

PRESIDENTIAL ADDRESS: TAPHONOMY AS AN AID TO AFRICAN PALAEOONTOLOGY*

by

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SUMMARY

Palaeontology has its roots in both the earth and life sciences. Its usefulness to geology comes from the light which the understanding of fossils may throw on the stratigraphic relationships of sediments, or the presence of economic deposits such as coal or oil. In biology, the study of fossils has the same objectives as does the study of living animals or plants and such objectives are generally reached in a series of steps which may be set out as follows:

STEP 1. *Discovering what forms of life are, or were, to be found in a particular place at a particular time.*

Each form is allocated a name and is fitted into a system of classification. These contributions are made by the taxonomist or the systematist.

STEP 2. *Gaining a fuller understanding of each described taxon as a living entity.*

Here the input is from the anatomist, developmental biologist, geneticist, physiologist or ethologist and the information gained is likely to modify earlier decisions taken on the systematic position of the forms involved.

STEP 3. *Understanding the position of each form in the living community or ecosystem.*

This step is usually taken by a population biologist or ecologist.

Hopefully, any competent neo- or palaeobiologist (I use the latter term deliberately in this context in preference to "palaeontologist") should be able to contribute to more than one of the steps outlined above. Although the taxonomic and systematic steps have traditionally been taken in museums or related institutions, it is encouraging to see that some of the steps subsequent to these very basic classificatory ones are now also being taken by museum biologists. The trend is a desirable one as it will ensure the continued viability of museums as research institutions in the mainstream of biological progress.

As I have mentioned, I believe that the aims of palaeobiologists should be similar to those of their neobiological colleagues. The two kinds of biologists should centre their aims on the complete understanding of living things, both as individual expressions of life's processes, and as integrated parts of communities and ecosystems. It is an obvious fact that palaeobiologists have to interpret traces of past life while neobiologists can study living things in the very act of living. The burden on the former group of scientists is an obvious one and it is not difficult to understand why the progress in palaeo-studies should have been so much slower than it has been in neobiology. Despite its problems and frustrations, the reconstruction of past life is an enthralling occupation, the fascination of which must surely have been experienced by all palaeontologists. I have frequently pondered on the psychological basis of palaeontological fascination — perhaps it is similar to that of detective work in which the attention of the investigator is held as each new scrap of evidence is uncovered and slots into place. Such work has the elements of a strip-tease performance which would doubtless be boring if all were to be laid bare at once. Fortunately for palaeontology (and strip-tease performances for that matter), the picture emerges but slowly and the work involved becomes pure fun, as all productive research ought to be. My friends in the field of animal behaviour tell me that the motivation for research has its origins in ritualised hunting — that excitement mounts as the time for the kill, or the major discovery, approaches. Maybe they are right, but their conclusion need not detract from the intense pleasure to be had from the pursuit of palaeontology.

The obvious point I wish to make is that fossils are the dead relics of once-living things — it is necessary to reconstruct them and, in our imagination, to bring them back to life, if we are to make any biological sense of them as individual once-living things, or as parts of once-living communities. It is in this reconstructive process that taphonomy has its usefulness, some aspects of which I hope to bring to your attention.

What is taphonomy?

It would be misleading to suggest that taphonomy is a new branch of science, as I am sure that geologists and palaeontologists have been thinking about those processes now regarded as taphonomic ones for a century or more. It would be true to say though that only recently has the study crystallised into what might be regarded as a discipline. The crystallisation process began when, in 1940, Prof. I.A. Efremov, a Russian geologist and palaeontologist, defined and

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described the term "Taphonomy" to mean, literally, the laws of burial. As Everett Olson has pointed out, taphonomy "concerns all aspects of the passage of organisms from the biosphere to the lithosphere" and, since Efremov's original definition was formulated, Olson has been prominent in his application of taphonomic concepts to his study of Triassic vertebrates in the United States. By the early 1970s, enough people were actively working on taphonomic problems to allow the planning of an international symposium on the subject. The symposium was hosted by the Wenner-Gren Foundation for Anthropological Research and took place in Austria during July 1976. Its theme was "Taphonomy and vertebrate palaeoecology with special reference to the late Cenozoic in sub-Saharan Africa" and it was jointly organised by Andrew Hill, Kay Behrensmeyer, Alan Walker and myself. Its proceedings are currently being published as a book entitled "Fossils in the Making" by the University of Chicago Press.

The aspects of taphonomy are many and varied but, from the palaeobiological point of view, I believe the central issue to be this: *fossils are relics of once-living things which have suffered a series of losses since they were last alive. It is in understanding these losses, and compensating for them, that taphonomy may serve as an aid to palaeontology.*

In the comments which follow, I will be referring almost entirely to the taphonomy of terrestrial, Caenozoic vertebrates simply because this is the field in which I have had practical experience. Hopefully, some wider principles are involved here so that extrapolation to other palaeontological fields will not be difficult.

Taphonomic reconstruction of individual animals

Upon death, an animal (or plant for that matter) gives up the fight to maintain the integrity of its body and the inevitable process of subtraction begins. Here it must be remembered that no animal, not even an amoeba, can be regarded as a homogeneous blob of protoplasm which will disintegrate and disappear in a uniform manner. It is inevitable that some parts of any body will be more susceptible to the processes of decay or predator action than others and that those particular parts will be more effective in their resistance to disintegration. The effect of fossilisation is to stop the progress of disintegration at a particular stage in the process and to maintain the *status quo* of that stage for as long as the enclosing sediment remains intact.

In the case of a vertebrate, various components of its body will vary considerably in their ability to resist destruction. At one end of this scale of destructibility will lie the blood and similar soft connective tissues, while, at the other, are the heavily mineralised parts of the skeleton. Regrettably, it is only some of the skeletal parts that can survive the destructive forces operating on them before fossilisation inhibits further degradation. It is possible, in the case of any vertebrate skeleton, to predict with confidence which parts of that skeleton will resist destruction most effectively and, I suspect, this kind of prediction will become a routine procedure in taphonomy.

I have had personal experience of how a taphonomic investigation can throw light on a problematic situation in palaeontology. When Prof. R.A. Dart published the results of his pioneering analysis of a large fossil sample from Makapansgat in 1955, he found that parts of the skeletons represented there occurred in very unnatural proportions. Primates and carnivores were largely represented by their skulls while, in the case of antelopes, certain skeletal parts were found to the partial or complete exclusion of others. Distal humeri for instance proved to be ten times as common as proximal ones, while parts such as caudal vertebrae could not be found at all. Never having encountered such a situation before, Prof. Dart assumed that such disproportions must surely have resulted from artificial selection by hominids. He postulated that those bones found in abundance were ones brought to the cave because of their suitability for tools. Those that were missing had simply not been brought back at all. On the basis of this and similar evidence, Prof. Dart built up his theory of the "osteodontokeratic culture" of *Australopithecus*.

In the hope of elucidating the situation, I made a study during the 1960s of goat bones discarded by Hottentots and subsequently gnawed by dogs in Namib desert villages. The skeletal parts remaining were those which had been able to survive the combined feeding action of the Hottentot/dog combination. To my surprise at the time, it was impossible to find the intact proximal humerus of a single goat, while distal humeri were extremely abundant. On the basis of the whole goat-bone assemblage, it was possible to work out percentage survival figures for each skeletal part and the correspondence between these figures and those for the Makapansgat fossil assemblage was certainly remarkable. Both samples were found to contain resistant skeletal elements to the complete or partial exclusion of delicate ones. The need to postulate artificial selection in the case of the Makapansgat bones fell away and other agents of accumulation could then be investigated.

The Hottentot study showed that any bone's ability to resist destruction could be correlated with some of its inherent characteristics. Foremost of these is compactness of the bone which may be expressed as specific gravity. Linked to this is the ratio of a bone's surface area to its volume. Consider the case of a thin flat bone such as a scapula. Although composed of compact bone, its surface area relative to its volume is so great that a scapula blade is a delicate structure, readily destroyed and thus frequently absent from fossil assemblages.

A bone's characteristics of compactness and shape are naturally of significance when that bone is transported in water before reaching its fossilisation site. The point about this is sim-

ply that a transported bone assemblage will consist of those skeletal elements which ended up where they did for good hydraulic reasons. Taphonomists such as Kay Behrensmeyer and Noel Boaz have studied bones as sedimentary particles in fluvial environments and their results should be of interest to any palaeontologist having to deal with a fossil assemblage which had undergone water transport.

Taphonomic reconstruction of communities

In attempting to reconstruct individual animals on the basis of their relics, a taphonomist will try to assess and interpret the losses which the bodies of each of these animals have suffered. When attention is turned to the reconstruction of communities, however, the preoccupation is with a preserved *assemblage* derived from that original community. During its transformation into an assemblage, a community has obviously lost a good deal of its substance, but the chances are good that this loss has not been uniformly suffered by all parts of the community. Those parts to have suffered more loss will obviously be less well represented in the assemblage, with the resultant appearance of a *bias*. The nature of biases will vary from one fossil assemblage to another and generalisations are probably pointless. However, I would like to mention two common predator-induced biases as examples of the kind of thing to be taken into account.

In the first case it should be remembered that a predator typically selects prey within a certain preferred size-range. Potentially edible animals whose size falls above or below this range are generally ignored with the result that, if an assemblage is built up by this particular predator, that assemblage will be seriously biased in favour of the carnivore's feeding preference.

Secondly, the time at which hunting takes place will determine what prey spectrum is taken. Most owls, for instance, restrict their hunting to the evening or night, resulting in a bias towards the remains of crepuscular or nocturnal prey species in the owl-accumulated assemblage.

When using an assemblage as an indicator of a community's original composition, it is important to consider the death rates of the various animals in that community. Consider the case of an area of land capable of supporting ten elephants and ten shrews at any one time. Each elephant lives for 50 years but each shrew for only one year. If remains of all these animals found their way into an assemblage, shrews would be over-represented in that assemblage by a factor of 50, simply because they die 50 times as frequently as elephants do. In reconstructing the composition of the community, as it was at any given moment in time, correction would have to be made for the death-rate bias.

I have said enough to make it clear that the major task of the taphonomist in reconstructing a community from an assemblage lies in the recognition of biases which affected the assemblage's composition, and in correcting for such biases. If the taphonomist does his work well, the assemblage can be used as a high-fidelity reproduction of the community which it represents. This is one of the ways whereby taphonomy may serve as an aid to palaeontology.

Some suggestions for further reading

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BIOZONATION OF THE BEAUFORT GROUP WITH SPECIAL REFERENCE TO THE WESTERN KAROO BASIN*

by

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ABSTRACT

The lithostratigraphic subdivision of the Beaufort Group is discussed in its historical perspective. The Adelaide Subgroup (lower Beaufort) is now divided into two formations, as the lithostratigraphic subdivision used in the Eastern Cape is not applicable in the western part of the Karoo Basin. The Ecce-Beaufort transition is discussed.

The *Abrahamskraal Formation* lies conformably on the Waterford Formation of the Ecce Group and is distinguished from the overlying Teekloof Formation by the presence of numerous continuous "chert bands", the higher percentage of sandstone and the paucity of red mudrock. Continuous "chert bands" do not occur in the Teekloof Formation.

The existing biostratigraphic subdivision of the Beaufort Group is examined.

The lower three-quarters of the existing *Tapinocephalus* zone is referred to as the *Dinocephalian Assemblage Zone*. The lowest "chert band" associated with the arenaceous Poortjie horizon coincides with the last occurrence of dinocephalian remains. The strata between this point and the first occurrence of *Tropidostoma* are referred to a *Priesterognathus-Diictodon Assemblage Zone*. This assemblage zone is now considered to be part of the Teekloof Formation.

The *Tropidostoma-Endothiodon Assemblage Zone* is associated with the Hoedemaker Member of the Teekloof Formation which contains very few sandstones. This is overlain by the *Aulacephalodon-Cistecephalus Assemblage Zone* which is mainly associated with the Oudekloof Member of the Teekloof Formation which contains numerous prominent channel sandstones. *Oudenodon bairni* also occurs in this sequence. This zone is followed by the *Dicynodon lacerticeps-Whaitsia Assemblage Zone*. These three zones are restricted to the Teekloof Formation in the western part of the basin.

The *Lystrosaurus-Thrinaxodon Assemblage Zone* is mainly associated with the Katberg Formation of the Tarkastad Subgroup (upper part of the Beaufort strata). The genus *Lystrosaurus* does, however, occur both above and below the Katberg Formation. The *Kannemeyeria-Diademodon Assemblage Zone* occurs in the upper two-thirds of the Burgersdorp Formation.

It is concluded that most of the larger uranium discoveries have been made in strata assigned to the *Priesterognathus-Diictodon* and *Tropidostoma-Endothiodon Assemblage zones* within a stratigraphic thickness of about 300 m.

It is expected that a more detailed biostratigraphic subdivision will become possible when taxonomic revisions of the genus *Diictodon* and the smaller endothiodonts are effected.

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SOME ASPECTS OF THE RELATIONSHIP BETWEEN TIME, MORPHOLOGICAL CHANGE AND THE ENVIRONMENT*

by

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ABSTRACT

What is the relationship between morphological change (along a lineage) and speciation? Must the environment always change in order to produce morphological change and/or speciation; or could the passage of time alone be responsible for producing morphochange in the form of increasingly better adaptation to the *same* environment? What is the distribution of rates of change along lineages? How many "modes" of evolution are there, and which one predominates? These questions are the essence of the hotly fought current debate on how evolution progresses. The majority of biologists either explicitly or implicitly believe, as did Darwin, that gradual, inexorable change predominates, with no increase in evolutionary rate with lineage splitting (phyletic gradualism). Some think that change is by no means gradual or inexorable; but that equilibrium is the rule while change/speciation is rare (punctuated equilibrium). These two models can be tested in a variety of ways, and particularly effectively by palaeontological data. This contribution contains a review of some tests suggested by others, as well as some new ideas on the subject.

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TOOTH FUNCTION AND REPLACEMENT IN HETERODONTOSAURID ORNITHISCHIAN OF THE STORMBERG SERIES — IMPLICATIONS FOR AESTIVATION*

by

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ABSTRACT

Thulborn (1978) suggests that ornithischian dinosaurs of the upper Stormberg Series (Late Triassic–Early Jurassic) of southern Africa underwent aestivation during an annual dry season. His argument, based on an interpretation of tooth function and replacement in heterodontosaurids, is: (1) unequivocal evidence of tooth replacement is not seen, and (2) piecemeal replacement of the dentition would be incompatible with maintenance of a fore-aft grinding function of the teeth; therefore, the entire dentition must have been rapidly replaced as a unit during periods of non-feeding, i.e. during aestivation. However, study of tooth wear patterns in *Lanasaurus*, *Lycorhinus*, and *Heterodontosaurus* show that jaw movements during mastication were orthal (open-and-close) and lateral to medial, not forwards and backwards. Differences in degree of tooth wear would not interfere with masticatory movements. Patterns of differential wear indicate that tooth replacement was not periodic but continuous, as in other reptiles. *Zahnreihen*, with a Z-spacing of about 3.0, are recognizable. Replacement ceased in mature individuals. The dentition shows adaptations for prolonging its effective life despite heavy wear. Differential tooth wear is incompatible with the idea of replacement of the entire dentition as a unit during an hypothesized period of aestivation.

FOSSIL HISTORY

Revised History

Discovery of the first ornithischian fossil was the *Protosuchus* and *Moschops* of southern Africa. The first type is an almost complete skull in the South African Museum (SAM 1922). It is a small herbivorous ornithischian dinosaur from the lower Gorgospondon zone of the Beaufort. It comes from the Karoo region near Beaufort West, Free State province, about 100 km from the first Triassic ornithischian *Scelionyx* from the Karoo. *Protosuchus* was named by Gertzel (1952) in a review of the identifiable fossil fish animals from southern Africa.

The first other specimens of the possible ancestor of Ornithischians, a small, early form, were the *Protosuchus* and *Moschops* from the Karoo. The Cape Province (McLachlan and Anderson 1974).

In southern Africa the fossil record was the *Protosuchus* and *Moschops*. Detailed information was from South African Triassic deposits are abundant and represent three families: the *Protosuchus* and *Moschops* (Gertzel and Gertzel 1952).

New Material

The discovery of ornithischian material was reported in the Karoo region of which the *Protosuchus* and *Moschops* are the most important.

The discovery of a shark rostrum associated with a large ornithischian fossil was reported by G. Gertzel in the *Protosuchus* district. This implies a close association between the ornithischian and shark fossils from Beaufort West and Karoo region. A shoulder blade and material in Namibia (South West Africa) after by and Woodward 1970. From Beaufort West, probably similar material was found at the top of the Beaufort formation and a small level from a quarry, Beaufort West 1970 and Woodward (1970). In late, however, an ornithischian material has been reported from the Gorgospondon locality. The South African fossil formation (Parsons) from the other hand has yielded an abundance of fossil shark teeth and spines (Ragotzke 1978) which were reported from the equivalent Witbank Formation of the South African Karoo basin (Gertzel 1981).

The ornithischian relationship was reported in a number of ornithischian teeth. The teeth of the skull (ornithischian) are found in the Karoo region and the greater part of the dentition is represented in the Karoo region. The teeth of which are found with the ornamentation of ornithischian teeth. The ornamentation was found in the Karoo region and the ornamentation was found in the Karoo region. The ornamentation was found in the Karoo region and the ornamentation was found in the Karoo region.

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THE FOSSIL RECORD OF THE CLASS CHONDRICHTHYES IN SOUTHERN AFRICA

by

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ABSTRACT

The fossil record of the class Chondrichthyes in southern Africa is reviewed and some important new fossil finds are announced.

INTRODUCTION

The fossil record of the Chondrichthyes is incomplete and usually restricted to material such as detached teeth and spines because the cartilaginous parts of the skeleton fossilise only under extremely favourable conditions. For this reason only a few three-dimensionally preserved specimens of chondrichthyan neurocrania are known and all of these come from Europe and North America.

Described fossils of this class from the Gondwana continents are virtually non-existent but for a few isolated teeth and spines mostly from Brazil (Silva Santos 1946, Pinto 1965, Silva Santos and Sardenberg 1970, Figueiredo 1972, Ragonha 1978).

FOSSIL RECORD

Record to Date

Only a single shark species has been described from the Palaeozoic and Mesozoic of southern Africa. The holotype is an almost complete fish in the South African Museum (SAM-1082). It is a small hybodont shark *Hybodus africanus* Broom from the lower *Cynognathus* zone of the Beaufort. It comes from Bekkerskraal near Rouxville, Orange Free State. Romer (1966) lists *Lissodus* from the lower Triassic of southern Africa but does not mention *Hybodus africanus* Broom. *Lissodus*, however, is not mentioned by Jubb and Gardiner (1975) in a review of the identifiable fossil fish material from southern Africa.

The only other indication of the possible presence of chondrichthyans is spiral coprolites from the shales above the Dwyka tillite from near Douglas, Cape Province (McLachlan and Anderson 1973).

In contrast to the limited record from the Palaeozoic and Mesozoic, detached elasmobranch teeth from South African Cenozoic deposits are plentiful and represent three families, six genera and 11 species of sharks (Jubb and Gardiner 1975).

New Material

New discoveries of chondrichthyan material were recently made in South Africa of which one specimen in particular is of great importance.

1. The oldest chondrichthyan material now known from South Africa comes from the third Bokkeveld shale and was found by Mr. A. de Vries

on his farm between Barrydale and Ladismith, Cape Province. Impressions of pleuracanth (ctenacanth)-type teeth occur together with placoderm fragments in a brown mudstone. The teeth have two large lateral cusps and a much reduced central cusp, on a button-like base. The middle to upper Devonian age of the upper Bokkeveld is equal to the oldest records for pleuracanth.

2. The tentative identification of spiral coprolites from nodules in a marine horizon in the Prince Albert formation near Douglas, Cape Province (McLachlan and Anderson 1973) is supported by the discovery of a shark neurocranium associated with spiral coprolites from the same stratigraphic horizon by R. Oosthuizen in the Prince Albert district. This marine horizon in the Prince Albert formation has yielded a fauna which includes osteichthyans and cephalopods from Douglas and, amongst other marine forms, a goniatite from near Mariental in Namibia (South West Africa) (Martin and Wilczhewski 1970). From Uruguay a stratigraphically similar nodular marine horizon at the top of the Itararé formation has yielded a similar fossil fauna of goniatites, Radiolaria (Closs 1967) and osteichthyans (Beltan 1978). To date, however, no chondrichthyan material has been reported from the Uruguayan nodules. The South American Irati Formation (Paraná basin) on the other hand has yielded an abundance of fossil shark teeth and spines (Ragonha 1978) whilst none are known from the equivalent Whitehill Formation of the South African Karoo basins (Oelofsen 1981).

The neurocranium mentioned above was preserved in a nodule of radiolarian tests. The cartilage of the skull disappeared after burial in the radiolarian ooze and the greater part of the cartilage is represented in the nodule as cavities, the walls of which are lined with the impressions of calcite crystals from the superficial layer of calcified cartilage. The radiolarian ooze flowed into the skull through apertures such as the nasal openings, foramen magnum and the foramina of the parietal fossa. In this way, internal structures such as the ampullae, sacculus, utriculus and lagena of the inner ear as well as the meninges were extensively preserved.

The cranial anatomy of this shark indicates a

close relationship to forms such as *Danaea* and *Co-belodus* and it is at the level of organisation which Shaeffer (1967) regards as clododont and which Zangerl (1973) calls the anacanthous design. A description of the neurocranium is in preparation and will be published elsewhere.

Apart from the fact that this is the first important record of chondrichthyans from the Palaeozoic of southern Africa or any other Gondwana country (Zangerl, pers. comm.) this braincase, as far as can be assessed from the literature (Romer 1964, Zangerl and Case 1967), seems to be the most complete and best preserved chondrichthyan braincase of Palaeozoic age known to date.

3. A nodule from the upper Witteberg shales collected by Mr. Oosthuizen in the Prince Albert district, Cape Province, contains a spine, numerous placoid scales and impressions of calcite crystals from the calcified layer of cartilage. That this nodule contains the remains of a shark is certain, but a study of the material has not yet been attempted, so a more specific identification is not yet possible.

4. From the Cretaceous deposits at Swartkops and Knysna (Brenton) Cape Province, Mr. Oosthuizen has retrieved three shark teeth. One of the teeth from the marine beds at Swartkops was lodged in a fossilised *Pinna* and it is therefore certain that it did not come from the overlying Alexandria beds. The one from Brenton was found with fossils of Cretaceous age. The other Swartkops specimen shows a strong resemblance to the teeth of *Charcharias taurus* Rafinesque which has a range from the upper Cretaceous to the present. Further collection and study will, however, be necessary to confirm this identification.

SUMMARY

In summary it can be said that although the fossil record of the chondrichthyans is still very incomplete, the new material has made an important contribution in filling in some of the gaps (see table 1).

ACKNOWLEDGEMENTS

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TABLE 1
The fossil record of the Class Chondrichthyes in Southern Africa

Rock Units	Age	Fossil material
Gravel member Varswater formation Langebaan	Latest Miocene–Early Pliocene	Detached shark teeth.
Uloa and Sapolwana Beds, Zululand	Miocene	Hendey (1976) Table 3 lists 11 families and 18 genera. 3 families, 6 genera with 11 species (Jubb and Gardiner 1975).
Alexandria beds	Eo- to Miocene	Haughton (1925) described teeth referred to <i>Isurus hastalis</i> and <i>I. silimani</i> .
Bogenfels, Namibia	Eocene	Detached teeth.
Umzamba beds, Pondoland	Upper Cretaceous (Senonian)	Detached shark teeth (Du Toit 1954).
Sundays River beds, Swartkops		2 teeth from the Sundays River beds, Swartkops; 1 possibly of <i>Charcharias taurus</i> ?
Knysna: Brenton Cretaceous beds	Upper Cretaceous	One tooth from Brenton beds. In the collection of R. Oosthuizen.
Beaufort	Upper Permian to Triassic	<i>Cynognathus</i> zone <i>Hybodus africanus</i> Broom; various specimens from Bekkerskraal, Rouxville. <i>Lissodus</i> ? mentioned by Romer (1966).
Prince Albert formation (Lower Ecca)	Upper Carboniferous to lower Permian	Spiral coprolites, upper Dwyka shales, Douglas (McLachlan and Anderson 1973). 3-dimensionally preserved neurocranium and spiral coprolites, Prince Albert district. Collection of R. Oosthuizen.
Lake Mentz formation, Witteberg Group	Lower Carboniferous	Placoid scales, spine and impressions of calcified cartilage from a nodule, Prince Albert district. Collection of R. Oosthuizen.
Bokkeveld Group	Upper Middle Devonian	Impressions of pleuracanth (ctenacanth)-type teeth in a dark-brown mudstone. Collected by A. de Vries, Barrydale.

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PACHYGENELUS, DIARTHROGNATHUS AND THE DOUBLE JAW ARTICULATION

by

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Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg 2001

The ictidosaur, *Diarthrognathus*, from the Clarens Formation (Cave Sandstone) (Crompton 1958) is generally held to exhibit the expected morphological grade intermediate between advanced cynodonts and mammals; more specifically, it is thought to have both reptilian and mammalian jaw joints. However, several of Crompton's interpretations of the morphology of the lower jaw and its articulation with the skull were wrong; some, but not all, of these he has conceded in print (Crompton 1972).

It is possible that there are only two species of ictidosaur in the Red Beds. The first specimen described was *Tritheledon* (Broom 1912), which comprises a pair of maxillae having mesiodistally compressed teeth of distinctive crown morphology. *Pachygenelus* (Watson 1913), a partial lower jaw with some teeth, is an apparently valid second genus but the position is complicated by the fact that upper and lower teeth are now known to be strikingly dissimilar in ictidosaur. Hopson and Kitching (1972) have synonymised *Diarthrognathus* under *Pachygenelus*.

Re-study (now in progress) of the types of all three genera in conjunction with new materials discovered since will probably clarify the taxonomy.

This is important, for, if it can be shown that most of the ictidosaur material is referable to a single species, the problem of understanding the jaw joint is considerably simplified.

Most of the confusion surrounding the nature of the jaw articulation of *Diarthrognathus* arises from Crompton's (1958) misidentification of the quadrate as the articular. Parts of the squamosal he thought to be quadrate and part of the articular. It was therefore possible for Crompton to conclude that: "The double articulation was possible because a single glenoid cavity was formed by both the quadrate and the squamosal." However, once the quadrate is correctly positioned such a glenoid configuration is no longer tenable. Crompton (1972) conceded this, although still maintaining that *Diarthrognathus* (but perhaps not *Pachygenelus*) had a dentary condyle.

On present evidence the author is disinclined to accept a dentary-squamosal jaw hinge in *Diarthrognathus*. It may be some time before clarity is obtained on this issue but it is useful at this stage to throw the whole question wide open.

The teeth of *Diarthrognathus* have now been prepared and described, and compared with those of *Pachygenelus* (Gow 1980).

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A FIRST RECORD OF A FOSSIL CEPHALOCHORDATE*

by

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ABSTRACT

An imprint from the White Band shales, interpreted as a fossil cephalochordate, is the first record of a fossil of this subphylum.

The anatomy of the specimen as well as the palaeosedimentary environment are suggestive of a pelagic mode of life in contrast to that of modern burrowing forms. This poses the question as to whether the burrowing habit of modern forms really is as primitive as generally believed.

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N.B. A further note was published by the same authors in the *South African Journal of Science*, **77**(7), p. 309.

ASPECTS OF THEROCEPHALIAN CLASSIFICATION AND FUNCTION*

by

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ABSTRACT

The so-called primitive or early Therocephalia of the Upper Permian of South Africa, typified by the Pristerognathidae, have up to the present largely eluded attempts at devising a satisfactory classification for them. The task has been generally complicated by the poor state of preservation, an intractable matrix, relatively few complete skulls and a paucity of postcranial material. Consequently external cranial features have predominated in past classifications with the emphasis on the number and type of teeth. This method is unsatisfactory since lost or replacing teeth may directly influence even the familial status of specimens. This is demonstrated by the Lycosuchidae where the second canine in each maxilla, which was considered to typify the family, turned out to be a replacement tooth. Additional preparation of selected material appears to show that certain differences which exist in the literature might not be valid, e.g. the postfrontal of *Lycosuchus vanderrieti*, and that the group might be more uniform than previous classifications indicate.

A programme involving the use of photoelasticity to determine possible jaw function in the early therocephalians has been initiated with the Department of Engineering at the University of Stellenbosch and preliminary investigations appear to indicate that a scavenging mode of life may have prevailed.

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PRELIMINARY REPORT ON A CLUTCH OF SIX DINOSAURIAN EGGS FROM THE
UPPER TRIASSIC ELLIOT FORMATION, NORTHERN ORANGE FREE STATE*

by

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Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg 2001

ABSTRACT

Up to the present time, dinosaurian egg remains have been described from the Upper Jurassic sediments of Spain and from the Tendaguru Formation of Tanzania, while the majority of known specimens came from the Cretaceous sediments of Mongolia, China, France and North and South America.

The discovery of a cluster of six dinosaurian eggs containing foetal skeletons, from the upper horizons of the Elliot Formation (Red Bed Stage) of the Orange Free State, seems to be the first record of fossil eggs of Upper Triassic age.

The specimens are embedded in a block of hard reddish-brown sandy mudstone blasted from a road-cutting locally known as Rooidraai (Red Bend) in the Golden Gate Highlands National Park, some 17 km east of Clarens, Orange Free State.

Prior to this discovery and the description of two small ornithischian dinosaurs, *Clarencea gracilis* Brink, the present author had on a number of occasions noted the occurrence of isolated long bones of the prosauropod *Massospondylus* weathering out of the face of the now much widened road-cutting; a partial skeleton is still embedded in the face.

From the remains of two partial eggs exposed on one side of the block of sandy mudstone, housed in the Bernard Price Institute, it seems evident that there were originally more than only six eggs in the cluster. Of the six eggs present, three contain foetal remains in an advanced stage of development while one juvenile seems to have hatched prior to the fossilisation of the others, leaving in the matrix a shapeless egg "shell".

The "wrinkled" and to a certain degree flattened state of the eggs seems to indicate that they were leathery as in the eggs of some modern-day reptiles. As preserved they have a long axis of 65 mm and a short axis of approximately 55 mm with an estimated thickness of the egg-shell of 0,5 mm. Microscopically the outer surface or upper prismatic zone shows a very finely roughened surface with minute, well-spaced respiratory pores.

Dinosaurian features that can at present be distinguished on the partially exposed embryonic skull include the very short parietal region, the position of the postorbital, the parietal/supraoccipital suture, and the position and shape of the lachrymal which forms the posterior border of the antorbital fenestra.

This skull is reasonably well preserved and measures 10 mm across the squamosals and 7 mm from the anterior border of the orbit to the supraoccipital. It is in the process of being prepared, but because of the hardness of the matrix and frail state of the bone this will be a long and tedious task, complicated by the fact that parts of the skeleton overlies the anterior portion of the skull.

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AN ILLUSTRATED BIBLIOGRAPHICAL CATALOGUE OF THE SYNAPSIDA

by

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At the Karoo Symposium held at the Bernard Price Institute in 1977 I briefly announced my intention of producing a loose-leaf illustrated bibliographical catalogue of the Synapsida. Each loose leaf deals with a separate species (Appendix A, B). The front page contains the text, which consists of a genus-species-author-date title and material is handled in a standard sequence under six headings: Synonyms, Bibliography, Holotype, Referred material, Generic diagnosis, and Specific diagnosis. The reverse side contains, as far as possible, four views of the skull: lateral, dorsal, ventral and posterior, to standard scale and style.

Any palaeontologist will be welcome to submit entries, each being treated as a separate contribution with the author's name and address.

The catalogue is at present confined to the Synapsida but the possibility of expanding it to other reptile groups and even the whole spectrum of vertebrates has been borne in mind. A major problem has been the numbering of separate entries in such a way that they could be arranged in taxonomic rather than alphabetical order. The solution was to devise a filing code embodying the taxonomy of every individual genus and species. The code extends from class to family and within each family the genera and species are arranged in alphabetical order. When families are arranged in numerical order, they will automatically sort into taxonomic order. This code appears at the top left hand corner of every page. For a typical entry the code would be:

J213C211B *Diademodon tetragonus*

where J refers to the Class

J2	Subclass
J21	Infraclass
J213	Superorder
J213C	Order
J213C2	Suborder
J213C211	Infraorder
J213C211B	Family

Two important matters emerge immediately:

Firstly, if only for the sake of convenience and uniformity in terms of the codal system, the Subphylum Vertebrata is regarded as if it comprises 12 Classes and would-be "Classes": the Agnatha, Placoderma, Chondrichthya, Osteichthya, Amphibia, "Anapsida", "Parapsida", "Euryapsida", "Diapsida", "Synapsida", Aves, and Mammalia.

The 12 Classes and would-be "Classes" of the Vertebrata will resort under 5 Superclasses:

- Superclass Pisces
 - A Class Agnatha
 - B Class Placoderma
 - C Class Chondrichthya
 - D Class Osteichthya
- Superclass Tetrapodes
 - E Class Amphibia
- "Superclass Reptiles"
 - F "Class" Anapsida
 - G "Class" Parapsida
 - H "Class" Euryapsida
 - I "Class" Diapsida
 - J "Class" Synapsida
- "Superclass Aves"
 - K Class Aves
- Superclass Theria
 - L Class Mammalia

Secondly, across the spectrum of vertebrate taxonomy there are many instances where a need is not felt for providing names for all ranks. In the codal system proposed for pagination and classification of entries it is imperative that every rank is properly designated to avoid the use of zero for any of the digits in the code. I have tentatively derived names from lower and higher levels, whichever alternative I have regarded as most appropriate.

In the process of adjusting vertebrate taxonomy in areas where there is no consensus of opinion, or in areas thus far left blank, it is felt that taxonomists in general will welcome any endeavour to standardise the terminations of ranks higher than that of Superfamily. There can be no doubt regarding the convenience of using ranks ending in *-oidea*, *-idae* and *-inae* without qualifying them additionally as Superfamily, Family or Subfamily respectively. Similarly it will be equally convenient to regard ranks terminating in *-ica*, *-ida* and *-ina* as those of Superorder, Order and Suborder respectively so that these can also be used without the rank qualifications.

Unfortunately at ranks above Superfamily one is confronted with some difficulties preventing perfect standardisation. A wide variety of terminations (*-ta*, *-da*, *-a*, *-es*, *-ii*, *-ini*, *-morpha*, *-formes*) — used rather haphazardly at present — are subject to gender, declension, the last letter(s) of the root, or otherwise mere custom or tradition.

Easton (1960) proposed that the following terminations be used consistently (while dealing with the Invertebrata):

Superorder	-ica	Superfamily	-icae
Order	-ida	Family	-idae
Suborder	-ina	Subfamily	-inae

While the termination *-icae* corresponds with *-ica* and could therefore pass for being more logical, it is suggested that its use be confined to the Invertebrata, while in the Vertebrata we adhere to the more traditional *-oidea*. In the botanical field there are other terminations at various levels which may remain customary for that field.

I should like to expand Easton's proposal to cover the full range as follows:

Phylum	-ta				
Subphylum	-ta				
Superclass	-es	Superorder	-ica	Superfamily	-oidea
Class	-a	Order	-ida	Family	-idae
Subclass	-ia	Suborder	-ina	Subfamily	-inae
Infraclass	-ii	Infraorder	-ini		

This proposal will sound less frightening if one bears in mind that these terminations are not supposed to be fixtures; that they are required to change with promotions and demotions — comparable to declensions of nouns in Latin. When a Family is promoted to Superfamily it will automatically, by existing custom, change its termination from *-idae* to *-oidea*.

From the following scale it can be seen that the matter is not problematical at all. The synapsid taxon "Anomodontia" is used here as if it could feature at any level from Phylum to Subfamily:

Phylum	Anomodont-ta (t part of termination)
Superclass	Anomodont-es
Class	Anomodont-a (t part of root)
Subclass	Anomodont-ia
Infraclass	Anomodont-ii
Superorder	Anomodont-ica
Order	Anomodont-ida
Suborder	Anomodont-ina
Infraorder	Anomodont-ini
Superfamily	Anomodont-oidea
Family	Anomodont-idae
Subfamily	Anomodont-inae

The classification used is by no means a final classification; the idea is that every contributor may submit his own recommendations for any adjustments. It is hoped that a final version will gradually evolve, embodying the consensus of opinion of the vast majority of vertebrate palaeontologists. Should this materialise, also for other vertebrate classes, the consequences could have immense value; to mention only one very useful repercussion: a standard universal codal system would become available for computer processing of museum collections. It is particularly with a view to computer processing that the standardisation of terminations is advocated — as standard "computer language".

The break-down is so designed that it remains unaffected upwards and downwards when a rank is added or subtracted, promoted or demoted, or transferred. This is achieved by the use of a combination of letters and digits. In computer programming digits within digital series should preferably not exceed nine. Fortunately across the entire vertebrate spectrum one rarely finds that super-, sub- or infra-ranks for any substantial taxon approach nine in number. Substantial ranks (Class, Order, Family) do tend to exceed nine in number, but they never exceed 26 — the alphabetic potential. The code can thus cope with more than nine Classes and the numerous osteichthyan and avian Orders approaching 26 in number within a single Superorder.

No doubt the eye will soon grow accustomed to this codal system where at a glance it can be seen that letters of the alphabet represent the three substantial ranks: Class, Order and Family. A digit in front of a letter indicates a super-rank and a digit following a letter indicates a sub-rank. The third digit in-between indicates an infra-rank.

APPENDIX A

J213B321B *Herpetogale marsupialis***HERPETOGALE MARSUPIALIS KEYSER AND BRINK, 1979****SYNONYMS***Herpetogale saccatus* (in errore) See Keyser and Brink 1979.**BIBLIOGRAPHY**

- 1973 Keyser, A.W. (*Sesamodon*-like), *S.Afr.J.Sci.*, **69**: 113-115; p.114; fig.3c.
 1973 Keyser, A.W. (*Sesamodon*-like), *Palaeont.afri.*, **16**: 1-15; p.7; fig.6a,b.
 1979 Keyser, A.W. and A.S. Brink, *Ann.geol.Surv.S.Afr.*, **12**: 91-105; p.91; fig.1.
 Idem (*Herpetogale saccatus*), p.103, table 5.1 (in errore).

HOLOTYPE

R337 GSO Good skull with lower jaw from Etjo mountain, Rhenosterfontein, Kalkfeld, Namibia - Anisian Omingonde Formation, M.Trias. See Keyser 1973; Keyser and Brink 1979.

REFERRED MATERIAL

Nil.

GENERIC DIAGNOSIS *Herpetogale* Keyser and Brink, 1979.

Bauriid therapsid with complete postorbital arches; short snout; short, wide intertemporal region; definite pineal foramen between postorbital bars, well in front of short, narrow intertemporal crest; snout tapering, nasals reaching far forward, rendering external nares barely visible in dorsal view; premaxillaries not penetrating between nasals; palatines situated far back, not reaching folds of soft secondary palate; hard secondary palate formed posteriorly by maxillaries only; posterior margins at internal choanae at level between second and third post-canines; small suborbital vacuities; interpterygoid vacuity a long, narrow slit reaching back to parashpenoid; pterygoid extensions to quadrates wide apart with straight outer margins; opisthotics massive; occipital condyle distinctly double; dentaries short and robust with distinct chin, and pronounced coronoid and angular processes; extensive fossae massetericae over lateral surfaces; dentition reduced to I4 : C1 : Pc5 upper and I3 : C1 : Pc5 lower; first lower incisors very large and inclined forward; lower canines tend to occlude on outside of upper alveolar margin; upper incisors and canines (worn ?) blunt at tips; all postcanines molari-form; upper incisors incline outward and increase in size from first to fourth; upper post-canine series extend far medially relative to the far laterally placed canines; cheek pockets thus formed, well defined dorsally by extensive crista faciales and ventrally by pronounced shelves on the dentaries.

SPECIFIC DIAGNOSIS

The only species on record.

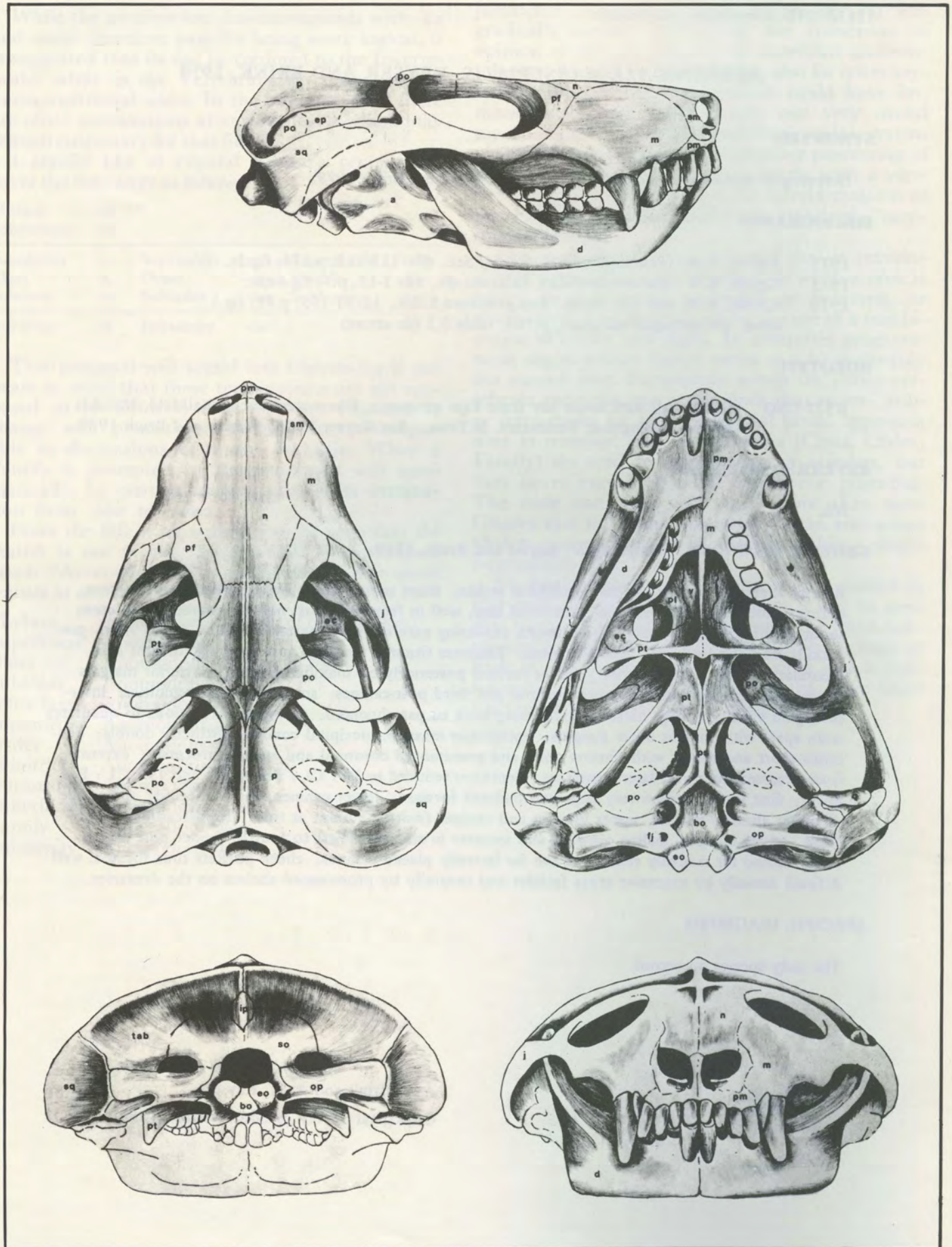
A. S. Brink and A. W. Keyser,
 Geological Survey of South Africa, 1980,

J213B321B

APPENDIX B

HERPETOGALE MARSUPIALIS R337 GSO

X 1



AN ATTEMPT TO DETERMINE THE PROVENANCE OF THE SOUTHERN DWYKA FROM PALAEOONTOLOGICAL EVIDENCE

by

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ABSTRACT

Conflicting evidence regarding the palaeo-iceflow direction of the Dwyka is discussed. A study by Debrenne of archaeocyathid-bearing erratics in Dwyka tillite is reviewed, and new material, associated fossils and their localities documented. The need for more intensive study is stressed to decide whether the Nama group could be the source of the fossiliferous erratics.

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INTRODUCTION

Since the recognition during the latter part of the last century of the Dwyka tillite as glacial in origin, there has been much speculation as to the provenance of these deposits in the extreme southern part of the Karoo basin. Du Toit (1954: 277, fig. 41) postulated a northern provenance for most of the tillite, including the outcrop belt from Laingsburg through Prince Albert to Willowmore, the area under discussion in this paper. Striated pavements, on which Du Toit partly based his conclusions, do not occur in the southern part of the Karoo basin. Du Toit also made use of comparisons of erratic rock-types with outcrops to the north. Stratten (1970: 483, fig. 1), through study of tillite fabric and erratic types, envisages a general iceflow direction from the west, while Theron and Blignaut (1975: 352, fig. 24.3), by analyses of structures associated with east-west striae (mostly relating to the western side of the basin), state that the palaeo-iceflow was in the opposite direction, i.e. from the east, with the ice sheet spreading-centre near the east coast of South Africa. Recently Visser (1979: 73, fig. 3) postulated a provenance to the south-east, based on striated pavements, fabric analyses and archaeocyathid-bearing erratics. It is, therefore, clear that to date no general agreement has been reached on the provenance of the glacial deposits in the south.

PALAEOONTOLOGICAL EVIDENCE

The abovementioned archaeocyathid-bearing erratics were first discovered by the author in 1965 on the farm Zwartzkraal in the Prince Albert district. One large, light-grey limestone erratic (c. 15 cm in diameter) was sent to F. Debrenne of the Palaeontological Department of the National Museum of Natural History, Paris. She found 18 spe-

cies of archaeocyathids, a new family (Pseudosyringocnemididae), two new genera (*Flexanulus* and *Statanulocyathus*) and three new species (*Flexanulus oosthuizeni*, *Statanulocyathus oosthuizeni* and *Andalusicyathus cooperi*) in the erratic (Debrenne 1975). Trilobite fragments were also present (Debrenne, pers. comm.). Debrenne compared the archaeocyathids from the erratics with archaeocyathids known from other parts of the world (see Debrenne 1975, table 1) and found that of the four species occurring most commonly, three are known only from Antarctica — *Erugatocyathus scutatus* (Hill), *Pseudosyringocnema* cf. *gracilis* (Gordon) and *P.* cf. *uniserialis* (Hill) — while the fourth, *Thalamocyathus tectus* (Debrenne), is known also from Australia. Species of the genus *Protopharetra* are cosmopolitan and of little value in this study. The rest are known only from Antarctica, and/or Australia. Another point of interest is the presence of equatorial forms with pectinate (comb-like) tabulae, e.g. *Thalamopectinus*, which occurred only in shallow equatorial seas in the early Cambrian (Debrenne 1973: 33, fig. 4). This could restrict the likely provenance of the fossils to a large extent, as it seems improbable that two widely separated lower Cambrian Gondwana areas (e.g. Antarctica and South West Africa, the two most likely sources) could both have been aligned on or near the equator and they would be difficult to fit into Zhuraveleva's Australo-Antarctic equatorial region (Hill 1972: E42, fig. 28). However, this would depend on the actual position of the Gondwana continent in relation to the equator in the Cambrian. Unfortunately, very little is known of this era.

A subsequent thorough search by the author of the tillite outcrops on the farms adjoining Zwartzkraal has produced scores of archaeocyathid-bearing limestone erratics. A number of these archaeo-

cyathid-bearing erratics were found *in situ*, embedded in the tillite matrix. These limestone erratics, though extremely rare, occur from the base of the tillite right to the very top, which would imply that during the deposition of the entire southern Dwyka at least some of the material was derived from an archaeocyathid-bearing source. The fossil-bearing limestone erratics vary in colour from medium-grey to off-white, the latter being predominant. The matrix is very fine-grained and fairly uniform. The fossil-bearing erratics were traced by the author over 70 km in an east-west direction, and over *c.* 10 km in a north-south direction. They have also recently been reported by J.C. Loock from Leeuwkloof (Willowmore district) and north of Gamka Poort dam (Loock, pers. comm.).

As the study of archaeocyathids is highly specialized (involving thin sectioning, differential solution, etc.), it is not yet possible to say with any certainty if new species were recovered, but at least a few large single-walled specimens were found which were not present in the material examined in the first study. A number of trilobite fragments, mostly sections of segments, one small complete pygidium and a librigena? (free-cheek) were also encountered. One large erratic contains numerous possible hyolithids which appear to belong to the genus *Quadrotheca*, a Cambrian form. Onkolites and stromatolites (both algal) were found. They all occur in the same type of limestone and all these forms are normally associated with archaeocyathids in biohermal strata (Hill 1972: E27).

The only other fossils from the tillite (obviously of a much later age), are of plant origin. One black carbonaceous boulder found *in situ* near the base of the tillite is packed with flattened plant stems. A striated reddish sandstone cobble with stem impressions was also found higher up in the tillite. Phosphatic erratics within tillite nodules from near the top of the succession contain possible radiolarians.

CONCLUSIONS

Although Debrenne's evidence points to an Australo-Antarctic provenance for the southern Dwyka tillite (see also Cooper and Oosthuizen 1974), in which case Visser's palaeo-iceflow direction is acceptable, one cannot completely discount the possibility of a northerly provenance. If one ignores the slight possibility that all the fossil-bearing lower Cambrian material that may have existed somewhere to the north was completely denuded by the Dwyka ice, then the Nama Group in South West Africa and the north-western Cape

seem to be the only other possible sources. The Kuibis subgroup is generally accepted to be of Precambrian age because of its "Ediacara-type" fossil assemblage. The latest dating of the Schwarzrand is based on Precambrian age (Vendian) acritarchs from this subgroup (Germs, pers. comm.). The limestones of this subgroup are moreover almost exclusively dark in colour. This seems to leave only the Fish River subgroup as a possible source. Germs suggests that a thorough search for subtidal carbonates in the Fish River subgroup in the Niewoudtville area of the north-western Cape could possibly produce a source for the archaeocyathids. Intertidal marine sandstones and shales have already been recognised in South West Africa (Germs, pers. comm.), so if subtidal carbonates do exist here they will probably be covered by the Kalahari sands to the east. Unfortunately the alleged archaeocyathids described from the Nama Group in South West Africa (Haughton 1960, Germs 1972, Kaever and Richter 1976) are not archaeocyathids at all, but trace fossils (Häntzschel 1975: W37), serpulids, or structures of mineral origin (Debrenne and Lafuste 1979: 143-144). Moreover, some of these fossils occur in sandstone, which excludes these rocks as a source for the archaeocyathids in the erratics (Hill 1972: E27).

The object of this paper is, therefore, to stress the necessity of: (a) widespread search of the Dwyka tillite for erratics containing archaeocyathids and associated fossils to establish their total distribution; and (b) a more intensive search of the calcareous members of the upper Nama Group in the north-western Cape Province and South West Africa for these fossils. If glacial material containing archaeocyathids was derived from both the north and the south, the distribution of different species may help to determine their respective depositional limits more accurately. (Incidentally, it should be stressed that the phylum Archaeocyatha — which occurs almost exclusively in limestone — could be an excellent age indicator if found in the Nama Group, as this phylum is known only from the Lower Cambrian to the base of the Middle Cambrian.) Because of the absence of striated pavements in the southern Cape and the controversies regarding the provenance of the tillite, it seems logical to make the best use of all evidence in solving this elusive problem.

ACKNOWLEDGEMENTS

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ABSTRACT

Thinly sectioned and multi-view analysis of the archaeocyathid *Buschmannia roeringi* from the Nama Group, South West Africa and Zambia shows that these specimens conform to a morphologically homogeneous ontogenetic growth series. The specimens, which include fossils attributed previously to several different genera and species, display a remarkable degree of morphometric similarity. It appears that only a single species, *Buschmannia roeringi*, is represented by the South African and Zambian material. The implications of this growth series are examined. It is postulated that whilst younger individuals were more isomorphic, the adults were more selectively heteromorphic. Also, it is concluded that *Buschmannia* exhibited polyphyty, possibly directed sequential shell replacement. The distribution of numerous specimens representing various ontogenetic stages seem to support these statements. Furthermore, the enamel of the postlarval shells is relatively thin and porous, and it was more slowly formed. *Buschmannia* shells exhibited radial deformation, the most pronounced morphological of these animals is that they housed soft glands. The absence of prominent longitudinal growth, polyphyty, shell replacement, porous enamel and the probable presence of soft glands indicates that *Buschmannia roeringi* was more typical than *Archaeocyathus* in its general morphological organization.

NEW EVIDENCE PERTAINING TO THE TAXONOMY AND PALAEOBIOLOGY OF *DIADEMODON* (REPTILIA; THERAPSIDA)*

by

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ABSTRACT

Bivariate (allometric) and multivariate analyses of diademodontine crania from South Africa and Zambia have shown that these specimens conform to a biometrically homogeneous ontogenetic growth series. The specimens, which include fossils attributed previously to several different genera and species, display a remarkable degree of morphometric similitude. It appears that only a single species, *Diademodon tetragonus*, is represented by the South African and Zambian material. The implications of this growth series are examined. It is postulated that whilst younger individuals were more insectivorous, the adults were more selectively herbivorous. Also, it is concluded that *Diademodon* exhibited polyphyodont, posteriorly directed sequential tooth replacement. The dentitions of numerous specimens representing various ontogenetic ages seem to support these statements. Furthermore, the enamel of the postcanine teeth is relatively thin and prismless, and it was worn away rapidly. *Diademodon* skulls exhibit rostral depressions; the most parsimonious interpretation of these cavities is that they housed salt glands. The evidence for prolonged ontogenetic growth, polyphyodont tooth replacement, prismless enamel and the probable possession of salt glands indicates that *Diademodon tetragenus* was more reptilian than mammalian in its general physiological organization.

* Full paper presented at PSSA First Conference, July 1979.

TRANSGRESSIVE EVENTS IN THE CRETACEOUS SEDIMENTS OF SOUTHERN AFRICA*

by

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ABSTRACT

There are three major transgressive events in the Cretaceous sediments of southern Africa: upper Lower Albian, Lower Coniacian and Middle Santonian. The faunal assemblages occurring in each of these transgressive sequences are well documented. Each of these transgressive sequences is characterized by a high proportion of endemic faunas, rapid rate of evolution, and extreme intraspecific variation.

The implications of these faunal features on our current concepts of evolutionary theory and stratigraphic principles are briefly discussed.

course of characters cannot be separated from the concept of evolution. If evolution takes place through imperceptible gradual changes of characters through time, then there can be no discrete species and consequently no "specific characters". Classification in such a case is bound to be artificial and the separation of species arbitrary. Species are, however, objective entities with constant essential characters if speciation events take place in a comparatively short time relative to the lifespan of species. The individual differences may then be evaluated as variations of constant specific characters.

The arbitrary separation of *Glossopteris* leaves in the 19th century has not resulted from acceptance of a "gradualist" model of evolution. There has indeed been very little theoretical explanation behind the introduction of "broad sense interpretations" of *Glossopteris* leaves; it was originally intended to be a practical means of naming leaf impressions which were believed to be mutually indistinguishable. This so-called "broad sense interpretation of leaves" has replaced the species as an objective entity. Some of the consequences of this approach are reviewed below.

THE HISTORY OF "BROAD SENSE INTERPRETATIONS" AS APPLIED TO *GLOSSOPTERIS* LEAVES

Seward (1897) was the first palaeobotanist to discuss in general "the extreme difficulty of drawing satisfactory distinctions between such forms as are included under *G. beccaria*, *G. indica* and *G. signata*" as "these three forms cannot be maintained as standing by their well-marked species of *Glossopteris*" (p. 57). The three species mentioned were the first ever described by Brongniart in 1839 and as such they formed the basis for comparison when other species were described later. Seward also found that the "very large number of leaves of this genus (i.e. *G. repens*) described by Feistmantel from different localities in the Gondwana series of India have in several instances formed the types

* Full paper presented at PSSA First Conference, July 1979.

"BROAD SENSE INTERPRETATION" OF *GLOSSOPTERIS* LEAVES: A CRITIQUE

by

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ABSTRACT

According to Arber (1905), palaeobotanists attempting to identify *Glossopteris* leaves must choose between the methods of "grouping broadly" or "distinguishing in detail". The taxonomic treatment of *Glossopteris* according to these two alternatives is briefly reviewed. It is concluded that if palaeobotanists are allowed to choose between different interpretations of specific names, disparity and taxonomic confusion are unavoidable. A plea is made for a return to traditional methods of identification based on objective criteria.

INTRODUCTION

Palaeobotany is considered by some researchers to be an empirical science. However, even the initial examination of a specimen usually implies more than mere observation alone. The application of a binomial name when a specimen is identified presupposes some conception of the term "species", especially in respect of the particular species to which the specimen is assigned. This cognitive aspect of the study is theoretically based and the species, as a concept, cannot be perceived empirically.

Different schools of philosophy, of evolutionary theories and of applied methodology affect the process of identification at all stages from the examination of characters to the designation of the specimen as belonging to a certain taxon. Debates ranging over a wide field, from the problems of nomenclature to those of the nature of evolution, have resulted in many published articles recently. The number of papers, and their often agitated tone (e.g. the recent debate about the use of cladistics at the British Museum of Natural History), testify to the importance of the whole complex problem. If knowledge was attainable on empirical grounds alone, the present theoretical controversy in systematics would not occur.

In the case of fossils, the problems of species-concept and of the evaluation of characters are more complicated by the time factor and by the fragmentary nature of specimens than is the case in identification of living plants and animals. Specific names must be used, but their meanings depend on the evaluation of the characters in the specimens studied. Irrespective of the aim of any study in this field, whether it deals with systematics or biostratigraphy, the first concern must be the accurate determination of specific characters.

This paper concentrates on aspects of specific identification of *Glossopteris*; these aspects are not connected directly with evolutionary theories although the author is aware that the concept of species, and thus the evaluation of the specific signifi-

cance of characters, cannot be separated from the concept of evolution. If evolution takes place through imperceptible gradual changes of characters through time, then there can be no discrete species and consequently no "specific characters". Classification in such a case is bound to be artificial and the separation of species arbitrary. Species are, however, objective entities with constant essential characters if speciation events take place in a comparatively short time relative to the lifespan of species. The individual differences may then be evaluated as variations of constant specific characters.

The arbitrary separation of *Glossopteris* leaves in the 20th century has not resulted from acceptance of a "gradualist" model of evolution. There has indeed been very little theoretical explanation behind the introduction of "broad sense interpretations" of *Glossopteris* leaves; it was originally intended to be a practical means of naming leaf-impressions which were believed to be mutually indistinguishable. This so-called "broad sense interpretation of leaves" has replaced the species as an objective entity. Some of the consequences of this approach are reviewed below.

THE HISTORY OF "BROAD SENSE INTERPRETATIONS" AS APPLIED TO *GLOSSOPTERIS* LEAVES

Seward (1897) was the first palaeobotanist to discuss in general "the extreme difficulty of drawing satisfactory distinctions between such forms as are included under *G. browniana*, *G. indica* and *G. angustifolia* . . . these three names cannot be maintained as standing for three well-marked species of *Glossopteris*" (p. 317). The three species mentioned were the first ones described by Brongniart in 1830 and as such they formed the basis for comparison when other species were described later. Seward also found that the "very large number of leaves of this genus (i.e. *Glossopteris*) described by Feistmantel from *different horizons* in the Gondwana series of India have in several instances formed the types

of new species founded on quite inadequate grounds . . . It is difficult, or indeed impossible, to admit the existence of adequate grounds for some of Bunbury's species . . ." (p. 316) (emphasis mine). In his descriptions of the specimens Seward (1897) repeatedly called attention to the lack of distinguishing specific characters in leaves: e.g. "This fragment is of interest as illustrating the difficulty of drawing any sharp line between *G. browniana* and *G. indica* . . . It is also identical, as regards both size and venation, with some of the large fronds described by Bunbury from Nagpur as *G. browniana* var. *indica*, *G. stricta*, Bunb., and other species . . ." (pp. 320—322).

These comments of Seward (1897) represented a new sceptical tone in *Glossopteris* studies. Seward maintained this attitude and consistently dealt with *Glossopteris* in this manner. He came to the conclusion that the "accurate identification or diagnosis of *Glossopteris* fronds, and their separation into specific types, is, I believe, a hopeless task . . ." (Seward 1903: 80). "The arbitrary separation of sterile leaves, which differ by small degrees from one another in form and in the details of venation, by the application of specific names is a thankless task necessitated by custom and convenience; it is, however, idle to ignore the artificial basis of such separation" (Seward 1910: 507). When it is recalled that Seward was at the time a professor at Cambridge and was therefore a recognised authority, and that megaplant fossils are generally impressions of sterile leaves, then the serious impact of Seward's scepticism can be appreciated.

Seward made no attempt to establish a method for the identification of indistinguishable leaves. It was Arber who put Seward's intentions into practice. In his Catalogue, Arber (1905) gave an identification key and re-defined, by "grouping broadly" (p. 46), the *Glossopteris* species already described. In doing so, he influenced the study more profoundly than Seward, his professor. His catalogue is an often-used and much quoted source of information to this day. Arber, too, was convinced that "It is a most difficult and thankless task to attempt a general revision of these specific determinations, for it is almost impossible to obtain any definite aggregate of characters to serve as a standard in dealing with details confined to the shape of the sterile frond and its nervation; the characters on which any classification must at present be based" (Arber 1905: 45).

Arber's first justification for creating an artificial classification was that "there has been considerable difference of opinion already on this subject." The second cause of his discouragement was "a considerable variation in the form and shape of the leaf of *Glossopteris*, and in the details of the nervation" (Arber 1905: 45); "Indeed, a detailed examination shows that there are hardly any characters which may be regarded as constant in fronds of the same species" (p. 46). Here the question arises: how did he know, then, which were the "fronds of the same species"? What did he regard as a spe-

cies? If he had formed a concept of species in general and of certain species in particular, then surely he should be able to evaluate the "considerable differences" of opinion; they could be "right" or "wrong" as compared with the diagnosis by the author of the species. In the same way, he should have been able to find those characters that were constant among the "considerable variations" of shapes and venation patterns of leaves.

Arber (1905) came to the conclusion that "since an artificial classification is without alternative, and seeing that the value of such a classification depends largely on its convenience, it would seem more convenient . . . to maintain comparatively few species, and to group together those fronds which, though they may differ in one or more details from the typical form, are not sufficiently dissimilar in the aggregate of their characters to warrant separate specific rank. . . . In this manner, it has been possible to reduce the number of specific determinations to thirteen" (pp. 46—47). It is left to the reader to decide which "one or more details" might "differ from the typical form" and thus which leaves are "not sufficiently dissimilar", to warrant separate specific rank. It is also not made clear what is to be regarded as the "typical form" in this method.

Consider, as an example in Arber's sense, the first described "species" of *Glossopteris*, *G. browniana* Brongniart: The shape of *G. browniana* was defined by Brongniart (1830) as "subspathulatis obtusis"; by Arber (1905) as "spathulate, oval-linear, suboval, or almost oblong" (p. 50). Arber (1905) synonymized many species under the name *G. browniana* (pp. 48—50), irrespective of the horizons of the localities of type specimens. The synonymized species are dissimilar to *G. browniana* either in the shape of leaf, or in the characters of venation. Indeed, *G. wilkinsoni* does not share any character with *G. browniana*. Arber had to adjust the description to embrace all these species. Despite the fact that Arber's definition of *G. browniana* is very general, some of the species he assigned to it still disagree with it in one or more characters. If it is permissible for a fossil at hand to "differ in one or more details" even from Arber's broad interpretation of *G. browniana*, then the name can be applied to any *Glossopteris* leaf. Thus the "differences of opinion" about the aggregate of specific characters have turned into confusion over the years since publication of Arber's Catalogue.

Arber doubted the specific value of characters of leaves, but he could not replace them with anything else in his circumscriptions of species. Not only did he broaden the specific circumscriptions, but he also changed them, as illustrated in the following examples from his key compared with the original definitions:

<i>Original definition</i>	<i>Arber's (1905) definition</i>
<i>Glossopteris indica</i>	"meshes . . . not as a
Schimper: "areolis	rule markedly broader
secum rachim positus	on the borders of the
abbreviatis, latiusculis"	midrib"

<i>G. stricta</i> Bunbury:	“lanceolate”
“frond narrow, strap-shaped, with nearly parallel edges.”	
<i>G. divergens</i> Feistmantel:	“Meshes . . . of nearly equal size through the lamina and very elongate”
“meshes being short close to the midrib, and becoming oblong towards the margin”	

Seward (1910) commented: “Mr Arber recently published, in his valuable *Glossopteris* Flora, an analytical key which serves to facilitate the description and determination of different types of frond.” Maheshwari (1966: 39) called Arber’s interpretation “broad-based specific circumscription” and found it “unsatisfactory”.

Lambrecht *et al.* (1972) proposed a new scheme of “broad sense interpretation” of glossopterid leaves; this differs from Arber’s, and is even broader.

THE CONSEQUENCES OF “BROAD SENSE INTERPRETATION” OF GLOSSOPTERIS LEAVES

By changing the specific characters, Arber (1905) changed the concepts of the specific names, too. He created artificial categories which could not be recognised in fossil leaves without accepting that “one or more details” could differ. Great freedom was given to personal opinion in deciding which characters could differ from Arber’s already flexible and vague definitions, and to what extent they could differ. Thus the “broad sense interpretation” is not one kind of comprehension, but many. The “broad sense” attribute means that it is not restricted by principles or standards. The broad-based specific circumscription itself has such a broad meaning that it allows different interpretations of similar fossils, or the use of the same name for different leaves.

Some palaeobotanists lost confidence in the taxonomic value of external characters of *Glossopteris* leaves and tried instead to identify the species according to epidermal characters. However, the external characters could not be completely ignored, because even the epiderms are attached to leaves. Furthermore, as Maithy (1965: 249) comments: “In recent years the evidences of the cuticular studies of Glossopteridalean remains have exhibited that leaves with a similar external morphology, may have different types of epidermal structures . . . , leaves with different morphological characters, may possess cuticles with similar epidermal structures”. Which, then, are the more reliable characters — the external, or the epidermal? Similar difficulties arise because different parts of fossil plants are classified separately: for example, even if a fructification is found in direct organic connection with *Glossopteris* leaves, the two are given separate names; in the hypothetical case of a leaf with an attached fructification, with seed in the fructification and with pollen in the pollen chamber, each part would be classified separately.

Biostratigraphy and intercontinental correlations are largely based on specific names summarised from the literature. Consequently, any geological conclusions drawn will be comparably as precise or as broad-based as the identifications of the fossils in the layers. If the separation of *Glossopteris* leaves into specific types is a “hopeless task”, then so is any stratigraphic analysis based on them. If the characters of *Glossopteris* leaves are unreliable and they cannot be identified, then any conclusion based on them would have to be regarded as unreliable, too. The author, however, does not share this pessimistic view.

ALTERNATIVES TO “BROAD SENSE INTERPRETATION” OF GLOSSOPTERIS LEAVES

More than 80 years have elapsed since Seward’s first sceptical comments on the taxonomic value of morphological characters of sterile leaves. However, as has been pointed out, the great majority of megaplant fossils are sterile leaves without preserved cuticles. Comparisons either for systematic or for stratigraphic purposes cannot be based on rarely preserved characters such as cuticles or fructifications. Leaf-impressions of *Glossopteris* are abundant in many fossiliferous layers; they represent the most readily available material for research. According to Arber, in their study “the choice lies between grouping broadly, and distinguishing in detail” (Arber 1905: 46). Grouping them broadly had led to confusion. Distinguishing in detail thus seems to be the better alternative. It means turning back to the traditional means of identification, i.e. to the exact evaluation and comparison of characters in the type specimens and in the studied fossil leaves.

There is only one kind of comprehension of species in the sense of traditional identification: the fossil at hand has to share the characters of the original diagnosis and type-specimen of the species. The fossil is misidentified if the researcher overlooks or misinterprets an essential character. All scientists make such mistakes, which is only human. Errors can be corrected by comparing against the reliable characters of objective entities, i.e. of species. In an artificial classification a species is a mental construction and the criterion for its size and definition is its usefulness. This criterion depends on personal inclination and, in consequence, so does the definition of the species. Artificial taxa that are useful to one researcher may be useless to another. The definition can be changed to such an extent that it can become the diametric opposite of the original description. For example, Bunbury (1861) distinguished *Glossopteris leptoneura* from *G. angustifolia* as follows: “In *G. angustifolia*, the veins appear to be coarse and rather distant”, in *G. leptoneura* “they are very fine and close” (Bunbury 1861: 330) — hence the descriptive specific name of the latter. On the other hand, Lacey *et al.* (1975: 361) perceived *G. angustifolia* “with closely set . . .

veins" and *G. leptoneura* "distinguished by the secondary veins producing wide meshes". In this definition the leaves have been "interpreted in a broad sense" (Lacey *et al.* 1975: 360). The limits of the broad sense interpretation are not set, not defined; thus the definition cannot be regarded as being "right" or "wrong". Errors can be corrected and by corrections science advances, but names with multiple meanings cannot be subjected to correction. The type-specimen or first diagnosis becomes meaningless for comparison, because the species is not comprehended as an objective entity; the meanings of specific names are formed and reformed by successive authors, and confusion reigns.

A species is an objective entity, a unit, which in neontology is represented by an interbreeding population, or a number of potentially interbreeding populations. The same gene-pool which determines the ability to interbreed is also responsible for all specific morphological characters in individuals. There is no reason to believe that the gene-pool which determines the characters of epiderms and fructifications acts differently with respect to the venation pattern of leaves. The genes also assure stability of species in time and provide the constancy in specific characters. In palaeontology similar fossils in a bedding plane, or within stratigraphically related horizons, represent a number of potentially interbreeding populations, or in other words, a species.

There are always certain characters in the diag-

noses and type specimens of *Glossopteris* species which together constitute a set of characters typical of the species. Seward (1897) stated that he could not distinguish between *Glossopteris browniana* and *G. indica*, but Schimper (1868: 645-646) clearly separated the two species on size, shape of leaf, shape of apex, and in characters of the venation. Seward (1897) also stated that it is impossible to distinguish between Feistmantel's and Bunbury's species. Such a serious allegation should be substantiated with a study of random transitions of characters illustrated by specimens. However, no such study has been offered thus far. The alleged taxonomic unreliability of external characters of *Glossopteris* leaves is not proved.

Seward and Arber proposed the method of "grouping broadly" because they could not find definite aggregates of characters which could be considered as specific. Even if their scepticism was justified, their broad sense interpretation has aggravated the difficulty. The reliability of characters was doubted and therefore artificial categories were created; these categories have been formulated in different ways by subsequent authors and consequently no definite aggregates of reliable characters have emerged from the different perceptions. Thus *Glossopteris* studies move in a vicious circle. One way to break out of the vicious circle and to check on the reliability of specific characters is to return to traditional methods of identification. The alternative to broad grouping is exact identification.

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QUANTITATIVE AND QUALITATIVE ASPECTS OF ONTOGENY AND SEXUAL DIMORPHISM IN THE PERMIAN ANOMODONT *AULACEPHALODON**

by

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ABSTRACT

A biometrical (allometric) analysis of a number of *Aulacephalodon* crania, several of which have been assigned to different species, was undertaken. The results suggest that this material represents a morphometrically homogeneous ontogenetic growth series. Features utilized previously in the diagnosis of *Aulacephalodon* species can be accounted for by the phenomenon of allometric growth. A quantitative assessment of sexual dimorphism was, for the most part, inconclusive. However, the results of a qualitative investigation of nasal boss and temporal arch morphologies suggest that these features are related to sexual dimorphism. It is proposed that adult females possessed somewhat flattened nasal bosses, whilst males showed bulbous nasal bosses and, with advanced size (age), thickened lateral borders of the temporal arches. Sexual dimorphism appears to have been expressed in individuals with a basal cranial length of between 190 mm and 245 mm. Locality and stratigraphic data were examined, and these data appear to support the hypothesis that we are dealing with a single species, *Aulacephalodon baini*, which showed sexual dimorphism.

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THE USE OF WAX IN CONTROLLED ACID PREPARATION

by

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For preparing blocks of cave breccia rich in microfaunal remains, some method was needed to confine acid action to the upper surface of the blocks and thus prevent delicate bones on the lower surface from being crushed by the weight of the rock as they become exposed, and generally to make the whole procedure more manageable. Conventional methods are either time consuming (latex) or expensive (silicone rubber). The method described here is quick and effective and the cost is negligible.

Blocks are first treated in 3 per cent formic acid, washed and dried. All exposed bone is coated with a solution of "Glyptal" G1276 cement diluted with

lacquer thinners. This treatment cleans and roughens the surface providing a good surface key for the wax. A string cradle is made to hold the block, which is then dipped in paraffin wax heated in a double boiler. Six to eight dippings are usually adequate. The first skin of wax chills immediately on contact with the breccia. Surplus string is then cut away and the block is ready for further acid preparation, using concentrations of 5 per cent to 10 per cent formic acid. The wax forms a perfect seal against acid penetration and it can be easily removed as preparation progresses. Wax can be written on using a felt pen; it can be cleaned and re-used.

INTRODUCTION - HISTORY OF RESEARCH AT THE LIDGETTONTA SITE

The history of palaeontological research at the Lidgettontla site is a long one, beginning with the discovery of a rich fossiliferous breccia in 1937 by the geologist, Dr. J. H. van der Merwe. This discovery led to a series of excavations and investigations by the geologist, Dr. J. H. van der Merwe, and the palaeontologist, Dr. C. E. Gow. The site is a rich source of fossiliferous breccia, and has been the subject of several studies, including the work of van der Merwe (1937), and the work of van der Merwe and Gow (1941). The site is a rich source of fossiliferous breccia, and has been the subject of several studies, including the work of van der Merwe (1937), and the work of van der Merwe and Gow (1941). The site is a rich source of fossiliferous breccia, and has been the subject of several studies, including the work of van der Merwe (1937), and the work of van der Merwe and Gow (1941).

An interesting letter was sent to Dr. A. J. H. van der Merwe on the 10th April 1976 (see also Levinson, 1976). He described the site as a rich source of fossiliferous breccia, and has been the subject of several studies, including the work of van der Merwe (1937), and the work of van der Merwe and Gow (1941).

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A STUDY OF THE TYPE LOCALITY OF *LIDGETTONIA AFRICANA* THOMAS 1958

by

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ABSTRACT

The circumstances of the discovery of the type locality of *Lidgettonia africana* Thomas 1958 and of Thomas's description of this fructification are placed on record and the fossils mentioned by him are listed. The horizon, depositional environment and modes of fossilization are discussed, and the present known flora and fauna are outlined, compared with Thomas's list and with those of other sites, and illustrated with particular regard to the variety of fossils and modes of fossilization. The presence of several species of *Glossopteris* and three fructification taxa show Thomas's associations of leaf taxa with *Lidgettonia* and *Eretmonia* to be arbitrary. On the basis of the present known flora and fauna the type locality of *Lidgettonia* is provisionally considered to be, like the Mooi River site, lower Beaufort.

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INTRODUCTION — HISTORY OF RESEARCH AT THE LIDGETTONIA SITE

Interest in *Lidgettonia africana* Thomas 1958 has recently been stimulated by the discovery at a different site (Mooi River) of numerous specimens of this important pteridosperm fructification (Lacey *et al.* 1975). Arising out of consequent interest in the type locality and the fortuitous finding of a portion of the wing of an homopteran plantbug, the site has been the subject of recent study; unusual preservation of the fossils at the site has been the subject of two reports (Van Dijk *et al.* 1975, 1978). Gordon-Gray *et al.* (1976) did a preliminary study of the equisetalean fossils, Riek (1976a) included two insects from the site in a description of new Permian fossil insects, and Van Dijk, Hobday and Tankard (1978) referred to the site as an example of one type of bay-fill facies. Apart from the paper in which *Lidgettonia* was described, these appear to be the only papers in which there is anything more than a mention of the site and its fossils. The present paper attempts to record something of the history of the discovery of the site, to assess the significance of the site, to list and illustrate its present known palaeoflora and -fauna and to elucidate the palaeoenvironmental setting.

An enquiring letter was sent to Dr. A.O.D. Mogg, the discoverer of the site, on 27th April 1976 (his 90th birthday). He described the discovery as follows:

"The Thompsons farm fossils I discovered June or July 1917 when I was working on Styfsiekte for Division of Veterinary Services, Dept. Agriculture.

I found some *Ecca* shale flakes in the stream with clearly defined *Glossopteris* Fossils & photographed them, my native driver holding one in his hand.

Working back a foot I came across doorsteps 3-6" thick & removed about half a dozen approx. 15" x 10" x 3-5".

These I sent to:

a/ Hamshaw Thomas, Cambridge, Eng.

b/Director Geological Survey, Pretoria

c/ Director Veterinary Services, Pretoria

d/ Curator Natal Museum, Durban,

& I believe to National Herbarium, Botany Dept., Pretoria."

Thomas (1958: 180) states of the site and material: "This plant bed was originally discovered by Mr. A.D.O. Mogg, he kindly sent two large blocks to the author, who visited the locality in 1929 and made a collection of specimens, which have only recently been studied." That the original material collected, and that collected by Dr. Thomas in 1929, was not entirely forgotten between 1929 and 1958 is known from a request made by Dr. Thomas in 1950 to Mr. M.P. Rilet while he was a student at Cambridge, for the col-

lection of more material when he returned to South Africa (M.P. Rilett, pers. comm.). Thomas does not refer to a second visit which he made to the site — in 1956, according to the present owner of Bella Vista, Mr. A.S. Thompson (pers. comm.). The publication of descriptions of *Glossopteris* fructifications by Dr. Edna Plumstead (1952, 1956) appears to have been the stimulus for Dr. Thomas to revisit the site and to publish a description of the site and of the new fructification, *Lidgettonia africana*.

Subsequent to the publication of Thomas's paper, visits were made to the site by Dr. Plumstead with Dr. Mogg and with students, and by Miss A.K. Benecke (now Dr. Malleson). Plumstead (1969) refers to material collected by Malleson: "On Pl. XVII, fig. 3 is a figure which I feel may add one more link in the chain of evidence. The specimen was collected by Miss Benecke from the same area as that described by Thomas (1958) and given to me to illustrate *Lidgettonia*. The photograph reveals an elongated 'scale' leaf with *Lidgettonia* 'flowers' on small pedicels and apparently, a small convex scale leaf attached to the top of the elongated scale leaf. Both *Arberiella* (top right) and small seeds can be seen in the vicinity. There is also a larger isolated scale leaf on the right hand side. The specimen suggests that much of the evidence of previous authors may be combined in this lucky specimen." (pp. 50–51). (The association of seeds with the cupules of *Lidgettonia* was suggested by Thomas (1958: 84) "A well preserved seed is seen lying in contact with one of the cupules, but its position may have been accidental".)

In 1974, Dr. W.S. Lacey visited South Africa to work on material from the Mooi River site discovered by the present author and Mr. B. Schaller, and he was taken to the Lidgetton site for comparative topotypical material. There the author collected a small slab of material from a point in the stream bed which Mr. A.S. Thompson (pers. comm.) later identified as precisely that on which Thomas concentrated in 1956. The slab contained, in addition to all the types of plants mentioned by Thomas, the distal half of an homopteran insect wing (cf. fig. 57). This was the first insect fossil from the site. The site was later visited by the present author with senior Botany students, and Mr. John Oliver discovered a plecopteran (stonefly) wing (fig. 56). In the latter half of the year the site was the subject of a third year Geology exercise by Mr. Owen R. Dix at the suggestion, and with the guidance, of the author. Mr. Dix found a beautiful homopteran wing (of the same species as the original fragment (fig. 57), a nymphal insect specimen (fig. 55), two *Glossopteris* specimens which were very distinctly different from those described by Thomas (figs. 7, 10), and a small slab which showed trackways (figs. 2, 3). The homopteran and plecopteran wings have already been studied (Riek, 1976a). Further work by the author has yielded many more specimens (e.g. figs. 54, 58–76).

Table 1 compares the present collection with that described by Thomas (1958).

METHODS

Besides unsystematic collecting of material, the orientation of which could not be retained during collection, systematic collection of slabs was attempted. Dips were recorded. Removal of coherent slabs was then attempted. So far this has rarely been successful through a succession of layers. The intactness of fossiliferous layers could rarely be retained when the slabs were split, because of the coherence and uniformity of texture of the sediments and the paucity of bedding planes. Appropriate material was clipped off, or sawn off with a dry saw, and embedded in polystyrene-polyester resin (Natal Chemicals Syndicate 7036); this material could then be sectioned with a water-cooled diamond saw to expose a surface without this disintegrating; after lapping and polishing with pumice suspension the surface could then be etched for examination under the scanning electron microscope (figs. 48–50), or for acetate peels using Schwann-Stabilo OHP-Transparent-Foils 0,08 mm (figs. 43–46). Acetate peels and replicas of the fossils, as exposed, were also made for optical microscope observation (figs. 40–42). Profiles of a few of the ripple-surfaced layers above the main fossiliferous layer were prepared by sawing, lapping, polishing on glass and coating with "dope" (fig. 1). Hydrofluoric Acid digests (concentrated, i.e. approx. 50 per cent, overnight) were made of portions of the most carbonaceous layer, which did not show clear fossils macroscopically and may have been overlooked by Thomas (fig. 47).

LOCATION, HORIZON AND NATURE OF THE EXPOSURE

The site is located at 29°25'55"S; 30°07'08"E at an altitude of approximately 1 180 m; the location is ringed in the map (fig. 80) and indicated by a white arrow in the aerial photograph (fig. 81), in which landmarks are shown to the east (pylon), south (spring) and north (fence).

Through the kindness of Dr. J.W. du Preez of the Geological Survey in Pietermaritzburg it was possible to include in the map information from geological mapping at present in progress for the Geological Map 2930A; beds which are lithologically Beaufort are shown hatched horizontally (towards the north-west and south-west), while the rest of the map area is lithologically Ecca or dolerite or alluvium. Plumstead (1969, caption Plate XVII, fig. 3) placed the Lidgetton site in the Upper Ecca without comment, while Thomas (1958: 180) comments: "Age of the specimens. The organic remains in the bed furnish no clear indications of its age, and there is a heavy cover of soil and vegetation in the area. According to the latest map published by the Geological Survey of South Africa the outcrop is of Ecca age in the Karoo System. The boundary between the Ecca and the Beaufort series is not far distant, and it is thus possible that the material is of Upper Ecca age.

TABLE 1

* Thomas 1958

N.B. including only one species of *Glossopteris*, compared by Thomas to three taxa.** Present Collection including specimens collected by D.E. van Dijk¹, O.R. Dix², J. Oliver³, G.H. Hickman⁴, Jacques van Dijk⁵, David Stuckenberg⁶, Miss J.R. John⁷, A.B. Cunningham⁸; identifications by D.E. van Dijk¹, K.D. Gordon-Gray⁹, E.P. Riek¹⁰.

PLANTAE		*	**
Thallophyta			
Eumycophyta			? Hyphae, on <i>Glossopteris</i>
Embryophyta			
Bryophyta			<i>Buthelezia mooiensis</i> Lacey, Van Dijk and Gordon-Gray (Bryophyte), including acetate peels and replicas

Tracheophyta			
Sphenopsida		cf. <i>Neocalamites carreri</i> Zeiller stems, pith-casts, branches, leaves	+ + + + diaphragms ^{1:ident.9} (some <i>in situ</i>) histological detail from acetate peels and replicas cytological detail from pyritized material by SEM and peels and replicas of etched sections

Pteropsida			<i>Sphenopteris</i> leaf fragments in HF digests

Cycadopsida			
Peridospermales		<i>Glossopteris</i> sp. leaves (cf. <i>indica</i> Schimper, <i>communis</i> Feistmantel, <i>arberi</i> Srivastava)	+ histological and cytological detail as above
		Scale leaves	+ <i>Vertebraria indica</i> Royle ^{1,3;ident.1}
		<i>Lidgettonia africana</i> Thomas (gen. et sp. nov.)	+
		<i>Samaropsis</i> cf. <i>S. seixasi</i> (White) Sew. seeds	+ <i>Plumsteadia</i> sp. 1 very good specimen <i>Eretmonia natalensis</i> Du Toit
		microsporangia cf. sporangia of <i>Eretmonia natalensis</i> Du Toit (microsporangia now known as <i>Arberiella</i> Pant and Nautiyal)	+

Coniferopsida			
Cordaitales			Pyritized wood, cytological detail by HF digests
Incertae sedis		Winged spores of various sizes	Winged spores of various sizes ? Spore similar to type known from Mooi River and Mt. West

ANIMALIA			
? Annelida			? Burrows (difficult to distinguish from post-depositional roots) Worm tracks
? Mollusca			Tracks, ? molluscan

Arthropoda			
Crustacea			Crustacean tracks Conchostracan shells, 14 specimens Type A, 13 specimens (7 with pyrites surface replication) Type B (cf. <i>Leaia</i>) ⁶ , 1 specimen, with pyrites surface replication

Insecta			120+ specimens, half of which fragmentary, mainly in the case of what are apparently exuviae of nymphs, of which there are 56 specimens Plecopteran <i>Euxenoperla</i> Riek ^{4:ident.1} sp. nov. ^{ident.10} 1 specimen ? Plecopteran nymphal exuviae ^{1,3} , ? of <i>Euxenoperla</i> , numerous specimens ^{ident.1} , rather small to be nymphs of <i>Euxenoperla</i> ^(1,10) Paraplecopteran <i>Miolopectera</i> Riek ^{5,1:ident.1} cf. <i>stuckenbergi</i> ^{ident.10} Homopterans ^{1,3,8} at least 20 specimens, including 1 very complete specimen 4 or more types ^{ident.1} , including Prosbolids ^{ident.10} Aleyrodid hemipteran <i>Aleuromypha</i> Riek 1 specimen, apparently late nymphal instar (cf. Riek 1974) 6 specimens of a smaller scale insect, ? earlier instar Scale insect ⁵ , possibly related to <i>Aleuromypha</i> Coleopteran ^{ident.1} (cf. <i>Molenocupes</i> Riek ^{ident.10}) 1 specimen Unclassified wings, body fragments ^{1,9} , legs

Chordata			
Osteichthyes			Fish scales (impressions) 6 specimens

But there is little lithological difference between the rocks of the Eccla and those of the Beaufort series, as is stated by du Toit, and it is also possible that the forms described are of Beaufort age." In a later publication than those referred to by Thomas, Du Toit (edited Haughton 1954) commented on the upper limit of the Upper Eccla having been undefined "since no clear line of demarcation from the overlying reptilian-bearing strata, styled the Beaufort Beds, was apparent" (p. 280). Haughton (1969: 352), discussing the problem of distinguishing Upper Eccla and Lower Beaufort, writes of characteristic Beaufort beds in the northern Karoo as follows: "The coloration of these argillaceous members tends to disappear in a north-easterly direction and, in the absence of vertebrate remains differentiation between the Upper Eccla and the Lower Beaufort in this region is partly a subjective exercise." The significance of vertebrate fossils follows immediately (new paragraph): "The advent of continental reptilian life within the main basin appears not to have preceded Beaufort times; but there are stretches of country near the presumed Eccla-Beaufort boundary in which reptilian fossils have not as yet been found and over these the boundary line is to a certain extent doubtfully placed." Barry (1970: 653) reported on the "recent discovery of vertebrate fossils in Eccla defined beds . . ." and discussed the Eccla-Beaufort boundary.

Two important sites lie close to the (lower) margin of the Beaufort, namely Bulwer and, north of Lidgetton, Mount West, while the rest of the main Beaufort sites are situated higher in the Beaufort — at an altitude of approximately 1 390 m in the case of the Mooi River site, i.e. 210 m higher than the Lidgetton site (see the map, fig. 1, p. 351 in Lacey *et al.* 1975). Figure 80 shows that the base of the Beaufort, on lithological criteria, lies between 1 200 m and somewhat more than 1 300 m in the south-west, while it lies at about 1 350 m in the north-west of the map area. If the beds at the level of the Lidgetton site have a similar regional dip, then they might be expected above 1 200 m (light shading) north of the Lions River valley and progressively further below 1 180 m southwards in the south-east of the map area (unshaded). New exposures are being sought; completion of the Geological map of this area, which will give details of the dips, will greatly aid the search. It should be mentioned that the immediate vicinity of the fossil site is influenced by dolerite intrusions, the dip of the beds being quite different at a point about 20 m south of the site.

Thomas (1958) refers to fine dark shales in which the fossils are carbonaceous compactions, to coarser grey shales, and to fine pale buff material in which the plant substance has disappeared or is represented by ferruginous material. The material in this study is in the dark shales; as mentioned above the material is from precisely the same point as that studied by Thomas. At this point the exposure is partially to wholly submerged in a stream. According to Mr. Thompson (pers.

comm.), Dr. Mogg stated, when visiting the site, that he had collected upstream from this point, but could not find further material upstream, while Dr. Plumstead collected material downstream from this point. The site studied lay immediately upstream of the roots of a large living wattle tree which had toppled downstream on the eastern edge of the stream before Thomas's 1956 visit. Recently this tree was removed to permit a systematic study of the site. Fortunately the beds dip at about 5° and 7° in the north-westerly direction and therefore emerge from the stream on its eastern edge. Excavations towards the eastern bank were begun in order to produce a vertical transect, and these excavations at the same time provided samples of the main fossiliferous layer and the layers immediately above. An accurate, detailed, transect is not yet possible.

DEPOSITIONAL ENVIRONMENT, FOSSILIZATION AND FOSSILS

A detailed study of the depositional environment at the Lidgetton site is intended in the future when further information is available about the lateral extent of the various layers. The beds studied lie at the bottom of an upwards-coarsening sequence which ranges from dark carbonaceous shales to lighter, less reducing, or oxidizing, conditions above. The upwards-coarsening sequence suggests a deltaic environment and the still reducing conditions suggest a backswamp environment in a delta. The northerly direction of the ripples in the upper layers (fig. 1) accord with observations elsewhere in the Beaufort.

The main fossiliferous unit, which is about 6–8 cm thick, contains most of the *Glossopteris* leaves and associated fructifications near the bottom, followed by slender sphenopsid stems with leaves, and then the larger sphenopsid stems, while the top of the unit is coarser and contains, in addition to *Glossopteris* leaves and small sphenopsids, rhizomes (*Vertebraria*, fig. 16) and evidence of superficial bioturbation. It is possible that the sequence of fossils represents in part a sorting phenomenon rather than a purely chronological sequence, since the larger sphenopsid stems may have settled more slowly because of contained air. In the sediments of this unit there is apparently a range from strongly reducing anaerobic at the bottom to aerobic at the top. A detailed analysis of this unit is intended concomitantly with study of the lateral extent of all the beds, somewhat in the manner so admirably pioneered in South Africa by Dr. Heidi Anderson for the various sites which she has studied (Anderson 1975). It is important to note that a statement of Thomas (1958: 180) gives the erroneous impression that the *Glossopteris* leaves and associated fructifications and sporangia are mainly found above the sphenopsids, when he states of the former: "With these, towards the bottom of the bed, are parts of equisetalean plants, stems, pith-casts, branches and leaves."

A few tentative comments are possible at this

stage on the fossils and their mode of fossilization. Firstly there is replication of the surfaces of *Glossopteris* leaves (figs. 24, 25, 28–30) and conchostracan shells (figs. 77, 78) by pyrites deposition, suggesting contemporaneous precipitation through the action of hydrogen sulphide from the rotting organisms with iron salts in solution in the pools or the connate water (see figs. 31–39, 78). The fact that pyrites is also found to be preferentially deposited on wound surfaces of some leaves, and other parts, such as *Lidgettonia* cupules and attached seeds, which may be presumed to have been actively growing at the time of detachment, is also strongly suggestive of contemporaneous deposition. Secondly, subsequent pyritization (by which is meant infilling and not substitution — *vide* Schopf 1971) appears to have occurred in hollow parts particularly, for instance the conducting tissue of sphenopsids, and to have occurred while much structure still remained (see figs. 31–39). Schopf (1971) discusses the process of silicification and much of what he says is, *mutatis mutandis*, relevant to pyritization. Preservation of so much cellular detail in the Permian Gondwana deposits has apparently very rarely been discovered: Plumstead (1962: 82) reported the absence of cellular detail in pyritized stems from the Triassic of Antarctica. Thirdly, there is evidence of a biocoenosis nearby with conchostracans, the whole bodies of which were deposited (figs. 77, 78), with fishes (or a fish, if all the scales are on precisely the same layer) which disintegrated in, or close to, the deposits (fig. 79), and with numerous aquatic nymphs the exuviae of which are preserved in the deposits, in some cases at least as HF-resistant body fossils (fig. 55 inset). In the most carbonaceous layer are fairly complete specimens of *Buthlezeria* (figs. 17, 42), which provides evidence that the plants described (from Mooi River, Lacey *et al.* 1975), which are of similar size and appearance, were fully grown, while the presence of rhizoids or root-hairs on one of the described specimens, and the completeness of the specimens in the Lidgetton deposits, suggests that *Buthlezeria* grew in swamps. Another moss-like plant is also present (fig. 18), while there is evidence of penetration of mud-covered leaves by roots and/or burrows (fig. 21), as well as evidence of fungal attack, probably during decay (fig. 20).

Of the insects so far obtained most are related to modern plant-piercing sap-sucking types (figs. 57–65, 69–74) and their wings appear to show the same kind of plant-dwelling camouflage as in present-day insects such as jassids (cf. fig. 71). Phytophagous (biting) types may be represented by the beetle (figs. 67, 75), while the plecopteran (fig. 56) probably lived near water as do living stone-flies. Several sporophylls of *Lidgettonia* with holes in them suggest that they may have been attractive to insects, as young shoots are today, and this might have facilitated pollination, or perhaps favoured out-breeding. The shapes of the *Lidgettonia* sporophylls (figs. 11, 12) suggest that they may have been aggregated into a cone-like structure,

but otherwise there is no evidence as to their relationship to other structures. It should be noted that inferences from associations are very risky, and in particular that Thomas's inclusion of the commonest type of sterile leaf in the diagnosis of *Lidgettonia* is particularly risky, as there appear to be at least three types of *Glossopteris* (figs. 5, 6, 7, 10), whatever they prove to be, as well as three fructifications — *Lidgettonia*, *Eretmonia* and *Plumsteadia* (figs. 11–13, 15, and 14 respectively). Any of the leaf taxa, or others not noted, could have been associated with any of the fructifications. (On the basis of his failure to find *Eretmonia*, Thomas 1958: 187, states: "It seems very probable that *Eretmonia* was a fertile structure from another plant with *Glossopteris* leaves, possibly *G. cordata* Feist. If this is so, *Lidgettonia* and *Eretmonia* may well be related, though they could scarcely be regarded as species of the same genus.") Leaves attributable to *G. cordata* had not been found at Lidgetton, thus providing some evidence against relationship between *G. cordata* and *Eretmonia*.

Thomas (1958: 181), in attributing all the *Glossopteris* leaves to one species in his diagnosis of *Lidgettonia africana*, remarks: "They vary considerably in size, their venation is uniform, but differs somewhat in appearance on the two sides of the leaf, and there is no reason to suppose that more than one species is represented." The types of difference between the leaves illustrated in Figures 5 and 6 (and together in fig. 4) would not be expected on the two sides of the same leaf, but Thomas's observation of differences (? between axial and abaxial surfaces) does emphasize the inadvisability of detailed descriptions of venations based on single, or even a few, specimens.

The absence, so far, of *Sphenophyllum* and glossopterid leaves with an open reticulation (of the *G. retifera* type), including *Belemnopteris* (*sensu* Lacey *et al.* 1974, 1975) is interesting, since these occur at Mooi River, Bulwer and Mt. West (see table 2 and van Dijk *et al.* 1977). Common to Lidgetton and Mt. West is the presence of apparently aquatic nymphs (fig. 55), and to these sites and Mooi River, and possibly (different species?) also Bulwer, are *Mioloptera* wings (fig. 54). *Aleuronympha* (figs. 64, 74) and *Euxenoperla* (fig. 56) occur at Lidgetton and Mooi River. A similar age (in the Upper Permian) of the Lidgetton site to that of Mooi River is suggested; when the fossils now available have been fully studied the advisability of placing the sites in a common zone can be considered. As noted above, the absence of tetrapod fossils can no longer be regarded as diagnostic of *Ecca* deposits, as is very strongly suggested by the work of Barry (1970).

DISCUSSION

Productivity of the site

The present account is based on a study of material collected during six excursions to the site, in addition to the basically geological study of Mr. O.R. Dix. Every full day of searching through the



1. Layer of shale about 15 cm above the fossiliferous layer, in vertical section NNW-SSE, x 1; showing rippled surface (current direction NNW, to left) and buried ripples, apparently with a similar wavelength and direction.

2. Surface of a layer immediately below the one in Figure 1, x 1; showing trackway of small arthropod and short tracks which are probably feeding grooves. Collected by Mr. O.R. Dix.

3. Same as Figure 2, x 2.

material has yielded at least one valuable insect fossil per searcher (the author or Jacques van Dijk); layers known to be productive yielded about four insect fragments per worker-hour, in the case of an experienced worker.

Significance of the site

The fossil site on the farm Bella Vista, near Lidgetton, will remain important as the type locality of a female fructification, *Lidgettonia africana*, which, like the male fructification, *Eretmonia natalensis*, is now known in considerable detail, differing in this respect from the several other fructifications to

which megaspores or microspores have not yet been found attached. In addition the site is already a fossil insect type locality (Riek 1976a: 769 and 779), and further fossil insect genera and species will be described from the site, the importance of which in this respect can be evaluated by considering the other Gondwana, and particularly African Palaeozoic, fossil insect sites.

Plumstead (1963) illustrated and discussed insect damage on fossil leaves, and discussed possible biotic interactions, particularly between insects and *Glossopteris* plants. She commented: "Winged insects of this age have not up to now been re-

Captions to Figures

- Figure Page 50
4. *Glossopteris* spp., x 1.
5. *Glossopteris* sp. from Figure 4 left, x 2,4 (*G. indica/communis*).
6. *Glossopteris* sp. from Figure 4 right, x 2,4.
7. *Glossopteris* sp., x 10; cf. *G. browniana*.
8. *Glossopteris* sp., x 1; bract-like, viewed from concave side.
9. Same as Figure 8, x 2.
10. *Glossopteris* sp., x 10; cf. *G. conspicua*.
- Figure Page 51
11. *Lidgettonia africana*, x 1.
12. *Lidgettonia africana*, x 1.
13. Cupule of *Lidgettonia africana*, x 10.
14. *Plumsteadia* sp., x 5, and counterpart x 10 (inset).
15. *Eretmonia natalensis*, x 1.
16. *Vertebraria indica*, x 1.
17. *Buthlezia mooiensis*, x 5.
18. Bryophyte? (Hepaticae), x 5.
19. Spore?, x 10 and 25.
20. Hypha of fungus?, x 250; scanning electron micrograph of *Glossopteris* leaf.
21. Leaf with chewed margins and penetrated by ? root, x 1.
22. Leaf with chewed margins (right side and top right), x 1.
23. Leaf with lesion, x 5; ? insect damage.
- Figure Page 52
24. *Glossopteris* leaf with pyritization, x 5; pyrites superficially covering carbonaceous cellular material.
25. Same as Figure 24, x 10.
26. *Glossopteris* leaf without cuticle, x 14, showing epithelial cells.
27. *Glossopteris* leaf with pyrites infilling, x 5.
28. Pyrites replica of *Glossopteris* cuticle (cf. figs. 24, 25), x circa 150; scanning electron micrograph, uncoated.
29. As Figure 28, x circa 150; epidermal cells at bottom left.
30. As Figures 28, 29, x circa 40; pyrites replica of cuticle viewed from within, and epidermal cells.
- Figure Page 53
31. Small sphenopsid stem infilled with pyrites, x 40.
32. Small specimen as Figure 31, x 40, scanning electron micrograph, uncoated.
33. Same as Figures 31, 32, x 80, scanning electron micrograph, uncoated.
34. Sphenopsid stem, acetate peel, x circa 40; scanning electron micrograph of surface opposite to the acetate film, coated.
35. Same as Figure 34, x circa 360; showing bordered pits.
36. Same as Figure 34, x circa 360; showing scalari-form thickening, probably tracheids.
37. Same as Figure 34, x circa 360; showing bordered pits.
38. Same as Figure 34, x circa 360; showing wall with numerous pits.
39. Same as Figure 38, x circa 600.
- Figure Page 54
40. Sphenopsid stem, acetate peel, x 55; showing the different modes which reveal the cells, the cell walls appearing clear in the upper internode and dark in the lower internode, while the large cells of the node are not visible in a mounted peel, except under phase contrast.
41. Sphenopsid stem, acetate peel, x 55; showing cells revealed by diffraction from the unmounted replica on acetate film, with narrower cells on the right near the ridges of conducting tissue.
42. *Buthlezia mooiensis*, acetate peel, x 100; showing thicker middle of the leaf and cells on one side.
43. Sphenopsid stem, acetate peel of etched face of a transverse section, x 55; showing effect of deep etching.
44. As Figure 43, different specimen, x 55; showing effect of light etching.
45. *Glossopteris* leaf, acetate peel of etched face of transverse section of pyritized region, x 55.
46. Same as Figure 45, different specimen, x 55.
47. Spore from hydrofluoric acid digest, x 600.
- Figure Page 55
48. Sphenopsid stem, etched face of a transverse section, x circa 40; scanning electron micrograph, coated (note supporting plastic on the right).
49. Same as Figures 48, x circa 400.
50. *Glossopteris* leaf, pyritized midrib, cracked and etched; scanning electron micrograph, x circa 250.
51. Coniferopsid stem, pyritized, broken open longitudinally, x 20.
52. Same as Figure 51, etched face, x circa 100; scanning electron micrograph
53. Same as Figure 51, different field, x circa 300.
- Figure Page 56
54. Paraplecopteran wing (cf. *Mioloptera stuckenbergi* Riek), x 5; collected by Dr. G.H. Hickman.
55. ? Plecopteran nymph (exuvia), x 5; collected by Mr. O. Dix. Inset: fragment of same taxon? from HF digest.
56. Plecopteran wing (*Euxenoperla* Riek), x 5; collected by Mr. J. Oliver.
57. Homopteran (prosbolid) wing, x 5; collected by Mr. O. Dix.
58. Homopteran (? prosbolid) wing, x 5; collected by Miss J. Johns.
- 59-62. ? Homopteran wings, x 5; see also enlargements, Figures 70, 71.
63. Homopteran insect, x 4,5.
64. Hemipteran (Aleyrodid) cf. *Aleuromypha* Riek, x 5; see also enlargement Figures 73, 74.
65. Hemipteran ("Scale insect"), x 5; collected by Jacques van Dijk.
- 66-68. Insects represented by more than just a single wing, x 5; Figure 67. Coleopteran (cf. *Moltenocupes* Riek), see also enlargement, Figure 76 — this is the first known Permian beetle in Africa.
- Figure Page 57
69. Same as Figure 63, x circa 9; showing stylet (passing behind a microsporangium), the characteristic, transversely ridged postclypeus, and legs with two rows of spines.
70. Same as Figure 61. (counterpart), x 10.
71. Same as Figure 60, x 10.
72. Same as Figure 65, x 10.
73. Same as Figure 64, x 10.
74. ? Aleyrodid hemipteran, ? earlier stage of the aleyrodid in Figure 73, x 10.
75. Same as Figure 67, x 10.
76. Unidentified arthropod fragment, c, x 10.
77. Conchostracan shell (cf. *Leaia*), x 10; collected by David Stuckenberg.
78. Conchostracan shell, type B, x 5.
79. Fish scale, x 10.





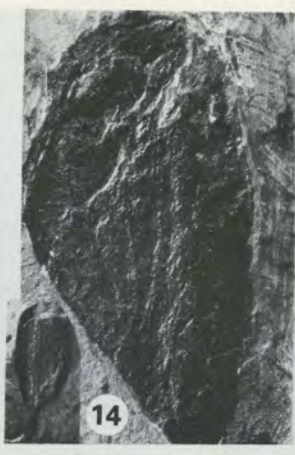
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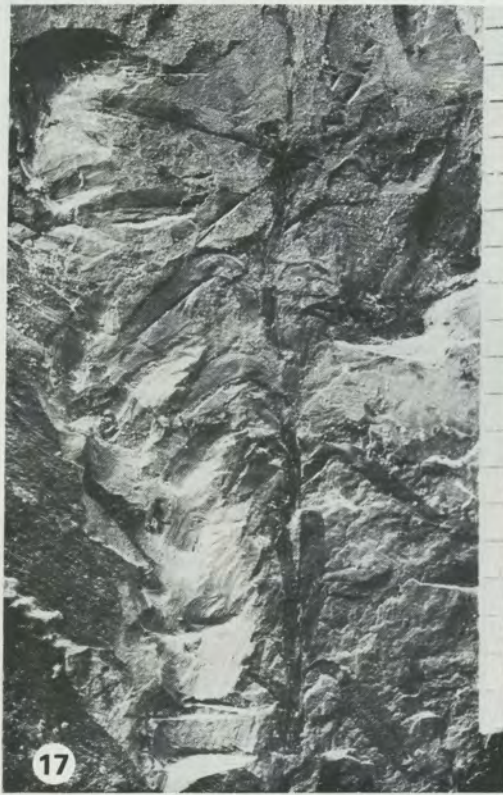
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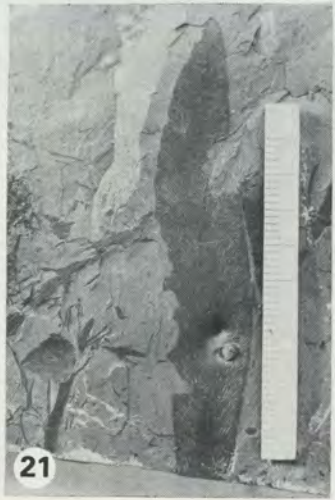
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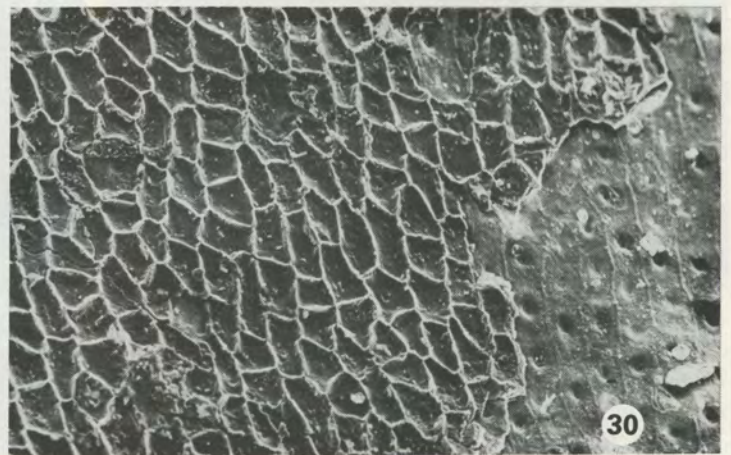
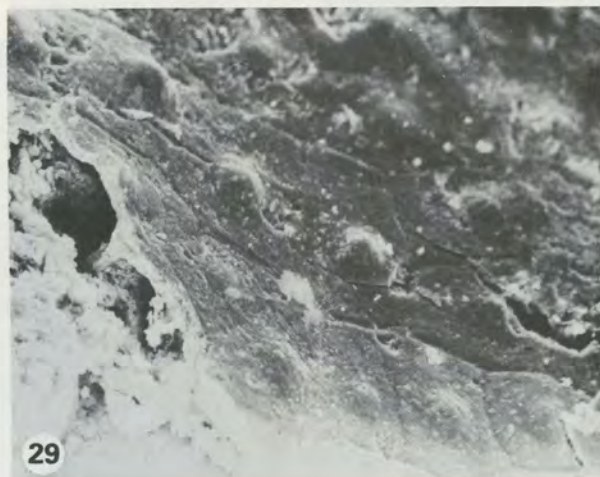
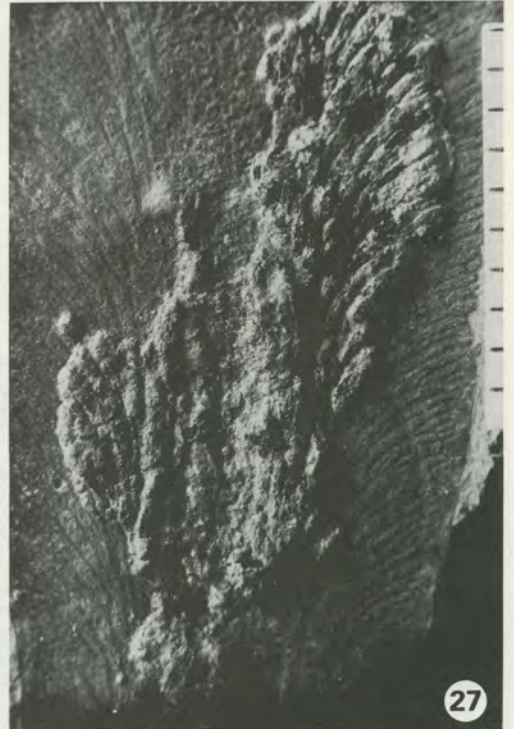
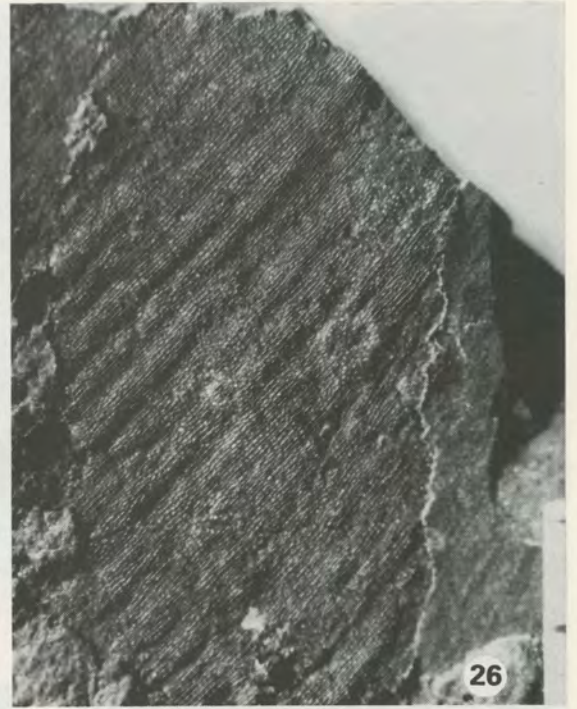
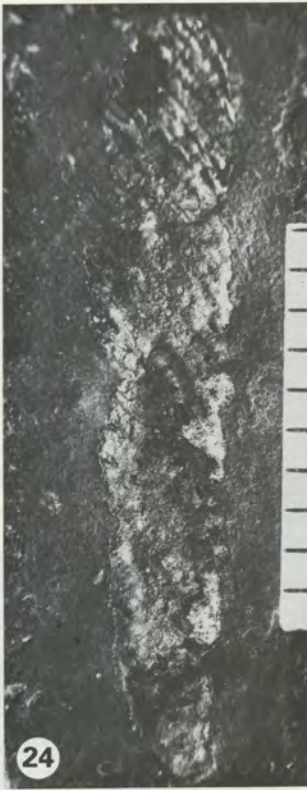
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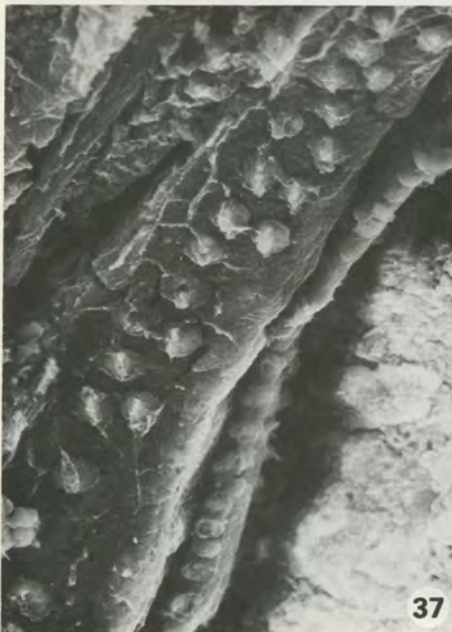
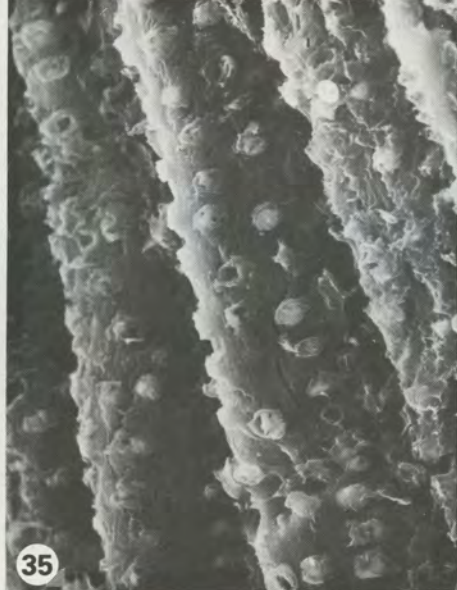


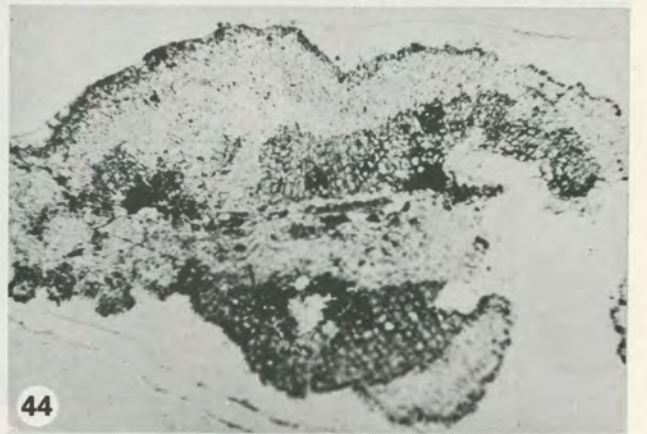
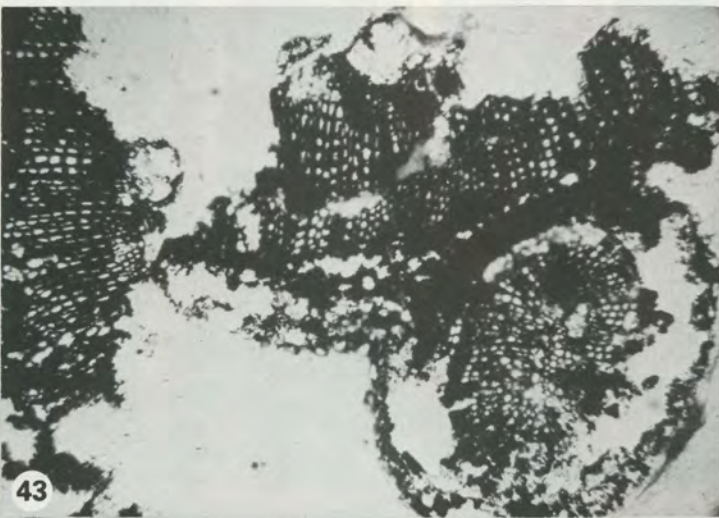
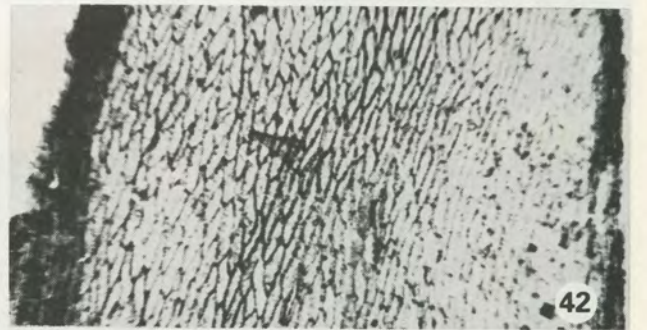
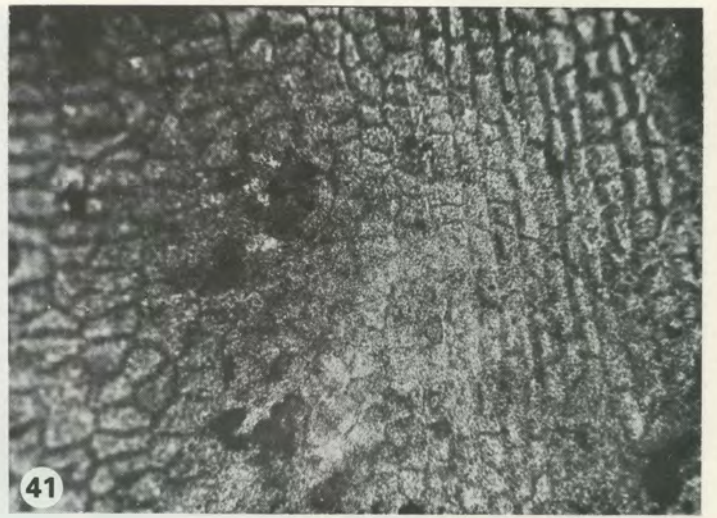
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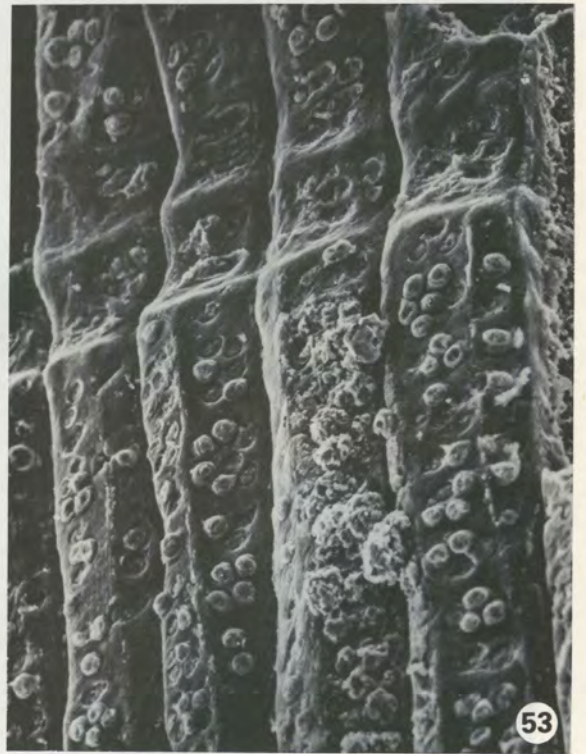
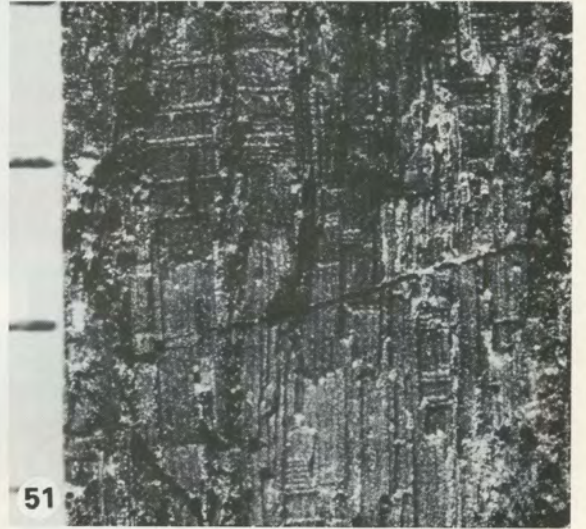
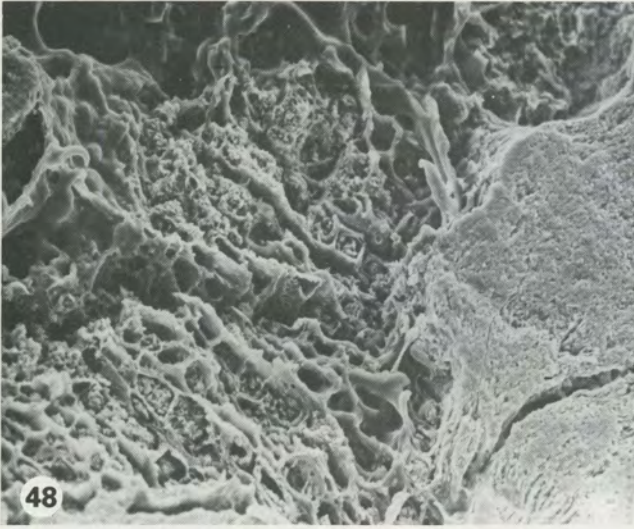


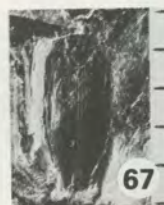
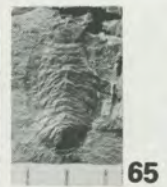
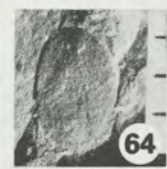
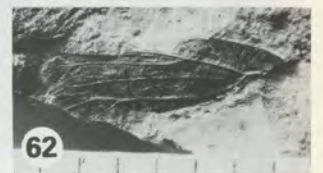
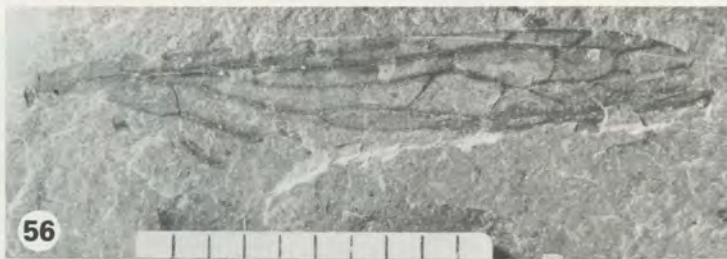
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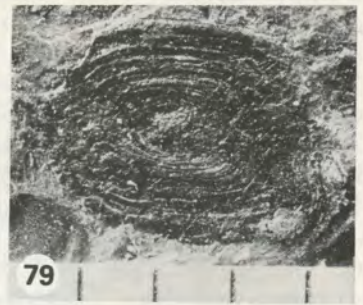
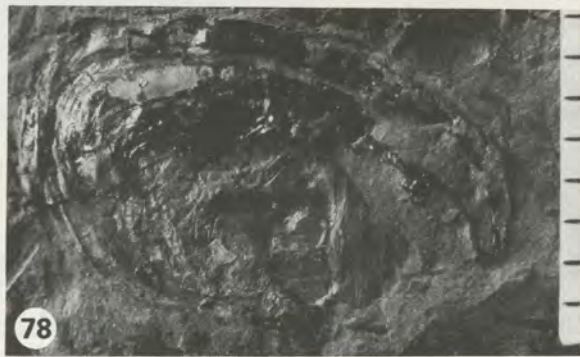
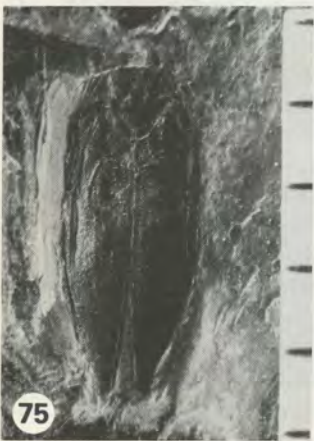
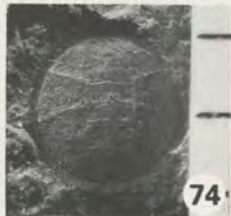
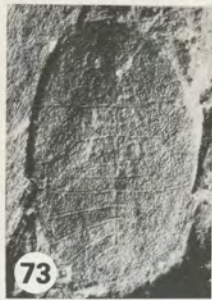
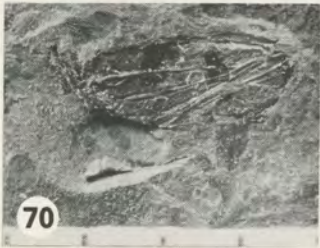


TABLE 2

Comparison of the fossils at the Lidgetton Site with the fossils of possible stratigraphic significance at three sites in the Lower Beaufort

Lithostrata	Sites			
	Beaufort	Mt. West	Bulwer	Mooi River
	Ecca	Lidgetton		
Taxa				
Plantae				
Bryophyta				
<i>Buthelezia (mooiensis)</i>		+	—	+
Tracheophyta				
Sphenopsida				
cf. <i>Equisetites</i> (cf. <i>Neocalamites carreri</i>)		+	+	+
<i>Sphenophyllum (speciosum)</i>		—	+	+
Pteropsida				
<i>Sphenopteris (alata)</i>		+(fragments)	+(? sp.)	+
Cycadopsida				
Pteridospermales				
<i>Glossopteris indica</i>		+	+	+
<i>G. communis</i>				
<i>G. browniana</i>		+(cf.)*		+
<i>G. conspicua</i>		+(cf.)*		+
<i>G. sp.</i>		+		— or few
<i>Belemnopteris (elongata)</i>		—	+	+
<i>Lidgettonia (africana)</i>		+	+	+
<i>Plumsteadia sp.</i>		+	+	+
<i>Eretomonium (natalensis)</i>		+		+
Coniferopsida		+(pyritized)		+(silicified)
Cordaitales				?+(carbonized)
Animalia				
Arthropoda				
Crustacea				
A and B (cf. <i>Leaia</i>)		A B	A B	A
Insecta				
Paraplecoptera (Liomopteridae)				
<i>Miolopectera (stuckenbergi)</i>		+	+	? Miolopectera
Plecoptera				
<i>Euxenoperla (spp.)</i>		+	?(fragment)	+
? Plecoptera				
Nymphs		+	+	?+
Homoptera				
<i>Aleuronympha (bibulla)</i>		+(? sp.)		+
Arthropoda (unclassified)				
C		C† (fig. 76)		

*For criteria see Lacey *et al.* 1975, Table 1

†Present at new locality at Balgowan.

corded from S. Africa. The difficulty in distinguishing a wing tracery from the reticulate venation of underlying and overlying leaves probably accounts for the paucity of the record and more detailed and determined hunting in the future should prove rewarding. That such insects existed contemporaneously with early Glossopteridae is proved by fossil impressions of wings found in formations of the same age in the Congo (Pruvost 1934), Falkland Islands (Halle 1912) and in Antarctica (Plumstead 1962)" (Plumstead 1963: 148–149). To the above could have been added Rhodesia (now Zimbabwe) (Zeuner 1955), Kashmir (Handlirsch 1906–1908), Brazil (Woodworth 1912, quoting Olivieri in litt. 1908, Carpenter 1930, Olivieri 1930, Petri 1945, Mezzalira 1948, this last not seen in the original — see Carpenter 1930 and Pinto 1972 for bibliography) and New South Wales (Tillyard 1917,

1921 and numerous other papers on the fossil insects of sites such as Belmont — see Riek 1976a for bibliography). Since 1963, 16 further African Palaeozoic insect sites have been discovered, of which eight, like Pruvost's Congo site and Zeuner's Rhodesian site, are represented by one specimen each — Loskop, Wagondrift, and Rondedraai, near Estcourt (Riek 1973), Emakwezini, near Empangeni (Riek 1976a), Matabola Flats, in Zimbabwe (Riek 1975b), Modderdrift and Krantz Poort in the southern Cape (McLachlan and Anderson 1977), and Kilburn dam-site, near Oliviershoek, where the author collected a wing fragment. The Matabola Flats is of Dwyka age with "apparently the oldest recorded insect in the Southern Hemisphere"; Modderdrift and Krantz Poort are Upper Dwyka; Hammanskraal, in Transvaal, with a collembolan and three insect

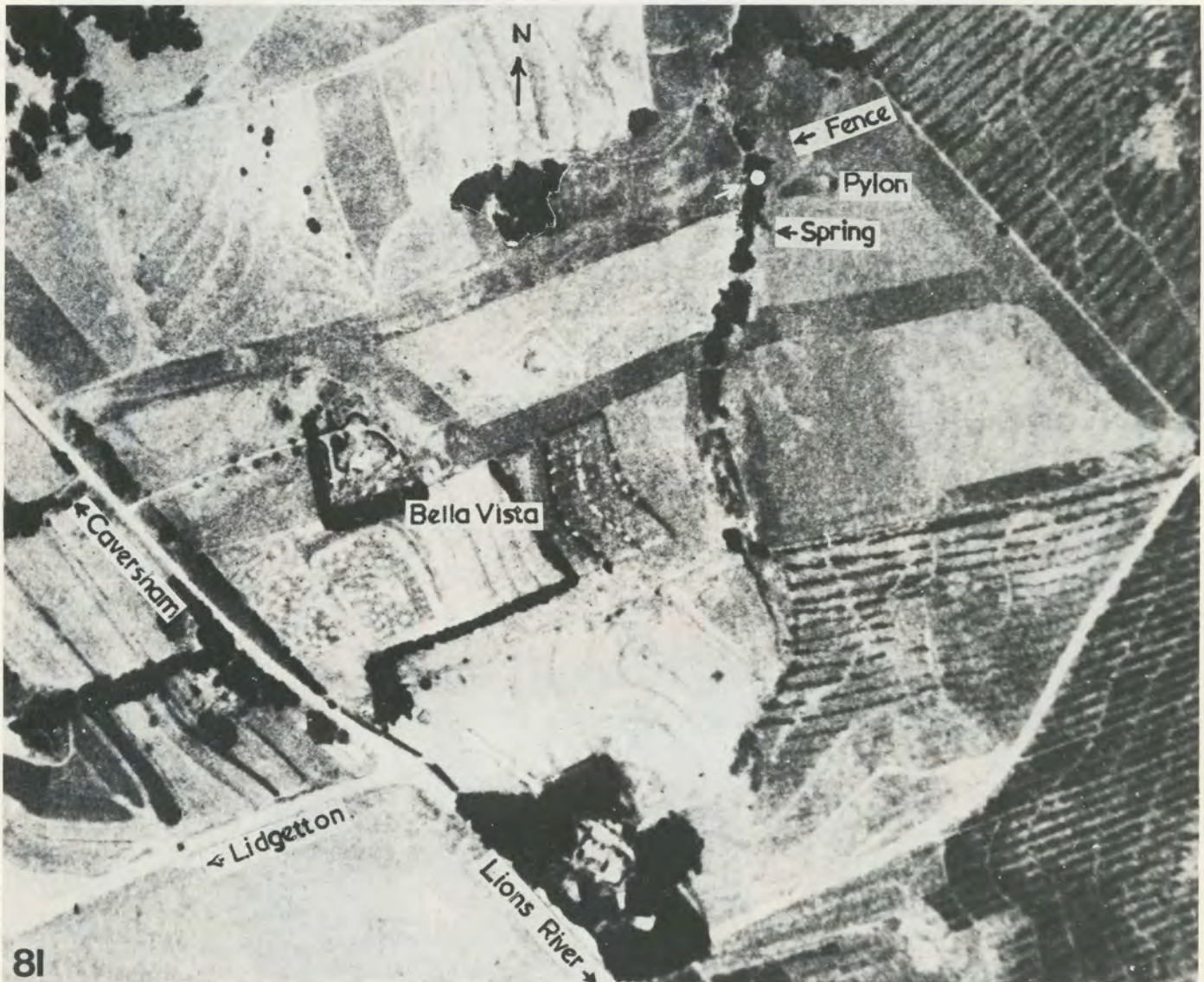


Figure 81. Aerial photograph of the farm Bella Vista, Lidgetton district, approximately 1 : 8 000; rephotographed from Trigonometrical Survey Aerial Photograph 1973, 1 : 50 000 Series, Job 717, Strip 6, Number 2680. The type locality of *Lidgettonia africana* Thomas 1958 is shown as a white spot indicated by a white arrow. For stereoscopic study the following pairs were used:

1973, 1 : 50 000 717 6 2680;	1963, 1 : 36 000 471 4 6800
717 6 2694;	471 4 6801

specimens (Riek 1976b,c), is in the Ecca; all the other sites are in the Beaufort of Natal, except for a Cape Upper Dwyka site with two specimens (B.W. Oelofsen, pers. comm.). The remaining six sites are Mooi River, Mooi River Quarry (farm Far End), Bulwer, Lidgetton (farm Bella Vista), Mount West (discovered 1975) and Balgowan (discovered August, 1976). The Bella Vista site is thus one of the six most productive sites among the 17 insect fossil sites in Africa of Permian age or older. In terms of the number of species represented, Lidgetton is second only to Mooi River in the Palaeozoic of Africa, and second only to Mooi River in number of fossil insect specimens of any age collected in Africa (cf. Riek 1975b, on Triassic insects and insect sites, and details of the Bella Vista collection presented here).

A very important feature of the Bella Vista site is

the exceptionally good state of preservation of some of the material in comparison with that of most other Palaeozoic Gondwana sites, particularly African ones. This applies to the detail of some replicas, to the presence of cellular layers, including epidermis, and, particularly, to the presence of pyritized material with cellular detail (Van Dijk *et al.* 1975, 1978). Pyritized vascular tissue from the midrib of *Glossopteris* leaves shows detail such as the presence of well-preserved scalariform thickening of the elements (fig. 50; Van Dijk, Hobday and Tankard 1978, fig. 8j). In August 1976 similar pyritization of *Glossopteris* leaves and sphenopsid stems was discovered at Wagondrift, but there is very much less material and preservation of cellular and subcellular detail is not as good as at Bella Vista. Poorer pyritization has also been observed at Estcourt (since 1979).

CONCLUSIONS

1. The fossil site discovered at Bella Vista in 1917, near Lidgetton, besides its importance as type locality of *Lidgettonia africana* Thomas 1958, has a considerable flora and extensive fauna, largely insect and largely new, as revealed by studies since 1974 by the present author and associates.
2. Some of the Bella Vista fossils, particularly pyritized material, is exceptionally well preserved when compared to other Gondwana Palaeozoic fossils, and warrants detailed study.
3. Studies of the Bella Vista site, and of a number of new Lower Beaufort sites in Natal, have provided a basis for biostratigraphic and palaeoecological comparisons; there is a clear need for early study and publication of the fossil floras and faunas of individual sites in the Karoo deposits, as well as compilations from many sites such as Anderson's (1975) — thus far only Indian Gondwana sites appear to have received

much detailed attention. Studies of this kind are intended for sites readily accessible from Pietermaritzburg, where material will be housed in the Natal Museum.

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THE OCCURRENCE, ORIGIN AND STRATIGRAPHIC SIGNIFICANCE OF BONE-BEARING MUDSTONE PELLET CONGLOMERATES FROM THE BEAUFORT GROUP IN THE JANSENVILLE DISTRICT, CAPE PROVINCE, SOUTH AFRICA

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ABSTRACT

The lack of useful lithostratigraphic markers in the Beaufort Group in the southern Karoo Basin has focused attention on the biostratigraphy of the sediments. As a result a more refined scheme of biostratigraphic classification is now possible which may prove useful in fixing the stratigraphic position of the uranium mineralized horizons. The most important mineralized horizon in the Beaufort West area (contains about 90 per cent of all known uranium occurrences) is associated with the *Priesterognathus/Diictodon* assemblage zone, but the way in which this relates to the important uranium occurrences farther east, between Graaff-Reinet and Jansenville, is uncertain because of the lack of biostratigraphic control.

Vertebrate remains have recently been found in mudstone pellet conglomerates in Beaufort channel sandstones along the Bullrivier in the Jansenville District, in an area that is extensively mineralized. The sandstones were deposited as point bar sands within a meandering river system flowing towards the north-east. The rivers drained a dry, arid to semi-arid alluvial plain and were characterized by fluctuating discharge and periods of low or negligible flow. These conditions promoted flood scour and fill activity and the deposition of internal mudstone pellet conglomerates. Hydrodynamic considerations suggest that estimates of bone transport velocity from their hydrodynamically equivalent quartz sphere is of limited value and can seldom, if ever, be applied to fossil bone accumulations.

Identification of the bones from the conglomerates indicates that they belong to the *Dinocephalia* biozone and not the overlying *Priesterognathus/Diictodon* zone. This suggests that the lower part of the Beaufort succession (formerly the *Tapinocephalus* zone) extends farther east than previously thought, and that the main mineralized horizon in this area occurs lower down in the succession than that around Beaufort West.

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INTRODUCTION

Uranium exploration in the upper Permian sediments of the Beaufort Group in the southern part of the Karoo Basin (west of longitude 25°E) has been handicapped by the lack of regional stratigraphic guides. The relationship between mineralized areas in different parts of the basin is a major problem: do they occur at a similar stratigraphic level or at different stratigraphic levels?

The lack of useful stratigraphic markers has focused attention on the biostratigraphy of the sediments with the result that a more refined scheme of biostratigraphic subdivision is now possible for the *Tapinocephalus* and *Cistecephalus* zones (Keyser and Smith 1978). These are the two lowermost zones in the Beaufort succession and the most important from the point of view of uranium mineralization. Although the scheme has only been applied to the

area between Sutherland, Beaufort West and Aberdeen, reconnaissance studies indicate that it may be possible to extend it farther east.

Dinocephalians have always been regarded as diagnostic of the lower and middle part of the *Tapinocephalus* zone (Kitching 1977); a fact that has been incorporated into the new biostratigraphic scheme which recognises the following biozones from the base upwards: (1) *Dinocephalia*; (2) *Pristerognathus/Diictodon*; (3) *Tropidostoma*; (4) *Aulacephalodon*; and (5) *Daptocephalus* (about to be changed to the *Dicynodon lacerticeps* zone). These zones may prove useful in fixing the stratigraphic position of mineralized horizons, especially as they appear to correspond with broad lithological divisions defined essentially on the changing ratio of sandstone to mudstone. For example, the most important mineralized horizon in the Sutherland, Beaufort West and Aberdeen areas coincides with the *Pristerognathus/Diictodon* zone and this in turn fixes the position of a thick (up to 150 m) sandy horizon, known as the Paalhuis Member of the Abrahamskraal Formation (Turner 1979). The base of this sandy horizon, which includes the Poortjie sandstone (Rossouw and De Villiers 1953), the Rietkuil sandstone and possibly the Rystkuil sandstone, contains something like 90 per cent of all known uranium occurrences. However, the way in which this mineralized horizon relates to the important uranium occurrences farther east, between Graaff-Reinet and Jansenville, is uncertain because of the lack of adequate biostratigraphic control.

Vertebrate fossil remains have recently been discovered in Beaufort sandstones along the Bullrivier in the Jansenville District (fig. 1) in an area that is extensively mineralized. Identification of the fossil material indicates that the lower part of the Beau-

fort succession (formerly the *Tapinocephalus* zone) extends much farther east than previously thought (Kitching 1973), and that the main mineralized horizon in this area occurs lower down in the succession than that around Beaufort West. Regional studies suggest that this part of the Beaufort succession was deposited mainly by high sinuosity meandering rivers (Turner 1978). The sandstones along the Bullrivier fit this regional pattern, and on the basis of their sedimentary properties and comparison with modern depositional environments, provide a means of interpreting the conditions under which they and the bone-bearing mudstone pellet conglomerates were deposited.

SEDIMENTOLOGICAL SETTING

Beaufort Group sediments in the southern part of the Karoo Basin cover an area of about 25 000 km², attain a maximum thickness of 2 700 m and consist mainly of sandstones and mudstones. A systematic upward decrease in the ratio of these two lithologies, together with changes in their sedimentary properties and comparison with modern depositional environments, enables the succession to be divided into low sinuosity channel, high sinuosity channel and floodbasin facies associations (Turner 1978). The facies associations are believed to represent the proximal, intermediate and distal components of an extensive fluvial depositional system which built out from a distant source to the south and west.

Uranium mineralization is only significantly developed in the upper part of the high sinuosity channel facies association where the ratio of mudstone to sandstone is about 4 to 1. The facies association is characterised by fining-upward sequences consisting of a basal scoured surface of low relief generally incised into mudstone, overlain by intraformational conglomerate, sandstone, siltstone and mudstone. In places mudstone is missing and the sequence is terminated by siltstone. The intraformational conglomerate consists predominantly of mudstone clasts, although siltstone clasts, reworked calcareous concretions, bone fragments and plant material are present locally. The sandstones are fine-grained, lenticular, and range from 1 to 24 m in thickness. Internally they are structured by horizontal lamination, cross-bedding (both trough and planar types with foresets directed to the north and east) and ripple cross-lamination. No preferred arrangement of these structures is discernible in the sandstones, although ripple cross-lamination tends to be most common in the finer-grained sandstone and siltstone higher in the sequence, and may include ripple drift cross-lamination. Current-rippled surfaces are common and confirm bimodal currents flowing to the north and east. The mudstones are maroon and bluish-grey, and contain calcareous concretions, red and green mottled horizons, thin sandstones and siltstones, which are commonly ripple cross-laminated, and desiccation cracks.

The fining-upward textures and sedimentary

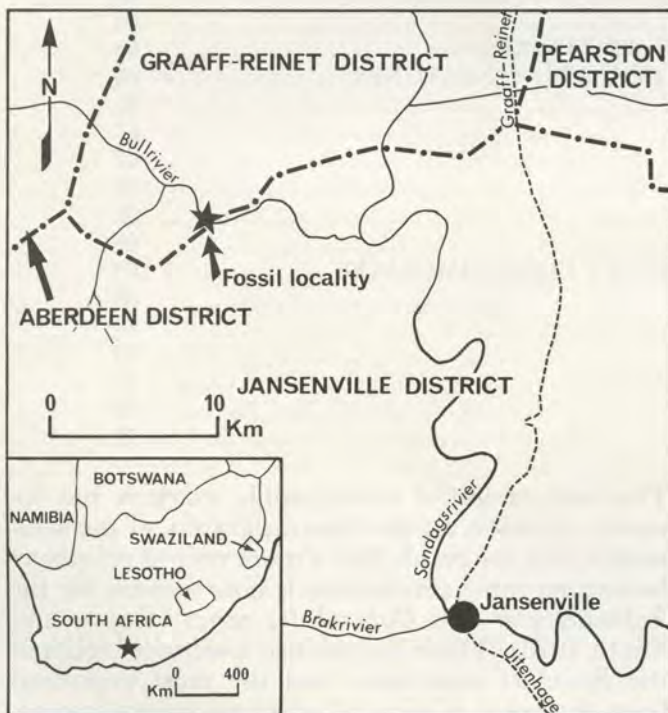


Figure 1. Map showing location of fossil site.

structures resemble the high sinuosity meandering stream model of Allen (1965, 1970) and Visser (1972). Thus the intraformational conglomerate overlying the scoured surface at the base of the sequence is interpreted as a channel lag derived from scouring of the floor and cutbank of the channel.

The sandstone records deposition on the sloping surface of a point bar — the sequence from horizontally laminated and cross-bedded sandstone lower down to ripple cross-laminated sandstones higher up corresponds closely with point bar development in meandering streams in response to

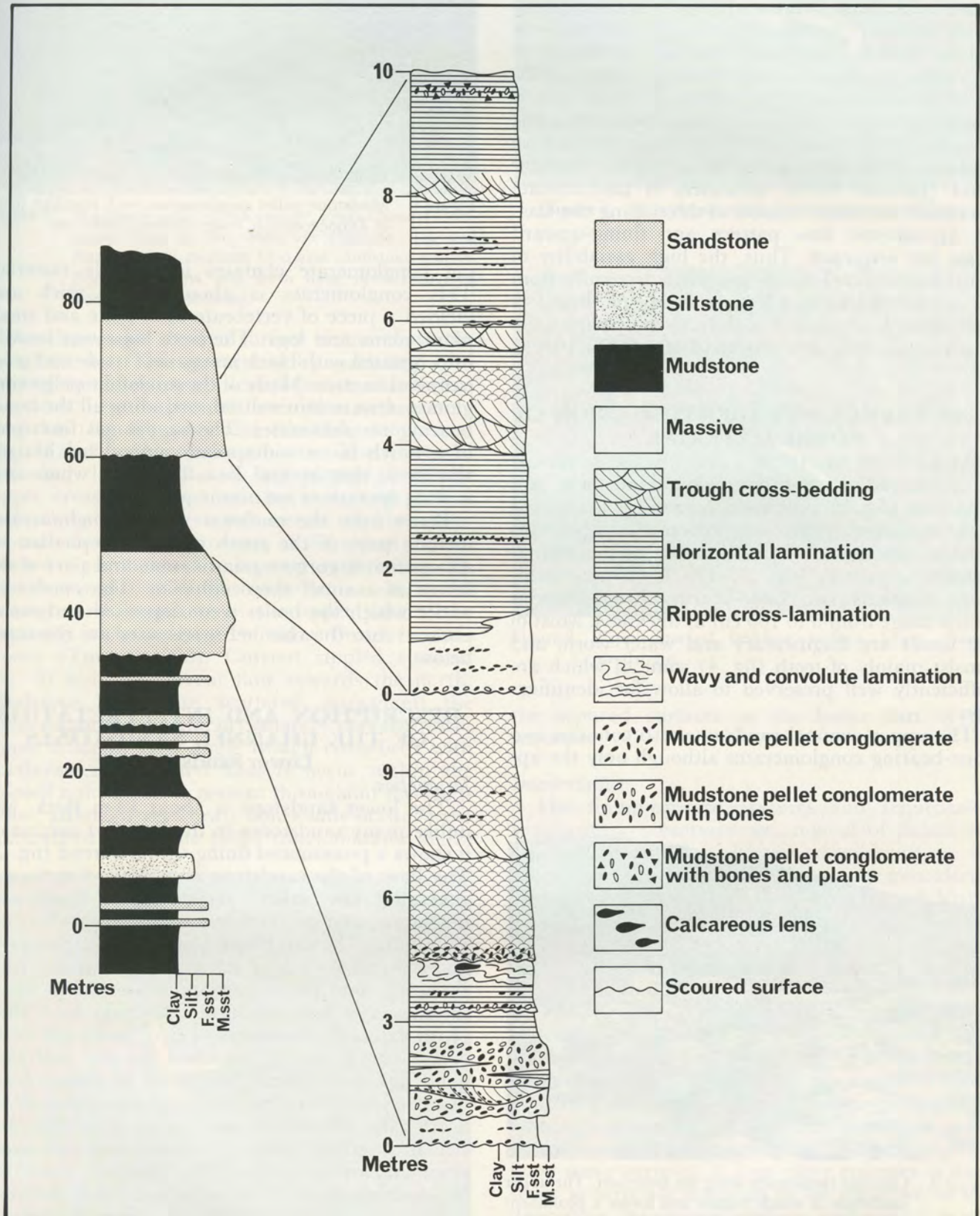


Figure 2. Generalized vertical section of the Beaufort Group sediments along the Bullriver showing fining-upwards channel sandstone sequences and distribution of bone-bearing mudstone pellet conglomerates.

declining bed shear stress as currents moved obliquely across the bar (Allen 1970). As the point bar accreted laterally, it became overlain by overbank fines, deposited mainly from suspension and subject to periodic desiccation. However, the classic fining-upward meander point bar model of Allen (1965) is seldom developed, probably because of the flashy (unsteady flow pattern) nature of the streams (locally simulates characteristics of braided low sinuosity streams) and the degree of curvature of the meander bends (Turner 1979). Modern studies indicate that tight or gently curved bends are unable to develop a strongly asymmetric flow pattern in which maximum flow velocities are confined to the outer cutbank part of the meander bend (Jackson 1975). Meanders of intermediate curvature are more capable of developing the classic asymmetric flow pattern and fining-upward point bar sequence. Thus, the high variability of point bar channel sands and their departure from the classic fining-upward trend in the Beaufort succession is attributed mainly to the complex geometry of the meander pattern (Turner 1978, 1979).

OCCURRENCE AND IDENTIFICATION OF FOSSIL MATERIAL

At the fossil site the Beaufort sediments consist of about 80 m of interbedded sandstone and mudstone (fig. 2). The fossil material is associated with mudstone pellet conglomerates within two channel sandstones (fig. 3) forming part of fining-upward sequences (fig. 2). The lowermost sandstone contains two bone-bearing conglomerates which range from 6 to 100 cm in thickness. Most of the bones are fragmentary and water worn, and consist mainly of teeth (fig. 4) some of which are sufficiently well preserved to allow for identification.

The upper channel sandstone also contains two bone-bearing conglomerates although only the up-



Figure 3. Channel sandstones along the Bullrivier. The upper sandstone is much thicker and forms a prominent cliff above the river. Both sandstones contain bone-bearing mudstone pellet conglomerates and are locally mineralized.



Figure 4. Mudstone pellet conglomerate with reptilian tooth cf. *Dinocephalian*, lower channel sandstone.

per conglomerate contains identifiable material. This conglomerate is about 11 cm thick and yielded a piece of vertebrate limb bone and small plant stems and logs. The limb bone was heavily impregnated with black manganese oxide and is locally radioactive. Many of the mudstone pellet conglomerates are mineralized, including all the bone-bearing conglomerates. The sandstones form part of a much more widespread mineralized horizon similar to that around Beaufort West, where trial mining operations are now in progress.

Bones from the mudstone pellet conglomerates include part of the tooth of a dinocephalian cf. *Anteosaurus*, a gorgonopsian canine and part of the femur of a small therocephalian. The conditions under which the bones were deposited and incorporated into the channel sandstones are discussed below.

DESCRIPTION AND INTERPRETATION OF THE CHANNEL SANDSTONES Lower Sandstone

Description

The lower sandstone is about 13 m thick, and unlike many sandstones in the Beaufort succession it shows a pronounced fining-upward trend (fig. 2). The base of the sandstone is a scoured surface of generally low relief, incised into bluish-grey mudstone, and overlain by a mudstone pellet conglomerate. The sandstone above the conglomerate and scoured surface is massive and contains a few scattered mudstone clasts. At about 0.5 m above the base is a scoured surface overlain by a thick (1 m) laterally persistent (40 m) mudstone pellet conglomerate. Mudstone clasts are flat and elongate (fig. 5) and locally display a pronounced imbrication with their long axes inclined towards the north-east. Within the conglomerate are thin, lenticular interbeds of horizontally laminated sandstone and trough-shaped scour and fill structures, in which the base of the scour and the foresets are lined with small mudstone clasts, particularly at the upcurrent end. Foreset orientation is towards the north-east.

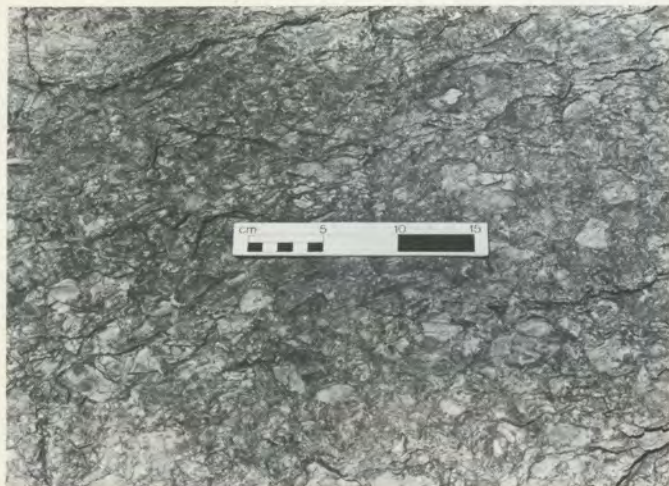


Figure 5. Mudstone pellet conglomerate, lower channel sandstone. Most of the clasts are elongate, flattened discs set in a medium to coarse sandstone matrix. Bone fragments and teeth have been recovered from the conglomerate.

Another major scoured surface occurs above the conglomerate. This is overlain by sandstone containing the following vertical sequence of sedimentary structures: horizontal lamination with parting lamination (fig. 6); wavy and convolute lamination (fig. 7) and ripple cross-lamination. The wavy and convolute laminated unit is separated from the ripple cross-laminated unit by a scoured surface and mudstone pellet conglomerate. A chocolate-brown calcareous lens occurs at the top of the deformed zone, below the scoured surface (fig. 2). The dominance of ripple cross-lamination in the finer-grained sandstone in the upper part of the sequence is characteristic of many Beaufort sandstones (Turner 1978). Current rippled surfaces (fig. 8) indicate current flow towards the north. Mudstone flakes are scattered throughout the rippled sandstones, and occasionally concentrate in ripple troughs. Low angle trough cross-beds with north-easterly directed foresets occur within the rippled unit. Pyrite is present throughout the sandstone, although vertebrate bones only occur in the mineralized mudstone pellet conglomerates above



Figure 6. Parting lamination on sandstone bedding surface, upper channel sandstone.



Figure 7. Wavy lamination, lower channel sandstone.



Figure 8. Ripple-marked bedding surface, lower channel sandstone.

the scoured surfaces in the lower part of the sequence.

Interpretation

The fining-upward textures and sequence of sedimentary structures are typical of fluvial deposits, and show a strong resemblance to the coarse member of the high sinuosity meandering river model (fig. 9) of Allen (1965) and Visser (1972). The lower scoured surface and mudstone pellet conglomerate are attributed to erosion of the floor and cutbank of the channel as it migrated laterally across its floodplain, and the incorporation of the eroded material into a channel lag gravel (Allen 1964, 1970). The structureless sandstone at the base of the sequence implies rapid dumping of sediment from decelerating floodwaters at a rate too fast for sorting processes to cope with. The scoured surface and thick mudstone pellet conglomerate above suggests a prolonged period of flood scour activity; at least three episodes of flood scour activity are apparent in the sequence, as evidenced by the scoured surfaces and mudstone pellet conglomerates. Trough-shaped scour and fill structures probably filled in channel floor depres-

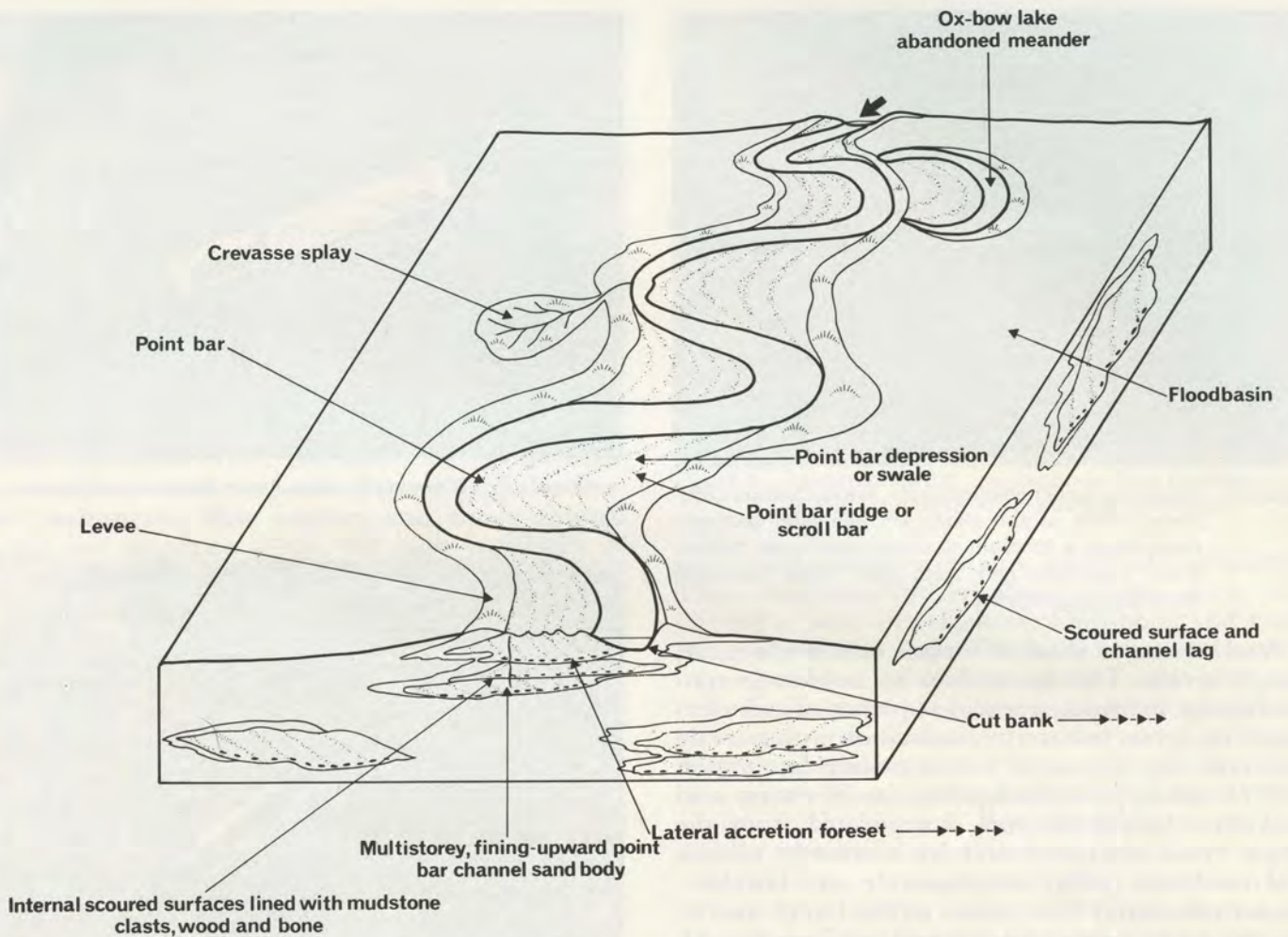


Figure 9. Depositional model of an idealized meander belt fluvial system showing various kinds of fluvial depositional units.

sions immediately following flood activity and scouring, whilst the horizontally laminated sandstone lenses may have been deposited as transitional or low flow regime plane beds (Harms *et al.* 1975).

The scoured surface overlain by horizontal laminations and wavy and convolute laminations suggests a similar pattern with flood scour followed by waning flow and the gradual emergence of the depositional surface. Liquefaction of the sediment due to expulsion of water during late falling stage (Reineck and Singh 1973) could explain the wavy and convolute lamination. Similar deposits have been described from channel sequences by Coleman (1969). Renewed flooding and scour was followed by the development of lower flow regime ripple bedforms during falling water stage, interrupted by the development of sinuous to curve-crested megaripples giving rise to the trough crossbeds in the middle of the rippled unit. The decay of vegetation growing within, and buried with the sediment (cutbank erosion), uses up the available oxygen and forms a reducing environment in which sulphides (pyrite) form. Coleman (1971) notes pyrite forming on the rootlets of living cypress trees along the lower Mississippi River at depths of up to 30 cm.

Upper Sandstone

Description

The uppermost sandstone is about 20 m thick and can be traced laterally for more than 1 km. It is a fine- to medium-grained, moderately sorted, arkosic wacke, with a basal scoured surface of low relief overlain by a mudstone pellet conglomerate. The sandstone immediately above the conglomerate is massive and contains a few scattered mudstone pellet conglomerate lenses, some of which are mineralized. The overlying sandstone shows the following sequence of sedimentary structures (fig. 2): horizontal lamination; trough cross-bedding; ripple cross-lamination; and horizontal lamination with locally developed trough cross-bedding (fig. 10) and scour surfaces associated with mudstone pellet conglomerates. The sequence is dominated by horizontal laminations in contrast to most fining-upward point bar sequences described from modern and ancient meandering river systems (Reineck and Singh 1973). Mudstone pellet conglomerates occur throughout the sandstone, although vertebrate bones are restricted to the thicker conglomerate horizons at the base of the sandstone and in the middle of the sandstone where the bones were found associated with oxidized plant material.



Figure 10. Horizontal lamination overlain by small scale trough cross-bedding, upper channel sandstone.

Interpretation

The general arrangement and type of sedimentary structures within the sandstone correspond with the deposits of modern meandering river channels (Bernard and Major 1963, Allen 1965, 1970). The scoured surface and mudstone pellet conglomerate at the base of the sandstone probably record erosion of the floor and cutbank of the channel during high discharge events, and the deposition of the eroded material as a lag gravel conglomerate (Arnborg 1958). The overlying sandstone has many modern counterparts in the deposits of point bar sands (fig. 9). The sequence from structureless to horizontal lamination, trough cross-bedding and ripple cross-lamination records deposition from decelerating currents during waning flood conditions, as the dominant bedform changed from upper flow regime plane bed to lower flow regime high intensity megaripples and low intensity ripples. Horizontal laminations in the upper part of the sequence may represent upper or lower flow regime plane bed conditions (Harms *et al.* 1975), with fluctuating energy levels during decelerating flow resulting in the local development of megaripples. The scoured surfaces and associated mudstone pellet conglomerates in the lower part of the horizontally laminated unit probably record minor flood scour events, similar to those described by Picard and High (1973) from modern ephemeral flood streams. The possibility that some of the horizontal laminations developed from downstream migration of megaripples (dunes) overriding the coarser material of the megaripple front (McBride *et al.* 1975) is suggested by their close association with trough cross-bedding.

ORIGIN OF THE BONE-BEARING MUDSTONE PELLET CONGLOMERATES

General

Mudstone pellet conglomerates occur at the base of channel sandstones, where they rest upon mudstone, and within the sandstones. The basal mudstone pellet conglomerates differ from the internal ones in that they are laterally more persistent and associated with major scoured surfaces. They are analogous to the channel floor lag concentrates of modern meandering rivers derived

from the erosion of the bank and floor of the channel as it migrates laterally across its own floodplain (Allen 1964, 1965).

The internal bone-bearing mudstone pellet conglomerates probably represent scouring and reworking by floodwaters of consolidated mud layers; the lateral persistence and thickness of the conglomerates implies a major episode of flood scour activity. Modern river systems show that point bar deposition is episodic and composed of more than one flood event (Reineck and Singh 1973). As floodwaters subside the more elevated portions of the river bed may become exposed, leaving behind pools of standing water in hollows and depressions (e.g. swales) away from the thalweg (line of maximum depth). Within such hollows and depressions clays settle out from suspension to form a mud layer, which with further drying may consolidate and form a mudcracked surface. With renewed flooding, scouring of the bed occurs and the mud is incorporated into a mudstone pellet conglomerate along with vertebrate bones and plants picked up by the floodwaters. In some cases turbulence on the downstream side of bones leads to the formation of a scour pit within which the bone accumulates and is then buried on falling river stage. In this situation the bone acts as a bedform modifying the flow, but if buried and preserved it is not normally associated with mudstone pellet conglomerates unless it acts as a sediment trap. Most bones in the conglomerates are too small to act as efficient sediment traps, whilst the larger bones such as ribs and limbs are hydrodynamically unsuitable for trapping because of their shape. These would tend to align in the direction of least resistance to flow with their long axes parallel to flow and the larger end (if present) pointing upcurrent (Blatt *et al.* 1972). In river channel deposits the majority of particles are orientated parallel to flow, particularly when the flow is heavily-laden with sediment, such as during flood events. The fact that many of the larger bones are not associated with highly concentrated mudstone pellet conglomerate zones also argues against sediment trapping by bones as an important mechanism in the formation of mudstone pellet conglomerates. The small size of the clasts and their fragile nature further suggests that they were not transported very far prior to deposition.

Climatic Factors and Contemporary Analogues

Repeated flood scour activity depends on flood periodicity which is largely determined by climatic factors (Friend *et al.* 1979). The presence of desiccation cracks, calcareous concretions of pedogenic origin (Turner 1978), colour mottling, and "desert roses" composed of pseudomorphs of calcite after gypsum (Keyser 1966) in the Beaufort, point to prolonged periods of exposure and desiccation. Comparison of pedogenic calcareous concretions with Quaternary calcretes of similar pedogenic origin (Goudie 1973) provides useful clues to the climatic conditions prevailing during Beaufort times.

The formation of pedogenic carbonate implies not only prolonged exposure, but a warm to hot climate (mean annual temperature of 16–20 °C) and a seasonally distributed rainfall (mean annual rainfall of 100–500 mm) but without any marked seasonality. The maximum monthly rainfall must be less than 25 per cent of the mean annual precipitation for calcrete to form; dry areas with one season of very heavy rainfall tend towards ferricrete and so far no sign of pedogenic iron enrichment has been found in the Beaufort. Other lines of evidence indicative of a warm, dry and possibly arid climate are: (1) the paucity of preserved plant remains (Kitching 1977) and the apparent dwarfism shown by *Glossopteris* leaves from the lower Beaufort (Smith 1978); (2) the catastrophic mass mortality of fish in an ephemeral pool (Keyser 1966); (3) the introduction at this time of new faunal and floral elements consistent with increasing temperatures (King 1963); (4) the presence of a widespread arid zone (desert) to the north of the Beaufort depositional site (King 1963); and (5) the palaeomagnetic data which places this part of Africa during Beaufort times between latitude 30 and 40°S (Creer *et al.* 1973). All this is consistent with rivers draining a dry, arid to semi-arid alluvial plain characterized by fluctuating discharge and periods of low or negligible flow. Such conditions would tend to promote flood scour and fill activity (Leopold *et al.* 1964), intraformational breaks and mudstone pellet conglomerates and the multistorey build-up of channel sands, a feature that is characteristic of most Beaufort channel sandstones (Turner 1979).

Similar conditions occur today in the southern part of the Karoo, between Pearston and Sutherland, which experiences climatic conditions not much different from those envisaged during deposition of the Beaufort sediments (mean annual temperature 15–21°C, and mean annual rainfall 120–380 mm). The rivers draining this part of the Karoo show both braided and meandering characteristics (e.g. Leeurivier) and deposit predominantly fine sand during flood events. The sands are structured mainly by horizontal lamination and ripple cross-lamination and may provide useful contemporary analogues for the Beaufort Group sandstones which are also dominated by these structures. Rivers in humid areas do not show the same frequency of scour and fill because of the removal of fines by perennial flows, leaving the more resistant coarser material behind (Leopold *et al.* 1964).

Derivation and Preservation of Bones

The bones in the mudstone pellet conglomerates are probably derived from upstream sources and from undercutting and reworking of the channel bank deposits during channel migration. Transportation and reworking of the bone in this manner would tend to concentrate the most resistant material such as teeth and compact bone fragments. Some of the bones show sun cracking, flaking, rounding and fragmentation consistent with long distance and often turbulent transport, inter-

persed with periods of subaerial exposure. In most fluvial settings, especially in arid climates, movement of particles is generally intermittent so that weathering during transport may be important.

The similarity in size of the bone (less than 5 cm in length) and its resistant nature suggest that it may represent hydrodynamic accumulations of the chemically most resistant material. Whilst this appears to be true for some of the bone-bearing conglomerates, others contain larger, less resistant bones such as limb bones and ribs (fig. 11). This suggests more locally derived material, probably



Figure 11. Reptilian rib in mudstone pellet conglomerate, lower channel sandstone.

from animals inhabiting the channel and channel bank environments (proximity to water and vegetation). Additional factors, such as the amount of surface weathering to which the bone was subjected prior to its inclusion in the conglomerate, may be important. For example, most bones break down quickly when subjected to surface weathering, especially under dry climatic conditions such as those envisaged for the Beaufort depositional site, unless they are buried quickly or protected from weathering by carbonate concentrations. In the Beaufort both of the latter processes seem to have operated in promoting preservation of bone. Carbonate concentrations are most common in the channel bank (levee) deposits, which contain the best preserved fossil material, as noted by Hotton (1967) and Smith (1978). The bone in some cases serves as a nucleus for CaCO₃ concretionary formation with the result that many well-preserved specimens are found within the concretions from channel bank environments. In addition carbonate formation implies alkaline soils which will also favour preservation of fossils (Behrensmeier 1975). Judging by the internal characteristics of the channel sandstones and the frequent preservation of sandstone palaeosurfaces in overbank environments (Turner 1979), flood periodicity was high and rapid burial and preservation of fossils common.

Hydrodynamic Factors

Bones and clasts carried by the flow will be deposited immediately the flood waters begin to subside and the current is no longer competent to carry the coarsest fraction of its load (bedload). The presence of mudclasts and bones above flood scour surfaces and their association with the coarsest fraction of the sand supports this interpretation. Factors which may increase the depositional potential are: (1) spill resistance and energy loss due to the chaotic deformation of flow around mudclasts and bones in transport (Leopold *et al.* 1964); and (2) the retardation of flow at the bed following the initial deposition of the coarse sand fraction of the bedload (Koster 1978). However, this simple picture of deposition in stream channels according to size grading is not realistic in many cases. For example, deposition often occurs in zones of local flow divergence where conditions are *non-uniform*, in contrast to most field and laboratory studies which have been mainly concerned with uniform flow conditions.

In the present study one important factor which must be explained is the fragile nature of many of the mudclasts and the short distance of transport prior to deposition, despite their association with water-worn bone derived from much farther away. Within alluvial channels preferential sites for the accumulation of bone and mudclasts occur due to local changes in flow conditions induced by bed topography. Hydrodynamic studies show that velocity increases with decrease in depth in the flow direction, whereas the velocity decreases with increasing depth in the flow direction (Allen 1970, Middleton and Southard 1977). These changes are fundamentally linked to two factors, channel shape and bed configuration (Allen 1964). The presence of hollows and depressions on the channel floor of sufficient relief constitute bed configuration which may locally affect flow conditions and the transport and deposition of particles (Leopold *et al.* 1964), assuming channel width and shape are constant. On encountering a hollow or depression lined with mudclasts, the flood waters will suddenly decelerate and tend to deposit the coarsest fraction of their load, including bones, along with the mudclasts as a local lag concentrate (Allen 1964). The sudden deceleration of the floodwaters may be accompanied by a change from upper to lower flow regime conditions and a hydraulic jump. Flume studies have shown that clasts are often deposited where this change takes place, and since these constitute the coarse fraction of the load, lower stage flows are incapable of modifying the deposit, which becomes "fossilized". Under these conditions transport of mudclasts would be short-lived, thereby increasing their potential for preservation. Deposition occurs at such sites because of the loss of competency of the flow to transport all its load due to factors such as particle size, shape and density.

In a situation like this, flume studies on bone transport dynamics and deposition are of limited

value. Estimates of transport velocity for bones from their hydrodynamically equivalent quartz grains suffer from the problem that the velocity component at a given point varies with depth. Thus, in principle it is not possible to estimate palaeovelocity from grain or bone size information alone, particularly when mean conditions are specified, since velocity is a probabilistic phenomenon dependent on the frequency and intensity of eddy impingement on a spatially varied bed (Church 1978). The data used by Behrensmeyer (1975) for this purpose was based on experimental work with bed material in a non-dilated state, without imbrication or packing, and with the grains in the uppermost layer available for transport. This condition is seldom found in nature and is not directly applicable to velocity estimates in river channels without introducing probability statements or empirical coefficients into the data base. Two other problems are apparent in attempts to estimate bone transport (as with sands and conglomerates). The first is that what one is measuring is the transport velocity of the bones at their site of deposition and the hydrodynamic conditions are not necessarily the same for deposition as for entrainment (velocity required for initiation of grain movement). Grain size-velocity diagrams such as those used by Behrensmeyer (1975, fig. 8) are based on data for grain entrainment, not deposition, and to date there has been little study devoted to the subject of grain movement once entrainment begins. However, recent studies indicate that sands are deposited at values for the dimensionless shear stress (θ) of 5 per cent lower than those for entrainment. Moreover, since the bones occur only in mudstone pellet conglomerates indicative of major flood events, the floodwaters may have been more heavily laden with sediment than usual, thereby increasing their competence and potential for producing poorly sorted bone debris. Some conglomerates contain bones of varying sizes (including limb bones up to 25 cm long), despite the preponderance of teeth. The absence of bones in the sandstones deposited between major flood events is consistent with the notion of increased competency of the flows (from increased sediment load and/or velocity) necessary for the transport of bone and its inclusion in the conglomerates, the bones coming either from within the channel or from undercutting of the channel bank. In this respect major flood events associated with the conglomerates may have two important effects, they promote channel erosion and undercutting of the bank, and they may be the cause of death among the animal population inhabiting the channel and near-channel environments. Under the dry, arid to semi-arid conditions prevailing at the time, drought and flash floods may have been common occurrences. Periods of drought would tend to concentrate the animals along major water courses, making them easy victims of flash floods. Because of the sparse plant cover and the fact that vegetation capable of colonising and stabilizing the inter-

fluvial hillslopes had not yet evolved (Schumm 1968), run-off and sediment yield were exceptionally high. Under these conditions major flood events of the type likely to cause mass drownings would occur frequently — normal flood recurrence interval for most rivers is 2,33 years (Leopold *et al.* 1964). The lack of vegetation beyond the confines of the channel environment may similarly be reflected in the almost complete absence of plant and vertebrate remains in distal floodplain sediments, far removed from the major active channels.

These same general conditions occur today east of Beaufort West where the Salt River drainage system is at present experiencing the effects of a prolonged drought. The drainage system is over 25 km wide and during exceptionally heavy rains the entire system and parts of the surrounding flats are flooded, although normally flow is confined to a narrow central channel.

Current velocities during deposition of the mudstone pellet conglomerate can be estimated from the grain size of the sandstone matrix which averages about 0,2 mm in diameter (medium-grained sand). As discussed earlier, this provides only an "order-of-magnitude" estimate of the flow and suggests that for shallow flows up to 40 cm deep a velocity of about 50 cm/s is required for grain transport (Blatt *et al.* 1972, Harms *et al.* 1975). For deeper flows, velocities up to 100 cm/s are required and during flood events this may increase to between 180 and 300 cm/s (Leopold *et al.* 1964). This is well within the values estimated by Behrensmeier (1975) for transport of large mammalian bones, including those of hippos and elephants.

CONCLUSIONS

Bone-bearing mudstone pellet conglomerates occur in channel sandstones of the Beaufort Group along the Bullrivier in the Jansenville District, in an area that is extensively mineralized. The sandstones were deposited as point bar sands within a meandering river system flowing towards the north-east. Mudstone pellet conglomerates within the sandstone represent episodes of flood scour and fill activity which were promoted by the flashy (unsteady) nature of the flow and the arid to semi-arid climate. Deposition occurred immediately flood waters began to subside because of the inability of the currents to carry the coarsest fraction of their load (bedload). Depositional potential may

have been further increased by: (1) deformation of flow around mudclasts resulting in spill resistance and energy loss; (2) retardation of flow at the bed due to deposition of the coarsest fraction of the bedload; (3) local flow divergence and the development of non-uniform flow conditions; and (4) local changes in flow conditions induced by bed topography.

Estimates of transport velocity for bones from their hydrodynamically equivalent quartz grains are of limited value because: (1) velocity varies with depth; (2) velocity is a probabilistic phenomenon dependent on eddy impingement on a spatially varied bed; (3) experimental work has been carried out on bed material in a non-dilated state which is seldom found in nature; (4) transport velocity is not necessarily the same for deposition as entrainment (initiation of movement); and (5) flood waters are generally heavily-laden with sediment, thereby increasing their competency. Current velocities based on the grain size of the mudstone pellet conglomerate matrix indicate flows of about 50 cm/s for depths of up to 40 cm, and 100 cm/s for deeper flows. During floods, this would probably increase to between 180 and 300 cm/s.

The bone-bearing mudstone pellet conglomerates represent the only known occurrences of vertebrates in this area and include part of the tooth of a dinocephalian cf. *Anteosaurus*, a gorgonopsian tooth and part of the femur of a small therocephalian. The presence of material characteristic of the Dinocephalia biozone has important stratigraphic implications and suggests that the lowermost part of the Beaufort succession, formerly assigned to the *Tapinocephalus* zone, extends much farther east than previously thought (Kitching 1977) and that the uranium mineralization in this area occurs lower down in the Beaufort succession than that around Beaufort West, which belongs mainly to the overlying *Pristerognathus/Diictodon* zone. The presence of a dinocephalian humerus in Beaufort Group strata near Somerset East suggests that the Dinocephalia zone may extend even farther to the east (Keyser 1978), although systematic collecting has still to be carried out in this part of the basin before this can be firmly established. It is also uncertain whether the *Pristerognathus/Diictodon* zone is represented in this area; the only evidence to date is a single pristerognathid and a gorgonopsian specimen with non-Dinocephalia zone affinities. There is considerable scope here for further study.

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