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PALAEONTOLOGIA AFRICANA

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

VOLUME 18, 1975

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Bernard Price Institute
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BERNARD PRICE INSTITUTE FOR PALAEONTOLOGICAL RESEARCH
UNIVERSITY OF THE WITWATERSRAND, JOHANNESBURG

REPORT OF THE HONORARY DIRECTOR (EM. PROFESSOR S. P. JACKSON) FOR THE CALENDAR YEAR 1974

Early in 1974 Dr. S. H. Haughton relinquished the office of Honorary Director. At a function held in the Institute's library, the Vice-Chancellor of the University, Dr. G. R. Bozzoli, paid a warm tribute to Dr. Haughton on behalf of the Council and Senate for the services which Dr. Haughton had rendered to the University and to Palaeontology during his long association with the Institute as its honorary director. The Vice-Chancellor was able to say that Dr. Haughton would not be severing his connection with the Institute, for he would continue to serve as Honorary Editor of Palaeontologia Africana, and as a scientific adviser to the Director and the Board of Control. Dr. Haughton has been succeeded by Em. Professor S. P. Jackson, who was Deputy Vice-Chancellor of the University until his retirement at the end of 1973.

There have also been some changes in the composition of the Board of Control. The Chairman is the Vice-Chancellor; Dr. A. P. Burger, Vice-President of the C.S.I.R. has been appointed in place of the President Dr. C. v.d.M. Brink; Dr. C. K. Brain, the Director of the Transvaal Museum, represents the Historical Monuments Council, and Professor T. R. Trevor-Jones is an additional representative of Senate.

Minor alterations in the Institute's buildings have been carried out in order to provide a teaching laboratory for second and third year undergraduate students, a new drawing office and photographic studio, and a small contamination-free laboratory for palynology. At the same time much improved washroom facilities were provided for the staff of preparators. The accommodation of the Institute is now expected to be adequate for many years to come, and it should be possible to continue to provide hospitality for such work as the micropalaeontology programme of the Southern Oil Exploration Corporation, and the Anglo American Swaziland Project. There is adequate office accommodation for visiting scientists and for the research students who offer themselves at present.

The annual budget of the Institute approaches R150 000 of which R22 000 is received in the form of a block grant from the South African Council for Scientific and Industrial Research.

STAFF MATTERS

The post of senior staff palaeobotanist, which fell vacant on the retirement of Dr. Edna Plumstead, was advertised again early in 1974. Dr. J. T. Brown, formerly of the University of Montana, was offered the post on a contract basis for three years in the first instance. Dr. Brown's departure from the United States was delayed, but he is due to arrive in South Africa late in August 1975.

Dr. E. P. Plumstead has continued to work in the Institute as an honorary Professorial Research Fellow of the University, supported by a special grant from the Council for Scientific and Industrial Research. Research in palaeobotany for higher degrees has, in the absence of a palaeobotanist on the Institute's staff, been supervised by Associate Professor R. Pienaar of the University's Department of Botany.

Mrs. D. King, formerly secretary to the Registrar of the University, was appointed at the end of the year to a new post of secretary in the Institute.

Mr. P. Nagel, who held the post of photographer-technician since the beginning of 1973, resigned in order to take up a commercial appointment. No successor has been appointed, but Mr. Nagel's duties have been assumed by Mr. Gerard Smith, who now combines the duties of photographer with those of illustrator.

Mrs. H. Anderson relinquished her appointment as Junior Research Officer at the end of 1974, but continues to work in the Institute on the Molteno Flora, the subject of her Ph.D. thesis.

During the course of the year, three higher degrees were confirmed by the University. Dr. C. E. Gow, who came to the Institute from the South African Museum in Cape Town, completed his thesis for the degree of Ph.D. about the middle of the year and graduated in December. Miss Ann Anderson, senior research bursar of the University, also completed her thesis for the degree of Ph.D. during 1974, and the degree was conferred in December. Miss Anderson has since married Mr. I. R. McLachlan, the officer in charge of the SOEKOR Micropalaeontology Unit. Dr. McLachlan was awarded a C.S.I.R. post-doctoral research grant and with this support she will continue to work in the

Institute during 1975. Miss G. E. Collings received the degree of M.Sc., early in 1974, and is now in the United Kingdom.

FIELD WORK

Dr. Gow, having completed his thesis, planned to undertake work on the Red Beds of the Karroo system. Accordingly, he entered into negotiations with the Ciskeian authorities to visit the District of Herschel, and to collect there. Dr. Gow undertook a collecting trip to Herschel at the end of the year.

Drs. Kitching and Cruickshank accompanied Dr. A. Keyser of the Geological Survey on a two-week field trip to the vicinity of Etjo Mountain in S.W.A. On this trip, some 30 anomodont fossils were collected and some fragments of archosaurs from the Otjiwarongo District.

Dr. Kitching spent the months of September and October on a fossil collecting trip in the Beaufort beds in the Victoria West, Pearston, Graaff Reinet and Rouxville Districts. On this trip, Dr. Kitching was accompanied by Mr. M. Kitching. Some 180 well preserved fossil reptiles were collected, and new data were obtained for the Cynognathus zone sediments in the Rouxville District.

Mr. B. R. Turner spent a week in the field in the early part of the year, clearing up various points in connection with his research on the stratigraphy and sedimentary history of the Molteno formation.

Mr. I. R. McLachlan undertook a two week field trip at the end of the year to follow up results of earlier visits to the southern and western Karroo Dwyka and Ecca outcrops in connection with his microfaunal studies.

Dr. Ann McLachlan, having finished her thesis on Arthropod trackways in the lower Karroo, visited the eastern Cape Province with a view to exploring the possibility of trackways having been made by crustaceans. At the same time she took the opportunity of visiting universities and museums in the eastern Cape Province area and making contact with other research workers with similar interests.

Several visits were made to Makapansgat and Sterkfontein. The University has now provided accommodation at Frankenwald for storage and partial preparation of specimens from the Makapansgat site.

Professor P. V. Tobias, who has a special interest in palaeoanthropology and human evolution and has published extensively on those topics, has for some time been in charge of the excavation at the University's Pleistocene cave site at Sterkfontein. Professor Tobias has published extensively in his special field of work and continues to do so. He reports to the Director before Board meetings.

The Sterkfontein caves are a popular attraction for visitors. Electric lighting has now been installed in the caves, and the preparation of audio-aids is proceeding.

The Department of Botany of the University has undertaken the compilation of an illustrated guide to the plants of the Sterkfontein area, and work is now proceeding on laying out a "natural trail" along which the plants illustrated in the guide will be identified.

Dr. C. K. Brain, Director of the Transvaal Museum, conducts an excavation at Swartkrans, another University site, on the understanding that all specimens excavated since the University acquired the site will be numbered and lodged in the Institute's collection.

RESEARCH WORK

During the year, Dr. Cruickshank continued his work on the early history of the archosaurs with special reference to the development of the ankle joint. He has also started a collaborative study with the Department of Mechanical Engineering on the hydrodynamic function of the extended "horns of Nectidian amphibia". He has completed two papers on the fossils which he had studied in Harvard and East London. He continues to work on the taxonomy of Triassic dicynodonts in collaboration with Dr. A. Keyser of the Geological Survey. Recently he has become interested in the relationship of the Omingonde Mudstone Formation (S.W.Africa) to the underlying Precambrian Damara metasediments.

Dr. C. Gow completed his work on the morphology and taxonomy of the genera *Youngina* and *Prolacerta*. At present he is engaged on a study of the skulls of certain thecodontosaurids and ornithischians. Another interest is the search for the still unknown ancestors of lizards in the upper Permian of the Karroo. Dr. Gow has prepared a paper on the problematic lizard-like form from the Daptocephalus zone and is presently engaged on describing the skull of *Owenetta*, a small procolophonid which is sometimes confused with juvenile *Procolophon*.

Dr. J. W. Kitching has continued his ongoing programme of collecting and describing fossils of reptiles from the South African Karroo and from the Limeworks Cave at Makapansgat. He has been collaborating with Prof. E. H. Colbert of the United States of America on a paper on the Triassic Cynodont *Thrinaxodon* and other small Lystrosaurus zone therocephalians in Antarctica. This work, which is now completed, arises from Kitching's own visit to Antarctica a year or two ago. He has also worked on fossil millipedes from the Lystrosaurus zone (Triassic) beds of South Africa.

Mr. Brian Turner has continued to work on the stratigraphy and sedimentary history of the Molteno formation in the main Karroo basin of South Africa and Lesotho. In addition, he has devoted some time to sedimentology and uranium deposition in the Beaufort Beds.

Mr. Brian Maguire's dissertation on the food plants of the Bushmen was almost completed in 1974.

Mrs. Judy Maguire was engaged throughout the year on a study of old world living and fossil porcupines and other South African Hystricid material from the australopithecine sites in the country. She has also worked on modern porcupine bone accumulations and a comparison of these with the Makapansgat bone accumulations and "osteodontokeratic" tools. All the work is expected to be completed and ready for submission for the degree of Ph.D. in 1975.

Dr. Ann McLachlan, after submitting her thesis, spent some of her time preparing the text for publication and went on two field trips, as detailed above. She has continued to gather information on the invertebrate animals which possibly made the trackways she has been working on, and also she is endeavouring to elucidate the lower Karroo palaeoenvironment from various angles with a view to effecting a facies correlation between the northern and southern Karroo.

The following post-graduate students are working in the Institute:

Mrs. H. M. Anderson
Mr. J. M. Anderson
Miss S. Chernin
Mrs. R. M. S. Falcon
Mrs. A. Malleson
Mr. I. R. McLachlan
Mrs. S. Smithies

In addition, Dr. R. Davies, a staff Geologist at Rand Mines, started a part-time project on a microfaunal analysis of material from the Cretaceous of Richards Bay.

The microfaunal and palynological laboratories maintained by SOEKOR at the Institute continued to operate at full capacity during 1974. The staff was maintained at four micropalaeontologists and six laboratory assistants and preparators. Material from the Mesozoic and Cenozoic of Zululand, Algoa Basin, the Agulhas Bank and the West Coast areas of South Africa was received for processing. Palynological research concentrated mainly on the Lower Cretaceous to Upper Jurassic sediments and the Microfaunal studies embraced the full section encountered in wells extending from the ?Upper Jurassic to Quaternary.

TEACHING

Staff members in the Institute continued to support the teaching programme of the Geology Department by giving courses in palaeontology, stratigraphy and sedimentology to all three years of study. Two students enrolled for Honours in Palaeontology this year and divided their course equally between options offered by both the Institute and the Department of Geology.

The micropalaeontological component of the teaching commitment was given by Mr. I. R. McLachlan of SOEKOR.

PUBLICATIONS

During 1974, Vol. 17 of *Palaeontologia Africana* appeared. The contents were as follows:

HAUGHTON, S. H. Report of the Honorary Director for 1973.

ANDERSON, H. M. A brief Review of the Flora of the Molteno Formation (Triassic) South Africa.

KOVACS-ENDRÖDY, E. Seed-bearing Glossopteris leaves.

RIEK, E. F. A Fossil Insect from the Dwyka series of Rhodesia.

————. Upper Triassic Insects from the Molteno "Formation", South Africa.

CHERNIN, S. Capitosaurid Amphibians from the Upper Luangwa Valley, Zambia.

KEYSER, A. W. Evolutionary Trends in Triassic Dicynodontia.

MENDREZ, Ch. H. A New Specimen of *Promoschorhyncus platyrhinus* Brink 1954 (Moschorhinidae) from the *Daptocephalus* zone (Upper Permian) of South Africa.

Apart from these papers, members of the Institute have written the following:

ANDERSON, A. M. Arthropod trackways and other trace fossils from the early Permian lower Karroo beds of South Africa. 2 vols. Pal. Thesis QE815 Ph.D. (1974).

BEAUMONT, P. B. Report on test excavations in a prehistoric pigment mine near Postmasburg, northern Cape. *S. Afr. Archaeol. Bull.* **29**, (113—114) 41—59 (1974).

COLLINGS, G. E. Some new Machaerodonts from the Makapansgat Limeworks. Pal. Thesis QE 4882 C.15. M.Sc. (1974).

GOW, C. E. The morphology and relationships of Youngina capensis Broom and Prolacerta broomi Parrington. Pal. thesis QU862. Ph.D. (1974).

HAUGHTON, S. H. Book review: "Environmental Remote Sensing: Applications and Achievements"; eds. Eric C. Barrett and Leonard F. Curtis. London, Edward Arnold, 1974. *S. Afr. geol. Soc. Quarterly News Bulletin,* **Vol. 17** No. 4 (December, 1974).

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MAGUIRE, B. and HEINZ, H. J. The ethno-biology of the !ko Bushmen: their etho-botanical knowledge and plant lore. Botswana society. Occasional paper No. 1, 54p. (1974).

PLUMSTEAD, E. P. Trees of the distant and more recent past in South Africa. *South African Forestry Journal* No. 88 : 1—5 (1974).

TOBIAS, P. V. Palaeoanthropological Progress: Problems and Perspectives *J. Hum. Evol.* 3(3): 1—2 (1974).

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———. "Taxonomy of the Taung Skull", comment on article by T. R. Olson. *Nature*, **252**: pp 85–6 (1974).

———. The Taung Skull Revisited. *Natural History* **83(10)**: pp 38—43 (1974).

———. Does the form of the inner contour of the mandible distinguish between *Australopithecus* and *Homo?* In: *Perspectives in Palaeoanthropology*: D. Sen Festschrift Volume (ed. A. K. Ghosh), pp 9—17. Firma K. L. Mukhopadhyay, Calcutta (1974).

———. Aspects of Pathology and Death among Early Hominids. *The Leech* **44(3)**: pp 119–24 (1974).

———. African Finds — comment on article by B. Wood, "*Australopithecus africanus* 50 years on". *Nature* **254**, p.478 (1974).

———. Die onstaan van die mens. In: *Die Verhaal van die Mensdom* by P. S. Fry, H. J. van Aswegen et al. Cape Town/Pretoria: Human and Rousseau: pp 10—15 (1974).

Palaeont. afr., **18**, 1—29 (1975)

PALYNO-STRATIGRAPHY OF THE LOWER KARROO SEQUENCE IN THE CENTRAL SEBUNGWE DISTRICT, MID-ZAMBEZI BASIN, RHODESIA

by

Rosemary M. S. Falcon

ABSTRACT

Hart (1962) was the first to discuss seriously the subject "palynology—key to stratigraphy" with regard to Southern Africa. Since then a number of publications have appeared on African Karroo palynology. However, to date only one large scale microfloral zonation scheme has been proposed—that of Hart (1967). In this, four major palynofloristic zones were outlined for Lower Karroo (Permian) sequences, drawn from surface and sub-surface material in South and Central Africa. Another scheme, dividing the Permian into eight zones in S. Africa (Great Karroo Basin) is as yet unpublished (Anderson, in press).

In an attempt to apply palynology to the problems of geological correlation and relative age determinations, specifically in the field of coal exploration in Rhodesia, a standard section in the form of one borehole, the Matabola Flats borehole, well-sited, deep and with apparently continuous deposition was chosen for palynological biostratigraphic analysis. Fifty-five miospore genera and ninety-eight species have been recognised in this study. Their systematic descriptions and statistical analyses are published elsewhere. Falcon 1975 a, b. Detailed analysis of the forty-eight productive samples show large scale micro-floral changes up the stratigraphic column. Four major assemblage zones and eight assemblage sub-zones are herein proposed, thereby expanding by four the palynofloristic zones of Hart.

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INTRODUCTION

Palynological research in Rhodesia was initially embarked upon by the author in 1969, on one borehole core situated in the Mid-Zambezi Basin, Rhodesia. This basin is one of a number of isolated troughs in Central and Southern Africa bearing thick Lower Karroo (Lower Gondwana) deposits of Permo-Carboniferous age. Due to mining exploration in search of coal in the Ecca Series of the Lower Karroo sequences, the stratigraphy is well known in certain areas such as the rich coalfields of Wankie. However, due to the widespread and undisturbed nature of these continental deposits, and the paucity of fossils in these thick and monotonous rock units, correlation within the basin and inter-regionally is difficult.

It was therefore considered necessary to seek a palynological basis for sub-dividing and correlating this series of strata. The initial study (Falcon, 1973) showed the miospore content to be of excellent quality and preservation, and broad age correlations were drawn between these sediments and those of other Lower Gondwanaland deposits in Africa, India, Antarctica and Australia.

Having established the potential of palynology in Rhodesia it is now considered necessary to describe in detail the taxonomic content of the borehole core, and to attempt a biostratigraphic sub-division of the sequences using a palynological basis for drawing the zonal boundaries.

Due to the ideal and relatively continuous nature of this core and its changing microfloras, it is ten-

tatively proposed (a) that the Matabola Flats borehole be regarded as a type section for Lower Karroo sediments in Rhodesia and (b) that the miospore assemblage zones found within this section be used as a standard reference on which to base future detailed regional correlation for the present.

Previous Palynological Work

No previous work has been published from Rhodesia, and those publications concerning Pre-Tertiary palynology from Zaire, Tanzania, Malagasy, Zambia, South West Africa and South Africa have been reviewed by Hart (1967), Falcon (1972, 1973), and Anderson (in prep.). Suffice it to say that of major stratigraphic importance only the four broad palynofloristic zones of Hart (1966, 1967, 1969, 1970) exist at present for Southern-Central Africa and these lack precise definition and type area. They are adequate to determine broad relative ages of miospore assemblages at regional levels, but are too generalised for local stratigraphic delineation.

Farther afield in Gondwana countries Goubin (1965) in Malagasy compiled a detailed stratigraphic scheme dividing the Middle and Upper Karroo sequences into four palynological zones. In Australia three zonal schemes exist to date — an original tripartite scheme of Balme (1964), further sub-divided into five units by Segroves (1969, 1970a,

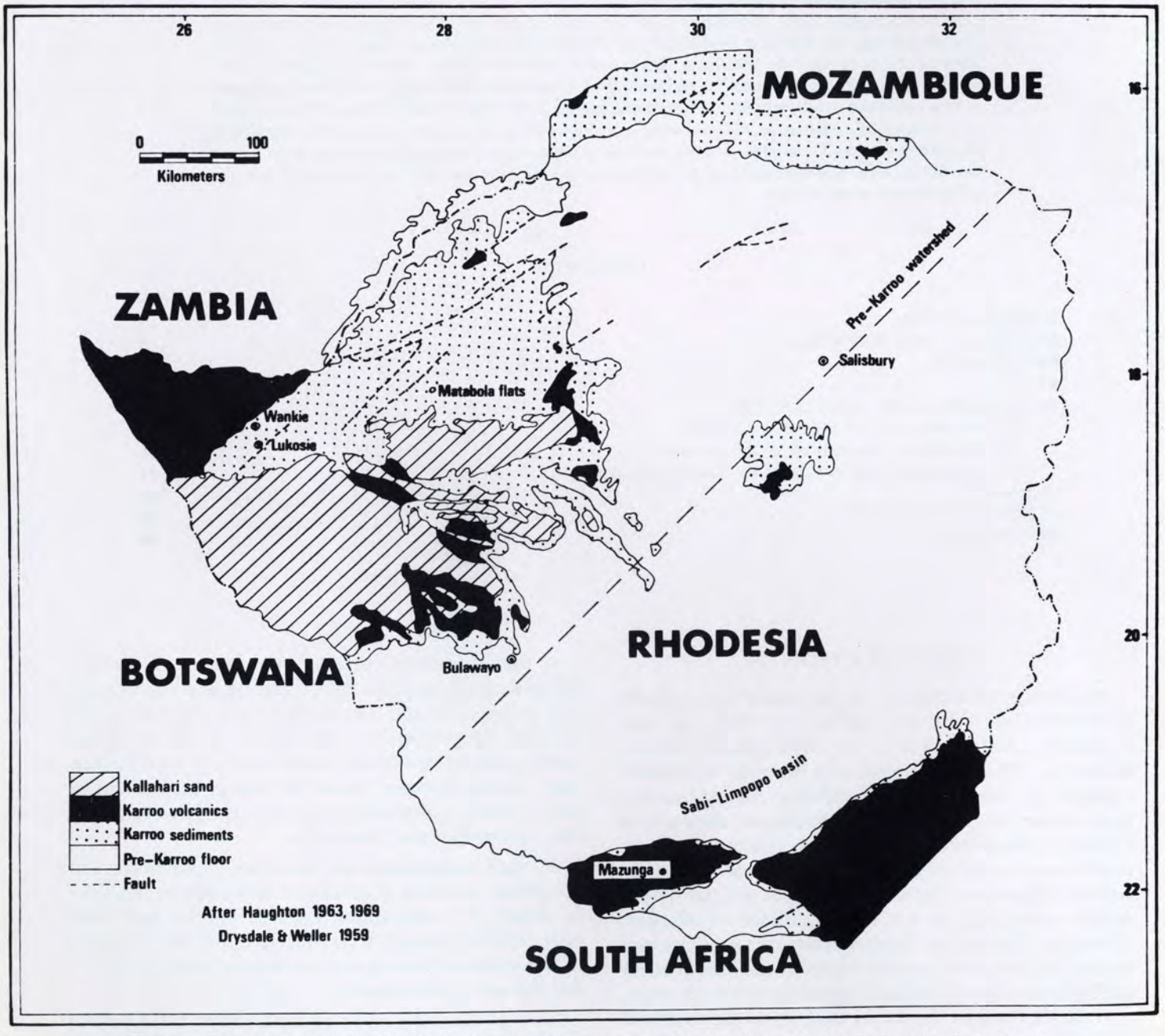


Figure 1. Geological Map of Rhodesia showing Karroo outcrops and the locality of the borehole. (Matabola Flats).

b) in the Perth Basin, Western Australia, and that of Evans (1967) in Eastern Australia. The last is extended into an *older* assemblage by Helby (1969). In India, only a very broad assemblage, related in general terms to Gondwana macrofloras, has been published (Bharadwaj, 1970).

In the Northern Hemisphere in Permo-Carboniferous times the micro- and macrofloras differ widely over the major floral provinces (as reviewed by Chaloner and Lacey, 1973) and large scale botanical and regional correlation by zonation is difficult. However, chronostratigraphic correlation is possible due to widespread marine intercalations. In contrast, in the Southern Hemisphere the macro- and microfloral Gondwanaland assemblages appear to be broadly similar but no widespread correlateable horizons exist in the dominantly continental deposits to confirm their relationships in time.

The palynological zonations so far offered in Gondwanaland may be regarded as generalisations in regional areas, as no true type-sections have been figured. These zonations serve to illustrate the common widespread microfloral changes occurring during these times, which in turn contribute to the evidence of the original composite landmass. However, due to the vast geographical extent of this supercontinent and the consequent variations of palaeolatitude, palaeoclimates and palaeoenvironments, close comparison of these microfloral zones at any one point in time would obviously show some degree of variation. In order to build up a more detailed understanding of the parent floras and their climates and environments during this long period of time finer analysis of regional areas is necessary. It is for this reason that the Matabola Flats assemblage zones are proposed as standard references for a future detailed analysis of the floral changes in Rhodesian and other Central African Basins.

MATERIALS AND METHODS

The material initially selected for palynological study was from a borehole drilled in 1963 in the course of water exploration. This is sited in the centre of the Matabola Flats in the Central Sebungwe District of the Mid-Zambezi Valley (co-ordinates 18° 13′ S; 27°45′ E; 1960 edition of the 1/1 000 000 geological map of Rhodesia). (See Figure 1.)

The selection of this borehole core hinges on three main factors:

(a) the position relative to the Mid-Zambezi trough is virtually central;

(b) the lithological successions throughout the core are apparently conformable, thereby presenting a continuous sequence of Lower Gondwana (Karroo) sediments. In particular the core passes through an unusually thick succession of Dwyka, the thickest yet published in Rhodesia.

(c) the absence of intrusions in the vicinity of this core probably accounts for the excellent preservation of the miospores in productive horizons.

Bond and Stocklmayer (1967) describe in detail the lithology of the Dwyka Series, and record the younger Lower Karroo sediments found within the 0′—1 206′ limits of the core. The lithological units are those based on Bond's work in the Central and Eastern parts of the Mid-Zambezi region (Bond, 1952, 1967).

In the region of the Matabola Flats borehole, no economic coal seams are encountered. The sequences consist of conformable tillites, conglomerates and varved and non-varved shales at the base, overlain in succession by the Lower Wankie Sandstone (sandstone and conglomerates), Black Shales and Coals (carbonaceous shales and coals), Upper Wankie Sandstone (sandstones and shale) and finally by Madumabisa Mudstones (shales, siltstones, mudstones and limestones).

Sampling and Preparation

Of 105 samples collected in the 1 206 ft. of core, 48 samples were productive (See Figure 2.) Samples are labelled by depth in feet. Core samples are housed in the Department of Geology, University of Rhodesia, Salisbury, and the slides are to be found at the Bernard Price Institute of Palaeontology, University of the Witwatersrand, Johannesburg.

Sampling and preparation techniques are fully discussed in Falcon (1973). The extraction techniques involved a standardised sequence of seven stages through which all types of lithologies passed. Slides were made from material taken at intervals during the extraction procedures, i.e. after demineralisation, and after two periods of oxidation (ten minutes and one hour).

Briefly the extraction technique involved crushing two to five grams of sample to pass through a 35 tyler mesh. Carbonate dispersal was conducted by use of 50 per cent hydrochloric acid followed by demineralisation in 40 per cent hydrofluoric acid and removal of the silicofluorite compounds by means of 50 per cent hydrochloric acid. Oxidation was effected by Schultz solution for periods of ten minutes and one hour, and the resultant humic acids were dispersed by means of 10 per cent sodium carbonate. The organic residue was mixed with Cellosize or Clearcol and mounted on glass slides by means of Canada Balsam.

Microscopy

A Laborlux D. Leitz Microscope was used for general scanning and statistical counts. Magnification for this purpose was 500X but, in the case of detailed miospore study, it was 1 250X. A Zeiss photographic microscope was made available for limited photographic use.

In scanning the slides for analysis, the entire surfaces of two or more slides per sample (within the

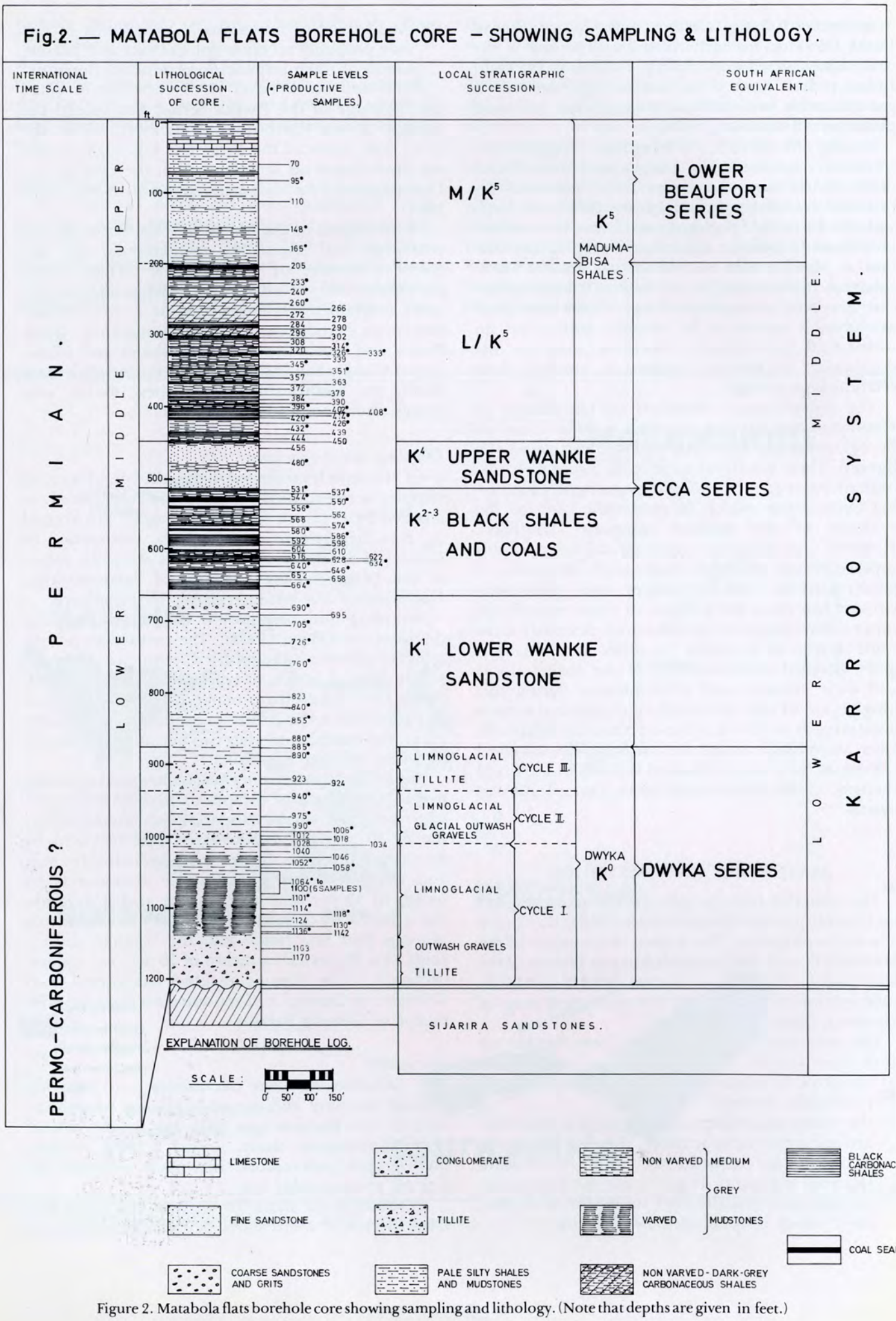


Figure 2. Matabola flats borehole core showing sampling and lithology. (Note that depths are given in feet.)

microspore co-ordinate range) was traversed for genera and species; whilst random traverses were scanned for the overall quantitative count.

Counting Techniques

Counting procedures were similar to those employed by Hart (1966), Segroves (1970a, b), and Balme (1970). Visual (as opposed to true statistical) counts of a minimum 250 and maximum 500 miospore specimens were conducted in the quantitative study and 2 000 or more in the qualitative study. Where preparation or preservation was too poor for reliable counts, a visual average was noted, and qualitative analysis pursued. Supra-generic analysis comprised straight percentage counts of the initial 250—500 miospores, whilst relative abundance of species involved absolute counts within the first 250—500, and thereafter, when noted during scanning, were recorded as 1 per cent on a presence/absence basis.

In relative abundance analysis five grades are used; very rare (not present in the 250—500 count but seen in scanning); rare (1 per cent or less): common (1—10 per cent); abundant (10—25 per cent); and dominant (more than 25 per cent).

Where Aletes dominate the assemblages, further percentage counts were taken disregarding the Alete content. Percentage counts thus obtained are seen in cross hatching in Figure 3.

Analyses

Analyses are (a) quantitative and (b) qualitative.

Quantitative analysis. The purpose of this analysis is to study the distribution throughout the borehole core of (i) the percentage relative abundance of the major supra-generic miospore taxa based on 250—500 miospores; and (ii) the relative abundance of species in each sample using the five grades of abundance as defined above.

Qualitative analysis: This represents the study of the generic and specific content of the microfloral assemblages of each sample. The purpose of this analysis is to plot the stratigraphic ranges of each species. These, combined with the relative abundance of each species at every productive level, are illustrated in Figures 4 and 5.

SYSTEMATICS

Approach to Systematics

The systematic problems facing the palynologist in Africa at present have been adequately summarised (Utting (in press), Anderson (in prep.), and Falcon 1972, 1973). These problems involve the several schools of systematic thought already introduced into pre-Tertiary African palynology. These broadly defined are—the European School (Bose, Kar, Maheshwari, Gosh, Sen, with Hoeg and Pierart in collaboration); and the South African School (Hart (subsequently), Anderson (with an Australian background)).

The basic taxonomic schemes range from morphological to phylogenetic philosophies, whilst the different species concepts involve the use of morphological, chronological, phylogenetic or preservational criteria. Frequently ill-defined taxonomic forms have been published often with inadequate illustrations.

The systematic approach adopted in this study has been, of necessity, a practical morphological one, and one major taxonomic system has been followed, that of Hart (1964a, b; 1965b, c, d; 1966a, b; 1969a, b, c). In order to supplement this system in which very few photographs appear and in which there is inadequate coverage of some major taxa, six other important authors of taxonomic works were consulted—those of Jansonius (1962), Bharadwaj (1962), Balme and Hennelly (1955, 1956a, b), Balme (1970), Segroves (1967, 1969) and Goubin (1965). Other relevant papers were consulted for lists of synonymies, e.g. the publications issued on the Congo miospores.

The supra-generic system of classification is basically that compiled by Hart (1965b) based on the original classification of R. Potonié (1956, 1958), and the information collated by the International Commission for the Microflora of the Palaeozoic. The names attributed to the miospores are primarily based on previously described African material, but do include forms referred to in the major sources of reference. The layout and proposed names of the genera and species are such that they may be relatively easily combined to fit any future improved classification system.

Terminology

The terminology employed is based on the suggested terms from the I.C.M.P. and modified by Hart (1965b). Other terms employed are followed by their author in parentheses.

List of Taxa

Triletes

Punctatisporites gretensis Balme and Hennelly, 1956b.
P. gretensis forma *minor* Hart, 1965c.
Deltoidospora directa (Balme and Hennelly, 1956) Hart, 1965c.
D. lukugaensis Kar and Bose, 1967.
Calamospora plicata (Luber and Valtz, 1941) Hart, 1965c.
Retusotriletes diversiformis Balme and Hennelly, 1956b.
Apiculatisporis levis Balme and Hennelly, 1956b.
A. filiformis Balme and Hennelly, 1956b.
A. cornutus Balme and Hennelly, 1956b.
A. minutus sp. nov.
Granulatisporites tentula (Tiwari, 1965) nov. comb.
Lophotriletes sp. cf. *L. rarus* Bharadwaj and Salujha.

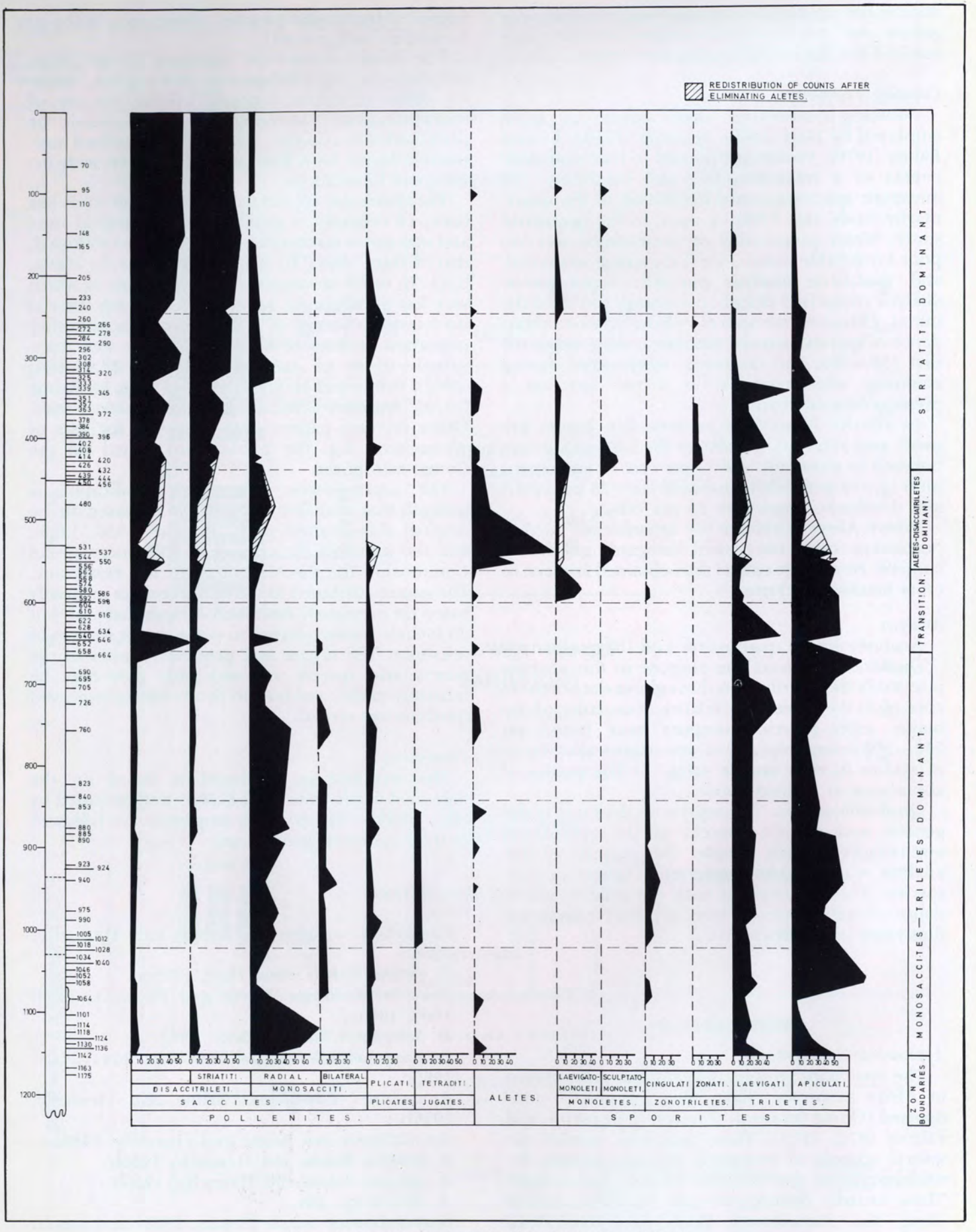


Figure 3. Quantitative Analysis of the Supra-Generic Taxa.

Microbactulatispora micronodosus (Balme and Hennelly, 1956b) nov. comb.
A. tereteangulatus Balme and Hennelly, 1956b
Acanthotriletes tereteangulatus Balme and Hennelly, 1956b. forma *minor* nov. comb.
Reinschospora sp.
Neoraistrickia ramosa (Balme and Hennelly, 1956) Hart, 1960.
N. sp. cf. *N. congoensis* Kar and Bose, 1967.
Reticulatisporites compactus (Luber and Valtz, 1941) Hart, 1965c.
Baculatisporites bharadwaj Hart, 1965c.
Verrucosisporites parmatus Balme and Hennelly, 1956b.
V. naumovai Hart, 1963.
V. sp. cf. *V. pseudoreticulatus* Balme and Hennelly, 1956b.
V. pseudotrisectus sp. nov.
V. bondii sp. nov.
Cirratriradites africanensis Hart, 1963.
Zinjispora bullata (Balme and Hennelly, 1956) Hart, 1965c.
Z. zonalis Hart, 1975c.
Densoporites rotundus sp. nov.
Denscsporites rotundus sp. nov.
Gondispora vrystaatensis Hart, 1965c.
G. novus sp. nov.

Monoletes
Laevigatosporites colliensis (Balme and Hennelly, 1956) Bharadwaj, 1962.
L. perpendiculus sp. nov.
Punctatosporites granulatus Imgrund, 1960.
Spinosporites spinosus sp. nov.
Thymospora thiesseni (Kosanke, 1943) Wilson and Venkatachala, 1963.
T. pseudothiesseni (Kosanke, 1950) Wilson and Venkatachala, 1963.

Jugates
Quadrisporites horridus Hennelly, 1958.

Aletes
Pilaspora calculus Balme and Hennelly, 1956a.
Circulisporites magnus sp. nov.
Granulatasporites sp.
Verrucosphaera colliensis Glickson, em.
Tetraporina sp.

Plicates
Marsupipollenites triradiatus Balme and Hennelly, 1956a.
M. striatus Balme and Hennelly, 1956a.
M. sp.
Cycadopites cymbatus Balme and Hennelly, 1956a.
C. nevesi (Hart, 1964) Hart, 1965c.

Monosaccates
Plicatipollenites indicus Lele, 1954.
Virkkipollenites obscurus Lele, 1964.
V. radiatus (Hennelly, 1958) Lele, 1964.
V. mehtae Lele, 1964.
V. densus Lele, 1964.
Parasaccites diffusus (Tiwari) Bose and Maheshwari, 1968.
Elilasaccites elilaensis Bose and Kar, 1966.
Florinites eremus Balme and Hennelly, 1956.
Densipollenites indicus Bharadwaj and Salujha, 1964.
Striomonosaccites sp.
Potonieisporites novicus Bharadwaj, 1962.
P. hennellyi (Hart, 1960) nov. comb.
P. thomasi (Pant, 1955) nov. comb.
Vestigisporites sp.
Caheniasaccites ovatus Bose and Kar, 1966.

Disaccates (Striatiti)
Protohaploxypinus globus (Hart, 1960) Hart, 1964b.
P. diagonalis Balme, 1966.
P. micros Hart, 1964b.
P. amplus (Balme and Hennelly) Hart em. Balme, 1970.
P. goraiensis R. Potonie and Lele, 1961.
P. limpidus (Balme and Hennelly, 1956) Segroves, 1969.
P. sulcatus sp. nov.
P. acutus sp. nov.
Striatopodocarpites octostriatus (Hart, 1960) em.
S. rarus (Bharadwaj and Salujha) Balme, 1970.
S. communis (Wilson, 1962) Hart, 1964b.
S. cancellatus (Balme and Hennelly, 1955) Hart, 1964b.
Taeniaesporites noviaulensis Leschik, 1956.
Striatoabietites multistriatus (Balme and Hennelly, 1955) Hart, 1964b.
Lueckisporites nyakapendensis (Hart, 1960) Hart, 1969b.
Guttulapollenites hannonicus Goubin, 1965.
Hemiapollenites karrooensis Hart, 1964b.
H. sp.
Vittatina africana Hart, 1966b.
V. minima Jansonius, 1962.

(Non-Striate)
Platysaccus radialis Leschik, Hart, 1965c nov. comb.

P. leschiki (Hart, 1960) Hart, 1965c.
Alisporites plicatus Jizba, 1962.
A. gracilis Segroves, 1969.
A. tenuicorpus Balme, 1970.
Sulcatisporites ovatus Balme and Hennelly, 1955.
S. splendens Leschik, 1956.
S. potoniei (Lakhanpal, Sah and Dube) Hart, 1965c.
Vesicaspora sp. A.
V. sp. B.
Jugasporites sp.
Illinites unicus Kosanke, 1950.
Limitisporites monstruosus (Luber and Valtz) Hart, 1965c.

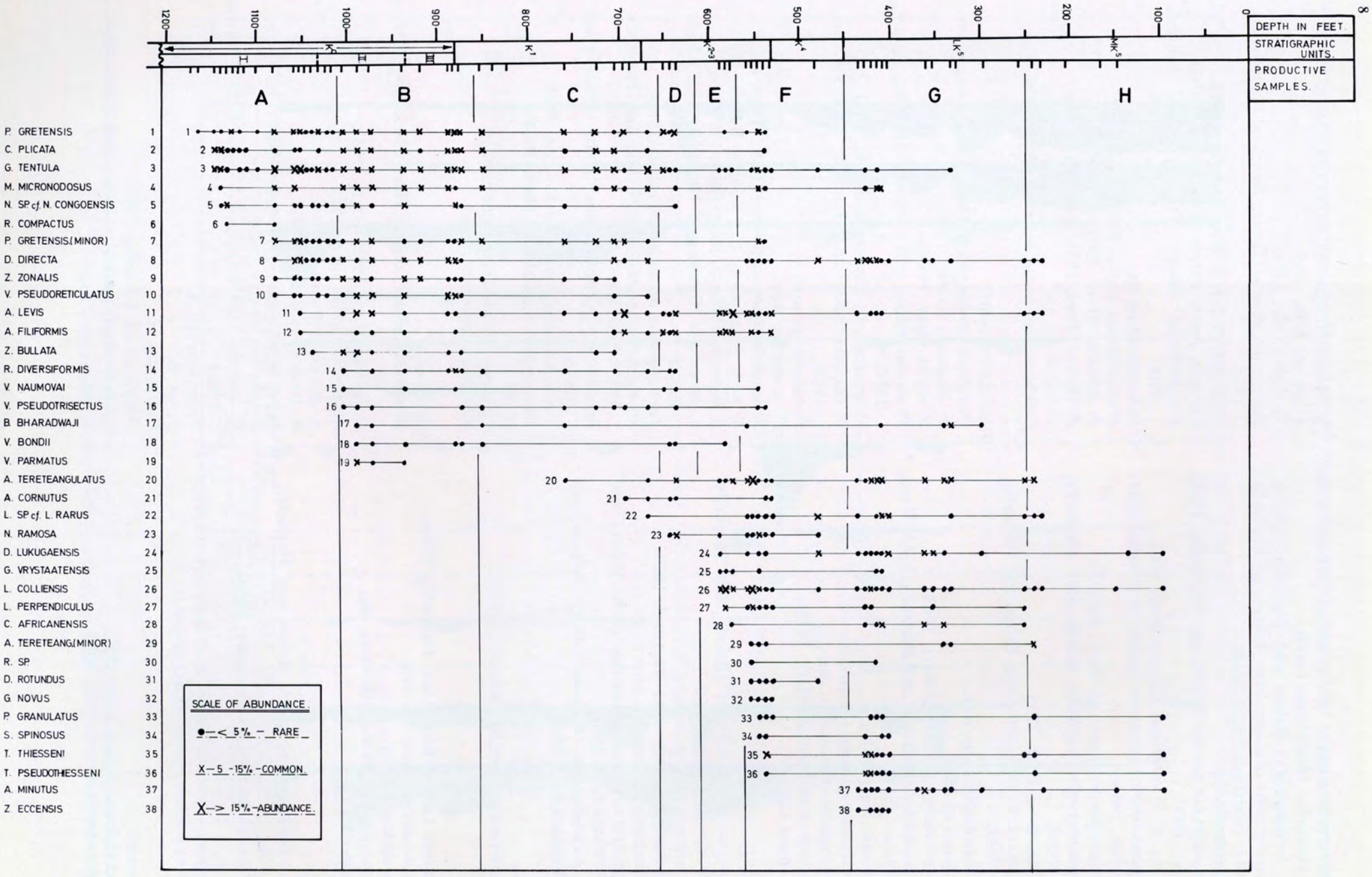


Figure 4. Qualitative Analysis and Range Chart for Sporites.

RESULTS

The microfloral content of the Matabola Flats borehole core is summarised and illustrated in Figures 3, 4, 5 and 6.

Quantitative Analysis

The quantitative variations of the supra-generic categories of miospores are shown in Figure 3. The major trends are easily definable and, beginning in the oldest sediments, may be noted as:

(i) decreasing Monosaccites,
(ii) decreasing Triletes,
(iii) increasing Disaccites, and
(iv) increasing ratio of striate to non-striate pollen in the Disaccites.

Of particular interest is the existence of two major pollen groups, the Monosaccites (dominant in the lower half of the core), and the Disaccites (abundant in the upper half). A transitional zone may be noted midway, i.e. above sample 664′ in which Disaccites (striate and non-striate) consistently represent more than 10 per cent of the assemblage, whilst Monosaccites equally consistently represent less than 20 per cent. From sample 556′ upwards, non-striate forms of the Disaccites always total more than 20 per cent and striate forms more than 10 per cent (excluding the Alete counts), making a combined Disaccate total of greater than 30 per cent of the entire assemblages. Above 260′, striate and non-striate forms equal each other in proportion, and total more than 60 per cent, whilst the Monosaccates drop to below 10 per cent.

Boundaries based on this quantitative data may therefore be placed above 664′ and 556′ and arbitrarily above 260′.

The Triletes show a marked decrease in abundance up the stratigraphic column, but this group is regarded as unreliable zonal indicators. This is due to their possible pteridophytic origin and consequent fluctuations in their response to minor climatological and ecological factors. Also of little zonal value due to local influence is the abundance of Aletes at specific horizons. These forms exist at varying times over the region of sedimentation, depending on the necessary conditions for their existence (salinity or other mineral content of the water). The peak abundance of this group between samples 556′ and 408′ is particularly noteworthy, but only on a local regional basis.

Of further stratigraphic interest is the occurrence of a rare form of Jugates between samples 1 006′ and 853′, and bilateral Monosaccates between 1 006′ and 586′. The sudden appearance of Laevigatomonoleti at 586′ and Sculptatomonoleti at 556′, and the apparently restricted ranges of Zonati and Cingulati also serve as further diagnostic potential.

In summary, three major zones are indicated, over and above the minor fluctuations of the histograms. (See Figure 6.) In these histograms smooth and more stable results have been obtained by redistribution of associated spore/pollen types (Punctatisporites with Monosaccites) and recalculation of the major taxa excluding certain irrelevant taxa (Aletes).

(i) *samples 1 142′ to 664′:* Monosaccite and Trilete dominated assemblages. This may be further divided into three sub-stages on the basis of restricted ranges and peak abundance of Cingulati, Jugates, and bilateral Monosaccates.
(ii) *samples 646′ to 580′:* equally low proportions of Disaccates and Monosaccates, with abundant Triletes. This may be divided into three stages by the appearance of Zonati and Laevigatomonoleti.
(iii) *samples 556′ to 0′:* dominant Disaccates over Monosaccates. A further two divisions are possible on the grounds of equal proportions of striate over non-striate Disaccates, and the apparent termination of Zonati.

This method of analysis for vertical sub-division is treated with caution due to obvious factors influencing the proportions of major taxa after dispersal and prior to extraction. However, references to other Gondwana palynological assemblages show closely similar trends, indicating parallel major vegetational change over this period of time.

Qualitative Analysis

Figures 4 and 5 represent the range charts of the species encountered in the productive horizons, whilst Figure 8 illustrates the distribution of the genera and their species in the assemblage zones subsequently made. Figure 6 summarises the ranges of selected genera and species, together with the smoothed histograms of supra-generic taxa.

Briefly, on analysis of the range charts, three groups of genera and species may be noted:

(i) those of long range: i.e. apparently present in most productive samples to a greater or lesser degree, e.g. *Apiculatisporis*, *Protohaploxypinus*, and *Sulcatisporites* and species *A. levis*, *P. amplus*, *S. ovatus*, *R. diversiformis* and *P. calculus*. These miospores are termed general and are of little stratigraphic use.
(ii) those of medium range, showing finite points of appearance or disappearance at one end of their stratigraphic range but apparently extending beyond the range of this borehole at the other end, e.g. genera *Punctatisporites*, *Calamospora*, and *Virkkipollenites-Plicatipollenites* (up to K^{2-3}); *Marsupipollenites* and *Florinites* (K^{1} onwards); *Striatopodocarpites*, *Laevigatosporites* and *Thymospora* (K^{2-3} onwards) and *Vittatina* and *Hamiapollenites* (LK^{5} onwards).
Examples of species noted for medium ranges, apart from forms attributed to the above genera are *Cycadopites cymbatus* (up to K^{2-3}) and *Acanthotriletes tereteangulatus* (K^{1} onwards).
(iii) those of short restricted ranges with apparently finite points of appearance and disappearance,

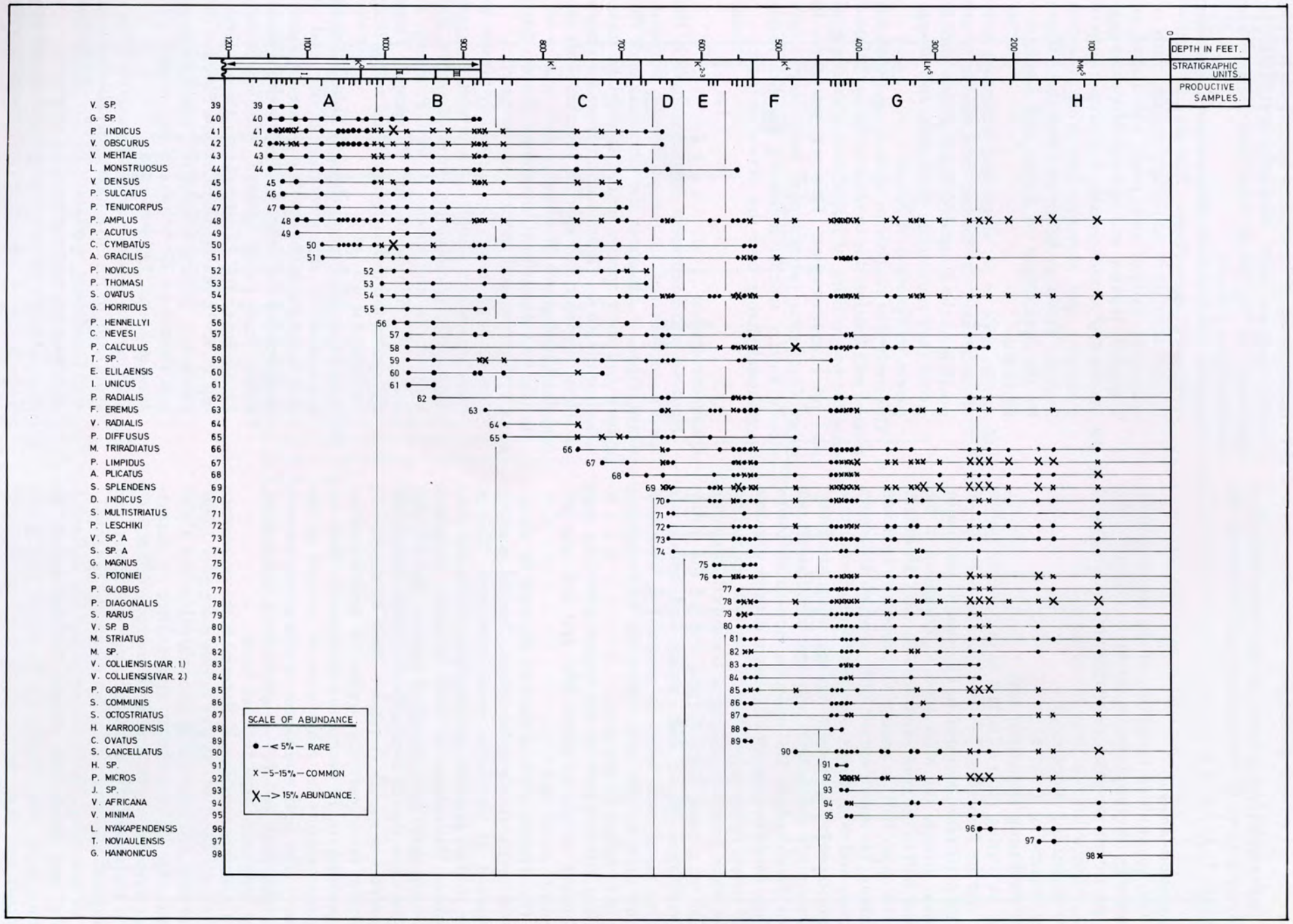


Figure 5. Qualitative Analysis and Range Chart for Pollenites and Aletes.

e.g. genera *Reticulatisporites*, *Quadrisporites*, *Potonieisporites*, *Cirratriradites* and *Guttulapollenites* and *Taeniaesporites*.
Examples of species are *P. acutus*, *V. parmatus*, *N. ramosa*, *C. novus*, *D. rotundus*, *Z. eccensis* and *L. nyakapendensis*.

From studying the proliferation of species and their relative abundance as seen on the range charts and in Figure 8, it becomes obvious that two major assemblages exist, overlapping between 646′ and 531′. Below this an abundance of Apiculate and Laevigate forms of Trilete spores are closely associated with an equal variety of Monosaccate pollen forms, a few early Disaccate striate and non-striate forms and two simple Monocolpate forms. Above the broad transition zone, the Sporites reduce in variation as well as number in favour of an overwhelming diversification in pollen forms, i.e. striate and non-striate Disaccates suffer an explosive evolution and so to a much less degree do Plicates and Aletes.

A further refinement of the study of species diversification may be seen in Figure 9. Here the total number of species counted per sample has been drawn in the form of a histogram in column 3. Data were collected on a presence-absence basis and only on samples bearing more than 200 specimens or more than 15 species. Species were presumed to be continuous (or potentially present) in samples between their oldest and youngest points of appearance. In column 1, account was taken of the number of new species occurring for the first time, and in column 2, the number of species disappearing.

Six distinct levels of increased species diversity are apparent, taking the arbitrary level at five species or more. In each case, several closely spaced samples are combined together to a period of change, during which time a large variety of miospore forms appear or disappear. Two major periods of species diversification occur, at 1 150′ to 1 140′ and 556′ to 544′, and four minor ones at the depths of 1 006′, 649′, 586′ and 432′,

Two significant periods of species disappearance or dying out occur, a major one at 556′ to 531′ reflecting the possible waning of the diverse older flora, evident in lower stratigraphic levels, and a minor one at 260′ to 240′.

DISCUSSIONS AND CONCLUSIONS

(a) Interpretations of Microfloral Trends

Quantitative Analysis

(a) The predominant trend is the swing from Monosaccate-Trilete dominance to Disaccate dominance. This is attributed to the large scale climatic and evolutionary factors which must have come into play during the long period of Lower Karroo sedimentation (Lacey, 1959, 1961, 1966). Fluctuations caused by local factors have not obliterated these trends to any marked degree.

(b) The high abundance and narrow stratigraphic occurrence of certain major taxa such as the very distinctive Alete group in Assemblage sub-zone F may be indicative of a specialised depositional environment, e.g. marine or brackish water conditions, or specific Eh/pH environment.

(c) Minor peaks and drops in the more or less continuous histograms are attributed to minor climatic fluctuations or changing depositional environments, or a combination of both. For example, in zone I inverse proportions of Monosaccites and Triletes coincide closely with tillitic and periglacial sedimentation. The presence of Striatiti and Cingulati are only noted in interglacial phases. In zone IV fluctuations gradually decrease until above 260′ the Disaccate-Striatiti flora appears to be constant, indicating little change in major conditions.

(d) The introduction of new major taxa may be considered as manifestations of climate amelioration and migration of these elements into the depositional area. Where the introduction is gradual, the possibility of evolution and natural selection of micro- and macrofloras must be considered, such an example being the slow introduction of striate Disaccate pollens. The more or less sudden occurrence of Sculptatomonoleti and Zonati may be considered as migrations from farther afield.

Qualitative Analysis

(a) From the range charts and Figure 8, it is possible to see the increase or decrease in diversification of the major evolving taxa, i.e. the Monosaccites and Disaccate Striatiti. In the oldest floral assemblage zone I, there are 12 species of Monosaccites but only three in zone IV, whilst in the Striatiti group, only four species occur in zone I but 18 in zone IV. Considerable evolutionary development assisted by climatic change is therefore interpreted throughout this period.

(b) By graphically illustrating the peaks of diversity and disappearance of miospore species (see Figure 9) further information may be noted regarding the gaps in time or apparent disconformities not hitherto realised in the stratigraphic sequence. Factors causing large scale qualitative rather than quantitative changes may be varied and interactive, and in particular are closely linked to the depositional history of the sediments. It is beyond the scope of the present paper to discuss at length the tectonic and

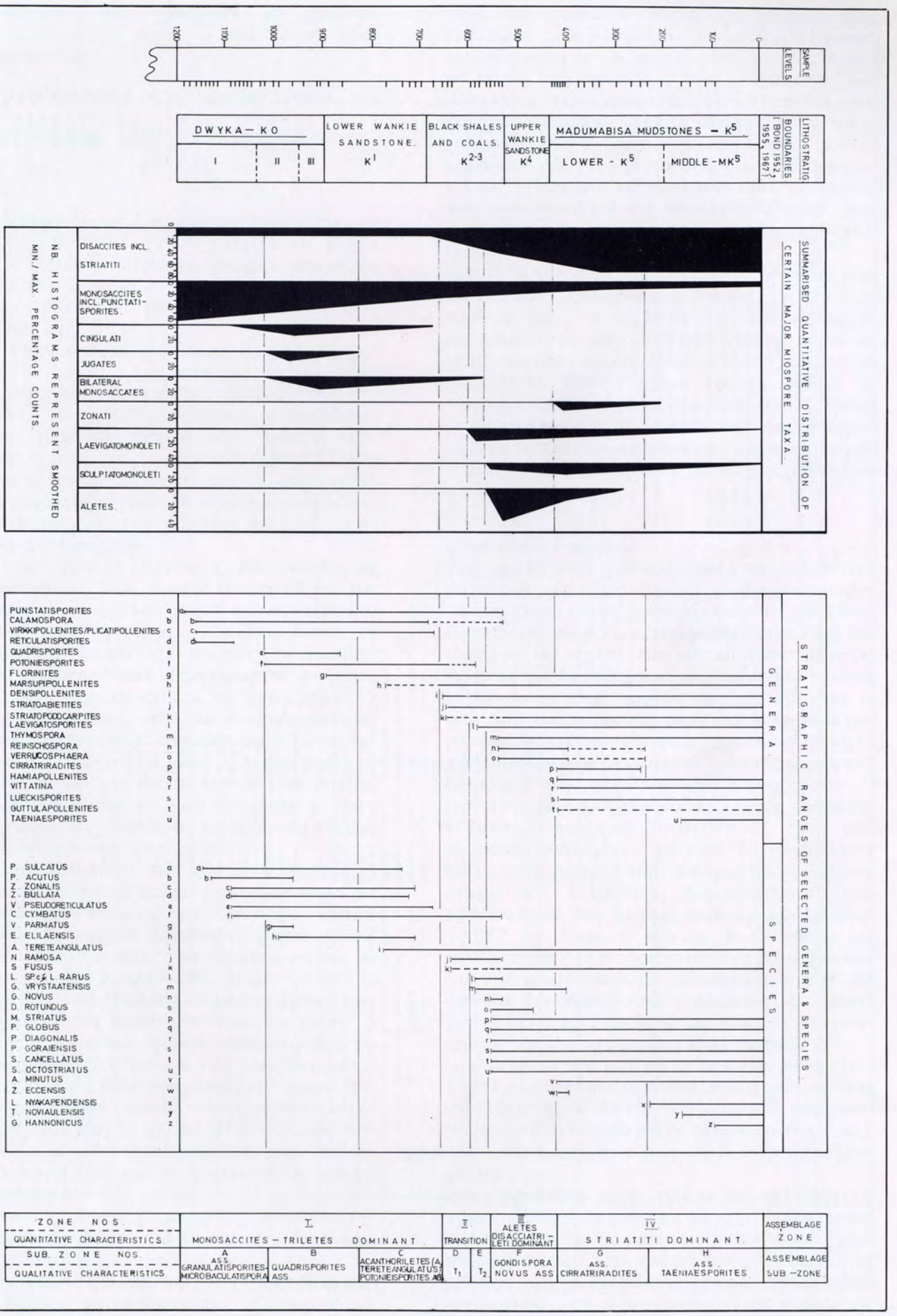


Figure 6. Summary of Significant Quantitative and Qualitative Data with Sub-division of the Borehole Core.

Litho-stratigraphic Units (Bond *et al.*)		Core samples	Bio-stratigraphic Units	Assemblage Characteristics	
				Assemblage Zones	Assemblage Sub-Zones
Madumabisa Mudstones	M		H	*Ass. Zone IV:* **Vittatina-Lueckisporites Ass.** *Notable Genera:* Protophloxypinus Striatopodocarpites Vittatina Hamiapollenites Lueckisporites Platysaccus Sulcatisporites Thymospora Marsupipollenites Rheinschospora	*Ass. Sub-Zone H:* **Taeniaesporites-guttulapollenites Ass.** *Introduction of:* Taeniaesporites Guttulapollenites N.B. Striatiti dominant > 50%
	L		G	*Notable Species:* A. Cornutus A. Minutus *Quantitative Content* Disaccites: 4C—75% Striatiti: 25—60% Monosacciti: < 5% Triletes: 0—20% Aletes: 0—15%	*Ass. Sub-Zone G:* **Cirratriradites africanensis Ass.** *Introduction of:* — *Restricted Species:* Cirratriradites — C. africanensis Hamiapollenites — Z. eccensis Vittatina — P. micros Lueckisporites — A. minutus
Upper Wankie Sandstone — K^4			F	*Ass. Zone III:* **Densosporites-Gondispora Ass.** *Final Disappearance of:* Punctatisporites, Parasaccites, Calamospora; A. levis, A.filliormis, V.naumovai *Restricted Species:* G. Novus, D. Sp. *Introduction of:* Verrucospharera, Circulisporites, Thymospora; Rheinschospora, M.striatus, P.globus	*Ass. Sub-Zone F:* *Quantitative content:* Disacites 20—40% Striatiti: 10—20% Monosacciti: < 5% Triletes: > 40% Aletes: 10—30% *P. Goraiensis*, *P. Diagonalis*, *S. Cancellatus*: S. octostriatus, Vesicaspora sp. A. and B., P. gracilis, etc.
Black Shales and coals — K^{2-3}			E	*Ass. Zone II:* *Transition Zone* Miospore genera and species characteristic of both adjacent Assemblages.	*Ass. Sub-Zone E: T.II* *Introduction of:* Laevigatosporites spp., Lophotriletes sp. B., G. vrystaatensis, D. lukugaensis, S. potoniei
			D	*Quantitative content:* Disaccites: 10—20% Monosacciti. < 10% Striatiti: 5—20% Triletes: 40—50%	Ass. Sub-Zone D: T.I. *Introduction of:* Striatopodocarpites spp., Striatoabietities, Platysaccus, Marsupipollenites; Densipollenites, N. ramosa, S. splendens, P. leschiki
Lower Wankie Sandstone — K^1			C	*Ass. Zone I:* **Virkkipollenites-Plicatipollenites Ass.** *Notable Genera:* Granulatisporites Microbaculispora Punctatisporites Calamospora Zinjispora Cycadopites Protohaploxypinus Apiculatisporis Acanthotriletes Lophotriletes Retusotriletes Potonieisporites	*Ass. Sub-Zone C:* **Acanthotriletes tereteangulatus Ass.** *Introduction of:* Florinites eremus Acanthotriletes tereteangulatus *Notably Abundant:* Monosaccites, especially Virkkipollenites Plicatipollenites Potonieisporites Parasaccites
Dwyka — K^0	III		B	*Notable Species:* S. ovatus A. tenuicorpus Granulatasporites sp.	*Ass. Sub-Zone B:* **Quadrisporites Horridus Ass.** *Introduction of:* Potonieisporites Elilasaccites Verrucosisporites Baculatisporites *Restricted Species:* Quadrisporites horridus
	II				
	I		A	*Quantitative Content* Disaccites: 1—5% Striatiti: 0—2% Monosacciti: 10—60% Triletes: 40—70%	*Ass. Sub-Zone A:* **Granulatisporites-Microbaculispora tentula Ass.** *Introduction of:* Granulatisporites sp., Microbaculatispora tentula } Dominant Punctatisporites Calamospora Cycadopites Zinjispora Plicatipollenites-Virkkipollenites Protohaploxypinus P. amplus, P. sp. A., P. sp. B. } Rare

Figure 7. Proposed Assemblage Zone Characteristics.

depositional history of the basin in which these sediments were deposited. Suffice it to say that, if it may be assumed that the climate and vegetation continued to change relatively constantly (as is inferred from other palaeontological evidence from arctic floras to those supporting *Tapinocephalus* vertebrates in the youngest sediments), then any large scale changes in microfloral diversity or disappearance may possibly represent a gap in time often difficult to interpret otherwise in a borehole sequence.

Diversity periods I and II (with a possible third just above I) coincide with the advent of two periglacial phases, thereby indicating an earlier gap in time consistent with periods of glaciation. In these two cases, the non-fossiliferous deposition of glacigene sediments (occurring whilst the prevailing flora continued to flourish farther afield) followed by climatic amelioration during glacial retreat may well explain the sudden introduction of new floral elements that had evolved or been introduced during the intervening gap in time.

Diversity periods III, IV and V all occur during deposition of Black Shales and Coal. These sediments are predominantly barren of plant cuticles and spores (Watson, 1960, suggests that exposure, oxidation and possibly excessive transport may be the cause of this). The fact that miospores are found at all in these three periods illustrates a change in depositional environment, possibly a cyclic change in base-level or Eh-pH conditions. The introduction of new species at these points does not necessarily mean a sudden influx to the area, but rather a sudden accumulation and fossilisation of a number of species that had already evolved or migrated into the area of deposition since the previous miospore assemblage was deposited. This theory is consistent with the idea of fluctuating base-level during this period of deposition which has been suggested from other geological information (Bond, 1967). The greatest of these three periods of diversity indicating a larger gap in time occurs ten to fifteen feet below the top of the Black Shales and Coal beds, at the base of sub-zone F.

Diversity period VI represents a vegetation now markedly different in quantitative and qualitative character from older floras (cf. Figure 3). It appears after a peak in Alete abundance and after a period of renewed tectonic activity resulting in the deposition of about one hundred feet of sandstones. Whatever the rate of deposition or the gap of time involved, the climate or environment appears to have changed considerably and the evolution of the Disaccate Striatiti seems to have progressed rapidly. Above this point in the borehole the increase in floral diversity appears to be minimal, whereas the dominance of the Disaccate group becomes rapidly apparent.

Disappearances of large numbers of species is obvious during two periods. Period I, in the upper ten to fifteen feet of Black Shales and Coals, coincides with a large period of diversity (V). A combination of fifteen species disappear at this point in time, whilst twenty-one new species occur. This may indicate a longer gap in time since the previous assemblages were deposited, or a rapid change in climate or environment. All these factors may be true as there is a rapid and substantial waning of early cold temperate floras and an introduction to an Alete-rich environment.

In zones I and II miospores appear to have diversified well in interglacial periods with a gradual waning of species proliferation in Lower Wankie Sandstones.

A second period of large scale disappearance occurs between 240′ and 260′, the base of sub-zone H. This coincides with a minor climatic or environmental factor, and during this apparent gap in time the new species already introduced in zone III remain more or less constant, but a number of microfloral elements that were introduced in zones II and III disappear.

(b) Microfloral Sub-Division of the Borehole

The problems of sub-division of sedimentary rock sequences by means of palynology have been discussed by such authors as Smith and Butterworth (1967) and Hart (1970), and general problems in stratigraphical procedure employing biostratigraphic methods have been enlarged upon by Eicher (1968) and Harland *et al.* (1972).

That broad floral changes occurred during these Lower Karroo times is obvious, when studying the quantitative analysis of the major supra-generic taxa. These major changes, gradual as they are, may be matched with those of Hart (the four florizones) and farther afield in Australia, India, Malagasy and Antarctica (Falcon, 1973). The causes of long term floral changes within the Gondwana sequences are postulated as rapid evolution and development of land plants after the Dwyka glaciation (Plumstead, 1968) and the broad climatic changes which must have occurred between the cold arctic conditions of the Dwyka and the ultimate hot, arid conditions of the Red Beds in the Stormberg Series (Bond , 1967; Lacey, 1967). Correlation is therefore possible on a broad developmental basis.

However, when finer biostratigraphic subdivision is required, an appreciation of local factors causing the minor microfloral fluctuations is necessary. These include, for example, the original amount of miospores produced by the parent plants, the climate and ecological niches affecting parent plants, the type of ultimate depositional environment of the miospores and the lithification and diagenetic process subsequently affecting the strata containing the miospores. These factors may be manifested in the miospore content in the form of fluctuations of relative abundances of different

Assemblage Sub-Zones	I A	I B	I C	II D	II E	III F	IV G	IV H
Punctatisporites gretensis	+	+	+	+	+	+		
P. gretensis forma minor	+	+	+	+	+	+		
Retusotriletes diversiformis		+	+	+				
Calamospora plicata	+	+	+	+	+	+		
Deltoidospora directa	+	+	+	+	+	+	+	
D. lukugaensis					+	+	+	+
Apiculatisporis levis	+	+	+	+	+	+	+	
A. filiformis	+	+	+	+	+	+		
A. cornutus			+	+	+	+		
A. minutus							+	+
Reticulatisporites bharadwaji		+	+	+	+	+	+	
Reticulatisporites compactus	+							
Granulatisporites tentula	+	+	+	+	+	+	+	
Microbaculatispora micronodosus	+	+	+	+	+	+	+	
Verrucosisporites pseudoreticulatus	+	+	+					
V. naumovai		+	+	+	+	+		
V. pseudotrisectus		+	+	+	+	+		
V. bondii		+	+	+	+			
V. parmatus		+						
Lophotriletes sp. cf. *L. rarus*			+	+	+	+	+	
Neoraistrickia ramosa				+	+	+		
N. sp. cf. *N. congoensis*	+	+	+	+				
Acanthotriletes tereteangulatus			+	+	+	+	+	
A. tereteangulatus forma minor						+	+	
Reinschospora sp.						+	+	
Cirratriradites africanensis						+	+	
Zinjispora bullata	+	+	+					
Z. eccensis							+	
Z. zonalis	+	+	+					
Densosporites rotundus						+		
Gondispora vrystaatensis					+	+	+	
G. novus						+		
Laevigatosporites colliensis					+	+	+	+
L. perpendiculus					+	+	+	
Punctatosporites granulatus						+	+	+
Spinosporites spinosus						+	+	+
Thymospora thiesseni						+	+	+
T. pseudothiesseni						+	+	+
Pilaspora calculus		+	+	+	+	+	+	
Circulisporites magnus					+	+		
Tetraporina sp.		+	+	+	+	+		
Granulatasporites sp.	+	+						
Verrucosphaera colliensis								
Var. 1						+	+	
Var. 2						+	+	
Marsupipollenites triradiatus			+	+	+	+	+	+
M. striatus						+	+	+
M. sp.						+	+	+
Cycadopites cymbatus	+	+	+	+	+	+		
C. nevesi		+	+	+	+	+	+	+

Quadrisporites horridus		+						
Plicatipollenites indicus	+	+	+	+				
Virkkipollenites obscurus	+	+	+	+				
V. radialis			+					
V. mehtae	+	+	+					
V. densus	+	+	+					
Parasaccites diffusus			+	+	+	+		
Elilasaccites elilaensis		+	+					
Florinites eremus			+	+	+	+	+	+
Densipollenites indicus						+	+	+
Striomonosaccites sp.						+	+	+
Potonieisporites novicus		+	+					
P. hennellyi		+	+	+				
P. thomasi		+	+					
Vestigisporites sp.	+							
Caheniasaccites ovatus							+	
Protohaploxypinus globus							+	+
P. diagonalis							+	+
P. micros								+
P. amplus	+	+	+	+	+	+	+	+
P. goraiensis							+	+
P. limpidus			+	+	+	+	+	+
P. sulcatus	+	+	+					
P. acutus	+	+						
Striatopodocarpites cancellatus							+	+
S. octostriatus							+	+
S. rarus							+	+
S. communis							+	+
Taeniaesporites noviaulensis								+
Striatoabietites multistriatus					+	+	+	+
Leuckisporites nyakapendensis								+
Guttulapollenites hannonicus								+
Hamiapollenites sp.								+
H. karrooensis							+	+
Vittatina africana								+
V. minima								+
Platysaccus radialis		+	+	+	+	+	+	+
P. leschiki				+	+	+	+	+
Alisporites plicatus			+	+	+	+	+	+
A. gracilis	+	+	+	+	+	+	+	+
A. tenuicorpus	+	+	+					
Sulcatisporites ovatus		+	+	+	+	+	+	+
S. splendens				+	+	+	+	+
S. potoniei					+	+	+	+
Vesicaspora sp-a				+	+	+	+	+
Vesicaspora sp-b							+	+
Jugasporites sp.								+
Illinites unicus		+						
Limitisporites monstruosus	+	+	+	+	+	+		

Figure 8. Qualitative Comparison of Assemblage Sub-Zones.

species, or the sudden dearth of a portion of or all the miospores, or a sudden influx of several new species. These changes occur within the broad gradually changing microfloral trends, and their uses in biozone delineation must be kept in perspective.

In terms of sub-dividing the present borehole core, these minor microfloral changes causing qualitative and quantitative differences in the miospore assemblages are very useful. However, these changes may not be synchronous chronostratigraphically with changes in other parts of the region, or in basins of sedimentation farther afield. Correlation on the basis of artificial changes is therefore somewhat suspect in anything other than restricted locality. It is for this reason that, in addition to the analysis of the minor changes for future local correlation, attention is paid to the qualitative analysis (local range charts) of the miospore assemblages in this borehole core, with particular reference to the development of the highly diagnostic new lineage, the Striate Disaccates. From the introduction of new and rapidly evolving genera and species in this infra-turma, as well as the association of other significant genera and species with them, a series of eight assemblage sub-zones are delineated, which it is hoped will prove more reliable for wider chronostratigraphic use. The ar-

tificial periods of maximum species influxes and disappearance as noted in Figure 9 coincide with the boundaries of six assemblage sub-zones.

Four major assemblage zones have been proposed, characterized by the presence of distinct genera and delineated by quantitative analysis of selected major supra-generic taxa showing in particular the distinctly evolving change from Monosaccate to non-striate and striate Disaccate dominated microfloras.

Analysis of Assemblage Zones

By definition (Harland *et al.*, 1972 and Eicher, 1968) a (bio)zone refers to all rocks deposited anywhere during the entire time a species existed. In order to provide the most accurate correlation, zones must be delineated by consistent boundaries and comprise the narrowest time stratigraphic sequence possible. The definition of the boundaries is therefore of prime importance, and must inherently rest on the bottoms and tops of species ranges, the positions of which can only be inferred from the actual distribution in the rocks. It has been proved (Oppel in Eicher, op. cit., p. 109) that greater precision results from overlapping ranges of several species than the range zone of one species alone and it is in this context that the present eight assemblage sub-zones have been defined. Although strictly known as *concurrent-range zones*, the term sub-zones has been retained in this paper to denote a rank subordinate to the four major assemblage zones which in turn may be defined as *acme zones* or epiboles (i.e. peak abundance) of selected major supra-generic taxa. The prefix *assemblage* to zone or sub-zone is adhered to in its original definition by Harland *et al.* (op. cit.) as referring to "a body of strata characterised by a certain assemblage of fossils without regard to their ranges". *Assemblage zones* therefore refer to biostratigraphic units bearing characteristic miospore genera associations and delineated by the acme zones of major taxa, whilst *assemblage sub-zones* are all composed of reliable time-stratigraphic fossils, delineated by the appearances of new species within evolving major miospore taxonomic groups (i.e. new lineages) and characterized by other selected species associations, not all of which need appear together. The sub-zones are named by selected species not always present or confined to that stratigraphic unit. The advantage of this type of concurrent-range sub-zone is that in terms of correlation, the characteristics and delineations can be carried into all depositional environments independent of facies change or thickness. This, however, applies typically to regional (provincial) correlation only, as factors affecting the minor changing microfloral assemblages may not be synchronous in other regions. Where larger changes occur, groups of zones or stages can be correlated between regions.

Assemblage Zones

From the peak abundances three major delineations are drawn, based on the arbitrary proportionate percentage levels of Monosaccates, Disaccates (striate and non-striate) and Aletes. The points of appearance, disappearance and periods of abundance of other major taxa (e.g. Jugates, Bilateral Monosaccates, Monoletes and Zonati) represent diagnostic parameters for further subdivision of the borehole core. In terms of chronostratigraphic correlation, the three primary epiboles may prove to be far reaching in Gondwanaland, although the abundance of Aletes is regarded as possibly only a local deep water (algal?) phase. The remaining epiboles would be of diagnostic interest in surrounding regions where the climate and ecology would suit the major parent floras, provided this abundance was recorded everywhere in the strata containing it. It may also be that maximum abundance may be found in some localities and not others, and where found they may not necessarily be entirely synchronous.

Therefore the interpretation of peak abundance of major taxa may be regarded as useful in dividing the stratigraphic sequence, and of great value in local and regional correlation, but only of broad, less chronostratigraphic value in correlation farther afield.

The associated genera within each assemblage are listed in Figure 7.

Assemblage Sub-Zones

By definition the ranges of the species as seen in Figures 4, 5 and 6 are termed local range (bio)zones (Harland *et al.*, op. cit.). They represent the total appearance of the individual taxa in this one locality, which in turn may be only a part of each life span, assuming that the ranges may extend into younger or older sediments elsewhere. Therefore in sub-dividing the biostratigraphic units appearances and disappearances of new miospore forms are of relative importance in one locality, but in terms of correlation their appearance and disappearance in other areas may not be contemporaneous due to a number of factors discussed earlier. Range zones may be said to fluctuate with environment in a province and are not therefore true chronostratigraphic units. For detailed local palaeoecological and palaeoclimatological interpretation this may well prove of interest, but in terms of age in a province, total ranges must be obtained from all the local ranges.

Of the length of ranges encountered within the borehole core, those of short restricted duration are particularly diagnostic in the assemblage zones and may prove of interest in correlation if the parent plant possessed a particularly low ecological or climatic tolerance. Such an example may well be *Quadrisporites horridus*, which has been seen equally rarely and at correlateable horizons in the Perth

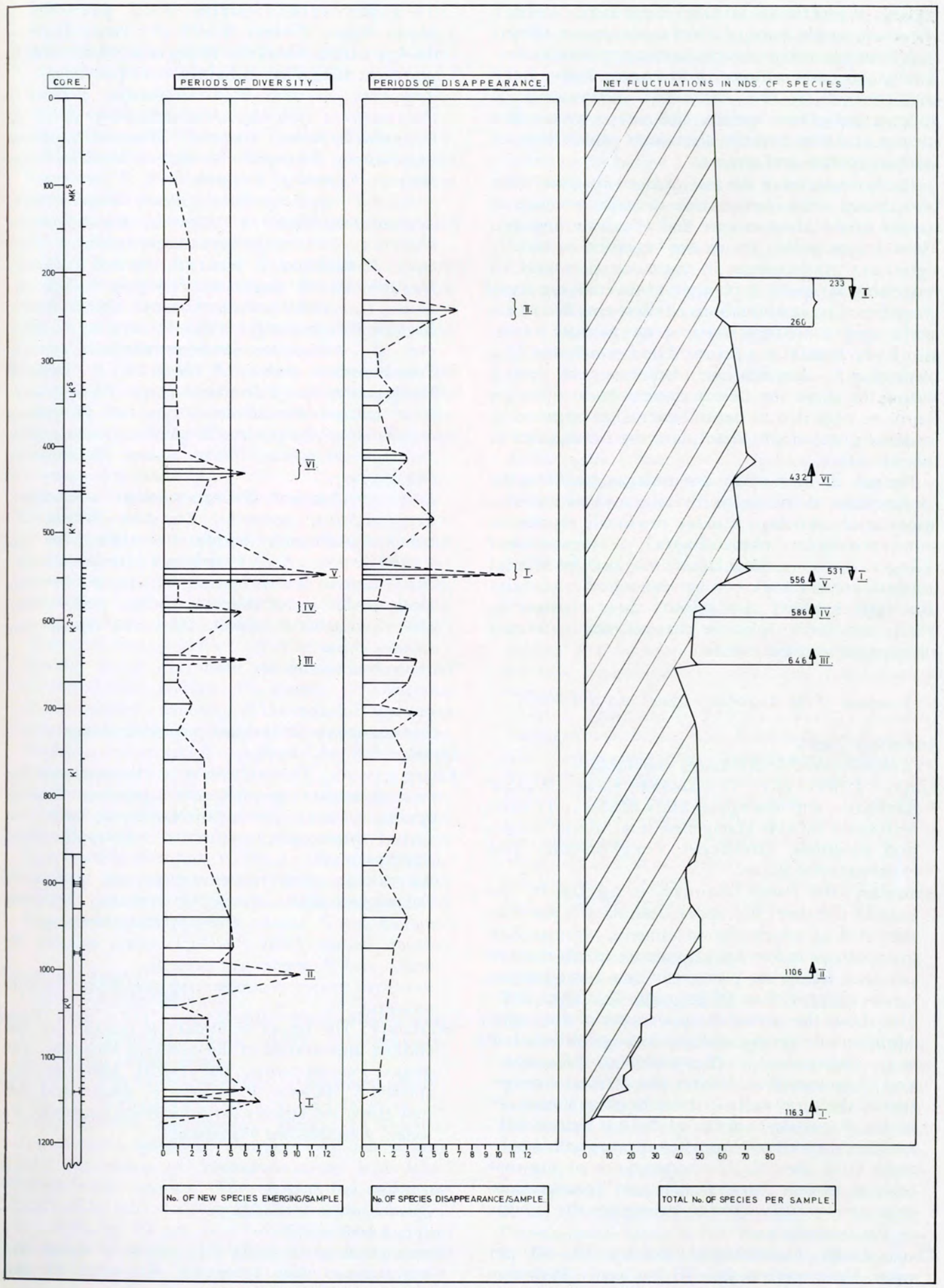


Figure 9. Periods of Apparent Miospore Diversification and Disappearance.

Basin, Western Australia (Segroves, 1970a). However, single lines of fossil evidence are subject to greater error than several lines interpreted collectively, so assemblage sub-zones have been characterized by the combined information of appearances of new species, disappearances of older species and the notably abundant associations of selected species and genera.

The boundaries of the assemblage sub-zones have been drawn at the introduction of major genera and species in the Monosaccate and Disaccate lineages. These major pollen forms are regarded as usually significant components in most samples and of possessing a rapidly evolving and diversifying array of species. The introductions of these new forms are fairly rapid, sometimes showing intermediate forms, all of which may at a future date be included in a phylogenetic classification (Anderson, in prep.). Within the above limitations these introductions are therefore regarded as natural events (as opposed to artificial ones) at which to place the boundaries in this locality.

The sub-division of the assemblages, based on the six horizons of miospore diversity and two of disappearance, although feasible obviously represents some ecological, climatological or depositional changes. However, these factors may only be of local importance. It remains to be seen whether correlation farther afield also reflects these changes in which case the cause of the changes may be termed chronostratigraphic events.

Summary of the Assemblage Zones and Sub-Zones

Assemblage Zone I:
Virkkipollenites-Plicatipollenites Assemblage.

Limits: 1 163′—664′, i.e. Dwyka, Lower Wankie Sandstone and lowermost Black Shales and Coals. Sediments include glacigenes, inter-glacial varves and siltstones, sandstones, conglomerates and carbonaceous shales.

Boundary: the lower boundary is marked by the base of the core; the upper boundary is taken at the level at which the prominent Monosaccate group drops in average abundance to less than 10 per cent, whilst the previously rare Disaccites increase to more than 10 per cent. This level, 646′, also shows the virtual disappearance of the major Monosaccate genera and species so prolific below (e.g. *Virkkipollenites*, *Plicatipollenites*, *Elilasaccites*, and *Caheniasaccites*). Within the Striatiti lineage, two of the three early *Protohaploxypinus* species (*P. acutus, P. sulcatus*) appear to die out before 664′, and a new species (*P. limpidus*) appears within sub-zone C of Zone I. The appearance of the new Striatiti genera *Striatoabietites* and *Striatopodocarpites* (rare) is also taken to strengthen the validity of the boundary.

Characteristic assemblages: Triletes 10—80 per cent; Monosaccites 10—70 per cent; Disaccites 0—5 per cent (Striatiti 0—2 per cent); Monocolpate Plicates 0—10 per cent; Jugates 0—4 per cent; Aletes 0—10 per cent; Monoletes 0 per cent; Cingulate Zonales 0—10 per cent.

Abundant species: Punctatisporites gretensis, Calamospora plicata, Deltoidospora directa, Granulatisporites tentula, Microbaculispora micronodosus, Plicatipollenites indicus, Virkkipollenites obscurus, V. mehtae, V. densus.

Associated species: Retusotriletes diversiformis, Apiculatisporis levis, A. filiformis, Baculatisporites bharadwaji, Verrucosisporites pseudoreticulatus, V. parmatus, V. naumovai, V. pseudotrisectus and *V. bondii, Neoraistrickia* cf. *congoensis, Zinjispora bullata, Z. zonalis, Cycadopites cymbatus, C. nevesi, Quadrisporites horridus, Tetraporina* sp., *Pilaspora calculus, Parasaccites* sp., *Elilasaccites elilaensis, Florinites eremus, Potonieisporites novicus, P. hennellyi, P. thomasi, Vestigisporites* sp., *Caheniasaccites* sp. *Protopaploxypinus amplus, P. salcatus, P. acutus, Platysaccus radialis, Alisporites plicatus, A. gracilis, A. tenuicorpus, Sulcatisporites ovatus, Illinites unicus, Limitisporites monstruosus.*

Restricted species: Reticulatisporites compactus, Verrucosisporites parmatus, Zinjispora bullata, Z. zonalis, Quadrisporites horridus, Granulatasporites sp., *Virkkipollenites radialis, V. mehtae, V. densus, Elilasaccites elilaensis, Potonieisporites novicus, P. thomasi, Vestigisporites* sp., *Caheniasaccites* sp., *Protohaploxypinus sulcatus, P. acutus, Alisporites tenuicorpus, Illinites unicus.*

Three sub-divisions are made:

Assemblage Sub-Zone A:
Granulatisporites-Microbaculispora Assemblage.

Limit: 1 163′ — 1 030′,

Characteristics: This sub-zone is characterized by two dominant groups, the apiculate Trilete genera *Granulatisporites-Microbaculispora* and the radial Monosaccate forms *Virkkipollenites-Plicatipollenites.*

Associated species: Punctatisporites gretensis, Calamospora plicata, Cycadopites cymbatus, Zinjispora bullata and *Z. zonalis*, and *Granulatasporites* sp.

Striate lineage: Only *Protohaploxypinus sulcatus, P. acutus* and *P. amplus* are present.

Restricted species: *Vestigisporites* sp., and *Reticulatisporites compactus.*

Boundary: The upper boundary is marked by the sudden appearance of the bilateral Monosaccites genus *Potonieisporites*, the radial Monosaccites species *E. elilaensis, V. radialis, V. densus*, and the new apiculate Triletes *Verrucosisporites naumovai, V. bondii, Baculatispora bharadwaji.*

Assemblage Sub-Zone B:
Quadrisporites Assemblage.

Limit: 1 006′—853′.

Characteristics: Typically this sub-zone shows the appearance and increased diversity of the

bilateral Monosaccites (20 per cent) (i.e. *Potonieisporites novicus, P. hennellyi* and *P. thomasi),* and of the Cingulate Zonotriletes (10 per cent) (*Zinjispora bullata* and *Z. zonalis*). The rare turma Jugates *(Quadrisporites horridus)* appear to be restricted to this sub-zone.

Associated species: These are typical of sub-zone I, with the introduction of species *Verrucosisporites naumovai, V. pseudotrisectus, V. bondii, V. parmatus* and *Baculatisporites bharadwaji.*

Species dying out: *Granulatisporites* sp. and *Protohaploxypinus acutus.*

Striatiti lineage: No new striate Disaccites were noted, only two non-striate forms (*Platysaccus radialis* and *Sulcatisporites ovatus).*

Restricted species: Include *V. parmatus, Illinites unicus* and *Quadrisporites horridus.*

Boundary: The upper boundary is drawn at the point of disappearance of *Quadrisporites horridus* and at the approximate introduction of the Monosaccites forms *Florinites* and *Parasaccites,* and species *V. radialis.*

Assemblage Sub-zone C:

Acanthotriletes tereteangulatus Assemblage.

Limit: 840′—664′.

Characteristics: Monosaccites are abundant, both bilaterial and radial forms.

Notable species: These are typical of Sub-zone B, with the further introduction of *Acanthotriletes tereteangulatus, Apiculatisporis cornutus, Lophotriletes rarus* and *Marsupipollenites triradiatus.*

Species dying out: The Monosaccites forms *Virkkipollenites mehtae, V. densus, V. obscurus, Potonieisporites novicus, P. thomasi, Elilasaccites elilaensis, Caheniasaccites* sp., the Zonotriletes forms *Zinjispora bullata* and *Z. zonalis* and the Trilete form *Verrucosisporites pseudoreticulatus.*

Striatiti lineage: Protohaploxypinus sulcatus dies out, whilst *P. limpidus* emerges within the sub-zone. In the Disacciatrileti range, *Alisporites tenuicorpus* significantly dies out, whilst *A. plicatus* emerges.

Boundary: The upper boundary is drawn at the level where the Striatiti genera *Striatoabietites* and *Striatopodocarpites* appear.

Assemblage Zone II:

Transition Assemblages.

Limit: 646′—574′, i.e. Middle Black Shales and Coals. Sediments include shales, carbonaceous shales and shaley coals.

Boundary: The lower boundary is discussed above, but is summarised as the appearance of *Striatoabietites multistriatus, Platysaccus leschiki, Sulcatisporites splendens, Densipollenites indicus* and rare specimens of *Striatopodocarpites* and *Marsupipollenites* species. The upper boundary is marked by the consistent appearance of Disaccites in excess of 20 per cent (when discounting the presence of Aletes), of which Striatiti represent more than 10 per cent. Aletes suddenly predominate from 550′ to 480′. This coincides with the appearance of sculptured Monoletes. No marked disappearances occur at the upper boundary, but a sudden increase in new genera and species within the Aletes, Monoletes, Plicates (Praecolpates), and Striatiti are noted at and above 556′. More specifically the boundary is taken to be below 556′ and above 574′ based on the Striatiti lineage, i.e. the emergence of three new *Protohaploxypinus* species (*P. globus, P. diagonalis* and *P. goraiensis*) and four *Striatopodocarpites* species *(S. cancellatus, S. octostriatus, S. rarus* and *S. communis).*

Characteristic assemblages: Triletes 40—50 per cent; Monosaccites less than 10 per cent; Disaccites 10—20 per cent (Striatiti 5—10 per cent); Monocolpate and Praecolpate Plicates 2—8 per cent; Jugates 0 per cent; Aletes 0—2 per cent; Laevigate Monoletes 0—20 per cent; Cingulate Zonotriletes 0—2 per cent.

Associated species: Punctatisporites gretensis, Retusotriletes diversiformis, Deltoidospora directa, Apiculatispora levis, A. filiformis, A. cornutus, Lophotriletes rarus, Baculatisporites bharadwaji, Granulatisporites tentula, Microbaculatispora micronodosus, Verrucosisporites naumovai, V. pseudotrisectus, V. bondii, Cycadopites nevesi, Pilaspora calculus, Tetraporina species, *Plicatipollenites indicus, Parasaccites* sp., *Virkkipollenites obscurus, Florinites eremus, Potonieisporites hennellyi, Protohaploxypinus amplus, Platysaccus radialus, Alisporites plicatus, A. gracilus, Sulcatisporites ovatus* and *Limitisporites monstruosus.*

Species dying out: Verrucosisporites bondii, Plicatipollenites indicus and *Potonieisporites hennellyi. New species appearing: Deltoidospora lukugaensis, Neoraistrickia ramosa, Laevigatosporites colliensis, Gondispora vrystaatensis, Marsupipollenites triradiatus, Circulisporites magnus, Densipollenites indicus, Striomonosaccites* sp., *Protohaploxypinus limpidus, Striatoabietites multistriatus, Platysaccus leschiki, Sulcatisporites splendens, S. potoniei, Vesicaspora* sp. A. and sp. B. There are no restricted species.

Two sub-divisions are made:

Assemblage Sub-Zone D:

Transition assemblage I (TI)

Limit: 646′—634′.

Characteristics: The assemblage in this sub-zone represents the first transition phase between the older essentially Monosaccate-Trilete dominated assemblage in Zone I, to the Disaccate-Striatiti dominated ones above. In common with the older floras are such species as *Punctatisporites gretensis, Granulatisporites tentula, Microbaculatispora micronodosus, Calamospora plicata, Cycadopites cymbatus, Protogaploxypinus amplus, P. limpidus, Potonieisporites hennellyi,* etc. New species emerging in this sub-zone include *Neoraistrickia ramosa, Densipollenites indicus, Striatoabietites multistriatus,*

Striatopodocarpites sp(?), *Sulcatisporites splendens* and *Platysaccus leschiki.*

Boundary: The upper boundary is taken at the introduction of Laevigatomonoletes.

Assemblage Sub-Zone E:

Transition assemblage II(TII)

Limit: 586′—574′.

Characteristics: This assemblage represents the second transition phase in the change towards the Zone III flora. Quantitative and qualitative data are similar to Sub-zone D, but for the sudden and abundant appearance of new laevigate Monoletes (*Laevigatisporites colliensis, L. colliensis* forma minor) together with *Deltoidospora lukugaensis, Gondispora vrystaatensis, Circulisporites magnus, Striomonosaccites* sp., and *Sulcatisporites potoniei.* No new Striatiti forms appear.

Boundary: The upper boundary is marked by a large influx (at 550′) of sculptured Monoletes, abundant Aletes and the Striatiti species *Protohaploxypinus goraiensis, P. diagonalis* and *P. globus.*

Assemblage Zone III:

Densosporites-Gondispora Assemblage.

Limit: 556′—below 432′. i.e. Upper Black Shales and Coals, and Upper Wankie Sandstone, possibly lowermost Madumabisa Mudstones. Sediments include carbonaceous shales, gray shales and mudstones.

Boundary: The lower boundary is discussed briefly above, but may be briefly be summarised as the introduction of the Striatiti species *Protohaploxypinus globus, P. diagonalis, P. goraiensis, Striatopodocarpites cancellatus, S. rarus, S. octostriatus* and *S. communis*, with a marked increase in variety and abundance of Aletes, Praecolpate Plicates and the new appearance of sculptured Monoletes. The upper boundary is drawn at the level at which Zonati Zonotriletes are introduced *(Cirratriradites)*, Disaccites begin to average 40 per cent or more, with Striatiti representing 25 per cent or more of this amount. Aletes, which are abundant in this zone, drop to less than 10 per cent. A large number of species disappear (remnants of Assemblage Zones I and II), and many new species emerge. Within the Striatiti lineage the upper boundary is marked more specifically by the appearance of one new *Protophaploxypinus* species *(P. micros)* and four new genera — *Vittatina, Hamiapollenites* and more rarely *Lueckisporites* and *Guttulapollenites.*

Characteristic assemblages: (Count exclusive of the Aletes). Triletes 40 per cent; Monosaccites average 5 per cent; Disaccites 20—40 per cent (Striatiti 10—20 per cent); Plicates 0—8 per cent; Jugates 0 per cent; Aletes 10—80 per cent; Monoletes 0—20 per cent; Zonotriletes 0 per cent.

Associated species: Deltoidospora directa, D. lukugaensis, Apiculatisporis levis, Granulatisporites tentula, Microbaculatispora micronodosus, Lophotriletes rarus, Acanthotriletes tereteangulatus, Laevigatosporites colliensis, Pilaspora calculus, Florinites eremus, Densipollenites indicus, Protohaploxypinus amplus, P. limpidus, P. radialis, Alisporites plicatus, A. gracilis, Sulcatisporites ovatus, S. splendens, S. potoniei.

Species disappearing: Punctatisporites gretensis, P. gretensis forma *minor, Calamospora plicata, Apiculatispora filiformis, A. cornutus, Verrucosisporites naumovai, V. pseudotrisectus, Lophotriletes rarus, Neoraistrickia ramosa, Cycadopites cymbatus, Circulisporites magnus, Parasaccites* sp. and *Limitisporites monstruosus.*

Species appearing: Acanthotriletes forma minor, *Reinschospora* sp., *Punctatosporites granulatus, Spinosporites* sp., *Thymospora thiesseni, T. pseudothiesseni, Marsupipollenites striatus, M.* sp., *Verrucosphaera colliensis* (varieties 1 and 2), *Protohaploxypinus globus, P. diagonalis, P. goraiensis, Striatopodocarpites cancellatus, S. octostriatus, S. rarus, S. communis, Hamiapollenites karrooensis, Vesicaspora* sp. B.

Restricted species: Densosporites rotundus, Gondispora novus.

Assemblage Zone IV:

Vittatina-Lueckisporites Assemblage.

Limit: 432′—0′: i.e. Lower and Mid-Madumabisa Mudstones. Sediments include mudstones, siltstones, carbonaceous shales and limestones.

Boundary: The lower boundary is taken as the level of introduction of *Protohaploxypinus micros, Vittatina africana, V. minima, Hamiapollenites karrooensis, Lueckisporites nyakapendensis* (rare) and *Cirratriradites africanensis.* The upper boundary is taken to be the top of the borehole.

Characteristic assemblages: Triletes 20 per cent; Monosaccites average 5 per cent; Disaccites 40—75 per cent (Striatiti 25—60 per cent); Plicates 0—10 per cent; Jugates 0 per cent; Aletes 0—15 per cent; Monoletes 0—5 per cent; Zonotriletes (Zonati) 0—8 per cent.

Abundant species: Acanthotriletes tereteangulatus, Cirratriradites africanensis, Florinites eremus, Densipollenites indicus, Protohaploxypinus diagonalis, P. amplus, P. goriensis, P. limpidus, P. micros, Sulcatisporites ovatus, S. splendens and *S. poteniei.*

Associated species: Deltoidospora directa, D. lukugaensis, Retusotriletes diversiformis, Apiculatisporis levis, Baculatisporites bharadwaji, Laevigatosporites colliensis, Punctatosporites granulatus, Thymospora thiesseni, T. pseudothiesseni, Marsupipollenites triradiatus, M. striatus M. sp., *Cycadopites nevesi, Pilaspora calculus, Verrucosphaera colliensis* (varieties 1 and 2), *Striomonosaccites* sp., *Protohaploxypinus globus, Striatopodocarpites cancellatus, S. octostriatus, S. rarus, S. communis, Striatoabietites multistriatus, Platysaccus*

radialis, *P. leschiki*, *P. plicatus*, *P. gracilis* and *Vesicaspora* sp. A. and *V.* sp. B.

Species disappearing: Granulatisporites tentula, *Microbaculatispora micronodosus*, *Lophotriletes rarus*, *Reinschospora* sp., *Gondispora vrystaatensis*, *Tetraporina* sp., and *Verrucosphaera colliensis* (varieties 1 and 2).

Species appearing: i.e. restricted to Zone IV; *Apiculatisporis minutus*, *Zinjispora eccensis*, *Cirratriradites africanensis*, *Protohaploxypinus micros*, *Leuckisporites nyakapendensis*, *Vittatina africana*, *V. minima*, *Taeniaesporites noviaulensis*, *Guttulapollenites hannonicus* and *Jugasporites* sp.

Two divisions are made:

Assemblage Sub-Zone G:

Cirratriradites africanensis Assemblage.

Limit: 438′—240′.

Characteristics: Striate and non-striate Disaccites (40—60 per cent) are now beginning to dominate the assemblages, with Aletes (dominant in Zone III) much reduced in abundance. Monoletes and Triletes are still prominent constituents of the assemblages. Zonati Zonotriletes appear for the first time.

Associated species: These are predominantly similar to those found in the uppermost levels of Zone III, with the exception of the new species listed above, all of which appear in this sub-zone except *Taeniaesporites noviaulensis*. In comparison with Zone III the relative abundance of certain species is seen to change significantly. *Protohaploxypinus* and *Sulcatisporites* species now become the dominant constituents of the assemblages, in favour of the abundant Trilete, Alete, Monolete and non-striate Disaccites species. Above 240′ the trend towards Disaccites dominance continues.

Striatiti lineage: Protohaploxypinus micros, *Vittatina africanensis*, *V. minima* and *Jugasporites* occur at the base of this sub-zone followed by *Hamiapollenites karrooensis* and *Leuckisporites nyakapendensis* in rare quantities.

Restricted species: Zinjispora eccensis and *Cirratriradites africanensis*.

Boundary: The introduction of the above striate Disaccites with Zonati Zonotriletes (*Cirratriradites*) serves as the lower boundary of this zone and sub-zone. The upper boundary may be delineated by the disappearance of the Zonati and the following species: *Deltoidospora directa*, *Apiculatisporis levis*, *Lophotriletes rarus*, *Acanthotriletes tereteangulatus*, *Pilaspora calculus*, and *Verrucosphaera colliensis*. More specifically, the boundary is drawn at the appearance of the striate Disaccites *Taeniaesporites noviaulensis*, *Lueckisporites nyakapendensis* and *Guttulapollenites hannonicus* (the latter two species in excess of 1 per cent).

Assemblage Sub-Zone H:

Taeniaesporites — Guttulapollenites Assemblage.

Limit: 233′—0′.

Characteristics: Striate and non-striate Disaccites now dominate the entire assemblages (60—80 per cent). Triletes (5 per cent) are only represented by *Retusotriletes diversiformis*, *Deltoidospora lukugaensis* and *Apiculatisporis minutus*. Laevigate and sculptures Monoletes are present in a small minority, whilst Zonotriletes and Aletes are almost absent.

Abundant species: Protohaploxypinus diagonalis, *P. micros*, *P. amplus*, *P. goraiensis*, *P. limpidus*, *Striatopodocarpites cancellatus*, *S. octostriatus*, *S. rarus*, *Guttulapollenites hannonicus*, *Platysaccus leschiki*, *Alisporites plicata*, *A. gracilis*, *Sulcatisporites ovatus*, *S. splendens* and *S. potoniei*.

Associated species: Laevigatosporites colliensis, *Punctatosporites granulatus*, *Thymospora thiesseni*, *T. pseudothiesseni*, *Marsupipollenites triradiatus*, *M. striatus*, *M.* sp., *Florinites eremus*, *Densipollenites indicus*, *Striomonosaccites* sp., *Protohaploxypinus globus*, *Striatoabietites multistriatus*, *Vittatina africana*, *V. minima*, *Vesicaspora* sp. A. and *V.* sp. B.

Boundary: As defined above the lower boundary occurs at the introduction of the striate Disaccites *Taeniaesporites noviaulensis* and at the consistent appearance (1 per cent) of *Leuckisporites nyakapendensis* and *Guttulapollenites hannonicus*. The boundary is emphasized by the disappearance of Zonati form *Cirratriaradites* and certain Trilete and Alete species (see above in Sub-zone G).

(c) Stratigraphic Correlation of the Assemblage Zones

Stratigraphic correlations have been considered previously (Falcon 1972, 1973), but are again summarised here in order to update some recent advances in Central African palynology. A point to emphasize in correlation of the coal sequences in South and Central Africa is the interest displayed currently in the exploration and age of the different coal-bearing strata. Basically three potential ages of coal are now noted—Lower to Middle Ecca, Upper Ecca, and Molteno (Stormberg) — and three distinct macrofloras are known to have flourished over this period (Plumstead, 1967).

Due to this rapidly changing vegetation throughout Lower Karroo times, the parent floras forming the original constituents of the coal must have varied and thereby to some degree the eventual organic constituents of the coal. Inversely, the recognition of particularly sought after coal sequences may be conducted by the spore / pollen-macroplant content. Further research is being conducted along these lines at present and will be published at a later date.

Assemblage Zone I:

Dwyka and Lower Wankie Sandstone (K^0 and K^1).

In terms of percentage abundance of the major miospore taxa, Zone I as seen in the Matabola Flats core is comparable to Hart's Cavati Zone in South Africa. Both zones possess dominant Trilete

miospores with abundant (±20 per cent) Monosaccites. Striatiti are present but are rare.

The comparison based on genera and species content is not as close. Hart (1967) selects sixteen representative genera to illustrate the Cavati Zone of which eleven are represented in the Matabola Flats Zone I sediments. Three of these are very rare and have not been included in the present microfloral lists: viz. *Grandispora*, *Gondispora* and *Lycospora*. Of particular interest is the fact that three elements exist in the South African Cavati Zone: (Hart, 1963); (i) the pre-Permian forms: *Grandispora, Lycospora, Endosporites*, *Reinschospora* and *Reticulatisporites*. Of these only *Reticulatisporites* (*R. compactus*) has been described and is very rare in Rhodesia. (ii) The Permian element, containing *Marsupipollenites*, *Plicatipollenites* (*Cordaitina*) and Striatiti genera; the latter two are present in Zone I. (iii) Forms restricted to Lower Permian times; of the eleven forms present in the South African Cavati Zone, six occur in the Rhodesian Zone I, viz. *Zinjispora*, *Verrucosisporites*, *Vestigisporites*, *Apiculatisporis*, *Punctatisporites* and *Cordaitina*.

Zone I (Rhodesia) also possesses four species characteristic of Hart's Cingulati Zone (Hart, 1966a), viz. *Cordaitina balmei*, *Vestigisporites thomasi*, *Cycadopites nevesi*, and *Reticulatisporites* sp.

In terms of correlation, the South African Cavati (Camerati) microfloral assemblage is regarded as somewhat heterogeneous and in need of revision and therefore it cannot represent an absolute standard of reference. The problem of age and wrong stratigraphic bases is a related problem. The sediments from which Hart (1963) extracted his Cavati assemblage may be regarded as Lower Ecca and not Dwyka (J. Anderson, in prep.). For the present purpose, the Rhodesian Zone I assemblage is regarded as possibly Upper Cavati Zone, on the basis of little pre-Permian miospore elements, abundant Lower Permian elements and the presence of Striatiti (although rare) from the base of the productive horizons.

The Rhodesian Zone I appears to be very similar to the lowest beds of the Lower Coal Measures in Tanzania (K2c) due to the common occurrence of *Punctatisporites*, *Zinjispora*, *Vesicaspora*, and *Cordaitina*. Due to the small representation of Striatiti, it may be further confined to Sub-zone C. Utting (in press) has recently shown a closely comparable sequence in the Upper Luangwa Valley in his Mukumba Siltstone Member. Sub-zone A may be correlated to the lower assemblages of these beds on the basis of overwhelming Monosaccate/Trilete dominance and lack of striate Disaccites, whilst the upper assemblages of this member become closely allied to Sub-zones B and C by the introduction of *S. ovatus*, *P. limpidus*, *Z. eccensis*, *N. congoensis*, *V. pseudoreticulatus* and *T. tereteangulatus*.

In Tanzania, Manum and Tien (1973) describe two spore/pollen assemblages from the Ketewaka coalfield, the oldest of which, the *Cordaitina-Zone*, occurs in sandstone coal sequences and is characteristic of Assemblage Zone I, Sub-zone B and C, with abundant Monosaccates and Triletes, two rare Striatiti forms, and a bilateral Monosaccate. Disaccates are rare. *N. ramosa* is typical of Zone II, Sub-zone D, but the Cordaitina-Zone, due to the high proportion of Monosaccates, is for the present purpose retained in Zone I. It is of particular interest to note that unlike other Zone I microfloras these assemblages occur in sandstone coal measures, thereby representing the oldest coal seams so far palynologically correlated in Southern and Central Africa. The two youngest samples in this Cordaitina-Zone (4 and 5) appear to represent a transition zone with high Disaccate content (22—74 per cent), and the appearance of Monoletes and the introduction of *P. amplus, P. sewardi (limpidus), S. cancellatus, V. ovata* and *V. potoniei*. These are forms typically found in Zone II, D and E and are therefore regarded as indicative of the transition phase seen in early Black Shales and Coals beds in Rhodesia.

In the Congo (Pierart, 1959; Hoeg and Bose, 1960; Bose and Kar, 1966), the generic content of the Assise de Schistes noirs de la Lukuga and Assise de Schistes noirs Walikale are both similar to the Rhodesian Zone I assemblage due to the presence of *Virkkipollenites*, *Plicatipollenites*, *Elilasaccites*, *Strotersporites (Protohaploxypinus)*, *Punctatisporites*, *Apicultatisporis*, *Ginkgocycadophytus (Cycadopites)*. On the basis of diversity of species, the Congo assemblages are far more varied and have many forms not yet encountered farther south. The Assise Periglaciaires et Glaciaires is represented by a very dominant Monosaccate assemblage unlike anything encountered elsewhere in Africa so far; the Assise Schiste noirs de Walikale has an equally high proportion of Disaccites, Monosaccites and Triletes, whilst the Assise de Schistes noirs de Lukuga assemblage is predominantly Trilete. The Rhodesian Zone I is tentatively correlated on the basis of the above common abundant genera and low percentage of Striatiti with the Assise des Schistes de Walikale and Assise des Schistes de Lukuga.

No parallel assemblages have as yet been described from Madagascar. In India, the Talchir Flora (Potonie and Lele, 1961) possess a very comparable Monosaccate-dominated flora (*Nuskoisporites* and *Potonieisporites*). Other genera are *Leiotriletes*, *Punctatisporites*, *Granulatisporites*, *Lophotriletes*, *Apiculatisporis*, *Quadrisporites*, *Lunatisporites* (*Protohaploxypinus*), *Pityosporites* and *Ginkgocycadophytus* (*Cycadopites*).

The presence of *Quadrisporites* in minor quantities, abundant *Botryococcus* and *Microbaculispora* (*M. tentula*) equate this miospore assemblage to zones Upper-1 and 2 of Segroves, Western Australia (1970) and Stage 2 of Evans, Eastern Australia (1967). Also Blame's (1964) lower *Nuskoisporites*-Complex K^1 would appear to be equivalent to the upper part of

this assemblage. These assemblages are characteristic of glacigene deposits and post-glacial shales in Australia and are represented by the Nangetty Formation-Holmwood Shale-Fossil Cliff Formation (K^1) of the Lochinvar-Allandale strata of the Sydney Basin (Evans, 1967).

Correlation on the basis of biostratigraphy (i.e. microfloral assemblages and percentage abundance patterns) is evident, but the *age relationship* or chronostratigraphic tally is somewhat problematic. The base of the Permian in Australia was taken by convention as being the introduction of the *Glossopteris-Gangamopteris* flora and striatitid disaccate pollen (Balme, 1964; Evans, 1967). In Western Australia, Balme assigns the lowermost glacials (containing striatitid pollen) as the base of the Permian, whilst Evans, in Eastern Australia, regards the glacials as starting earlier, but still regards the occurrence of *Glossopteris-Gangamopteris* and striate pollen as the introduction of the Permian.

Plumstead, however, is of the opinion that the mixed *Glossopteris-Gangamopteris* macroflora in Southern Africa began in Upper Carboniferous times (Plumstead, 1967), and that this flora, her Zone III, was introduced prior to the end of the glaciation in Africa. This implies a fair discrepancy in age.

Earlier microfloral assemblages are found and defined in Australia in Evans' Stage I (Seaham and Kuttung Series, Sydney Basin) and the lowest part of Segroves' Zone I (lower part of the Nangetty Formation, Perth Basin). In these assemblages, Disaccites are rare, no Striatiti are found, and a few Monosaccites appear in the uppermost beds. An abundance of Sporites occurs. This microfloral content may be equivalent to the early *Proto-Glossopterideae* and Lycopod Assemblages of Plumstead (Zone II, macrofloral), for which she gives a Middle Carboniferous age in Southern Africa.

These floral assemblages are not considered present in the Matabola Flats sediments as Striatiti Disaccites are represented from the base. Also Monosaccites are fairly abundant and diverse, and Plicates are present in significant numbers. This miospore content is thought to indicate a flora equivalent to Plumstead's early Zone III. It is relevant to note here that palaeomagnetism has inferred a Lower to Middle Carboniferous age for the Dwyka Series in Rhodesia. In the light of microfloral evidence taken from the Matabola Flats glacigene sediments, this dating would seem to be somewhat early.

If the South African Cavati florizone (in Dwyka sediments) is of Stephanian-Sakmarian age (Hart, 1967b) then the age of the Rhodesian Dwyka, based on comparable miospore assemblages, may be very similar. This agrees with Bond's proposals (1952, 1967) based on climatic and lithological evidence, i.e. the occurrence of glacial tillites and conglomerates and varved sediments.

Assemblage Zone II:

Lower Black Shales and Coals (lower K^2-K^3).

This portion of the Black shales and coals series is correlated with the Tanzanian $K2e_1$ beds in the Mchuchuma-Ketewaka coalfields on the grounds of quantitative and qualitative content (Hart, 1965, 1966, 1967). Manum and Tien (1973) illustrate the presence of this Transition Zone (Assemlage Sub-Zones D and E) very clearly in the Ketewaka Coalfield. In Zambia, the lowermost Mpwashi carbonaceous shales and coals, as in Rhodesia, are assigned to this assemblage zone. Bar minor variations, the introduction of Monoletes occurs at the top of these beds together with the gradual introduction of the Plicate infra-turma group Monocolpates (*Marsupipollenites*) from the base. There is a comparable decrease in Sporites, a rapid increase in Disaccites (to a higher percentage in Tanzania), gradually increasing Striatiti and reduction in Monosaccites.

Generic content is essentially similar, with reduction in *Zinjispora* and *Punctatisporites*, and the introduction of *Acanthotriletes* (*A. tereteangulatus*), *Laevigatosporites*, *Marsupipollenites*, *Striatopodocarpites* and new species of *Protohaploxypinus* (= *Striatopinites*). In particular, the appearance of *L. colliensis, S. plicatus, S. potoniei, V. saccata* (*S. multistriatus*), *P. limpidus* and *S. fusus* (*S. rarus*) are diagnostic.

On comparison with the miospore florizones of South Africa, Hart places his $K2e_1$ (and therefore the Rhodesian Zone II) on the border of the Cavati and Cingulati Zones. This, on South African standards, is in the Lower Ecca. Bond (pers. comm.) assigns these beds, together with K^1 (Lower Wankie Sandstone) to Lower Ecca on the grounds of *Glossopteris/Gangamopteris* occurrences.

On detailed comparison with Australian microfloral assemblages, this microflora would appear to be comparable to Balme's (1963) upper *Nuskoisporites* Complex, Segroves' lower *Acanthotriletes* Assemblage (= High Cliff Sandstone, Northern Perth Basin), and Evans' (1967) lower stage 3 (= Rutherford and Farley sequences, Sydney Basin).

Assemblage Zone III:

Upper Black Shales and Coals (Upper K2-3).

The palynological content of this sequence is closely comparable to $K2e_2$ (Shale-Coal Measures) in the Tanzanian stratigraphy, more on the basis of generic content (qualitative) than quantitative content (Hart, 1966, 1967a, b; Manum and Tien, 1973). In the Upper Luangwa Valley, Utting (in press) also describes assemblages occurring mid-way up his Mpwashi Carbonaceous Member (Luwumba Coal Formation) closely resembling Assemblage Zone III. In the Rhodesian material a noticeable increase (up to 35 per cent) in Alete forms tends to mar the closer tally between the Disaccites and Striatiti percentage abundances of the three regions.

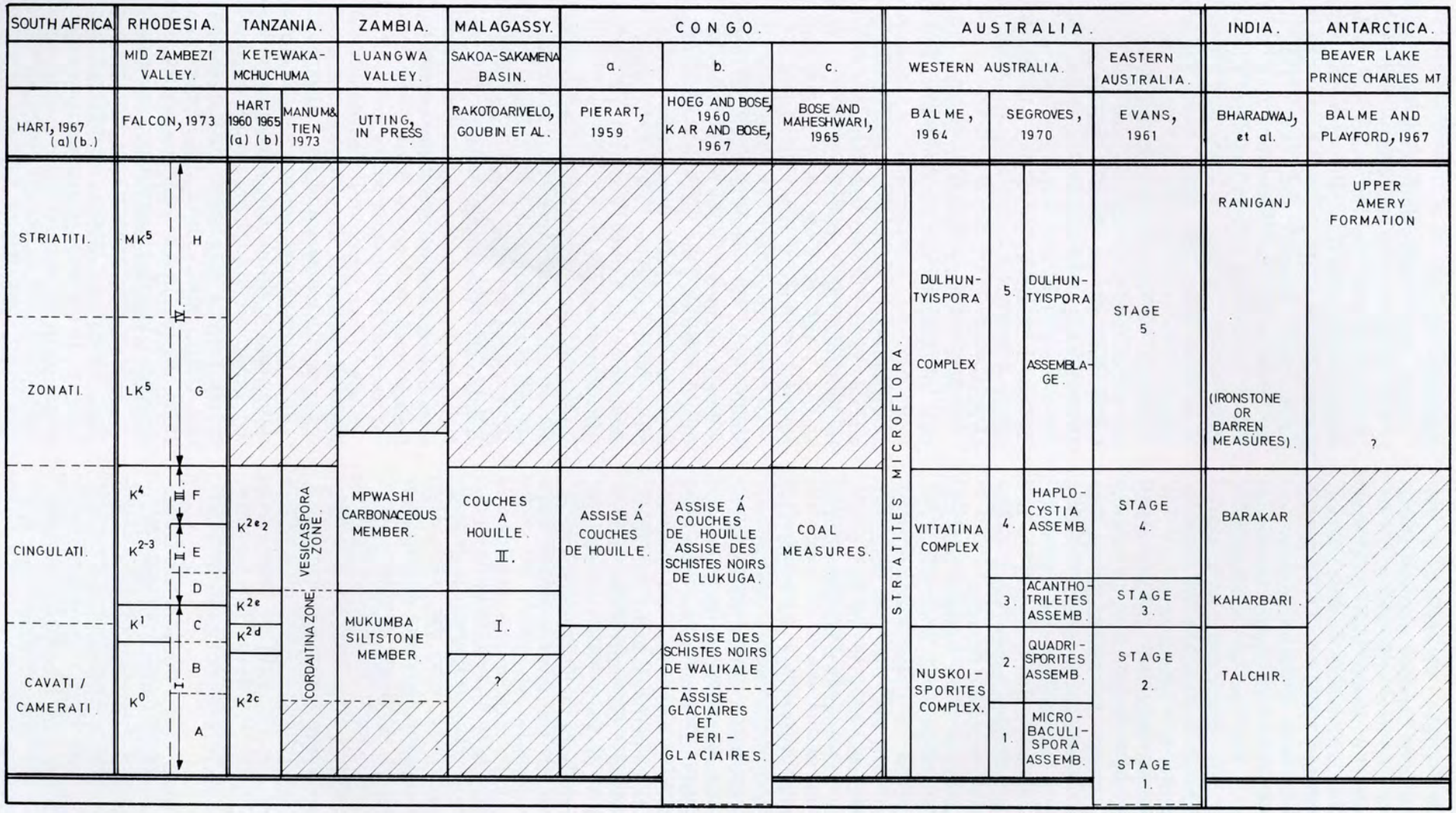


Figure 10. Broad Stratigraphic Correlations.

However, despite their reduction in abundance, both major miospore taxa continue to increase in the three areas under consideration, with Striatiti comprising roughly one third of the total Disaccites content. Monosaccites drop to 10 per cent or less in both regions, Monocolpates and Monoletes increase up to 8 per cent and 10 per cent and Sporites vary with samples, but are generally reduced.

Genera coincide markedly with the common abundance of *Acanthotriletes* (*A. tereteangulatus*), *Laevigatosporites*, *Marsupipollenites*, *Protohaploxypinus* species, *Striatopodocarpites*, *Sulcatisporites* and *Platysaccus*. *Circulisporites* (= *Chomotriletes*) and *Verrucosphaera* are amongst the diagnostic abundant Aletes. The introduction of *Striatoabietites*, *Vittatina*, *Florinites*, *Densipollenites* and *Cirratriradites* is apparent, but these genera are relatively rare in occurrence. In particular, the following species are diagnostic: *S. potoniei*, *S. rarus*, *M. striatus*, *S. communis* and *S. octostriatus*.

On the basis of the overall microfloral similarity to the Cingulati Zone, implying a South African lithostratigraphic equivalence of Middle Ecca, the correlateable $K2e_2$ beds in the Tanzanian Coal Measures and the Mid-Mpwashi Member of the Zambian Luwumba Coal Formation are also tentatively assigned to a Middle Ecca age. In Rhodesia, this confirms Bond's (pers. comm.) chronostratigraphic assignment of these beds on macrofloral and lithological (concretions) grounds. It is of interest to note that the Zone III microfloral assemblages have proved the existence of a facies change in the Ketewaka Coalfield ($K2e^2$). This is basically an arenaceous sequence and unlike the shale-coal units found elsewhere associated with this assemblage.

Australian comparisons illustrate differences due to marine incursions. However, basic quantitative and qualitative analyses of major taxa and genera are possible. K^{2-3} (upper sequences) and K^4 appear to be equivalent to Balme's *Vittatina* Complex, Segroves' Upper *Acanthotriletes* Assemblage and *Haplocystia* Assemblage (Irwin Coals-Carynginia Sequences, Perth Basin) and Evans' (1967) Upper Stage 3 and Lower Stage 4 (Greta Coal Measures and Branxton Formation, Sydney Basin).

On the quantitative and qualitative information supplied by Rakatoarivelo (1970), the two zones of the Couches à Houille of the Sakoa-Sakamena Basin in Madagascar fit in very closely to the lower and upper K^{2-3} beds and their characteristic assemblages. The Barakar microfloral assemblages in India (Tiwari, 1965), and the Assise à Couches de Houille of the Congo (Hoeg and Bose, 1960; Pierart, 1959) and Coal Measures South of Albertville near Lake Tanganyika, Congo (Bose and Maheshwari, 1968) are all considered equivalent to the Cingulati Zone.

Assemblage Zone IV:

Madumabisa Mudstones (K^5).

Assemblage Sub-Zone G:

Lower Madumabisa Mudstones (LK^5).

The Rhodesian Zone IV (Sub-zone G) appears to be very similar to the Upper Mpwashi Carbonaceous sequences in Zambia both quantitatively and qualitatively. Specifically there is in common the introduction of *P. micros*, *H. karrooensis* and the presence of other more prominent forms such as *V. africana*, *Striatoabietites*, *P. leschiki*, *V. saccata*, *L. lukugaensis*, *M. striatus*, *S. communis* and *S. cancellatus*. The uppermost beds encountered by Manum and Tien in the Tanzanian Ketewaka Coalfield (Bh II) are typically those of Sub-zone F, but they possibly grade into early Sub-zone G based on the quantitative comparisons. The typical and diagnostic genera of this sub-zone (*Lueckisporites* and *Cirratriradites*) are, however, missing.

The quantitative values of the Disaccites and Striatiti and the associated genera found in Subzone G do indicate a close resemblance to the South African Zonati Zone. Common genera to both assemblages in significant quantities are: *Vittatina*, *Striatoabietites*, new species of *Striatopodocarpites*, *Florinites*, *Densipollenites* and *Cirratriradites*. *Apiculatisporis* and *Marsupipollenites* are found in greater abundance. Minor variations within the Matabola Flats assemblage are the rare occurrences of *Hamiapollenites*, *Lueckisporites* and *Reinschospora*.

Hart places the Zonati florizone, and therefore by extrapolation the Lower Madumabisa Mudstones (LK^5) and Upper Mpwashi Member of the Luwumba Coal Formation, in South African Upper Ecca lithostratigraphy (Kazanian in age). Bond (pers. comm.) once again agrees with this on the basis of macrofloral evidence. *Gangamopteris* has now all but disappeared in the Mid-Zambezi Valley, whilst *Glossopteris* species continue. Plumstead's Zone IV (Transition Zone), with an abundance of *Glossopteris* and lack of *Gangamopteris* and abundance of swamp lovers (*Phyllotheca* and *Schizoneura*), is apparently equivalent and to this she assigns an Upper Ecca, Middle to Upper Permian dating.

The comparative Australian florizones are the lower *Dulhuntyispora* Complex of Balme (1963), the lower *Dulhuntyispora* Assemblage of Segroves (1970) (lower Wagina Sandstone, Perth Basin) and lower stage 5 of Evans (Muree Formation). The main features common to all these zones is the high percentage of Disaccites and Striatiti, and *Marsupipollenites*. A fair number of genera are common to the Rhodesian and South African microflora, but possibly marine incursions and ecological and climatic factors would have been the cause of a break away and development of different microfloral elements.

Assemblage Sub-Zone H:

Mid-Madumabisa Shales (MK^5).

The microfloral content of this sub-zone appears to be very closely allied to Hart's (1967) South

African Striatiti Zone. The percentage relative abundance of Sporites, total Disaccites, Striatiti, Monosaccites, Monocolpates and Monoletes are all closely comparable.

Generically, *Guttulapollenites* and *Taeniaesporites* are minor but significant introductions into the Matabola Flats MK[5] assemblage, while *Vittatina*, *Lueckisporites*, *Thymospora* and new species of *Striatopodocarpites* and *Platysaccus*—all of which are common to the Striatiti Zone—are in more substantial evidence.

As yet no other comparable Central African assemblages have been published.

Hart (op. cit.) assigns this zone to the Lower Beaufort in South Africa, whilst Bond (pers. comm.) proposes a Lower Beaufort correlation on the presence of *Tapinocephalus* Zone reptiles and other vertebrate and invertebrate macrofaunal fossils.

The MK[5] assemblages, via Hart's Striatiti Zone, is considered equivalent to the Raniganj Stage in India, and the *Dulhuntyispora* Assemblages in Australia (Wagina Sandstone, Perth Basin, and Newcastle-Tomago-Mulbring Formations, Sydney Basin). Hart (1967b) suggests the inclusion here of the dominantly striatitid assemblage reported by Balme and Playford (1967) from Beaver Lake, Prince Charles Mountains, Antarctica.

The Middle Madumabisa Shales, like the Lower Madumabisa Shales, are placed by Plumstead (1967) in her Zone IV, with a Middle to Upper Permian dating. The *Glossopteris* woodlands and equisetalians on the mudflats would seem to be even more pronounced in this zone (higher percentage of Striatiti) than in the lower one, probably creating an excellent environment for the fairly abundant reptilia and amphibia reported by Bond.

SUMMARY

A detailed palynological analysis has been conducted on the microfloral assemblages encountered in the Matabola Flats borehole. This has included quantitative (major taxa) and qualitative (species and their relative abundancies) research, the establishment of an evolutionary sequence in the Disaccate Striatiti and the discovery of microfloral diversification and disappearance periods.

An attempt has been made to establish the major microfloral trends, throughout this Lower Karroo sequence, and to interpret, to some degree, the possible factors affecting these trends and their fluctuations.

Based on the above information, a number of sub-divisions of the microfloral assemblages have been investigated. This has resulted in the establishment of eight assemblage sub-zones which have been incorporated into four major assemblage zones.

Stratigraphic correlation of these assemblage zones, and in some cases sub-zones in South and Central Africa and in Gondwanaland has been attempted. This has illustrated the remarkably uniform parallel trends in changing microfloral patterns throughout this period of time. It has also been shown that lithofacies changes can be detected through assemblage correlation, and that the broad ages of the coal sequences may now be established. Further work is necessary before correlations can be refined to the point where coal seams or their intercalated sediments can be reliably linked.

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Palaeont. afr., **18**, 31—34 (1975)

A PROBLEMATICAL ELEMENT IN THE GLOSSOPTERIS FLORA OF VEREENIGING

by
S. F. Le Roux

INTRODUCTION

An unusual element, not previously recorded from the mixed *Glossopteris* Flora of Vereeniging, is described here. The type material was obtained from a rich fossiliferous zone, previously described by the author (Le Roux, 1963, pp. 1—2). The material available for study consists of a single specimen of an incomplete frond preserved in the form of an impression in fine-grained laminated clay.

NAMING AND CLASSIFICATION OF THE FOSSIL

A frond of this nature presents a most difficult problem of identification owing to the fact that one has to depend on gross morphology only. This task becomes even more hazardous where the preservation is poor and the material fragmentary such as in the case concerned here. Under the circumstances it is proposed to refer the fossil provisionally to Plantae Incertae Sedis. The name proposed for the new plant is *Thomasleslia vereenigensis* in commemoration of the late Dr. Thomas Leslie and the locality which he made famous through his palaeobotanical discoveries at Vereeniging.

DESCRIPTION OF THE MATERIAL

Incertae sedis

Thomasleslia vereenigensis gen. et sp. nov.

(Figures 1 and 2)

Combined diagnosis

Sterile vegetative frond, imparipinnate with falciform leaflets borne on a stout rachis. Leaflets arranged in opposite pairs spaced at a wide interval and confined to the region immediately subtending the terminal leaflet. Leaf laminae borne on strong petioles attached to rachis at a wide angle; margins of leaf blades entire, oppositely curved. Greatest width of blade in centre, tapering gradually towards apex; veins strong, more or less parallel, with shallow grooves between adjacent veins; midrib absent; rachis prominent, tapering gradually towards apex.

Holotype — Specimen TLV/I, Museum of the Bernard Price Institute for Palaeontological Research, Johannesburg.

Locality — Leeuwkuil, Vereeniging, Transvaal.

Horizon — Transvaal Coal-measures, Lower Permian.

Zone — Clay layer "A", Leeuwkuil Quarry No. 2 (Le Roux, 1963, p. 2).

Description

Leaflet slightly curved in basal portion with gradual increase in curvature until a distinct sickle-shape is produced; maximum length of lamina approximately 80 mm and having a maximum width of 6 mm in central region; parallel venation, five veins running 1 mm apart; petiole about 40 mm long and 3 mm wide; leaflets arranged in two opposite pairs and spaced approximately 20 mm apart on rachis. Rachis bare of foliage except 5 leaflets in apical region; maximum width of rachis at point of fracture 13 mm, tapering gradually to 6 mm at the terminal end; traversed longitudinally by a faint median ridge.

Comparisons and discussions

As far as is known the only plant showing some resemblance to the new Vereeniging plant is *Glossophyllum florini* Kraüsel, a ginkgoalean plant from the Triassic of Austria. The foliage of both plants includes falciform leaves. It is doubtful whether this feature should be considered as being of important diagnostic value owing to the possibility that the sickle shape may have been induced under certain conditions of preservation. Both plants show parallel venation, with distinct forking of veins in the case of *G. florini*, indicating affinity with the Ginkgoales. No such evidence is afforded, however, in the case of the Vereeniging plant.

There is a marked difference between the habits of growth of the two plants, a fact which seems to rule out the possibility of mutual affinity with the Ginkgoales.

The specimen described in this paper shows a superficial resemblance to the frond of a small palmaceous or cycadaceous plant. This raises the interesting possibility that the new plant may be of cycadophytic stock. Such a surmise would not be too far-fetched considering the fact that remains of cycadeoidalean plants have previously been recorded from Vereeniging (Plumstead, 1961; Le Roux, 1966). For the present the evidence is too meagre and inadequate to establish relationship with the Cycadophyta, however, and the taxonomic position of the plant will have to remain problematical pending the discovery of more conclusive evidence.

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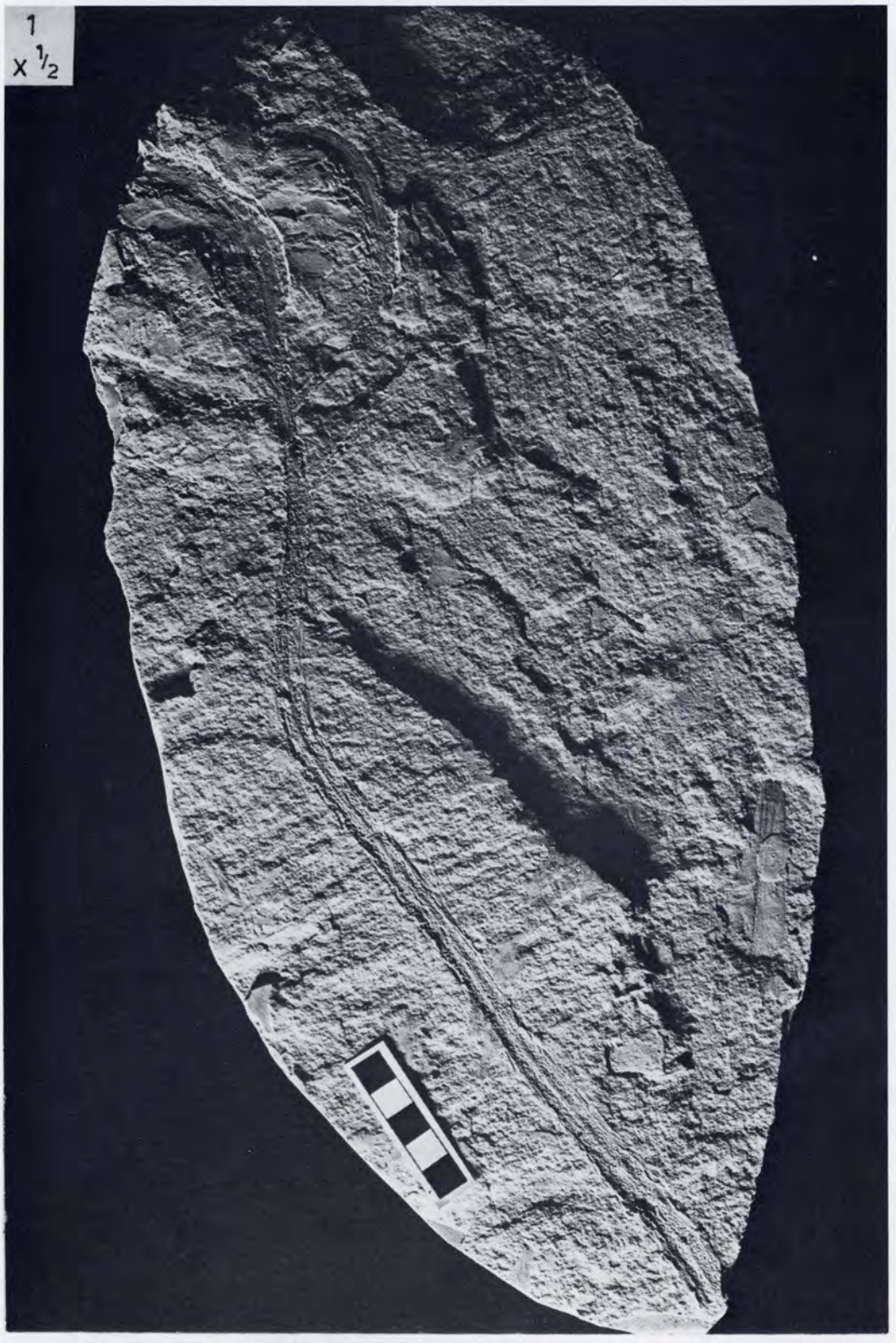
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Thomasleslia vereenigensis gen. et sp. nov.

Figure 1. Incomplete frond showing strong rachis with cluster of falciform leaflets. Note the distinct curvature in the rachis and the faint median longitudinal ridge. (Magnification X$\frac{1}{2}$)



Thomasleslia vereenigensis gen. et sp. nov

Figure 2. Apical portion of the specimen figured in Figure 1. Note the imparipinnate arrangement of the leaflets on the rachis, the comparatively wide spacing between the two pairs of leaflets, the prominent petiole and the parallel nature of the veins shown in the leaflet on the right. (Natural size)

Palaeont. afr., **18**, 35—45 (1975)

THE "TRILOBITE" TRACKWAYS IN THE TABLE MOUNTAIN GROUP (ORDOVICIAN) OF SOUTH AFRICA

by

Ann M. Anderson

ABSTRACT

A terminology for arthropod trackways is defined and the nomenclature of trace fossils is discussed briefly. Most of the trackways from the reddish sandstone Graafwater Formation are assigned to the ichnospecies *Petalichnus capensis* sp. nov. which includes bilaterally symmetrical walking trails consisting of a repetition of 9—12 pairs of unifid tracks sometimes accompanied by a median drag line. These trackways are associated with hemispherical burrows *Metaichna rustica* gen. et sp. nov. The same animals possibly made both the trackways and the burrows, but whether or not they were trilobites is not clear.

INTRODUCTION

In 1962 Taljaard recorded trilobite trackways from the Table Mountain Sandstone series on the farm Brandenburg 25 km west-south-west of Clanwilliam in the western Cape Province. He presented a sketch of a 7 m² slab, now mounted in an entrance hall of the Department of Geology at Stellenbosch University (Figure 2), and two photographs: one is of a specimen 1,5 m² housed at the South African Museum in Cape Town, the other is of a specimen retained on the farm (18° 38′ E, 32° 16′ S).

Rust (1967; 1969) elucidated the stratigraphic setting of trackways and discovered further occurrences (1967, p. 60):

> ". . . at Tierhoek and Waterval [farms], and in the vicinity of Stellenbosch and Hout Bay, Simonstown. In these localities the tracks occur in the Graafwater Formation [reddish sandstone and siltstone] but tracks have also been found [stratigraphically higher] in the Peninsula Formation [white quartz sandstone] at Matjiesgoedkloof, Urionskraal".

However, the material from Brandenburg remains the most useful because of its relatively good preservation and wide surface exposure; the other examples have been left in situ in the field. Rust (1967, Pl. 14, 18, 19, Figs. 70—78) provided photographs of the trackways and full-size carbon paper rubbings made directly from the rock.

Although both Taljaard (1958; 1962) and Rust (1967) described the morphology of the trackways and burrows, and discussed their possible origin, there has been no previous attempt at a formal systematic classification of these trace fossils.

TRACK TERMINOLOGY

To facilitate definition of the trackways it is necessary to define a few terms.

Tracks, Trails, Trackways

Pettijohn (1957, p. 220) defined "TRACKS . . . [as] impressions left in soft materials by the feet of birds

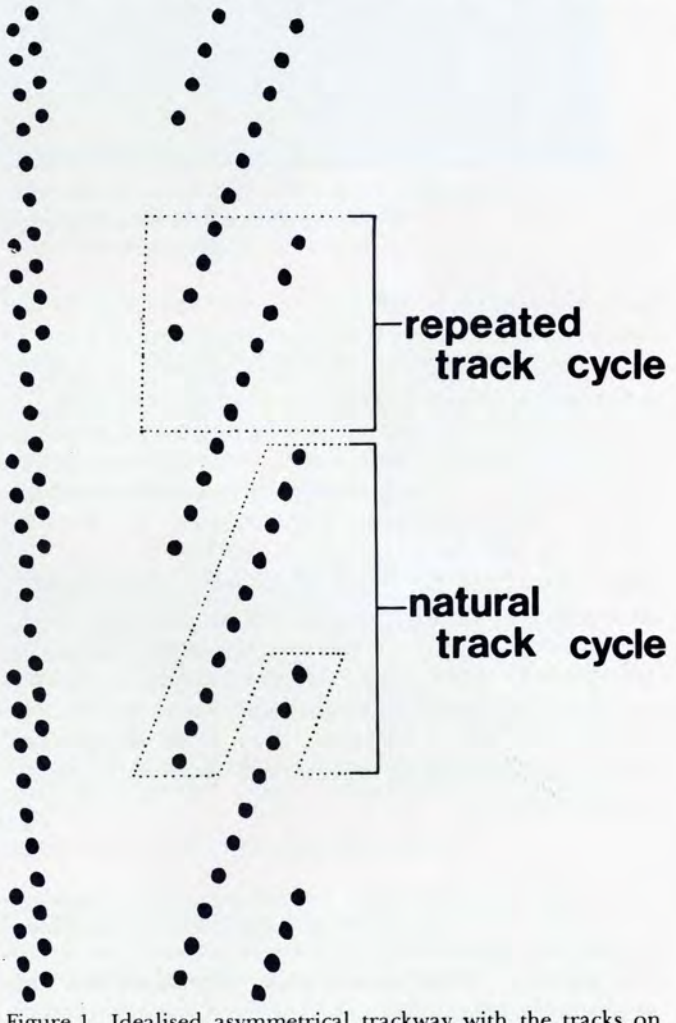


Figure 1. Idealised asymmetrical trackway with the tracks on one side separated into oblique lines of ten set *en echelon*. One such line is a natural track cycle, while the tracks between any two identical tracks in adjacent natural cycles form a repeated track cycle.



Figure 2. Part of the "Brandenburg slab" which is mounted in a wall in the Stellenbosch University Geology Department. It is the type specimen for both the *Petalichnus capensis* trackways and the *Metaichna rustica* burrows. (x0,1)

and other animals. TRAILS . . . [as] the more or less continuous markings left by an organism as it moves . . .". With reference to the markings left by walking arthropods, Bandel (1967, p. 5) explained that "In . . . current American usage the individual imprints of organs of locomotion are . . . referred to as tracks, while a series of tracks made by one individual is a trail." This usage was implemented by Packard (1900, p. 63) and Osgood (1970, p. 351). To emphasise that an arthropod trail consists of a succession of discrete tracks (unlike the trails of the recent amphipod *Corophium volutator* shown by Häntzschel, 1939, Figures 1, 2), it could be termed an arthropod walking trail. Alternatively, it may be termed a TRACKWAY (Frey, 1971, p. 94; Bergström, 1973, p. 53). The latter is preferred because of its comparative brevity.

Track Cycles

A track cycle is a unit sequence of tracks which is repeatedly reproduced to form a continuous length of trackway. Track cycles can be distinguished only where individual tracks are sufficiently characteristic to allow their differentiation. A REPEATED TRACK CYCLE is the sequence between two successive identical tracks; a NATURAL TRACK CYCLE is the consecutive sequence of tracks left by the walking appendages when each, starting with the fore- or hind-most, has pivotted on the substrate once. The natural track cycles usually overlap, i.e. they tend to be longer than the repeated track cycles (see Figure 1). Of course, in one trackway both natural and repeated cycles involve the same number of tracks.

TRACE FOSSIL NOMENCLATURE

A binomial nomenclature usually is employed for the classification of trace fossils (see Häntzschel, 1962; Sarjeant and Kennedy, 1973). This is a "form" nomenclature based on the morphologies of the traces themselves, and the connotation of "ichno-genera" and "ichno-species" is necessarily different from that of phylogenetic genera and species.

Seilacher (1953; 1967; 1974) has demonstrated that behaviour is a significant factor in trace formation. In general, the more meagre the anatomical information in a trace, the more prominent the behavioural aspect. Trackways potentially reveal more about the anatomy of the creature responsible than do most trails. Indeed, the ichno-generic and ichno-specific names of trackways can be almost phylogenetic if the diagnoses are based on a sufficiently extensive collection from one locality. The behavioural change implicit in a change in morphology along the length of a single trail then

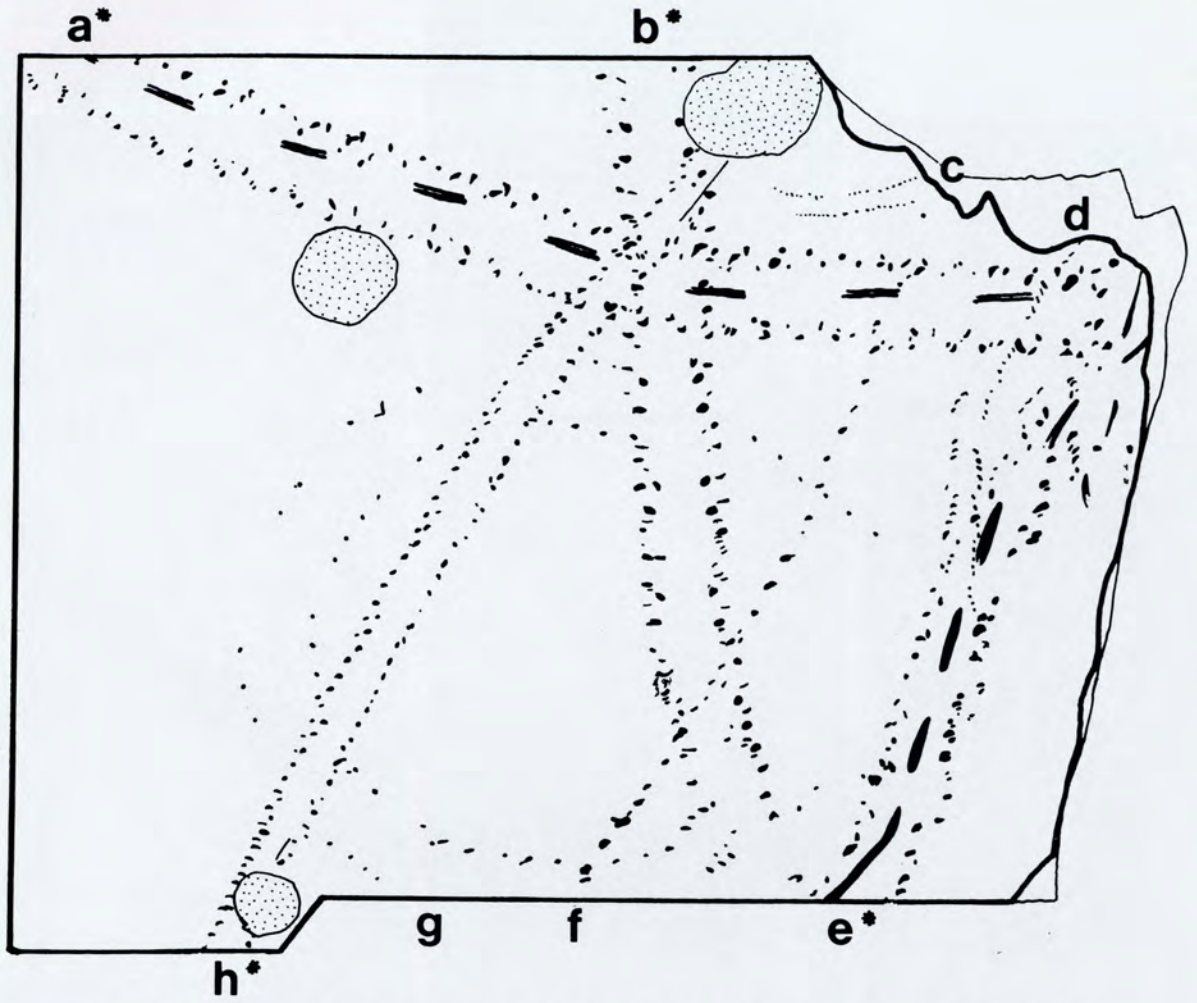


Figure 3. Diagram of the Brandenburg slab (cf. Figure 2). To facilitate reference to particular trackways each is arbitrarily assigned an identifying letter, placed where one end of the trackway intersects the outline of the photographed slab surface. These letters do not correspond with Rust's (1967) individuals A to E described from the slab. The definite *Petalichnus capensis* trackways are marked with an asterisk.

Trackway **a*** is the paratype figured in Figure 4c. (It is Rust's individual A.)

Trackway **b*** is the holotype figured in Figure 4b.

Trackway **c** is Rust's (1967) individual E.

Trackway **d** has the tracks on both sides divided into series set *en echelon*. There are only four or five tracks per series and the series do not overlap. This is probably a deep "undertrack" version of a symmetrical *P. capensis* trackway in which the more superficial tracks are not recorded (see Goldring and Seilacher, 1971).

Trackway **e*** is the one reported by both Taljaard (1962) and Rust (1967, individual B) as having a median drag line for only part of its length. The portion without the drag line is now elsewhere (cf. Taljaard, 1962, Figure 1).

Trackway **f** is represented by a single straight row of tracks; those in the other row have not been recorded probably as a result of "undertrack fallout" in an initially asymmetrical trackway similar to trackway g.

Trackway **g** consists of two curving rows of identical tracks. This is apparently Rust's individual D.

Trackway **h*** is the paratype illustrated in Figure 4a. (Apparently Rust's individual C.) The animal moved from the top to the bottom of the slab as figured (cf. Seilacher, 1959, Figure 2a, b).

There are three *Metaichna rustica* burrows: one on each end of trackway h* and another alongside trackway a*.

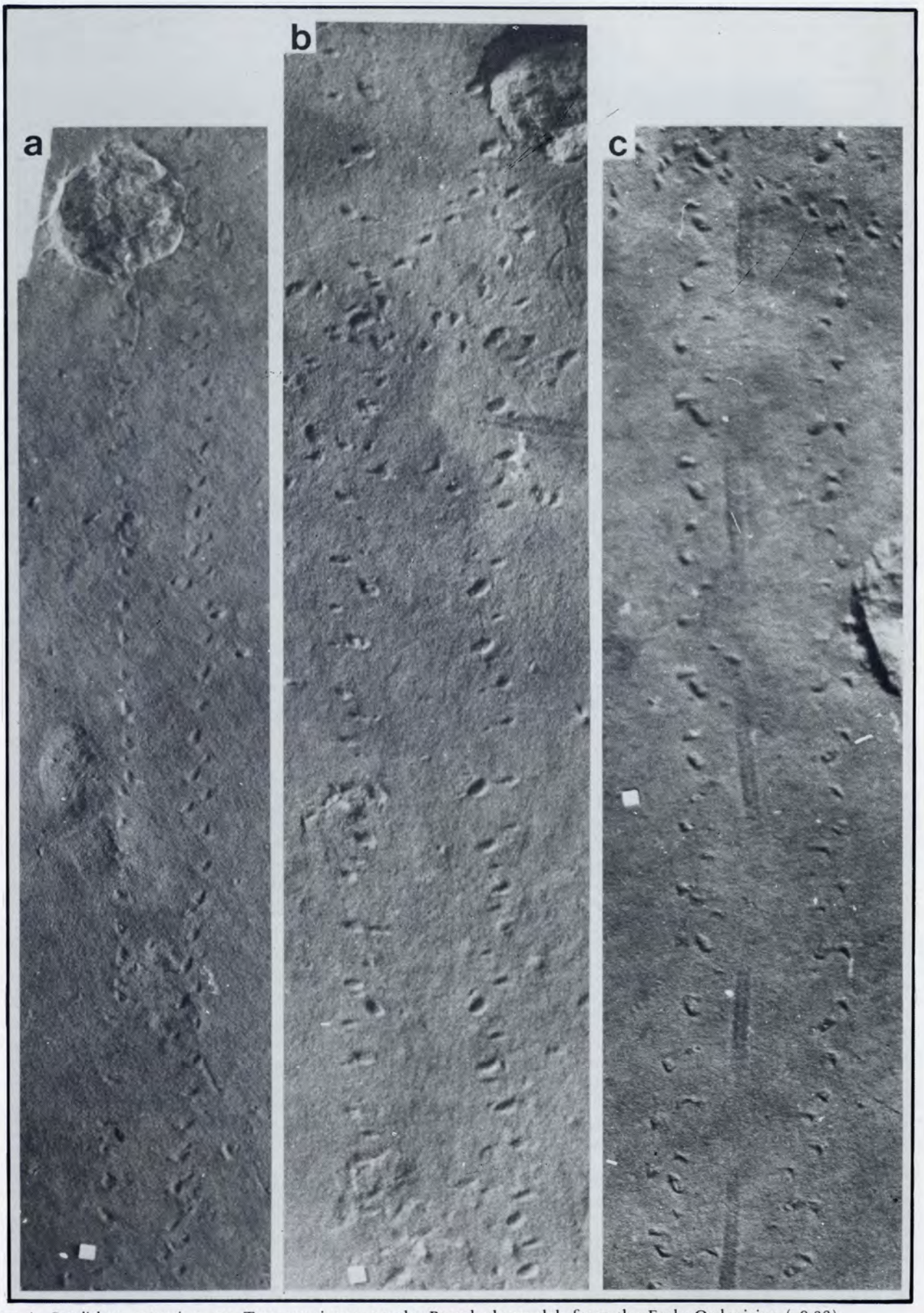


Figure 4. *Petalichnus capensis* n. sp. Type specimens on the Brandenburg slab from the Early Ordovician (x0,33).

(a) Example in which the tracks on the right side are in series of 9, possibly 10, set *en echelon* (see Figure 5a). The circular structure at the top is a *Metaichna rustica* n. gen. et sp. burrow in plan view. The contact between the two is coincidental: the tracks on one side of the trackway continue unaffected past the burrow.

(b) Holotype of the trackway ichnogenus *Petalichnus capensis*. Unlike the specimen in Figure 4a, direction of movement was straight ahead and it is difficult to distinguish the natural track cycles. There are nine or ten tracks in each repeated cycle (see Figure 5b).

(c) Example with a discontinuous median drag line, which does not maintain a strictly median position. The drag line has a distinct median ridge along its length, suggesting that the inscribing organ, probably the tail of the animal, was bifurcate. Each section of the drag line is accompanied by one of the repeated cycles of nine or ten tracks.

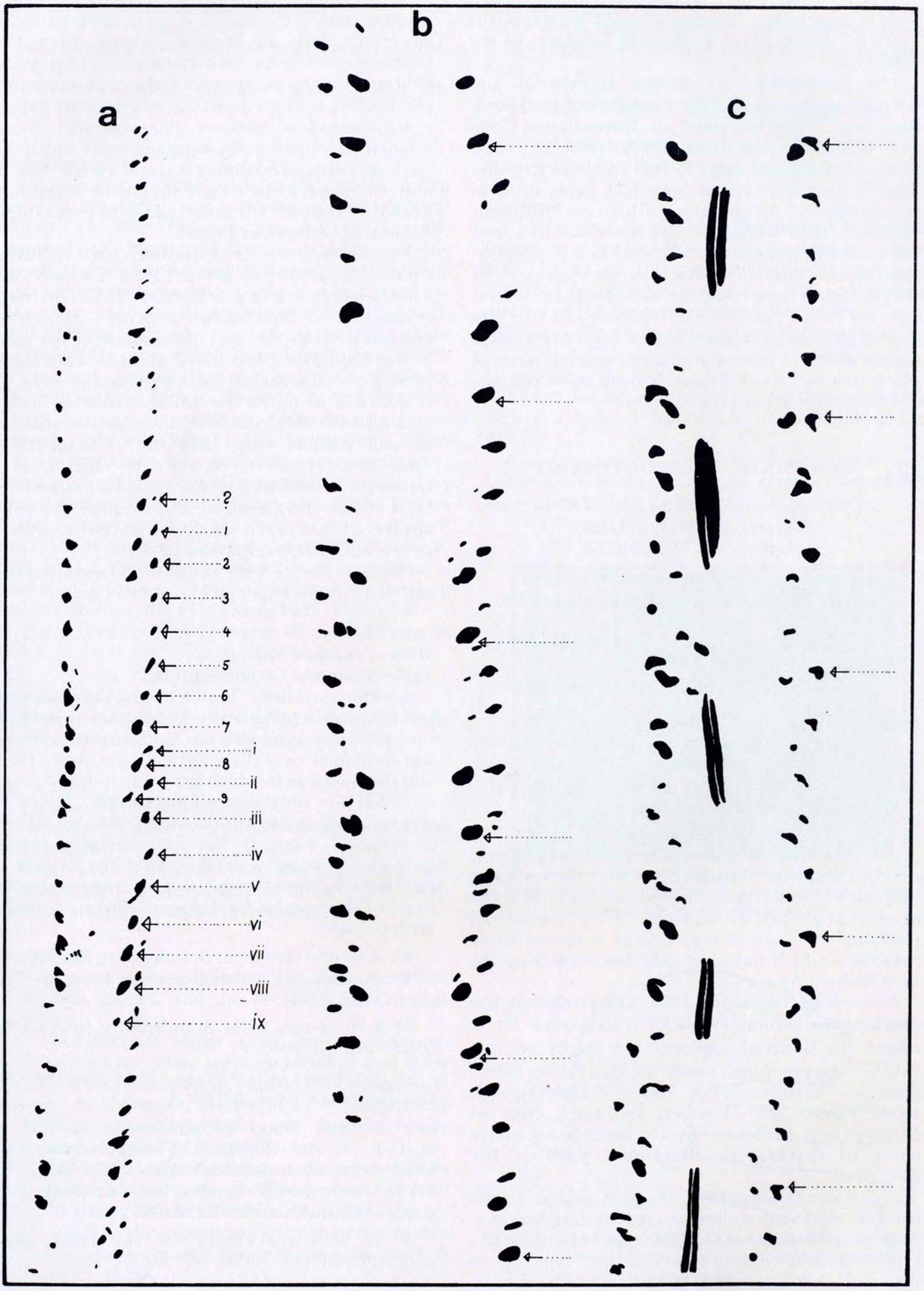


Figure 5. Tracings of the *Petalichnus capensis* trackways shown in Figure 4. In (a) the individual tracks in two natural cycles are numbered, one with Arabic symbols, the other with Roman symbols. In (b) and (c) repeated cycles are marked. In the latter, one portion of the intermittent median drag line is accompanied by one repeated cycle of tracks.

finds no expression. (Perhaps it could be reflected in "variety" names given to the end members of the gradation.)

The morphology of resting impressions and burrows is entirely distinct from that of trackways. Each is an "imperfect state" (cf. International Code of Botanical Nomenclature, 1972, Article 59), none being the complete animal. It is customary to distinguish between various imperfect states in form nomenclature by assigning them to different "genera", each within its own form classification; the levels of phylogenetic implication are independent of one another. Thus, a single "species" of resting impression may be affiliated to several "species" (even "genera") of trackway and vice versa, and one animal species will be responsible for a variety of ichno-genera and ichno-species, some of which may be indistinguishable from those produced by another animal species.

SYSTEMATIC PALAEONTOLOGY

Kingdom INVERTEBRATA
Phylum ARTHROPODA
Subphylum TRILOBITA

Ichnogenus PETALICHNUS Miller 1880.

Type species: *Petalichnus multipartitum* Miller 1880, monotypic.

1863 undesignated trackways, Roberts, Figure 4.
1909 *Acripes* Matthew.
1955 *Diplichnites* Dawson 1873, sensu Seilacher.

Diagnosis (from Osgood, 1970, p. 362):

"Trilobite tracks showing straight-ahead or slightly oblique movement. Each series [track cycle] consists of 9—12 unifid or bifid imprints. Generic designation of producer unknown"

Comparison

Acripes Matthew 1909 has, at least in the species *A. incertipes* (lectotype, Häntzschel, 1965), the tracks on one side of the trackway divided into series of about nine tracks set *en echelon*. This Devonian trackway therefore is regarded as a synonym for *Petalichnus* which was originally described from the Late Ordovician.

Dimorphichnus Seilacher 1955, like *Petalichnus*, has overlapping natural cycles of tracks often set *en echelon*. In both ichnogenera the tracks on one side may be sigmoidal, produced by a raking movement (cf. Seilacher, 1955, Figure 2 and Osgood, 1970, Figure 22). However, the track cycle of *Dimorphichnus* seems to involve more than twelve pairs of tracks, the maximum number for *Petalichnus*.

Diplichnites Dawson 1873 has been used to denote trilobite trackways without a median drag line (e.g. Seilacher, 1955). Osgood (1970, p. 352) remarked that "Dawson's illustration of the type is so schematic that it is impossible to determine if it is a trilobite track". It certainly is not possible to discern any track cycle in Dawson's sketch of a Carboniferous trackway with transverse linear tracks, although the tracks are not a constant distance from one another or from the midline of the trackway.

Merostomichnites Packard 1900 includes in the original description *M. narragansettensis* which is a trackway with overlapping natural cycles, but the number of tracks in a cycle cannot be determined from the diagram. The same applies to the examples illustrated by Størmer (1934).

Protichnites Owen 1852 has been used to denote trilobite (and other cf. Sharpe, 1932) trackways with a median drag line (e.g. Seilacher, 1955). This usage, unlike that of *Diplichnites*, conforms well with the original descriptions and illustrations of the genus in the Cambrian. The moot point is whether the presence or absence, in itself, of a median drag line is sufficient to justify the differentiation of genera. Häntzschel (1962) included trackways both with and without median drag lines in his diagnosis of *Protichnites*. However, he restricted the name to trackways with trifid tracks; *Petalichnus* has unifid or bifid tracks. Furthermore, the original *Protichnites* apparently had no more than eight pairs of tracks per cycle; *Petalichnus* has nine to twelve.

Umfolozia Savage 1971 from the Permian has only half as many tracks per cycle as *Petalichnus*.

Material examined in this study

Table Mountain Group examples:

(a) The so-called "Brandenburg slab", Stellenbosch University (Figure 2). Unfortunately a significant portion of the slab has been removed since it was described by Taljaard (1962) and Rust (1967), and the trackway in which the median drag line was recorded for only part of the length (Rust's individual B illustrated in his Figures 71 and 72, and in Taljaard's Figure 1 has been truncated, leaving only the portion with the drag line (Figure 3, trackway e). The other portion is now mounted in front of the fireplace at 4 Anreith Street, Karindal, Stellenbosch.

(b) A second slab from Brandenburg locality now in the custody of the South African Museum (Taljaard, 1962, Pl. I).

(c) A third slab from Brandenburg, still on the farm (Taljaard, 1962, Pl. II).

(d) Trackways in situ in the hills east of the town Graafwater (18° 38′ E, 32° 09′ S).

(e) Bernard Price Institute casts Hb./C.T. 1, St./C.T. 1 and Th./C.T. 1 respectively from Helderberg near Somerset West (18° 53′ E, 34° 01′ S), Stellenbosch vicinity and Tierhoek farm south of Clanwilliam (18° 51′ E, 32° 24′ S).

(f) In situ trackways on the farm Matjiesgoedkloof (18° 59′ E, 31° 39′ S), about 35 km south-south-west of Nieuwoudtville (Figure 8c).

Petalichnus capensis sp. nov.
Figs. 2—5

1962 undesignated trilobite trackways, Taljaard, Pl. I, II.

1967 undesignated trilobite trackways, Rust, Pl. 14 -D, -F; 19 -C; Figures 70—72, 76, 78.

Definition

Petalichnus trackways with unifid tracks, often laterally elongated and not necessarily identical (Figure 4). The trackways are rarely bilaterally asymmetrical. When they are, the tracks on one side are set *en echelon* and a slight taper is revealed in the distance between opposite tracks in one natural cycle (Figure 4a; see also photograph in Taljaard, 1958). There generally are not more than three natural cycles represented in the longitudinal length of trackway occupied by one such cycle of tracks. There mostly are nine tracks per cycle (see Figure 5). There may or may not be a median drag line, continuous (Taljaard, 1962, Pl. I) or intermittent. When it is discontinuous, one section accompanies one cycle of tracks (Figure 4c). The median drag line does not maintain a strictly median position (see Figures 2 and 3). On occasion, the median drag line itself has a slight median ridge (on the epichnial surface) (Figure 4c). Sometimes the adjacent sediment is puckered to form a "chevron" pattern over the drag line (Taljaard, 1962, Pl. I; Rust, 1967, Figure 76).

The trackways vary between 50 and 125 mm in width.

Derivation of name

Capensis (Latin adjective) derived from the Cape in Cape Province and Cape Supergroup.

Types

Type Locality: Brandenburg.

Holotype: Trackway on Brandenburg slab shown in Figure 4b.

Paratypes: Trackways on Brandenburg slab shown in Figures 4a and 4c, plus those on the South African Museum specimen (Taljaard, 1962, Pl. I).

Comparison

P. capensis is generally larger than other described *Petalichnus* species, and the presence of a median drag line is unusual.

P. multipartitum Miller 1880 (amend. Osgood, 1970) trackways often are asymmetrical and there usually is more overlap of natural cycles than in *P. capensis*. Furthermore, the tracks of *P. multipartitum* sometimes are clearly bifid and they are more elongate than those of *P. capensis*.

P. incertipes Matthew 1909 and the other species originally described under the ichnogenus *Acripes* all have the tracks on one side set *en echelon*, an arrangement which is the exception rather than the rule in *P. capensis* (however, see Figure 4a and photograph in Taljaard, 1958).

Museum specimens

(a) Brandenburg slab at Stellenbosch University.

(b) South African Museum slab from Brandenburg.

Phylum — ARTHROPODA?

Ichnogenus METAICHNA nov.
Type species: *Metaichna rustica* sp. nov.

Definition

This regular conical or hemispherical burrow transgresses the bedding planes (Figures 6, 7; Rust, 1967, Pl. 14 -C). It is orientated with the apex pointing stratigraphically downwards. The wall and the interior of the cone usually are structureless. The infill material is always coarser than the host rock.

Comparison

Conostichus Lesquereux 1876 (cf. Häntzschel, 1962, Figures 116 -2, -3) has structured outer wall and infill.

Kulindrichnus Hallam 1960 is also a conical body, but it is oriented subvertically, is composed of shell aggregates and the matrix may be phosphatic.



Figure 6. *Metaichna rustica* burrow viewed laterally in situ at Tierhoek, south of Clanwilliam (x0,33).

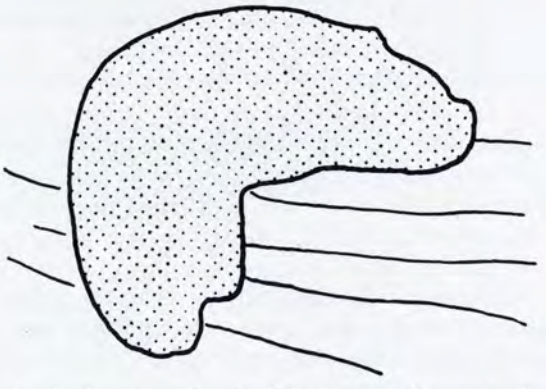


Figure 7. Explanatory sketch of the burrow shown in Figure 6 above. The burrow infill is stippled. It cuts across the bedding of the host strata.

Rusophycus Hall 1852 (cf. Häntzschel, 1962), the typical resting impression made by trilobites (Seilacher, 1955, 1959; Crimes, 1970, 1975; Bergström, 1973), has a bilobed outline reminiscent of a coffee bean. Each lobe is transversely scratched. *Metaichna* therefore is not a typical trilobite excavation.

Material examined in this study

Besides the material mentioned under *Petalichnus*, burrows were observed in situ on the farm Tierhoek south of Clanwilllam.

Metaichna rustica nov.
Figures 2, 4a, 6, 7, 8c.

1962 undesignated trilobite "nests", Taljaard, Pl. I.

1967 undesignated trilobite burrows, Rust, Pl. 14.

Definition

As for genus.

The diameter of the mouth of the burrow (see Figures 4a, 8c) seldom exceeds 15 cm.

Derivation of name

Metaichna = meta-ae f.(L): cone + ichna;
rusticus -a -um (L.): homely, simple.

Types

Type locality: Brandenburg.
Holotype: Brandenburg slab.

Museum specimens

As for *Petalichnus capensis* trackways.

THE ARTHROPOD TRACKWAYS AND ASSOCIATED BURROWS IN THE TABLE MOUNTAIN GROUP

Cocks *et al.* (1970) described marine invertebrate body fossils from the Table Mountain Group. They concluded that the horizon is uppermost Ordovician in age and they estimated that the stratigraphically lower Graafwater Formation, which has yielded most of the "trilobite" tracks, is Early Ordovician.

Not all the trackways in the Table Mountain Group can be referred to *Petalichnus capensis*. Most of the walking trails in which the tracks are a variable distance from one another and from the midline of the trackway probably belong in the ichnospecies (e.g. Figure 8a): the youngest trackways occurring in the Peninsula Formation at Matjiesgoedkloof (Figure 8c; Rust, 1967, Pl. 14 -D) fall into that category. However, even with the expanded definition, there are some trackways that are obviously different, notably Rust's (op. cit.) individuals D, E, H and I. There is no illustration of H, but in the other three the tracks are evenly spaced in straight rows. In trackway D the two rows and the component tracks in them are far apart, while in trackway E the rows and tracks are both relatively close together. These two trackways (c and g in Figure 3) are on the Brandenburg slab; trackway I is from Tierhoek. It has two continuous parallel median drag lines (Figure 8b).

The sediment in which the Table Mountain trackways are recorded is usually too coarse to allow the preservation of fine detail. Nonetheless, at Helderberg near Somerset West and in the vicinity of Stellenbosch there are some tracks that show striations along their long axes. These are each preserved as moulds on the sole of a sandstone which overlay a shale horizon, while the other examples are all impressions on the upper surfaces of sandstone beds. This difference could account for the finer detail, the original impressions having been made in finer sediment. Although no track cycles can be discerned in the museum specimens (B.P.I.P.R. casts Hb./C.T. 1 and St./C.T. 1) it is likely that these striated tracks were left by the animals responsible for the *Petalichnus capensis* trackways.

The *Metaichna rustica* burrows are more widely preserved than the associated trackways, largely because they are more robust structures. The coarse material filling the cones includes ". . . shale gritty sand with pebbles 5—6 mm in diameter at Gansekraal, Worcester" (Rust, 1967, p. 65). The structures stand proud or weather out to form hollows depending on the relative cohesion of the infill. Rust (ibid.) observed that "On the Brandenburg bedding plane the filling of the burrows projects above the bedding surface, thereby indicating that the burrows were dug from a higher level than the surface on which the tracks occur." This is not necessarily so as trackways frequently are preserved as "undertracks" made by the walking appendages penetrating the substrate and intersecting buried laminae just below the free surface (Goldring and Seilacher, 1971). As a result, the burrows could have commenced from the surface on which the arthropods walked.

THE POSSIBLE ORIGIN OF THE *PETALICHNUS CAPENSIS* TRACKWAYS AND THE *METAICHNA RUSTICA* BURROWS

There are four arthropod subphyla in which as many as nine pairs of limbs are employed in walking: the Onychophora, the Trilobita, the Myriapoda and the crustacean Malacostraca.

Taljaard (1958, p. 60; 1962, p. 27) decided that the Table Mountain Group arthropods most probably were trilobites. Rust (1967, p. 67) reached the same conclusion, and Seilacher confirmed that opinion in a private communication. The association of the trackways with burrows apparently atypical of trilobite activity and the absence of the characteristic

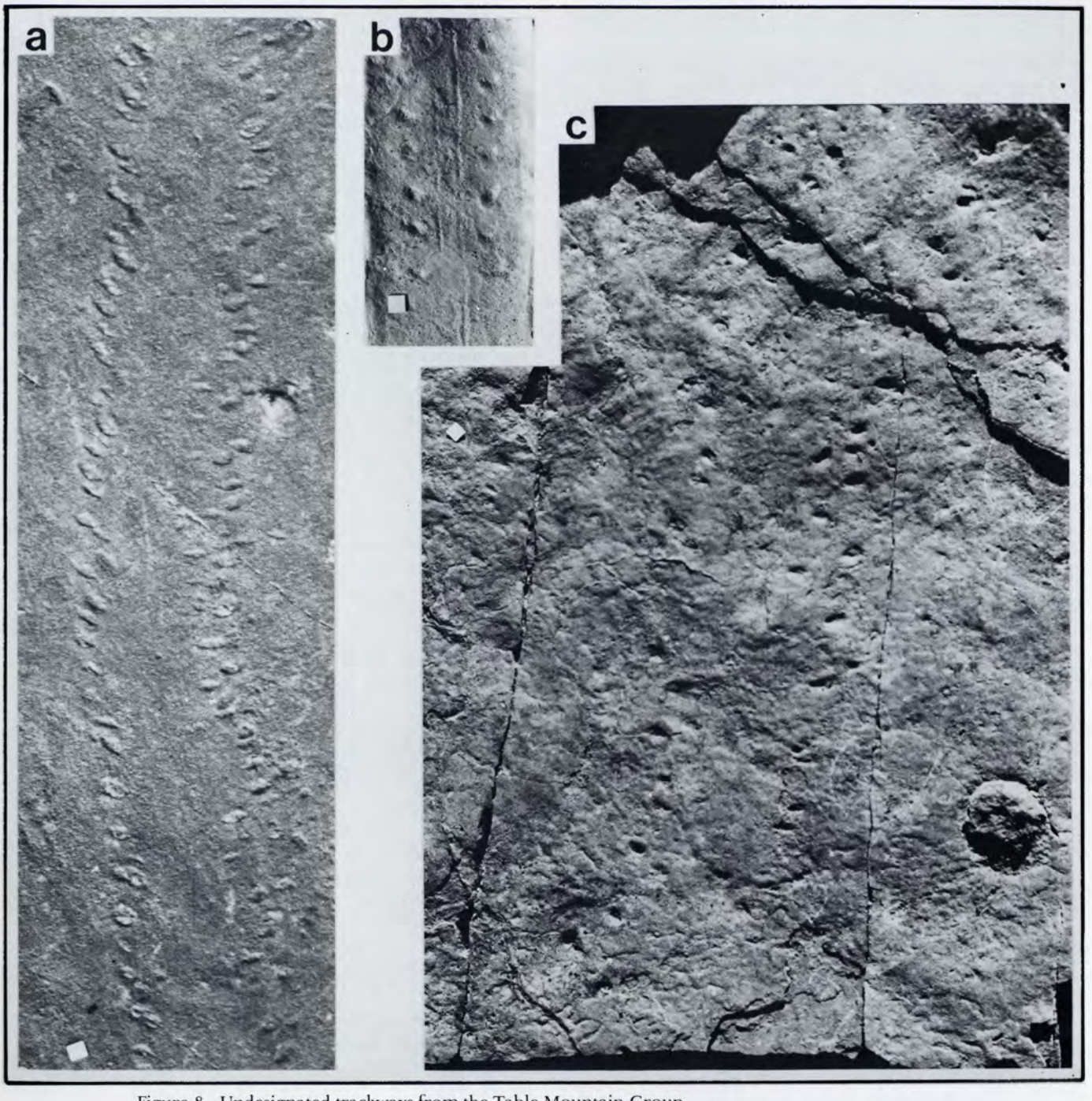


Figure 8. Undesignated trackways from the Table Mountain Group.
(a) Trackway on the Brandenburg slab (not included in Figure 2) with individual tracks a variable distance from one another and from the midline of the trail (x0,33).
(b) Trackway from Tierhoek with opposite paired tracks and a double median drag line (x0,33).
(c) This trackway from Matjiesgoedkloof is slightly younger than the others figured. It has its individual tracks a variable distance from one another and from the midline of the trail, but no cycle is discernible. Note the *Metaichna rustica* burrow on the right (x 0,25).

"raking" tracks cast some doubt on this identification.

The Myriapoda are not particularly promising candidates because they usually have identical legs which pivot on the substrate at a generally constant distance from the animal's axis of bilateral symmetry. In the Diplopoda the legs are very numerous and those on each side produce a continuous furrow rather than individual tracks; in the Chilopoda there are fewer legs, but the footprints on one side are often all superimposed, with the composite "tracks" on one side alternating with those

on the other, simulating the trackway of a bipedal animal (cf. Manton, 1952).

The more "primitive" Onychophora produce overlapping natural cycles similar to those in *Petalichus capensis*, but as their speed increases they superimpose their footprints to produce identical composite "tracks" which may be opposite or alternate (Manton, 1950). The undesignated trackways in the Table Mountain Group could bear the same relationship to *P. capensis*. However, until examples are found which exhibit both forms in one trackway, any relationship between the more common *P. capensis* trails and those with little differentiation between individual tracks must remain speculative.

The Malacostraca, like the Trilobita, have a posteriorly decreasing distance between the distal tips of opposite limbs; this is suitable for the production of a tapering natural cycle of tracks. Seilacher (1955; 1959) considered the direction of movement of creatures responsible for walking trails in which the tracks in one natural cycle are arranged in a "V". Where there are more than four pairs of tracks involved it does seem unlikely that there would be sufficient overstepping to form the long-armed acute-angled "V" developed in *Petalichnus* trails: he concluded that the trackway probably reflects the taper of the limb extremities directly and that the angle of the "V" points backwards. Osgood (1970, p. 351) did not altogether agree, stressing that while Seilacher's hypothesis is logical, it is nevertheless only a theory. Crimes (1970) and Bergström (1973) supported Seilacher's theory.

The *Metaichna rustica* burrows are as enigmatic as the associated trackways. Taljaard (1962) supposed that they were:

> ". . . nests, scooped out for 'egg repositing'. *Limulus*, a present-day distant relative of trilobites, still does that. The hollows could also be the hollows scooped out in search of food, but their small number militates against such a suggestion."

The structures are in fact numerous in some beds, so Rust (1967) favoured the interpretation as feeding burrows (pascichnia), but he noted that they

> ". . . differ from those ascribed by Seilacher (1959; 1960; 1967) to trilobites in that the burrows . . . are not elongated scooped out grooves, but are hemispherical hollows which show no digging marks or any internal structures."

The lack of digging marks and internal structures admittedly could be a preservational feature; the Table Mountain Group sediment is very coarse-grained and not generally suitable for the preservation of fine detail. Rust (pers. comm.) argues that the very coarse nature of the infill might have been the result of an active winnowing away of the finer sediment particles during feeding.

Another explanation is suggested by the extant isopod *Tylos granulatos* Krauss which gains temporary shelter by burying itself backwards in dry beach sand: it rotates around its firmly down-turned tail and a conical or hemispherical depression is produced. The Table Mountain Group conical burrows are also in coarse sediment, and they might have originated in the same way. The heavier particles in the subsequent influx of sediment would accumulate in the open hollows, thus accounting for the relatively coarser infill in the burrows. However, the substrate would need to be damp, at least, for the walls to be sufficiently cohesive to survive an overflow of water bearing coarse detritus.

This interpretation of the *Metaichna* burrows lends support to the Malacostraca as possible authors of the *Petalichnus capensis* trackways. Nevertheless, the evidence is far from conclusive, and it may well be that trilobites or other early arthropods were responsible. It is not even certain that burrows and trackways were made by the same animals; it is only the similar widths of the two traces that provokes the inference.

ACKNOWLEDGEMENTS

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Palaeont. afr., **18**, 47—52 (1975)

TRACE FOSSILS IN THE ECCA OF NORTHERN NATAL AND THEIR PALAEOENVIROMENTAL SIGNIFICANCE

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ABSTRACT

Because of the rarity of body fossils in the Ecca Group fossil burrows, tracks and trails are of potential value in supplementing primary sedimentary evidence concerning the palaeoenvironmental factors of bathymetry, energy level and food supply. The three most important ichnogenera are *Skolithos*, *Corophioides* and *Scolicia*. The first two are restricted to the upper portions of Middle Ecca upward-coarsening regressive cycles attributed to delta progradation. They are representatives of Seilacher's (1967) *Skolithos* and *Glossifungites* communities, indicating shallow water conditions with diastems. *Scolicia* occurs at lower levels in the cycles and corresponds to Seilacher's deeper water *Cruziana* community. Meandering trails *Helminthopsis* and *Taphrhelminthopsis* in the Lower Ecca belong to Seilacher's deep water *Nereites* community. Less common ichnogenera include the U-burrows *Diplocraterion* and *Rhizocorallium*. It has proved impossible positively to identify many trace fossils such as short ramifying burrows, chevron trails, dumbell-shaped surface impressions, digitate tracks and problematic elliptical casts. Trace fossils have not been recognised with certainty in the fluviatile deposits which comprise the bulk of the coal-bearing strata of northern Natal.

INTRODUCTION

The Ecca Group of the Karroo Supergroup (provisional stratigraphic nomenclature pending recommendations of S.A.C.S.) has been studied in the region extending northwards from Pietermaritzburg to the Transvaal border (Hobday, 1973; Hobday, Tavener-Smith and Mathew, in press; Hobday and Mathew, in press). In the course of these investigations it has become evident that a significant relationship exists between some of the trace fossils and the lithology and sedimentary structures with which they are associated. Body fossils have rarely been encountered in these rocks (see Rilett, 1963; McLachlan, 1973), and apart from these few specimens further biological indications of the nature of the palaeoenvironment are dependent entirely upon trace fossils which are fortunately common.

The Middle Ecca has been attributed by Hobday and co-workers to the southward progradation of deltaic and fluviatile complexes. These clastic wedges apparently overrode the Lower Ecca epicontinental platform facies of mud and silt. The deltaic deposits are distinguished, among other characteristics, by the presence of numerous trace fossils. The regressive deltaic sequences are vertically repetitive, and certain varieties of burrows and trails tend to recur at particular levels within a given cycle. Except for occasional rootlet markings and fragments of lithified wood, biogenic structures are absent from most fluviatile deposits.

It follows from the above statement that trace fossils in the Middle Ecca are not only of intrinsic descriptive interest, but may also be used for predictive purposes. In limited exposures of incomplete cycles they can be used, in conjunction with other sedimentary criteria, to recognise the position of the strata within the modal cycle (Figure 1).

THE MODAL UPWARD-COARSENING REGRESSIVE CYCLE

These cycles vary in thickness from 30 to over 150 metres. At the base of the lowermost cycle, which extends into the Lower Ecca, are shelf mudstones. Above these, and forming the basal component of each succeeding cycle, are considerable thicknesses of alternating thin beds of siltstone and sandstone in roughly equal proportions. A prodelta environment, in which gentle tractional processes alternated with suspensional settling of fines, is envisaged for these rocks. Overlying them are cross-laminated and/or horizontally-laminated sandstones of the distal distributary mouth bar facies. These pass upward into coarse-grained, cross-bedded and massive sandstones of the proximal mouth bar and distributary channel.

In addition to the above pattern of beds there are thinner, less regular upward-coarsening cycles averaging under 10 metres in thickness. These are attributed to deposition in interdistributary embayments and delta plain depressions. In these cases the siltstones are highly carbonaceous and coarsen upward by the progressive intercalation of erosively-based, cross-laminated to massive, lenticular sandstones of crevasse origin. These sequences may include finely-laminated, oxidised, root-penetrated levee splay sandstones.

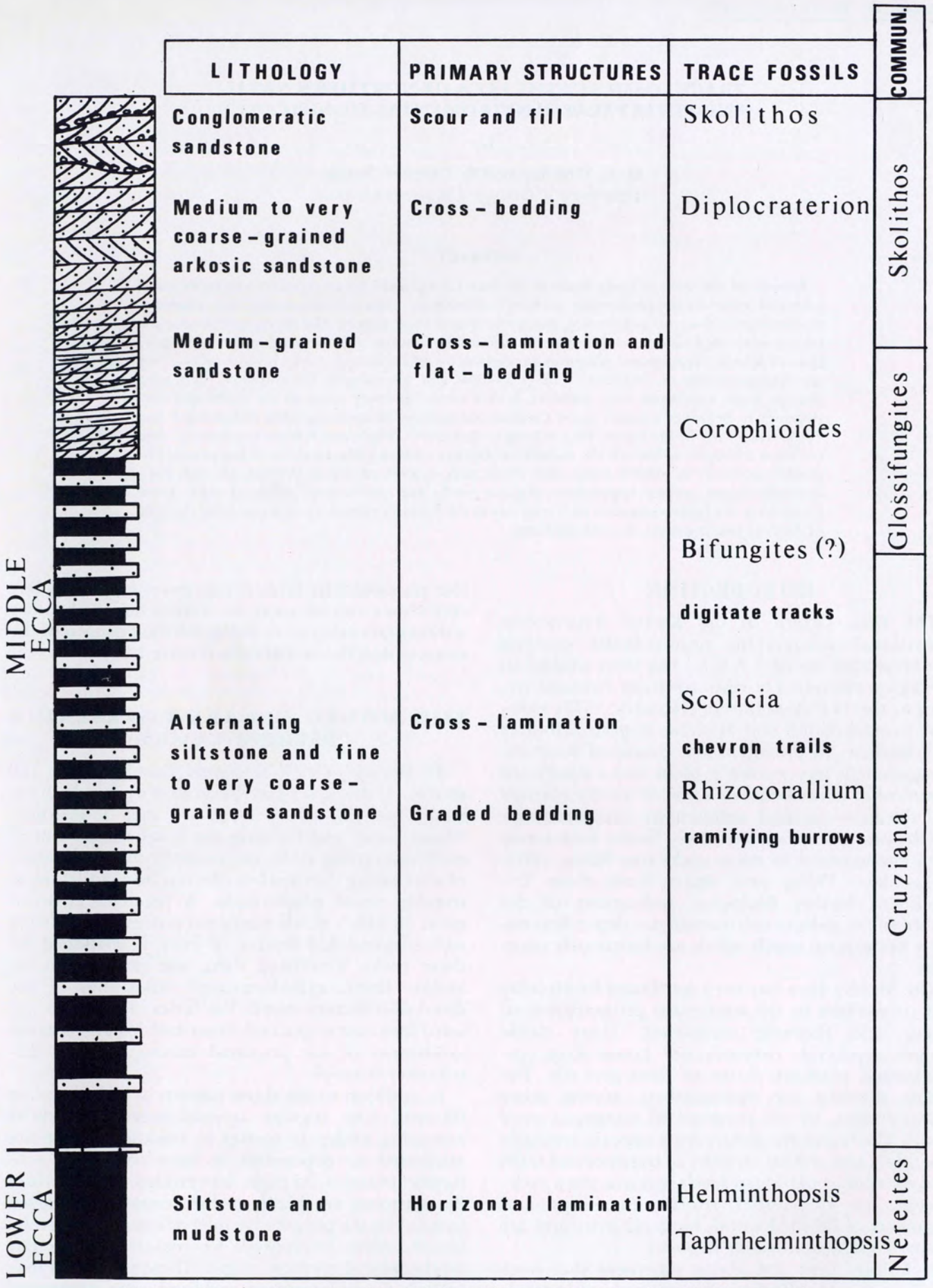


Figure 1. The top of the Lower Ecca and the modal regressive cycle of the Middle Ecca with associated primary structures, trace fossils and Seilacher community.

TRACE FOSSILS

Description and Possible Mode of Origin

(i) Ichnogenus *Skolithos* Haldeman, 1840

These structures are vertical, unbranching tubular burrows between 6 and 20 mm in diameter, and up to 30 cm long. Two subtypes are recognised in the Middle Ecca. The first is circular in transverse section with an axial filling of structureless sandstone which is surrounded by one or more dark bands of sandy carbonaceous mustone (Figure 2). An outer concentric band of light coloured sandstone is also commonly present. The burrows are closely spaced and more or less equidistant. They bear strong resemblance to the well-known "pipe-rock" in the lower Cambrian of north-west Scotland. The second variety may be circular to irregularly elliptical in transverse section. Concentric banding is only weakly developed or absent. The tubes are very closely spaced, and may be mutually interpenetrant.

Skolithos tubes were recognised as *domichnia* by Seilacher (1964), in that they afforded permanent shelter to animals which procured food from above the water-sediment interface. Hallam and Swett (1966) attributed such burrows to suspension-feeding worm-like organisms.

(ii) Ichnogenus *Corophioides* Smith, 1893

Vertically disposed U-shaped burrows corresponding to this ichnogenus have a width between the two arms of the burrow approximately equal to its depth (6–10 cm). The tube limbs are parallel in some cases, but in others are symmetrically inclined. The latter may have resulted from erosion of the sediment containing the upper vertically-disposed portions of the limbs. Spreiten are well developed (Figure 3). According to Seilacher (1967) the growth of these structures represents an adjustment to the increasing size of the inhabitants of the *domichnia*. Alternatively, vertical migration of the burrow through the sediment may have been accompanied by backfilling.

(iii) Ichnogenus *Diplocraterion* Torell, 1970

These long narrow vertical U-tubes have been positively identified only in cores from the Middle Ecca. It is likely that the very fine spreiten are rapidly obliterated in outcrop by weathering.

(iv) Ichnogenus *Rhizocorallium* Zenker, 1836

Narrow U-tubes of this type, oblique or parallel to the bedding (Figure 4), are seldom well preserved. Faint spreiten are the product of feeding activities (Häntzschel, 1962, p. 210) which involved the excavation of sediment which was subsequently repacked in the apex of the U-bend. These burrows therefore correspond to Seilacher's (1967) *fodinichnia*.

(v) Ichnogenus *Scolicia* de Quatrefages, 1849

These trails occur in a variety of forms preserved in convex epirelief (on the top of a sandstone bed). Some show well-developed lateral lobes (Figure 5). Others appear as relatively featureless bands with faint laterally convex striations extending across the entire width (Figure 6). The trails range between 2 mm and 4 cm in width.

The grain size of the material comprising the trail is usually somewhat coarser than that of the surrounding sediment. These traces are probably the sole trails of gastropods which ploughed through the sediment in search of food.

(vi) Ichnogenus *Helminthopsis* Heer, 1877

According to Ksiazkiewicz (1970) this ichnogenus, as amended by Sacco (1888, p. 174), includes irregularly meandering sole trails. Such forms occur infrequently in the Lower Ecca as semi-cylindrical tubes up to 3 mm in diameter (Figure 7). Some are partly pyritised.

(vii) Ichnogenus *Taphrhelminthopsis* Sacco, 1888

This group includes all meandering trails with a central furrow. Good examples have been documented in the Ecca by Hosking (1973).

(viii) Other trace fossils of unknown ichnogenera

It has proved impossible to classify many of the biogenic structures encountered. Some traces display no distinctive features while others are rendered unidentifiable as a result of interpenetration. Intense bioturbation has rendered certain sandstones almost structureless. Such activity belies the generally held impression that Ecca sediments contain little evidence of the former existence of animal life. Nondescript endichnial burrows and exichnial casts (nomenclature of Martinsson, 1970, p. 327) are particularly common. Some of these have a distinct spiral form (Figure 8). Short near-vertical tubular burrows in arenaceous material are in many cases seen to ramify on reaching fine-grained organic rich sedimentary laminae to form an extensive complex of horizontal burrows.

Chevron trails, seldom exceeding 2 mm in width and 8 cm in length, occur as traces on the upper surfaces of sandstone beds. The trails are straight or slightly curving, with angular intersections and random orientation. Sole trails, preserved in positive hyporelief (on the base of a sandstone bed) are sometimes bunched after the manner of *Phycodes* (see Häntzschel, 1962, p. 206).

Dumb-bell-shaped surface impressions, superficially resembling *Bifungites,* occur in large numbers on certain sandstones (Figure 10). The spheres at the extremities of the dumb-bell are, however, much smaller than those illustrated by Häntzschel (1962, p. 186). Excellent examples from the Ecca have been illustrated by Hosking (1973, Figure d. vi.).

Digitate tracks in positive hyporelief (Figure 11) appear to be crawling impressions or repichnia, possibly to be associated with arthropod-type

animals. The tracks are occasionally paired, with a spacing of between 2 and 4 cm, but most have an apparently disordered arrangement. Each impression consists of 3 to 5 divergent rays between approximately 0,5 and 2 cm long.

Problematic casts in mudstone, illustrated in Figure 9, are possibly of biogenic origin. They take the form of flattened triaxial ellipsoids lying in the plane of the bedding. A longitudinal depression is commonly present in both the upper and lower surfaces. This axis is the origin of very large numbers of closely-spaced radiating striae which cover the entire surface of the cast. These structures were first interpreted as concretionary bodies, but this seems unlikely since those examined were compositionally identical with the surrounding mudstone. Neither are they fossilised vegetal material.

Distribution of Trace Fossils in the Modal Upward-Coarsening Regressive Cycle

All the forms described, apart from *Helminthopsis*, *Taphrhelminthopsis* and the problematic elliptical casts, were encountered in the upward-coarsening sequences of the Middle Ecca. The three exceptions are all from the Lower Ecca, but these are of infrequent occurrence and sporadic in their distribution.

The vertical distribution of trace fossils within a cycle follows a particular pattern. There is a predominance of horizontal types such as *Scolicia*, chevron trails, *Rhizocorallium* and *Bifungites* (?) in the lower prodelta alternations of siltstone and mudstone. These strata also contain occasional digitate tracks and the vertical burrows with ramifying horizontal extensions.

Corophioides occurs within the uppermost alternating beds, but is more common within the cross-laminated and horizontally-laminated sandstones above. These trace fossils are generally concentrated at particular horizons. There is an upward increase in the abundance of *Skolithos* from the alternating beds to the cross-bedded sandstones at the top of a cycle. The upper limit of the cycle, where sandstone is succeeded by siltstone of the overlying cycle, is commonly riddled with these burrows. *Diplocraterion* appears to be confined to the cross-bedded sandstones.

Palaeoenvironmental Significance of Trace Fossil Distribution

As pointed out by Seilacher (1967) trace fossil morphology is controlled by the behavioural rather than the anatomical characteristics of organisms. Almost identical trace fossils may be produced by quite different animals, representing a similar response by these animals to the same environment. Seilacher (op. cit.) stressed the bathymetric significance of trace fossil assemblages. He maintained that the *Skolithos* and *Glossifingites* communities are associated with littoral sands and omission surfaces respectively, that the *Cruziana* community reflects epicontinental platform deposits, and that the *Zoophycos* and *Nereites* communities occur in progressively deeper water facies.

Representatives of the *Skolithos*, *Glossifungites* and *Cruziana* communities are present in the Middle Ecca, while the *Nereites* community is recognised in the Lower Ecca, which was of deeper water origin. Deep vertical burrows such as *Skolithos* and *Diplocraterion* are characteristic of shallow water. Their position near the top of each of the Middle Ecca regressive cycles confirms the contention that these sediments were deposited on proximal, shallow water, distributary mouth bars.

Burrows such as *Corophioides* were the shelters of filter-feeding organisms of the *Glossifungites* community. These burrows were not subjected to appreciable erosion or sedimentation and their concentration at certain levels is in each case indicative of a depositional hiatus. Such horizons are common in the lower distal distributary mouth bar facies where there was a seasonal reduction in sediment influx and little reworking of the material by waves or currents.

The ramifying feeding burrows associated with the *Cruziana* community indicate that the organisms burrowed vertically until they encountered nutrient-rich organic layers, which they followed laterally. Other feeding furrows, such as *Scolicia* and chevron trails, were produced by the reworking of surface layers. Seilacher (op. cit.) pointed out that a greater volume of sediment can be processed if the furrowing follows a winding, digitate or helicoid pattern. All these trace fossils belonging to the *Cruziana* community occur most abundantly in the fine-grained prodelta facies, generally between 20 and 80 metres below the top of a cycle.

Crimes (personal communication) commented that he has observed *Scolicia* very similar to the example shown in Figure 5 in the Eocene flysch of northern Spain. It is possibly unusual to find these traces in relatively shallow water deposits of the Ecca.

The *Nereites* traces of the Lower Ecca are also somewhat anomalous in this respct although these shales have been ascribed to a deep water environment by Ryan (1967, p. 199). However, a maximum water depth of no more than a few hundred metres at most is indicated by the thickness to the top of the lowermost delta-front sandstone. Even allowing for the effects of sediment compaction and possible shallowing, water depth was certainly only a small fraction of that usually occupied by this community.

As Crimes (1970) has pointed out, however, the factors which control behavioural responses in organisms are energy conditions, substrate type and the nature of the food supply. While these parameters are to a large degree depth-dependent

there may be exceptions, as in sheltered shallow water, where conditions strongly resemble those of deeper water environments. This is consistent with the observation that in the north-eastern part of the Karroo Basin the only evidence of high energy processes is that which is associated with fluvial discharge. We have encountered no features indicative of even weak wave activity. Furthermore there is no evidence of tidal processes, and the effects of offshore currents appear to have been negligible.

ACKNOWLEDGEMENTS

Dr. T. P. Crimes of Liverpool University kindly commented on photographs of certain trace fossils. We are grateful to the C.S.I.R. for a grant awarded to R.T.-S. which helped to finance the field investigations. David Mathew assisted in the field and with photography.

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Explanation of Figures 2—11 (see next page).

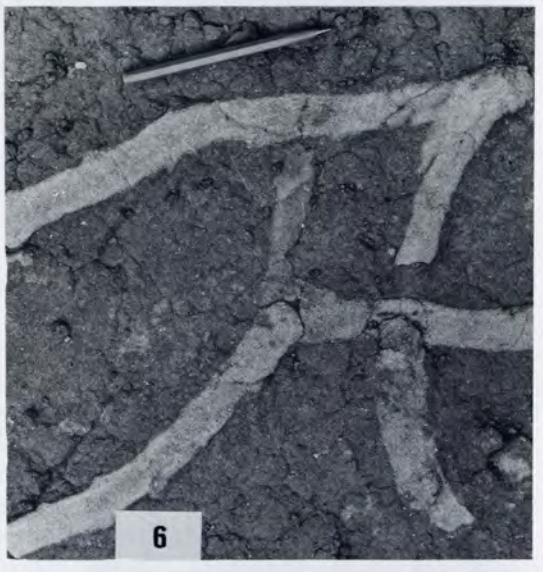
Figure 2. Bedding plane exposure of *Skolithos.*
Figure 3. *Corophioides* with well-developed spreiten.
Figure 4. *Rhizocorallium*, a horizontal U-tube.
Figure 5. *Scolicia* with clearly defined lateral lobes. x1.
Figure 6. Bedding plane exposure of intersecting *Scolicia* trails.
Figure 7. *Helminthopsis* preserved in convex epirelief on sandy parting near top of Lower Ecca.
Figure 8. Vertical spiral burrow. x2.
Figure 9. Problematic elliptical cast preserved in convex epirelief in Lower Ecca mudstone.
Figure 10. Dumb-bell-shaped surface impressions on bedding plane.
Figure 11. Digitate scratch marks preserved in positive hyporelief with *Skolithos.*


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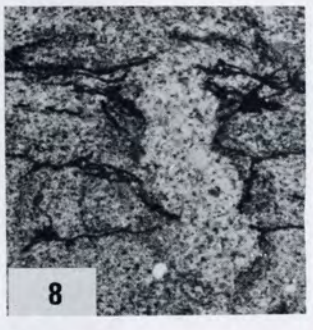

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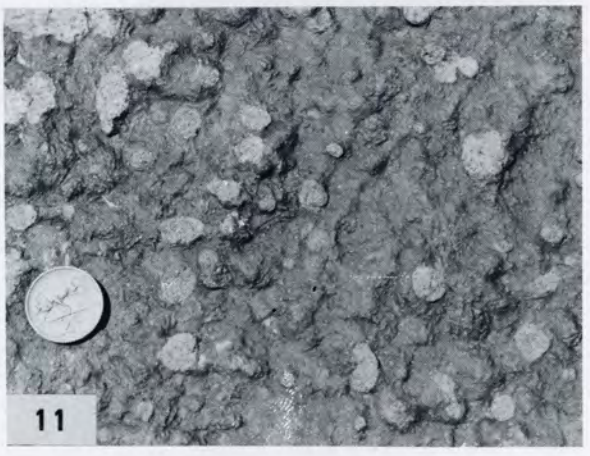

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Palaeont. afr., **18**, 53—69 (1975)

PLANKTONIC FORAMINIFERA AND CALCAREOUS NANNOFOSSILS AT THE CRETACEOUS-TERTIARY CONTACT IN ZULULAND

by

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ABSTRACT

Assemblages of planktonic foraminifera and calcareous nannofossils for the Maestrichtian and Danian of Zululand are listed and illustrated. The *Globotruncana gansseri* and *G. mayorensis* foraminiferal zones are present in the Maestrichtian. The *Globigerina triloculinoides* and *Globorotalia compressa* foraminiferal subzones are present in the Danian. The Maestrichtian in this area cannot be subdivided on the basis of calcareous nannofossils. Danian nannofossil zones present are those of *Cruciplacolithus tenuis* and *Chiasmolithus danicus*. The Cretaceous-Tertiary faunal extinctions are briefly discussed and it is concluded that lowered temperatures were a factor in this extinction.

INTRODUCTION

The presence of lowermost Tertiary sediments in Zululand was first noted by Orr and Chapman (1974) who reported early Paleocene planktonic foraminifera from an excavation at Richards Bay. Maud and Orr (in press) described the subsurface stratigraphy of the Richards Bay area and listed some of the more important species of planktonic foraminifera present in the uppermost Cretaceous and lowermost Tertiary. Numerous test boreholes have since revealed that a narrow belt of early Paleocene sediments is present in the subsurface parallel to the coast. Several of these boreholes passed through the Cretaceous-Tertiary (Maestrichtian-Danian) contact and from two of these boreholes (see location map, Fig. 1), a continuous sequence of core was recovered.

This is the only known area on land in southern Africa where the Maestrichtian-Danian contact occurs although similar contacts have been extensively studied in other parts of the world. The purpose of this paper is to document the assemblages of the two most important microfossil groups — the planktonic foraminifera and the calcareous nannofossils — within this interval in Zululand.

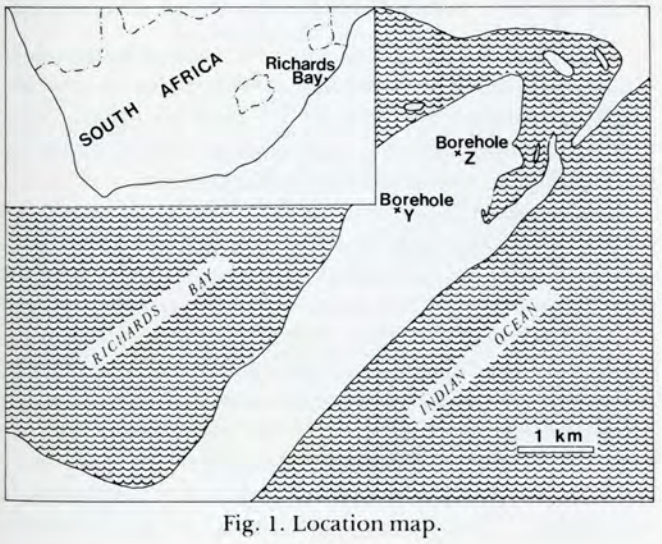


Fig. 1. Location map.

ZONATION

Postuma (1971) erected a threefold division for the Maestrichtian based on planktonic foraminifera. For the Danian, he recognized a single zone of *Globigerina daubjergensis*. Berggren (1969) subdivided the *G. daubjergensis* zone into three subzones.

There is as yet no satisfactory nannofossil zonation for the Maestrichtian. Martini's (1970) nannofossil zonation is used for the Danian. The zonations are shown in Fig. 2. Original zone names are used although the species *Globotruncana mayorensis*

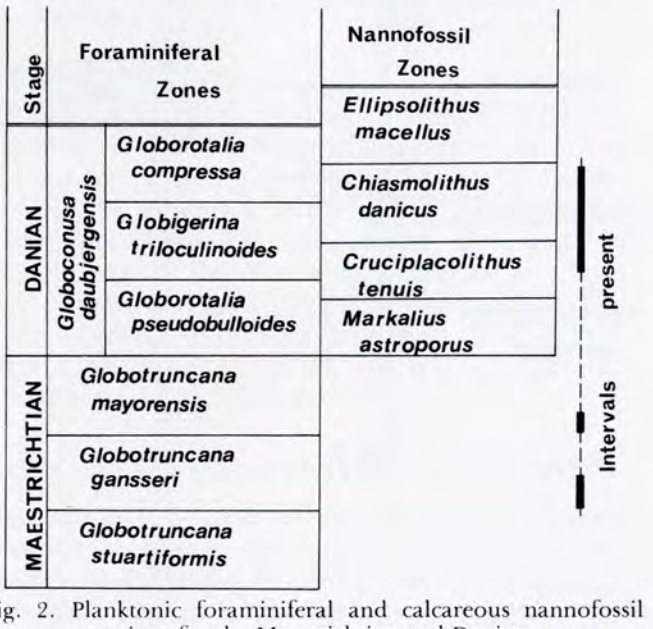


Fig. 2. Planktonic foraminiferal and calcareous nannofossil zonations for the Maestrichtian and Danian.

is usually placed in the genus *Abathomphalus* and *Markalius astroporus* is considered to be a junior synonym of *M. inversus*.

Borehole Z was sampled at one metre intervals and Borehole Y at three metre intervals. Borehole Z had a collar elevation of 4 m above sea level with first sample recovered at 18 m and total depth of 92 m. Borehole Y with a collar elevation of 5 m above sea level was drilled to 103 m with top samples at a depth of 30 m. The zones encountered and their depths are shown in Fig. 3.

Both boreholes bottomed in the middle Maestrichtian foraminiferal zone of *Globotruncana gansseri* which extended upward to 67 m in Borehole Z and 58 m in Borehole Y. The presence of *Globotruncana fornicata* and *G. stuarti* throughout this interval indicates that only the lower portion of the zone is present. Above the *G. gansseri* zone, there was a 1 m thick interval in both boreholes containing a microfauna of the uppermost Maestrichtian zone of *Globotruncana mayorensis*. A few specimens of *Globotruncana arca* were present, suggesting that the interval falls into the lower portion of the zone.

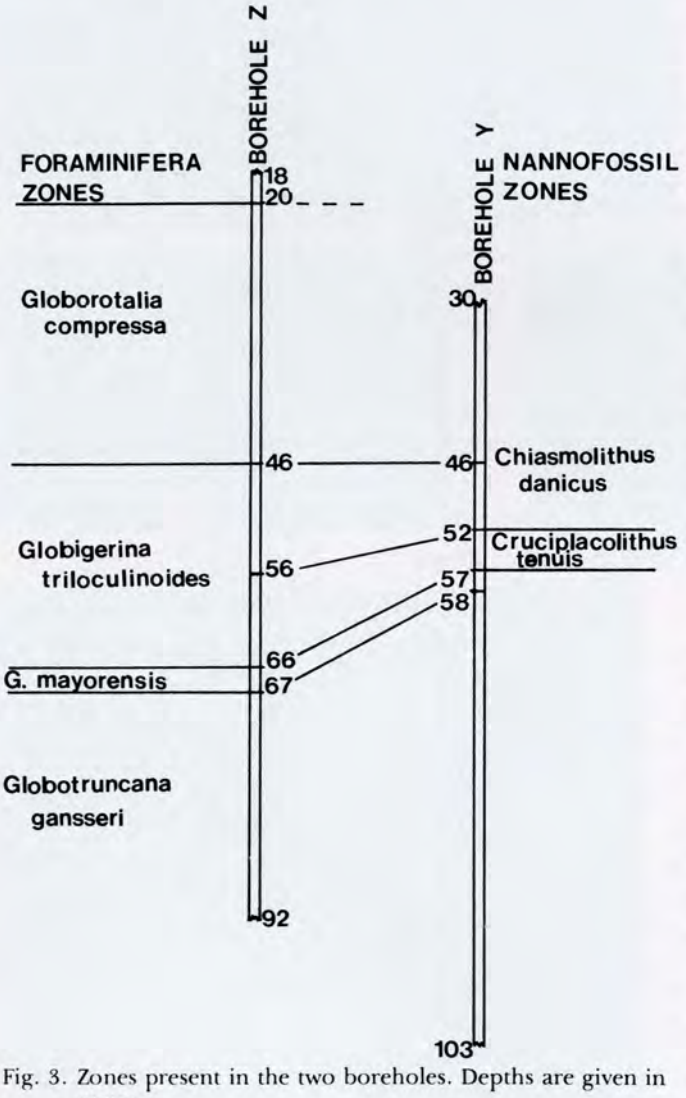


Fig. 3. Zones present in the two boreholes. Depths are given in metres.

Nannofossils in both foraminiferal zones were virtually identical. *Tetralithus pyramidus* and *Zygolithus rhombicus* were present in the *G. gansseri* zone but not in the *G. mayorensis* zone. However, both species were extremely rare and their presence or absence cannot be considered significant.

Above the Maestrichtian, the middle Danian foraminiferal subzone of *Globigerina triloculinoides* was present to 46 m in both boreholes. The *Globorotalia compressa* subzone extended from 46 m to the uppermost sample at 30 m in Borehole Y and to 20 m in Borehole Z. In the latter borehole, a few metres of unfossiliferous sand occur above the Danian.

The lowermost Danian samples (66 m in Borehole Z and 57 m in Borehole Y) were within the *Cruciplacolithus tenuis* nannofossil zone which extended upward to 56 m in Borehole Z and 52 m in Borehole Y. Above this, all Danian material was within the *Chiasmolithus danicus* zone.

Deposition during the Danian appears to have been continuous. There are no abrupt changes in assemblages to suggest hiati.

The hiatus at the Maestrichtian-Danian contact extends from within the *G. mayorensis* zone, through the *Globorotalia pseudobulloides* subzone and into the *Globigerina triloculinoides* subzone. The absence of the *Globorotalia pseudobulloides* foraminiferal subzone is confirmed by the absence of the nannofossil zone of *Markalius astroporus*.

The absence of the upper portion of the *Globotruncana gansseri* zone indicates a second hiatus between that zone and the overlying zone of *G. mayorensis*. Although neither borehole penetrates below the *G. gansseri* zone, the absence of the lowermost Maestrichtian zone of *G. stuarti* elsewhere in Zululand suggests that there may be a third hiatus lower in the succession.

The persistence of the thin *G. mayorensis* zone throughout the area suggests that the hiati are depositional rather than erosional.

NOTES ON NANNOFOSSIL OCCURRENCES

There are a number of known cases of anomalous chronological distributions of nannofossil species. Such anomalies are caused by provincialism, local environmental factors, reworking, faulty observation and inadequate stratigraphic control.

Chiasmolithus bidens and *Toweius craticulus* were present in the *Chiasmolithus danicus* zone although both Gartner (1971) and Perch-Nielsen (1972) indicate that the species do not occur until the overlying zone of *Ellipsolithus macellus*. Perch-Nielsen (1972) indicates *Braarudosphaera discula* as restricted to Danian or younger, but the species was common in the Maestrichtian of Zululand. *Micula staurophora* has been reported throughout the Tertiary but such reports are generally considered to be examples of reworking. The species was present in the Zululand

Danian, even in samples which contained no other Cretaceous species, and it is possible that it does extend into the Tertiary.

The uniformity of the nannofossil assemblages in the upper two Maestrichtian foraminiferal zones indicates that these zones cannot be separated on a nannofossil basis in this area. Characteristic early Maestrichtian species such as *Arkhangelskiella parca, Microrhabdulus decoratus* and *Tetralithus obscurus* were not seen in the *Globotruncana gansseri* zone.

ASSEMBLAGES

No new species were seen and the author would be sceptical of the existence of undescribed species in a portion of the section which has been so frequently studied. Perhaps more significant is the absence of many characteristic Maestrichtian species: *Globotruncana conica, G. falsostuarti, Rugoglobigerina rotundata, Kamptnerius magnificus, Ceratolithoides kamptneri* and *Tetralithus* spp. The species present are listed in Tables 1 and 2 and are illustrated in the plates.

Worsley (1974) used the presence of *Abathomphalus mayorensis* and *Racemiguembelina fructicosa* together as an indicator of the tropical zone. Other planktonic foraminifera and the calcareous nannofossils in the Maestrichtian are consistent with this interpretation. This would place the southern boundary of the tropical zone somewhat farther south than indicated by Worsley. Danian assemblages are fairly uniform from the tropics into the temperate zone and little can be said of Danian water temperatures. The relative abundance of both groups in the borehole samples indicates normal marine conditions, probably inner to middle neritic.

Table 1
Species of planktonic foraminifera present.

ZONES				
G. gansseri	*G. mayorensis*	*G. triloculinoides*	*G. compressa*	
+				*Globotruncana fornicata* Plummer
+				*Globotruncana marginata* (Reuss)
+				*Globotruncana stuartiformis* Dalbiez
+				*Globotruncana tilevi* (Brönnimann & Brown)
+				*Heterohelix plummerae* (Loetterle)
+				*Heterohelix pulchra* (Brotzen)
+	+			*Globigerinelloides aspera* (Ehrenberg)
+	+			*Globigerinelloides messinae* (Brönnimann)
+	+			*Globigerinelloides subpetaloidea* (Gandolfi)
+	+			*Globotruncana arca* (Cushman)
+	+			*Globotruncana contusa* (Cushman)
+	+			*Globotruncana gagnebini* Tilev
+	+			*Globotruncana gansseri* Bolli
+	+			*Globotruncana leupoldi* Bolli
+	+			*Globotruncana rosetta* (Carsey)
+	+			*Globotruncana stuarti* (de Lapparent)
+	+			*Heterohelix carseyae* (Plummer)
+	+			*Heterohelix glabrans* (Cushman)
+	+			*Heterohelix globulosa* (Ehrenberg)
+	+			*Heterohelix ornatissima* (Cushman & Church)
+	+			*Heterohelix striata* (Ehrenberg)
+	+			*Planoglobulina acervulinoides* (Egger)
+	+			*Rugoglobigerina macrocephela* Brönnimann
+	+			*Rugoglobigerina rugosa* (Plummer)
	+			*Abathomphalus mayorensis* (Bolli)
	+			*Globigerinelloides subcarinata* (Brönnimann)
	+			*Racemiguembelina fructicosa* (Egger)
	+			*Trinitella scotti* (Brönnimann)
		+	+	*Globigerina triloculinoides* Plummer
		+	+	*Globoconusa daubjergensis* (Brönnimann)
		+	+	*Globorotalia pseudobulloides* (Plummer)
			+	*Globorotalia compressa* (Plummer)
			+	*Chiloguembelina morsei* (Kline)

Table 2
Species of calcareous nannofossil present.

ZONES				
G. gansseri	*G. mayorensis*	*C. tenuis*	*C. danicus*	
+				*Tetralithus pyramidus* Gardet
+				*Zygolithus rhombicus* Stradner & Adamiker
+	+			*Actinozygus splendens* (Deflandre)
+	+			*Ahmuellerella octoradiata* (Gorka)
+	+			*Arkhangelskiella cymbiformis* Vershina
+	+			*Corollithion exiguum* Stradner
+	+			*Cretarhabdus conicus* Bramlette & Martini
+	+			*Cretarhabdus decorus* (Deflandre)
+	+			*Cribrosphaerella ehrenbergi* (Arkhangelsky)
+	+			*Cylindralithus gallicus* (Stradner)
+	+			*Deflandrius cretaceus* (Arkhangelsky)
+	+			*Deflandrius intercisus* (Deflandre)
+	+			*Deflandrius spinosus* Bramlette & Martini
+	+			*Eiffellithus turriseiffeli* (Deflandre)
+	+			*Lithraphidites quadratus* Bramlette & Martini
+	+			*Markalius circumradiatus* (Stover)
+	+			*Microrhabdulus attenuatus* (Deflandre)
+	+			*Microrhabdulus nodosus* Stradner
+	+			*Nephrolithus frequens* Gorka
+	+			*Polypodorhabdus crenulatus* (Bramlette & Martini)
+	+			*Reinhardtites anthophorus* (Deflandre)
+	+			*Staurolithites mielnicensis* (Gorka)
+	+			*Stephanolithion laffittei* Noël
+	+			*Thoracosphaera operculata* Bramlette & Martini
+	+			*Watznaueria barnesae* (Black)
+	+			*Zygodiscus spiralis* Bramlette & Martini
+	+			*Zygolithus dubius* Deflandre
+	+	+	+	*Braarudosphaera bigelowi* (Gran & Braarud)
+	+	+	+	*Braarudosphaera discula* Bramlette & Riedel
+	+	+	+	*Markalius inversus* (Deflandre)
+	+	+	+	*Micula staurophora* (Gardet)
		+	+	*Cruciplacolithus tenuis* (Stradner)
		+	+	*Micrantholithus attenuatus* Bramlette & Sullivan
		+	+	*Micrantholithus pinguis* Bramlette & Sullivan
			+	*Chiasmolithus bidens* (Bramlette & Sullivan)
			+	*Chiasmolithus danicus* (Brotzen)
			+	*Coccolithus pelagicua* (Wallich)
			+	*Cruciplacolithus staurion* (Bramlette & Sullivan)
			+	*Heliorthus concinnus* (Martini)
			+	*Toweius craticulus* Hay & Mohler
			+	*Zygodiscus plectopons* Bramlette & Sullivan
			+	*Zygodiscus sigmoides* Bramlette & Sullivan

THE CRETACEOUS-TERTIARY EXTINCTION

Numerous fossil groups became extinct at the end of the Cretaceous. In some cases, this extinction was gradual, lasting throughout the later Cretaceous; in other cases, the extinction was incomplete with some species persisting well into the Tertiary. Among the

calcareous nannofossils and the planktonic foraminifera, however, a massive and abrupt extinction took place between the end of the Maestrichtian and the beginning of the Danian. Nearly forty species from each group disappeared. No species of Maestrichtian planktonic foraminifera and only a few species of calcareous nannofossils persisted into the Danian.

The time interval during which the extinction took place is unknown since there is an hiatus at all known contacts, even those in the deep ocean basins.

Numerous explanations have been offered for extinctions at system boundaries. Most of these are discussed and criticised by Rhodes (1967). One of the more plausible explanations, first advanced by Bramlette (1965), postulated a crisis in the nutrient cycle. Tappan (1968) suggested that the critical nutrient was carbonate, depleted by massive phytoplankton blooms, and Worsley (1974) proposed a model in which the carbonate compensation depth was elevated into the photic zone.

There is no firm evidence for such a crisis. The end of the Cretaceous was a period of active orogeny with increasing sedimentation. Even if, as Bramlette suggested, most sedimentation took place in non-marine basins, the soluble nutrients should still have been carried out to sea. All evidence points to shrinking tropical regions at the end of the Cretaceous which should have produced an increase in vertical mixing and replenishment from the deep basins. Massive phytoplankton blooms would be ephemeral, with immediate destruction of the blooms and stabilization. Worsley's model for an elevated carbonate compensation depth was not borne out by later drilling (Anonymous, 1975; van Andel, 1975). Finally, such hypotheses do not explain why meroplanktonic groups such as the benthonic foraminifera were largely unaffected.

The only major ecological factor for which evidence is available is temperature and most evidence points to the latest Cretaceous as a period of cooling with a minimum occurring late in the Maestrichtian or early in the Danian. By the end of the Cretaceous, the tropical zone had shrunk to within the 30° parallels (Bandy, 1967; Worsley, 1974). Although this reduction in living area, along with possible lowered surface water temperatures, may have been the critical factor, it is possible that some asylum areas with higher temperatures would have persisted. However, lowered temperatures and a reduced living area may have produced critical conditions under which some other factor or factors could have operated to produce the extinction.

It is perhaps significant that Danian planktonic foraminifera are forms whose morphology suggests a cold-water environment and that the few calcareous nannofossil species which persisted into the Tertiary are either cold-water forms such as *Markalius inversus* or tolerant forms such as *Braarudosphaera* spp. The earliest new species of calcareous nannofossil to appear in the Danian, *Biantholithus sparsus,* is a cold-water form.

SUMMARY AND CONCLUSIONS

Assemblages of calcareous nannofossils and planktonic foraminifera from the Maestrichtian and Danian of Zululand show no major divergences from assemblages reported for the same stages in other parts of the world. The Zululand assemblages are somewhat smaller than usual and some common species were not seen. At least two and possibly three hiati are present in the Zululand Maestrichtian. The hiatus at the Maestrichtian-Danian contact is relatively long.

The assemblages indicate that this area was within the tropical zone during the Maestrichtian. It is suggested that shrinkage of the tropical zone in the Danian produced conditions which resulted in the Cretaceous-Tertiary extinctions.

ACKNOWLEDGEMENTS

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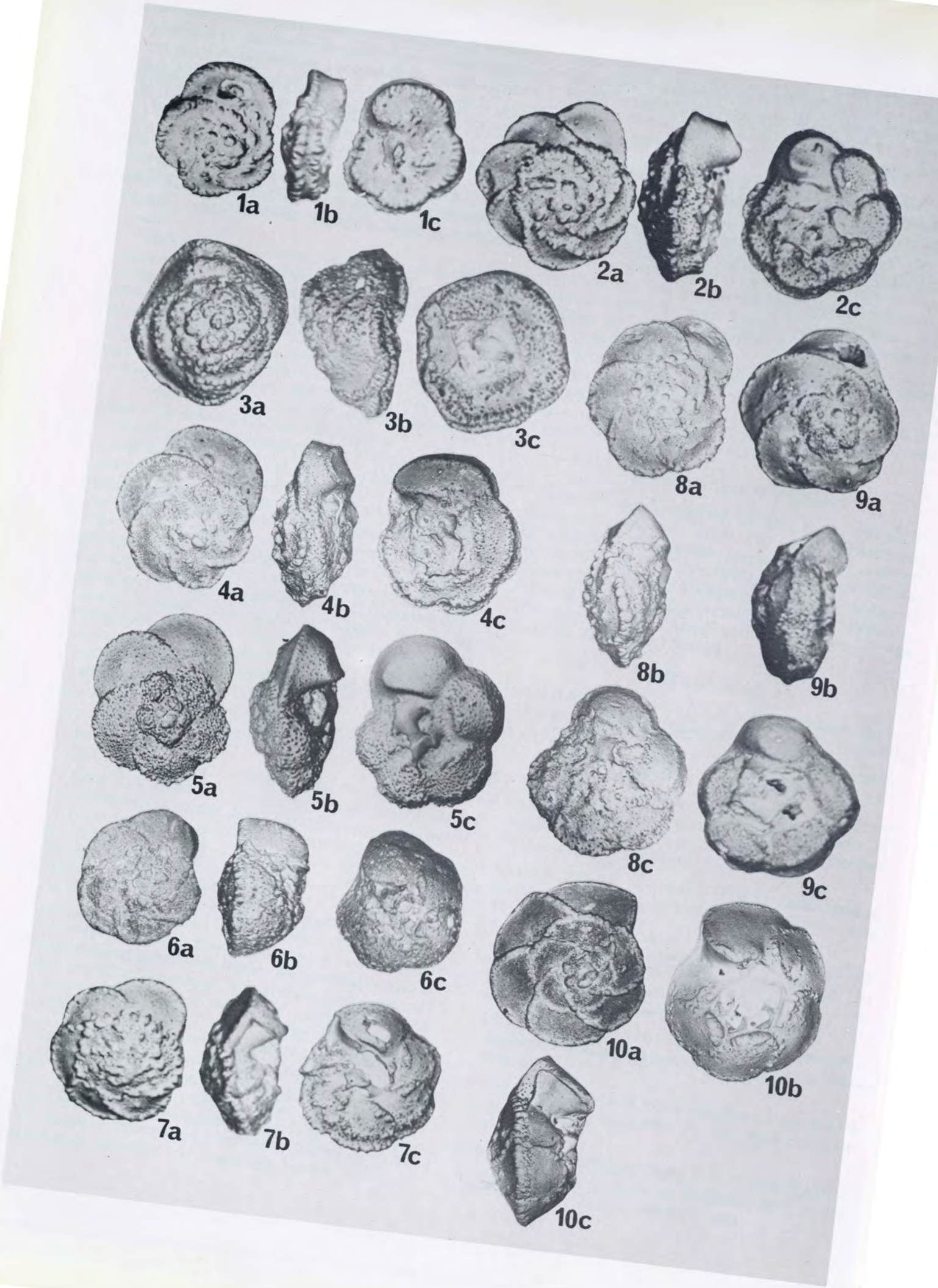

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PLATE I

Fig. 1a—c. *Abathomphalus mayorensis* (Bolli), X60.
Fig. 2a—c. *Globotruncana arca* (Cushman), X60.
Fig. 3a—c. *Globotruncana contusa* (Cushman), X50.
Fig. 4a—c. *Globotruncana fornicata* Plummer, X75.
Fig. 5a—c. *Globotruncana gagnebini* Tilev, X100.
Fig. 6a—c. *Globotruncana gansseri* Bolli, X50.
Fig. 7a—c. *Globotruncana leupoldi* Bolli, X60.
Fig. 8a—c. *Globotruncana marginata* (Reuss), X75
Fig. 9a—c. *Globotruncana rosetta* (Carsey), X60.
Fig. 10a—c. *Globotruncana stuarti* (de Lapparent), X50.

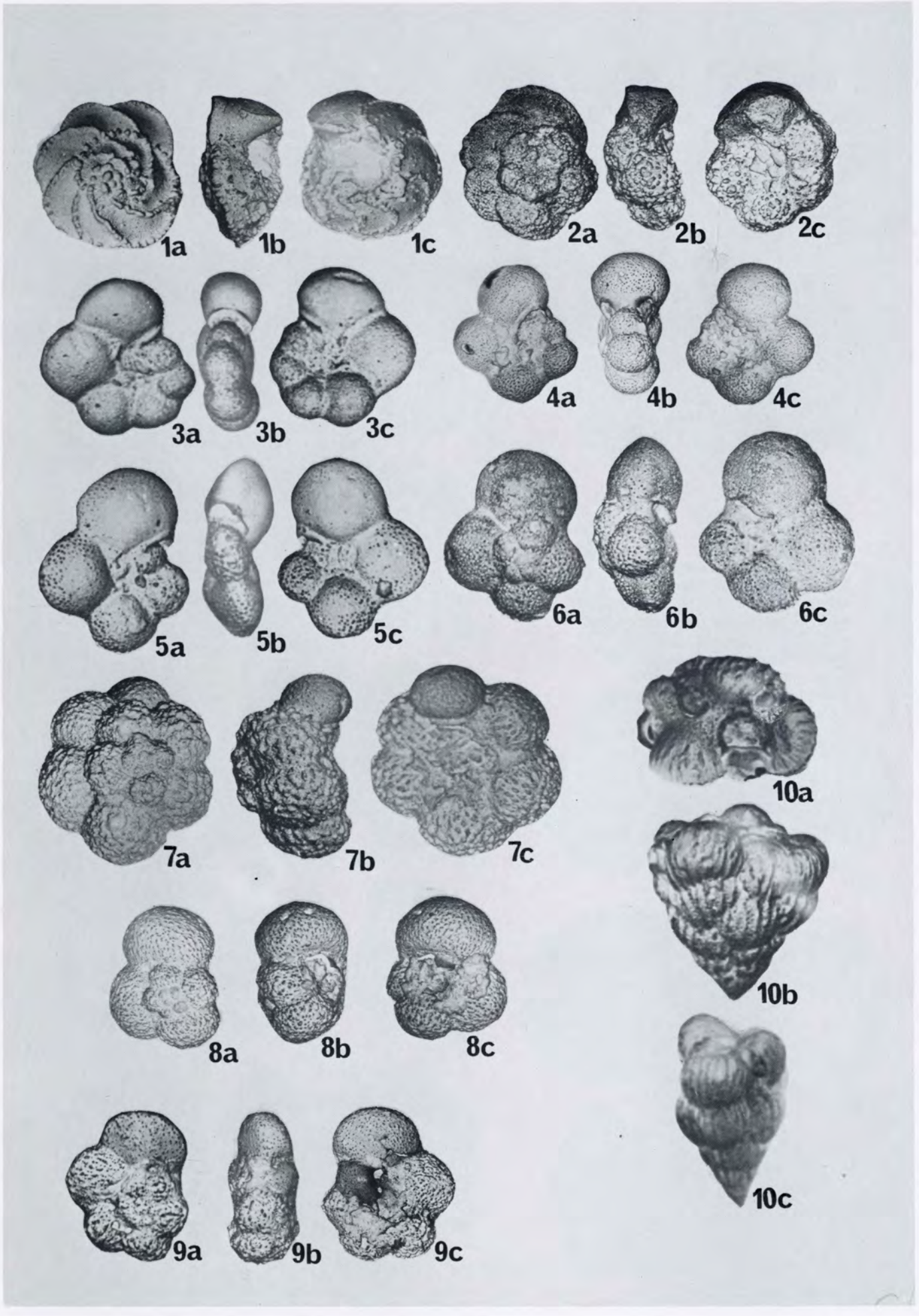

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PLATE II

Fig. 1a—c. *Globotruncana stuartiformis* Dalbiez, X50.
Fig. 2a—c. *Globotruncana tilevi* (Brönnimann and Brown), X100.
Fig. 3a—c. *Globigerinelloides aspera* (Ehrenberg), X100.
Fig. 4a—c. *Globigerinelloides messinae* (Brönnimann), X75.
Fig. 5a—c. *Globigerinelloides subcarinata* (Brönnimann), X100.
Fig. 6a—c. *Globigerinelloides subpetaloidea* (Gandolfi), X100.
Fig. 7a—c. *Rugoglobigerina rugosa* (Plummer), X75.
Fig. 8a—c. *Rugoglobigerina macrocephela* Brönnimann, X75.
Fig. 9a—c. *Trinitella scotti* (Brönnimann), X75.
Fig 10a—c. *Racemiguembelina fructicosa* (Egger), X60.

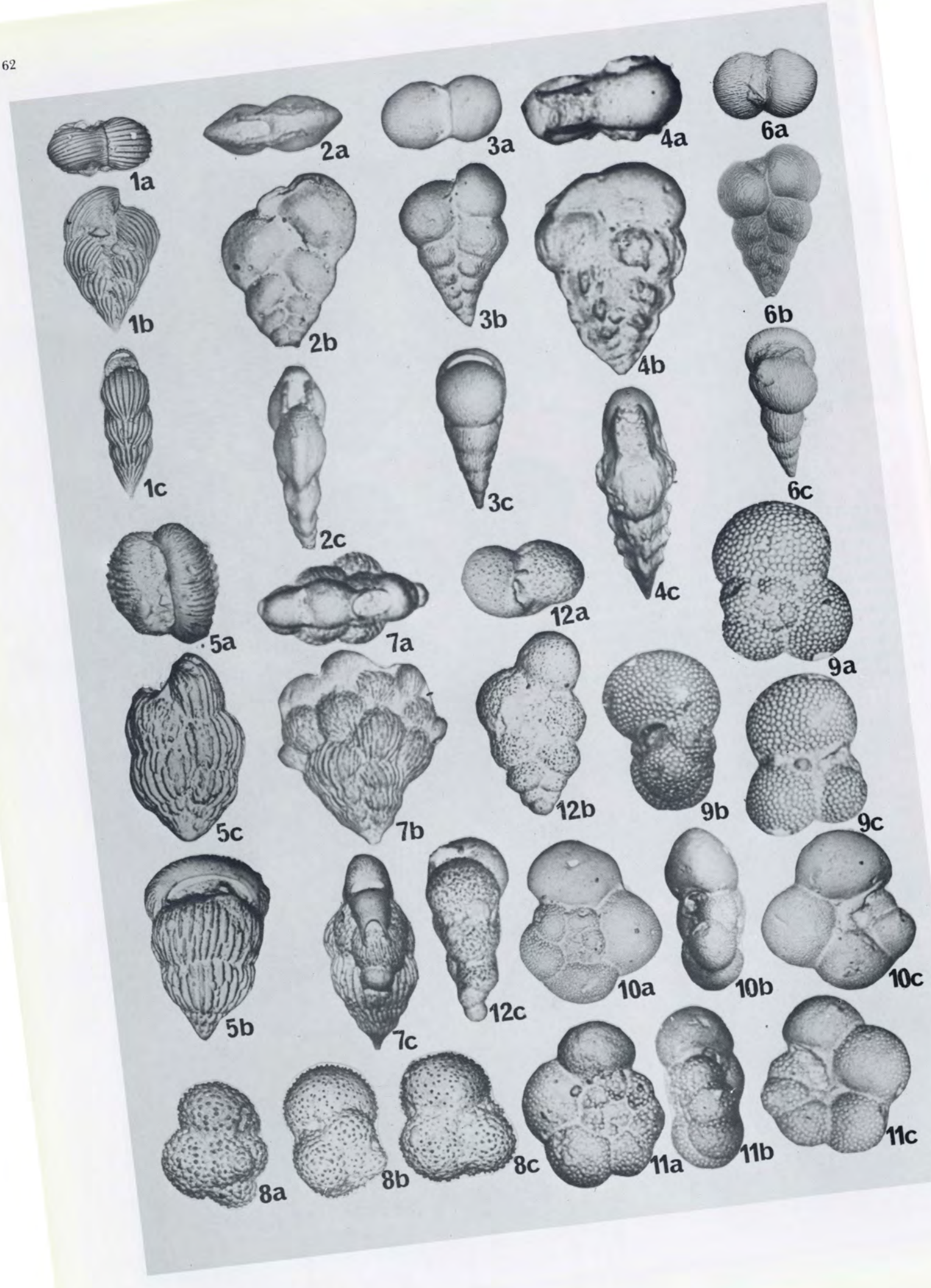

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PLATE III

Fig. 1a—c. *Heterohelix carseyae* (Plummer), X100.
Fig. 2a—c. *Heterohelix glabrans* (Cushman), X100.
Fig. 3a—c. *Heterohelix globulosa* (Ehrenberg), X100.
Fig. 4a—c. *Heterohelix ornatissima* (Cushman and Church), X100.
Fig. 5a—c. *Heterohelix plummerae* (Loetterle), X75.
Fig. 6a—c. *Heterohelix striata* (Ehrenberg), X100.
Fig. 7a—c. *Planoglobulina acervulinoides* (Egger), X60.
Fig. 8a—c. *Globoconusa daubjergensis* (Brönnimann), X150.
Fig. 9a—c. *Globigerina triloculinoides* Plummer, X100.
Fig. 10a—c. *Globorotalia compressa* (Plummer), X75.
Fig. 11a—c. *Globorotalia pseudobulloides* (Plummer), X100.
Fig. 12a—c. *Chiloguembelina morsei* (Kline), X90.

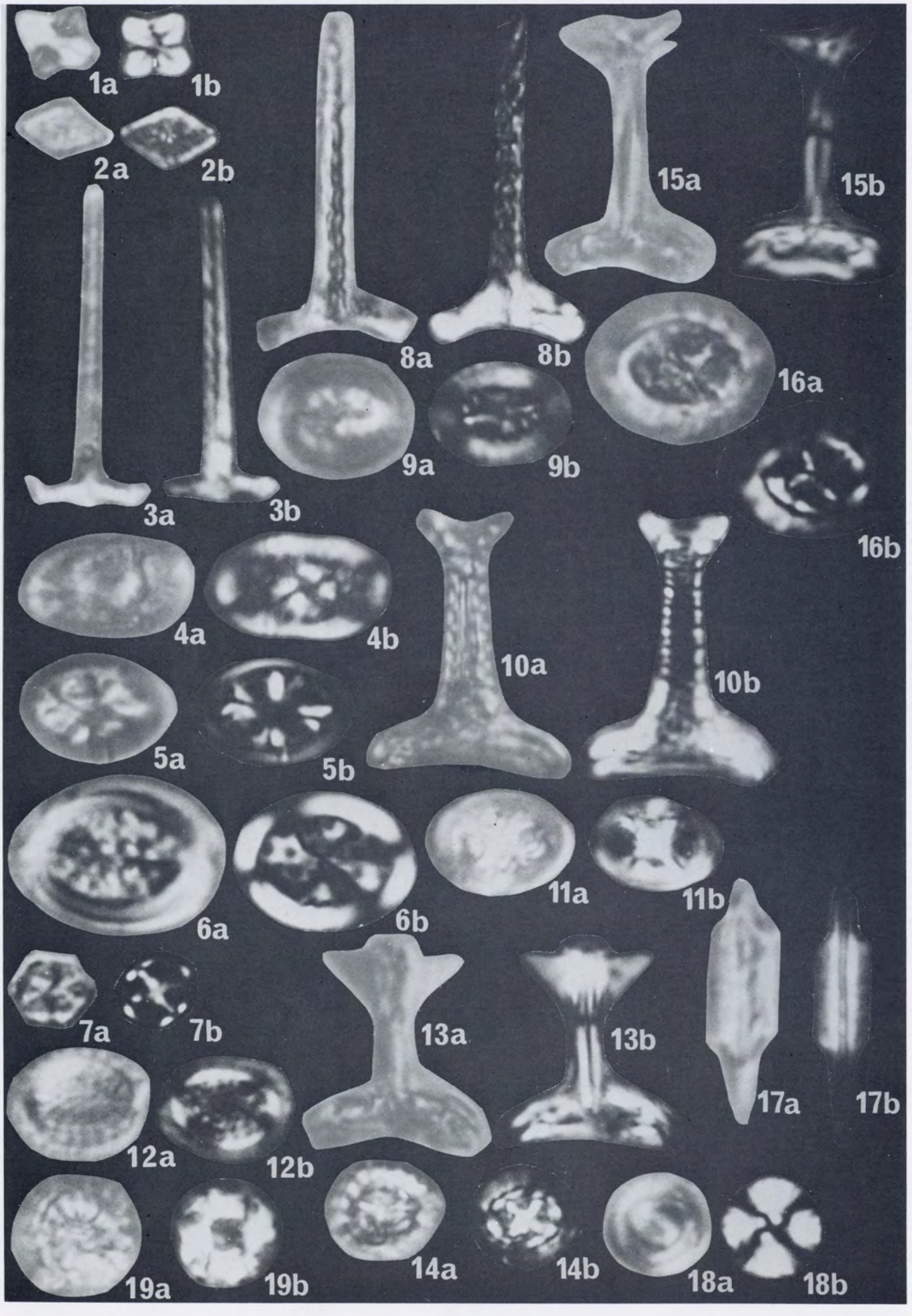

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PLATE IV

All figures X3 500. Figures 'a' are under interference contrast; figures 'b' under crossed polarizers.

Fig. 1a—b. *Tetralithus pyramidus* Gardet.
Fig. 2a—b. *Zygolithus rhombicus* Stradner and Adamiker.
Fig. 3a—b. *Actinozygus splendens* (Deflandre), spine.
Fig. 4a—b. *Actinozygus splendens* (Deflandre), base.
Fig. 5a—b. *Ahmuellerella octoradiata* (Gorka).
Fig. 6a—b. *Arkhangelskiella cymbiformis* Vershina.
Fig. 7a—b. *Corollithion exiguum* Stradner.
Fig. 8a—b. *Cretarhabdus conicus* Bramlette and Martini, spine.
Fig. 9a—b. *Cretarhabdus conicus* Bramlette and Martini, base.
Fig. 10a—b. *Cretarhabdus decorus* (Deflandre), spine.
Fig. 11a—b. *Cretarhabdus decorus* (Deflandre), base.
Fig. 12a—b. *Cribrosphaerella ehrenbergi* Arkhangelsky.
Fig. 13a—b. *Deflandrius cretaceus* (Arkhangelsky), spine.
Fig. 14a—b. *Deflandrius cretaceus* (Arkhangelsky), base.
Fig. 15a—b. *Deflandrius intercisus* (Deflandre), spine.
Fig. 16a—b. *Deflandrius intercisus* (Deflandre), base.
Fig. 17a—b. *Lithraphidites quadratus* Bramlette and Martini.
Fig. 18a—b. *Markalius circumradiatus* (Stover).
Fig. 19a—b. *Cylindralithus gallicus* (Stradner).

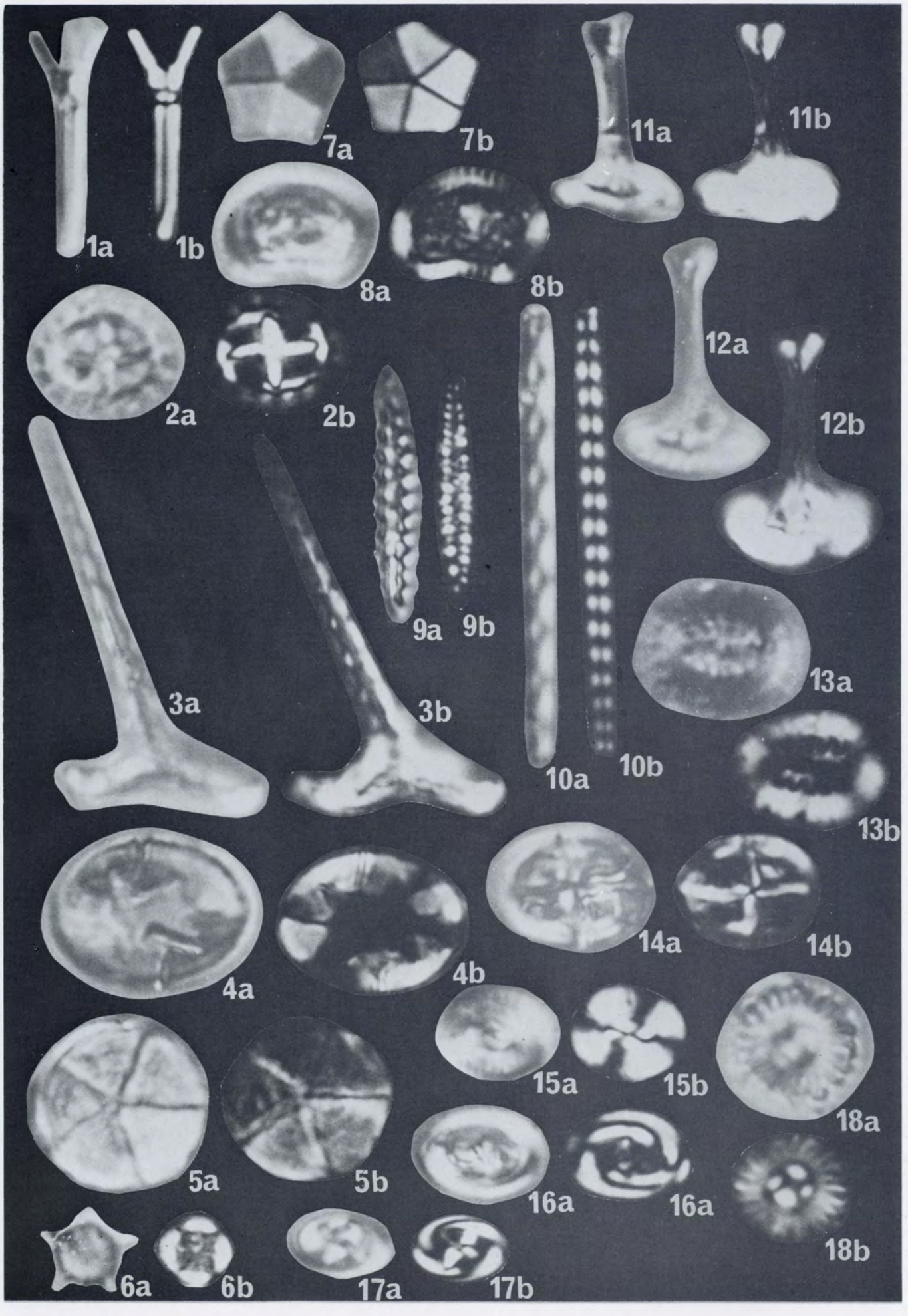

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PLATE V

All figures X3 500. Figures 'a' are under interference contrast; figures 'b' under crossed polarizers.

Fig. 1a—b. *Deflandrius spinosus* Bramlette and Martini, spine.
Fig. 2a—b. *Deflandrius spinosus* Bramlette and Martini, base.
Fig. 3a—b. *Eiffellithus turriseiffeli* (Deflandre), spine.
Fig. 4a—b. *Effellithus turriseiffeli* (Deflandre), base.
Fig. 5a—b. *Braarudosphaera discula* Bramlette and Riedel.
Fig. 6a—b. *Stephanolithion laffittei* Noël.
Fig. 7a—b. *Braarudosphaera bigelowi* (Gran and Braarud).
Fig. 8a—b. *Nephrolithus frequens* Gorka.
Fig. 9a—b. *Microrhabdulus nodosus* Stradner.
Fig. 10a—b. *Microrhabdulus attenuatus* (Deflandre).
Fig. 11a—b. *Reinhardtites anthophorus* (Deflandre).
Fig. 12a—b. *Polypodorhabdus crenulatus* (Bramlette and Martini), spine.
Fig. 13a—b. *Polypodorhabdus crenulatus* (Bramlette and Martini), base.
Fig. 14a—b. *Staurolithites mielnicensis* (Gorka).
Fig. 15a—b. *Watznaueria barnesae* (Black).
Fig. 16a—b. *Zygodiscus spiralis* Bramlette and Martini.
Fig. 17a—b. *Zygolithus dubius* Deflandre.
Fig. 18a—b. *Markalius inversus* (Deflandre).

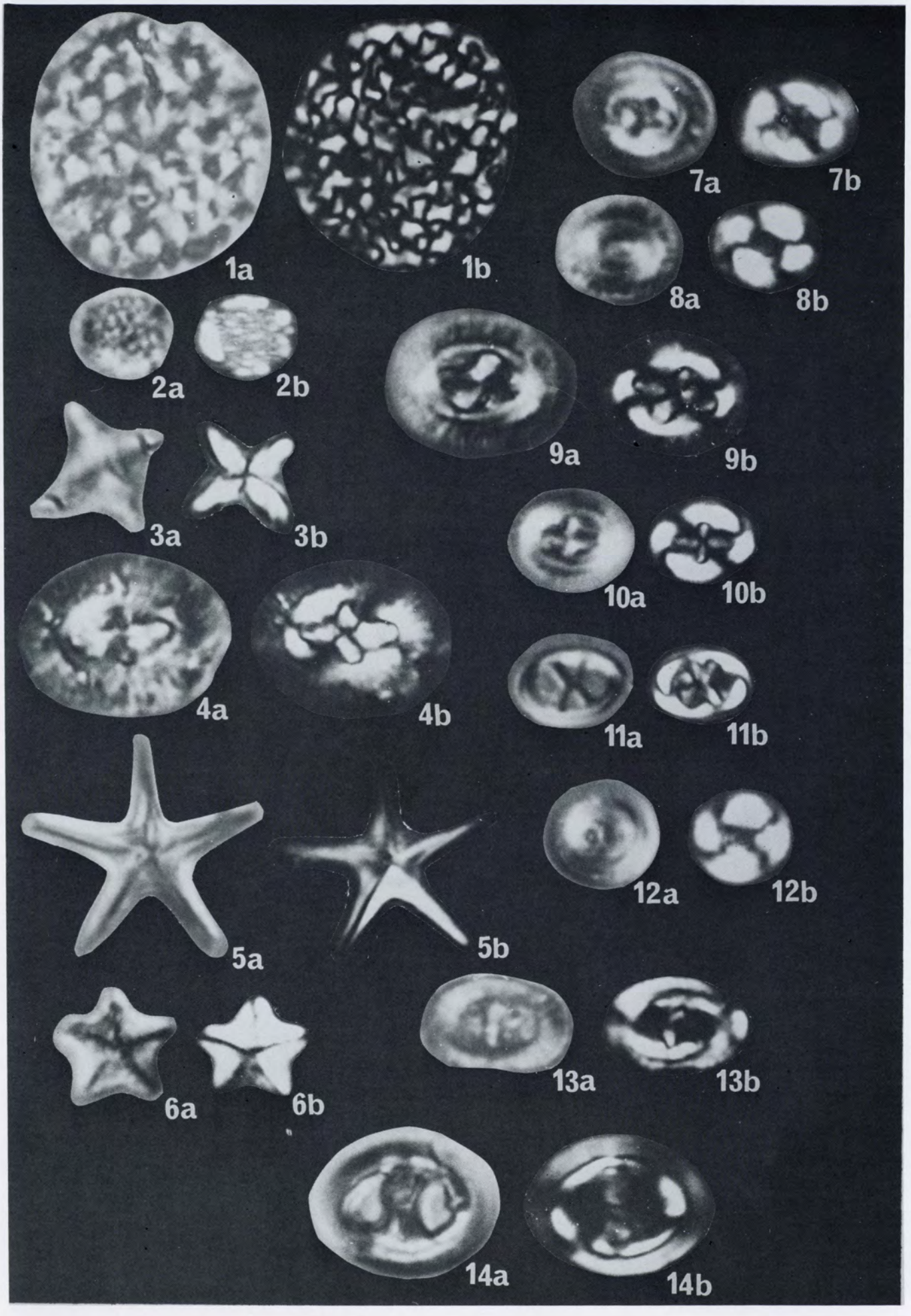

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PLATE VI

All figures X3 500. Figures 'a' are under interference contrast; figures 'b' under crossed polarizers.

Fig. 1a—b. *Thoracosphaera operculata* Bramlette and Martini.
Fig. 2a—b. *Thoracosphaera operculata* Bramlette and Martini, operculum.
Fig. 3a—b. *Micula staurophora* (Gardet).
Fig. 4a—b. *Cruciplacolithus tenuis* (Stradner).
Fig. 5a—b. *Micrantholithus attenuatus* Bramlette and Sullivan.
Fig. 6a—b. *Micrantholithus pinguis* Bramlette and Sullivan.
Fig. 7a—b. *Chiasmolithus danicus* (Brotzen).
Fig. 8a—b. *Coccolithus pelagicus* (Wallich).
Fig. 9a—b. *Chiasmolithus bidens* (Bramlette and Sullivan).
Fig. 10a—b. *Cruciplacolithus staurion* (Bramlette and Sullivan).
Fig. 11a—b. *Heliorthus concinnus* (Martini).
Fig. 12a—b. *Toweius craticulus* Hay and Mohler.
Fig. 13a—b. *Zygodiscus sigmoides* Bramlette and Sullivan.
Fig. 14a—b. *Zygodiscus plectopons* Bramlette and Sullivan.

Palaeont. afr., **18**, 71—87 (1975)

PERMO-TRIASSIC "LIZARDS" FROM THE KARROO

by

Robert L. Carroll

Redpath Museum, McGill University
P.O. Box 6070, Station A Montreal, P.Q. Canada.

ABSTRACT

Three genera of sauropsid reptiles from the Permo-Triassic beds of South Africa — *Saurosternon* Huxley, *Paliguana* Broom and *Palaegama* Broom — were originally described as lizards, or the immediate ancestors of that group. Restudy of these forms confirms that they are close to the ancestry of later Mesozoic and Cenozoic squamates. The skull is somewhat primitive, but in size, proportions and function extremely similar to that of *Kuehneosaurus*. The pectoral girdle is lacertoid in the proportions and orientation of the clavicles and interclavicle; the anterior margin of the scapulocoracoid is fenestrate, and the articulating surface of the glenoid is very short. A sternum is present and one specimen shows ventral connections between the ribs and the sternum. In *Saurosternon*, the forelimb can be seen as very similar to that of living lizards, with special epiphyseal articulating surfaces on the proximal end of the humerus and distal end of the ulna. The pelvic girdle remains primitive, but the rear limb is close to the pattern in lizards. The fifth metatarsal is not obviously hooked, and all five distal tarsals are retained, but the proportions and functions of the ankle presage the condition in living lizards. Epidermal scales are present. Following Romer, these forms are all included in the Family Paliguanidae. They are placed in the Suborder Lacertilia, provisionally in the Infraorder Eolacertilia.

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INTRODUCTION

The lacertoid habitus has been an extremely important way of life throughout the history of the Class Reptilia. The earliest of all reptiles were small lizard-like forms, and the assumption of this pattern was probably basic to the emergence of the group from the labyrinthodont amphibians (Carroll, 1969). Today, the Lacertilia are the most successful reptiles in terms of number of species and habitus diversity.

This suborder is characterized by having a streptostylic quadrate and total elimination of the lower temporal bar. Animals already exhibiting these features and otherwise close to the ancestry of the modern forms are known from the Upper Triassic (Robinson, 1967). Despite the relatively early appearance of these forms, they are already completely lacertoid in their general anatomy and some genera are extremely highly specialized in having enormously elongated ribs which served to support a gliding "wing", as in the living genus *Draco*. Clearly, lizards had a long previous history.

It has long been accepted that true lizards had evolved from Permo-Triassic eosuchians originally possessing a diapsid skull configuration, by the reduction of the lower temporal bar and the freeing of the quadrate. The genus *Prolacerta* from the *Lystrosaurus* zone of South Africa illustrates an intermediate stage in this process. This genus has long figured prominently in considerations of the origin of lizards as a result of the careful descriptions of the skull by Parrington (1935) and Camp (1945). Genera other than *Prolacerta* have been described from the Karroo as lizards or their antecedents, but curiously have been largely ignored since their original descriptions. *Paliguana* and *Palaeagama* were both described by Broom (1903 and 1926), yet they do not figure in more recent considerations of the origin of squamates (e.g. Robinson, 1967). These forms, in both cases represented solely by the type specimens, have been re-examined as part of a general study of primitive sauropsids from the Karroo. In addition, the type of *Saurosternon bainii* (Huxley, 1868) and one other previously undescribed specimen have been studied. All are found to ex-

hibit a number of important characteristics typically associated with squamates. These specimens are significant in demonstrating that lacertoid forms had evolved by the late Permian or early Triassic, independently and in advance of the pattern shown by *Prolacerta*.

A major difficulty in working with this material is the lack of reliable or precise information on the locality or geological horizon of the specimens. Some have no field data at all. What information is available suggests that all are from the late Permian to early Triassic — *Cistecephalus, Daptocephalus* and *Lystrosaurus* zones.

All of the known specimens from South Africa are described here. Aside from *Prolacerta*, there are only four, collected over a period of 100 years. They are clearly very rare elements in the Karroo fauna, possibly as a result of living in an environment not normally leading to fossilization. It is somewhat surprising that lizard-like forms should be so uncommon in the Karroo, especially over such a long period of time. Small size and fragility of skeleton may contribute to the rarity of recognizable fossils, and small insectivorous therapsids may have successfully filled the role of lizards at this time, at least in this region. The paucity of diapsids of any type in the early Karroo beds strongly suggests some general bias against this group (perhaps climatological). The morphological diversity of the few known forms also suggests that we are seeing only a small portion of their total radiation.

At the beginning of this study, it was assumed that Permo-Triassic fossils would represent a comparatively primitive stage in the origin of lizards and exhibit few of the specializations evident in the late Mesozoic and Tertiary genera. Closer examination revealed a host of specific similarities with later forms. There may be some question as to whether the genera from the South African Karroo should be included within the Suborder Lacertilia, but they are certainly members of the group that was ancestral to later lizards.

Unfortunately, the fossil record of lizards is very incomplete throughout the Mesozoic and Tertiary. Determination of the interrelationships of the various living families must be based to a large extent on the anatomy of modern forms and their geographical distribution. The fossil record may confirm or weaken phylogenetic schemes based on the latter criteria, but does not in itself form the primary basis for classification within the group (Camp, 1923; Estes, 1970). It is evident that the basic diversification of lizards was well underway by the end of the Jurassic and Camp indicates that the origin of the various major types was considerably earlier. Gekkonids and iguanids have both been considered as exemplifying the most primitive of modern lizards. From the standpoint of the skull, however, there can be no question but that the configuration common to the iguanids is closest to that of primitive diapsids. Their current geographic distribution supports an early origin, although this is apparently not confirmed by positive evidence of an ancient fossil record. In comparing the skeletons of the South African forms with a wide range of living lizards, overall similarities are greatest with the iguanids and it is with this group that the most detailed comparisons have been made.

Because it is the most completely known of the Karroo "lizards", *Palaeagama vielhaueri* will be described first.

PALAEAGAMA VIELHAUERI Broom

(Figs. 1, 2 and 3)

The type and only specimen, No. 3707 in the McGregor Museum, Kimberley, is a nearly complete skeleton exposed in ventral view. Broom reported that it had been discovered by Mr. P. F. Vielhauer at Kinira in the Mount Frere District. According to Dr. Kitching (personal communication), the horizon is most probably the Eotriassic *Lystrosaurus* zone, although the specimen might have come from the Uppermost Permian *Daptocephalus* zone. It is surely not from higher in the section than the early Triassic. The specimen is in a slab of fine-grained argillaceous sandstone. It consists of the greater portion of the skeleton, in some parts split through with the fracture of the rock. The skull roof is preserved, visible in ventral view. Although the restorations are shown in customary dorsal and lateral views, the specimen shows primarily the internal surface of the bone. The external surface can be seen only where the bone has been lost and a cast could be made to recreate the original surface. The most obvious feature is the relatively great size of the orbits and the corresponding shortness of both the snout and cheek region. This, together with the similarity in size, gives this skull a very similar appearance to *Kuehneosaurus* (Robinson, 1962) and *Icarosaurus* (Colbert, 1970), the only described Upper Triassic lizards. Although the cheek region as a whole is not well preserved, the jugal is well exposed on both sides. The left jugal is nearly complete, lacking only the end of the dorsal process. The ventral margin of the bone is slightly crushed, but with no substantial portion missing. The posterior margin is complete on both sides, demonstrating the complete absence of a posterior process. As restored, this margin slopes posteriorly at an angle of approximately 10° from the vertical. Much of the bone of the right jugal is lost. An impression shows much of its original anteroposterior extent, but the ventral margin is missing, except posteriorly. No trace of either quadratojugal is evident, but the nature of preservation of this area is too poor to assume that it was originally absent.

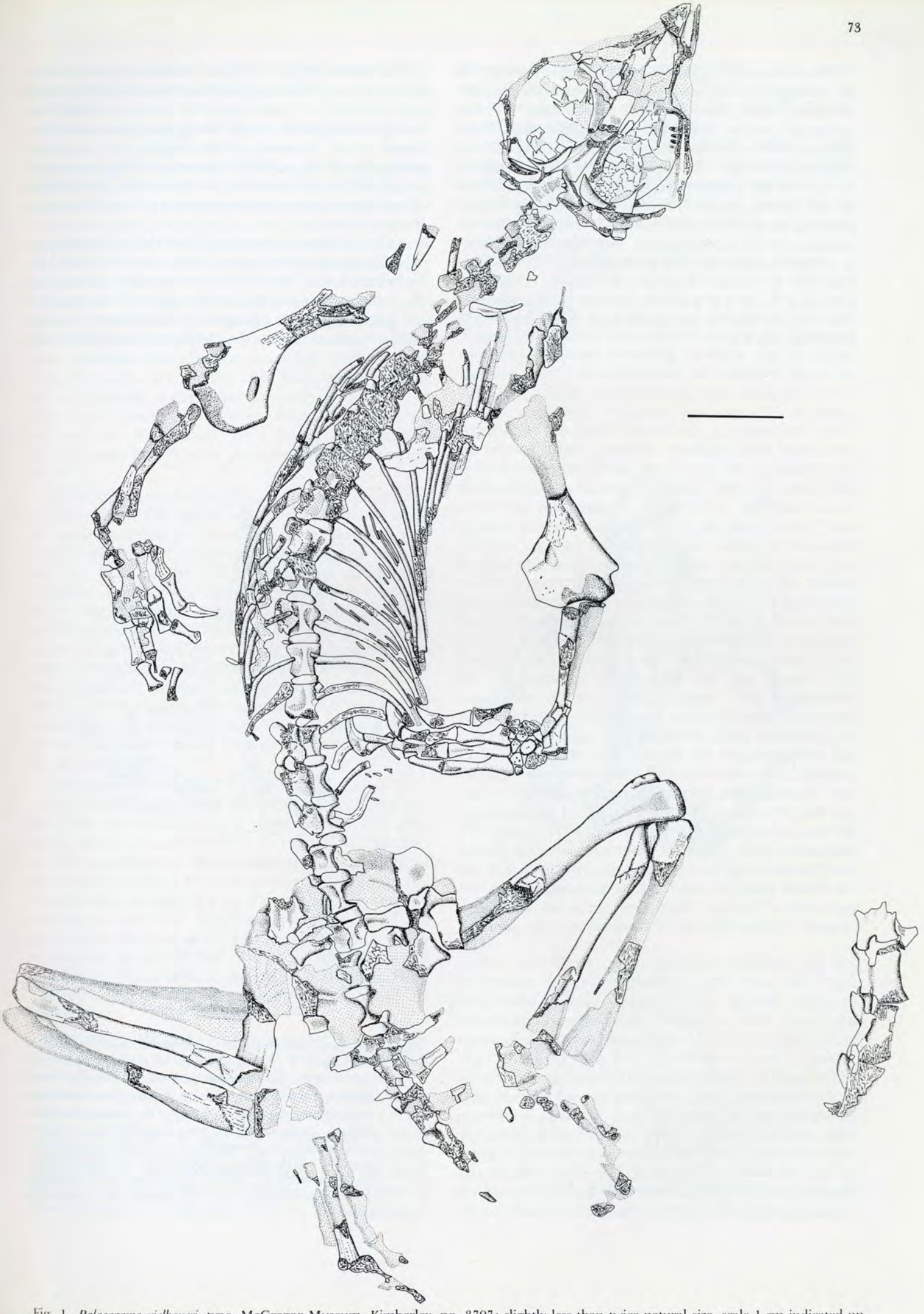


Fig. 1. *Palaeagama vielhaueri*, type, McGregor Museum, Kimberley, no. 3707; slightly less than twice natural size, scale 1 cm indicated on figure.

The temporal region is astonishingly modern in its anatomy. The elements are somewhat disarticulated and portions are represented by impressions rather than the actual bone, but comparison with a modern lizard discloses their identity without question. On both sides, the squamosal can be seen to be a simple strap-shaped bone, much as in the genus *Iguana*. There is definitely no ventral process, as in *Prolacerta*, nor even the posterior extension seen in *Kuehneosaurus*. As preserved, the bone is oriented more or less perpendicular to the long axis of the skull, but this is clearly unnatural, resulting from the anteroposterior compression of this region. The bone must have been essentially horizontal in life.

The postorbital is a flat triradiate bone as in *Keuhneosaurus*; the margin is in contact with the jugal and borders the lower temporal opening in nearly a straight line, rather than being conspicuously embayed as in *Prolacerta*. Unfortunately, the posterior extremity of the posterior process of the postorbital is covered by other bones on both sides, precluding determination of its exact manner of attachment to the squamosal.

The quadrate is represented on the left side by an impression and bone scrap in the shape of a vertically oriented rod. It terminates dorsally adjacent to the paroccipital process and the lateral extremity of the parietal. This is presumably the anterior margin of the tympanic crest. The configuration of the jugal

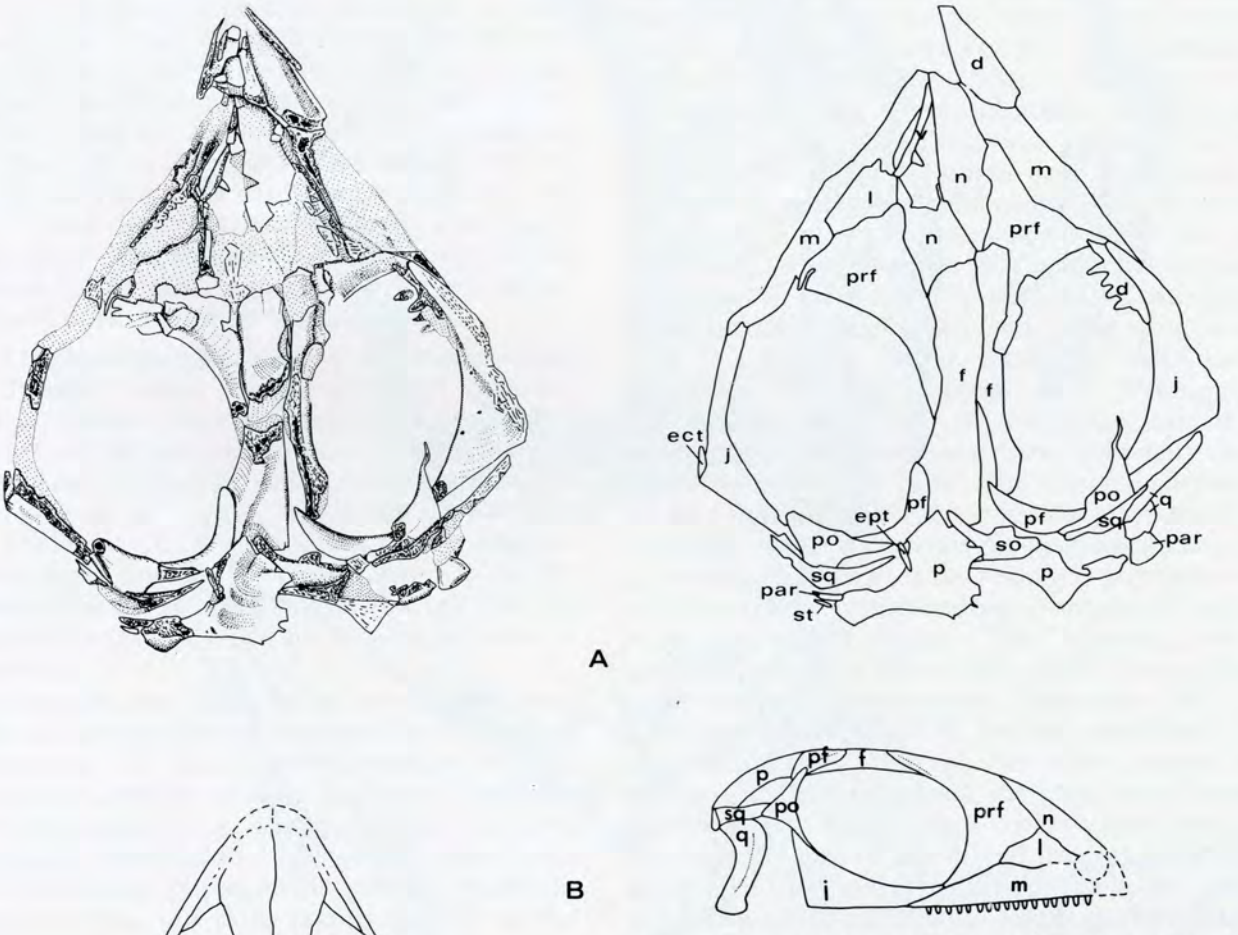


Fig. 2 *Palaeagama vielhaueri*, type. A. detail of ventral surface of skull roof, × 3. B. restoration of skull, in dorsal and lateral views, based almost entirely on the medioventral surface; teeth restored on the basis of the lower jaw, ×2. Abbreviations: d — dentary; ect — ectopterygoid; ept — epipterygoid; f — frontal; j — jugal; l — lacrimal; m — maxilla; n — nasal; p — parietal; par — paroccipital process; pf — postfrontal; po — postorbital; prf — prefrontal; q — quadrate; so — supraoccipital; sq — squamosal; st — supratemporal.

and squamosal indicates that the quadrate was freely movable; the streptostylic condition was fully achieved.

The parietal resembles that of *Kuehneosaurus* except for the slightly shorter extent of the lateral process and the presence of a large pineal opening midway in the length of the bone. A small fragment of bone at the end of the lateral process may be the supratemporal, retaining a primitive position comparable with that of *Youngina*. The ventral surface of the parietal is markedly concave. No postparietals or tabulars are preserved. At the end of the lateral extremity of the right parietal is a small portion of a discrete ossification. Although the fragment is too small to identify on the basis of its anatomy, its position indicates that it is the distal end of the paroccipital process. On the left side, just beyond the end of the parietal, is the other paroccipital process, in this case clearly identifiable despite its peculiar orientation. A fragment of a large supraoccipital may be seen beneath the anterior margin of the left parietal.

Breaking through the edge of the right parietal at the margin of the upper temporal opening is a rod of bone that can be identified by its position and orientation as the epipterygoid, similar to that of modern lizards. The frontals are long narrow rectangular bones, considerably thickened ventrally where they enter the margins of the orbit and buttress the pre- and postfrontals. The frontals, like the other circumorbital bones, lack the ornamentation seen in *Keuhneosaurus*. The postfrontal has a large area expanded medially on the orbital margin. The nasals are as long as the frontals, but considerably wider and very much thinner. The telescoping of the bones in this area makes their exact lateral limits difficult to establish.

The posterior margin of the prefrontal is preserved in the bone on both sides. It apparently reached the level of the maxilla, at least on the left side, eliminating the lacrimal from the margin of the orbit, at least superficially. More anteriorly, the pattern of the roofing bones is difficult to interpret. Much of the bone itself is missing, but enough remains to preclude making a clear cast. The bones in the area of the prefrontal, lacrimal and nasal have been extensively telescoped on the left side. The lacrimal appears as a small area of bone between the prefrontal and maxilla. The top of the snout is obscured by the bones of the lower jaw.

Nothing of the premaxillae is visible. Little of the bone of either maxilla is preserved, but much is represented as an impression. On the left side, the ventral margin lies at the limit of the matrix so that the curvature of the bone may be seen where it extends medially at the base of the teeth, but the teeth themselves are not visible. The posterior extremity of the maxilla is represented by bone on both sides; here it is considerably wider than that of *Kuehneosaurus*. It extends only a short distance posterior to the anterior margin of the orbit. At the end of the snout, the bone itself is present but obscured by other elements. The maxilla curves medially to be exposed dorsally.

Nothing of the palate is preserved, unless a small piece of bone medial to the posterior end of the right jugal is a fragment of the ectopterygoid.

A short section of the dentary is preserved, indicating the presence of small, peg-like, apparently sub-pleurodont teeth.

The postcranial skeleton is in general primitive — eosuchian rather than lizard-like in most observed features. The cervical vertebrae are very poorly preserved. After completion of the whole specimen drawing, the small amount of bone in this area was removed and the resulting cavities cast in latex. Despite their incompleteness, it is immediately obvious that these vertebrae are not elongate as are the cervicals of *Prolacerta* but are, if anything, somewhat shorter than the succeeding trunk vertebrae. Their general configuration resembles that of primitive living lizards and the Jurassic genus *Eichstattosaurus* (Cocude-Michel, 1963, pl. xxx). The count in this region is somewhat difficult to establish, but there appear to be 23 presacrals. There are two sacrals; six caudals are visible in sequence behind the sacrum, and remains of five more are visible a short distance away. Judging by the related species, the tail was probably originally a great deal longer. Except for the cervicals, in which the impression of the dorsal surface is exposed, the column is visible primarily in ventral view. Intercentra are visible throughout the length of the trunk. The zygapophyses are widely spaced and apparently relatively flat. There is no evidence that the neural spines were long. The anterior trunk vertebrae are extremely badly crushed. In the remainder of the column the arches of the vertebrae are crushed down on the centra, obscuring the normal configuration of the pedicle and the transverse process. The bases of the centra show rounded keels, with the lateral surfaces markedly concave. The intercentra are thin crescents whose length is approximately one half that of the centra. They bear no facets for rib articulation. Between the last two isolated caudals may be seen the dorsal part of an incomplete haemal arch.

The ribs of the most anterior cervicals are not preserved, or, as in lizards, they may not have originally been present. The second cervical vertebra, however, does exhibit a well developed transverse process. Assuming a correct count of cervical vertebrae, the first rib preserved is the fourth. which is long, with a cylindrical shaft. In most of the ribs, neither the proximal nor distal extremity is well preserved, making determination of the nature of the heads and the total length difficult. Where adequately preserved, two distinct heads may be seen. Cartilaginous ventral extensions of the ribs in the central portion of the trunk are visible on the right side. A maximum length is attained at approximately

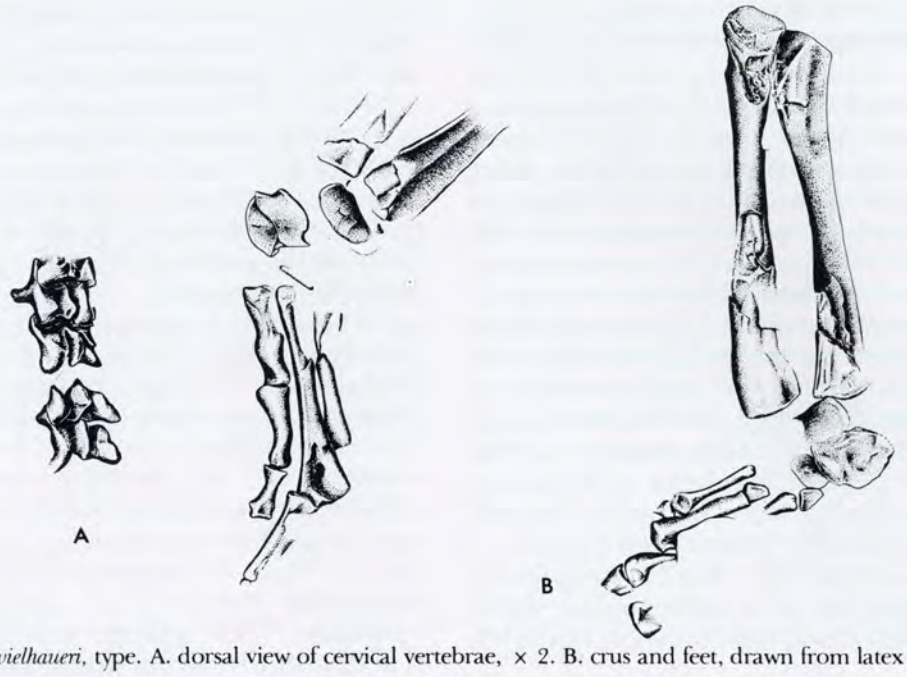


Fig. 3. *Palaeagama vielhaueri*, type. A. dorsal view of cervical vertebrae, × 2. B. crus and feet, drawn from latex casts, ×2.

the 12th rib. The length decreases sharply behind the 17th. The last presacral rib is a narrow rod, apparently shorter than the centrum. The penultimate is not preserved. The antepenultimate is as thick as those more anterior and approximately twice the length of the centra. The anterior sacral ribs are well exposed ventrally. They are not fused to the vertebrae. A shallow constriction demarcates the barely separate heads. The distal end is not greatly expanded and does not curve ventrally to provide a large area for attachment with the illum. Such a narrow sacral attachment is common in modern lizards. Only a small portion of the second sacral rib is visible on the left side. The distal portion resembles that of the first. The ribs of the first three caudals can be seen as fused to the transverse processes and extending horizontally at right angles to the long axis of the tail. They are dorsoventrally flattened. No ribs are preserved more posteriorly.

The most notable feature of the shoulder girdle is the presence of an ossified sternum posterior to the coracoid. The outline of the structure is not well defined, but it must have been the length of at least three centra. The scapulocoracoid is very poorly preserved. There appears to be a narrow anterior projection from the scapula, suggestive of the lattice-like margin seen in the lizards. This cannot be established with any certainty, however. The dermal shoulder girdle is also represented only by fragments, establishing that the plates of the clavicles were narrow, as was the stem of the interclavicle.

The humeri are represented only by impressions proximally, but much of the shaft of the right and the distal portions of both are present as bone. In contrast to late Triassic lizards, the distal ends of the shafts are expanded, much as in romeriids and captorhinids, with a long slit-like entepicondylar foramen and a short supinator process. Only the ventral surface of the area of distal expansion is exposed, showing large areas of unfinished bone for the articulation of the ulna and radius. The ulna and radius are poorly preserved, but clearly short and slender. There is only a slight ossification of the olecranon. The distal elements of the left wrist are well exposed, but the proximal bones are badly crushed and broken, making establishment of the margins impractical. Much better preservation of the area would be necessary to establish any significant features, since there are few dramatic changes in the wrist from romeriids to true lizards. In both hands, only the first four digits are exposed. The first three are almost completely preserved, but only the proximal two phalanges of the fourth. The terminal phalanges are large curved claws. As a unit, the hand is surprisingly massive in appearance.

The puboischiadic plate is largely preserved as an impression. It is generally plate-like in appearance. There is no evidence of ossification where the pubis and ischium would have joined, but it is quite possible that this area was deformed by the sacral ribs and so was not preserved in the plane of the block as it is exposed. There are certainly no clear margins indicating the presence of a thyroid fenestra, as is the case in the late Triassic lizard *Icarosaurus*. On the right side, a small circular obturator foramen is visible. The girdle extends the length of five vertebrae. The ilium is a broad blade of indeterminate length extending posterodorsally.

The femur is the length of seven trunk vertebrae. The head is robust, with the internal trochanter descending ventrally as an extension from the shaft. The distal elements of the rear limb are almost as long as the femur, the tibia and fibula both reaching

93% of its length; both are lightly built bones. The feet are unfortunately represented only by scraps of bone and poor impressions of the dorsal surface (Fig. 3). The astragalus and calcaneum are clearly large, flat, more or less square bones, as in the romeriids and the primitive eosuchian *Galesphyrus*, in contrast to the shorter thicker elements seen in true lizards. Little of the distal tarsals is visible and nothing worth describing. Between the two feet, most of the metatarsals can be reconstructed. The bones are long, with the fifth almost certainly not hooked, in contrast to Broom's interpretation, but substantially shorter than the fourth.

Ventral scales can be seen, scattered among the more posterior ribs. Their configuration resembles that of other small primitive reptiles.

PALIGUANA WHITEI Broom

(Fig. 4)

A second form known from the skull alone, *Paliguana whitei*, was described by Broom in 1903 and discussed again in 1925. It is in the collection of the Albany Museum, Grahamstown, No. 3585. It comes from Donnybrook, between Tarkastad and Queenstown. According to Kitching (personal communication), the specimen may be either Upper Permian or Lower Triassic since strata of both the *Daptocephalus* and *Lystrosaurus* zones are exposed in this area. The bone is soft and white, the matrix a red sandy clay. Very little preparation was attempted, beyond that initiated by Broom. The skull remains essentially as he saw it. The present interpretation differs only in details from that offered by Broom in 1903. The restorations given in his 1925 paper are, however, quite different. The present interpretation owes much to comparison with the Upper Triassic lizard *Kuehneosaurus*. The two forms are of almost exactly the same size and agree in most significant anatomical details.

The outlines of almost the entire skull roof and jaws are apparent, but most of the bone in the antorbital region has gone, leaving only an impression, and the tip of the snout is totally missing. Bones are present in the area of the palate, but so badly broken that no description is possible. The

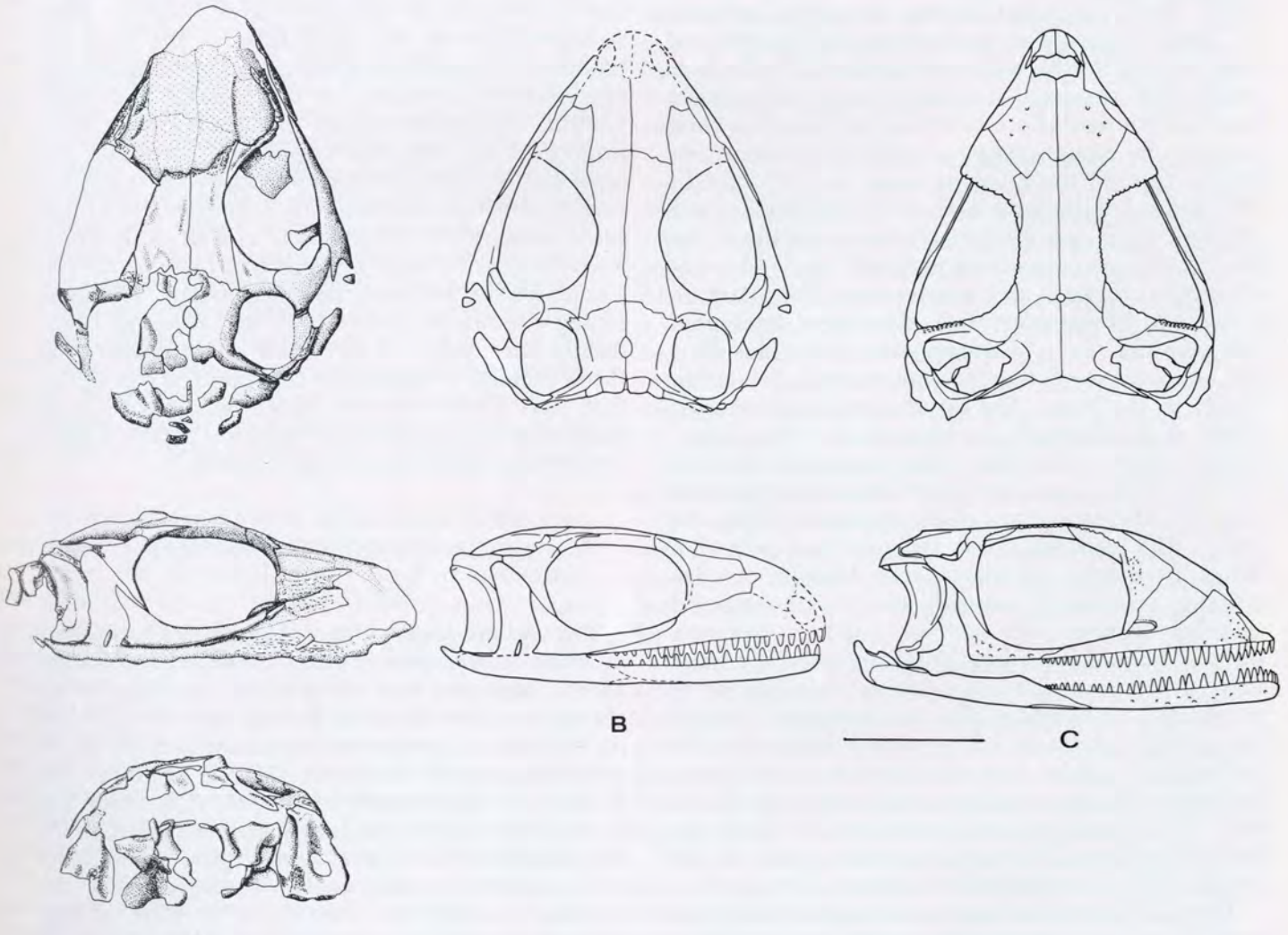


Fig. 4. *Paliguana whitei*, type, Albany Museum, Grahamstown, no. 3585. A. skull in dorsal, lateral and posterior views. B. restoration of skull in dorsal and lateral views. C. skull of the Upper Triassic lizard *Kuehneosaurus*, from Robinson. All × 2.

right lower jaw is present, but shows no details. Fortunately, the temporal region is quite well preserved. The parietals differ from those of *Kuehneosaurus* in the presence of a large pineal opening midway in their length, but are otherwise similar in configuration. A long process extends posterior to the upper temporal opening to make contact with the squamosal laterally. Posteriorly, this process is recessed, probably for a small supratemporal, a bone that has this general position in captorhinomorphs, eosuchians and many lizards. Medially there are two pairs of small quadrangular bones exposed on the occipital surface of the parietal. They surely represent vestiges of both postparietals and tabulars — bones lost in all typical squamates. Little of the actual bone of either squamosal is present, but most of the outline is retained as an impression of the right side, together with traces of the bone. It is in the form of a narrow band, inserting on the anterodorsal surface of the posterior process of the parietal posteriorly, and extending across the dorsal surface of the quadrate. Anteriorly it is overlapped by the posterior bar of the postorbital. There is no evidence of the great extension down over the quadrate shown by Broom (1925, Fig. 5), although it does extend farther than in *Kuehneosaurus*. The postorbital and postfrontal have essentially the same configuration as in that genus. The quadrate is a large bone, of typically lacertoid configuration. Laterally, the bone has been pierced by weathering or earlier preparation. Broom figured the bone as entire in 1903, but in 1925 indicated the bone in front of this opening as a quadratojugal, restoring that bone as L-shaped, the ventral process connecting with the jugal. There is no support for such an interpretation. The quadrate is exposed in posterior view, showing a configuration very like that of *Kuehneosaurus*. A rounded crest for attachment of the tympanum runs the entire height of the bone. The dorsal surface is rounded where it fits beneath the squamosal. The paroccipital process must have fitted against the medial surface of the quadrate just beneath the parietal. The articulating surface of the quadrate is not exposed. The jugal has a very long anterior extension beneath the orbit. There is a very short process extending posteriorly beneath the lower temporal opening. Between this and the quadrate is a tiny piece of bone that Broom (1903) identified as a fragment of the lower jaw. It is just as plausibly interpreted as a rudiment of the quadratojugal. Despite the possible remnant of a quadratojugal and the presence of a short posterior process of the jugal, the temporal region is functionally very similar to that of *Kuehneosaurus* and *Icarosaurus*, in both size and proportions. The area is much closer to the pattern of true lizards than it is to that of *Prolacerta*.

In occipital view can be seen poorly preserved exoccipitals and otic-paroccipital bones. The posterior portions of the pterygoids are visible ventrally. The frontals are long paired rectangular bones, much as in *Kuehneosaurus*, except that their orbital margin is smooth rather than crenulated. The prefrontals have a large dorsal exposure, but probably do not extend ventrally on to the maxilla in front of the orbit as in the Upper Triassic lizards. Only the posterior portion of the nasals are represented, and that only by an impression of the inner surface. There is no evidence of the premaxilla, nor of either the position or configuration of the external nares. The lacrimal, lacking the surface layer, is exposed on the right side. As preserved, it shows a narrow rectangular shape, extending halfway between the orbit and the end of the snout.

Only the broken inner bone of the posterodorsal portion of the maxilla is visible on the right side. A small peg-shaped tooth is present adjacent to the lower jaw. A dentition similar to that of *Kuehneosaurus* has been restored on the basis of it.

The jaw is slender and has a short retroarticular process. No other features are evident.

Palaeagama and *Paliguana* are the only genera from the Karroo that provide evidence of the skull roof of forms directly ancestral to lizards. There is no evidence that either of these forms is any younger than the *Lystrosaurus* zone, at the base of the Triassic, yet the basic pattern is fundamentally the same as that exhibited by Upper Triassic lizards. What primitive features they do exhibit — the large size and posterior position of the pineal opening and the retention of remnants of the tabular and postparietal — are not related to the important functioning of the temporal region. Of particular importance is the relative shortness of the temporal region as recently discussed by Robinson (1973). The great similarity in proportions as well as in size to *Kuehneosaurus* strongly suggests that these forms had a functionally lacertoid jaw mechanism. This is in strong contrast to *Prolacerta*, which, although structurally intermediate between the diapsid pattern of the eosuchian *Youngina* and the lacertoid configuration, has much different skull proportions from *Kuehneosaurus*; details of the temporal region suggest a much less lizard-like jaw mechanism.

SAUROSTERNON BAINII Huxley

(Figs. 5, 6 and 7)

The earliest description of a lizard-like form from the Karroo was that of *Saurosternon bainii* (Huxley, 1868). The only known specimen consists of an almost complete skeleton, lacking only the head and part of the tail, preserved in counterpart blocks of very fine-grained sandstone (British Museum No. R.1234). It was discovered by Mr. Bain from Styl Krantz, Sneeuwberg, South Africa. According to Dr. Kitching, both *Cistecephalus* and *Daptocephalus* zones are exposed in this area. Whichever bed the specimen came from, it is Upper Permian in age. When originally described, the counterparts were essentially mirror images of each other; the bone was split through the middle with little if any of the

original surface exposed. Consequently, Huxley's illustrations show little more than the outline of the bones. Mr. Croucher at the British Museum (Natural History) very kindly prepared the specimen by etching away the bone in hydrochloric acid, leaving the matrix as a high fidelity mould of the original surface. This was cast with silicon and latex rubber. The detailed anatomy of the specimen has been studied from these casts.

The casts of the counterparts represent primarily dorsal and ventral views of the animal. The overall appearance is similar to that of the type of *Palaeagama*. Although there are structural differences that may be used to support the retention of the previously indicated taxonomic difference, several areas of particular significance are not comparably preserved in both specimens. The specimen of *Saurosternon* is certainly less mature, with correspondingly less complete ossification of the distal end of the humerus and most of the other articulating surfaces of the limb bones.

The body is spread out flat, with the tail curving around the front of the block. The forelimbs are bent back with the hands inserted into the rib cage; the rear limbs are strongly flexed, with the feet drawn in just behind the pelvis. The preservation of the individual bones is exceedingly good in this specimen. So good, in fact, that it is necessary to base this description largely on comparisons with living forms. Some primitive features correspond with those seen in *Sphenodon*, but more extensive comparison is possible with lizards. The greatest similarity was found with the common iguanid, *Iguana iguana*, but comparison was also made with a variety of other forms representing many of the living families. Among iguanids, the greatest similarity in proportions was found not with forms of the same size but with animals of considerably greater linear dimensions. For its size, *Saurosternon* has noticeably stouter limbs than modern equivalents, although the detailed structural similarity is very close.

The cervical vertebrae as well as the skull are missing in this specimen. Ten vertebrae are exposed between the pectoral girdle and the sacrum. Presumably, up to 12 had been present more anteriorly. Five can be glimpsed above the puboischiadic plate. From comparison with *Palaeagama* and modern lizards, it is probable that the last of these is the first caudal, although it might be the more posterior of the two sacrals. No trace of the vertebrae in this region can be seen in dorsal view. Twenty-one caudal vertebrae can be seen in articulation behind the pelvis. Extending around the opposite side of the block, over the left shoulder, can be seen 10 distal caudals. Assuming that the tail had been coiled evenly about the body, that the length of the intervening segments was intermediate between those of the extreme ends of the tail, and that no appreciable gaps developed during preservation, there would be 35—40 vertebrae in this area, for a total caudal count approaching 70.

The general configuration of the vertebrae resembles more that of sphenodontids than lizards. Throughout the trunk and sacral region, large intercentra, with proportions similar to those in *Sphenodon*, are apparent. The centra are notched to receive them. They are presumably still deeply notochordal. Laterally, the centra are deeply constricted near the base, but the ventral surface remains rounded rather than keeled. There is no trace of the neurocentral suture. The transverse processes extend a very short distance laterally from the pedicles and slope anteroventrally to the margin of the centra. The articulating surface is essentially flat and faces straight laterally. The neural arches are crushed down into the neural canal, making detailed observation of this surface difficult. The neural spines are short and triangular, with the apex above the posterior zygaphophyses. Anteriorly, the spine continues as a low ridge, passing beneath the preceding arch. Here it bifurcates, as in some lizards, to form laterally facing accessory articulating processes. These are also developed in *Sphenodon* (Hoffstetter and Gasc. 1969). The zygapophyses themselves appear to be quite steeply angled, but this is difficult to quantify due to crushing. In contrast to primitive eosuchians such as *Galesphyrus* and *Youngina*, the zygapophyses are close to the midline, as in most lizards.

As in lizards, sphenodontids and advanced eosuchians, the anterior caudal ribs are indistinguishably fused to the transverse processes. These fused structures extend at essentially right angles to the tail. Those of the most anterior exposed caudals, the first or second of the series, extend at a slight angle anterior to the transverse plane. The next several extend slightly posteriorly. These prominent processes extend for only about five segments. Short pointed ribs are evident to the end of the anterior portion of the tail as preserved. The apparent break in the pattern of the ribs is probably a result of preservation, rather than being natural.

Although not all of the anterior caudal centra are ideally preserved, enough are sufficiently well exposed to indicate the absence of any tail-break mechanism in the portion of the tail where it might be expected.

Intercentra are present anterior to the first centrum behind the ischium. More posteriorly, well developed haemal arches are present in the anterior portion of the tail. The length of the centra does not appreciably shorten even in the terminal caudals, but the height and width are greatly reduced and the zygapophyses become almost indistinguishable.

The shoulder girdle presages the lacertoid condition to a striking degree. The dermal elements are similarly reduced, with the plate of the interclavicle reduced to a narrow bar. The similarity of this bone to that of the monitor was noted by Huxley. In iguanids, the lateral processes angle posteriorly at

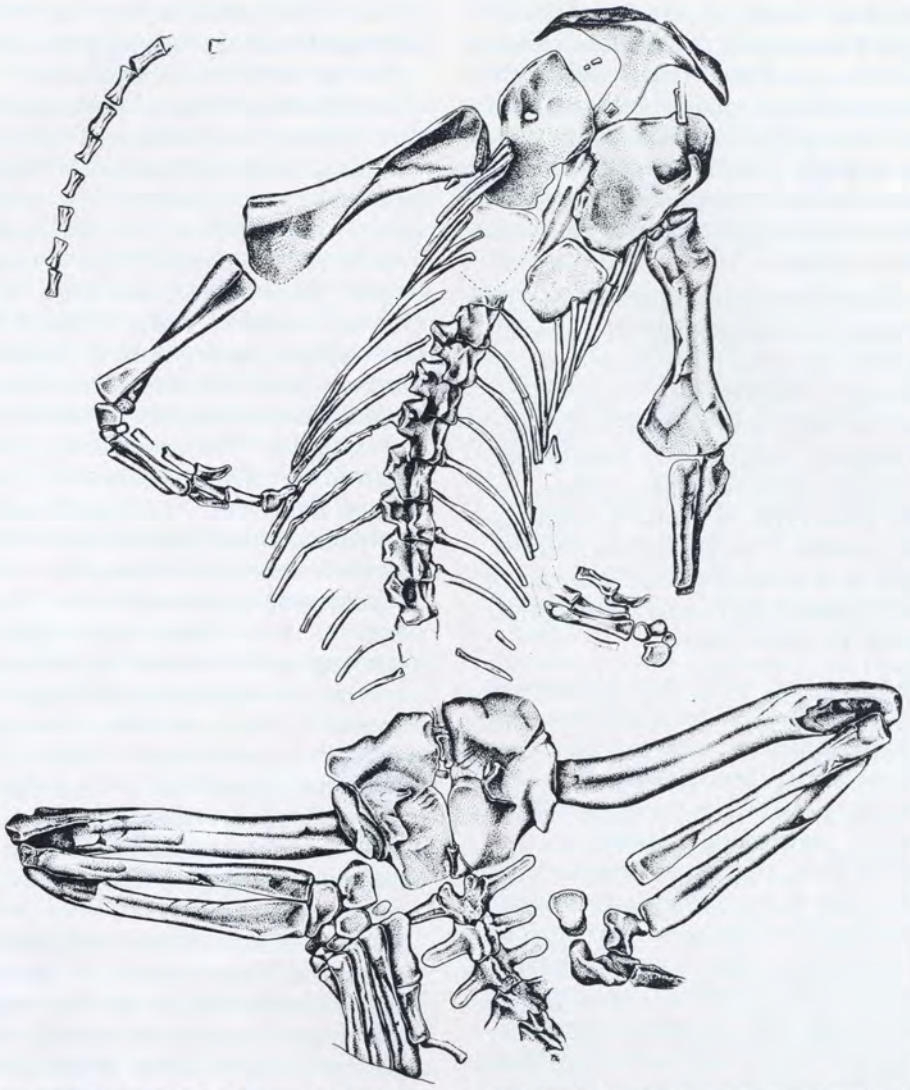


Fig. 5. *Saurosternon bainii*, type, British Museum (Natural History), no. 1234; dorsal view, drawing based on latex cast, ×2.

about 25° to the transverse plane. The angle is approximately 15° in *Saurosternon*. In both forms, there is a midventral ridge extending from the area of the clavicular attachment back to the level of the sternum. In both, the stem extends posteriorly nearly, but not completely, to the posterior limit of the sternum. The clavicular blades are very narrow. Since the specimen is flattened into almost a single plane, it is difficult to reconstruct the original angle of the blades. Their appearance above the dorsal surface of the interclavicle suggests, however, that as in lizards they were angled dorsally from the level of the interclavicle. Only the very base of the shaft is preserved. No trace of the cleithrum is preserved. There is no way to judge whether this element had been eliminated by this stage in the origin of lizards.

Only the ventral portion of the scapulocoracoid is present. This area is very important, however, in showing the inception of lacertoid characteristics. Lizards typically have a fenestrated structure anteriorly in contrast to a more or less continuously ossified anterior portion of the scapulocoracoid of most Paleozoic forms. In the latter group, the anterior margin may be smooth, but is more often irregular as a result of incomplete ossificaton; there are never narrow extensions of tissue between large openings. In *Saurosternon*, there is a large gap ventrally behind the plate of the interclavicle. The margin of this area is clearly defined, but across it are narrow, poorly ossified rods of tissue, clearly comparable to those seen in lizards. *Saurosternon* appears more primitive than iguanids in the lesser extent of the fenestration and possibly in the lower degree of ossification of the separate bars.

In lizards, the scapula and coracoid tend to be separately ossified. Although only the base of the scapula is preserved in this specimen, there is no evidence of a suture separating it from the coracoid. Making allowance for dorsoventral crushing, the glenoid appears essentially like that of iguanids. The shortness of its articulating surface is in marked contrast to the great extent common in Paleozoic reptiles. The scapular portion has been crushed into the ventral plane, but the orientation of this portion of

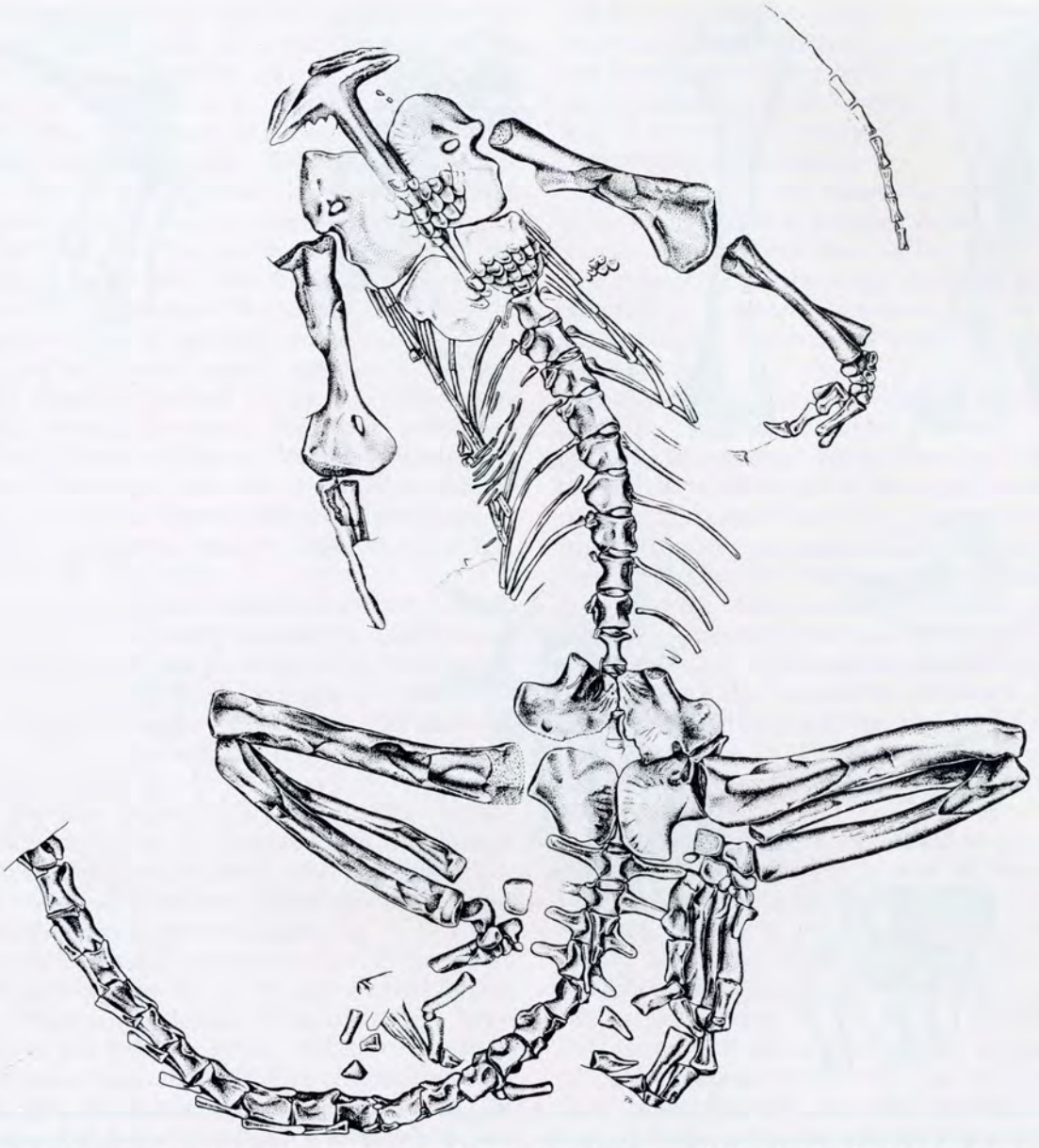


Fig. 6. *Saurosternon bainii*, type, British Museum (Natural History), no. 1234; ventral view, drawing based on latex cast, ×2.

the glenoid was probably obliquely posteroventral, as well as somewhat lateral. There is, as in iguanids, a small opening just anterior to the supraglenoid buttress. Anteromedial to the glenoid is a large coracoid foramen, again as in iguanids. Medially, the configuration of the area appears more primitive, with this foramen opening into a substantial subcoracoscapular fossa.

Saurosternon exhibits a substantial but paired sternum. This bone extends the length of slightly more than two vertebral centra. It has essentially the same proportions and dimensions as those of some modern lizards. The relationship of the coracoid and the sternum is very similar, with a slight gap between them laterally and a larger space medially. The apparent immaturity of the specimen indicates the possibility that the sternum might be co-ossified in an adult. The sternum does appear median in the slightly larger but generally similar specimen from the Albany Museum collection (Fig. 8). The ventral surface of the sternum in *Saurosternon* is somewhat obscured by overlapping scales, but there do not appear to be the lateral projections for the attachment of the ventral extremities of the ribs as seen in modern lizards and also in the Permo-Triassic eosuchians *Tangasaurus* and *Kenyasaurus* (Harris and Carroll, 1975). Cartilaginous ventral extensions of the sternal ribs may not have been well developed in this form, in contrast to the condition seen in *Palaeagama*. Considering the preservation of other delicate structures in this area, their absence in the fossil probably indicates that they were not substantial elements in the living animal.

The humerus is essentially lacertoid, although with some retention of primitive features. In comparing this and other limb bones, it is important to



Fig. 7. *Saurosternon bainii*, type, details of appendicular skeleton, compared with modern lizard. A. *Saurosternon*, dorsal view of humerus (dotted line indicates extent of articulating surface, based on the nature of the glenoid), × 3. B. *Iguana iguana*, dorsal view of humerus, × 1.5. C. *Saurosternon*, medial and lateral views of left carpus, × 4.5. D. *Saurosternon*, restoration of carpus in dorsal view, × 4.5. E. *Saurosternon*, head of left femur, posterior view (dotted line indicates probable extent of articulating surface based on condition in modern lizards), × 3. F. *Iguana iguana*, head of left femur, posterior view (dotted line indicates extent of articulating surface), × 1.5. G. *Saurosternon*, left foot, ventral view, × 4.5. H. *Iguana iguana*, left foot in dorsal view, showing epiphyses, × 2. Abbreviations: a — astragalus; c — calcaneum; cen — centrale; i — intermedium; lc — lateral centrale; mc — medial centrale; p — pisiform; r — radiale; R — radius; U — ulna; u — ulnare; 1-5 — distal carpals and tarsals; i-v — metacarpals and metatarsals.

keep in mind that the ends are incompletely ossified; it should therefore be matched with an immature lizard, or one in which the epiphyses have been removed. In lizards and *Sphenodon* there is a ball-shaped proximal articulating surface of the humerus, extending from the general proximal surface of the bone, and of much less anterior-posterior extent. Such a structure is not visible in this specimen, but such a head must have been present in the living animal since the total width of the proximal end of the humerus is much greater than the available articulating surface of the glenoid. There is some crushing, which probably accentuates the width of the shaft. It is certain that the area of distal expansion is wider than in lizards, since posteriorly the entepicondyle surrounds the entepicondylar foramen so that this opening, as in *Sphenodon,* opens ventrally well anterior to the margin of the bone. Dorsally it is revealed, as in that genus, by a diagonal slit on the margin of the bone. Anteriorly there is a narrow groove running parallel to the margin at the distal extremity indicating the presence of a small ectepicondylar foramen. Except for the reduction in the posterior extent in living forms, the distal portion of the humerus is essentially like that of iguanids.

The ulna and radius are directly comparable with those elements in iguanids, if lack of the epiphyses is taken into consideration. Even without the olecranon, the proximal articulating surface of the ulna slopes ventrally toward the humerus. The shaft of the ulna is slim and about 70% the length of the humerus. Distally it is flattened in the plane of the carpus. More proximally, the shaft is laterally compressed. In living lizards, the distal epiphysis of the ulna develops as a convex head for a ball and socket joint between that bone and the ulnare. This pattern has already evolved in *Saurosternon*. In ventral view, the distal end of the left ulna is concave at the tip, apparently showing the end of the bony shaft. On the dorsal surface, however, the bone continues slightly more than a millimetre longer in tissue that is slightly differentiated in surface detail from that of the shaft. For some reason, the acid preparation removed this epiphyseal area on the dorsal surface, but not ventrally (Fig. 7C).

There are relatively few features for comparison, but the radius is essentially indistinguishable from that of an iguanid. It has a slender shaft; the proximal end is a flat oval at right angles to the shaft. Distally the bone is slightly flattened in the plane of the carpus. The distal articulating surface forms a gently convex arc.

All of the left carpus is preserved. The medial elements are visible in the ventral block, the lateral in the dorsal. The overall pattern and detailed structure of the individual bones closely resemble those of *Sphenodon* and primitive living lizards.

The pisiform lies adjacent to the end of the ulna; it is small, nearly spherical, with only a small finished bone surface anterodorsally. The ulnare is a large oval with an extensive anterior surface of finished bone; the posteroproximal face is concave, for articulation with the specialized surface at the end of the ulna. As in lizards, the radiale is a flattened oval of unfinished bone. There is a small diamond-shaped intermedium which has a very limited surface for articulation with the radius and none with the ulna. It is much smaller than the intermedium of fossil and living sphenodontids. A primitive feature is the presence of a relatively large medial centrale, similar in shape and directly beneath the radiale. A smaller spherical bone can be identified as a second centrale.

The first distal carpal is a tiny spherical bone, occupying less than half the proximal surface of the first metacarpal as in iguanids. The second distal carpal is considerably larger than the first. The third distal carpal is partially obscured beneath the other elements. The fourth distal carpal is the largest, and a small area of the dorsal surface is of finished bone. The fifth distal carpal is a small sphere with no finished surface. Comparison of this carpus with that of specific lizards is difficult due to the presence in the latter group of ossified epiphyseal elements at the proximal ends of the metacarpals and elsewhere. There were apparently no such elements in the fossil, but smaller distal tarsals resemble those elements in their size and position and it is possible that confusion might arise in differentiating between small elements of the central series, distal carpals and metacarpal epiphyses in both fossils and prepared lizard skeletons.

In *Saurosternon,* the length of the metacarpals increases in primitive fashion from the first to the fourth, with the fifth close to the length of the first. The remainder of the hand resembles that of large iguanids in its general structure, but on neither side are enough of the distal elements preserved for restoration.

In ventral view, the pelvic girdle can be seen to be basically primitive, with a nearly continuous puboischiadic plate. Ventrolaterally, the margin of the pubis is thickened to form an anteriorly facing process that ends bluntly in a surface of unfinished bone. This area, conspicuous in many primitive reptiles, served for the attachment of abdominal muscles and tendons. On the dorsal surface, the anterior margin — the only portion of the pubis that is ossified in lizards — is much thickened in this form. In *Saurosternon,* the obturator foramen pierces this thickened portion near the margin of the ischium. The area that in lizards remained open as the thyroid fenestra is still ossified, but the bone is quite thin.

A diamond-shaped unossified area characterizes the juncture of the pubis and ischium. This may have marked the initial development of the thyroid fenestra, but it is equally probable that this area would have been ossified at a more mature stage. It is difficult to determine the natural orientation of the pubis because of crushing. In modern lizards, the major surface of this bone is angled obliquely from the transverse plane so that the largest surface faces anterodorsally. In primitive reptiles, the surface of the bone faces predominantly dorsomedially. In this flattened specimen, it is difficult to determine whether the large dorsal exposure is entirely natural, or if the bone has been twisted as well as flattened during preservation. The symphysis between the pubes appears to extend at least half the length of these bones, in contrast to its very narrow extent in small iguanids, but the length of the symphysis is quite long in larger modern forms such as *Varanus*.

The ischium approaches the lacertoid configuration in its short posterior extent, but the anterior border is certainly not recessed where it might have bordered a thyroid fenestra, in contrast to even the Triassic lizard *Icarosaurus*. Only the bases of the ilia are preserved. This area resembles that of lizards, but there are likewise no distinguishable differences from more primitive forms. In sum, this pelvis shows no specifically lizard-like features in advance of the general eosuchian pattern.

Like the humerus, the femur resembles that of a lizard in which the epiphyses are not ossified. Comparison with an iguanid femur in which these elements are lost shows almost no distinguishing

features. The proximal end of the femur of *Saurosternon* has a large oval area of unfinished bone, ridged at the margins, that must have been covered in life by an extensive, hemispherical, cartilaginous or bony articulating surface, as in modern lizards. Posteroventrally the bone extends as an internal trochanter, arising gradually from the general ventral surface of the bone. The shaft is slightly sigmoidal, with the articulating surfaces twisted relative to one another. The posterior portion of the distal articulating area has an unfinished surface, suggesting the original presence of a bony epiphysis.

The bony shafts of the tibia and fibula are both 20 mm in length, 85% that of the femur. In a specimen of *Iguana iguana* of comparable size, the tibia is 90% the length of the femur. The general proportions, configuration and relative size of these elements resemble those of iguanids; the only notable exception is the relatively smaller size of the proximal head of the tibia in *Saurosternon*. This bone also lacks the proximal crest expressed on the posteromedial margin of the shaft in many lizards. No epiphyses are ossified on either the tibia or fibula. The configuration of the ossified extremities of these bones closely resembles that in lizards. There is no evidence bearing on the presence or absence of proximal ossifications or cartilaginous developments such as the patella or the epiphysis of the fibula. Distally, the configuration of the ventral surface of the proximal tarsals suggests the presence in the living animal of a triangular epiphyseal extension of the fibula such as that seen in an iguanid. The configuration of this area in more specialized lizards such as varanids, however, is not comparable with that of *Saurosternon*.

The left tarsus, with all of the elements in nearly their natural positions, is visible in both dorsal and ventral views. At first glance, it appears to lack all the specializations characteristic of lizards. The fifth metatarsal is not hooked, and all five distal tarsals are retained, along with a substantial centrale. The astragalus and calcaneum are clearly not co-ossified. Comparison with a series of more primitive reptiles, captorhinomorphs and eosuchians, as well as primitive lizards, indicates that the tarsus as a unit was functionally approaching the lacertoid condition. This is particularly noticeable if we consider proportions. Although exact measurements are impractical as a result of the angular contact between the elements, the ratio between the posterodistal extent of the tarsus and the length of the crus shows a general decrease from primitive romeriids, through the primitive eosuchian *Galesphyrus* to *Saurosternon* and later lizards.

In primitive reptiles, romeriids, captorhinids and primitive eosuchians such as *Galesphyrus,* the astragalus and calcaneum are large flat elements, with the articulating surfaces for the tibia and fibula broad, sharply separated and at a considerable angle to one another. In *Saurosternon,* the astragalus and calcaneum are relatively extensive dorsally, with the perforating foramen still evident at the margin of the calcaneum. Ventrally, the extent of the bones is much less. The articulating surface for the fibula is in the shape of a very open V, formed equally by the astragalus and calcaneum. Dorsally, the calcaneum appears as a flattened oval. The astragulus is basically triangular in dorsal view, with the dorsomedial margin sloping toward the centrale. The surface for articulation with the tibia is separated from that for the fibula by a considerable gap. In ventral view, the two surfaces appear to be confluent. Dorsally, the centrale appears as a narrow, more or less flat plate; ventrally, none of the surface is finished bone. Proximally, the bone is deeply grooved so as to be closely integrated with the astragalus. It is probable that the two bones functioned as a unit, presaging the condition in true lizards where the centrale is not retained as a discrete element. The fourth distal tarsal articulates broadly with both the astragalus and calcaneum proximally, with the centrale medially, and both the fifth distal tarsal and the fifth metatarsal laterally. The nearly spherical third distal tarsal fits into the mediodistal surface. Much of the ventral surface of the fourth distal tarsal is flat, finished bone. The remainder of the distal tarsals are rounded and show no finished surfaces. This suggests that the surrounding elements moved over them with extensive flexure of the foot. The extent of the first distal tarsal seems great in this specimen, but this is a result of displacement, with the proximal articulating surface extensively exposed in ventral view. In its natural orientation, this bone would have appeared as only a narrow oval. The second is a tiny spherical structure. The third is in the form of a somewhat larger, laterally compressed oval. The fifth is also a small oval element, occupying much less than the total articulating surface of the fifth metatarsal. The presence of distal tarsals one, two and five may be considered to be a primitive condition, distinguishing this form in a clear and obvious way from modern lizards. Close examination of lizards of various families reveals epiphyses in essentially the same position as these distal tarsals. Although the similarity in position does not in itself necessitate accepting homology between these elements, it would certainly be difficult to differentiate the epiphyses from small distal tarsals in fossil members of living lizard groups. The homology of traction epiphyses with originally distinct ossifications within tendons has been suggested by Parsons (1908). Most pressure epiphyses presumably evolved from cartilaginous tissue primitively associated with the growing extremities of the bones, but comparison with traction epiphyses raises the possibility that epiphyses of the metatarsals and metacarpals have evolved from distal tarsals and carpals.

Of the left foot, the first metatarsal is incomplete and the remainder of the first digit is missing. The remainder of the metatarsals are closely appressed and overlapping throughout their length. The proximal ends would have overlapped when the bones were in their normal position. The third and fourth

metatarsals appear to be of approximately equal length. The fifth is about half this length. It is not conspicuously hooked, as this configuration has been specified by Robinson (1975). The proximal articulating surface is somewhat expanded, and proximally it is tilted slightly medially where it is in articulation with the fourth distal tarsal. The proximal end appears to be somewhat bent medially from the long axis of the bone. It is possible that the fifth digit was strongly divergent in the living animal, but it seems doubtful that the role of the fifth metatarsal as a "heel bone" was far developed in this form. There is no evidence for the development of either the outer process or either of the plantar tubercles.

Distally, the foot is incomplete: of the second digit, there is only the proximal phalanx; of the third, the first and second phalanges and the base of the third; of the fourth digit, only the first phalanx. The fifth digit has two phalanges in place. The right foot is badly scattered, but the individual elements are well preserved. One of the terminal phalanges shows a well developed tubercle for a flexor tendon. The ventral surface is keeled and sharply recurved.

A scattering of typical primitive reptilian scales can be seen adjacent to the ribs at the level of the distal end of the right humerus. Individually they are long and narrow, pointed at one end and thinner and flatter at the other. Of much greater interest is the presence of epidermal scales. These can be seen covering the ventral surface of the sternum, with a few lying more laterally. The size and pattern of the scales is essentially similar to those of some living lizards, e.g. *Sceloperus*, of similar body size. They are diamond-shaped and overlapping, and appear quite thick. Presumably they were preserved initially as impressions and contain no bone.

ALBANY MUSEUM 4133

(Fig. 8)

Despite a fairly thorough search for lizard-like forms in the major South African museums in 1972—73, only one previously undescribed specimen was located. This one, in fact, does not add appreciably to our knowledge, since it has no horizon, locality or collector data, and shows no anatomical features not seen in other specimens. It consists of a natural cast of the trunk region in ventral view, including much of the pectoral girdle and the anterior portion of the puboischiadic plate. It is preserved in a fine-grained sandstone, from which casts can readily be made. The specimen is catalogued as no. 4133 in the Albany Museum, Grahamstown.

The portion preserved measures 94 mm in length, 20% greater than the comparable portion of the type of *Saurosternon bainii*. Apart from size, there are few features to differentiate the two specimens. The distal ends of the humeri appear poorly ossified, even in the larger specimen, suggesting that it had not reached maturity. The sternum, however, appears to be a unitary structure, rather than paired as is that of *Saurosternon*. The bone is in two pieces, but this is apparently a result of crushing against the overlying vertebrae, and does not appear to have taken place at the midline. The Albany Museum specimen does not show the anterior processes extending from the margin of the scapulocoracoid, as reported in the smaller form. The glenoid and other features of the scapulocoracoid are of lacertoid configuration. Ventral extensions of the sternal ribs are not preserved, nor are processes of the sternum for their attachment. Only a few intercentra are exposed, but they were presumably present the full length of the column.

THE PALIGUANIDAE AND THE ORIGIN OF LIZARDS

Of the four lizard-like forms described from the South African Karroo, three have been named as the types of monotypic genera. It is very difficult to evaluate taxonomic distinctions where one genus, *Paliguana*, is a disembodied head, and another, *Saurosternon*, a headless body. *Palaeagama* is represented by an essentially complete skeleton, but the skull is extremely poorly preserved, and the specimen certainly represents a much more mature individual than that by which *Saurosternon* is known. Many differences in detail of structure and proportions might be cited between the latter two specimens, but at least some may be related to degree of ossification and maturity. The difficulty of evaluating the possible taxonomic diversity of these specimens is compounded by the absence of firm stratigraphic data. The probable distribution in both Upper Permian and Lower Triassic might justify recognition of specific or even generic distinction between forms, even if they were morphologically quite similar. A further problem is that we have almost no notion of the probable diversity among lizard-like forms of this age. Most of the modern infraorders had probably differentiated by the end of the Jurassic, but it is impossible to suggest how far this process might have proceeded by the early Triassic. Whether one or three genera should be recognized, it seems reasonable to include all these forms in a single family, Paliguanidae, a practice followed by Romer (1956).

The genera discussed here have long been included within the Eosuchia, but with the acceptance that they possessed some characteristics suggestive of affinities with lizards. The current work has shown a multitude of very significant similarities with primitive lizards. In terms of size, proportions and functional characteristics, the skull of *Paliguana* and, to the extent that it is known, that of *Palaeagama* are essentially similar to those of *Kuehneosaurus* and *Icarosaurus*. The postcranial skeleton demonstrates a

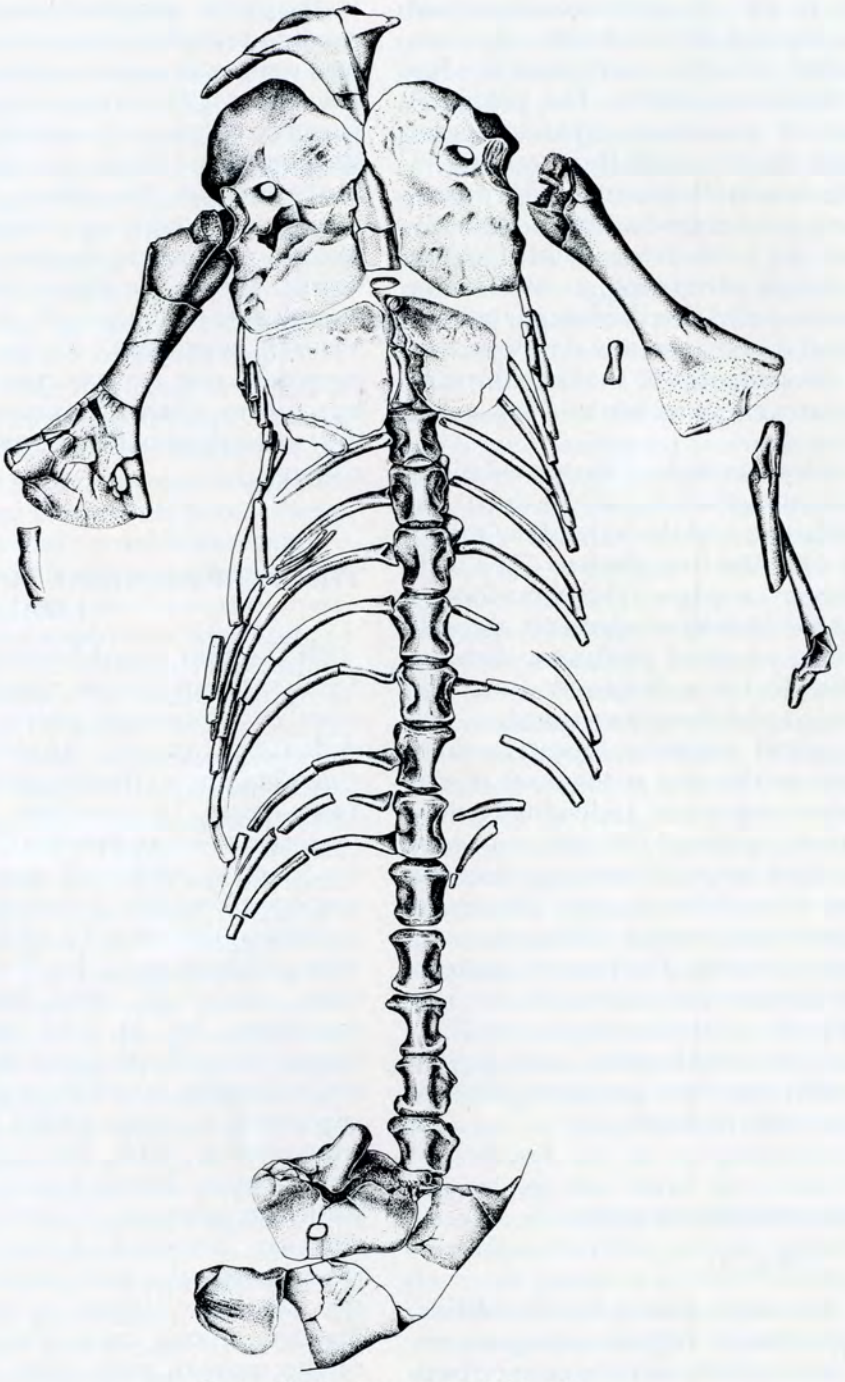


Fig. 8. Albany Museum no. 4133, ×2.

striking mosaic of primitive and lacertoid characteristics. The vertebral column resembles closely that of *Sphenodon,* but shows no features that would not be expected in an ancestor of lizards. In this, it contrasts strongly with *Prolacerta*, in which the cervical vertebrae are of an entirely different nature from those seen in any primitive lizards. The structure of the pectoral girdle and forelimb is comparable even in small details with that of iguanids. The only primitive feature is the retention of the entepicondylar foramen. The configuration of the glenoid and the necessity of a special epiphyseal articulating surface of the humerus are especially striking, as is the nature of the articulation between the ulna and the ulnare.

The pelvic girdle does not appear to show any specializations above the eosuchian level, but the femur, tibia and fibula are almost identical with those of primitive lizards. The tarsus is basically primitive in retaining all the eosuchian elements, but the overall proportions and the functional relationships of the units approach the lacertoid condition. Squamate epidermal scales are present.

The detailed similarities of the paliguanids with primitive living lizards and, as far as they are known, primitive Mesozoic squamates, are so numerous that it may be assumed that they are very closely related. It seems almost impossible for such a complex of characteristics to have evolved in this family if it

were not intimately associated with the ancestry of Mesozoic and Cenozoic lizards.

Although there are some features, such as the structure of the pelvic girdle, and some aspects of the foot structure, of the Paliguanidae that are eosuchian rather than lacertoid in their configuration, the overall anatomy of these forms is that of a very primitive lizard. It is thus suggested that they be included in the Suborder Lacertilia. Since published descriptions of members of the otherwise most primitive lizard infraorder, Eolacertilia, are limited to the highly specialized gliding genera *Kuehneosaurus* and *Icarosaurus,* it is difficult to determine whether the Paliguanidae should be included within this group. In so far as comparable parts of the skeleton are known, the Paliguanidae fit most of the criteria outlined by Robinson and Colbert.

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Palaeont. afr., **18**, 89—131 (1975)

THE MORPHOLOGY AND RELATIONSHIPS OF *YOUNGINA CAPENSIS* BROOM AND *PROLACERTA BROOMI* PARRINGTON

by
C. E. Gow

ABSTRACT

Comprehensive descriptions of the osteology of *Youngina capensis* Broom and *Prolacerta broomi* Parrington are presented. New details of the braincase of *Proterosuchus fergusi* Broom are given as these became necessary for comparative purposes. It is suggested that the initial radiation of sauropsid reptiles was a Permian event as yet poorly documented. The phylogenetic position of *Youngina* both forward and backward in time cannot be narrowly defined, though certain characters seem specifically to preclude it from lizard ancestry. *Prolacerta*, on the basis of tooth implantation, braincase morphology and postcranial anatomy is shown to be closest to the proterosuchian thecodonts. It is very definitely not concerned with lizard origins, but would on available evidence seem to be a perfectly good ancestor for the middle Triassic forms *Macrocnemus* and *Tanystropheus*, which latter must cease to be regarded as lizard ancestors. We have here a rather distinct reptilian lineage which branched off from common ancestral stock just prior to the advent of archosaurs.

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INTRODUCTION

The Permian eosuchians, typified by *Youngina,* are generally considered the hub of later diapsid reptilian diversification (e.g. Romer, 1956).

Youngina is relatively poorly known; thus part of the present study will describe the anatomy of this animal in detail. To begin with it will be necessary to decide just what we mean by Eosuchia and to try to decide what is to be understood as comprising the genus *Youngina*. Here it is necessary to be very explicit as it is becoming clear that the Upper Permian was a crucial period in sauropsid evolution and that relationships are not as generalised as has until now been believed.

The Eosuchia are an order within the Subclass Lepidosauria and in the light of the present study must be added to Romer's (1956) otherwise satisfactory definition that dorsal dermal armour was present. The genera comprising Romer's family Younginidae are a reasonably homogeneous group, with the exception of *Noteosuchus*, which shows rhynchocephalian affinities (Carroll, pers. com.). Of the rest the best material in existence is that of *Youngina* (with its taxonomic variants), and these with their smooth peg-like marginal dentition can be distinguished from *Heleosaurus* (Carroll, in press) which has serrated

marginal dentition and certain other features which put it more closely in line with the Archosaurs.

Broom (1914 et seq.) was responsible for the three generic and five specific names with which what is manifestly one form (*Youngina capensis*) is presently encumbered. This string of names is misleading; all the specimens come from the same horizon, differing only in size, state of preservation and preparation, and nature of deformation, which factors adequately account for all supposed taxonomic differences. One can have no doubts about synonymising them all under *Youngina capensis* to stress the probability that this was a single monospecific genus. This work will present a detailed description of this animal based on all useful material.

Prolacerta (Parrington, 1935), on the basis of its incomplete lower temporal bar, has been considered to represent a stage between the Eosuchia and the Squamata, but this concept must be rejected. A critical re-examination of the true position of *Prolacerta* is necessary. Until now *Prolacerta* (which includes *Pricea*) has been known from a few skulls and some cervical vertebrae. Largely on the basis of an incomplete lower temporal bar it has been regarded as ancestral to the Squamata. The present study describes the whole skeleton and the animal is shown to be Archosaurian in almost every respect.

The braincase of *Proterosuchus* is here re-described in some detail for comparative purposes.

YOUNGINA

MATERIAL AND METHODS

The descriptions of *Youngina* are based on material in the Bernard Price Institute (BPI) and one partial skull from the Transvaal Museum (TM). The several specimens in the Rubidge Collection (RC) were examined. Professor Crompton kindly provided copies of his unpublished drawings of *Youngina rubidgei;* these, though useful, have not been used here, and there are one or two points where we differ. These points of difference are those which it has been possible to prepare more fully. A cast and photographs of the Chicago specimen (*Youngoides romeri*) were made available to the author.

All *Youngina* material comes from the *Daptocephalus* zone of the Karroo. The state of preservation is rather different from that of the millerettids (Gow, 1972) of the same age, which might imply some ecological differences in life. While the millerettids are articulated and distortion free, the younginids are disarticulated and the skulls are distorted.

Most of the *Youngina* material has in the past been subjected to mechanical preparation which had caused some damage and also restricted the scope of further work. Fortunately it was possible to prepare a good braincase and skeleton in formic acid; other details were pieced together from mechanical preparation of selected areas of different skulls.

Material referable to *Youngina capensis* Broom 1914.

A.M.N.H. 5561: *Youngina capensis* Broom 1914. Skull and vertebrae, in American Museum of Natural History.
Locality: New Bethesda, Graaff-Reinet.
Collected: R. Broom.

U.C. 1528: *Youngoides romeri* Olson and Broom 1937. Skull in University of Chicago.
Locality: Towerwater, Murraysburg.

R.C. 90: *Youngopsis rubidgei* Broom and Robinson 1948. Very good skull.
Locality: Doornkloof, Graaff-Reinet.
Collected: J. W. Kitching, 1939.

R. C. 91: *Youngoides minor* Broom and Robinson 1948. A poor partial skull. A second undescribed specimen with the same number is also *Youngina*.
Locality: New Bethesda, Graaff-Reinet.
Collected: Kitching Bros., 1940.

T.M. 1490: *Youngopsis kitchingi* Broom 1937. A very poor skull.
Locality: New Bethesda, Graaff-Reinet.
Collected: J. W. Kitching.

T.M. 200: *Youngina capensis* Broom 1922. Fragments of postcranial skeleton, now even fewer than when described by Broom, but certainly of *Youngina*.
Locality: New Bethesda, Graaff-Reinet.
Collected: I. Venter, circa 1920.

T.M. 3603: Posterior half of a large skull, now acid prepared.
No catalogue data.

R.C. 625 and 626: Two poorly preserved skulls.
Locality: Wellwood, Graaff-Reinet.
Collected: S. H. Rubidge, 1936—45.

R.C. 714: Incomplete skull.
Locality: Ganora, New Bethesda, Graaff-Reinet.
Collected: S. H. Rubidge, 1940.

K. 106: Badly flattened skull in the collections of the Geological Survey, Pretoria.
Locality: Blaaukranz.
Collected: A. W. Keyser.

B.P.I. 375: Skull.
Locality: von der Waltzhoek, Graaff-Reinet.
Collected: J. W. Kitching, 1946.

B.P.I. 2459: Small flattened partial skull.
Locality: Klipplaat, Richmond.
Collected: J. W. Kitching, 1951.

B.P.I. 2871: Skull.
Locality: Beeldhouersfontein, Murraysburg.
Collected: J. W. Kitching, 1958.

B.P.I. 2859: Skull and skeleton.
Locality: Doornplaas, Graaff-Reinet.
Collected: J. W. Kitching, 1964.

OSTEOLOGY OF *YOUNGINA*

The Skull

Dermal bones of the skull roof

Premaxilla (Figures 1 and 6). The premaxilla is fairly well represented only in B.P.I. 2871. There

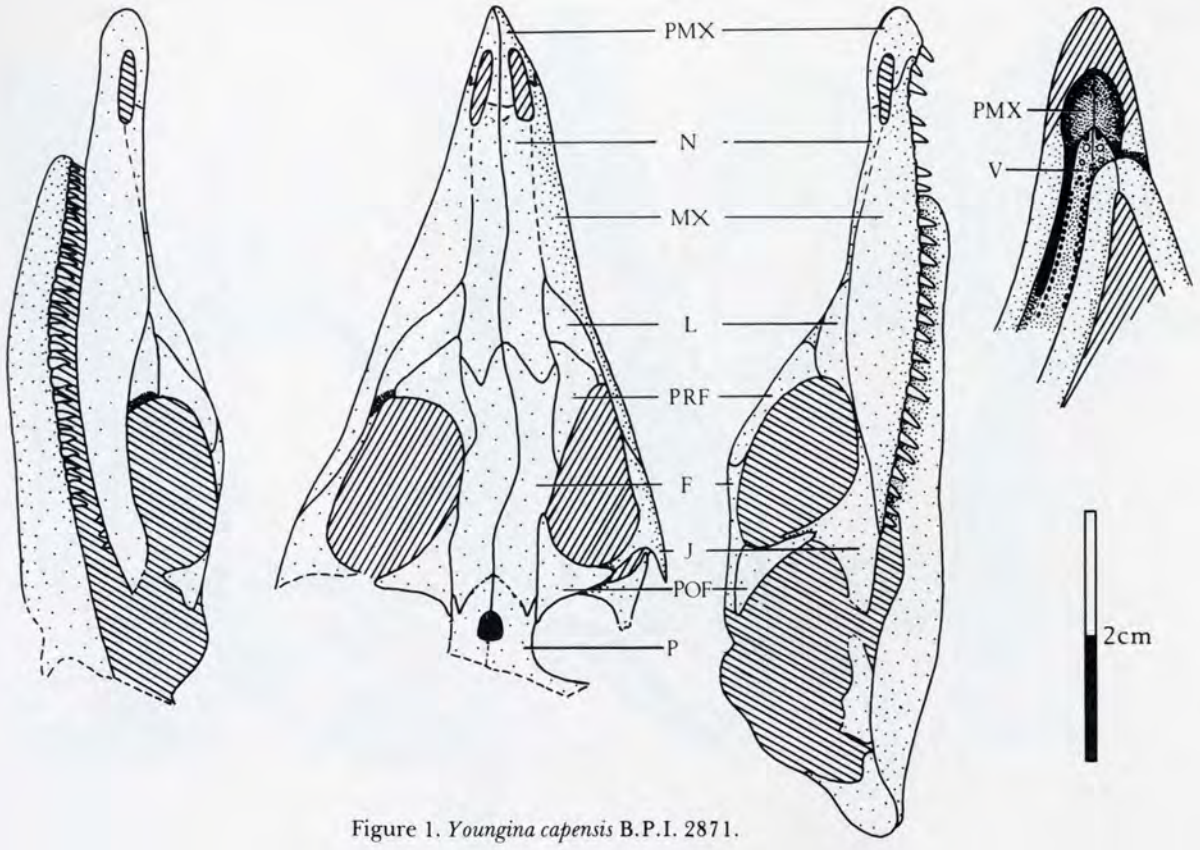


Figure 1. *Youngina capensis* B.P.I. 2871.

appear to have been three premaxillary teeth. The important feature of the premaxilla is its medial extent in the palate: the premaxillae run well back inside the maxillae in a strong contact and meet in the midline.

Maxilla (Most Figures). The maxilla sheaths most of the slender, rather shallow snout, and has an extensive contact with the palatine. The teeth are conical, sharply pointed and not serrated; they thicken lingually at the base much as described for *Milleretta* (Gow, 1972); they are sub-thecodont and become firmly ankylosed in deep pits. An exact count is not possible but there are about 30 tooth positions with alternate replacement so that one gets a count of about 20 functional teeth of different ages. An important aspect of the maxillary tooth row is that it extends back to below the postorbital bar (c.f. *Proterosuchus* Cruickshank, 1972, and crocodilians, but not lizards).

Septomaxilla. Details of this bone are totally lacking.

Nasal (Figures 1 and 6). The relationships of the nasals are clear except anteriorly where there is some doubt as to the exact position of the sutures with the premaxillae, but this is of little consequence.

Lacrimal (Figures 1 and 6). The lateral exposure of the lacrimal is reduced to a short distance in front of the orbit. A single foramen runs the full antorbital extent of the bone (as seen in section in R.C. 625).

Prefrontal. As figured, requires no special description.

Frontal (Figures 2 and 6). The frontals are the only skull roofing elements which have roughened surfaces, notably between the postfrontals and above the orbits. The frontals are rigidly sutured to the parietals.

Parietal (Figures 2, 4, 5 and 6). The parietals enclose a large pineal opening and send out posterolaterally directed wings. The area bordering the upper temporal opening is deep and has a shallow pocket in the posterior corner affording a strong area of origin for part of the jaw adductor muscle complex. The wings are joined by a slight ridge between skull table and occiput. Each lateral wing forms important attachments; anteriorly there is an extensive firm contact with the squamosal (Figures 4 and 6): applied to the posterior surface are a post-parietal and tabular, while the tip is sheathed by a supratemporal whose exact relationships will be discussed separately. The lateral wings roof large post-temporal fossae and there is no firm contact with the supraoccipital.

Postfrontal. The postfrontal is firmly sutured between frontal and postorbital.

Postorbital. The postorbital is overlapped above by the post-frontal (this region, the anterior border of the upper temporal opening, is deep); ventrally it has a rigid sloping contact with the jugal, and posteriorly a broad flat sheet has an extensive overlap onto the squamosal.

Jugal (Figures 2, 5 and 6). This is a straightforward element having a long sloping contact with the maxilla and short rigid connections with post-orbital and quadratojugal. Where it forms the anterior border of the lower temporal opening there is a distinctive depression (indicated in Figure 6, lateral view). Internally the jugal has the ectopterygoid abutting against it. It has not been possible to expose the inner surface of this region of the jugal.

Quadratojugal (Figures 2 and 6). This is an element

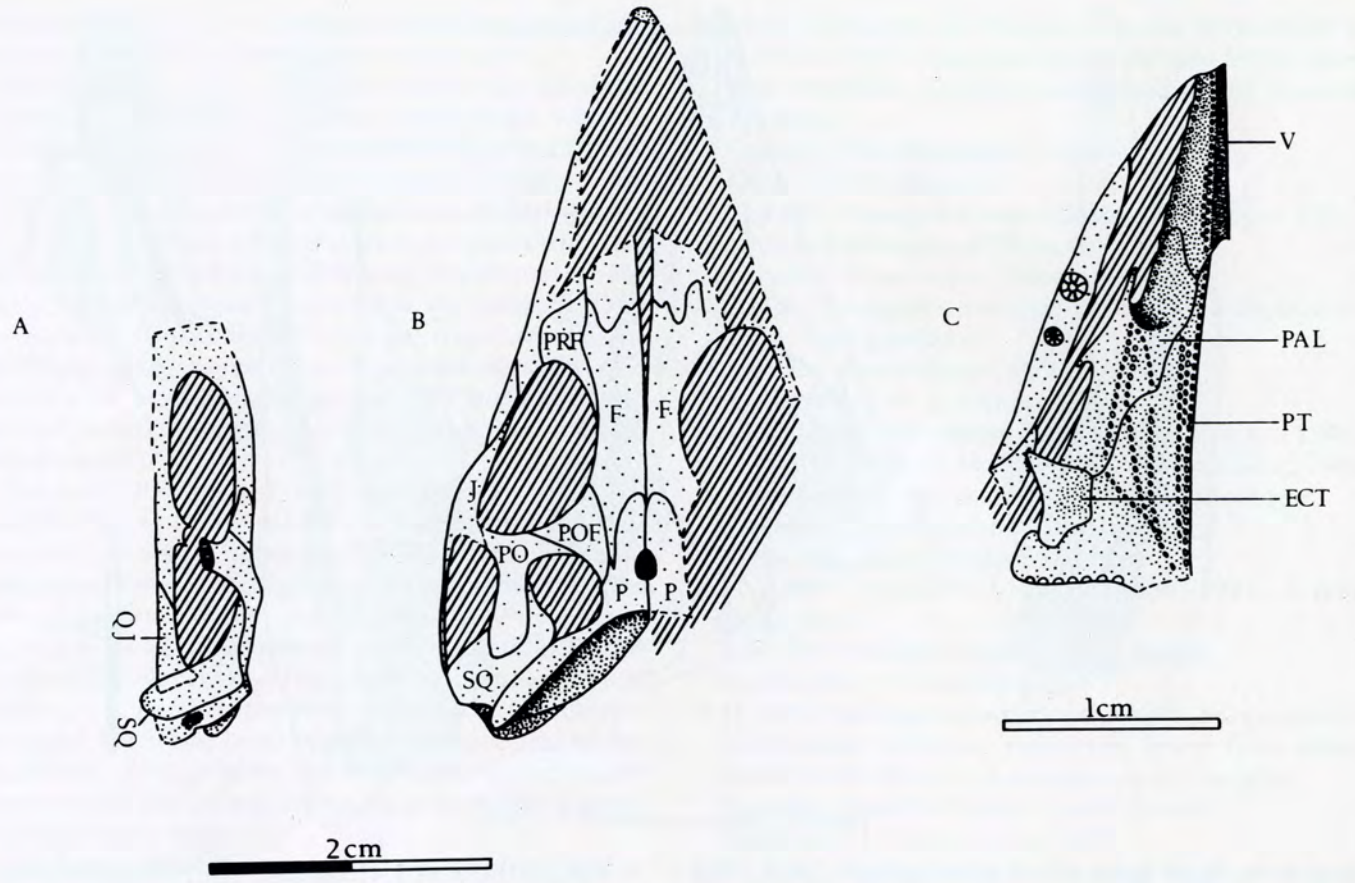


Figure 2. *Youngina capensis* B.P.I. 3859.

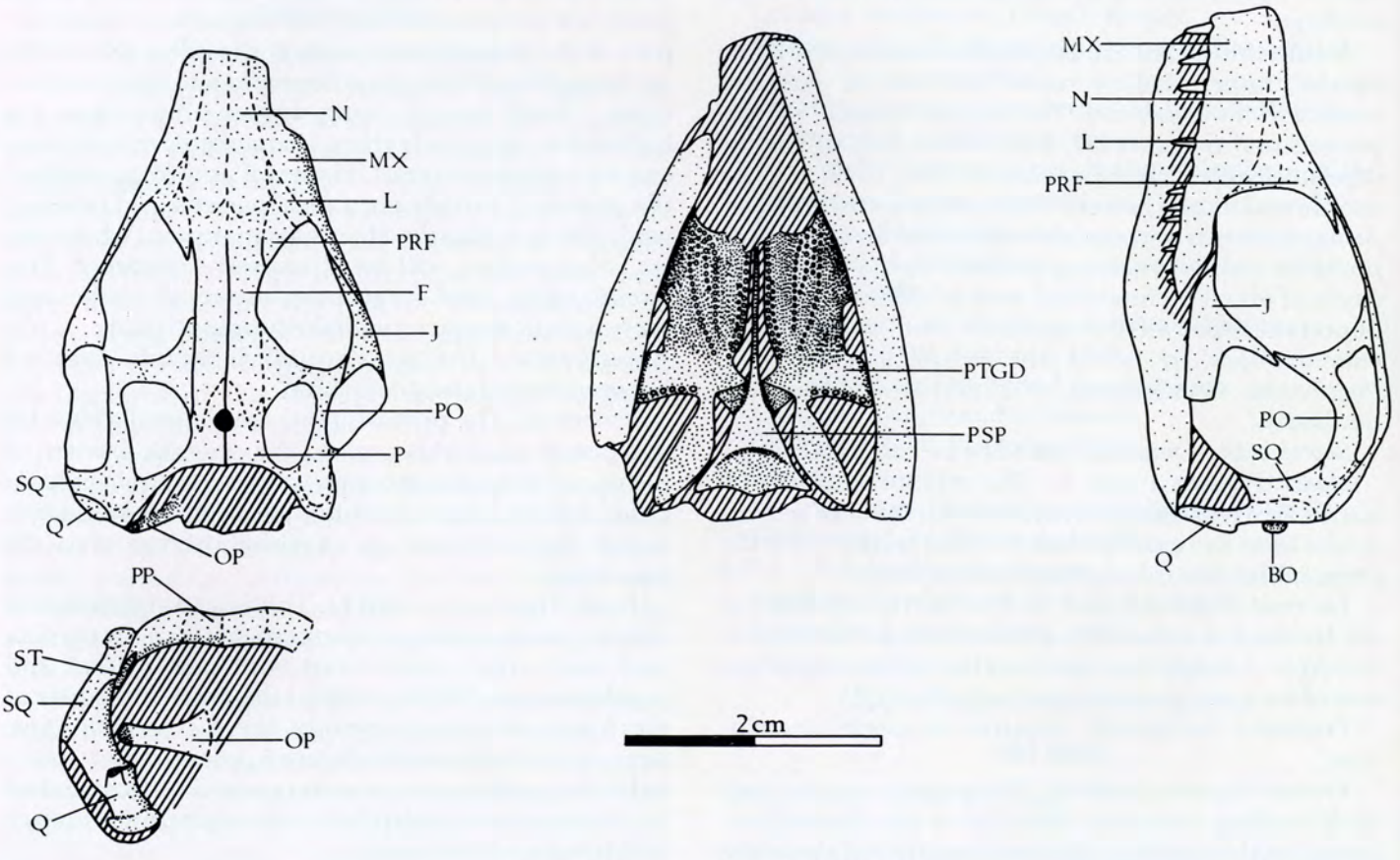


Figure 3. *Youngina capensis* B.P.I. 375.

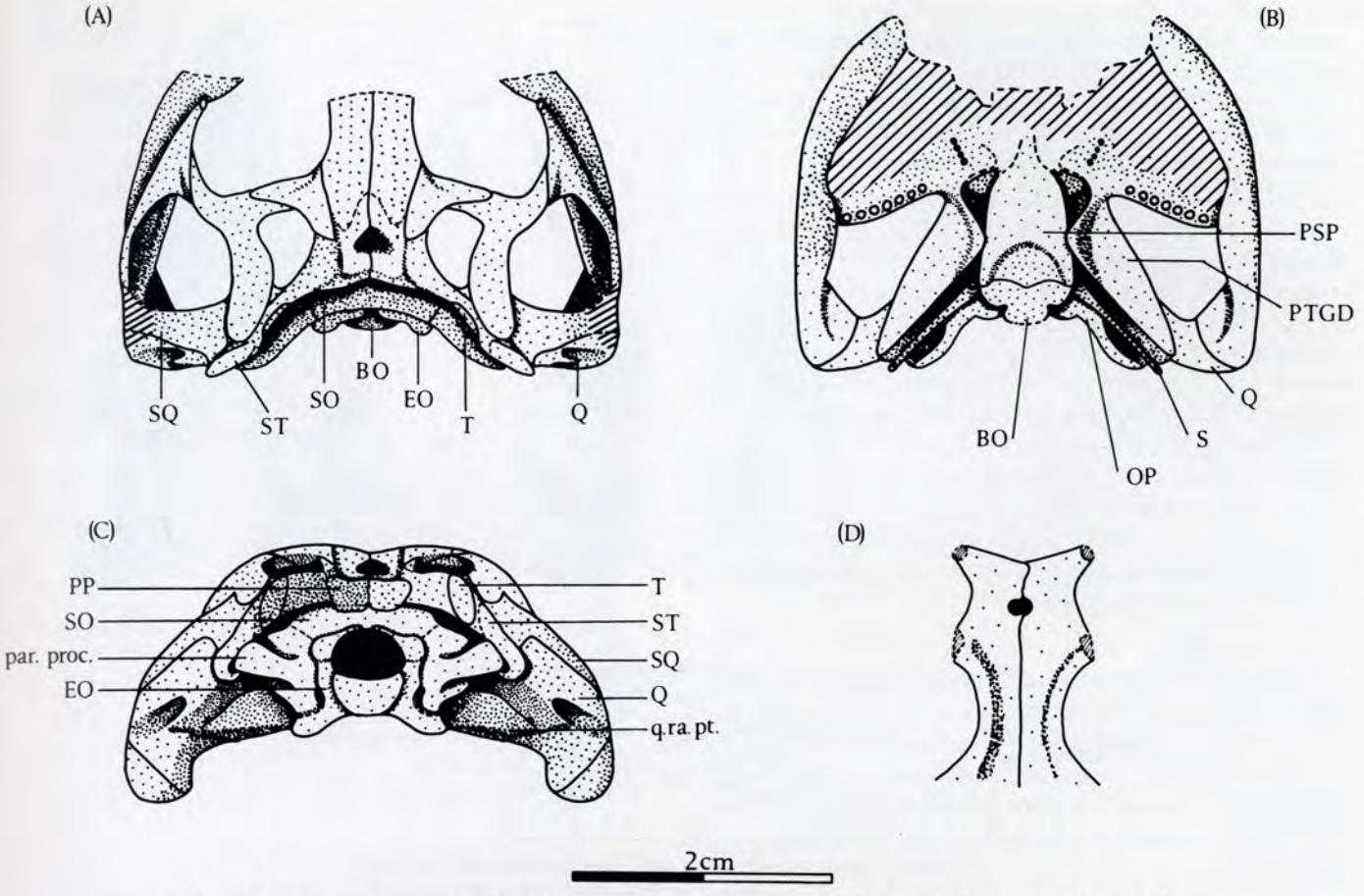


Figure 4. *Youngina capensis* T.M. 3603. A, Dorsal; B, Ventral; C, Occipital; D, Internal detail of frontoparietal region.

critical to phylogenetic discussion. The contact with the jugal presents no problem; it is the relationships to squamosal and quadrate which are important. With B.P.I. 3859 (Figure 2) it was possible to remove part of the squamosal to reveal the full extent of the quadratojugal beneath it. T.M. 3603 provides a check in that the upper two-thirds of the inner surface of the squamosal are clean and there is no sign of any dorsal continuation of the quadratojugal. Unfortunately no specimen shows the contact of quadrate and quadratojugal.

Squamosal (Figures 2, 4, 5 and 6). The squamosal overlies part of the quadratojugal below, then rises up in contact with the quadrate, finally turning inwards to cap the quadrate, running under a facet of the post-orbital and lapping against the parietal wing.

Postparietal, Tabular and Supratemporal (Figures 4, 5 and 6). There is reasonable certainty regarding the presence of these three elements. Postparietal and tabular are simply applied against the back of the parietal. The supratemporal on the other hand is more complex; it lies against the back of the parietal wing and extends beyond its tip, turning down and forwards to form a hook which lies against the top of the pterygoid flange of the quadrate. This hooked supratemporal possibly supported a cartilaginous pad which could rotate against the paroccipital process.

Sclera. These are present in B.P.I. 2871 and suggest a ring of ± 12 flat plates.

The palate. The palate of *Youngina* has to date been poorly known and imaginatively drawn. Olson's (1936) reconstruction is poor and has been used by Romer (1956): in this, the anterior of the palate is quite wrong as is the epipterygoid stuck in the basal articulation.

Vomer (Figures 2 and 6). The vomers are fused in the midline. Anteriorly they disappear above the palatal extensions of the premaxillae which are also united in the midline. Relationships with palatine and pterygoid are clear. Median and lateral borders of each vomer bear a row of small teeth: the median row divides into two along the posterior third of its length. Medial to the tooth rows where the vomers meet they are upturned to form what in palatal view is a narrow smoothly rounded trough. There are two or three larger teeth grouped at the tip of each vomer.

Palatine (Figure 2). The relationships of the palatine are clear; it bears four rows of teeth, one a continuation of the lateral row on the vomer, the others of corresponding rows on the palatine. The foot in contact with the maxilla projects downwards somewhat from the level of the palate.

Ectopterygoid (Figures 2 and 6). The ectopterygoid overlaps onto the palatal surface of the pterygoid,

extending well down the pterygoid flange. This element is poorly known in more primitive reptiles, but by analogy with Millerettids it appears that the infraorbital fenestra in *Youngina* is formed by reduction of the ectopterygoid. The extent of the surface abutting against the jugal is not clear.

Pterygoid (Figures 2, 3, 4, 5 and 6). The palatal portion of the pterygoid bears a double row of teeth on the mesial edge continuous with a double row on the vomer. Three rows of teeth fan out from near the basal articulation and continue onto the palatine. The strongly down-turned flange of the pterygoid bears a row of 6 or 7 robust teeth. The articulation with the basisphenoid is freely movable. The quadrate ramus of the pterygoid is a rigid triradiate structure with its edges directed laterally, mesially and dorsally, enclosing a dorso-mesial depression (for the protractor pterygoideus). There is a considerable overlap between pterygoid and quadrate, and a marked supporting ridge on the quadrate.

The palatoquadrate

Epipterygoid (Figure 5E). Both epipterygoids are partially exposed in T.M. 3603. The upper portion of the shaft is missing; there is no sign of an attachment area on the parietal. A broad footplate rests on the pterygoid very much as illustrated for *Milleretta* (Gow, 1972, Figure 8) and, by analogy, probably caps the basal articulation.

Quadrate (Figures 3, 4, 5 and 6). The quadrate is held laterally and dorsally by the squamosal and internally by parietal and supratemporal above and the pterygoid below. Anteriorly it is braced by the quadratojugal. This is a rigid system. The pterygoid ramus is a tall flat sheet. The ridge supporting the quadrate ramus of the pterygoid extends to the back of the quadrate, as is clear from Figures 3, 5 and 6; lateral to this and sloping in from the back of the outer condyle is an abrupt depression. The stapes would have passed across this region. As is plain from the reconstructed lateral view the quadrate is held vertically and the term "otic notch" hardly applies.

The braincase (Figure 5)

Supraoccipital. The relationships of this element are largely evident from the figures. The supraoccipital runs in under the parietals, this area being bridged by the postparietals. The bone slopes obliquely down and backwards.

Opisthotic. The structure and relationships of the opisthotic are clear from the figures. The point to note here is that the paroccipital process articulates in a pocket formed by the supratemporal (Figure 5E).

Exoccipitals and Basioccipital (Figures 4, 5 and 6). These form a fused unit. The exoccipitals almost meet above the foramen magnum behind the supraoccipital. The overlap between parasphenoid and basioccipital is clear from Figure 5C.

Proötic (Figure 5C, D and E). The region of the fenestra ovalis is poorly ossified (and this is a large

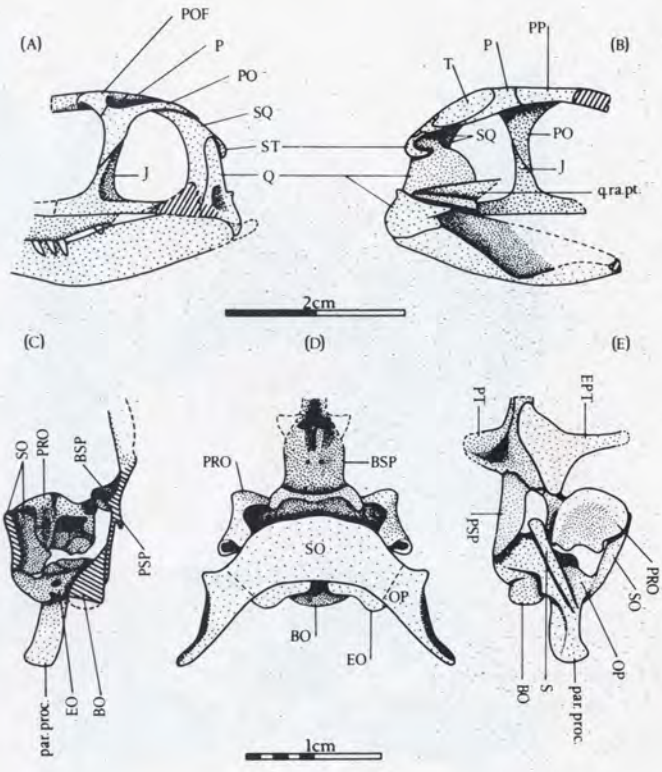


Figure 5. *Youngina capensis* T.M. 3603. A, Lateral view; B. Mesial view of quadrate and cheek region; C, Saggital section through braincase; D, Braincase dorsal view; E, Braincase lateral view.

specimen), so that the proötic appears suspended from a strong suture with the supraoccipital while ventrally it rests on the basisphenoid. The system of inner ear canals converging at the fenestra ovalis from supraoccipital, opisthosthotic and proötic is well displayed in the specimen.

Basisphenoid (Figures 3, 4, 5 and 6). Basisphenoid material is poor. The nature of the basipterygoid processes is clear and the articulation possible here is very similar to that described for millerettids (Gow, 1972); the low clinoid processes too are very similar.

Parasphenoid (Figures 3, 4, 5 and 6). The parasphenoid is edentulous. It overlaps the basioccipital extensively and has a pronounced semicircular lip posteroventrally (seen in section in Figure 5C).

Stapes (Figure 6). The stapes is a thin rod pierced near the proximal end by a stapedial foramen. The foramen is bounded by an extremely thin bridge which is bowed slightly outwards; such a foramen could well disappear in later forms.

The lower jaw (Figure 6)

There is no good lower jaw material: the region of the retroarticular process is eroded off in all specimens. The tooth-bearing rami are rather slender while the region of the adductor fossa is considerably deeper.

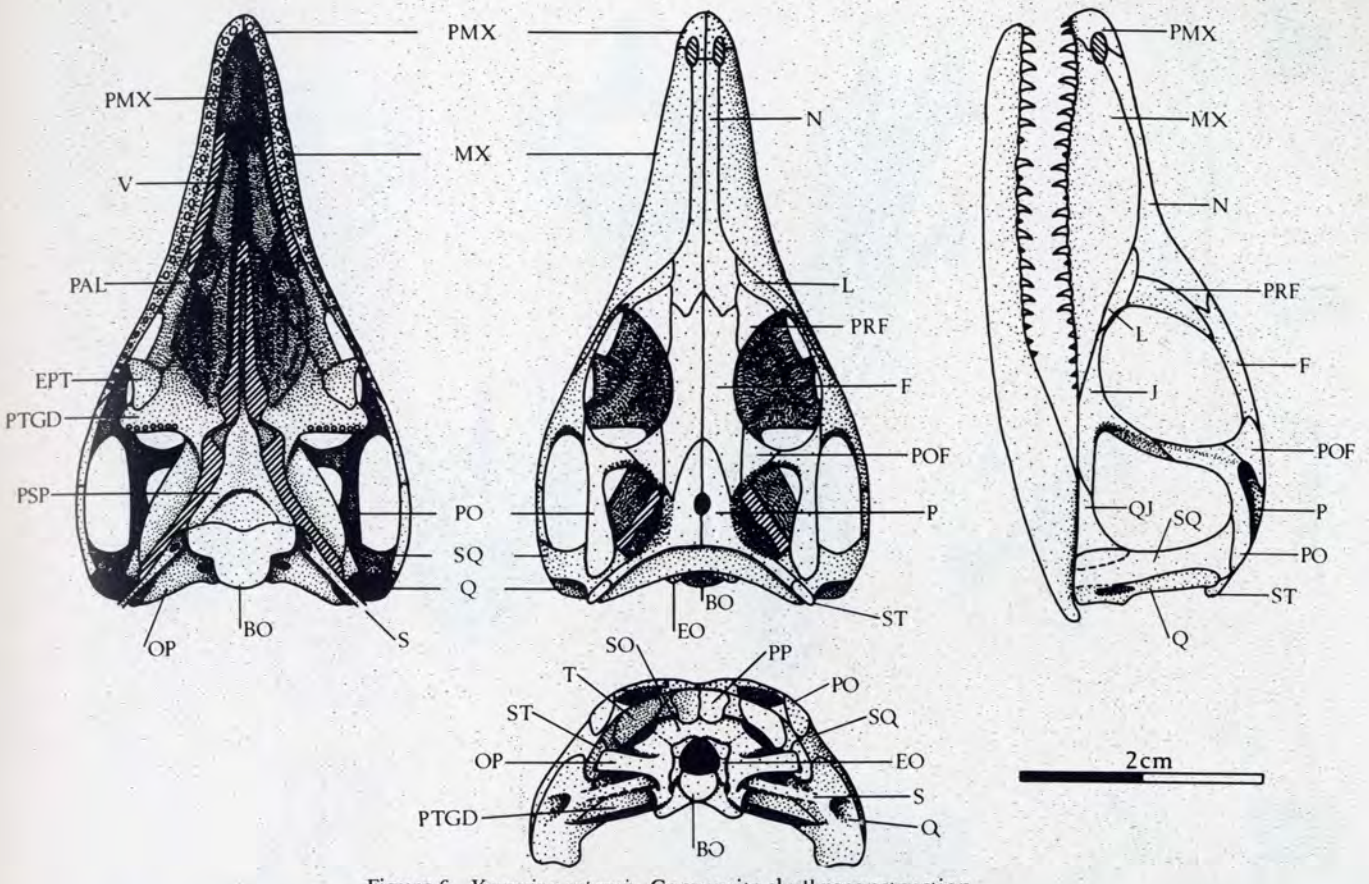


Figure 6. *Youngina capensis*. Composite skull reconstruction.

The postcranial skeleton of YOUNGINA

The skeleton of B.P.I. 2859 was jumbled together in a tight bundle behind the skull and part of it had already rotted away. Before acid preparation could commence the skull which had been extensively mechanically prepared had to be removed along a natural joint. The forelimb too was prepared mechanically and removed. The remainder was then disentangled by the repeated use of formic acid. The skeleton comprises a nearly complete set of presacral vertebrae apparently lacking only the atlas, axis and first sacral. The second sacral and first caudal are attached and there are two other caudals and two haemal arches (thought absent by Broom, 1922). There are several plates of middorsal armour. There are several ribs. All elements of both girdles are represented. The left forelimb is complete, also the right humerus. The left femur and the proximal end of the tibia and a presumed fourth metatarsal are all that remain of the hind limb. Thus it is only the hind limb which is incomplete.

Vertebrae (Figure 7) *and ribs*

The neural arches are broad and flat with moderately tall spines. The zygapophyses are horizontal, the transverse processes are pronounced, slanted, and have facets for single rib heads. The centra are amphicoelous and notochordal and invisibly fused to the neural arches. Intercentra are present.

The first sacral is missing; in the second the ribs are directed forwards and the distal ends bifurcate, the more anterior branch articulating with the ilium and the posterior branch forming a continuation of the caudal transverse processes and a site of attachment for caudal musculature. The caudal vertebrae with their strong transverse processes and deep haemal arches indicate a deep and powerful tail. A small number of symmetrical middorsal scutes are preserved (Figure 8), sufficient to indicate that there was one to each vertebra but there is no indication as to the extent of the row.

Girdles and limbs (Figures 9 and 31)

The pectoral girdle comprises a T-shaped interclavicle (with anteroventral notches for the clavicles), and a scapulocoracoid anteriorly notched to leave a gap between it and the clavicle. The ends of the humerus are rotated at 90° to each other. There is an entepicondylar foramen and a pronounced ectepicondylar groove. Radius and ulna require no additional description. The wrist is practically intact: there is a large ulnare and a rather small radiale, an intermedium, lateral and medial centrales, and five distal carpals. The digits are complete and bear powerful, laterally compressed, curved claws. The pelvic girdle is rather similar to that of *Howesia* (Broom, 1906). The ilium has a short, almost vertical blade, the pubis a pronounced thickened outturned antero-ventral

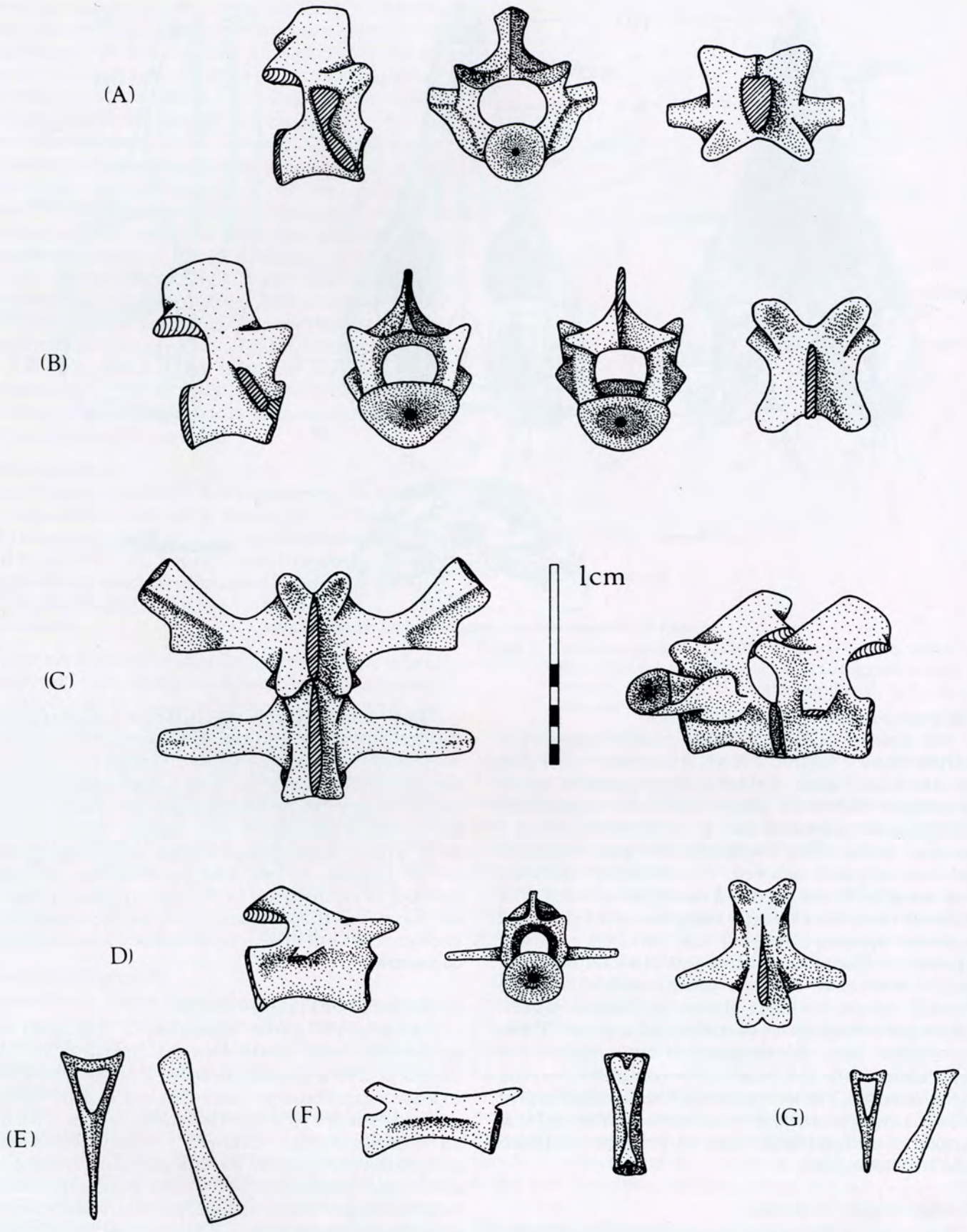


Figure 7. *Youngina capensis* B.P.I. 3859. A, Cervical vertebra; B, Anterior dorsal vertebra; C, Second sacral and first caudal vertebrae; D, Proximal caudal vertebra; E, Proximal haemal arch; F, Distal caudal vertebra; G, Distal haemal arch.
(Cross hatching of neural spines and articular facets does not indicate damaged surfaces.)

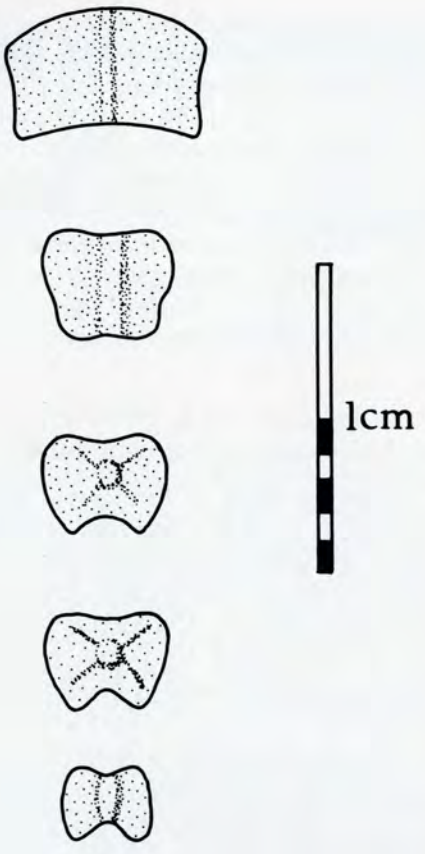


Figure 8. *Youngina capensis* B.P.I. 3859. Mid-dorsal scutes.

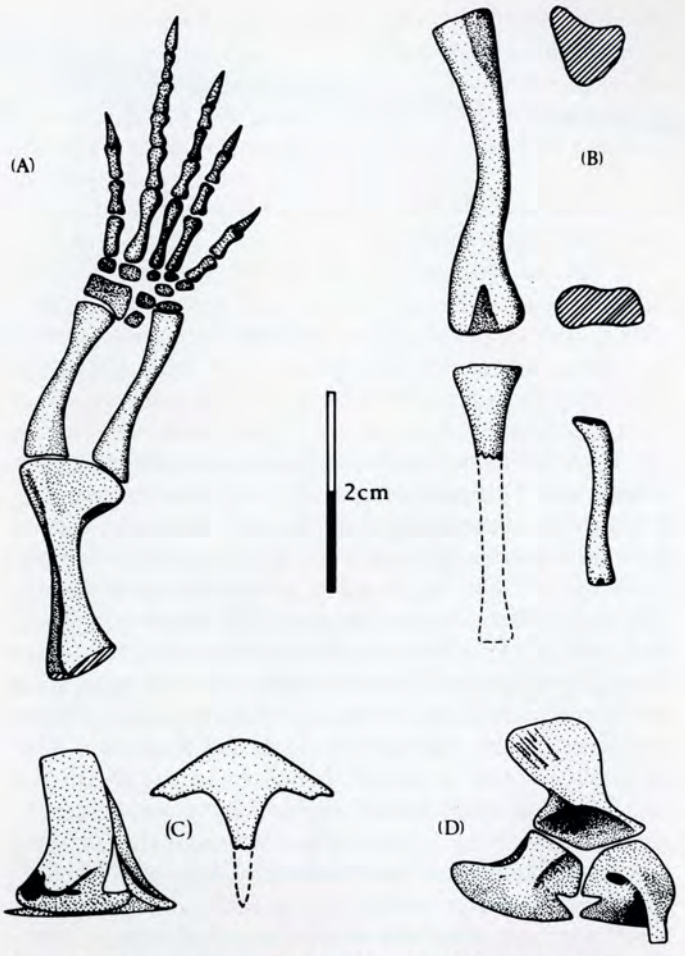


Figure 9. *Youngina capensis* B.P.I. 3859. A, Left forelimb; B, Femur, tibia and fourth metatarsal in anterior view; proximal and distal ends of femur; C, Right aspect of pectoral girdle; D, Right pelvic girdle.

process, and the ischium extends well back. The acetabulum is confined to the ilium. The notch between pubis and ischium would, according to Romer (1956, p. 318), indicate incomplete ossification and not an incipient thyroid fenestra.

The femur is primitive, though with a marked curvature which seems natural. The tibia is unfortunately incomplete. There is a single metatarsal which is almost certainly the fourth.

The following are the limb element measurements in mm:

Humerus			23
Ulna	16	Radius	18
Femur			34

The skeletal fragments described by Broom (1922) were almost certainly correctly assigned to *Youngina,* and as he illustrated a humerus and tibia it is possible to deduce that the femur and tibia were of closely similar length, as shown in the reconstruction (Figure 10).

The ankle described by Broom (1922) is now apparently irretrievably lost, but it is quite clear from Broom's figure and text that it is very like that of early rhynchocephalians and archosaurs.

YOUNGINA FUNCTION

With its long, low, and rather narrow snout, sharp pointed teeth and dermal sculpturing, the *Youngina* skull has a rather crocodilian appearance. Belying this impression are the apparently unspecialised terminal nares.

Broom (1922) figured the humerus and tibia of *Youngina;* combining measurements from these with data available from the present study we can conclude with a fair degree of certainty that the tibia was shorter than the femur, but not dramatically so—this points towards a terrestrial quadrupedal existence.

The tail is important, but as the interpretation of tail function is important with *Prolacerta* as well, and as this is a complex and neglected field, some general remarks about tails are in order at this point. Several parameters control the shape and weight distribution of the reptilian tail and some may change according to their position along its length. One may cite: height, breadth and thickness of neural spines; breadth across the transverse processes; position, depth, breadth and thickness of chevrons, and the rate of reduction in size of all the above from root to tip of tail. Clearly a detailed study of tail morphology and function would fill an important gap in present knowledge.

The *Youngina* tail has very low neural spines, which could possibly be simply the retention of a primitive captorhinomorph character. The chevrons on the other hand are long in proportion. Looking for com-

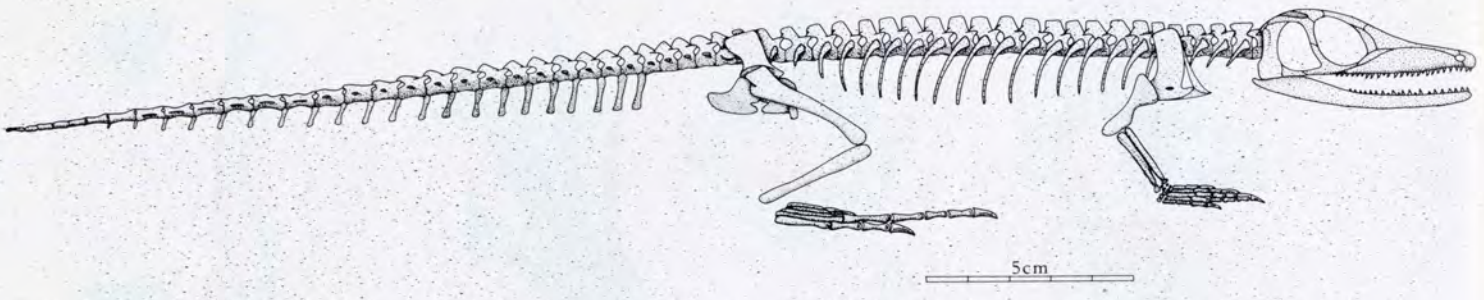


Figure 10. *Youngina capensis*. Reconstruction of the skeleton.

parisons we find that in *Sphenodon* the chevrons are substantial but balanced by tall neural spines. Something closely approaching the *Youngina* condition is seen in one of our local lizards, *Cordylus giganteus*, a fairly large spiky armoured lizard of the grassveld. Pairs live in burrows of their own making, and judging by the even distribution of burrows are strongly territorial. In this animal neural spines are very poorly developed throughout and the chevrons are comparable in size to those of *Youngina*. This similarity of tail structure, however, may be just that and no more, and it is interesting that *Sphenodon* and *C. giganteus* which have more or less the same way of life in several respects should have such different tails. *C. giganteus* would probably fare poorly as a swimmer. This may be a case where it is not possible to explain the observed differences in functional terms.

It should be noted that in swimming reptiles (e.g. crocodiles, monitors) the distal caudal vertebrae have tall neural spines which balance long chevrons in supporting a flattened, more or less symmetrical, tail.

There can be little doubt that *Youngina* was a terrestrial animal. Girdle measurements relating to body sections are given in Table 1.

YOUNGINA RELATIONSHIPS

While the skull of *Youngina* is essentially Permian (braincase, palatal dentition) it exhibits certain advances which foreshadow the Triassic early thecodont grade (considerable palatal extent of premaxillae, suborbital vacuity, and slender stapes). This should not be construed to imply a direct relationship between *Youngina* and a possible *Proterosuchus-Prolacerta* ancestor. These are simply time grades of reptilian evolution, and while it is useful to know what the "Eosuchian" skull looks like there are other small little known U. Permian eosuchians which may prove to be more directly on specific lines to the Triassic Thecodonts (e.g. *Heleosaurus*).

One must concede that the diapsid upper temporal opening is a rigid distinctive feature shared by *Youngina* and its kin plus all later diapsids. The one serious drawback to *Youngina* as a thecodont ancestor is in the structure and relationships of the quadratojugal. Both the tall "archosaurian" quadratojugal of e.g. *Proterosuchus* and the small articulating slip of a bone in *Prolacerta* are readily derivable from the sort of condition seen in millerettids (Gow, 1972, Figures 8 and 22) but not from the arrangement in *Youngina*.

Table 1

	Crocodylus niloticus	*Youngina capensis*	*Sphenodon punctatus*	*Chamaeleo dilepis*	*Prolacerta parringtoni*
	Measurements in mm.				
Interglenoid width IGW	241	28	34	11	32
Interacetabular width IAW	127	19	28	9	30
Pectoral girdle depth	178	18	33	18	50
Pelvic girdle depth					
Taken together as girdle depth GD	178	22	34	16	46
Ratios					
IGW : IAW	2 : 1	3 : 2	1 : 1	1 : 1	1 : 1
IGW : GD	4 : 3	3 : 2	1 : 1	1 : 2	3 : 5
IAW : GD	2 : 3	1 : 1	1 : 1	1 : 2	3 : 5
Body Shape	Dorsoventrally compressed		Round bodied	Laterally compressed	

This is *not* to suggest a relationship between millerettids and thecodonts. This quadratojugal objection does not apply to rhynchocephalian derivation from *Youngina*, but it does reject a too close relationship between rhynchocephalians and early thecodonts.

It seems likely that where the small Permian eosuchians are concerned details of the postcranial skeleton will prove significant in assigning affinities. The girdles and limbs of *Youngina* (the pelvic girdle in particular) are strikingly similar to those of the rhynchocephalian *Howesia* (Broom, 1906).

YOUNGINA — SYNONYMY AND DIAGNOSIS

It is not desirable at this stage to consider the ordinal and familial status of *Youngina*. Future work must decide whether the Order Eosuchia will remain as a depository for unrelated primitive diapsids of doubtful affinity. Certainly several unrelated families are represented in the Younginidae as presently constituted. *Youngina* almost certainly cannot be regarded as more than one palaeontologic species.

Genus *YOUNGINA* Broom (1914 skull, 1922 skeleton)

Species *YOUNGINA CAPENSIS* Broom 1914

= *Youngoides romeri* Olson and Broom 1937
= *Youngopsis kitchingi* Broom 1937
= *Youngopsis rubidgei* Broom and Robinson 1948
= *Youngoides minor* Broom and Robinson 1948

Small upper Permian diapsid reptiles occurring in the *Daptocephalus* zone of the Karroo beds of South Africa. Skull rather shallow snouted with terminal external nares. Some roughening of the frontals particularly above the orbits. Simple plate-like quadratojugal no taller than lower third of quadrate. Postparietals, tabulars and supratemporals present, the latter with ventrally recurved hooks distally for reception of the paroccipital processes. Marginal teeth conical and subthecodont with alternate replacement with approximately 20 functional maxillary teeth. Maxillary tooth row extending well back beneath the orbit. Considerable palatal extent of premaxilla, particularly lateral to the internal choanae. Vomer bearing teeth on both edges, with two or three anterior median "vomerine fangs". Parasphenoid edentulous. Infraorbital fenestra present.

Vertebrae amphicoelous and notochordal with broad flat arches. A middorsal row of scutes, one per vertebra. Second sacral rib bifurcated distally (first not known). Tail with low neural spines and deep haemal arches. Body dorso-ventrally compressed in crocodilian fashion. Proximal limb segments marginally longer than distal.

PROLACERTA

REVIEW OF LITERATURE AND MATERIAL

All the *Prolacerta* material comes from the *Lystrosaurus* zone of South Africa of Lower Triassic age. (Colbert has undescribed material of equivalent age collected by Kitching in Antarctica.) *Prolacerta broomi* was first described by Parrington in 1935. Parrington's specimen lacks the posterior spur of the jugal. With this exception, Parrington's reconstruction is good and the specimen is an acceptable type.

Camp (1945) described a second skull and six cervical vertebrae. This is an excellent specimen and Camp's reconstructions are, on the whole, good.

Broom and Robinson (1948) described a third skull as *Pricea longiceps*, but the only respect in which this differs from the previous two skulls is in the nature of its preservation; strikingly different types of preservation of the same species are typical of the *Lystrosaurus* zone, as all familiar with the zone fossils will know.

A fourth skull, in the collections of the South African Museum, Cape Town, has been worked on by Crompton who has kindly given the writer copies of his detailed drawings.

In 1970 Barry Hughes came across some patently sauropsid material in the collections of the Bernard Price Institute; this soon proved to be prolacertid, and the Institute's material can now be listed as follows:

471 Skull *Pricea longiceps* Broom and Robinson 1948.
Locality: Heuning Krans, Burghersdorp.
Collected: J. W. Kitching.

4196 Very small broken and distorted skull in nodule.
Locality: Tweefontein, Bethulie.
Collected: J. W. Kitching.

2675 A skull and skeleton minus sacrum, pelvis, tail and hind legs and including a third scapula.
Locality: Harrismith.
Collected: J. W. Kitching.

2676 An almost complete, articulated postcranial skeleton, lacking the head and first three cervicals.
Locality: Harrismith.
Collected: J. W. Kitching.

4005 Tibia, fibia, ankle and part of foot.
Locality: Old Brickfields Donga, Harrismith.
Collected: J. W. Kitching.

MATERIAL AND METHODS OF PRESENT STUDY

B.P.I. 2675 was almost completely disarticulated with acetic acid; the skull is now entirely reduced to its elements, and only one hand has been left intact, prepared from one side only. As this took an inordinately long time and as the material is not entirely suited to acid preparation, B.P.I. 2676 was first prepared mechanically in lateral aspect; acid was used on the sacrum and tail which were left articulated, and only the pelvis and hind limbs have been completely cleaned in acid. B.P.I. 4005 was entirely amenable to acid preparation and has been completely cleared of matrix to yield a useful additional ankle. B.P.I. 471, the type of *Pricea*, would be ruined by acid but it has been possible to remove the anterior third of the lower

jaws with a saw cut between upper and lower teeth and so to prepare mechanically the anterior of the palate—notably the premaxillae and tips of the vomers. This material then yields the complete osteology of *Prolacerta*.

OSTEOLOGY OF *PROLACERTA*

The skull

Though the following description refers to B.P.I. 2675, points of difference with the interpretations of other workers are noted.

Dermal bones of the skull roof

Premaxilla (Figures 11 and 12). In lateral aspect the premaxilla is somewhat downturned. There appear to be five tooth positions. The premaxillae extend back beyond the tips of the maxillae in the palate and unite in the midline beneath the tips of the vomers.

Maxilla (Figures 11, 12, 13, 13A and 32). Figure 13 clearly shows the structure of the maxilla with its thickened tooth-bearing margin dropping away internally to an extremely delicate vertical sheet with internal thickening behind the nasal capsule. The maxilla is excluded from the nasal opening by the premaxilla. There are 25 (+ 2?) maxillary tooth positions and active alternate replacement. The thecodont teeth are laterally compressed, with sharp unserrated edges and are recurved; they are deep rooted, extending the full depth of the thickened alveolar portion of the maxilla which is extremely thin walled.

Marginal dentition (Figures 13, 13A and 32). It is essential that the marginal dentition be described in full detail. Thecodont teeth are known in only one group of lizards, the Cretaceous mosasaurs (Edmund, 1967; Russel, D. A., 1967): these teeth are distinguished by having enamel-coated crowns one third the length of the dentine base; resorption pits affect the tooth base and the adjoining bone and arise in the posterior half of the lingual surface of the tooth.

By contrast the teeth of *Prolacerta* appear entirely coated by enamel and are held in deep alveoli by bone of attachment; resorption pits are medially situated in the lingual base of each tooth, and do not affect the adjoining bone of the mandible. In Figure 32A the groove for the dental lamina can be seen clearly, Figure 13A supplements the photographs, giving the pattern of resorption pits and replacement teeth. Among known dentitions this is typical only of the Archosauria.

Nasal (Figures 11 and 14). Little can be added to Camp's description. The nasal is overlapped considerably by the maxilla. A clear suture with the frontal is seen in Figure 14A.

Lacrimal (Figures 11 and 12). The lacrimal is exposed as a narrow strip on the side of the snout. There are two lacrimal foramina as indicated.

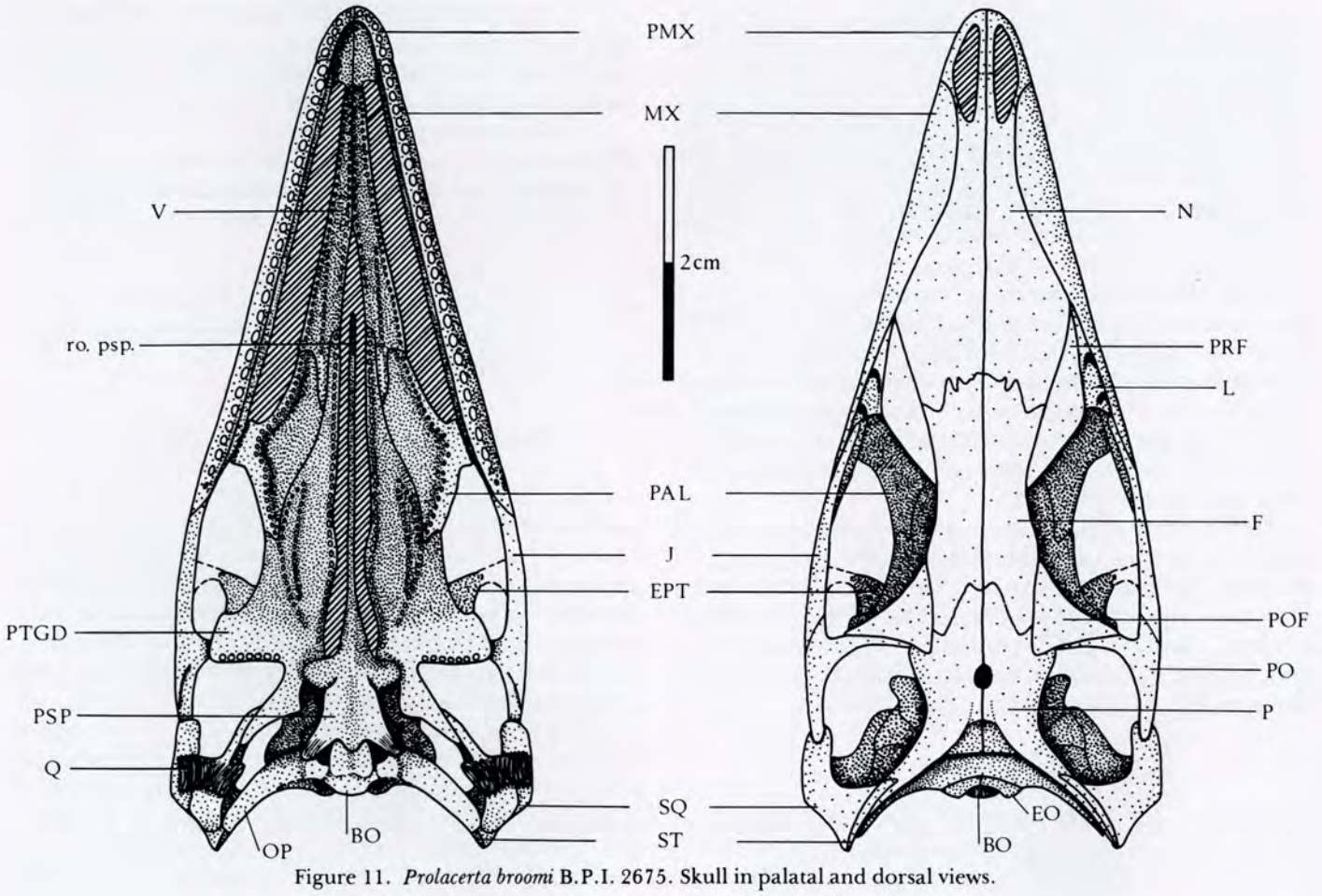


Figure 11. *Prolacerta broomi* B.P.I. 2675. Skull in palatal and dorsal views.

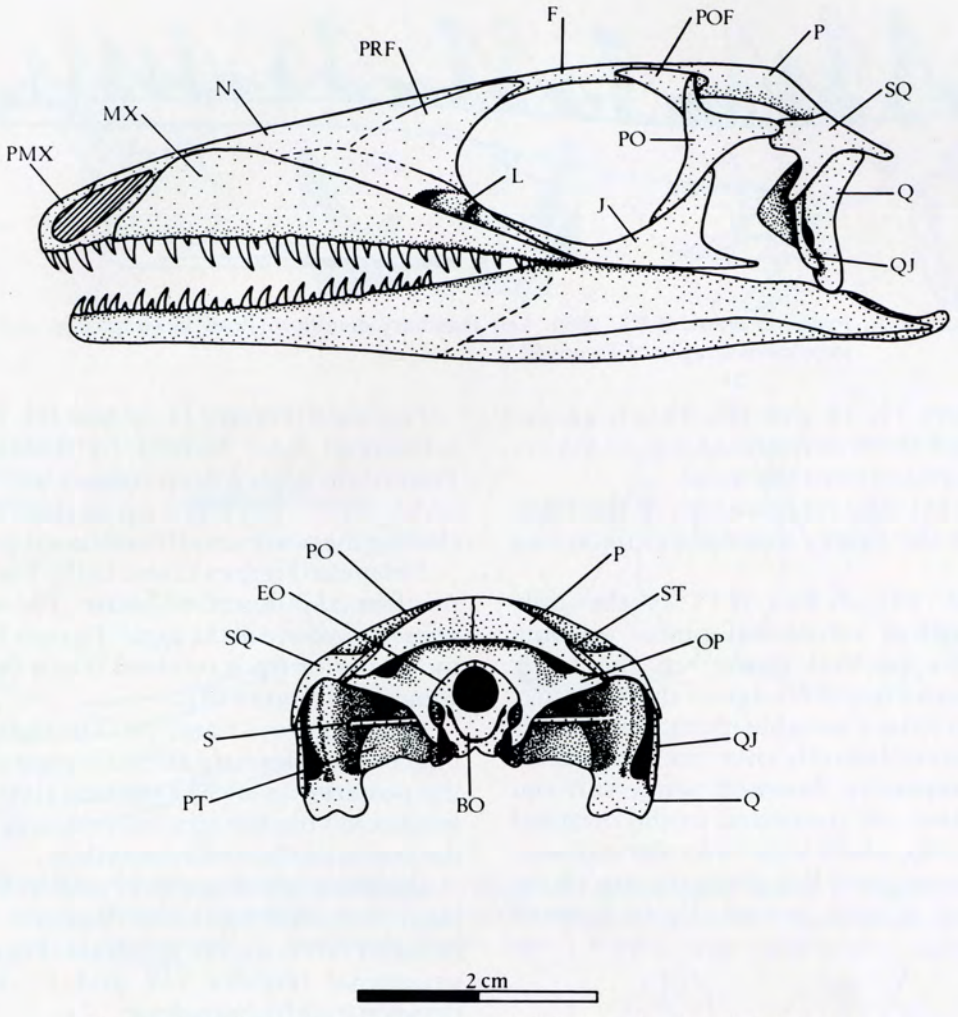


Figure 12. *Prolacerta broomi* B.P.I. 2675. Skull in lateral and occipital views.

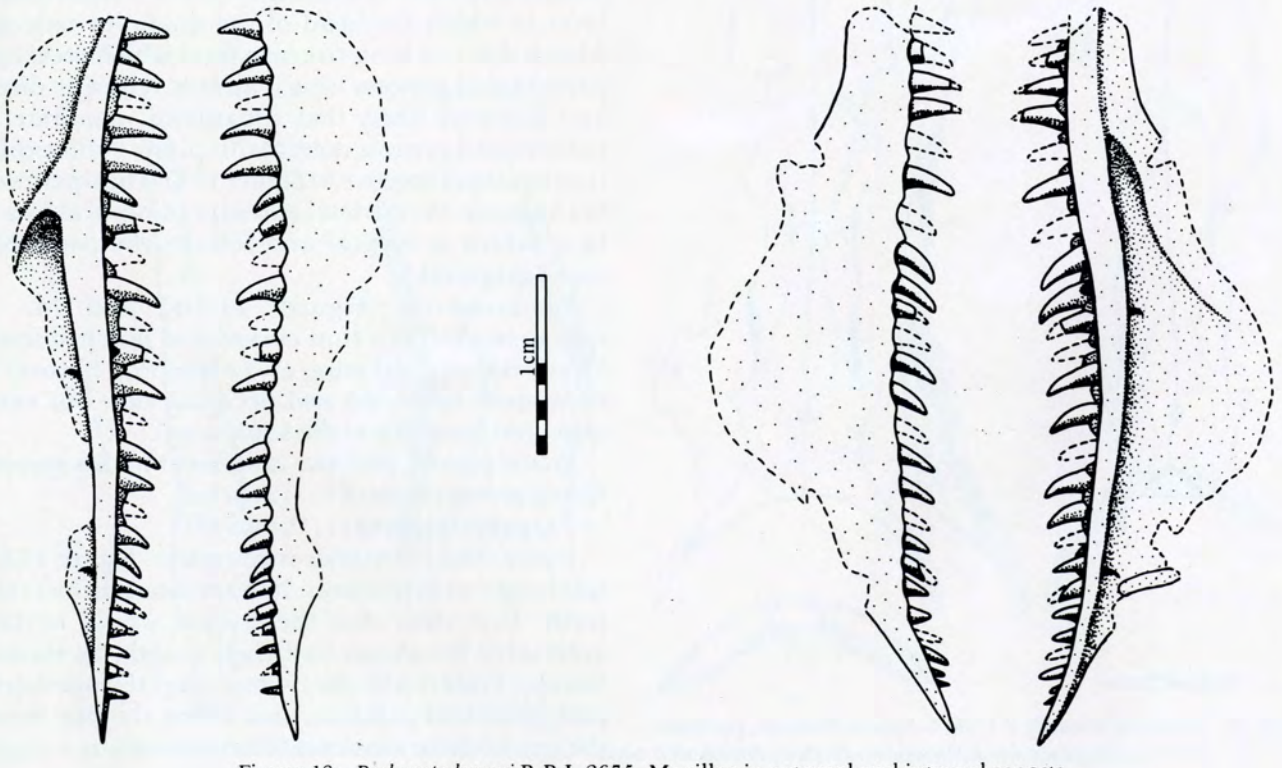


Figure 13. *Prolacerta broomi* B.P.I. 2675. Maxillae in external and internal aspects.

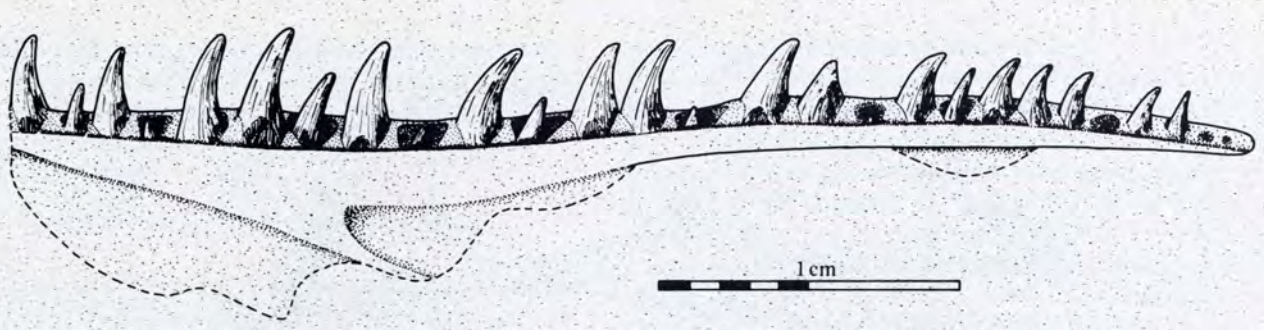


Figure 13A. *Prolacerta broomi* B.P.I. 2675. Left maxillary dentition. Read in conjuction with stereophotographs of Figure 32.

Prefrontal (Figures 11, 12 and 14). This is an extremely thin walled element rimming part of the orbit and wrapping round onto the snout.

Frontal (Figure 14). The relationships of the frontal are clear from the figure; supraorbital thickening is indicated in C.

Parietal (Figure 14). B.P.I. 2675 is the only *Prolacerta* skull with a substantial pineal opening midway along the parietal suture; in the other described specimens there is no sign of this opening; this must be taken to be a variable character. Dorsally the parietals curve laterally over the brain area. Posterolaterally vertically flattened wings run out and back, and these are connected in the occipital plane by a thin bridge which slides over the supraoccipital. The supratemporal lies along the top of the parietal wing and is held proximally in a small notch.

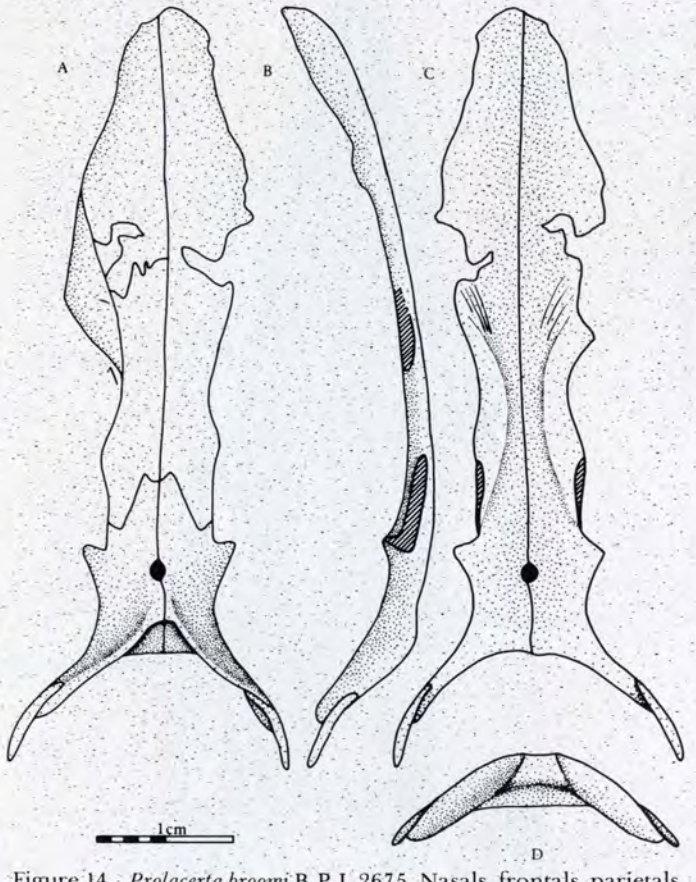


Figure 14. *Prolacerta broomi* B.P.I. 2675. Nasals, frontals, parietals and supratemporals. A, Dorsal (includes prefrontal); B, Left lateral; C, Ventral; D, Occipital.

Postfrontal (Figures 11, 12 and 14). This lies against a substantial facet formed by frontal and parietal. Posteriorly it has a deep contact with the postorbital, which latter runs right up against the parietal, excluding the postfrontal from the temporal fossa.

Postorbital (Figures 12 and 15G). The contact with the postfrontal is described above. The ventral prong inserts in a groove in the jugal (Figures 15H and I), while the posterior tip is received into a depression on the squamosal (Figure 15E).

Jugal (Figures 12 and 15). The right jugal is present intact which clears up all doubt regarding the extent of the posterior spur. The portion rimming the orbit is substantial but the spur and the area above it behind the postorbital are extremely thin.

Quadratojugal (Figures 12 and 15). The quadratojugal is a small bent and flattened rod articulating between facets on the quadrate (Figure 15A) and the squamosal (Figures 15E and F), with a foramen between it and the quadrate.

Squamosal (Figures 11, 12 and 15). Facets for postorbital and quadratojugal have already been described. Posteriorly there is a mesially directed hemispherical facet in which the head of the quadrate articulates. Above this is a long concave facet which receives the paroccipital process (this is almost ventrally directed and it seems likely that squamosal, quadrate, and paroccipital process meet at this point—this explanation lends perspective to Figure 15F). The squamosal is held against the parietal and supratemporal by a fifth facet which is vertical and follows the curve of the supratemporal.

Supratemporal (Figures 11, 12 and 14). The supratemporal is a thin curved rod notched into the top of the parietal wing and extending beyond it: it is exposed in dorsal and occipital view but entirely obscured laterally by the squamosal.

Scleral plates. Sclerotics are absent in this specimen. Camp gives a count of 11-12 for his.

The palate (Figures 11, 16 and 17)

Vomer. The left vomer is complete (Figure 16A) but was lying out of position. It bears three distinct rows of teeth. It is clear that the vomers would be united anteriorly for about half their length, as shown by Camp. Posteriorly the vomer slightly overlaps the pterygoid and palatine, also filling the gap between the tips of these elements (Camp illustrates a gap here but this is improbable).

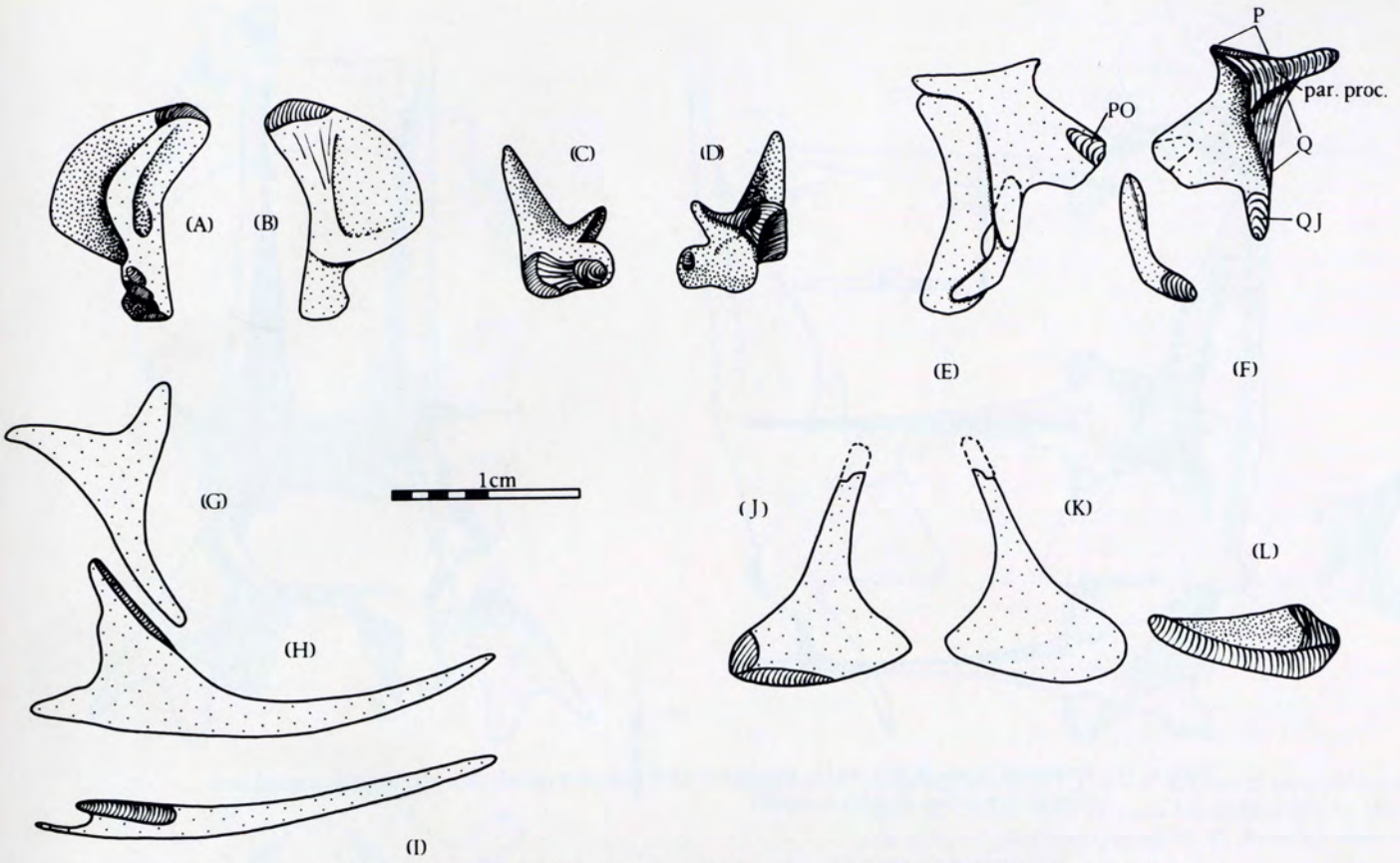


Figure 15. *Prolacerta broomi* B.P.I.2675. A—D, Quadrate; A, Lateral; B, Mesial; C, Ventral; D, Dorsal; E, Squamosal, quadrate and quadratojugal; F, Squamosal in internal aspect and quadratojugal; G, Postorbital; H and I, Jugal; J, K and L, Epipterygoid in lateral, mesial and ventral views.

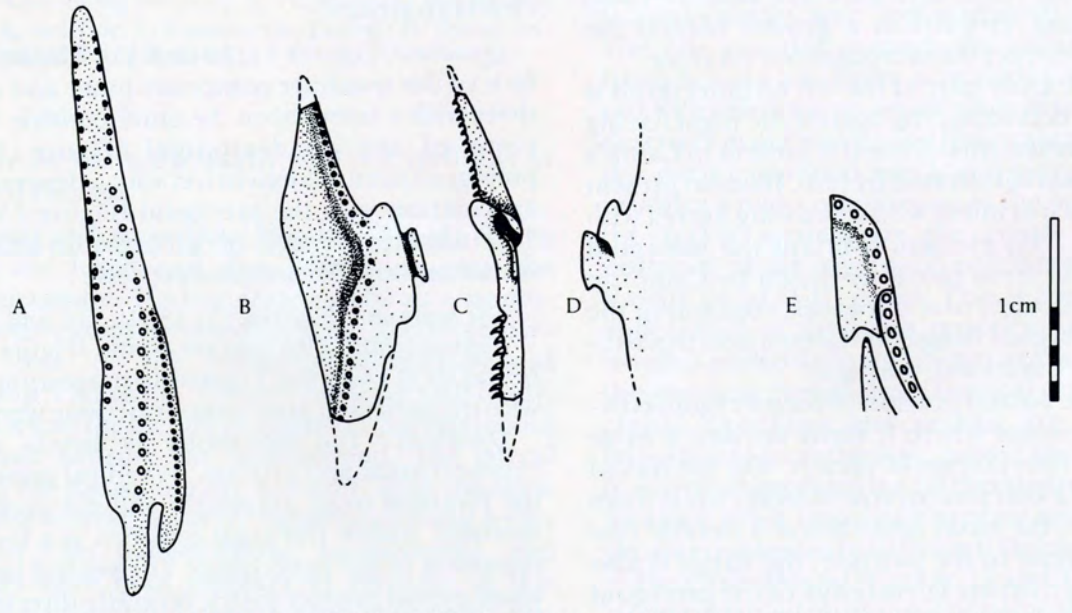


Figure 16. *Prolacerta broomi* B.P.I. 2675. A, Vomer; B, Palatine; C, Palatine in lateral view; D, Dorsal view of palatine foot; E, Palatal extent of premaxilla.

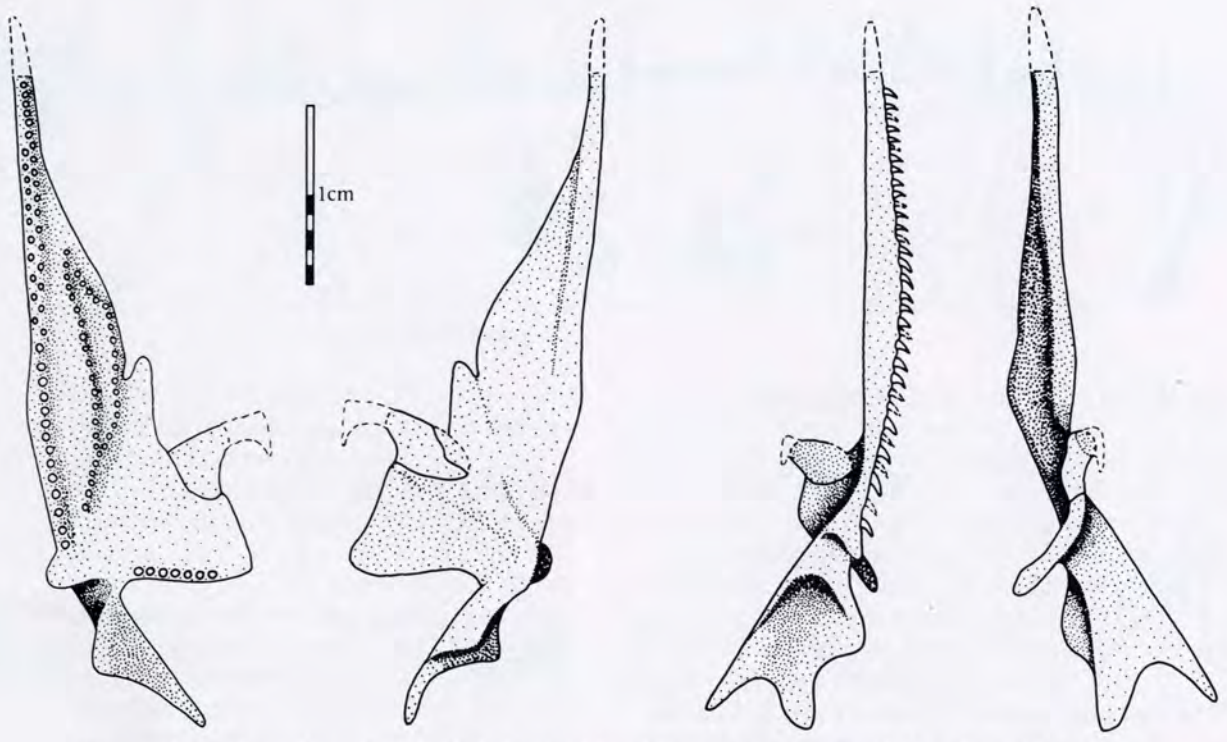


Figure 17. *Prolacerta broomi* B.P.I. 2675. Pterygoid and Ectopterygoid: palatal, dorsal, mesial and lateral views (last slightly rotated).

Palatine. The mesial portion of the palatine is an extremely thin sheet; laterally the bone thickens and turns downwards, this thickened edge bearing a single row of teeth continuous with those of pterygoid and vomer. The foot of the palatine is applied against the alveolar border of the maxilla and has a small dorsal process which rests on top of the alveolar ledge (Figure 16B and D). Above this latter process is the palatine groove which transmits the maxillary artery and superior alveolar nerve (Figure 16C) which then enter a foramen in the maxilla (Figure 13), branches also possibly running forward in a groove behind the alveolar ledge to enter the more anterior foramen.

Ectopterygoid. Only part of the left ectopterygoid is present, the process abutting against the jugal having been lost. However, this element is present in Camp's specimen and well illustrated by him. It is also present in Crompton's specimen, whose drawing agrees with that of Camp. This element overlaps the pterygoid from above (not from below as shown by Camp); it curves gently forward and outwards, continuing the edge of the pterygoid flange, and terminates in a substantial foot in contact with the jugal.

Pterygoid. The palatal portion of the pterygoid is extremely thin, except where it turns up into a ridge bordering the interpterygoid vacuity. On the mesial border there is a continuous row of teeth, while from just anterior to the basal articulation a double row runs towards those of the palatine; the flange is also toothed. A notch on the lateral edge of the pterygoid receives the palatine. The articulation for the basipterygoid process is deep, hemicylindrical, and directed obliquely posteriad. The quadrate ramus is deeply concave on its mesial surface with a pit situated anteriorly. The ornate margins of this process (Figure 17) are genuine. The area of origin of the *pterygomandibularis* is marked by a ridge on the inwardly sloping lower portion of the quadrate ramus.

Epipterygoid. The lower half of each epipterygoid is preserved. It is very similar to that of *Youngina*, including a facet capping the basal articulation. Camp's description and figure of a thin quadrate process is clearly an artifact.

Quadrate (Figures 11, 12 and 15). The articular surface of the quadrate comprises inner and outer condyles with a facet above the outer condyle for attachment of the quadratojugal (Figure 15A). The pterygoid ramus is extensive, with a depressed area of articulation with the pterygoid (Figure 15B). Figure 15D indicates the areas of cartilaginous attachment to squamosal and paroccipital process.

The braincase (Figures 12, 18, 19, 34 and 35).

Supraoccipital. The supraoccipital (Figure 18A-D) is broad, as in *Youngina.* There is no suggestion of contact with the parietals; post-temporal fossae were present.

Opisthotic. The opisthotic is firmly united to supraoccipital and proötic. Its ventral ramus borders the foramen ovale anteriorly and the jugal foramen mesially. Above the jugal foramen is a facet for the reception of the exoccipital. The ventral ramus has a loose mesial contact with a ventrally directed process of the basioccipital. The paroccipital process is flattened, as in *Varanus*, but meets the squamosal/quadrate

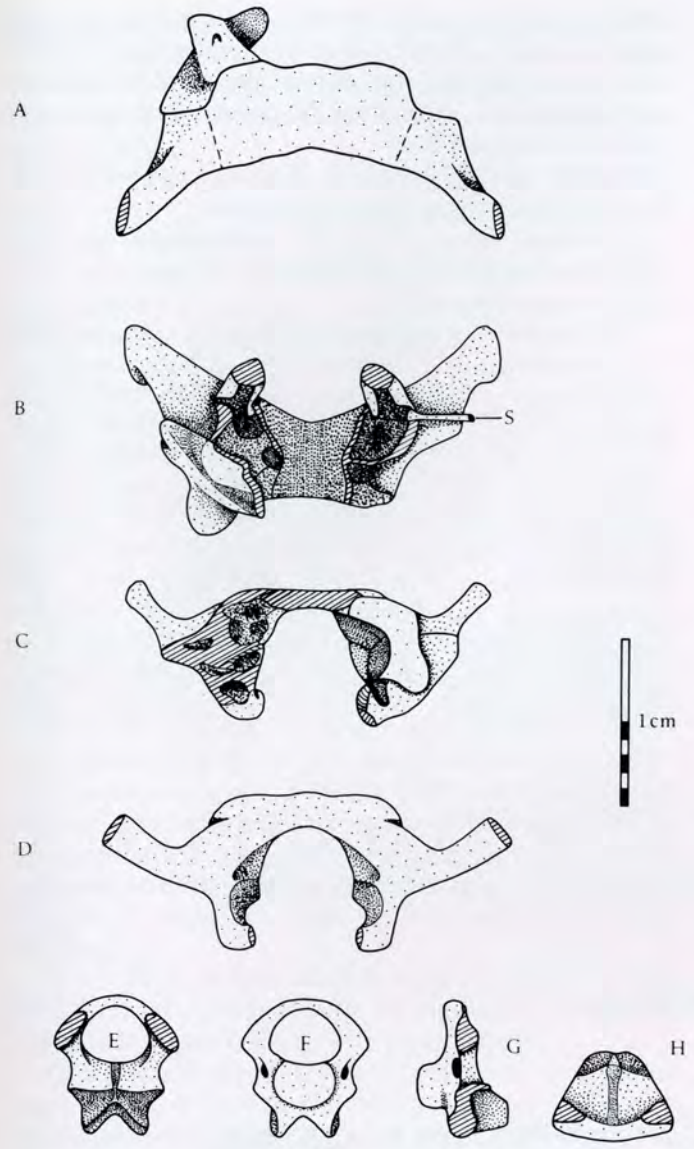


Figure 18. *Prolacerta broomi* B.P.I. 2675. A – D, Supraoccipital, proötic and opisthotic; A, Dorsal; B, Ventral; C, Anterior; D, Posterior; E—G, Basi- and exoccipitals; E, Anterior; F, Posterior; G, Lateral; H, Dorsal (exoccipital ring removed).

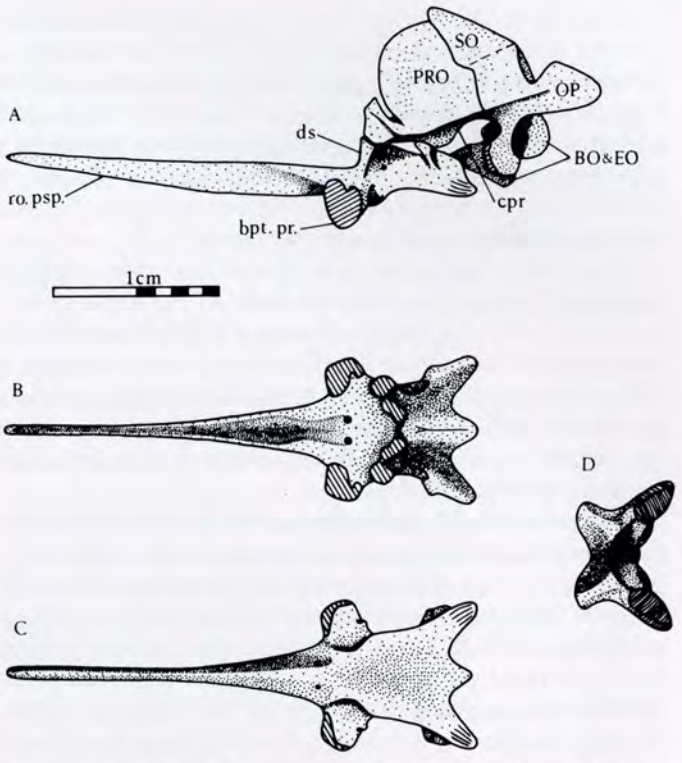


Figure 19. *Prolacerta broomi* B.P.I. 2675. A, Lateral view of braincase; B, Dorsal view of para-basisphenoid; C, Ventral view of para-basisphenoid; D, Anterior view of para-basisphenoid.

joint more or less horizontally, and not vertically as does that of *Varanus*.

Exoccipital and basioccipital (Figure 18E-H). These elements are fused and they completely ring the foramen magnum. The braincase is difficult to assemble as so many joints involved cartilage, and this is particularly true of the basioccipital/parasphenoid relationship (Figure 11). These bones separated freely, though it seems the medial prong of the parasphenoid was applied beneath the basioccipital. The lateral prongs of the parasphenoid, however, span the same width as the ventral tips of the opisthotics and it seems very likely that parasphenoid, basioccipital, and opisthotics were held together in cartilage at this point, the basioccipital contributing reasonably discrete basal tubera.

Before leaving the occiput it should be noted that Camp's (1945) reconstruction of this area is completely wrong. Robinson's (1966) is better, but the tips of the paroccipital processes are out of position, the tops of the exoccipitals are the wrong shape and do not meet, the top of the quadratojugal is shown touching the outer surface of the squamosal instead of the inner, and the quadrate squamosal contact is too low.

Proötic (Figures 18 and 19). The proötic has extensive sutural contact with supraoccipital and opisthotic. The pila antotica contacts the dorsum sella of the basisphenoid and there is an additional ventral contact with a delicate posterior ridge of parasphenoid (cf. description of *Proterosuchus* braincase to follow). There is a deep trigeminal notch and a pronounced crista proötica which continues on to the opisthotic; within the recess formed by the crista and somewhat posterior of the trigeminal notch is a small foramen for the facial (VII) nerve. This is the earliest known appearance of the crista proötica s.s. (see *Youngina*) which is particularly significant as a point of origin for the *protractor pterygoideus*. (Internal canals in supraoccipital, opisthotic and proötic are clearly displayed—should comparison prove necessary.) Medial to the crista proötica is a further depression above the foramen ovale (involving proötic and opisthotic) for the anterior semicircular canal (Oelrich, 1956, p. 15).

Para/Basisphenoid (Figures 11 and 19). This element is completely edentulous. The parasphenoid rostrum, V-shaped in cross section, extends a little farther

forward than the pterygoids. Posteromedially there is a light overlapping contact with the basioccipital, while posterolaterally a gap exists which, when closed by cartilage, would connect basisphenoid and opisthotic. Prominent basipterygoid processes (orientation Figure 19D) correspond with deep pockets in the pterygoids already described. The vidian (parabasal) canal is a deep groove.

The only foramina are those for the internal carotids. The course of the abducens (VI) is marked by a groove on the posterior dorsal surface between alar process and dorsum sella. The alar process meets the pila antotica, its lateral edge continuous with the crista proötica. Behind the dorsum sella the bony sheet (parasphenoid) is W-shaped in cross section, with tall lateral walls.

The posterolateral extremities of the parasphenoid do not contact the ventral processes of the opisthotics in the region where the sternohyoideus muscles would attach. This area would have been filled in by cartilage. A distinctive ridge on the posterolateral wall of the parasphenoid terminates in a knob which meets the proötic below and in front of the lagena recess. Between this point of contact and the alar process there is a sharp smooth edge of parasphenoid; by contrast the corresponding edge of the proötic is broad and channelled, indicating the presence of a connecting membranous sheet.

Stapes (Figures 12 and 18). The stapes is a thin rod, the stapedial foramen having been lost.

Ceratobranchial. A long thin ceratobranchial I is present—this has been described by Camp.

The lower jaw (Figure 20).

The elements of the lower jaw, like those of the skull, are rather delicate. The Meckelian canal runs to the tip of the dentary. There is a large Meckelian fossa on the lingual surface. The glenoid, with two distinct facets, was probably reinforced anteriorly by a wad of cartilage. The large broad retroarticular process bears muscle attachment scars (*pterygomandibularis*). Twenty-seven tooth positions are indicated, the teeth being somewhat smaller than the maxillary teeth. The symphysis is extremely light and was probably movable. The relationships of the bones are clear from the figures, though some notes are in order. The *surangular* contributes the lateral glenoid facet, and

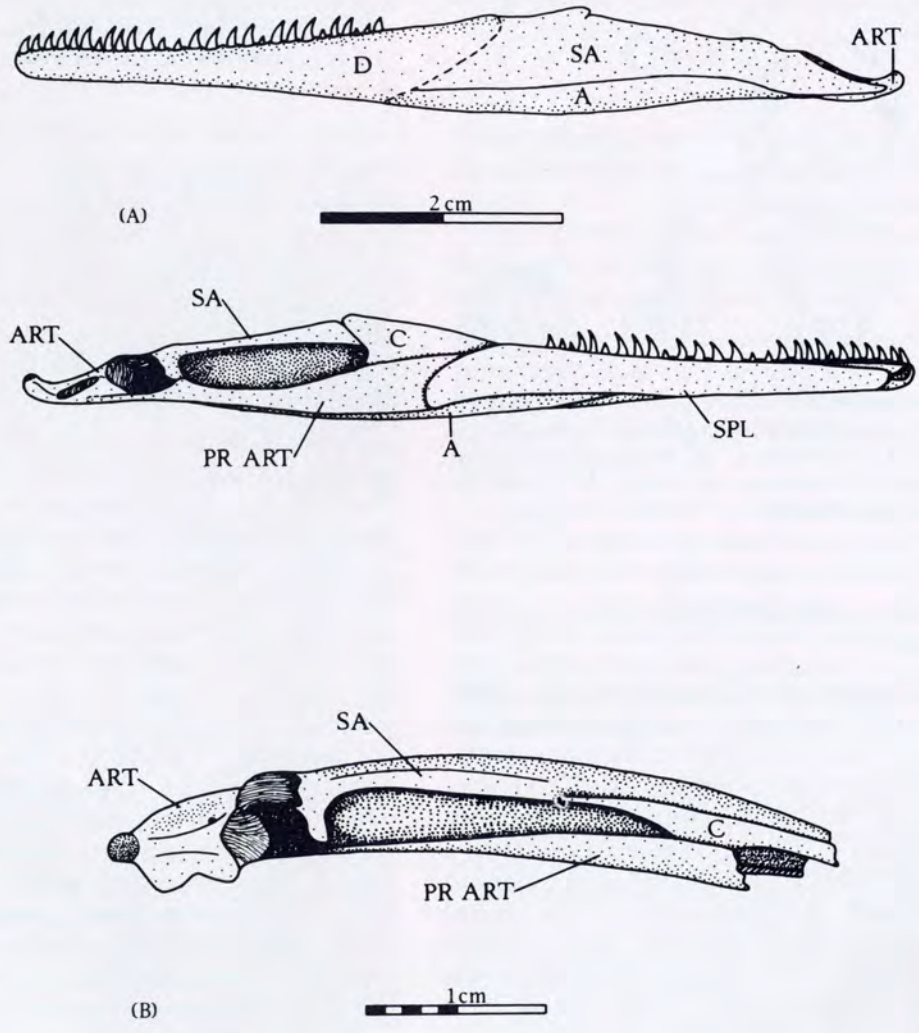


Figure 20. *Prolacerta broomi* B.P.I. 2675. A, Reconstructions of the lower jaw; B, Dorsal view of posterior half of left ramus.

sends a projection mesially to contact the prearticular.

The *angular*, which forms the postero-ventral border of the jaw, terminates beneath the glenoid. The tip of the *coronoid* is barely raised above the dorsal surface of the jaw.

The *articular* contributes the mesial glenoid facet; its recurved tip forms the site of attachment for the *depressor mandibularis*. There is good evidence for a tympanic crest on the lateral border. The chorda tympani/posterior condylar artery foramen is present. There is an incipient angular process.

The postcranial skeleton

The nearly complete articulated skeleton, B.P.I. 2676, lacks the first three cervicals and of the forelimbs only the proximal ends of the humeri are present. B.P.I. 2675 which contains the forelimbs and skull is truncated anterior to the pelvis. The overlap between these two specimens then is only in the vertebral column and the scapulocoracoids.

It must be stated at the outset that scales in the drawings are true for the smaller specimen (B.P.I. 2675) while the larger specimen has been reduced by 1/6th to bring it to the same size: this figure was arrived at by measuring the scapulocoracoids and this reduction produced a very good fit of the vertebrae. While this appears to be satisfactory it is unfortunate that an approximation was necessary, though the critical proportions of the skeleton are of a far greater order of magnitude than any error of scale which may have resulted.

B.P.I. 4005 yielded additional information on the hindlimb, and here there is no problem of equating size with undistorted tibiae for comparison.

Camp has described the first six cervical vertebrae and suggested they might indicate aquatic habits—a significant remark in view of the close affinity of bipedal lizards for water (Neill, 1971). *Prolacerta* was clearly a bipedal runner with a large tail to counterbalance the weight of the body. That the head and neck were highly manoeuvrable is shown by thickening of the tips of the neural spines in the shoulder region. Like the skull, the skeleton is extremely light, with hollow limb bones, and centra thin walled but supported by a delicate web of internal bony struts (there is no sign of pneumatopores). The ankle and hooked fifth metatarsal are similar to those of rhynchocephalians and *Proterosuchus*, yet not much different from those of *Euparkeria*. Intercentra are one primitive character in an otherwise very advanced, typically Triassic, skeleton.

The whole animal is so closely comparable to *Macrocnemus* (Peyer, 1937; Kuhn Schyder, 1962) as to assure very close relationship. It seems ridiculous to think of these distinctive thecodonts as lizards: they are yet another group which has dispensed with the lower temporal arcade. *Glevosaurus hudsoni* (Robinson, 1973) is an undoubted sphenodontid which has an incomplete lower temporal arcade. Clearly this feature evolved independently in squamates, thecodonts and rhynchocephalia.

Axial skeleton

There are 26 presacral vertebrae, including proatlas, deeply amphicoelous but not notochordal. There are two sacrals and a string of 13 proximal caudals plus several isolated more terminal caudals. Intercentra are present only as far back as between the first two caudals, after which they are succeeded by very long, flat haemal arches. The vertebrae are very lightly constructed: there is no sign of separation between centrum and neural arch; the centra are hollow with an intricate system of internal supporting struts.

Atlas and axis (Figure 21). The atlas complex is primitive. The proatlas connects the atlas arch to the exoccipital above the foramen magnum. The paired atlas arch elements just meet in the midline anteriorly and rest on a large pleurocentrum. The atlas intercentrum articulates between the occipital condyle and the axis intercentrum. This gives the appearance of being a highly mobile joint. The axis has a long neural spine typical of this bone, and it has a facet for the first cervical rib.

Cervicals (Figure 21, (7)). The following six vertebrae may be termed cervicals; they are greatly elongated. The last three cervicals and first three dorsals have thickened neural spines—clearly points of attachment for important neck muscles. In the neck region capitular facets are all on the centra and do not involve the intercentra. Rather long, slightly inclined zygapophyses would permit great freedom of movement, both lateral and dorsoventral.

Anterior dorsals. A lateral ridge leading towards the tubercular facet becomes increasingly pronounced posteriad until the first dorsal, which is characterized by transverse processes with their leading edges almost at right angles to the column (Figure 21, (10)). The length of the neural spines decreases to a minimum on 10 before picking up again over the back. This is also the point at which the rib facets start to merge, forming a continuous articular region. This process is complete by 15.

Posterior dorsals. Here there is a slight but distinct alternation in the length of the neural spines. By 19 all trace of two rib facets has gone leaving a single circular facet (Figure 22, (21)).

Sacrals (Figure 22). The narrow-necked transverse processes (or pleurapophyses) widen into substantial facets which touch and interlock slightly as shown. The transverse processes of the second sacral bifurcate into two functionally distinct processes; the anterior process is thick and broad and abuts against the ilium. The posterior process is thin and narrow and does not touch the ilium; it in fact constitutes an additional caudal transverse process and would no doubt strengthen the attachment of tail muscles, helping to support and control the large powerful tail which is such an important organ to a bipedal lizard-like animal. (This seems to be a rather different arrangement from that described for *Proterosuchus* by Cruickshank, though I am not convinced that the

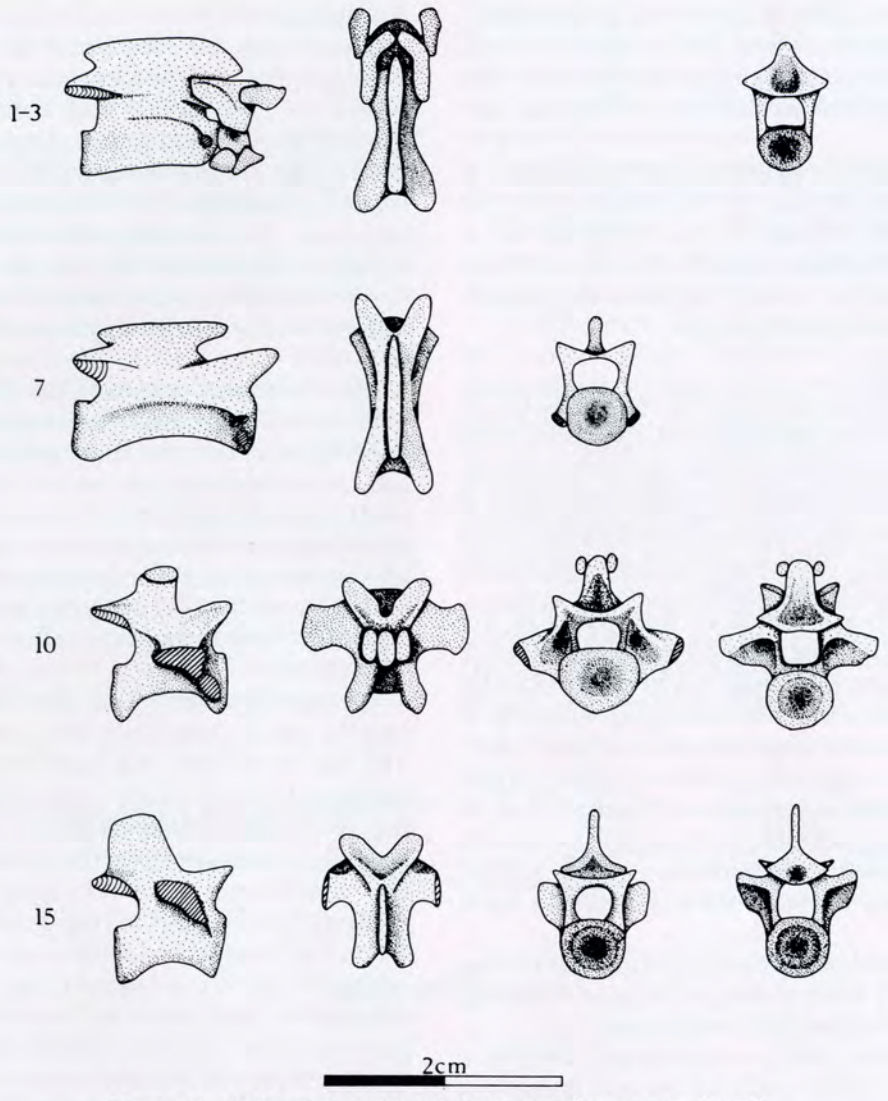


Figure 21. *Prolacerta broomi* B.P.I. 2675. Vertebrae as numbered.

posterior process contacts the ilium as he has shown.) The beginnings of a *Prolacerta*-like condition can be seen in *Youngina*, and several modern lizards trend the same way (Hoffsetter and Gasc, 1969, p.265).

Caudals (Figures 22 and 27). The string of 13 proximal caudals all have strong transverse processes diminishing gradually in size in the same way as do the neural spines and haemal arches. The chevron bones or haemal arches are laterally compressed and anteroposteriorly broadened: they are extremely long ($1\frac{1}{2}$ × the depth of the preceding vertebra). The enormously powerful tail indicated by the osteology almost certainly relates purely to the animal's bipedal mode of locomotion and active feeding movements of the head and neck, though the possible importance of lateral threat display cannot be overlooked.

Ribs (Figure 22). The cervical ribs have extremely slender shafts tapering to fine points; they have two distinct articular facets and an anterior dorsal process. Ribs 10 and 11 (in the pectoral region) are rather stout proximally; here the two rib heads have merged into a single articular facet. For the rest the ribs have slender shafts circular in section. From 19 to 26 the ribs are rather weak with expanded circular attachment facets, shafts very slender proximally, expanding a little distally.

Pectoral girdle and forelimb (Figures 23 and 30). The scapulocoracoid is extremely delicate, particularly that portion of the scapula anterior to the shaded line in the figure, which is paper thin. The posterior third of the suture between the two elements can be seen on the mesial surface. A coracoid foramen is present immediately in front of the screw-shaped glenoid.

Clavicles appear to elaborate with age (F is larger than G and therefore probably older, or possibly a male); unfortunately most of the medial shaft is missing. The vertical shaft is grooved on the inner surface where it would lie against the scapula. A prominent anteriorly directed boss appears to form with age in the angle between the two shafts.

The interclavicle is somewhat damaged though its essential structure is clear—it has a narrow medial shaft and a broad crosspiece notched anteriorly and with depressed facets on the ventral surface which receive the clavicles.

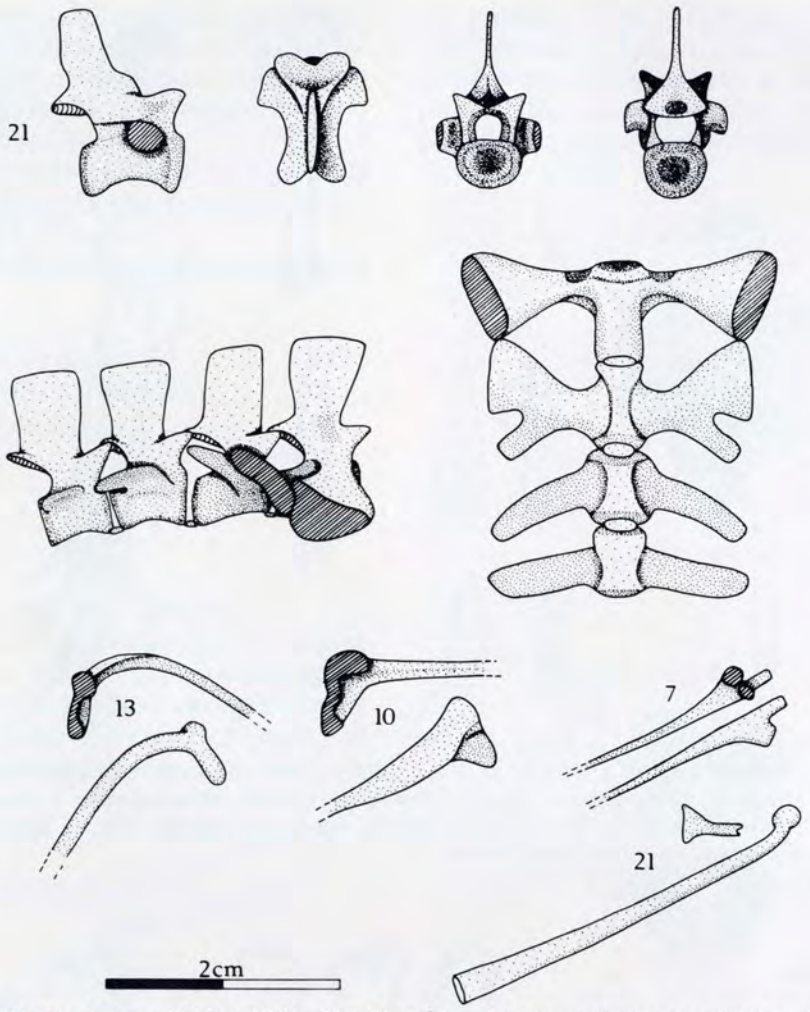


Figure 22. *Prolacerta broomi* B.P.I. 2675. 21st Vertebra; Sacrum and two proximal caudals in lateral and ventral aspect; Ribs as numbered.

The humerus is primitive and simple, though the entepicondylar foramen has been lost; there is a deep ectepicondylar groove.

Radius and ulna are long and slender. The small wrist elements preserved are as shown, but as they are somewhat disarticulated nothing definite can be said regarding the missing elements. The phalangeal count for the hand is the standard reptilian one.

Pelvic girdle and hindlimb (Figures 24, 31 and 33). All the elements of the pelvic girdle have smoothly rounded margins. All three contribute to the acetabulum which has no upper rim as such (though it is rimmed anteriorly by a ridge angled towards the posterior tip of the iliac blade)—this could be to allow the femur to be raised rather high during bipedal locomotion. The pubo-ischiadic plate is broad; the central area is extremely thin. There is a thickened out-turned antero-ventral process of the pubis, with the obturator foramen immediately behind it. Girdle measurements relating to body sections are given in Table 1. p. 98.

The femur has marked posteriad curvature at the distal end. The head is concave and would thus have been capped by an epiphysis which would effectively increase the length of the femur. There is an internal trochanter, with intertrochanteric fossa, very much restricted to the head. The shaft is devoid of muscle attachment protruberances and scars. The tibia is large and robust, particularly at the proximal articulation; the distal end is concave and poorly ossified, suggesting the involvement of cartilage at this point. The fibula is rather slender and is laterally compressed.

The ankle comprises a proximal assemblage of astragalus and calcaneum in loose articulation with a large foramen between them, and a centrale in firm contact with the mesial surface of the astragalus. There are four distal elements of which the first three are small and featureless while the fourth is large with a lateral facet for the fifth metatarsal and a terminal facet for the fourth; it lies in the junction between astragalus and calcaneum.

There is a standard phalangeal count of 2:3:4:5 : 4. The fifth metatarsal is hooked with a ventrolateral scar indicating the insertion of the gastrocnemius.

The astragalus has a large proximal facet which receives the tibia; this is followed by a smooth narrow neck before a second facet at right angles to the first.

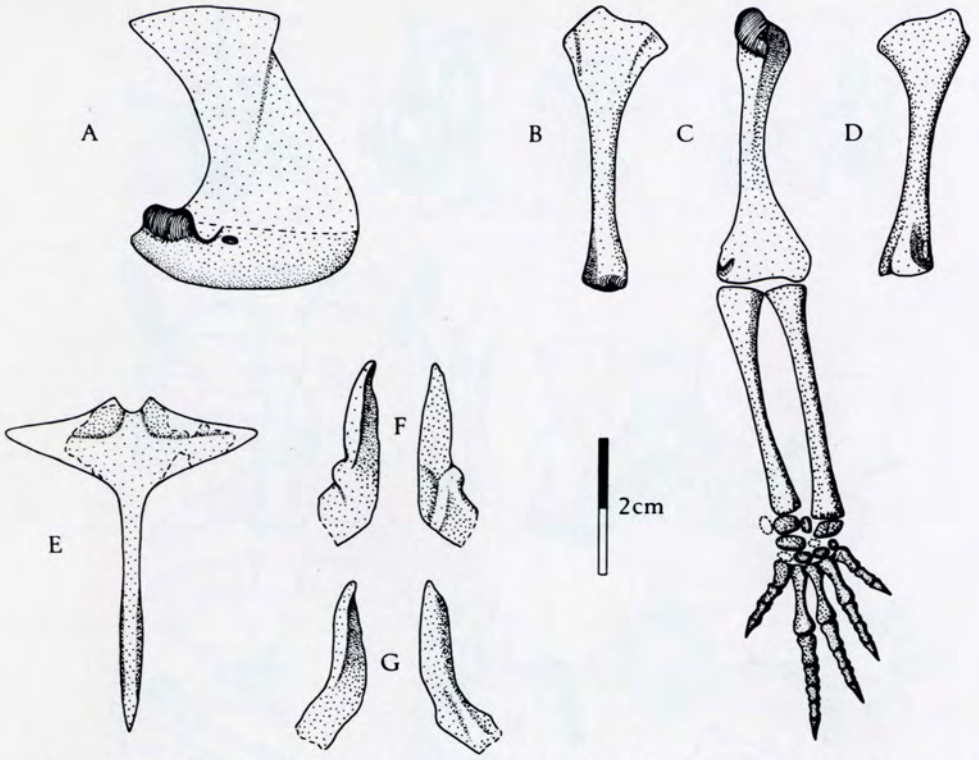


Figure 23. *Prolacerta broomi.* (A – E and G, B.P.I. 2675; F, B.P.I. 2676.) A, Scapulocoracoid; B, Humerus mesial view; C, Right forelimb; D, Humerus in lateral view; E, Interclavicle ventral view; F, Dorsal limb of clavicle, mesial and lateral views: G, Dorsal limb of clavicle, mesial and lateral views.

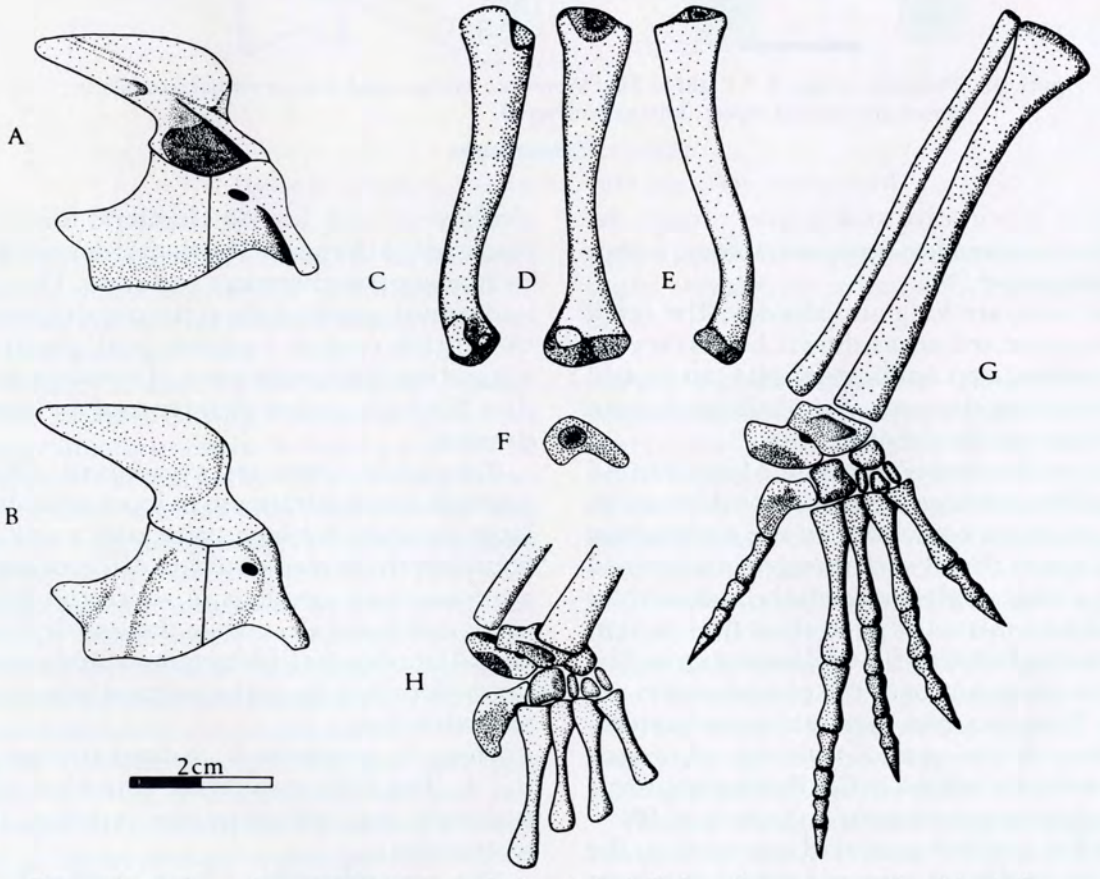


Figure 24. *Prolacerta broomi* B.P.I. 2676. A, Right pelvic girdle lateral aspect; B, Left pelvic girdle internal aspect; C – F, Left femur; C, lateral view; D, Posterior view; E, Mesial view; F, Proximal end; G, Right hind limb flat; H, Ankle flexed.

The calcaneum below this is of equivalent thickness, thinning a little from here towards its lateral edge. One can thus envisage a mass of cartilage here for reception of the fibula. The astragalus bears a marked depression in its dorsal surface as indicated.

Figure 24 G shows the hind-foot in one plane while in H a natural positioning has been attempted with the ankle flexed at the mesotarsal joint.

Some of the more important length measurements are as follows in mm:

Skull (occipital condyle to snout)	67
Neck (condyle through ninth vertebra)	100
Trunk (glenoid to acetabulum)	130
Femur	54
Tibia	58
Humerus	42
Radius	37

PROTEROSUCHUS BRAINCASE

The braincase in B.P.I. 3993 (Figures 25, 26, 36 and 37) has suffered from the vertical compression which has affected the whole skull; no corrections have been made in the drawings except in Figure 26B which has been restored to symmetry.

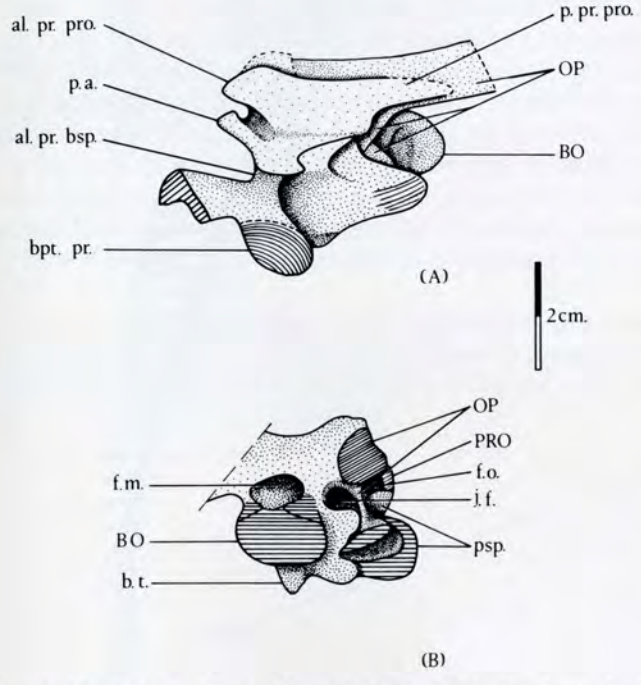


Figure 25. *Proterosuchus vanhoepeni* B.P.I. 3993, (Braincase); A, Lateral view; B, Somewhat oblique occipital view.

The *proötic* has an open trigeminal notch between well developed alar process and pila antotica: it has a long posterior process running along the paroccipital process of the opisthotic. A distinct ventral process meets the alar process of the basisphenoid; behind this a second process from the basisphenoid contacts the proötic. Anteriorly the proötics are united in the midline by a substantial sheet of bone, stretching from one pila antotica to the other, which roofs the pituitary fossa. This sheet is continuous with the dorsum sella; the exit for the VIth cranial nerve can be clearly seen (Figure 26A) between them. This condition also occurs in *Euparkeria*. The *basisphenoid* has several notable features. In lateral view

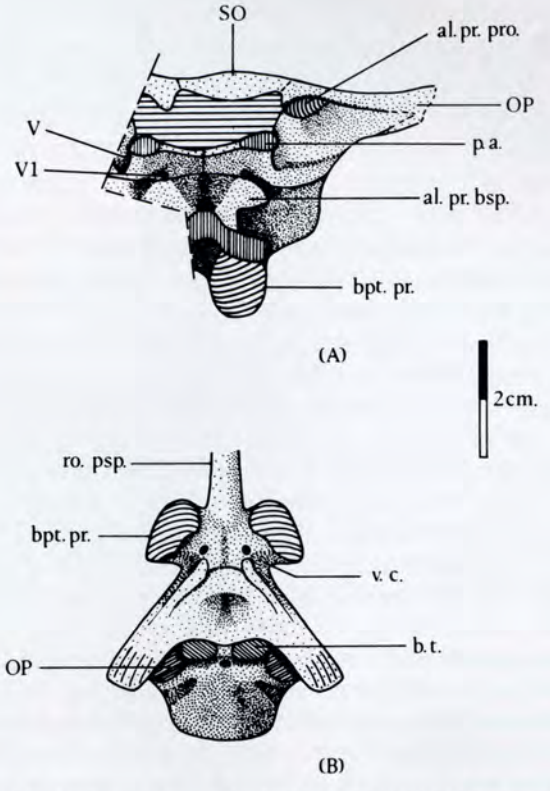


Figure 26. *Proterosuchus vanhoepeni* B.P.I. 3993, (Braincase); A, Anterior view; B, Ventral view.

(Figure 25A) can be seen the prominent process coming in behind the ventral process of the proötic; and thin bone behind it is folded inwards, as indicated also in Figure 25B. This arrangement floors the foramen ovale. The large postero-lateral processes of the basisphenoid bearing the grooves of muscle attachment scars run out beyond and below the ventral processes of the opisthotics—this is indicated in Figure 25B, a somewhat oblique view. In ventral aspect (Figure 26B) the basisphenoid runs anterior to and closely applied against the prominent basal tubera of the basioccipital, while just anterior to this is a deep depression. The open videan canals lie mesial to the posterior edge of the basipterygoid processes, while immediately in front of them are a pair of foramina (present also in *Prolacerta*) which possibly transmitted a branch of the palatine artery.

The ear region poses a problem. The foramen ovale is very small. A stapes if present would have been restricted to a channel between opisthotic and proötic and would thus have run obliquely backwards to the head of the quadrate, indicating a tympanum in the position postulated by Ewer (1965) for *Euparkeria*. There is in any case no room for the attachment of a tympanum on the retro-articular process.

Palatine

Cruickshank (1972) shows the palatine forming the entire lateral margin of the suborbital fenestra. In fact it only runs halfway back. (B.P.I. 3993 and *P. fergusi*.)

Streptostyly

Cruickshank suggested that the quadrate of *Proterosuchus* might be movable. This is clearly not possible in an animal with a solid lower temporal bar. Variations in the position of the quadrate are apparently due solely to post-mortem distortion just as in *Youngina*.

PROLACTERTA FUNCTION

(a) *Cranial kinesis*. It is well known that most if not all predatory squamates have kinetic skills. These are generally speaking small animals which swallow their prey whole. *Prolacerta*, though not a squamate, is functionally similar. A small, lightly built predator, it is the epitome of the sort of animal to which cranial kinesis is of advantage. In *Prolacerta* the skull can move in a vertical plane relative to the braincase, pivoting on the paroccipital processes, the palate being guided by the basal articulations of the basisphenoid. The quadrate is free to move anteroposteriorly as a result of the loss of the lower temporal bar; this is the only acceptable explanation for the retention of the quadratojugal as a delicate strut articulating between squamosal and quadrate. (One can readily accept that slight refinement to the quadrate controlling mechanism in a more advanced form would render the quadratojugal superfluous, but there is no reason to believe that this type of quadratojugal mechanism formed part of the lizard evolutionary story.)

Certain less obvious movements are also possible. These involve the jugal and postorbital, and may be connected with either streptostyly (fore and aft movements or quadrate spreading) or muzzle movements, or both.

Some lateral movement of the postorbital along its vertical contact with the postfrontal would have been possible though slight. The postorbital/squamosal contact is loose and would allow free movement in anteroposterior and dorsoventral planes. The tongue and groove contact between postorbital and jugal would allow sliding movement, and it seems logical to assume a fair degree of the same sort of sliding at the long curving jugal-maxillary junction. The great reduction of jugal and postorbital in recent lizards and the loss of contact between them, as for example in *Varanus*, would suggest that jugal/postorbital sliding is necessary in the early stages of the development of mesokinesis. Movements at the upper extremities of the postorbital in *Prolacerta* might be related more to quadrate movements. Although there is no mesokinetic joint as such, yet the bones of the snout are extremely thin and the fenestrae exochoanis very long, so that muzzle flexure by actual bending of particularly the nasals almost certainly occurred.

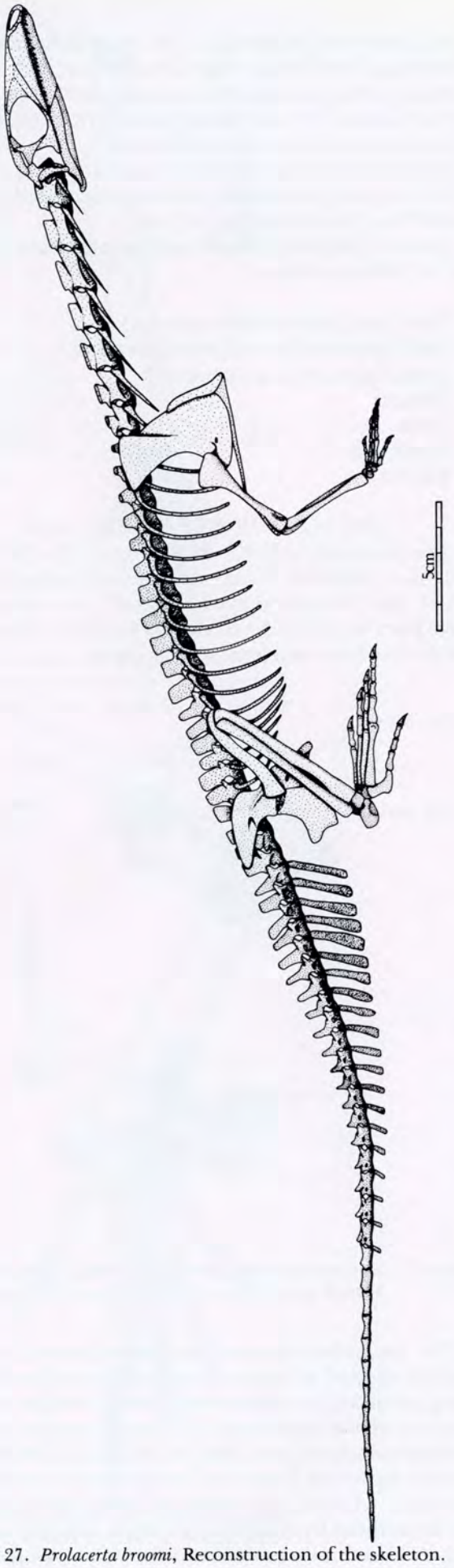
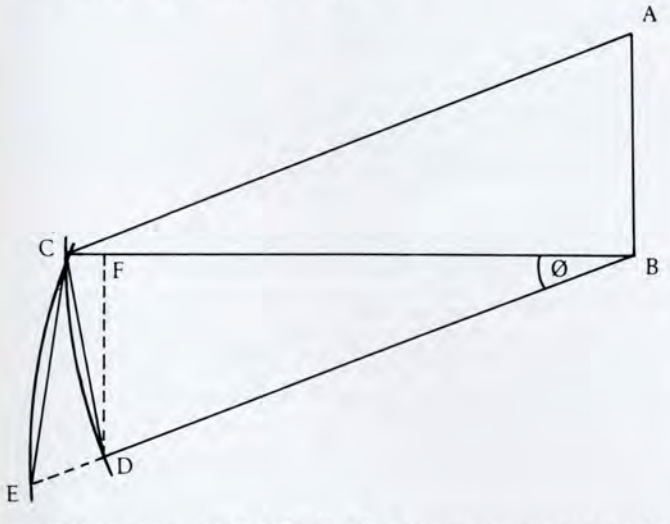


Figure 27. *Prolacerta broomi*, Reconstruction of the skeleton.

It is interesting to note the movable joints present in lizard skulls (Frazzetta, 1962) which are not present in *Prolacerta*. In all lizards which have a mesokinetic (fronto-parietal) joint, the skull roof is broadest at the straight transverse fronto-parietal suture. In millerosaurs, younginids and *Prolacerta* this marked broadening is lacking and the fronto-parietal suture is W-shaped, effectively preventing flexure at this point. In this context the keuhneosaurs are intermediate in morphology, though apparently not yet mesokinetic (Robinson, 1966). Associated with mesokinesis in lizards is antero-posterior movement of the pterygoids. This is reflected in a sliding basal articulation and a rod-like epipterygoid which pivots at both ends. In *Prolacerta* there is no suggestion that the basal articulation is moving in this direction and the epipterygoid has an antero-posteriorly elongated footplate which could not conceivably have pivoted. Relative movement between pterygoid and quadrate certainly occurred.

Slight spreading of the pterygoids and hence of the quadrates and lower jaw rami is a possibility, but until both the movements and their functional importance can be convincingly demonstrated in living lizards, there is no purpose served by discussion at this stage. Frazzetta (op. cit.) has shown that the lizard quadrate moves forward as the jaws open; it would thus be reasonable to assume that the same is true of *Prolacerta*. Now while kinesis in *Prolacerta* is not as complex as that described by Frazzetta for lizards, there appears to be a very simple explanation for quadrate protrusion. Upward movement of the skull on the braincase as the jaws open is slight, and any upward movement of the whole head will not alter the fact that the lower jaws are dropped through a considerable arc relative to the upper.

This means that without protrusion of the quadrate the lower teeth move posteriad relative to the upper, and consequently move forward during the bite, as shown in the following diagram.



ABC represents the skull. The snout moves upwards hinging at A. This movement is slight and for present purposes can be ignored.

BD represents the lower jaw, hinging at B.

CF represents the extent of posteriad movement of lower teeth relative to upper in an akinetic skull.

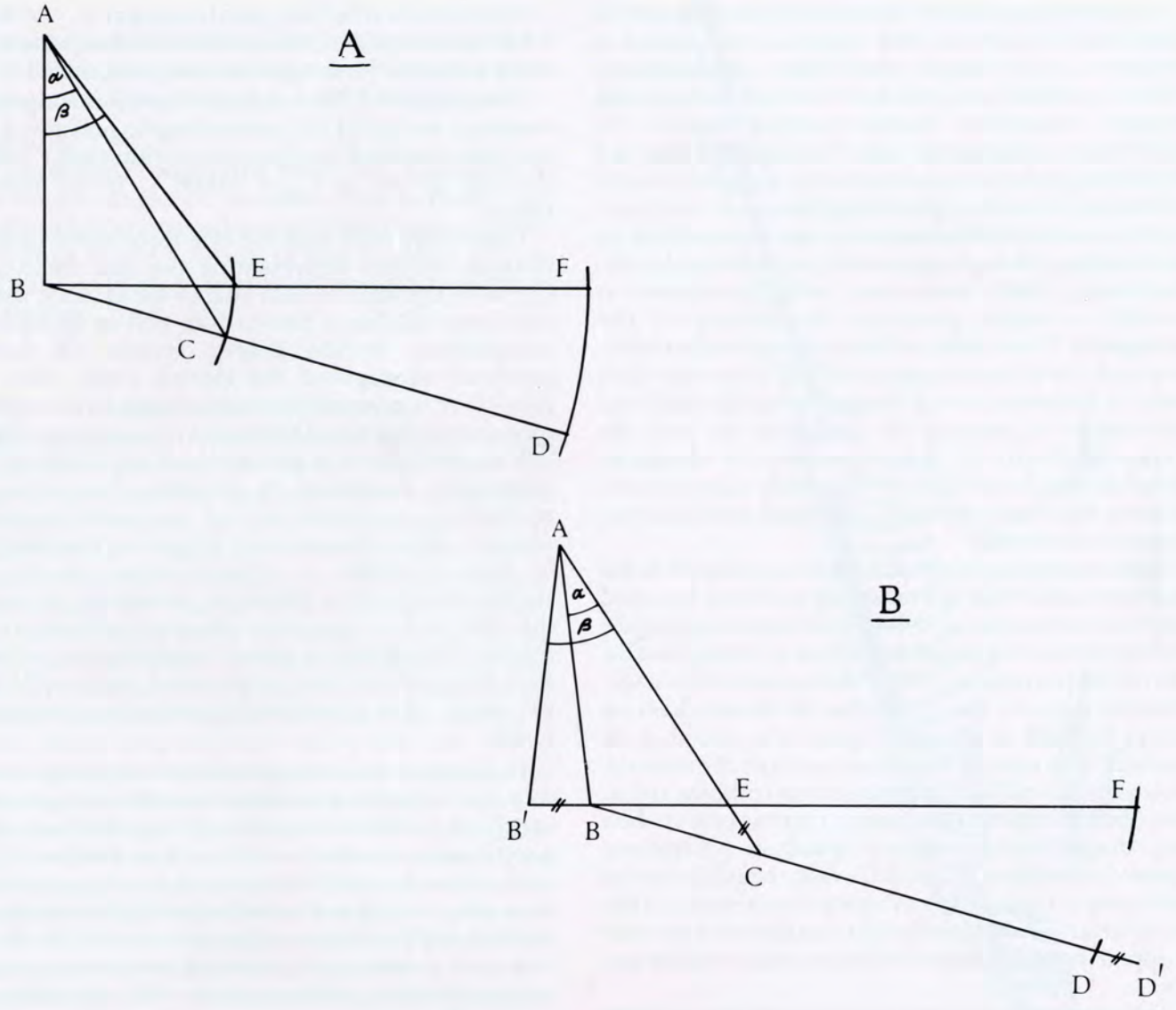
Protraction of the quadrate during jaw opening results in the tip of the jaw moving to position E. As the jaws close and the quadrate is retracted E moves through an arc to C, as would D in an akinetic system.

Clearly the teeth and the bite force move upward through an arc. Representing the bite force as a chord on this arc it is clear that in the akinetic system this force CD has a forward as well as an upward component. In the kinetic system CE moves posteriad throughout the closing cycle. This circumstance is governed by two variables, the angle of the jaw opening θ and the extent of protrusion DE.

θ as used above is greater than any angle of jaw depression illustrated by Frazzetta, but it is still necessary to determine DE for live lizards to decide whether natural movements fall within the limits set by these variables. It certainly seems plausible to suggest that there could be an advantage in having the teeth and the bite force directed backwards during jaw closing for an animal capturing active prey. It is surely more than coincidental too that ECD is the shape of a generalised carnivorous thecodont tooth.

Compare the akinetic system (A) with the kinetic system (B) p. 114. In both the muscles contract from length AC to length AE. In both α decreases to β. But, whereas in A the direction of pull shifts from AC to AE, in B AE and AC lie on the same line, with C moving to E as B moves to B^1. Note that in B quadrate retraction B B′ = adductor shortening CE = degree of jaw protrusion D D′. As any biological system can be expected to represent a compromise between conflicting ideals, B B′ is probably too short to allow perfection of system B though the system yet holds considerable advantage by virtue of the extra linkage and more nearly constant line of action of the adductors.

Streptostyly seems to hold an irresistible fascination which has led to some curious statements in the literature. Some of these merit brief consideration. Walker (1961) suggested that the quadrate of *Stagonolepis* (a pseudosuchian) might have been movable and have played a part in that animal's shovel-snouted foraging mechanism. Ewer (1965) suggested that some movement of the quadrate may have been possible in *Euparkeria*, a thecodont, and suggested the presence of an additional wholly unnecessary and improbable protractor muscle attaching to the mesial surface of the quadrate ramus of the pterygoid, i.e. that portion which lines the throat. Cruickshank (1972) has suggested that the *Proterosuchus* quadrate may have been movable—this to account for the variability in the slope of the quadrate exhibited by several skulls. The fact remains that *Proterosuchus* has a solid lower temporal bar and the quadrate always bears the same relationship to it; it



therefore seems more reasonable to attribute this variability to distortion of the specimens. It would be unexpected to find a streptostylic quadrate in any diapsid, as meaningful movement is only possible once the lower temporal arcade has been breached as in *Prolacerta*.

There is merit in Robinson's (1966) suggestion that the quadrate (of lizards) might rock back and forth during chewing movements thus aiding swallowing. Whether this is true of any lizards will require experimental determination. In particular it is necessary to determine what sequence of muscle actions is responsible for quadrate retraction and to what extent these movements are independent of jaw adduction.

(b) *The postcranial skeleton.* It is no exaggeration to say that the combination of characters which make up the skeleton of *Prolacerta* (and *Macrocnemus*) is unique.

This is a small, very light-boned animal, unquestionably built for speed and/or agility. Limb disparity *per se* is a vague and misleading term. What is important as a clue as to whether an animal was terrestrial quadrupedal, aquatic or bipedal, is the relative lengths of femur and tibia: in a terrestrial quadruped these are subequal in length, in aquatic animals the tibia is markedly shorter and in bipedal animals the tibia is the longer bone. Hence we can say that *Prolacerta*, on the basis of limb proportion, was bipedal (at least at speed). This, however, is the only immediately apparent indicator of bipedality; there is no indication, particularly in the pelvic girdle, of supporting modifications for this mode of locomotion.

Looking for comparisons then we can look first at the lizards. Several lizards are known to adopt a bipedal stance and/or gait at times. This subject has been well covered in a delightful chapter by Neill (1971), whose main thesis it is that bipedality arose in arboreal lizards as a predator confrontation and escape mechanism and is only employed by them as such. The bipedal lizards are characterized by long slender tails which are important in counterbalancing the weight of the head and trunk during this rather ungainly gait (described by Snyder, 1949, 1954, 1962). One aspect of this crude bipedal gait which has seemingly escaped notice is the rotation which occurs

at the foot in contact with the ground as the opposite limb is swung forward in stiff-legged fashion: this can easily be seen in the scratch marks of the toe impressions left by a basilisc chased across a damp clay surface. This is worth recording for the implications it may have for ankle structure, though *Prolacerta* itself has a typical early thecodont ankle and it is remarkable that very little osteological modification, limb disparity excepted, is seen in the early stages of bipedalism.

A disconcerting aspect of bipedal lizard morphology from the point of view of this discussion is that they all have short necks and trunks; however, we can immediately remark that perhaps the deep rooted tail of *Prolacerta* is designed in part to counteract the added weight of the long neck. There are at least two other factors to consider here.

Leaving the lizards for the moment it is pertinent at this stage to introduce another tentative comparison. Both the long neck and the large flattened chevrons of *Prolacerta* invite comparison with the incipiently bipedal prosauropod dinosaurs.

We are now at the stage where we can embark on detailed argument on the function of the *Prolacerta* skeleton. To start with the tail. The bipedal lizards have long slender tails with rather insignificant chevrons; one aspect of the function of this tail has been overlooked. While it is clear from Snyder's (op. cit.) drawings and photographs that the distal part of the tail is flung out to counterbalance the body, it is equally clear that the base of the tail is held in line with the pelvis and both it and the trunk are thrown over to the same side as the limb executing the powerstroke. This probably ensures that the direction of pull of the femoral retractors places the arc of travel of the femur in the required plane, and it also helps distribute the necessary weight over the sacral region (weight against which the limb is pushing). As far as the use of the tail as a counterbalance to the weight of the body is concerned this is something which requires further explanation as we are dealing with a state of dynamic equilibrium in which weight distribution clearly changes considerably through the stride sequence.

The above remarks serve to highlight the importance of the second sacral rib of *Prolacerta* doubling as a caudal transverse process tending to lock the base of the tail to the sacral region; this also suggests a reason for the impression of relative rigidity conveyed by the *Prolacerta* chevrons (one may note by way of contrast that in the varanids which use their tails as lashes the chevrons are centrally situated on the centra, thus not impeding flexure in any way).

The caudal chevrons of *Prolacerta*, in proportion, must be among the largest on record. At the base of the tail they are 1,5 times as long as the depth of the preceding vertebra and this ratio gradually decreases to unity. The only acceptable explanation for this is that of concentrating the bulk of the muscle mass ventrally at the proximal end of the tail. There is almost certainly more than a simple weight factor involved here; as the pelvis shows no evidence of improvement of the locomotor musculature for bipedal locomotion it is quite likely that the main femoral retractor, the *caudifemoralis longus*, would be considerably enlarged in an animal of this size (the size limit of bipedal lizards). Femur morphology shows that the caudifemoralis inserted near its proximal end, an arrangement which sacrifices power for speed.

The shape of caudal chevrons in reptiles is rather variable; as this is an aspect largely ignored one can find little help in the literature, but comparison with the incipiently bipedal dinosaurs is striking, in that the chevrons are rather large and laterally compressed: while these prosauropods have long necks, there is not much skull weight to counterbalance, and in any case one cannot compare locomotion in early thecodonts and dinosaurs too closely. It is instructive to note, however, that in *Saltoposuchus*, a bipedal dinosaur with large head and carnivorous dentition, the cervical vertebrae are extremely short.

A deep tail must inevitably raise the possibility of its being an adaptation to swimming. Fortunately that possibility is easy to discount in this case. In the crocodile which is adapted to an aquatic existence the chevrons are of more moderate size, narrow, and circular in section; the tail is dorso-ventrally symmetrical with tall neural spines extending almost to the tip. In *Prolacerta* the neural spines become insignificant in the distal half of the tail. In the extinct marine reptiles caudal chevrons become very small and insignificant. A piece of circumstantial evidence against an aquatic existence is worth mention. *Macrocnemus* occurs in association with a highly adapted aquatic fauna which tends to underpin the non-aquatic nature of *Macrocnemus*.

The long neck of *Prolacerta* may account in part for the extra weight at the root of the tail. The long neck is a typically thecodont specialisation common to Proterosuchians, certain dinosaurs and birds. This is a specialisation which considerably enhances the predatory capability of the animal. The thickened neural spines at the base of the neck and in the pectoral region are sites of attachment for powerful, quick-acting muscles concerned with raising the head and neck and with lateral movements.

With regard to the limbs and girdles the latter are extraordinarily primitive for such an advanced animal, conveying no hint of the animal's obviously rapid, often bipedal, gait. Though the hind limb is long with tibia longer than femur, yet it shares a primitive ankle pattern with *Proterosuchus* and rhynchocephalians. The hammate process of the fifth metatarsal shows no sign of turning inwards underneath as is the case in bipedal lizards (Snyder, 1954). The forelimb is not reduced and probably functioned during slow locomotion, basking (Figure 27) and tree climbing.

ECOLOGY

Possible environment and habits

The *Lystrosaurus* zone presents many problems of interpretation of ecology of its fauna. A regional sedimentological study is an essential prerequisite as a framework in which to place the fauna, but this is as yet lacking. This is a zone notable for its omissions; there is, for instance, little evidence of vegetation. Another notable omission is the total absence of fish to date, though these must have been present in an environment which supported labyrinthodonts. Of the many invertebrates, including insects which must have been present, only millipedes have so far been recorded.

Considering its early thecodont ancestry it is possible that sharp blade-like teeth were the only option available to *Prolacerta*; these are small in relation to the size of the skull, compared with the teeth of, for example, *Euparkeria*. (This applies as well to *Proterosuchus*.) Unfortunately no living reptiles have comparable dentitions with the possible exception of *Varanus komodoensis*. *Prolacerta* might be envisaged as feeding on small prey which it would grab, kill, and swallow whole, such as the young of the many small synapsids, procolophonids and labyrinthodonts known from the *Lystrosaurus* zone, as well as insects. It seems very likely that the prolacertids were replaced by true (pleurodont) lizards.

The rather larger *Proterosuchus* on the other hand probably fed by tearing pieces of meat off a carcass much as does *Varanus komodoensis*, as the teeth of these two animals are closely comparable in size relative to the skull, in shape, and in having finely serrated posterior edges. *Prolacerta* lacks serrations on the teeth and as these are present in *Heleosaurus* and *Proterosuchus* they have presumably been secondarily lost in *Prolacerta*.

Stealth more than agility would be required in hunting. Why then this light, swift creature? Presumably no contemporaries could match *Prolacerta* for speed, though some Galesaurids and Therocephalians would certainly have eaten them, given a chance. The most likely explanation is that it was to an extent arboreal—here lightness and agility are of advantage. This would support Neill's (op. cit.) argument for a close link between an arboreal existence and the evolution of bipedality (in animals of this size).

RELATIONSHIPS OF *PROLACERTA*

Comparisons of all the possibly significant features of *Prolacerta* cover a very wide field indeed. Some of them are rapidly discountable, most flounder on inadequate knowledge of many forms, but in the end the reasonable options are few and a stable picture seems to emerge.

Some of the earlier Permian diapsids should be mentioned. *Petrolacosaurus* is a Pennsylvanian form technically diapsid but remote in time and lacking the strong morphological features which link the late Permian and Triassic forms. *Areoscelis* merits attention as the only fairly well known protorosaurian. Relationship to *Prolacerta* has been argued by Camp (1945), Romer (1947) and Vaughn (1955). The only striking parallel is in the elongation of the cervical vertebrae, but this feature is common to several unrelated groups. *Areoscelis* has in fact a curious specialised postcranial skeleton (e.g. the elongate limbs) behind a primitive skull—certainly not a good generalised ancestor. The double coracoid is another point against it.

One animal which must be revived in this discussion is the Russian Permian *Mesenosaurus*. Here is an animal with powerful carnivorous dentition (mode of implantation unknown), a lower temporal opening with lower temporal bar, several primitive characters such as the maxilla entering the external naris, which should merit consideration with early thecodonts, but about which too little is known.

An early Permian diapsid is *Mesosaurus*, a curious, little known, highly specialised form, but which with *Petrolacosaurus* stands as a caution that diapsid sauropsids became established early on. Hopefully, the Brazilian material, reputedly of excellent potential, will yield a good account of this animal.

One arrives then at the Eosuchia, the millerosaurs, younginids, rhynchocephalians (sphenodontids), squamates and archosaurs (Thecodontia) for present purposes, and the problem of relationships of these groups.

The millerosaurs, which may or may not have direct bearing on later phylogenies, nevertheless exhibit certain morphological details which are not shown by, for instance, the younginids but which go a long way to explain the derivation of early thecodont characters (particularly one may mention the quadratojugal and its relationships).

Among the younginids, *Youngina* as described above gives an apparently satisfactory rhynchocephalian ancestor, but it is necessary to note here that all the known rhynchocephalians have basically crushing dentitions and virtually akinetic skulls.

Heleosaurus (to be described by Carroll) is a good thecodont ancestor with its blade-like marginal dentition and advanced femur indicating bipedality.

Much use has been made here of the term "thecodont" as *Prolacerta* is so obviously a thecodont while the squamates are typically acrodont or more commonly pleurodont (Edmund, 1969). This applies to the earliest recognised true lizards, the keuneosaurids, which are defined as having subpleurodont teeth.

Paliguana, contemporaneous with *Prolacerta*, is a poor specimen, yet it has very much the morphology and proportions of the keuneosaurids. One or two probable lizard skeletons are known from the Permian of South Africa, of which *Palaeagama* (Broom, 1926) has been described; unfortunately the temporal region is badly damaged. Carroll believes he can reconstruct it to look much like the keuneosaurids.

The lizard-like animals mentioned in this paragraph are to be described by Carroll. There is thus some evidence to suggest that the Squamata had evolved before the end of the Permian, though more collecting is needed to strengthen this.

To place *Prolacerta* then we are left with two options. Detailed comparisons with primitive thecodonts prove instructive, as do comparisons to the Protorosauria (sensu Romer, 1956). Comparisons between *Prolacerta* and *Macrocnemus* are so close there can be little doubt of a close relationship. Other Protorosaurs are so poorly known that they cannot be drawn into this relationship with certainty.

Proterosuchus (Cruickshank, 1972) is the one animal close to *Prolacerta* known in sufficient detail for meaningful comparison. Much of the material has also been available to the writer when additional information was required. *Proterosuchus* occurs consistently lower in the *Lystrosaurus* zone than does *Prolacerta*, but this probably does no more than reflect an ecological separation. *Proterosuchus* is a larger, more heavily built, and quadrupedal animal, while *Prolacerta* is small, light and bipedal. *Proterosuchus* has an antorbital fenestra which puts it among the Archosauria, but Cruickshank has suggested with some justification the derivation of *Proterosuchus* from a "rhynchocephalian" ancestor; such an animal would be required not to possess an antorbital fenestra, and this step would not have been far back in time.

Strip *Proterosuchus* of its archosaurian label and compare with *Prolacerta*. The skull morphology and detailed relationships of the bones are remarkably close. The writer does not accept Cruickshank's interparietal, nor the jugal process of the quadratojugal which he shows. The palatine does not form the entire lateral margin of the suborbital vacuity as he shows, but only runs halfway back. Cruickshank failed to note that the teeth of *Proterosuchus* are serrated on their posterior margins.

Having disposed of these points the differences are now only of degree and quite consistent with the basic differences of size and build.

Proterosuchus has apparently a proportionately longer snout, achieved by compressing the orbit, with a more downturned premaxilla; it has a very odd retroarticular process (for which a functional interpretation is required). It is difficult to accept Cruickshank's assertion that the quadrate was streptostylic. Surely this can only occur once the lower temporal bar has been breached?

The postcranial skeletons of the two animals present a very similar morphological grade. The girdles of *Proterosuchus* are heavier, interclavicle and ilium having distinctive shapes. The bifurcations of the sacral processes were one of the first points of strong similarity noted in this study.

Similarity extends to the hind foot and ankle, though there is some doubt regarding the phalangeal count of *Proterosuchus*. Cruickshank has called the astragalus intermedium when it is really a compounding of intermedium and tibiale, and the centrale he calls astragalus. Names aside, the feet of *Prolacerta* and *Proterosuchus* are identical down to the hooked fifth metatarsal.

The vertebral columns are very similar, though *Proterosuchus* does not have such elongate cervicals. This similarity extends to the large blade-like caudal chevrons, though these are only two-thirds the length in *Proterosuchus*.

All the above gave sufficient grounds for expecting to find an explanation for the braincase of *Prolacerta* in *Proterosuchus*. One may expect braincases to be fairly conservative at this level; also, while that of *Prolacerta* is poorly ossified in places, this is consistent with a light kinetic skull, while in the larger *Proterosuchus* the braincase is well ossified. This comparison, detailed elsewhere, is so striking in every detail as to put the seal on a very close relationship.

The quadratojugal may be one of the more important elements in deciding lizard/rhynchocephalian/archosaurian relationships. Gow (1972) has described the relationships of this bone in millerosaurs in detail, and this pattern could very easily give rise to what we see in *Prolacerta* and *Proterosuchus* and the later archosaurs, e.g. *Euparkeria* (Ewer, 1965) where the quadratojugal rests on a facet on the lateral condyle of the quadrate running up to meet the squamosal above, lateral to a quadrate foramen. From the reduced condition in *Prolacerta* it is of little consequence whether this bone is lost or retained by *Macrocnemus*. It is difficult to see how this quadratojugal arrangement could be derived from *Youngina*.

The Triassic reptiles of Monte San Giorgio (Kuhn-Schnyder, 1963 and others) are a diverse collection mostly of specialised marine forms; it is thus surprising to find amongst them an animal very close indeed to *Prolacerta*, namely *Macrocnemus bassanii* Nopsca. Owing to their poor mode of occurrence these fossils are not as well known as one would like, particularly in details of skull structure. Nonetheless Kuhn-Schnyder (1963) described a skull of *Macrocnemus* in sufficient detail to conclude convincingly that this animal is closely allied to *Prolacerta*. In that paper he suggested the possibility that the lower temporal opening of diapsids evolved before the upper. The writer has suggested (Gow, 1972) this might apply in the origin of squamates. In view of the standard morphology of upper temporal openings of younginids and early thecodonts and bearing in mind the presence of two temporal openings in the upper Carboniferous *Petrolacosaurus* these suggestions are open to doubt. It seems likely that the lower temporal bar has been lost (along with the quadratojugal?) in *Macrocnemus* and *Tanystropheus*. *Prolacerta* constitutes the ideal starting point for the derivation of these forms.

In Kuhn-Schnyder's 1963 paper there is an excellent photograph of an almost complete skeleton of *Macrocnemus*. The resemblance to *Prolacerta* is so close

as hardly to bear detailing and should dispel all doubt regarding the close relationship of these animals. Further checks against Peyer's (1937) original detailed description of *Macrocnemus* with its many excellent photographs also serve as a good standard of comparison.

Size, proportion and morphology are closely comparable in the two animals. The few concrete differences are predictable and only slight advances occur in *Macrocnemus*.

As far as the *Macrocnemus* skull is known it is very similar to that of *Prolacerta*. Doubt exists as to the nature of the snout and the position of the external nares. The hind margin of the jugal is not known with certainty, nor can the presence of a quadratojugal be shown, though it seems certain that no lower temporal bar was present. Details of squamosal, quadrate and upper temporal fenestra are identical to the condition in *Prolacerta*. Dentitions are very similar in the two animals. What can be seen of the palate of *Macrocnemus* agrees well, and the shape of the basisphenoid is identical.

The vertebrae and ribs agree very closely, even to the divided second sacral transverse process and the large flattened caudal chevrons.

Ossification of the girdles in *Macrocnemus* shows a considerable reduction over that in *Prolacerta* but this is almost universal in middle Triassic reptiles and to be expected and involves just those areas that are extremely thin in the girdles of *Prolacerta*. The ilium and inter-clavicle are still virtually interchangeable between the two animals. Limb proportions are the same in both animals, both have hooked fifth metatarsals and the same digital formulae. Slight differences in ankle morphology reflect only the time gap.

It is thus clear that *Prolacerta* is representative of an as yet poorly known group of early Triassic prearchosaurian thecodonts which in all probability gave rise to the later *Macrocnemus* and *Tanystropheus*. These can then be regarded as a sterile group which paralleled the Squamata in the loss of the lower temporal arcade.

PROLACERTA—SYNONYMY AND DIAGNOSIS

Subclass: Incertae sedis

Probably most workers would favour retention in the Lepidosauria

Order **Parathecodontia** nov.

Thecodont reptiles of diapsid origin in which the lower temporal arcade has been breached. Very closely allied to proterosuchian thecodonts in most aspects of skeletal morphology but precluded from the Subclass Archosauria by the almost certainly primitive absence of antorbital fenestrae.

Family Prolacertidae Parrington 1935.

Small agile light-boned bipedal animals. Quadrate streptostylic and quadratojugal reduced or absent.

Prolacerta broomi Parrington 1935.

= *Pricea longiceps* Broom and Robinson, 1948.

Lower Triassic prolacertids from the *Lystrosaurus* zone of South Africa. Girdles large, unfenestrated, plate-like structures. Jugal spur and quadratojugal present.

Macrocnemus bassanii Nopcsa 1930

European Middle Triassic prolacertids. Girdles reduced. Posterior border of jugal smooth, quadratojugal absent.

Family Tanystropheidae Romer 1956.

Tanystropheus longobardicus Meyer 1852.

Skull very similar to that of Prolacertidae but with heterodonty in juveniles, in which the teeth in the posterior half of both jaws are tricuspid. Greatly elongate neck with longest neck vertebra five times as long as the longest trunk vertebra. Considerably larger than Prolacertidae—in excess of four metres in length.

DISCUSSION

The reptilian braincase

Although it is now known that the incomplete lower temporal bar is not confined to lizards but is present also in the sphenodontid *Glevosaurus* (Robinson, 1973) and certain millerettids (Gow, 1972), and in spite of the fact that *Prolacerta* has blade-like carnivorous theodont dentition, it seems desirable to establish the differences between squamates and archosaurs on as many features as possible, particularly those of a predictably conservative nature. Clear differences in braincase morphology would provide this additional distinction. Here good comparative information is scarce, particularly as regards good illustrations, but this situation is starting to change and new work on reptilian braincases can be expected to appear in the near future. There is enough material available for certain trends to be discernible and putting these forward at this stage may provide guidelines and ideas for future work.

A problem is that several strong features of typical lizard braincases tend to lose significance the farther one goes back in time, and in any case squamate history below the upper Triassic is vague at the least. To illustrate the point, take the foramen rotundum found in lizards; this is lacking in *Youngina*, millerettids and *Sphenodon*; it is lacking in archosaurs, some of which develop a foramen pseudo-rotundum. Apparently the Kuehneosaur braincase is still Permian in this respect (Robinson, 1973).

The ventral process of the opisthotic thought by Robinson (1967) to be a unique character linking *Prolacerta* and *Kuehneosaurus* is in fact typical of the lower Triassic proterosuchians and were it not for the fusion of opisthotic and exoccipitals in later forms it might be possible to extend this to modern lizards and the sauropod dinosaurs at least.

However, the negation of the usefulness of the above points notwithstanding, there does seem to be a concrete basis for separation on braincase features. The millerettid-younginid grade braincase could lead

anywhere, but approaching the problem from the other end a clear difference between lizard and archosaur is in the extent of participation of the parasphenoid (basisphenoid when the two are no longer distinguishable) in the sidewall of the braincase. In *Prolacerta, Proterosuchus, Euparkeria* and *Stagonolepis* this is extensive, while in lizards the braincase is walled completely by proötic and the basisphenoid terminates abruptly much farther forward (e.g. *Varanus*, Figure 28). On this basis it seems there can be no ambiguity regarding the correct assignment of Triassic fossils, though it appears at this stage that the archosaurian condition became firmly established earlier than that of lizards.

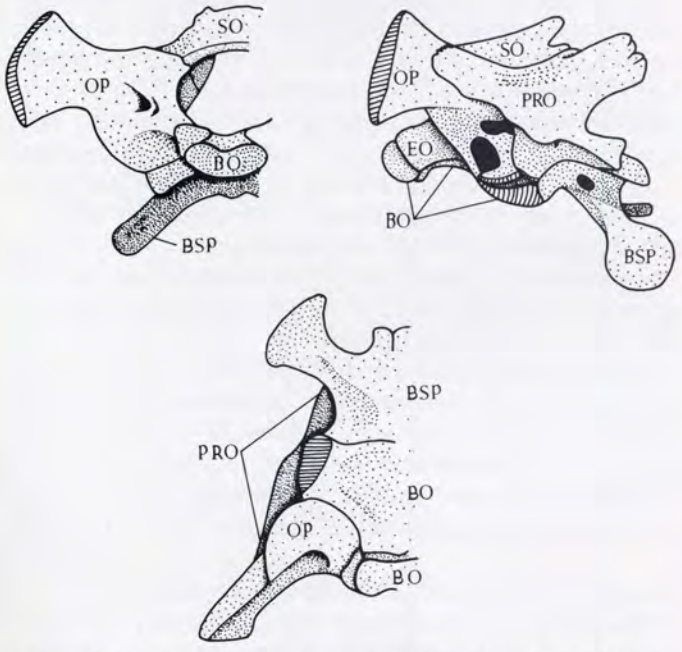


Figure 28. *Varanus*, Braincase in occipital, lateral and ventral views. Note particularly the restricted extent of the basisphenoid, both laterally and posteriorly.

The above suggestions are now considered in greater detail.

At the level of *Youngina* and *Milleretta* the braincase is essentially captorhinid (*Milleretta* has an odd stapes while that of *Youngina* is more like the slender rod seen in later reptiles, but this does not affect braincase morphology). Perhaps the braincase in these animals could be said to represent an upper Permian level of development, just prior to considerable changes taking place, but it is necessary to bridge the middle Permian gap in the reptile story before this can be stated with certainty. A feature of this braincase is the nature of the parasphenoid. Gow (op. cit., Figure 9C and p. 239) was able to demonstrate that the parasphenoid in millerettids runs right back beneath the basioccipital almost to the condyle. The basisphenoid, comprising the basipterygoid processess, sella turcica and dorsum sellae lies on top of the parasphenoid, while between basisphenoid and basioccipital is an extensive gap bridged only by parasphenoid. An exactly similar condition is indicated for *Youngina* (Figure 5C). The millerettid parasphenoid is characterized by a toothed rostrum plus two teeth on either side of the base of the rostral row; this is very similar to the condition in *Petrolacosaurus* (Figure 30). In *Icarosaurus* (Colbert, 1970) and *Kuehneosaurus* (privileged data from P. L. Robinson) these parasphenoid teeth are retained. In recent lizards, typified by *Varanus* (Figure 30), the parasphenoid seems to be reduced to the cartilaginous rostrum, leaving only basisphenoid flooring the braincase anteriorly.

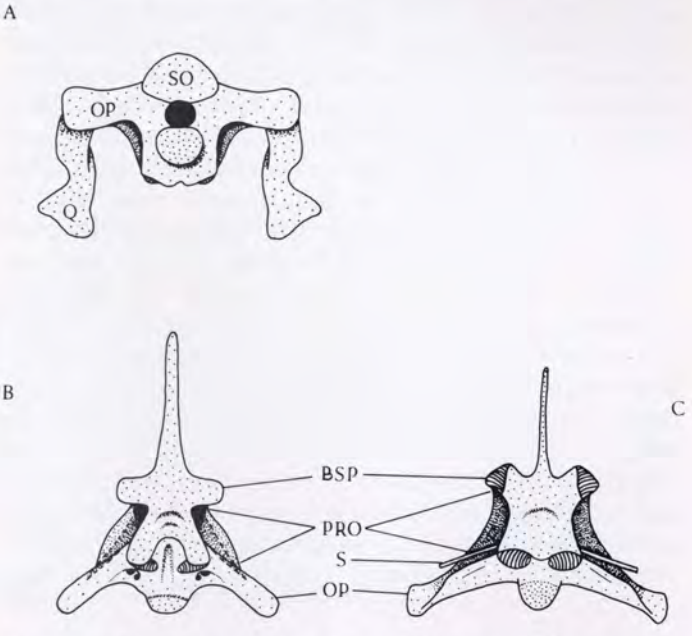


Figure 29. A & B, *Massospondylus*. From photographs of the specimen K1314 in the South African Museum; C, *Dromaeosaurus*. From a photograph in Colbert and Ostrom (1958).

On the thecodont line the picture is somewhat different. The *Youngina* parasphenoid is a rather different shape from that of *Milleropsis*; it too could be derived from that of *Petrolacosaurus*. In both animals there is a pair of parabolic depressions in the ventral surface of the parasphenoid plate, and this pattern tends to persist through the Proterosuchia to some of the dinosaurs, a possible inference being that the parasphenoid as such tends to be retained in these archosaurs. The depressions in the parasphenoids of *Kuehneosaurus* and *Icarosaurus* would tend to reinforce the identity of this element based on the teeth.

Figure 29 shows two dinosaur braincases which look to be extraordinarily primitive in their closeness to the proterosuchian condition. A and B are of *Massospondylus*, an upper Triassic Prosauropod, drawn from photographs of the specimen (S. A. Museum No. K1314). C is of *Dromaeosaurus* (Colbert and Ostrom, 1958), an upper Cretaceous theropod (drawn from published photograph). *Camarasaurus* (Ostrom and McIntosh, 1966), a Jurassic to Cretaceous sauropod, also conforms to this primitive pattern. What is not clear in these seemingly primitive dinosaur braincases

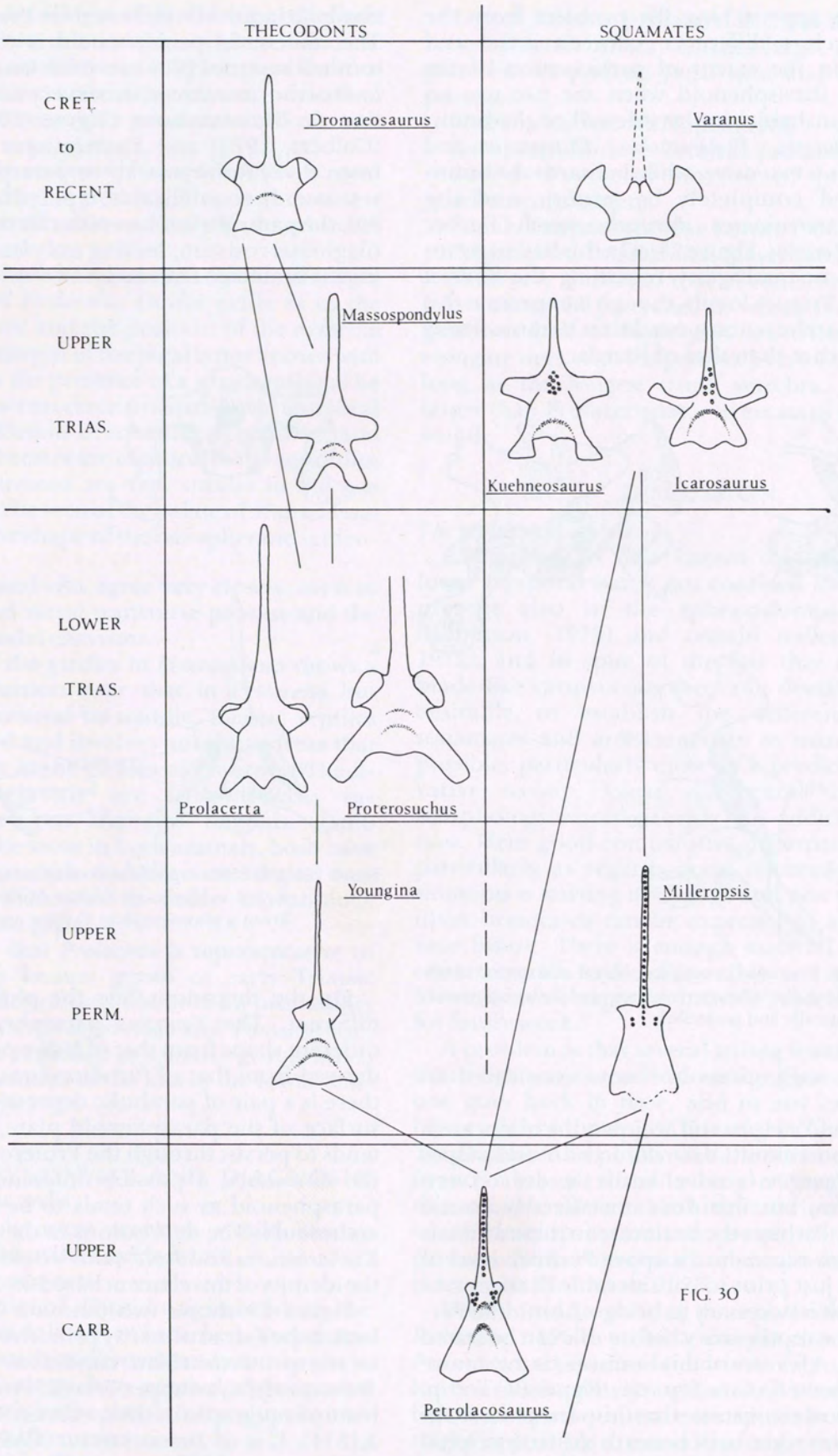


Figure 30. An attempted separation of thecodonts and squamates through time based solely on ventral views of the para-basisphenoid. The several possible interpretations of the position of *Milleropsis* do not affect the overall picture. *Heleosaurus* is a better archosaur ancestor than *Youngina* but there is no difference in the parasphenoids of the two. The lack of Permo-Triassic lizards is clear.

is the extent of participation of the basisphenoid in the sidewall of the braincase, but with good material in existence this information should soon become available.

In the present context the position of *Euparkeria* is still not clear. Ewer's (1965) drawing of the basisphenoid seems open to question.

Another area where one might expect to be able to make meaningful comparisons is the middle ear region. In *Milleretta* and *Youngina* the region of the fenestra ovale is a large irregular opening bordered by good edges of proötic, opisthotic, basioccipital, para- and basisphenoid. The pattern of exits for cranial nerves IX to XII is primitive; in *Milleretta* IX—XI and jugular vein emerge between exoccipital and opisthotic, XII through the opisthotic (Gow, op. cit.). *Youngina* is similar except that the foramen for XII discharges externally into that which transmits IX to XI and jugular. The stapes of *Milleretta* is peculiar, but that of *Youngina* has the typical rod shape of later sauropsids and runs out under the paroccipital process towards the back of the head of the quadrate.

Typical lizards are characterized by the presence below the foramen ovale of a foramen rotundum, the former bordered anteriorly by proötic, the latter piercing the opisthotic alone. In iguanids these formina are separated by the crista interfenestralis of the opisthotic, in varanids both are anterior to that sheet of bone. The footplate of the stapes is applied against the foramen ovale while a membrane at the foramen rotundum compensates for vibrations of the stapes (Romer, 1956; Robinson, 1973). According to Robinson the required physical effect is attained in *Sphenodon* as follows:

> "an unossified portion of the inner wall of the otic capsule, and the large vagus foramen, serve to allow compensatory movements of the fluids of the inner ear, and probably *Kuehneosaurus* had a condition similar to *Sphenodon* in these respects."

This leads to consideration of the fact that in a typical lizard the otic capsule is encased in bone and this is what makes the foramen rotundum necessary. In *Milleretta, Youngina*, and the early thecodonts listed above the otic capsule is either known, or can safely be inferred, to be open internally.

In crocodiles and birds in which the middle ear is enclosed in bone a foramen pseudorotundum is developed to perform the necessary compensatory movements (Romer, 1956; Baird, 1970; Walker, 1972). In this context the importance of Walker's work on *Sphenosuchus* is that he was able to demonstrate the presence of a foramen pseudorotundum in an upper Triassic pseudosuchian.

Another feature which distinguishes lizards from archosaurs is the extent of the contribution of the parasphenoid/basisphenoid to the sidewall of the braincase. In *Milleretta* the parasphenoid plate is flat, in *Youngina* the lateral edges are slightly upturned. In *Prolacerta* this upturning is pronounced, with a lateral ridge of parasphenoid contacting the proötic, while in *Proterosuchus* contact between parasphenoid and proötic is complete. An extension of this condition can be seen in for example *Stagonolepis* (Walker, 1961) and *Euparkeria* (Cruickshank, 1970). By contrast it appears that in lizards the basisphenoid remains essentially a flooring plate giving no significant contribution to the sidewall of the braincase, which is formed entirely of proötic and opisthotic—this is true of *Varanus* (Bahl, 1937 and personal observation) and *Ctenosaurus* (an Iguanid, Oelrich, 1956). A crista lateroventralis in some lizards gives an impression of lateral depth of basisphenoid, but this is simply a downwardly projecting ridge (Säve Säderbergh, 1947, Figure 9A). The question of changes in the ventral extent of the opisthotic becomes difficult due to fusion of that bone with exoccipital; hence para/basisphenoid morphology is possibly the best indicator of reptilian relationships in the lower Triassic particularly.

The order Thecodontia is considered basal to all later archosaurian radiation. A spate of recent work on the classification of these animals is brought together by Romer (1972c). In Romer's tentative classification we have a suborder Proterosuchia containing four families. Now it is striking that in the Proterosuchidae the archosaurian antorbital fenestra is rather poorly defined (having formed in a thin-boned minimum stress area) and does not yet show the strengthened outlines of more advanced forms. In the light of the above it seems reasonable to assume that the earliest thecodonts lacked the antorbital fenestra and possibly to include a fifth family, the Prolacertidae.

To do this purely on the basis of dermal bones might never prove entirely convincing, but reinforced by what is now known about braincases such an arrangement could make sense. The braincase is well known in *Prolacerta* and *Proterosuchus,* it is reasonably well figured and described in ventral view for *Chanaresuchus* (Romer, 1971) which seems reasonably primitive (further description of this braincase is necessary). Virtually nothing is known of the braincase in Erythrosuchids and Prestosuchids, with genera like *Mandasuchus* being little more than words on paper. The braincase of phytosaurs (Camp, 1930) and aetosaurs (Walker, 1961) is well known; these are fairly advanced in several respects, notably in the presence of a laterosphenoid.

Of Romer's Pseudosuchia the braincase of *Euparkeria* (Cruickshank, 1970) is fairly well known, and considerably more primitive than that of Phytosaurs and Aetosaurs though somewhat advanced over that of the Proterosuchids. Of the Ornithosuchidae the braincase is very inadequately known, though the close proximity of the basal articulations of the pterygoids in *Gracilisuchus* (Romer, 1972a) and *Ornithosuchus* (Walker, 1964) suggest similar specialisations which might be reflected in several other aspects of braincase morphology.

Among Romer's miscellaneous Pseudosuchia is *Lewisuchus*. Romer's (1972b) figure and description of

the braincase of this animal seem open to a different interpretation: the possibility exists that there is no laterosphenoid, that the notch for V in the proötic has closed and that Romer's V should be VII.

As far as other later groups of archosaurs are concerned there is a certain amount of information on the braincase in the Crocodilia (fossil and recent) and birds (Walker, 1972), but one wonders whether discussion of this material, *in vacuo* as it were, need be taken too seriously. Little is known about dinosaur origins or of the braincase in the different lines. There is enough to suggest that the Prosauropod braincase was exceedingly primitive (Figure 29A and B), so much so that it is probably derivable only from the Proterosuchian level. The same may be true of theropods based on what little information there is on the braincase in the upper Cretaceous *Dromaeosaurus* (Figure 29C). It seems reasonable to suggest from this that the Saurischia are derivable only from the Proterosuchia. A little more work on existing material will establish this point.

Nothing can be said at this stage about the Ornithischia, though here again good material exists and awaits only description.

The foregoing is a tentative outline of the importance of archosaur braincases in phylogeny and is offered here in the hope of stimulating further work of this nature. These are deep structures well obscured by other bones, but they can be removed successfully and the suggestion is made that where possible braincases be illustrated in lateral, ventral, occipital and saggital and frontal views.

NOTE: I have recently had the opportunity to examine a good braincase of *Euparkeria*. The similarity between the proötics and the foramen for VI in anterior view between *Proterosuchus* and *Euparkeria* is clear from Figure 26 and Figure 37.

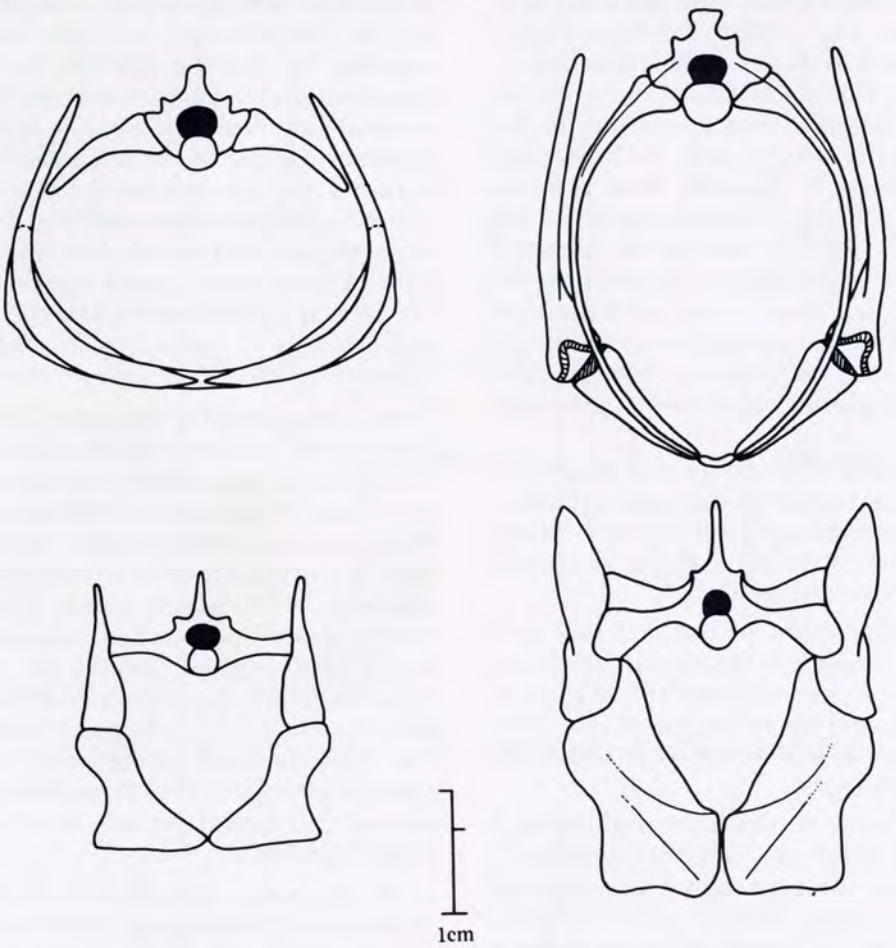


Figure 31 depicts the girdles of *Youngina* (left) and *Prolacerta* (right); all but the pectoral girdle of *Prolacerta* in anterior view, the latter as seen from behind. This gives a clear impression of dorsoventral flattening in *Youngina* and lateral flattening in *Prolacerta*. In order to see how body shape relates to way of life the fossil forms are compared in Table I (page 98) with a selected number of extant forms; when girdle measurements are converted to ratios the animals form an interesting series. This lends itself to misinterpretation as the broad pectoral girdle of crocodiles and *Youngina* is associated with vertical carriage of the humerus and probably does not as such relate to aquatic habits. Bakker's (pers. comm.) thoughts on this aspect are far advanced so it will not be pursued here. Likewise it is misleading to compare the agile *Prolacerta* and slow moving chamaeleon too closely, though the more closely spaced glenoids clearly afford climbers better balance.

SUMMARY

1. The osteology of *Youngina capensis* is described in detail. There is every indication that this was a terrestrial animal. *Youngopsis* and *Youngoides* are relegated to junior synonyms. No tidy phylogenetic associations are proposed either backwards or forwards in time; there are objections to close association with *Prolacerta*, squamates and archosaurs.
2. The complete osteology of *Prolacerta* is described. A description of the braincase of *Proterosuchus* is included for comparison. It is shown that *Prolacerta* was a swift bipedal animal morphologically very close to the proterosuchian thecodonts, which was probably on a direct line to *Macrocnemus* at least among the lizard-like forms of the European middle Triassic. *Pricea* is relegated to a synonym of *Prolacerta*.
3. Discussion of sauropsid braincases suggest fundamental differences exist between those of lizards and thecodonts—a situation which helps to dispel the concept of *Prolacerta* as an ancestral squamate.

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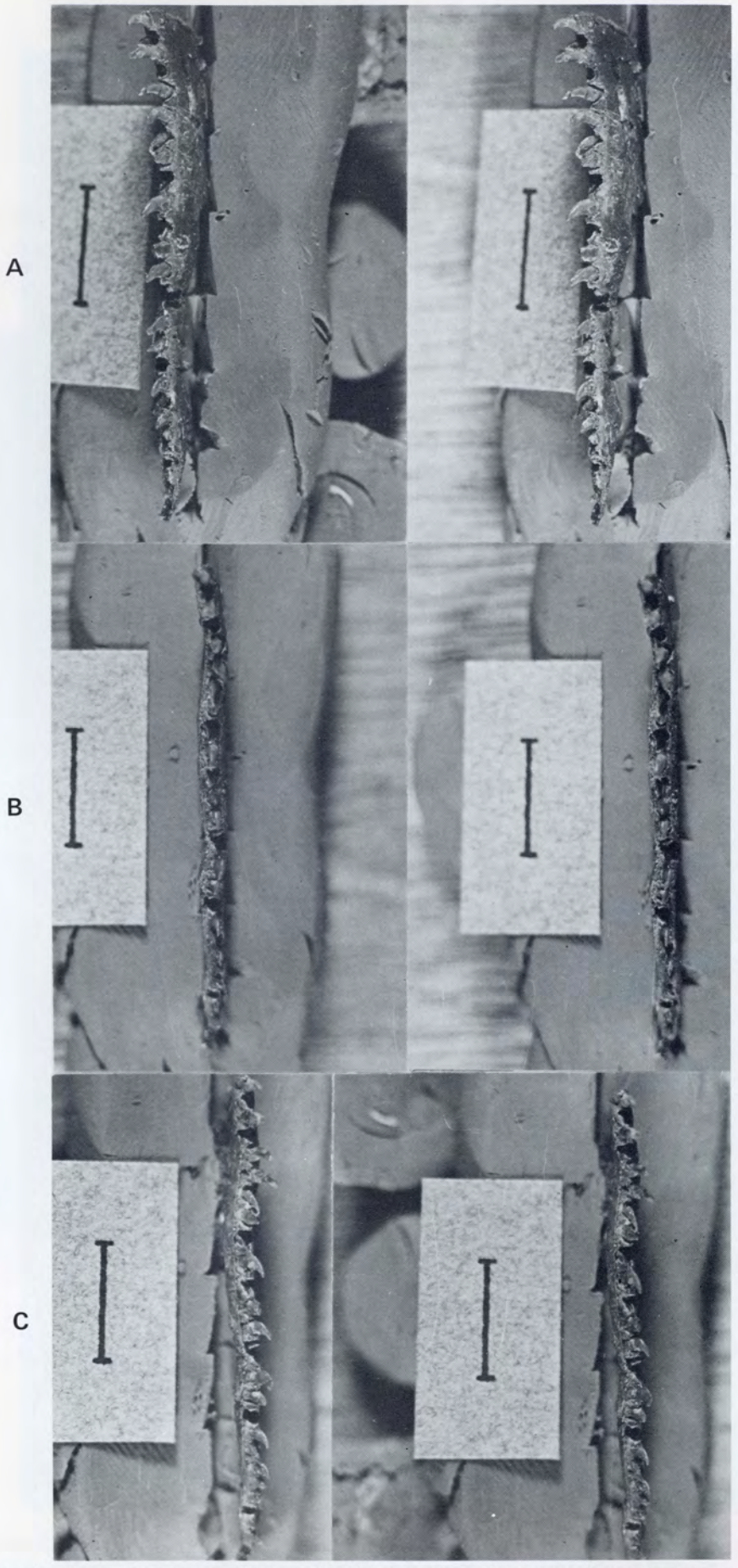


Figure 32. Stereo-photographs of left maxilla of *Prolacerta broomi* B.P.I. 2675. A, Labial oblique; B, Straight occlusal; C, Lingual oblique. Scale is 1 cm long.

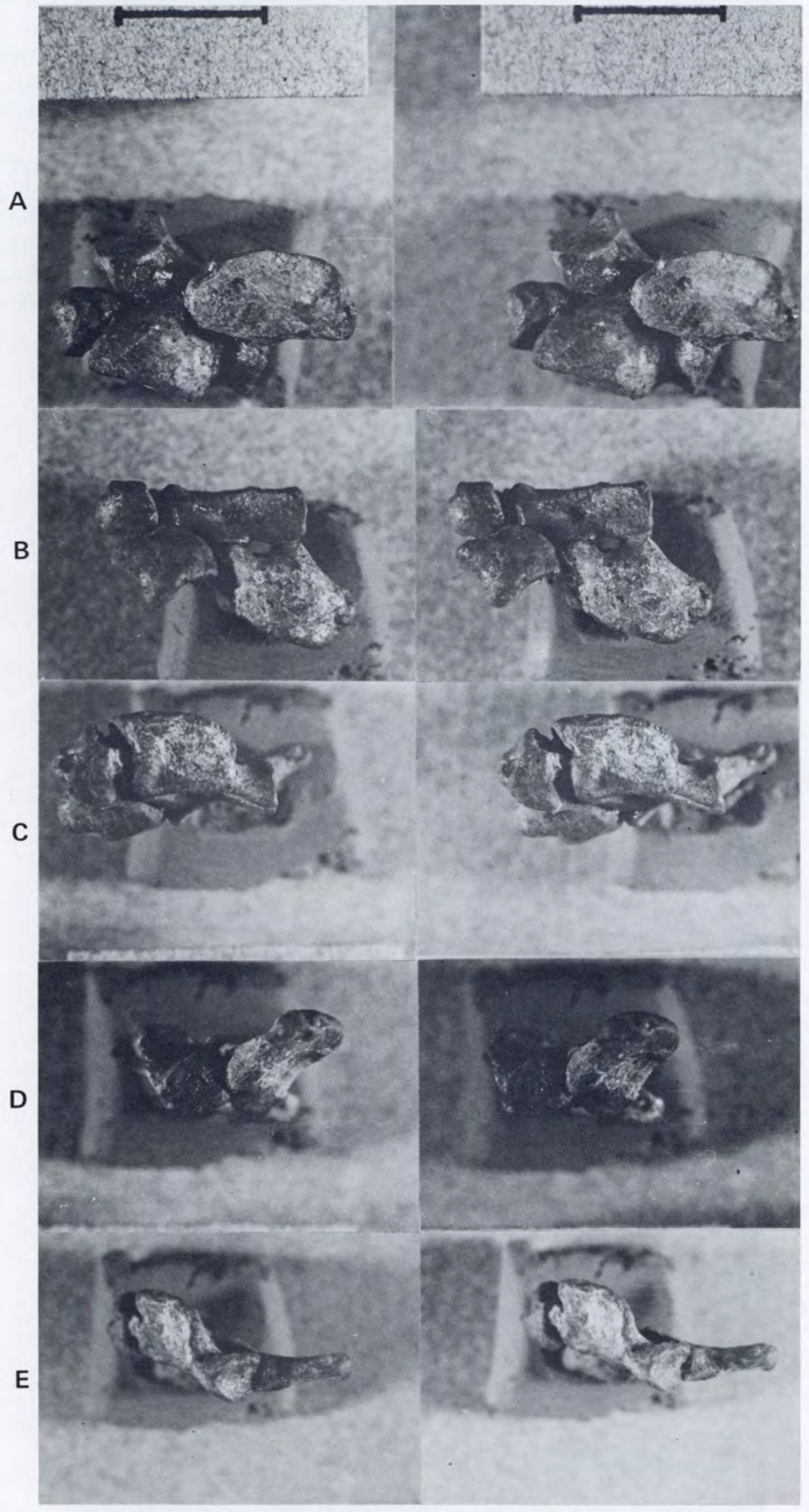


Figure 33. Stereo-photographs of ankle of *Prolacerta broomi* B.P.I. 2675. A, Ventral; B, Dorsal; C, Normal to tibial facet; D, Normal to fibial facet on astragulus; E, Both facets oblique. Scale is 1 cm long.

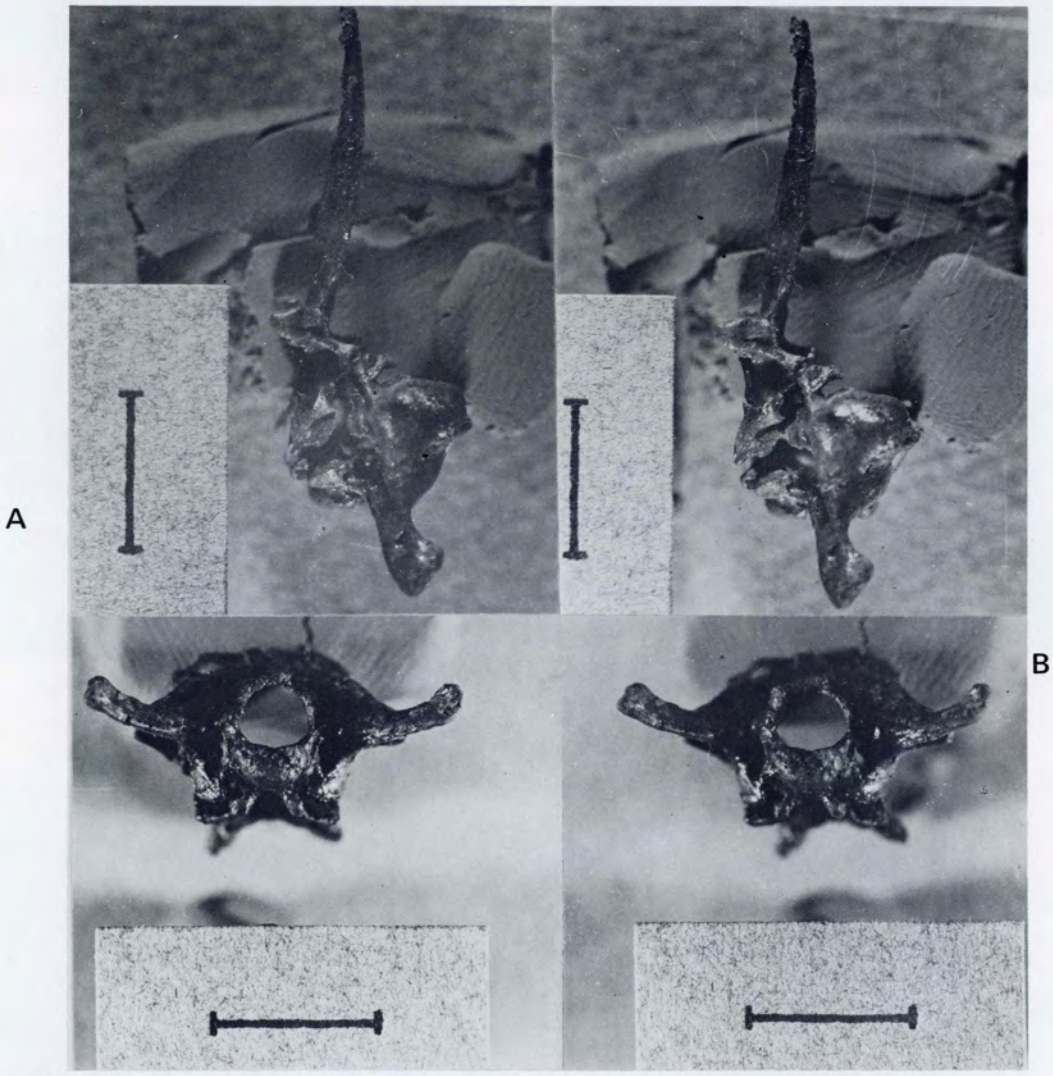


Figure 34. Stereo-photographs of braincase of *Prolacerta broomi* B.P.I. 2675. A, Left lateral view; B, Posterior view. Scale is 1 cm long.

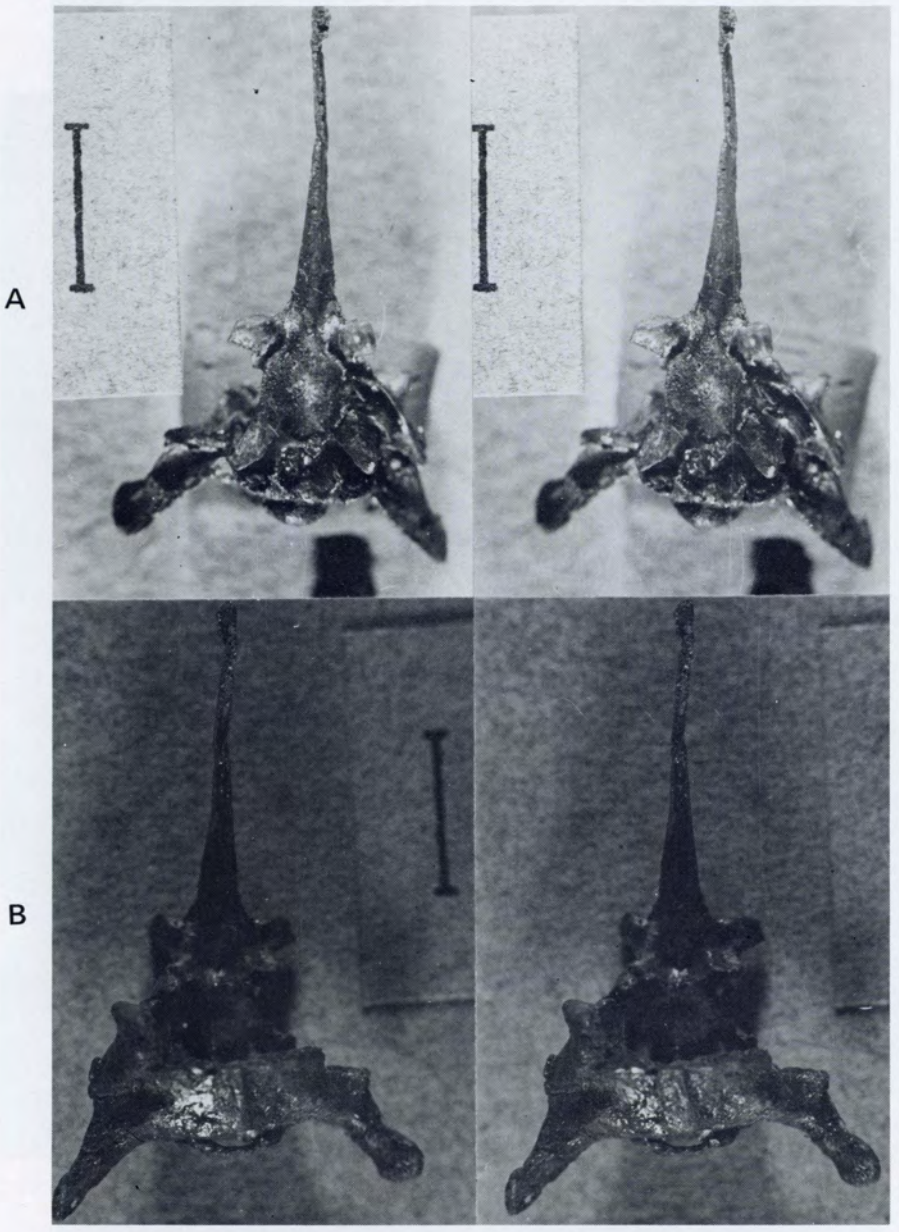


Figure 35. Stereo-photographs of braincase of *Prolacerta broomi* B.P.I. 2675. A, Ventral view; B, Dorsal view. Scale is 1 cm long.

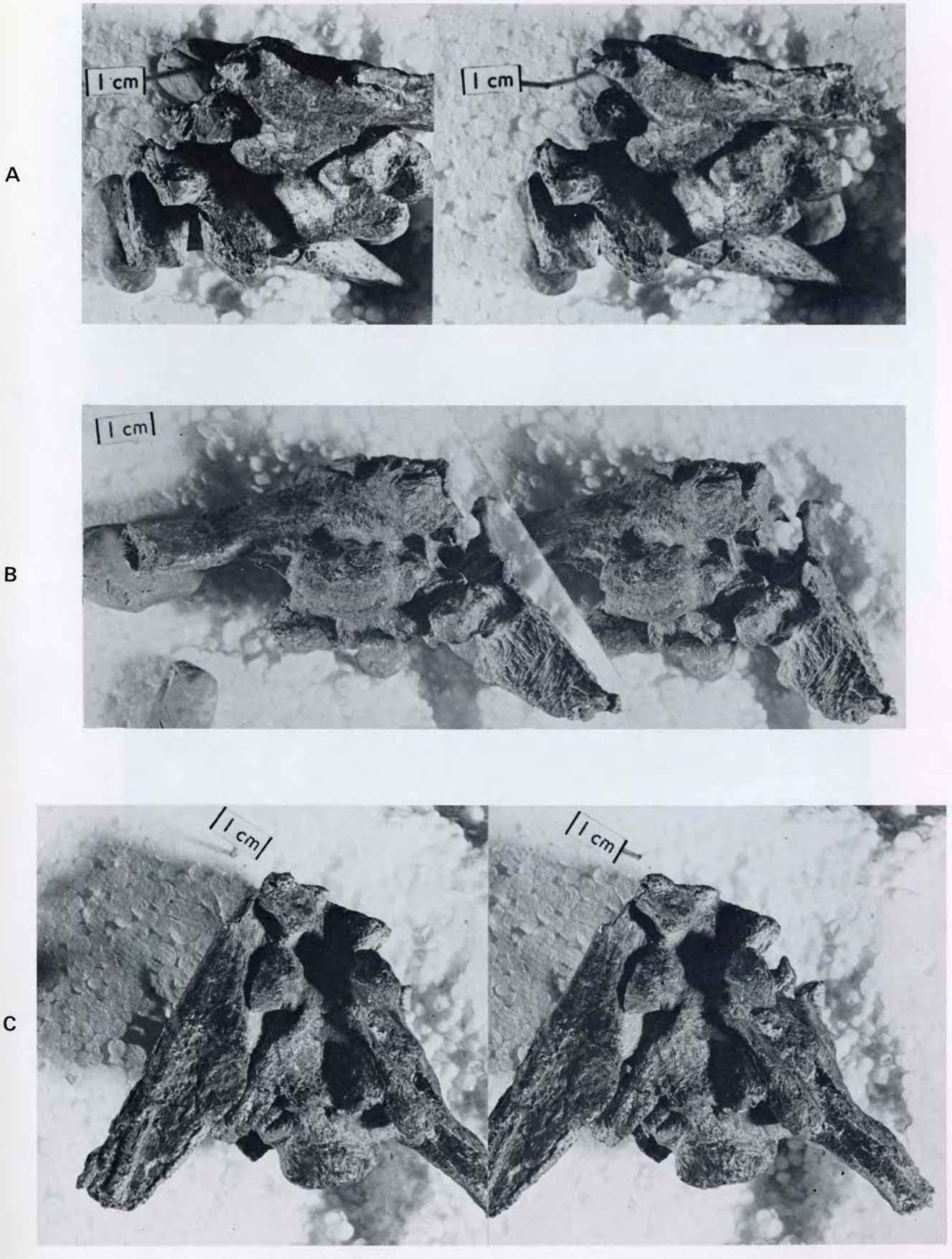


Figure 36. Stereo photographs of braincase of *Proterosuchus fergusi* B.P.I. 3993. A, Left lateral; B, Posterior; C, Ventral. Scale is 1 cm long.

A



B

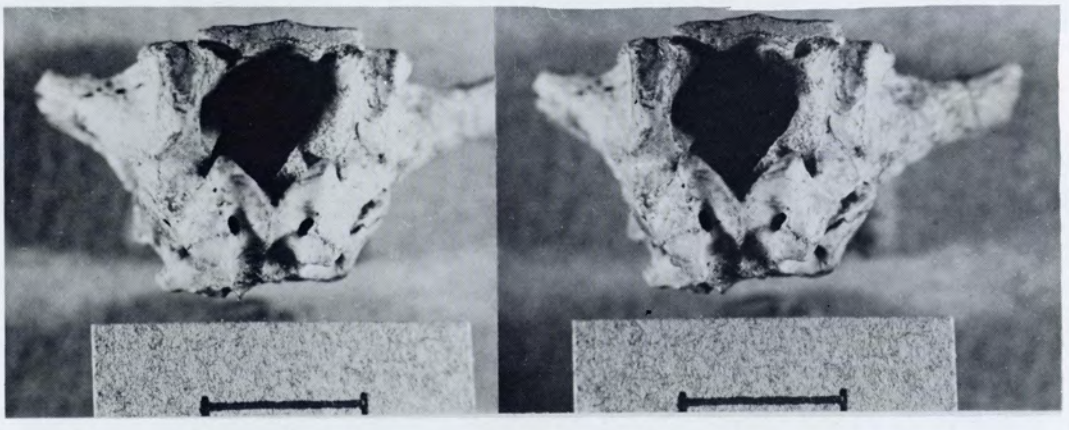


Figure 37. Stereo-photographs of: A, Braincase of *Proterosuchus fergusi* B.P.I. 3993, anterior view; B, Braincase of *Euparkeria capensis* S.A.M. 7696, anterior view. Scale is 1 cm long.

ABBREVIATIONS

A. —angular
al.pr.bsp. —alar process of basisphenoid
al.pr.pro. —alar process of proötic
ART. —articular
BO. —basioccipital
BSP. —basisphenoid
bpt.pr. —basipterygoid process
b.t. —basal tubera
cpr. —crista proötica
ds. —dorsum sella
EO. —exoccipital
EPT. —epipterygoid
F. —frontal
f.o. —foramen ovale
f.m. —foramen magnum
J. —jugal
j.f. —jugular foramen
L. —lacrimal
MX. —maxilla
N. —nasal
OP. —opisthotic
P. —parietal
PAL. —palatine
PMX. —premaxilla
PO. —postorbital
POF. —postfrontal
PP. —postparietal
PRF. —prefrontal
PRO. —proötic
PR.ART. —prearticular
PSP. —parasphenoid
PTDG. —pterygoid
P. —parietal facet
p.a. —pila antotica
par.proc. —paroccipital process
p.pr.pro. —posterior process of proötic
Q. —quadrate
QJ. —quadratojugal
q.ra.pt. —quadrate ramus of pterygoid
ro.psp. —parasphenoid rostrum
S. —stapes
SA —surangular
SO. —supraoccipital
SPL —splenial
SQ. —squamosal
ST. —supratemporal
T. —tabular
V. —vomer
v.c. —vidian canal

Palaeont. afr., **18**, 133—135 (1975)

THE AFFINITIES OF *PROTEROCHAMPSA BARRIONEUVOI* REIG

by

A. R. I. Cruickshank

ABSTRACT

Proterochampsa barrioneuvoi Reig is re-examined and is confirmed as a proterosuchian thecodont. None of the features previously thought to ally it to the Crocodilia are solely characteristic of that group. On the other hand it is not a phytosaur nor phytosaur ancestor, only showing one real trend towards these animals in the rearward migration of the internal and external nares. *Proterochampsa* and its relatives *Chanaresuchus*, *Gualosuchus* and *Cerritosaurus* are too late in time to be phytosaur ancestors. They are grouped together in the Proterochampsidae, a family within the Proterosuchia.

INTRODUCTION

Recently while visiting the Museum of Comparative Zoology in Harvard I had the opportunity to examine skull material ascribed to this taxon and which had been dealt with in some detail by Sill (1967). In addition there were available casts of the type and one other skull (Reig, 1959). In view of the comments made by Walker (1968) and Romer (1972) concerning the affinities of this species it seemed advisable to re-examine it and the observations made form the body of the following notes, which have been made possible largely as a result of my recent work on the Proterosuchia.

MATERIAL

MCZ 3323; Cast of the type PVC 2063 (Instituto Lillo, Tucuman) (Figured Reig, 1959, Figures 1 and 2).

MCZ 3408; a well preserved but crushed skull with few of the sutures clearly seen. Associated with this skull are a series of cervical and anterior dorsal vertebrae and ribs. (Figured Sill, 1967, Figures 1, 2, 3, 4b, 5 (in part), 6b, 7b, 8a and 9b; plates I—V, VIII and IX.)

MCZ 3409; cast of skull MACN 18165. (Museo Argentino de Ciencas Naturales.) The original lacks the greater part of the left maxilla, all the bones of the left side behind the antorbital fenestra, the entire occiput, the braincase and parts of the right squamosal and quadratojugal. It is dorso-ventrally crushed. (Figured Sill, 1967, plates VI and VII.)

Of the three, the type is apparently the best preserved but is damaged in the snout region so that the external nares were reconstructed as being lateral and terminal by Reig in contradiction to the real state of affairs where they are dorsally situated against the midline of the skull, a situation which was ascertained only after more material was found subsequent to Reig's description.

All the specimens came from the Ischigualasto Formation. Romer and Jensen (1966, p. 16) are in doubt as to whether it is Ladinian or Carnian but feel that it ". . . is essentially Middle Triassic". On the other hand others (summarised in Anderson and Anderson, 1970) place the age of these beds as high as the Norian. The weight of evidence would seem to prefer an Upper Triassic age, though not as late as the Norian.

THE AFFINITIES OF PROTEROCHAMPSA

Reig in his original description stressed the crocodilian affinities of *Proterochampsa* and his view was followed by Sill who believed that it should be included formally in the Crocodilia as representative of the family Proterochampsidae of the new suborder Archaeosuchia. Included in this new suborder was a second family, the Notochampsidae comprising *Notochampsa* and *Erythrochampsa* (Reig, 1959; Sill, 1967).

Walker (1968) took strong exception to this classification and raised fourteen points (op. cit., pp. 6—11) to deny its crocodilian affinities and concluded (p.11) that "there seems ample evidence then for regarding *Proterochampsa* as a very primitive phytosaur and not a crocodile".

Romer (1972, p. 5) concludes his discussion on the family Proterochampsidae (in which he places the additional genera *Chanaresuchus, Gualosuchus* and *Cerritosaurus*) with the statement that "the proterochampsids are long-snouted amphibious forms which have advanced little beyond the proterosuchian grade of organisation and may well be placed in the Proterosuchia".

It is quite clear therefore that there are three views on the matter. Is *Proterochampsa* a crocodile, a phytosaur or a proterosuchian?

Crocodilian features of Proterochampsa (Sill, 1967)

1. Flat broad skull with long snout.

2. Highly sculptured surface to bones of skull.
3. Large dorsally placed orbits.
4. Small supra-temporal fenestrae.
5. External nares near midline of snout.
6. Similarities to crocodilian conditions in the otic notch and external auditory meatus.

There are in addition other features of doubtful validity but quoted by Sill as being diagnostic of the Crocodilia, e.g. the relationship of the exoccipital to supraoccipital.

Considering the points listed above, the flattening of the skull is a result of dorso-ventral crushing as much as a natural shape. This feature also exaggerates the orientation of the orbits. The sculptured surface of the skull is paralleled in the undoubted proterosuchians *Chanaresuchus* and *Gualosuchus* and is therefore not exclusive to the Crocodilia. Likewise the position of the nares — both internal and external — are similar in all three genera, as are the small supra-temporal fenestrae. These latter are also much the same as in *Proterosuchus*.

However, the point which was emphasised by Sill was the presumed similarity of the crocodilian external ear region to that of *Proterochampsa*. It is now believed that incorrect information on this region in the Proterosuchia led Sill to misinterpret these structures in *Proterochampsa*.

In MCZ 3408 considerable dorso-ventral crushing has occurred so that the exoccipitals (with the opisthotics attached) have been moved laterally and have thus allowed the basisphenoid to ride up against the interior of the braincase. As a result of this, the two prominent openings ". . . assumed to be the carotid foramina" (Sill, op. cit., p. 423) have been misidentified. They are in fact the ventral portions of the large vagus foramina. The two "flange-like processes" are the basal tubera (somewhat weathered) and the median cleft between them runs antero-dorsally into an area of crushed bone and is clearly part of the median backwardly facing excavation similar to that seen on the basisphenoid of *Proterosuchus* and figured as such by Reig (1959, p. 262, Figure 2). It has nothing to do with the eustachian system.

The groove that Sill figures (op. cit., Figure 5) purporting to be the homologue of the crocodilian external auditory meatus is in fact the stapedial groove running on the anterior face of the paroccipital process of the opisthotic and exactly similar to that in *Proterosuchus*. From what can be seen of the rest of the braincase in MCZ 3408 it is clear, moreover, that it is essentially the same as in *Proterosuchus* (Cruickshank, 1972). The inward slope of the head of the quadrates has been exaggerated by the dorso-ventral crushing and their relationship to the palatal bones is strictly as in *Proterosuchus*. In addition, there seems no evidence for the quadrate head being in primary contact with the prootic as might be expected in a crocodile (Walker, 1972). The reconstruction of the occiput figured by Sill (op. cit., Figure 3) does not seem to have taken into account this very obvious dorso-ventral crushing and thus the quadrates have been splayed too far laterally in his figure; so much so that the lower jaw, if in natural articulation with the quadrates, would be far removed from the steadying influence of the pterygoid flanges. This is borne out by a close examination of specimen MCZ 3408 itself. For greater realism, the quadrate should therefore be orientated more vertically, which would deepen the line of the skull posteriorly in lateral view, narrow it slightly in dorsal view and bring the lower jaw nearer the pterygoid flange, and in all make it less superfically crocodile-like. There is present a small triangular interparietal and it would also seem that the parietals at least are not fused on their midline for their entire length. *Proterochampsa* has no post-temporal fenestrae, another character in common with *Proterosuchus*. Therefore it would seem that there are no real grounds for allying this form with the Crocodilia as Walker has already pointed out.

Phytosaurian features of Proterochampsa

Walker (1968) enumerated fourteen points in his claim for phytosaurian affinities of *Proterochampsa*. It is not necessary to repeat them here except to comment on his conclusions and to note that, with the exception of the relationship of the internal nares, the majority of them are primitive for the Phytosauria or are similar to the conditions seen in the Proterosuchia.

The most important of Walker's points (No. X) is that dealing with the position of the internal nares, which in *Proterochampsa* agree proportionately more with the Phytosauria than with the Crocodilia. However, Romer (1971) described subsequently to Sill's paper two genera of closely related proterosuchian thecodonts (*Chanaresuchus* and *Gualosuchus*) with, in the former, a palate closely comparable to *Proterochampsa* and additionally a braincase and ankle of the proterosuchian pattern, showing that the palatal characters of *Proterochampsa* cannot be taken to indicate relationships higher than the Proterosuchia. The ratio of posterior margin of the "primitive" internal nares to a line joining the posterior ends of maxillae/length of maxillae in the midline is in *Chanaresuchus* 15,5%, a slightly lower value than in *Proterochampsa* (Walker, 1968).

Proterosuchian features of Proterochampsa

Proterochampsa has many features characteristic of primitive thecodonts which were recognised by both Walker and Sill. It is in fact these characters which are the more important in assessing the affinities of *Proterochampsa*.

The palate, apart from the backwardly placed internal nares, is basically primitive and very similar to that of *Proterosuchus*. There are teeth on the pterygoids and the basal articulation seems to have been free. Associated with this feature is an almost

certain lack of an ossified laterosphenoid element. Although the rearward movement of the internal nares is cited by Walker as being the most important feature of this genus linking it to the phytosaurs, they are hardly a significant distance farther back than in *Chanaresuchus* (see above) which is clearly a proterosuchian. The outline of the lower temporal opening is very much more like that of *Chanaresuchus* and *Gualosuchus* than is indicated in Sill's figures, having among other characters a small postero-ventral extension as in the two aforementioned genera. The position of the external nares is almost identical in all three of these and the occiput of *Proterochampsa* has no post-temporal fenestra, in common with most other Proterosuchia.

CONCLUSIONS

It must therefore be clear that, as Romer pointed out, and after a re-examination of skull material, *Proterochampsa* has strong affinities with the Proterosuchia in general and *Chanaresuchus* and *Gualosuchus* in particular. All three, plus *Cerritosaurus*, can conveniently be placed together in the same family (the Proterochampsidae) within the Proterosuchia. They probably represent a lineage of primitive thecodonts, evolving in parallel with the phytosaurs, but they themselves, particularly *Proterochampsa*, because of the time relationships involved, are too late to be phytosaur ancestors, and were probably the last representatives of the Proterosuchia. This family shows advances over the earlier proterosuchians in the rearward migration of both the external and internal nares, the tendency to acquire ornamentation on the skull roof, the loss of post-frontals and the development of a fenestra in the lower jaw.

ACKNOWLEDGEMENTS

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Palaeont. afr., **18**, 137—142 (1975)

THE SKELETON OF THE TRIASSIC ANOMODONT *KANNEMEYERIA WILSONI* BROOM

by

A. R. I. Cruickshank

ABSTRACT

The general structure of the post-cranial skeleton of many Triassic anomodonts is now well known, but in Africa that of the stratigraphically important Lower Triassic (? Scythian) genus *Kannemeyeria* is known only from dissociated elements. A brief description is given for the first time of an almost complete skeleton ascribed to this genus. The environment of deposition is described briefly. The locality of the type species of the genus is also noted.

INTRODUCTION

In December 1934 Mr. R. McEwan the (then) owner of the farm Ravenskloof, Tarkastad District (Long. 31° 50′, Lat. 26° 20′), situated 24 km (15 miles) north-east of Tarkastad, brought into the East London Museum some bone fragments he found 100 m (300 yards) north-east of the old homestead. The farm Ravenskloof is composed of portions of the farms Van Wyk's Kraal, Hartebeeste Fontein and Honde Nek where they meet. The name Ravenskloof does not appear on the 1 : 250 000 Topocadastral series of the Republic of South Africa.

The Curator of the museum, Miss (now Dr.) M. Courtenay-Latimer, mounted an expedition in January of the following year which recovered most of the specimen as it now exists, and a further trip was made in 1936 to try to recover the missing portions (Table 1) (Broom, 1937; Courtenay-Latimer, 1948).

The purpose of this short paper is to place on record the salient features of this specimen in recognition of the extremely careful way that it was excavated. It is unfortunate that with the passage of the years other as complete specimens of Triassic anomodonts have been described, which has robbed this individual of the impact it might have had on their study.

I am grateful to Dr. Courtenay-Latimer for allowing me access to her personal and correspondence files covering this period, from which the following extracts are taken.

The locality is described as follows:
"Sandstones, mudstones and shales were the prevailing rocks; the banks of the intermediate sandstone could be seen thickening and thinning out within varying distances . . . the site was found to be . . . at the top of an erosion ravine and immediately below a horizontal outcrop of sandstone" (letter M. C-L to National Monuments Commission dated 12th November, 1941).

The skeleton was excavated from four levels and some additional remains were recovered from the surface.

On the surface lay (i) portion of a femur, (ii) portion of a tibia, (iii) 6 vertebrae, (iv) portion of left shoulder girdle, (v) 4 ribs.

Under this was Layer A. "Fine red gravel shale, 9″ thick" from which was recovered (i) lower jaw, (ii) right hand ramus of lower jaw (two feet away), (iii) humerus, (iv) portion of radius, (v) ulna, (vi) collar bone [*sic*], (vii) three vertebrae. Layer B was a "coarse compact red shale 15″ thick" and held (i) eighteen ribs (numbered 1—18), (ii) sixteen vertebrae (numbered 19—34) with twelve of them (21—32) in a natural articulation, (iii) complete shoulder girdle, (iv) humerus. Layer C, a solid red shale, was 12″ thick. It yielded (i) the ?RH pelvis, (ii) the ?RH shoulder girdle, (iii) five ribs, (iv) radius, (v) ulna, (vi) tibia, (vii) fibula, (viii) clavicle. The final productive layer, D, comprised a loose coarse red shale and was 12″ thick. It yielded (i) the skull, partly embedded in the underlying gray shale, (ii) one quadrate, (iii) sternum, (iv) the ?LH pelvis, (v) two feet, (vi) the other quadrate (M. C-L Field notes January, 1935).

The subsequent expedition in 1936 recovered, by sieving, isolated fragments of bone from the spoil heap and most of the missing femur.

Miss Courtenay-Latimer communicated news of her find to Dr. Robert Broom at the Transvaal Museum, having started to make a mounted reconstruction of the skeleton following Pearson's (1924b) reconstruction of the dissociated material in the British Museum and with the aid of her father.

Broom replied on the 26th July, 1935 (TM 33/33) "Your beast is grand. You have I think, the leg bones wrongly arranged, and also the pelvis. Your supposed tibia is clearly the ulna."

There follows a suggestion that he should be sent one each of all the limb-bones, which would be marked as to place and orientation on a diagram.

"All this would cost you nothing as the specimens can come O.H.M.S. and be returned similarly and it ought not to take more than a couple of weeks."

Nonetheless, the overall impression gained from the skeleton as reconstructed is of an animal which had suddenly come to a halt after running headlong, and as will be discussed below, several errors in identification of the bones have resulted in only a generally accurate reconstruction of the skeleton.

The taxonomy of the genus *Kannemeyeria* has been discussed recently (Cruickshank, 1970, 1972) and it was concluded that the genus contains only four species, viz. the large commonly found South African species *K. simocephalus* (Weit.), the equally large but rarer form *K. wilsoni* Broom (the subject of this description), *K. argentinensis* Bonaparte, a small form from S. America, otherwise similar to *K. simocephalus,* and *K. latirostris* Crozier, a medium-sized species which may be based on a juvenile specimen and which may warrant a new taxonomic placing. All are known from the Lower Trias (Scythian, (Anderson and Anderson, 1970)) except *K. latirostris* which is from the Zambian Middle Triassic (? Anisian) N'tawere Formation. *K. simocephalus* is also known from an Anisian (?) horizon in the East African Manda Formation (see Cruickshank, 1965, 1970, 1972 for details) and from S.W.A. (Keyser, 1973), in the Omingonde Formation which is very close to the *Cynognathus* zone in age.

It is possible that the relatively minor differences between *K. simocephalus* and *K. wilsoni* could be ascribed to sexual dimorphism, but the evidence is inconclusive at present and the two species are here recognised as separate (Cruickshank, 1970, 1972).

The importance of *Kannemeyeria* in South Africa is that it is of very common occurrence in the Upper Beaufort and in many ways a better zone fossil than *Cynognathus*, at the time of writing, being present on eighteen of the 33 *Cynognathus* zone localities recorded by Kitching (1972) whereas *Cynognathus* is known from only seventeen. Until recently the locality of the holotype of *K. simocephalus* was not even vaguely known (Cruickshank, 1970), but it seems to be from the fram Dwaarsvley (Alt. Q. 1—11) in the Aliwal North District (letter from R. L. Dorrington, Elandshoek, Aliwal North dated 24th October, 1970 refers. See also Cruickshank (1970, Table 1)). The information in the catalogue of the Natural History Museum, Vienna reads:

Type *Dicynodon simocephalus* Weit. 1888.

Museum No. 8178. Acquisition 1886 xv. 4.

Altersstufe — Karroo

Fundort — Südafrika

Coll — Adler. (the then German Consul in Port Elizabeth. [Ed.])

Dorrington (litt. cit.) says "He (Alfred Brown) strongly maintained . . . that the blocks of stone containing the fossil (were) to be shipped to British Museum but . . . ended up in Vienna and that (he) was always annoyed that he never received money or recognition for his efforts." At this distance in time the truth may never be discovered, and this is probably the best approximation likely as to the original site of this specimen.

MATERIAL

It was very difficult to examine this specimen properly as it was mounted in a close fitting glass case with the vertebrae strung on an iron rod and the limbs and skull supported by an iron pipe-and-strip framework. However, by kind permission of Dr. Courtenay-Latimer I was able to dismount some of the bones.

The majority of the photographs taken for record purposes were made using a "Polaroid" Model 180 camera with type 107 black and white film rated at 3 000 ASA and with a flash gun. A "Stereo-tach" stereo attachment proved invaluable and was used wherever possible. Colour and black and white photographs were taken with a conventional 35 mm camera as a backup service. The Polaroid films were frequently overdrawn with details taken from the specimen at hand.

This specimen is numbered E.L.M. 1.

DESCRIPTION

Skull

Further detailed description of the skull of *Kannemeyeria* is unnecessary since several adequate accounts have already been given in the past (Pearson, 1924a; Camp, 1956; Bonaparte, 1966; Cruickshank, 1965, 1970). Let it suffice to say that the skull of *K. wilsoni* differs from that of *K. simocephalus* only in the flatter snout region which is also less ridged and in the maxillary flanges which are smaller. These differences may be due to sexual dimorphism (Cruickshank, 1970, p. 50).

This skull was found in 53 pieces and the tusks are reconstructed in wood. Although their tips point downwards on leaving the maxilla, the roots run in line with the jugal arches (Cruickshank, 1970, p. 50).

The palate is not visible as the skull is mounted, and no description can therefore be given of it.

The lower jaw is typical of the anomodont's except that the tip appears to be horizontal rather than turned up as is the more usual case (Cruickshank, 1970).

Axial skeleton

As the vertebrae are rigidly mounted, it was not possible to examine each one individually, and the numbers recorded by Courtenay-Latimer at the time of collection could not be seen. Therefore, the sequence of articulated vertebrae she excavated from "Layer B" could not be identified.

The axial skeleton as preserved comprises forty-six vertebrae. It is difficult to distinguish between those that are cervical and thoracicolumbar, but it seems clear that there are at least 15 caudals present.

Nine of the remainder have been restored to a greater or lesser extent. The atlas/axis has not been completely prepared, but seems little different from those already described.

If there were six sacral vertebrae (Cruickshank, 1967, p. 194), then the presacral count amounts to 25. Therefore this specimen seems to possess an almost complete vertebral column, a fact almost unique among the recorded Triassic anomodonts. Likewise, the skeletal proportions of the specimen can be regarded as being realistic, if not exactly correct.

There was nothing to indicate that these vertebrae would differ from those described by Pearson (1924b).

Ribs

Twenty-four ribs are mounted on the skeleton, all on the left-hand side. It would appear likely that no cervical ribs are preserved (but see below) and no record was found of the remaining three ribs not incorporated into the mounted skeleton.

There are a number of errors of positioning of the ribs, viz. those that are mounted ahead of the scapula being in fact posterior thoracic or lumbar ribs, having the small triangular single head as described for *Tetragonias* (Cruickshank, 1967, Figure 7). Six ribs with swollen ends, and thus likely to be originally in contact with the sternum and hence anterior thoracic ribs, have been mounted in the mid-region of the rib cage. Several ribs from the right-hand side were included in this sequence on the left.

In more detail, it would appear that the first rib as mounted is the only one which might be a cervical, as it seems to have the remnant of a divided head, but in all probability it is a posterior lumbar rib as are numbers two to four. Numbers five to ten inclusive are from the thoracic-lumbar region anterior to the foregoing. Number eleven is a true first thoracic rib as it has both the divided head and a swollen end for contact with the sternum (Cruickshank, 1967). Rib number twelve as mounted is probably an anterior thoracic rib, as are ribs numbers thirteen and fourteen. Rib number fifteen is in all probability the matching first thoracic for number eleven, but its identity is in doubt because of damage to the head region. Rib number sixteen is clearly an anterior thoracic and the remaining smaller ribs are clearly from the posterior thorax-lumbar region.

In summary there is little in the rib-cage of this species to indicate any special adaptations or to distinguish it in detail from *Tetragonias*. The reconstruction should show therefore that the rib-cage was deep anteriorly becoming gradually shallower towards the pelvis (e.g. Cox, 1965, p. 478, Figure 11).

Pectoral girdle

Both pectoral girdles are more or less completely preserved and in addition there was the remnant of a sternum. It is regrettable that nothing resembling an interclavicle was recovered from the excavation (Cruickshank, 1967, p. 208). Bonaparte (1966) illustrates one from *K. argentinensis*.

The left scapula has a broken acromion process, but the right is complete in this respect.

The prespinous fossae are much smaller than in the scapula figured by Pearson (1924b), but nonetheless are still relatively much bigger than in *Tetragonias* (Cruickshank, 1967, Figure 8). In this respect the scapula is much more advanced than those normally associated with the Triassic anomodonts. The scapulae are tall narrow bones in the typically anomodont pattern. The glenoid is large and faces almost entirely backwards with only a small proportion of the articulating surface facing outwards. The articulating surfaces are equally divided between the scapula and the coracoid. It is therefore likely that the elbow was drawn into the side of the animal and that protraction was limited during each stride. The humerus must have been held horizontally, because the lower lip to the glenoid, formed by the coracoid, would have prevented much adduction. Also, the remains of the substantial sternum seem to indicate large ventral pectoral muscles and hence a clumsy posture and slow gait.

The coracoid and precoracoid are subequal and the precoracoid seems to be excluded from the glenoid. The coracoid foramen is entirely on the precoracoid, equally spaced from the posterior and dorsal margins.

Clavicle

The clavicles in *K. wilsoni* are relatively long, flat bones. The one from the right-hand side of the mounted skeleton is the more complete of the pair, although only the left-hand one shows a knob or boss towards its distal end as mounted, which may have served to locate it against the interclavicle.

Humerus

Both humeri are present and almost complete, although crushed. The condyles were apparently poorly ossified and the proportion seems different from the humerus figured by Pearson (1924b), but this feature is at most certainly due to the crushing they have suffered.

Sternum

The sternum is a poorly preserved irregularly-shaped flat plate of bone, which has been wrongly mounted at an angle, in contact with the clavicles.

Radius and ulna

Only the left ulna is preserved, although both radii were present. The radius and ulna are subequal, and there is no evidence of there having been a separately ossified olecranon process as described in some other Triassic anomodonts (Cox, 1965) and it is possible that this feature is not as universally

present as Cox believed. The ulna is flattened antero-posteriorly. The radii have moderately expanded ends and are rounded in section. The ulna seems broadly similar to that figured by Pearson (1924b).

Fore-foot

In describing the feet of this specimen, reference is made to the field notes kept by Dr. Courtenay-Latimer in which she states that two feet were recovered from layer "D" (see p. 137 above). However, as reconstructed, 29 elements have been incorporated into the fore-foot and 33 into the hind. Therefore, at least two extra bones have been used in the reconstruction of the fore-foot (27 bones used by Camp, 1956, Figure 58a; 25 bones used by Cruickshank, 1967, Figure 17) and eight extra in the hind foot (25 bones used by Camp, 1956, Figure 58b; 23 bones used by Cruickshank, 1967, Figure 22). Therefore, although only 10 terminal phalanges have been incorporated into the two reconstructed feet, at least 10 supernumerary foot bones are also present and quite clearly the remains of more than two feet must have been present in this specimen.

Owing to the fact that it was almost impossible to remove the fore-limb from the mounted skeleton, no attempt has been made to describe the foot bones in detail. Likewise, at this interval of time it is almost impossible to make an accurate reconstruction from the remembered field association, if any, of the foot bones.

The impression gained from an examination of the preserved material is that the fore-feet of *K. wilsoni* were shorter and broader than in *Tetragonias*, and certainly the terminal phalanges were considerably different in proportion. The fore-feet of *Tetragonias* have long sub-rectangular claws, whereas these are broad and triangular. Camp's *Kannemeyeria* material had no complete terminal phalanges (1956, Figure 58) and Cox's descriptions and figures of *Dinodontosaurus turpior* are also different (1965, Figure 18).

Pelvis

Both halves of the pelvis are preserved, though the left pubo-ischiadic plate has been reversed on mounting and is thus viewed from the inside. The ilium is remarkable for its distinct "hook" on the long anterior blade, which is partly matched in *Ischigualastia* (Cox, 1965, Figure 9), but apparently not in the material described by Pearson (1924b, Figure 29). This character has also been noted by Cruickshank (1970) as being of taxonomic importance in association with the similarly contrasting scapula characters, and serves at present to help distinguish *K. simocephalus* and *K. wilsoni*.

The dorsal rim of the ilium is a regular curve and the external surface is smooth. On the internal face there seem to be six facets for the sacral vertebrae, though this is not clear on the left ilium. On the right ilium, immediately behind the front edge of the pillar-like ventral part of this bone, there is a buttress, behind which, at its dorsal extremity, is a small depression. Following posteriorly from this there are a further five clear sets of sacral-vertebrae attachments, and thus it would seem that the sacral count in this species is six, confirming Pearson's (1924b) estimate.

The ischium and pubis are very similar to those described by Pearson. The former has the same inturned posterior portion and the latter a pubic process similar to the one figured by Pearson. There is a large obturator foramen placed high up under the cup-shaped acetabulum.

Femur

The femora are substantial bones, not nearly as flattened as in the specimen figured by Pearson and possessing inturned and rounded heads. The proportions of the femora of this specimen are very similar to the femur of *Tetragonias* (Cruickshank, 1967, Figure 19).

The head of the femur is not separated from the body of the bone by any constriction and there does not seem to be any indication of a trochanter minor. A small step on the proximal end of the femur similar to that in *Tetragonias* might likewise indicate the limit of the trochanter major. The distal condyles are somewhat ventrally placed, showing that the femur was probably held horizontally out from the body, with the lower limbs in a splayed position. However, there is not the prominent adductor femoris tubercle as is seen in *Tetragonias*.

Tibia and fibula

Only the left tibia is preserved. It is a massive bone, and had been subjected to considerable crushing during fossilisation. As a result of this, the cnemial crest had been flattened into the main body of the bone and the ends are now in fact much thinner than the columnar shaft of the bone. The fibula is in comparison an almost insignificant bone, with the proximal end tapering to fit against the lateral condyle of the femur. It is slightly shorter than the tibia and distinctly rounded in section.

Hind feet

As with the fore-foot, no genuine reconstruction of the hind foot can be attempted, at this late stage in time. However, a selection of foot bones corresponding to those illustrated by Camp (1956, Figure 58) can be arranged to make up a hind foot. Only one fibulare (calcaneum) is present. As in the fore-foot the terminal phalanges are short triangular bones, and they do not seem to have been offset as in the *Tetragonias* specimen described by Cruickshank (1967, Figure 22).

DISCUSSION

Affinities

The affinities of this specimen are clearly with the genus *Kannemeyeria* as redefined (Cruickshank,

1970), and the possibility is that it is either a female of *K. simocephalus* or a different species as is assumed here. As the whole question of the interrelationship of the Triassic anomodonts is under review at the present time, any further discussion under this heading is unwarranted.

Depositional environment

The descriptions given above by Dr. Courtenay-Latimer can quite clearly be interpreted in terms of the similar Molteno sequence described by Turner (1969, 1972a). The main differences between the Molteno and the Upper Beaufort are the coarser sandstones of the former and the persistent red colour of the latter. Turner (1972a, p. 313) concludes that the Molteno sediments were laid down on a river flood plain crossed by braided river channels with the sandstones representing point-bar complexes fining upwards into coals and carbonaceous shales, which in turn represent back swamp areas. However, in the Upper Beaufort no coals are found and of course the Molteno is almost totally devoid of known vertebrate fossils (Turner, 1972b; Jubb, 1973). The fauna of the Upper Beaufort on the other hand contains lungfish (cf. *Neoceratodus*), palaeoniscids (Hutchinson, 1972), labyrinthodont amphibians and a rich reptilian fauna.

Therefore in summary it seems that the Upper Beaufort environment comprised a slow-flowing seasonal river system with adjacent swamps. The large anomodont *Kannemeyeria* would have fed on the vegetation growing along the riverbanks, and the specimen recorded here was probably mired in a somewhat deeper mud pool than it might have expected. The carcase was clearly not disturbed by either scavengers or secondary reworking by river currents and on the body disintegrating the heavy head sank to the bottom, the remainder floating for a while to give the depth distribution recorded by Dr. Courtenay-Latimer when she excavated the specimen.

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TABLE 1
Principal measurements of *Kannemeyeria wilsoni* Broom E.L.M. 1

CLAVICLES	LEFT	29 cm long
	RIGHT	30 cm long; 9,5 cm wide proximally; 6,5 cm wide distally
SCAPULAE	LEFT	46 cm overall height; 15 cm wide at top
	RIGHT	44 cm overall height; 19 cm wide at top
CORACOID PLATES	LEFT	24 cm along dorsal edge; 12 cm high
	RIGHT	22 cm along dorsal edge; 12 cm high
HUMERI	LEFT	35 cm overall length; 24 cm wide proximally; 21 cm across distal condyles
	RIGHT	36 cm overall length; 23 cm wide proximally; 21 cm across distal condyles
LEFT ULNA		29 cm overall length; 11 cm wide at sigmoid notch; 8 cm wide distally
RADII	LEFT	23 cm overall length; 9 cm wide proximally; 8 cm wide distally
	RIGHT	23 cm overall length; 8,5 cm wide proximally; 6 cm wide distally
LEFT ILIUM		33 cm maximum length of blade; 28 cm depth of ilium (acetabulum to dorsal rim); 10 cm width of acetabular pillar; 8,5 cm diameter of acetabulum
FEMORA	LEFT	34,5 cm overall length; 16,5 cm wide proximally; 14,5 cm wide over distal condyles
	RIGHT	33 cm overall length; 14,5 cm wide proximally; 15,5 cm wide over distal condyles
LEFT TIBIA		26,5 cm overall length; 11 cm wide proximally; 8,5 cm wide distally
FIBULAE	LEFT	23 cm overall length; 6 cm wide proximally; 5 cm wide distally; shaft 2,4 cm diameter
	RIGHT	22 cm overall length; 7 cm wide proximally; 6 cm wide distally
OVERALL LENGTH MOUNTED SKELETON		1,93 metres
GLENOID-ACETABULUM DISTANCE		80 cm approximately

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FURTHER CONSIDERATION OF THE CAPITOSAURIDS FROM THE UPPER LUANGWA VALLEY, ZAMBIA

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and

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Recently Chernin (1974) described the capitosaurid material collected from the Upper Horizon of the N'tawere Formation by Drysdall and Kitching in 1961, and tentatively assigned the two most complete specimens to *Parotosaurus pronus* (Howie, 1970). This taxon was founded for material collected from the Middle Triassic Manda Formation in the Ruhuhu Valley, Tanzania. The material from the N'tawere Formation is probably of Early Middle Triassic age, perhaps somewhat older than the Manda Formation specimens (Chernin and Cruickshank, 1970).

Welles and Cosgriff (1965) reviewed the Superfamily Capitosauroidea, relegating a large number of generic and specific names to the *nomen vanum* category and reducing the taxonomic content to 3 families, 6 genera and 18 species. The families retained are Benthosuchidae, Mastodonsauridae and Capitosauridae. The first two hold one genus each and the remaining 4 genera are grouped in the Capitosauridae. The Benthosuchidae comprises only the one species *Benthosuchus sushkini* (Efremov) 1928, and two species of *Mastodonsaurus, M. cappelensis* Wepfer (1923) and *M. jaegeri* Meyer (1844) constitute the Mastodonsauridae. Within the Capitosauridae, *Parotosaurus* has 8 species, *P. nasutus* (Meyer) 1858, *P. helgolandicus* (Schroeder) 1913, *P. haughtoni* (Broili and Schroeder) 1937, *P. semiclausus* (Swinton) 1927, *P. angustifrons* (Riabinin) 1930, *P. brookvalensis* (Watson) 1958, *P. birdi* (Brown) 1933 and *P. peabodyi* Welles and Cosgriff, 1965. *Cyclotosaurus* has 4 species, *C. robustus* (Quenstedt) 1850, *C. stantonensis* (Woodward) 1904, *C. ebrachensis* Kuhn, 1932 and *C. hemprichi* Kuhn, 1942. *Kestrosaurus* has one species, *K. dreyeri* Haughton, 1925 and *Paracyclotosaurus* has one species, *P. davidi* Watson, 1958.

Since the time of the Welles and Cosgriff revision the contents of the superfamily have been enlarged and many changes in its structure have been proposed. Subsequent literature has included taxonomic alterations within the superfamily as it was constituted at that time and, in addition, a number of new taxa have been added. These alterations and additions have greatly added to the knowledge of the morphology, diversity and geographic distribution of the group and have raised numerous and provocative questions regarding its evolutionary radiation. As a result of this expansion, however, the capitosauroid taxonomy is currently in a confused and unreconciled state. A complete new revision of the superfamily is called for but this is beyond the scope of the present paper which is confined to justifying a new specific designation for the Luangwa Valley capitosaur. Clearly, however, the present uncertainty in the classification must affect this effort. The revised diagnosis for the species (see below) is necessarily incomplete and its allocation to genus and family provisional pending a new review and integrated new structuring of the group. Also, it is possible that subfamilies will have to be interjected in the new classification. Such a review should preferably be conducted through direct inspection and comparison of all or most of the specimens currently assigned to the superfamily. A brief summary in rough chronologic order is presented here without comment merely to indicate the problems involved.

Welles and Cosgriff (1965) overlooked the following new taxa that were described in the years just previous to the publication of their review: *Cyclotosaurus mechernichensis* Jux and Pflug (1958) from the Muschelkalk of West Germany; *Promastodonsaurus bellmani* Bonaparte (1963) from the Ischigualasto Formation of Argentina; and *Parotosaurus orenburgensis* (Konzhukova, 1965) from zone VI of the Cis-Uralian sequence of the Soviet Union. All three of these were placed in the family Capitosauridae by the authors describing them. A new species of *Mastodonsaurus*, *M. torvus*, was added by Konzhukova (1955) but also overlooked by Welles and Cosgriff.

Otschev (1966) contributed an extensive consideration and revision of capitosauroid systematics and phylogeny, summarized in detail (pages 157—160) in a classification that is at considerable variance with that provided by Welles

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and Cosgriff (1965, pages 5 and 97). Otschev conducted his research contemporaneously with that conducted by Welles and Cosgriff but each party was, at the time, unaware of the work of the other. The points of difference are best summarized by beginning with genera and proceeding up through the subfamilies (not employed by Welles and Cosgriff) to the families. The variance in treatment of species is omitted here as none of it is presently relevant to determining a provisional taxonomic position for the Luangwa Valley capitosaur. The reader is referred to the two reviews for a comparison of the listings of species regarded as valid. Otschev's list is more extensive than that of Welles and Cosgriff as he retains a number of species that the latter place either as junior synonyms of other species or relegate to the *nomen vanum* category and a few species that the latter overlooked or considered as non-capitosauroid. The Welles and Cosgriff review places a number of other species in *nomen vanum* status or in synonymy that are not mentioned in Otschev's review.

Regarding capitosauroid genera, Otschev recognised a number that were disposed of in various ways by Welles and Cosgriff. These, in chronologic order and with the dispositions of Welles and Cosgriff parenthetically following each, are:

Capitosaurus Münster, 1836 (*nomen vanum*);
Mentosaurus Roepke, 1930 (not mentioned);
Wetlugasaurus Riabinin, 1930 (synonym of *Parotosaurus*);
Stanocephalosaurus Brown, 1933 (synonym of *Parotosaurus*);
Heptasaurus Säve-Söderbergh, 1935 (synonym of *Mastodonsaurus*);
Austropelor Longman, 1941 (not mentioned);
Sassenisaurus Nilsson, 1942 (*nomen vanum*);
Stenotosaurus Romer, 1947 (synonym of *Parotosaurus*);
Procyclotosaurus Watson, 1958 (synonym of *Cyclotosaurus*);
Subcyclotosaurus Watson, 1958 (synonym of *Parotosaurus*); and
Jarengia Shishkin, 1960 (*nomen vanum*).

In addition, Otschev proposed the new generic designations: *Karoosuchus* for *Parotosaurus haughtoni*, Broili and Schroeder 1937; *Watsonisuchus* for *Wetlugasaurus magnus* Watson, 1962 (regarded as *nomen vanum* by Welles and Cosgriff); and *Meyerosuchus* for *Labyrinthodon fürstenbergianus* Meyer, 1855 (regarded as a synonym for *Parotosaurus semiclausus* by Welles and Cosgriff). Also, he included *Mastodonsaurus silesiacus* Kunisch, 1885 with question in his new genus *Eryosuchus* founded for material from the U.S.S.R. (Welles and Cosgriff regarded *M. silesiacus* as a *nomen vanum*).

New species erected by Otschev (1966) for material from the Cis-Uralian sequence include *Wetlugasaurus kzilsajensis*, *Wetlugasaurus ? lehmani*, *Parotosaurus orientalis*, *Parotosaurus panteleevi*, *Bukobaja enigmatica*, *Eryosuchus antiquus*, *Eryosuchus tverdochlebovi*, and *Eryosuchus garjainovi*. *Benthosuchus uralensis* Otschev, 1958 is also listed. Most of these were described in more detail by Otschev (1972).

The classification of the Capitosauroidea of Otschev (1966) down through the category genus is as follows:

Superfamily Capitosauroidea
- Family Rhinesuchidae Watson, 1919
  - *Rhinesuchus* Broom, 1908
  - *Rhinesuchoides* Broom and Olson, 1937
  - *? Jugosaurus* Riabinin, 1962
- Family Uranocentrodontidae Romer, 1947
  - *Uranocentrodon* van Hoepen, 1917
  - *Laccocephalus* Watson, 1919
  - *? Muchocephalus* Watson, 1962
  - *? Gondwanosaurus* Lydekker, 1885
  - *? Pachygonia* Huxley, 1865
- Family Rhinecepidae Otschev, 1966
  - *Rhineceps* Watson, 1962
- Family Lydekkerinidae Watson, 1919
  - *Lydekkerina* Broom, 1915
- Family Sclerothoracidae von Huene, 1931
  - *Sclerothorax* von Huene, 1931
- Family Capitosauridae, Watson, 1919
  - Subfamily Wetlugasaurinae Otschev, 1958
    - *Wetlugasaurus* Riabinin, 1930
    - *Sassenisaurus* Nilsson, 1942
    - *Parotosaurus* Jaekel, 1922
    - *Karoosuchus* Otschev, 1966
    - *Watsonisuchus* Otschev, 1966
    - *Stenotosaurus* Romer, 1947
    - *Eryosuchus* Otschev, 1966
    - *Mentosaurus* Roepke, 1930
    - *Capitosaurus* Münster, 1836
  - Subfamily Cyclotosaurinae Otschev, 1966
    - *Procyclotosaurus* Watson, 1958
    - *Cyclotosaurus* Fraas, 1889
  - Subfamily Paracyclotosaurinae Otschev, 1966
    - *Subcyclotosaurus* Watson, 1958
    - *Paracyclotosaurus* Watson, 1948
    - *Austropelor* Longman, 1941
    - *Stanocephalosaurus* Brown, 1933
    - *Moenkopisaurus* Shishkin, 1960
    - *Rhadalognathus* Welles, 1947
- Family Mastodonsauridae Lydekker, 1885
  - *Heptasaurus* Säve-Söderbergh, 1935
  - *Mastodonsaurus* Jaeger, 1828
  - *Promastodonsaurus* Bonaparte, 1963
- Family Bukobajidae Otschev, 1966
  - *Bukobaja* Otschev, 1966
  - *Kestrosaurus* Haughton, 1925
  - *Meyerosuchus* Otschev, 1966
- Family Benthosuchidae Efremov, 1931
  - *Benthosuchus* Efremov, 1929
  - *Yarengia* Shishkin, 1960

In comparing this classification with that of Welles and Cosgriff (1965) many differences will be noted. Among these are the much greater number of

previously described genera recognised by Otschev, the addition of new genera and families, the inclusion of the families Rhinesuchidae, Uranocentrodontidae, Lydekkerinidae and Sclerothoracidae in the superfamily and the division of the Capitosauridae into subfamilies.

New genera and species have been added to the superfamily since the revisions of Welles and Cosgriff (1965) and Otschev (1966). These are, by stratigraphic unit and region: from the Triassic portion of the Cis-Uralian region of the U.S.S.R. — *Benthosuchus bashkirikus* Otschev (1972); from the Lower Triassic of Sinkiang — *Parotosaurus turfanensis* Young (1965); from the Upper Bunter of West Germany — *Eocyclotosaurus woschmidti* Ortlam (1970); from the Lower Triassic of the Vosges, France — *Stenotosaurus lehmani* Heyler (1969); from the Lower Triassic Zarzaitine Series of Algeria — *Parotosaurus lapparenti* Lehman (1971) and *Wellesaurus bussoni* Lehman (1971); from the Yerrapalli Formation of India — *Parotosaurus rajareddyi* Chowdhury (1970); from the Middle Triassic Manda Formation of Tanzania — *Parotosaurus pronus* Howie (1970); and from the Lower Triassic Gosford Formation of New South Wales — *Parotosaurus wadei* Cosgriff (1972).

Further alterations in generic assignments and familial grouping have also appeared in the recent literature. Jux (1962) changed the generic designation of the form described by Jux and Pflug (1958) from *Cyclotosaurus mechernichensis* to *Procyclotosaurus mechernichensis* and, later, Jux (1966) to *Parotosaurus mechernichensis*; Heyler (1969) removed *Stenotosaurus* from the Capitosauridae, placing it in its own family, Stenotosauridae; Lehman (1970) changed *Parotosaurus peabodyi* to *Wellesaurus peabodyi*; Paton (1974) revalidated the three species *Labyrinthodon leptognathus* Owen (1842), *Labyrinthodon pachygnathus* Owen (1842) and *Labyrinthodon lavisi* Seeley (1876), placing the first two in *Cyclotosaurus* and the last in *Mastodonsaurus*. Paton placed *Cyclotosaurus stantonensis* (Woodward, 1904) as referred specimen of *C. leptognathus* and supported Heyler's segregation of *Stenotosaurus* in its own family, Stenotosauridae, adding to this family *Kestrosaurus dreyeri* Haughton (1925).

A recent inspection of the capitosaurids from the Karroo by both authors suggests that reconsiderations of this complex will be necessary. *Parotosaurus africanus* Broom (1909) was considered *nomen vanum* by Welles and Cosgriff, 1965 as they believed the holotype of this form was too incomplete for meaningful comparisons. The specimen, however, consists of most of the postorbital portions of the skull which are well prepared and capable of being compared directly with these portions on other taxa. It may well prove to be a distinct and definable species. *Kestrosaurus dreyeri* Haughton (1925) is obviously close to other parotosaurs and it is doubtful if it should be retained in a separate genus. It seems distinct, however, from *Parotosaurus africanus* and its status as a separate species is probably firm. *Parotosaurus haughtoni* Broili and Schroeder (1937) will probably also retain its species status but should be compared again with both *Parotosaurus africanus* and *Kestrosaurus dreyeri*. A reappraisal of *Parotosaurus* sp. Welles and Cosgriff (1965) (*Wetlugasaurus magnus* Watson, 1962) is also desirable.

Reliable comparisons within the genus *Parotosaurus* are presently limited to those species for which extensive sets of measurements of the skull roof have been provided. These include, first, the species recognised by Welles and Cosgriff (1965): *P. nasutus*, *P. helgolandicus*, *P. haughtoni*, *P. semiclausus*, *P. angustifrons*, *P. brookvalensis*, *P. birdi* and *P. peabodyi*. Comparisons of this nature are also possible with *P. mechernichensis*, *P. pronus*, *P. rajareddyi* and *P. wadei*. In Table 2 the computed indices are listed. The eight species considered by Welles and Cosgriff (1965) are given in one column as a range for each index. All but one of these are taken directly from Table I of that work. The exception is the range for the O:C index which is computed directly from the illustrations in Welles and Cosgriff. The range shown for this index (57—68) actually falls within the range for the species population of *P. peabodyi* as computed from Welles and Cosgriff (1965, Table II). For *P. mechernichensis*, *P. pronus*, *P. rajareddyi* and *P. wadei* the indices cited are those listed in the respective descriptions of these species (Jux, 1966, Howie, 1970, Chowdhury, 1970 and Cosgriff, 1972) or are taken from measurements of the published illustrations.

The Luangwa Valley capitosaurs were assigned with question to *P. pronus* primarily because of the marked resemblance in the construction of their otic notches to that form and because of general morphologic similarities. In spite of the correspondence of the otic notches the senior author has always entertained misgivings regarding even a tentative assignment to *P. pronus* and, therefore, in conjunction with the junior author, has undertaken a new reconstruction (Fig. 1) of the outlines of the best preserved specimen, B.P.I. No. 414 (specimen B of Chernin, 1974) which has led us to create a new species, based on this specimen, which we propose to call *Parotosaurus megarhinus* Chernin and Cosgriff, 1975. This new reconstruction of the dorsal surface was accomplished by making separate drawings of the distorted parts of the skull, reassembling them and checking their accuracy by direct measurements from the skull. The measurements that form the basis for the reconstruction were taken with allowances for distortion and are listed in Table I. It will be noted that some of these are at appreciable variance with those listed in Table I of Chernin (1974) which were taken not directly from the specimen, but from a reconstruction based on

photographs. These new measurements, in turn, have produced a new set of indices that are listed in the first column of Table 2. It must be noted that the new method of reconstruction was only attempted in the case of specimen B. Specimen A (B.P.I. No. 424) proved to be too distorted and incomplete for line drawing restoration and is referred with question to the new species for which

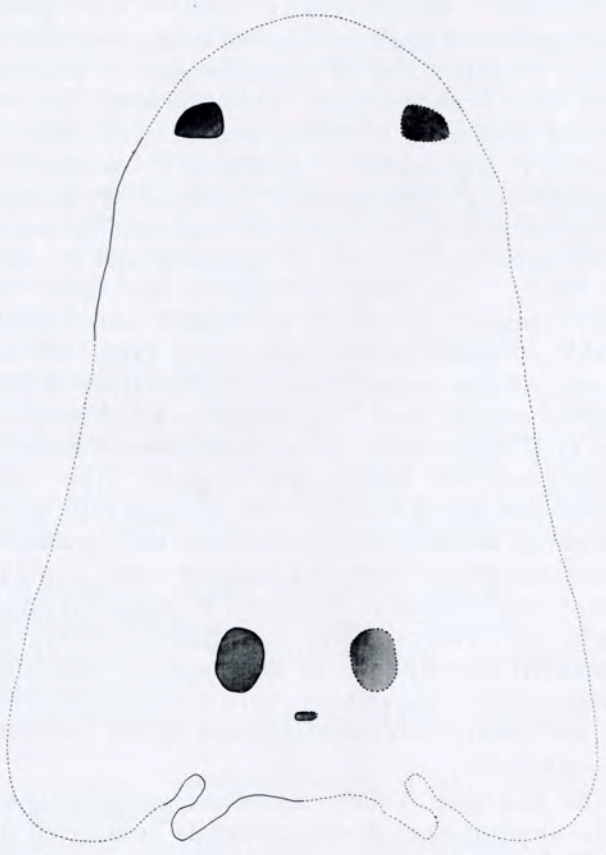


FIG. 1 **10 CMS**

Table 1
Measurements of skull roof of B.P.I. No. 414 (in millimetres)

1. Breadth of skull across quadrates (B)	575
2. Length of skull (L)	787
3. Interorbital distance taken at mid-length of orbit (A)	87
4. Distance from tip of snout to level of anterior edge of orbit (O)	613
5. Distance from level of posterior limit of orbit to level of centre limit of skull (D)	110
6. Distance from postero-lateral corner of eye to otic notch (N)	87
7. Midline distance from centre posterior limit of skull to level of posterior limit of tabular horn (K)	46
8. Inter-otic distance (least) (C)	192
9. Distance from mid-length of orbit to lateral edge of same side (I)	190
10. Distance from posterior mid-point of nares to anterior mid-point of orbit (F)	491
11. Internarial distance taken at mid-length of nares (J)	165
12. Distance from level of anterior limit of nares to edge of snout (M)	90
Breadth of snout 1/5th of skull length from tip (S)	370
14. Distance from level of posterior limit of orbit to parietal foramen taken at centre of skull (P)	18
15. Midline distance from level of anterior limit of otic notch to parietal foramen (T)	53
16. Orbit length	64

Table 2
Comparison of some indices with some specimens of Parotosaurs

Indices (Welles and Cosgriff, 1965)	Specimen B B.P.I. No. 414	*Parotosaurus pronus* (Howie, 1969)	Welles and Cosgriff, 1965 Tables I and II	*Parotosaurus rajareddyi* (Chowdhury, 1970)	*Parotosaurus wadei* (Cosgriff, 1972)	*Parotosaurus mechernichensis* (Jux, 1966)
B:L	73	75	60—85	84	91	
S:L	47	32	28—43	38	47	
A:L	11	(1)* 13	14—17	16	15	
C:L	24	(1)* 30	31—38	36	42	
A:C	45	(1)* 45	41—49	45	36	42
N:C	45	(1)* 43	42—63	46	46	68,5
P:C	9	(1)* 8	6,1—13,7	6,3	(1)* 0	27
T:C	28	(1)* 28	25—38	31	(1)* 41	31
K:C	24	(1)* 30	17—38	20,1	(1)* 25	24
O:L	78	(1)* 70	(2)* 57—68	(1)* 65	(1)* 56	

(1)* These indices were obtained by taking measurements from the plates of the dorsal view of the skull that were available in the respective descriptions of these species.
(2)* Taken only from paratypes of *P. peabodyi*.

specimen B is designated holotype. As a result of the new interpretations, specimen B is somewhat different in gross outline and in the shapes of the tabular horns and external nares from conditions shown in Fig. 7 of Chernin, 1974.

As compared in Table 2, the type of the new species differs from *Parotosaurus pronus*, *P. rajareddyi*, *P. wadei* and the eight parotosaur species of Welles and Cosgriff (1965) by having a very broad snout (S:L index), a very long preorbital region (O:L index), orbits and otic notches closely spaced on the skull roof relative to skull length (A:L and C:L indices). *P. wadei* is identical to our new type in breadth of snout but differs from it in the other proportions. The species considered by Welles and Cosgriff (1965) and also *P. rajareddyi* differ from *P. megarhinus* in all respects. They have shorter preorbital regions, narrower snouts and more widely spaced orbits and otic notches. *P. pronus* shows the nearest approach to the new species in the relative length of the preorbital region but differs from it in having a very narrow snout and more widely spaced orbits and otic notches.

Skull roof indices of *Parotosaurus mechernichensis* are available only for the postorbital region (Jux, 1966). In this species the measurements (a) least distance between orbit and otic notch (N) and (b) orbits to parietal foramen (P) are much greater relative to least interotic distance (C) than in *P. megarhinus* or the other species of the genus.

Comparisons of *P. megarhinus* with the remainder of capitosauroid species that have been described in recent years are less reliable than the foregoing comparisons, as the literature concerning them does not cite the measurements and indices that serve as the base for our comparative work. Many of the described species are based either on postcranial or jaw material or on skull material that is complete enough for quantitative analysis. Among those species founded on adequate skulls, those possessing open otic notches are certain to bear fairly close evolutionary relationship to *P. megarhinus*. Some of these have been assigned to *Parotosaurus* and some placed in other genera. The list of these, with reference to published illustrations cited parenthetically, includes *Parotosaurus orenburgensis* (Konzhukova, 1965, fig. 1), *Parotosaurus orientalis* (Otschev, 1972, pl. VIII), *Parotosaurus lapparenti* (Lehman, 1971, figs. 4 and 6), *Eryosuchus tverdochlebovi* (Otschev, 1972, pl. XVI), *Eryosuchus garjainovi* (Otschev, 1972, pla. XXV and XXVI), *Promastodonsaurus bellmanni* (Bonaparte, 1963, fig. 1) and *Wellesaurus bussoni* (Lehman, 1971, fig. 3). Rough comparisons by eye suggest that *P. megarhinus* is distinguishable for the most part from these recently described species through the same indices (S:L, O:L, A:L and C:L) used in distinguishing it from the more familiar species. Generally, *P. megarhinus* appears to have a longer and broader snout (O:L and S:L indices) and more closely spaced orbits and otic notches (A:L and C:L indices) than any of the forms in this list of newly described species. However, *Parotosaurus lapparenti* and *Parotosaurus orientalis* may approach *P. megarhinus* in relative length of snout and *P. orientalis* may have orbits proportionately as close together.

B.P.I. No. 414 (Specimen B), therefore, represents a distinct species of *Parotosaurus*. B.P.I. No. 424 (Specimen A) is referred with question to this species but possibly represents still another species. Its orbits seem farther apart and the texture of its surface sculpture is decidedly coarser.

Parotosaurus megarhinus sp. nov.

Parotosaurus cf. *pronus* Chernin and Cruickshank (1970); Chernin (1974).

Holotype: B.P.I. No. 414 (Specimen B).

? Referred specimen: B.P.I. No. 424 (Specimen A).

Locality and *Horizon*: Locality 15 of the N'tawere Formation in the Upper Luangwa Valley, Zambia. Probably Middle Triassic.

Diagnosis: Skull broad posteriorly (B:L index 73), tapering slightly to a broad snout (S:L index 47). Orbits close together (A:L index 11) and otic notches close together (C:L index 24). Snout relatively very long (O:L index 78). Parietal foramen rectangular, just posterior to rear borders of orbits.

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