
PALAEONTOLOGIA

AFRICANA

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

VOLUME 20, 1977

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Bernard Price Institute
for Palaeontological Research

University of the Witwatersrand
Johannesburg

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BERNARD PRICE INSTITUTE FOR PALAEONTOLOGICAL RESEARCH

1977

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BERNARD PRICE INSTITUTE FOR PALAEOONTOLOGICAL RESEARCH,
UNIVERSITY OF THE WITWATERSRAND, JOHANNESBURG

REPORT OF THE HONORARY DIRECTOR FOR 1976

Financial depression, which has affected not only the universities but the economy of the whole country, has affected the Institute in 1976 less severely than might have been expected. Two posts — one a research post and the other a technical post — could not be filled but otherwise the Institute's budget, though it did not expand, remained at the level for the previous year.

STAFF MATTERS

Dr. Brian Turner, who qualified for the degree of Ph.D. at the end of 1975, with the aid of a post-doctoral research fellowship from the Council for Scientific and Industrial Research and some support from the University, left for a year's study leave in Europe in the middle of 1976. Though based in the Department of Geology of the University of Oxford, he has spent some time in Scandinavia and North Africa, paying special attention to some problems of basin sedimentology which are likely to contribute to the understanding of the deposits of coal and uranium in South Africa.

Dr. Judy Maguire, who submitted her extensive thesis on the old world and living porcupines and other Hystriid material from Pleistocene sites, received the degree of Ph.D. at the November graduation ceremony.

Dr. Heidi Anderson's thesis on the Molteno Flora was submitted and accepted for the degree of Ph.D. in the University.

Dr. Elizabeth Vrba of the Transvaal Museum, Pretoria, has been appointed Hon. Research Associate of this Institute, and Mr. A. Hughes, principal technical assistant in the Department of Anatomy, has been appointed Honorary Senior Field Research Officer in recognition of his services at the Sterkfontein excavations.

Towards the end of the year the Dean of the Faculty of Science, Professor P. D. Tyson, attended an informal function in the Institute and presented Mr. Regent (Lucas) Huma with a watch as a gift from the staff of this Institute in recognition of more than 30 years of service. Lucas (as he is known to us) replied in Afrikaans.

The Southern Oil Exploration programme, started in the Institute some years ago, continues. In terms of the arrangement, a micropalaeontological facility has been established for the analysis of bore-hole cores with a view to stratigraphic correlation of sediments that may contain oil, and seeking evi-

dence of environments favourable to oil formation. The Unit at present consists of 2 technicians and five laboratory assistants, in charge of a scientific officer, Mr. I. McLachlan, who takes part in the Institute's teaching and research programme.

The new accommodation for African staff at Sterkfontein was brought into use in February 1976. This now falls directly under the personnel officer of the University who arranges for supervision and the provision of services to the residents.

In August 1976 the long awaited tape recorders were installed at convenient places in the Sterkfontein caves, making it possible for the guides to switch on recordings — in English and Afrikaans — which explain to the visitors the history and the formation of the caves and their significance in the record of man's evolution. This service was formally inaugurated at a function held on August 12, 1976.

Mr. C. J. M. Kitching has spent some time in the Department of Geology undergoing special training and, more especially, gaining experience of cutting thin rock sections. A visit to the South African Museum in Cape Town is planned for the early part of 1977.

STUDENTS

The following post-graduate students are working for higher degrees:

Mrs. R. M. Falcon
Mrs. S. Isernhinke (S. Chernin)
Mr. I. R. McLachlan
Mrs. A. Malleson
Mrs. S. Smithies
Mr. C. MacRae
Mr. I. M. Macgregor
Miss M. Makrides

Dr. J. M. Anderson's thesis on Permian Palynology, submitted in October 1975, was accepted for the degree of Ph.D.

FIELD WORK

Excavations at Sterkfontein continued under the direction of Professor P. V. Tobias and at least one important find was reported during the course of the year. Improvements in the facilities at the site of the Sterkfontein excavation has been recommended by the Director and are being carried out by the University's Maintenance Department.

Dr. Kitching, in addition to a number of short

field excursions, has spent several weeks in the recovery of fossil reptilian remains from the middle and upper Beaufort exposures in the Bethulie and Rouxville districts. Ninety-eight well-preserved specimens were collected and new data were obtained on the deposition of *Lystrosaurus* and *Cynognathus* zones in these districts.

During the course of a short field expedition in November 1976, Dr. James Kitching visited a dump of Red Bed mudstone blasted from a road cutting near Golden Gate in the Clarens district of the Orange Free State. There he found a cluster of five fossil reptilian eggs containing embryos. These eggs are the first to be found in South Africa and may be the first of Triassic age to be found anywhere in the world. It is hoped that the preparation work now in progress will reveal in time whether these eggs are of crocodilian or dinosaurian origin.

Dr. J. T. Brown and Dr. C. Gow undertook a collecting excursion to the Lower Cretaceous beds in the Algoa Basin.

Professor Yves Lemoigne of the Université Claude Bernard, Lyon 1, France, visited the Institute in October 1976. He was escorted on a field excursion by Dr. Kitching and Dr. Brown to the Permian and Triassic fossil plant sites at Lidgetton, Mooi River, Estcourt, and Little Switzerland. As a result of this visit Professor Lemoigne and Dr. Brown are engaged on a joint project dealing with Lower Permian Lycophyta.

The work of extracting fossil remains of mammalian fauna from the grey breccia of the limeworks deposit continues. Mr. Brian Maguire and Dr. Kitching have devoted short periods to this work intermittently throughout the year.

The guide book, "Important Plants of Sterkfontein", prepared by A. O. D. Mogg and illustrated by Rita Lloyd, is now completed and published. Dr. A. R. I. Cruickshank undertook the exacting task of seeing the work through the press.

RESEARCH WORK

Dr. A. R. I. Cruickshank is engaged on a revised classification of Triassic Anomodonts in collaboration with Dr. A. W. Keyser of the South African Geological Survey. A short paper on the Waterberg Thrust Fault in South West Africa has been accepted for publication by the Geological Society of South Africa. The joint project with B. W. Skews of Mechanical Engineering, analysing the behaviour of Nectridian amphibia in a wind tunnel, reached a stage at which the experimental work is completed.

Dr. C. E. Gow has been working on tooth function and succession in *Procolophon trigoniceps*, new procolophonids from the Triassic *Cynognathus* zone of South Africa, and on a skin impression of *Procolophon*. He is also working on a description of *Owenetta* and on the jaw function in *Procolophon*. Three papers were accepted for publication during the year. He has also spent some time on papers entitled "*Diarth-*

rognathus — it isn't and it hasn't" and "Possible non-anomodont herbivores of the Triassic", intended as contributions to the 1977 symposium on Karroo palaeontology.

Dr. J. T. Brown's research in 1976 has been concerned chiefly with the Lower Cretaceous flora of the Algoa Basin and with the Lycophyta from the Lower Permian. He has assisted Mr. Murray Macgregor on the biostratigraphy of stromatolites from pre-Cambrian dolomites of the Cape Province, and Mr. Colin MacRae with the Palaeozoic palynology of Botswana. Three papers have been accepted for publication.

Dr. Brian Turner spent most of 1976 on study leave at the University of Oxford.

Dr. J. W. Kitching has continued his work on the rocephalians found in Antarctica which he is pursuing in collaboration with Prof. E. H. Colbert. Two joint papers have been published already. Towards the end of the year Dr. Kitching devoted considerable attention to Mrs. Sharon Isernhinke's research on Amphibians. "Distribution of Karroo Vertebrate Fauna — Memoir No. 1" was completed ready for publication early in 1977.

It is a pleasure once again to acknowledge the Institute's gratitude to the Council for Scientific and Industrial Research for substantial financial aid to the Institute and to the Department of National Education for continued assistance with the publication of *Palaeontologia Africana*.

PUBLICATIONS

During 1976, Volume 19 of *Palaeontologia Africana* appeared in the form of a special number — issued as a tribute to Dr. Edna Plumstead's notable work in the field of fossil plants. The contents were as follows:

EDITOR'S NOTE AND PUBLICATIONS OF DR. EDNA P. PLUMSTEAD 1923 — 1975

REPORT OF THE HONORARY DIRECTOR FOR 1975

FALCON, Rosemary M. S. Numerical Methods in the Definition of Palynological Assemblage Zones in the Lower Karroo (Gondwana) of Rhodesia.

ANDERSON, Heidi M. A Review of the Bryophyta from the Upper Triassic Molteno Formation, Karroo Basin, South Africa.

ANDERSON, Ann M. and McLACHLAN, I. R. The Plant Record in the Dwyka and Ecca Series (Permian) of the South-Western half of the Great Karroo Basin, South Africa.

GORDON-GRAY, Kathleen D., VAN DIJK E. E. and LACEY, W. S. Preliminary Report on Equisetalean Plants from Lidgetton, Natal.

LE ROUX, S. F. On some "Northern" Elements in the Lower Gondwana Flora of Vereeniging, Transvaal.

KOVÁCS-ENDRÖDY, Eva. Notes on some *Glossopteris* species from Hammanskraal (Transvaal).

BENECKE, Anna K. Several new forms of *Glossopteris* Fructifications from the Beaufort *Daptocephalus*-Zone (Upper Permian) of Natal, South Africa.

ERASMUS, T. On the Anatomy of *Dadoxylon arberi* Seward, with some remarks on the Phylogenetical tendencies of its Tracheid Pits.

———. A New Species of *Dammaroxylon* Schultze-Motel, *D. natalense* Sp. Nov., from the Cretaceous of Natal, South Africa.

- RIEK, E. F. An Entomobryid Collembolan (Hexapoda: Collembola) from the Lower Permian of Southern Africa.
- . Fossil Insects from the Middle Ecca (Lower Permian) of Southern Africa.
- . An unusual Mayfly (Insecta: Ephemeroptera) from the Triassic of South Africa.

Members of the Institute have written and published the following additional papers:

- BROWN, J. T. and ROBISON, C. R. Observations of the Structure of Marchantiolites blairmorensis (Berry) n. comb., from the Lower Cretaceous of Montana, U.S.A. *J. of Palaeontology*, 50(2), 309–311. 1976.

- . Observations on the hypodermis of *Equisetum*. *S. Afr. J. Sci.*, 72(10), 303–305. 1976.
- , and GOW, C. E. Fossil plants as indicators of the rate of sedimentation of the Kirkwood Formation of the Algoa Basin, South Africa. *S. Afr. J. Sci.*, 72(9), 278–279. 1976.
- CRUICKSHANK, A.R.I. Old Bones Rattling Well. *S. Afr. J. Sci.*, 72, 37–40. 1976.
- HAUGHTON, S. H. Some early remembrances. *Geol. Soc. S. Afr.*, 19(3), 1976. Quart. News. Bull.
- COLLINGS, G. E., CRUICKSHANK, A. R. I., MAGUIRE, J. M. and RANDALL, R. M. Recent faunal studies at Makapansgat limeworks, Transvaal, South Africa. *Ann. S. Afr. Mus.*, 71, 153–165. 1976.

COLUMNAR STROMATOLITES FROM THE EARLY PROTEROZOIC SCHMIDTSDRIFT FORMATION, NORTHERN CAPE PROVINCE, SOUTH AFRICA — PART I: SYSTEMATIC AND DIAGNOSTIC FEATURES

by

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ABSTRACT

The Schmidtsdrift Formation (Transvaal Dolomite) is a Lower Proterozoic stromatolite-bearing carbonate unit. A good succession of columnar stromatolites occurs along the Boetsap River (Northern Cape Province). Using the method of serial sections to draw the gross morphology of columns and following the actual classification based on a succession of different characters, many new groups and forms have been found: *Topinamboura insulata* is a bulbous column with wart-like projections spreading out everywhere on the smooth surface. *Radiatina isotropa* presents closely packed radiating columns forming compact bioherms. The small rhythmically superposed columns of *Tibia cristata*, *Tibia plumata* and *Sapinia fucoides* offer tiny bushy columns with a constant crestal zone, a very unusual feature, giving an angular shape to the laminae. Some of the stromatolites belong to previously described groups, from the same area as *Katernia africana* or *Katernia perlina* new form, which present true bushy columns forming thin biostromes; or, from other parts of the world, as *Pilbaria boetsapia* and *Pilbaria inzeriaformis*, two new forms, attributed to a Lower Proterozoic group described in Australia. Besides description of morphologies and mode of occurrences, detailed studies of lamina microstructures have been carried out. Very interesting fabrics have been described but, until now, no true organic remains (cells) have been found. The conclusions emphasize the importance of detailed systematic description of stromatolites in order to make a biostratigraphical model of the Lower Proterozoic and to clear up confusions with Upper Proterozoic stromatolites which also present varied assemblages of ramified stromatolites.

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*Contribution CGG n° 204

INTRODUCTION

The Schmidtsdrift Formation is a facies equivalent of the Malmani Dolomite in the Transvaal (Eriksson *et al.*, 1976) which is dated relative to younger lavas at greater than $2\,224 \pm 21$ m.y. (D. Crampton, personal communication, 1972).

Early work on the Schmidtsdrift Formation was undertaken by Young between 1928 and 1943. In three of his contributions (1933, 1934, 1940), Young made reference to columnar stromatolites from the Schmidtsdrift Formation and Groot Boetsap River. These two localities have subsequently been studied

in more detail in a palaeoenvironmental context by Visser and Grobler (1972) and Truswell and Eriksson (1973) respectively. Columnar stromatolites are especially well developed in the Groot Boetsap River section where Truswell and Eriksson (1973) noted a great diversity of morphologies. Samples have been taken in this area in order to describe columnar stromatolites in terms of the presently known Russian classification. Linnean binary names are used. In this classification different characters enter dealing with shape of columns, ramification, nature of marginal surface, mode of occurrence, and micro-

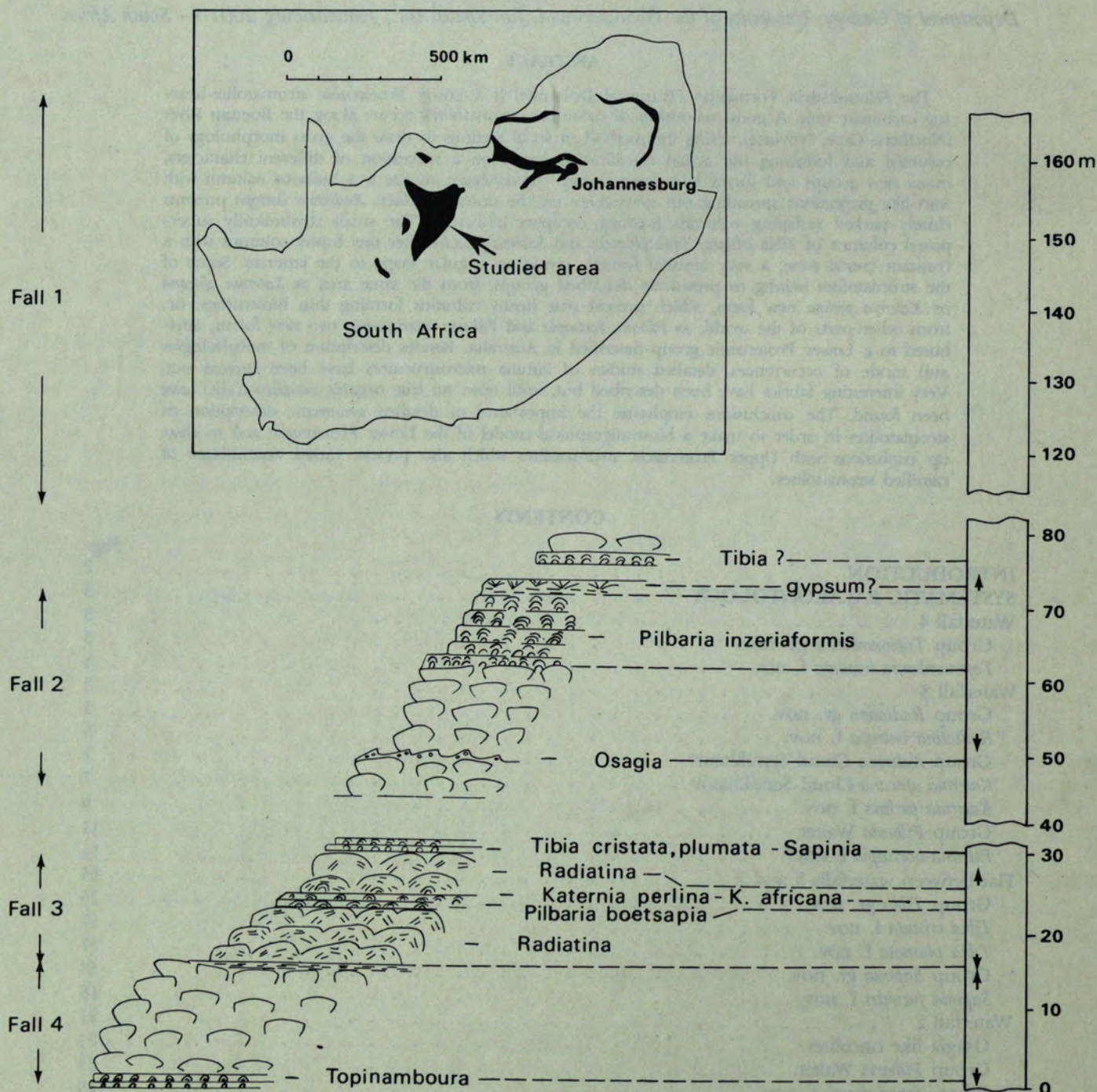


Figure 1. Section of the Groot Boetsap River on the right (according to Truswell and Eriksson, 1973, p. 20); on the left schema of the outcrop showing location of the different stromatolite groups. The individual thickness of domes is greatly exaggerated; inset, locality map of the Transvaal Dolomite.

structure of laminae. For this purpose, in addition to thin section studies, reconstructions of the columns were made by drawing of serial sections through the samples (Krylov, 1963). These were compared with other stromatolites described in the available literature. In the present case, few of them are known from lower Proterozoic carbonates, and comparisons have mainly been made with Riphean stromatolites and a few Australian forms circa 2 000 m.y.

We will now describe the stromatolites following their chronological succession along the Groot Boetsap River. Four waterfalls along the river provided well exposed outcrops (fig. 1).

SYSTEMATIC PALAEONTOLOGY

Waterfall 4 (fig. 1)

At the very base of the waterfall is a 1,2 m thick bed of contorted and bulbous *Topinamboura* (gr. nov.). The ramified columns form small bushes 20 to 30 cm high. Overlying this bed in a sharp contact with the columns is a thick sequence of domical stromatolites, with few discrete columns. Domes are linked, oblate to convex-shaped. Dolomitization retains sometimes few structures (Truswell and Eriksson, 1973, p. 9). The sequence ends with a thin bed of shales and spheroids.

Group *Topinamboura* gr. nov.

Type form

Topinamboura insulata

Group Name

From Topinambour, French name of an American plant with potato-like tubers.

Diagnosis

Bulbous sparsely distributed columns with small wart-like projections and slightly divergent branching, with the daughter columns spreading out laterally at various angles. Marginal surface is very smooth with a well defined wall. The microstructure shows trapped particles without defined lamina boundaries.

Topinamboura insulata f. nov.
(figs. 2a-d, 4a-c)

Holotype

SA 2, from three samples in the same horizon and one from an outcrop near the previous one.

Form Name

From the Latin *insula* (island) for the isolated, widely spaced column.

Description

The discrete columns are generally vertical or slightly oblique, never horizontal. They are bulbous with short straight portions which rapidly ramify.

Diameter varies greatly (2–10 cm) and some parts increase laterally to three or four times their initial size, overlapping smaller columns. Horizontal section is lobate with complex contour form. Axes of columns changed during growth. Ramification shows separate daughter-columns in divergent position continuing to grow for a few centimetres and also lots of small bumps (one or two centimetres as a maximum) spreading out at right angles, in every direction. Along the surface are long deep depressions differing from niches; they may be horizontal, oblique or vertical. The column margins show no peaks, bridges or coalescence. The surface is smooth, outlined by a continuous wall (less than 2 mm thick). Laminae are moderately convex, generally asymmetric with a slightly visible stratification. In horizontal portions they are quite flat but in the oblique one they are vertical to recumbent. The total relief of the walled column is variable, sometimes as high as 10 to 15 cm. A crust envelops the columns prior to sedimentary filling.

Microstructure

The succession of laminae is regular but without clear physical discontinuity between mats. Different laminae are defined by the rough alternation of microsparitic and corruscular layers. The microsparitic one is made of xenotopic dolo-microsparite with dark limits of crystals, probably due to recrystallization of a muddy carbonate. The corruscular layer contains dark grains (micritic pelloids) in a matrix of larger crystals. The black grains appear as rounded or elongate pelloids of micrite obviously different from the stromatolite laminae but probably also algal (organic matter content). They are relatively well sorted (between 0,05 to 0,12 mm with a length up to 0,9 mm). The layers are not very thick and never show graded-bedding. Elongate grains lie parallel to the surface of curved laminae.

The wall changes from thin mats (no more than 0,02 mm for a doublet and up to 15 doublets) to an homogeneous texture in the curved upward portions where it reaches a thickness of 4–5 mm. In some cases the continuity with stromatolite mats is clearly visible, especially on the small bumps.

Interspace filling

(a) Prior to the sediment deposition, the column is enveloped by a non-algal crust. In the overlapping portions it is a thick dolomitic radiaxial crust made by the superposition of very thin laminae (up to ten). When the column flattens some grains are trapped between these layers and in the flat portions big grains falling by gravity are coated by the clear bladed crystal layers. The continuity of the crust prevents interpretation as a vadose cement. The crust also can extend upon sediment interspace filling.

(b) The sedimentation of the interspaces takes place following, not during, the column and crust growth. It presents layers of microsparitic carbonate (muddy) containing thin beds of small particles with

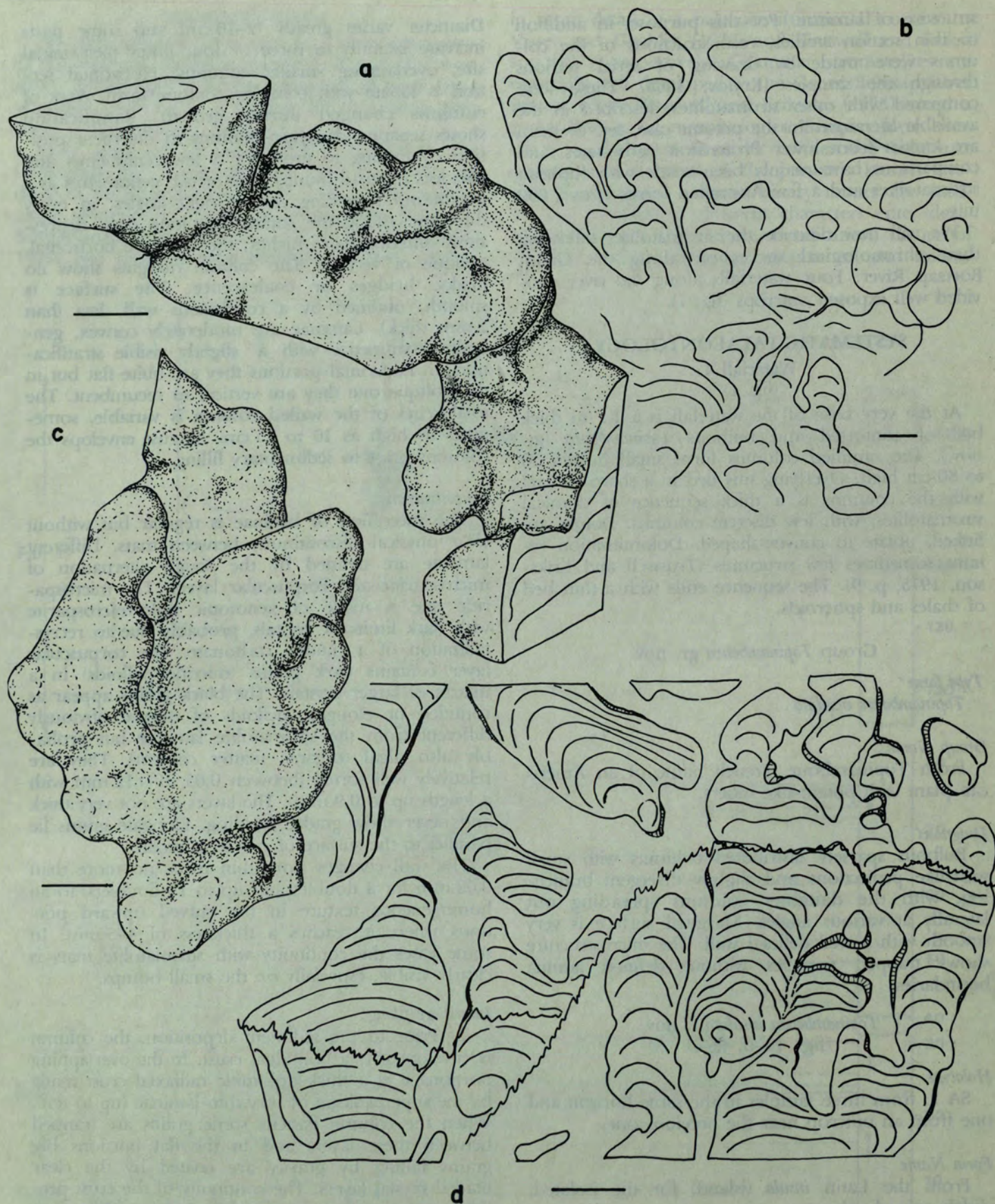


Figure 2. *Topinamboura insulata*
 (a) contorted column (SA 2, JBS coll.);
 (b) ramified columns (drawing from JBS field photograph);
 (c) bulbous columns with small bumps on the surface (SA 1, JBS coll.);
 (d) clear dolomitic envelope (e) along the overlapping portions of columns (SA 31, drawing from a peel, Young coll.).
 Scale bars, all 2 cm.

small sized slumps and micritized surfaces. Abundant lenses of coarse material alternate with them forming small pockets in depressions of the column surface. The grains are not genetically different from those found within the laminae but are much bigger. They are dark micritic peloids or aggregates, very poorly sorted (minimum at 0,12–0,2 mm, maximum at 1 to 1,5 mm, and thin films 0,03 mm thick). They show rounded and elongated bodies and strange vermiform, thin, and very dark micritic elements of probably algal origin. Nevertheless they are not comparable to the stromatolitic laminae of the neighbouring columns. They seem to come from elsewhere, perhaps from leathery algal mats disrupted prior to lithification. Peeling of mats can be due to biological activity (Monty, 1972, p. 777). This could explain their contorted appearance and, as they were richer in organic matter, their black colour. They are cemented by clear carbonate.

(c) There are many signs of pauses in the sediment filling indicated by micritized surfaces. They can be seen on eroded portions of the columns, on sharply cut laminae without crust or wall, on part of the crust and on muddy sediment upper surfaces. This sediment is an homogeneous micritic mud with silt-size particles and graded-bedded coarser grains in a sparry matrix; the upper flat surface with smaller grains testifies a discontinuous sedimentation in an agitated environment. No cracks have been found in the sediment and the particles are not *in situ* intraclasts.

(d) Along the overlapping portions of the columns outlined by the crust are protected voids, generally between crust and coarse sediment. These cavities were later filled by clear anhedral dolomite crystals.

They are fringed along the surface of the crust by small dolomite rhombs.

Comparisons

This form is a very unusual one. Irregular shape of column restricts the comparison to only few of the presently described stromatolites: *Baicalia* Krylov and *Poludia* Rabben. *Baicalia* and *B. burra* Preiss and especially *B. cf. burra* from Nabberu Basin present bulbous columns, some of them (Preiss, 1976, p. 27, fig. 16g) very similar to our form, but they are differentiated by the absence of wall and the close spacing of *Baicalia*. *Poludia* is defined by angular axes of growth as in *Topinamboura* but it has also a variable surface and coalescing closely spaced columns with oblique ramification. The association of the different characters of *Topinamboura* is completely new, also the type of microstructure.

Waterfall 3

The outcrop is composed of superposed large elongate flat domes interbedded with flat biostromes:

(a) At the base low relief domes (1,5–2,5 m long and 0,5–0,8 m thick) overlap each other. These bio-

herms are built by fan radially arranged columns of *Radiatina* (g. nov.) and upwards mixed bioherms are built by successive layers of *Radiatina* and *Katernia africana* Cloud Semikh. The tops of the bioherms are capped by slightly undulated laminae. On the edges rough columns are in continuity with the laminae making up the bioherms. Small pockets of carbonate breccia are found between some of the domes. Sometimes beds of shales are interbedded between the domes.

(b) A biostrome (0,8 m high) built by the straight discrete large columns of *Pilbaria boetsapia* (f. nov.) is sharply cut at the top by an erosional surface and overlain by flat laminae filling the irregularities and giving rise to the small vertical columns of *Katernia perlina* (f. nov.) and *K. africana*. The small bushy columns are often interbedded with flat lying or slightly undulate laminae of the same microstructure.

(c) At the top of the waterfall, new bioherms of *Radiatina* appear obviously the same as the previous, surrounding without any discordance a central zone built by short *Pilbaria*-like columns.

Group *Radiatina* gr. nov.

Type form

Radiatina isotropa

Group Name

From the latin *radiatus* in relation to the fan-like radial arrangement of the convex part of laminae.

Diagnosis

Very closely spaced columns with connecting laminae, fan-like radially arranged in a bioherm. The laminae are nearly flat with an asymmetric bumpy convex zone just before the interruption of laminae. Ramifications begin in the crestal zone at a constant angle.

Radiatina isotropa f. nov.

(figs. 3a, c; 7a)

Holotype

SA 6; base of fall 3; from five samples from different bioherms, beneath and above *Pilbaria* and *Katernia* biostromes.

Form Name

From the Greek *iso* + *tropos* (equal + turn) because of the regular repartition of crestal zone lines all over the bioherm.

Description

The close spacing of the columns prevents one from drawing them. Column shape is moderately turbinate with an horizontal section elongate at the base and lobate at the top of the bioherm. In vertical section the interspace filling appears in relief due to weathering. The laminae run almost flat and parallel with a very low total relief. On one side of the column, generally external, the lamina bumps, thick-

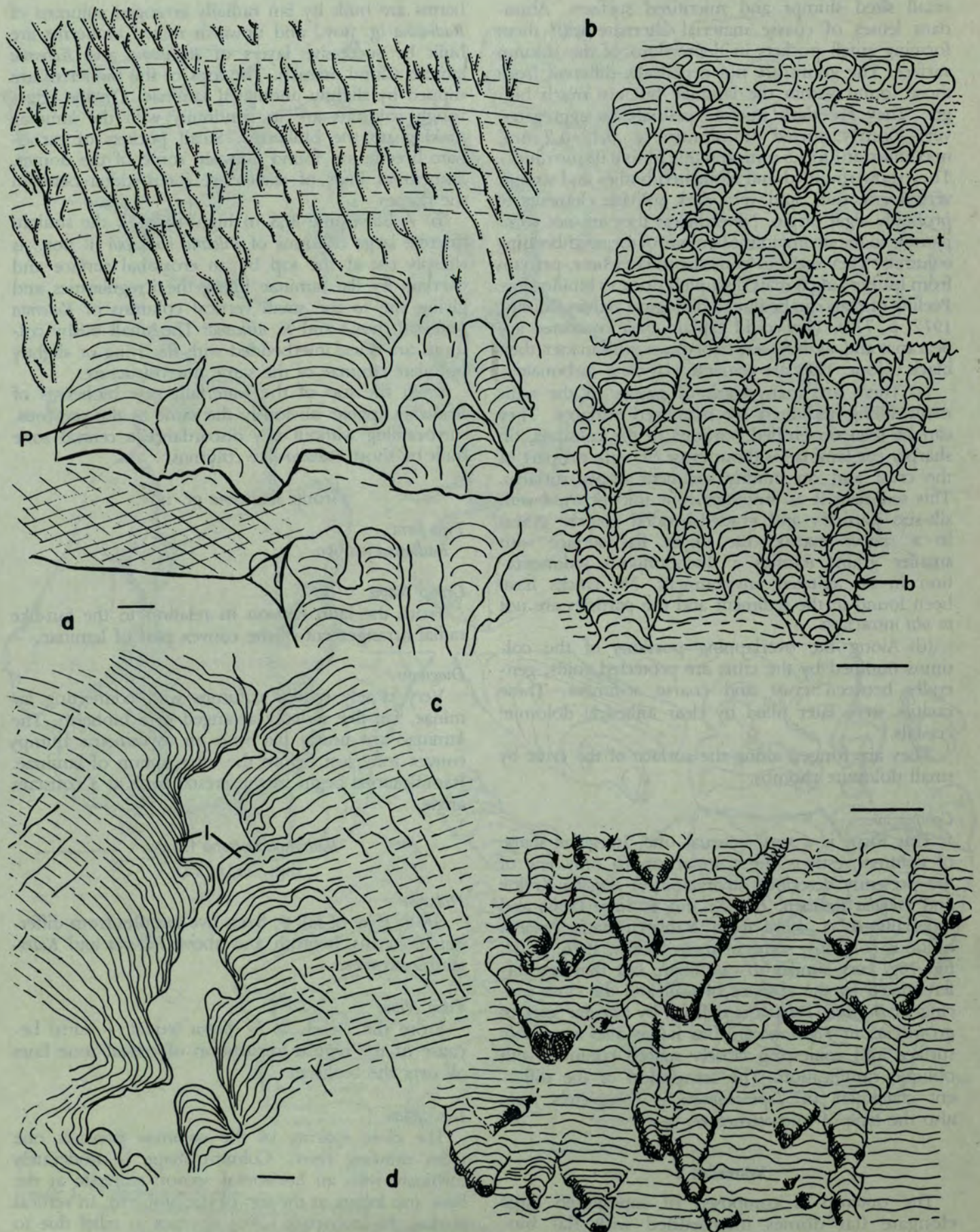


Figure 3. (a) *Radiatina isotropa* ramified columns directly growing on *Pilbaria*-like columns (P) forming the central part of the bioherms (top of waterfall 3), (drawing from JBS field photograph);
 (c) roughly columnar laminae (l) on the edges of two adjacent bioherms (drawing from JBS field photograph).
Katernia africana
 (b) columnar form with slightly different shape from base (b) to top (t) (SA 35, Eriks. coll.).
 (d) columnar to pseudo-columnar forms intermediate with *Radiatina* (Young coll.).
 (b) and (d) drawing from peels.
 Scale bars, all 2 cm.

ens, curls back and stops. This feature is called here a "crestal zone". It is generally thin, with a high degree of inheritance. A sparitic zone outlines it along the sharp edge followed by a cup-like laminated thin (2–3 mm) interspace. Then the new flat lamina begins, forming the other side of the column. The ramification, more abundant near the top and the edges of the bioherm, begins in the crestal zone with an upward displacement of the second crestal zone, following an angle of approximately 60°.

Microstructure

The laminae are poorly defined with no boundaries between them, except a discontinuous more or less clear carbonate layer at the base. Very small grains are found, especially in the more micritic layers, with few silt-size quartz and thin straight flat lying "filaments". The dark micritic pelloids are mostly rounded, with sometimes a clear central zone and darker envelope, and could be unicell colonies developed *in situ*, especially in *Radiatina* from the top of fall 3. They are generally small and well sorted. The flat-lying thin "filaments" are found especially in the stromatolite laminae. They are short, generally with thin dark limits defining a tube of clear carbonate (less than 0,012 mm). Some of them are monocrystals. On its sharp edge, the crestal zone is outlined by a sparitic pseudo-wall made of big crystals of sparite with dark boundaries. It differs from a wall made of coalescing laminae because of its sparitic nature. It cannot be confused with infilling carbonate, because of its relationship with the plunging laminae. This sparitic coating gives a strange relief to the crestal zone.

Interspace filling

It represents a very thin zone along the crestal zone frequently laminated with an upward convexity. The matrix is sparitic, different from the pseudo-wall and containing rounded, dark micritic grains of bigger size than in the stromatolite layers. They never present flat "filaments".

Comparisons

This form stands completely apart: fan-ramified columnar forms are known from the Riphean, especially *Anabaria* Komar, and in the Saharian area, *Serizia radians* Bertrand-Sarfati and *Tifounkeia* Bertrand-Sarfati but the three of them have normally spaced columns with convex-shaped laminae and true ramification (*Anabaria* in one plan and others in all directions) and none of them have a crestal zone. On the other hand, the crestal zone is completely different from that of *Conophyton* Maslov, which is more convex, made of vertical films or mats generally folded, and larger in size (up to 2 or 3 cm in diameter).

Group *Katernia* Cloud and Semikhatov

Type form

Katernia africana Cloud-Semikhatov, 1969, pp.

1046–47, Plate 3, Figures 4–5; the sample comes from Schmidtsdrift and is compared to a Boetsap columnar form.

Revised Diagnosis

Luxuriantly branching columns with many connecting layers and lateral surfaces ragged, in domal bioherms.

Katernia africana Cloud and Semikhatov

(figs. 3b and d; 7b and c)

Description

In Boetsap, they are mainly columnar with a laminated infilling that resembles interconnecting laminae. Columns are turbinate and straight. Horizontal section is generally sub-circular. The ramification begins upon an enlarged portion of column by two convex zones on the laminae, in external positions, so the ramification leads to daughter columns placed laterally on the ramification which is sometimes parallel and sometimes markedly divergent. The ramification rate increases upward with a size diminution, and columns become more bulbous and short. The laminae are slightly convex to flat in the larger portions of the columns and show a sudden plunging of the lamina on the edges in a kind of crestal zone. Tangential cutting presents very deeply convex laminae. Surfaces of columns are smooth with a pseudo-wall along the margins of the deeply convex laminae. In the flat laminated portions the laminae end sharply and sometimes extend through the infilling.

Microstructure

The laminae differ according to their shape. The convex laminae are mats of micrite-microsparite with sharp upper limits and a more sparitic layer at the base; radial alignments of small crystals that could be ghosts of filaments are visible within the micritic laminae. The crestal zone (inherited convex portion of laminae) is, most of the time, visible on each side of columns and along the edges there is a pseudo-wall of clear calcite crystals. In the flat laminae, small rounded pelloids (0,01 to 0,05 mm) are found most of the time in the sparitic zone at the base of the lamina. The rate of detrital material increases as the size of columns decreases.

Recrystallization is important, especially in the sparitic pseudo-wall (dolomite rhombs), but this wall cannot be only a recrystallization feature.

Interspace filling

Small rounded micritic pelloids (not larger than 0,15 mm) are found in a microsparitic to sparitic matrix. In the upper parts, where columns are smaller, the infilling is more thin-grained and alternating with sparitic layers in a convex downward laminated pattern.

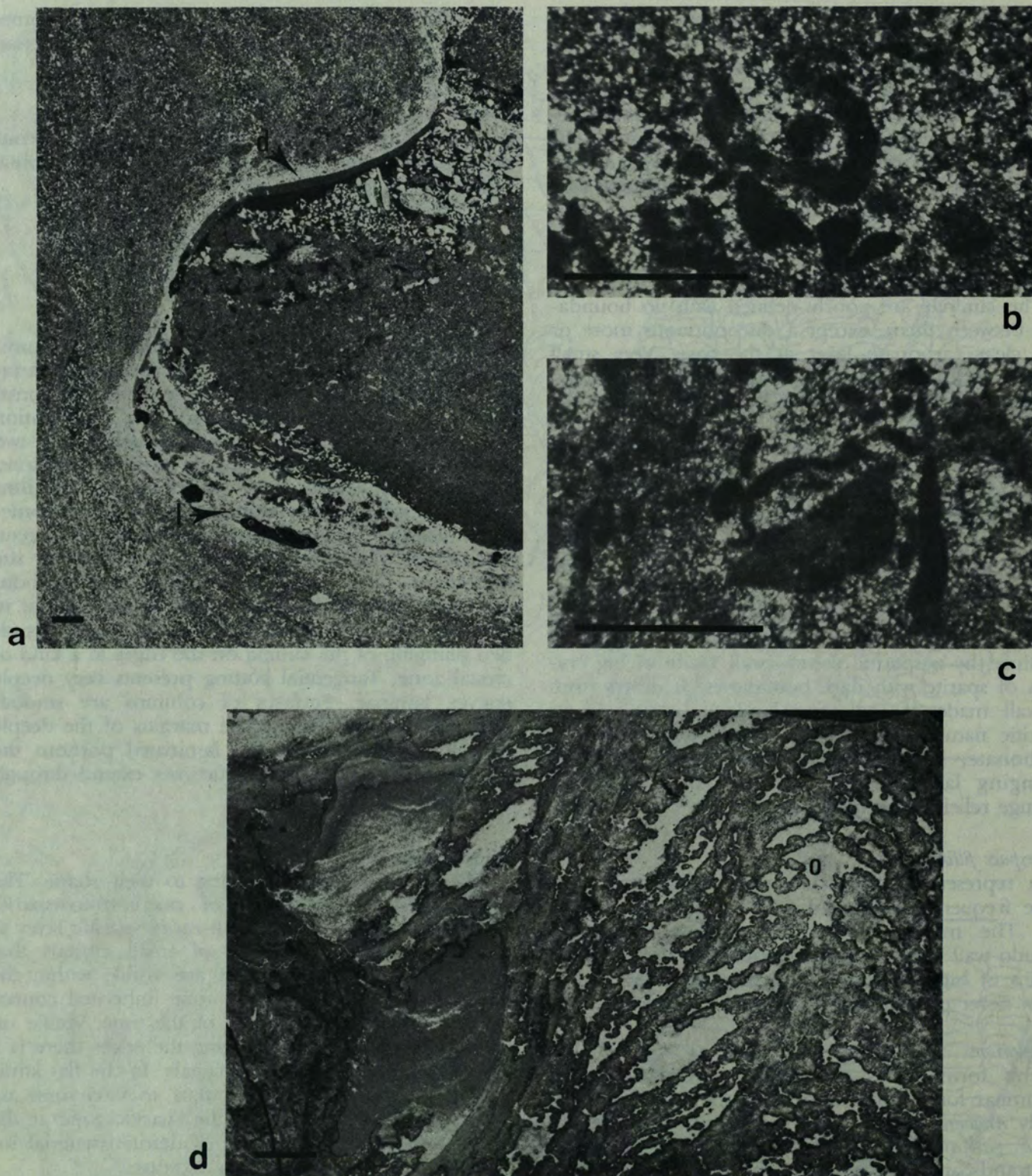


Figure 4. *Topinamboura insulata*

(a) column showing the drusy crust (d) along the columns at the top, passing to separate layers (1) on the flat portion (SA 2, JBS coll.). Scale bar, 1 cm;

(b) and (c) vermiciform structures in the sedimentary infilling (SA 2, JBS coll.); Scale bars, all 1 mm.

Pilbaria boetsapia

(d) recrystallization of the central zone in rounded pseudo-oid (o) (SA 10, JBS coll.);

Scale bar, 1 cm.

Negative prints from thin sections.

Comparisons

This form presents relationships in the field with both *Radiatina* and *Katernia perlina*. Their relationships are also found in the structure of the columns where the main features are present in the three forms: crestal zone in *Radiatina* and *K. africana*; pseudo-wall in the three of them; angle of ramification also the same for the three forms. We do not agree with the definition of *K. africana* given by Cloud and Semikhatov which insists on the interconnecting laminae. (See Revised Diagnosis). Here we have a true columnar form and the interconnecting algal laminae are often distinct from the stromatolite-laminae. In the Sibley group of Aphebian age, Hofmann (1969, Pl. 4) described very tiny columns, more often coalescing: they expand in every direction and have different microstructures. *Gruneria*

Cloud-Semikhatov has been compared to *K. africana* but has too many connecting laminae and larger columns. *Alcheringa narrina* Walter is of approximately the same age but has a very compact growth forming coalescing bushes with thicker laminae. *Alcheringa* has also well-defined laminae very different from this one.

Katernia perlina f. nov.

(figs. 5a-e, 6a-d, 7d)

Holotype

SA 11, from eight samples, three from the Young collection.

Form Name

From the vulgar Latin *perla* (pearl) because the columns have branches reminiscent of a string of pearls.

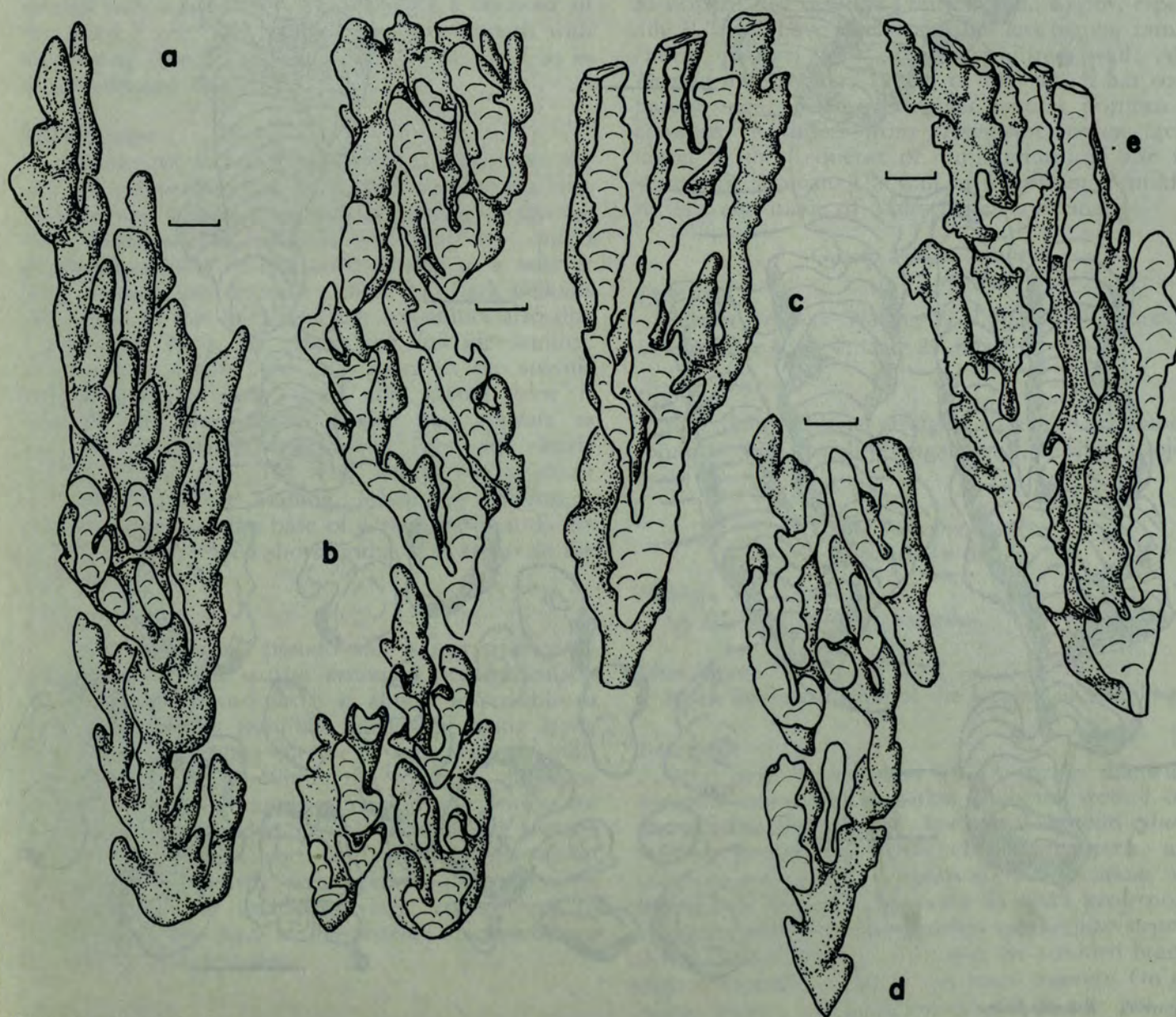


Figure 5. *Katernia perlina*
(a), (b), (d) holotype (SA 11, JBS coll.);
(c), (e) similar form from Schmidtsdrift syndinorium (SA 38, Young coll.).
Scale bars, all 1 cm.

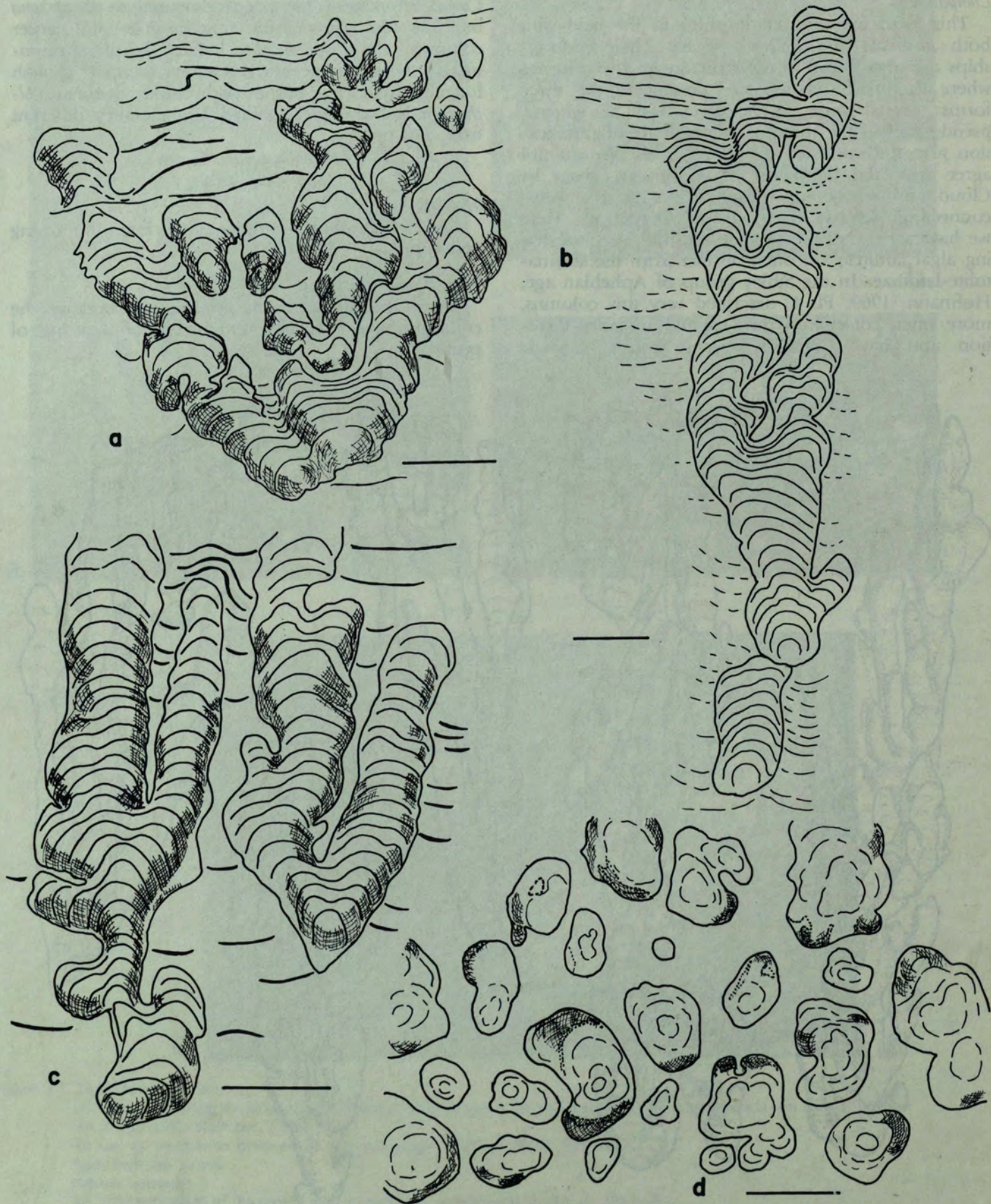


Figure 6. *Katernia perlina*
 (a), (b), (c) different mode of ramification showing small projections (SA 30 and 36 from Eriks. coll.; SA 11, JBS coll.);
 (d) horizontal section:
 (drawing from enlarged peels)
 Scale bars, all 1 cm.

Description

Small pearl-like, slightly turbinate, vertical columns with a diameter less than one centimetre and subcircular or slightly lobate horizontal section. Interspace between columns reaches ten centimetres, but every small straight and unramified portion is never more than 1,5 to 2 cm high. The ramification resembles parts of *K. africana*, especially the smaller columns of this type. As columns enlarge, laminae flatten and are disrupted in the middle and two smaller columns develop with steeply convex laminae on the outer edges. One of the new columns stops and the other ramifies after 1 or 2 cm. The digitations are sometimes very short and the whole column presents a characteristically bumped shape. Very often the continuity of the different portions of one bush is not visible on the surface of the sample and appears only on the drawing. The laminae are convex with a relief of 0,5 to 1 cm for a diameter of less than 1 cm. The margin surface is smooth with enveloping laminae and a sparitic pseudo-wall as in *K. africana* and *Radiatina*.

Microstructure

Laminae are not well defined but, when they are not too recrystallized, it is possible to see at the bottom of the lamina discontinuous lenses of sparite, with small micritic pelloids and very few quartz grains (from 0,01 to 0,03 mm) passing to a micritic layer without any boundary. Few thin dark pelloids are found in this layer which is sometimes also discontinuous. Near the edges, the micritic laminae only plunge deeply and fade away in the sparitic pseudo-wall. In some cases, the sparitic base is reduced and the micritic upper mat appears as cushions irregularly superposed. They are clearly limited at the top. The wall always has a sharp boundary with the infilling. When the column is tangentially cut at the base of a ramified branch the wall is well developed showing that it is a part of the algal growth.

Secondary alteration

First, the sparitic pseudo-wall is recrystallized in bladed crystals of sparite arranged perpendicularly to the edges. Sometimes it is almost impossible to see the continuity with the micritic plunging layer. Sometimes late joints cut the crystals with an infilling of clear calcite. Within the columns, the same type of recrystallization occurs and the lenses are surrounded by bladed crystals leading to pseudo ooids with a dark core and a dark dissolution boundary. In heavily weathered samples, ferrous oxide appears in undulated rings, concentric to the margins. No trace of the primary microstructure of laminae then remains.

Interspace filling

It is often more detrital than in *K. africana*: intra-clasts of dark micrite (up to 1,5 to 2 mm) are embedded in a sparite. Surfaces of the layers are of dark

micrite with a precise upper limit. They probably are algal but they have no continuity with the stromatolite layers.

Comparisons

It differs from *Radiatina* by the convex shape of laminae giving rise to small straight ramified columns. It differs from *K. africana* by the true columnar growth, spacing of columns, smooth margin, less turbinate shape and more important rate of ramification. In the Transvaal dolomite they are comparable to a small ramified column from Schmidtsdrift, also mixed with *K. africana*, differing only by the absence of the sparitic pseudo-wall. There are similarities also with columns of *Sapinia* (see p. 18 et sqq.) with lots of ramification and sparitic wall but different other features. Besides these local comparisons, they are so small that it is difficult to compare them to normal size columns: only *Patomia* Krylov, especially *P. ossica*, have similar size but less regular ramification pattern and no recrystallized wall. Also *Patomia* ind. (Walter, 1972b, p. 165) which has comparable age presents straighter vertical portions of columns. It differs from *Gymnosolen ramsayi* Steinmann by the frequency of ramification and also the texture of laminae. The wall in *Gymnosolen* is multilamellate and made of coalescing micritic mats.

Group *Pilbaria* Walter

Type form

Pilbaria perplexa Walter 1972, p. 167, Figures 7, 51–52, Plate 4, fig 4; Plate 29, figs 2–7.

Diagnosis

Subcylindrical long, straight, parallel, very smooth columns with small elongate niches with projections.

Pilbaria boetsapia f. nov.
(figs. 4d, 8a–d, 9)

Holotype

SA 10, from two big samples.

Form Name

From Boetsap; name of the locality of sampling.

Description

Very large (more than 10–12 cm in diameter), straight, subcylindrical, rather bulbous, vertical columns. The multilobate horizontal section shows lateral projections generally asymmetric and without preferential orientation. Ramifications are moderately frequent and occur as small projections, always protected in deep niches (pocket-like depressions, Walter, 1972, p. 167), and the ramified branch stays completely inside of the main column. On the edges appear small digitations which are just depressions in the laminae and do not lead to true branching. In the upper third of the columns appears parallel true ramification, leading to a size di-

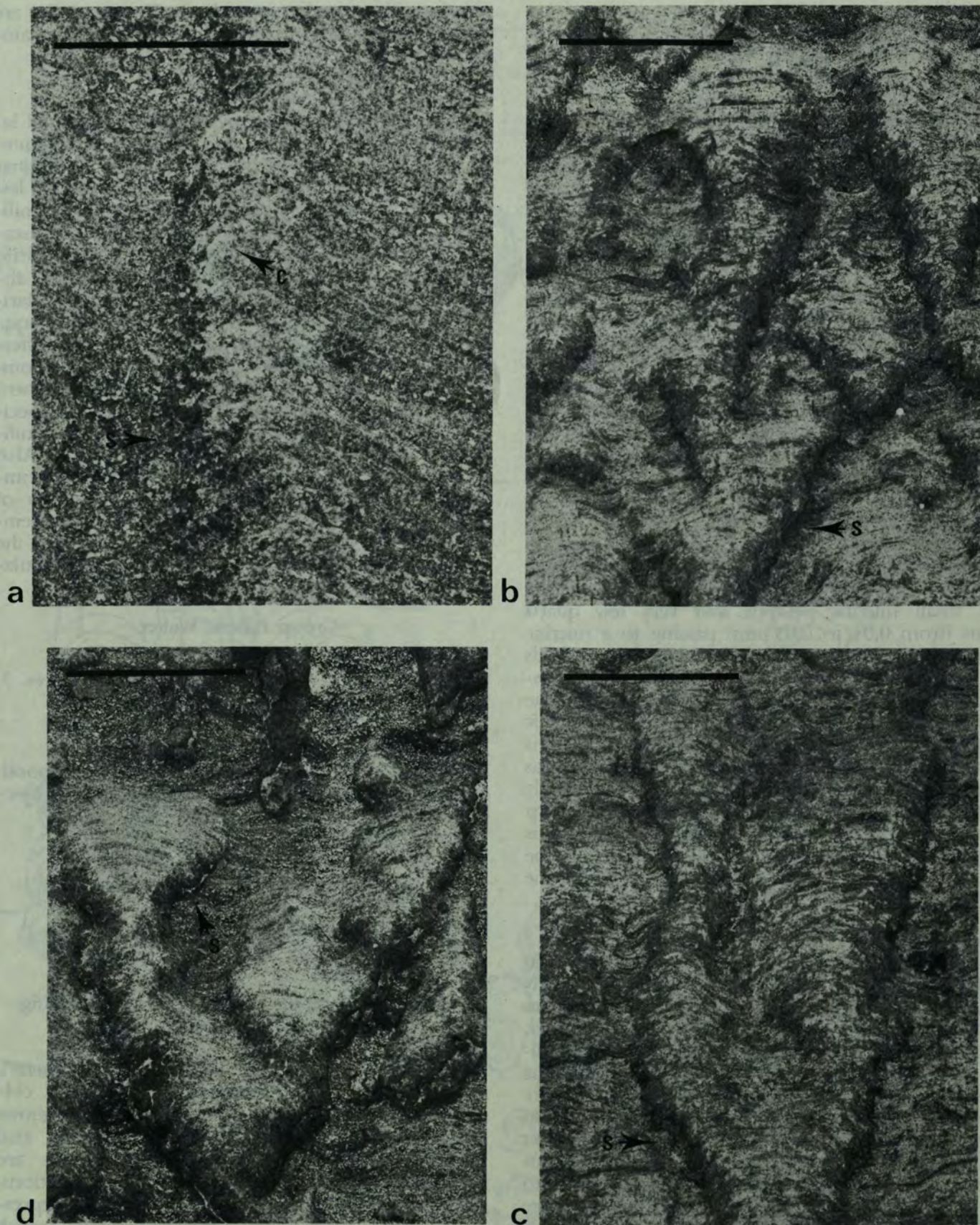


Figure 7. *Radiatina isotropa*
 (a) crestal zone (c) and sparitic pseudo-wall (s) outlining the small interspace (SA 12, JBS coll.).
Katernia africana
 (b) higher part and (c) lower part of one sample (cf. Fig. 3b, d), pseudo-wall (s) (SA 35, Eriks. coll.).
Katernia perlina
 (d) holotype, pseudo-wall (s) (SA 11, JBS coll.).
 Negative prints from peels or thin section
 Scale bars, all 1 cm.

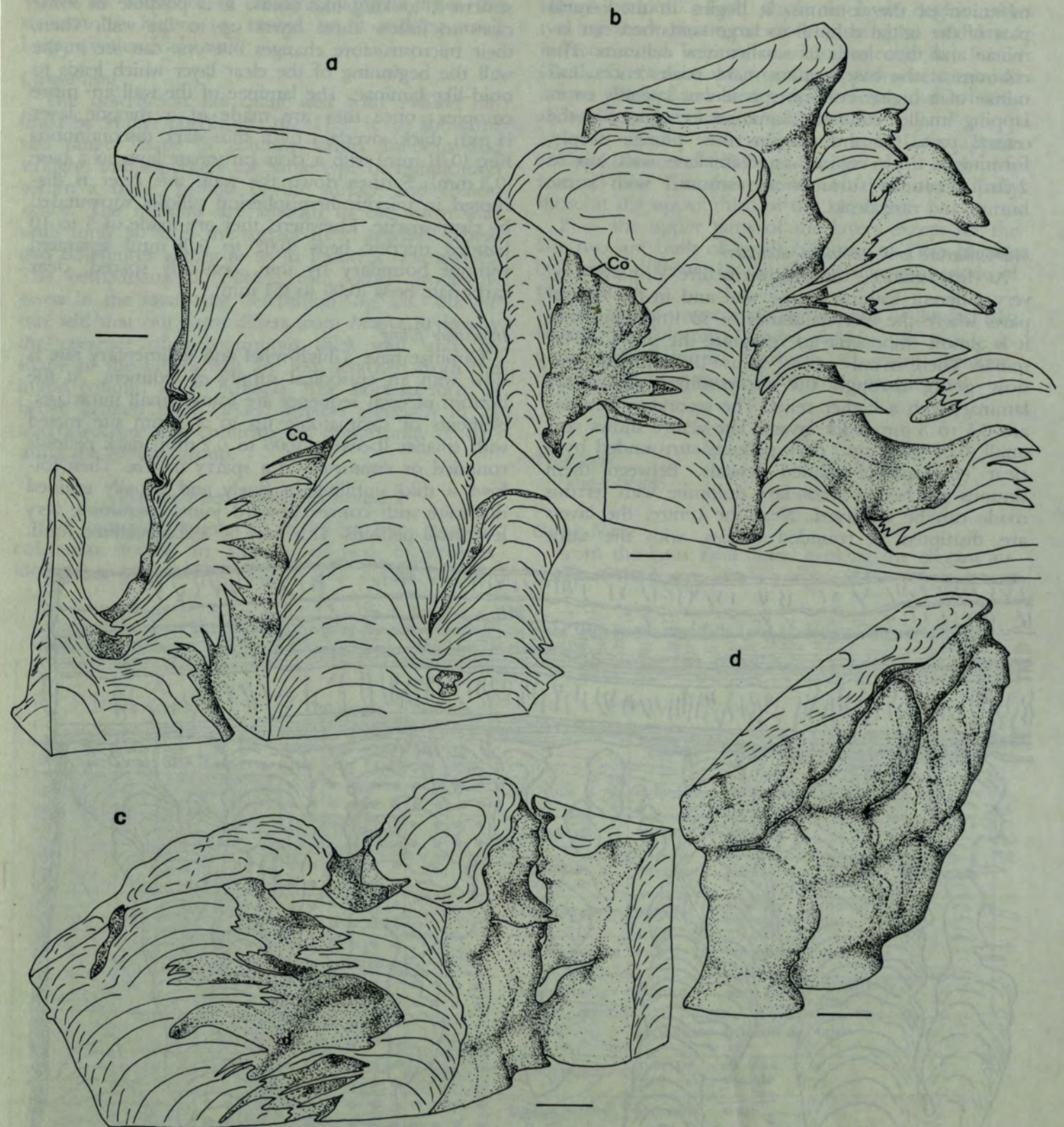


Figure 8. *Pilbaria boetsapia*
 (a) coalescence (Co) and small bumps on the surface;
 (b) coalescence (Co) and ramification in a niche; on the right small individual short columns isolated within the matrix;
 (c) ramification in the upper third of columns beginning with a series of depressions (d) in the central part of columns;
 (d) ramification in deep niche.
 (SA 10, JBS coll.).
 Scale bars, all 2 cm

minution of the columns. It begins in the central part of the initial column as large voids between laminae and then leads to smaller new columns. The columns at the base present many coalescences. Laminae of a higher column spread out laterally overlapping smaller columns. Laminae are convex in the central part. On the margins they plunge deeply, forming a thick vertical multilamellate wall (up to 2 cm). Column surfaces are smooth with some bumps and rare peaks.

Microstructure and secondary alteration

At first glance, the microstructure displays two very different features in the wall and in the central parts where the recrystallization is so important that it is almost impossible to recognize the primitive laminae. There is only a very diffuse dark micritic shadow going through the recrystallized secondary laminae, with a higher relief. The secondary laminae are 0,5 to 3 mm thick layers. The centre shows very small (0,01–0,06 mm) dark pelloids surrounded by a clear envelope of bladed crystals. Between them sinuous patches of secondary dolomite with ferrous oxide can be observed. Near the centre, the layers are disrupted in rounded bodies, with the same

structure, looking like ooids. It is possible in some cases to follow these layers up to the wall. Then, their microstructure changes but one can see in the wall the beginning of the clear layer which leads to ooid-like laminae. The laminae of the wall are more complex: once they are made of a micritic layer (1 mm thick) overlain by a thin dark discontinuous film (0,01 mm) with a clear carbonate layer as a base (0,3 mm). Farther down the wall, this layer is disrupted in micritic hemispherical pillows surrounded by clear sparite. Elsewhere, they are made of 5 to 10 banded micritic beds (0,02 to 0,06 mm) separated without boundary by thin, regularly spaced, clear carbonate beds (0,06 to 0,1 mm).

Interspace filling

Laminae have a high relief and sedimentary rate is slow with an episodic supply of sediment. At the bottom of each sequence are found small intraclasts: elements of stromatolite up to 2–3 mm size mixed with smaller (between 0,06 to 0,2 mm) dark pelloids rounded or contorted in a sparry matrix. Then follows a thick infilling of finely and equally grained dolomite with convex upward joints containing very few small pelloids. This may be a recrystallized mud.



Figure 9. *Pilbaria boetsapia*

Flat laminae overly *Pilbaria* ramified columns, filling the surface irregularities, then pass to an alternation of tiny columns of *Katemia perlina* and flat laminae.

(drawing from Eriks. field photograph)

Scale bar, 15 cm.

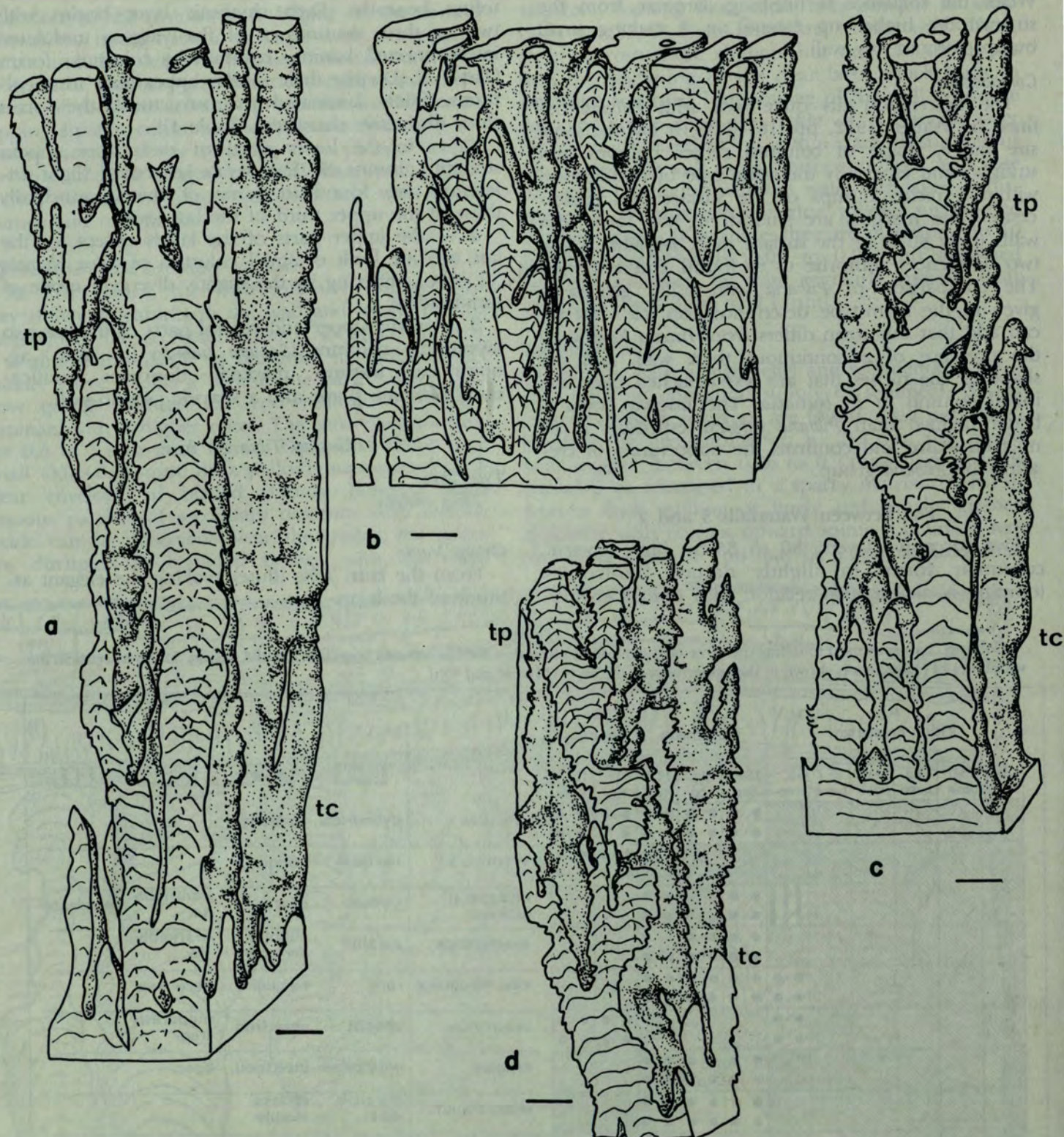


Figure 10. *Tibia cristata* (tc) at the base and *Tibia plumata* (tp) at the upper part (a), (c), (d) (respectively SA 13b, 13a, 14a, JBS coll.); (b) *Tibia cristata* isolate base of (a). Scale bars, all 1 cm.

Diagnosis

Tiny, discrete, straight columns, ramification running from parallel to slightly divergent. The microstructure is composed of micritic mats very regularly superposed, presenting in the centre of columns a small (less than 1 mm) wart-like protuberance. The high inheritance of this crestal zone leads to deeply convex laminae shape.

Tibia cristata f. nov.

(figs. 10a-d; 11a, b, d and f; 12a)

Holotype

Base of SA 13-a, from seven samples of the same area.

Form Name

From the Latin *crista* (crest) in respect to the crestal zone shown by these forms.

Description

Small (between 1 and 2 cm of diameter) closely spaced vertical columns with a more or less circular horizontal section. Ramification is rare and generally passive (parallel), ramified branch stops quickly after branching. Coalescences are quite frequent, also interconnecting laminae. At the passage to *Tibia plumata* many small columns disappear and the others enlarge and begin to ramify.

The surface of the columns is very smooth, even if laminae are sharply interrupted along the edges. Laminae are very regularly stratified with a very equal thickness. They are moderately convex, except when they present a crestal zone which leads to a deeply convex pattern, in vertical section. This crestal zone appears mainly in the central parts of columns. It has a good inheritance and could be followed for tens of centimetres. Seasonal laminae appear in some of the layers.

Microstructure

As the microstructures of *Tibia cristata* and *Tibia plumata* are very similar, we will describe them together. They appear as a "doublet" dark and clear layer with an upper limit well defined. The dark micritic layer is continuous with less than 0,2 mm thickness. The clear microsparitic layer is generally discontinuous and its thickness is around 0,4 mm. In fact there are few differences between them. On the margin, laminae are sharply interrupted and present in *T. plumata* small peaks and irregularities capping small voids filled by sparry calcite. The upper dark mat extends often through the interspace, joining adjacent columns by a convex upward lamina. The main feature is the crestal zone. It is very difficult to define because it has no special structure. The crestal zone appears as a conical micritic bump on the top of a normally convex lamina and cross-cutting the clear layer. It extends in every direction as a very small bump (up to 1,2 to 1,3 mm). The next lamina then has a more deeply

convex shape and it reproduces also the crestal zone, so the feature goes on for one to five centimetres. It seems, but we cannot prove it, that there are very small (5 to 10 microns thick) tabular filaments through the dark laminae and radiating in the crestal zone. It differs from the *Radiatina* crestal zone by its central position and its smaller size. Sometimes the crestal zone ramification leads to short branches. In a S.E.M. study Macgregor *et al.* have described "tapering filaments" in these columns (1974, fig. 5).

Secondary alteration

All over the rock, and forming a roughly banded pattern, is a dolomitic angular network of crystals easier to see in the infilling where they could be confused with detrital grains. It is not present in the small voids on the edges of *T. plumata*.

Interspace filling

Microsparitic thick layers with very few grains are overlapped by thin discontinuous micritic dark laminae convex downwards and sometimes in continuity with the upper part of the darker layer of the columns. The probably muddy sediment is contemporaneous with the column growth.

Comparisons

Early Proterozoic forms comparable to *Tibia* are *Gruneria* and *Eucapsiphora* Cloud-Semikhatov. *Gruneria*, however, has rarely discrete columns. Comparison with *Eucapsiphora* is more interesting but the gross form of *Tibia* is more evenly cylindrical without enlargement before branching and no connecting layers throughout the whole colony. The mode of occurrence is very different: *Eucapsiphora* grows encrusting high places and sometimes overhangs. This form can be compared to many of the small branching columns of upper Riphean stromatolites: *Gymnosolen* Steinmann, *Jurusania* Krylov, *Boxonia* Koroliuk or *Kulparia* Preiss and Walter. It differs from both *Gymnosolen* and *Boxonia* by the absence of wall and the type of branching. From *Jurusania*, the distinction is based on the smoothness of surface and absence of peak and cornices. Also it is easily distinguished from *Kulparia* by the presence of a wall and the biostrome setting. But even if there are some affinities between *Tibia* and Riphean stromatolites, they mainly differ by the existence in *Tibia* of the unusual crestal zone structure giving an angular shape to the laminae and the smooth surface without enveloping laminae or wall.

Tibia plumata f. nov.

(figs. 10a, c and d; 11c; 12b)

Holotype

Upper part of SA 13-b, from four samples in the same area.

Form Name

From the Latin *pluma* (feather), because the form has a light ramified framework.

Description

Small tiny columns straight and more or less turbinate with a lobate horizontal section. The ramification is more frequent than in *Tibia cristata* and is either parallel or slightly divergent. The digitations are in small straight columns (2 cm high) or less frequently in permanent columns of equal diameter. The surface of columns is ragged and the laminae projected as angular peaks. The crestal zone is also present but less continuous. Laminae super-position is very even and no seasonal differentiations are visible. The lamina shape is gently convex to angular and near the edges there is an interruption of laminae which continues afterward for a few millimetres, making a kind of projection that is more striking in *Sapinia*.

Microstructure and interspace filling

They do not differ from *Tibia cristata*. Most of the time, the microstructure is less defined and interspaces are larger with small pockets of very small pelloids.

Comparisons

Comparable Riphean forms are *Kulparia* Preiss and Walter and *Eucapsiphora* Cloud-Semikhatov, ex-

Table 2

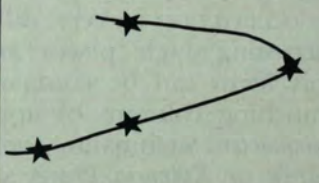
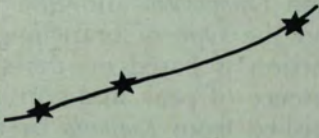
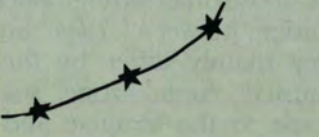
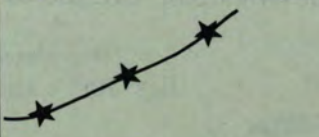
Rhythmicity in the chronological succession.

A: *Tibia cristata*;

C: *Sapinia fucoides*

B: *Tibia plumata*;

L.pl.: Planar laminations.

n° Sample	Form	Lam. Pl.	A	B	C
15	A C A L. Pl.				
14 b	C A L. Pl.				
14 a	B A L. Pl.				
13 b	B A L. Pl.				
13 a	B A L. Pl.				

cept for the crestal zone and bioherm setting. They differ from *T. cristata* only by the turbinate attitude and divergently mode of ramification. One form mentioned by Hoffman (1974, p. 863, fig. 10) as a basin floor stromatolite can be compared to *T. plumata* of Aphebian age by the conical shape and low relief of laminae, absence of wall. Unfortunately there are no indications about microstructure, ramification, etc.

Group *Sapinia* gr. nov.

Type form

Sapinia fucoides

Group Name

Sapinia, from the French "sapin", a conifer tree.

Diagnosis

Tiny regular columns with very frequent ramification always at the same angle, and small bumpy digitations on the surface. The surface is outlined by a sparitic pseudo-wall.

Sapinia fucoides f. nov.

(figs. 12c-d; 13a-e)

Holotype

SA 14-b, from four samples coming from the same area.

Form Name

From the Latin *fucus*, name given to a forking brown algae.

Description

The columns are tiny, oblique and turbinate with a diameter between 0,5 and 2,5 cm. The horizontal section is multilobate. Interspaces between columns are larger than in *Tibia* (between a third and half of the total volume). The ramification has two different settings: one in two small markedly divergent columns. In some of the samples, daughter-columns are asymmetrical and the shorter ones are always in the same position in respect to the main column. The other type is a very short digitation, as the small pseudo-columns are not longer than 4-5 mm. They are made by a short, straight interruption of the laminae parallel to the direction of normal ramification and they are really distinct from the main column. The discontinuity is filled by sparry calcite. They appear only in the outer portion of columns. In the inner portion, columns show more inter-connecting laminae. The surface of columns is smooth with short enveloping laminae and a sparitic pseudo-wall along the crestal zone, larger than in *Tibia* (2-3 mm).

Microstructure

The lamina microstructure is the same as that of *Tibia* with perhaps a little more silt-size pelloids and quartz in the flat laminae. Crestal zone resembles more *Radiatina*, with a larger bumping of the lamina outlined by a sparitic pseudo-wall. It is possible to see the plunging micritic laminae overlapping crystals of the pseudo-wall arranged perpendicularly to

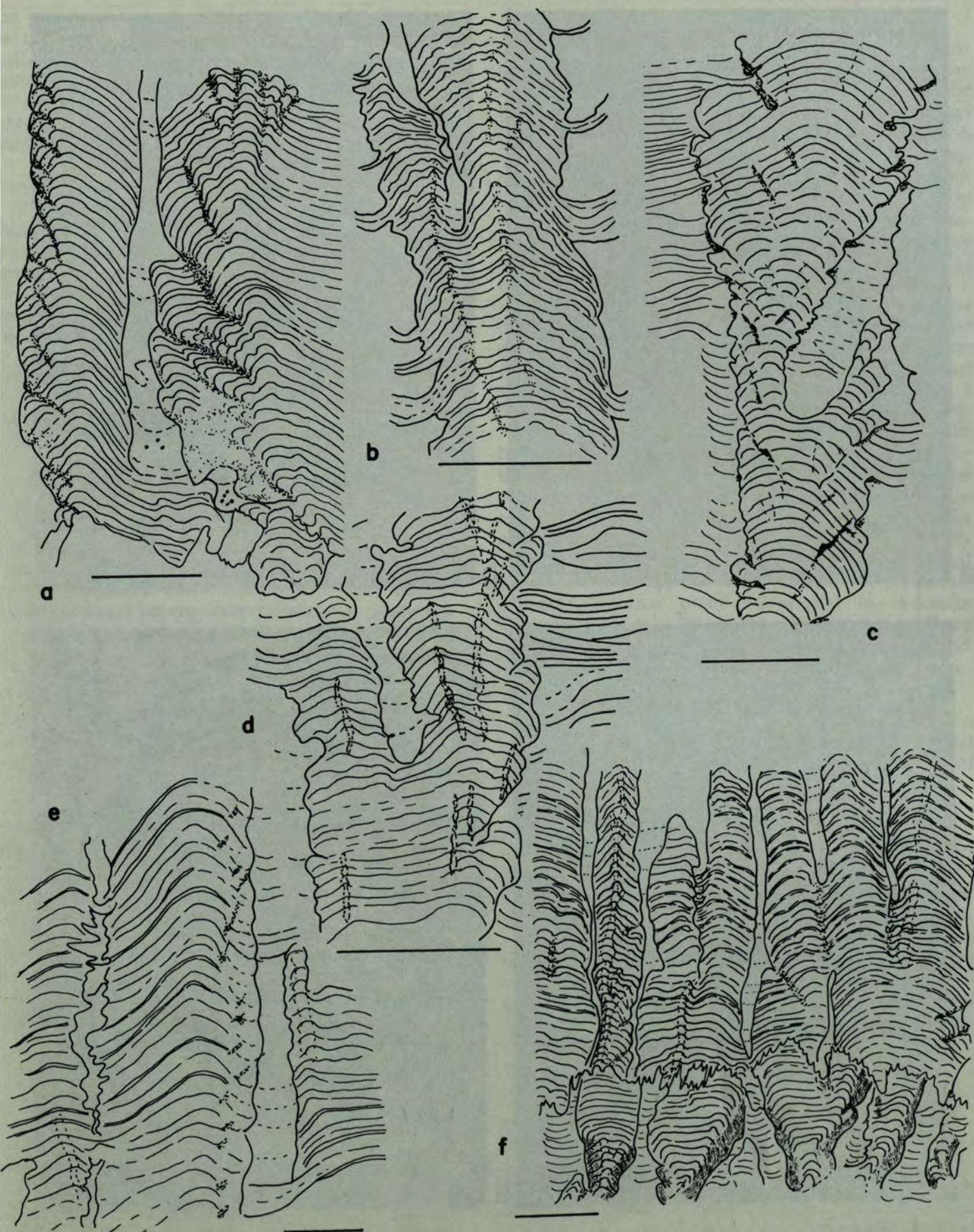


Figure 11. *Tibia cristata*

- (a) and (f) columns overlying *Sapinia* (SA 15, JBS coll.);
 (b) holotype: base of the first layer of *T. plumata* (SA 13a, JBS coll.);
 (d) base of *Sapinia* (SA 14b, JBS coll.)
 (e) base of SA 13b (JBS coll.)

Tibia plumata

- (c) SA 13a (JBS coll.).

Drawings from enlarged peels.

Scale bars, all 1 cm.

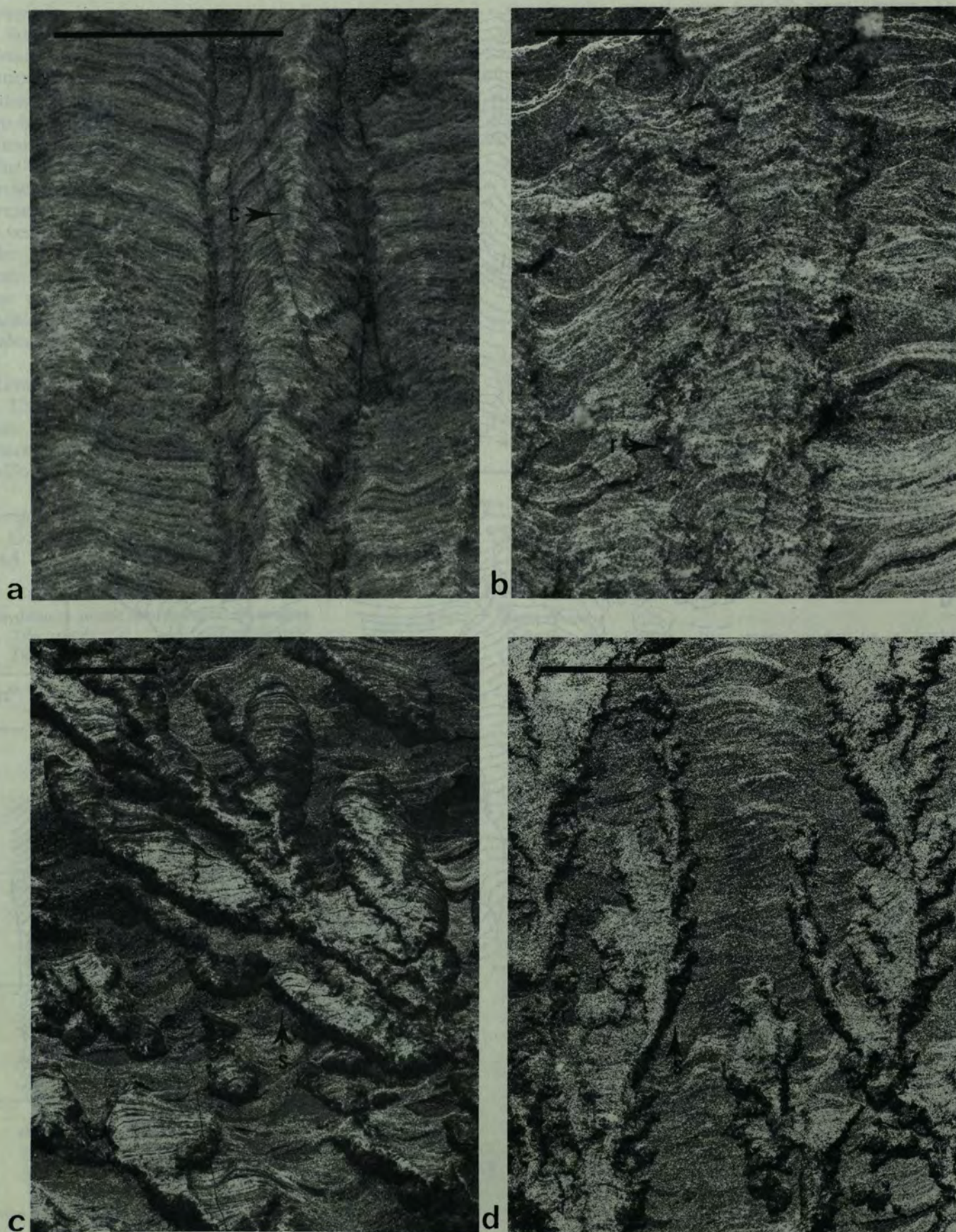


Figure 12. *Tibia cristata*

(a) crestal zone (c) (SA 15, JBS coll.).

Tibia plumata

(b) rugged surface (r) (SA 13b, JBS coll.).

Sapinia fucoides

(c) inclined columns, sparitic pseudo-wall (s) (SA 48, Eriks. coll.)

(d) straight columns cut perpendicularly to the direction of the general inclination; sparitic pseudo-wall (s) (Young coll.).

Negative prints from peels.

Scale bars, all 1 cm.

the margins of previous laminae. This fabric cannot be related to a neomorphic origin of the pseudo-wall. The sparry filling of small discontinuity separating digitations is different from the sparite filling the voids on the margins of *Tibia plumata* and it presents an undubitable boundary with the sediment filling of the columns.

Interspace filling

It is a very finely laminated sediment, perhaps algal but not connected directly to stromatolite laminae. Micritic thin laminae are frequently convex upward and along the column margins are crescents of microsparite with small pelloids at the base and a fringe of sparite crystals at the top. They are generally discontinuous.

Comparisons

First of all we will discuss the reasons why we make three distinct forms. The microstructures are fairly similar and can support the idea that there are no changes in the algal coenose throughout the whole biostrome. The sediment infilling, carbonate mud and algal laminae, is also quite the same. Nevertheless gross morphologies present several characters that differ (Table 1) and in absence of clear use and definition of what Krylov (1975, p. 73) named "bioherm series" we have to give different names to forms having several distinctive characters.

We will now compare *Sapinia* to tiny columns of the same age.

One of them is the *Patomia* ind. described by Walter (1972b, pp. 165–166) which shows, as the Riphean one, small tiny ramified columns with bumpy surfaces. However, they differ by the wall which is multilamellate in *Patomia* Krylov and the ramificated pattern which is more complex (two sets of ramification) and more regular in *Sapinia*. At least *Patomia* Walter has no defined microstructure and the Riphean one shows undulate highly convex laminae with a multilamellate wall. The other possible comparison is with *Katernia perlina* with which it has some common features, especially the sparitic pseudo-wall and the mode of ramification. But in *K. perlina* are never found the small marginal digitations nor the asymmetric wall, and the microstructure is completely distinct. Other possible comparisons could be made with Riphean stromatolites such as *Tungussida* which presents active and frequent ramification. *Tifounkeia* Bertrand-Sarfati is comparable by the size and the slightly divergent ramification, but does not present any of the other features of *Sapinia*. *Parmites* Raaben has turbinate columns, often ramified but with a radiating pattern and also it has ragged surface and flat laminae. *Katavia* Krylov presents bumpy but less ramified and bigger columns. Differences with *Vetella uschbasica* Krylov are present as this form is more compact with interconnected laminae, no crestal zone. We conclude that *Sapinia* and *Tibia* are completely original forms.

Waterfall 2

Low elongate domes with few ramified stromatolites and generally flat-lying to undulated laminae are found at the base of the fall. In the middle of the fall, a massive bed of oncolitic grainstone displays big ripples interpreted by Truswell and Eriksson (1973, fig. 15, p. 14) as deposited in a high energy environment. Above them new domes occur not very different from the previous ones. Near the top of the outcrop appear biostromes of straight columnar forms. They present several layers separated by erosional surfaces and overlain by new columns of the same structure and shape: *Pilbaria inzeriaformis*, f. nov. Upon the undulate surface the new columns begin in continuity or not with the previous one (fig. 15f). One of the layers presents straight discrete columns (eroded?) enveloped by the uppermost concordant laminae to the very base. Acquiring a mushroom-like shape, they touch each other at the top. Around the heart-like cavity between columns at the base concentric layers of sparry calcite are separated by thin dark boundaries (fig. 14f). Coarse dolomite fills the central core. The general column size decreases from base to top and they present less seasonal laminae. On the flat above the fall, small domical stromatolites, generally non-columnar, contain one layer of flat-lying cryptalgal laminae with juxtaposed big "rosettes" of crystals of probably gypsum pseudomorphosed in dolomite (Bertrand-Sarfati, 1976). At the very top of the fall are elongate columns and shales marking (Truswell and Eriksson, 1973, p. 20) the end of a regressive sequence.

Osagia-like oncolites

The mega ripples described by Truswell and Eriksson (op. cit.) are made by an accumulation of small spherical bodies.

Description

The sediment is a dolomitic grainstone with lenses of "grumelous" matrix (Cayeux, 1935) formed by small grains (between 20 to 200 microns) cemented by large crystals. The big grains forming the framework (0.5 to 3 mm) are poorly sorted. They are more or less spherical built by a thick well-defined cortex of concentric sparitic layers (up to 40 for biggest grains). Many grains present a discontinuous growth of this envelope with inverted pattern (Logan *et al.*, 1964) preventing us from attributing them to oolites. Very few envelopes present disrupted external laminae.

Interpretation

It is not easy to recognize the original framework: is it a grainstone or a recrystallized packstone? Two features favour this latter interpretation: (a) existence of syntaxial crystals through the cement and the oncoid testify that cement is of second order; (b) presence of large quantities of very small elements contained within larger crystals could signify an initial muddy or silty matrix. The origin of the grains is also uncertain: con-

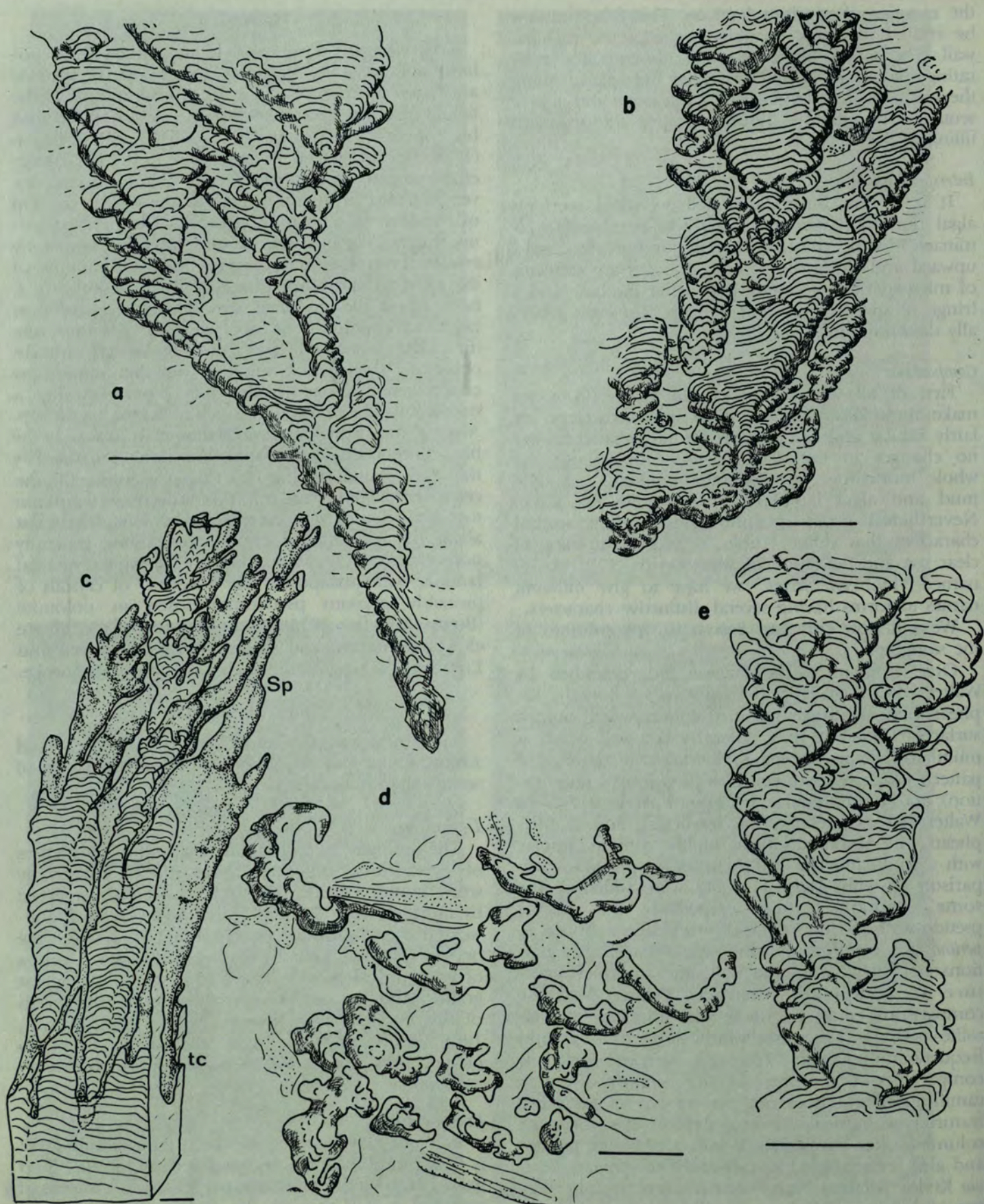


Figure 13. *Sapinia fucoides*

(a), (b) and (e) drawing from enlarged peels; (e) cut perpendicularly to the direction of the inclination i.e. in a plan perpendicular to b (SA 14b, 15, 48 from JBS and Eriks. coll.);

(c) succession of *T. cristata* (tc) and *Sapinia* (Sp) (SA 14b, JBS coll.);

(d) horizontal section of the top of (c).

Scale bars, all 1 cm.

cretionary grains (caliche pisolites) or oncolites: (a) as many vadose pisolites, the grains are highly asymmetric with sometimes strange re-entrant angles of new laminae upon the previous laminated spheroid (Dunham, 1969). But here asymmetry is not evenly oriented on each grain and we find none of the other features of vadose pisolites (Scholle and Kinsman, review 1974, pp. 912–913); (b) the possibility of an algal origin in the absence of true organic remains is supported by the existence of normal spherical *Osagia*-like grains but there is no true analogue in modern environments (Loreau, personal communication). Modern forming oncolites have a smaller size with a large nucleus and only few concentric laminae (Loreau and Purser, 1973). Asymmetric oncolites are known from quiet water environments (Freeman, 1962) and they often present an incomplete envelope with internal unconformity.

Conclusion

We cannot be sure of the original structure of the rock but there are good possibilities that it has been first a packstone. Oncolites are asymmetric and therefore could have been generated either in a shallow and protected quiet water environment or in deeper water beneath the wave action zone. The surface of oncolites presents very few abrasion features and transportation in highly agitated environment cannot be proven: fore-reef ripples in the Australian Great Barrier Reef are present in quiet water (Monty, 1974, film).

Group *Pilbaria* Walter

Type form

Pilbaria perplexa Walter 1972, p. 167.

Plate 4, fig. 4; Plate 29, figs 2–7; text figs. 7, 51–52.

Pilbaria inzeriaformis f. nov.

(figs. 14 a–f, 15)

Holotype

SA 23, from four samples from the same area.

Form Name

From *Inzeria* Krylov, Riphean stromatolite group to which this form is very similar.

Description

Straight, subcylindrical columns with a diameter varying between 2 and 10 centimetres. Horizontal section shows closely spaced subcircular shape of columns with deep invagination when a ramification is cut. Frequency of ramification is variable from one layer to another. Most of the time it shows a parallel type which leads to smaller columns or to one short column quickly stopped. In this case it is included in a niche within the initial column. Columns show periodic enlargements and constrictions outlined by a depression of the surface. They correspond to the same kind of digitation found in *Sapinia* or in *P. boetsapia*. The relief of deeply convex

laminae reaches 3 to 5 cm and the column surface is smooth with enveloping laminae forming a multilamellate wall less continuous than in *P. boetsapia*. There are few interconnecting laminae. Some layers present seasonal differentiation of laminae zone with distinct microstructure. Laminae unconformities appear in the central portion with bumps or folds. They are soon rubbed out by the following lamina rapidly filling the depressions. This produces a discontinuous conical shape to the laminae.

Microstructure and secondary alteration

There are few differences between central portions of columns and walls, just a decrease of the laminae thickness (from 1,5–3 mm to 0,2–0,8 mm in the wall). Microstructure is complex and presents four different elements: (a) a micritic mat with small dark pelloids sometimes vermiform (0,06 mm); (b) bigger grains of brown micrite and a clearer centre (0,1 to 0,3 mm) in a sparry matrix appearing within the mat; (c) a dark filmy upper limit; (d) clear sparitic layers striated by dark thin films (less than 0,006 mm) most of the time discontinuous. The succession of these elements is relatively variable. The big grains occur in continuous mats or within hemispherical bumpy fenestrae, with a somewhat inverted graded bedding. The filmy and sparitic doublets could develop separately giving rise to distinct zones of laminae. Then the regular thin films pinch and swell separating microsparitic layers (up to 1,5 to 2 mm high) containing few pelloids. Along the slopes the thickness of the whole zone decreases, films are grouped interbedded with sparite and some of them overlap the interspaces. A clear sparitic zone then appears under the films as a cement. The recrystallized central part of columns (as for *P. boetsapia*) contains rounded bodies with bladed crystals arranged around a core where few pelloids remain. On their surface and between them are dark insoluble residue in a dolomite network. Sheathed filaments have been described by Macgregor *et al.*, (1974, fig. 3).

Interspace filling

It is more detrital than the *P. boetsapia* infilling, with few layers of muddy neomorphic dolomite. The detrital elements are of the usual kind in this area: rounded pelloids and vermiform black algal debris. As in *P. boetsapia* there are stromatolitic mats expanding over the infilling, making small bumps. They are most of the time distinct from the columns mats.

Comparisons

We have attributed the different columns from distinct layers to the same form because they show very slight changes: a decrease in size and a variability of the seasonal differentiation of the laminae zones. *Pilbaria inzeriaformis* has features reminiscent of *P. boetsapia*: niches, short small digitations on the margins of columns, wall, laminae expanding upon

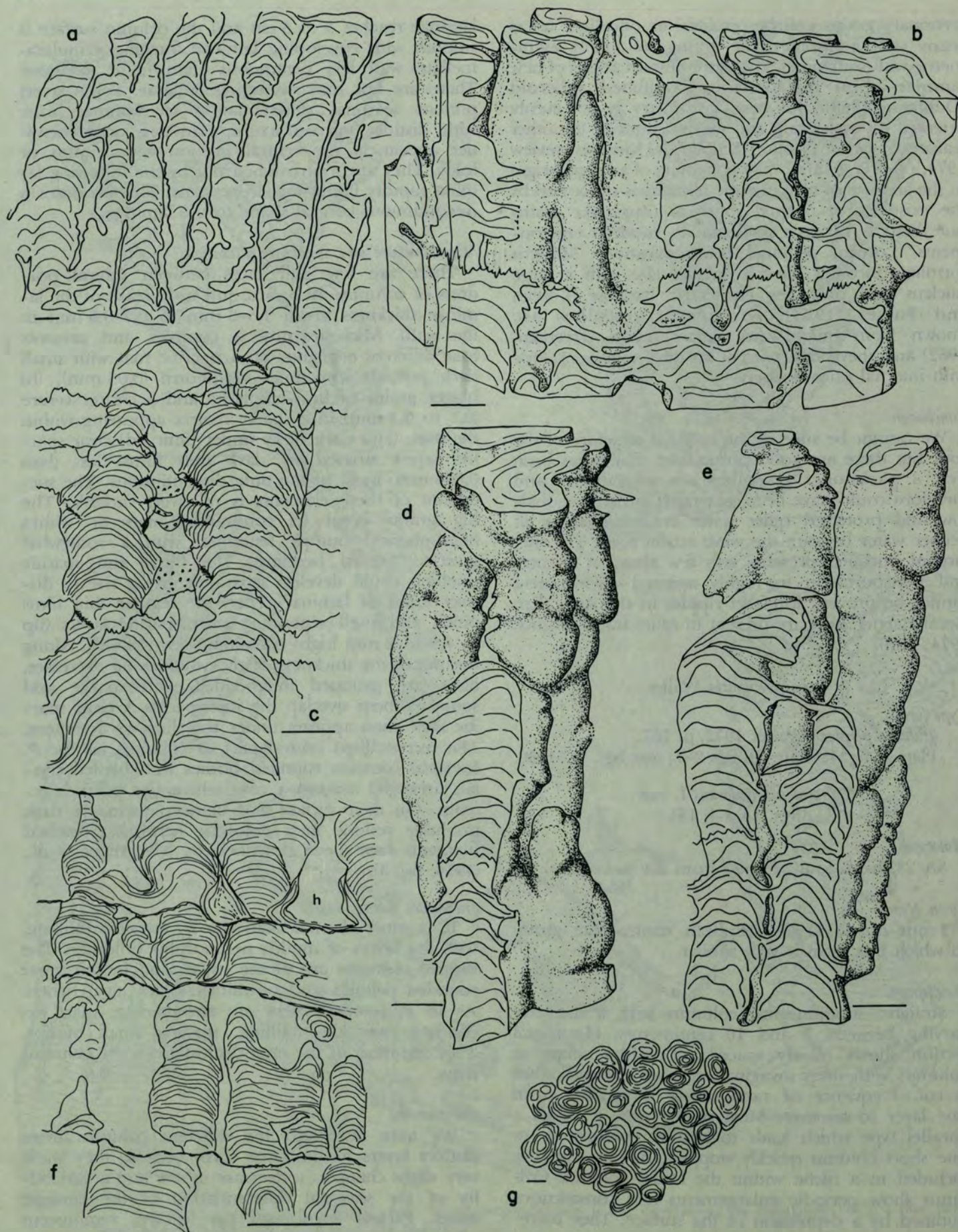


Figure 14. *Pilbaria inzeriaformis*

(a) holotype

(f) successive layers of columns; the upper one showing heart-like (h) cavities.

Drawing from field photographs, (a) from JBS, (f) from Eriks.

(b) small forms at the top of the waterfall 2 (SA 16, JBS coll.);

(c), (d) and (e) holotype (SA 23, JBS coll.); (c) drawing from peel;

(g) horizontal section (drawing from JBS field photograph).

Scale bars all 2 cm, except (f) = 17 cm.

the interspaces, superposition of loosely packed laminae in the central portions with fenestrae. Differences are few: columns straighten without coalescences, they display true ramifications and a



Figure 15. *Philbaria inzeriaformis* Microstructure (SA 23, JBS coll.). Scale bar, 1 cm.

more complex microstructure especially by the existence of films and seasonal zones of laminae. *Pilbaria* group has been compared to *Inzeria* Krylov and this form is perhaps more comparable to *Inzeria* than *P. boetsapia*. It differs principally by the shape of laminae, the microstructure with films and a more continuous wall. Its resemblance to *P. boetsapia* has determined the attribution to *Pilbaria* group.

CONCLUSION

Palaeoenvironment of stromatolites

This was not the aim of our study, but an actualistic tidal model has been proposed for this Schmidtsdrift Formation in Boetsap (Truswell and Eriksson, 1973, pp. 7–18). Two sequences are distinguished: a transgressive one, from the *Topinamboura* beds to the shales beneath *Radiatina* bioherms; the second, regressive, begins with pulses during the growth of *Radiatina* domes, then through an agitated zone with oncolitic megaripples, finishes in the intertidal zone with the upper columns of *Pilbaria inzeriaformis*. We must remember that interpreting stromatolites sequences in terms of tidal environment according to columnar forms, in the lack of associated evidences of subaerial exposure (desiccation cracks, etc.) is a dangerous simplification. Many authors emphasize the number of factors involved in stromatolite morphology: biological (Awramik, 1973, 1976) and environmental (Serebriakov, 1975) as well as the environmental diversity of stromatolites (Monty, 1973; Hoffman, 1974, 1976; Donaldson, 1976b).

Mechanisms of the laminae microstructure

The microstructures are particularly well preserved in the Schmidtsdrift sequence and show great similarities in their mechanisms of growth with pre-

sent-day algal laminae. But everywhere in Precambrian stromatolites, the microstructures, even for complex laminae, are characterized by a very evenly repeated superposition of laminae for long periods. This gigantism is also presented by the *Osagia*-like oncolites with up to forty concentric laminae for two to five in modern analogue. This is one of the more unusual features of Precambrian stromatolites.

Complexity of the ramification

Until recently, stromatolite studies have been concentrated on Soviet Union Riphean Formations and they outlined an increase in the ramification complexity throughout Lower and Middle Riphean, leading to an explosion of columnar forms during Upper Riphean. With the increasing number of studies on Lower Proterozoic assemblages it becomes evident that stromatolites of this age contain lots of ramified forms presenting every kind of ramifications previously known from Upper Riphean. Our study illustrates also this fact and we can compare *Pilbaria* ramification type to the *Gymnosolenid*, *Tibia cristata* to the *Kussiellid* type and *Sapinia* and *Katernia* to the *Tungussid* type. Other works emphasize also this fact: in Australia Walter (1972b) and Preiss (1976), in Canada Campbell (1975), Donaldson (1976a) and Hoffman (1974, 1976). It is now evident that one can find in Lower Proterozoic as many types of ramification as in the Upper Riphean.

Biostratigraphic importance

As a consequence of this point, criticisms have been made regarding the biostratigraphic importance of stromatolites. They are founded on the fact that typical Riphean groups are represented in Aphebian formations (Donaldson, 1976a, p. 377). These comparisons are based on two sets of characters only: ramification and/or nature of the lateral surface. These characters lead in the best case to a rough definition of the group only. If one wants a better definition, it appears necessary to take account of a bulk of characters (see Table 1) that is to work at the form level instead of the group level (Preiss and Walter, 1975; Preiss, 1976).

In this study we have described columnar stromatolites presenting original features: the crestal zone which is quite different from that of *Conophyton* and the sparitic pseudo-wall distinct from a multilamellate wall. Beside these peculiar features, the association of characters leading to the definition of groups and forms are very distinctive and we have been able to define new groups and forms completely different from Riphean ones. These stromatolites built successive layers, the lateral evolution of which are not known, except for *Sapinia* and *Tibia* found in the vicinity of the Boetsap River outcrop and for *Katernia* found in the Potchefstroom synclorium.

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A REVIEW OF THE LOCALITIES AND FLORA OF THE LOWER PERMIAN KAROO STRATA AT VEREENIGING, SOUTH AFRICA

by

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ABSTRACT

The Vereeniging fossil floras are particularly well known and often referred to, as it is among them that attached glossopteridophyte fructifications were first recorded. No recent review of the localities, flora and age of the deposits is available. The history of collecting and description of fossil plants from Vereeniging dates from 1879. Ten localities have been recorded to date, the most important of which are the three Leeukuil quarries from which a diverse flora has been collected and described over the past thirty years. Two of the localities are considered to fall within the Lower Eccla and the remaining eight within a restricted section of the Middle Eccla coal measures. The older flora is poorly known and is represented only by the genera *Gangamopteris* and *Noeggerathiopsis*. The younger flora is fairly comprehensively known and includes some 23 genera and 33 species of plants.

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STRATIGRAPHY, CORRELATION AND AGE

Where Vereeniging is mentioned below, the area being considered is that covered by the map in Figure 1.

Basement

The Karoo sediments at Vereeniging lie on a very irregular basement topography of the Precambrian Transvaal System (Supergroup). The northern half of the map area (with localities 2, B, C and E) is underlain by dolomites, the south-western portion (with localities 1, 3, 4, 5, A and D) essentially by quartzites and shales. In view of this irregular floor, forming part of the northern shore region of the Karoo basin (Figure 1), the strata are lenticular in nature, are variable in thickness and are not readily correlated.

Dwyka Tillite

No unequivocal Dwyka Tillite is known to occur at Vereeniging.

Lower Eccla

The monotonous succession of shales and siltstones typical of the Lower Eccla stable shelf deposits farther to the south are not developed along the northern shore region of the basin (Ryan, 1968). The time equivalent, filling the low-lying portions of the pre-Karoo surface at Vereeniging, is a coarse-grained conglomeratic facies. This resembles concrete, with a fine-grained siliceous matrix and a wide variety of included pebbles. It weathers dirty white and is of very variable thickness, reaching a maximum of 4 m. This deposit has in the past often been regarded as Dwyka Tillite, but it is now generally agreed that it represents the Lower Eccla (Nel and Jansen, 1957; Cillie and Savage, 1961; Stratten, 1968; J. M. Anderson, 1975).

Localities B (Dolomite Quarry) and C (Suikerbosrand River) occur in this horizon. The senior author has searched extensively through the exposures of this conglomerate at Vereeniging but has been unable to find any further plant material within it. One

locality was found, however, which yielded thin laminated shales with arthropod trackways (A. M. Anderson, 1974).

Middle Ecca

The remaining eight localities all fall within the Middle Ecca coal measures, which are, at Vereeniging, very incomplete relative to their development elsewhere in the northern Karoo region. Whereas, in the Cornelia, Clydesdale and Sigma Collieries to the south and south-west of Vereeniging (extending from just south of the Vaal River for some 25 km) three workable coal seams occur; only one is developed in the map area. This seam can be shown through mine workings and borehole cores to be the topmost of the three (Cillie and Savage, 1961).

The plant-bearing horizons at all eight remaining localities fall within 20 m or so of Middle Ecca strata overlying this coal seam. It is interesting to note that abundant leaf impressions occur in the carbona-

ceous shales immediately overlying the top seam in the Cornelia Colliery (Smith, pers. comm. 1972). It might be assumed that all these fossiliferous beds represent a relatively narrow span of time.

Although much palynological work has been done throughout the Permian succession of the northern Karoo region (J. M. Anderson, 1977) no results have been obtained from Vereeniging as such. According to J. M. Anderson (1976, pers. comm.) the samples analysed from the fossiliferous horizons at the Leeukuil quarries all proved to be barren. The nearest locality yielding spores and pollens was the Sigma Colliery where typical Middle Ecca assemblages were obtained.

Overburden

No Karoo strata younger than Middle Ecca occur at Vereeniging, the coal measures being directly overlain over much of the area by about 0.5 m of Recent river gravels, followed by about 0.5 m of top-soil.

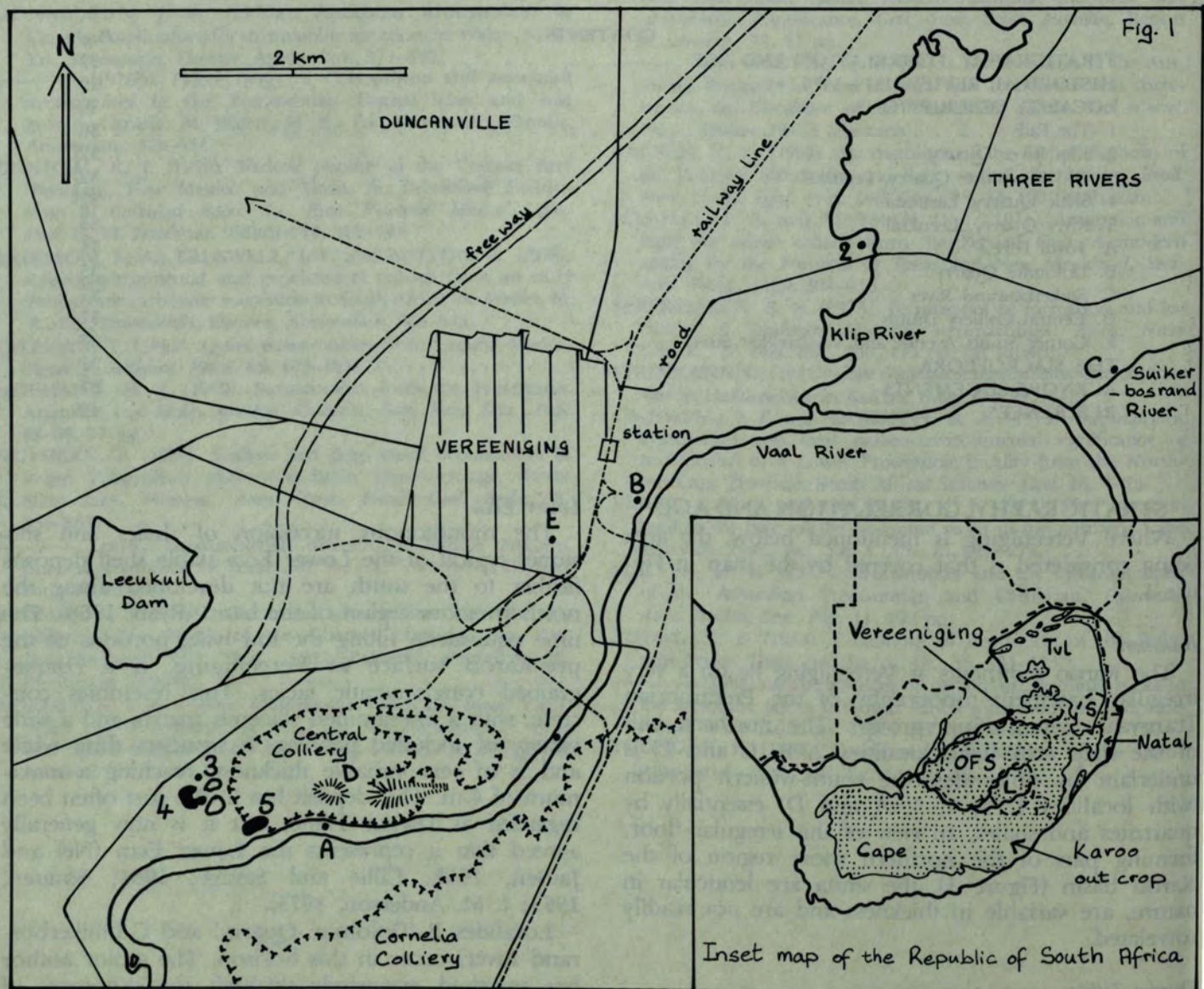


Figure 1. Map showing (a) the position of Vereeniging and (b) the localities, 1-5, and A-E, in the Vereeniging district described herein.

Age

According to the correlation charts (J. M. Anderson, 1973; 1975) using all available palaeontological and other data, the following ages for the Karoo strata occurring at Vereeniging may be postulated:

Middle Ecce — Lower Artinskian } Lower Permian
Lower Ecce — Middle Sakmarian }

HISTORICAL REVIEW 1879–1976

In the following review where original and revised generic designations are given in brackets, the author is recorded in Table 1.

Stow, 1879.

The first person on record to discover and collect plant fossils from the Vereeniging area (locality 1 as numbered in this paper) was G. W. Stow, who described the coal field of the central Vaal valley in his geological report of 1879. The subsequent exploitation of this coal field led to the establishment of Vereeniging which was proclaimed a town in 1892. It was T. N. Leslie (1922) who first brought to notice the good collection of fossil plants Stow had made and donated to Bloemfontein Museum. This material had hitherto gone unnoticed.

Leslie, 1892 to early 1900s.

T. N. Leslie, one of the pioneers of the town of Vereeniging, combined his trade as stone mason with his hobby, geology. During the early 1890s and 1900s he collected numerous fossil plants from two exposures he worked in his capacity as a stone mason. One of these was the original site in the bed of the Vaal River (locality 1) from which Stow had collected and the second was the Klip River Quarry (locality 2).

Draper, 1897.

D. Draper described a locality in the following terms "two miles east of Vereeniging, and close to the junction of Klip and Vaal Rivers, a sandstone-quarry was opened". From this locality, Draper sent a collection of fossil plants to A. C. Seward, who described them (Seward, 1897). The position of this locality is uncertain but in the authors' opinion it is probably equivalent to the Klip River Quarry (locality 2). However, it is strange that Seward and Leslie (1908) do not clarify this and that they refer to it in terms that suggest it may be a separate locality.

Seward, 1897, 1898, 1903.

A. C. Seward published the first systematic descriptions of fossil plants from Vereeniging in 1897. These comprised various species of *Glossopteris*, *Gangamopteris*, *Noeggerathiopsis*, *Sigillaria* (*Lycopodiopsis*) and *Conites* (?*Scutum*) and were derived from the uncertain quarry (probably locality 2), mentioned above. Based on comparisons with floras from other countries he suggested that the coal-bearing strata around Vereeniging were of Permo-Carboniferous age. A further short account of various species fol-

lowed in 1898, based on material sent by a geologist, Hatch, from the same locality. Species belonging to the genera *Glossopteris*, *Gangamopteris*, *Neuropteridium* (*Gondwanidium*), *Bothrodendron* (*Cyclodendron*), *Psyg-mophyllum* and *Noeggerathiopsis* were described by Seward in 1903 from material collected by Leslie.

Leslie, 1904.

T. N. Leslie clarified that the fossils described by Seward in 1903 were obtained from two of his sandstone quarries. These two localities (localities 1 and 2) were briefly described and a short account of the flora was included.

Mellor and Leslie, 1906 described a fossil forest in the bed of the Vaal River (locality A) which became exposed due to extreme low water and has never been seen again.

Seward and Leslie, 1908 discussed the geology and age of the fossiliferous strata at Vereeniging and drew up a generalized geological section for the area. Various species (some new) belonging to the genera *Glossopteris*, *Gangamopteris*, *Callipteridium* (?*Pecopteris*), *Lepidodendron* (*Lycopodiopsis*), *Cordaites* (*Noeggerathiopsis*) and *Conites* (*Scutum*) were described.

Thomas, 1921, described a fructification (from locality 2) and placed it in the genus *Ottokaria* which was subsequently regarded as a *Scutum* by Plumstead (1952).

Leslie, 1922, referred to a further plant locality, namely his Dolomite quarry (locality B) near Vereeniging station, where thin bands of laminated shale yielded numerous *Gangamopteris* impressions.

Du Toit, 1926, 1932.

In his text book on South African geology (1926) Du Toit gave a general review of the "Ecce Series" fossil flora which included the Vereeniging plants. In 1932 he described *Stigmara ficoides* from the Central Colliery dump (Locality D).

Le Roux, 1949.

The description of *Pecopteris* (from locality 3, Le Roux, 1949) heralded the publishing of numerous further papers after an interim of seventeen years. This renewed activity was largely due to extensive collecting by the senior author. From 1941 onwards, collections were made at Leslie's Klip River quarry (locality 2) and at an abandoned sandstone quarry (locality 3) on the farm Leeukuil where a series of fossiliferous shale bands was discovered. During 1946 large scale excavations were commenced by the Vereeniging Brick and Tile Company. This developed into extensive quarrying of the refractory shales from four closely situated quarries. The senior author then transferred his activities in late 1946 to two of these (localities 4 and 5) which were

fossiliferous. Over a period of three years a comprehensive collection was accumulated, including numerous specimens of attached *Glossopteris* fructifications. These were handed over to Dr. E. P. Plumstead for description.

The majority of the following papers describing new genera and species deal solely with material from localities 3, 4 and 5.

Plumstead, 1952, 1956a and b, 1958a, 1962.

In this series of papers the now famous *Glossopteris* and *Gangamopteris* fructifications, including 6 new genera and 19 new species, were described.

Plumstead, 1957, 1961, 1963, 1966a and b, 1967, 1969, 1970, 1973.

These papers include general reviews of a variety of aspects of the "Permo-Carboniferous" macrofloras of Southern Africa. The Vereeniging Coal Measure assemblages play a significant role throughout. Only in the 1961 paper were new taxa described — *Jongmansia transvaalensis* (regarded as a pteridospermous male fructification), *Lerouxia transvaalensis* (taken to be a bennettitalean flower) and *Taeniopteris gemmina*.

Le Roux, 1960, described a conchostracan (*Cyzicus*) from the River Quarry (locality 5). This remains the only invertebrate to be described from Vereeniging.

Kräusel, 1960a and b, 1961.

In the 1960a and 1961 papers, R. Kräusel described a number of lycopods from Vereeniging belonging to the genera *Lycopodiopsis*, *Cyclodendron*, and *Lycopodophlois*, whilst in the 1960b paper brief general reference to the fossils at Vereeniging was included.

Le Roux, 1963a and b, 1965, 1966, 1970, 1975, 1976.

In this series of papers S. F. le Roux described the bulk of the Leeukuil quarry material belonging to the Cycadophyta, Ginkgophyta and Coniferophyta. Two new genera and three new species were introduced.

LOCALITY DESCRIPTIONS

Intermittent collecting from the Shale and River Quarries (localities 4 and 5) was undertaken by Dr. Plumstead, the senior author and various students throughout the fifties and sixties. By 1954 large-scale quarrying operations by Vereeniging Refractories ceased and the quarries have in part been inundated by water (locality 5) or overgrown by vegetation. Recently (November, 1975) quarrying operations were recommenced at the north-eastern border of the River Quarry (locality 5). Should the quarrying be continued and the rich fossiliferous horizons be exposed, a third phase of palaeobotanical investigations at Vereeniging may be initiated.

The palaeobotanical localities of Vereeniging are here divided into two groups, based on their relative

importance: localities 1–5 which have yielded the majority of fossil plants to date and localities A–E which are of only minor importance. Within each group in turn the localities are described in order of discovery and excavation. As far as can be ascertained this is a comprehensive list of localities.

(1) The Falls (Bed of Vaal River)

Location: 27°55'53"E/26°41'56"S. This locality is no longer exposed and Leslie's (1904) original description is thus quoted

"... about 1½ miles west of Vereeniging. It is a sandstone bar across the Vaal River, and is known as the 'Falls'. The coal is exposed, and it was at this spot that Stow discovered the coal in 1879. (It was here that he died, and his remains lie within a stone's throw of the spot.)".

(N.B. The word "West" was applied in error by Leslie and should read "South".)

This locality is situated in the bed of the Vaal in an area which is now permanently under water. The reason for the change of water level was the building of the Barrage (damming up the river's flow) 32 kilometres downstream, in 1924. Before that date the river bed during the winter months was, to a large extent, exposed. Leslie's reference to Stow's grave in the above quotation does not throw any light on the problem either, since all attempts to locate Stow's grave have failed in spite of intensive research by several workers.

Description

Leslie (1904) described the exposure as follows: "the bar consists of about five feet of the lower beds of the sandstone. It has been faulted up rather sharply. The top beds have been eroded". The relationship of the sandstone to the coal horizon was not indicated by Leslie.

History

It was at this spot that Stow originally discovered coal in 1879 and the specimens he collected are in the Bloemfontein Museum. Leslie collected actively from this site (probably between 1892–1904) and in 1904 recorded that "quarrying operations gradually removed the bar exposed during low water".

Material

The following statement enables some of the material to be traced:

"It is a dark grey sandstone with the leaf impressions beautifully black, but generally too coarse to get the delicate markings requisite for determination". (Leslie, 1904)

Such specimens are to be seen in the following museums: Bloemfontein Museum; S.A. Museum, Cape Town; Geological Museum, Johannesburg; Transvaal Museum, Pretoria; Bernard Price Institute for Palaeontological Research, Johannesburg; and the Vereeniging Museum. The most common genera represented in the above collections are

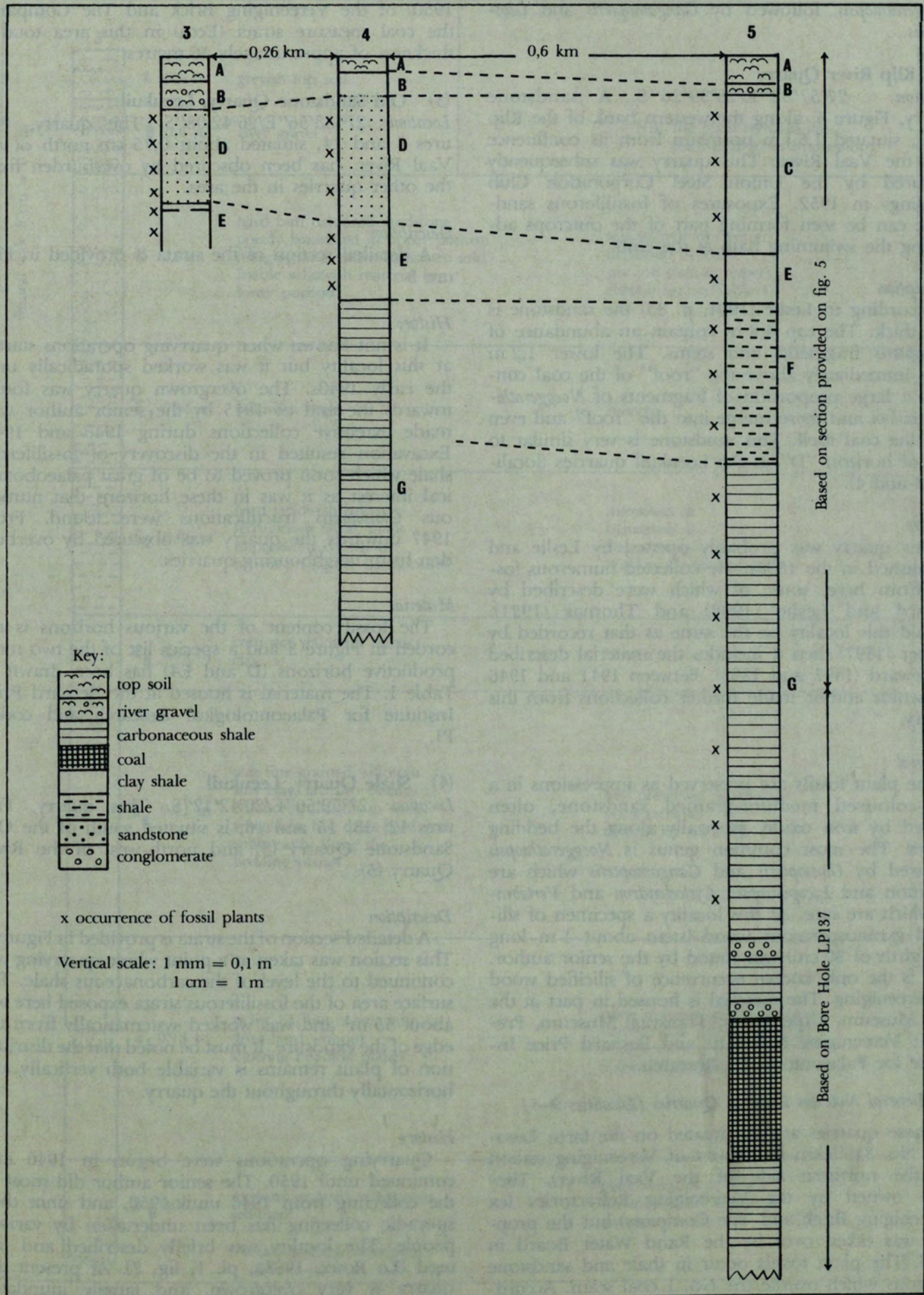


Figure 2. Generalised sections of the three Leeukuil Quarries (localities 3-5)

Noeggerathiopsis, followed by *Gangamopteris* and *Glossopteris*.

(2) Klip River Quarry

Location: 27°57'32"E/26°39'26"S. A sandstone quarry, Figure 6, along the western bank of the Klip River, situated 1,6 km upstream from its confluence with the Vaal River. This quarry was subsequently obscured by the Union Steel Corporation Club buildings in 1952. Exposures of fossiliferous sandstone can be seen forming part of the outcrops adjoining the swimming bath at the club.

Description

According to Leslie (1904, p. 85) the sandstone is 6 m thick. The top 4,8 m contain an abundance of *Glossopteris* fragments and stems. The lower 1,2 m lying immediately above the "roof" of the coal contains a large proportion of fragments of *Noeggerathiopsis hislopi* and these merge into the "roof" and even into the coal itself. This sandstone is very similar to that of horizon "D" in the Leeukuil quarries (localities 3 and 4).

History

This quarry was probably opened by Leslie and established in the 1890s. He collected numerous fossils from here, some of which were described by Seward and Leslie (1908) and Thomas (1921). Should this locality be the same as that recorded by Draper (1897) then it includes the material described by Seward (1897 and 1898). Between 1941 and 1946 the senior author made further collections from this quarry.

Material

The plant fossils are preserved as impressions in a buff-coloured medium-grained sandstone, often stained by iron oxide, especially along the bedding planes. The most common genus is *Noeggerathiopsis* followed by *Glossopteris* and *Gangamopteris* which are common and *Lycopodiopsis*, *Cyclodendron* and *Vertebraria* which are rare. At this locality a specimen of silicified gymnospermous wood (stem about 1 m long and girth of 30 cm) was found by the senior author. This is the only known occurrence of silicified wood at Vereeniging. The material is housed in part at the S.A. Museum, Cape Town; Transvaal Museum, Pretoria; Vereeniging Museum; and Bernard Price Institute for Palaeontological Research.

General Note on Leeukuil Quarries (Localities 3–5)

These quarries are all situated on the farm Leeukuil No. 81 (5 km south-west of Vereeniging station on the northern side of the Vaal River). They were owned by the Vereeniging Refractories (ex Vereeniging Brick and Tile Company) but the property was taken over by the Rand Water Board in 1963. The plant fossils occur in shale and sandstone horizons which overlie the No. 1 coal seam. According to the borehole records (nos. 158–160, sunk in

1950) of the Vereeniging Brick and Tile Company, the coal measure strata (Ecca) in this area total a thickness of approximately 16 metres.

(3) Old Sandstone Quarry, Leeukuil

Location: 27° 53'56"E/26°42'08"S. The quarry, Figures 7 and 14, situated about 0,75 km north of the Vaal River, has been obscured by overburden from the other quarries in the area.

Description

A detailed section of the strata is provided in Figure 3.

History

It is not known when quarrying operations started at this locality but it was worked sporadically until the early 1940s. The overgrown quarry was found towards the end of 1945 by the senior author who made extensive collections during 1946 and 1947. Excavation resulted in the discovery of fossiliferous shale which soon proved to be of great palaeobotanical interest as it was in these horizons that numerous *Glossopteris* fructifications were found. From 1947 onwards the quarry was obscured by overburden from neighbouring quarries.

Material

The fossil content of the various horizons is recorded in Figure 3 and a species list of the two most productive horizons (D and E4) has been drawn in Table 1. The material is housed at the Bernard Price Institute for Palaeontological Research and coded PI.

(4) Shale Quarry, Leeukuil

Location: 27°52'56"E/20°42'12"S. This quarry, Figures 12, 13, 15 and 16, is situated south of the Old Sandstone Quarry (3) and north-west of the River Quarry (5).

Description

A detailed section of the strata is provided in Figure 4. This section was taken at a point where quarrying was continued to the level of the carbonaceous shale. The surface area of the fossiliferous strata exposed here was about 55 m² and was worked systematically from the edge of the exposure. It must be noted that the distribution of plant remains is variable both vertically and horizontally throughout the quarry.

History

Quarrying operations were begun in 1946 and continued until 1950. The senior author did most of the collecting from 1946 until 1950, and since then sporadic collecting has been undertaken by various people. The locality was briefly described and figured (Le Roux, 1963a, pl. 1, fig. 2). At present the quarry is very overgrown, and largely inundated with water.

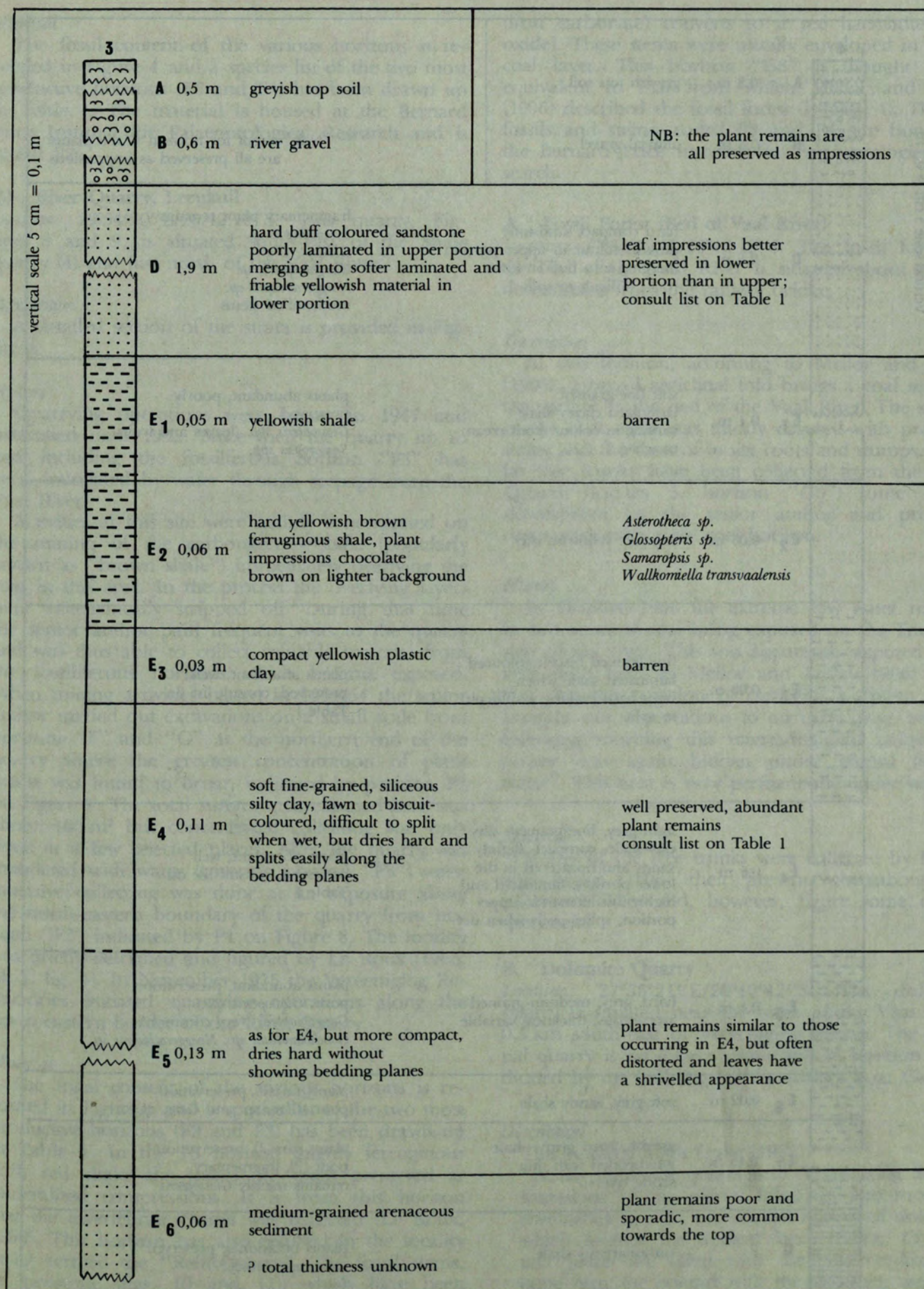


Figure 3. Section of strata at locality 3, Old Sandstone Quarry, Leeukuil.

Vertical scale 5 cm = 0,1 m	4			N.B. except for horizon G the plants are all preserved as impressions
	A	0,3 m	greyish top soil	
	B	0,6 m	alluvial gravel	
	D	2,6 m	hard compact sandstone pinkish colour in upper portion merging to a buff in lower rock; difficult to split	fragmentary plant remains <i>Lycopodiopsis</i> sp. <i>Glossopteris</i> sp. <i>Gangamopteris</i> sp. <i>Noeggerathiopsis</i> sp. unidentified stems
	E ₁	0,1 m	soft fine-grained laminated clayey shale varying in colour from cream to white	plants abundant, poorly preserved <i>Glossopteris</i> spp. (leaves and fruits) <i>Samaropsis</i> spp.
	E ₂	0,05 m	compact yellowish clay	barren
	E ₃	0,08 m	fine-grained biscuit coloured laminated shale which dries hard making it difficult to split	plants abundant, well preserved, consult list on Table 1
	E ₄	0,6 m	light grey, fine-grained, silty clay-shale, compact, slightly sandy and micaceous in the lower portion, laminated and highly fossiliferous in upper portion, splits easily when dry	plants abundant, well preserved, consult list on Table 1
	E ₅	0,4 m	hard, grey, medium-grained arenaceous, thickness variable	plants abundant, preservation poor, <i>Glossopteris</i> spp. <i>Gangamopteris</i> (very common) <i>Gondwanidium</i> sp., <i>Noeggerathiopsis</i> sp.
	E ₆	0,02 m	soft grey, sandy shale	plants rare(?), preservation poor, <i>Gloss.</i> sp. and <i>Gang.</i> sp.
E ₇	0,15 m	greyish, hard gritty, shale interbedded with thin sandy layers	plants rare(?), preservation poor (?), fragmentary remains mainly <i>Glossopteris</i>	
G	?	carbonaceous shale	plants occasional, preserved as compressions (?)	

Figure 4. Section of strata at locality 4, Shale Quarry, Leeukuil.

Material

The fossil content of the various horizons is recorded in Figure 4 and a species list of the two most productive horizons (E3 and E4) has been drawn up in Table 1. The material is housed at the Bernard Price Institute for Palaeontological Research and is coded P2.

(5) River Quarry, Leeukuil

Location: 29°54'20"E/26°42'18"S. This quarry, Figures 8 and 9, is situated south-east of the Shale quarry (4) and just north of the Vaal River.

Description

A detailed section of the strata is provided in Figure 5.

History

Quarrying operations were begun in 1947 and continued until 1952. Since then the quarry up to and including the fossiliferous horizon "F3" has been inundated by water through seepage from the Vaal River.

Activities at this site were mainly concentrated on the mining of the carbonaceous shale (popularly known as "brown shale") immediately overlying the coal in this area. In the process the overlying layers were systematically stripped off. During that time the senior author paid frequent visits to the quarry and was thus able to collect valuable material from the fossiliferous horizons which became exposed. When mining activities ceased in 1953/54 the senior author carried out excavations on a small scale from horizons "F" and "G" at the northern end of the quarry where the greatest concentration of plant fossils was found to occur, indicated by position P3 on Figure 9. The total surface area exposed here was about 100 m² but concentrated collecting was only done at a few selected places. After the quarry was inundated with water (covering horizon "F3") some intensive collecting was done at an exposure along the north-eastern boundary of the quarry from horizon "F2" indicated by P4 on Figure 8. The locality was briefly described and figured by Le Roux (1963, pl. 1, fig. 1). In November 1975 the Vereeniging Refractories initiated quarrying operations along the north-eastern border of the River Quarry.

Material

The fossil content of the various horizons is recorded in Figure 5 and a species list of the two most productive horizons (F2 and F3) has been drawn up in Table 1. In the F3 horizon (highly ferruginous dark red shale) the fossils are often preserved as mineralized compressions. It is from this horizon that the invertebrate *Cyzicus* was collected (Le Roux, 1960). This horizon has also resulted in the locality being termed the "Red Quarry". The fossil stems, all prostrate (figs. 10 and 11), which have been found in horizon "G3" are mineralized compressions. Upon exposure the grey coloured siderite

(iron carbonate) converts to a red haematite (iron oxide). These stems were usually enveloped in a thin coal layer. This horizon "G3" is thought to be equivalent to that from which Mellor and Leslie (1906) described the fossil forest (locality A). The leaf fossils and stems, coded P3 and P4, are housed at the Bernard Price Institute for Palaeontological Research.

A. Fossil Forest (Bed of Vaal River)

Location: 27°54'42"E/26°42'19"S. The fossil forest in the bed of the Vaal River is situated about 2,8 km downstream from the railway bridge.

Description

At this location, according to Mellor and Leslie (1906), a broad anticlinal fold brings a coal seam to the surface in the bed of the Vaal River. The surface of the coal seam was thickly covered with prostrate stems and the casts of *in situ* roots and stumps. Similar tree trunks have been collected from the River Quarry (locality 5, horizon "G3") some 700 m downstream by the senior author and probably occur above the same coal horizon.

History

In October 1906 the extreme low water resulted in two acres of coal being exposed on the Transvaal side of the river. This was apparently exposed for a very short time as Mellor and Leslie (1906) wrote that "on the occasion of our visit a violent storm brought our observations to an early close, and the following morning this interesting and unique exposure was again hidden under several feet of water". This area is now permanently under water.

Material

If any of the tree trunks were collected by Mellor and Leslie (1906) their present whereabouts are unknown. They did, however, figure some of the specimens.

B. Dolomite Quarry

Location: 27°56'21"E/26°40'42"S. The dolomite quarry is situated near the bank of the Vaal River, 0,5 km south-east of Vereeniging station. The original quarry is no longer visible and its position is indicated by the buildings of the Riviera Boat Club.

Description

This is taken from Leslie (1922):

"At my dolomite quarry near Vereeniging Station intrusions of the glacial filled up and moulded themselves around the uneven masses of dolomite which formed the ancient land surface. Crevices and joints are filled with the concrete-like till; quite near the contact with the dolomite are usually a few thin bands of laminated clay shale, the lamina being a $\frac{1}{4}$ inch thick or even less."

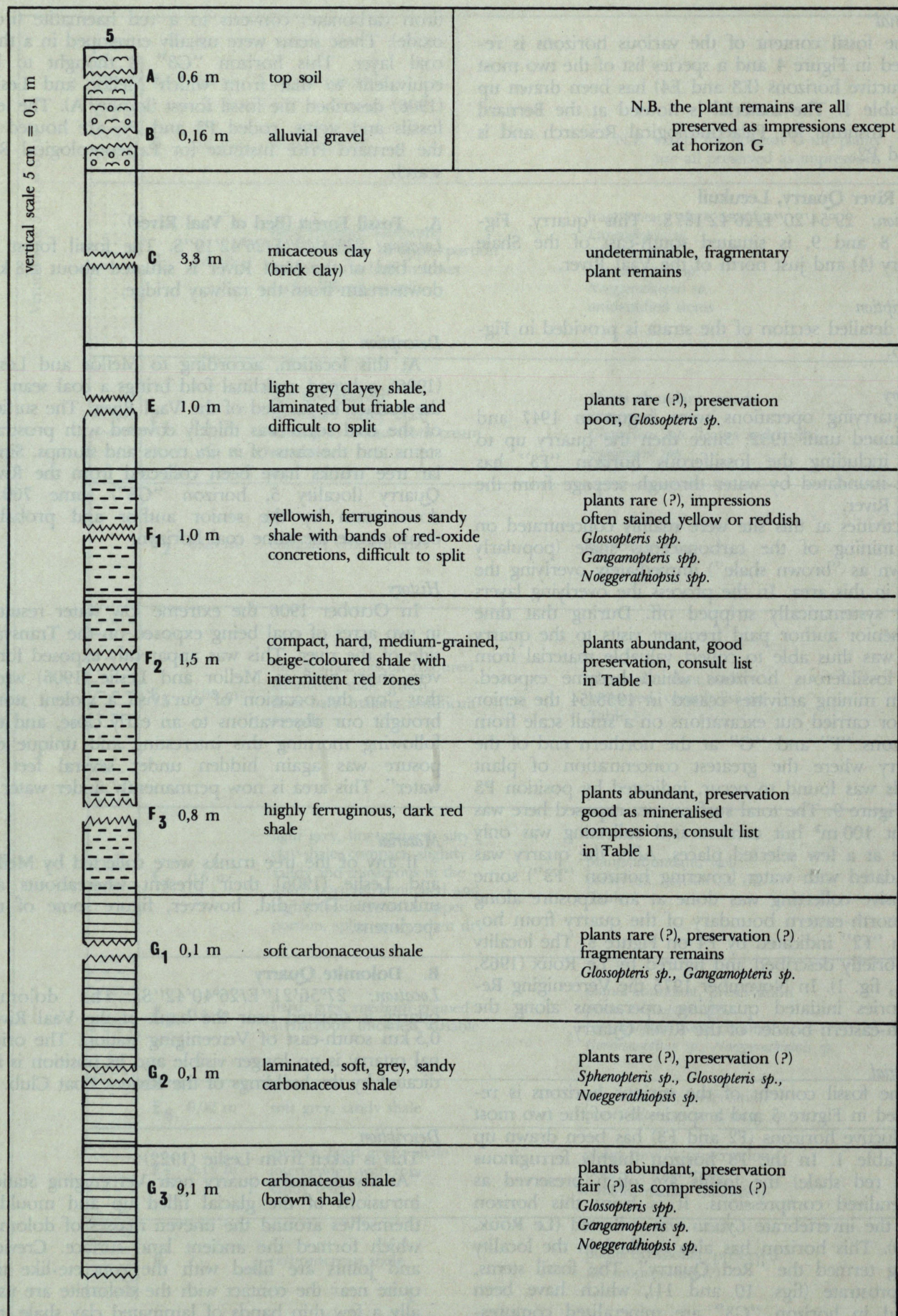


Figure 5. Section of strata at locality 5, River Quarry, Leeukuil.

History

Quarrying operations started some time prior to 1922 and continued until 1939. The fossils were first reported by Leslie (1922) and have been figured by Plumstead (1969, Pl. 7, figs. 2-4).

Material

The only genus to be recorded was *Gangamopteris* of which the few available specimens are housed at the Bernard Price Institute for Palaeontological Research and form part of the Leslie Collection.

C. Suikerbosrand River

Although no collections are available from this locality it is included here to complete the overall record of plant fossils at Vereeniging.

Location: 27°58'47"E/26°40'05"S. Exposures along the banks of the Suikerbosrand River, 500 m from its confluence with the Vaal River.

Description

The only information provided by Leslie (1922) is the observation that long strap-shaped leaves of *Cor-daites* (*Noeggerathiopsis*) existed in stratified beds. These he regarded as occurring in the "Dwyka". The same "concrete-like till" of locality B is well exposed along the Suikerbosrand River and overlies the dolomite more or less directly. It can be safely assumed that the leaves Leslie referred to were preserved in this horizon, and probably in thin intercalated laminated shales as at locality B.

D. Central Colliery Dump

Although this dump cannot be considered a true locality it is nevertheless included.

Location

The dump lies 4 km south-west of the Vereeniging station. The subsurface extent of the colliery workings is indicated on Figure 1.

History and material

Du Toit (1932) described a single specimen of *Stigmaria ficoides* (supposedly a lycopod root fragment). He writes of the specimen which was loaned to him by Dr. T. N. Leslie:

"It was picked up not far from a waste dump at the Central Coal Mine at Vereeniging by R. H. Smith of that town and is presumed to have come from the workings of that colliery, though unfortunately such presumption cannot be established."

The Central Coal Mine was opened in 1890 and closed in 1910. The present whereabouts of the specimen are not known.

E. Corner Smuts Avenue and Voortrekker Street

Location: 27°55'51"E/26°40'54"S. On the south-west corner of the intersection of Smuts Avenue and Voortrekker Street, in the town of Vereeniging.

History and Description

In 1947 some workmen excavating a stormwater drain encountered a fossiliferous sandstone about 4 m below surface. The top 0,5 m or so of this horizon was removed. The senior author, on continuous alert for new sites, came across these workings at the time. The dark grey sandstone with black leaf impressions is very similar to that from locality 1, which suggests possible equivalence. Sandstones of this description have not, beyond these two localities, been encountered in the Vereeniging area.

Material

Only leaves of the genus *Glossopteris* occurred in the sandstone. A single specimen is housed in the Vereeniging Museum.

THE MACROFLORA

Lower Ecca

The Lower Ecca flora recorded to date is very meagre and is recorded from only two localities. It consists of the two genera, *Gangamopteris* and *Noeggerathiopsis*.

Middle Ecca

The Middle Ecca flora, on the other hand, is well represented, relatively diverse, and has been recorded from eight localities to date, and is best known from the three Leeukuil quarries. A comprehensive check list, with relative abundance ratings for all the species found to date, from the most prolifically bearing strata at these three quarries is presented on Table 1. In summary the flora may be recorded as follows (by Divisions according to Boureau 1970):

Lycophyta	— 3 genera, 4 species
Sphenophyta	— 3 genera, 3 species
Filicophyta	— 3 genera, 5 species
Glossopteridophyta	— 4 genera, 7 species
Pteridospermophyta	— 1 genus, 1 species
Cycadophyta	— 3 genera, 4 species
Ginkgophyta	— 4 genera, 6 species
Coniferophyta	— 2 genera, 3 species
Total—	23 genera, 33 species

This is based solely on the leaves and non-gymnospermous stems which are listed in Table 1. This tally is presumed to reflect reasonably accurately the flora growing at Vereeniging after the cessation of coal swamp development. The gymnospermous fructifications and fossil wood (which remain unstudied) have not been counted as they are probably largely represented by the equivalent leaf species.

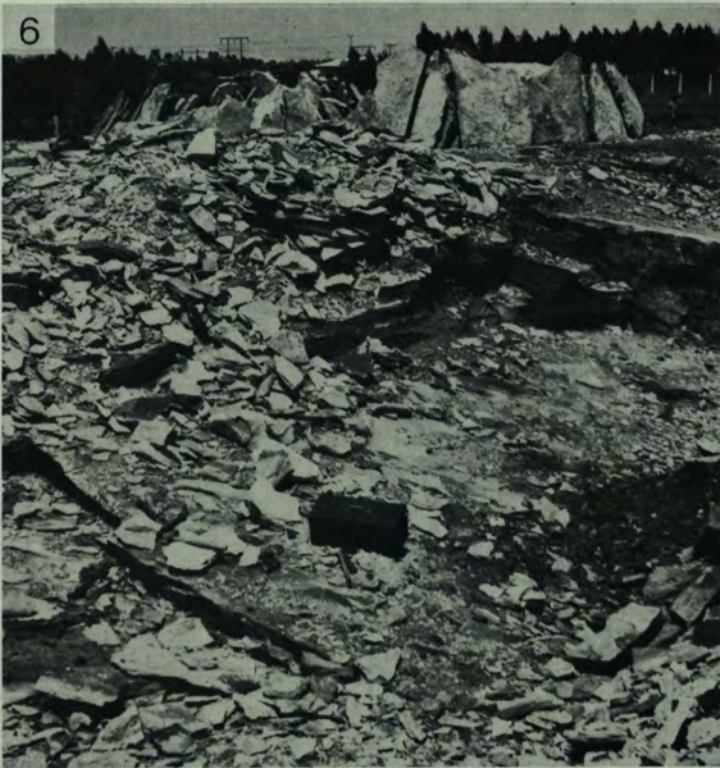
ACKNOWLEDGEMENTS

Grateful thanks are due to Vereeniging Refractories Limited (formerly known as Vereeniging Brick and Tile Company) and also to the management of the Rand Water Board for permission to collect plant fossils on their properties.

This paper was in an advanced state of preparation when the senior author regrettably died (2 August 1976). The greater part of the paper is a result of his work, while the junior author helped mainly in compilation of the text and figures.

TABLE 1. THE VERENIGING MACROFLORA FROM THE LEEUKUL QUARRIES (localities 3-5)

Relative abundance:		Abbreviations for references:		Notes:	
1	extremely rare	Kr. Kräusel		This check list consists of all the species found to date, from the most prolifically bearing strata at these localities.	
2	rare	LeR. Le Roux			
3	occasional	Pl. Plumstead			
4	common-to-abundant	* undescribed material			
		Major groups after Boureau 1970		non-Gymnosperms (leaves & stems)	Gymnosperms (mainly leaves)
Genus	Species	Reference			
Cyclodendron	leslii (Sew.) Kr.	Kr. 1961		LYCOPHYTA	
Lycopodiophloios	dolianitii Kr.	Kr. 1961			
L.	edwardsi Kr.	Kr. 1961			
Lycopodiopsis	derbyi Renault	Pl. 1966		SPHENOPHYTA	
? Phyllothea (only stems)		Pl. 1957, 61, 66			
? Schizoneura (only stems)		Pl. 1961			
Sphenophyllum	sp.	LeR. 1976		FILICOPHYTA	
Pecopteris (Asterotheca)	cf. thonii Mahr	LeR. 1976			
P. (A)	singeri Arch.	LeR. 1976			
P.	cf plumsteadiae H-M	LeR. 1976		GLOSSEPTERIDOPHYTA	
Cladophlebis	sp.	LeR. 1949			
Sphenopteris	cf. nebbensis Brong.	LeR. 1976			
Glossopteris	spp.	Pl. 1961		GLOSSEPTERIDOPHYTA	
G.	stricta Bunb.	Pl. 1958a	1 A		
G.	indica Schimper	Pl. 1952	3 B		
G.	intermittens Feist.	Pl. 1958a	4 B		
G.	longicaulis Feist	Pl. 1958a	5 C		
G.	damudica Feist.	Pl. 1958a	7 C		
G.	conspicua Feist	Pl. 1952	8 C		
G.	browniana Brong.	Pl. 1952	9 C		
G.	b.var cornelium Pl.	Pl. 1958a	10 D		
G.	tortuosa Zeiller	Pl. 1952	11 D		
G.	t. var. vaalense Pl.	Pl. 1958a	12 D		
G.	decipiens Feist.	Pl. 1958a	14 D		
G.	retifera Feist.	Pl. 1952	16 E		
Palaeovittaria	kurzi Feist.	Pl. 1958a	17 E		
Gangamopteris	buriadica Feist.	Pl. 1956b	18 F		
G.	obovata (Carr.) White	Pl. 1956b	19 F		
G.	cf. clarkiana Feist.	Pl. 1962	20 G		
scale leaves	spp.	*		Pteridospermophyta	
Gondwanidium	validum (Feist) Gothan	Pl. 1961			
Taeniopteris	gemmina Pl.	Pl. 1961			
T.	sp.	Pl. 1961		?CYCADOPHYTA	
Thomaslesia	vereenigensis	LeR. 1975			
Old Sandstone Quarry (locality 3)	D 3	1	1	1	1
Shale Quarry (locality 4)	E ₃	4 3 2 1	2	2 1	1 3
River Quarry (locality 5)	F ₂	1	1	1	2 2
	F ₃	1	1	1	2 2 2 1 1 3 3 2





- Figure 6. Locality 2, Klip River Quarry as it appeared in 1942 (direction of view not available).
- Figure 7. Locality 3, Old Sandstone Quarry, Leeukuil, showing sandstone layer "D" overlying a succession of fine grained sediments E_1 - E_6 (direction of view not available).
- Figure 8. Locality 5, River Quarry, Leeukuil, showing succession of fossiliferous strata "G-G" (as viewed from the south-west) and position of collecting place P4.
- Figure 9. Legend as for Figure 8, but viewed from the south-east and showing position of collecting place P3 and localities 3 and 4. A small portion of the Vaal River is visible at upper left. Position of tree trunk (fig. 10) marked by a x.
- Figure 10. A prostrate tree trunk in position of discovery at locality 5, total length exposed was more than 10 m.
- Figure 11. Portion of tree trunk X-Y shown in Figure 8, with coaly matrix removed to show the lateral branching; now housed at Bernard Price Institute for Palaeontological Research, PB 312.
- Figure 12. Locality 4, Shale Quarry, Leeukuil, showing fossiliferous horizons "D-G" and collecting point P2 at right (viewed from the south-east).
- Figure 13. Legend as for Figure 12, showing detail of collecting point P2 and fossiliferous strata (viewed from the south-east).
- Figure 14. Locality 3, Old Sandstone Quarry, Leeukuil, showing small scale excavation in progress in sandstone "D" (viewed from the west).
- Figures 15. and 16: Locality 4, Shale Quarry, Leeukuil, showing method of excavating the fossiliferous strata " E_4 and E_5 ".



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THE MORPHOLOGY AND TAXONOMY OF *CYCADOLEPIS JENKINSIANA* AND *ZAMITES RECTA* FROM THE LOWER CRETACEOUS KIRKWOOD FORMATION OF SOUTH AFRICA

by

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ABSTRACT

Cycadolepis jenkinsiana, a bennettitalean scale-leaf, is shown to have had two types of venation, is shown not to be covered by hairs as had previously been thought and has a strong association with *Zamites recta*, the most common vegetative leaf species to be found in the Kirkwood Formation of the Algoa Basin. The morphology of *Zamites recta* is reasonably clear and this species has definite affinities with the Bennettitales based on its gross morphology and a single microscopic character, i.e. sinuous epidermal cell walls of the pinnae. *Zamites morrisii* is shown to be only a variant of the better represented *Z. recta*. Two of the previously described species of *Zamites*, *Z. rubidgei* and *Z. africana* are excluded from *Zamites*.

INTRODUCTION

Four species of *Zamites* were reported from near Geelhoutboom, Cape Province in the Uitenhage series by Seward (1903) who based his work on specimens described earlier by Tate (1867) and new material collected for him. With his work as a background and more specimens now available from this locality, it is clear that only one morphological species, *Zamites recta* (Tate) Seward, is recognizable in the Kirkwood Formation. One species, *Zamites africana* (Tate) Seward, should be excluded from the genus *Zamites* particularly because of the form of its pinna base and mode of attachment to the rachis. A second of the four species, *Zamites rubidgei* (Tate) Seward, is based on a single incomplete specimen, which shows only five parallel tapering leaves or pinnae but with no distinctive structure by which it could be assigned with confidence to any genus. Of the two remaining species, *Zamites morrisii* (Tate) Seward and *Zamites recta*, the latter has nomenclatural priority due to its occurring first in the treatment of Tate (1867). This paper will outline the reasons for combining the two species into one more comprehensive species and review the morphology of the leaves and their association with a bennettitalean scale leaf *Cycadolepis jenkinsiana* (Tate) Seward which occurs exclusively with them.

The large scale leaves of *Cycadolepis jenkinsiana* (Tate) Seward form a conspicuous, if numerically minor, portion of the flora from the Kirkwood Formation of the Algoa Basin. *Cycadolepis* here is used in the broadest sense following the diagnosis as amended by Harris (1953, 1969). The morphological features of these scale leaves require amplification since the study by Seward (1903) seems inadequate in his interpretation of the pattern of veins on the leaf surface.

SYSTEMATIC PALAEOBOTANY

Order Bennettitales

Genus: *Cycadolepis* Saporta, 1875 (emend. Harris, 1953)

Species: *Cycadolepis jenkinsiana* (Tate) Seward, 1903
(Figures 1, 2)

Synonymy

Cyclopteris jenkinsiana Tate 1867, p. 146, Plate 6, Figure 4

Diagnosis emended

Scale-leaves, ovate to orbicular; margin entire; base truncate; apex obtuse; surface with midrib which may extend to apex; larger veins numerous, 2 mm apart, forking, curving from base to margin with occasional anastomoses; smaller veins between larger, generally parallel with large veins, irregularly anastomosing, 2-10 mm; cuticle thick with occasional sinuous walled cells; stomata not seen.

Locality

Specimens utilized in this study were collected from the Kirkwood Formation 3/4 km west of Dunbrody Station on the west-facing cliff of the Bezuidenhout's River, 14 km east of Kirkwood, Cape Province, South Africa. The illustrated specimens are held in the type collection of the Bernard Price Institute for Palaeontological Research of the University of the Witwatersrand, Johannesburg and catalogued under their BPI (Pal) PB numbers. Other specimens are catalogued with their accession code 276.



Figure 1. *Cycadolepis jenkinsiana*. PB 313 $\times 0.6$. A single nearly complete leaf.

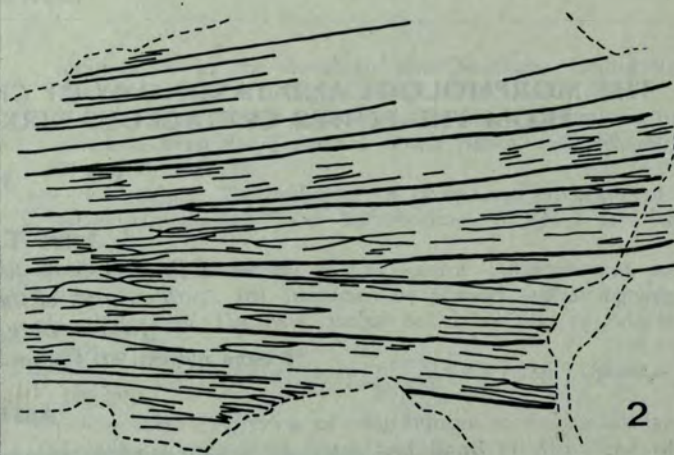


Figure 2. *Cycadolepis jenkinsiana*. PB 314 $\times 3$. Line drawing of minor vein pattern.

Description

Complete specimens of this scale leaf measure up to 13.5 cm long by 12 cm or more wide; most are broadest about half way along the length of the leaf. The margin is entire and without ornamentation. The base is one-third of the total width of the leaf and shows no evidence of a petiole. A large number of sub-parallel veins enter the base about 1 to 1.5 mm apart. Specimen PB 313 (fig. 1) has 22 veins across a width of 4.0 cm. The veins nearest the midline are essentially straight, paralleling the midvein; those entering the base nearer the margin arch gently outward and curve to become perpendicular to the margin in the proximal half of the leaf, but the angle with the margin is less for those ending in the distal portion (fig. 1). These veins end blindly near the margin. The midvein is of a complex nature. It seems to be composed of a central bundle of veins similar to those which occur in the laminar portion of the leaf. Smaller lamina veins do not seem to branch off this midvein but rather arise from the repeated forking of those which enter the lamina independently at the leaf base. This midvein may not have been a vein at all but a strand of supporting tissue. Veins which traverse the lamina dichotomize repeatedly but at irregular intervals to near the margin; then at about 1 to 2 cm from the margin each vein dichotomizes several times and the spaces between them become quite small. Anastomoses are rare, usually only seen at isolated intervals across the leaf (fig. 1). The specimen (PB 313) shown in Figure 1 has only 6 anastomoses visible on its surface.

The smaller veins which lie between the larger are very fine and generally parallel the larger veins. They fork and fuse frequently and irregularly; some cross connections between these fine veins are perpendicular to the vein courses, others more oblique or even acute. In areas where the larger veins are distant there may be 6 to 10 veins between the larger (fig. 2). Occasionally the smaller veins are seen to arise at an acute angle from the larger veins (fig. 2).

The cuticle of these leaves is very poorly preserved and the matrix surface is coarse and has not yielded adequate surface replicas for SEM preparations. Many small fragments of the cuticle have been mounted for optical examination and the only structure seen is an occasional impression of a thick very sinuous anticlinal wall.

Stomata were apparently very widely scattered, as occasional nearly circular holes of uniform size appear in the cuticle but nothing of their structure is preserved.

Discussion

The original attribution of this group of scale leaves to Saporta's (1874) genus was based entirely upon the macroscopic features of the leaves (Seward, 1903). Seward (1895) had enlarged Saporta's genus to include petiole bases and isolated scales which may have been fertile but which have lost evidence of either pollen- or megaspore-bearing structures. Later when the more precise taxonomic distinctions between the Cycadales and Bennettitales based on cuticular morphology became apparent, the diagnosis of *Cycadolepis* was restricted to those scale leaves of this general form having syndetocheilic stomata and restricted to the Bennettitales (Harris, 1953).

The Kirkwood specimens can be attributed to the Bennettitales only on two grounds: first, the sinuous walls of the epidermal cells as shown by their cuticular remains and, second, their restricted appearance with *Zamites recta* and no other bennettitalean leaf at this locality. These are not sufficient criteria to allow a dogmatic attribution of these leaves to *Cycadolepis*, but at least they give some evidence for the choice of the genus.

Our more recently collected specimens from Be-zuidenhout's River locality near Dunbrody Station certainly belong to the same taxon as those described and illustrated by Seward (1903).

There is one interpretation based on the newly collected specimens which differs considerably from

that of Seward (1903). He interpreted the fine dark lines between the major veins as a ramentum of anastomosing or at least overlapping hairs. This seems unlikely for several reasons: the consistently parallel orientation of the network, its anastomosing character and the length of the individual members which make up the reticulum (fig. 2).

All of these taken together seem to indicate a network of small veins rather than a surface covered with long and very unusual epidermal hairs. It is possible that the larger structures were not conducting tissue but a ramifying series of supportive strands of sclerenchymatous or collenchymatous nature, with the fine network representing the veins.

The state of preservation does not allow other identification of the cell types which make up the two networks which would be necessary to distinguish between conductive or supportive tissues. It is also possible that the larger structures were complex fibrovascular bundles having both types of tissue and serving the combined function of support and conduction.

At present *Cycadolepis jenkinsiana* must stand as a possible bennettitalean scale-leaf with a complex and unusual surface pattern of two distinct types of branching and anastomosing fibrous networks.

Genus: *Zamites* Brongniart, 1828

Species: *Zamites recta* (Tate) Seward, 1903 (figs. 3, 4).

Synonymy

Palaeozamia (*Otozamites*) *recta* Tate, 1867. p. 144, Plate 5, Figure 7a, b.

Palaeozamia (*Podozamites*) *morrisii* Tate 1867. p. 145, Plate 5, Figure 4.

Zamites morrisii (Tate) Seward, 1903. p. 25, Plate 5, Figure 4.

Diagnosis emended. Compound frond, lanceolate, up to 60 cm in length; apex acute; pinnae attached to upper surface of rachis, opposite or alternate; lanceolate, margin entire, base contracted, truncate,

with callosity or thickening on upper surface at point of attachment to rachis, apex acute; veins sub-parallel from base, or spreading slightly, 10 per mm; rachis woody, with hexagonal raised scars at point of pinna abscission; petiole not represented; cuticle thick, with impressions of sinuous anticlinal wall thickenings.

Locality

Kirkwood Formation, 3/4 km west of Dunbrody Station on west-facing cliff of Bezuidenhout's River, Cape Province, South Africa.

Description

A large number of incomplete fronds of *Zamites recta* are now known, but none of these is complete at its base so no specimen has been obtained with a petiole. The most proximal leaflets are also unknown. Seward (1903) estimated that the fronds of *Zamites recta* were up to 60 cm in length but this is an unsupported suggestion. Pinnae of *Z. recta* range from quite small, less than 3 cm long near the apex of the frond to 7 cm long from wider portions of the leaf. Pinnae range in shape from nearly straight to markedly falcate but all have the characteristic vein pattern and relatively obvious constriction at the base of the pinna. The rachis as shown by Seward (1903) has very prominent ribbed cushions where individual pinnae have abscised naturally or been torn away. The veins which enter through the constricted point of attachment of the pinnae bifurcate and spread to occupy evenly the entire width of the pinnae (fig. 3). Beyond the near basal region they run nearly parallel to the margins of the pinna and do not fork or anastomose further. Near the apex of the pinna the veins may be slightly closer together but generally run directly to the margin and end blindly there.

Cuticle fragments have been macerated from a single specimen of *Zamites recta* (fig. 4) but show very little structure except for occasional sinuousities as



Figure 3. *Zamites recta*. PB 315 $\times$ 1.5. Portion of frond showing pinna bases and venation.

Figure 4. *Zamites recta*. PB 316. $\times$ 1.5. Portion of frond with complete pinna.

are found in almost all bennettitalean leaf cuticles. No other cuticular structure is visible and surface replicas of impression specimens have failed to provide any further information on the cell pattern of the pinnae or rachis.

Discussion

Typical *Zamites recta* comprises the bulk of both Seward's material and that collected recently. *Zamites morrisii* was known only from a single specimen which appeared to be smaller and to represent only a slight variant of the general pattern of the pinnae of *Z. recta*. The range of variation in *Zamites recta* is sufficient to include *Z. morrisii* easily and the relatively broader form of the pinnae of *Z. morrisii* is found in larger specimens of *Z. recta*.

Zamites africana is clearly distinct from *Zamites*. The pinnae are not constricted at their point of attachment to the rachis and the proximal basal margin is decurrent on the rachis where it seems continuous with the distal margin of the adjacent pinna (Seward, 1903). This form of leaf would better be classified as *Pterophyllum* if the pinnae are set laterally on the rachis as they seem to be in Seward's Plate 5, Figure 3. This is assuming that they are bennettitalean and do not belong to the Cycadales.

Zamites rubidgei is known only from five large (13.5 cm long × 1 cm wide) leaf fragments with parallel veins lying on a single block of shale (Seward, 1903). Neither the apex nor base is shown in any of the five fragments. With so little data to work with, no convincing classification is possible.

Frankel (1960) has reported the occurrence of both *Zamites recta* and *Zamites rubidgei* from the Lower Cretaceous rocks along the Umfolosi River in Natal. His illustration of *Zamites recta* (fig. 4) appears very similar to Seward's *Zamites africana* with laterally

attached broad-based pinnae of the *Pterophyllum* type. The illustrated specimen of *Zamites rubidgei* (plate 35, fig. 2) is more like *Zamites recta* as it is defined now. The original *Z. rubidgei* had not sufficient taxonomic characters present to justify its erection as a separate species and the Umfolosi specimens are better preserved and more complete than the type specimen of *Z. rubidgei*. It is best to include these as representatives of the most completely known species whose characters they match than to refer them to an ill-defined species thus creating two equivalent species with the same morphology.

Seward listed several species of *Zamites* known from other Mesozoic localities which resemble *Z. recta*. The most closely allied species seems to be, as Seward (1903) mentioned, *Zamites gigas* (L. and H.) Morris from the Jurassic of Yorkshire. This is a very well-defined species of *Zamites* which has recently been studied extensively in its macro- and microscopic morphology (Harris, 1969). The South African specimens have unfortunately not sufficiently well preserved cuticle for a close comparison with *Z. gigas*, but appear in general to fit very close to the English species within the genus. It is interesting to note that Harris (1969), in his taxonomic treatment of *Z. gigas*, lists nine species of *Zamites* which are similar to *Z. gigas* but have no known cuticle, including four of the six species used by Seward (1903) in his comparisons with *Z. recta*, but Harris does not include *Z. recta*.

The association with scale leaves assigned by Seward to *Cycadolepis jenkinsiana* is a strong one. No other known species of bennettitalean foliage leaf occurs with the scale-leaves at any of the Kirkwood Formation plant fossil localities.

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ON *ARAUCARITES ROGERSII* SEWARD FROM THE LOWER CRETACEOUS KIRKWOOD FORMATION OF THE ALGOA BASIN, CAPE PROVINCE, SOUTH AFRICA

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ABSTRACT

Araucarites rogersii Seward from the Kirkwood Formation (Lower Cretaceous) of South Africa, is redescribed based on new fossil material including a single compressed cone. Some additional observations on the flora and environment of the Early Cretaceous in the Algoa Basin are made.

INTRODUCTION

Araucarites rogersii Seward is one of the most common fossil plant organs found in the Kirkwood Formation of South Africa. The genus *Araucarites* Presl is a widespread Mesozoic group of coniferous foliage and seed cone scales with affinities to those of the extant *Araucariaceae*.

Since Seward's (1903) description of the flora of the Uitenhage Series is the latest detailed work on the Lower Cretaceous fossil flora of South Africa, the present work will attempt to update Seward's description of *Araucarites rogersii* based on the increased number of specimens now available and particularly on a new find of a partially compressed cone assigned to this species.

SYSTEMATIC PALAEOBOTANY

Order: Coniferales

Family: *Araucariaceae*

Genus: *Araucarites* Presl

Araucarites rogersii Seward 1903

Araucarites rogersii Seward 1903: 37-38, Plate 6, Figures 4-7.

Diagnosis emended

Ovulate conifer cone, subcylindrical, compact, bearing helically inserted seed scales, fused to subtending bracts. Bract-scale complexes subcircular to deltoid, as long as broad, central 1/3 thick, fibrous, lateral extensions of scale thin, laminar, with fine elongate hexagonal reticulations; scale free near bract apex, semi-circular in outline, and scale with a single obovate seed, per scale.

Locality

Kirkwood Formation, Lower Cretaceous. 14 km east of Kirkwood 3/4 km south-west of Dunbrody Station. Along the west facing bluff on the east side of Bezuidenhout's River, Cape Province, South Africa.

Nomenclature

Seward's specific epithet *rogersi* is altered to *rogersii* according to the recommendations of the International Code of Botanical Nomenclature. This

change requires no alteration in the species authorship.

Description

Seward's description and diagnosis are quite accurate except for his failure to note the "ligule" or free seed scale apex. Measurements of the specimens of isolated seed scales give an average median length of 2.5 to 3.0 cm with the width of the broadest portion of the scale measuring 2.0-3.0 cm. The very thin laminar wings of the seed scales are most often indifferently preserved but, when present, give a more nearly subcircular outline to the whole scale (figs. 4, 7, 8). The central one-third of the scale is a massive, very fibrous, narrowly deltoid area that widens smoothly from the base to the apex (figs. 1-8). Only rarely is there evidence of a continuation of the thin lateral wings across the distal portion of the apex. Usually the apex is truncate with the fibrous central portion extending to the distal edge (figs. 1-8).

Seward's (1903) Plate 6, Figure 4 and description includes a mucronate or narrowly prolonged apex for the bracts; these extensions of the apex have not been found in any of the recently collected material. Clearly defined seeds have not been found either, and the original description of these is accepted (Seward, 1903).

The abaxial surface of several scales shows, near the bract apex, the impression of a semicircular or acutely pointed free scale tip (figs. 3, 4, 5, 7). The shape and position of these structures is consistent with the position of free scale apices in extant *araucarian* scales. It is most probable that these are only visible in adaxial view since not all the scales show such impressions (fig. 6).

The cone here assigned to *Araucarites rogersii* is obliquely compressed but is 4.5 cm long and about 2.5 cm wide (figs. 1, 2). Because most of the cone-scale specimens of *Araucarites rogersii* are found detached, it seems likely that the cones shattered when mature to facilitate seed dispersal as in modern *Araucariaceae* (Dallimore and Jackson, 1966). The small size of the cone would then be consistent with

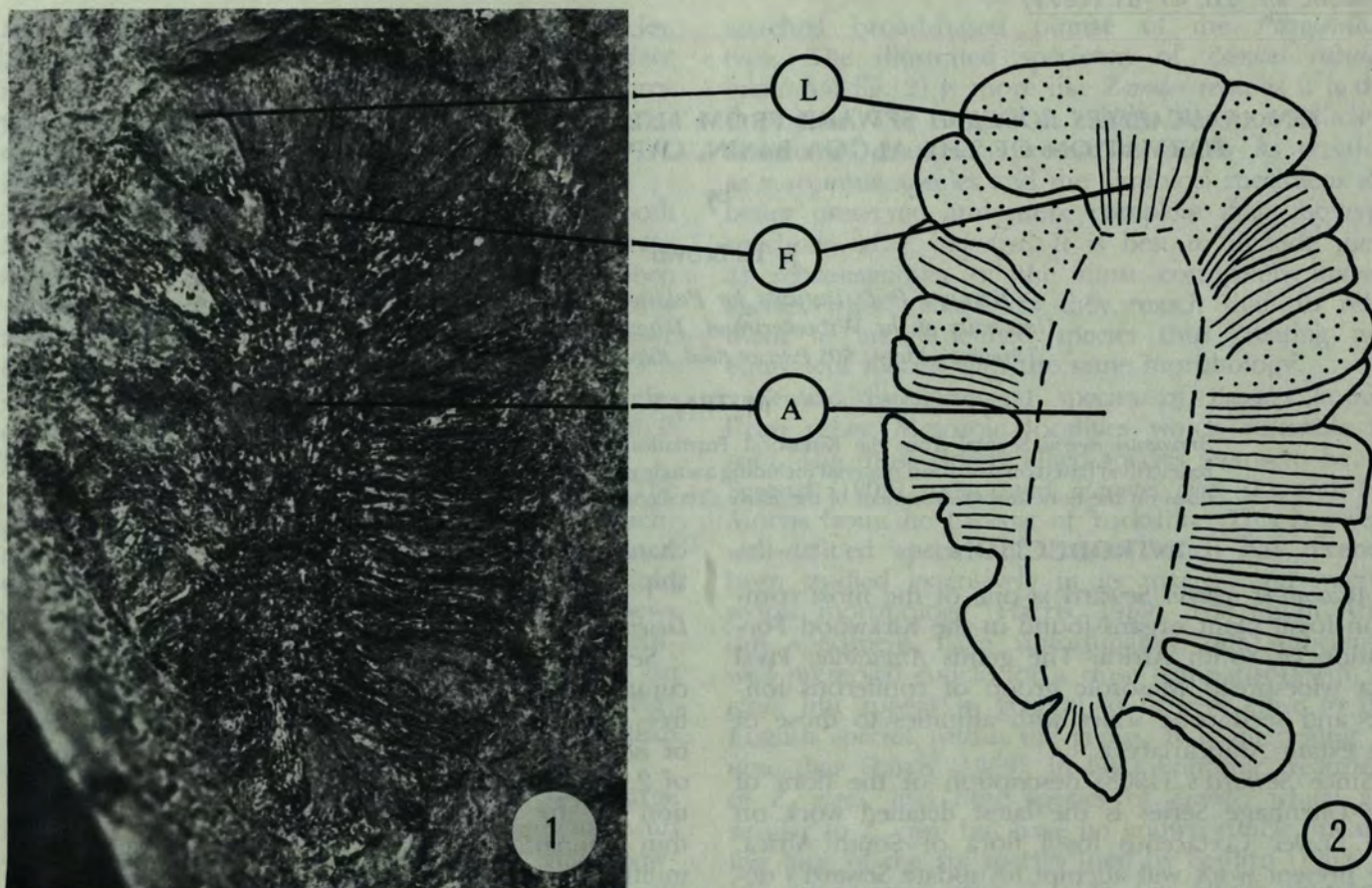


Figure 1. *Araucarites rogersii* BPI (Pal) PB 163. $\times 2$. L. laminar wing of cone scale. F. fibrous centre of cone scale. A. fibrous axis of cone.

Figure 2. *Araucarites rogersii*. Interpretation of cone PB 163. As shown in Figure 1.

an assumption of immaturity. Scales of the cone measure 1,0 cm long, about 1/3 that of dispersed scales. The axis of the cone is about 0,5 cm in diameter (figs. 1, 2).

The best evidence for assigning the cone to this species lies in the massive fibrous nature of the central portion of the scales. These fibrous areas are easily seen on the fractured surfaces of the scales attached to the cone axis (fig. 1). They are also abundant in the exposed end of the cone axis itself (fig. 1). Where the matrix of the rock is evenly broken near the cone apex, the scales can be seen in cross section as flattened ellipsoidal bodies extending laterally into fine laminar extensions. This configuration too is consistent with the known structure of the isolated scales of *A. rogersii*.

Discussion

Morphologically *Araucarites rogersii* is rather securely established as a coniferous megasporangiate cone with affinities in its structure to the modern Araucariaceae. Structurally, *Araucarites rogersii* has many superficial similarities to the seed cone of the extant genus *Araucaria*, a genus which is known to extend from the Jurassic through to the present.

However, there are not enough detailed characters known for *Araucarites rogersii* to include it confi-

dently in the modern genus *Araucaria*. We know at present nothing of the vegetative leaves, stem anatomy, or even the cone anatomy, all of which should be available before a fossil cone is definitely assigned to a genus with living representatives. It seems more precise to indicate this lack of knowledge by using a fossil organ genus with less demanding characters than to create a possibly mistaken correlation based on insufficient evidence.

Seward (1903, 1919) mentions the close resemblance of this South African species to *Araucarites* species recorded from India and the Lower Cretaceous of North America.

One species, *A. cutchensis* Feistmantel, has been reported from both the Lower Cretaceous of India and the Grahamland flora of Antarctica (Halle, 1913). *Araucarites cutchensis* chiefly differs from *A. rogersii* in the shape and size of the free scale apex. Halle (1913, fig. 16) clearly illustrates the elongate attenuate free scale apex of *A. cutchensis*. This is quite distinct from the semicircular acute free scale apex of *A. rogersii*. *Araucarites wyomingensis* Fontaine is a second species compared by Seward to *A. rogersii*; it is, however, consistently smaller than *A. rogersii*, measuring 1,2 cm in length by 0,9 cm in width.

There are two well-defined species of *Araucarites* from the Lower Cretaceous Ticó flora of Argentina

(Archangelsky, 1966). *Araucarites bagueroensis* Archangelsky is smaller than *A. rogersii* and has a very different shaped free scale which is separated from the bract laterally by a prominent ridge. The second species from Ticó, *Araucarites minimus* Archangelsky, is as the name implies very small, only 0,8 cm wide by 0,7 cm long, far smaller than *A. rogersii*.

Other Indian species of *Araucarites* also differ in detail from *A. rogersii*. *Araucarites fibrosa* Sukh-Dev and Bose is larger than *A. rogersii*, measuring up to 6 cm long by 4,4 cm wide and has an obviously mucronate tip which has seldom been encountered in *A. rogersii*. *Araucarites macropterus* Feistmantel is deltoid in shape with a less pronounced laminar wing (Sukh-Dev and Bose, 1972). Two Jurassic *Araucarites* from India, *A. bindrabunensis* Vishnu-Mittre and *A. nipaniensis* Singh, are also quite distinct. *Araucarites*

bindrabunensis is known from a petrification but its scales are less than one-third the size of those of *A. rogersii* and wedge-shaped with a 3 to 5 mm long tip (Vishnu-Mittre, 1954). *Araucarites nipaniensis* has a very extensive wing, a much less fibrous central area, and has no free scale (Singh, 1956). Seemingly, *A. rogersii* is a morphologically distinct form when compared to these other species of *Araucarites* from similar age strata.

Araucarites rogersii is not a distinct indicator of an Early Cretaceous age for the flora. Species of *Araucarites* have been reported from the Jurassic and Cretaceous (Seward, 1919). The best evidence from megafossil remains comes from the abundant occurrence of *Onychiopsis psilotoides* (Stokes and Webb) Ward (= *O. mantelli* Seward), a widespread species of fern usually assigned to the Wealden or its equiva-

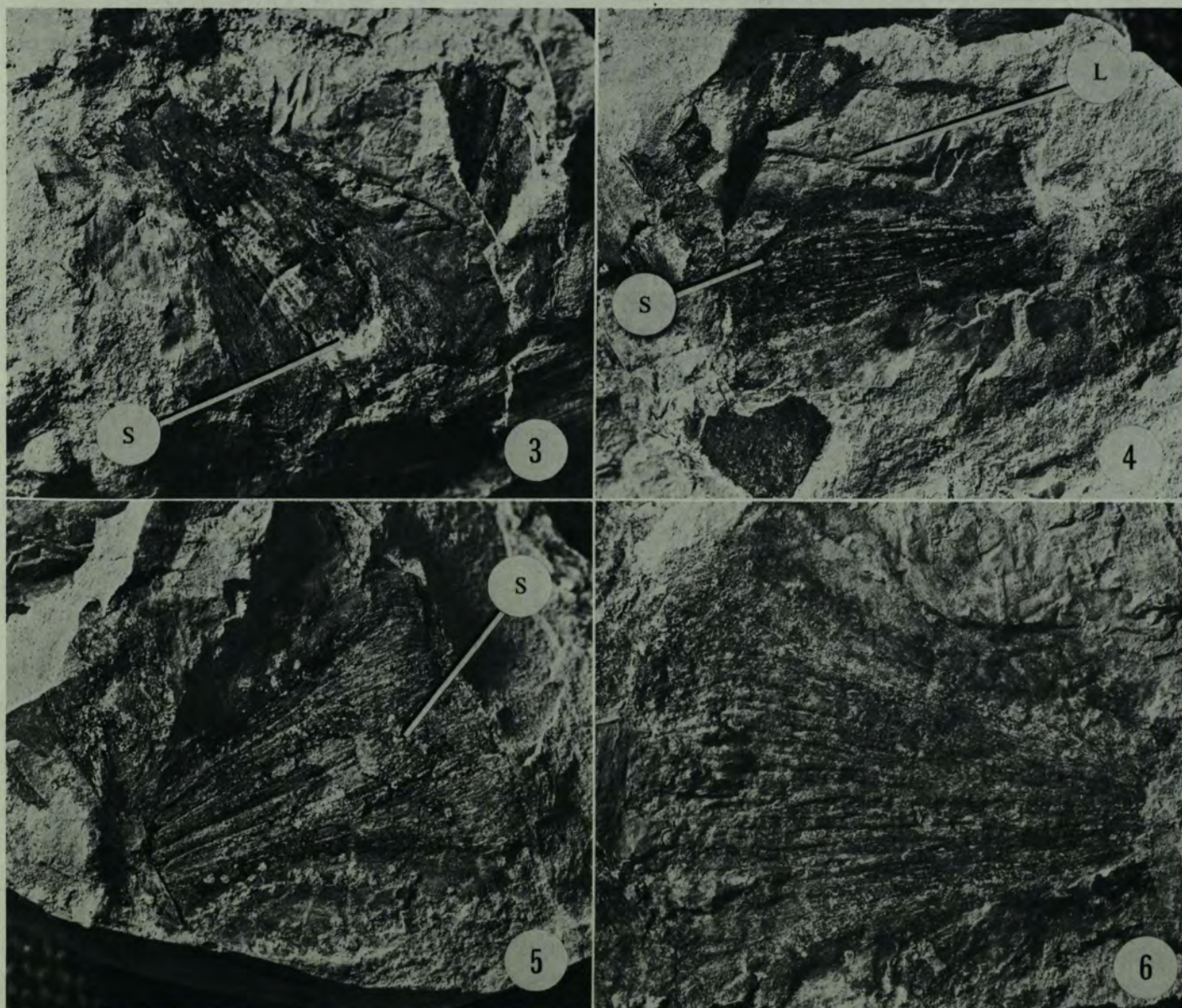


Figure 3. *Araucarites rogersii* BPI (Pal) PB 164. $\times 2$. Single detached cone scale with a free scale apex shown S.

Figure 4. *Araucarites rogersii* BPI (Pal) PB 165. $\times 2$. Cone scale with broad laminary wing L.

Figure 5. *Araucarites rogersii* BPI (Pal) PB 166. $\times 2$. Cone scale with free scale apex S.

Figure 6. *Araucarites rogersii* BPI (Pal) PB 167. $\times 2,5$. Detached cone scale.

lent (Barnard, 1973). This fern occurs almost alone at the nearby Sunday's River locality, and several smaller fronds have been found with *Araucarites rogersii* at the Bezuidenhout's River locality.

An interesting feature of the deposits in which *A. rogersii* is found is the relative lack of vegetative remains of conifers. Seward (1903) reported only two forms, *Brachyphyllum* and a single specimen he referred to *Taxites*. The collections available here have only a very few, small, poorly preserved fragments of a *Brachyphyllum* sp. and these do not occur at the same level as the cone scales. The *Taxites* type of conifer is unknown from the Bezuidenhout's River locality. It must be assumed that in the light of our present knowledge the cones of *Araucarites rogersii* were borne on the same tree that bore the *Brachyphyllum* foliage. Because some species of *Brachyphyllum* have cuticular characters which align them with the Araucariaceae, this seems to support the alliance based on cone-scale morphology (Kendall, 1947).

Little can be said to further our knowledge of the habit or surrounding environment based on the occurrence or morphology of *A. rogersii*. It has been noted that in Lower Cretaceous times conifers occupied a much broader geographic and physiographic range than at present (Hughes, 1973). The Kirkwood Formation is believed to have been laid down rapidly in the Algoa Bay-Kirkwood area and represents the continental-lacustrine facies of the series of strata of Early Cretaceous age in this area (Shone, 1976). An earlier paper pointed out one aspect of the rate of sedimentation during this time based on other plant fossils and their preservation (Brown and Gow, 1976). *Araucarites rogersii* was probably at-

tached to a tree of considerable size, if its assignment to the family Araucariaceae is correct, which grew very near an area where rapid deposition took place due to periodic inundation with complete burial of the smaller plants which grew along the margins of the watercourses (Brown and Gow, 1976).

Since *A. rogersii* is assumed to have been attached to a large tree, the scattered organs which are found today must have been present on the soil when burial took place. Perhaps a seasonal variation in the shedding of the plant organs could account for the greater number of cone scales preserved relative to the vegetative leaves, if burial took place shortly after a large drop of cones and scales. This could account for the relative scarcity of vegetative parts compared to cone scales. The trees themselves may have been unaffected by the flooding which buried the isolated organs. Large pieces of silicified coniferous wood are found at different levels of the Kirkwood Formation; these may represent the trunks of *Araucarites rogersii*.

We may assume that there was a significant area of land which was covered with large coniferous trees close enough to the area for their scattered seed scales to be buried with the ferns which grew along the margins of the streams.

The picture of the flora in Early Cretaceous times of the area now surrounding the present Bezuidenhout's River near its entry into the Sunday's River is that of low-lying, well-watered land with bryophytes, ferns and cycads occupying the watercourse margins, while large coniferous trees bearing *Brachyphyllum* type foliage and *Araucarites* cones occupied the higher ground.

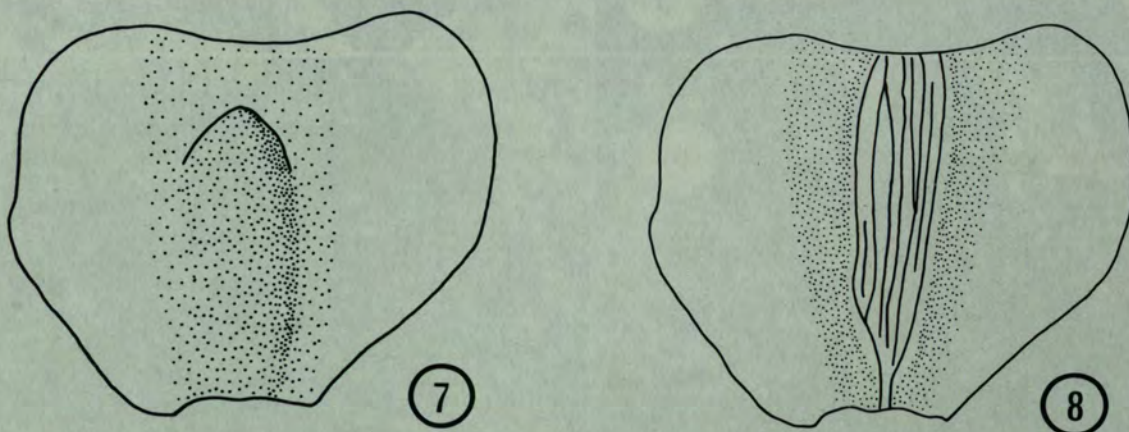


Figure 7. *Araucarites rogersii*. Diagrammatic reconstruction of the adaxial view showing free ovuliferous scale. Stipple represents thicker area of central bract and scale. $\times 2$.

Figure 8. *Araucarites rogersii*. Diagrammatic view of abaxial surface showing central fibrous area of bract. $\times 2$.

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INTRODUCTION

The Algoa Basin, situated in the south-eastern part of South Africa, is a small, isolated, and relatively recent, but geologically important, basin. It is situated in the south-eastern part of the Cape Province, between the Orange and the Tugela rivers, and is bounded to the north by the Orange River, to the east by the Tugela River, to the south by the Tugela River, and to the west by the Orange River. The basin is situated in the south-eastern part of the Cape Province, between the Orange and the Tugela rivers, and is bounded to the north by the Orange River, to the east by the Tugela River, to the south by the Tugela River, and to the west by the Orange River. The basin is situated in the south-eastern part of the Cape Province, between the Orange and the Tugela rivers, and is bounded to the north by the Orange River, to the east by the Tugela River, to the south by the Tugela River, and to the west by the Orange River.

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AN INVESTIGATION OF THE LOWER PERMIAN MIDDLE ECCA AMMONITE LOCALITY AT ALLETA, NATAL

by

I. R. McLachlan

ABSTRACT

The problematic ammonite *Paraceltites bowdeni* Teichert & Rilett has been recorded only from the Alleta iron-ore mine near Dundee in Natal. It is unique in the Early Permian Ecca Series as it suggests a normal salinity for the depositional environment of sediments that have yielded no other clearly marine fossils. An investigation of the matrix of the specimen slabs, however, yields information which is incompatible with equivalent data from the Alleta mine and the Ecca sediments in general. The matrix contains the distinctive pollen *Classopollis* which is not known from elsewhere in the world in deposits older than Late Triassic. Comparative tests of the degree of thermal diagenesis of the contained organic material suggests that the ammonite specimens have not been subjected to the same degree of alteration as the sediments at the Alleta mine. Results of other tests have not been definitive but do not contradict the suggestion that the ammonites were mistakenly accredited to the Alleta mine. It is concluded that the ammonites derived originally from sediments of Late Triassic to Early Jurassic age at an unknown locality outside of South Africa.

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INTRODUCTION

The Middle Ecca sediments of the northern Karoo facies form a sandy wedge of fluvio-deltaic origin (Ryan, 1968; Hobday and Mathew, 1975) which built out into the basin, being supplied from source areas mainly in the north-east. Economic coal deposits occur at several levels in a broad arc extending from near Welkom in the north-western Orange Free State across the southern Transvaal and into northern Natal as far south as Dundee. Although the basin of deposition has been loosely referred to as being a "sea" or "marine", the invertebrate record is notably sparse. In the course of a review of the paleontological information relating to the nature of the depositional environment of the northern Karoo Ecca sediments, McLachlan (1973, p. 10) concluded that the fossil content (fish scales, fresh

water bivalves, Conchostracha, acanthomorph acritarchs, monaxon siliceous sponge spicules) suggests fresh to brackish water and provides no support for normal marine conditions. Anderson (1975) has since described limulid trackways from the top of the Upper Ecca shales in the Orange Free State. Although it was recognised that they might record a restricted relict fauna surviving in the basin after withdrawal of the marine incursion which followed the retreat of the Dwyka glaciers (McLachlan and Anderson, 1973), it was tentatively suggested that their presence might reflect the existence of a link with the world oceans (Anderson, 1975). As the alternative explanation is equally acceptable the evidence provided by the limulid trackways in favour of a marine environment must remain inconclusive. The only real exception to have emerged in nearly

70 years of coal mining and exploration of the Ecça is the ammonite from the Alleta* mine described by Rilett (1963) as *Discetoceras bowdeni* and recently re-described by Teichert and Rilett (1974) as *Paraceltites bowdeni*. It was cited by Teichert and Rilett as evidence for a marine paralic depositional environment within the Middle Ecça coal measures and was considered to indicate a late Early to Late Permian age. According to Rossouw (1976) the Alleta iron-ore deposit lies approximately in the middle of the Middle Ecça sequence.

The Alleta mine was worked on a small scale between 1939 and 1953 (MacGillivray, written comm. 1975) to exploit a metre thick carbonaceous siderite band as a source of iron. A few years before the mine shut down, Rilett (1951) described a number of specimens of the fresh-water bivalve *Unio alettaensis* which had been recovered from the siderite band by the mine staff in the course of operations. He considered the lenticular iron ore deposit to be clearly lacustrine in origin. In 1963, a decade after the closure of the mine, he described a few compressed but otherwise well preserved cephalopods (*Discetoceras bowdeni*) which he reported had been recovered by the Inspector of Mines, Mr. Bowden, from the shale roof of the small coal seam overlying the siderite deposit at the Alleta mine (fig. 1). He observed that the Middle Ecça beds in northern Natal were laid down in a cyclic manner and that the cephalopods were found in a thin shale above a small coal seam where marine beds would be expected if the classical cyclothem of the European coal measures was used as a model. He pointed out that cyclothems are normally incomplete with the marine portions almost invariably being absent (Teichert and Rilett, 1974).

The present investigation arose from an interest in the depositional environments of the Dwyka and

Ecça sediments as revealed by micropalaeontology. The matrix of the ammonite specimen slab was initially studied in 1971, in the hope that marine microfaunas or acritarchs might be present which would shed further light on the environment and age of the sediments and which could perhaps aid recognition of the horizon in boreholes further afield. These studies were inconclusive because of the difficulty of effectively disaggregating the sample material. In June, 1973, the ammonite specimen was examined at the Natal Museum. The manner of preservation, particularly the bright fresh appearance, seemed anomalous when compared with other invertebrate fossils known from the Karoo. A comparative study was accordingly undertaken to discover whether there is any positive information to confirm that the ammonite specimens did derive from the Karoo sediments or whether they were from some other source and had been mistakenly credited to the Alleta mine.

A. Description of Alleta Mine

The mine is situated 12 km north of Dundee, near the southern limit of the Natal Middle Ecça coal fields (fig. 2). The geology of the area is described in some detail by Rossouw (1976). A schematic section, (fig. 3) shows the relative positions of the main elements. The mine was briefly visited in 1973 to obtain a set of comparative samples. A number of adits and stopes extended from an open cut and followed the horizontally bedded siderite into the hillside for 600 m. The workings are in a dangerous condition and in most cases falls of hanging-wall strata have buried the siderite and coal bands. Only one adit was open and safe for a short distance. A careful search did not reveal any sediment resembling that of the ammonite matrix. This absence could be explained by the weathered state of sediments and the poor exposures. Furthermore, Teichert and Rilett (1974) pointed out that the thin layer was probably impermissibly developed. Figure 3 shows a sketch of an exposure in the easternmost open pit and the positions of the samples collected.

The extensive Zuinguin dolerite sill (fig. 1) lies 15 metres above the workings and is about 30 metres thick.

B. The Ammonite Specimen Slabs

Teichert and Rilett (1974) provided a careful description of the specimens and matrix, so only the main points and any new observations are recorded here. The most striking feature of the fossils is the bright fresh orange colour of the ? aragonitic shells and their relatively good state of preservation. They occur as compressions on a pale grey matrix of highly calcareous shale. Teichert and Rilett observed

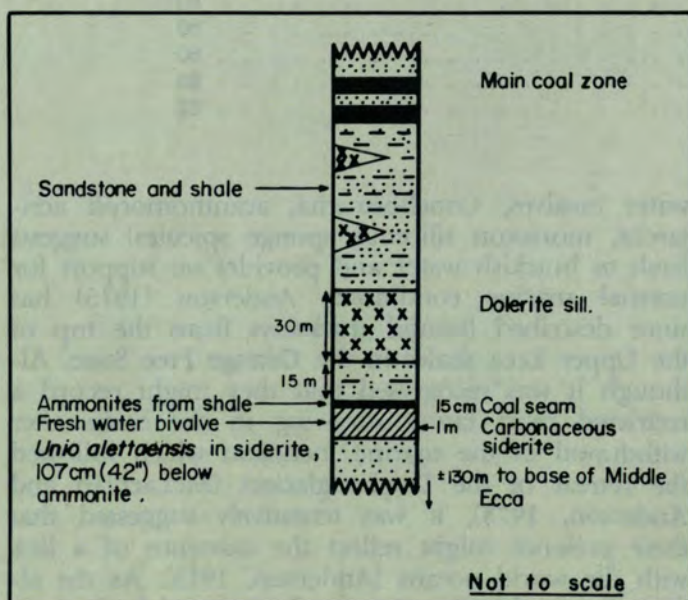


Figure 1. Schematic stratigraphic section at Alleta, compiled from information in Rilett (1951, 1963), Teichert and Rilett (1974), Rossouw (1976) and personal observation.

* This spelling follows the usage of the 1:125 000 geology map of the area (Elandslaagte 2829B and Dundee 2830A, printed 1967) and the 1:50 000 topographic map 2830AA (printed 1973). The farm name on the latter is spelt Alletta. Rilett (1951) used the spelling Aletta.

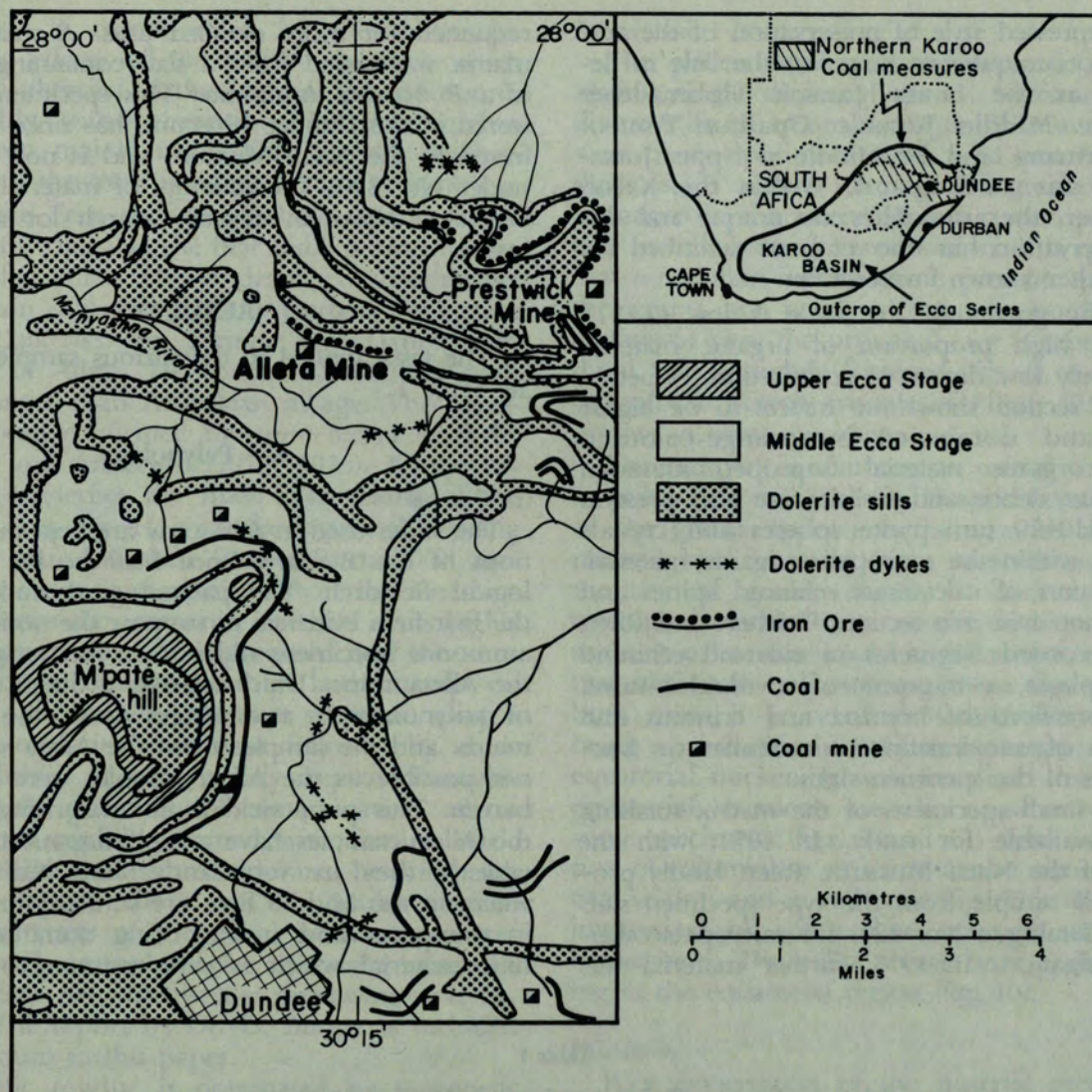


Figure 2. Plan showing regional geological setting of the Alleta iron-ore mine from which the ammonite *Paracelites bowdeni* is said to have originated. (Modified after Figure 1 of Teichert and Rilett, (1974). Baseplan: 1/125 000 Geol. map. 2829B Elands-laagte and 2830A Dundee, Geol. Surv. S. Afr.)

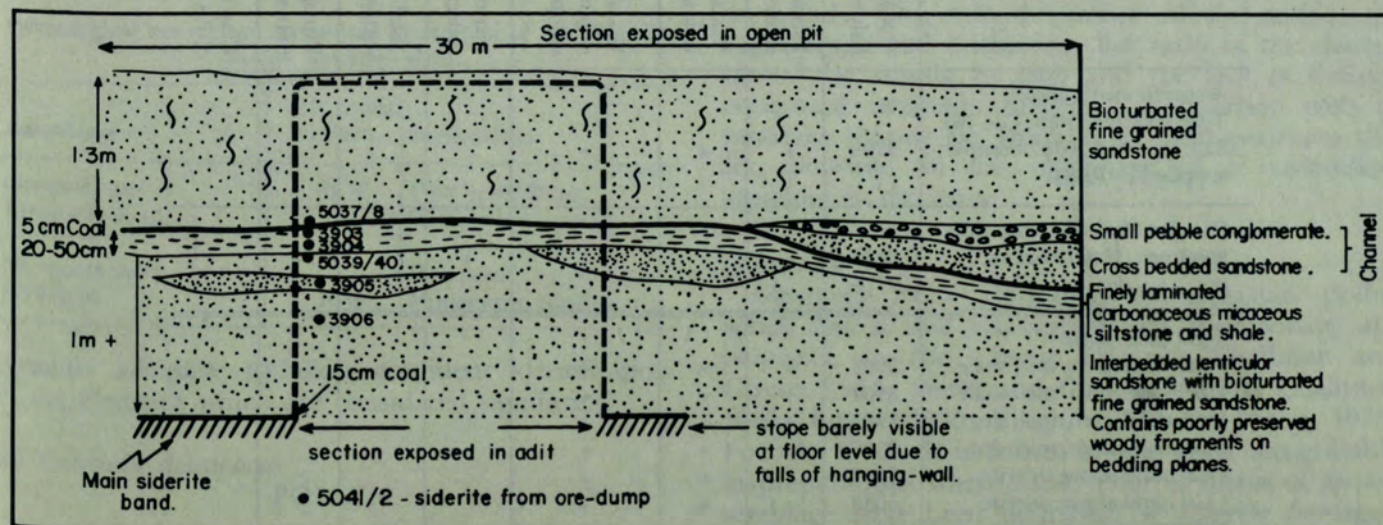


Figure 3. Sketch of section exposed at Alleta mine. Sample positions 3903 to 3906 and 5037 to 5042 are shown.

that the compressed style of preservation of the ammonites is not unique but is in fact the rule in deposits such as the Lower Jurassic Holzmadener Schiefer, the Middle Jurassic Opalinus-Ton of southern Germany, and the Middle to Upper Jurassic Oxford clay of England. Within the Karoo basin, however, the ammonites are unique and this style of preservation has not yet been described for any of the other known invertebrates.

The specific gravity of the shale is low (2.131), suggesting a high proportion of organic material and a relatively low degree of compaction. A petrographic thin section shows the matrix to be highly calcareous and dominated by orange-coloured amorphous organic material (sapropel) although tracheitic plant debris and fusinite are also present. Very small (10–20 μm) pyrite spheres and crystals are crowded within the sapropelic organic material. A few fragments of calcareous echinoid spines and plates were noted in thin section; Teichert and Rilett previously recorded fragments of cidaroid echinoid spines and plates, a fragment of mytiloid bivalve, possible impressions of bryozoa and crinoids and the remnants of one indefinite foraminifer on fractured surfaces of the specimen slabs.

Only two small specimens of the matrix totalling 7 g were available for study. In 1971, with the permission of the Natal Museum, Rilett kindly provided a small sample from the type specimen slab (No. 1012, Catalogue No. 820) for micropalaeontological investigation. In 1973, further material was

requested for more detailed tests. A small piece of matrix was sawed from a slab containing a portion of a *P. bowdeni* ammonite. This specimen, originally stored in the Dundee Museum, has since been transferred to the Natal Museum and is now catalogued under No. 820. The quantity of material was insufficient to allow an effective search for microfaunal fossils.

RESULTS

The tests applied to the various samples are listed in Table 1.

A. Palynology

(i) General

The slides used in this study are kept in the collections of the Bernard Price Institute for Palaeontological Research. The palynological study provided the first firm evidence to support the notion that the ammonite specimens did not, in fact, originate from the Alleta mine. Unfortunately, a direct comparison of palynomorph assemblages from the ammonite matrix and the samples from the Alleta samples was not possible as the Alleta samples were very nearly barren. This poor yield is not surprising. Although the Alleta samples have a high organic content (see table 3) they are very sandy. Such sediments elsewhere in the Middle Ecca are similarly impoverished in miospores and cuticle, being dominated by lignitic material which is very resistant to oxidation.

Table 1
Schedule of tests applied to samples from the ammonite specimen slabs and from the Alleta mine.

Sample Description	SOEKOR palynology No.	Palynology studied	Visually estimated TAI	Visual estimate of organic material composition	Vitrinite reflectance	Total organic material (T. org.)	Petrographic thin section	Clay mineralogy by X-ray diffraction
<i>Ammonite matrix samples</i>								
Type specimen slab. Cat. No. 820, type No. 1012. (Sample supplied by Rilett).	3769	+	+	+				
<i>Dundee Museum ammonite specimen. Natal Museum Cat. No. 820</i>	3834	+	+	+	+	+	+	+
<i>Alleta mine samples</i>								
Finely lam. carb. mic. shale	3903	+	+	+	+	+		+
Finely lam. carb. mic. shale	3904	+	+	+				
Bioturb. sl. carb. mic. sltst.	3905	+	+	+				
Bioturb. sl. carb. mic. sltst.	3906	+	+	+				
Coal band above siderite	5037	+	+	+				
Coal band above siderite	5038	+	+	+				
Siderite ore from dump.	5041	+	+	+				
Siderite ore from dump.	5042	+	+	+				

The situation is compounded by the destructive metamorphic effects of the nearby dolerites which have caused thermal darkening of the miospores and probably some corrosion. Weathering has probably been mainly responsible for the destruction of all but the most resistant organic material.

The Middle Ecca unit as a whole is nonetheless well dated. In what was the first publication on Ecca palynomorphs, Rilett (1954) described assemblages from the main coal seams of the Durban Navigation Group of Collieries No. 3 mine near Dannhauser, 25 km west of Alleta. He concluded that the coals are not younger than Artinskian in age. This assessment has been confirmed by more recent work by Hart (1967) and Anderson (1973, 1975). As the Alleta deposit underlies the main coal seams of the Dannhauser area (fig. 1), it can be regarded as being not younger than Artinskian (Lower Permian) in age.

Very poor yields were obtained from the initial attempt to process the ammonite material as its highly sapropelic nature was not appreciated and the sample could not be disaggregated. A later attempt on the matrix of the Dundee Museum specimen using a fairly severe oxidation treatment followed by staining with safranin O gave greatly improved results. To preclude the possibility of contamination, all receptacles were carefully cleaned with fuming nitric acid mixed with potassium chlorate, before being used. As a further check on the results detailed below, the director of the Natal Museum was requested to send a sample of the ammonite matrix to an independent palynologist for processing and examination. The report by Dr. D. Burger is included as an addendum to this paper.

The organic residue is dominated by sapropelic material with miospores constituting less than 5 % of the whole (table 3). The palynological assemblage consists almost entirely of *Classopollis* with minor amounts of other pollen grains and acritarchs (table 2). Preservation of the microfossils is not good but is

Table 2

Palynological assemblage recognised in samples of the *Paraceltites bowdeni* specimen slabs.

Assemblage	% in count of 200	Preservation
<i>Classopollis</i> spp.	82 %	Poor to moderate
? <i>Araucariacites</i> sp.	8 %	Moderate
Miospores indet.		Very poor
Acritarchs	10 %	Moderate to good

certainly adequate to allow confident identification of the elements which are considered significant.

(ii) Systematic descriptions

POLLEN

Genus: *CLASSOPOLLIS* Pflug emend. Reyre, 1970

Classopollis sp. cf. *C. meyeriana* (Klaus), De Jersey, 1973
Figures 4–11

Description

The pollen occurs as tetrads in a ratio of 1:4 against single dispersed grains. Specimens range in diameter from 44 µm to 20 µm. The average dimensions of ten specimens is 36 × 31 µm. Average exine thickness is about 1.6 µm. The grains show some variations in character. While a certain part of this is due to differences in preservation, it is quite possible that more than one species is present. In polar view, the grains are nearly circular in outline while in equatorial view the proximal face is tapered and the distal face is slightly flattened (fig. 4). A sub-equatorial circular furrow (rimula of Pflug, 1953) is clearly present in most specimens.

The ratio of its diameter to overall amb diameter in polar view is 0.78:1 for 10 specimens. The surface of the grains appears to be smooth and unornamented but this may be a preservational effect. A number of grains display a distinct pseudopore (average diameter 9 µm) on the distal surface (figs. 4 to 7). A trilete scar could be discerned on the proximal surface in only two specimens (figs. 8 and 9); in both cases it is relatively small with the laesurae being approximately 2–3 µm in length. No marked equatorial thickening was seen, and definite circum-equatorial striations are also apparently absent. In some specimens (figs. 7 and 11) there is the suggestion of columellate structure in the exine seen in optical section and in only one (fig. 7) is there a distinct impression of columellate structure on the distal hemisphere. The exine shows only a slight thickening in the equatorial region (fig. 10).

Discussion

Poor preservation of the material precludes confident specific allocation.

The presence of the following features leaves little room for doubt (see Pocock and Jansonius, 1961; Reyre, 1970) that the genus represented is *Classopollis*: general shape of the grains, sub-equatorial furrow, proximal trilete scar and distal pseudopore, columellate structure of exine, common occurrence as tetrads. The smooth surface of the grains, the slight equatorial thickening, the ratio of the diameter of the rimula to amb and the lack of definite equatorial striations suggest a comparison with *C. meyeriana* (Klaus) De Jersey, 1973. The specimens differ, however, in the suggestion of a columellate structure in the exine.

Occurrence

Classopollis is a distinctive cosmopolitan pollen which has a well established first evolutionary appearance in the Upper Triassic (Chaloner and Clarke, 1961; Pettitt and Chaloner, 1964; Chaloner, 1969; Reyre, 1970; Singh, 1971; De Jersey, 1973; Pocock, 1972). It is robust and is often recognisable in preparations where most other elements of an assemblage have been destroyed or severely damaged by corrosion. It characteristically dominates Jurassic and Lower Cretaceous ("Neocomian") assemblages

and thereafter declines in importance until it finally disappears in the Senonian.

The record of *C. belloyensis* by Pocock and Janso-nius (1961) from the Permian has been shown by Chaloner and Clarke (1961) to be erroneous. *Classopollis* has not been recorded from the Karoo basin Permian or Triassic rocks in spite of extensive sampling by Hart (1967), Anderson and Anderson (1970) and Anderson (1973, 1975), nor has it been reported from Karoo sediments of the age in Rhodesia (Mrs. R. Falcon. pers. comm.) or Zambia (Dr. J. Utting, pers. comm.). De Jersey (1973) gives the range of *C. meyeriana* as being Upper Triassic (Carnian) to Lower Jurassic.

Genus: ARAUCARIACITES Cookson ex Cooper, 1953

Araucariacites sp.

Figure 12

Description

The pollen is oval to circular in outline and has a finely granular exine. No evidence of apertures was seen. The dimensions of four specimens average $50 \times 41 \mu\text{m}$ with a maximum dimension of $54 \mu\text{m}$ and a minimum of $38 \mu\text{m}$.

Discussion

Because of poor preservation, the identification is not confidently made; it is not a distinctive pollen and especially when poorly preserved could easily be confused with other similar long ranging genera.

Occurrence

The range of *Araucariacites* is given by Singh (1971) as Jurassic to Tertiary. It commonly occurs as a dominant element in Jurassic to Lower Cretaceous assemblages in association with *Classopollis*.

ACRITARCHS

The relative abundance of this group in the assemblages is probably due to their superior resistance to diagenetic alteration as well as to depositional environment factors. Preservation is moderate; in the case of *Leiosphaeridia* and *Dictyotidium*, it is good. Unfortunately, the acritarchs provide little positive age information. Most are simple conservative forms that have changed little with time and it seems unwise to place reliance on the age ranges given below.

Subgroup: SPHAEROMORPHITAE Downie, Evitt and Sarjeant, 1963.

Genus: LEIOSPHAERIDIA Eisenack, 1958

Leiosphaeridia granulosa Pocock, 1972

Figure 13

Discussion

Three specimens were noted. The description by Pocock (1972, p. 105) applies very well to these and need not be repeated here. There is no sign of an aperture. Vesicle diameter averages $32 \mu\text{m}$ and the

granules are 0.4 to $0.8 \mu\text{m}$ wide.

Occurrence

Pocock recorded *L. granulosa* from the Lower to Middle Jurassic of Canada.

Leiosphaeridia sp. B

Figure 14

Description

Vesicle circular in outline and 12 to $14 \mu\text{m}$ in diameter. Surface uniformly ornamented with short conical granules spaced a little more than their own diameter apart. No apertures seen.

Discussion

Similar to *L. minutaespinoza* Pocock (1972) but the dimensions are consistently smaller. Three specimens seen.

Subgroup: HERKOMORPHITAE Downie, Evitt and Sarjeant, 1963

Genus: DICTYOTIDIUM (Wetzel) Staplin, 1961

Dictyotidium sp.

Figures 15–17

Description

Vesicle circular in outline. Preservation is not sufficiently good to allow the wall structure to be distinguished. Surface ornamentation consists of low membranes which outline polygonal fields of irregular shape and size. No aperture was seen. Vesicle diameter varies from 13 to $19 \mu\text{m}$, the height of the ornament membranes is 0.2 to $0.4 \mu\text{m}$ and the width of the polygonal fields is 0.8 to $3 \mu\text{m}$. Seven specimens seen.

Discussion

The specimens studied are all similar in basic organisation but there seems to be a certain amount of gradational variation in vesicle size and the coarseness of ornament reticulation. Some of the specimens are closely similar to *D. eastensis* Pocock but the dimensions are smaller.

Subgroup: ACANTHOMORPHITAE Downie, Evitt and Sarjeant, 1963.

Genus: MICRHYSTRIDIUM (Defl.) Staplin, Janso-nius and Pocock, 1969.

Michrystidium lymensis Wall, 1965

Figures 19–20

Description

Vesicle spherical, thin walled ($\pm 0.8 \mu\text{m}$) smooth and bearing 15 to 32 spines of variable length in different specimens. Preservation not sufficiently good to allow details of wall or spines to be discerned. The spines are conical and solid, and taper rapidly to a fine point. Vesicle diameter ranges from 17 to $28 \mu\text{m}$ and averages $26 \mu\text{m}$. Nine specimens seen.

Discussion

Riley and Sarjeant (1972) gave the range of *M.*

lymensis Wall as being confined to the Jurassic but it is very probable that simple indistinctive acritarchs of very similar appearance also occur much earlier and later.

Michrystidium deflandrei Valensi, 1948

Figure 18.

Description

Vesicle oval to circular in outline and bearing numerous short straight or slightly curved solid spines which taper to a fine point. No aperture seen. Three specimens recorded.

Discussion

The specimens fit the description of Davey (1970) well but are consistently larger in size.

Occurrence

Riley and Sarjeant (1972) recorded the age range of *M. deflandrei* as being Jurassic and pre-Jurassic. Davey (1970) recorded it from the Cenomanian.

(iii) Conclusions

The only palynomorph from the ammonite specimen slab which gives any definite age information is *Classopollis*. It clearly indicates a post Late Triassic age for the ammonites. The remainder of the assemblage, although not in itself of age significance, is compatible with this dating and, together with the dominance of *Classopollis*, forms a typical Jurassic or Lower Cretaceous (Neocomian) microflora. If the age range of *C. meyeriana* is also taken into account, it is considered that the most probable age for the ammonites is Late Triassic to Early Jurassic.

B. Diagenetic Studies

An extensive literature exists on the determination of maximum palaeotemperature employing the degree of carbonisation of dispersed organic material in sediments (Correia, 1971). For this exercise it is reasonable to suppose that, if the ammonites did originate from Alleta, they would have been exposed to the same temperature as the samples 3903 to 3906 and 5037 to 5042, collected stratigraphically a few metres away in the old workings (fig. 3). The nearest dolerite sill lies 15 m above the siderite; over the small area of the mine, temperatures are likely to have been nearly uniform at the time of maximum heating.

The laboratories of Société des Pétroles d'Aquitaine (S.N.P.A.) undertook the quantitative measurements of total organic carbon, CR/CT ratios and vitrinite reflectance, and also made a visual estimate of the composition of the organic material under reflected light. The samples they received were identified only by code numbers. The author completed visual estimates of the composition of the organic material and the thermal alteration index with transmitted light using standard unoxidised palynological preparations. Results of the tests are shown in Table 3.

The composition of the organic material of the two samples tested is quite different. The palynological assessment indicates a dominance of amorphous organic material in the ammonite specimen and, in contrast, a dominance of lignitic material in the Alleta mine samples. This is supported by S.N.P.A.'s reflected light estimates of 80 % exinite, 15 % vitrinite and 5 % inertinite, with strong and

Table 3

Results of tests on content, composition and degree of thermal alteration of organic material.

	Total organic carbon	CR/CT	Palynological assessment of composition of O.M.				T.A.I.	Vitrinite reflectance	EXPLANATION
			Amorphous O.M. (sapropel)	Cuticle, spores, etc.	Tracheids	Lignite			
Ammonite specimen	*1 0,25 %	*2 0,80	80 %	< 5 %	10 %	5 %	2,75	1,00	CR/CT = Proportion of residual to total carbon. It provides a rough indication of organic matter type and maturity.
Alleta mine 3903	4,15 %	0,91	—	< 5 %	< 5 %	90 %	3,50	1,35	OM = Organic material.
3904			—	< 5 %	< 5 %	90 %	3,50		T.A.I. = Visually estimated thermal alteration index. (S.P. of Correia, 1971).
3905			—	< 5 %	< 5 %	90 %	3,50		*1 = Low T.O.C. probably due to loss of O.M. which floated on surface of preparation.
3906			—	< 5 %	< 5 %	90 %	3,50		*2 = Result possibly not accurate because of low total organic carbon, but S.N.P.A. feel it is compatible with other information.
5037			—	< 5 %	< 5 %	90 %	4,00		
5041			—	—	—	100 %	—		

Analysts: Société Nationale Pétroles d'Aquitaine. Palynological assessment by I. R. McLachlan.

abundant fluorescence, for the ammonite specimen and 75 % vitrinite, 25 % inertinite for the Alleta mine samples. It is suspected that the measured total organic content of the ammonite specimen is low because of inadvertent loss of organic material due to small sample size: the petrographic thin section shows a high content of organic material. The quantitative measurements of thermal alteration also show clear differences, with the Alleta mine sample vitrinite reflectance index of 1,35 % (equivalent to a temperature of about 135 °C) being compatible with the values measured elsewhere in this area by SOE-KOR (Rowell and De Swardt, 1976) and the ammonite matrix giving the anticipated lower value of 1,00 % (equivalent to a temperature of ± 100 °C). The palynological visual estimates (TAI's) of the degree of thermally induced carbonisation also indicate a significant difference: the Alleta miospores and cuticle are dark brown in colour and correspond to a TAI of about 3,5 while the material from the ammonite specimen is clearly less carbonised and has a TAI of about 2,75. The CR/CT ratios are in accord with the above data.

These results strongly suggest that the Alleta sediments have been distinctly more heated than the ammonite samples which are reported to originate from the same site.

C. Mineralogy

The results of X-ray diffraction analyses are shown in Table 4. The composition of the Alleta mine samples is not particularly distinctive.

Table 4

Comparison of minerals identified by X-ray diffraction of a sample from the Alleta mine and one from the ammonite specimen slab.

ALLETA MINE Sample No. 3903 *1	AMMONITE SLAB	Natal Museum *2 Catalogue No. 820
Illite 80 %	Sericite	
Illite-montmorillonite ± 20 % No carbonate	Calcite Aragonite	Results qualitative only
Abundant quartz	Minor quartz	

*1 Analyst: Société Nationale
Pétrole d'Aquitaine

*2 Analyst: Geological Survey of
South Africa

The presence of aragonite in the ammonite specimen seems incompatible with its supposed origin as aragonite is normally unstable at the temperature determined for the Alleta mine sample. However, Kennedy and Hall (1967) gave examples of situations

in which the mineral has retained its crystallographic form at higher temperature due to the protective effect of large concentrations of sapropelic organic material. Nevertheless, aragonite has not previously been recorded from the Ecca sediments (Rowell, pers. comm.) and its presence at Alleta is anomalous.

CONCLUSIONS

The palynomorph assemblage recovered from the matrix of the ammonite specimen slabs indicates a definite minimum age limit of Early Jurassic. This is corroborated by the results obtained by Dr. D. Burger (see appendix) who independently processed and studied the ammonite material which was sent to him by the Natal Museum. The dating is clearly incompatible with the well established Lower Permian age of the Middle Ecca sediments which occur at Alleta. Thermal diagenesis studies support this conclusion and indicate that the ammonites were not subjected to the temperatures which were attained by the sediments at the Alleta mine.

A clue to the origin of the ammonites is perhaps contained in the discussion by Teichert and Rilett (1974). They mentioned that the type of preservation seen in the *Paraceltites bowdeni* specimens is the rule in Jurassic deposits in Germany and Britain: the similarities of preservation and the nature of the enclosing sediments are certainly compelling, while the opposite is the case when a comparison is made with the sediments and mode of preservation of known Karoo fossils.

Clearly, a direct comparison of *P. bowdeni* with ammonites of this age should be made. It is relevant to note in passing that no marine sediments of Upper Triassic or Lower Jurassic age are known within southern Africa (McLachlan, McMillan and Brenner, in press).

It is concluded that the *Paraceltites bowdeni* ammonite specimens did not originate from the Karoo sediments of the Alleta mine and that the environmental conclusions based on them are therefore invalid.

ACKNOWLEDGEMENTS

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ADDENDUM

PALYNOLOGICAL NOTES CONCERNING THE ALLETA AMMONITE

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Palynological examination was carried out in the Bureau of Mineral Resources on a rock sample forwarded by the Natal Museum from matrix adhering to the Alleta ammonite. The sample yielded a moderately rich assemblage mainly consisting of pollen grains, and including sporadic smooth-walled and sparsely spinose unicellular organisms determined as acritarchs belonging to the genera *Leiosphaeridia* Eisenack and *Michrystidium* Deflandre.

The pollen assemblage is restricted to the extent that it contains only one type of pollen. The grains are spherical; they have an unlamellated and structureless, psilate wall. Many display a circular aperture (pore) and triradiate feature, respectively in distal and proximal polar areas. A circum-equatorial exine thickening is bordered distally by a narrow ring-shaped zone ("rimula") where the exine is thinner and which in equatorial view is apparent as a

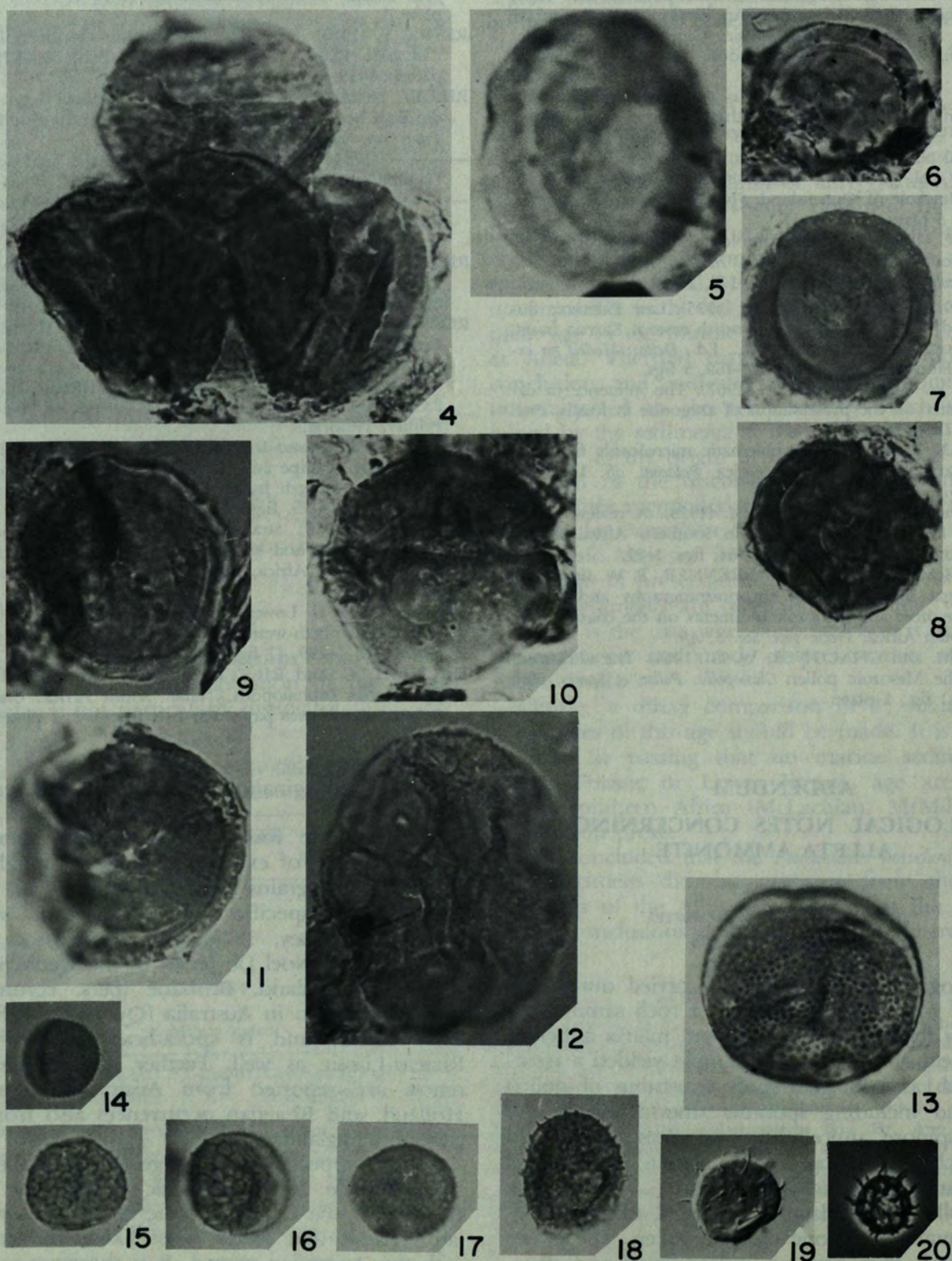
local slight invagination of the outline of the pollen grain.

Although the fossils are extremely poorly preserved the lack of exinous features is thought to be authentic. The grains show close affinity to, and are probably conspecific with, *Classopollis meyeriana* (Klaus) De Jersey, 1973. This comparison is confirmed by Dr. Noel De Jersey of the Geological Survey of Queensland, Brisbane (pers. comm.). The species is known in Australia (Queensland) from the late Triassic, and is sporadically present in the Rhaeto-Liassic as well. Further late Triassic occurrences are reported from Austria, Germany and Holland, and Rhaetian occurrences also from Hungary and England.

It thus appears that the age limits of the assemblage include the late Triassic and earliest Jurassic. In view of the exclusive presence of *C. meyeriana*, a late Triassic age seems most likely, in accordance with the Australian record. It is therefore concluded that the matrix sediment, and by inference also the ammonite, is of late Triassic age.

DE JERSEY, N. J. (1973). Rimulate pollen grains from the Lower Mesozoic of Queenstown. *Geol. Soc. Aust. Spec. Publ.* 4, 127–40.

Canberra, 30th July, 1976.



Figures 4 to 11. *Classopollis* sp. cf. *C. meyeriana*

- Figure 4. Slide 3834 (b) 109, 5/10,4 (R-439/1) Tetrad. A distal pore and sub-equatorial furrow (rimula) can be seen on the top pollen grain.
- Figure 5. Slide 3834 (b) 84,5/20,5 (R-V13/4) Polar view. The rimula and distal pore are clearly visible.
- Figure 6. Slide 3834 (a) 83/19,3 (R-U12/1) Polar view. Grain showing rimula and distal pore.
- Figure 7. Slide 3834 (b) 82/16,6 (R-R11/3) Polar view. The rimula and distal pore can be seen, as well as an indistinct columellate structure in the exine at the top right hand margin of the grain and also on the exine of the distal hemisphere.
- Figure 8. Slide 3834 (b) 103,3/2,5. (R-B 33/3) Polar view, showing small trilete mark on proximal hemisphere.
- Figure 9. Slide 3834 (a) 118/9,4. (R-K 47/2) Polar view, showing small trilete mark on proximal hemisphere.
- Figure 10. Slide 3834 (b) 89,3/5,5. (R-F18/2) Equatorial view showing sub-equatorial furrow, smaller distal hemisphere and columellate structure of exine near equator at right.
- Figure 11. Slide 3834 (b) 115,5/10,8. (R-L45/4) Polar view, showing columellate structure of exine at edge of grain.
- Figure 12. ? *Araucariacites* sp. Slide 3834 (b) 78,4/7,9 (R-H 7/3) Equatorial view showing granular surface ornament.
- Figure 13. *Leiosphaeridia granulosa* Pocock. Slide 3834 (b) 122,2/11,2. (R-M 52/2).
- Figure 14. *Leiosphaeridia* sp. Slide 3834 (b) 106/3. (R-C 35/4).
- Figures 15–17. *Dictyotidium* sp. Slide 3834 (b) 102,3/4,8 (R-E 31/2), 83/17 (R-S 11/2), 91,5/17 (R-R 20/4).
- Figure 18. *Michrystidium deflandrei* Valensi. Slide 3834 (b) 103, 2/2,7 (R-C 32/2).
- Figures 19–20. *Michrystidium lymensis*.Wall. Slide 3834 (b) 99,4/23 (R-Y 29/1), 119,6/22,6 (R-X49/4). Fig. 19 interference contrast, Fig. 20, phase contrast.

UPPER CRETACEOUS BRYOZOA FROM NEED'S CAMP, SOUTH AFRICA

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ABSTRACT

The bryozoan fauna from the Upper Cretaceous limestones of the lower quarry at Need's Camp, South Africa is revised. Eighteen cyclostomatous species are identified, of which twelve are new: *Desmeplagioecia primitiva*, *Diastopora solida*, *Pustulopora minuta*, *Spiropora irregularis*, *Clausia crassa*, *Foliopora expansa*, *Idmidronea robusta*, *Idmidronea africana*, *Idmidronea capensis*, *Idmidronea langi*, *Idmonea compressa*, and *Multicavea rotunda*. The fauna seems to indicate a shallow-water, strongly agitated environment and differs in composition from the probably contemporaneous fauna from Madagascar. There is a suggestion that distinct biogeographical provinces may be represented.

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<i>Idmonea compressa</i> n.sp.	70
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<i>Idmidronea africana</i> n.sp.	73
<i>Idmidronea langi</i> n.sp.	74
<i>Idmidronea capensis</i> n.sp.	76
<i>Pustulopora virgula</i> von Hagenow, 1840	76
<i>Pustulopora variabilis</i> von Hagenow, 1851	76
<i>Pustulopora minuta</i> n.sp.	77
<i>Spiropora irregularis</i> n.sp.	78
<i>Clausia crassa</i> n.sp.	79
<i>Lichenopora betsibokensis</i> Brood, 1976	80
<i>Multicavea rotunda</i> n.sp.	80
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INTRODUCTION

The Bryozoa discussed in this study are from the lower limestone quarry of Need's Camp, approximately halfway between East London and King William's Town in the Cape Province of South Africa. Limestone has been quarried from two small sites in the area, which lie 5 km apart, and in the topographically lower, eastern quarry a small, 1,5 m thick patch of limestone is currently exposed. This limestone is highly fossiliferous and is composed largely of bryozoa together with echinoids, brachiopods, corals and bivalves. Benthic foraminifera and ostracodes are also present.

Cyclostomatous bryozoa have been described previously from the quarry by Lang (1908), but unfortunately his type material appears to be lost and it is not possible to be certain of all his identifications on the basis of his illustrations alone (cf. table 1).

Other cyclostomatous bryozoa have also been described previously from the Upper Cretaceous of the southern hemisphere, but knowledge of these faunas is very incomplete. Canu (1911) described 69 species from the Upper Cretaceous of the Argentine, of which 18 were cyclostomes and later (Canu, 1922) described 22 species from the Maastrichtian of the East Coast of Madagascar, including eight cyclostomes.

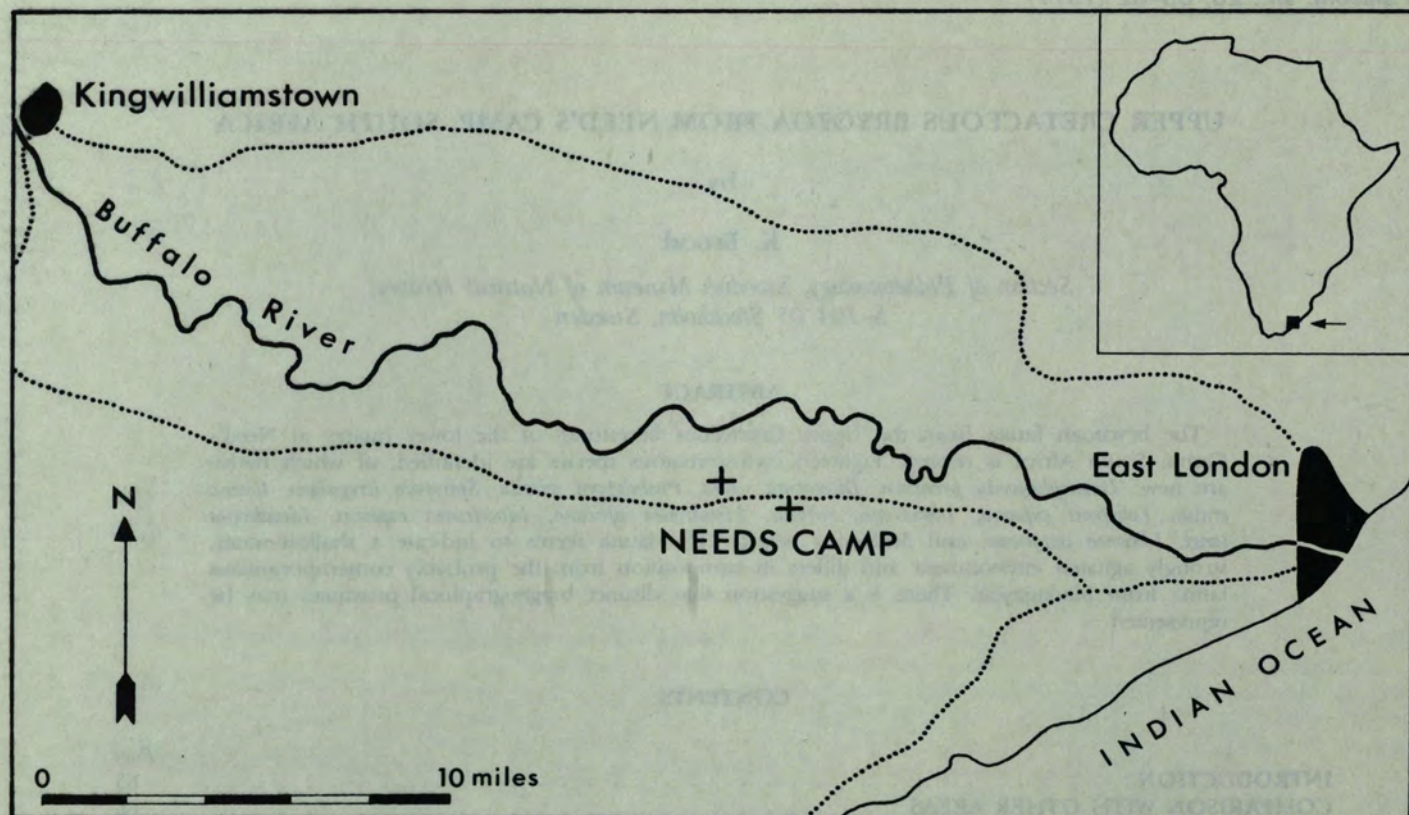


Figure 1. Map showing the situation of the Need's Camp quarries.

Recently, Maastrichtian and Palaeocene cyclostomes have been described from the west coast of Madagascar (Brood, 1976).

Generally each of these earlier authors identified their material with European species, but revision of the Southern Hemisphere faunas reveals that commonly these identifications are incorrect and that Asian and African specimens are specifically distinct from European ones. There are, however, exceptions.

The terminology used in this study is the same as in Brood (1972) unless otherwise stated. The following abbreviations are used:

- azap = autozooeal aperture, width
- azp = autozooeal peristome, width
- daf = distance between fascicles of autozooea
- az/mm² = number of autozooeal apertures in 1 mm²
- O.R. = observed range
- s = standard deviation
- $\bar{x}$ = arithmetical mean (given with confidence interval)
- V = coefficient of variation

The type specimens are deposited in the collections of the Palaeozoological Department, the Swedish Museum of Natural History, Stockholm, Sweden (serial numbers RM By 23600 — 23685). A set of topotypes is deposited in the collections of the Department of Palaeontology of the British Museum (Natural History), London.

COMPARISON WITH OTHER AREAS

Since few bryozoan faunas are known in detail from the Upper Cretaceous outside Europe a comparison between different areas for stratigraphical and biogeographical purposes is difficult. However, some similarities and dissimilarities may be pointed out despite the incomplete nature of the material.

In previous work the cyclostomatous faunas of the northern and southern hemispheres were considered to be basically similar (Lang, 1908; Canu, 1911, 1922). In fact, despite the common presence of certain species such as *Pustulopora variabilis* and *P. virgula*, the faunas are quite distinct. It should also be realised that some identifications of widely distributed cyclostomatous species, or rather species groups, in the southern part of the world are based on material which is imperfectly preserved and may later have to be revised when better material becomes available.

Eighteen cyclostomatous species have been identified from the Need's Camp material, of which four also occur in the Upper Maastrichtian of Madagascar, namely: *Lichenopora betsibokensis*, *Diastopora madagascarensis*, *Pustulopora virgula* and *P. variabilis*. The remaining 14 are as yet known only from South Africa. However, this discrepancy between a South African and a Madagascan fauna should perhaps not be stressed since the ecological settings were not identical. There is nevertheless the suggestion of a

Table 1.

Comparison of Lang's specific determinations and those used in the present paper.

Lang, 1908	This paper
<i>Filisparsa ramosa</i> d'Orbigny	<i>Foliopora expansa</i> n.sp.
<i>Filisparsa fragilis</i> Marsson	<i>Foliopora expansa</i> n.sp.
<i>Diastopora compressa</i> (Goldfuss)	<i>Diastopora solida</i> n.sp.
<i>Idmonea virgula</i> d'Orbigny	<i>Idmidronea africana</i> n.sp.
<i>Crisina cenomana</i> d'Orbigny	<i>Idmidronea africana</i> n.sp.
<i>Crisina excavata</i> (d'Orbigny)	?
<i>Crisina marginata</i> (d'Orbigny)	?
<i>Tervia dorsata</i> (von Hagenow)	<i>Idmidronea langi</i> n.sp.
<i>Tervia gibbera</i> Gregory	<i>Idmidronea capensis</i> n.sp.
<i>Tervia decurrens</i> (Pocta)	?
<i>Entalophora virgula</i> (von Hagenow)	<i>Pustulopora virgula</i> (von Hagenow)
<i>Entalophora conjugata</i> von Reuss	<i>Pustulopora variabilis</i> von Hagenow
<i>Entalophora echinata</i> (Römer)	<i>Pustulopora variabilis</i> von Hagenow
<i>Entalophora madreporacea</i> Goldfuss	<i>Clausia crassa</i> n.sp.
<i>Spiropora verticellata</i> (Goldfuss)	<i>Spiropora irregularis</i> n.sp.

biogeographical difference.

Two species from Need's Camp occur also in the Upper Cretaceous of South America (Canu, 1911) and suggest a link between these regions. However, the Argentine fauna consists almost entirely of encrusting forms on shells, whereas that from Need's Camp consists chiefly of erect species.

Two species, *Pustulopora virgula* and *P. variabilis*, also occur in Europe and are apparently widely distributed since they also occur in Madagascar.

AGE AND ENVIRONMENT

The limestone at the lower quarry of Need's Camp has been suggested by Lang (1908) to be of Campanian or Maastrichtian age from investigation of the bryozoans. Although most of the identifications made by Lang are now rejected, the present study supports his age assessment. This date is suggested by the presence of the species *Lichenopora betsi-bokensis*, *Diastopora madagascarensis* and *Pustulopora variabilis*. All occur both in the Need's Camp material and in the Maastrichtian of Madagascar. An Upper Campanian or Maastrichtian age is also suggested by MacGowran and Moore (1971).

Lang (1908) suggested a resemblance between the faunas of Need's Camp (Lower Quarry) limestone and the bryozoan limestone from Faxø in Denmark, but although bryozoa are common in both localities, the similarity is not very close. In the Danian of Scandinavia at localities such as Faxø, the cyclostomatous bryozoans consist chiefly of pustuloporids (erect, cylindrical stems), hornerids (double walled with idmidronid growth) and idmidronids (Brood, 1972). At Need's Camp the idmidronids are dominant among the cyclostomes and constitute more than 90 % of these if counted as specimens. The bryozoan fauna of Need's Camp therefore provides a closer ecological similarity in gross composition with the shallow water Campanian of southern Sweden (Brood, 1972), where the idmidronids are the

dominating growth form. The bryozoan fauna therefore suggest a shallow water, reasonably high energy environment. Agitation of the water is further suggested by the presence of dorsal supports of kenozoecia and the stout shape of many bryozoan colonies.

SYSTEMATIC DESCRIPTIONS

Desmeplagioecia primitiva n.sp.
(figs. 4, 5)

Type specimens

Holotype: RM By 23626. Paratypes: RM By 23627–23628.

Diagnosis

A *Desmeplagioecia* with small, crowded autozoecia and a small gonozoecium.

Description

The zoarium is encrusting, forming small circular discs. The autozoecia are irregularly arranged in the centre of the colony, but tend to become arranged in uniserial rows near the margin, and are densely crowded. The autozoecial peristomes are short and open obliquely towards the surface of the colony. The autozoecial aperture is generally circular. The surfaces of the zooecia are faintly striated transversally.

The gonozoecium is situated near the margin of the colony. It is small and transversely elongated, approximately twice as wide as long and measures 0,35 × 0,70 mm in the holotype. Its oeciostome is terminal and tubular. The oeciopore is smaller than the aperture of an autozoecium, measures 0,040 mm in the holotype, and is transversely oval in outline.

Dimensions

Holotype and paratype.

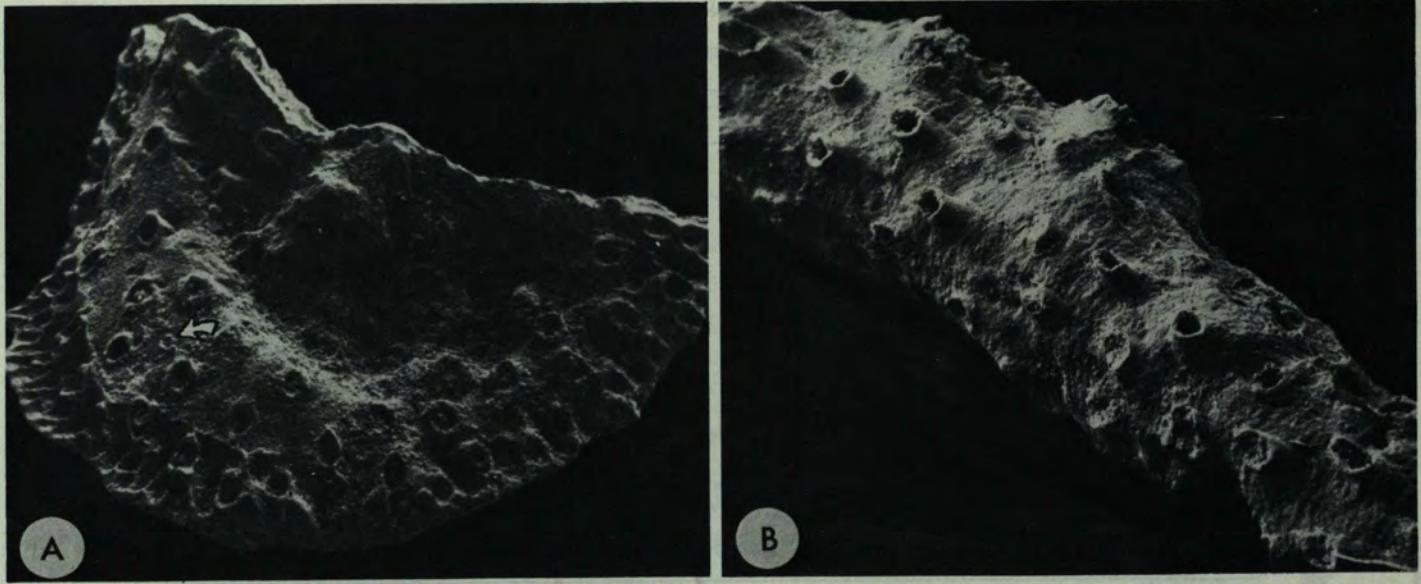


Figure 2. *Diastopora madagascarensis* Brood. A. Specimen with gonozoecium. Oeciopore at arrow. RM By 23643. X 35. B. Surface of encrusting specimen. RM By 23644. X 40.

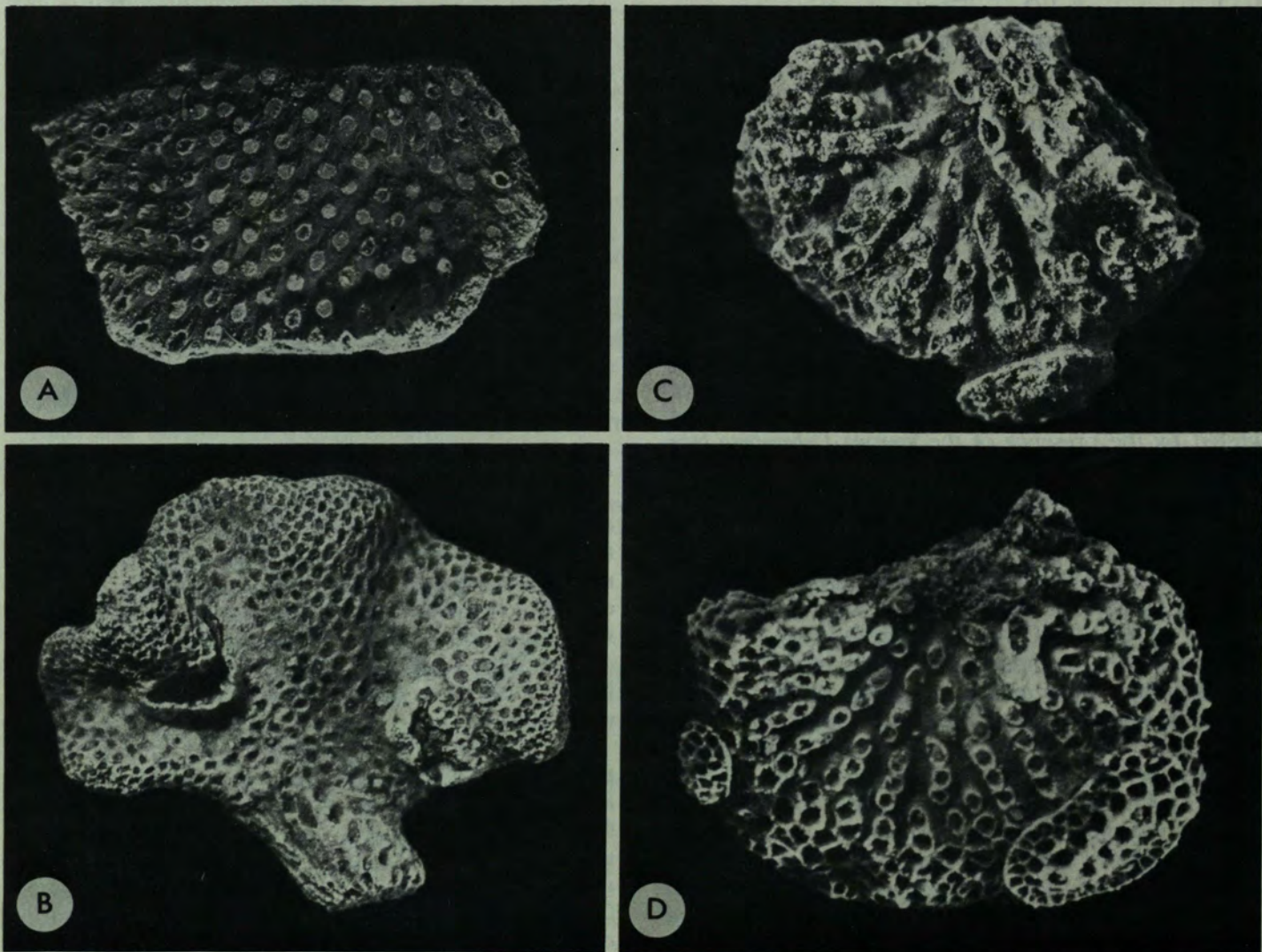


Figure 3. *Diastopora solida* n.sp. A. Specimen with well preserved peristomes. RM By 23647, paratype. X 20. B. Surface of bifoliate specimen with two gonozoecia. RM By 23645, holotype. X 14. *Theonoe striata* (Canu). C. Fragment of colony with subcolony. RM By 23635. X 25. D. Specimen with two subcolonies. RM By 23636. X 25.

	O.R.	$\bar{x}$	V	S	N
azap . .	0,050 — 0,068	0,057 $\pm$ 0,001	8,63	0,004 9	47
azp . . .	0,067 — 0,090	0,077 $\pm$ 0,004	16,72	0,012 8	47

Remarks

This species is characterized by its small dimensions and crowded autozooezia.

Diastopora madagascarensis Brood, 1976

(fig. 2)

1922 *Diaperoecia papyracea* (d'Orbigny); Canu, p. 137, Pl. XI, Figures 9, 10.

1976 *Diastopora madagascarensis* Brood, p. 400.

Referred Material 23643 — 23644.

Remarks

This species also occurs in the Maastrichtian and Palaeocene of Madagascar (Canu, 1922; Brood, 1976).

Diastopora solida n.sp.

(fig. 3 A, B)

Type specimens

Holotype: RM By 23645. Paratypes: RM By 23646–23649.

Diagnosis

A *Diastopora* with comparatively thick zoaria, autozooezia of moderate size and a large gonozooecium.

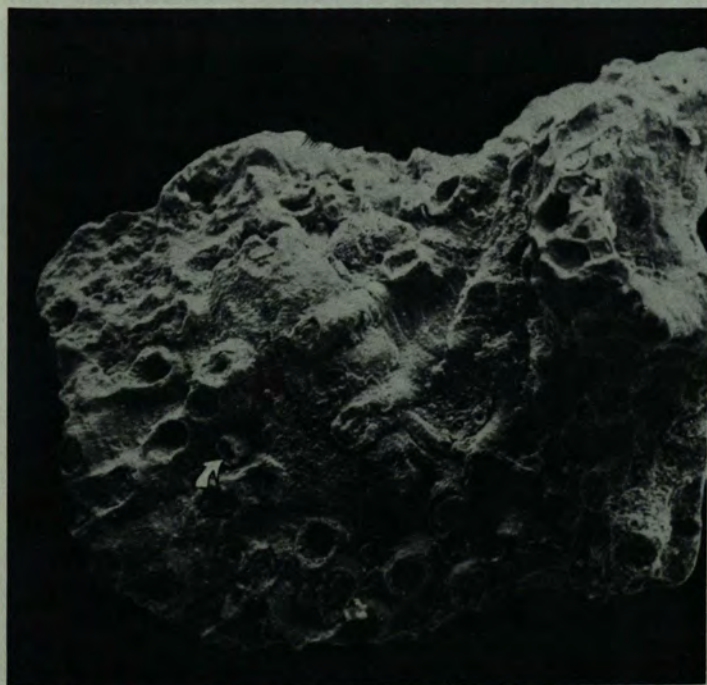


Figure 4. *Desmeplagioecia primitiva* n.sp. Specimen with gonozooecium. RM By 23626, holotype. X 50. Oeciopore at arrow.

Description

The zoarium is encrusting or erect, forming thick bilaminar fronds which are up to 1 mm thick. The autozooezia are long in section, curve gently outwards, and open in quincunx or irregularly. They are crowded, with short peristomes. The autozooezial aperture is circular and of moderate size. Commonly, the autozooezial peristome is absorbed especially near the margin of the bilaminar fronds.

The gonozooecium is large and transversely expanded. It is approximately 1 mm long and 1,5 mm wide.

Dimensions

Holotype and paratypes.

	O.R.	$\bar{x}$	V	s	N
azap. . .	0,065 — 0,080	0,069 $\pm$ 0,001	5,79	0,004 0	49
azp . . .	0,077 — 0,112	0,087 $\pm$ 0,004	16,43	0,014 3	49
az/mm ² . 26	— 33	30,7 $\pm$ 1,2	13,44	4,128	49

Remarks

This species is characterized by its massive zoarium with small autozooezial dimensions. The most common growth form in Need's Camp material is the bilaminar "Mesenteripora" type, which would normally be indicative of a shallow water environment.

D. solida differs from *D. madagascarensis* in having larger autozooezia and a thicker zoarium. It differs from *Diaperoecia formosa* (Canu, 1922) in having a thicker zoarium and a smaller gonozooecium.

Theonoo striata (Canu, 1911)

(fig. 3 C, D)

1911 *Actinopora striata* Canu, p. 276, Pl. XII, Figure 4.

Referred material

RM By 23634—23637.

Remarks

In the Need's Camp material there are several small fragments of a species which agree well with *T. striata* from the Upper Cretaceous of the Argentine.

Foliopora n.gen.

Type species. *Foliopora expansa* n.sp.

Derivation

Folium (Latin) = leaf, referring to the leaf-like shape of the zoarium.

Diagnosis

A tubuliporid genus with a leaf-like zoarium, where the autozooezia open on one side only. The reverse side lacks kenozooezia. Gonozooecium a much expanded sac, enveloping several autozooezial peristomes.

Description

The zoarium consists of an erect, leaf- or fan-shaped stem. The autozooezia open irregularly on one side

of the stem. The reverse side is free from kenozoecia.

The gonozoecium is large and flat, enclosing several autozooeal peristomes. The gonozooeal oeciopore is approximately of the same size as the autozooeal aperture and is transversely oval.

Remarks

Foliopora is characterized by its short, erect stems with the autozooea opening on one side only. Superficially, the genus resembles *Nevianopora* or *Filisarsa*, but differs from *Nevianopora* in lacking the regular arrangement of autozooea. It differs from *Filisarsa* in having much shorter and more expanded stems and a larger gonozoecium. This new genus may be related to *Filisarsa* and may therefore be tentatively referred to the family Filisarsidae Brood.

A modern species which possibly belongs to this genus is *Diaperoecia arcuata* Harmelin from the Mediterranean (Harmelin, 1976). There are other modern species commonly referred to *Diaperoecia* which might also be placed here.

Foliopora expansa n.sp.
(figs. 7 B, E, F; 8)

1908 *Filisarsa ramosa* d'Orbigny; Lang, p. 2, Pl. I, Figure 1.

Type material

Holotype: RM By 23678. Paratypes: RM By 23679—23684.

Diagnosis

Flat, erect stems with autozooea opening on one side. Autozooea of moderate size. Gonozoecium flat, much expanded, enclosing several autozooeal peristomes.

Description

The zoarium is erect and consists of single or dichotomously branching stems, which are flat and approximately 1 mm wide. Generally, the stems are curved towards the reverse side. The autozooea open irregularly on the frontal side and are densely crowded. Peristomes of the autozooea are generally short with a circular aperture. The dorsal side of the colony is smooth and free from autozooea, but may be transversely striated. Kenozoecia are lacking.

The gonozoecium is large and much expanded. It encloses several autozooeal peristomes. The oeciopore is smaller than an autozooeal aperture, is circular in outline and not adjacent to an autozooeal peristome.

Dimensions

Holotype and paratypes.

	O.R.	$\bar{x}$	V	s	N
azap . . .	0,070 — 0,100	0,078 ± 0,002	7,74	0,006 1	46
azp . . .	0,093 — 0,120	0,109 ± 0,002	6,99	0,007 6	46

Remarks

F. expansa has a superficial likeness to species of *Filisarsa* and Lang (1908) identified it with *F. ramosa* from the Turonian of Europe. It differs, however, from that species in general shape and size.

Idmonea compressa n.sp.

(figs. 6; 7 A, C, D)

Type specimens

Holotype: RM By 23650. Paratypes: RM By 23651—23657.

Diagnosis

An *Idmonea* with a compound zoarium consisting of small subcolonies which are approximately 1 mm long and 0,5 mm wide. Autozooea are arranged in lateral rows, but do not form fascicles. Subcolonies are surrounded by many small kenozoecia with hexagonal distal walls.

Description

The zoarium consists of small, elongate or oval subcolonies united by areas of kenozoecia. The subcolonies consist of short transverse rows of autozooea which contain three to four zooea each. There are approximately 5—15 rows of zooea in each subcolony. Fascicles are never formed. Generally the innermost zoecium is the largest and the lateral ones decrease in size outwards. The exterior part of the autozoecium is short and hexagonal in outline. Autozooeal apertures are circular and small.

Between the subcolonies there are areas of kenozoecia. These are long in section but terminate with a hexagonal or rhombic distal wall. Kenozooeal walls form a reticulate pattern on the zoarial surface.

The interzooeal walls are thick and measure up to 0,050 mm. Exterior walls may be up to 0,100 mm thick. Diaphragms are generally absent.

The gonozoecium is narrow and placed in the centre of a subcolony and forms a thin immersed elongation between the autozooeal rows. It is approximately 1 mm long and 0,2 mm wide.

Dimensions

Holotype and paratypes.

	O.R.	$\bar{x}$	V	s	N
azap . . .	0,070 — 0,110	0,090 ± 0,002	6,37	0,005 7	59
azp . . .	0,125 — 0,140	0,129 ± 0,001	3,57	0,004 6	59
az length	0,150 — 0,400	0,335 ± 0,015	16,89	0,056 9	59

(All measurements taken from the inner autozooea.)

Remarks

This species differs from the contemporary *Reptoclausia jugum* Voigt from the Turkmenistan in having shorter kenozoecia and three to four autozooea per row.

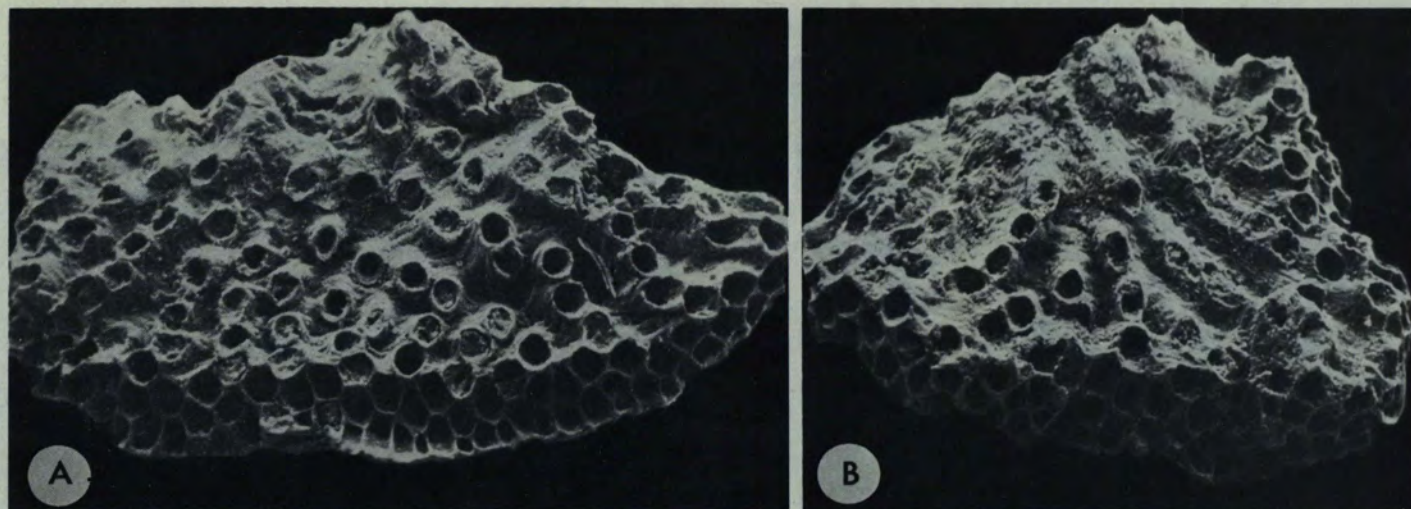


Figure 5. *Desmeplagioecia primitiva* n.sp. A. Broken specimen. RM By 23627, paratype. X 40. B. Small specimen. RM By 23628, paratype. X 40.

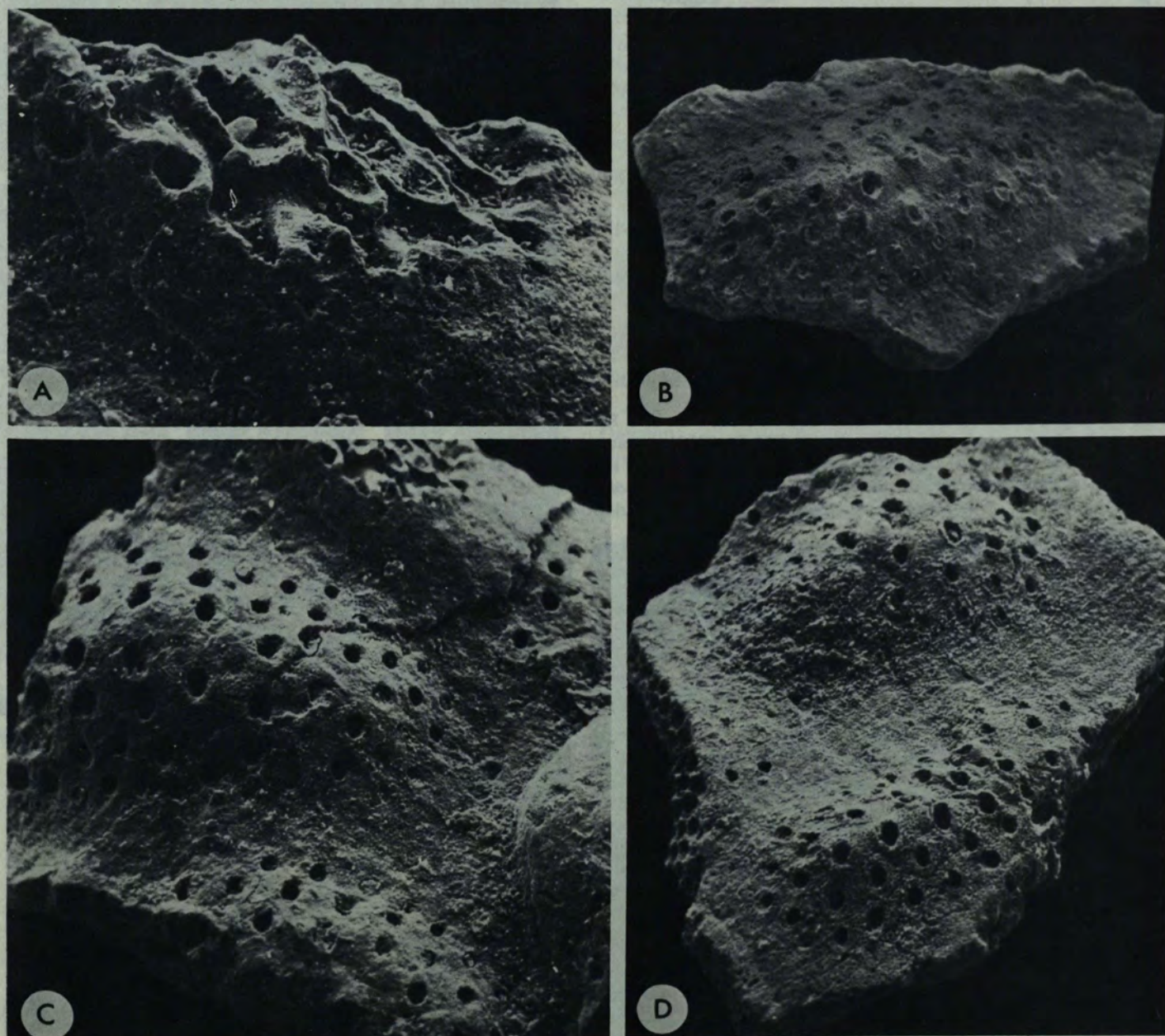


Figure 6. *Idmonea compressa* n.sp. A. Surface of specimen with broken gonozoecium. RM By 23650, holotype. X 100. B. Subcolony with gonozoecium. RM By 23652, paratype. X 50. C. Specimen with several subcolonies. RM By 23650, holotype. X 40. D. Specimen with two subcolonies. RM By 23652, paratype. X 30.

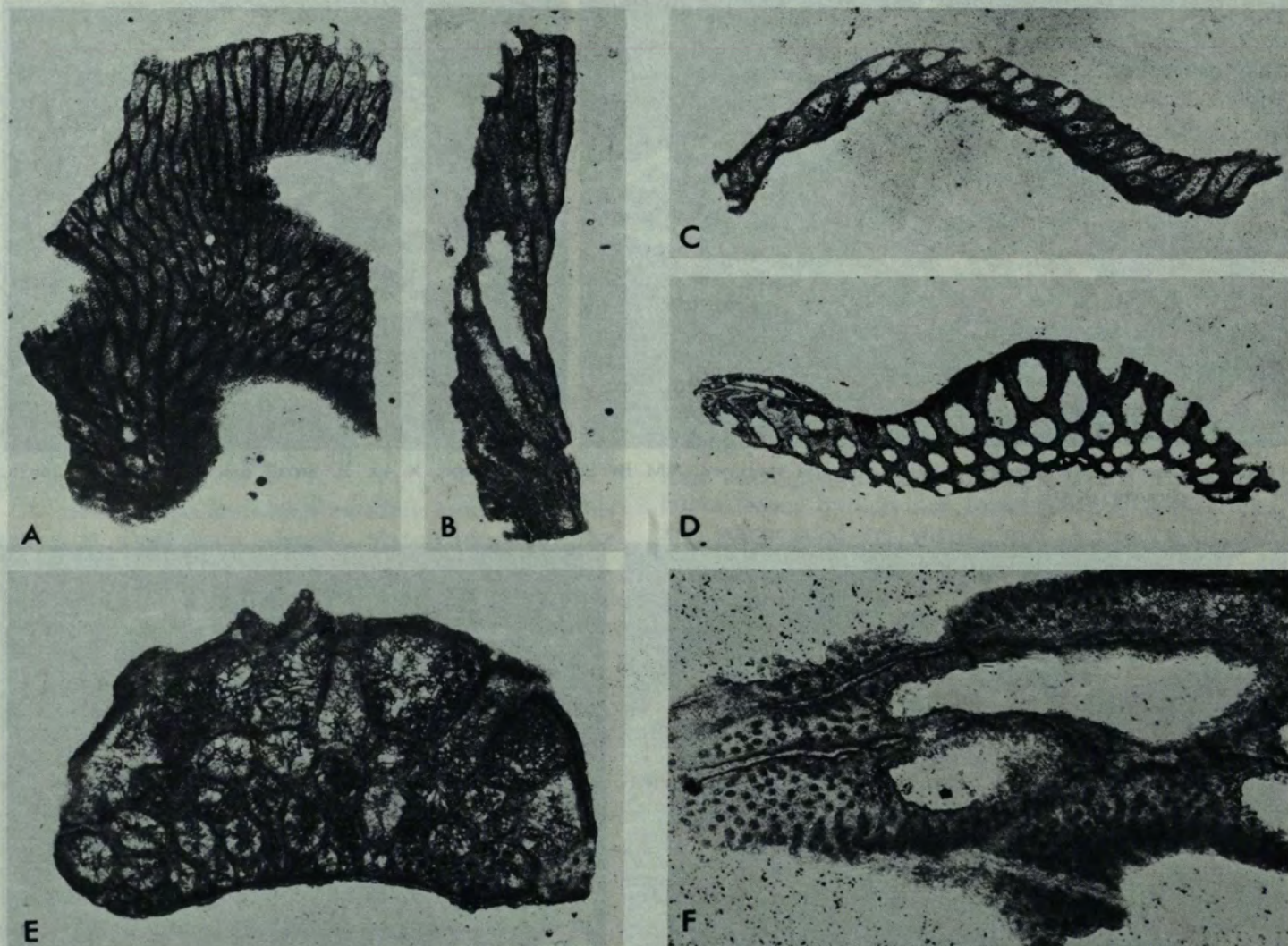


Figure 7. *Idmonea compressa* n.sp. A. Tangential thin section. RM By 23657, paratype. X 25. C. Longitudinal thin section showing short zooecia and thin zoarium. RM By 23655, paratype. X 25. D. Transverse section of subcolony. Note multilayered part to the left. RM By 23654, paratype. X 35. *Foliopora expansa* n.sp. B. Longitudinal thin section showing autozooecia. RM By 23682, paratype. X 30. E. Transverse thin section showing gonozooecium. RM By 23683, paratype. X 55. F. Tangential section of frontal part of autozooecia showing pseudopores. RM By 23684, paratype. X 100.

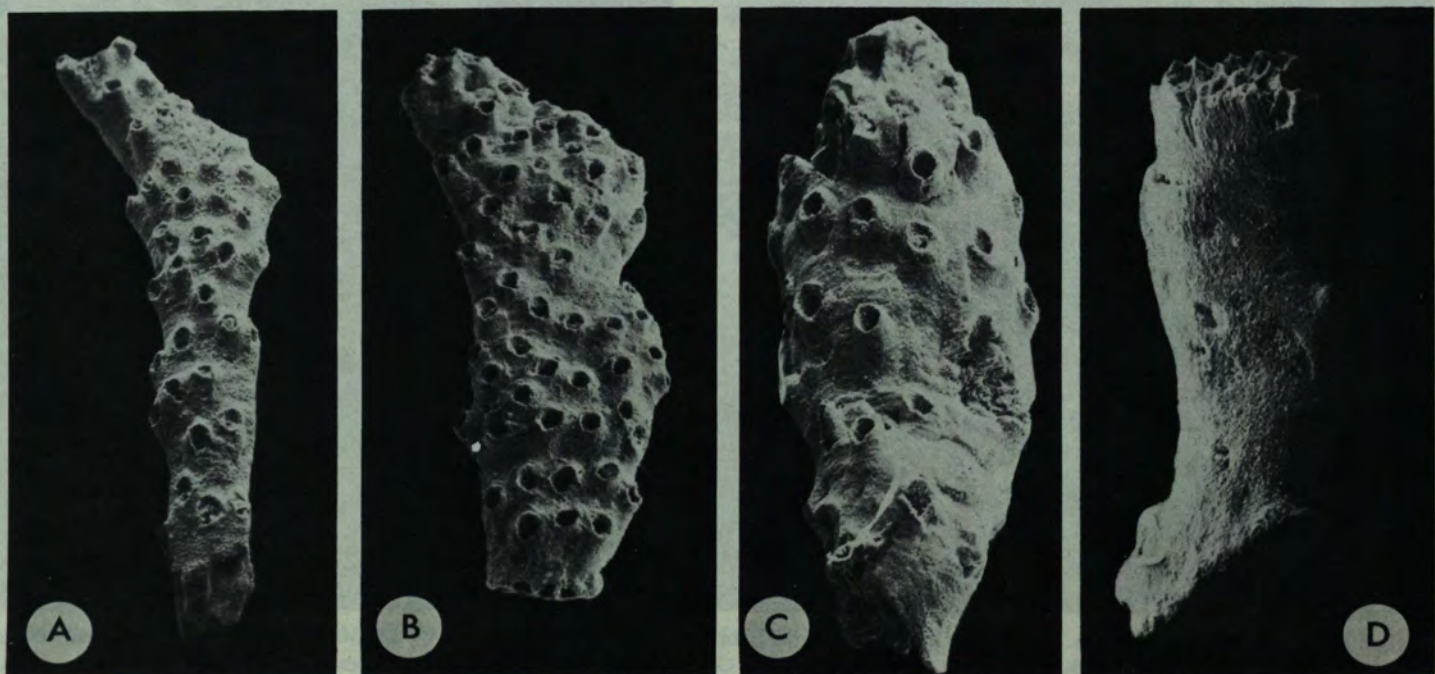


Figure 8. *Foliopora expansa* n.sp. A. Specimen seen from frontal side. RM By 23679, paratype. X 20. B. Specimen seen from frontal side. RM By 23678, holotype. X 20. C. Specimen with gonozooecium seen from frontal side. RM By 23680, paratype. X 30. D. Specimen from reverse side. RM By 23681, paratype. X 40.

Idmidronea robusta n.sp.

(figs. 11 A; 13 A)

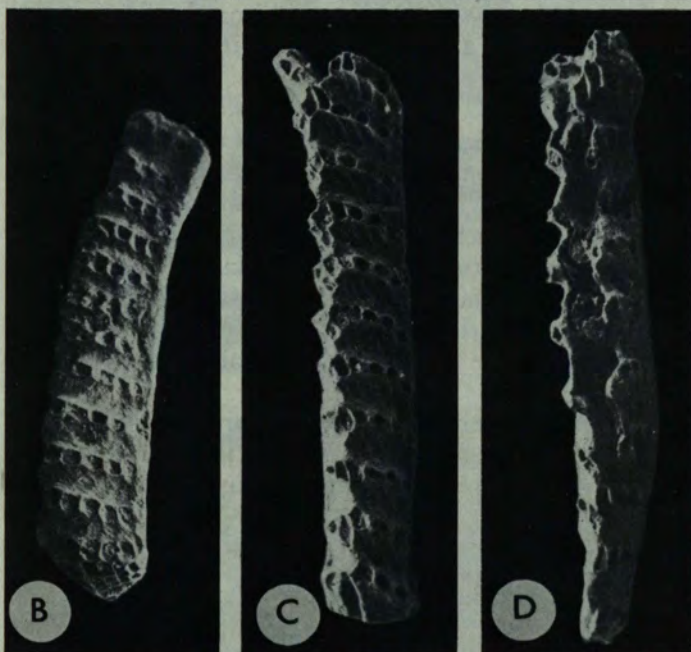
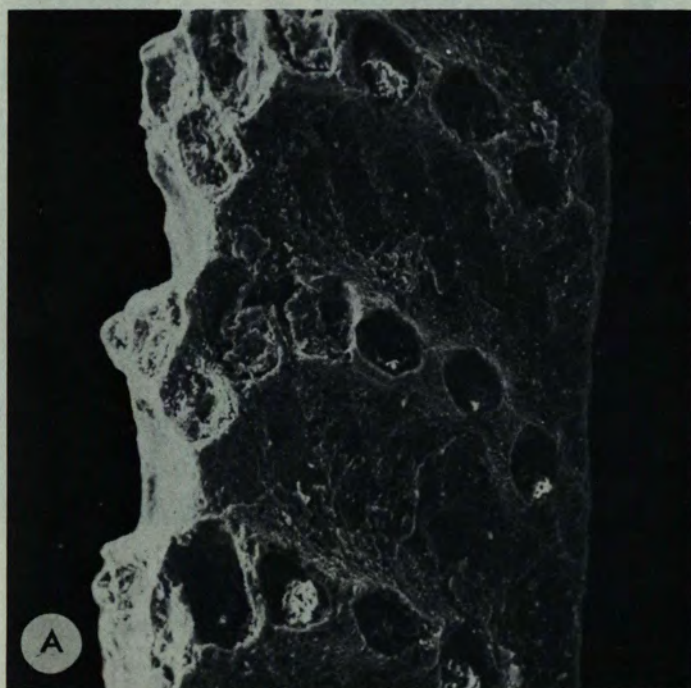


Figure 9. *Idmidronea langi* n.sp. A. Lateral view showing autozoecial rows. RM By 23658, holotype. X 80. B. Another lateral view. RM By 23659, paratype. X 17. C. Frontal view of specimen. RM By 23658, holotype. X 17. D. Specimen with broken gonozoecium seen from frontal side. RM By 23660, paratype. X 17.

Type specimens

Holotype: RM By 23638. Paratypes: RM By 23639–23641.

Diagnosis

A large *Idmidronea* with seven to eight autozoecia per fascicle.

Description

The zoarium is erect, composed of dichotomously branching triangular stems, which are on the average 1,5 mm wide. The autozoecia are large and are each arranged in alternating fascicles of seven or eight zooecia. The interfascicular space is small. The dorsal side of the stem is flat and transversely striated. Gonozoecium not observed.

Dimensions

Holotype and paratypes.

	O.R.	$\bar{x}$	V	s	N
azap . . .	0,113 — 0,146	0,124 $\pm$ 0,003	7,23	0,009 0	43
azp . . .	0,135 — 0,180	0,157 $\pm$ 0,004	7,77	0,012 2	43
daf . . .	0,175 — 0,525	0,371 $\pm$ 0,027	23,48	0,087 5	43

Remarks

This species is characterized by its large dimensions, which separate it from other Upper Cretaceous species of *Idmidronea*.

Idmidronea africana n.sp.

(figs. 10; 11 C, E, F, H, I)

1908 *Crisina cenomana* d'Orbigny; Lang, p. 5, Pl. I, Figure 5.

1908 *Idmonea virgula* d'Orbigny; Lang, p. 4, Pl. I, Figure 4.

1908 *Crisina excavata* (d'Orbigny); Lang, p. 6, Pl. I, Figure 6.

Type specimens

Holotype: RM By 23665. Paratypes: RM By 23666–23673.

Diagnosis

An *Idmidronea* with four to eight autozoecia in each fascicle and a long gonozoecium. Dorsal side flattened. The oeciopore is adjacent to a fascicle of autozoecia and is small. Autozoecia are of moderate size.

Description

The zoarium is erect, composed of dichotomously branching stems with triangular cross section. The stems are approximately 0,8 mm wide and commonly curved dorsally. The autozoecia are of moderate size and open in alternating fascicles, each containing four to eight autozoecia. The kenozoecia are few and may form a thin layer on the dorsal side of the stem. Commonly kenozoecia are lacking. The dorsal side is flat, sometimes slightly concave, and shows growth striations. Kenozoecia may have dorsal supports.

Autozoecia are of moderate length and generally lack diaphragms.

The gonozoecium is long and narrow, and placed on the mid-part of the frontal side between fascicles of autozoecia. It extends along three to seven interfascicular areas. The curved, tabular oe-

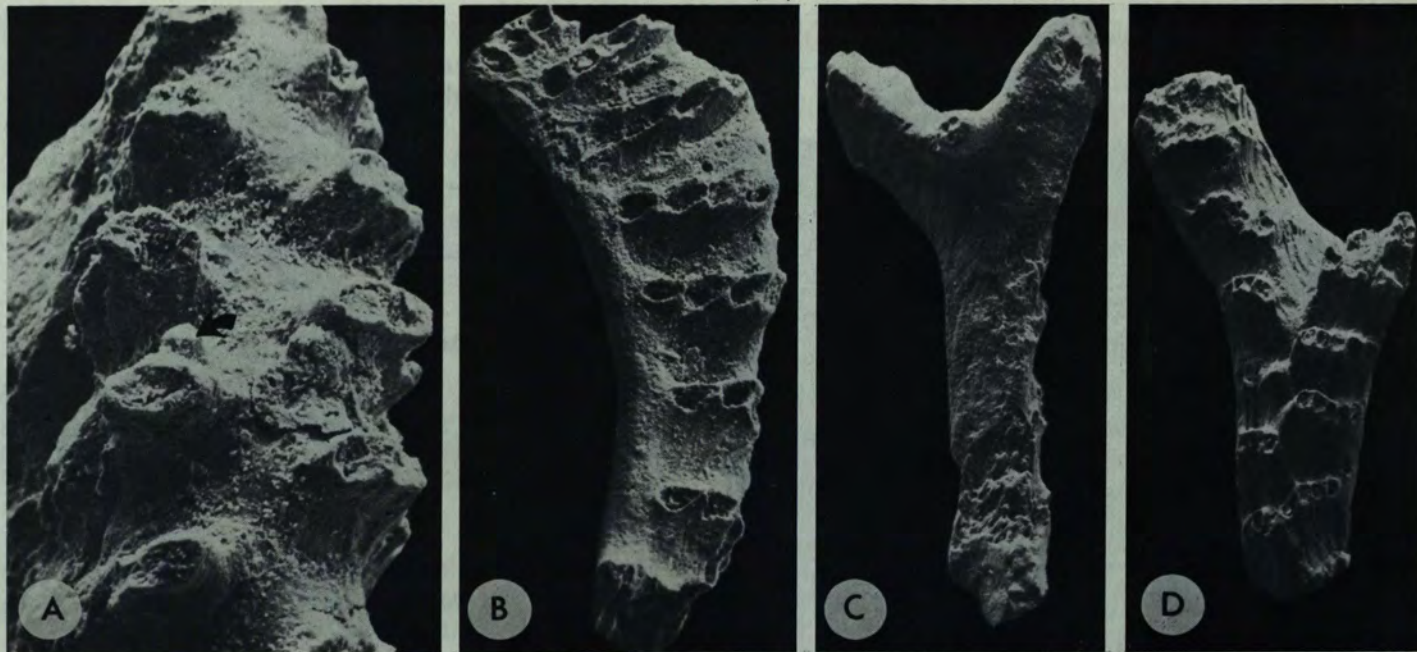


Figure 10. *Idmidronea africana* n.sp. A. Frontal view showing gonozooecium with oeciopore. RM By 23666, paratype. X 90. B. Lateral view of specimen with gonozooecium. RM By 23665, holotype. X 35. C. Dorsal view showing kenozooecial support at bifurcation. RM By 23667, paratype. X 30. D. Bifurcating specimen seen from frontal side. RM By 23669, paratype. X 30.

ciostome is placed near the middle of the gonozooecium and opens adjacent to an autozooecial fascicle. The oeciopore is circular in outline and its diameter less than an autozooecial aperture. It measures 0,040 mm and its oeciostome 0,045 mm in the holotype.

Dimensions

Holotype and paratypes.

	O.R.	$\bar{x}$	V	s	N
azap . . .	0,046 — 0,066	$0,053 \pm 0,001$	9,19	0,004 9	46
azp . . .	0,063 — 0,093	$0,075 \pm 0,002$	10,89	0,008 2	46
daf . . .	0,150 — 0,325	$0,220 \pm 0,012$	18,35	0,040 4	46
gl. . . .	0,70 — 2,50	$1,41 \pm 0,039$	41,49	0,587	11
gw	0,35 — 0,70	$0,50 \pm 0,007$	20,85	0,105	11

Remarks

This species is common in the material from Need's Camp. It is characterized by relatively small dimensions, by having many autozooecia in the fascicles, and by a long gonozooecium. It differs from the contemporary European species *I. filiformis* (D'Orbigny) in having a much longer gonozooecium and more autozooecia per fascicle.

Idmidronea langi n.sp.

(figs. 9; 11 B, D)

1908 *Tervia dorsata* (von Hagenow); Lang, p. 7, Pl. I, Figure 8.

1911 *Idmonea carinata* Römer; Canu, p. 275, Pl. VI, Figures 8, 9.

Type specimens

Holotype: RM By 23658. Paratypes: RM By 23659–23664.

Diagnosis

A large *Idmidronea* with approximately five zooecia per fascicle and a long, narrow gonozooecium.

Description

The zoarium is erect, composed of triangular, dichotomously branching stems, which are approximately 1 mm in cross section. Autozooecia open in alternating fascicles, each composed of five, rarely six or four, autozooecia. The dorsal side is flat with faint growth striations. Generally there are no kenozooecia on the dorsal side, but a thin layer may be present in some specimens. The autozooecia are of moderate size.

Autozooecia are of moderate length and lack diaphragms. The gonozooecium is long and narrow. It extends along six to eight interfascicular areas.

Dimensions

Holotype and paratypes.

	O.R.	$\bar{x}$	V	s	N
azap . . .	0,065 — 0,087	$0,073 \pm 0,002$	7,82	0,006 8	47
azp . . .	0,085 — 0,114	$0,099 \pm 0,002$	6,84	0,006 7	47
daf . . .	0,150 — 0,275	$0,230 \pm 0,010$	14,47	0,033 3	47
gl. . . .	1,80 — 2,80	$2,30 \pm 0,45$	17,75	0,408	4
gw	0,40 — 0,80	$0,64 \pm 0,22$	30,96	0,197	4

Remarks

This species is characterized by its triangular stems with crowded autozooecial fascicles, its long gonozooecium and moderate autozooecial size. It differs from the contemporary *I. suecica* Brood from Europe in having smaller autozooecia and a longer gonozooecium.

The species from the Rocanian of Argentine identified by Canu as *Idmonea carinata* Römer may be the

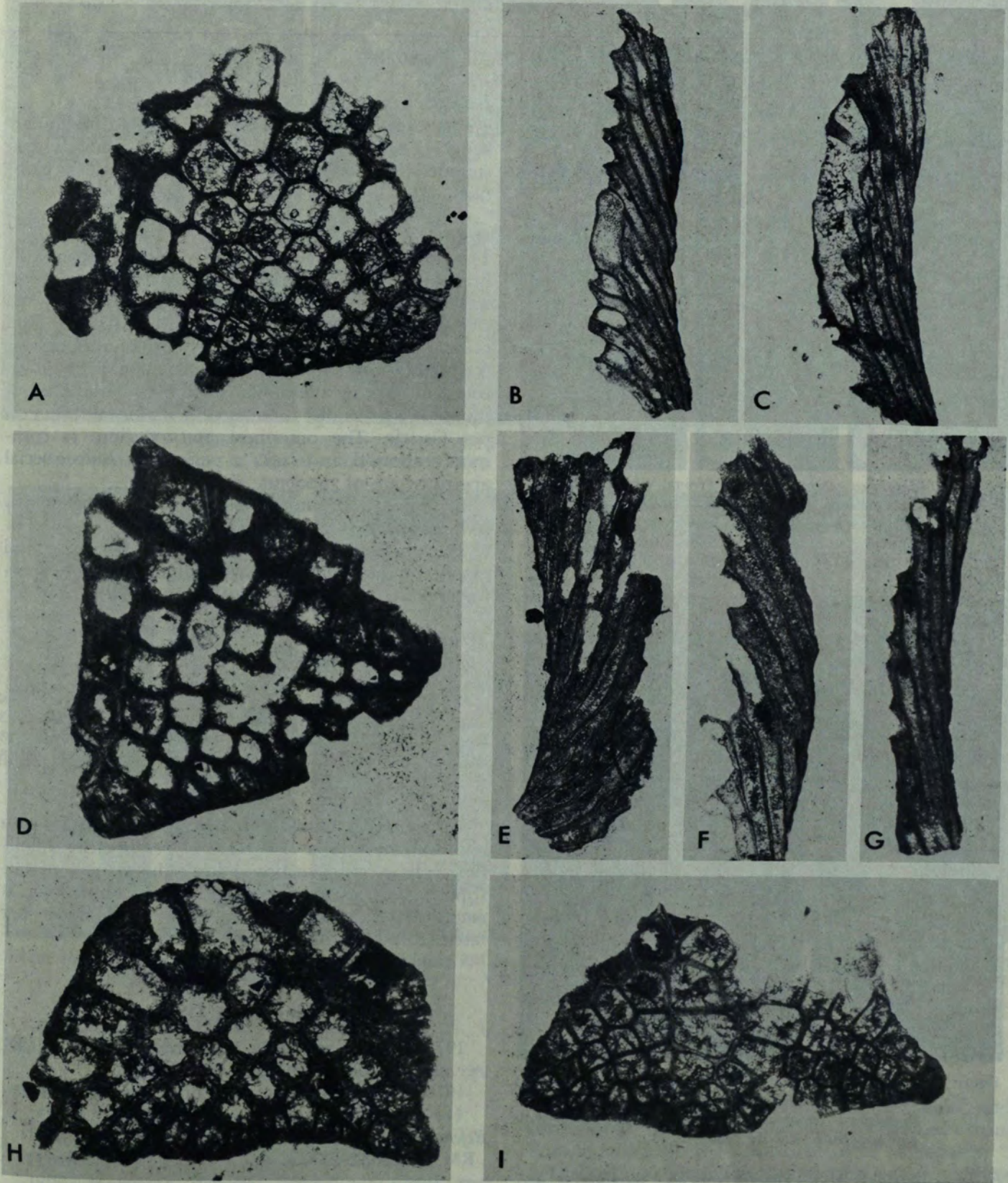


Figure 11. *Idmidronea robusta* n.sp. A. Transverse section of stem. RM By 23641, paratype. X 50. *Idmidronea langi* n.sp. B. Longitudinal section of stem with gonozoecium. RM By 23662, paratype. X 30. D. Transverse section of stem. RM By 23663, paratype. X 65. *Idmidronea africana* n.sp. C. Longitudinal section showing stem with gonozoecium. RM By 23670, paratype. X 30. E. Longitudinal section of stem. RM By 23656, paratype. X 35. F. Longitudinal section of stem. RM By 23673, paratype. X 35. H. Transverse section of stem with gonozoecium. RM By 23672, paratype. X 80. I. Transverse section of bifurcating stem. RM By 23671, paratype. X 60. *Idmidronea capensis* n.sp. G. Longitudinal section through stem showing long autozooecia. RM By 23677, paratype. X 30.

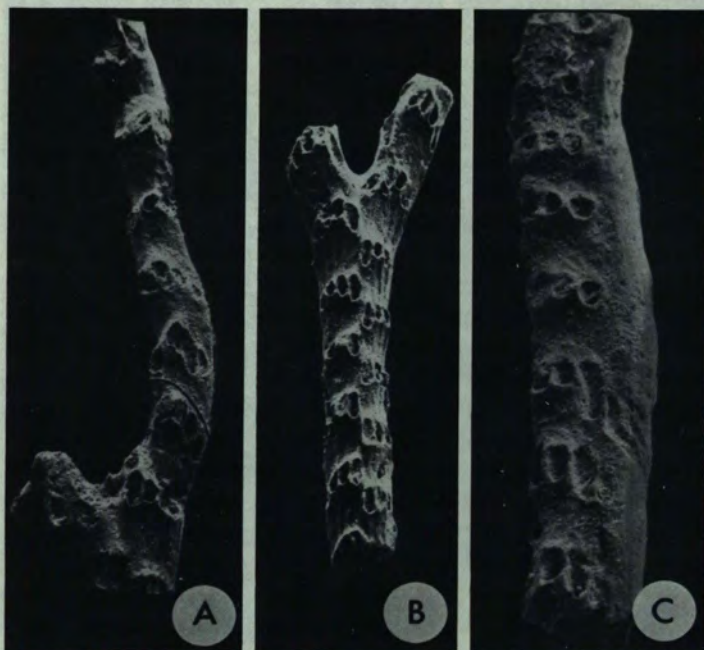


Figure 12. *Idmidronea capensis* n.sp. A. Frontal view of bifurcating specimen. RM By 23674, holotype. X 20. B. Frontal view of bifurcating specimen. RM By 23675, paratype. X 20. C. Lateral view of small specimen. RM By 23676, paratype. X 28.

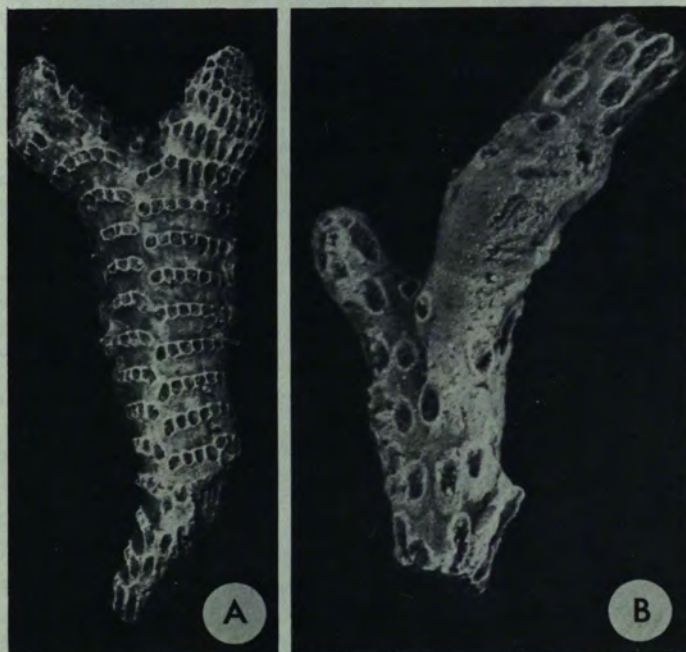


Figure 13. *Idmidronea robusta* n.sp. A. Bifurcating specimen seen from frontal side. RM By 23638, holotype. X 8. *Pustulopora variabilis* Hagenow. B. Specimen with gonozooecium. RM By 23629. X 18.

conspecific with the present species, though it appears to have slightly larger autozooeal dimensions.

Idmidronea capensis n.sp.
(figs. 11 G; 12)

1908 *Tervia gibbera* (Gregory); Lang, p. 7, Pl. I, Figure 9.

Type specimens

Holotype: RM By 23674. Paratypes: RM By 23675–23677.

Diagnosis

A medium-sized *Idmidronea* with three to four autozooeia per fascicle. The stem is smooth and rounded on the reverse. The gonozooecium is globular.

Description

The zoarium is erect, composed of dichotomously branching stems, which are subtriangular in cross section. The stems are approximately 0,5 mm wide. The reverse of the stems is rounded and shows faint growth striations. A thin layer of kenozooeia is commonly present on the dorsal side. The autozooeia open in alternating fascicles on the sides of the stem, generally with three to four autozooeia per fascicle. The outermost autozooeium is commonly aborted and lacks a peristome. Autozooeal apertures are of moderate size.

In section the autozooeia are long and generally lack diaphragms.

The gonozooecium is more or less globular and placed in the middle of the stem. In the only specimen examined it is 1,1 mm long and 0,4 mm wide.

Dimensions

Holotype and paratypes.

	O.R.	$\bar{x}$	V	s	N
azap . . .	0,053 — 0,085	$0,071 \pm 0,003$	12,04	0,008 5	43
azp . . .	0,073 — 0,110	$0,092 \pm 0,003$	10,12	0,009 3	43
daf . . .	0,175 — 0,325	$0,265 \pm 0,009$	10,95	0,029 0	43

Remarks

This species is characterized by rounded stems with approximately three autozooeia per fascicle. It differs from *I. globulosa* Brood from the Danian of Europe in its rounded stem and longer autozooeia. *I. langi* has triangular stems, more autozooeia per fascicle, and a longer gonozooecium.

Pustulopora virgula von Hagenow, 1840

(figs. 14 C, D)

1972 *Pustulopora virgula* Hagenow; Brood, p. 283 (see also for older synonyms).

1976 *Pustulopora virgula* Hagenow; Brood, p. 402.

Referred Material

RM By 23632–23633.

Remarks

This species is fairly common at Need's Camp. The specimens agree well in size and shape with those of the same age from Europe and Madagascar.

Pustulopora variabilis Hagenow, 1851

(figs. 13 B; 14 A, B)

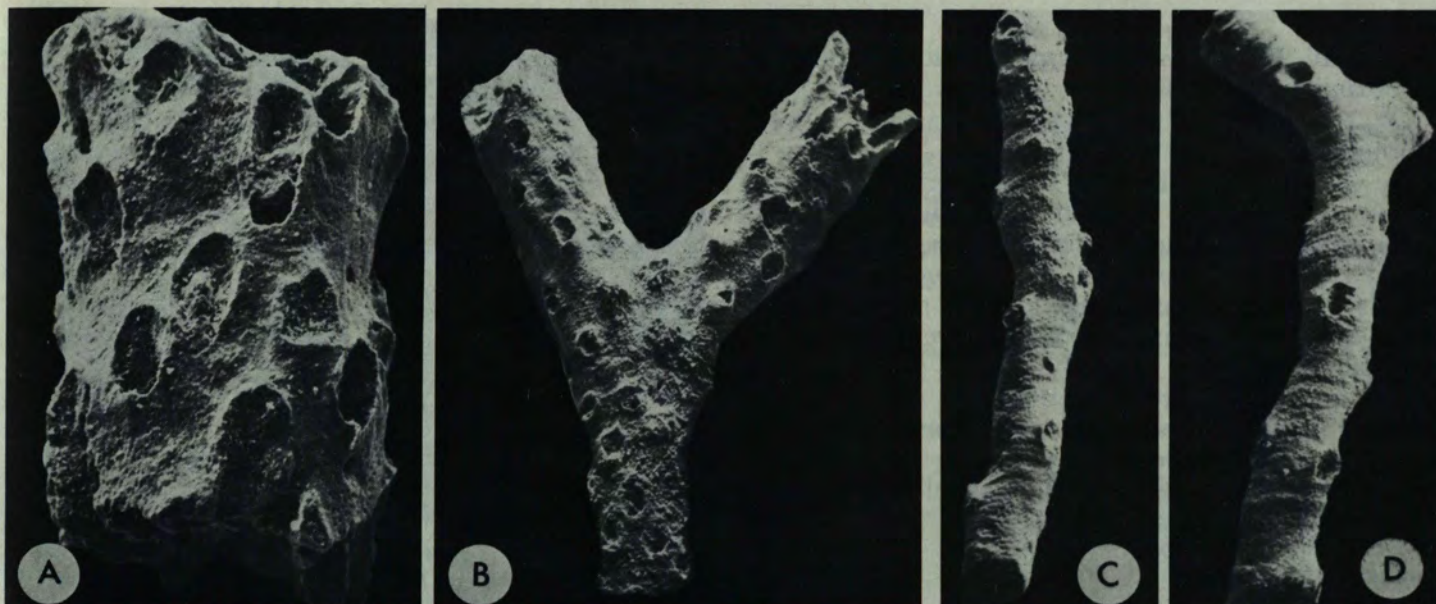


Figure 14. *Pustulopora variabilis* Hagenow. A. short specimen. RM By 23630. X 40. B. Bifurcating specimen. RM By 23631. X 20. *Pustulopora virgula* Hagenow. C. Thin stem. RM By 23632. X 20. D. Bifurcating specimen. RM By 23633. X 20.

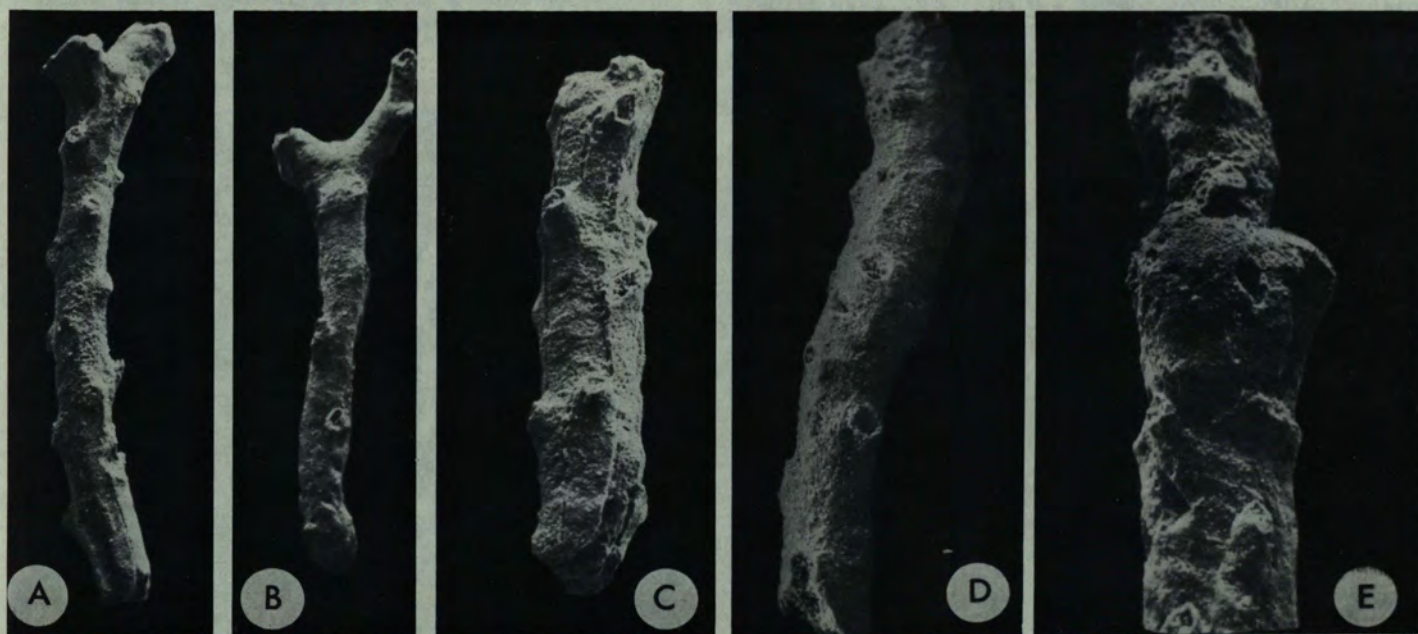


Figure 15. *Pustulopora minuta* n. sp. A. Bifurcating specimen. RM By 23623, paratype. X 20. B. RM By 23624, paratype. X 20. C. RM By 23625, paratype. X 30. D. RM By 23626, paratype. X 20. E. Specimen with gonozoecium. RM By 23622, holotype. X 30.

1840 *Pustulopora variabilis* Hagenow, p. 19, Pl. I, Figure 9.

1888 *Entalophora variabilis* Hagenow; Pergens, p. 205.

1899 *Clausa variabilis* Hagenow; Gregory, p. 417.

1908 *Entalophora echinata* (Römer); Lang, p. 9, Pl. I, Figure 12.

1922 *Mecynoecia variabilis* Hagenow; Canu and Bassler, p. 17, Pl. I, Figure 14.

1972 *Pustulopora variabilis* Hagenow; Brood, p. 289, Pl. XLI, Figures 1, 2.

1976 *Pustulopora variabilis* Hagenow; Brood, p. 403, Pl. 6, Figures 8, 9.

?1872 *Entalophora pavimentata* Stolizcka, p. 32, Pl. III, Figure 11.

Referred Material
RM By 23629–23631.

Remarks

This species is fairly common in the fauna, and corresponds well with specimens described from Europe and from the Maastrichtian of Madagascar.

Lang (1908) identified this species with *E. echinata* Römer from the European Turonian.

Pustulopora minuta n.sp.
(figs. 15; 18 B, C)

Holotype

RM By 23622. Paratypes: RM By 23620–23621, 23623–23625.

Diagnosis

A small *Pustulopora* with long autozooezia and a globular gonozoecium.

Description

The zoarium consists of thin, erect, cylindrical stems approximately 0,4 mm wide which bifurcate dichotomously. Autozooezia are long with well marked zooecial boundaries. The autozooezial apertures are directed transversely towards the stem surface. The peristome is short with a circular aperture of small diameter.

The autozooezia are long in section and generally lack diaphragms. New zooecia are generally budded from the centre of the stem.

The gonozoecium is small and globular. It is 0,4 mm long and 0,35 mm wide in the holotype.

Dimensions

Holotype and paratypes.

	O.R.	$\bar{x}$	V	s	N
apaz . . .	0,043 — 0,055	$0,046 \pm 0,001$	8,07	0,003 7	49
azp . . .	0,058 — 0,073	$0,064 \pm 0,001$	7,76	0,005 0	49
azw . . .	0,067 — 0,094	$0,073 \pm 0,002$	8,22	0,006 0	49
fwl . . .	0,450 — 1,000	$0,708 \pm 0,032$	15,11	0,107	49

Remarks

This species is characterized by its small dimensions. It resembles *P. pulchra* Brood from the Campanian of Scandinavia in general shape, but differs in having smaller autozooezia.

P. bonamaryi Brood from the Palaeocene of Madagascar differs in having larger autozooezial dimensions.

Spiropora irregularis n.sp.

(figs. 18 D–F; 19)

1908 *Spiropora verticellata* (Goldfuss); Lang, p. 10, Pl. I, Figure 13.

Type specimen

Holotype: RM By 23615. Paratypes: RM By 23613–23614, 23616–23619.

Diagnosis

A *Spiropora* with thick stems, large autozooezial apertures and incompletely developed verticells.

Description

The zoarium is erect, composed of dichotomously branching cylindrical stems, which are 0,5 — 1,5 mm wide. Autozooezial apertures open in annular cycles around the stems. The rings are commonly not fully developed and can be replaced by ascending spirals or rarely by an irregular arrangement of autozooezial apertures. The frontal walls of autozooezia are flat with well-marked zooecial boundaries. The autozooezial aperture is circular in outline.

Autozooezia are long in section, generally without diaphragms. The interzooecial walls are thick, ap-

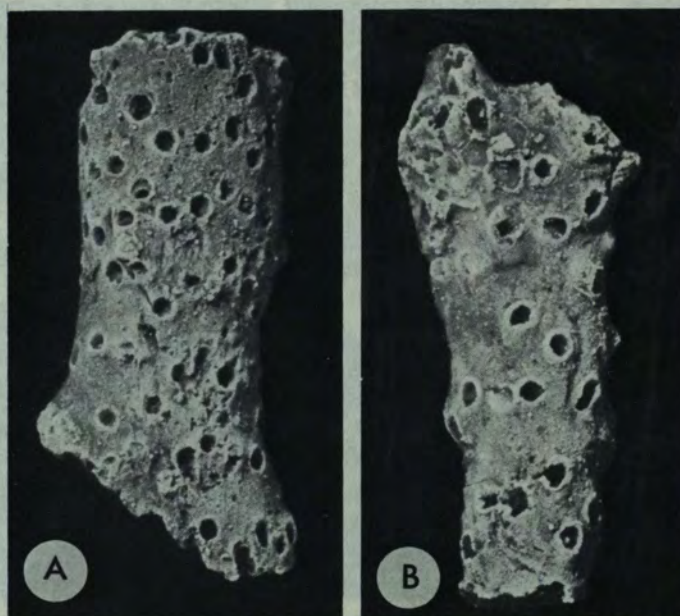


Figure 16. *Clausia crassa* n.sp. A. Short specimen. RM By 23611, paratype. X 13. B. Thin specimen. RM By 23612, paratype. X 15.

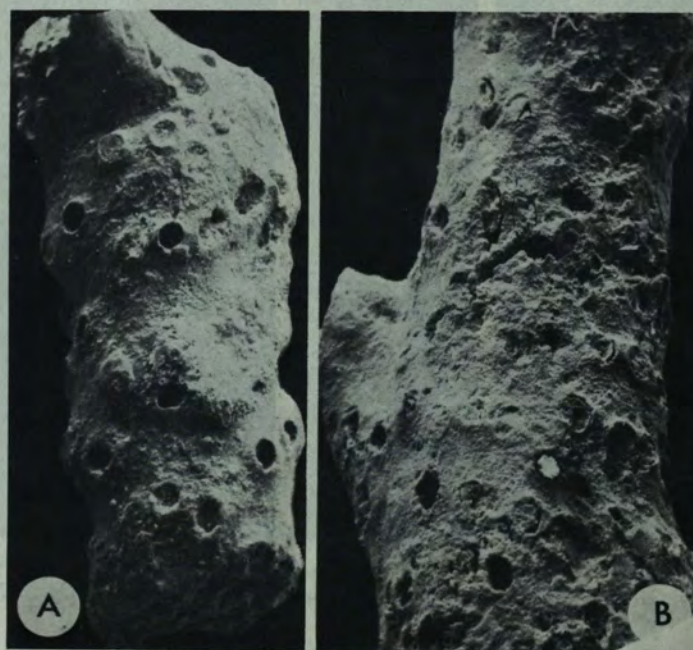


Figure 17. *Clausia crassa* n.sp. A. Small specimen. RM By 23610, paratype. X 20. B. Bifurcating specimen. RM By 23609, holotype. X 20.

proximately 0,030 mm at the distal end. The exterior walls are approximately 0,040 mm thick. The gonozoecium is not known.

Dimensions

Holotype and paratypes.

	O.R.	$\bar{x}$	V	s	N
azap . . .	0,080 — 0,120	$0,103 \pm 0,003$	10,14	0,010 5	46
azp . . .	0,110 — 0,160	$0,137 \pm 0,004$	9,63	0,013 2	46
fwl . . .	0,650 — 1,050	$0,828 \pm 0,034$	13,18	0,131	46

Remarks

This species is characterized by its tendency to have incomplete verticells so that the apertures of autozooecia are commonly arranged in spirals. It differs from the contemporary *S. verticellata* (Goldfuss) from Europe in the arrangement of autozooecia and in having smaller autozooecial dimensions. *S. ingens* Voigt from the Santonian of Europe is a larger species.

Clausa crassa n.sp.
(figs. 16; 17; 18 A)

1908 *Entalophora madreporacea* (Goldfuss); Lang, p. 10, Pl. I, Figure 14.

Referred specimens

Holotype: RM By 23609. Paratypes: RM By 23607, 23608, 23610–23612.

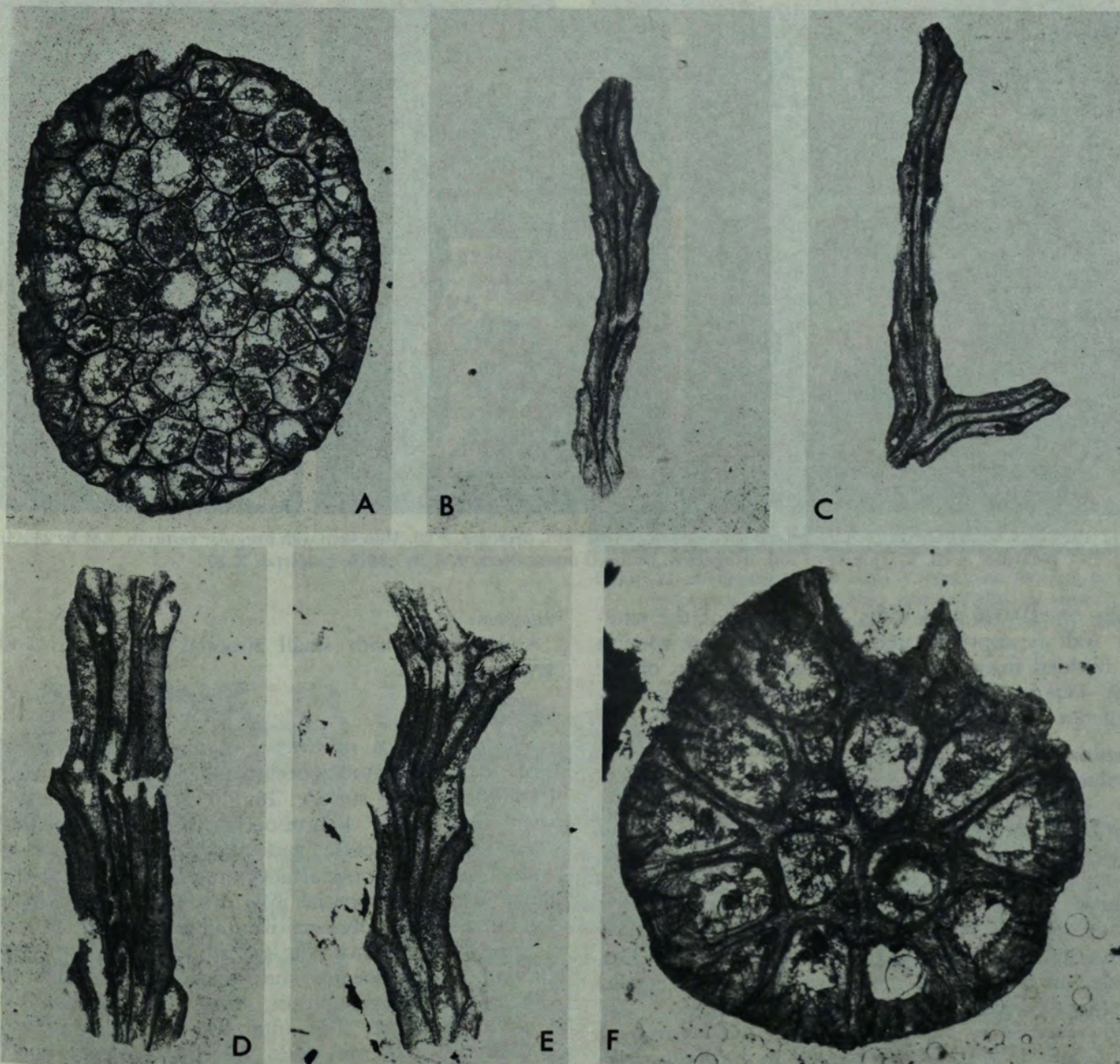


Figure 18. *Clausa crassa* n.sp. A. Transverse section of stem showing thin interzooecial walls and small kenozoecia in the exozone. RM By 23608, paratype. X 30. B. *Pustulopora minuta* n.sp. B. Longitudinal section of stem. RM By 23620, paratype. X 25. C. Longitudinal section of bifurcating stem. RM By 23621, paratype. X 25. *Spiropora irregularis* n.sp. D. Longitudinal section of stem. RM By 23616, paratype. X 20. Longitudinal section of stem. RM By 23618, paratype. X 20. F. Transverse section of stem showing granular middle layer within interzooecial walls and flanking laminar layers. Note thick zooecial walls. RM By 23619, paratype. X 95.

Diagnosis

A large *Clausa* with few kenozoecia and large, crowded autozoecia. Interzooecial walls are very thin.

Description

The zoarium consists of dichotomously branching, cylindrical stems, approximately 2 mm wide. The autozoecia are irregularly arranged on the stem surface. Their peristomes are short with large, circular apertures. Box-like kenozoecia are present between the autozoecia. Young stems may lack kenozoecia.

The interzooecial walls are comparatively thin,

Type Material

RM By 23642.

Remarks

This species is common in the samples from Need's Camp, the specimens agreeing well with contemporary material from the Maastrichtian of Madagascar.

Multicavea rotunda n.sp.

(figs. 21; 22)

Type specimens

Holotype: RM By 23600. Paratypes: RM By 23601–23606.

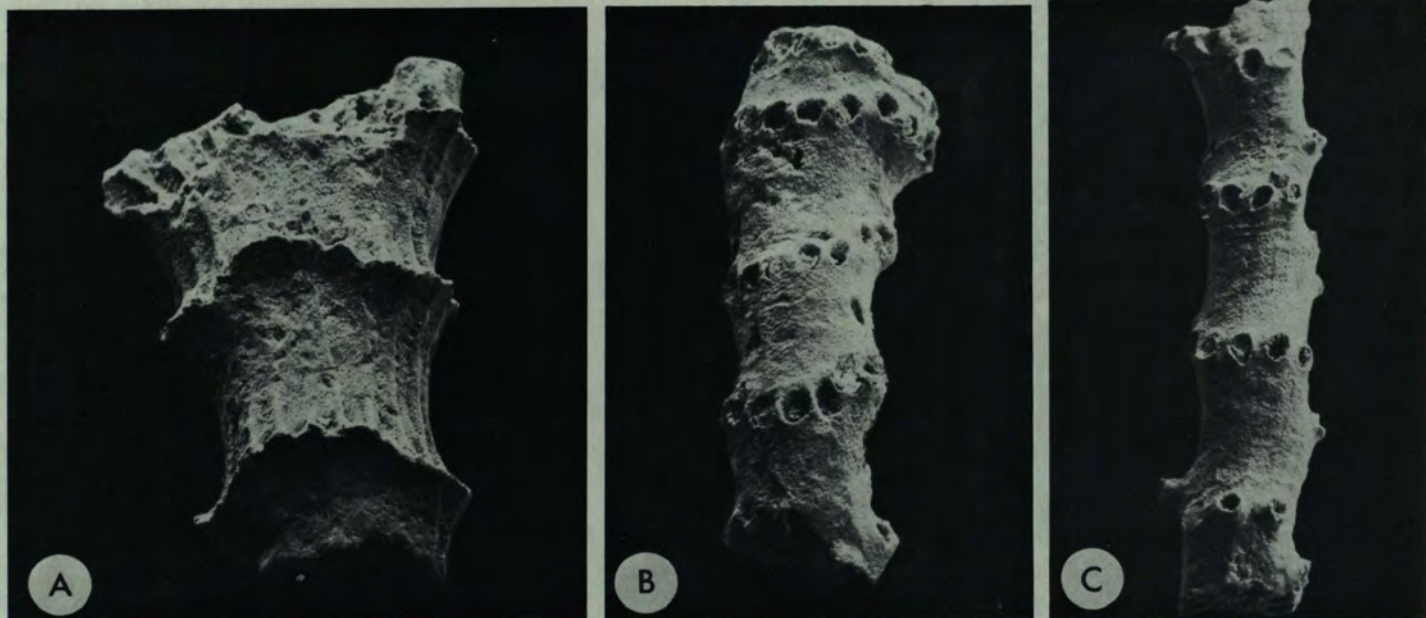


Figure 19. *Spiropora irregularis* n.sp. A. Corroded specimen. RM By 23613, paratype. X 20. Thin stem with irregular verticells. RM By 23614, paratype. X 20. C. Thin stem with irregularly arranged autozoecia. RM By 23615, holotype. X 20.

being only 0,010 mm wide. The width of the exterior wall is approximately 0,050 mm. New zooecia are budded from the whole of the axial part of the stem. Diaphragms are generally lacking. Gonozoecium not observed.

Dimensions

Holotype and paratypes.

	O.R.	$\bar{x}$	V	s	N
azap . . .	0,107 — 0,147	0,122 $\pm$ 0,003	8,67	0,010 5	46
azp . . .	0,147 — 0,168	0,168 $\pm$ 0,003	6,88	0,011 5	46

Remarks

C. crassa has comparatively few kenozoecia in the stems, and some young stems may lack them altogether. In this respect this species resembles the living *Clausi* (*Bientalophora regularis* MacGillivray).

C. crassa differs from *C. globulosa* D'Orbigny from the Upper Cretaceous of Europe in having smaller autozoecia.

Lichenopora betsibokensis Brood, 1976

1976 *Lichenopora betsibokensis* Brood, p. 407, Pl. 4, Figures 1, 2, 4.

Diagnosis

A *Multicavea* with small zooecial dimensions and few diaphragms.

Description

The zoarium is massive, globular or forms erect stout branches. Autozoecia are grouped irregularly over the zoarial surface. Rarely, a stellate arrangement is present. Kenozoecia are slightly smaller than the autozoecia and approximately twice as numerous. Autozoecial apertures are small and circular. The kenozoecial aperture is generally circular but may be polygonal in younger zooecia.

Thin sections show the growth of the zoarium to be episodic. Generally autozoecia are continuous through the regeneration areas, but overgrowths commonly occur. The interzooecial walls are approximately 0,04 mm wide, but may be even wider at the distal end. Diaphragms are generally lacking except for terminal ones. Several stout longitudinal rods occur within the zooecial walls. These are built by laminar crystals and apparently lack a central rod; they are similar to the pseudolunaria of the dis-



Figure 20. *Lichenopora betsibokensis* Brood. Specimen with zoarial brood-chambers. RM By 23684. X 20.

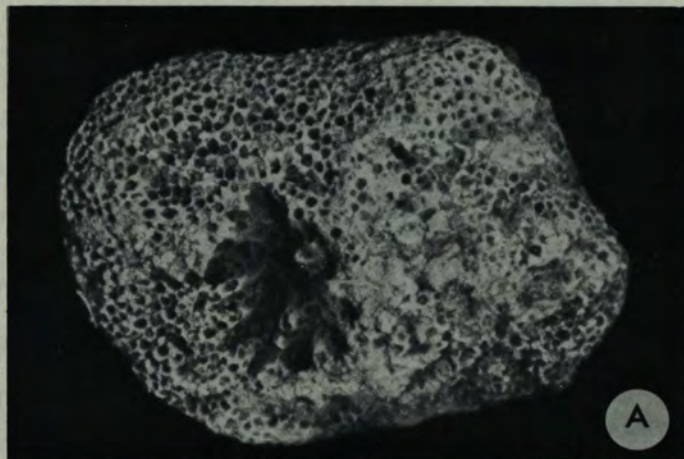


Figure 21. *Multicavea rotunda* n.sp. A. Specimen showing broken zoarial brood-chamber. RM By 23601, paratype, X 15. B. Bifurcating, massive zoarium. RM By 23600, holotype.

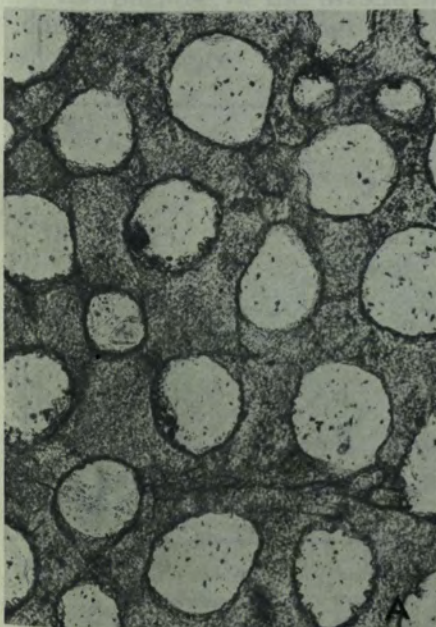


Figure 22. *Multicavea rotunda* n.sp. A. Tangential section showing auto- and kenozoecia. RM By 23605, paratype, X 120. B. Longitudinal section showing club-shaped growth units of zoecial walls. Specimen partly recrystallized. RM By 23604. X 100. C. Longitudinal section of colony showing growth lines. RM By 23602, paratype. X 6.

porellids but are placed deeper within the zooecial walls and are smaller.

The zoarial brood-chamber is small and placed near the zoarial surface.

Dimensions

Holotype and paratypes.

	O.R.		$\bar{x}$	V	s	N
azap . . .	0,053 — 0,070		0,061 $\pm$ 0,001	7,59	0,004 6	48
kzap . . .	0,045 — 0,053		0,049 $\pm$ 0,001	5,63	0,002 8	48
z/mm ² . .	45,000 — 62,000		55,1 $\pm$ 1,9	11,55	6,371	48

Remarks

Due to partial recrystallization of the available specimens the exact microstructure cannot be determined with accuracy. However, the structure appears to be very similar to that of *Multicavea*

(*Canuella*), and the present species is tentatively referred to that genus. It differs, however, in having the autozooecia irregularly placed, and the tendency to form clusters and radiating lines seems to be lacking in the specimens examined except around an ovicell.

M. rotunda differs from the Danian species *M. danica* Levinsen in having larger autozooecia. It differs from the Maastrichtian *M. pustulosa* Hamm in having smaller autozooecia.

ACKNOWLEDGEMENTS

I am grateful to Dr. Herbert Klinger, the South African Museum, Dr. Brian Lock, University of Exeter, Professor Ron Tavener-Smith, University of Natal, and Professor I. C. Rust, University of Port Elizabeth for sending me material from Need's Camp and for valuable suggestions. Technical assistance was given by Uno and Sif Samuelson and Göran Blom. Stylistic corrections were made by Mike Bassett.

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FOSSIL INSECT WINGS FROM THE EARLY PERMIAN WHITE BAND FORMATION, SOUTH AFRICA

by

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ABSTRACT

Fossil insect remains are reported for the first time from the Lower Karroo White Band in South Africa. The wings of two individuals have been recovered from separate localities 140 km apart in the southern Cape fold-belt. They unfortunately supply little useful information on the depositional environment of the White Band as they were probably transported some distance to their final site of preservation.

INTRODUCTION

A variety of fossil insects has been recorded from the Irati Formation in Brazil (Pinto, 1972a, b). The White Band in South Africa is the time and lithological equivalent of the Irati (Du Toit, 1937; Martin, 1961), but no insect remains have previously been reported from the White Band.

In 1975 we fortuitously discovered the remains of two isolated insects at separate localities in the southern Cape Province; the material is now housed at the Bernard Price Institute for Palaeontological Research. In July 1975 we sent latex moulds of the specimens to Professor Irajá D. Pinto at the Federal University of Rio Grande do Sul, Brazil, followed later by the photographs and line drawings reproduced here. He supplied us with preliminary identifications of the specimens and, with L. Pinto de Ornellas, will be publishing the formal taxonomy elsewhere (Pinto and De Ornellas, in press).

The purpose of the present note is to record and illustrate the insect wings and comment briefly on their significance.

GENERAL GEOLOGY AND PALAEOONTOLOGY OF THE WHITE BAND

The White Band is a black pyritic shale formation which contains subordinate bands and lenses of fine-grained dolomite. The insect wings are preserved as compressions within the dolomite.

The discovery of insect wings augments the fossil record from the White Band. The assemblage includes the aquatic reptile *Mesosaurus tenuidens* Gervais 1865, the fish *Palaeoniscus capensis* Broom 1913, the crustacean *Notocaris tapscotti* Broom 1931 (McLachlan and Anderson, 1973), rare limulid trackways (Anderson, 1975), plant fragments (Anderson and McLachlan, 1976) and monaxon sponge spicules.

In combination, the lithological and palaeontological evidence indicates that the White Band sediments probably accumulated in an enormous stratified lake with little or no access to the world ocean (McLachlan and Anderson, 1977; Anderson, McLachlan and Oelofsen, in press). The sites at which the insects were preserved were apparently a considerable distance from land.

THE INSECT WING LOCALITIES

(i) Modderdrift (33°09'S; 22°32'E)

The insect remains from the farm Modderdrift P.A. Q. 2–21 (fig. 1) were found in a loose boulder of finely laminated slump-deformed dolomite resting on the persistent metre-thick band of dolomite near the middle of the White Band succession (McLachlan and Anderson, 1977), and there is no reason to believe that it did not derive from this band. Fragmentary crustacean remains, presumably *Notocaris*, are widespread in the metre-thick dolomite and also occur in the boulder containing the insect wings.

Two similar but incomplete wings are present and a torn fragment between them may represent a third wing (fig. 2). The most complete wing is 6 mm long.

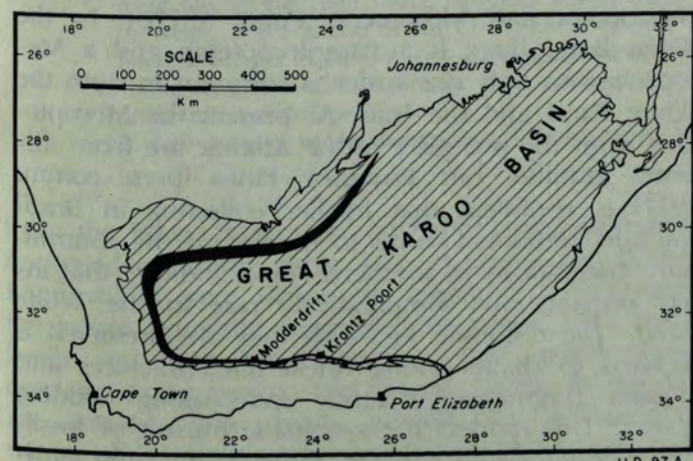


Figure 1. Sketch map of the Karoo Basin in South Africa showing the two insect wing localities in the White Band. The White Band outcrop is indicated in heavy black.

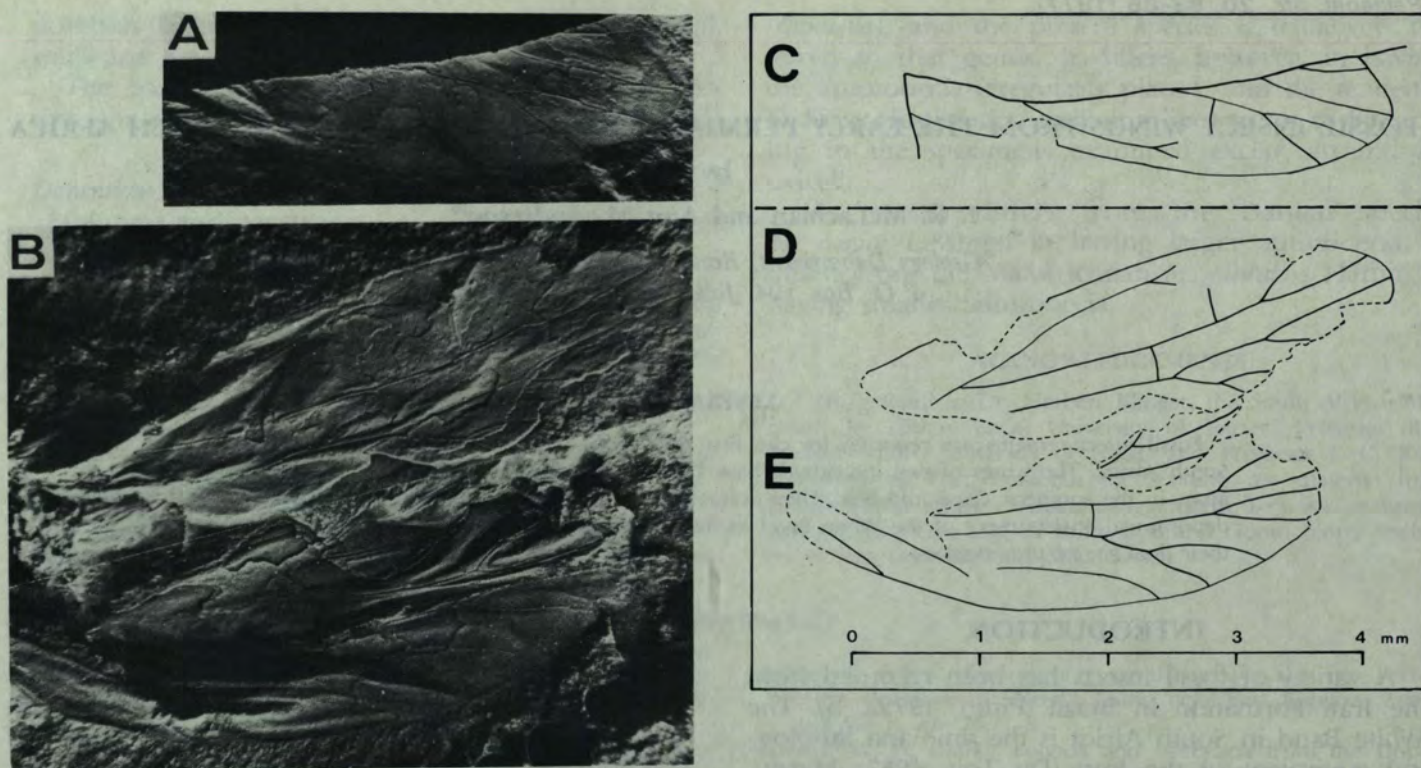


Figure 2. The Mecopteran insect wings from Modderdrift. Mod./K W.B.1 (Approx. $\times 20$).

A. and B. Photographs of the specimens. The wing tip in A is the only surviving portion of the counterpart of the more complete specimen shown in B. It is the counterpart of the upper wing in B as figured. There are two large wings in B. As they are on slightly different levels, the photograph is a composite constructed from two frames, with one wing in focus in each. The configuration of the specimens illustrated in both this figure and the next is such that it is not possible to illuminate them correctly with the lighting from the top/left: the photographs as printed, with the leading edge of the wings towards the top of the page, therefore present a misleading visual impression of the relief, the positive areas appearing to be negative and vice versa.

C. to E. Line drawings of the venation on the wings shown in A and B above. There appears to be a disconnected wing fragment lying between the major wings D and E. Point of attachment to the body was on the left.

The two large wing surfaces are preserved on slightly different levels and each is a little folded. This may be a reflection of the original disposition of the wings or the result of differential compaction of the dolomite.

All the fragments clearly belonged to one individual, apparently a member of the order Mecoptera.

(ii) *Krantz Poort* ($33^{\circ}2'30''S$; $24^{\circ}03'E$)

The insect remains from the farm Krantz Poort Uit. Q. 10-57 were found in a loose block of dolomite in a roadside quarry within the White Band (fig. 1).

A large part of the venation belongs to one wing with its tip torn away (fig. 3). The venation in the proximal half of the wing is superimposed on what appears to be a separate venation. This suggests that a second wing may be present. Three or four body segments appear to be present as well, but they are very indistinctly preserved. The long, straight, cylindrical moulds might represent legs, although there are no discernible joints. The entire complex spans 3 cm. The proximal part of the major wing is slightly folded longitudinally. The membrane between the veins is frequently finely pleated. The pleating may be a preservational feature or the re-

sult of desiccation shrinkage before deposition.

The remains appear to be those of a member of the order Paraplecoptera.

CONCLUSION

The diverse insect fauna recovered from the Irati Formation in the Parana Basin in Brazil (Rio Grande do Sul State) includes Homoptera, Coleoptera, Neuroptera and Mecoptera (Pinto, 1972b). In the White Band there is a Paraplecopteran and a Mecopteran, so only one order is common to both the White Band and the Irati. At present the Mecopterans from the two sides of the Atlantic are from different families, but Professor Pinto (pers. comm. 1977) is confident that further collecting in Brazil will add additional forms to the record. By contrast, our observations in southern Africa indicate that insect remains are comparatively rare in the White Band. The dolomite in which they are preserved is inclined to shatter along calcite-filled fractures into angular fragments: it rarely splits along bedding planes. This renders the systematic pursuit of fossils on bedding plane surfaces difficult and unrewarding. A determined search would nevertheless probably produce more specimens.

The larval stages of the insects recovered to date

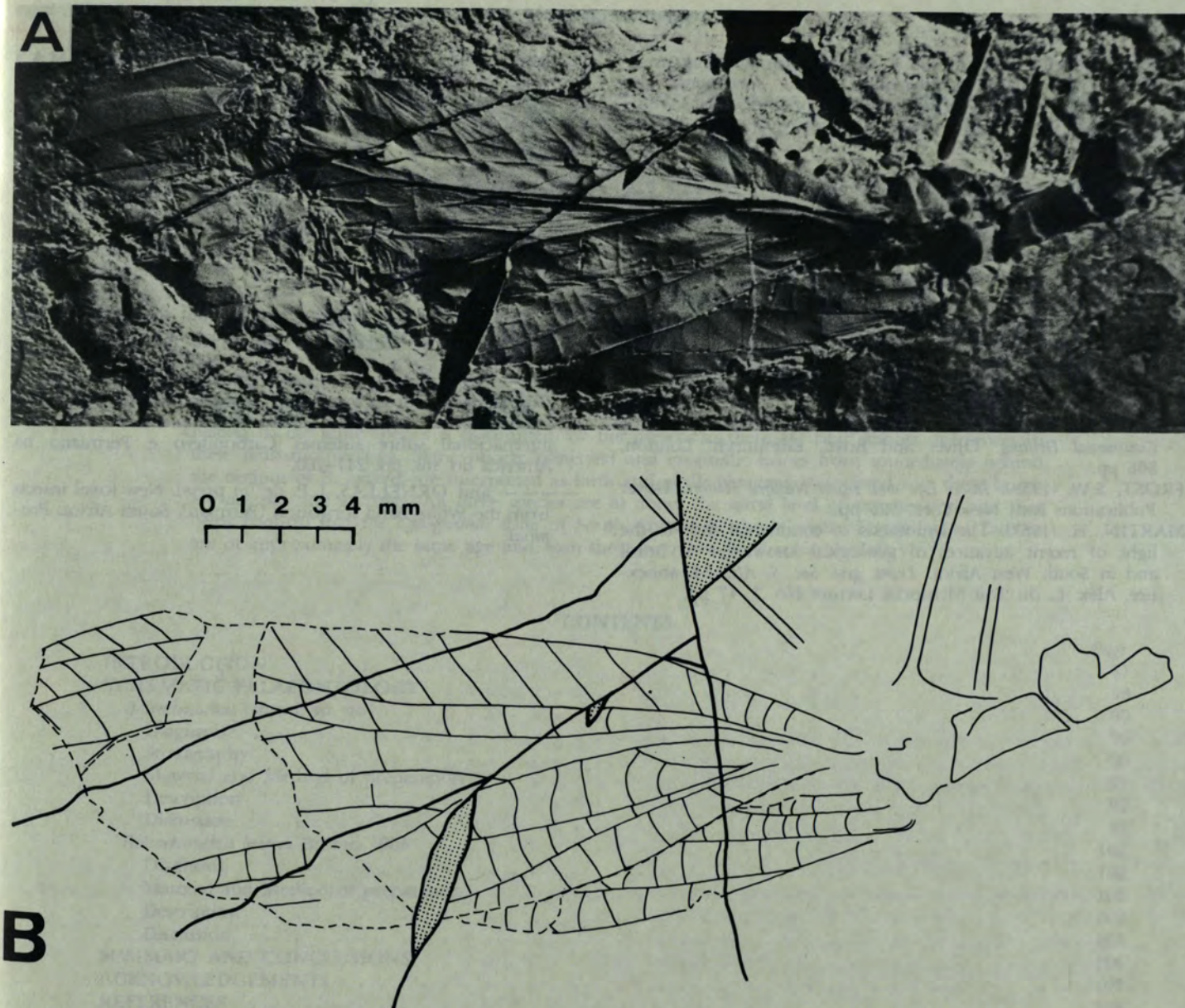


Figure 3. The Paraplecopteran insect fragments from Krantz Poort. K.P./K. W.B.1 (Approx. $\times 6$).

A. Photograph of the specimen. (There is no counterpart.) Most of the venation clearly derives from one wing, but the triangle of venation at the bottom/right appears to be distinct and may be portion of another, underlying, wing. The attachment was on the right; some indistinct bits of body remain. Notice the fine pleating of the membranous areas between the veins. There is also a mat of disjointed pleated fragments at the distal end of the large intact wing. The prominent linear structures in the top right hand quadrant of the picture may be the proximal segments of long legs, but no joints are visible. The row of three circular holes alongside the proximal upper edge of the veined surface is an artifact produced in preparation of the specimen.

B. Line drawing of the insect remains shown in A above.

from the White Band were probably land based and not resident in the great lake in which the White Band shales were deposited. Mecopteran (scorpion fly) larvae generally resemble caterpillars, and both larvae and adults are believed to feed largely upon dead or dying insects; Plecopteran (stone fly) larvae are aquatic, but usually inhabit the well-aerated waters of fast-flowing streams, where the larvae and the adults (which tend to stay in the vicinity of the streams) both feed chiefly on plants, including algae (Frost, 1959). The winged Mecopteran and Paraple-

copteran adults were at any rate tree fliers and might easily have been blown, dead or alive, far from their usual haunts to the sites of fossilisation. The wings might also have floated in the lake waters for some distance, as the occasional fragment of leaf and twig (Anderson and McLachlan, 1976) might have done as well. The application of the fossils will therefore be in providing information on the evolution and general distribution of the insect groups rather than in the elucidation of the depositional environment of the White Band itself.

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A NEW BRACHYOPID, *BATRACHOSUCHUS CONCORDI* SP. NOV. FROM THE UPPER LUANGWA VALLEY, ZAMBIA WITH A REDESCRIPTION OF *BATRACHOSUCHUS BROWNI* BROOM, 1903

by

Sharon Chernin

ABSTRACT

Two brachyopid skulls from southern Africa are described: one from the N'tawere Formation, Zambia is assigned to *Batrachosuchus concordi* sp. nov. and the other, *B. browni* Broom from the Cynognathus zone of South Africa is used as comparative material after further preparation had been effected on it. Both are assessed in relation to published descriptions of *B. watsoni* and it is concluded that *B. concordi* is closest to *B. watsoni*. The possibility that *B. watsoni* and *B. browni* belong to the same species is discounted for the present as there are four distinct differences in their skull morphology. Some poorly preserved and enigmatic bones from immediately behind the occiput of *B. concordi* are interpreted as limb and girdle elements. Associated with these bones are an axis and an atlas. All three species are at about the same level of organisation and that helps confirm that the Cynognathus zone of South Africa and the N'tawere Formation of Zambia are of approximately the same age and span the Lower-Middle Triassic boundary.

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INTRODUCTION

The brachyopid labyrinthodonts existed from the Upper Permian to the Upper Triassic. Some reached six feet in length and all are characterized by large orbits, a Ω -shaped palate, a long retroarticular process and a more or less parabolic skull outline.

Watson (1919, 1956), Cosgriff (1969) and Welles and Estes (1969) are among those who have reviewed the contents and taxonomic history of the family. Based on work by previous authors, a composite diagnosis of the family Brachyopidae may be given as follows: skull short and broad; B : L index 110 to 150; no zones of relative intensive growth; occipital condyles project well behind posterior edge of skull roof; basicranial joints absent; pterygoid bones joined by suture to parasphenoid bones; squamosal and quadratojugal with strong occipital flanges forming a vertical, transversely concave trough lateral to the pterygoid; pterygoid forming a large

vertical plate laterally which is posteriorly elongated beyond squamosal-quadratojugal trough, making a steeply arched flat-roofed palate.

Workers have at various times removed genera and families from the Brachyopidae. Panchen (1959) removed the plagiosaurs from the family. Cosgriff (1969) removed the Dvinosauridae, forming a separate family, which together with the Brachyopidae constitute the Superfamily Brachyopoidea. Welles and Estes (1969) removed *Dvinosaurus primus* Amalitzki 1921, because of its primitive structure as indicated by the lack of development of the pterygoid-parasphenoid suture. They also removed the following species: *Tungussogyrinus bergi* Efremov 1939, from the Korwuntchan (upper Angara) series near Tungus, Siberia; *Boreosaurus thorslundi* Nilsson 1943, from the Early Triassic of Spitsbergen; *Pelorocephalus mendozensis* Cabrera 1944, from Potrerillos Village, Mendoza Province, Argentina, in the Upper Ca-

cheuta beds of Early or Middle Triassic age; *Tupilakosaurus heilmani* Nielsen 1954, from the Early Triassic of Greenland; *Enosuchus breviceps* Efremov (in Konjukova) 1955, from the Russian Zone II (Late Permian) of the Ishevo site in the Tatar A.S.S.R.; *Eobrachyops townsendae* Watson 1956, from the Upper Permian Clear Fork beds of Texas; *Indobrachyops panchetensis* Huene and Sahni 1958, from the Upper Panchet rocks (Early Triassic) of India; *Plagiorophus paraboliceps* Konjukova (1955) from the Early Triassic Zone V of Chkalov province, U.S.S.R.

The species retained in the Brachyopidae are:

(i) *Brachyops laticeps* Owen 1855. Only one specimen (B.M.N.H. No. R4414) was found from the Mangali beds in Nagpur, Central India (possibly equivalent to the *Lystrosaurus* zone). A composite definition of *Brachyops laticeps* Owen 1855 is: small brachyopid with parabolic skull; snout tapered to point; large orbits anterior to mid-length of skull; antero-posterior axis of orbits directed parallel to skull border; very large choanae; cultriform process of parasphenoid overlain by vomer; no denticles present on cultriform process; lateral line grooves relatively narrow; sculpture pattern linear.

(ii) *Bothriceps australis* Huxley 1859. Only one specimen comprising a skull and attached incomplete lower jaw (B.M.N.H. No. 23110) has been found from an unknown locality in Australia. The midline length of the skull is approximately 8 cm. A composite definition of *Bothriceps australis* is: small brachyopid with narrow skull; skull roof roughly triangular in dorsal view; large orbits set close together, relatively far back on skull roof; preorbital length of skull roof is 33 % of skull length; broad subtemporal fossa, indented on medial margin by a projection of the Pterygoid bone.

(iii) *Blinasaurus wilkinsoni* (Stephens) Cosgriff 1969

= *Platyceps wilkinsoni* Stephens 1887

Proc. Linn. Soc. N.S.W. 2, 1175–1195

= *Bothriceps wilkinsoni* (Stephens) Lydekker 1890

Q. Jl. geol. Soc. Lond., 46, 289–294

= *Platyceps wilkinsoni* (Watson 1956)

Bull. Br. Mus. nat. Hist. (Geol.), 2, 317–391.

A partial skeleton (N.S.W.G.S. No. F12872) consisting of the skull roof, a number of branchial bars, the dermal shoulder girdle and a series of ribs and vertebral elements was found at the Railway Ballast Quarry near Gosford, New South Wales, in the uppermost part of the Gosford Formation, Narrabeen Group (Middle Triassic).

A composite definition of *Blinasaurus wilkinsoni* is: very small brachyopid with narrow parabolic skull; orbits close together; parietal foramen very close to orbits; in dorsal view skull nearly circular.

(iv) *Blinasaurus henwoodi*, Cosgriff 1969. A fairly complete skull (W.A.M. No. 62.142) found in the Erskine Range on Blina Station, West Kimberley District, Western Australia, from the Upper Blina Shale, ? *Otocerat* Division of the Scythian Stage.

The skull is approximately 11.2 cm in length.

A composite definition of *Blinasaurus henwoodi* is: small brachyopid with narrow parabolic skull; orbits close together; parietal bone separated from postorbital bone by postfrontal-supratemporal suture; frontal forms part of medial margin of orbit.

(v) *Bothriceps major* Woodward 1909. This specimen, from the Late Permian Upper Coal Measures, Airly, New South Wales, consists of a skull and associated partial skeleton, which was divided after its discovery, part remaining at the Mining Museum of the New South Wales Geological Survey as No. F12697, and part sent to the British Museum (B.M.N.H. No. R3728). The portion at the Mining Museum contains the dorsal impression of the skull roof (length of skull approximately 15.3 cm), the part described by Woodward (1909).

Watson (1919 and 1956) commented on the portion in the British Museum, redescribed and re-illustrated B.M.N.H. No. R3728 and placed the species in a new genus, *Trucheosaurus*.

Cosgriff (1969) retains the name *Trucheosaurus major* for this specimen. A composite definition of this species is: large brachyopid with skull roughly triangular in dorsal view; preorbital length of skull 34 % of skull length; orbits relatively smaller and more widely spaced than in *Bothriceps australis*; orbit length 20 % of total skull length; tabulars longer than in *B. australis*.

(vi) *Batrachosuchus browni* Broom 1903. (Redescribed below)

(vii) *Batrachosuchus watsoni* Houghton 1925. The specimen (B.M.N.H. No. 3589) is a complete skull (skull length approximately 12 cm) found in the *Cynognathus* zone (Lower-Middle Triassic?) of the Burgersdorp district, C.P., South Africa (Watson, 1956). It was first described by Watson (1919) as *Batrachosuchus* sp.

A composite definition of *Batrachosuchus watsoni* is: large brachyopid with broadly parabolic skull outline; orbits far forward, postorbital part of skull long; interpterygoid vacuity short; narrow inter-narial area; lateral line grooves well defined and broad.

(viii) *Batrachosuchus lacer* (Shishkin 1966)

(*Batrachosuchoides lacer*, Shishkin 1966)

This species is based on the anterior part of a skull, along with much fragmentary referred material from the Early Triassic Federov horizon, Baskunchakskaya Series, Viatki Basin, European U.S.S.R. This is a small brachyopid, about two-thirds the size of *Batrachosuchus watsoni*. Welles and Estes (1969) comment on this species: "In the generic diagnosis Shishkin (1966) lists a number of features, with nine derived from the type and three more based on referred material. The present state of our knowledge of brachyopid skull details is so poor that it is not possible to diagnose a genus or even a species on the basis of the characters listed." Welles and Estes draw no conclusions from the available and scanty data, but as yet find no reason to exclude the Viatki bra-

chyopid from the genus *Batrachosuchus*.

(ix) *Hadrokkosaurus bradyi* (Welles) 1947. This species was originally described as *Taphrognathus bradyi* (Welles 1947) but the generic name was found to be preoccupied and was changed to *Hadrokkosaurus* Welles (1957). The type, U.C.M.P., No. 36199, is a nearly complete right ramus of a lower jaw found in the Holbrook Member of the Moenkopi Formation some 10 km west of Holbrook, Arizona (probably Lower-Middle Triassic). The hypodigm contains skull material; length of skull approximately 23,4 cm.

A composite definition of *Hadrokkosaurus bradyi* is: extremely large brachyopid with smoothly parabolic skull outline; nares far apart; broad interpterygoid vacuities; quadrate ramus of pterygoid a vertical plate projecting far behind squamosal; lower jaw smooth-surfaced; large lateral mandibular fenestra.

(x) *Boreosaurus thorslundi* Nilsson 1943. The material included in this taxon by Nilsson consists entirely of lower jaw fragments from the Sticky Keep Formation of Spitsbergen (Lower Triassic). Welles and Estes (1969) exclude this genus from the Brachyopidae because of the very short retro-articular process.

Cosgriff (1969), however, includes this species in the Brachyopidae believing that the retroarticular process of the holotype was broken off close to its base and was probably elongate as in other brachyopids. A composite definition of *Boreosaurus thorslundi* is: jaw very slender; posterior meckelian foramen and angular-prearticular suture located low on lingual surface of lower jaw; adductor fossa long and narrow; jaw ramus bowed strongly upward in lingual view; labial wall of adductor fossa very high.

(xi) *Brachyops allos* Howie 1972. The specimen (Queensland Museum No. F.6572) consists of a more or less complete skull (skull length approximately 11,1 cm) found in Locality 0,6 Duckworth Creek, South Central Queensland. The horizon is the Lower Upper Rewan Formation of the Mimosa Group (Lower Triassic).

A composite definition of *Brachyops allos* is: brachyopid with more or less triangular shaped skull; small orbits anterior to mid-length of skull with the antero-posterior axis directed parallel to skull border; exoccipital condyles very near to level of quadrate condyles; sloping portion of occiput greatly reduced; cultriform process of parasphenoid clasped laterally by posteriorly directed processes of vomer; denticles present on posteromedial portion of cultriform process; long tripartite anterior palatal foramen.

(xii) *Notobrachyops picketti* Cosgriff 1973. This specimen (New South Wales Geological Survey No. F.8258) consists of an external impression of most of a skull roof (length of skull approximately 3,1 cm) and part of the right lower jaw ramus. It was found at the Huntsville Brick Company quarry, Mortdale, New South Wales. The horizon is the Ashfield Shale of Liverpool sub-group, Wiannamatta Group of the Sydney Basin (?Upper Triassic).

A composite definition of *Notobrachyops picketti* is: very small brachyopid with narrow skull and round snout; antorbital portion of skull roof approximately one-third of skull length; orbits close together; each element of skull roof elevated in central region and depressed around sutural edges; posterior edge of skull roof strongly convex.

(xiii) *Austrobrachyops jenseni* Colbert and Cosgriff,

TABLE 1
World Distribution of Brachyopidae

	U.S.A.	SPITZBERGEN AND U.S.S.R.	INDIA	AFRICA	AUSTRALIA	ANTARCTICA
UPPER TRIASSIC					<i>Notobrachyops picketti</i>	
MIDDLE TRIASSIC	<i>Hadrokkosaurus bradyi</i>			<i>Batrachosuchus concordi</i> <i>Batrachosuchus watsoni</i> *	<i>Blinasaurus wilkinsoni</i>	
LOWER TRIASSIC		<i>Batrachosuchus lacer</i> <i>Boreosaurus thorslundi</i>	<i>Brachyops laticeps</i>	<i>Batrachosuchus browni</i> *	<i>Blinasaurus hemwoodi</i> <i>Brachyops allos</i>	<i>Austrobrachyops jenseni</i>
UPPER PERMIAN					<i>Bothriceps australis</i> <i>Tracheosaurus major</i>	

* *Cynognathus* zone of South Africa which may well be Scythian (Cruickshank, 1967)

1974. This species was based on a left pterygoid bone more or less intact (American Museum of Natural History No. 9346) from Coalsack Bluff and a referred fragment of lower jaw (A.M.N.H. No. 9301) from Graphite Peak in the Transantarctic Mountains. These two localities are approximately 140 km apart. The horizon is the lower part of the Fremouw Formation (Lower Triassic).

A composite definition of *Austrobrachyops jenseni* is: brachyopid in which the pterygoid bone possesses a distinct angle in the middle of its course; ventrolateral corner of stapedial fossa incised by groove for internal carotid artery; labial wall of adductor fossa of lower jaw considerably higher than lingual wall; retroarticular process three times longer than articular facet; labial surface bears sculpture of elongate pits; oral and mandibular grooves well marked.

SYSTEMATIC PALAEONTOLOGY

In the following paragraphs *Batrachosuchus concordi* sp. nov. from the Upper Luangwa Valley, Zambia is described. Also, *Batrachosuchus browni* Haughton is redescribed, as the type specimen has been further prepared revealing more detail and some new characters.

Batrachosuchus concordi sp. nov.

Holotype. BPI Cat. No. F3728. Imperfect skull, lower jaws and some postcranial material

Locality. N'tawere Formation, Upper Luangwa Valley, Zambia. Locality 15 (Drysdall and Kitching, 1961)

Horizon. ? Lower Middle Triassic

Derivation. From a fancied similarity to the Concord supersonic airliner as seen in lateral view.

Diagnosis

Small *Batrachosuchus* with skull narrower than *B. browni* and much narrower than *B. watsoni*; interorbital breadth very much narrower than both; shorter preorbital length than both; orbit slightly smaller than *B. browni*; postorbital length greater than *B. browni*, but shorter than *B. watsoni*; interpterygoid vacuity shorter than *B. browni* and much shorter than *B. watsoni*, interpterygoid vacuity narrower than in both; distance of parietal foramen in front end of skull table greater than *B. browni* (T:L = 23) and *B. watsoni* (T:L = 23), (*B. concordi* T:L = 37); lateral line canals weakly defined; parasphenoid extends to basal limit of skull; exoccipital does not reach as far posteriorly as in either *B. watsoni* or *B. browni*; a lingual process of the angular is present.

Stratigraphy (see table 3)

This specimen was collected from the Upper Horizon of the N'tawere Formation by Drysdall and Kitching in 1961. The fossiliferous beds of their Locality 15 consist of dark red, soft mudstones with

characteristic feldspathic grit bands, containing angular vein-quartz fragments. The N'tawere Formation contains two fossiliferous zones, the Lower with *Diademodon*, and an Upper (Red Marl) horizon which includes Locality 15. Towards the base of the beds, amphibians and molluscs are present. The molluscs have been identified as *Unio karrooensis* by Drysdall and Kitching (1963, p. 22). From the same locality, two cynodonts were also collected, the smaller perhaps belonging to the genus *Trirachodon*, and the larger a *Scalendon*-like form resembling material described by Crompton (1955) from the Manda Beds of Tanganyika.

The author has previously described two large capitosaurians from Locality 15 (Chernin and Cruickshank, 1970; Chernin, 1974; Chernin and Cosgriff, 1975) which were assigned to the species *Parotosaurus megarhinus*. This species is very similar to *P. pronus* (Howie, 1970) but distinct from it and perhaps somewhat stratigraphically older. *P. pronus* was collected from Mkongoleko, Ruhuhu Valley, Tanzania in the Manda Formation of East Africa (Middle Triassic) by Parrington, 1933.

Welles and Estes (1969) state that comparison of certain indices obtained by measuring the brachyopids shows trends which are probably indicative of the relative evolutionary level of the various genera. Of the 10 values obtained for the indices of *B. concordi*, one is more advanced than that of the *Cynognathus* zone batrachosuchians as given by Welles and Estes (the author has included her own values obtained by measurement of *B. browni*; Welles and Estes 1969 indices appear in parenthesis):

$$\begin{aligned} \text{U:L} &= 23 - B. \text{watsoni} \\ &23 - B. \text{browni} \quad (24) \\ &25 - B. \text{concordi} \end{aligned}$$

Two values lie between the other species:

$$\begin{aligned} \text{Q:R} &= 31 - B. \text{watsoni} \\ &27 - B. \text{browni} \quad (26) \\ &30 - B. \text{concordi} \end{aligned}$$

$$\begin{aligned} \text{D:L} &= 58 - B. \text{watsoni} \\ &50 - B. \text{browni} \quad (55) \\ &57 - B. \text{concordi} \end{aligned}$$

Five values are more primitive than the other two species:

$$\begin{aligned} \text{B:L} &= 149 - B. \text{watsoni} \\ &120 - B. \text{browni} \quad (133) \\ &118 - B. \text{concordi} \end{aligned}$$

$$\begin{aligned} \text{A:L} &= 46 - B. \text{watsoni} \\ &45 - B. \text{browni} \quad (43) \\ &28 - B. \text{concordi} \end{aligned}$$

$$\begin{aligned} \text{O:L} &= 25 - B. \text{watsoni} \\ &24 - B. \text{browni} \quad (21) \\ &17 - B. \text{concordi} \end{aligned}$$

$$\begin{aligned} \text{Y:L} &= 53 - B. \text{watsoni} \\ &50 - B. \text{browni} \quad (49) \\ &46 - B. \text{concordi} \end{aligned}$$

$$\begin{aligned} \text{Z:Y} &= 56 - B. \text{watsoni} \\ &66 - B. \text{browni} \quad (55) \\ &52 - B. \text{concordi} \end{aligned}$$

Finally two values are so much more advanced as to be out of the range of the Brachyopidae as considered by Welles and Estes:

$$\begin{aligned} P:A &= 69 - B. watsoni \\ &55 - B. browni \quad (55) \\ &80 - B. concordi \\ T:A &= 49 - B. watsoni \\ &55 - B. browni \quad (53) \\ &107 - B. concordi \end{aligned}$$

The latter two values are the result of the interorbital breadth being so small in *B. concordi*. This could be a juvenile feature (no growth series of the Brachyopidae is available for study). However, taking the other indices as evolutionary guides, it seems that *B. concordi* is more or less on the same level as the *Cynognathus* zone forms. Welles and Estes (1969) place the batrachosuchians between Early and Mid-

dle Triassic. This agrees with the earlier conclusion that the N'tawere Formation is probably of Early Middle Triassic age (Chernin and Cosgriff, 1975) (see table 3).

Material and Method of Preparation

The material consists of a weathered and badly shattered skull, slightly dorsoventrally compressed with the anterolateral borders missing. Both lower jaw rami are present, the left one being firmly attached to the skull; the right one has been freed. The anterior parts are missing. A little of the postcranial skeleton is preserved, including parts of the pectoral girdle and forelimbs.

The skull is badly cracked, making the sutures difficult to discern. The material was prepared by Dr C. E. Gow who used a weak acetic acid solution.

TABLE 2
Comparison of the Indices of the Genus *Batrachosuchus*

* Indices	<i>B. watsoni</i> *	<i>B. browni</i> *	<i>B. browni</i> ***	<i>B. concordi</i>	From direct skull measurements of <i>B. concordi</i>
B:L	149	133	120	118	107
A:L	41,6	43	45	28	33
O:L	25	21	24	17	9
U:L	23	24	23	25	—
D:L	58	55	50	57	64
P:A	69	55	55	75	80**
T:A	49	53	50	107**	100**
Q:R	31	26	27	30	29
Y:L	53	49	50	46	52
Z:Y	56	55	66	52	50

* From Welles and Estes (1969).

** Out of range of Brachyopidae as stated by Welles and Estes (1969).

*** As measured in the new reconstruction of *B. browni*.

TABLE 3
Stratigraphy

	SOUTH AFRICA	ZAMBIA	EAST AFRICA
UPPER T R I A S S I C	Cave Sandstone Red Beds Molteno		
MIDDLE	Cynognathus zone Lystrosaurus zone	Red Marls? N'tawere Formation	Manda Formation
LOWER		?Escarpment Grits (<i>Lystrosaurus</i> absent)	?Kingori Sandstone (<i>Lystrosaurus</i> absent)

Modified after Drysdall and Kitching (1963)

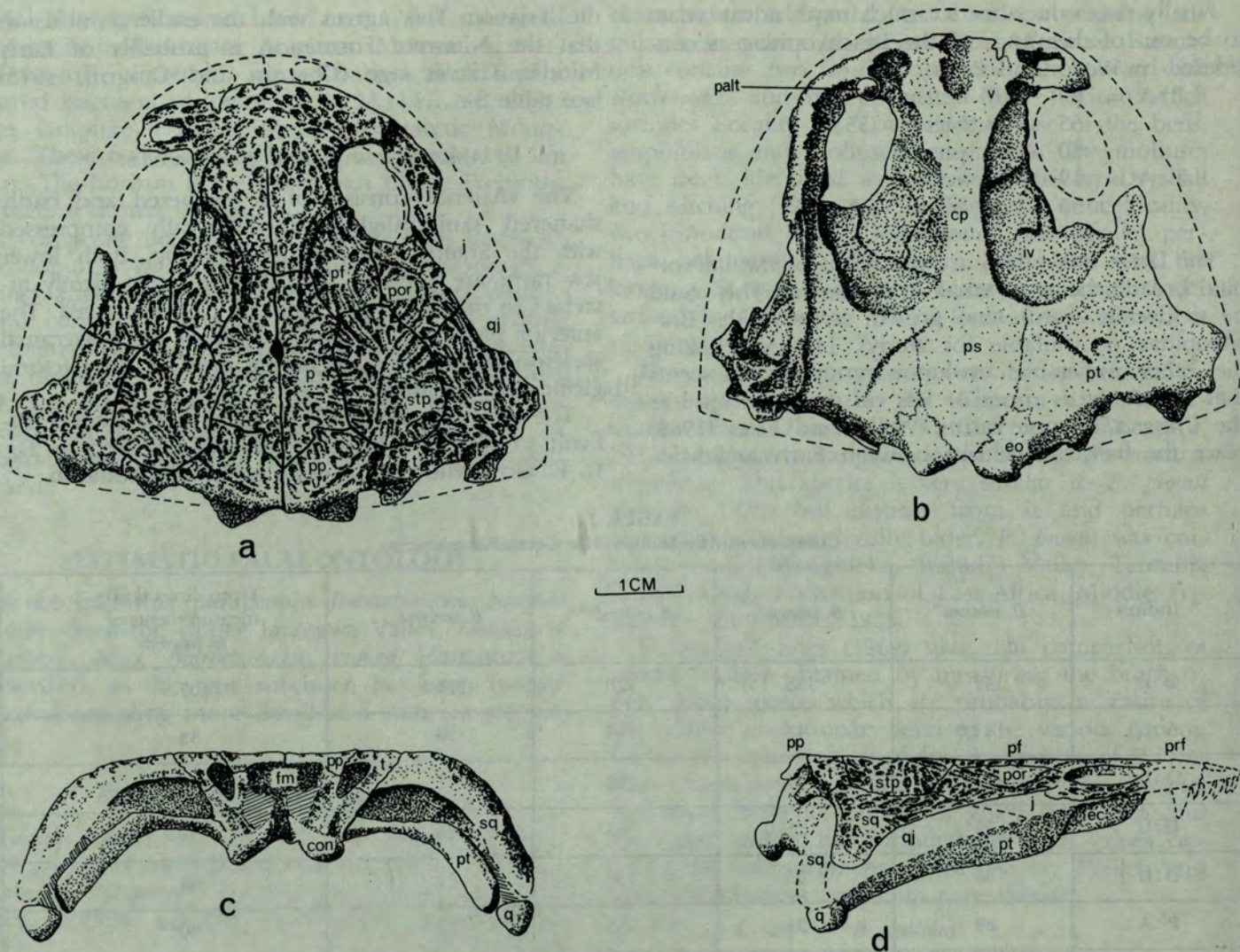


Figure 1. The skull of *Batrachosuchus concordi*

- (a) dorsal view
- (b) palatal view
- (c) occipital view
- (d) lateral view

Description

The bones of the skull (figs. 1 and 7)

Due to the loss of the whole skull border except some of the posterior border (which has been slightly distorted) reconstruction of the shape of the skull is subject to error. Also, the left lower jaw is attached firmly to the skull and a broken smooth-edged fragment of jugal lies loosely to the right of the right orbit.

Anterior to the midpoint of the frontal, the bone is severely damaged and no detail of sutures is evident. However, lateral line canals are easily recognized from anterior to the midpoint of the orbit.

Frontal. Only the posterior and part of the lateral sutures of the frontal are visible. The lateral suture is slightly slanted towards the midline and the somewhat indistinct posterior suture is almost transverse and straight.

Postfrontal. The postfrontal is a roughly pentagonal bone pointed posteriorly between the parietal and supratemporal and anterolaterally the edge of the postfrontal forms part of the posteromedial border of the orbit. The suture with the postorbital is straight and parallel to the midline and then slopes medially, where it sutures with the supratemporal; the anteromedial suture with the frontal slopes towards the midline.

Postorbital. The postorbital is also roughly pentagonal. The anterior edge of the bone forms the posterior border of the orbit. Anterolaterally the suture with the jugal (whose limits are unknown) is slightly slanted in a posterolateral direction while the posterolateral suture with the squamosal slants posteromedially. This results in the postorbital forming an obtuse point between the squamosal laterally and the supratemporal medially.

Parietal. The medial suture of the parietal is a straight line. Halfway along this suture a circular parietal foramen is visible. The anterior suture with the frontal is almost straight. This suture is badly damaged. Posterolaterally, the bone meets the supratemporal which forms a concave edge to the parietal. The posterior border of the parietal is laterally convex and medially slopes posteriorly so that the parietals form a sharp point in the midline.

Supratemporal. This is a roughly pentagonal bone. The posterolateral border with the squamosal and most of the medial border with the parietal are more or less parallel to each other and slightly slanted posterolaterally. The posteromedial corner abuts the postparietal in a posterolaterally-directed curved suture. The posterior border meets the tabular posteromedially. The posterolateral corner of the bone overlies part of the squamosal.

Squamosal. Anteriorly the squamosal forms an acute angle between the postorbital medially and the jugal and presumed position of the quadratojugal laterally. The latter bones are missing, except for a narrow piece of jugal which lies disarticulated on the lateral side of the right orbit. The posterolateral corner was probably gently rounded. Posteromedially, the bone has a slightly slanted border with the supratemporal and a concave suture with the tabular. The posterior dorsal edge turns at right angles from the skull table to form an occipital flange which probably overlay most of the quadrate bone. The occipital flange is badly damaged, but it leaves an impression in the underlying matrix. This shows that the bone has a curved border above a large otic recess and expands ventrally to cover most of the quadrate.

Postparietal. The anterior suture of the postparietal has a lateral concave and medial posteriorly slanted suture with the parietal. Anterolaterally it forms a posterolaterally directed curved border with the supratemporal. Posterolaterally the postparietal abuts the tabular in a short curved suture. The bone turns through 90° on to the occiput. The occipital flange of the postparietal when viewed dorsally is triangular in shape and when viewed laterally is a short round knob on the posterodorsal corner of the skull. In occipital view the bones form the roof over the large space above the foramen magnum that was probably occupied by the cartilaginous supraoccipital. The lateral edge of the postparietal forms the dorsomedial corner of the posttemporal foramen.

Tabular. Most of the right tabular is present. The anterior border is a transverse straight suture with the supratemporal. The tabular has both an occipital and dorsal component. The ventral limit is straight medially, then laterally forms a ventromedially directed rounded pillar which sutures with the dorsolateral extension of the exoccipital and forms the posterolateral corner of the posttemporal foramen.

Quadrate. The only part of the quadrate that is visible is the condyle. Seen posteriorly this is shaped

like a rounded triangle, the apex of which lies ventrally. A rounded articular boss lies most posteriorly with the bone expanded laterally and anteriorly from each side of this projection.

Exoccipital. In lateral view, the exoccipital condyle is clearly seen with a rounded articular area. The foramen magnum is not visible in this view, only solid exoccipital is seen rising dorsally and anterolaterally from the condyle.

Seen posteriorly, each exoccipital forms an oval condyle, which project approximately 3 mm from the posterior end of the occipital flange of the postparietal. From the condyle a flange of exoccipital which borders the foramen magnum extends dorsally but is broken off a few millimetres above the condyle. Dorsolaterally to the condyle a broad flange rises to meet the occipital flange of the postparietal.

On the occiput the pterygoid meets the exoccipital below the otic recess. The suture is not visible. The pterygoid continues laterally in a smooth curve and then turns through 90° to form a vertical flange which continues ventrally internal to the squamosal. The bones are distorted in this region. The basioccipital is evidently not ossified.

The Sculpture

The superficial sculpture of the skull roof is of typical brachyopid pattern, similar to that found in capitosaurids, and consists of pits in the centre of ossification of each bone, from which ridges and grooves radiate outwards, but show no areas of disproportionate growth, unlike in capitosaurids.

The Lateral Line System

The characteristic pattern of the anterior lateral line system is visible on the skull roof as a series of irregular pits which have slightly broader-based bordering ridges than those of normal sculpture. The distribution of the canals differs from that of the other two species but is closer to *B. watsoni* as illustrated by Welles and Estes (1969, p. 25).

Supraorbital canal. From the antero-lateral corners of the parietals the canals pass along the posterolateral sutures of the frontals and enter the prefrontals. Although the limits of the prefrontals and the nasals are damaged and not recognizable, the lateral line canals are visible. The supraorbital canals then turn medially and are lost to view.

Temporal canal. These canals run from the posterior border of the skull table where they form a curve, from the postero-medial borders of the postparietals to the anterolateral limits of those bones. They then traverse the supratemporals from the posteromedial to the anterolateral corners displaying a sharp curve midway along their length. The temporal canals then enter the postfrontals medially along their posterolateral borders and continue straight on to the posterior borders of the orbits. From here they do not follow the pattern of the *Batrachosuchus* species as illustrated by Watson (1956),

where the temporal canals continue laterally around the orbit as well. This is probably due to the fact that in *B. concordi*, where the relevant bones are present, the surface detail is damaged and obscure. In *B. concordi* the temporal canals continue medially along the medial borders of the orbits to join the supra-orbital canals halfway along the length of the orbits.

No other canals are discernible, probably due to the fragmentation of the relevant bones and the sculpture pattern itself which makes it difficult to follow irregularities.

Palate

Very little of morphological significance is preserved in the palate. Anteriorly, the choanae are visible as being transversely oval and relatively large. The stump of a large tusk is present lateral to each choana. The parasphenoid forms a flat plate which blends into the exoccipitals and pterygoids without a visible suture. Anteriorly, it sends out a cultriform process which is broad and flat.

The pterygoids extend outward from the parasphenoid until at their anterolateral extremity they end in a curved border, clearly part of the antero-medial limit of the subtemporal vacuity. Laterally, the pterygoids curve through 90° to form vertical flanges. When viewed laterally, the pterygoid sweeps anterodorsally from the quadrate condyle posteriorly to a position directly ventral to the posterior border of the orbit. The ectopterygoid, which sutures at this point with the pterygoid, continues anteriorly to a point beneath the anterior limit of the orbit. The pterygoid and ectopterygoid form a characteristic shape very similar to that illustrated by Watson (1956) for *Batrachosuchus watsoni* Haughton.

The exoccipitals form rounded condyles which project outwards from the midline. Each condyle measures 5 mm horizontally and 4 mm vertically. The less distorted left condyle projects 3 mm behind the dorsal edge of the skull table. The two condyles are 1.2 mm apart and 12 mm across. A flat parasphenoid separates the two condyles.

Lower Jaw (figs. 2 a-c)

The jaw is bowed upward to match the concavity of the palate. The area between the symphyseal region (the anterior part of which is missing in this specimen) and the adductor fossa is high and narrow and is inclined ventromedially. This area does not have a keeled ventral surface as in *Blinasaurus henwoodi* (Cosgriff 1969). In dorsal view the jaw widens through the region of the adductor fossa and the articular facet. A flat ventral surface underlies the anterior half of the adductor fossa. The ventral surface from the centre of the adductor fossa to the tip of the retroarticular process is keeled. The large adductor fossa is spear-shaped in dorsal view with a flat posterior margin and an acute anterior margin. The labial wall is very high and has a rounded upper margin. The lingual wall is low and its upper margin is concave downward. Lingually, the articular facet

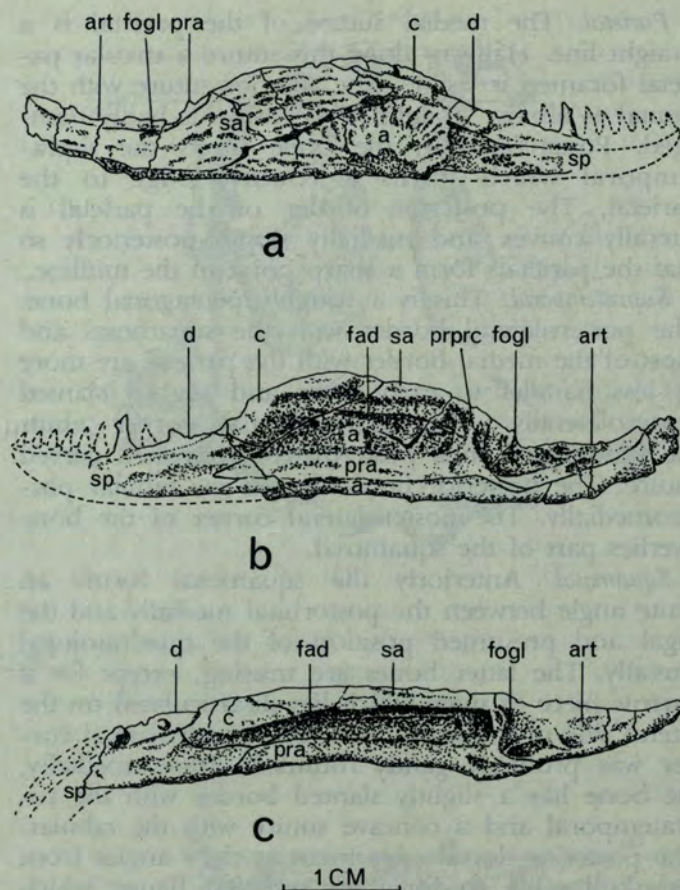


Figure 2. The right lower jaw of *Batrachosuchus concordi*

- (a) labial view
- (b) lingual view
- (c) dorsal view

of the glenoid forms a ledge which overhangs the surface of the jaw below it. The narrow retroarticular process is triangular in section. The posterior meckelian foramen is not preserved.

The left jaw ramus is firmly attached to the skull with the retroarticular process extending approximately 1 cm behind the skull table. The right jaw ramus is free and seems to be almost undistorted, although the anterior part is missing.

Dentary

Anteriorly there are two large teeth. Posteriorly and dorsally the dentary is capped by the coronoid. The dentary extends on to the labial wall of the adductor fossa as a slender and pointed process.

Splenial

Only the posterior part of the second splenial is preserved. It lies ventral to the dentary and forms the antero-ventral border of the jaw ramus.

Angular

The angular covers a large area on the labial surface, where it forms a suture with the splenial anteriorly, the dentary dorsally and the surangular posteriorly.

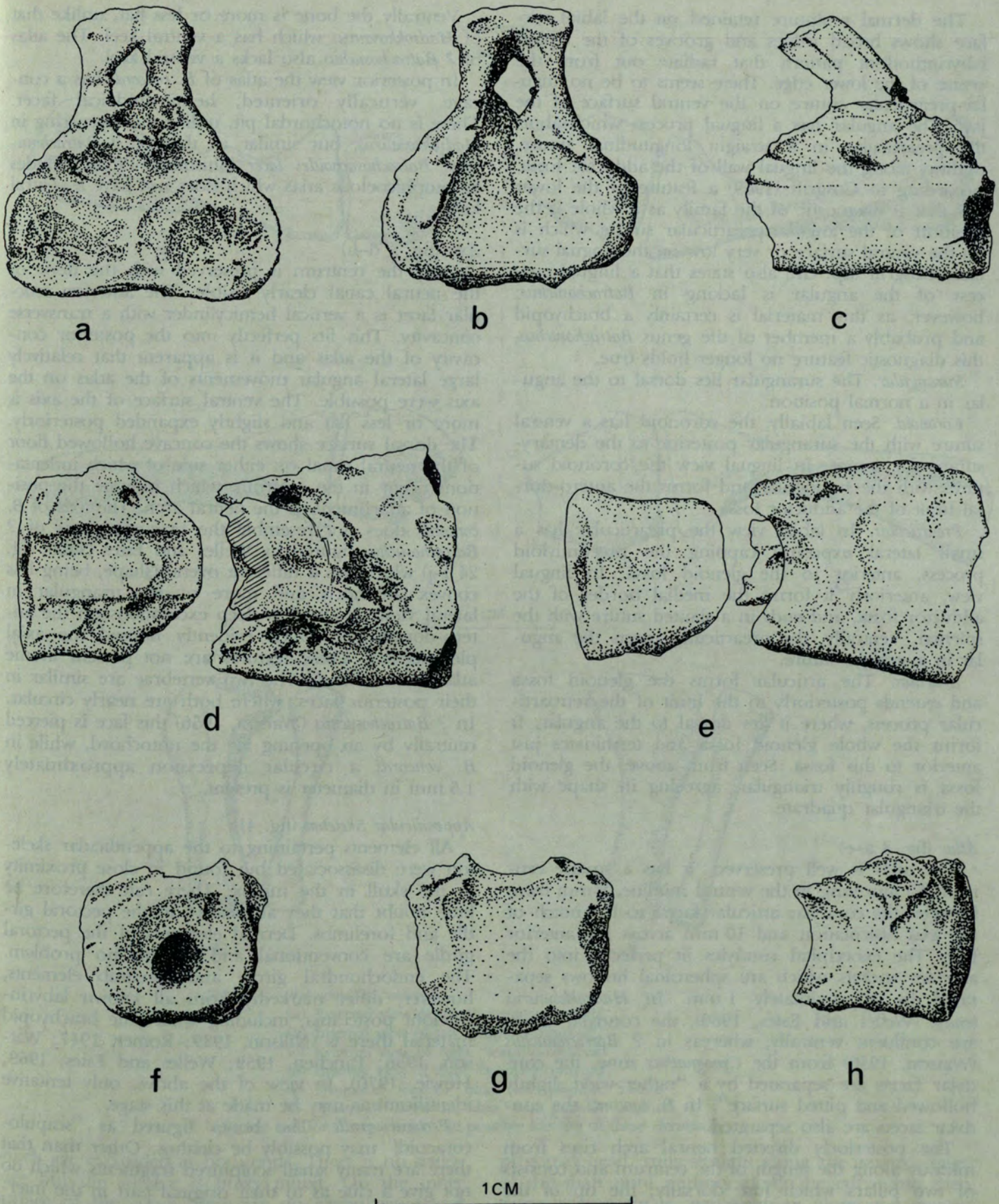


Figure 3. *Batrachosuchus concordi*

- (a) Anterior view of atlas
- (b) Posterior view of atlas
- (c) Lateral view of atlas
- (d) Dorsal view of atlas and axis

- (e) Ventral view of atlas and axis
- (f) Posterior view of axis
- (g) Anterior view of axis
- (h) Lateral view of axis

The dermal sculpture retained on the labial surface shows broad ridges and grooves of the typical labyrinthodont pattern that radiate out from the centre of the lower edge. There seems to be no angular-prearticular suture on the ventral surface of the jaw. The angular has a lingual process which abuts the prearticular in a straight longitudinal suture, midway along the lingual wall of the adductor fossa. According to Cosgriff (1969) a feature of the lower jaw that is diagnostic of the family as a whole is the position of the angular-prearticular suture which is on the ventral surface or very low on the lingual surface. Cosgriff (op. cit.) also states that a lingual process of the angular is lacking in *Batrachosuchus*; however, as this material is certainly a brachyopid and probably a member of the genus *Batrachosuchus*, this diagnostic feature no longer holds true.

Surangular. The surangular lies dorsal to the angular in a normal position.

Coronoid. Seen labially, the coronoid has a ventral suture with the surangular posterior to the dentary-surangular suture. In lingual view the coronoid sutures with the surangular and forms the antero-dorsal limit of the adductor fossa.

Preatricular. In labial view the prearticular has a small lateral exposure capping the precondyloid process, anterior to the glenoid fossa. In lingual view, anteriorly it forms the medial border of the adductor fossa, and ends in a slanted suture with the splenial. Ventrally, the prearticular meets the angular in a straight suture.

Articular. The articular forms the glenoid fossa and extends posteriorly to the limit of the retroarticular process, where it lies dorsal to the angular. It forms the whole glenoid fossa and terminates just anterior to this fossa. Seen from above, the glenoid fossa is roughly triangular, agreeing in shape with the triangular quadrate.

Atlas (fig. 3 a-e)

The atlas is well preserved. It has a square centrum 10 mm long in the ventral midline, 8 mm from between the condylar articular facets to the notch of the axis articulation and 10 mm across the anterior face. The exoccipital condyles fit perfectly into the anterior sockets which are spheroidal hollows separated by approximately 1 mm. In *Hadrokkosaurus bradyi* (Welles and Estes, 1969), the condylar facets are confluent ventrally, whereas in ? *Batrachosuchus* (Watson, 1956) from the *Cynognathus* zone, the condylar facets are separated by a "rather wide slightly hollowed and pitted surface". In *B. concordi* the condylar facets are also separated.

The posteriorly directed neural arch rises from midway along the length of the centrum and consists of two pillars which fuse dorsally; the tip of the neural arch is broken off. On either side of the neural arch on the lateral surface of the centrum a deep indentation is present, probably for muscle attachment. The floor of the neural canal is wide and slightly hollowed along its length.

Ventrally the bone is more or less flat, unlike that of *Hadrokkosaurus* which has a ventral keel. The atlas of ? *Batrachosuchus* also lacks a ventral keel.

In posterior view the atlas of *B. concordi* has a concave, vertically oriented, hemicylindrical facet. There is no notochordal pit, unlike that occurring in *Hadrokkosaurus*, but similar to that of ? *Batrachosuchus*: *Batrachosuchoides lacer* (Shishkin, 1966) includes an amphicoelous atlas which does not have a ventral keel.

Axis (fig. 3 d-h)

Only the centrum is preserved with the floor of the neural canal clearly visible. The anterior articular facet is a vertical hemicylinder with a transverse concavity. This fits perfectly into the posterior concavity of the atlas and it is apparent that relatively large lateral angular movements of the atlas on the axis were possible. The ventral surface of the axis is more or less flat and slightly expanded posteriorly. The dorsal surface shows the concave hollowed floor of the neural canal on either side of which indentations occur in the centrum, which indicate the position of attachment of the neural arch. The axis of *B. concordi* does not resemble the presumed axis of ? *Batrachosuchus* figured by Welles and Estes (1969, fig. 24 f-j) which has a different overall shape, being less convex anteriorly and more or less triangular in lateral view. It also has deep excavations on the antero-dorsal face which evidently housed the axial pleurocentra. These features are not present in the atlas of *B. concordi*. The two vertebrae are similar in their posterior faces, where both are nearly circular. In ? *Batrachosuchus* (Watson, 1956) this face is pierced centrally by an opening for the notochord, while in *B. concordi* a circular depression approximately 1.5 mm in diameter is present.

Appendicular Skeleton (fig. 4)

All elements pertaining to the appendicular skeleton were disassociated but found in close proximity to the skull in the matrix. There can therefore be little doubt that they all pertain to the pectoral girdle and forelimbs. Dermal elements of the pectoral girdle are conventional and present no problem. The endochondral girdle and forelimb elements, however, differ markedly from all known labyrinthodont postcrania, including what little brachyopid material there is (Nillson, 1939; Romer, 1947; Watson, 1956; Panchen, 1959; Welles and Estes, 1969; Howie, 1970). In view of the above, only tentative identifications may be made at this stage.

Pectoral girdle. The bones figured as "scapulo-coracoid" may possibly be cleithra. Other than that there are many small sculptured fragments which do not give a clue as to their original part in the interclavicle/clavicle configuration, which are thin and smooth medially with fine sculpturing externally. Not much more can be said about these fragments.

The scapulo-coracoid/cleithra elements may be described as follows: they are gently curved elements

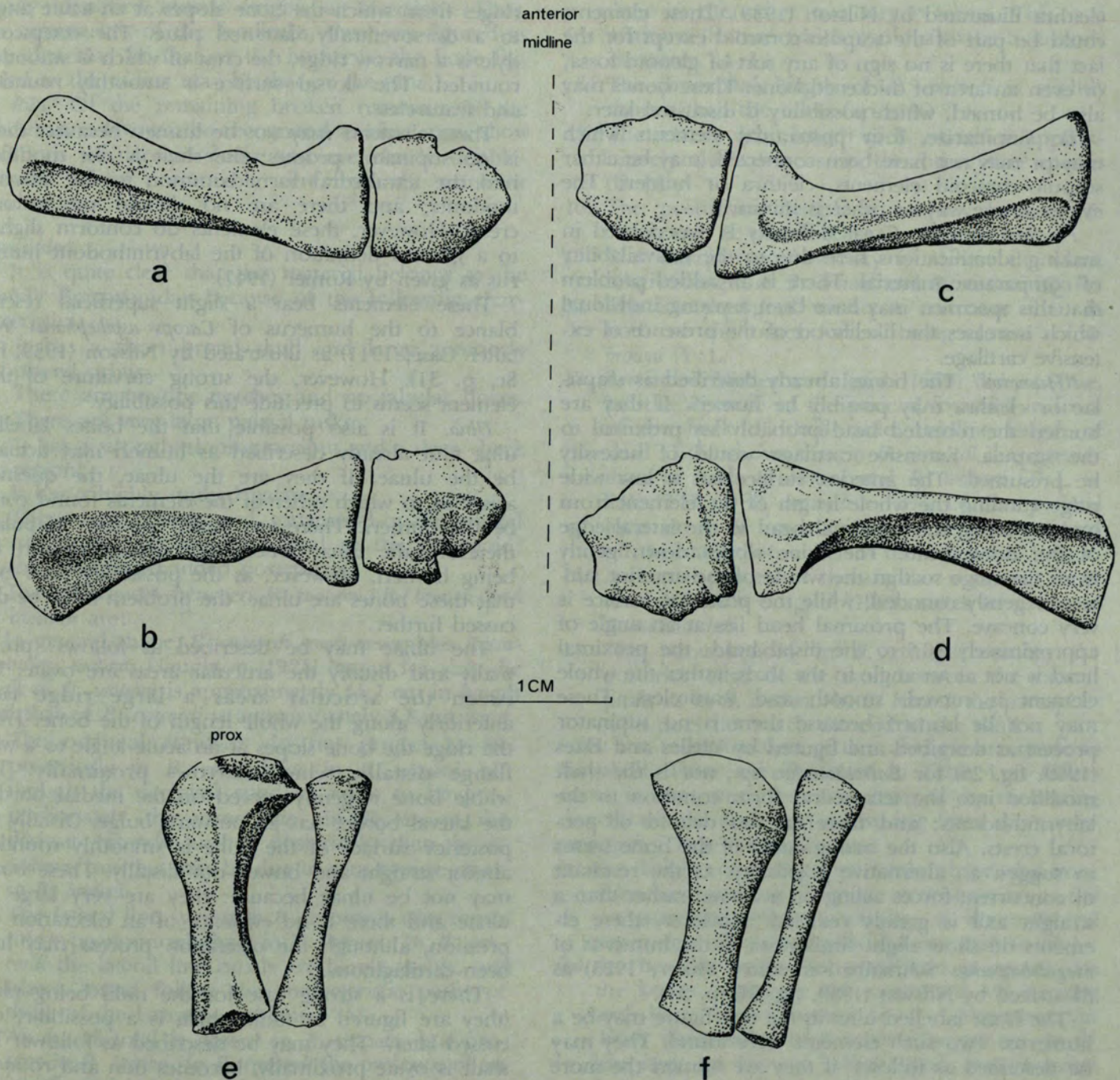


Figure 4. *Batrachosuchus concordi*

- (a) External view of left "scapulo-coracoid"
- (b) Internal view of left "scapulo-coracoid";
- (c) External view of right "scapulo-coracoid"
- (d) Internal view of right "scapulo-coracoid"
- (e) "Anterior" view of "ulna" with possible "radius"
- (f) "Posterior" view of "ulna" with possible "radius"

N.B. See text for discussion on the possible identity of these elements.

which are expanded at both ends. There is no sculpture but the surface is finely pitted. On the inner surface of the curve there are no irregularities and the surface is smooth. On the outer surface of the curve, a ridge runs from end to end. The end nearest the midline as illustrated ends in a flat border, while the distal end is gently curved. The ridge on the outer surface starts at the anterior corner of the flat

proximal head, runs straight along the anterior edge of the shaft until midway along the curve and then turns posteriorly to end midway along the curved distal end. Panchen (1959) described the cleithrum in typical labyrinthodonts as being a bony rod clasping the edge of the scapula in a deep groove. No such groove is found in the element described. Also these elements bear no similarity to any of the

cleithra illustrated by Nilsson (1939). These elements could be part of the scapulo-coracoid except for the fact that there is no sign of any sort of glenoid fossa, or even an area of thickened bone. These bones may also be humeri, which possibility is discussed later.

To summarize, four postcranial elements which may or may not have been connected, may be either scapulo-coracoid elements, cleithra or humeri. The evidence one way or other is minimal.

Forelimb elements. Great difficulty is experienced in making identifications here due to the unavailability of comparative material. There is an added problem that this specimen may have been a young individual which increases the likelihood of the presence of extensive cartilage.

"Humerus". The bones already described as scapulae or cleithra may possibly be humeri. If they are humeri the rounded head probably lay proximal to the scapula. Extensive cartilage would of necessity be presumed. The anterior surface has a low wide ridge running the whole length of the element from midway along the proximal head to the lateral edge of the distal head. The bone slopes down gently from the ridge so that the whole of the anterior surface is gently rounded, while the posterior surface is very concave. The proximal head lies at an angle of approximately 30° to the distal head; the proximal head is not at an angle to the shaft, rather the whole element is curved, smooth and featureless. These may not be humeri because there is no supinator process as described and figured by Welles and Estes (1969, fig. 25) for *Batrachosuchus* sp., nor is the shaft modified into the tetrahedral form common to the labyrinthodonts; and there are no deltoid or pectoral crests. Also the strong curve of the bone seems to suggest an alternative possibility, as the resultant of concurrent forces acting on a curved rather than a straight axis is greatly reduced. However, these elements do show slight similarities to the humerus of *Megalobatrachus* Schmalhausen (after Miner, 1925) as illustrated by Nilsson (1939, fig. 8E, p. 31).

The bone labelled ulna in the text figure may be a humerus. Two such elements were found. They may be described as follows: if they are humeri the more expanded head probably lay proximal to the scapula. Both proximal and distal ends were probably covered extensively by cartilage in life. The larger proximal surface of each element is gently rounded and relatively featureless except for an ovate articular area at the end of a wide ridge on the posterior edge of the ventral surface.

The slightly hollowed ovate articular area is turned obliquely at a 45° angle from the shaft. In primitive tetrapods this is typical in contrast to a strap-shaped proximal articulation of the humerus (Romer, 1947). The proximal entepicondylar region tapers from the breadth of the head to the narrow posteriorly curved ectepicondylar border.

On the ventral surface there is one large ridge which extends the entire length of the element. At the distal end, this ridge divides into two confluent

ridges from which the bone slopes at an acute angle to a dorsoventrally flattened plate. The ectepicondyle is a narrow ridge, the crest of which is smoothly rounded. The dorsal surface is smoothly rounded and featureless.

These elements may not be humeri because: there is no supinator process; the shaft is not modified into the tetrahedral form common to the labyrinthodonts; and there are no deltoid or pectoral crests. However, these elements do conform slightly to a general definition of the labyrinthodont humerus as given by Romer (1947).

These elements bear a slight superficial resemblance to the humerus of *Cacops aspihephorus* Will (after Case, 1911) as illustrated by Nilsson (1939, fig. 8c, p. 31). However, the strong curvature of that element seems to preclude this possibility.

Ulna. It is also possible that the bones labelled ulna and already described as humeri may actually be the ulnae. If they are the ulnae, the question arises as to which other of the elements found could be the humeri. There are none, bar the "scapula"; therefore the ulna bones have strong support for being humeri. However, as the possibility does exist that these bones are ulnae, the problem must be discussed further.

The ulnae may be described as follows: proximally and distally the articular areas are ovate. Between the articular areas a large ridge runs anteriorly along the whole length of the bone. From the ridge the bone slopes at an acute angle to a wide flange distally, which narrows proximally. The whole bone is gently curved on the medial border; the lateral border has an outward bulge. Distally the posterior surface of the bone is smoothly rounded, almost straight and bowed-out distally. These bones may not be ulnae because: they are very large for ulnae and there is no evidence of an olecranon depression, although the olecranon process may have been cartilaginous.

There is a strong case for the radii being ulnae (they are figured as radii which is a possibility discussed later). They may be described as follows: The shaft is ovate proximally, becomes thin and rounded in the middle and becomes expanded distally in an anteroposterior plane. The medial border is gently curved and the lateral border is almost straight and slightly bowed-out proximally so that the proximal and distal ends of the bone are expanded towards the radius. The characteristic olecranon depression as well as the olecranon process are not preserved. If these bones are the ulnae, the radii are probably missing; some cylindrical smooth shattered fragments possibly belonging to the radii exist.

An alternative description of the "radii" bones as radii is as follows: The bones are columnar with proximal and distal ends expanded. Seen anteriorly, the gently incurved dorsal surface is rounded and the ventral surface is flattened. Both of the terminal surfaces are shallowly cupped for the rather extensive cartilages of the articular surfaces. There are no

easily identified muscle origins or insertions. Thus, to summarize: of the forelimbs, the bone figured as an ulna may be that or the humerus; the bone figured as the radius may be that or the ulna.

Ribs. Of the remaining broken remnants of the skeleton, a few can be recognized as ribs; most show portions of narrow shafts and are clearly double-headed. These presumably were from the trunk or neck region.

Discussion

It is quite clear that this material belongs to the family Brachyopidae because of the following characteristics:

1. It has a short broad skull and large anteriorly placed orbits.
2. There are no otic notches and no tabular horns.
3. There are very large palatal tusks.
4. It has a strongly sloping occiput and a deep cheek region.
5. It has a highly vaulted palate.
6. There is a pronounced squamosal-quadratojugal trough on the occiput lateral to the pterygoid; the latter is expanded posteriorly.

The differences between *B. watsoni*, *B. browni* and *B. concordi* are:

In general shape, *B. concordi* most resembles *Batrachosuchus watsoni* Houghton (1925) except for size; the skull of *B. watsoni* is approximately 15,7 cm in length and that of *B. concordi* is approximately 3,8 cm long.

1. The occipital condyles do not project as far posteriorly in *B. concordi* as in *B. watsoni*, although the occipital condyles seem to be proportionately the same size. In *B. browni* the occiput extends further posteriorly than in *B. watsoni*, but this may be due to a transverse crack in *B. browni*.
2. The lateral line system in *B. watsoni* is very much more pronounced than in *B. browni*. In *B. concordi* the lateral line canals are barely visible, but where found follow the characteristic paths of those of the batrachosuchians.
3. An interfrontal is absent in *B. watsoni*, but present in *B. browni*. In *B. concordi* the presence of an interfrontal is indeterminate.
4. The shapes of the individual bones of the skull roof are essentially the same in *B. concordi* as in the other two batrachosuchian species where the sutures can be positively identified.
5. The shape of the posterior skull table is slightly convex, which agrees with *B. watsoni*, but not *B. browni*. (Further preparation has revealed a parabolic crack in *B. browni* which passes through the pineal foramen; the crack is filled with matrix, which distorts the posterior curvature of the skull.)
6. The skull of *B. concordi* is much narrower than in both *B. browni* and *B. watsoni*, but it is closer in breadth to *B. browni* (B:L). This character of *B. concordi* may be a juvenile feature.
7. The interorbital breadth is very much narrower

than in the other two larger forms. This is a primitive feature which could also be a juvenile character. (A:L).

8. The preorbital length of *B. concordi* is slightly shorter than the other forms (O:L).
9. The relative orbit length of *B. concordi* is approximately the same as in the other two species (U:L).
10. The postorbital length is midway between *B. browni* and *B. watsoni* (D:L).
11. The interpterygoid vacuity is almost the same relative length as *B. browni* and *B. watsoni* (Q:R).
12. The interpterygoid vacuity is narrower than in both of the other forms, being closest to *B. browni* (Y:L).
13. An index Welles and Estes (1969) did not use, i.e. the distance of the parietal foramen in front of the back of skull table: midline length of skull (T:L) shows that in *B. concordi* it is greater than in both *B. browni* and *B. watsoni* (T:L = 23); (T:L in *B. concordi* = 37), i.e. the parietal foramen in *B. concordi* is more anteriorly placed on the skull than either of the other two forms.
14. A lingual process of the angular is present in *B. concordi* which Cosgriff (1969) states is absent in *Batrachosuchus*.
15. The parasphenoid in *B. concordi* reaches the posterior edge of the skull between the exoccipitals as in *B. watsoni*. In *B. browni*, the parasphenoid does not reach the end of the skull.

In the reconstruction certain changes are made to the skull. These are illustrated in Table 4 as differences in the measurements obtained by measuring directly off the skull and measuring from the reconstruction. These differences are:

- (a) the height of the postparietals above the condyles has been raised in the reconstruction as the postparietals definitely display a dorso-ventral depression which probably did not exist in life;
- (b) the breadth across the quadrates is greater, as the bones lateral to the squamosal are missing and have been inserted in the reconstruction from illustrations of *Batrachosuchus watsoni*, as illustrated by Watson (1959) and *Batrachosuchus browni* as redescribed here;
- (c) the length of the skull is consistent with that of the reconstruction as some of the preorbital bones are present in the skull although badly damaged and the postorbital region has been reduced in the reconstruction. These two reasons, i.e. the presence of preorbital bones in the skull and the shortening of the postorbital region (which is discussed later), keep the skull length constant;
- (d) the interorbital distance is shorter in the reconstruction as the borders of the left orbit are extremely distorted where not actually missing;
- (e) the distance from the tip of the snout to the level of the anterior edge of the orbit is greater in the reconstruction as the maxilla and premaxilla have been inserted in the reconstruction as being

- similar to those of *B. browni* and *B. watsoni*;
- (f) midline postorbital length has been shortened in the reconstruction because in this region the bones are not closely sutured, but have considerable gaps between them. These gaps are removed in the reconstruction;
 - (g) the distance from the mid-line of the orbit to the lateral edge of the same side is increased in the reconstruction because only the right side of the skull gives any indication of this area and even here only a small disarticulated part of the jugal lies next to the orbit though somewhat displaced. In the reconstruction, a larger jugal is added lateral to the orbit to cover the underlying pterygoid completely (in dorsal aspect) which seems to be more or less in its correct position;
 - (h) the breadth of the snout one-fifth of the skull length from the tip of the snout is narrower in the reconstruction than would appear to be the case from the photograph, as the left lower jaw is firmly attached dorsally on the lateral part of the skull;
 - (i) the distance from the level of the posterior limit of the orbit to the parietal foramen is less in the reconstruction because, as mentioned above, the gaps between the bones in the skull are not present in the reconstruction.

Welles and Cosgriff (1965) adopted a method of analysis for capitosaurians whereby a series of arbitrary measurements is made on the skulls and indices are then derived from these measurements. Comparison of these indices lead to significant phylogenetic and taxonomic conclusions. The validity of the conclusions is dependent upon the accuracy of the measurements, the number of characters that are susceptible to numerical analysis and the number of specimens available (fig. 6).

Welles and Estes (1969) developed this method by assuming that the sum of the differences between indices for any two species is a useful indication of the relationship between these species, which can then be compared with the sum of the differences between indices for any other two species. They acknowledge the various shortcomings of this method of analysis of which the most serious is that even though large numbers of species are included, there is a strong likelihood that in any group with a long geologic time span, those forms at a similar stage of evolution will be closer together numerically than later forms in a phylogenetic sequence. If there is a large number of specimens from each species, this objection can be reduced by measuring differences from trend lines if such exist. This was useful in the analysis of capitosaurians (Welles and Cosgriff, 1965) but it is of less value in dealing with the small number of known brachyopids. However, nine of the indices used by Welles and Estes (1969) do show trends and these are probably indicative of the relative evolutionary level of the various genera.

Other objections are that non-numerical characters are excluded from this analysis and must be

considered separately, but adequate knowledge of ontogenetic changes within a species is not available nor is it known just how much or how little these changes affect the validity of the indices.

Nevertheless, as Welles and Estes (1969) point out, this index method of analysis does have the advantage of presenting in tabular form a series of summaries that are not otherwise readily comprehensible. This methodology can only be improved with accurate data, and it is important that accompanying every description of a specimen accurate indices are included. By the collection of such data the probability of the validity of the results is increased so that a revision every few years, including new data, should add to the clarity of our understanding of the group.

The reconstruction of the specimen is an essential ingredient in this flow of data. Where much of the skull is shattered, missing or severely distorted, measurements taken directly off the skull are misleading and bear no relationship to indices taken from undistorted skulls, thus the onus falls on the palaeontologist to reconstruct with the utmost accuracy (i.e. as far as the specimen allows) a skull which takes into account the limitations of the material.

In conclusion, index methodology is important with regard to many aspects of palaeontology, and it should be regarded as standard practice to include in descriptions accurate data which can be used in the future to correlate the mass of information which has been and is being collected.

Indices for *B. concordi*

B:L	118	D:L	57	Q:R	30
A:L	28	P:A	75	Y:L	46
O:L	17	T:A	107	Z:Y	52
U:L	25	H:B	19		

Sums of differences

	Using 6 indices	Using 11 indices
<i>Batrachosuchus concordi</i>	82	224
<i>Hadrokkosaurus bradyi</i>		
<i>B. concordi</i>	35	110
<i>B. watsoni</i>		
<i>B. concordi</i>	37	121
<i>B. browni</i>		
<i>B. concordi</i>	59	168
<i>B. laticeps</i>		
<i>B. concordi</i>	44	111
<i>Blinasaurus henwoodi</i>		
<i>B. concordi</i>	43	122
<i>Bothriceps australis</i>		
<i>B. concordi</i>	52	142
<i>Brachyops allos</i>		

TABLE 4

Batrachosuchus concordi — showing differences in measurements between reconstruction and fossil

	Directly from skull (mean of 5 measurements) in cm	From reconstruction in cm
Height of postparietals above parasphenoid, H	0,9	1,0
Breadth of skull across quadrates, B	5,2	5,7
Length of skull, L	4,8	4,8
Interorbital distance taken at mid-length of orbit, A	1,6	1,3
Distance from tip of snout to level of anterior edge of orbit, O	0,5	0,8
Distance from level of posterior limit of orbit to level of centre limit of skull, D	3,1	2,8
Distance from mid-length of orbit to lateral edge of same side, I	0,2	0,6
Breadth of snout 1/5th of skull length from tip, S	3,7	3,5
Distance from level of posterior limit of orbit to parietal foramen taken at centre of skull, P	1,3	1,0
Distance of parietal foramen in front of end skull table, T	1,6	1,8

Using 11 indices *B. concordi* seems to be closely related to *Blinasaurus henwoodi*. The T:A index which is not included for the computation of the 6-index figure is the reason for this low figure. *Blinasaurus henwoodi* and *Batrachosuchus concordi* both have orbits relatively very close together, compared with other brachyopids, but as far as *B. concordi* is concerned, this character seems to be a juvenile feature. Thus it may be possible to add another shortcoming of the methodology, i.e. a young individual may show similar proportions to an unrelated adult form at a different evolutionary level. However, other than the above disparity, assuming that the smaller totals of index differences are real measures of relationship, the conclusion is reached that the new material is indeed a species of the genus *Batrachosuchus*.

Batrachosuchus concordi could possibly be a small member of either *B. browni* or *B. watsoni*, but for two characteristics which may not be completely explained by ontogenetic growth, i.e. the close proximity of the orbits and the very small projection of the occiput. There is a possibility that the orbits move laterally during growth and it is known that the occipital region acquires a greater posterior pro-

jection during development in anurans. The sculpture in the interorbital bones is pitted, rather than having ridges and grooves. According to Bystrow (1935) and Welles and Cosgriff (1965) longitudinal grooves are probably regions of intense growth and where growth is slow, transverse ridges are able to develop so that such bones consist mostly of pits. Thus it seems unlikely that the interorbital region was in a state of intense growth that would be needed to separate the orbits to a position comparable to either *B. browni* or *B. watsoni*. If it is a juvenile form of *Batrachosuchus* it would more likely be a small *B. watsoni* as the parasphenoid of *B. concordi*, as in *B. watsoni*, extends to the edge of the skull, whereas in *B. browni* the parasphenoid does not reach the edge.

TABLE 5
Measurements of the skulls of the Genus *Batrachosuchus*

	<i>B. browni</i> cm	<i>B. watsoni</i> * cm	<i>B. concordi</i> cm
Interorbital breadth, A	9,0	5,0	1,3
Breadth of skull roof across quadratojugals, B	24,0	16,5	5,7
Midline postorbital length, D	10,0	7,0	2,8
Midline distance between nostrils and orbits, F	3,0	1,0	0,4
Height of parasphenoid, H	4,5	3,5	1,0
Internarial breadth, J		1,1	
Length of skull roof, L	20,0	11,5	4,8
Midline preorbital length, O	4,8	2,4	0,8
Distance behind orbits of parietal foramen, P	5,0	3,3	1,0
Length of body of pterygoid, Q	4,9	3,4	1,5
Breadth across pterygoids at concavity, R	18,0	11,2	5,0
Distance of parietal foramen in front of end skull table, T		3,0	1,8
Breadth of snout 1/5th of skull length from tip, S	16,0	9,2	4,0
Midline orbital length, U		2,5	1,3
Length of interpterygoid, Y	10,0	5,7	2,4
Breadth of interpterygoid, Z	6,6	3,3	1,4
Distance between choanae, G	4,9	3,0	1,3
Distance exoccipital projects behind skull deck	5,0	2,0	0,3

* From Welles and Estes (1969, p. 24)

Batrachosuchus browni Broom 1903

Type: Skull only. S.A.M. Cat. No. 5868

Locality: Aliwal North, Cape Province

Horizon: Cynognathus zone

Diagnosis

Large brachyopid with broadly parabolic skull outline; orbits far forward, postorbital part of skull long; extremely narrow internarial area; interfrontal present; lateral line grooves well defined, but relatively much narrower and possibly more U-shaped in section than in *B. watsoni*; well developed vomerine foramen in centre of vomer; parasphenoid does not reach posterior limit of skull; three lateral line canals present on post-frontal; evidence of paired tusks on vomer, palatine ectopterygoid.

The differences between *B. watsoni* and *B. browni* according to Welles and Estes (1969) are at least of specific degree and might even justify erection of a new genus. However, they consider *B. watsoni* a more advanced species with a much broader skull than *B. browni*.

Material and Method of Preparation

The material consists of a well-preserved skull whose antero-lateral borders are missing. The skull does not seem to be very distorted. Additional preparation was undertaken on the skull by Dr. J. W. Kitching by means of a vibro-tool and needles.

Description (figs. 5 and 8)

The bones of the skull

The antero-lateral limits of the skull are missing; no premaxillary or maxillary sutures are discernible and only the posterior half of the right narial border is preserved as an impression. Unless otherwise stated the left side of the skull is described, because the bones on the right hand side have suffered some displacement and slight damage.

Nasals. The posterior part of the right nasal is preserved. The mid-line suture is sinuous; posteriorly the nasal sutures with the interfrontal in an antero-laterally slanted suture. Laterally part of the suture with the prefrontal is visible as a posteromedially

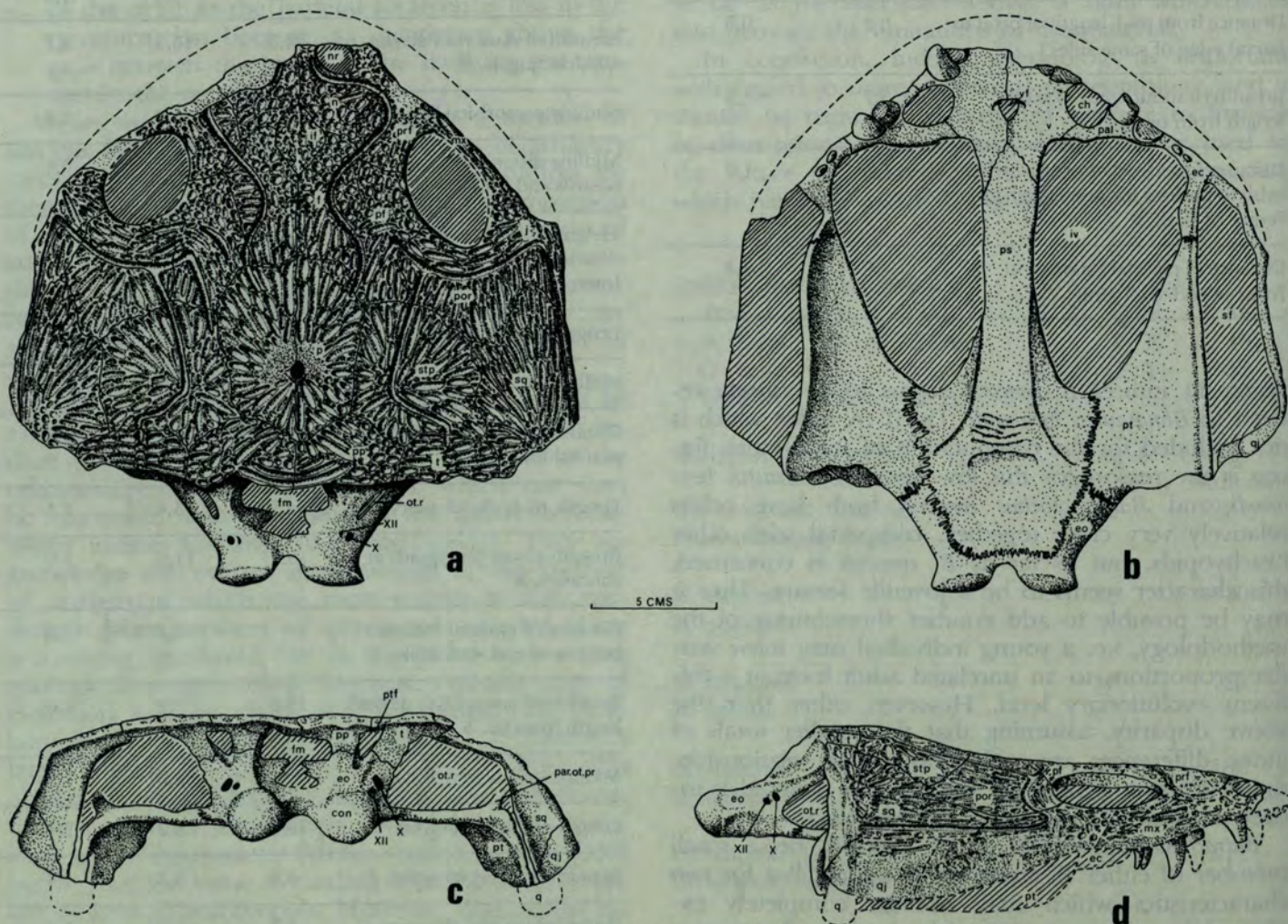


Figure 5. The skull of *Batrachosuchus browni*

(a) dorsal view

(b) palatal view

(c) occipital view

(d) lateral view

slanted suture, so that at the posterolateral corner, the nasal forms a sharp point. The posterior suture with the prefrontal is curved.

Interfrontal. The interfrontal is roughly diamond-shaped bone with its anterior extremity lying between the two nasals and its posterior end between the frontals. It is widest at the naso-frontal suture.

Prefrontal. The prefrontal forms part of the anterior border of the orbit but the exact limits are not visible. The posterior border with the postfrontal is curved laterally towards the orbit. Part of the anteromedial suture with the nasal is visible.

Frontal. The frontal is a fairly large bone; antero-medially the posterior half of the interfrontal is wedged between the two frontals. The lateral limit of the bone is a more or less straight suture with the postfrontal.

Postfrontal. The postfrontal forms the posteromedial border of the orbit. The posterolateral suture with the parietal is slanted posterolaterally so that the lateral suture of the postfrontal has an obtuse angle along its length. Laterally the suture with the postorbital is almost transverse anteriorly and parallel to the midline posteriorly, so that the lateral border forms a rough right angle along its length. The posterior border is straight and almost transverse.

Postorbital. The postorbital is a roughly pentagonal bone. The anterior median part forms the posterior border of the orbit. On either side of the orbital border formed by the postorbital the anterior sutures meet with the jugal laterally and the prefrontal medially and are almost transverse and straight, sloping slightly posteriorly. The anterolateral suture with the jugal is almost parallel to the midline. Posterolaterally, the suture with the squamosal is antero-medially directed so that the apex of the rough pentagon is solely projected into the squamosal and not between the squamosal-supratemporal suture.

Jugal. The lateral limits are not preserved. The postero-lateral border of the orbit is formed by the jugal. Posteriorly, the jugal sutures with the squamosal in a curved suture.

Parietal. The parietal is longer and wider than the frontal. The anterior suture with the frontal is curved on the left and almost straight and transverse on the right. A circular parietal foramen lies just posterior to the mid-length of the bone. Posterolaterally, the suture with the supratemporal is more or less parallel to the midline on the right side of the skull and posteromedially slanted on the left side of the skull. The posterior border of the parietal is also different on either side of the midline. On the right side it is almost straight and transverse, while on the left medially it projects into the postparietal and lateral to this rounded projection it is almost straight and transverse, so that its posterior limit forms a rough point.

Supratemporal. Laterally, the supratemporal sutures meet with the squamosal in a sinuous suture almost parallel to the midline. The posterior limit medially is a curved suture with the postparietal,

while laterally the suture with the tabular is firstly straight and then turns suddenly posteriorly so that the supratemporal forms a sharp point between the tabular and postparietal.

Squamosal. The lateral limits of the bone are not preserved. It forms most of the dorsolateral border of the skull, then turns through 90° to form a large occipital flange whose lateral edge forms the dorsolateral wall of the otic recess. In occipital view its ventral edge meets the occipital flange of the quadratojugal (which is not seen on the skull roof) in a straight, almost transverse, suture.

Postparietal. Anteriorly the postparietal sutures laterally with the supratemporal. On the right side of the skull, the postparietal seems to have pushed the parietal anteriorly so that it appears larger than the left postparietal. The lateral suture with the tabular is almost straight and parallel to the midline. The postparietal forms the posterior border of the skull table in the midline and then turns through 90° to form an occipital flange which ventrally sutures with the vertical flange of the exoccipital. Seen posteriorly, the ventromedial limits of the postparietals form the roof of a transversely elongate opening that probably housed a cartilaginous supraoccipital. The ventrolateral edge of the bone in occipital view forms the medial border of the posttemporal fenestra. Dorsolaterally, it meets the occipital flange of the tabular in a straight, dorsolaterally slanted suture.

Tabular. The tabular forms a slightly curved suture anteriorly with the supratemporal. Medially it meets the postparietal in a straight suture parallel to the midline. The lateral suture with the squamosal is also straight and parallel to the midline on the right. The tabular forms part of the posterior border of the skull table, then turns through 90° to form an occipital flange which joins with the dorsolateral flange of the exoccipital, in an interdigitated angled suture. Ventromedially, the tabular forms the lateral and dorsal borders of the posttemporal fenestra. Ventrolaterally the bone forms the dorsolateral corner of the otic recess. Seen posteriorly, it meets the squamosal in a straight dorsolaterally slanted suture.

Exoccipital. Seen posteriorly, each exoccipital forms a rounded condyle from which two thick processes rise dorsally and one thinner process laterally. The exoccipital condyles project 5 cm beyond the edge of the skull table. Anterolateral to the condyle is a large foramen for the exit of the Xth nerve and just posterolateral to this is a second smaller foramen for the exit of the XIth nerve. The vertical postparietal process has two medial extensions, the larger dorsal one, the *processus lamellosus*, evidently underlay a cartilaginous supraoccipital. The ventral process, the *processus basalis*, which is a small, sharp projection, overlies the space presumably occupied by the cartilaginous basioccipital. Thus the true foramen magnum is smaller and narrower than the dorsal opening with its long axis transverse to the

midline. Dorsolaterally the bone meets the tabular in a suture which has an acute angle halfway along its length. The dorsolateral limit of the bone forms the ventromedial border of the otic recess. The lateral process meets the pterygoid in a dorso-laterally directed suture.

In palatal view each exoccipital forms a rounded condyle posteriorly and extends anterolaterally to suture with the pterygoid in an interdigitating posterolaterally directed suture. Its medial suture with the body of the parasphenoid is curved and interdigitated.

Sculpture

The surface sculpture is exceptionally well preserved, consisting of round or rectangular pits in the centres of ossification from which ridges and grooves radiate outwards. Along some of the longer grooves cross struts have formed. A striking feature of the sculpture occurs on the postparietals and parietals where the sculpture pattern forms two triangles with their bases on the midline and the apices extending laterally towards the quadrates. The anterior angle of each triangle extends into the parietal and fades before reaching the parietal foramen. This pattern is different from that of *Hydrokkosaurus bradyi* (Welles and Estes, 1969), where the sculpture pattern is also triangular and extends to the midline of the frontals. However, both patterns include the centres of the postparietals.

Lateral Line System

The lateral line system conforms to Watson's (1956) illustration of *B. browni* except for one detail; within the left postfrontal three separate canals are visible and not two. The new canal is almost parallel to the midline, extending from just behind the anterior one-third of the postfrontal and fading just anterior to the posterior suture of that bone. It lies between the temporal and the supraorbital canal.

Supraorbital canal. This canal forms an hour-glass pattern in the centre of the skull. Posteriorly each groove enters the anterolateral corners of the parietals. From this point the groove curves laterally passing through the postfrontal. It then swings medially into the frontal. Halfway along the length of the frontal the groove changes direction and curves laterally again to exit from the frontal at its anterolateral corner. The groove then continues laterally into the prefrontal, where anteriorly it changes direction again, curving medially to leave the prefrontal at its anterior suture. The groove continues into the nasal following the curve of the nare. It fades at the medial border of the nare.

Temporal canal. The temporal canal issues from the postorbital and circles the orbit anteriorly giving off a posteriorly directed branch which crosses the postorbital at its posteromedial corner, and passes into the supratemporal and enters the tabular midway along the suture. The temporal canal which passes

into the postfrontal sends off another branch which swings posteriorly to enter the anterolateral corner of the supratemporal where it stops. Also from the postorbital a lateral branch extends onto the jugal where it turns posteriorly and extends along the lateral part of the squamosal.

Palate

Unless otherwise stated the left side of the skull is described. The antero-lateral borders of the palate are not preserved, but a striking feature is the presence of a large foramen situated in the centre of the vomer on the midline. The position of this foramen seems to correspond to the cartilaginous area in *Hydrokkosaurus bradyi* (Welles and Estes, 1969). In *Batrachosuchus watsoni* (Haughton, 1925) a depression in the vomer is indicated by Watson (1956) and Welles and Estes (1969), but this depression is more posterior than the foramen found in *B. browni*. This foramen probably housed a gland. It is roughly triangular with the apex pointing posteriorly. The base is 9 mm across and the midline length is 9 mm.

The matrix has not been removed from the subtemporal vacuities, due to the delicacy of the surrounding bones and the overlying skull roof.

Vomers. The most anterior limits of the vomers are not preserved. In the anterolateral corner of each vomer, a large tusk next to a tusk depression is present. Posterolateral to the tusk the suture with the palatine is interrupted by the choana. From the posteromedial corner of the choana the suture with the palatine slants posteromedially to the anterolateral corner of the interpterygoid vacuity. The posterior ends of the vomers project on either side of the cultriform process of the parasphenoid. There is no depression in this area as in *Batrachosuchus watsoni*, but the two elements blend smoothly together.

Palatine. The most anterior limits of the palatine are not preserved. Posterolateral to the choana is a large tusk adjoining a broken tusk base and further posterolaterally to this pair of tusks the sinuous anterolaterally directed suture with the ectopterygoid is visible extending to the anterolateral corner of the interpterygoid vacuity.

Ectopterygoid. The anterolateral limits of the ectopterygoid are not preserved. Two teeth (tusks) smaller than the vomerine and palatine tusks are present just lateral to the anterolateral corner of the interpterygoid vacuity. Posteriorly, an interdigitated almost straight transverse suture with the pterygoid enters the anterolateral border of the interpterygoid vacuity.

Parasphenoid. The parasphenoid forms a large polygonal body underlying the exoccipitals posteriorly and the pterygoids laterally. The body is smooth and slightly concave. Two grooves following the lateral margins of the cultriform process extend into the body, at the centre of which is a very shallow transverse depression which is probably homologous with the *crista muscularis* of the capitosaur. The cultriform process narrows from 4.2 cm at its base

to 1,9 cm almost halfway along its length. The process then broadens to 2,5 cm at its anterolateral sutures with the vomers. The parasphenoid does not extend to the posterior limit of the skull as it does in *Batrachosuchus watsoni* but leaves a gap of 1 cm from this border. The quadrate is missing.

Pterygoid. The pterygoid displays the typical condition found in the brachyopids in that the lateral edge of the palatine flange turns through 90° forming the vertical inner wall of the subtemporal vacuity. Posterolaterally, the pterygoid sutures with the exoccipital on an almost straight posterolaterally directed line. The quadrate ramus of the pterygoid is expanded so that the posterolateral corner of the vertical flange lies 1,2 cm posterior to the edge of the palatal portion.

In occipital view the pterygoid sutures medially with the exoccipital in a dorsolaterally slanted suture. It then extends laterally forming the ventral border of the otic recess before turning vertically. A part of the parotic plate of the pterygoid is visible on the dorsolateral surface of the pterygoid (as in *Batrachosuchus watsoni*, illustrated by Watson, 1956).

Choanae. The right choana measures 1,8 cm at its narrowest breadth by 2,6 cm at its long axis. The anterior limits of the left choana are not preserved and the shape seems to be distorted. The right choana has its long axis transverse to the midline.

Interpterygoid vacuity. The interpterygoid vacuity has its greatest width along its anterior border. The right measures 6,1 cm at its anterior border by 10 cm; the left measures 5,6 cm at its anterior border by 10 cm, this discrepancy being due to distortion.

Subtemporal vacuity. The subtemporal vacuity is obscured by matrix which, if removed, may endanger the skull roof. Its inner border is formed by the vertical flange of the pterygoid.

Discussion

When comparing *B. browni* to *B. watsoni* confusion is encountered (see table 6) as the three existing sets of plates and illustrations of *B. watsoni* show different skull proportions; e.g. in Watson's (1919) plate which is "½ approximately", the skull length is 19,2 cm, whereas in Watson's 1956 reconstruction the skull length is 16 cm. In Welles and Estes (1969) their new reconstruction of the skull length is only 11,5 cm, but this is taken from new casts provided by the British Museum of Natural History and probably provides the most reliable information. However, when comparing the plate in Watson (1919) to *B. browni* as now reconstructed, the two skulls look very similar and the possibility exists that they are of the same species. This would explain away the inconsistency of there being two sympatric species of brachyopid in the same horizon (*Cynognathus* zone). Excluding the general skull morphology which is difficult to assess for reasons already given, there are supposedly four main differences; these are:

(1) the presence of an interfrontal in *B. browni*;

- (2) the presence of a vomerine foramen in *B. browni*;
- (3) the parasphenoid does not reach the edge of the palate as it does in *B. watsoni*;
- (4) the wider lateral line canals of *B. watsoni* and their distribution.

Looking at the plate of *B. watsoni*, the area where an interfrontal would be found is rather unclear but it seems that there is a possibility that sutures of an interfrontal are in fact discernible. This point could be resolved with microscopic examination of the area.

Considering Watson's (1919) plate showing the palate, in the position of the vomerine foramen found in *B. browni*, a distinctly triangular depression is visible. Although Welles and Estes (1969) describe the area as a depression perhaps further preparation, if possible in this area, would uncover a foramen in *B. watsoni*.

The parasphenoid of *B. watsoni* may not reach the edge of the palate. In Watson's (1919) plate there seems to be a suture running just anterior to that margin. The wider lateral line canals could be due to a lateral compression which widened the canals, or *B. watsoni* may be a young individual and perhaps the lateral line canals would close together as the animal got older. The variation of their distribution may also be due to sexual dimorphism or individual variation. However, there is no evidence as yet available to verify these theories and as the wider lateral line canals of *B. watsoni* could have been an adaptation to faster-flowing water speciation may well have occurred even though the two localities are approximately 56 km apart.

Thus, until these four characters are explained away, it seems advisable to retain the two South African species and Welles and Estes (1969) indices are used by the author for comparisons.

One further factor which emerged from discussion and which may have a bearing on the relationships and function of the three Southern African members of the genus *Batrachosuchus* is the degree to which the occipital condyles protrude behind the skull roof. Measured on the dorsal surface this character is greatest in *B. watsoni* (29%), less so in *B. browni* (20%), and is very much reduced in *B. concordi* (<5%). Thus the last-named species has a reduced ability to raise the upper jaw for mouth-opening and hence, by implication, there is a requirement for the skull to be kept well clear of the ground so as to allow the lower jaw sufficient movement to clear the palatal fangs. This also would require relatively robust forelimbs and pectoral girdle to support the body; this requirement is met in the well-ossified bones described from the post-cranial remains.

By comparison the other two species would appear well suited to a greater degree to a bottom-living, aquatic existence where mouth-opening movements would be effected by a combination of powerful nuchal and depressor mandibuli muscles. A comparison of the anterior vertebrae of these forms with the axis and atlas of *B. concordi* would be of great value here,

as would a knowledge of their limb morphologies. In this case *B. browni* seems less well adapted to the bottom-dwelling habit which, with the difference in development of the lateral line canals when compared with *B. watsoni*, might help explain the presence of these two closely related species in the *Cynognathus* zone, *B. watsoni* being a permanent dweller in swift-flowing waters and *B. browni* perhaps preferring more transient waters.

In this case it is interesting to note that *B. concordi* might show an unusual reversal of the normal evolutionary trends of the temnospondyls in seemingly being less well-adapted to an aquatic environment. If the age of the N'tawere Formation is the same as the *Cynognathus* zone (and the large geographical separation of the two not significant) then the three species would occupy three separate niches in river ecology. If, as is more likely, the N'tawere Formation is the younger of the two, then an evolutionary sequence within the genus *Batrachosuchus* can be demonstrated based on this one character.

SUMMARY AND CONCLUSIONS

1. The family Brachyopidae, which in South Africa is part of the *Cynognathus* zone fauna of the Beaufort series, may be defined as: labyrinthodonts; orbits large; palate Ω -shaped; retroarticular process long; skull outline more or less parabolic; occipital condyles project far behind the posterior edge of skull roof; no zones of relative intensive growth; basicranial joints absent; pterygoids joined by suture to parasphenoid; palatal teeth present on vomer and palatine.
2. Only one genus *Batrachosuchus* is represented in Southern Africa by three species: *B. browni* and *B. watsoni* from the *Cynognathus* zone of South Africa and *B. concordi* from the N'tawere Formation in the Upper Luangwa Valley, Zambia. The genus may be defined as brachyopids with broad parabolic skulls; orbits far forward; postorbital part of skull very long; narrow internarial width; lateral line grooves well defined; extension of supraorbital lateral line canal onto parietal bone.
3. *B. watsoni* may be defined as a large *Batrachosuchus*; skull broader than that of *B. browni*; greater internarial width; greater interorbital breadth; longer preorbital region; shorter orbits; longer postorbital deck; lateral line canals well defined and broad; parasphenoid reaches limit of skull base; depression in centre of vomer; one lateral line canal present on postfrontal.
4. *B. browni* may be defined as a large *Batrachosuchus*; skull relatively narrower than that of *B. watsoni*; narrower interorbital breadth; shorter preorbital region; longer orbits; shorter postorbital deck; lateral line canals well defined, but relatively much narrower and of more Ω -shape in section than in *B. watsoni*; parasphenoid does not reach skull limit; vomerine foramen in centre of vomer; 3 lateral line canals present on postfrontal;

TABLE 6

Differences in Measurements of the Three Illustrations of *Batrachosuchus watsoni*

	Watson 1919 cm	Watson 1956 cm	Welles and Estes 1969 cm
Interorbital breadth, A	9,8	7,2	5,0
Breadth of skull roof across quadratojugals, B	27,5	18,5	16,5
Midline postorbital length, D	12,2	10,0	7,0
Midline distance between nostrils and orbits, F	2,2	1,4	1,0
Height of parasphenoid, H	—	4,2	3,5
Internarial breadth, J	2,0	1,5	1,1
Length of skull roof, L	19,2	16,0	11,5
Midline preorbital length, O	4,4	2,7	2,4
Distance behind orbits of parietal foramen, P	6,0	5,0	3,3
Length of body of pterygoid, Q	5,0	3,8	3,4
Breadth across pterygoids at concavity, R	20,8	12,4	11,2
Distance of parietal foramen in front of end skull table, T	4,8	4,0	3,0
Breadth of snout 1/5th of skull length from tip, S	17,4	10,8	9,2
Midline orbital length, U	3,8	3,3	2,5
Length of interpterygoid, Y	10,4	7,2	5,7
Breadth of interpterygoid, Z	6,0	4,0	3,3
Distance of exoccipital behind skull table	5,0	2,2	2,0

tal; evidence of paired tusks on vomer, palatine and ectopterygoid.

5. *B. concordi* may be defined as a small *Batrachosuchus* with a skull narrower than *B. browni* and much narrower than *B. watsoni*; interorbital breadth very much narrower than both *B. browni* and *B. watsoni*; shorter preorbital length than *B. browni*, much shorter than *B. watsoni*; orbit slightly smaller than *B. browni*; postorbital length greater than *B. browni*, but shorter than *B. watsoni*; interpterygoid vacuity shorter than *B. browni* and much shorter than *B. watsoni*; interpterygoid vacuity narrower than both *B. watsoni* and *B. browni*; distance of parietal foramen from posterior of skull table greater than both *B. browni* and *B. watsoni*; lateral line canals weakly defined; parasphenoid reaches limit of skull; exoccipital

does not project as far posteriorly as in either *B. browni* or *B. watsoni*; in addition a lingual process of the angular is present (the jaws of the other two species of *Batrachosuchus* are unknown).

6. *B. concordi* is more or less on the same evolution-

ary level as the *Cynognathus* zone brachyopids, in agreement with other evidence that the N'tawere Formation is probably of a similar age, and probably Early Middle Triassic (Chernin and Cosgriff, 1975).

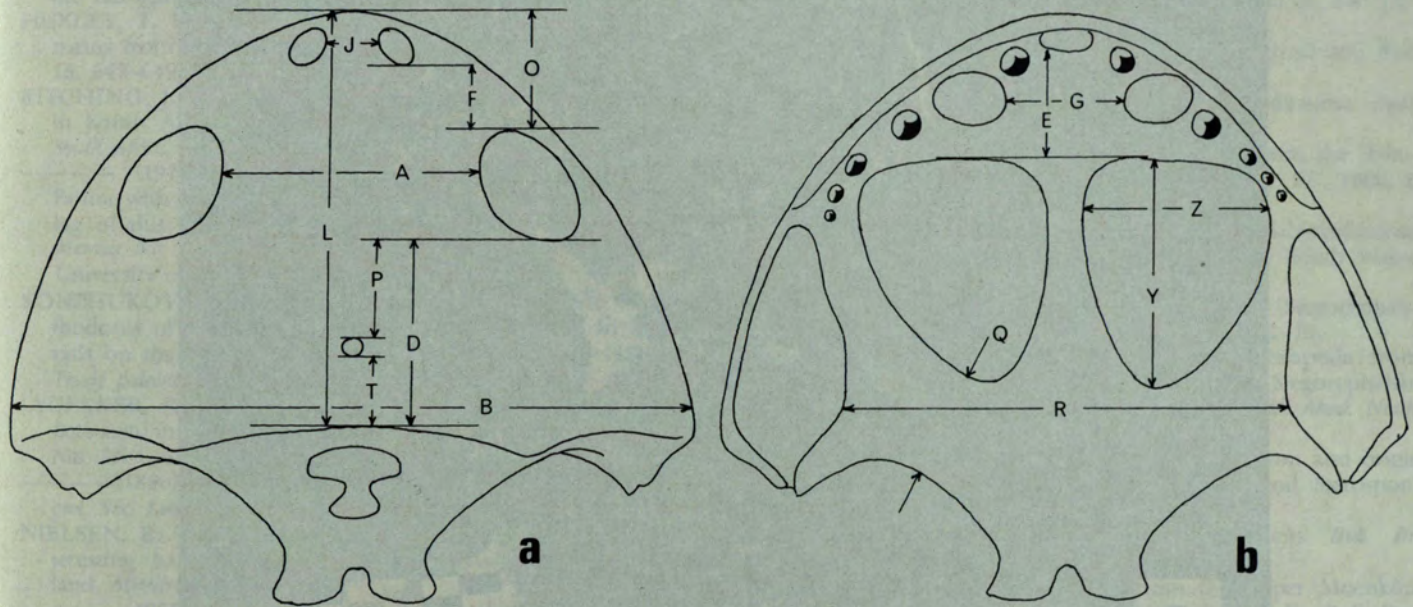


Figure 6. Diagrams of brachyopid skull showing measurements of dorsal surface and palate from Welles and Estes (1969, fig. 1, p. 5).

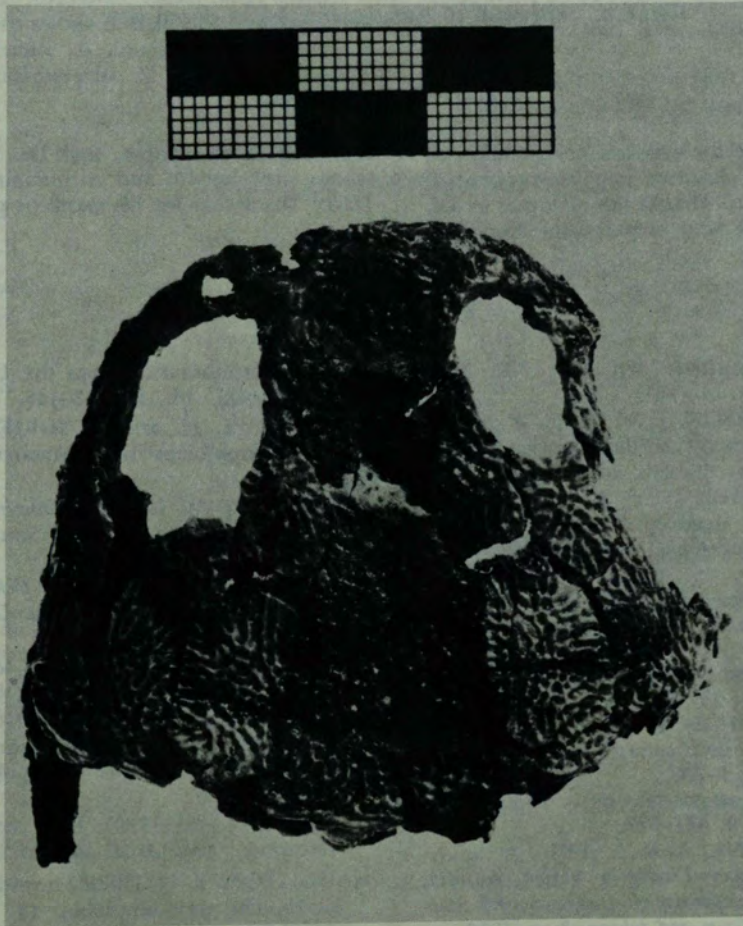


Figure 7. The skull of *Batrachosuchus concordi* dorsal view.

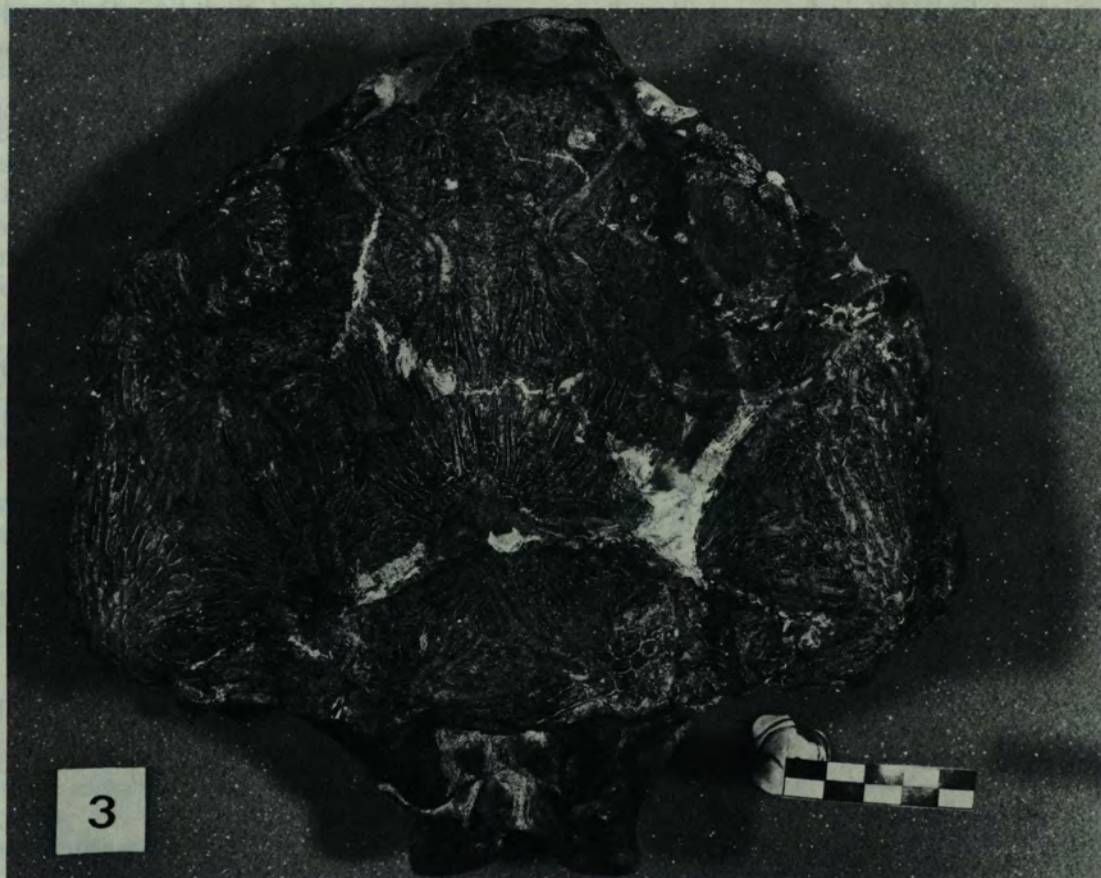


Figure 8. The skull of *Batrachosuchus browni* dorsal view.

ACKNOWLEDGEMENTS

With deep gratitude I acknowledge the constant co-operation of the Director of the Bernard Price Institute for Palaeontological Research, Professor Stanley Jackson. Thanks are also due to Dr. C. E. Gow and Dr. J. W. Kitching who prepared the specimens

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LIST OF ABBREVIATIONS

a	— angular	inl	— infraorbital canal	pref	— premaxillary foramen
art	— articular	iv	— interpterygoid vacuity	prf	— prefrontal
bac	— basioccipital chamber	j	— jugal	prprc	— precondylar process
bas	— basal process	la	— lacrimal	prptc	— postcondylar process
c	— coronoid	mx	— maxilla	ps	— parasphenoid
ch	— choana	n	— nasal	ptf	— posttemporal fossa
cm	— crista muscularis	nr	— nare	q	— quadrate
con	— condyle	otr	— otic recess	qj	— quadratojugal
cp	— cultriform process	p	— parietal	qpt	— quadrate ramus of pterygoid
d	— dentary	paf	— paraquadrate foramen	rp	— retroarticular process
dor	— dorsal process	pal	— palatine	sa	— surangular
ec	— ectopterygoid	palt	— palatine tusk	sf	— subtemporal vacuity
eo	— exoccipital	par	— paroccipital process	sp	— splenial
epi	— epipterygoid	par. ot. pr.	— parotic part of pterygoid as far as exposed	sq	— squamosal
f	— frontal	pc	— precoronoid	stp	— supratemporal
fad	— adductor fossa	pf	— postfrontal	sul	— supraorbital canal
fm	— foramen magnum	pmx	— premaxilla	sym	— symphysis
fma	— anterior meckelian foramen	por	— postorbital	t	— tabular
fmp	— posterior meckelian foramen	pos	— postsplenial	tl	— temporal canal
fogl	— glenoid fossa	pp	— postparietal	v	— vomer
fpsym	— postsymphysial foramen	ppt	— palatine ramus of pterygoid	ven	— ventral process
ic	— intercoronoid	pra	— prearticular	vf	— vomerine foramen
if	— interfrontal				

A REASSESSMENT OF *PHRYNOSUCHUS WHAITSI* BROOM

by

Sharon Chernin and J. W. Kitching

ABSTRACT

Phrynosuchus whaitsi Broom 1913, from either the *Tapinocephalus* or *Cistecephalus* zones of South Africa, is reassessed and is now considered a *nomen vanum* due to the poor state of preservation of the specimen. The specimen shows some rhinesuchid characters, and is tentatively assigned to *Rhinesuchus* sp. indet. and in all probability is that of a juvenile.

INTRODUCTION

Phrynosuchus whaitsi Broom 1913

Locality

Droogvoets, Fraserburg, Cape Province.

Zone

Tapinocephalus or *Cistecephalus* (Broom, 1913, “*Endothiodon*”)

In reconsidering the locality Droogvoets, Fraserburg, given by Broom (1913) as “*Endothiodon*” zone, it has been established in more recent years that both the uppermost horizons of the *Tapinocephalus* and the lowermost horizons of the *Cistecephalus* zone are exposed in the area around Fraserburg. So the horizon of *Phrynosuchus whaitsi* is unreliable, although it seems from the morphology or texture of the very hard matrix that the specimen in all probability came from the former zone.

Phrynosuchus has only been referred to on two occasions since it was described by Broom (1913) — probably due to its state of preservation — by Haughton (1925) and by Romer (1966).

Romer (1966, p. 363) assigns this “type” to the family Brachyopidae, probably based on Broom’s drawing which gives the impression that the skull outline is parabolic. However, the relative position of what is left of the orbital margins and the approximate position of the orbits as well as the oblong and lateral position of the nares close to the lateral margins of the skull seem to indicate that the specimen in all probability belongs to the family Rhinesuchidae.

State of preservation of type skull S.A.M. 235F

Further preparation has been undertaken by one of the authors, J. W. Kitching, along the perimeter

of the skull, and based on what is discernible of the skull an attempt at a redescription and reinterpretation is given in the following paragraphs.

The skull is embedded in a hard fine-grained sandstone containing biotite and is badly weathered, depressed and distorted. The posterior half of the skull together with a small part of the postfrontal is preserved as an impression. In places on the matrix faint traces of sutures are discernible.

Part of the left side and the anterior region of what was most probably also represented as an impression is completely missing, so that part of the much crushed and distorted anterior palatal region is exposed. Only a small part of the posterior border of the left orbit is preserved as an impression while the right orbit is badly distorted.

Posteromedially, in the area of the occipital region there is a projection of thin bone underlying the skull which could either be interpreted as severely flattened occipital condyles or as part of the pectoral girdle — possibly the interclavicle. Due to the thinness of the bone it could in all probability be assigned to the latter as it is almost inconceivable that the occipital condyle could have been flattened to such an extent by distortion and into such a shape.

The hardness of the matrix and exceptionally depressed state of the specimen unfortunately prevent further preparation of the palatal or ventral region of the skull.

An almost complete right as well as the greater part of the left mandibles are preserved, but due to compression these are firmly attached to the skull.

The following is a brief description of what can be discerned of the respective bone structures of the skull.

Postparietal. The postparietals are relatively large, square-shaped bones which are in the normal rhinesuchid position.

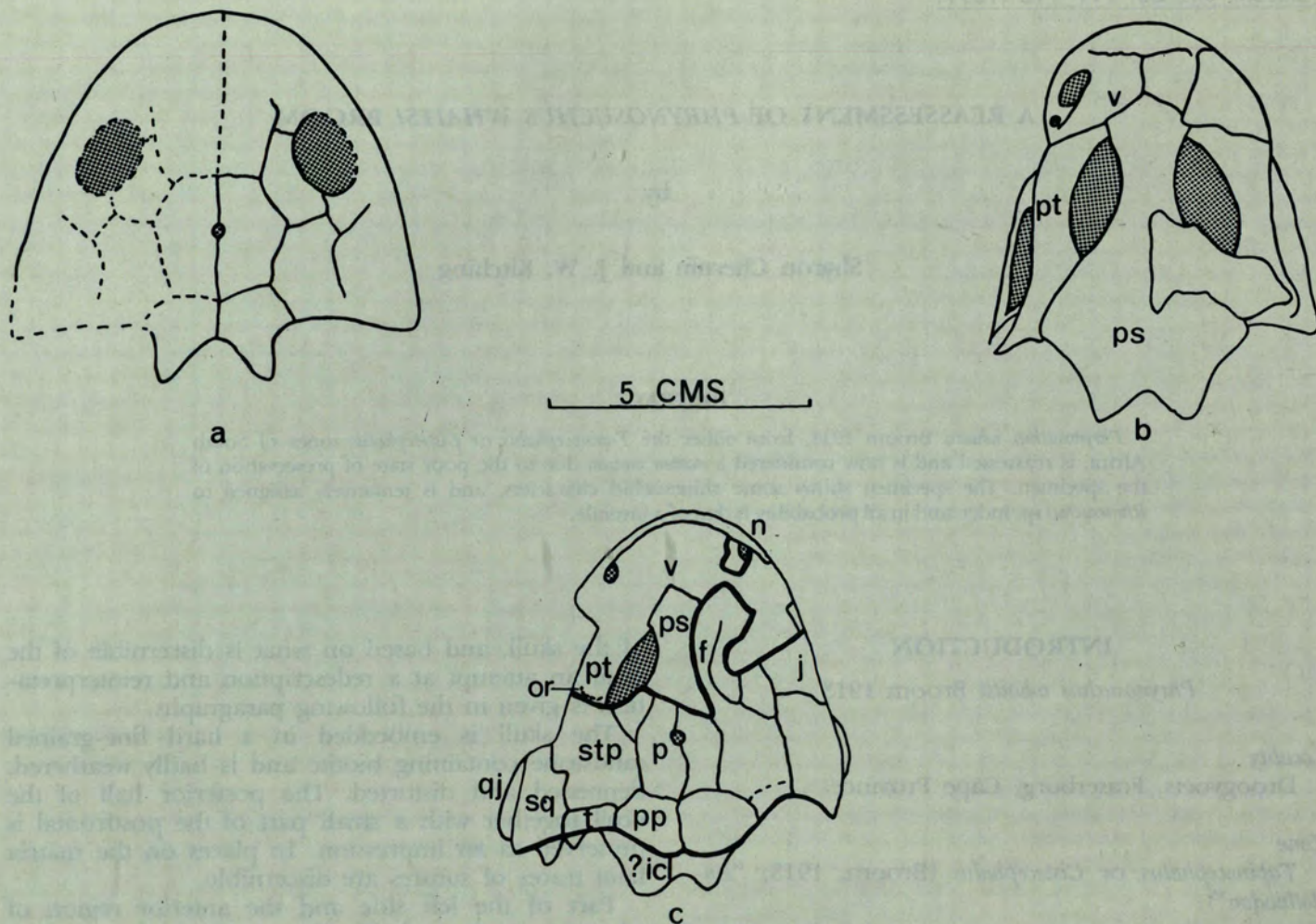


Figure 1. a. *Phrynosuchus whaitsi*. After Broom, 1913.
b. *Phrynosuchus whaitsi*. Dorsal view of palate. After Haughton, 1925.
c. *Phrynosuchus whaitsi*. Reassessment of dorsal view of skull.

Major portion of tabular. The anterior suture of the left tabular runs transversely and its lateral posterior limit appears to have been produced outwards to form a finger-like tabular horn.

Squamosal. The squamosal lies lateral to the tabular as in *Rhinesuchus*. The squamosal has been depressed in such a way that it seems to have a posterior projection behind the skull table in the probable position of the otic notch. The shape of the squamosal is thus very distorted.

Quadratojugal. Lateral to the squamosal lies the strap-shaped quadratojugal, which conforms in shape and position to that of *Rhinesuchus*.

Parietal. The parietals lie anterior to the postparietals, abutting on the mid-line. The anterior limits of the parietals are missing. A fairly large circular parietal foramen lies within the parietals on the midline, almost halfway along their length.

Supratemporal. Posterolateral to the parietals on the left side lies the only preserved supratemporal whose sutures, where visible, are highly distorted with regard to their position. However, the supratemporal seems to be a relatively large bone.

Postorbital. The postorbital is clearly preserved on

the right side of the skull, but on the left side no definite sutures can be differentiated.

Postfrontal. The postfrontal is a curved bone which follows the line of the rim of the orbit. On the right side of the skull, the postfrontal extends from a lateral, longitudinal suture with the postorbital following a curved suture medially, presumably with the frontal which follows the curvature of the orbit. The anterior limit of the postfrontal is not preserved. The postfrontal forms part of the medial border of the orbit. The positions of the postorbital and postparietal are indicated in the reconstruction.

Orbits. Only a small part of the left posterior border of the orbit is preserved. The orbits are situated almost in the mid-length of the skull roof slightly more within the posterior part of the skull and, before distortion, were probably closer together.

Nares. The shape and position of the nares are indicated by a small piece of the nasal bone, preserved as an impression, on the right side and which lies disarticulated on the dorsal surface of the palate. The nares were oblong, average in size, with their long axes parallel to the lateral borders of the skull, very similar to those in the *Rhinesuchidae*.



Figure 2. Stereo view of the dorsal surface of the skull of *Phrynosuchus whaitsi* Broom.

The palate. A very flattened cultriform process of the palate meets a fused complex of vomer and palatines in a sharp, almost triangular, anterior point. The shape of the anterior part of the interpterygoid vacuity as seen dorsally is indicative of the normal rhinesuchid structure. Numerous small teeth are present along the outer edge of the premaxillae and maxillae whose limits are not known. No other sutures are discernible on the palate as preserved.

DISCUSSION

From the foregoing it is evident that only insufficient information can be gained from the specimen as preserved and it is thus suggested that *Phrynosuchus whaitsi* be considered a *nomen vanum*. With the almost mid-length position of the orbits in the skull roof and other scanty information, a rhinesuchid-like creature is indicated, and it is proposed that this specimen be assigned as *Rhinesuchus* sp. indet., possibly that of a juvenile.

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LIST OF ABBREVIATIONS

f	— frontal
icl	— interclavicle
j	— jugal
n	— nasal
or	— orbit rim
p	— parietal
pp	— postparietal
ps	— parasphenoid
pt	— pterygoid
qj	— quadratojugal
sq	— squamosal
stp	— supratemporal
t	— tabular
v	— vomer

OWENETTA IN PERSPECTIVE

by

C. E. Gow

ABSTRACT

This paper adds detail to the existing description of the small procolophonid *Owenetta rubidgei* Broom. The relationships of this animal are assessed with reference to other South African procolophonids and pareiasaurs. All are broadly related but a mosaic of characters precludes any direct phyletic relationships.

INTRODUCTION

The order Cotylosauria is represented in the Karoo beds of South Africa by the Millerettidae (Gow, 1972) and the Procolophonidae and Pareiasauridae. The common well-known lower Triassic genus *Procolophon* and the poorly-known and rare upper Permian genus *Owenetta* are included by Romer (1956) within a subfamily Procolophoninae, to distinguish them from the supposedly related and more primitive Nycteroleterinae and Nyctiphruetinae.

Procolophonids and pareiasaurs are distinguished from other cotylosaurs by having a large tabular which projects posteriorly, and in lacking a supratemporal. The palate is broad and typically has a distinctive, short, rounded interpterygoid vacuity. The basal articulation is said to be fused (Romer op. cit.): this is true of pareiasaurs and old *Procolophon*, but *Owenetta* and young *Procolophon* have a free articulation (personal observation). Procolophonids are typified by having the posterior border of the orbit emarginated, pareiasaurs by their much larger size and rugose dermal skull bones.

The small upper Permian procolophonid *Owenetta rubidgei* has not been restudied since its description by Broom in 1939. Due perhaps to their small size and delicate construction these animals are not common in the fossil record; however, there are seven skulls in the collection of this Institute, and these all contribute to the reconstructions presented here. This paper presents more details of the cranial anatomy of *Owenetta*, and offers certain interpretations regarding its biology. Comparisons are made with the well-known procolophonids and pareiasaurs, resulting in a better understanding of the relationships between these animals.

MATERIALS AND METHODS

Following are the field numbers of the skulls of *Owenetta* used in this study: BPI 301; 1175 (two); 1395; 1396; 3819 and 4195b. A particularly well-preserved skull of *Procolophon trigoniceps* was used for comparison, number BPI 4014.

As well as being extremely thin and delicate the finer elements of the skull of *Owenetta* tend to be translucent (a condition which is aggravated by moisture). The matrix in some cases was not homogeneous, tending to break along parting planes. For these reasons preparation has been mechanical, using fine needles.

CRANIAL ANATOMY

The various elements of the skull do not require formal description — relationships are clear from the figures. *Owenetta* (fig. 1) has the same emargination of the posterior borders of the orbit so characteristic of procolophonids. The form of the maxilla, very high just behind the external nares, is also typically procolophonid, though *Owenetta* lacks the depression for a maxillary gland (Ivachnenko, 1973) seen in other procolophonids (stippled area in fig. 2). In *Owenetta* there is a gap between the posterior border of the jugal and the quadratojugal, a feature apparently unique to this genus among procolophonids; the jugal is pitted as shown for the attachment of a connective tissue sheet in this region.

Despite overall similarity there are pronounced differences in the skull roof between *Owenetta* and *Procolophon*. The postfrontal in *Procolophon* is a thin sliver of bone held out of contact with the postorbital by the parietal, which enters the posterior border of the orbit. (In some specimens this

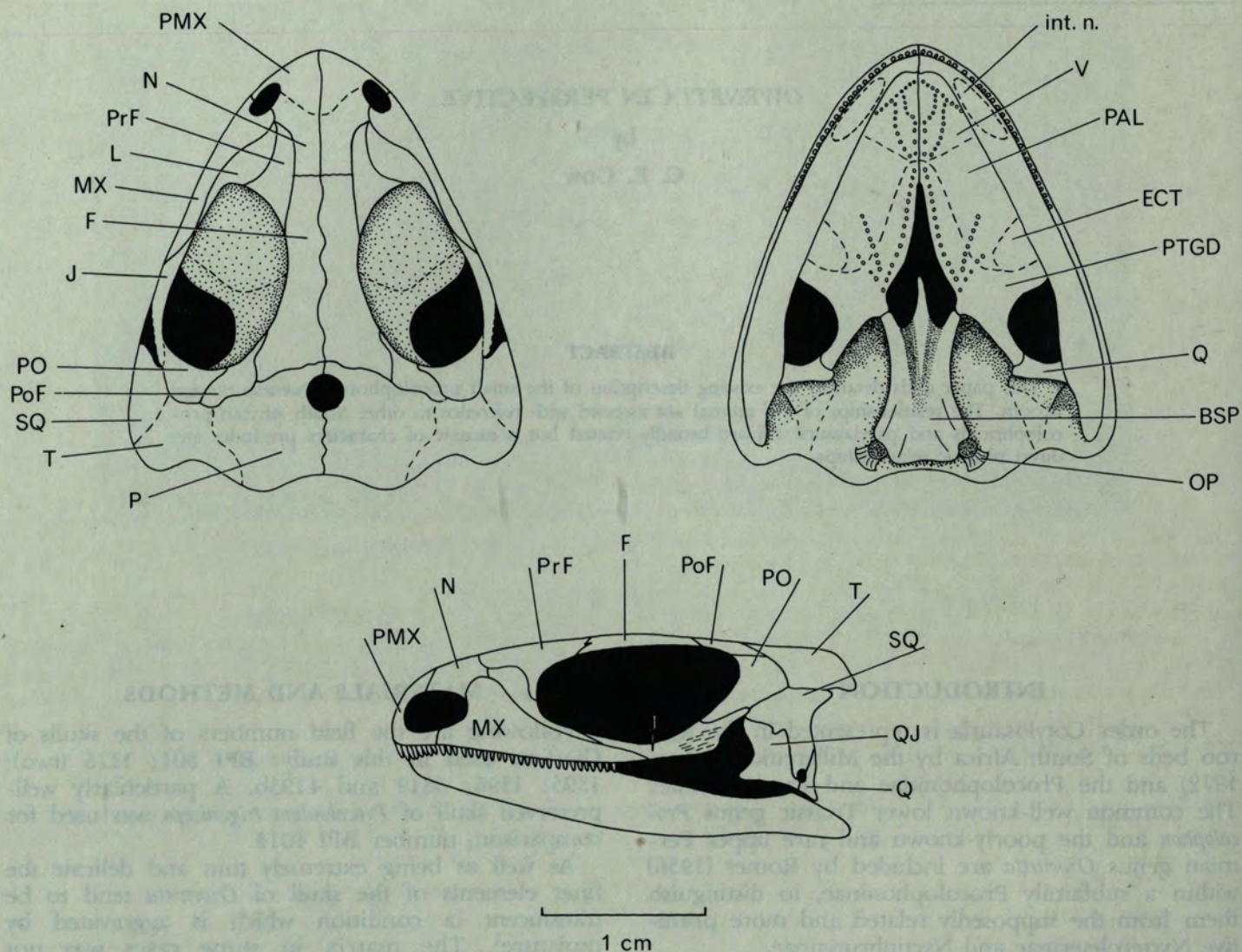


Figure 1. *Owenetta rubidgei*. Skull reconstruction. Dorsal, ventral and lateral views.

relationship may be obscured by the tabular extending forward to the orbit.) In *Owenetta* the position and relationships of the postfrontal are typically cotylosaurian. This suggests that emargination of the skull roof behind the orbit has proceeded further in *Procolophon*.

In *Owenetta* there are eight teeth in the premaxilla and 25 in the maxilla, twice as many as in the smallest known *Procolophon* (Gow, 1977). These teeth are slender, circular in section, and slightly recurved at the tips. Lower teeth occlude within the upper arcade as in pareiasaurs and quite unlike the tooth to tooth occlusion in procolophonids. The arrangement of the palatal bones, with a long palatal vacuity reaching almost to the vomers, is typical of primitive captorhinomorphs and contrasts with the palates of typical procolophonids and pareiasaurs. Tooth fields on the palate are primitive, except that teeth are absent from the pterygoid flanges as in *Procolophon* (these are still present in pareiasaurs).

Boonstra (1932) described the pareiasaurian

hyoid apparatus (fig. 3 A). One of the *Procolophon* skulls examined in the present study has a very similar hyoid apparatus (BPI 2504, fig. 3 B) while several of the *Owenetta* skulls have the hyoid apparatus in position (fig. 3 C). These bones in the three forms are strikingly similar, comprising in each case an ossified hyoid body with obvious points of attachment for two ceratobranchial arches, and the proximal portions of ceratobranchials I.

DISCUSSION

(a) Ecologic

Pareiasaurs and procolophonids were undoubtedly herbivorous. *Owenetta* was almost certainly insectivorous, which was the primitive condition in cotylosaurs as a group. The skull of *Owenetta* is reminiscent of modern geckos. *Owenetta* may well have been a cryptic nocturnal animal, as there is no hint of the defensive structures common to procolophonids (spiny cheeks) and pareiasaurs (dense bone and dermal armour; sheer size).

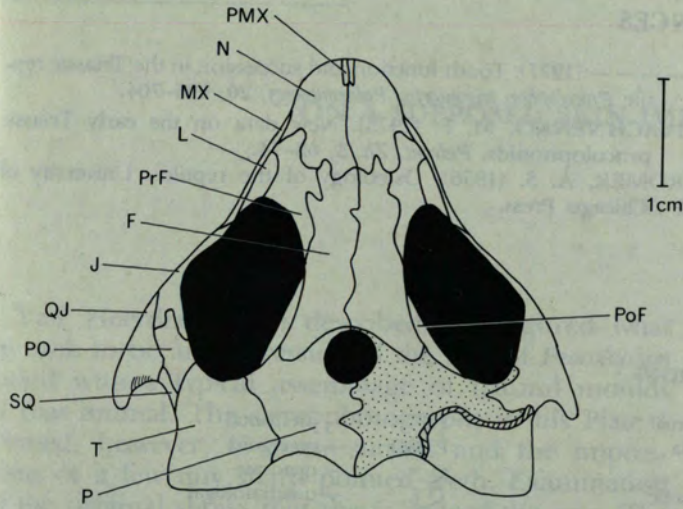
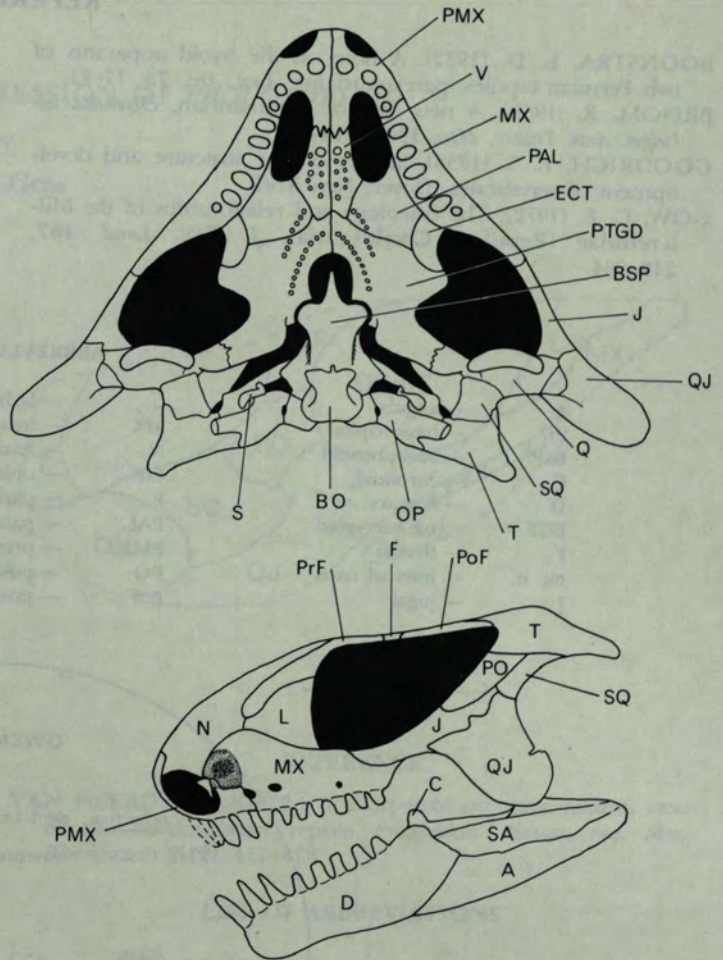


Figure 2. *Procolophon trigoniceps*. Dorsal, ventral and lateral views. Dorsal and lateral based on BPI 4014, ventral a composite reconstruction. In dorsal view the right tabular has been broken away to expose almost the full extent of the parietal (stippled). Depression for maxillary gland stippled in lateral view.



(b) *Phylogenetic*

Owenetta is discussed here in comparison with South African procolophonids and pareiasaurs (which are in all essentials similar to Russian and other described forms). As regards the more primitive forms, from published illustrations *Nyctiphruetus* is very similar to *Owenetta* but more primitive in having toothed pterygoid flanges and unmodified jugal and quadratojugal. If *Nycteroleter* is representative of a form ancestral to all procolophonids and pareiasaurs as suggested by Romer and as seems quite acceptable, and if its large amphibian type otic notch is primitive, which also seems likely, then these animals may have originated independently of other cotylosaurian groups.

All characters of seeming phylogenetic importance in *Owenetta*, procolophonids and pareiasaurs are schematised in Figure 4. All three share a distinctive, apparently unique, hyoid apparatus. (Here comparative information is scanty, but of all described hyoid elements this is closest to that of the *Chelonina* (e.g. Romer, 1956; Goodrich, 1958) which typically consists of an ossified hyoid body, two ossified ceratobranchials, and a much reduced cartilaginous lingual process.) Other characters can be divided as shown into those shared by any two of the three groups and those which are found in only one.

Figure 3. Hyoid apparatus of:
(a) Pareiasaur (after Boonstra, 1932)
(b) *Procolophon* (BPI 2504)
(c) *Owenetta* (BPI 1395, 1396).

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ABBREVIATIONS

A — angular
BO — basioccipital
BSP — basisphenoid
C — coronoid
D — dentary
ECT — ectopterygoid
F — frontal
int. n. — internal naris
J — jugal

L — lachrymal
MX — maxilla
N — nasal
OP — opisthotic
P — parietal
PAL — palatine
PMX — premaxilla
PO — postorbital
PoF — postfrontal

PrF — prefrontal
PTGD — pterygoid
Q — quadrate
QJ — quadratojugal
S — stapes
SA — surangular
SQ — squamosal
T — tabular
V — vomer

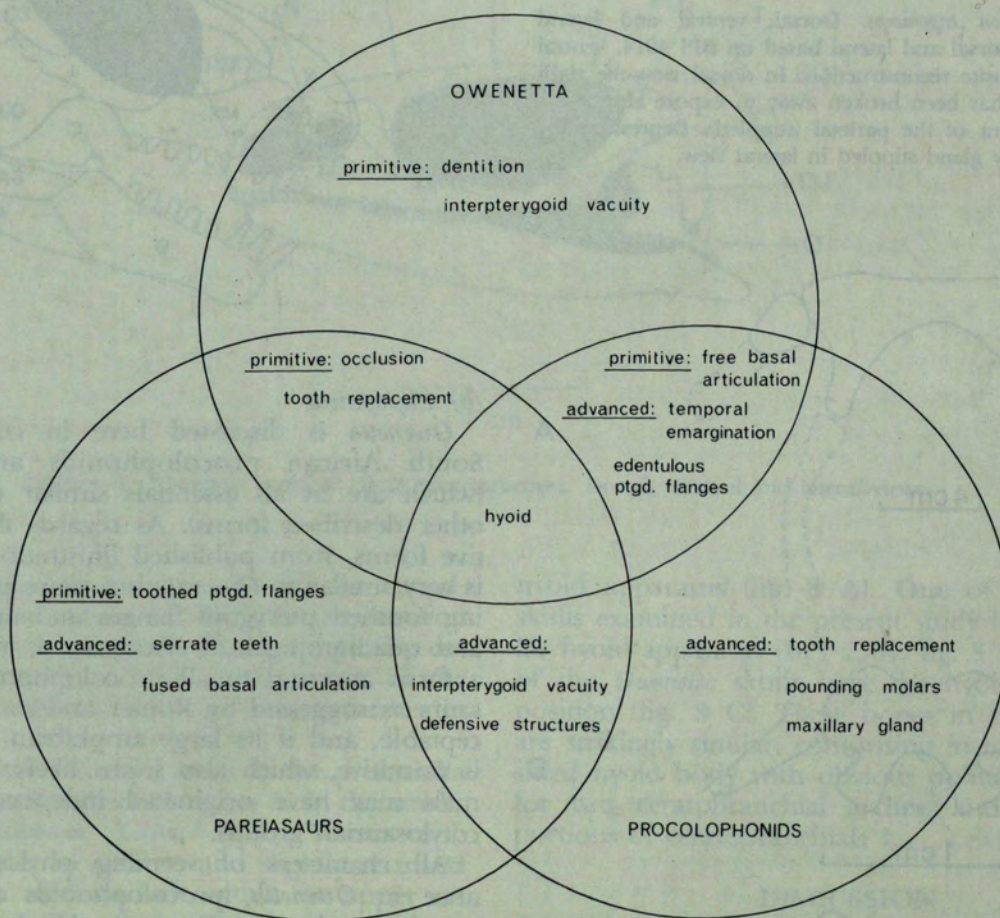


Figure 4. Diagrammatic presentation of the degree of relatedness of *Owenetta* to pareiasaurs and procolophonids using only those characters of seeming phylogenetic importance.

ON A SUPPOSED SKIN IMPRESSION OF *PROCOLOPHON*

by

C. E. Gow

Van Heerden (1974) described and figured what he took to be an impression of the skin of *Procolophon* found with a typical assemblage of natural moulds of that animal. The stereophotographs in his Plate 4 seemed, however, to show sutures and the impressions of a few tiny sharp pointed teeth. Examination of the original shows that this is indeed the case. The accompanying explanatory sketch (fig. 1), which may be read in conjunction with Van Heerden's published photographs, shows that the pattern of dermal bones is typically amphibian and quite unlike that of *Procolophon*, as too are the teeth. The conclusion is reached that the specimen (QR 1597) shows normal bones of the skull and is not a skin impression.

In the collection of the Bernard Price Institute there are at least three small skulls pertaining to an as yet undescribed amphibian, which have been collected in association with *Procolophon* (B.P.I. Nos 1366, 2507, 2510). It was possible to split some of the extremely hard matrix off 2507, and after removing adhering bone with dilute HCl an impression was obtained identical to that attributed by Van Heerden to *Procolophon*.

The purpose of this note is simply to dispel the illusion of the existence of a piece of *Procolophon* skin, which, had it existed, would have held important implications.

I thank Jacques van Heerden for the loan of the specimen.

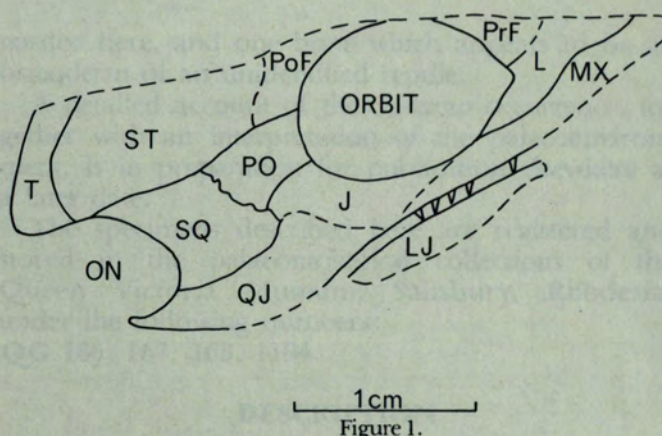


Figure 1.

REFERENCE

- VAN HEERDEN, J. (1974). A short note on some natural casts of the cotylosaurian reptile *Procolophon*. *Navors. nas. Mus. Bloemfontein* 2(12), 417-428.

LIST OF ABBREVIATIONS

J	jugal
L	lachrymal
LJ	lower jaw
MX	maxilla
ON	otic notch
PoF	postfrontal
PrF	prefrontal
PO	postorbital
QJ	quadratojugal
SQ	squamosal
ST	supratemporal
T	tabular

FOSSIL VERTEBRATE STUDIES IN RHODESIA: SPHENODONTID REMAINS FROM THE UPPER TRIAS OF RHODESIA

by

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INTRODUCTION

Small sphenodontid rhynchocephalians are known from the upper Trias in Britain (Robinson, 1973). This paper records for the first time the presence of sphenodontids of very similar age, size, and morphology from the Upper Trias of Rhodesia.

The material was recovered from a locality yielding concentrated coelurosaurian dinosaur remains in the Forest Sandstone (U. Triassic) of the Chitake River, Zambezi Valley, Rhodesia (16°07'S; 29°30'E). At least 26 individuals of the coelurosaurian genus *Syntarsus* have been recovered from a restricted site in the Chitake River exposure, the site evidently representing an ephemeral waterbody, or pan, in the arid Triassic landscape of that part of the country.

Although prosauropod dinosaur remains are common in the surrounding sediments they are absent from the immediate site of *Syntarsus* concentration. The only associated non-coelurosaurian remains in the "pan" are the sphenodontid jaws re-

corded here, and one bone which appears to be an osteoderm of an unidentified reptile.

A detailed account of the *Syntarsus* occurrence, together with an interpretation of the palaeoenvironment, is in preparation for publication elsewhere at a later date.

The specimens described here are registered and stored in the palaeontological collections of the Queen Victoria Museum, Salisbury, Rhodesia, under the following numbers:

QG 166, 167, 168, 1104.

DESCRIPTION

All of the sphenodontid material examined to date consists of broken lower jaws. The material is very well preserved and easily prepared with needles. Four of the best jaw fragments are shown in the camera lucida drawings in the accompanying figure (fig. 1).

QG 166 (fig. 1A) has three large conical acrodont

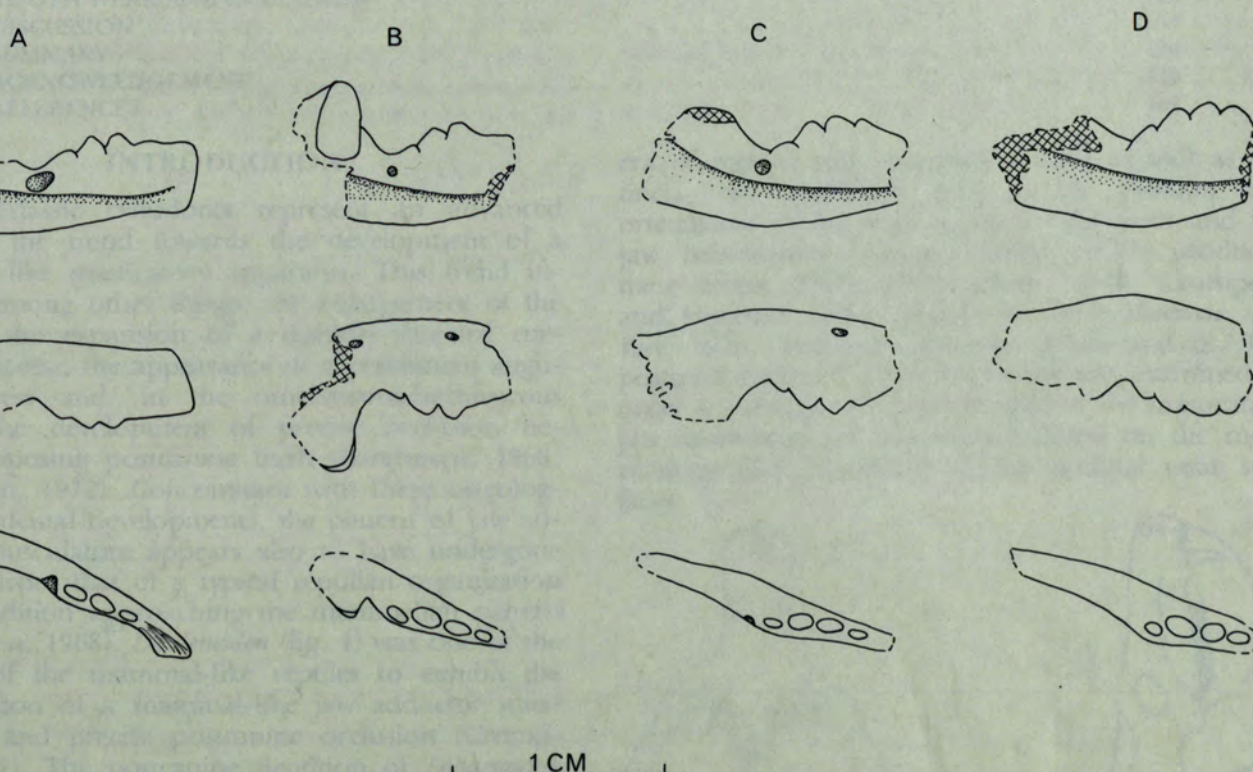


Figure 1. Sphenodontid lower jaws.

A QG 166 C QG 168

B QG 167 D QG 1104

All orientated with anterior ends to the right. Top to bottom, lingual, labial and occlusal views.

teeth followed by a large posterolabial pit from which the developing tooth has been lost (this pit is present in three of the four specimens, the size varying considerably). In QG 166 the symphyseal region of the jaw is undamaged; the anterior teeth have been obliterated by wear to leave a hard ridge or "beak".

QG 167 (fig. 1B) has three teeth and the recognisable base of a more anterior fourth. An intact coronoid bone is preserved in position in this specimen.

Jaws QG 168 and QG 1104 (fig 1 C & D) each have four large teeth. Four seems to be the maximum number of teeth recognisable at any time in these apparently mature individuals.

ROBINSON, P. L. (1973). A problematic reptile from the British upper Trias. *Jl. geol. Soc. Lond.*, **129**, 457-479.

——— (1976). How *Sphenodon* and *Uromastyx* grow their teeth

and use them. From *Morphology and Biology of Reptiles*. A de A'Beilairs & C. Barry Cox., Eds. Linn. Soc. Symp. ser. 3, 43-64.

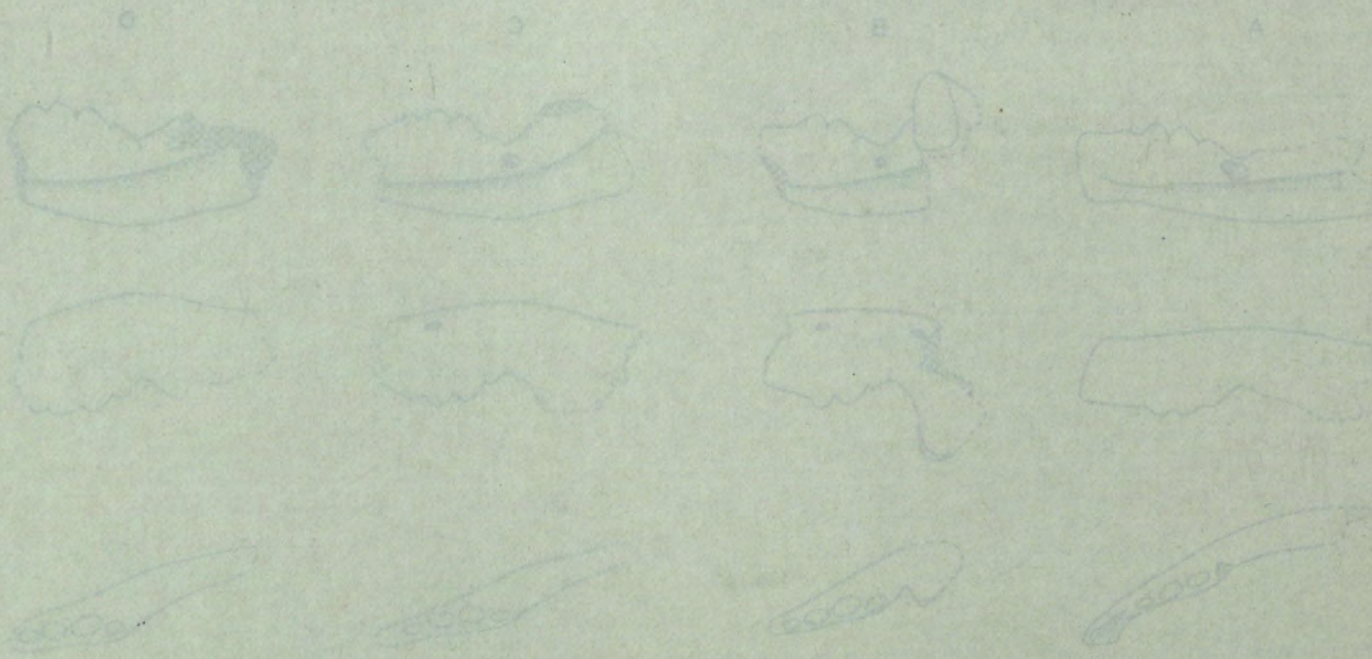
DISCUSSION

Compared with *Sphenodon* the tooth row in the new material is rather short, and the teeth, though fewer, are relatively much larger. This would suggest a rather shorter snout for the fossil form. These jaws correspond well with Robinson's (1973) description of the jaw of *Glevosaurus*.

The development of the dentition in *Sphenodon* has recently been elucidated fully by Robinson (1976). In the material described above anterior teeth are obliterated by wear, while the four large posterior teeth are added in sequence from the back as described by Robinson for *Sphenodon*.

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- ROBINSON, P. L. (1973). A problematic reptile from the British upper Trias. *Jl. geol. Soc. Lond.*, **129**, 457-479.
- (1976). How *Sphenodon* and *Uromastyx* grow their teeth and use them. From *Morphology and Biology of Reptiles*. A de A'Beilairs & C. Barry Cox., Eds. Linn. Soc. Symp. ser. 3, 43-64.



POSTCANINE TOOTH FUNCTION AND JAW MOVEMENT IN THE GOMPHODONT CYNODONT *DIADEMODON* (REPTILIA; THERAPSIDA)

by

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ABSTRACT

The postcanine dentition of *Diademodon* was well adapted, in both morphology and pattern of replacement, to exercising and maintaining precise occlusion. These teeth may be grouped into three morphological classes, consisting of conical, gomphodont and sectorial teeth. The anterior conicals may have acted as gripping teeth, and the posterior sectorials may have been utilized as food "tenderizers" or shredders, while the intermediate gomphodont teeth were utilized in the mastication of food items. The gomphodont teeth, which show evidence of heavy wear, were examined in the scanning electron microscope (SEM), in order to attempt a reconstruction of the masticatory jaw movements in this animal, based on the morphology and orientation of the occlusal wear facets. The occlusal surfaces of the gomphodont teeth are pitted. The pitted occlusal surface texture is an indication of either abrasion or attrition, resulting from direct pounding of the lower teeth against their maxillary antagonists. It is concluded that masticatory jaw movements in *Diademodon* were wholly orthal. There is no dental evidence to support the contention that this reptile exercised either propalinal (Hopson, 1971) or ectental chewing movements. The jaw closing action in *Diademodon* appears to have been equivalent to the masticatory power stroke.

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INTRODUCTION

The Triassic cynodonts represent an advanced stage in the trend towards the development of a mammal-like masticatory apparatus. This trend involved, among other things, the enlargement of the dentary, the expansion of a dorsally directed coronoid process, the appearance of a prominent angular process and, in the omnivorous-herbivorous forms, the development of precise occlusion between opposing postcanine teeth (Barghusen, 1968; Crompton, 1972). Concomitant with these osteological and dental developments, the pattern of jaw adductor musculature appears also to have undergone changes from that of a typical reptilian organization to a condition approaching the mammalian pattern (Barghusen, 1968). *Diademodon* (fig. 1) was one of the earliest of the mammal-like reptiles to exhibit the combination of a mammal-like jaw adductor musculature and precise postcanine occlusion (Crompton, 1972). The postcanine dentition of *Diademodon* was well adapted, in both morphology and pattern of replacement, to exercising and maintaining occlusion.

Numerous workers have shown, for various gen-

era of reptiles and mammals (extant as well as extinct), the correlation between the position and orientation of the wear facets on the teeth and the jaw movements during chewing which produced these facets (Mills, 1966; Every, 1970; Crompton and Hiiemae, 1970; Crompton, 1972; Hiiemae and Kay, 1973; Kay and Hiiemae, 1974a and b). The postcanine dentition of *Diademodon* was examined in order to attempt a reconstruction of the masticatory jaw movements in this animal, based on the morphology and orientation of the occlusal wear surfaces.

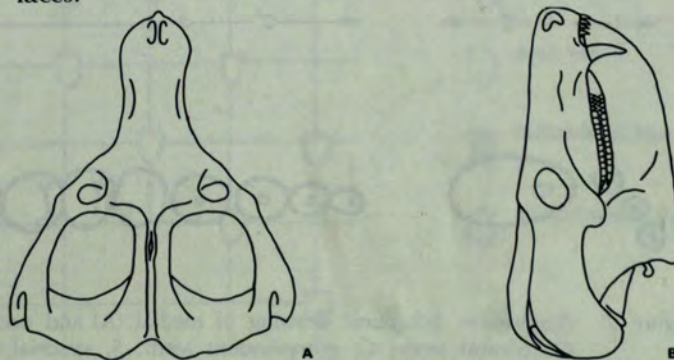


Figure 1. *Diademodon*. Dorsal (A) and lateral (B) views of the skull.

A moderately advanced cynodont, *Diademodon* is well known from the *Cynognathus* zone sediments of the Orange Free State and Cape Province, South Africa (Kitching, 1972). The fossil remains of this reptile have been recovered also from the Ntawere Formation, Upper Luangwa Valley, Zambia (Kitching, 1963; Brink, 1963a), and more recently from the Omingonde Mudstone Formation (Lower Etjo Beds) of South West Africa (Keyser, 1973). Thus *Diademodon* appears to have been late Early Triassic to early Middle Triassic in age (Du Toit, 1954; Cox, 1967; Keyser, 1973).

Tooth Morphology

The postcanine teeth of *Diademodon* may be grouped into three morphological classes (fig. 2). Conical teeth occupy the anterior end of the tooth row; behind these is a series of gomphodont teeth, and multicuspidate (sectorial) teeth constitute the posterior end of the tooth row.

The homodont, conical teeth are usually three to four in number. These teeth have been considered as "premolars" by several authors (e.g. Broom, 1905, 1913; Brink, 1955) by analogy with mammalian dentitions; but, in view of more recent work (Hopson, 1971) on the replacement of these teeth, it would appear that their classification as "premolars" is unwarranted. These homodont teeth do, however, appear to represent a morphological and morphogenetic class distinct from the gomphodont teeth; thus their classification as a discrete group, i.e. conical teeth, appears to be justified.

Like the conical teeth, the sectorial teeth at the back of the tooth row are also usually three to four in number. Each sectorial tooth is multicuspidate

and elongated mesio-distally. The crown is dominated by a large, somewhat recurved buccal cusp, and this is surrounded lingually by a well developed cingulum, which generally supports from five to seven small cusps. In overall morphology these teeth resemble the cheek teeth of the galesaurid *Thrinaxodon*. Fourie (1963) classified the sectorial teeth of *Diademodon* into two types — "sectorial" at the very back of the series (fig. 2, c and d) and, just anterior to these, "large sectorial" (fig. 2, b). From the most posterior to the most anterior tooth, however, this group of teeth exhibits an almost continuous morphological gradient, any one tooth being nearly indistinguishable from its immediate neighbour. It is unlikely, therefore, that these posterior teeth represent more than one morphological class or "tooth family". They are, however, morphologically distinct from the gomphodont series; thus their classification as a distinct rather homogeneous group, i.e. sectorial teeth, appears to be warranted.

The gomphodont teeth, the so-called "molars" of *Diademodon*, are fairly constant in general crown form or gestalt. The maxillary gomphodont teeth are consistently larger bucco-lingually than mesio-distally, i.e. they are broader than long; and unworn teeth possess a larger buccal cusp and a smaller lingual cusp, connected by a transverse crest. There are usually three to five small mesio-lingual, and three to five small disto-lingual accessory cusps surrounding the perimeter of the crown. These cusps were quickly obliterated by wear. The lower gomphodont crowns are generally circular in outline; the bucco-lingual dimension is usually slightly greater than the mesio-distal, but these two dimensions may be equal or, in some instances, the mesio-distal may exceed the bucco-lingual dimension. As

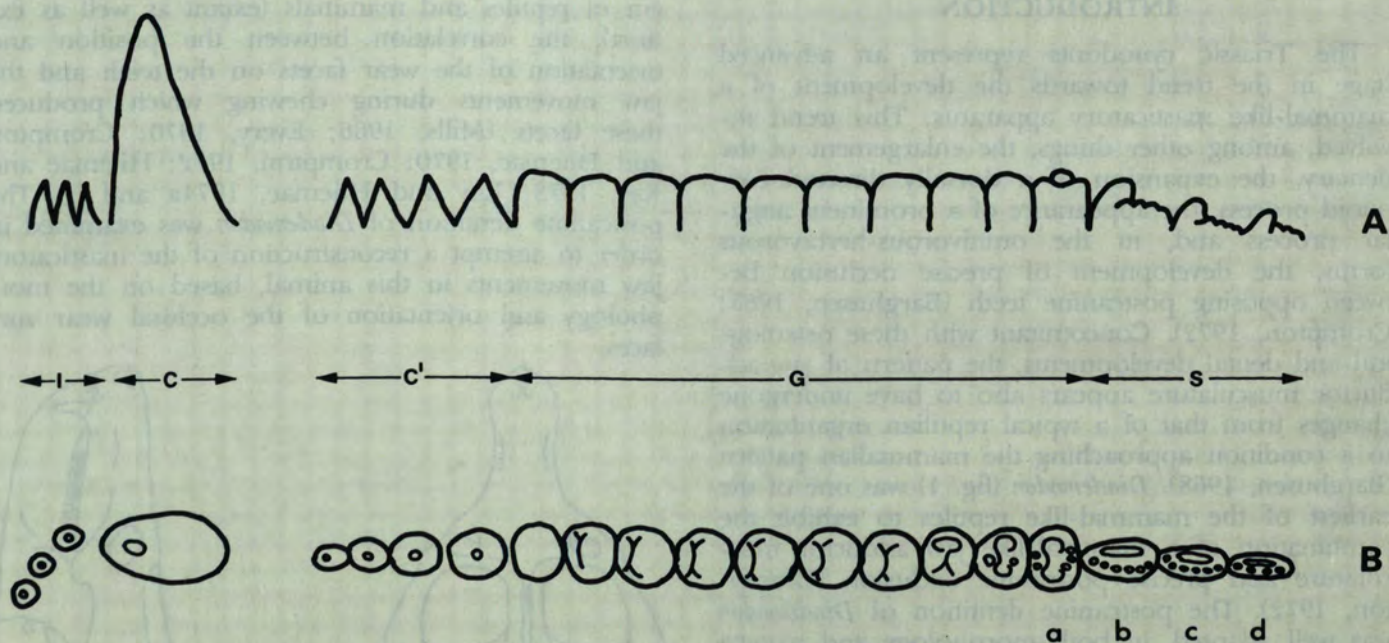


Figure 2. *Diademodon*. Schematic drawing of medial (A) and occlusal (B) views of the lower right dentition. I, incisors; C, canine; C', conical teeth; G, gomphodont teeth; S, sectorial teeth; a, intermediate gomphodont tooth; b, large sectorial tooth; c-d, sectorial teeth. See text for explanation.

in the upper gomphodont teeth, a moderately large buccal cusp and a subequal lingual cusp are present and connected by a low transverse ridge. A variable number of small peripheral cusps are usually present. The variations in position, size and number of these cingular accessory cusps on the gomphodont crown have been utilized by several authors (e.g. Seeley, 1894; Broom, 1932; Brink, 1955) as the foundation for numerous genera and species presently synonymized under *Diademodon tetragonus* (Hopson and Kitching, 1972). Fourie (1963) classified the most posterior teeth in the gomphodont series as "intermediate gomphodont". It appears that these "intermediate gomphodont" teeth are merely unworn, or very slightly worn, gomphodont teeth, the accessory cusps of which have not been effaced by wear. Morphologically and, by the latest evidence on replacement, morphogenetically, the "intermediate gomphodont" teeth are inseparable from the rest of the gomphodont group; thus their inclusion in the latter appears to be justified. The number of gomphodont teeth in *Diademodon* may vary greatly, from five to eleven, dependent on the size of the animal. The smaller (ontogenetically younger?) specimens usually possess fewer gomphodont teeth than do the larger specimens.

Tooth Replacement

Tooth replacement in *Diademodon* has been scrutinized by numerous workers (Broom, 1913; Parrington, 1936; Crompton, 1955, 1963b; Fourie, 1963;

Ziegler, 1969; Hopson, 1971; Osborn, 1974), resulting in varied conclusions concerning the detail and morphogenesis of the replacement pattern; but the gross pattern seems to be fairly well substantiated. Unlike the typical reptilian pattern of alternate replacement, *Diademodon* appears to have replaced teeth sequentially at the posterior end of each tooth class. The most anterior tooth of each class was shed and subsequently replaced by a tooth of the type in the preceding or immediately mesial class. Thus the most anterior sectorial tooth was shed and replaced by a gomphodont, and likewise, the most anterior gomphodont tooth was shed and replaced by a conical tooth. The most anterior conical tooth, however, was shed and was not replaced; rather, the vacated socket was "plugged" with bone (fig. 3). The conical and gomphodont tooth series both exhibit a size gradient, the most anterior tooth being considerably smaller than the most posterior tooth of each class (fig. 4). It seems reasonable to assume, therefore, that the conical and gomphodont teeth of each succeeding replacement generation were larger than those of the preceding generation (fig. 3). Thus, as replacement proceeded, the teeth became larger with each subsequent generation; in a teleological sense, the size of the teeth thus kept with the size of the animal possessing them.

As a result of this mode replacement, the more anterior teeth of each tooth class were exposed to the rigours of mastication for a longer period of time than those at the back of the series. This accounts for the often observed gradient of wear along

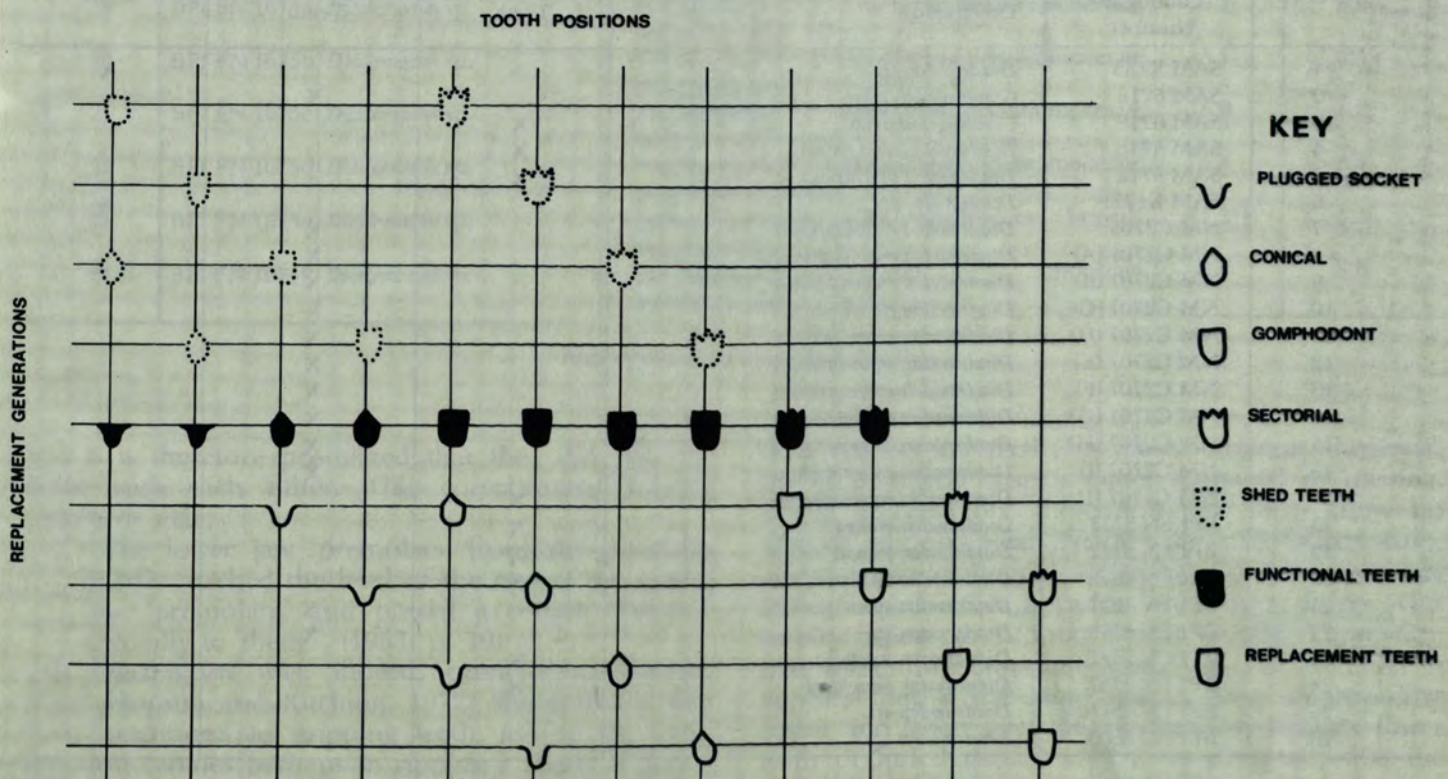


Figure 3. *Diademodon*. Schematic diagram of postcanine tooth replacement. Modified from Osborn, 1974. See text for explanation.

the gomphodont tooth row (fig. 4). Sequential replacement is a prerequisite for precise occlusion (Hopson, 1971). The relevance of sequential replacement to the mechanics of mastication in *Diademodon* will be discussed later.

MATERIALS AND METHODS

The maxillary and mandibular postcanine teeth of 26 different *Diademodon* specimens housed in the South African Museum, Cape Town, the National Museum, Bloemfontein and the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, were examined with either a hand lens or a binocular dissecting microscope under strong, oblique light (table 1). Neither the conical nor the sectorial teeth evinced any sign of occlusal wear, whereas the gomphodont teeth showed evidence of heavy masticatory use. Thus the gomphodont teeth were further scrutinized in the scanning electron microscope (SEM).

Fifty-one peels were made of the occlusal surfaces of both maxillary and mandibular gomphodont teeth, from 18 different *Diademodon* specimens. Peels were made of only those teeth which had been mechanically prepared and were entirely free of matrix. The peels were made using Xantopren impression material combined with Xantopren "soft" hardener catalyst. This material yields reliable results at magnifications up to 200x in the scanning electron microscope. Of these peels, some 22 were

chosen for examination (table 2). The peels were trimmed, cleaned for 15 minutes in an ultrasonic bath of 95 % ethanol, mounted and then coated with gold and palladium for examination.

Three isolated and broken gomphodont teeth from the collection in the Bernard Price Institute for Palaeontological Research (BPI FN 1675a, b and c) were chosen for direct examination in the SEM. Two of the specimens possessed fragmented, uneven root tips, and these ragged portions were cut-off and ground flat to facilitate mounting. The teeth were then cleaned in an ultrasonic bath of 95% ethanol for from one to two hours, mounted and subsequently coated with gold and palladium for examination. The peels and actual specimens were examined in the Cambridge S4 Stereoscan microscope at the University of the Witwatersrand.

The sample teeth were orientated in the microscope at low magnification (20x), and examined at magnifications up to 200x (peels) and 1 000x (actual specimens) for observation of occlusal wear.

TOOTH WEAR AND OCCLUSION

In the majority of specimens examined, the conical teeth are either damaged or, more often, missing as a result of post-mortem trauma. When present, however, these teeth evince no indication of wear;

Table 1
List of specimens examined with intact postcanine teeth.

Specimen	Institution Catalogue Number	Taxonomic Designation	Maxillary Teeth	Mandibular Teeth	Both
1	SAM K185	<i>Diademodon</i> sp.			X
2	SAM 6216	<i>Gomphognathus</i> sp.		X	
3	SAM 6219	<i>Gomphognathus</i> sp.	X		
4	SAM 571b	<i>Diademodon tetragonus</i>	X		
5	SAM 571a	<i>Diademodon brachytisus</i>	X		
6	SAM K177	<i>Diademodon</i> sp.			X
7	NM C2705	<i>Diademodon entomophonus</i>		X	
8	NM C2707 (A)	<i>Diademodon entomophonus</i>		X	
9	NM C2707 (B)	<i>Diademodon entomophonus</i>		X	
10	NM C2707 (C)	<i>Diademodon entomophonus</i>		X	
11	NM C2707 (D)	<i>Diademodon entomophonus</i>		X	
12	NM C2707 (E)	<i>Diademodon entomophonus</i>		X	
13	NM C2707 (F)	<i>Diademodon entomophonus</i>		X	
14	NM C2707 (G)	<i>Diademodon entomophonus</i>		X	
15	NM C2707 (H)	<i>Diademodon entomophonus</i>		X	
16	NM C2707 (I)	<i>Diademodon entomophonus</i>		X	
17	NM C2707 (J)	<i>Diademodon entomophonus</i>	X		
18	BPI FN 3773	<i>Diademodon browni</i>	X		
19	BPI FN 3772	<i>Diademodon browni</i>	X		
20	BPI FN 4652	<i>Diademodon</i> sp.	X		
21	BPI FN 4647	<i>Diademodon</i> sp.		X	
22	BPI FN 1169	<i>Diademodon</i> sp.		X	
23	BPI FN 2522	<i>Diademodon mastacus</i>	X		
24	BPI FN 3757	<i>Diademodon haughtoni</i>	X		
25	BPI FN 1675a-f	<i>Diademodon</i> sp.			X
26	BPI FN 2665	<i>Diademodon</i> sp.		X	

Abbreviations: SAM, South African Museum; NM, National Museum; BPI FN, Bernard Price Institute for Palaeontological Research, Field Number.

Table 2
List of the specimens and teeth examined in the scanning electron microscope.

Specimen	Institution Catalogue Number	Taxonomic Designation	Locality	Tooth Type	Wear	M-D Diameter	B-L Diameter
1	SAM K185	<i>Diademodon</i> sp.	Beersheba, Burghersdorp	upper gomphodont	slight	6,4	9,3
2	SAM 6216	<i>Gomphognathus</i> sp.	Sesamondon spot, Aliwal North	lower gomphodont	heavy	6,6	(6,7)
3	SAM 6219	<i>Gomphognathus</i> sp.	Aliwal North	upper gomphodont	heavy	6,5	10,8
4	SAM 571b	<i>Diademodon tetragonus</i>	Wonderboom	upper gomphodont	absent	4,5	5,4
5	SAM 571b	<i>Diademodon tetragonus</i>	Wonderboom	upper gomphodont	absent	4,8	6,2
6	SAM 571a	<i>Diademodon brachytisus</i>	Wonderboom	upper gomphodont	slight	4,1	6,0
7	SAM 571a	<i>Diademodon brachytisus</i>	Wonderboom	upper gomphodont	slight	3,9	5,5
8	SAM K177	<i>Diademodon</i> sp.	Waternat, Burghersdorp	lower gomphodont	heavy	5,0	5,3
9	SAM K177	<i>Diademodon</i> sp.	Waternat, Burghersdorp	lower gomphodont	heavy	5,0	6,2
10	SAM K177	<i>Diademodon</i> sp.	Waternat, Burghersdorp	lower gomphodont	heavy	5,4	6,6
11	SAM K177	<i>Diademodon</i> sp.	Waternat, Burghersdorp	lower gomphodont	heavy	7,7	7,6
12	NM C2705	<i>Diademodon entomophonus</i>	Nooitgedacht, Burghersdorp	lower gomphodont	slight	6,8	7,5
13	NM C2705	<i>Diademodon entomophonus</i>	Nooitgedacht, Burghersdorp	lower gomphodont	slight	7,0	8,1
14	NM C2707(A)	<i>Diademodon entomophonus</i>	Nooitgedacht, Burghersdorp	lower gomphodont	moderate	5,8	5,6
15	NM C2707(A)	<i>Diademodon entomophonus</i>	Nooitgedacht, Burghersdorp	lower gomphodont	moderate	6,3	6,5
16	NM C2707(I)	<i>Diademodon entomophonus</i>	Nooitgedacht, Burghersdorp	lower gomphodont	moderate	5,4	4,6
17	NM C2707(J)	<i>Diademodon entomophonus</i>	Nooitgedacht, Burghersdorp	upper gomphodont	heavy	5,0	5,9
18	NM C2707(J)	<i>Diademodon entomophonus</i>	Nooitgedacht, Burghersdorp	upper gomphodont	heavy	5,7	7,5
19	BPI FN 1675a	<i>Diademodon</i> sp.	Nooitgedacht, Burghersdorp	lower gomphodont	moderate	6,1	5,8
20	BPI FN 1675b	<i>Diademodon</i> sp.	Nooitgedacht, Burghersdorp	upper gomphodont	moderate	(5,1)	6,5
21	BPI FN 1675c	<i>Diademodon</i> sp.	Nooitgedacht, Burghersdorp	upper gomphodont	moderate	6,0	8,8
22	BPI FN 1675d	<i>Diademodon</i> sp.	Nooitgedacht, Burghersdorp	lower gomphodont	moderate	5,4	5,5
23	BPI FN 1675e	<i>Diademodon</i> sp.	Nooitgedacht, Burghersdorp	lower gomphodont	heavy	(5,2)	5,3
24	BPI FN 1675f	<i>Diademodon</i> sp.	Nooitgedacht, Burghersdorp	(?)lower gomphodont	moderate	6,3	5,0

Abbreviations same as for Table 1.

and it is therefore postulated that they did not occlude with each other. This corroborates Brink's statement that:

"The lower jaw 'premolars' [conicals] generally hardly reached the level of the tips of the upper jaw 'premolars' and passed a certain distance medially to them". (1955, p. 19)

If *Diademodon* was, indeed, omnivorous (Brink, 1955; Hopson and Kitching, 1972), the conicals may have functioned as gripping teeth, aiding the incisors and canines perhaps in ripping a piece of fleshy tissue from a carcass.

Generally, the sectorial teeth are better preserved

than the conical teeth; in many instances, however, the large buccal cusp is either damaged or missing. Upon examination, these posterior teeth show no signs of occlusal wear. Neither the large buccal cusp, nor the smaller lingual accessory cuspules evince any indication of either abrasion or attrition facets. This would appear to support Fourie's (1963) contention that these multicuspidate teeth did not occlude. It appears that if the large buccal cusps of opposing upper and lower teeth did, in fact, overlap, the lower teeth occluded medial to the uppers, such that the occlusal surfaces of opposing teeth never contacted one another. The multicuspidate sectorial teeth

probably served to "tenderize" or perhaps shred a food bolus as it passed to the back of the jaw from the chewing battery of gomphodont cheek teeth.

The gomphodont series of teeth was responsible for the mastication of food items. As pointed out above, this series of cheek teeth exhibits a gradient of wear from the heavily worn most anterior teeth to the newly erupted, unworn, posterior gomphodonts (fig. 4).

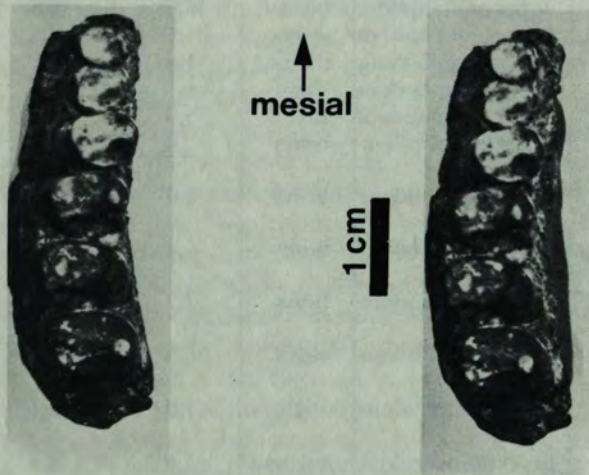


Figure 4. Stereophotograph of the left maxillary gomphodont teeth showing the heaviest wear on the lingual side of the crowns. NM C2707 J. Note the gradient of wear from the heavily worn anterior teeth to the slightly worn posterior teeth. The most anterior tooth is probably the first gomphodont; the erupting tooth at the posterior end of the row is a sectorial.

When the gomphodont teeth occluded, the upper overlapped the lowers both buccally and lingually; the lowers fitted into the embrasure formed between the transverse crests of adjacent upper teeth (Crompton, 1972) (fig. 5 A). This difference in size between the transversely broadened upper and circular lower crowns is perhaps significant, in as much as it may have permitted a rather liberal expression of mandibular adduction. That is, closing of the jaws could feasibly have brought the lower teeth into occlusion with their maxillary antagonists, several millimetres buccal (fig. 5 B) or lingual (fig. 5 C) to what might be termed the point of central occlusion, and an effective occlusal relationship still would have resulted. This situation may, perhaps, be correlated with the relative development (mass) and differentiation of the various jaw adductor muscle groups. Possibly, the jaw adductor musculature of *Diademodon* was incapable of performing the complex, controlled movements which are characteristically expressed in mammalian mastication (Grine, in preparation).

Brink (1955) noted that:

"the lower jaw 'molars' [gomphodont teeth] wear over the whole of their surfaces, while the upper jaw 'molars' wear only over the middle of the crowns". (p. 19)

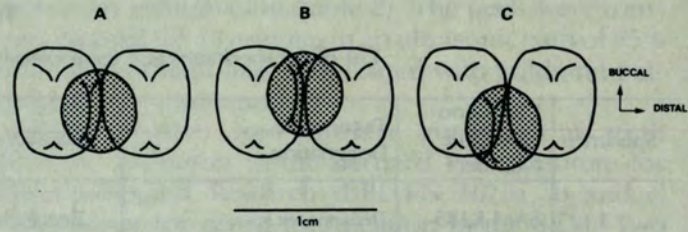


Figure 5. Dorsal view of the occlusal relationships between upper and lower gomphodont teeth. The lower tooth is shaded. A, "central" occlusal relationship; B, possible relationship with lower tooth occluding buccal of "central"; C, possible relationship with lower tooth occluding lingual of "central". See text for explanation.

Examination of *Diademodon* maxillae containing gomphodont teeth revealed, however, a number of specimens with teeth worn disproportionately on the buccal side (e.g. BPI FN 2522), and several specimens exhibiting heavier lingual wear on the gomphodont teeth (cf. fig. 4). It is not clear at present what, if any, taxonomic, ontogenetic or ecological significance these differences in gomphodont tooth wear among various specimens might indicate.

The occlusal surface relationships between unworn opposing upper and lower gomphodont teeth were not precisely matched. The cusps, crests and accessory cuspules did not exhibit the complex occlusal relationships which characterize the homologous structures of mammalian molar teeth. Rather, in *Diademodon* effective matching wear surfaces were produced only after considerable wear (Crompton, 1972); thus in those teeth exhibiting slight to moderate wear (fig. 6 B and C respectively), precise occlusion was manifested. The enamel covering the

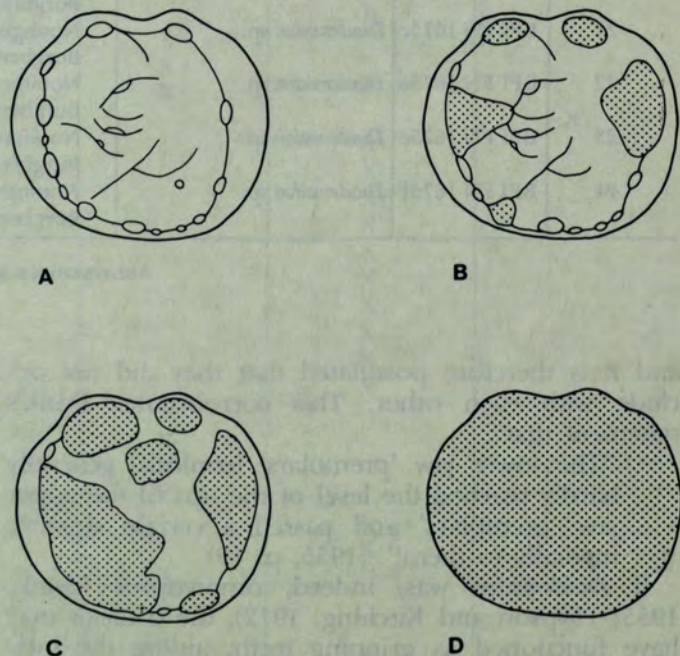


Figure 6. Lower gomphodont teeth in various stages of wear. A, unworn; B, slightly worn; C, moderately worn; D, heavily worn. Not to scale. Drawings by C. Gow.

gomphodont crown is thin, and probably non-prismatic (Poole, 1956; Moss, 1969), and as a result it was rapidly worn away; thus the occlusal surfaces of these teeth were quick to expose dentine. The main cusps and transverse crests of both upper and lower gomphodonts retained the thin enamel covering longer than the rest of the occlusal surface (fig. 7); however, continued wear rapidly obliterated all traces of occlusal surface morphology, resulting in featureless, flat-surfaced crowns pounding against one another. With time these teeth were shed sequentially, and replaced by conical teeth.

The occlusal surfaces of the gomphodont teeth, in various stages of wear (fig. 6), evince no indication of the presence of what might be called shearing surfaces (as indicated by wear facets possessing parallel striations or grooves). The only striations which are present are very short grooves running in a mesio-distal direction off the summit of the transverse crest in some slight to moderately worn teeth (fig. 8). These grooves are most likely an artefact of the imprecise matching of opposing occlusal faces in these teeth, and as such they can hardly be considered as representing an effective shearing surface (Crompton, 1972). The occlusal aspects of the gomphodont teeth characteristically reveal pitted, pock-marked surfaces (figs. 9; 10 A and C), an indication of either abrasion or attrition, resulting from direct pounding of the lower teeth against their maxillary antagonists. This corroborates Crompton's statement that the "external main cusp (actually the main buccal and lingual cusps and transverse crest) of the lowers pounded into the basin formed between two adjacent upper postcanines" (1972, p. 38); but no dental evidence exists to support his contention that vertical shearing planes were developed between the crests and cusps of the upper and lower gomphodont teeth.

Examination of the occlusal surfaces of worn gomphodont teeth in the SEM at high magnification (1 000x) yields pictures of surface textures which superficially resemble those encountered on aeolian sand grains (fig. 10 B and D). Neither the remnant enamel on the occlusal surfaces (fig. 7), nor the enamel on the sides of the tooth crowns (figs. 11 and 12), exhibited surface textures like that evinced by the dentine. Likewise, the cementum surfaces of the exposed roots of isolated gomphodont teeth, although showing more textural relief than the enamel surfaces, do not show the same rugged, pitted surfaces which characterize the occlusal dentine surfaces of the same teeth (fig. 12). Thus neither the enamel nor the cementum surfaces evince the same textural morphology as is found on the occlusal dentine surfaces of the selfsame teeth. It therefore seems reasonable to conclude that the dentine surface texture encountered on the worn gomphodont teeth is a result, primarily, of masticatory rigours, and is not an artefact of secondary, post-mortem processes such as sand-blasting, traction or freeze-fracturing.

Clearly then, the function of the gomphodont teeth was the preparation of food items for deglutition. The occlusal surfaces of these teeth indicate that the lower pounded against the uppers, thus crushing or pulverizing the food during mastication; and that the jaw movements which brought

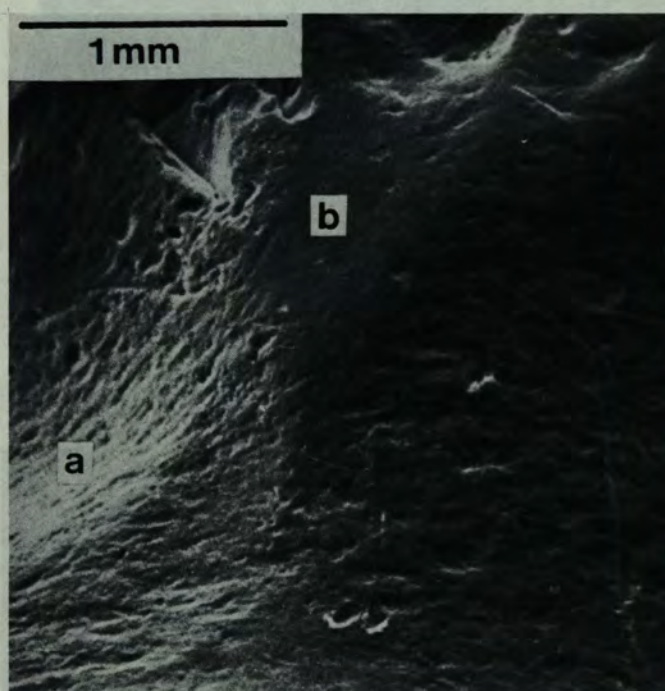


Figure 7. Scanning electron micrograph of the occlusal surface of a (? right) upper gomphodont tooth. The figure shows the pitted dentine surface, a, and the remnant of enamel covering the lingual cusp, b. Note the difference in surface textures. BPI FN 1675b. Oblique angle of 40° from the buccal side.

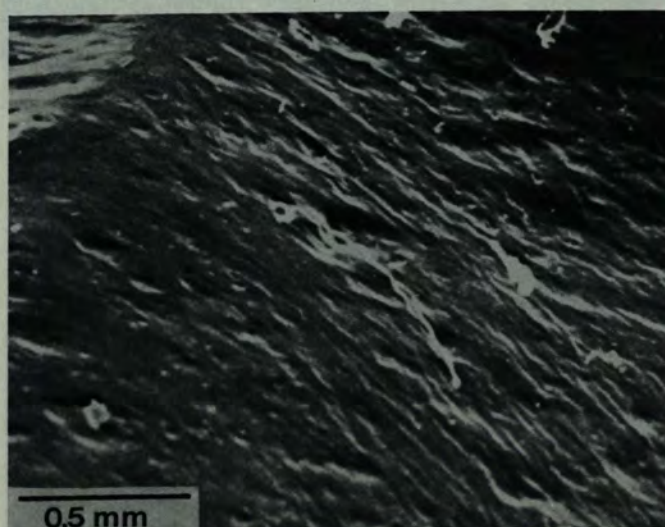
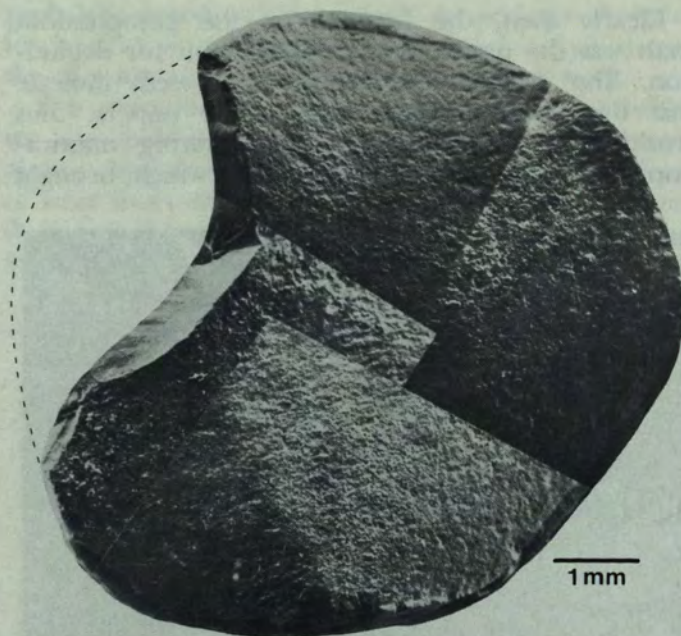


Figure 8. Scanning electron micrograph of a peel from the occlusal surface of a (? right) lower "intermediate" gomphodont tooth, exhibiting moderate wear. Note the grooves running off the summit of the transverse crest and the relatively smooth surface of the ridge. Note also that no grooves cross the summit of the crest. Oblique angle of 37°, taken from lingual side. BPI FN 1675f. Picture inverted in order to show surface in positive relief.



these teeth into occlusion were wholly orthal (that is, directly up and down). There is no dental evidence to support the contention that *Diademodon* exhibited propalinal (fore and aft) masticatory movements (Parrington, 1934, 1936; Hopson, 1971); nor is there any dental evidence to support the statement that a "postero-dorsally directed power stroke may have been initiated in *Diademodon*" (Crompton 1972). By the same token, the teeth evince no indication that this reptile exercised ectental (side to side) chewing movements, corroborating Brink's contention that "there could have been little lateral movement of the lower jaw when the jaw was closed" (1955, p. 19).

Figure 9. Composite scanning electron micrograph of the occlusal surface of a heavily worn (? right) lower gomphodont tooth. The outlined broken area represents post-mortem damage. Note the pitted surface texture of the dentine over the entire occlusal surface. BPI FN 1675a. Direct occlusal views.

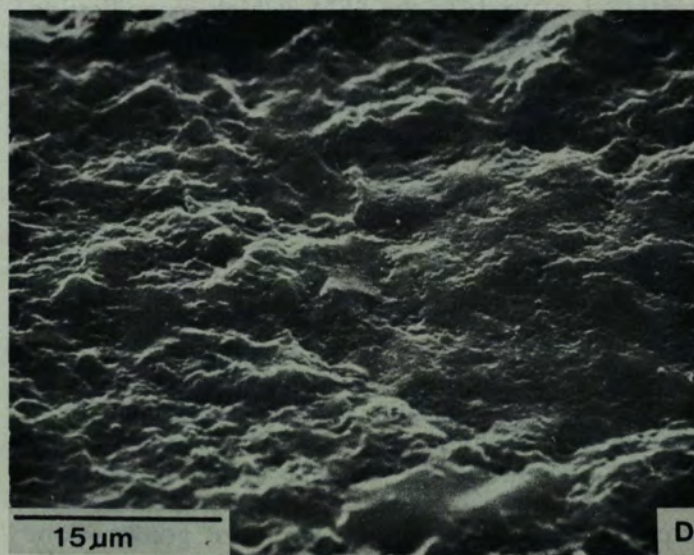
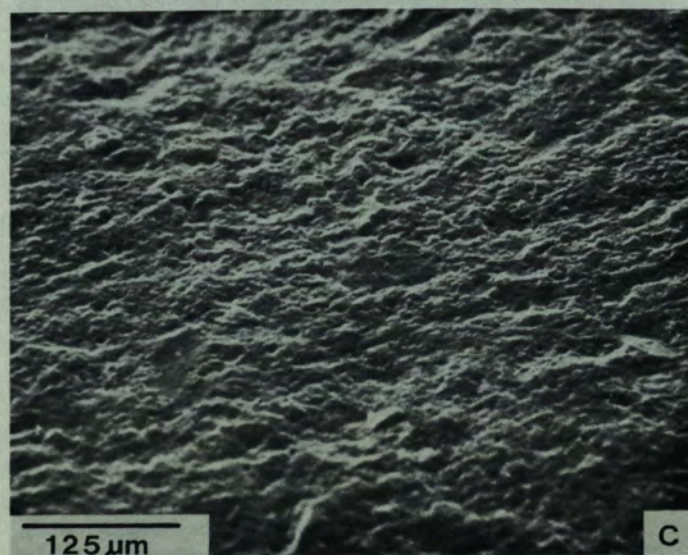
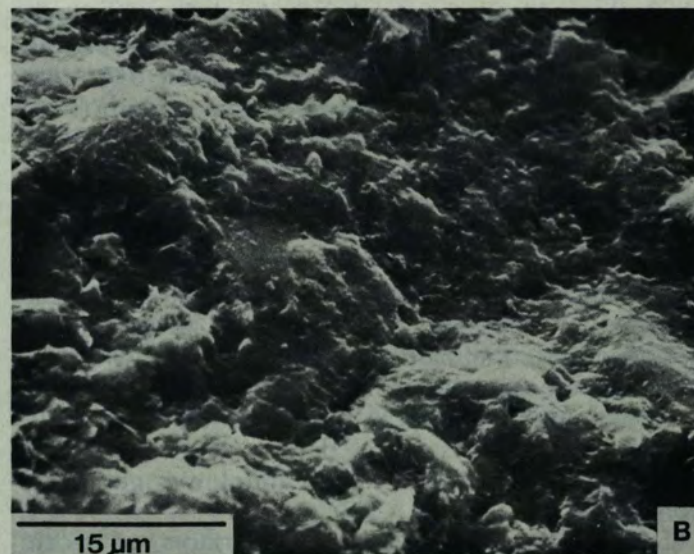
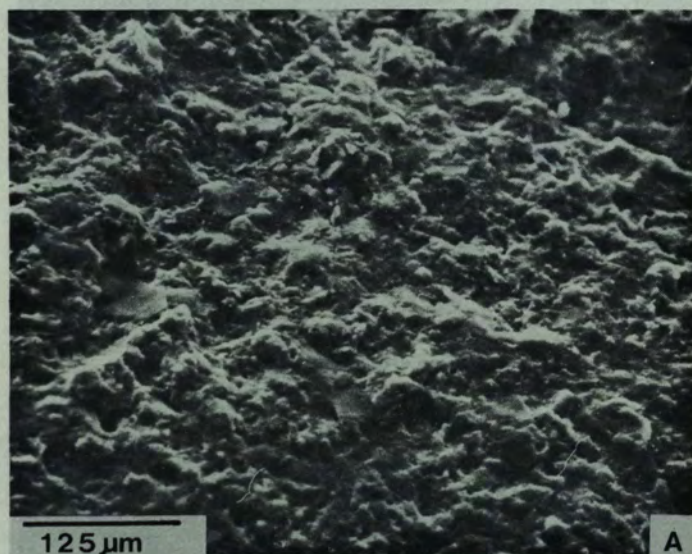


Figure 10. Scanning electron micrographs of the occlusal surface of the same tooth pictured in Figure 9. BPI FN 1675a. A, enlargement of area on the buccal (?) side of the tooth (see fig. 9), tilt angle of 25°; B, enlargement of the same area, tilt angle of 25°; C, enlargement of area on lingual (?) side of tooth, just distal to remnant of transverse crest, tilt angle of 25°; D, enlargement of the same area as shown in C, tilt angle of 25°.

The gomphodont teeth exhibited precise occlusion, in as much as the lower and upper teeth possessed matching wear faces; and the sequential replacement of these teeth permitted the maintenance of this type of occlusion. Furthermore, the shapes of the opposing upper and lower crowns, coupled with their mode of alternate occlusion (see fig. 5 A), may have served to retain their functional crown shapes for as long as possible under conditions of heavy, pounding wear. A similar mechanical design characterized the molariform teeth of the coelurosaur *Procolophon trigoniceps* (Gow, 1977).

DISCUSSION

The foregoing analysis of the occlusal surfaces of the postcanine dentition of *Diademodon* lends itself to the conclusion that masticatory jaw movements in this mammal-like reptile were wholly orthal. The pitted occlusal surfaces of the worn gomphodont teeth attest to an orthal movement of the lower jaw during chewing. The evidence against propalinal and ectental masticatory jaw movements in *Diademodon*, as gleaned from the dentition is, however, negative evidence. Several features of the cranium and lower jaw of *Diademodon*, however, do appear to provide further evidence against any significant propalinal or ectental jaw movements having been manifested in this animal during chewing.

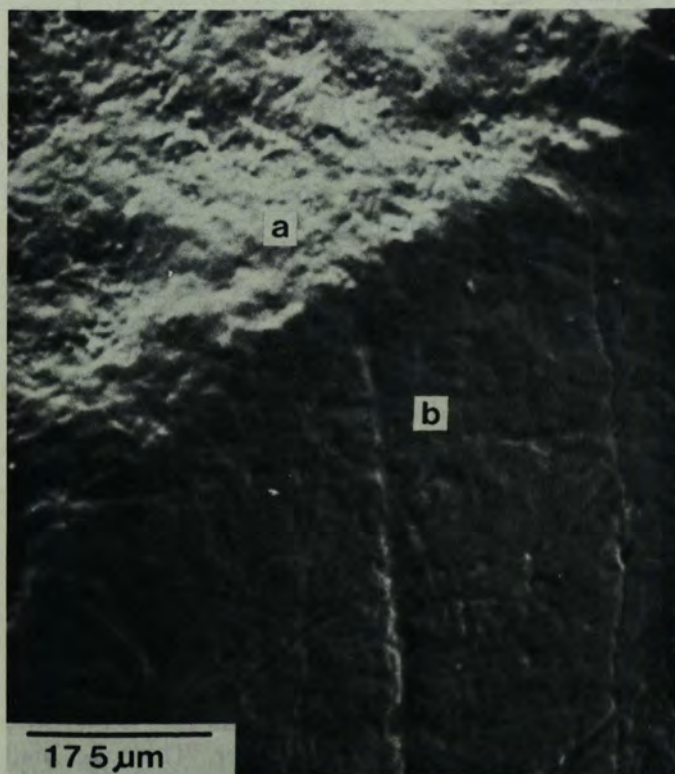


Figure 11. Scanning electron micrograph of an upper gomphodont tooth, showing the differences in surface textures between the occlusal dentine surface, a; and the non-occlusal enamel surface, b. BPI FN 1675c. Tilt angle of 51°, oblique from buccal.

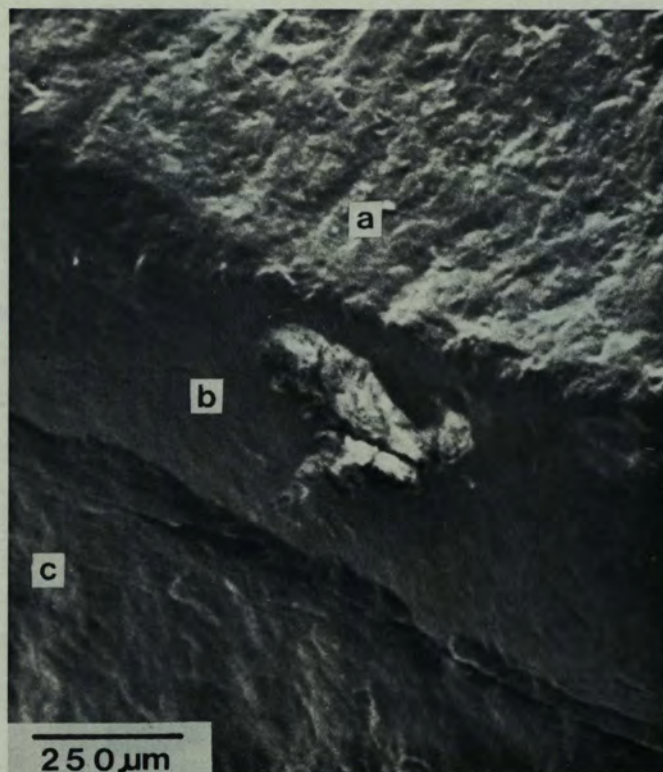


Figure 12. Scanning electron micrograph of an upper gomphodont tooth, showing the differences in surface textures between the occlusal dentine surface, a; the non-occlusal enamel surface, b; and the cementum surface, c. BPI FN 1675b. Tilt angle of 140°, oblique from buccal.

The anterior region of the hard palate possesses two fossae which housed the crowns of the lower canines when the jaws were closed. These excavations are located antero-medial to the maxillary canines, and postero-lateral to the incisive canal. The premaxilla contributes the anterior wall of each fossa, while the medial, lateral and posterior walls are formed by the maxilla (Brink, 1955, and personal observation). When the jaws are closed, such that the gomphodont teeth were in occlusion, much of the lower canine crowns would have been "locked" into these fossae. Although these palatal excavations are rather large, they would have been lined with oral epithelium, thus decreasing their diameters. The amount of movement that the lower canines would have enjoyed, once lodged in these fossae, would probably have been negligible; but it is debatable whether this "locking" of the lower canines would have effectively restricted either lateral or fore-aft masticatory movements.

The pterygoids support long, robust, ventrally directed flanges. These processes are situated just medial to the inner border of the lower jaw, and in life would have been covered with soft tissue (as would the inner border of the mandible), thereby placing the flanges in even closer juxtaposition with the medial sides of the lower jaw. Thus, the pterygoid flanges may have been situated close enough to the

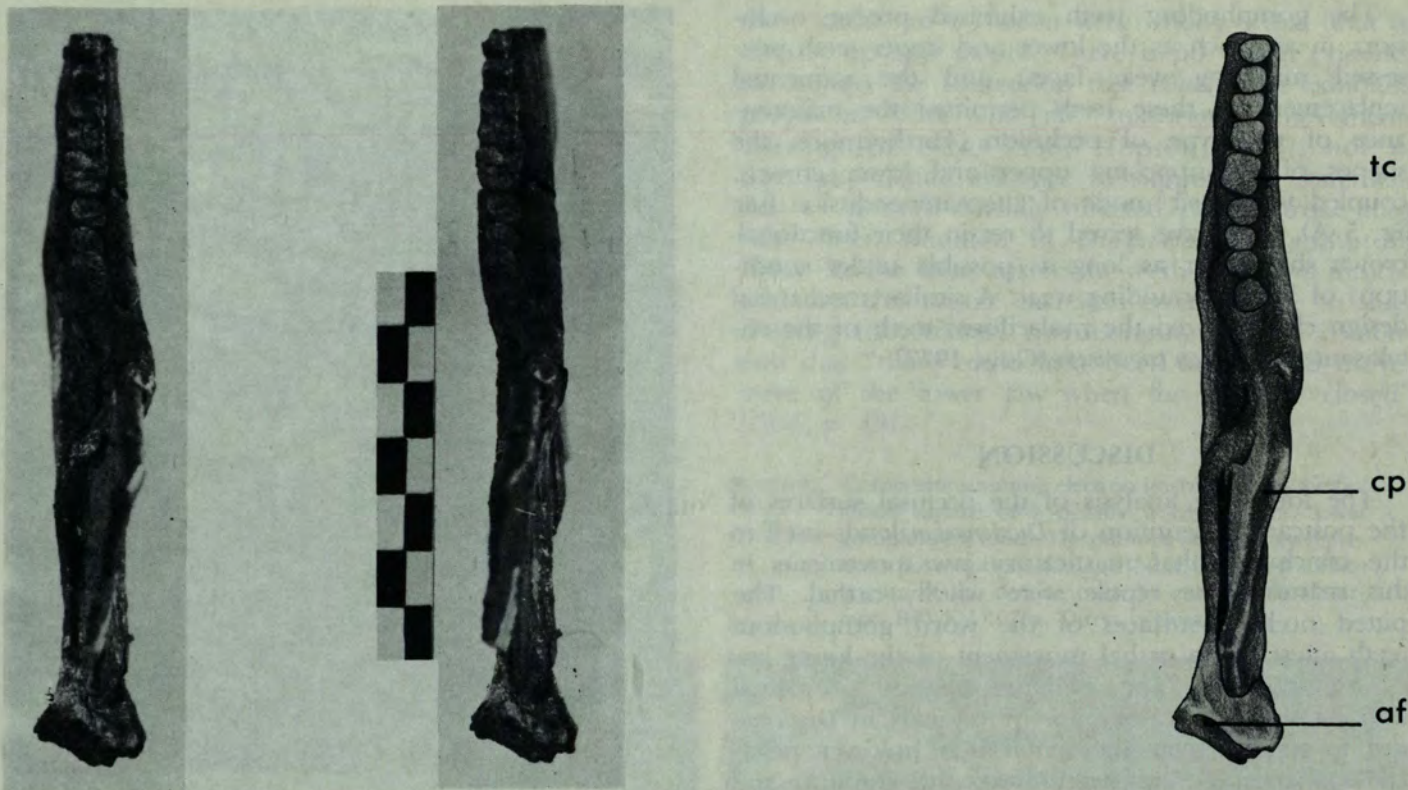


Figure 13. *Diademodon*. Left, stereophotograph of the right lower jaw; Right, drawing of same. Note the depth and orientation of the articular fossa; tc, tooth crown; cp, coronoid process; af, articular fossa. SAM K177. Scale in cm. Drawing by C. Richards.

inner sides of the lower jaw to have restricted effectively any gross lateral movement on the part of the mandible.

Finally, the jaw articulation in *Diademodon* is small compared to the size of the dentary. The articular bone possesses a divided, or double, glenoid fossa, consisting of a concave lateral fossa and a nearly flat medial fossa (Crompton, 1963b). The lateral fossa is elongated medio-laterally and convex from top to bottom; it is obliquely orientated, with the medial side higher and more anterior than the lateral side (fig. 13). It appears that only the lateral fossa articulated with the quadrate, and this articulation was probably rather weak (Crompton, 1963b). The structure and orientation of the lateral articular fossae are such that any lateral movement of the lower jaw (which possesses a very strongly fused symphysis) would have necessitated the dislocation of one of the joints. Similarly, in order to have effected propalinal jaw movement, both of the articular joints would have had to be dislocated. It appears, therefore, that the articular-quadrate joint in *Diademodon* was not constructed (adapted) so as to withstand either the movements or the resulting forces of lateral translation and rotation. Rather, the joint, by its construction and orientation, acted as a hinge (turning moment) for the lower jaw (fig. 14).

The mechanics of mandibular adduction in *Diademodon*, as determined by the relative development

and differentiation of the jaw adductor musculature, were such that little strain was placed on the relatively weak jaw joint. The pattern of sequential tooth replacement may have contributed also to a lessening of the stresses placed on the articular-quadrate joint and, at the same time, may have increased the efficiency of mastication.

Replacement at the posterior end of the tooth row, coupled with sequential loss of gomphodont teeth and their replacement by conical teeth at the anterior end of the row, perhaps served effectively to move the tooth row posteriorly, concomitantly with the growth of the dentary, thus maintaining younger (that is, relatively unworn) gomphodont teeth in the region of greatest occlusal pressure (fig. 14). Assuming the "bite point", or centre of greatest occlusal pressure, to be located near (probably slightly posterior to) the middle of the gomphodont series (fig. 14 BP), this point would have been moved posteriorly one tooth position with each replacement of sectorial teeth by gomphodont teeth. Owing to continuous, and possibly fairly rapid replacement, the bite point would have effectively moved posteriorly as the jaws grew larger and longer. Thus the load arm of the lower jaw (fig. 14 L) would have maintained a fairly constant length even as the tooth-bearing portion of the dentary enlarged. By the same token, it is possible that the pressure exerted at the bite point may have been increased as this point

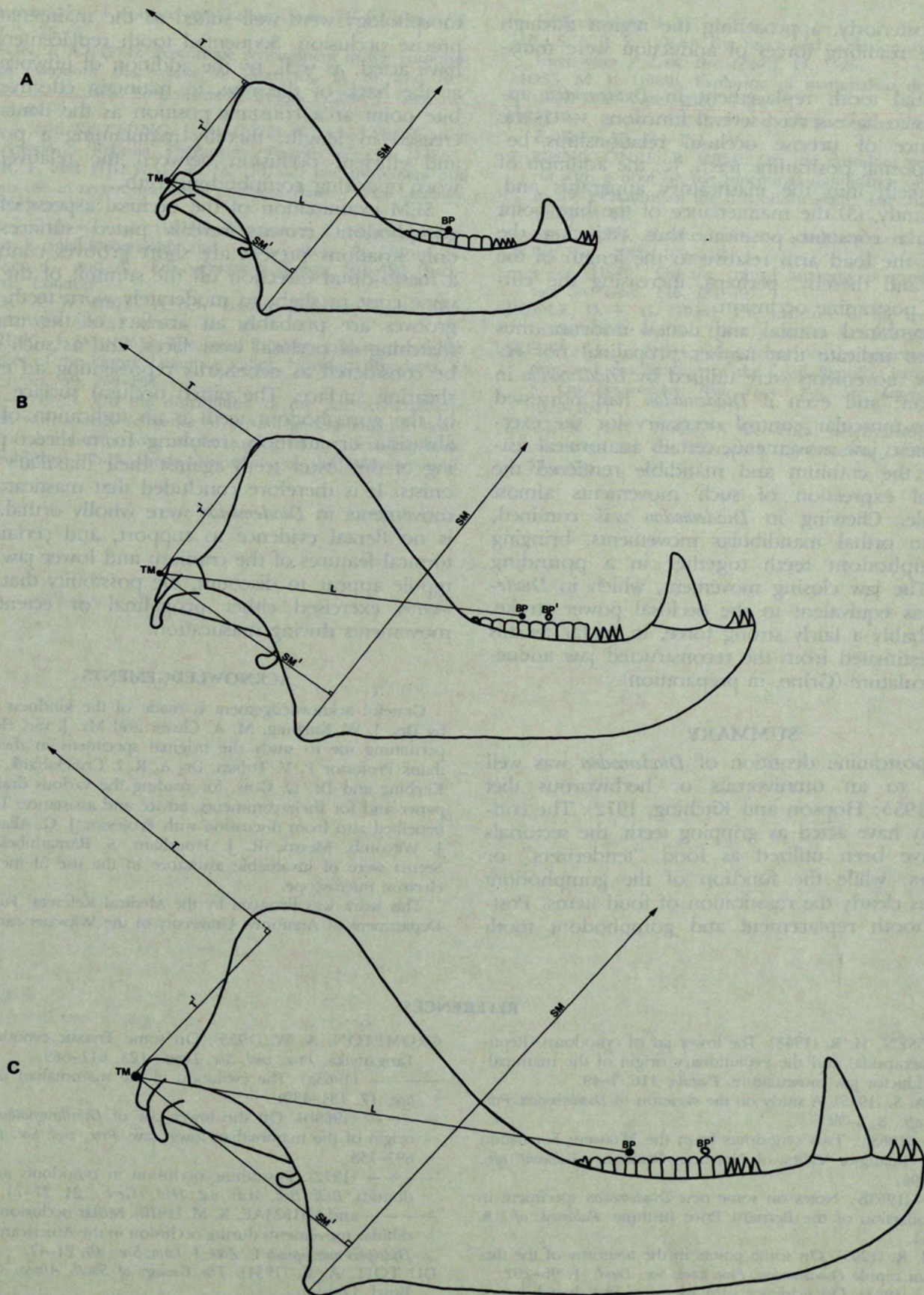


Figure 14. *Diademodon*. The correlation between sequential tooth replacement and jaw growth. A, hypothetical lower jaw of a young individual; B, lower jaw of an individual 1.33x larger, indicating the relative positions of the "static" bite point, BP' and the "actual" (moved) bite point BP; C, lower jaw of an individual 1.33x larger, indicating the relationships between the two bite points. BP, "actual" bite point; BP' "static" bite point; L, load arm of the jaw to bite point; SM, moment arm of *M. masseter superficialis*; SM', power arm of SM; T, moment arm of *M. temporalis*; T', power arm of T; TM, turning moment of the lower jaw. Lower jaw from Crompton (1963b). See text for explanation.

moved posteriorly, approaching the region through which the resulting forces of adduction were translated.

Sequential tooth replacement in *Diademodon* appears thus to have served several functions — (1) the maintenance of precise occlusal relationships between opposing postcanine teeth, (2) the addition of unworn teeth into the masticatory apparatus and, concomitantly, (3) the maintenance of the bite point at a fairly constant position, thus reducing the length of the load arm relative to the length of the dentary, and thereby, perhaps, increasing the efficiency of postcanine occlusion.

The combined cranial and dental evidence thus appears to indicate that neither propalinal nor ectental jaw movements were utilized by *Diademodon* in mastication; and even if *Diademodon* had possessed the neuro-muscular control necessary for the exercise of these jaw movements, certain anatomical features of the cranium and mandible rendered the functional expression of such movements almost impossible. Chewing in *Diademodon* was confined, rather, to orthal mandibular movements, bringing the gomphodont teeth together in a pounding action. The jaw closing movement, which in *Diademodon* was equivalent to the occlusal power stroke, was probably a fairly strong force, in so far as this can be estimated from the reconstructed jaw adductor musculature (Grine, in preparation).

SUMMARY

The postcanine dentition of *Diademodon* was well adapted to an omnivorous or herbivorous diet (Brink, 1955; Hopson and Kitching, 1972). The conicals may have acted as gripping teeth, the sectorials may have been utilized as food "tenderizers" or shredders; while the function of the gomphodont teeth was clearly the mastication of food items. Postcanine tooth replacement and gomphodont tooth

morphology were well suited to the maintenance of precise occlusion. Sequential tooth replacement may have acted, as well, by the addition of unworn teeth at the back of the row, to maintain effectively the bite point at a constant position as the dentary increased in length, thereby maintaining a powerful and efficient occlusion between the relatively unworn opposing gomphodont teeth.

SEM examination of the occlusal aspects of worn gomphodont crowns reveals pitted surfaces. The only striations present are short grooves running in a mesio-distal direction off the summit of the transverse crest in slight to moderately worn teeth. These grooves are probably an artefact of the imprecise matching of occlusal wear faces, and as such cannot be considered as necessarily representing an effective shearing surface. The pitted occlusal surface texture of the gomphodont teeth is an indication of either abrasion or attrition, resulting from direct pounding of the lower teeth against their maxillary antagonists. It is therefore concluded that masticatory jaw movements in *Diademodon* were wholly orthal. There is no dental evidence to support, and certain anatomical features of the cranium and lower jaw of this reptile appear to discount, the possibility that *Diademodon* exercised either propalinal or ectental jaw movements during mastication.

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NEW SPECIES OF *PARMULARIUS* HOPWOOD AND *DAMALISCUS* SCLATER AND THOMAS (ALCELAPHINI, BOVIDAE, MAMMALIA) FROM MAKAPANGS GAT, AND COMMENTS ON FAUNAL CHRONOLOGICAL CORRELATION

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ABSTRACT

Two new species of Alcelaphini, based on fossils from the Makapansgat Limeworks, are described. One is an early member species of the extinct genus *Parmularius* Hopwood. The present description is the first record of a *Parmularius* from any southern African fossil site. The other new species belongs to *Damaliscus* Sclater and Thomas, and is closely related to the extinct *Damaliscus niro* (Hopwood). The phylogenetic relationships of the new species to other extant and extinct alcelaphines are discussed. Comparison with fossils of the same, and/or related, species elsewhere in Africa gives rise to comments on faunal chronological correlation.

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INTRODUCTION

Among new species described by Wells and Cooke (1956), in their extensive paper on fossil Bovidae from the Makapansgat Limeworks, are the first three named in this quote (op. cit., p. 48): "In point of numbers the Makapan fauna is dominated by four species, *Redunca darti*, *Phenacotragus vanhoepeni*, *Makapania broomi* and the wildebeest". (*P. vanhoepeni* was subsequently placed in the genus *Gazella* De Blainville by Wells, 1969.) In the more than 20 years since then, none of these three species has been recorded from any site outside the Transvaal, i.e. they remain unique to the local australopithecine-associated faunas (see Vrba, 1975). After seeing more material than was available at the time that Wells and Cooke were working, it has become clear to me that the remains of the fourth species, the "wildebeest" (loc. cit.) belong to a new species of the extinct alcelaphine genus *Parmularius*. The description which follows below is the first record of a *Parmularius* from any southern African fossil site. Although Gentry (1970b) tentatively assigned some Langebaanweg remains to *Parmularius*, he subsequently (pers. comm.) retracted his opinion. Three other species of the genus (see table 1) have to date been recorded in East African assemblages. It will be further discussed

below that the new *Parmularius* species was widely distributed in Africa.

It is no accident that the alcelaphine species, alone of the four most abundant Makapan bovid species, appears to have had a wide distribution (I agree with Gentry, 1970a, that *Makapania broomi* is an ovibovine, and not an alcelaphine as originally suggested by Wells and Cooke in 1956). Alcelaphine size and cursorial adaptation has resulted in high dispersal rates, as attested to by the trans-African distributions, apparently at any one time, of several past and present species (Vrba, 1978). This factor, together with a correlated high speciation rate (op. cit.), renders the group suitable for chronological correlation between fossil assemblages. At the base of the high alcelaphine dispersal and speciation rates lies the strong environmental specialization of this tribe for vegetationally open habitats. Alcelaphine frequencies in modern and (by fairly secure morphological extrapolation) fossil contexts serve as excellent ecological indicators (Vrba, 1974, 1975, 1976, n.d.).

Partridge has recently revised the stratigraphy of Makapansgat (as briefly outlined in Brock, McFadden and Partridge, 1977) and I refer in this paper to Members 1-5 of the Makapansgat Formation as described by him.

DESCRIPTION OF NEW SPECIES

The description of each new species is preceded by the relevant generic diagnosis. The diagnoses and horizons here given for the genera *Parmularius* and *Damaliscus* differ from those of Gentry and Gentry (1977) with respect to certain additions and several minor alterations. In a phylogenetic, or cladistic, analysis of recent and fossil Alcelaphini (Vrba, 1978) I concluded that the genera *Parmularius* and *Damaliscus* are more closely related to each other (i.e.

with a more recent common ancestry) than either is to any other published alcelaphine genus. The phylogenetic hypotheses for alcelaphine genera, and for species of the *Damaliscus-Parmularius* group, suggested in that paper (op. cit.) are reproduced in Figures 1 and 2.

Consultation with these cladograms, while reading the generic and specific diagnoses which follow below, will point out to the reader which of the diagnostic features constitute synapomorphies (i.e.

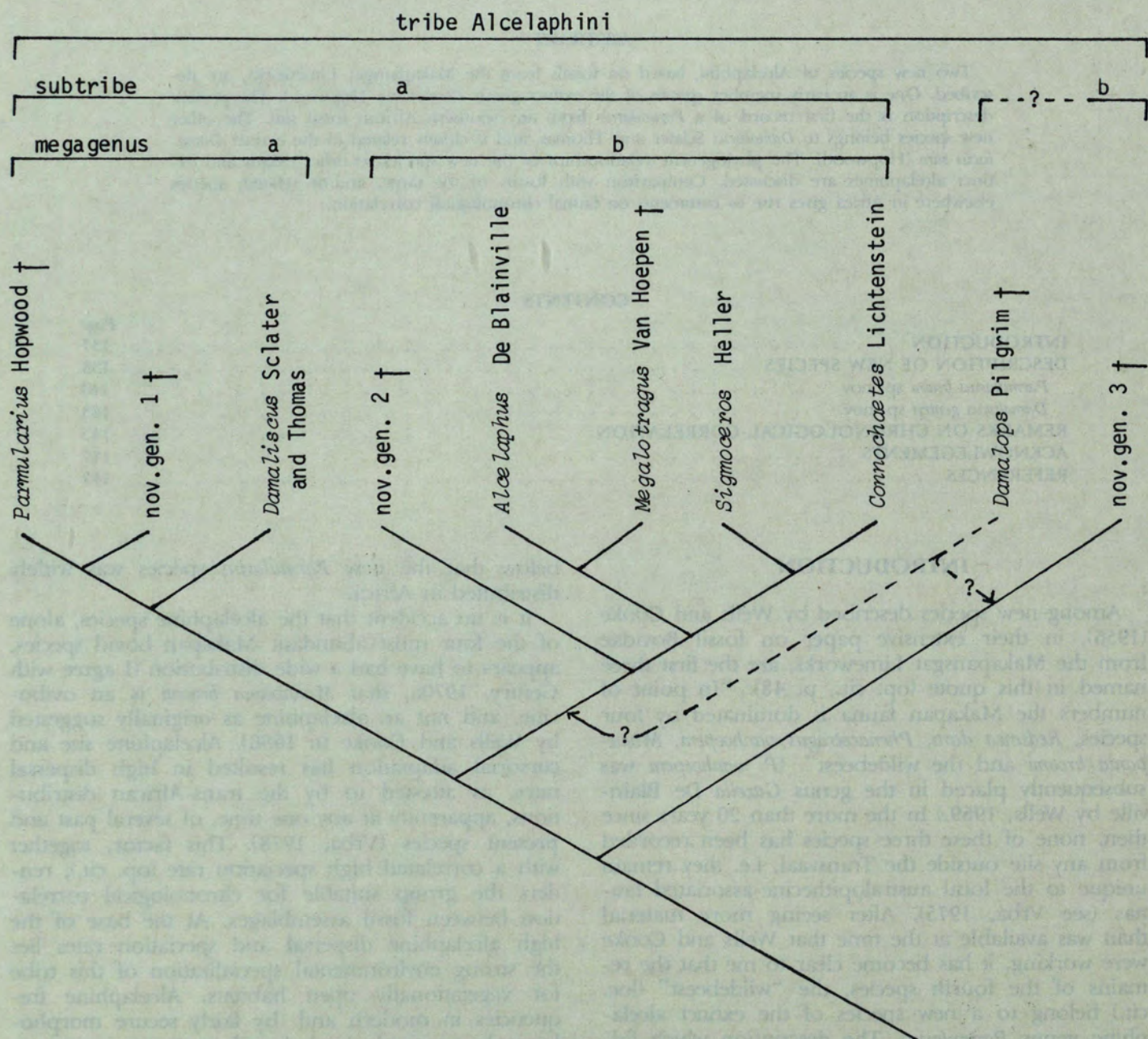


Figure 1. Phylogenetic relationships of alcelaphine genera (adapted from fig. 1 in Vrba, 1978).

nov.gen. 1 based on (Lit.) 1959.277, i.e. on nov.sp.A, from the Laetolil Beds;

nov.gen. 2 based either on a new species from the Hadar Formation, Ethiopia (specimen AL 208-7), or on a new species from the Laetolil Beds (specimen (Lit.) 1959.233).

nov.gen. 3 based on two new alcelaphine species (the only alcelaphine material) from Langebaanweg, Cape Province (material here referred to nov.gen. 1-3 is being studied by Dr. A. W. Gentry, who has kindly allowed me to refer to it prior to description).

† = extinct.

uniquely shared derived character states). Background to phylogenetic systematics may be found in Hennig (1966), Cracraft (1974), Griffiths (1972) and Nelson (1970).

Genus *Parmularius* Hopwood 1934

Type species *Parmularius altidens* Hopwood 1934

Generic diagnosis

Extinct medium-sized alcelaphines with high nar-

row skulls. Horn cores without torsion; generally not very compressed; the greatest basal horn core diameter is hardly angled to the metopic suture; horn cores inserted closely with little basal, but more distal, divergence; the presence of transverse ridges along the anterior horn core surface varies from moderately strongly marked along the entire horn core length to very weakly marked in the distal parts only; there are distinct localized basal horn core swellings situated either postero-laterally, pos-

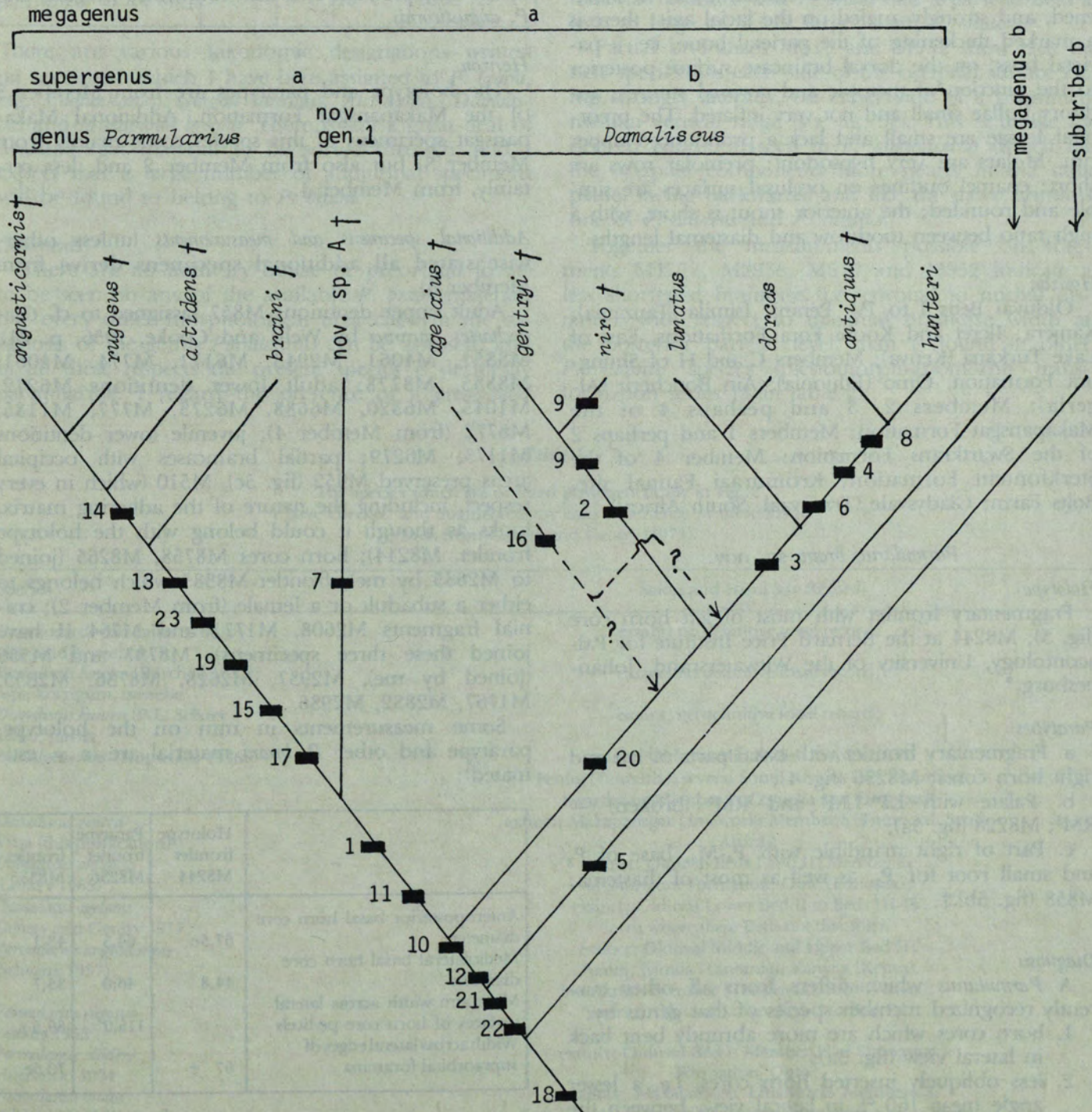


Figure 2. Phylogenetic relationships of species in the *Damaliscus-Parmularius* complex (i.e. megagenus a of fig. 1) (adapted from fig. 2 in Vrba, 1978).

■ = apomorphy, or derived character state, shared by species cluster below which it appears; apomorphies 1-23 as defined in Table 2; details of species are given in Table 1.

† = extinct.

teriorly, or postero-medially; in lateral view the horn core-pedicel boundary is oblique, being anteriorly higher than posteriorly (probably connected with the previous character of basal swelling). Horn pedicels are well defined, with near parallel sides, and are long. The basal horn core to orbit distance is long, partly resulting from pedicel length but also from elongation of the frontal anteriorly and laterally to the pedicels. The supraorbital foramina are not markedly far apart. The dorsal braincase, between coronal suture and nuchal crest, is shortened, and strongly angled on the facial axis; there is a marked thickening of the parietal bone, i.e. a parietal boss, on the dorsal braincase surface posterior to the junction of metopic and coronal sutures; auditory bullae small and not very inflated. The preorbital fossae are small and lack a pronounced upper rim. Molars are very hypsodont; premolar rows are short; enamel outlines on occlusal surfaces are simple and rounded; the anterior snout is short, with a high ratio between toothrow and diasternal lengths.

Horizon

Olduvai Beds I to IV; Peninj; Isimila (Tanzania); Kanjera; Ileret and Koobi Fora Formations, East of Lake Turkana (Kenya); Members C and H of Shungura Formation, Omo (Ethiopia); Ain Boucherit (Algeria); Members 2, 3 and perhaps 4 of the Makapansgat Formation; Members 1 and perhaps 2 of the Swartkrans Formation; Member 4 of the Sterkfontein Formation; Kromdraai Faunal site, Bolts Farm; Gladysvale (Transvaal, South Africa).

Parmularius braini sp. nov.

Holotype

Fragmentary frontlet with most of left horn core (fig. 3); M8244 at the Bernard Price Institute for Palaeontology, University of the Witwatersrand, Johannesburg.*

Paratypes

- Fragmentary frontlet with basal parts of left and right horn cores; M8236 (fig. 4);
- Palate with LP⁴-LM³ and RM¹ (broken) — RM³; M8228 (fig. 5a);
- Part of right mandible with P₄-M₃, base of P₃ and small root for P₂, as well as most of diastema; M858 (fig. 5b).†

Diagnosis

A *Parmularius* which differs from all other currently recognized member species of that genus by:

- horn cores which are more abruptly bent back in lateral view (fig. 3a);
- less obliquely inserted horn cores, i.e. a lesser angle (near 160 °), in lateral view, between the basal horn core and the face anterior to the pedicels than is found in other *Parmularius* species (near 180 °) (Fig. 3a);
- stronger basal horn core compression;

- more prominent transverse ridges on the anterior horn core surface, which extend over a greater part of the horn core length;
- supraorbital foramina which are wider apart, although they appear to be closer together than in the genus *Damaliscus* (fig. 3b).

The posteromedial positions of the basal horn core swellings in the type material (figs. 3a and 4) are shared by specimens belonging to *P. altidens*. The straight coronal suture, without forward indentation at the metopic suture, is also found in *P. rugosus* and *P. angusticornis*.

Horizon

The holotype and paratypes are from Member 3 of the Makapansgat Formation. Additional Makapansgat specimens of this species come mainly from Member 3, but also from Member 2 and, less certainly, from Member 4.

Additional specimens and measurements (unless otherwise stated all additional specimens derive from Member 3)

Adult upper dentitions M857 (assigned to cf. *Connochaetes taurinus* by Wells and Cooke, 1956, p. 24), M8351, M4061, M2943, M6171, M774, M1061, M8835, M8778; adult lower dentitions M6272, M1045, M6320, M6688, M6273, M777, M1185, M8772 (from Member 4); juvenile lower dentitions M1173, M6279; partial braincases with occipital areas preserved M952 (fig. 5c), M510 (which in every respect, including the nature of the adhering matrix, looks as though it could belong with the holotype frontlet, M8244); horn cores M8758, M8265 (joined to M2635 by me); frontlet M8385 which belongs to either a subadult or a female (from Member 2); cranial fragments M2608, M1771 and M764 (I have joined these three specimens), M8737 and M556 (joined by me), M2937, M2628, M8736, M2655, M1767, M2832, M2936.

Some measurements in mm on the holotype, paratype and other *P. braini* material are (e = estimated):

	Holotype frontlet M8244	Paratype frontlet M8236	frontlet M8385
Anteroposterior basal horn core diameter	67,5e	64,5	43,1
Mediolateral basal horn core diameter	44,8	46,0	35,7
Minimum width across lateral surfaces of horn core pedicels		116,0	89,5
Width across lateral edges of supraorbital foramina	67 e		70,5e

* All type specimens described, as well as all other Makapan fossils (catalogue numbers preceded by M) mentioned, are housed in this institution.

† This specimen was assigned to cf. *Connochaetes taurinus* Burchell by Wells and Cooke (1956, p. 24).

	Paratype palate M8228	Paratype palate M857	Paratype r. man- dible M858	l. man- dible M1045	l. man- dible M6272
LM ¹⁻³ length (maximal buccal occlusal length)	71,8				
Palatal width (across buccal surfaces of M ²⁻⁵)	89,5	93,5			
M ₁₋₃ length (maximal lingual occlusal length)			68,5	68,5	75 e
P ₂₋₄ length (as for M ₁₋₃)			26 e	26,5e	29 e

There are various taxonomic designations written on specimens which I have here assigned to *P. braini*, e.g. *Connochaetes*, *Gorgon taurinus*, *Alcelaphus*, *Damaliscus* and *Makapania broomi*. There is still a great deal of Makapansgat material to be sorted through, and I expect that a large number of additional specimens will be found to belong to *P. braini*.

Comments

There are no auditory bullae or preorbital fossae to be seen on any of the available *P. braini* material, but every other morphological area cited in the diagnosis of the genus *Parmularius* can be assessed; and in all these respects the present species is decidedly parmularine. I regard the presence of a pronounced

parietal boss as the single most diagnostic feature of this genus, because it alone among the five derived cranial character states shared by members of *Parmularius* (fig. 2) is unique among all Bovidae. The parietal boss of *P. braini*, only partially visible (as a result of damage) on the paratype M8236 (fig. 4) and cranial roofs M2936 and M1777, is best seen in specimens M2628 and M2832. Of previously described *Parmularius* species *P. altidens* has a larger boss than have either *P. angusticornis* or *P. rugosus*. The present material indicates that *P. braini* had a parietal boss at least as large as, if not larger than, *P. altidens*.

Partial braincases M510 and M952 show that the new species has each side of the occipital surface facing strongly laterally, on either side of a prominent median vertical ridge (see fig. 5c). This is unlike the derived condition seen in *P. angusticornis* (which has the occipital components more nearly in the same plane, facing backwards) and like the more primitive one of *P. altidens* and *P. rugosus*.

Together the measurements possible on fragments M1777, M2936, M510 and M952 indicate a less shortened braincase (i.e. coronal to nuchal distance), with respect to maximal braincase width at the posterior parietal level, than is found in other *Parmularius* species (plesiomorph-apomorph transformation series 14 in table 2).

Table 1

The species which are ordered phylogenetically in Fig. 2
I have checked and augmented my own experience of these fossil records from Gentry and Gentry (1977).

Species	Status and Fossil Site Record
<i>Damaliscus dorcas</i> (Pallas 1766) bles- and bontebok	extant; no definitive fossil record;
<i>Damaliscus lunatus</i> (Burchell 1832); topi, korrigum, tsessebe	extant; no definitive fossil record;
<i>Damaliscus hunteri</i> (P.L. Sclater 1889); hirola	extant; no definitive fossil record;
<i>Damaliscus niro</i> (Hopwood 1936)	extinct; Olduvai Middle Bed II to Bed IV; Peninj (Tanzania); several South African sites including Swartkrans Member 2, Cornelia and Florisbad.
<i>Damaliscus gentryi</i> Vrba (this publication)	extinct; Makapansgat Limeworks Member 5 (Transvaal, South Africa);
<i>Damaliscus antiquus</i> (Leakey 1965)	extinct; Olduvai Beds I and II; Member G of Shungura Formation, Omo (Ethiopia);
<i>Damaliscus agelaius</i> Gentry and Gentry 1977	extinct; Olduvai Lower Bed II to Beds III-IV (area where these Beds not divisible).
<i>Parmularius angusticornis</i> (Schwarz 1937)	extinct; Olduvai Middle and Upper Bed II; Peninj; Isimila (Tanzania); Kanjera (Kenya) Swartkrans Member I (Transvaal, South Africa);
<i>Parmularius rugosus</i> Leakey 1965	extinct; Olduvai Lower Bed II to Bed IV
<i>Parmularius altidens</i> Hopwood 1934	extinct; Olduvai Bed I; Member H of Shungura Formation, Omo;
<i>Parmularius braini</i> Vrba (this publication)	extinct; Makapansgat Limeworks Members 2, 3 and 4; Member C of Shungura Formation, Omo; Ileret and Koobi Fora Formations, East of Lake Turkana (Kenya); Ain Boucherit (Algeria);
nov.sp. A, based on Laetolil (Lit.) 1959.277	extinct; Laetolil Beds <i>sensu stricto</i> (M. D. Leakey <i>et al.</i> , 1976) (Tanzania)

If the joined horn core, M8265 + M2635, belongs to this species (the compression, nature of anterior transverse ridges and basal horn core hollowing make this highly likely), then *P. braini* horn cores must have varied quite a bit in the degree of back-bending in lateral view. This horn core is considerably less bent than is that of the holotype, M8244 (fig. 3a).

The paratype mandible M858 is sufficiently well preserved to allow an estimate of diastemal length. The ratio between P_3 - M_3 occlusal length and diastemal length (character 21 in table 2) would have been well over 110 %. I have measured this ratio on samples of all modern alcelaphine species and have not found a single individual of any species (other than *Connochaetes gnou* (Zimmermann) with a mean ratio of 121 %) with a ratio larger than 110 %. On the other hand this short snouted condition is definitely also found in mandibles of *P. altidens* from Olduvai Bed I and in Olduvai Bed II and Swartkrans Member I specimens which I attribute to *P. angusticornis*. I interpret this feature, and the simple, rounded, occlusal enamel morphology of the teeth, as primitive character states retained by the genus *Parmularius*, which I suspect may be found to separate it from the genus *Damaliscus* once mandibles of fossil damaliscines are better known.

Gentry and Gentry (1977) mention that about half the mandibles of Olduvai Bed I *P. altidens* lacked P_2 during life. In presumed *P. angusticornis* mandibles, which I have seen, the proportion of mandibles lacking P_2 (and its alveolus) was even greater. Of three *P. braini* mandibles from Member 3, and one from Member 4, all four had the tooth during life. This is a meagre sample, but it suggests that *P. braini* may have undergone less premolar reduction than the other *Parmularius* species.

The paratype frontlet, M8236, has a tendency to anterior horn core keels, a feature which I have not seen on other fossil and recent Alcelaphini. It is reminiscent of the condition in some caprines, an African fossil example being *Pachytragus solignaci* Robinson from the late Miocene Beglia Formation of Tunisia. I mention caprines, rather than other bovid groups, because I interpret the origin of the tribe Alcelaphini, and of the closely related Aepycerotini, as being from caprine stock.

Apart from its close relationship to other *Parmularius* species, particularly *P. altidens*, *P. braini* is most similar to the new Laetolil species based on skull (Lit.) 1959.277 (nov.sp.A in fig. 2, which I interpret as belonging to a genus separate from *Parmularius*) and to *Damaliscus niro* (Hopwood).

In what I have termed "supergenous a" (fig. 2), each temporally succeeding species branch has straighter horn cores in lateral view than the preceding one. While the strong lateral bending (character 7 in table 2) of nov.sp.A. does represent an apomorphy, stepwise reversal of the trend in *P. braini*, *P. altidens* and finally the species pair *P. angusticornis* and *P. rugosus*, would be a possible explanation. If this were

acceptable, the Laetolil species would qualify as a possible ancestor for *P. braini* (and for the genus *Parmularius*), because in every other respect it appears to be either less advanced than, or equally as primitive or advanced as, the latter. It has more uprightly inserted horn cores, which are less compressed and lacking transverse ridges and have basal swellings situated postero-laterally rather than postero-medially. The horn core to orbit distance is relatively short as in *Damaliscus*, and unlike *Parmularius*, in spite of the fact that the horn pedicels are distinctly lengthened, an apomorphy shared uniquely among alcelaphines with *Parmularius* (fig. 2). The supra-orbital foramina are probably (size independently) somewhat closer together than in *P. braini*. The braincase is less bent with respect to the facial axis, and longer and thinner, than in all *parmularines*. The occipital surfaces face at least as strongly laterally as in *P. braini*. The coronal suture is straight as in *P. braini*, while the parietal boss behind it is much less marked and more like that of *Damaliscus* species (fig.2).

Five features were cited above in the diagnosis of *P. braini*, as removing it from other *Parmularius* species. Four of these represent close approaches to the respective character states in *Damaliscus niro*: the lesser angle (than in other *parmularines*) between basal horn core and face in lateral view is as in *D. niro*; the stronger basal horn core compression is only slightly less marked; the stronger and more extensive transverse ridges on the anterior horn core surface, while not as marked nor as widely spaced as those of *D. niro*, nevertheless represent a closer approach to the latter than do their homologues in other *Parmularius* species; the wider separation of supraorbital foramina is probably (size independently) only slightly less marked than in *D. niro*. Some Olduvai Bed II horn cores, which Gentry and Gentry (1977) termed "type A" horn cores and doubtfully included in *D. niro*, are reminiscent of *P. braini*: they have a more marked change in backward curvature halfway between base and tip than other *D. niro* specimens, transverse ridges which are closer together and a small basal postero-lateral swelling. However, the elongated horn pedicels and horn core-orbit distance, as well as the pronounced parietal boss, remove *P. braini* decisively from all *D. niro* specimens on which these features can be seen. I prefer to place greater weight on these three apomorph character states, and to interpret the other resemblances as resulting from homoplasy (i.e. "resemblance not due to inheritance from a common ancestor"; Simpson, 1961). This preference is expressed in Figure 2.

Parmularius braini appears to have had a wide distribution in Africa. There are several well-preserved specimens among the fossil assemblages from East of Lake Turkana (previously Lake Rudolf), Kenya, which could belong to *P. braini*: e.g. left horn core KNM-ER270 (ER 68 FS-140), right horn core KNM-ER282 (ER 69 FS-87), frontlet KNM-ER 1596 (ER72

FS-153) and others. They differ from the Makapansgat specimens in having horn cores that are inserted more widely apart, basal horn core swellings that are situated postero-laterally rather than postero-medially, slightly less compressed basal horn cores, a lesser brain-face angle, more uprightly inserted horn cores (i.e. a smaller angle between the anterior basal horn core and the face in lateral view), and probably by a more abrupt backbending of the horn core in lateral view. With respect to the four last mentioned features, the East Turkana form appears to be less advanced than the Makapansgat one. I interpret these differences as indicating no more than subspecific differentiation. Two further fossil specimens from additional African sites probably belong to *Parmularius braini*: right horn core L.292-29 from Member C of the Shungura Formation (Omo, Ethiopia); and left horn core 1954-15-72 from Ain Boucherit (Algeria). Both specimens resemble Makapansgat *P. braini* horn cores in that the widest part of the basal transverse section is not situated anteriorly, as is the case in several *Damaliscus* species (including *D. niro*, except, according to Gentry and Gentry, 1977, some "Type A" horn cores); in the size and spacing of anterior transverse ridges; and in a comparable backward curvature in lateral view.

The specific name is after Dr. C. K. Brain in recognition of all he has done towards elucidating stratigraphical, geomorphological, taphonomic and faunal aspects of the Transvaal australopithecine cave assemblages.

Genus *Damaliscus* Sclater and Thomas 1894

Type species *Damaliscus dorcas* (Pallas 1766)

Generic diagnosis

Small to medium-sized alcelaphines with high narrow skulls. Horn core torsion may be absent, or incipient to pronounced anticlockwise*; there is a tendency for horn core tips to be directed upwards, when seen in lateral view, which increases proportionally to the degree of anticlockwise torsion; transverse ridges on anterior horn cores have a tendency to be present over the entire surface rather than just near the tips, and vary in expression from very slight to pronounced; there is little tendency to basal horn core swelling; the greatest basal horn core diameter may be slightly to strongly angled with respect to the metopic suture (angulation brought about by posterior horn core swinging laterally). Horn pedicels are well defined with near-parallel sides, but short. The basal horn core to orbit distance is short, partly resulting from the shortness of the horn pedicel but also from a lack of elongation of the frontal anteriorly and laterally to the pedicels. Supraorbital foramina are widely separated. The dorsal braincase, between coronal and nuchal crest, is shortened but longer than in *Parmularius*; the braincase is less bent with respect to the facial axis than in *Parmularius* and *Alcelaphus*. The coronal suture is straight, or only slightly indented

anteriorly at the metopic. There is a slight tendency to a parietal boss on the dorsal braincase. The surfaces of the occipital face mainly backwards, rather than laterally (i.e. they are more in one plane). The preorbital fossae are fairly large, larger than in *Parmularius*, with pronounced upper rims. The occlusal enamel configurations on dentitions have a tendency to greater complexity than those of *Parmularius*; premolar rows are fairly long in living species with P_2 's often retained.

Horizon

Olduvai Beds I to IV; Peninj (Tanzania); Member G of Shungura Formation, Omo (Ethiopia); Makapansgat Limeworks Member 5; Swartkrans Member 2; Sterkfontein Members 5 and 6 (Transvaal, South Africa); several mid-Pleistocene to later South African sites including Cornelia and Florisbad.

Damaliscus gentryi sp. nov.

Holotype

Fragmentary frontlet with basal parts of both horn cores, all surfaces extensively weathered; M8874 (figs. 6 and 7).

Diagnosis

A large *Damaliscus*, larger than *D. lunatus* and comparable in size to the larger specimens of *D. niro*. Backbending of the lower half of the horn core in lateral view is pronounced and commences almost immediately above the level of the anterior horn core-pedicel boundary, i.e. sooner than in any currently available specimens assigned to *D. niro*. In lateral view the horn core-pedicel boundary is oblique being anteriorly considerably higher than posteriorly; basal horn core swellings are absent. The frontal sinus extends far up (more than 2 cm above the anterior horn core-pedicel boundary in the holotype) into the horn core. Horn cores are more uprightly inserted than in extant *Damaliscus* species (i.e. with a lesser angle, in lateral view, between the basal horn core and the face anterior to the pedicels), as they are in *D. niro*. The horn cores diverge quite strongly and evenly from the base with a mutual angle between 40° and 50°. The mediolateral width of the horn core cross section is wider anteriorly than posteriorly, a tendency which becomes increasingly marked as one proceeds upward from the base. Horn pedicels and horn core-to-orbit distance are short, with orbital rims hardly projecting.

Horizon

The holotype was found low in Member 5 (Bed A) of the Makapansgat Formation. No additional specimens are known.

Measurements

Some measurements in mm on the holotype, M8874, are (e = estimated):

* Measured in the right horn core as seen from the base up.

Table 2
Hypothesis of apomorphy
 (all orientational terms in relation to a horizontal tooththrow)

character	state	
	plesiomorph (=primitive)	apomorph (=derived, or advanced)
<i>horn cores</i>		
1. basal swelling	absent	localized swelling present
2. surface contours	lateral and/or medial surfaces not flattened	lateral and medial surfaces flattened
3. torsion I (assessed on right core from base up)	no torsion	at least weak (i.e. involving mainly distal part) anticlockwise
4. torsion II	not pronounced	pronounced anticlockwise
5. torsion III	no torsion	at least weak clockwise
6. angle of max. basal diameter to metopic suture	$\pm < 60^\circ$	$\pm > 60^\circ$ with posterior margin swivelling laterally
7. course in lateral view I	less so	whole anterior surface strongly convex resulting from abrupt backward curvature about half way up
8. course in lateral view II	absent	tips elongated, straight, near parallel, pointing up
9. anterior transverse ridges	absent to weakly marked; where present ridges are closely spaced	strongly marked ridges spaced far apart
<i>horn pedicels</i>		
10. definition	absent to poorly defined with sloping sides	well-demarcated from horn core and rest of frontal, with near parallel sides
11. length	short	long
<i>braincase</i>		
12. parietal boss incidence I	boss absent	distinct localized "bump" or boss (a thickening of the parietal) posterior to the junction of metopic and coronal sutures
13. parietal boss II incidence	not enlarged	boss enlarged
14. brain proportion	ratio $\pm > 60\%$	length/width ratio $\pm < 60\%$ (coronal to nuchal length/max. width in midregion)
15. brain-face angulation	angle (1) $\pm > 100^\circ$; angle (2) $\pm < 130^\circ$	angle (1) between occiput-bregma line and anterior frontal $\pm \leq 100^\circ$ (and by inverse correlation an angle (2) between occiput-bregma line and occipital surface of $\pm \geq 130^\circ$)
16. dorsal parietal in lateral view	not markedly convex	marked convexity forming dome
<i>miscellaneous</i>		
17. horn core to orbit distance (assessed independently of character 11)	short	long
18. internal frontal hollowing	absent to poorly developed	extensive (i.e. past supraorbital canals and into orbital rims) with a single large smoothwalled sinus which extends into basal horn core
19. preorbital fossa	pronounced upper rim present, foss deep and extensive	loss of pronounced upper rim, and fossa less deep and extensive (or more reduced)
20. separation of supraorbital foramina	not wide apart	wide apart
21. face length	ratio $\pm > 120\%$	tooththrow/diastema ratio $\pm \leq 120\%$ (P_3 - M_3 occlusal length/min. distance between bone-tooth contacts of P_3 and C)
22. tooth morphology	basal pillars (ectostylids) present on adult lower molars; occlusal enamel pattern less rounded and more angular	basal pillars absent; occlusal enamel pattern markedly rounded (i.e. medial lobes of upper molars and lateral lobes of lowers rounded, wide out-bowing of ribs on uppers, central cavities with anterior and posterior rounding and tendency to central constrictions)
23. premolar length	P_2 present and large	P_2 absent or very reduced

Anteroposterior basal horn core diameter	62 e
Mediolateral basal horn core diameter	48,5e
Minimum width across lateral surfaces of horn pedicels	112,0
Basal horn core separation	30 e
Width across lateral edges of supraorbital foramina	62 e

Comments

Only a few of the diagnostic features for the genus *Damaliscus* are preserved on M8874. With respect to each of these the new form is decidedly damaliscine, and seems to be very closely related to *Damaliscus niro*. Gentry and Gentry (1977), in addition to the main body of typical *D. niro* specimens, doubtfully include in the species two horn core varieties (which they called Types A and B) from the BK site in Upper Bed II, Olduvai. This species appears to have undergone a size decrease, from the large specimens of Peninj and typical Olduvai *D. niro*, through the smaller Cornelia material, to the smallest from Florisbad and other late Pleistocene South African sites. *Damaliscus gentryi* is closest in size to the larger Olduvai and Peninj specimens and, according to Gentry and Gentry's (op. cit.) measurements, decidedly larger than Olduvai Type A and B varieties. However, in the following morphological respects it appears to resemble Type A specimens rather than any typical *D. niro*: type A horn cores have a more marked change in backward curvature, less basal compression and closer spacing of transverse ridges (op. cit.). (The latter comparison rests very tentatively on faint hints of ridges present on the anterior surface of the left horn core fragment of M8874). I am hoping that further Makapansgat finds may clarify whether M8874 really belongs to a species closely related to but separate from *D. niro*, as here suggested, or merely to a subspecies of that taxon.

The specific name is after Dr. A. W. Gentry, who has contributed more than anyone else to an understanding of the phylogenetic relationships of African fossil and recent Bovidae.

REMARKS ON CHRONOLOGICAL CORRELATION

A few general remarks, on faunal chronological correlation, may serve to place into perspective the particular ones concerning Makapansgat alcelaphines. The basic limitations stated here may seem obvious. While they are probably generally tacitly understood, they seem to be only rarely incorporated into published reasoning and conclusions.

1. *Temporal ranges of species.* Species have temporal ranges, and are generally not "flash" occurrences in time (although the palaeontologist often only glimpses "flashes"). In terms of the species definition it would be nonsense to postulate anything other than that temporal ranges of one species in geographically separate areas must overlap. On the other hand, chronological matching of sepa-

rate fossil occurrences of the same species, without recognizing the error limits imposed by the total duration time of that species, is simplistic.

2. *Interpretation of morphoclines.* There is a time-honoured and ubiquitous practice among palaeontologists: states of particular morphological characters (most frequently of dentitions in the case of higher vertebrates) are ordered into a primitive-to-advanced series. Then phyletic gradualism, and consequently temporal succession, are assumed for fossils showing that series of character states. We know that comparable advances in homologous structures frequently occur in separate lineages (some writers have referred to such convergence as being "rampant"). We also know that the rates of evolutionary advance may differ in different lineages. We should further consider that, in accordance with the allopatric speciation (as distinct from the phyletic gradualist) model, the ancestral morphology may survive together with the descendant one and indeed may outlast it. The fact that a primitive-to-advanced series for one morphological character may be encountered in a closely related group *at any one time* is amply demonstrated among recent faunal elements (for instance dentitions of some modern member species of the tribe Alcelaphini, as well as of other mammalian groups, might well be interpreted erroneously as temporally successive, if found in isolation in the fossil record). From all this it follows that an assertion of reasonably precise temporal correlations, based on stages of a morphological series, is logically indefensible unless it can be demonstrated independently (of the character from which time is inferred) that the series is a true transformation series, or belongs to a single lineage. I stress "independently", because all too often both the temporal correlation, as well as the necessary underlying assumption of presence on a single lineage, are deduced in circular fashion from the same morphocline.

3. *Interpretation of overall faunal similarity.* An important palaeontological task concerns the interpretation of differences between faunal compositions of fossil assemblages. It seems to be difficult to remember (judging by literature on chronological correlation) that, once taphonomic influences have been considered, observed differences need not necessarily be attributed to time, or to time only. Thus ecological factors may in reality be responsible for observed effects that are attributed to time, and vice versa. As an example may be cited the faunal compositions of the Wankie and Kalahari Gemsbok National Parks. From census data (Vrba, n.d.) I computed faunal similarity for the large mammalian genera, by means of a formula which has in the past been used to make chronological deductions on certain Pleistocene fossil assemblages (similarity values being interpreted as inversely propor-

tional to time difference). Similarity of Kalahari to Wankie (contemporaneous and some 800 km apart) was found to be low, much lower than to some fossil assemblages. Clearly ecology is responsible in this case. Even when both time and environment are held constant, geographic separation may produce differences. For example, the apparent restriction to the Transvaal of the three most abundant bovid species of Makapansgat, mentioned in the introduction, probably results from geographical/environmental factors.

Numerous specialists, working on problems relating to the Plio-Pleistocene hominid-associated fossil record, accord importance to time differences of the order of fractions of a million years. In attempts to date South African australopithecine assemblages we still depend heavily on faunal correlation. Perhaps the brief and simple reservations expressed here will help the reader (especially the non-palaeontologist) to evaluate realistically the few remarks which follow, as well as other faunal correlations.

The facts concerning the record of *Parmularius braini* and related taxa are:

I am satisfied that specimens from Makapansgat Members 2 and 3 belong to *P. braini*. From Member 4 only a single fragmentary mandible, M8772, which could belong to this species, has so far come to light. It had a well-developed P_2 during life, and thus (in view of my previous discussion on premolar length in parmularines) is more likely to belong to *P. braini* than to another *Parmularius* species. Nonetheless I will confine these remarks to the secure Member 2 and 3 *P. braini* representations.

The more advanced, but closely related (fig. 2), *Parmularius altidens* is not recorded prior to its abundant occurrence in Olduvai Bed I, while *P. braini* is absent from this alcelaphine-rich site. The most advanced *Parmularius* species, *P. angusticornis*, occurs in Swartkrans Member 1, Olduvai Middle and Upper Bed II, Peninj, Isimila and Kanjera. From the Laetolil Beds *sensu stricto*, with an upper age limit of 3,6 m.y. (M. D. Leakey *et al.*, 1976), we have the species based on (Lit.) 1959.277 (nov.sp.A. in fig. 2). I have discussed above that all we know of this species qualifies it for ancestry of *P. braini* and of the genus *Parmularius*.

P. braini is probably present in Member C of the Shungura Formation, which covers a time range of approximately 2,6–2,4 m.y. (Brown and Nash, 1976; Brown and Shuey, 1976). In the alcelaphine sample from the Hadar Formation, Ethiopia (dated near 3 m.y. ago, Aronson *et al.*, 1977), which I saw in October 1976, *P. braini* was absent.

East of Lake Turkana, specimens belonging either to *P. braini* or to a closely related species, as well as a cranium of *P. altidens*, all derive from what is currently referred to as Collection Unit 4 (J. M. Harris, pers. comm.). Samples referred to Collection Unit 4 have been loosely temporally correlated on the basis of evolutionary change exhibited by suid species

(White and Harris, 1977), although their correlation cannot at present be demonstrated lithostratigraphically. The suid correlation tentatively implies that the temporal ranges of these samples belong to the period later than the date of the KBS tuff (and preceding that of the Koobi Fora tuff). However, the authors (op. cit.) are quite clear in pointing out that the identity of the KBS tuff can only be established in two of the numerous fossiliferous areas of East Turkana. Unfortunately the latter do not include the sources of the *Parmularius* specimens which I have seen. On the basis of radiation damage and isotopic decay series techniques several dates have been suggested for (1) The KBS tuff in type area 105; $2,61 \pm 0,26$ m.y. (Fitch and Miller, 1970; Fitch *et al.*, 1974), $1,60 \pm 0,05$ m.y. (Curtis *et al.*, 1975), $2,42 \pm 0,01$ m.y. (Fitch *et al.*, 1976); and for (2) What was previously considered to be the KBS tuff in areas other than the type area: $1,60 \pm 0,05$ m.y. in area 10 (Curtis *et al.*, 1975), $1,82 \pm 0,04$ m.y. in area 131 (op. cit.), $2,44 \pm 0,08$ m.y. in area 131 (Hurford *et al.*, 1976). Palaeomagnetic results appear to be compatible with both earlier and later alternatives (Hillhouse *et al.*, 1977).

From all this, on the basis of occurrence of *P. braini* alone, I would have extracted a tentative hypothesis that the time ranges of *P. braini*, and of Makapansgat Members 2 and 3, may belong between 2–3 m.y. ago with the latter part of that time range preferable to the earlier. Among the East Turkana dating alternatives quoted above the earlier are more apposite to the present case than the later ones.

The first dating estimates, which are more rigorously based than solely on faunal correlation, for Makapansgat (or indeed for any South African australopithecine breccia) come from Brock, McFadden and Partridge (1977). In the interpretation of their preliminary palaeomagnetic results (op. cit.) they suggest that the upwards transition from reversed to normal polarity low in Member 2 is likely to have an age of either 3,32, 2,94, or 2,80 m.y., using Cox's (1969) time scale. On the basis of additional research they prefer the 3,32 m.y. alternative (reported at the May 1977 conference of the South African Society for Quaternary Research), and further suggest that the Kaena and Mammoth events within the Gauss normal epoch might be represented in Member 4. According to this interpretation most of Member 2 and all of Member 3 are bracketed between 3,32 and 3,06 m.y. or between 3,32 and 2,90 m.y.

If one rejects a later alternative in the interpretation of these palaeomagnetic results, a temporal distribution for *P. braini*, roughly spanning the time gap between the Laetolil and *P. altidens* members of the same lineage (fig. 2), must be considered. A second implication would be that the temporal distributions of the fossil finds of *P. braini* (not of the species itself) in East and South Africa are disjunct. Neither of these implications presents any difficulty: temporal ranges of near 1,5 m.y. are on record for

several alcelaphine species (Vrba, 1978, fig. 4). Concerning the second point one must remember that probably less than 10 % of the 2–4 m.y. time span is sampled in present Southern African fossil assemblages: the entire 2–3 m.y. "slice", from the point of view of identifiable alcelaphine remains (here I except Sterkfontein Member 4, formerly the Type Site, and Taung with their poor bovid remains), may be lacking.

The *Damaliscus* specimen M8874 from low in Member 5, here described as *Damaliscus gentryi*, suggests temporal correlation with the larger *D. niro* specimens of Peninj and Olduvai Bed II, or possibly with a somewhat earlier date than the base of Bed II. Such an interpretation, taken together with the estimates for Members 2–4 of Brock, McFadden and Partridge (1977), which were mentioned above, necessitates recognition of a substantial time lag between Members 4 and 5. This appears to be in

agreement with Partridge's brief description of Makapansgat stratigraphy. He writes (op. cit., p. 249) that Member 5 rests unconformably upon an eroded surface of Member 4, and that this unconformity probably represents a considerable lapse of time.

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Figure 3. *Parmularius braini*. Holotype frontlet M8244.

a = left lateral view;

b = anterior view.

(scales in Figures 3–7 in centimetres)



Figure 4. *Parmularius braini*. Paratype frontlet M8236 in left lateral view.

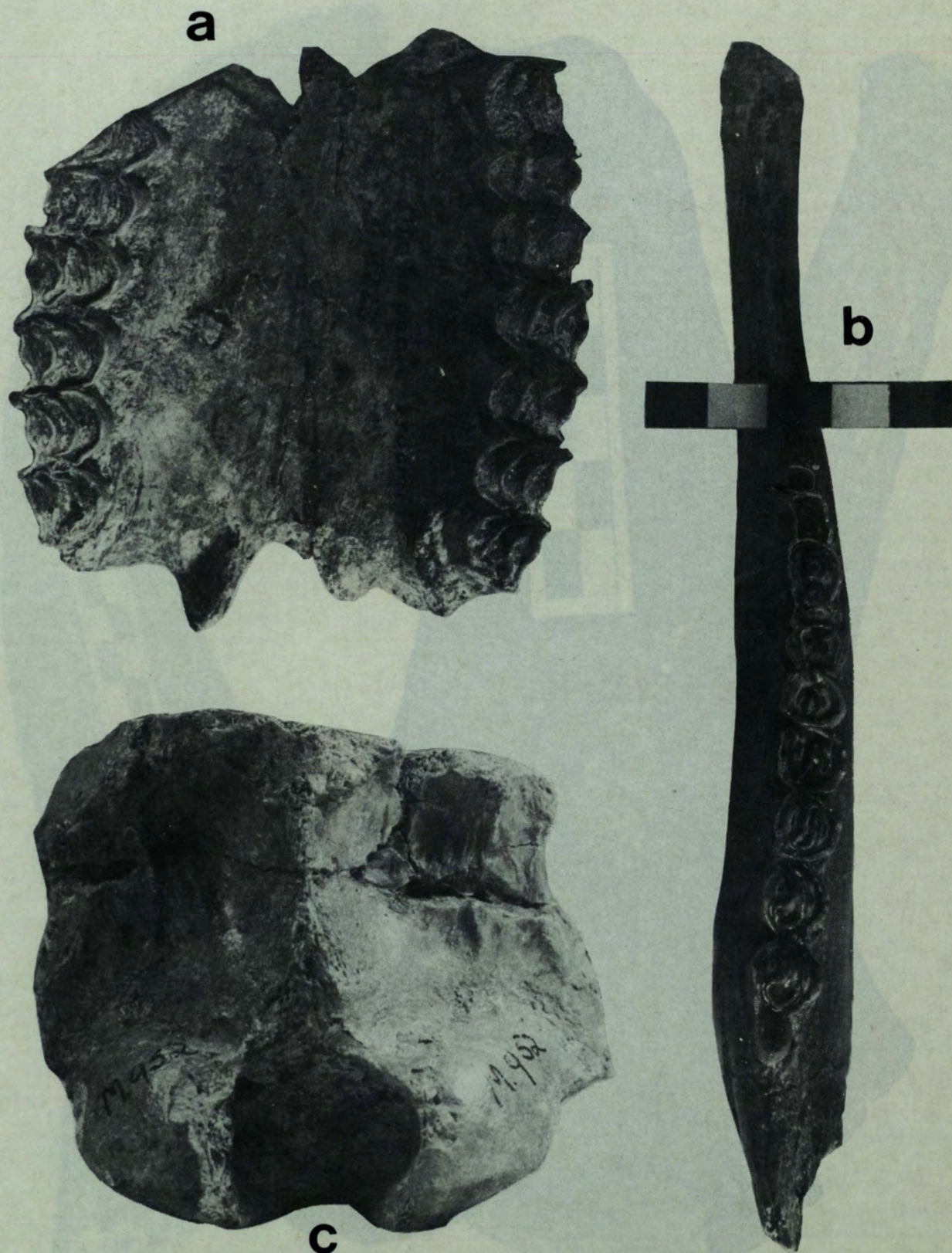


Figure 5. *Parmularius braini*.

- a = Paratype palate M8228 in occlusal view, anterior towards top of page;
 b = Paratype right mandible M858 in occlusal view; note sizes of hole for P_2 and root of P_3 ;
 c = partial cranium M952 in occipital view.



Figure 6. *Damaliscus gentryi*. Holotype frontlet M8874 in anterior view.



Figure 7. *Damaliscus gentryi*. Holotype frontlet M8874 in right lateral view.

DISCUSSION ON: NUMERICAL METHODS IN THE DEFINITION OF PALYNOLOGICAL ASSEMBLAGE ZONES IN THE LOWER KARROO (GONDWANA) OF RHODESIA

(*Palaeont. afr.*, 19, 1-20, 1976)

by

R. M. S. Falcon

Subsequent to the publication of the above paper (in which a number of errata appeared) certain points of discussion have been raised regarding the interpretation of the single axis spatial ordinations. In particular delineation of the numerical assemblage zones based upon the spacings between the clustered groups has been in question. In order to understand fully the significance of these groupings the following points should be borne in mind.

The degree of resolution (or spacing) between, and the detailed associations within, these groupings have been seen to vary depending on the reference samples chosen. However, the overall pattern of major grouping of stratigraphically adjacent samples into the major microfloral biozones appears to occur repeatedly, irrespective of stratigraphic bias or distance, in high D_{jk} valued reference pairs.

Theoretically, these results may be explained as follows: the projections of the data onto different reference axes will provide different arrangements of the sample points. If, in fact, the data points are clustered into a number of broad groups in n -dimensional space, this clustering will be evident when the data is projected onto a number of different axes, although some projections will tend to high-

light the clusters while others will tend to obscure them. If the same basic picture emerges from each axial projection (remembering that some of the clusters could overlap on some projections) then the observed clusters are likely to represent true clusterings of the data. This is the case in the present exercise, where in fact the reference pairs chosen herein do emphasize the clusterings of adjacent or associated samples with a maximum of resolution between them thereby highlighting the constant overall pattern seen in other reference projections.

The concepts may therefore be summarised as follows: the repeated clustering together of stratigraphically adjacent samples is regarded in this context as constituting a numerical biozone or unit. However, the delineation of such a group by means of spatial definition, although distinct in pairs with high D_{jk} values, must be regarded as a variable factor due to a certain degree of overlap on certain other projections.

The same philosophy and approach applies to the double axis ordination technique, with the exception that an added dimension may enhance the clusterings so far shown.

TECHNOLOGICAL NOTE: A CHEAP STEREOPHOTOGRAPH APPARATUS

by

H. O. Thackwray

The need for a gadget for taking stereo pairs of photographs has been evident for some time. What was needed was a cheap, pocket-sized gadget that would fit all makes of cameras, could be used for close-up photos, large immovable objects and even landscapes. It had to be simple and easy to operate.

Beam splitters were looked at, as were stereo-rocking boards. Beam splitters were found to be limited in close-up work, and stereo-rocking boards have serious limitations when it comes to size and immovable objects.

The principle of stereo-vision involves an understanding of the significance of inter-pupillary distance and the angle of the retina to the visual mid-line. Thought was therefore applied along these lines.

Some years ago when the author was Technician in the Zoology Department of Rhodes University, Grahamstown, the late Dr. Robin Bolt and he had experimented with stereo-photography. The stereo-plate and technique now described were the outcome of the experiment and the need for such apparatus in the Bernard Price Institute for Palaeontological Research at the present time.

The Plate

A 6 mm thick aluminium plate 20 cm x 7,5 cm is slotted as per the drawing in Figure 1. A tripod screw hole is drilled as shown.

The Technique

The plate is fitted to a tripod, the camera is fitted to the screw in the slot and tightened up in the central position and focused on the object to be photographed. A reference point is chosen on the object, usually in the centre of the field of view. The camera is now moved to the extreme right and again the reference point is centred. The camera should now be at an angle to the object photographed. An exposure is made and the camera moved to the extreme left and the procedure repeated.

To help line up the reference point on this specimen a dry transfer dot was placed on the view finder of the camera used by the author.

Figure 2 is a photo of the apparatus set up for use.

Figures 3, 4 and 5 are stereo-pairs of a close-up of a fossil, a moderate sized fossil skull and a landscape scene, which all show that a very good illusion of depth is obtained.

Stereo-pair enlargements for use with a large type stereo-viewer are possible and very successful.

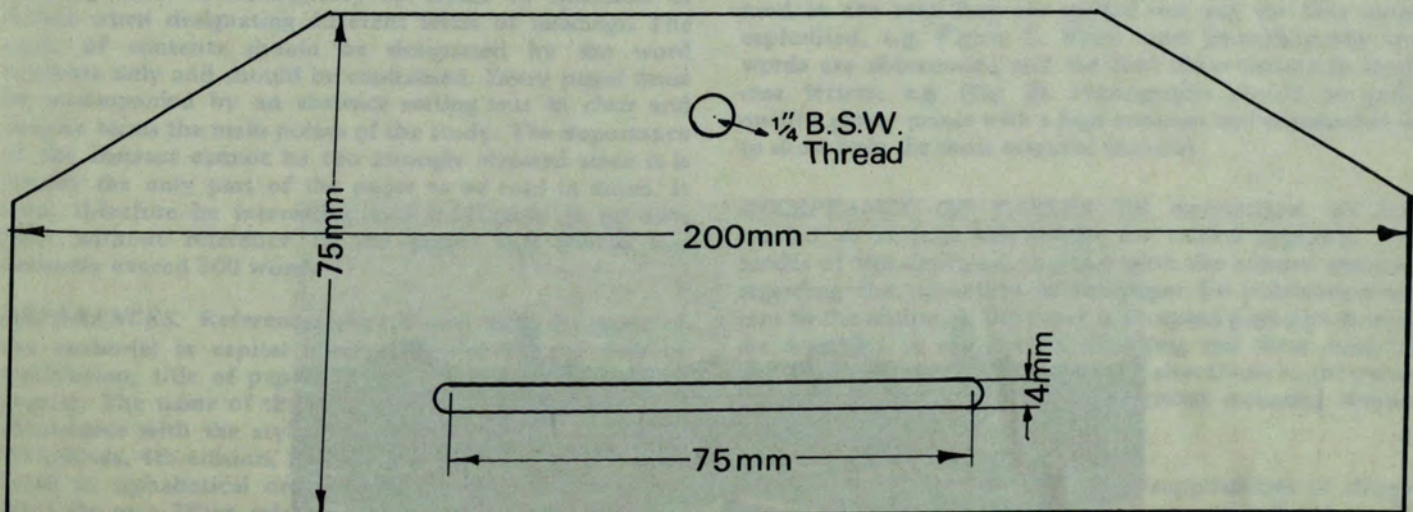


Figure 1.

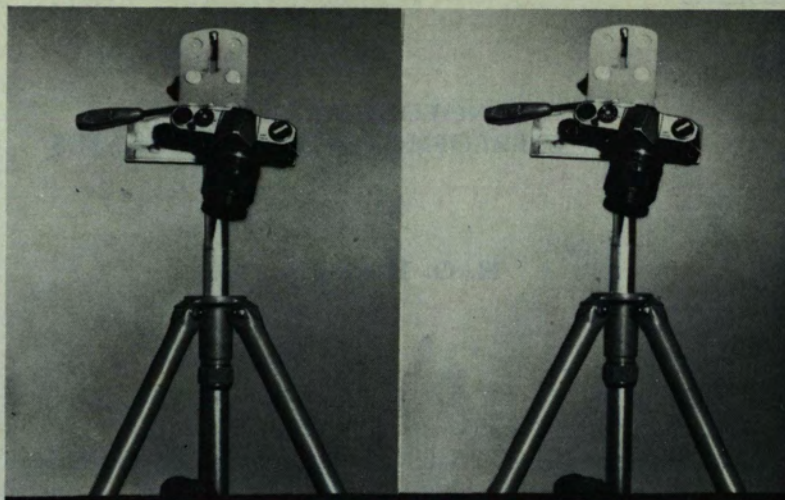


Figure 2.

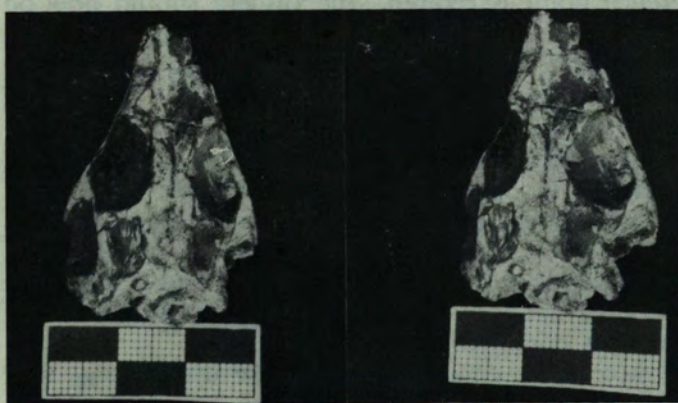


Figure 3.

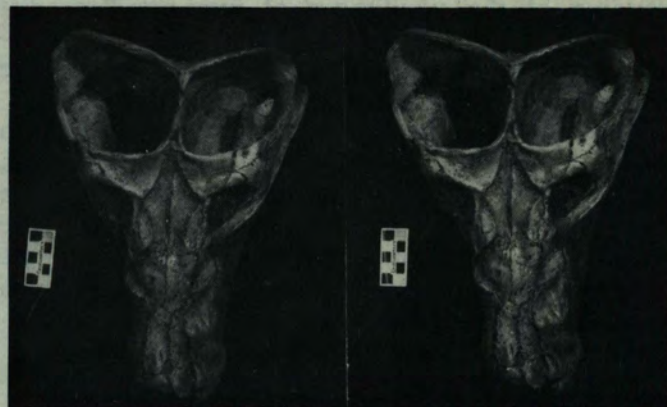


Figure 4.



Figure 5.

NOTES FOR THE GUIDANCE OF AUTHORS

GENERAL. The increase in size and scope of the journal during the last two years has emphasised the need for a greater degree of consistency in the style of manuscripts submitted for publication. The suggestions to authors given here is an attempt to ensure consistency and avoid unnecessary delays in publication. Authors are urged to follow these suggestions when preparing papers and especially where changes in the general style of the journal have been introduced. These are not only aimed at consistency but to help speed up editorial work and cut down publication time. For general style requirements and layout of papers authors should consult recent issues of the journal. *Palaeontologia Africana* is published annually in separate parts; the number of parts being largely determined by the number of contributions. In this way rapid publication of research material is assured. All aspects of palaeontological research are published and contributions from other related branches of the earth sciences are also welcome. There is no subscription rate although separate parts or volumes may be purchased. Free exchange with other institutes is encouraged and information about this can be obtained from the editors.

MANUSCRIPT. Manuscripts should be typewritten with double spacing and wide margins. The full title of the work followed by the author(s) name and the place where the work was carried out should also be included. The present postal address of the author(s) is also required for correspondence and the checking of proofs. All pages should be numbered consecutively in the top right hand corner beginning with 1 on the title page. Two copies of the manuscript and two copies of the illustrations should be sent to the Editor, *Palaeontologia Africana*, Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Milner Park, Johannesburg, South Africa. Except for very short papers and discussions a table of contents is required containing the headings of all sections of the paper. Three levels of headings are used by *Palaeontologia Africana*: first order, second order, and third order headings. First order headings are printed in capitals in the centre of the columns, second order headings are printed in small case letters in the centre of the column with the first letter capitalised and third order headings are underlined in the manuscript and italicized in the journal; they are printed in lower case letters to the left of centre of the column with the first letter capitalised. The headings adopted make it unnecessary to resort to numerals or letters when designating different levels of headings. The table of contents should be designated by the word contents only and should be capitalised. Every paper must be accompanied by an abstract setting out in clear and concise terms the main points of the study. The importance of the abstract cannot be too strongly stressed since it is usually the only part of the paper to be read in detail. It must therefore be interesting and intelligible in its own right without reference to the paper and should not normally exceed 300 words.

REFERENCES. References should start with the name of the author(s) in capital letters followed by the year of publication, title of paper, name of journal, volume, and page(s). The name of the journal should be abbreviated in accordance with the style of the World List of Scientific Periodicals, 4th edition, London. The references should be listed in alphabetical order and typed on sheets separate from the text. When references are cited in the text either parenthetically or otherwise only the name of the author(s) and the date need be included unless only part of an article

is cited in which case the page numbers should also be given.

TABLES. Tables should be typed on separate sheets and the table headings capitalised. They are numbered consecutively with arabic numerals and when referred to in the text the words Table and Tables are spelled out and the first letter capitalised, e.g. Table 2. When given parenthetically the words are likewise spelled out but with the first letter written in lower case letters, e.g. (table 2). Tables are normally placed in their appropriate position in the text unless otherwise stated; however, it would help if authors indicated the position of the tables by some form of notation in the margin of the text.

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REPRINTS. Fifty reprints will be supplied free of charge to authors. Additional reprints can be purchased and should be ordered on the appropriate form which is included with the proofs.

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