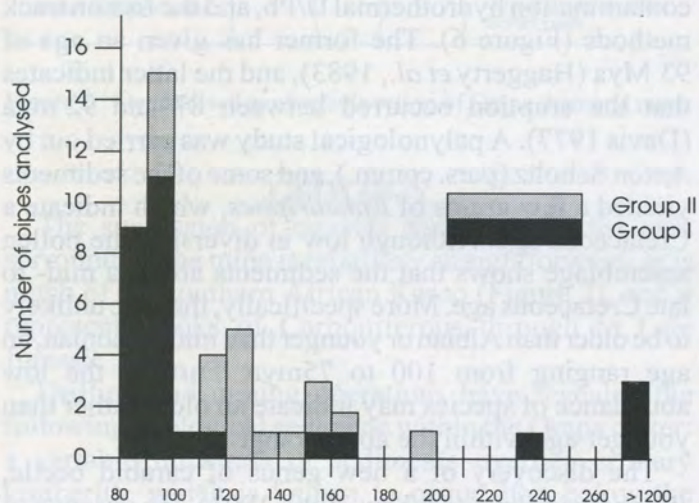


Figure 5: Histogram showing the ages of the Southern Africa Group I and Group II kimberlites (data from Anglo American internal report).

removed by oxidising groundwaters. Many insect structures, particularly the wings, and some plant fragments are highly reflective to light. This posed a problem in microscopy, particularly when taking photographs or when producing *camera lucida* drawings. A method using polarised light was developed which not only removed glare, but also enhanced the natural contrast of the specimens (Rayner 1992).

Fossil fauna

The fauna is overwhelmingly dominated by insects, with a few spiders. Most of the insects are beetles (Coleoptera) (Figure 7). This is in keeping with today's pattern of insect diversity and shows that the

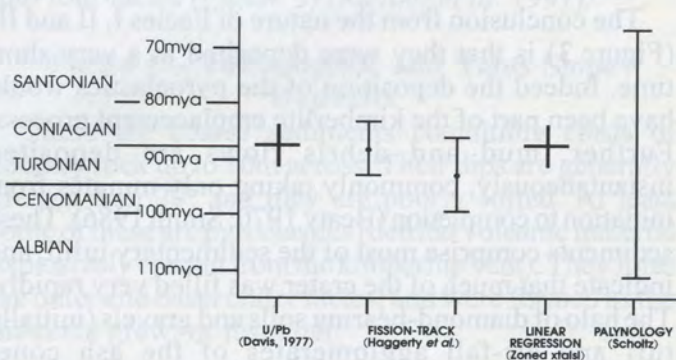


Figure 6: Summary of the age determinations for both the kimberlite and crater lake sediments of Orapa diamond mine. U/Pb data from Davis (1977), fission track and linear regression of zoned crystals from Haggerty *et al.* (1983) and palynology from Scholtz (pers. comm.).

overwhelming abundance of Coleoptera was established early.

McKay (1990, 1991) erected a new genus of carabid, or ground beetle, *Palaeoaxinidium* (Figure 8). This places the origin of the sub-family Promecognathinae in or before the Cretaceous and provides an explanation for a teasing biogeographic problem. Living examples of this sub-family are extremely rare, and little is known about their biology. Indeed, of the six southern African species, only one specimen has been collected in the last 25 years (McKay 1990). In addition, the two tribes in the sub family, Axinidiini and Promecognathini (the latter contains only two species), have disjunct distributions, the former in southern Africa, the latter in North America. For such a species-rich order, this low number of species is anomalous.

A cladistic analysis (McKay 1990) confirmed the division of the Promecognathinae into two sister tribes (Basilewsky 1958), but both constitute a sister clade to *Palaeoaxinidium*. The assumption is, therefore, that a common ancestor existed before the disintegration of Gondwana and that this taxon enjoyed an extremely wide distribution, taking in both southern Africa and North America. The distribution suggests that climatic zones typical of today were much broader in pre-Cretaceous times, and the promecognathines were spread from the Cretaceous equator to 35° S. After the separation of Gondwana, two sister tribes were established and were restricted to similar climates to those in which they are found today. The extremely low numbers of species in an otherwise species-abundant clade is presumably related to their flightless nature making them somewhat susceptible to environmental degradation.

A member of the Staphylinidae, not formally described but figured, is of considerable interest because of curious structures attached to its abdomen (Rayner & Waters 1991). These structures are small and approximately spherical, and generally consistent in both size and general morphology with pollen or spores. The highly mobile, predatory beetle may have lain in wait on primitive angiosperms or ferns for its prey – and may thereby have inadvertently carried pollen from plant to plant or inflorescence to inflorescence and acted as a pollinator. In addition, a scarab (family Scarabaeidae) has been described (McKay & Rayner 1986). The presence of a possible dung beetle in the absence of other fossil evidence for its large herbivore benefactors invites the suggestion that they were associated with large dinosaur herbivores in the mid-Cretaceous (cf. Chin 1995).

A new genus and species of weevil (Curculionoidea), *Orapaues cretaceus* (Kuschel *et al.* 1994), was placed in the tribe Eurhynchini of the family Brentidae. Several other weevils have also been described, but not named. There are only 30 living species in the tribe Eurhynchini. These occur in the eastern, wetter parts of Australia, from Tasmania to northern Queensland and in New Guinea. They seem to be absent from the drier western parts of Australia and Africa. A Gondwanan distribution is, therefore, established with the Orapa material. From

an ecological perspective, one extant species burrows into the stems of a protea. Proteaceae have a distribution which includes southern Africa and Australia and it is tempting to suggest that they may have been present on both land masses prior to their splitting and, further, that the association with weevil parasites was already established in the mid-Cretaceous.

Hymenoptera are well-represented in the Orapa sediments. The description of a new species of wasp (Brothers 1992), was the first of its kind from the southern hemisphere Mesozoic. *Curiosivespa orapa* (Figure 9) was well enough preserved to be placed in a pre-existing fossil genus. A previous cladistic analysis had indicated that the subfamily containing *Curiosivespa*, the Euparagiinae, probably had a southern hemisphere origin (Carpenter 1981). However, the only previously known fossils were from Russia and the subfamily was regarded as having a Laurasian origin (Carpenter & Rasnitsyn 1990). *Curiosivespa orapa* possibly re-establishes that southern origin. A few other well-preserved parasitic and stinging Hymenoptera (including a putative ant) are currently being studied.

A large number of Diptera have been discovered in the sediments (Waters 1990). Most Diptera are classified partly on the details of their wing venation, and this is often preserved in exquisite detail in the Orapa material, allowing reliable comparisons with modern representatives. The predatory *Pseudoacarterus orapaensis* (Figure 10) put the origin of the subfamily Hybotinae back to at least the early Mesozoic, and extended the evolution of the family Hybotidae back at least 40 million years (Waters 1989a).

Several specimens of a species of *Bibio* were found (Figures 11 & 12). All of them had identical wing venation, but more unusually they also possess evidence of wing spots, or stigmata (Rayner 1987). Such pigmentation is extremely rare in the fossil record (see also the spider, Figure 16). Bibionids are phytophagous insects and indicate the presence of substantial vegetation nearby. The living members are called March Flies, for they commonly swarm in the northern hemisphere spring. The presence of several of them on the same bedding plane indicates a similar behaviour in the mid-Cretaceous, and suggests a seasonal climate.

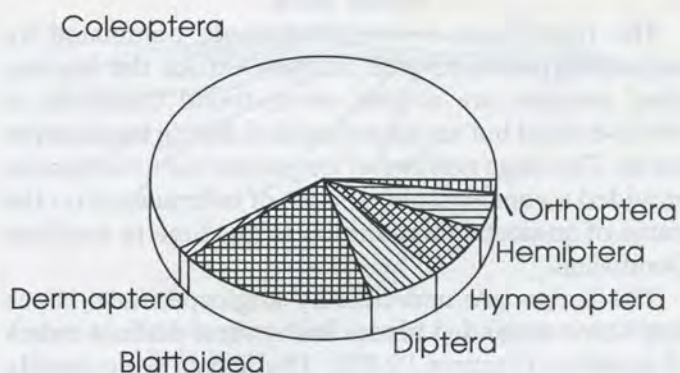


Figure 7. Summary of the relative abundance of the identified insect remains from Orapa mine.

A dance fly, *Empis (s.s.) orapaensis* Waters, was described from a single male specimen (Waters 1989b) (Figure 13). This dipteran was placed in a modern sub-genus, the representatives of which have a particularly interesting and elaborate courtship display. The male, which is exclusively predatory, captures an item of prey (many species coat it in a silken "balloon") and during their courtship "dance", offers it uneaten to the female prior to copulation. This "nuptial gift" is the only animal protein she receives and is essential for her ovarian cycle. At all other times, she feeds at flowers.

A crane-fly (Tipulidae) exhibited remarkable morphological stasis (Figure 14). Indeed, it was placed with ease in an extant cosmopolitan genus, *Helius*, and its feeding apparatus strongly suggests that it was a pollinator (Rayner & Waters 1991).

There are other indications of the close association between early flowering plants and insects at Orapa. An extremely rare find of a single wing of a fossil aphid (Figure 15), the first from Africa, resulted in a tentative assignment of the specimen to the genus *Siphonophoroides* in the family Drepanosiphidae (Rayner & Waters 1989). This representative of a group that exclusively parasitises angiosperms today suggests that the association between aphids and their angiosperm hosts developed early.

The fauna also contains large numbers of cockroaches. The Blattoidea is an ancient group and its presence at Orapa is somewhat predictable. Some of the fossil cockroaches are large and powerful animals, and yet there are no signs of disturbance in the very fine-grained sediment. It seems from this and other evidence that the waters may have been poisonous or inhospitable, and the insects therefore died soon after landing in the mud. Additional finds of interest were an orthopteran hind leg and a cricket (McKay & Rayner 1986).

The non-insect elements of the fauna included spiders. One well-preserved, almost complete specimen was placed in the superfamily Lycosoidea (Figure 16). Spider compressions are particularly rare in the fossil record, and this is the first to be described from Africa (Rayner & Dippenaar-Schoeman 1995). Such is the quality of preservation that pigmentation is even preserved on the legs (Figure 17).

Fossil flora

The fossil flora is overwhelmingly dominated by angiosperm remains (see below). Unlike the insects, plant remains are almost never found complete or whole-bodied but are disarticulated during transport or burial. The large number of fragments has nevertheless provided a considerable amount of information on the status of angiosperm evolution at this time in southern Gondwana.

The leaves are undoubtedly angiospermous, since they show expanded blades and several distinct orders of venation (Figures 19-23). The leaves were readily divided into groups on the basis of this venation (Bamford 1991). This ranged from simple-pinnate, and pinnate-compound (Figure 18) through to more complex

forms where three or more primary veins originate at one point (Figures 20, 22 & 23), and in some specimens these primary veins branch dichotomously (Figure 21). Most of the leaves were deciduous, indicating seasonality.

The flora is unique. There is nothing with which to compare it in the southern hemisphere, and the plants are unlike anything that has been described from the Northern Hemisphere. A total of 29 leaf types has been described and given formal generic and specific names (Bamford 1991). Only one of them, based on two specimens, could be placed in an existing fossil genus. This is the North American *Sapindopsis* Fontaine, a deeply lobed type. The Orapa leaf (Figure 18) is much smaller, however, and is arguably distinct generically. The leaves show similarities in levels of organisation and complexity to northern hemisphere material from the Aptian-Albian (Hickey & Wolfe 1975; Hickey & Doyle 1977).

A complex fruit from a compound inflorescence has been described (Bamford 1991) (Figure 24). In addition, three new genera and species of flowers, together with another six unnamed forms; 13 genera and 14 species of seeds and fruits; and five ferns were also described. The morphology of the flowers indicates both wind (Figures 27 & 28) and insect (Figures 26 & 29) pollination. The closed corolla tube at the base of the flower in Figure 26 indicates insect pollination and further suggests faithful pollination. However, some of the flowers show a higher level of organisation than their northern hemisphere counterparts (Friis & Crepet 1987). The tubular flower (Figure 26), for example, is considerably earlier than such structures from the north. Lower plants were also represented and several delicate ferns were found. These were presumably growing close to the lake shore.

Plant fossils were noticeably a lot less common and less diverse than the fauna. This presumably reflects the greater mobility of the flying insects which blundered into the fine-grained muds associated with the shallow crater lake. Plants were, however, more common at the top of the exposed succession than in the lower parts. We have interpreted this as possibly indicating that the volcanic explosion, or series of explosions, was so violent that it cleared vegetation for a considerable distance from the crater. The lower parts of the sedimentary succession were deposited too rapidly to permit complete colonisation by vegetation, which was only achieved later.

As the leaves cannot be compared directly with any other fossilized flora, their morphology and size characteristics are considered. The leaves are mostly small (microphyllous size class of Webb 1959). This would indicate a cool temperate or wet montane climate, the latter being unrealistic. The percentage of entire-margined leaves (45%) indicates a warm temperate and moist climate. The data are conflicting but the overriding feature of the leaves is their diversity. The flora is a successional one and inhabited the unstable inner cone slopes surrounding the crater lake and would therefore be an unreliable climatic indicator.

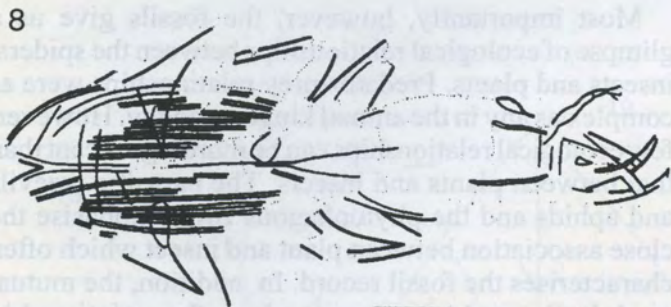


Figure 8. *Palaeoaxinidium* (McKay 1991). Scale bar 1mm.

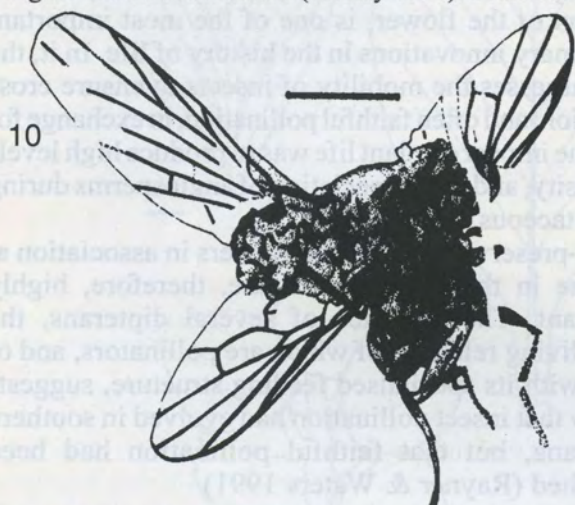


Figure 10. *Pseudoacarterus orapaensis* (Waters 1989a). Scale bar 1mm.



Figure 13. *Empis orapaensis* (Waters 1989b). Scale bar 1mm.

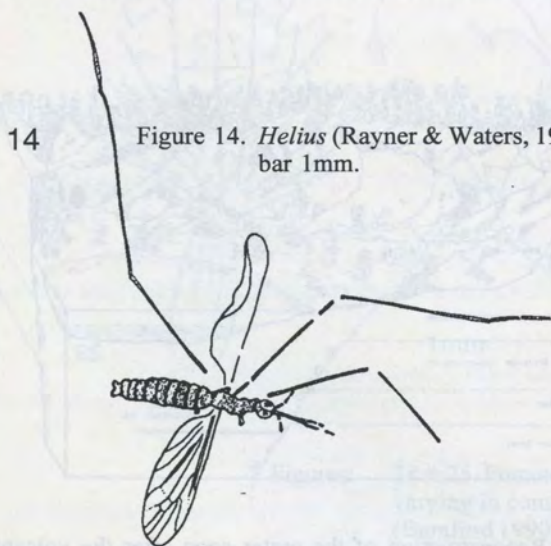


Figure 14. *Helius* (Rayner & Waters, 1990). Scale bar 1mm.

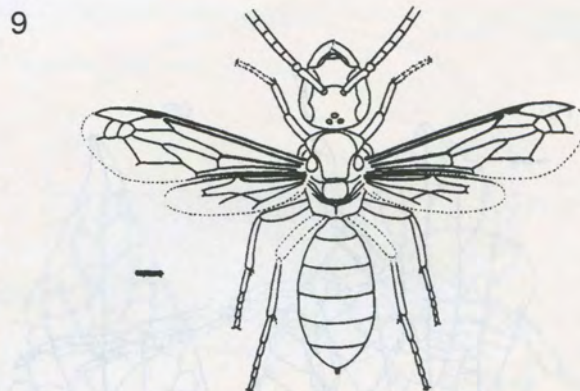
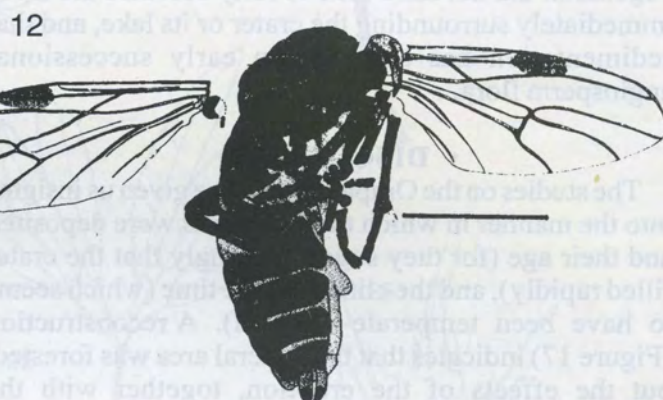


Figure 9. *Curiosivespa orapa* (Brothers 1992). Scale bar 1mm.



Figures 11 & 12. *Bibio* (Rayner 1987). Scale bar 1mm.

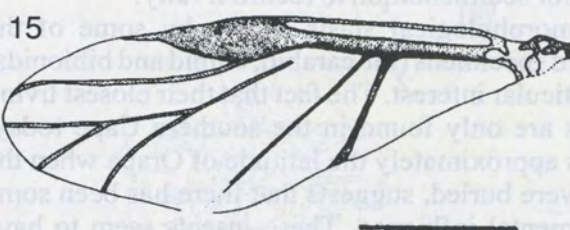


Figure 15. *Siphonophoroides? orapaensis* (Rayner & Waters 1989). Scale bar 1mm.

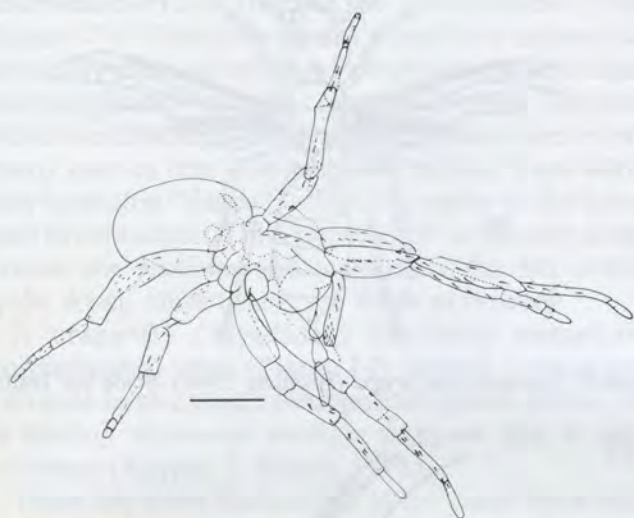


Figure 16. Spider from the family Lycosoidea (Rayner & Dippenaar-Schoeman 1995). Scale bar 10mm.

In addition, there is a notable absence of gymnosperm macrofossils in the flora (Figure 30). Today there are very few Southern African indigenous gymnosperms. However, pollen belonging to *Araucariaceae* and *Cupressaceae* and *Ephedripites* has been found in the sediments. These were wind pollinated, but are represented by very few grains. We suggest that, since these sediments represent the lower parts of the sedimentary succession, and since gymnosperms tend to be slow growing, this is further confirmation that the vegetation did not have time to fully colonise the areas immediately surrounding the crater or its lake, and that sedimentation has sampled an early successional angiosperm flora.

DISCUSSION

The studies on the Orapa fossils have given us insights into the manner in which the sediments were deposited and their age (for they suggest strongly that the crater filled rapidly), and the climate at the time (which seems to have been temperate-seasonal). A reconstruction (Figure 17) indicates that the general area was forested, but the effects of the eruption, together with the inhospitable nature of the groundwaters, prevented this vegetation being re-established in the crater soon enough for sedimentation to record it fully.

The morphological stasis shown by some of the described specimens (the carabid, empid and bibionids) is of particular interest. The fact that their closest living relatives are only found in the southern Cape today, which is approximately the latitude of Orapa when the fossils were buried, suggests that there has been some environmental influence. These insects seem to have persisted in their preferred habitat and, as Africa moved north, they remained at approximately the same latitude. Such habitat tracking has been described for Pleistocene beetles, which moved in response to periods of glaciation (Coope 1978, 1979). The unique nature of the angiosperms bears testimony to the highly derived nature of the extant members of the group.

Most importantly, however, the fossils give us a glimpse of ecological relationships between the spiders, insects and plants. Predator-prey relationships were as complex as any in the animal kingdom today. However, few ecological relationships can be more significant than that between plants and insects. The parasitic weevils and aphids and the phytophagous flies emphasise the close association between plant and insect which often characterises the fossil record. In addition, the mutual exploitation which characterises the relationship between plants and animals, and which climaxed in the evolution of the flower, is one of the most important evolutionary innovations in the history of life. In it, the plant harnesses the mobility of insects to ensure cross pollination, and often faithful pollination, in exchange for food. The impact on plant life was to produce high levels of diversity, and rapid speciation of angiosperms during the Cretaceous.

Well-preserved insects and flowers in association at this time in the fossil record are, therefore, highly significant. The presence of several dipterans, the closest living relatives of which are pollinators, and of *Helius* with its specialised feeding structure, suggests not only that insect pollination had evolved in southern Gondwana, but that faithful pollination had been established (Rayner & Waters 1991).

CONCLUSION

The Orapa diamond mine is surely only one of many such exceptional fossil localities in southern Africa waiting to be discovered. The conditions within kimberlite craters are ideal for such preservation: the basin is created suddenly; there is the opportunity for rapid burial in fine grained sediment which remains undisturbed; the normal agents of decay may be chemically excluded; and there is minimal tectonic disturbance. There is therefore a combination of conditions suitable for fossilisation: severe enough to exclude scavengers but not too severe to exclude organisms for fossilization. Rarity produces interest and the chance of further discovery. More will certainly follow.

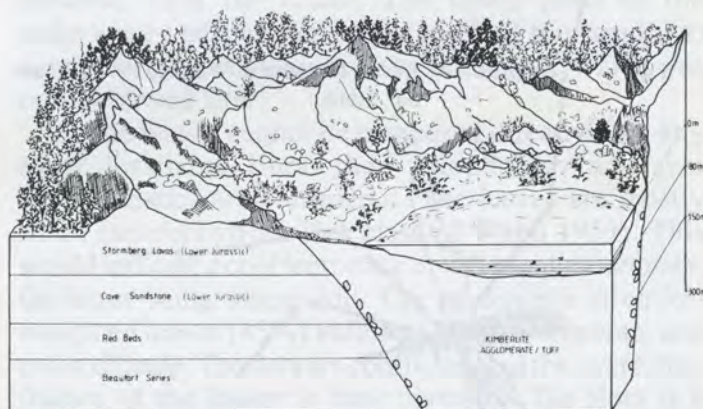
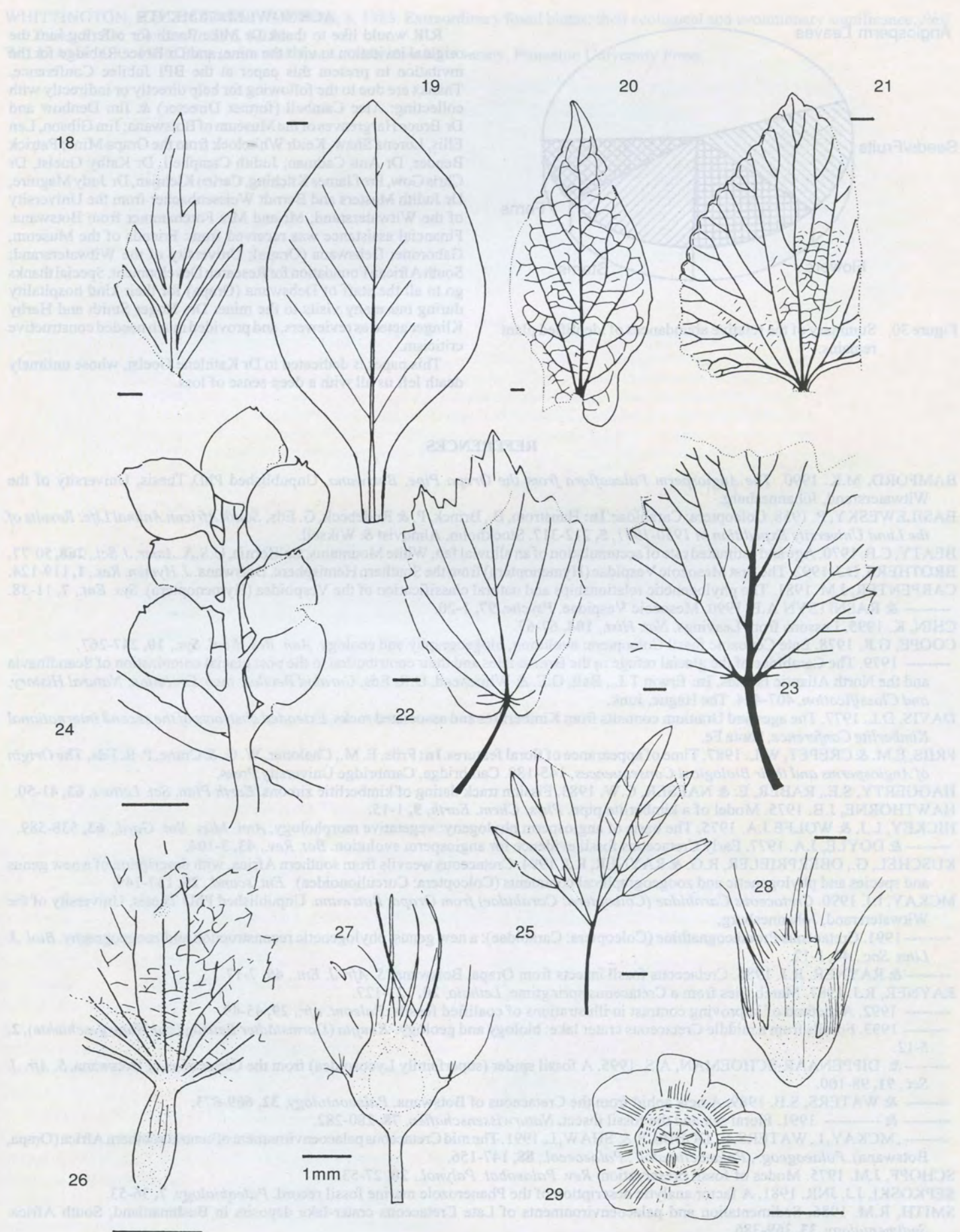


Figure 17. Reconstruction of the crater soon after the volcanic eruption (Waters 1990).



Figures: 18 & 25. Pinnate compound leaf (Bamford 1990); scale bar 5mm. Figures 19-23. Angiosperm leaves varying in complexity and venation (Bamford 1990); scale bar 5mm. Figure 24. Compound fruit (Bamford 1990); scale bar 5mm. Figures 26 & 29. Insect pollinated flowers (Bamford 1990); scale bar 5mm. Figures 27 & 28. Wind pollinated flower (Bamford 1990); scale bar 1mm.

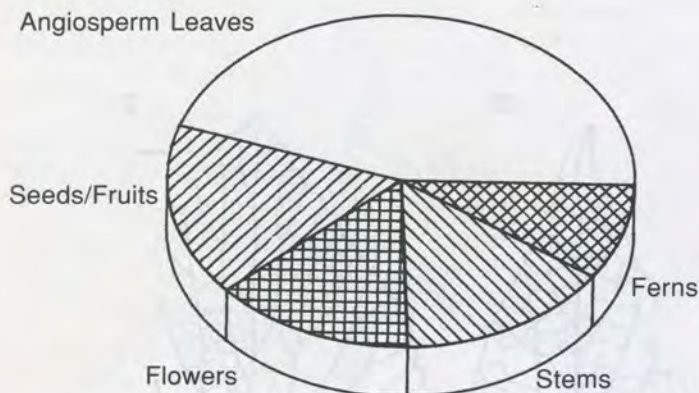


Figure 30. Summary of the relative abundances of identified plant remains.

ACKNOWLEDGEMENTS

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This paper is dedicated to Dr Kathlene Goelst, whose untimely death left us all with a deep sense of loss.

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SOME LITTLE KNOWN CHAPTERS IN THE EARLY HISTORY OF THE MAKAPANSGAT FOSSIL HOMINID SITE

by

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ABSTRACT

The opening up of the Makapansgat Lineworks deposit as an early hominid site was closely linked with the early years of the Bernard Price Institute for Palaeontological Research. Much of the history of the events leading up to James Kitching's recovery of the first australopithecine partial calvaria in 1947 is either scattered or remains unrecorded. An attempt is made here to recount the roles of W.L. Eitzman, R.A. Dart, R. Broom, C. van Riet Lowe, B. de Matas, J. Kitching and his brother Ben and Schoepes, R.J. Meunier and Dr. Bernard Price in the revelation of the scientific significance of those Lineworks and of other important sites in the area, the Cave of Hearths, Rainbow Cave, Historic Cave and Mweni's Cave. The historical part played by six student expeditions to the area in 1945-1947 is described. Save for palaeontological papers by J.S. Jernigan, O.D. van der Merwe and M.M. Dole, and archaeological ones by P.V. Tobias, the major impact of these ventures has not hitherto been analysed. It is shown that the first expedition was responsible for drawing R.A. Dart back into the field after 20 years of virtual absence, for setting about a series of further ventures in that area, and for leading to the uncovering of the first hominid specimen from the Lineworks from 1947 onwards. New evidence is presented bearing on the relationships between R.A. Dart and R. Broom, which suffered strain after both the Broom family's discovery of *Paranthropus* fossils in 1936 and those at the Makapansgat Lineworks in 1945. A note is added about the original extensive report on the first student expedition, which independent referees had recommended to the Wit University Principal, H.R. Raikes, should be published. As a result of the unexplained loss of this report, at or enroute to the publisher, it remains unpublished to this day.

KEYWORDS: Makapansgat, *Australopithecus*, *Chimpanzee*, Buffalo Cave.

INTRODUCTION

The Makapansgat Lineworks near Potgietersrus in the northern Transvaal was the fifth South African site to yield fossilized remains of early hominids. In September 1947, James Kitching discovered the posterior part of a calvaria which Dart made the holotype of a proposed new species, *Australopithecus prometheus*. This discovery followed the prior revelation of early hominids at four sites, namely those of Taung, Sterkfontein, Kromdraai and Cooper's B. Although Makapansgat is not the richest South African site to judge by the numbers of hominid specimens, it includes some of the most beautifully preserved Plio-Pleistocene fossil remains yet recovered from South and East Africa (Tobias 1972).

The recorded history of the complex of caverns in the Makapansgat area goes back to 1854, the year of the siege by the Boers of hundreds of Ndebele people of the Kekana lineage in the Historic Cave on the farm *Makapansgat* (Hofmeyr 1993). From then until 1925, these caves and that historical episode are mentioned in the accounts of W.L. Distini (1892), Paul Kruger (1902), G.G. Mannik (n.d.), G. Preller (1918-1925) and others (Figure 1). It was not, however, until the 1920s that the scientific potential of some of the caves was realised. At that time Wilfrid J. Eitzman, a teacher of

mathematics and science, and sometime vice-principal of Pieterburg High School (1919-1941), first drew the attention of the world of science to the rich fossil hoards at the Makapansgat Lineworks.

THE ROLE OF WILFRID J. EITZMAN

According to his own account, Eitzman (1958) first set eyes on the Makapansgat Valley in September-

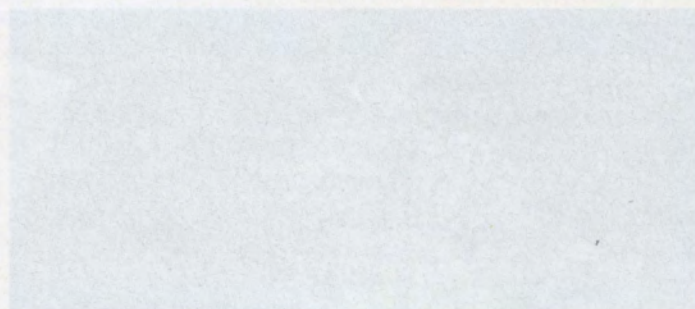


Figure 1: A photograph stated to have been taken at the entrance to the Historic Cave in the Makapansgat Valley in 1912. At that date, 58 years after the siege of Kekana people in the cave, the picture shows that large parts of the defensive walling which they constructed across the mouth of the cave were still relatively intact. The identity of the person is unknown. The photo was given to the author by the late Mr. Derryl Humphries of Beaufort.

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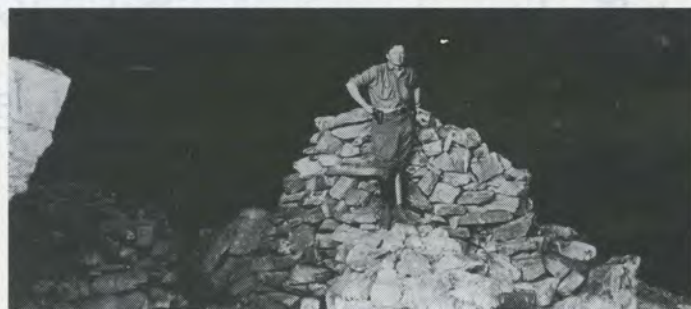


Figure 1: A photograph stated to have been taken at the entrance to the Historic Cave in the Makapan Valley in 1912. At that date, 58 years after the siege of Kekana people in the cave, the picture shows that large parts of the defensive walling which they constructed across the mouth of the cave were still relatively intact. The identity of the person is unknown. The photo was given to the author by the late Mr. Derryck Humphriss of Benoni.

October, 1922. At the main limeworks the removal of lime had already resulted in a quarry "about 15 feet deep". On the other side of the valley, "exactly opposite the quarry", he found bones embedded in brick-red breccia. This probably referred to what came to be known later as the Buffalo Cave, though we cannot exclude the possibility that he was referring to one of a number of other breccial outcrops along the south-facing scarp of Swartkrans. In fact, after mentioning the putative Buffalo Cave deposit, Eitzman states, "I wandered about in the valley and found several more such outcrops." (Eitzman 1958, p. 178). These "Swartkrans prospects" were later explored on the student expeditions of 1945-1946 and mapped by H.B.S. Cooke, whose plan of the sites on *Makapansgat* and *Swartkrans* was reproduced by Dart & Craig (1959, p. 90), and is reprinted here (Figure 2).

By the time Eitzman returned to the valley in 1924, in the company of D.J.J. Bezuidenhout, the road inspector for the district, the White Limes Company was operating vigorously at the Makapansgat Limeworks. Eitzman speaks of the miners penetrating into the hill and of fossil bone being apparent "on both sides of the tunnel". The breccia, he states, was similar to the brick red-brown breccia which he had seen two years earlier, on the opposite side of the valley (?Buffalo Cave). Lime kilns were being erected and a wood and iron dwelling was being constructed on the rising ground east of the Limeworks.

Through the courtesy of the White Limes Company, Eitzman collected samples of fossil bone in breccia, and sent some to the South African Museum (Haughton

1922; Malan 1988), but he failed to gain the attention of any South African scientist until 1925. In February 1925, the Taung skull, which R.A. Dart (1925a) made the type specimen of *Australopithecus africanus*, was announced to the world. During April 1925, Dart gave a series of lectures on physical anthropology in a vacation course for teachers at the University of the Witwatersrand. Among those who attended was Eitzman. He told Dart about Makapansgat. On his return to the northern Transvaal (now officially named the Northern Province), Eitzman revisited the Limeworks and stood amazed at the thick seams of bone which the further penetration of the limeworkings into the hillside had laid bare.

Large pieces of breccia rich in bones were sent to Dart's Department of Anatomy at the University of the Witwatersrand Medical School. According to Dart (1925b, p. 454),

"The material consists of a bone breccia containing thousands of comminuted bone fragments. The pieces of bone are so small that the animals to which they belonged cannot be ascertained with certainty, but here and there are teeth of Ungulates, small and large, of the "bok" family. As the deposit seemed to be of the cave variety and some of the bone fragments had a blackened, charred appearance, the agency of man in its formation was highly probable."

Intrigued by the blackening, and impressed by the results of some chemical tests that Eitzman had performed in the school laboratory at Pietersburg, Dart arranged for Dr. J. Moir of the Government Chemical Laboratories and Dr. F.W. Fox of the South African

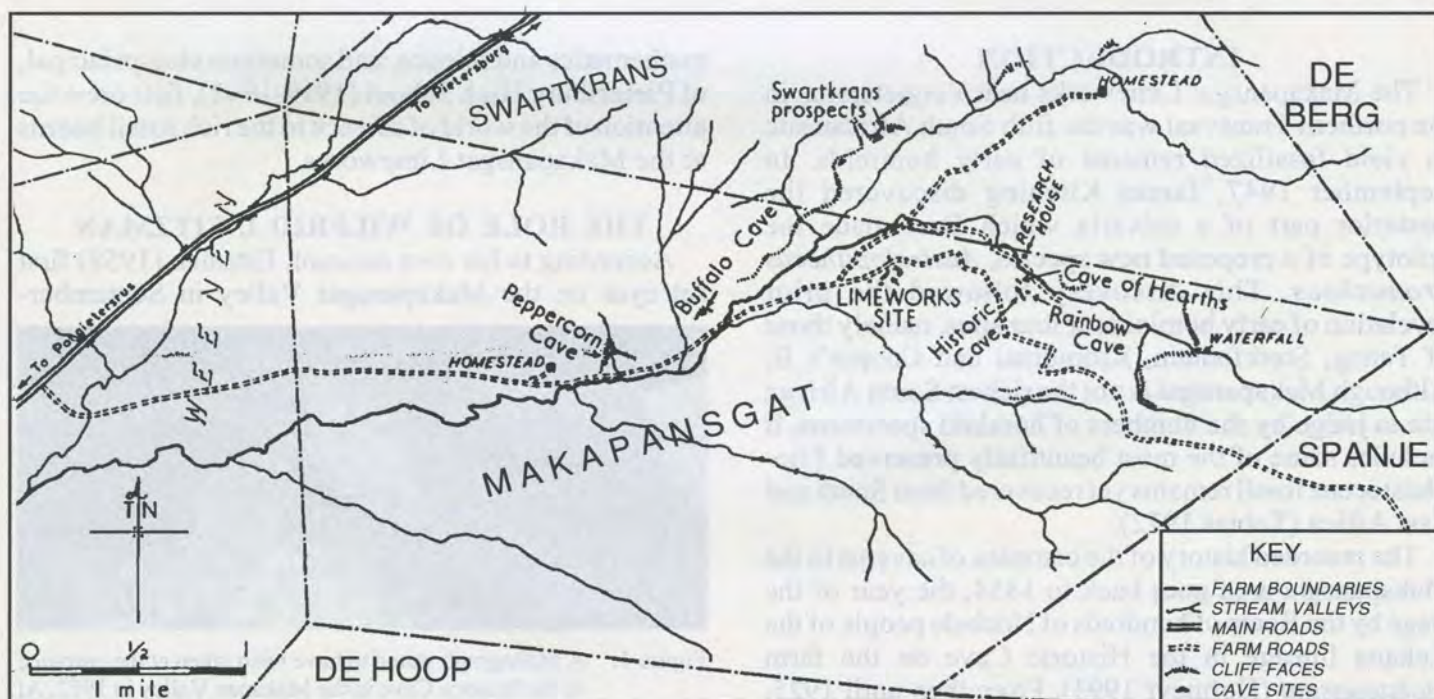


Figure 2: Plan by Dr. H.B.S. Cooke of the farm *Makapansgat* and parts of the adjacent farms, showing the positions of the principal named sites referred to in the text. The "Swartkrans prospects" were explored on the second and third student expeditions in 1945-1946 and a set of weathered hand-bones was discovered *in situ* in one of these deposits along the cliff face. This *Swartkrans* farm is not to be confused with the *Swartkrans* hominid site close to Sterkfontein. *Mwulu's* cave lies on the *Spanje* and *Portugal* farms to the east (off the map). *Peppercorn* cave and *Ficus* cave (not shown) were not visited on the six student expeditions of 1945-1947.



Figure 3: Some of the manganese-blackened bones *in situ* in the Makapansgat Limeworks deposit. Bones of this colour were sent to R.A. Dart by W.I. Eitzman in 1925 and, following chemical analysis, led to Dart's inference that they had been blackened by the action of fire and that the deposit represented a kitchen midden resulting from human occupation. Later it was concluded that the blackening was induced by the presence of manganese derived from the dolomite walls of the cave.

Institute for Medical Research to investigate some of the bone fragments (Figure 3). Their examination appeared to indicate the presence of a high percentage of free carbon. When Dart presented a brief report at the meeting of the South African Association for the Advancement of Science at Oudtshoorn on 7th July 1925, he claimed that the Makapansgat bone bed was the "kitchen-midden" result of human occupation at a remote epoch (Dart 1925b). Dart ended his communication with an appeal for the careful invigilation of the process of blasting at the site and for the complete geological history of the deposit to be investigated at the earliest opportunity. However, we have no evidence that Dart visited the site at the time, nor did it rate a mention in his chapter, "Anthropology" (Dart 1929), in the handbook on *South Africa and Science* (McCrae 1929) which was prepared for the meeting of the British Association for the Advancement of Science in Cape Town and Johannesburg in that year. [In the historical foreword to R.J. Mason's book *Cave of Hearths, Makapansgat, Transvaal* (1988), B.D. Malan states, "Two years later [1927] he himself collected fossils from the site now known as the 'Limeworks'...", but as both Eitzman and Dart had just been mentioned, it is not absolutely clear to which of the two men 'he' refers (Malan 1988, p. 9).]

Eitzman's account tells us that he conducted numbers of visitors over the Limeworks in the later 1920s, such as the Austrian palaeobiologist, Othenio Abel in 1928, and Lidio Cipriani, the Italian physical anthropologist in 1929. He apparently also played a part when some of the British Association visitors called at

Makapansgat, on their way to the Zimbabwe Ruins in 1929. By that time, recalled Eitzman, "The mining had penetrated to the end of the first great cavern but some of the large bone stacks were still intact." (Eitzman 1958, p. 179).

Eitzman's visits continued as late as 1933-1937, by which time, he reports, at least 60,000 tons of lime had been removed from the Limeworks. From memory he drew in 1958 the stratigraphic sequence he had observed at the Limeworks in the early years of the mining of the lime deposit. The layer shown as Bone Breccia 2 matches the grey breccia which Partridge (1979) recognised as Member 3 of the Makapansgat Formation. It was apparently from Eitzman's Bone Breccia 3 that he obtained the water-worn cobble "of many faces" which H.B.S. Cooke reported "is probably a piece of banded ironstone but could possibly be a banded jaspertite" (cited by Eitzman 1958, p. 181).

Eitzman recognised the semblance of a human face on this cobble. Although he reported that both R.B. Young and H.B.S. Cooke regarded the impression as due to natural wear, Eitzman held that even if it were so, "the material is alien to the dolomite, so it must have been picked up and treasured by those responsible for the bone layer. That is why I have kept it ever since I first showed it to Professor Dart in 1925: and have now handed it over to him . . . I regard it as certain that this water-worn pebble of foreign material was carried there by *Australopithecus*." (Eitzman 1958, p. 182). Turning the cobble over and inverting it, Dart thought he could find not one, but three or four human faces caricatured on it and he supported Eitzman's claim that it had been deliberately collected and cherished by the Makapansgat *Australopithecus*: "This pebble, in brief, may not have been 'the god of those people', but it could have played an appreciable role in awakening the thinking and exciting the imagination of those nascent intelligences in ways beyond our comprehension, profound as we may deem them to be." (Dart 1974, p. 169). Building on these ideas, Irwin (1974) speculated: "Was this the beginning of magic and ritual, or was it simply the first exhibit in an ape-man's art gallery?"

Long before ape-man remains came to light, there was the common story of human remains found and lost. Says Eitzman,

"In 1925 a complete fossil man was found just near the end of the first great tunnel in a crevice above the grey breccia on the east side. This fossil was destroyed and cast into the lime kilns. A certain person employed by the Northern Limes was responsible. The truth of this was beyond doubt; schoolboys heard about it independently. I questioned many natives who worked at the quarry and they confirmed it. The same person boasted about it as late as 1929 in the presence of Professors de Sitter [an astronomer from Leiden], [Ruggles] Gates [of London] and others."

(Eitzman 1958, p. 182).

Eitzman indicates also that, after the lime company stopped working in 1935, another company removed from the dumps even the lowest grade of limestone to put

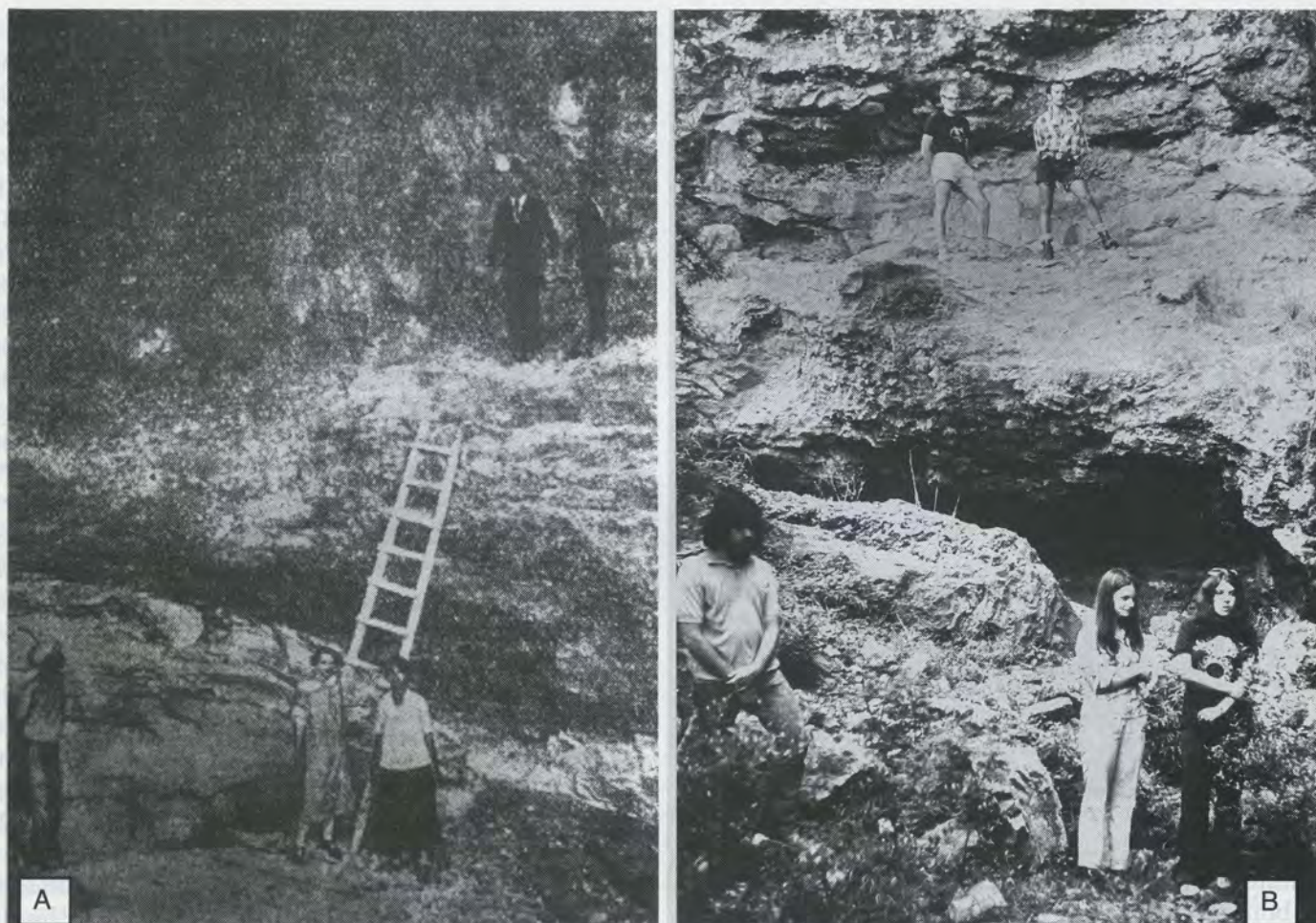


Figure 4: A comparison between (A) a photograph taken by W.I. Eitzman in the Makapansgat area in May 1925 and (B) one taken at Buffalo Cave by P.V. Tobias in 1973, with students posed in similar positions to the figures in the earlier picture. In the Eitzman photograph (published by courtesy of *The Star* newspaper), the two figures of men on the ledge were touched up about 1957, as they had faded and appeared to be reproduced indistinctly in the two earlier published versions in 1925 (*The Star*) and 1958 (*South African Journal of Science*).

into kilns at Potgietersrus. This resorting of the dumps, he says, explains why only a fraction of the original bone breccia had been recovered.

MISIDENTIFICATION OF A PHOTOGRAPH?

In the middle of May 1925, Eitzman took a photograph in the Makapansgat area and it appeared in *The Star*, Johannesburg, of 10th August, 1925. Eitzman later wrote of that photograph, "... it is the only photographic evidence available today of what the Makapansgat cavern looked like before the lime and bone-breccia had been almost completely removed from [it]" (Eitzman 1958, p. 178). The photograph thus purported to be of the Makapansgat Limeworks and the caption read, "*A storehouse of fossils: The Lime working at Makapans, in the Northern Transvaal, which are described today. The strata in which numbers of fossils exist is [sic] at the level where the two men are standing in the upper part of the photograph.*" (Figure 4A). The persons shown are Mr. Mahlala (left), Wilfrid Eitzman's wife Annie (middle) and Mrs. Petrus Verceuil née Martins (right) who died in 1928. Above are the mine manager, Mr. Darling (left) and his assistant (right).

When Eitzman showed this photograph to Dart in August 1957, Eitzman indicated that the breccial layers shown were the bone and lime beds at the Makapansgat Limeworks. Dart accepted Eitzman's identification of the photograph as showing what the Limeworks had looked like 32 years earlier. A copy of the photograph was reproduced with Eitzman's (1958) article in the *South African Journal of Science* in July 1958. In that article Eitzman stated, "My copy of that issue [of *The Star*] had [faded] so badly by 1957 that Professor Dart tried to get the original block from *The Star*, but it had been destroyed. The editor, however, kindly arranged for a reproduction to be made from their own copy of that issue. It also has faded..." (Eitzman 1958, p. 178).

From the first time I set eyes on that photograph, I strongly suspected that it had been taken not at the Makapansgat Limeworks but at the Buffalo Cave, which I had visited and worked at repeatedly from 1945. Among the features shown in the old photograph which tally with those to be seen in the Buffalo Cave, are the following: As in Buffalo Cave, there is a thick ledge on which Mr. Darling and his assistant are standing and this is sufficiently difficult to climb on to

that they have preferred to use a ladder. "The strata in which numbers of fossils exist" (*The Star*) including the bone-bed being pointed out by the manager's assistant match the layers of bone which formerly contained several crania and horn-cores of *Bos makapaani* at the time of our visits to Buffalo Cave in 1945-1946: although subsequently vandalised, these layers of very white bone are still evident *in situ* above the ledge in Buffalo Cave. The hollow beneath the ledge in the 1925 photograph matches a similar recess on the under surface of the thick ledge at Buffalo Cave. [In passing, it may be mentioned that the author extracted a bovid calvaria with endocranial cast in position from the dark red breccia in this recess in 1945-1946; and this breccia which is more accessible than the pink breccia above the ledge might have been the deposit from which Broom extracted the type specimen of *Bos makapaani* eight or nine years earlier (Broom 1937).] There is a large fallen mass in the left foreground, which in the old photograph and in Buffalo Cave tapers from the left (where Mahlala is standing) to the right (where the ladies are). The contour of the lower margin of the ledge – with a right-angled downward dip and a curving away to the right, and a semidetached fragment partially separated by a crack from the curved margin above it (some distance to the right of the ladder), are virtually identical in the 1925 photo and Buffalo Cave. Moreover, there is in both a smaller collapsed block beneath the ledge, reducing the darkly-shadowed recess to a narrow space running to the right.

To bring these resemblances out more clearly, in 1973, I posed some of my students in corresponding positions at Buffalo Cave. The resulting photograph (although taken from a slightly different angle from the 1925 picture) is a close match of Eitzman's photograph in general topography and in all details mentioned (Figure 4B). We know that Eitzman visited the side of the valley where Buffalo Cave is situated. Moreover, limeworking operations were carried on at Buffalo Cave and the old limeworkers' roadway is still in evidence. The most reasonable interpretation is that when he examined his photographs after the May 1925 visit, Eitzman could well have confused a picture taken of Buffalo Cave with a view of the rapidly changing face of the Makapansgat Limeworks.

ROBERT BROOM AND THE MAKAPANGSAT VALLEY

In September 1936, Broom visited the valley and recovered from the large cave deposit opposite the Limeworks part of the skull of a dwarf buffalo which he made the type of a new species *Bos makapani* (Broom 1937). The cave subsequently came to be called the Cave of the Buffalo, or simply Buffalo Cave. Gentry (1978) considers this form to be an ovibovine species, though of uncertain generic identity. Because of the distance from Pretoria, Broom did not continue his collecting activities in the Makapansgat valley, but he did receive at the Transvaal Museum part of the

lower jaw of a large fossil giraffid that a lady had picked up, presumably at the Limeworks. Broom states that "This giant giraffe may prove to be *Griquatherium cingulatum* Htn., but as the type is only an upper molar it is impossible to be sure whether this fragment of lower jaw is the same or different." (Broom & Jensen 1946, p. 337).

Broom's association, in 1945 and 1946, with the Wits Anatomy Science students and their expeditions to the Makapansgat Valley is discussed below.

VAN RIET LOWE, MALAN AND THE MAKAPANGSAT VALLEY

In 1936, the Historical Monuments Commission (later the National Monuments Council) considered the possibility of declaring the Historic Cave a national monument and asked C. van Riet Lowe to report on the cave. Lowe was not only a member of the Commission, but also Director of the Archaeological Survey of the Union of South Africa. He visited the site in January 1937. Close to the Historic Cave, he found an adit which had previously been abandoned by lime workers. Their drive had laid bare a wall of breccia from which the supporting lime and dolomite had been removed. In the exposed face Lowe observed an ashy layer which he regarded as a hearth and he named the site the Cave of Hearths.

In June 1937, Lowe visited the site again, together with Professor and Mrs. R.F.A. Hoernlé of Wits University and Mr. F.R. Paver, the Editor of *The Star* (Johannesburg). Between the January and the June visits, the breccia forming the right face of the drive had collapsed along a presumed horizontal plane of weakness thought due to an occupational level. Numerous stone tools, including polyhedrals, a hand-axe and a cleaver, and many flakes were recovered from the collapsed breccia, and their features suggested a late phase of the Earlier Stone Age. Bone fragments were apparent in the overhanging roof above the collapse. A further visit was paid to the Cave of Hearths in October 1937 by Lowe, B.D. Malan, Mrs. Alice Bowler-Kelly from Paris, and Mr. John Marcus (whose name is recalled in the archaeological site known as Marcus Donga at Germiston). Further collapsing had meantime occurred. It was clear that propping of the unsupported overhang and examination of the fallen debris were urgent necessities. Mrs. Bowler-Kelly offered to defray the costs of the initial shoring of the overhang. On this third visit, the Rainbow Cave was discovered and named thus, because of the multi-coloured layers of ash in an extensive system of hearths. Middle Stone Age tools were recovered.

In 1938, Lowe published his first account of the Cave of Hearths and in the same year Dart, Broom and Cooke visited the site. Malan and A.G. White of the Transvaal Museum broke up some 13 tons of the collapsed breccia in September 1938, recovering numerous stone tools. Cooke and two senior students made a geological survey of the area in 1939. A report

on the Cave of Hearths and the Rainbow Cave was published by Lowe in 1943. After World War II, L.C. King (1951) published the results of a geomorphological survey of the caves in the Makapansgat valley, and still later, C.K. Brain (1958) made comprehensive and detailed studies of the cave deposits as part of his doctoral work.

Interest was revived in the area in 1945 when P.V. Tobias organised the first of a series of student expeditions from the Wits University to the Valley, these having as objectives studies and collecting in the Cave of Hearths, Rainbow Cave, Historic Cave, Makapansgat Limeworks, Buffalo Cave and Mwulu's Cave.

THE CAVE OF HEARTHS, DR. BERNARD PRICE AND DR. R.J. MASON

That remarkable benefactor, Dr. Bernard Price, served the University of the Witwatersrand in many ways including the benefaction which enabled the University to establish the Bernard Price Institute for Geophysical Research. He offered to provide the funds for the resumption of work in the Cave of Hearths. The Bernard Price Foundation for Palaeontological Research was set up with a Board of Control which included H.R. Raikes (Principal of Wits University), Dr. Price himself, R.A. Dart (Anatomy), T.W. Gevers (Geology), C.J. van der Horst (Zoology), R. Broom (Transvaal Museum, Palaeontology), C. van Riet Lowe (Archaeological Survey), F.G. Hill of the Wits University Council, and subsequently S.H. Haughton (Geological Survey). Following Bernard Price's death in 1948, he endowed the University with a large sum which ensured the conversion of the Foundation into a permanent Institute.

It was with this generous financial support that the excavation of the Cave of Hearths was begun in April 1947 by Captain Guy Atwater Gardner, who had excavated in Egypt and under Leo Fouché at Mapungubwe, northern Transvaal. After Gardner resigned six months later, James Kitching was appointed to excavate the Cave of Hearths from October 1947, under the direction of Lowe, Malan and Cooke, and with the help of his brothers, Ben and Scheepers Kitching. The visits by Teilhard de Chardin in 1951 [followed by a second visit in 1953] and by George B. Barbour (1949), both of whom had worked at Zhoukoudian in China, led late in 1952 to a generous grant by the Wenner-Gren Foundation for Anthropological Research to Lowe for the Cave of Hearths dig (Malan 1988). In 1953 the Archaeological Survey was joined by Revil J. Mason and he was placed in charge of the field operations at the Cave of Hearths. To him, in the main, is owing the monumental excavation of the Cave of Hearths, while members of the Bernard Price Institute continued to help with the field work from time to time. At Mason's hands it became, and remains, the first excavated and completely published South African site showing a remarkable stratigraphic sequence that embraces Early Stone Age, Middle Stone Age, Late Stone Age, Iron Age and historical artefacts, fauna and human remains (Mason 1988).

THE FIRST OF THE STUDENT EXPEDITIONS OF 1945-1946

Ever since R.A. Dart set up the Medical BSc course in Anatomy and Anthropology at the Wits Medical School in 1923, there had been a tradition of fieldwork by third year medical science students. In 1924, a member of the first such class, Josephine Salmons, had borrowed from her fellow-student, 'Pat' Izod, a fossil baboon that his father E.G. Izod, had brought to Johannesburg from Taung. This unleashed a chain of circumstances leading to the recovery of the Taung child skull in November 1924 (Tobias 1984). In 1935, another of Dart's students, Trevor Jones, recovered baboon crania from Sterkfontein (Jones 1937). Bachelor of Science student Harding Le Riche, and a lecturer G.W.H. Schepers, in 1936 obtained more cercopithecids from Sterkfontein: when they took these to Broom, another sequence of events was set on foot, leading to the recovery of the first adult *Australopithecus* nine days later, on 17th August 1936 (Broom 1936, 1951).

A similar train of events started when, in July 1945, members of my own Science class discovered the first cercopithecoid fossil specimens to be found at the Makapansgat Limeworks and the first hominid specimen was recovered there by J.W. Kitching two years and two months later. Shortly after our first Makapansgat expedition, we obtained the first fossil baboon specimen at Gladysvale: but in this case the latent period before the first hominid remains were found was 47 years (Berger, Keyser & Tobias 1993).

Lectures which my third year medical B.Sc. class received from Broom once a week fired us with enthusiasm for field-work and palaeo-anthropology. This must have been apparent to our mentor for, on 12th May 1945, Broom wrote to Mrs Eunice Wells (the wife of Doctor, later Professor L.H. Wells), "My lectures at the University...seem to have given some pleasure to the students." We made our first excursion from 5th to 10th May 1945 to Sterkfontein, Kromdraai, Bolt's Farm and Gladysvale. So successful was this venture that we determined to plan a larger undertaking in the July vacation and to make it multidisciplinary.

It was almost by chance that we chose Makapansgat for the winter expedition. We first consulted Professor John Phillips, head of the Botany Department, and he suggested the Zoutpansberg as the most suitable spot. When we found from our atlas that this was nearly 400 miles from Johannesburg, we presumed that the rail fare would be exorbitant. Halfway, approximately, lies Potgietersrus, which I thereupon suggested. We returned to Phillips and, as soon as we mentioned Potgietersrus, he told us about the Makapan Valley, including its patch of relic, Knysna-type forest (which he had previously surveyed). He wrote to the Maguires of Potgietersrus on our behalf, helped us to obtain a railway concession, and sent us across to Professor Van Riet Lowe. Like Phillips, Lowe was extremely helpful, giving unfettered access to his Makapansgat files and with B.D. Malan aided us in a myriad ways. Enthusiastic support was



Figure 5: View of the Makapansgat Limeworks forty years ago, as captured by telephoto lens from a point across the valley close to the boundary between *Makapansgat* and *Swartkrans*. Of the Limeworks itself, three tiers may be seen: in the foreground, nearest the road, are white dumps of spent lime. In the second tier behind the lime dumps are dumps of breccia interspersed among deep lime kilns through which passed many thousands of tons of limestone between the 1920s and about 1940: it is from this second tier that enormous quantities of bones were recovered between 1945 and about 1965. The third tier is marked by *in situ* material penetrated by the limeworkers' major drives.
Photo by Alun R. Hughes.

given also by Professor T.W. Gevers of Geology. When Broom lectured to my class on 6th June 1945, we asked him to tell us about the palaeontological remains in the Makapansgat area and he, too, was most encouraging. As part of our preparations we received talks from Lowe and Malan on South African archaeology and on how to recognise stone tools. (There was at the time no Department of Archaeology at Wits and Lowe was designated an Honorary Professor.) We interviewed the Abbé Henri P. Breuil as he was on the eve of returning from South Africa to France: his chief advice was that we avoid the nettles near the entrance to the caves. Professor C.J. van der Horst was most helpful and materials needed by the zoology students were loaned by his department. Professor Dart was favourably disposed and encouraging: he reminded us that it was exactly 20 years since he had first drawn attention to the significance of the Makapansgat Limeworks as "a site of early human occupation" (Dart 1925b).

Our expedition lasted from 28th June to 8th July 1945. We took the train to Potgietersrus, spent the night camped in and around the Maguires' house, and hired Mr. Amm's truck to take us out to the Makapansgat Valley, where we lived under canvas.

Apart from the work of the geology, botany and zoology students, some of the medical science students spent their time breaking up collapsed breccia at the Cave of Hearths and the Rainbow Cave, and collecting the archaeological objects laid bare. From the Rainbow Cave breccia, I recall recovering a superb circular scraper, with which Lowe was later so impressed that he declared it alone had justified the entire expedition! The other group of medical BSc. students worked at the Makapansgat Limeworks (Figure 5). On 2nd July, they recovered the first primate known from the Limeworks: there were a cranium, endocast and close by a mandible. The jaw which was recovered by the deputy leader, Joseph Stokes Jensen, was subsequently made the type of a new species, *Papio darti*, named in honour of Prof. R.A. Dart (Broom & Jensen 1946). However, the authors added, "So markedly different is the 3rd molar that there seems some reason for regarding the fossil form as being worthy of being placed in a distinct genus." (p.340). Later, a number of other specimens from Makapansgat were referred to the same species and Kitching (1953) proposed to transfer the species to the genus *Gorgopithecus*. However, Freedman (1957) demonstrated that this Makapansgat taxon belonged to the genus

Simopithecus. The latter genus, in turn, has since been relegated to the status of a subgenus under *Theropithecus* (Jolly 1972). Eisenhart (1974) thus pointed out that the valid name for the species would be *Theropithecus (Simopithecus) darti* (Broom & Jensen 1946). Later usage has tended to drop the subgeneric nomen and the species is most commonly referred to simply as *T. darti* (e.g. Delson 1984). Other fauna which we recovered from the Limeworks included equid and bovid specimens.

Broom was very pleased with what we had achieved and was especially impressed that we had found a new type specimen of cercopithecoid. As class representative and expedition leader, I found myself writing to him on 8th August 1945 –

"We were all very encouraged by the favourable manner in which you viewed our recent expedition, and the several finds which were made. You have more than kindled a spark for the future, in several of us, and I am sure that your work on anthropology and palaeontology will be taken up and pursued in this fruitful field of South Africa."

In reply he wrote to me on 10th August 1945,

"...I saw enough [of your Makapan finds] to know that you are on a good wicket. A brief look over your fossils showed that you have two skulls of Primates which when cleaned out may prove to be new and may help us to date the other fossils. You have one or two antelopes which should be identifiable at least generically. You appear to have the tooth of [a] new animal quite unknown to me. All this shows you have been working in a bed of an age different from the Kromdraai and Sterkfontein deposits. In fact you are exploring a Terra Nova. Quite likely in the same deposit you may find some new sort of early man or pre-man which may be even more important than the discoveries made at Taungs or Sterkfontein or Kromdraai.

"Good luck to you all. Your explorations may prove to be quite as important – far more important than Stanley's opening up of The Dark Continent.

Sincerely - R. Broom"

On 27th September, Broom followed this up with a letter to our lecturer Dr. Alexander Galloway:

"You might tell the students that they have made a discovery of considerable importance. The 'baboon' they found at P.P. Rust [=Potgietersrus] appears to represent a new genus. Probably it is also a new species. I have named a fossil "baboon" *Parapapio major* from Kromdraai, but this is only known from a few upper molars. Of the P.P. Rust specimen we only have lower jaw teeth. Still I feel almost sure that it will turn out to be new. Certainly it is not a *Parapapio*.

Please ask them to do no further development till I see them – as they may do harm. Of course the beast is clearly a Cercopithecoid, and not a *Papio*, a *Parapapio*, nor a *Dinopithecus*... This will cheer them."

FURTHER EXPEDITIONS TO THE MAKAPANGS GAT AREA, 1945-1947

That first student expedition to Makapangs gat had important consequences. Our revelation of extinct cercopithecoids at the site kindled in us the high

expectation that hominids would follow (Tobias 1945a). We were well aware that, at both Taung and Sterkfontein, the recovery of cercopithecoids had presaged the discovery of hominid specimens.

There followed six more expeditions from the Anatomy Department in the ensuing eighteen months. In September 1945, I led a team on our second expedition to break up breccia and collect fossils at the Makapangs gat Limeworks. On our third expedition in December 1945 (our student group this time being joined by Eric Williams, the Senior Technician of the Anatomy Department and his brother Dennis), we recovered a number of additional "baboons" and monkeys. Our finds in December 1945 included the type specimen of a new genus and species. It was described by one of the Anatomy Honours students, Olleris Mollett (1947), and named *Cercopithecoides williamsi*, after Eric Williams who recovered it. Its affinities were not appreciated at the time, but on a later visit to Johannesburg, L.S.B. Leakey declared it to be a colobine and after careful comparative studies this reassignment is now accepted: *Cercopithecoides* is one of the recognised genera of the Colobinae, though it appears to be closely related to *Paracolobus* (Simons & Delson 1978).

The fourth expedition took place from 30th May to 2nd June 1946: we were accompanied by Professor and Mrs. Dart and their two children. Physically, it marked the return of Dart to the field. It might well have been his first visit to the Limeworks or, at least, the first since 1927 (Malan 1988), for his visit in 1938 had had the express purpose of seeing the Cave of Hearths.

The fifth student expedition, in July 1946, was led by a fellow Honours student of the Anatomy Department, M. Maureen Dale. She afterwards published an account of suid fossils from the Makapangs gat Limeworks, for one of which she created the new genus *Potamochoeroides* (Dale 1948). At the same time I participated in the excavation of the Rose Cottage Cave at Ladybrand, O.F.S., under Malan and Lowe. On this dig, I learned systematic excavation technique which thus equipped me to obtain a permit for the ensuing venture.

As the sixth venture, in January 1947 I took a student team, as well as anatomy technician Owen Jones, to make a systematic excavation of Mwulu's Cave, about eight kilometres from the Makapangs gat Limeworks. Brian Maguire had first shown us this cave on one of the preceding expeditions, his interest having been aroused by a botanical feature, the rooting in the deposit, and the growth in creeper fashion along the surface, of a *Podocarpus* tree. It was while I, on all fours, was being shown this tree by Maguire that my hand, grovelling just below the surface of the soft, sandy deposit, lighted on a stone tool with affinities to the Pietersburg Industry. This find and additional specimens then recovered from the talus slope determined me to conduct an excavation of this cave deposit. I named the site Mwulu's Cave after a recluse called Mwulu who Mr. C.D. Maguire stated in 1949 had lived in the cave about 1820 and whose pots still littered the surface of the deposit on our

early visits. It proved to contain a sequence of three occupation levels rich in stone tools of several phases of the Pietersburg Industry. This was the first systematic archaeological excavation of a cave deposit ever made in the Transvaal (Tobias 1949, 1954).

SOME OTHER CONSEQUENCES OF THE JULY 1945 EXPEDITION TO THE MAKAPANGS GAT VALLEY

An intensified programme of field activities followed these six student expeditions and led to the discovery of an australopithecine specimen by James Kitching in September 1947 (Figure 6). The Makapansgat hominid had at last been found, 26 months after the first student expedition.

Secondly, the role of the first student expedition in coaxing Dart back into palaeo-anthropology is best recounted in Dart's own words: "It is improbable that I would ever have returned to the Australopithecinae had it not been for the strange series of events set in train . . . in 1945 by the student expedition to Makapansgat Valley organised by P.V. Tobias . . ." (Dart 1957, p. viii). More explicitly, in his autobiographical *Adventures with the Missing Link* (Dart & Craig 1959), we read,

"Then in 1945 a student adventure led by a member of my science class, P.V. Tobias – the man who succeeded me as professor of anatomy on my retirement this year – was responsible for thrusting me back into the maelstrom of man's beginnings. Tobias and his group, thirty strong [actually 21], visited the Makapansgat Valley...and brought back a story so astonishing that I could no longer resist returning to that earlier field of activity." (Dart & Craig 1959, p. 83)

"When the party returned they said that the two sites [those from which stone tools and fossil ash came and the source of Eitzman's 1925 bones] were a mile apart. There were many Old Stone Age implements at the Cave of Hearths and plenty of Middle Stone Age implements at the Rainbow Cave. However, at the limeworks site a mile lower down the valley – where the fossil-bearing gray breccia was found – there were no traces of implements. But they had brought back something much more significant than Stone Age tools. Among the gray breccia they collected was the skull of a fossil baboon, indistinguishable from the *Parapapio broomi* first found by Trevor Jones at Sterkfontein in 1936 and now recognized as a characteristic of australopithecine deposits.

"Doesn't this mean, sir," Tobias asked, 'that Makapansgat may be far older than you or anyone else imagined?' 'It does indeed. It certainly looks that way,' I replied. 'Then,' asked the young student, 'doesn't this tempt you back into the field of anthropological research?' Hesitantly, he added, 'It might even prove to be contemporaneous with Sterkfontein.'

"It was almost as if he had read my thoughts. It might not only prove to be as old as anything yet discovered but might also yield a more complete man-ape than those found by Broom. Summoning Tobias to follow, I went to my workshop and took down my hammers, chisels and other anthropological tools which had lain neglected for so many years.

'You have my answer,' I told him." (Dart & Craig 1959, pp. 90-92)

Dart's return to palaeo-anthropology was marked by the revelation of a series of hominid specimens from the Limeworks, recovered for Dart by James Kitching and his brothers Ben and Scheepers, and by Alun Hughes (see account of Hughes's role by Tobias 1991a). It produced also Dart's ingenious but flawed concept of the Osteodontokeratic Culture which he supposed had been practised by *Australopithecus*. The work at Makapansgat gave Dart a major new scientific career between 1947 and 1966, beginning some twenty years after his earlier meteoric phase with the Taung child (Figure 7).

Thirdly, there was another interesting and slightly amusing consequence of our 1945-1946 expeditions. We handed over to Dart and Wells a number of primate crania, among other fossils from the Limeworks. One day, Dart came into the Medical B.Sc. Laboratory with a beatific expression on his face and, without saying a word, walked around the room shaking hands with each one of us who had been on the expedition. Then he stated simply, "Congratulations. You have discovered the Makapansgat apeman." He had identified one of our primate skulls as that of an australopithecine! As leader of the expedition I was privileged to be allowed into the technical laboratory two doors away, where, under powerful lights, the telltale specimen was being photographed. Dart had already sent a note to *Nature* in



Figure 6: James Kitching searching for bone-bearing breccia in the "Exit Quarry" of the Makapansgat Limeworks in 1947. In September of that year he found the first specimen of a hominid in the Limeworks: it was the posterior part of an australopithecine calvaria (MLD 1). Photo: by courtesy of *The Star*.



Figure 7: A gathering at the Makapansgat Limeworks on 13th March 1965 on the day following the delivery of the 2nd Raymond Dart Lecture by Sir Wilfrid Edward Le Gros Clark and his receipt of a doctorate of science *honoris causa* from the University of the Witwatersrand. Right to left: Lady Le Gros Clark, Sir Wilfrid, Raymond Dart, Peter Brain, Phillip Tobias and, from above down, Professor N.W.G. MacIntosh of Sydney University, Anne MacIntosh and Brian Maguire (shoulder to camera).

which he announced the discovery of the first hominid from Makapansgat. Mindful of the earlier finding of blackened bones there, which, following laboratory tests by Moir and Fox, he had interpreted as having been darkened by fire, he had even named the new hominid, *Australopithecus prometheus* (Dart & Craig 1959, p. 51).

It will be recalled that Prometheus was one of the Titans, those gigantic mortals who lived on earth before the creation of man. Prometheus and his brother Epimetheus made man – but with what could they endow him? – for Epimetheus had given away most resources, such as courage, strength, swiftness, sagacity, to the other animals. So Prometheus, with the help of Minerva, went up to Heaven, stole fire from the chariot of the sun...and brought fire down to man. With this story in mind and remembering the apparently cooked meat-bones, Dart named the new hominid from Makapansgat after Prometheus.

The name had been created, the paper had gone off, and it remained only for the photographs to be taken and sent to *Nature*. There, in the laboratory, the specimen was posed, the lights were adjusted, the camera was poised – when I saw Lawrie Wells, his head on one side, frowning slightly. He then turned his head the other way and frowned more deeply. In a small voice, he said, “Professor, if you look at it this way, it looks like the skull of a baboon.” Indeed that is what it turned out to be! The note to *Nature* was withdrawn, feelings were doubtless bruised, the name was left hanging fire, as one might say,

and Wells’s powers of observation and his morphological skills had won the day. When two years later James Kitching recovered a genuine australopithecine at the Limeworks (Figure 8), Dart resurrected the same name (Dart 1948).

Was there perhaps another – fourth – consequence of these early student endeavours which started when I was not yet out of my teens? An onlooker would doubtless claim that these undrilled and rather rough-hewn adventures played a seminal role in determining the direction of my own future career (Tobias 1991b).

A fifth sequel of our expedition was the flaring up of a feud that had simmered between the Anatomy Department and Broom in and after 1936. The fact that we were students from **Dart’s** anatomy department, but that **Broom** (with Jensen) published the first identified Makapansgat fossil baboon in 1946, certainly generated some tension which echoed the hard feelings of 1936.

To hark back, there had been pain in Johannesburg over Broom’s having made Sterkfontein his own site, in 1936. Trevor Rubidge Jones, a student of Dart, had obtained cercopithecoid specimens at Sterkfontein in 1935 and was working on them for an MSc dissertation project in 1936. In that year Harding le Riche, another science student of Dart, visited Sterkfontein and received from G.W. Barlow (the manager who had earlier worked at Taung) a baboon endocranial cast. G.W.H. Schepers, a neuro-anatomist in the Anatomy Department, accompanied Le Riche on further visits during which they recovered a number of baboon crania,

mandibles and endocasts. Dart being away at the time, and Broom having recently announced his discovery of a giant baboon (*Dinopithecus ingens*) in a cave near Hennops River in the Skurweberg, Le Riche and Schepers took the material to Broom. He accompanied them to Sterkfontein on Sunday 9th August 1936 and eight days later, on 17th August, Barlow handed Broom fragments of the first adult australopithecine.

Apparently both Trevor Jones and Schepers were irate at these developments. Jones was upset that the latest baboon finds from Sterkfontein had been taken to Broom: thereby, he said, Le Riche “had mucked up his MSc thesis which was to have been on the Sterkfontein fossils” (Findlay 1972, p. 65). Jones (1937) described and named the new genus and species, *Parapapio broomi*, from Sterkfontein. The hard feelings in the Wits Anatomy Department towards Broom are portrayed in George Findlay’s biography of *Dr. Robert Broom* (1972): “[G.W.H.] Schepers felt that Broom minimised the importance of their [the students’] contribution, and after cooling their ardour took over the site for his own work. He apparently echoed the sentiments of others in the department: that Broom had seized the opportunity to take over ‘their’ site.” (Findlay 1972, p. 66).

Findlay defended Broom’s actions in the following terms:

“Broom felt hurt at this view. In any case he could put the question of “rights to the cave” very simply. Dart and his staff were not actually working at the site in any real sense. The limestone was being burnt commercially all the time, and no arrangements had been made to preserve fossils disclosed during working operations. In fact, had Broom not gone out when he did, the Sterkfontein ape [sic] may not have been preserved. For this risk it seems strange to resent Broom’s success.



Figure 8: Parieto-occipital fragment with many sutural ossicles of an australopithecine calvaria found in the Limeworks by James Kitching in September 1947. This was the first hominid specimen from Makapansgat and initially it was made the type of a new species, *Australopithecus prometheus* Dart. Subsequently John T. Robinson re-assigned it to *A. africanus transvaalensis*, the same subspecies as that to which he assigned the Sterkfontein [Member 4] hominid.

“Harding Le Riche summed the matter up neatly. On getting the baboon brain cast back from Broom...he wrote to Broom: ‘I fetched the little brain at the station. I am going to keep it as a memento of a rather interesting bit of unpleasantness which led to your fine discovery.’ Dart’s position was equivocal. It would have been nicest had his students been less disobedient and consulted him first, but who could guarantee that the discovery, which was to vindicate his reputation over the Taungs skull, would then have been made?”

(Findlay 1972, p. 66)

Ten years later, neither the Anatomy Department nor Broom had forgotten the disgruntlement of 1936. Eunice Wells, the wife of L.H. Wells, apparently raised the matter in a letter to Broom in 1946. He explains his attitude in a series of letters to her in August and September 1946:

“...neither [Jones] nor anyone else of the dept. was working there in 1936. The rule in all such investigations is that if one man or expedition is working at a spot he is left alone while he works. But as soon as he is finished at the spot anyone else is at liberty to work there ... Neither Trevor Jones nor Dart nor anyone else from the Dept. ever went to Sterkfontein so far as I know after 1936. If it is argued that I should not have gone to Sterkfontein because T. Jones had worked there, the same argument would hold against any one going to P.P. Rust because I had been working there.”

In a more expansive tone, Broom adds, “The field is so large that there is room for all.” (Broom to E. Wells, 21st August 1946).

Then it emerges, in Broom’s letter of 28th August and in another dated simply “Sunday afternoon” (probably 1st or 8th September 1946), that her husband, Lawrence Wells, had himself cherished ambitions to carry on working at Sterkfontein after the students’ recovery of cercopithecids a decade earlier. However, “D.” [presumably Dart] would not allow him. Comments Broom:

“What a pity. It is like Turner and Girton. Turner said ‘Had Girton lived I would have starved.’ So had Wells been working at Sterkfontein I would not have barged in, and to day he would have been a famous man, and I just an ordinary authority on fossil reptiles.” (Broom to E. Wells, 28th August 1946).

Broom refers to this again in his Sunday afternoon letter:

“But what was to stop him [L.H.Wells] going [to Sterkfontein] on a Sunday? In the 1935-6-7 period and probably before this Mr. Barlow always kept a big collection of all the best things he came across on a large table in the rondavel to dispose of to visitors – and something of value could have been had every Sunday. When I first went there I thought the collection was a sort of museum or I would have bought a valuable specimen. It was an arm – with much of hand – of perhaps *Plesianthropus*. When I was there the next week this was gone. Barlow had no idea or wouldn’t tell me who got it. I tried to recover it thro’ the press but without success. Barlow said ‘You should have taken it when you got the chance’. In the two years that I worked at Sterkfontein I always searched Barlow’s table, and found there many valuable things. It was there I got the fragment of femur. Of course Dart himself should have visited [Sterkfontein] every Sunday from 1925 onwards, and

if he could not have gone he should have arranged for G. [Galloway] or your husband or one of his students or assistants to go, and never to miss a Sunday. What a collection he would have made! Alas we all have regrets for the 'might have been'."

It is clear from these quotations and other letters that Broom was shocked that Dart and his Department had for so long neglected their opportunities at Sterkfontein and elsewhere. Unfortunately, no relevant correspondence by Dart has come to light.

This was the background to a new bout of pique following our first student expedition in July 1945. Apparently there was chagrin that Broom had published Jensen's baboon. Dart was apparently aggrieved over this, as emerges clearly in the correspondence between Broom and Eunice Wells. Thus, in his letter of 15th August 1946, Broom states,

"You told me that those at the Med. School are jealous of my even looking at the stuff the Kitchings collected at P.P. Rust. So though I was at the Medical School last week I didn't go near the cave stuff. I'll soon have plenty of stuff of my own."

Although I have not had access to Mrs. Wells's letters to Broom, his replies are frequent and explicit. Thus, a few days later, he writes:

"I am sorry to learn of all my sins re Dart and others.
"Re Jensen. Jensen was one of my students.

[This refers to Joseph Stokes Jensen who was my deputy leader of the July 1945 expedition and who recovered the type specimen of *Theropithecus darti*. He was co-author with Broom of the article on this cercopithecoid that appeared in the *Annals of the Transvaal Museum* in 1946 and which seems to have angered Dart.] Broom continues in his letter to Eunice Wells,

"It was I who suggested going to P.P. Rust. [Broom is not accurate in this respect: see my earlier account, based on my detailed day-by-day record of the preparations for the first 1945 expedition to Makapansgat.] "I mapped out all the route where finds can be made. He and others went there – shown me all the specimens. One is a new Baboon which was partly worked out by Jensen – partly by me. In fact I worked out all the delicate teeth which had been much broken. As Jensen found the specimen and he and I had worked it out I have described it (with Jensen). Dart had nothing whatever to do with it – (except the University partly financing the trip). P.P. Rust caves have been there for 20 or more years. I doubt if Dart has been there. Certainly he had never been nor anyone else till I started working there in 1936 or 37. Dart has no *locus standi* in this matter. Of course there is no objection to anyone working there."

(Broom to E. Wells, 21st August 1946)

It is interesting that, whereas in 1936 everyone (Schepers, Jones, Le Riche, Wells, Galloway) seemed to have known about the dissonance between the Anatomy

Department and Broom, in 1946 neither I nor, I believe, any of us (other than the most senior people such as Lawrie Wells) had the slightest presentiment that vexation had flowed from Jensen's baboon being given to Broom for evaluation. Broom, after all, was our teacher of primate evolution, in his capacity as a part-time lecturer in Dart's Anatomy Department. It was only years later, in discussion with the late Professor Wells, and very recently from my study of the letters from Broom to Eunice Wells, which had been generously made available to me by Dr. Gregory Wells, that I became aware of these strains. Happily these problems seem to be well behind us and inter-institutional and interpersonal relationships have been kept on a somewhat more even keel by the later generations of palaeontologists.

TAILPIECE

My colleagues and I prepared a lengthy, 60-page report on the pioneering expedition of July 1945. This comprised an Introduction by Tobias; Geological Report by J. Kirkness; Archaeological Report by Tobias and Jensen; Palaeontological Report by Jensen; Botanical Report by B. Maguire; Ornithological Report by A.C. Allison; Conclusion and Recommendations by Tobias (1945b). Our professors were eager for the report to be published and C. van Riet Lowe was especially helpful and enthusiastic. They persuaded the Principal of the University, Mr. H.R. Raikes, to agree to pay for the publication. Then a tragedy befell. After I had devoted a substantial part of several vacations and of my Honours year to the preparation of the Report, the entire manuscript disappeared at the publishers – or somewhere between the office of the Science Students' Council and the publishers. Heavily involved in Honours and MSc projects, I was not able to find the time to prepare another clean copy of text and illustrations after this severe loss. The clean copy has never been found and the Report remains unpublished to this day. I have only an imperfect carbon copy. Thus, I welcome the opportunity to place these facts on record on the historical occasion of the golden jubilee of the Bernard Price Institute for Palaeontological Research.

ACKNOWLEDGEMENTS

I pay tribute to the memory of Dr. Bernard Price much of whose concept of the Bernard Price Institute for Palaeontological Research evolved in the caves of the Makapansgat Valley. After 50 years I extend my thanks to my fellow-members of the first Makapansgat Student Expedition, to our professors and mentors. I thank Dr. Gregory Wells for making available to me the correspondence from Dr. Robert Broom to his mother, Mrs. Eunice Wells. My thanks are extended to the Editor of *The Star* for permission to reproduce part of Figure 4 and Figure 6 and to Heather White for her uncomplaining and cheerful response to eleven years of publication pressures. My thanks are due also to Peter Faugust for valuable help with illustrations.

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THE CONTRIBUTION OF RAYMOND DART TO THE DEVELOPMENT OF CAVE TAPHONOMY

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ABSTRACT

The basic principles of African cave taphonomy were formulated in 1976, but twenty years earlier, Raymond Dart embarked on a pioneering taphonomic investigation into a hominid-bearing fossil assemblage from the Makapansgat Limeworks cave. He asked the questions that are typically addressed in contemporary cave-taphonomic studies, such as: how did the bones find their way into the cave? From what animals were the bones derived? What parts of the skeleton are represented and what damage have the bones suffered? What can be said about the behaviour of the hominids and other animals whose remains are preserved in the cave?

Dart concluded that hominids had been responsible for collecting the very large number of bones preserved in the Member 3 grey breccia unit. He set up a theory of the "osteodontokeratic" culture of *Australopithecus* and drew some remarkable conclusions about the nature and behaviour of early hominids. These conclusions, presented in powerful prose, provoked a good deal of subsequent research that set the discipline of cave taphonomy on its course.

KEYWORDS: Taphonomy, Cave-taphonomy, Raymond Dart, Makapansgat.

INTRODUCTION

Any review of research activities at the Bernard Price Institute for Palaeontological Research, during the last 50 years, would be incomplete without mention of Raymond Dart's remarkable study of a large bone assemblage from the Makapansgat Limeworks, undertaken in the early days of the Institute's existence. This was a pioneering investigation that had far-reaching consequences and it served to bring the Institute into palaeo-anthropological prominence.

Dart's attention was drawn to the fossil potential of the Makapansgat Limeworks cave by a local school teacher, Wilfred Eitzman, during the early 1920s. Among the numerous fossils that Eitzman sent to Dart at that time were several blackened bones, enclosed in the calcified cave earth, that Dart suspected of having been burnt. He arranged for chemical analyses of the bones to be done and these showed the presence of free carbon, suggesting that the bones had indeed been in a fire. On the strength of this evidence, together with that of the broken bones from a wide variety of animals, Dart (1925) suggested that Makapansgat had been "a site of early human occupation". Subsequently, following a Witwatersrand University student expedition, led by Phillip Tobias in 1945, new fossils were found at the Limeworks that led Dart to visit there the following year (Tobias, this volume). Dart immediately recognised the importance of the cave as a potential early hominid locality and employed James Kitching, Alun Hughes and their helpers to sort the lime-miners' dumps. This resulted in the finding of the first Makapansgat hominid specimens (Dart, 1948), which Dart named *Australopithecus prometheus*, assuming that they had been responsible for the burning

of blackened bones found in the deposit. Subsequent research on this topic by Kenneth Oakley (1956) failed to confirm the presence of free carbon in the bones and the conclusion was reached that the blackening was caused by the presence of manganese dioxide. It has been suggested that the carbon initially detected in the first samples may have come from the blasting activities of the lime-miners.

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

DART'S ANALYSIS AND INTERPRETATION OF THE MAKAPANGSAT FOSSIL ASSEMBLAGE

At the Third Pan-African Congress on Prehistory held at Livingstone in 1955, Dart (1957a) presented the results of his taphonomic investigation of the Makapansgat grey breccia (now termed Member 3) fossil assemblage. His sample consisted of 7159 pieces of fossil bone that had been laboriously prepared from the breccia blocks sorted from the lime-miners' dumps. Of these, 4560 were found to be sufficiently complete to allow allocation to skeletal part and taxon; the remaining specimens consisted of bone flakes and fragments. Dart found that 91,7% of the identifiable fossils were of bovid origin, 4,0% came from non-bovid ungulates and the rest were from non-ungulates, such as primates and carnivores. Among the 293 individual antelope represented, 39 were large such as kudu, 126

were medium-sized, 100 were from gazelle-sized antelope and 28 were from small species such as duiker. Non-bovid ungulates were represented by four equids, six chalicotheres, five rhinos, 20 pigs, one hippo and six giraffids. Among the primates, there were remains of 45 baboons and five australopithecines, together with a variety of other animals that included 17 hyaenas, a sabre-toothed cat, porcupines, as well as other small mammals and reptiles, including terrapins.

Non-ungulate mammals were typically represented by skull-parts only, but the antelope had contributed a wide variety of skeletal parts which, however, showed striking and unexpected disproportionate representations. Most common of all parts were skull pieces, particularly mandibles; neck vertebrae, particularly the atlas and axis, were well-represented, but thoracic vertebrae were scarce and those from the tail were absent. Among the limb-bones, disproportions were most striking of all: in the case of the humerus, for instance, the distal ends were ten times more common than the proximal ends.

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

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

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

In his 1957 monograph, Dart elaborated his theory of the "osteodontokeratic" (bone, tooth and horn) culture of *Australopithecus prometheus*. He explained the striking disproportions in skeletal parts apparent in the Makapansgat assemblage in terms of deliberate selection of certain bones in view of their potential as tools and weapons. Parts of antelope skeletons not suitable for tool-use were simply left at the kill-sites, hence their absence from the cave. Uses were suggested for virtually all the bones in the fossil assemblage: the tooth-rows of mandibles made good

saws, for instance, while the distal ends of humeri served as convenient clubs. Early in the investigation, Dart (1949) had suggested that humeral clubs had been responsible for the depressed fractures he observed on the calvaria of baboons and hominids from the caves of Taung, Sterkfontein and Makapansgat. In the case of fossil animals, such as baboons and carnivores, where only skulls are found in the Limeworks assemblage, Dart suggested that the exclusive presence of these, too, represented deliberate selection, concluding that the hominids had been "head-hunters" and "professional decapitators".

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

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

Dart's conclusions on early human nature were obviously of interest to a wide variety of people and his concepts generated lively debate. They so impressed the American dramatist Robert Ardrey that he wrote a series of widely-read books, starting with *African Genesis* (1961). They also provoked a number of palaeontologists, including myself, into undertaking further taphonomic investigations that would confirm or disprove Dart's wide-ranging conclusions. One such investigation was my 21-year-long excavation of the Swartkrans cave and associated taphonomic studies. This work quickly showed that many of the observations made by Dart, such as the striking disproportions of skeletal parts in the fossil assemblage, had explanations different from those that Dart had proposed. For instance, my work (Brain 1981) showed that the disproportions were linked to the varied robusticity of skeletal parts: some bones are simply better able to survive destructive treatment than others. In fact, it is possible to predict which parts of a skeleton will survive any given destructive process and which will disappear. It is no longer necessary to invoke deliberate hominid selection of bones to account for disproportions in a fossil assemblage. Similarly, subsequent work on hyaenas (Maguire *et al.* 1980; Skinner *et al.* 1980), particularly the striped hyaena, *Hyaena hyaena* whose fossils are found in the Makapansgat assemblage, have shown that these scavengers do, in fact, accumulate large numbers of bones in their breeding lairs. It now seems highly probable that they were more important as bone-collectors at Makapansgat than hominids had been.

It can be said that African cave taphonomy crystallised as a discipline at a symposium, held under the auspices of the Wenner-Gren Foundation for Anthropological Research, at Burg Wartenstein, Austria, during July 1976. The conference proceedings

were published as a book, "*Fossils in the Making*" (Behrensmeyer & Hill 1980). However, it will always be to Raymond Dart's credit that he embarked on a pioneering taphonomic investigation years before the basic principles of cave taphonomy had been formulated. His generosity of spirit was shown by the fact that he enthusiastically welcomed new

interpretations, even when these conflicted with his own published views.

ACKNOWLEDGEMENTS

I would like to thank Bruce Rubidge for inviting me to participate in the BPI-50 celebrations and to contribute this paper. I have greatly appreciated my long association with the Bernard Price Institute and wish it well for the years to come. My thanks are also due to Chris Gow and Judy Maguire for editorial help.

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THE BEGINNING

During the initial years of my involvement in the history of the Bernard Price Institute (BPI), I was a completely naive, slightly over-enthusiastic young man, and when the Institute was coming from the start it is hard to see what it is doing. In particular, James Kitching, who has been at the helm of the Institute since the very beginning, gave me some useful pointers to the early history of the BPI. From these discussions it was clear that it was the determination, enthusiasm and a certain break with the past on the part of Sir Robert Brown, combined with the philanthropic generosity of Sir Ernest Cassel, the vision of Percy Marshall Lee Smith, and the enlightened attitude of the University of the Witwatersrand that led to the Institute's birth. Implicitly it was because James was deeply convinced that South Africa was facing a large part of its prehistoric palaeontological heritage in serious peril that he planned this as what he regarded as an essential, unqualified and unadorned action on the part of state burgomasters who, by failing to provide sufficient money to ensure that this heritage was properly cared for, were failing in their duty to the country.

The main motive for the establishment of the Institute was therefore to carry out a task that was actually the responsibility of the State, but was being badly neglected. It was to initiate a systematic programme to find and collect fossils, especially the fossil remains of the Karoo, and to ensure that they were properly prepared, stored, catalogued and made

available for study by local and foreign specialists. It was to be part of a university, the Institute would also have an obligation to develop local palaeontological expertise by teaching students.

Robert's initiative came towards the end of World War II and no wonder was his war over than the first full-time member of staff was appointed and the programme of work got under way. That person was James Kitching — soon to be joined by his two brothers — and in their hands a two-pronged campaign of serious scholarly provision swung into action. Half the work went to the Karoo collecting fossil reptiles and the other half partly at handi-crafts, virtually where the Institute stands today, doing the necessary preparation and curation work, and pursuing the Karoo collecting. Percy Marshall Lee Smith's motto — 'our hope is that a fossil or two might turn up' — was a good one.

THE FRUIT OF WILL DOUBT

Over the half-century since then the collection has grown enormously, adding the best of the collection of mammal-like reptiles from the Karoo of the largest, most comprehensive best prepared and better known in the world. It now has the best of thousands of specimens that were never before known to exist in this country and its equivalent in or out of other parts of the world. In the BPI's 50th anniversary year, the 'big man' is served by a 1,200,000 m² of the southern part of the country with national parks, the BPI's 50th anniversary year is the Institute's

COAXING HISTORY FROM THE ROCKS: THE CONTRIBUTION OF THE BPI (PALAEONTOLOGY)

by

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ABSTRACT

From humble beginnings at the conclusion of the Second World War, the Bernard Price Institute for Palaeontological Research has developed into a major centre of palaeontological research and training whose contribution extends far beyond the borders of South Africa. Over the 50 years of its existence it has amassed large collections of fossils from most of the fossiliferous deposits of South Africa, covering a large segment of geological time and a broad sweep of the diversity of life. These collections have provided the foundation for ongoing research by its staff and students, as well as by visiting scientists from many other parts of the world. As a component of the University of the Witwatersrand, the Institute incorporates the only separate teaching department of palaeontology in any South African university, through which a steady stream of undergraduate and graduate students has passed over the years. Many of those students now occupy senior research and management positions in institutions and corporations scattered across the world. Under its current leadership, the Institute looks set fair for the next 50 years of solid contribution to world palaeontology.

KEYWORDS: Bernard Price Institute.

THE BEGINNING

During the mini-symposium to commemorate the jubilee of the Bernard Price Institute ('BPI', as it is commonly known), several contributors gave personal accounts of where the Institute has come from and what it is busy doing today. In particular, James Kitching, who has been at the hub of the Institute since the very beginning, gave some unique personal reminiscences of the early history of the BPI. From these discussions it was clear that it was the determination, enthusiasm and a certain brash pushiness on the part of Dr Robert Broom, combined with the philanthropic generosity of Dr Bernard Price, the vision of Field Marshal Jan Smuts, and the enlightened attitude of the University of the Witwatersrand that led to the Institute's birth. Basically it was because Broom was deeply concerned that South Africa was losing a large part of its priceless palaeontological heritage to erosion each year. He blamed this on what he regarded as an unwilling, unenlightened and mean attitude on the part of state bureaucrats who, by failing to provide sufficient money to ensure that this heritage was properly cared for, were failing in their duty to the nation.

The main motive for the establishment of the Institute was therefore to carry out a task that was actually the responsibility of the State, but was being badly neglected – namely, to initiate a systematic programme to find and collect fossils, especially the fossil reptiles of the Karoo, and to ensure that they were properly prepared, stored, curated, and made

available for study by local and foreign specialists. As it was to be part of a university, the Institute would also have an obligation to develop local palaeontological expertise by teaching students.

Broom's initiative came towards the end of World War II, and no sooner was the war over than the first full-time member of staff was appointed and the programme of work got under way. That person was James Kitching – soon to be joined by his two brothers – and in their hands a two-pronged campaign of almost military precision swung into action: half the year spent in the Karoo collecting fossil reptiles, and the other half partly at headquarters, virtually where the Institute stands today, doing the necessary preparation and curation work, and partly at Makapansgat collecting Plio-Pleistocene mammal fossils – ever hopeful that a hominid or two might turn up.

THE FRUITS OF FIELDWORK

Over the half-century since then the collections have grown enormously, making the Institute's collection of mammal-like reptiles from the Karoo one of the largest, most comprehensive, best prepared and better curated in the world. It now runs into tens of thousands of specimens from right across the Karoo rock sequence in this country and its equivalents in several other parts of the world. Inside the BPI almost one entire wall of the 'map room' is covered by a 1:250 000 map of the southern part of the country with coloured pins showing the localities from which specimens in the Institute's

collections – and in those of several other institutions – have been collected. It is affectionately and simply known as ‘The Map’, and it is awesome to stand in front of it and reflect on the fact that one man – James Kitching – has personally walked over virtually every one of those localities, and laboured to remove the fossils and carry them out on his back. In this task over more than forty years he was usually helped by his long-time field assistant and special friend, the late Regent (‘Lukas’) Huma. Whether anyone has ever counted the number of pins on the map I don’t know, but it certainly runs into many hundreds. It alone is a monument to the commitment and dedication of James Kitching as a field collector of fossils, under conditions that were often physically punishing.

One major shortcoming of South African fossil collections in the era of Broom and afterwards was that they consisted almost exclusively of skulls. In this, let it be said, collectors were following Broom’s own example, usually targeting only skulls, and leaving behind in the rock whatever other parts of the skeleton might still be there. Over the years the Karoo became littered with these sad victims of palaeontological decapitation, and collectors working the Karoo became derisively known as ‘head-hunters’. To some extent this criticism also applied to the early material in the BPI’s own Karoo reptile collections, but it is no longer true and is not as much of a problem here as it is in other collections. The BPI now houses significant numbers of well collected complete skeletons of many fossil forms which have proved a great boon to those trying to interpret these ancient life forms correctly. In particular, they have helped to trace the evolutionary transition from reptiles to mammals, and this remains one of the Institute’s greatest and most enduring contributions over the years.

The Institute’s early work at Makapansgat, sparked originally by the discoveries of Wilfred Eitzman in the ’20s, which galvanised Raymond Dart and later his student and successor, Phillip Tobias, produced vast quantities of generally fragmentary bone. Out of that work arose what is to my mind a very unfortunate split in the University’s Plio-Pleistocene fossil collections: all hominid specimens were to go to the Anatomy Department at the Medical School, and the BPI was to keep the rest, including non-hominid primates. This is still so to the best of my knowledge, and I regard it as regrettable – it is undesirable to split collections from the same locality in this frankly rather arbitrary way, with its unfortunate overtones of “first class” and “second class” collections.

BREAKING NEW GROUND

An important new direction which soon grew out of the Institute’s interests at Makapansgat was the detailed analysis of bone accumulations in the various ancient cavern infills at Makapansgat, in an effort to find out how and why they accumulated there. The BPI and the Transvaal Museum tackled this question at sites in the Northern Transvaal and the Swartkrans

localities respectively. From it there developed considerable taphonomic expertise in the institute, especially of Plio-Pleistocene cave deposits under the stimulating leadership of Judy Maguire. Linked to this has also been the detailed analysis of cave stratigraphy to unravel the often enormously complex stratigraphic relationships of the various separate but interlinked depositories in these complex systems.

BIRTH OF A JOURNAL

With a steadily increasing flow of studies by staff, research students and visiting scientists, the need was soon felt for a journal in which these studies could be published, thus making the work of the Institute known to a wider scientific world. This need gave rise to the birth of the only specialist journal in South Africa devoted entirely to palaeontology, *Palaeontologia africana*, now in its 33rd volume. This journal is widely circulated to many countries of the world, but I think it would be fair to say that it is better appreciated outside South Africa than it is at home. Over the nearly forty years of its existence it has published hundreds of papers, most dealing with some aspect of palaeontology related to the Institute’s own extensive collections.

FORGING LINKS WITH INDUSTRY

From the initial two-pronged collecting programme, it wasn’t long before the fledgling Institute branched out into other areas of palaeontology which were equally exciting academically, but were also important from other points of view. Palaeontology is sometimes dismissed by people with a ‘bean-counting mentality’ as being of no economic importance and therefore of no value other than a mild curiosity value at best. But the new areas into which the Institute was moving started to change that; these were the fields of palaeobotany and micropalaeontology – both with strong links to industry through the fossil fuels (coal and oil) with which they are associated. The illustrious Edna Plumstead initiated and led the palaeobotanical programme, and through her efforts and those of her students, very large and important collections of fossil plants of many kinds were built up. It was she who first put before the scientific world the intriguing fruiting structures of the plant forms which dominated the extensive Ecca coal flora, and interpreted their importance as showing the path of the evolutionary transition from non-flowering to flowering plants. These highly attractive fossils, and their promise of exciting new information, attracted several students, some of whom have gone on to build significant international reputations of their own as palaeobotanists of note.

One important application which grew out of this palaeobotanical initiative, and which now serves industry directly in a meaningful way, was the development and refinement of laboratory techniques to assess coal quality and its suitability for a variety of industrial uses. This aspect was developed in the Institute by Rosemary Falcon, herself one of Plumstead’s original students.

The other move into applied palaeontology was in the field of micropalaeontology related to the oil industry. This was greatly boosted by a decision by the oil exploration corporation SOEKOR to locate its micropalaeontology laboratory within the institute, under the direction of Ian McLachlan, himself a former student. Throughout its active prospecting phase, and before its move to the Western Cape, SOEKOR ran this lab and an excellent co-operative relationship built up between the Institute and the local oil prospecting industry.

TRAINING NEW PALAEOLOGISTS

Whatever other contributions the Institute has made, one of its most important has been the training of students in palaeontology. Attached to the Institute is the only separate teaching department of palaeontology at any university in South Africa. Although it offers no undergraduate courses of its own, it contributes to the undergraduate teaching of both the School of Earth Sciences and the School of Biological Sciences in the Faculty of Science. At postgraduate level it runs its own courses and caters for its own graduate students. Students who have received their training through the Institute have found their way into senior research and management posts not only in museums and universities, which is where one would normally expect to find palaeontologists, but also in industry and in various quasi-governmental bodies. Some have even successfully entered the precarious world of the entrepreneur – including one professional astrologer!

Although systematic work has continued to underpin the Institute's research, other avenues have been progressively added as new approaches and imaginative ideas have emerged from the many talented people who have worked at or been associated with the BPI. The large Karoo reptile collections, painstakingly and meticulously collected especially by James Kitching, clearly lend themselves to more than mere classification. Indeed, from the earliest moments of research on Karoo reptiles – even before the seminal early work of Broom – the fossils of the Beaufort Group have been used as biostratigraphic tools, and the Institute's contribution to biostratigraphy has been and continues to be notable. Since the Task Group on Biostratigraphy of the South African Commission on Stratigraphy was established a little more than ten years ago, it has been chaired by the Director of the BPI, and Professor Bruce Rubidge, the current Director, is playing his role as chairman with flair and distinction.

One could say that the late forties and the fifties represented the 'alpha-phase' of work in the Institute, in which the emphasis was on growing the collections, and identifying, describing and classifying the forms found. In keeping with trends in the rest of the scientific world, in the sixties and seventies the Institute's net was cast wider. Although alpha-taxonomic studies continued, the focus began to shift more towards syntheses aimed at providing insights into the way ancient ecosystems functioned, and the

applied aspects of palaeontology became increasingly important. Sedimentology and palaeoecology assumed a central importance in the work, and this helped to bring the Institute's work much closer to that of the University's Geology Department. Where links with the earth sciences had been at best tenuous before, these new directions forged new links which have progressively strengthened. For a palaeontological institute which grew out of zoology, this was a healthy development because the true heritage of the discipline embraces the life sciences and the earth sciences equally.

It was also during this period that a School of Earth Sciences was established at the University, with the Institute itself playing a leading role in its establishment. One of the great benefits of that development was the adoption of a 'topic' system for teaching courses in the Earth Sciences, and as a result students from a much wider spread of academic backgrounds – including the Arts – were exposed to palaeontology, out of which some important graduate research in palaeontology grew. There is no doubt in my mind that this was a valuable and healthy development for the Institute.

Since the eighties the Institute has further broadened its interests, and has now added other 'micro' aspects of the study of fossils – including fossil wood, which has for so long been a seriously neglected corner of palaeobotany, and osteohistology, which holds out so much promise of new insights into aspects of the lives of animals which are usually beyond the reach of traditional palaeontological methods. A further exciting project has been the ongoing investigation of the volcanic crater-lake deposits at Orapa in Botswana, with its astonishingly well preserved fossils, including not only insects and other delicate soft-bodied invertebrates, but also some of the earliest flowers in southern Africa. These deposits have opened up the very real possibility of study of the co-evolution of plants and their insect pollinators over the last 100 million years. Such studies again promise interesting insights into the ways plants and animals lived in a vanished world of long ago.

The Institute remains loyal to its original mission in that it recognises that the fossil fauna and flora of this part of the world is still far from being completely known, so there is still ample room for 'alpha' studies. But its study base is broadening all the time as innovative and imaginative new approaches are brought to bear on problems old and new, and as new areas of research open up to the fresh minds entering the field.

THE IMPORTANCE OF CROSS-POLLINATION

Finally, a very valuable contribution of the BPI is that it has always been an important magnet drawing visiting foreign specialists here, even during the height of the academic boycott of South Africa during the seventies and eighties. This has been true despite the strenuous efforts of some within this University (and

even one within the Institute itself) to intensify the boycott. It was satisfying for those of us opposed to the boycott to see their campaign against academic contacts with the BPI fail; even in the darkest, deepest days of the boycott a steady stream of foreign specialists came to the Institute to study its fossils and to interact with its staff, students and associates. This value as an academic magnet is an important one of which the University should take due note; in any academic institution, intellectual cross-pollination with specialists from elsewhere is a crucially important factor which largely determines an institution's academic relevance, viability and progress.

FROM SMALL ACORNS ...

The permanent staff of the BPI has always been small – some would say sub-critically small. But hopefully this brief review has shown that not only is the Institute alive and kicking, but buzzing with a vitality and enthusiasm that will carry it in healthy state into the next half century, if only it can be assured of the

support it deserves from the University, from important research funding sources such as the FRD, and from other potential benefactors. As someone said, "From small acorns tall oaks grow". May this acorn continue to yield tall oaks – none taller than the 'oke' we all know as 'Oom James'. If I look for one abiding contribution of the Bernard Price Institute to the world, I personally need to look no further than him. He is a legend in his own lifetime, and there are many of us who feel immensely privileged and proud to call him friend; all who are associated with him as a colleague admire him and hold him in the deepest affection.

Under the dynamic leadership of the present Director, Bruce Rubidge, the Bernard Price Institute indeed looks set fair to sail on into another half-century of exciting palaeontological achievement. One wonders what Broom or Price hoped for when they dreamed their first dreams of a palaeontological institute, and how they would feel now if they could see what had become of it in the intervening half-century. I suspect we would see smiles of deep satisfaction and contentment.

STYLE GUIDE FOR AUTHORS

(revised 1997)

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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.

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----- 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., MacLean, P.D., 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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