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# **PALAEONTOLOGIA**

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# **AFRICANA**

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

**VOLUME 19, 1976**



# **PALAEONTOLOGIA AFRICANA**

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BERNARD PRICE INSTITUTE  
FOR  
PALAEONTOLOGICAL RESEARCH  
UNIVERSITY OF THE WITWATERSRAND  
JOHANNESBURG

**VOLUME 19, 1976**

(Papers prepared especially in honour of  
Dr. Edna P. Plumstead)



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Bernard Price Institute  
for Palaeontological Research

University of the Witwatersrand  
Johannesburg  
1976



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Dr. Edna P. Plumstead, D.Sc., F.R.S. S.Afr.



## EDITOR'S NOTE

The papers in this volume have been prepared and are issued as a tribute to the work in the field of fossil plants that has been done, both as a researcher and a teacher, by Dr. Edna Pauline Plumstead (née Janisch) who has for slightly more than 50 years been associated actively with the University of the Witwatersrand and, almost from its inception, with its Bernard Price Institute for Palaeontological Research.

Edna Plumstead's scientific career started with the award of a B.Sc. from Witwatersrand University in 1923. She went on to take an Honours degree in Geology the following year and her M.Sc. with distinction in 1925. In the same year she became the first recipient of the Geological Society of South Africa's Corstorphine Medal and was awarded an H. B. Webb Research Scholarship. Her parent university, recognising her abilities, had already appointed her a Junior Lecturer in her Honours year and confirmed this appointment in 1925. During 1927, while on study leave in Cambridge, she was recalled to assist Professor R. B. Young in the Department of Geology because of the grave lack of staff.

Her career as a scientist seemed settled and these early years resulted in the publication of a number of papers and a standard mapping text book. However, in 1934 another call came, even more imperious than that of Professor Young seven years previously, and Edna Janisch left the service of the University to marry and change her name to Plumstead. This second career was followed as conscientiously as the first. The Plumsteads are now the very proud and happy owners of seven grandchildren, in which they delight.

In 1946, with the pressure applied by the returning ex-servicemen, Edna was once more recalled to duty with her University and has been, ever since, associated with it in one form or another. At present she is Honorary Research Associate in the Bernard Price Institute for Palaeontological Research with special reference to her own special subject, Karroo Palaeobotany.

During the years from 1946, Edna Plumstead has

achieved a world-wide reputation as a palaeobotanist and stratigrapher. Her publications now total about fifty, all of which are substantial contributions to the understanding of her two loves, palaeobotany and continental drift. In recognition of her work she was, in 1959, awarded a D.Sc. degree by the University of the Witwatersrand and the Geological Society of India made her the recipient of its Christian Mica Gondwanaland Medal.

She has been, among other things, vice-president of the Palaeobotanical section of the International Botanical Association, and a member of the Executive and South African representative on the International Committee for Carboniferous Stratigraphy. In 1964 she was elected a member of the Executive Committee of the International Organisation for Palaeobotany and, also in that year, she was elected to the Executive of the International Union of Biological Sciences. To crown her achievements in 1964 she was invited to act as Chairman of the I.U.G.S. Sub-Commission on Gondwana Stratigraphy and Palaeontology, a position from which she has recently retired.

Nearer home, among her more important posts, we find her a Fellow of the Royal Society of South Africa, a member of the Council, and a member of the Council of the Federation of University Women. She has served on the Joint Council of Scientific Societies of South Africa and she naturally took a leading part in the 2nd International Gondwana Symposium in 1970. In 1973, she was honoured by the South African Association for the Advancement of Science by the award of its South African Medal.

The palaeobotanical contributions in this volume have been written by younger palaeobotanists resident in South Africa who, acquainted with her personally, have freely acknowledged the value of her contributions to palaeobotanical information, particularly related to the study of the Karroo beds, and of the valuable advice which she has freely given to them. The other papers in the volume describe fossil insects from the plant-bearing beds of the Beaufort series.

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2. ——— (1931). Notes on the Central Part of the Zoutspanberg Range and on the origin of Lake Funduzi. *Trans. geol. Soc. S. Afr.*, **34**, 151-162.
3. ——— (1933). *Section drawing from simple geological maps*. Johannesburg, Hortors Ltd. 50 pp.
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5. ——— (1946). *Section drawing from simple geological maps*. (with G. N. G. Hamilton). 3rd Ed. Johannesburg, University of the Witwatersrand Press. 194 pp.
6. PLUMSTEAD, E. P. (1952). Description of two new genera and six new species of fructifications borne on *Glossopteris* leaves. *Trans. geol. Soc. S. Afr.*, **55**, 281-328.
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11. ——— (1956e). The dynamic-chemical stage in coal formation in South Africa. *Coal base miner. sth. Afr.*, **4**(10).



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18. ——— (1961c). A reassessment, based on fossil plants, of the relative ages of Karroo sediments in South Africa and of their position in a world time scale (Abstract only). C.C.T.A. Rep., 4th meeting, Pretoria. Publication **80**, 124–125.
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27. ——— (1965b). Glimpses into the history and prehistory of Antarctica. *Antarktische Bulletin*, **9**, 1–5.
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BERNARD PRICE INSTITUTE FOR PALAEOONTOLOGICAL RESEARCH  
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REPORT OF THE HONORARY DIRECTOR FOR 1975

The year 1975 has been one of normal progress in the Institute. No important changes have been made at the Institute itself but it is a pleasure to record that new brick buildings have been erected at Sterkfontein to provide living accommodation for the African staff working on the excavations near the cave site. The electric lighting installed in the caves makes the excursion to Sterkfontein much more interesting and less arduous than it has been. Attendances are rising to some hundreds per week and the caves are expected to become even more popular when the tape recordings — now being prepared in English and Afrikaans, explaining the history and formation of the caves — are installed at suitable points in the caves for operation at the touch of a button.

The Institute's lecture theatre, almost unusable on account of noise from Showground Road at times when traffic is busy, has now been improved by installing a forced ventilation system.

The financial crisis in the University has led to the freezing of certain approved posts in the Institute's establishment but, as in the rest of the University, temporary hardship seems to have encouraged activity rather than diminished it. The annual budget for 1975 was fixed at the 1974 level and consequently no new research ventures could be undertaken.

#### STAFF MATTERS

Dr. J. T. Brown — from the University of Montana — who had accepted the post of palaeobotanist, which fell vacant on the retirement of Dr. E. P. Plumstead, arrived in the latter part of 1975. He has devoted himself with much energy to the problems of curating the collection of fossil plants and has assumed responsibility for supervision of higher degree theses in palaeobotany. His appointment has added notably to the Institute's scientific staff.

At the University graduation ceremony in December, Dr. Brian Turner received the degree of doctor of philosophy for his work on the stratigraphy and sedimentary history of the Molteno formation. He has since been awarded a C.S.I.R. post-doctoral research fellowship and is now on a year's study leave in the United Kingdom.

During the course of 1975 the male African staff in the SOEKOR laboratory were replaced by African females. This change has resulted in a substantial improvement in the efficiency of the work performance.

Dr. A. R. I. Cruickshank attended the 23rd symposium on vertebrate palaeontology and comparative anatomy in Edinburgh in September 1975 and presented a paper on the evolution of ankle joints in some early archosaurs.

Dr. J. T. Brown and Mrs. R. Falcon attended a week long symposium on coal geology held in the University of Pretoria.

Dr. J. W. Kitching has again been approached to join the American Antarctic expedition as a palaeontologist. He will probably go to Antarctica in the summer of 1977–78. The South African National Committee for Antarctic Research has recognised Dr. Kitching's participation in the American programme as part of the South African National Antarctic effort.

In September 1975 Dr. C. Gow attended a symposium arranged by the Zoological Society of South Africa on Herpetology and Ichthyology. The symposium provided opportunities for contacts with South African zoologists and visitors from Europe and America.

Mr. Brian Maguire has spent several short periods at Makapansgat sorting out breccia blocks and bringing them back to Johannesburg for storage at Frankenswald and subsequent development in the Institute. He has assisted with several parties of visitors to Makapansgat including a large party of army cadets from Northern Command who visited Makapansgat in the course of a period of field instruction in October. In the last month of the year he began work with the pleistocene section of the Institute's museum which is now being reorganised with the assistance of the Director of the Transvaal Museum.

Staff, students and former associates of the Institute have spent much time during this year preparing a special volume of *Palaeontologia africana* — devoted to palaeobotany and to be issued in honour of Dr. E. P. Plumstead who retired from the staff of the Institute in 1972 but has continued as an Honorary Research Associate with financial support from the C.S.I.R.

#### FIELD WORK

Excavations continued at Sterkfontein and Swartkrans, the former under the direction of Professor P. V. Tobias of the Department of Anatomy and the latter under Dr. C. K. Brain of the Transvaal Museum.

Dr. Brian Turner has undertaken two field excursions — one in connection with his work on the sedimentary history of the Molteno and the other in the southern part of the Karroo basin with a view to determining required stratigraphic relations and depositional environments in the lower Beaufort beds, emphasis being placed on how this relates to uranium mineralisation. As a result of this work it seems that the *Tapinocephalus* zone of the lower Beaufort extends much farther east than was thought previously, and that the broad lithographic units can be traced across the southern margins of the basin.



For many years the Institute has concentrated on the extraction of fossil mammalian fauna in the grey breccia within the limeworks deposit. A considerable number and variety of fossil elements from this member are known. It is now felt that preparation work should be devoted to the fossil fauna in the upper phase breccia overlying the grey about which much less is known. Early in the year Dr. James Kitching, Mr. M. Kitching and Mr. Brian Maguire spent some time in the Makapansgat valley sorting and selecting upper phase breccias from the "Breccia Camp" at the limeworks.

In May 1975 Dr. John Cosgriff of Wayne State University visited the Institute. Dr. Kitching and Dr. Cruickshank accompanied him on a field expedition to the Beaufort exposures near Harrismith and the Oliviershoek Pass. The purpose of this expedition was to view the exposures of the lower and middle Beaufort sediments and to collect specimens of fossil Karroo reptiles for exhibition and teaching purposes in the Wayne State University, Detroit, U.S.A.

In November 1975 Dr. Kitching and Dr. Brown joined Dr. Turner on a field excursion in the Pearston District of the Cape Province.

During July 1975 a large party from the Institute, the Department of Anatomy and the Transvaal Museum visited Makapansgat in order to discuss with Dr. T. Partridge some views on the stratigraphy and dating of the cave deposits which he had put forward at a recent meeting in Cape Town.

The Department of Botany has now completed the illustrated guide to the plants and the nature trail of the Sterkfontein area and the printing of the work is now in progress.

## RESEARCH WORK

Dr. A. R. I. Cruickshank has now completed and written up his research on the archosaur ankle. Two papers — a short one entitled "The pes of *Erythrosuchus africanus* Broom" and a longer one "The ankle joint in some early archosaurs" have been submitted to the Linnean Society of London. A minor experimental project concerned with the functional significance of nectridean tabular horns, being carried out in the wind tunnel of the Department of Mechanical Engineering, in collaboration with Professor Skews, continued with the support of a small grant for interdepartmental research from the Senate Research Committee.

Dr. C. Gow, having completed and published his work on the morphology and taxonomy of *Youngina* and *Prolacerta*, has been engaged on two research topics: (1) Cranial morphology of Prosauropod dinosaurs and (2) on several aspects of the family Procolophonia. The latter includes a phylogenetic review of the family, tooth morphology and succession and taxonomy of the genus *Procolophon*, and the use of procolophonians in Permo-Triassic stratigraphic correlations.

Dr. Brian Turner has become interested in a sulphur

isotope study on the desert roses found in the Beaufort beds. This work has been initiated in collaboration with Dr. T. O. Reimer of Anglo Alpha Cement and Professor Vinogradov, Director of the Geochemical Laboratories of the Academy of Sciences, Moscow.

Dr. J. W. Kitching, in addition to his continuing work on the collection and curation of fossils from the Karroo and the Transvaal limestone cave deposits, collaborates with Professor E. H. Colbert of the United States of America. Their joint paper on *Thrinaxodon* is published and they are now working on the *Ictidosuchops*-like theriodonts from Antarctica. In addition to playing a role in the planning of a forthcoming expedition to Antarctica, in which he will almost certainly take part, Dr. Kitching is writing for publication in an American journal some practical hints for fastening fossil fragments together in the Antarctic climate, using Glyptol cement and plaster of Paris.

Mrs. Judy Maguire has completed and submitted a very extensive thesis, dealing with old-world and living porcupines and other Hystricid material from pleistocene sites in South Africa. She has included an account of her work on porcupine bone accumulations and their comparison with the Makapansgat accumulations around the "osteodontokeratic tools".

Mrs. H. Anderson's thesis work on the Molteno flora is nearing completion. Mrs. Rosemary Falcon has reached the stage of carrying out final microscopic analyses of the borehole material on which she is working for the degree of Ph.D. Only statistical analysis and photographic recording remains to be done before the thesis can be completed.

During the last quarter of 1975 Mrs. Falcon was invited by Ruhrkohle, West Germany to visit their laboratories in Essen in order to study coal petrography, diagenesis and their applications to coal research in Southern Africa.

Mr. J. M. Anderson completed his research on Permian palynology in Southern Africa, and presented his thesis in October 1975.

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

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

The microfaunal and palynological laboratories maintained by SOEKOR have been expanded by the appointment of two additional technical assistants. A provisional microfaunal biostratigraphic zonation and interpreted chronostratigraphy has been prepared, using data obtained from Agulhas bank wells. Palaeontological data from the Algoa basin is being used in a programme of investigation aimed at locating potential drilling prospects. Ostracods are proving useful in aiding correlation between wells.

We continue to be very grateful to the C.S.I.R. and the Department of National Education for substantial



financial support, respectively contributing towards the running costs of the Institute and subvention of publication costs of this journal.

#### PUBLICATIONS

During 1975 Volume 18 of *Palaeontologia Africana* appeared. The contents were as follows:

JACKSON, S. P. Prof. Report of the Honorary Director for 1974.

FALCON, R. M. S. Palynostratigraphy of the Lower Karroo sequence in the central Sebungwe district, mid-Zambezi Basin, Rhodesia.

LE ROUX, S. F. A problematical element in the *Glossopteris* flora of Vereeniging.

ANDERSON, A. M. The trilobite trackways in the Table Mountain Group (Ordovician) of South Africa.

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# NUMERICAL METHODS IN THE DEFINITION OF PALYNOLOGICAL ASSEMBLAGE ZONES IN THE LOWER KARROO (GONDWANA) OF RHODESIA

by

Rosemary M. S. Falcon

## ABSTRACT

The aim of this paper is to explore the possibility of using numerical methods in the sub-division of the palynological assemblages encountered upwards in the stratigraphic sequence in one borehole core situated in a central position in the Mid-Zambezi Basin, Rhodesia. Due to its apparently conformable thick succession and the variable micro-floras already encountered within it, this borehole has been proposed as a palynological type section for the Zambezi Basin, Rhodesia.

The numerical methods used to delineate zones of similar assemblages were basically very simple, using only presence-absence data of a set range of species. The formulae employed were those of Jaccard, Simpson and Sokal (the only linear method), and the methods of classification were simplified forms of divisive or shaded half matrices, agglomerative using single linkage clustering, and spatial ordination techniques.

The results support the concept of distinct changes of microfloras up the stratigraphic sequence. Groups of assemblages bearing similar microfloras appear stratigraphically adjacent to one another, barring certain minor instances of transition floras in the younger sequences. Measurable delineations or boundaries between these assemblage zones are illustrated. These numerically defined zones coincide very closely with the assemblage zones already proposed on a visual (quantitative and qualitative) basis.

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## INTRODUCTION

The apparently conformable stratigraphic sequence in the Matabola Flats borehole, which penetrates twelve hundred feet or about 400 metres of Lower Karroo (Gondwana) sediments and is situated centrally in the Mid-Zambezi Basin, Rhodesia, was regarded as an excellent means of testing the concept of applying detailed biostratigraphy to the region, i.e. to establish whether, from the palynological content, sufficiently clear assemblage changes occur up the stratigraphic

column to warrant delineation of zones or assemblages which may be useful in future correlation. (N.B.— The use of feet rather than metres is retained due to its practical application in Rhodesia.)

Previous statistical work, summarised by Hart (1970), has been initiated elsewhere in this field. Later Hart and Fiehler (1971) created a computer-aided storage and retrieval system for Lower Karroo stratigraphic palynology, taking for a first analysis a sequence of rocks in the Mchuchuma River Valley, Tanzania. The eventual aim of these authors is to es-



establish a complete taxonomic and stratigraphic analysis of samples from any section or borehole. Methods, results and conclusions are as yet to be fully published, and the basic taxonomy, whether coded or linear in type, has not been established. It is therefore primarily a retrieval system at present.

Christopher and Hart (1971) have shown statistically the effects of extraneous sources of variation on miospore analysis. They establish a method of measurement "by defining their operating level in the geological maze", and further erect a simplified method of zonation based on frequency of genera, independent of lithological bias. The same sequence of rocks as used by Hart and Fiehler (above) was used, and 25 genera were analysed relative to their distance above basal glacial deposits and the rock-type of the respective samples. Of the 25 genera analysed only three showed significant and lithologically independent changes in their frequency of occurrence. The distribution of the remaining 22 genera could not be used in establishing biostratigraphic florizones due to their large fluctuations in occurrence related to factors other than lithology.

The conclusions reached by Christopher and Hart (op. cit.) on this Tanzanian sequence were that two major biostratigraphic zones with one narrow intermediate transition zone could be recognised, based upon regression equations and curves for the genera *Cordaitina* and *Protohaploxylinus*.

In the transition zone a major change in distribution pattern of these two genera occur.

These statistical subdivisions are shown to be similar to the visual zones published earlier by Hart (op. cit.) based on conventional quantitative and qualitative methods.

The conclusions reached by Hart (op. cit.) confirm that major macro- and microfloral changes were occurring during this period in the Lower Karroo, and that the relative frequencies of occurrence of certain selected genera do in fact represent good parameters for distinguishing distance or time above the glacials, i.e. biostratigraphic zones. This method may well prove to be more than adequate in defining relatively narrow stratigraphic units and in periods of time when climate change and evolution are known to have been active (Falcon, 1975), but it may prove too cumbersome or ineffective when attempting to define biostratigraphic units over a large span of time and in much thicker stratigraphic sequences. Hence the attempt to apply less sophisticated numerical techniques as seen in this paper.

In Rhodesia, to date, biostratigraphic subdivision has involved the application of visual methods including the standard use of qualitative and quantitative microfloral data from samples taken at intervals up the stratigraphic column in one type section. Delineation of miospore assemblage boundaries was based primarily on the qualitative and quantitative

assemblage characteristics (assemblage zones) and secondly on the finite stratigraphic ranges of zonal or restricted species. Results of this analysis have appeared elsewhere (Falcon, 1975).

In terms of numerical and statistical techniques this visual and somewhat generalised concept of zonation is regarded as inadequate. Modern methods require that subjective and intuitive influences be superseded and that, with the advent of computerised techniques, information be objective and concise in order to obtain repeatable results.

Therefore, in order to obtain an unbiased method of grouping samples from the borehole core into groups exhibiting similar microfloral characteristics, certain numerical methods of analysis have been applied. It is the purpose of this paper to outline the methods and coefficients used, and to compare the microfloral assemblage changes thus illustrated with the zonal boundaries already proposed in the visual analysis. If it is shown that results from both methods coincide and complement one another, then the existence of objective boundaries and biostratigraphic units can be accepted, at least within the context of this one borehole core.

More detailed analysis of the data using computer techniques might yield a basis for consistently recognising finer sub-divisions of the units proposed here, which would be of use in local correlation.

## PROBLEMS IN METHODS OF SUB-DIVISION OF THE KARROO

The initial problem in sub-division of Karroo sequences, as summarised by Hart (1970) and Falcon (1975), is their continental origin. The Karroo in Africa is made up of thick horizontal and originally widespread terrestrial deposits of sandstone, shale, mudstone, carbonaceous and coal deposits, some of which are economically important. These sequences are now encountered in isolated basins in central and southern Africa, the largest of which is the South African Karroo Basin. There is a very low macrofossil yield in the Lower Karroo with the result that sub-division and correlation has depended to a large extent on lithological criteria and to a very small extent on classical biostratigraphic techniques.

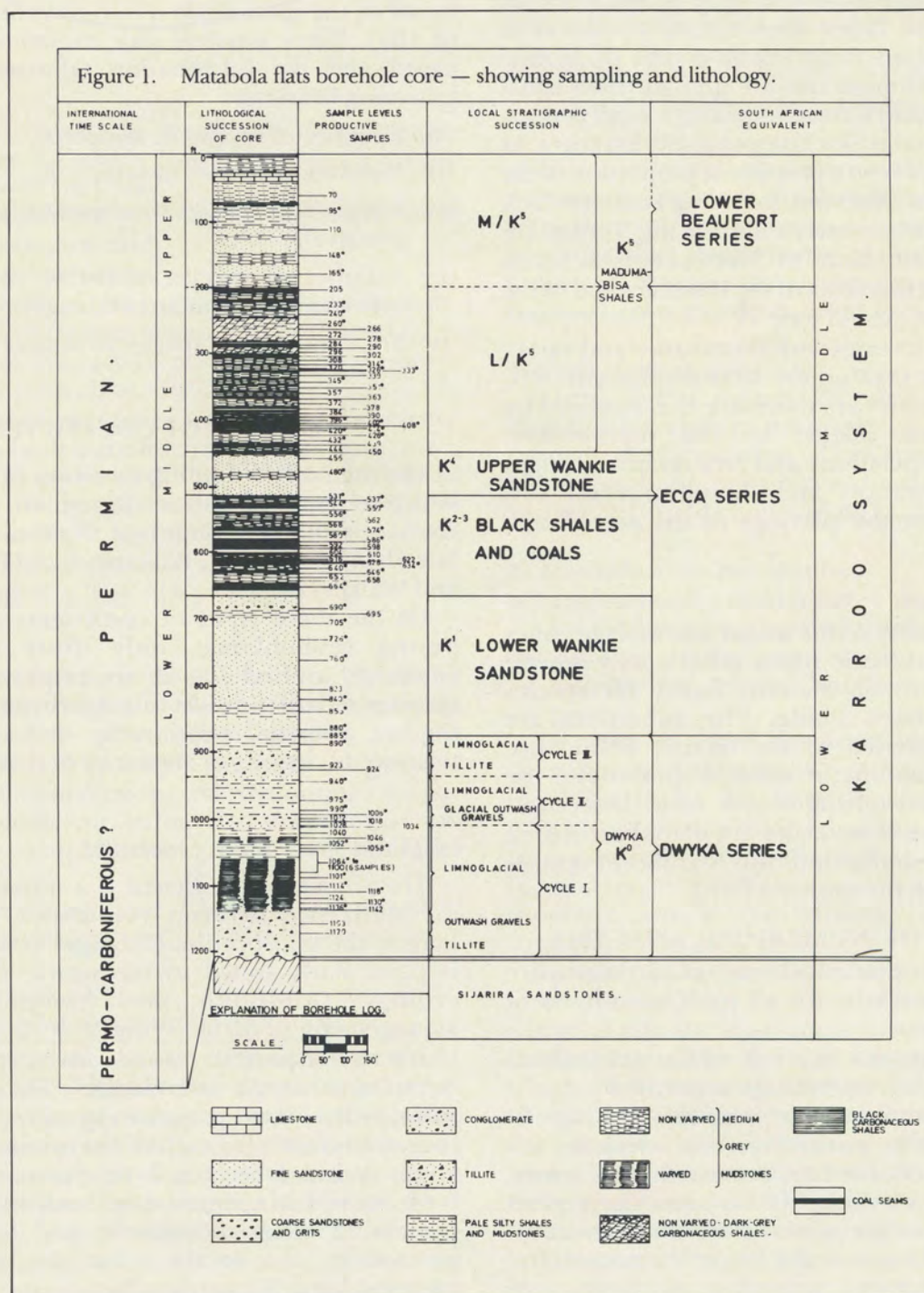
The fundamental problems of visual biostratigraphic zonation in the Karroo using palynology is a taxonomy which is unsteady and highly variable in interpretation, and thus methods in Gondwana palynological sub-division are basically subjective, with zonal boundaries drawn at arbitrary levels dependent on visual quantitative and qualitative microfloral characteristics and from samples taken over wide geographic areas. The biostratigraphic units themselves have been described in terms of microfloral assemblages found typically in them and none of these has been clearly related to any one section or series of specified sections.



However, particularly in pre-Tertiary times, the variables affecting spore/pollen production in the living plant communities (ecological, depositional climatic influences and geographic separation (Dale, 1971)) and the conditions encountered after fossilisation (diagenesis, erosion, re-deposition, etc.) are now well acknowledged and biostratigraphic unit sub-division based on visual qualitative and quantitative characteristics is approached with caution (Dale and Walker, 1970; Hughes and Moody-Stewart, 1969).

For regional and local sub-division and correla-

tion, an independent numerical approach based purely on presence/absence data is examined and analysed in this paper in the hope that this may prove more reliable than visual methods. The numerical approach in Gondwana provinces is still in its infancy, the only previous attempt known to the author being that of Hart (1970) who reports the existence of a computerised miospore retrieval system for African Karroo sequences. This, however, has a basically taxonomic emphasis and is inapplicable for the present purpose of finely delineating the Lower Karroo sequences.





## PREVIOUS SUB-DIVISION OF THE MATABOLA FLATS BOREHOLE CORE

This is discussed in detail (Falcon, 1975) and is only summarised here for the purpose of comparison (see Figure 1).

### *Assemblage zones*

These are based on characteristic quantities of suprageneric taxa, and contain distinctive assemblages of notable genera. The boundaries are placed at points in the stratigraphic column where marked changes occur in qualitative and quantitative characteristics.

Four assemblage zones are described with boundaries at about 432 feet, at about 556 feet and at about 645 feet. The major quantitative differences lie in the change in dominance from Trilete-Monosaccate miospores in zone I to the Disaccate-Striatiti forms in zone IV. In zone II, Disaccites and Monosaccites are approximately equal in proportion (Striatiti forms comprising a small percentage of the Disaccites), whilst Triletes are still dominant. In zone III, Aletes represent a prominent proportion of the assemblages, whilst Disaccites, including Striatiti (which now represent approximately a third of this Turma) are about equal in abundance to Triletes. Striatiti forms become dominant members of the Disaccites and of the total supra-generic taxa in zone IV.

Generic content varies with dominance and variation of the major taxa up the stratigraphic column. The assemblage zones are therefore characterised by associated genera related to the suprageneric groups. Their associations and stratigraphic ranges (including appearances and disappearances) add more emphasis to the placings of the assemblage zone boundaries.

### *Assemblage sub-zones*

Within the context of the major assemblage zones (with their characteristic supra-generic and generic contents), further sub-division based on species variations has been made. The sub-zones are therefore characterised by the relative abundance and group associations of selected species and the diversification in evolving major taxa (Disaccites-Striatiti) whilst the boundaries are placed according to the ranges of stratigraphically significant species particularly within the evolving flora.

## METHODS OF NUMERICAL ANALYSIS

The aim of this numerical analysis is to compare the degrees of similarity for all pairs of samples in order to establish:

- (i) groups of samples bearing similar microfloral assemblages, i.e. assemblage zones, and
- (ii) levels in the stratigraphic column where significant changes in assemblage characteristics occur, i.e. boundaries between assemblage zones. The degrees of similarity vary and the greater the difference (or *dissimilarity*) between compared assemblages so the larger the microfloral change.

## PREPARATION OF INFORMATION

The numerical methods chosen for this study are those employing only qualitative species information, i.e. presence/absence data. The presence of species not seen in samples located within their known stratigraphic range is not presumed.

Many methods employing quantitative information have been successfully tried on Tertiary and younger microfloral assemblage schemes (Dale and Walker, 1970; Williams and Dale, 1965; Williams *et al.* 1966), but due to the many variable factors affecting pre-Tertiary fossils the presence/absence of species is preferred at present.

The initial information was obtained by tabulating the sample numbers (43 in all) against a list of all the species taken into consideration (a total of 105). Every possible pair of samples was compared and the information tabulated under the following headings:

- (i) Number of species in sample A,
- (ii) Number of species in sample B,
- (iii) Number of species common to both (matched, positive),
- (iv) Number of species occurring in only one or other sample (unmatched, negative),
- (v) Total number of species in samples A and B.

## CHOICE OF COEFFICIENT

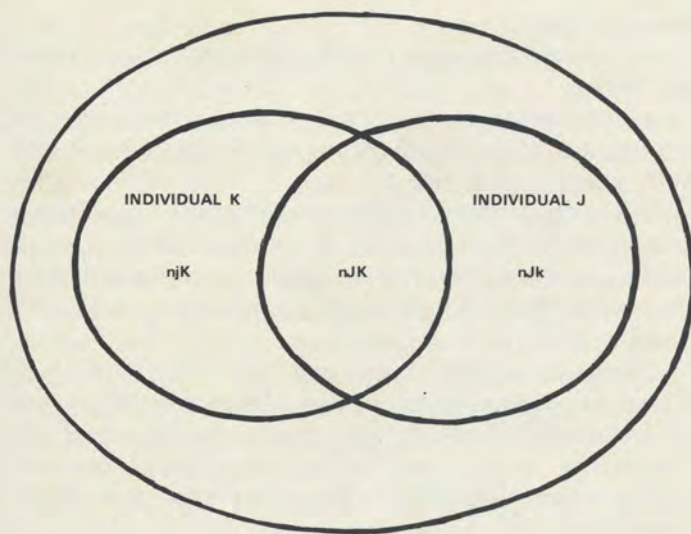
The methods of finding measures of resemblances between pairs of entities based on a number of characteristics is summarised in detail by Sokal and Sneath (1963, p. 123), Williams *et al.* (1966) and Dale and Walker (1970).

Of the three types of coefficients used in computing resemblance, only those of *association* (*similarity*) and of *distance* are employed expressing direct similarity, whilst the coefficient of distance implies a spatial relationship and a quantitative measure of degrees of similarity or dissimilarity.

### *Coefficient of association (similarity)*

The similarity coefficient is a numerical value of the difference between two entities or, as used herein, the miospore assemblages in two samples. It is particularly suited to measuring associations in ecology (Goldsmith, pers. comm.). The basic arrangement of data is the  $2 \times 2$  table, with  $n$  characters (species) scored for two individuals (samples or sample assemblages). The characters are sub-divided into presence (positive) or absence (negative) classes for each of the two individuals. The count is then taken for those characters positive to both individuals, negative to both individuals (but present in other individuals) and for those only positive in one or the other. In two imaginary samples, J and K, one then has:





$n$  = no. of characters (species) in the whole sequence, of which J and K possess a certain number. Therefore

$JK$  = shows positive presence of one character in both samples, and

$jk$  = negative presence;

$nJK$  = no. of characters *positive* to both individuals;

$njk$  = no. of characters negative to both; and

$nJk$  } = no. of characters positive to only one or other individual.

The number of characters with common presence or absence in both samples are termed "matched", and their sum is termed " $m$ ". The number of characters occurring only in one or other sample is termed "unmatched", and their sum is termed " $u$ ". The total number of characters,  $n$ , is therefore:

$$\begin{aligned} n &= nJK + njk + nJk + nk \\ &= nJ + nJ = nK + nk \\ &= m + u \end{aligned}$$

The fundamental formula as defined by Sokal and Sneath (op. cit.) consists of the number of matches (or total number of common species) — the numerator, divided by a term implying the possible number of comparisons — the denominator. The larger the coefficient value for the comparison between two samples, the greater the similarity between them.

The formula or coefficient of similarity employed in this study is that of *Simpson*<sup>(m2)</sup> in Mortimer (1969).

$$\begin{aligned} \text{i.e. } C &= \frac{nJK}{\min(nJ, nK)} \\ &= \frac{\text{total no. of spp. common to both}}{\text{no. of spp. in the less diverse assemblage}} \end{aligned}$$

This coefficient allows for wide variation in numbers of species per sample, from rich to poor. An assemblage poor in species variation may therefore possess a high degree of similarity (up to 100%) when compared with another rich in species.

The coefficient of distance is a measure of similarity utilising distance or dissimilarity based on Pythagoras's theorem. The techniques employed are

therefore geometric and are here only being considered in two dimensions. (See Sokal and Sneath, op. cit., p. 143.)

The measure of distance is estimated on the basis of quantitative values of negative matches of species between two samples or microspore assemblages. These values may be plotted on single or rectangular co-ordinates. If the two samples under consideration are identical, their spatial position will coincide, and the distance between them will be zero. The greater the dissimilarity, the greater the distance between them. Therefore distance complements similarity.

The coefficient of distance employed in this study is that of Sokal (Sokal and Sneath, 1963, p. 147).

$$D_{jk} = \sqrt{\sum_i (X_{ij} - X_{ik})^2}$$

where  $X_{ij}$  = 0 if the species  $i$  is absent from sample  $j$ ;  
= 1 if species  $i$  is present in sample  $j$ .

This coefficient of distance ( $D$ ) generalises the concept of Euclidean distance between two points in an  $n$ -dimensional space, i.e. it embraces information regarding the presence or absence of the whole range of species in a two-dimensional setting, relative to two standard points or samples.

#### Methods of classification

There are a variety of ways of constructing classification systems for grouping assemblages with similar characteristics. The system is basically hierarchical or non-hierarchical (see Dale and Walker, 1970; Gordon and Birks, 1972).

##### I. Hierarchical methods involve:

- agglomerative techniques, a monothetic form of singly clustering together similar entities; and
- divisive techniques, dividing up the total number of entities into smaller and smaller groups.

In order to make significant hierarchies clumped distribution of samples is required, i.e. nests within the hierarchies. Random distribution of samples may give some nested groups, but due to too many intermediate or transitional members, the hierarchies or divisions may not be as clear cut as those in which the samples are retained in stratigraphic order.

In making clusters of similar groups, the dividing lines or assemblage zone boundaries must be placed where there are significant breaks in microfloral composition. The level of termination (or rank) at which the hierarchical schemes are divided (in order to establish the groups of similar assemblages and the degrees of dissimilarity between them) is somewhat arbitrary. The level of rank adopted in this paper is that which illustrates most clearly the maximum number of assemblage sub-zones without omitting transitional single members and with the least amount of overlapping between nests or clusters.



It is an accepted fact (Sokal and Sneath, 1963; Goldsmith, pers. comm.) that in ecological analysis of extant organisms, overlapping of assemblages or communities is inevitable. However, due to the long time span represented by this borehole sequence, microfloral assemblage changes are expected to be more marked. Climatic and ecological conditions are the accepted causes of community changes, but other factors to be considered when covering a long period of time are those of evolution, disconformities in the stratigraphic sequence, long erosional periods, deposition of reworked sediments bearing older microfloral elements and repetition of climatic cycles. These conditions will influence the final interpretation of the assemblages analysis, or indeed may show up in the course of the analyses.

The methods of illustration or graphic representation of the hierarchical methods applied in this paper are (a) shaded half matrices and (b) single linkage clusters. These are considered useful preliminary techniques in terms of analysis of the Matabola Flats borehole core, and were drawn using the Simpson coefficient.

II. *Non-hierarchical methods* include ordination, a further method of sub-division of assemblages into similar groups based on spatial linear relationships. This technique is based on the distance-measure of all sample assemblages relative to two reference assemblages on a standard axis. *Sub-division* of assemblage zones is by means of magnitude of distance between two nests or groups of assemblages; the larger the measure between them, the greater the microfloral dissimilarity.

Illustration of this method of classification adopted in this paper includes (a) single axis ordination, and (b) spatial ordination (clustering). In single axis ordination the intercept of the perpendicular from the point at which the arcs meet (i.e. the measured distance of each sample from the two standard samples) and the axis gives the relative distance of dissimilarity along the axis of the sample assemblage from the two reference samples. The closer the sample assemblages, the greater their similarity. Ideally assemblages from samples closely adjacent would fall into neat clustered groups or nests to form assemblage zones or biostratigraphic units (if all members are stratigraphically adjacent).

Spatial ordination comprises the composite spatial relationship of two single axis ordinations. The sample assemblages relative to four basal axial samples appear as points where the perpendiculars meet. Those samples most closely grouped are recognised to be most similar. Ideally, nested or clustered groups of samples would represent biostratigraphic units if stratigraphically discrete, or "associated assemblages" if randomly scattered in the stratigraphic sequence. The larger the gaps between the nests, the greater the microfloral change.

## Nomenclature

A few relevant terms used in this paper are defined below:

*Sample* denotes the small rock unit at a specific depth in the borehole core from which the miospores are obtained.

*Assemblage* refers to the characteristic qualitative microfloral content of each sample. Both sample and assemblage refer to a single entity. Samples are named in feet (depth) and assemblages numbered 1–43 as in Figure 7.

*Visual assemblage zones and sub-zones (VAZ)* are biostratigraphic units, having distinct stratigraphic delineations (boundaries) and characterised by qualitative and quantitative microfloral content. Analysis and definition is based on inspection alone. (See Figure 12).

*Numerical assemblage zones (NAZ)* are units consisting of assemblages (=samples) grouped together on the basis of similarity or dissimilarity of the microfloral content, irrespective of the stratigraphic positions. The microfloral analysis is based solely on presence-absence data while delineations of the NAZs are based on the magnitudes of spatial breaks between them.

## Results

These will be discussed under the headings of classification methods and comparisons made between the two coefficients involved in this study.

### (a) Divisive Techniques in Classification

The technique applied is that of *differential shading of a similarity matrix*. The coefficient used was that of Simpson. This is the simplest method of illustrating the sub-division among the assemblages, as groupings may be seen at a glance. (See Figure 2.)

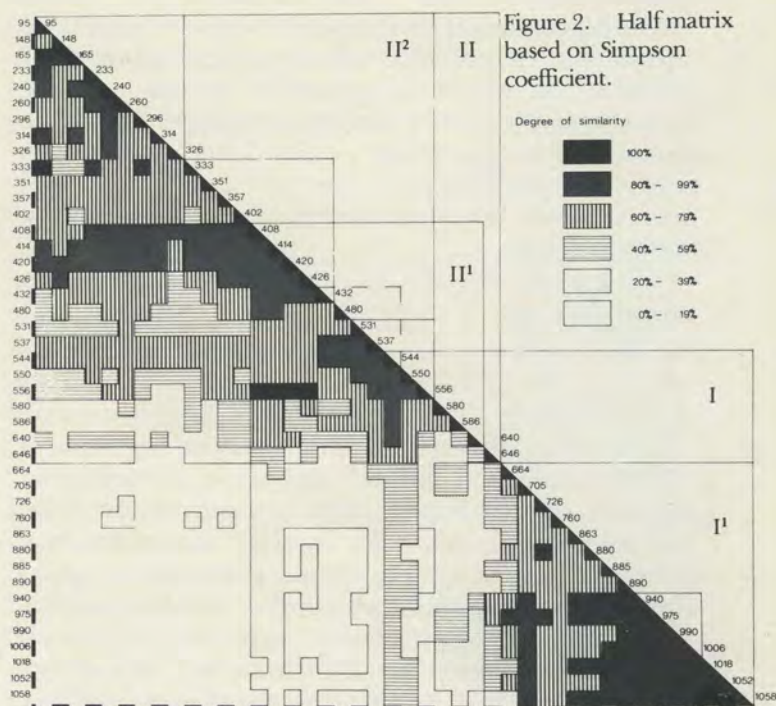


Figure 2. Half matrix based on Simpson coefficient.



The coefficient values for all possible pairs of assemblages are placed into a half matrix. These values are divided into five equal classes of magnitude between 0 and 100%, the sixth indicating absolute similarity or 100%. Each class possesses a different degree of shading proportional to its magnitude and when applied to the values in the squares of the half matrix should show dark areas of high value and light areas of low value.

In the present application, the assemblage values in the half matrix were arranged in stratigraphic order so that the clusters of similar assemblage groups, although appearing rearranged due to their marked nestings or groupings, are in fact unbiased and merely arranged according to depth.

The half matrix shading illustrates that samples (assemblages) are grouped together in large distinct clusters in ascending or descending stratigraphic order. At a glance, four major groups of clustering are obvious but on coefficient value analysis (i.e. according to the percentage units) a different and more complex picture emerges.

At the low similarity value of 40–59%, two large overlapping groups are seen: NAZ I = 1,058–544 and II = 646–95 ft. The overlap or transition area is between samples 544 and 646 — which coincides with the proposed transition zones in the visual assemblage zones. A further sub-division at the 60–79% level shows one large microfloral unit, NAZ I<sup>1</sup>, below 664 ft and two overlapping above 640 ft, NAZ II<sup>1</sup> and NAZ II<sup>2</sup>.

NAZ I is characterised by one large cluster of samples centred around samples 940 ft, 975 ft, 990 ft, and 1 006 ft. No further assemblage breaks occur of any significance. It is of interest to note that all the samples above 890 ft and below 1 018 ft do not show any greater similarity to each other — their uniform value is 60–79%. But all these samples have greater values when compared to 940–1 006 ft. This is considered to be a function of the coefficient in that the richest and most varied miospore taxa occur in samples 940–1 006 ft; all other samples with similar species but fewer in variety therefore show extremely high values when compared with these rich samples.

NAZ II is divided into two overlapping zones with values of 60–79%: 640–408 ft (II<sup>1</sup>) and 556–95 ft (II<sup>2</sup>). A further three sub-zones may be sub-divided. These are arbitrary units based on careful comparison of all samples, and are not clearly seen in the visual assemblage zones. Overlapping, clustering and repetition of high similar values account for this. One small transition zone occurs. Sample assemblages down to a level of 333 ft show close comparisons between each other and samples 408–420 (80–99%), i.e. repetitive or associated assemblages. But samples 35 to 402 show closer affinity to 408–426 only. There would seem therefore to be a break of some small order in the region of sample 333. Similarly, assemblages 420–408 compare at a similarity of 80–99% not only with assemblage 480 below (and 556, a relatively weak sample),

but all possible assemblages above, possibly illustrating a new flora at level 426–432 ft which continues through the younger sediments — this agrees with the *Vittatina-Lueckisporites* visual assemblage zone. Sample 480, a stratigraphically isolated sample, shows equal affinity up to 408 ft and down to 544 ft. This may therefore be termed a transition assemblage.

The “problem” assemblages in samples 640, 646 and 664 are indicated by the Simpson coefficient as being transitional, but with a major dividing point in sample 646. This assemblage bears a 60–79% similarity to the adjacent major assemblage groups above and below (537–550 and 940, 975). The younger assemblage 640 is moderately similar to 646 but below this a break occurs in older assemblages. The natural affinity is to the younger assemblage group 408–556. Alternately sample 664 ft shows a moderate break ( $\pm 50\%$ ) with younger assemblages above but a close affinity to older ones below.

Figure 3 shows the numerical assemblage zones as analysed in Simpson's coefficient. Four breaks shown in Simpson's analysis coincide with four visual assemblage zones delineations at 885 ft, 664 ft,

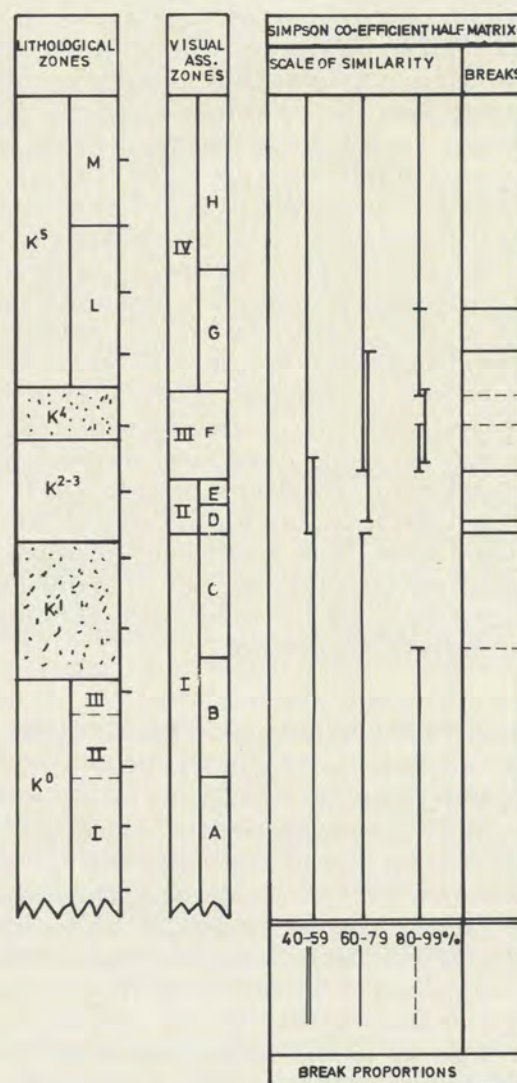


Figure 3. Divisive classification — half matrix shaded.



556 ft and 432 ft, i.e. boundaries between visual assemblage zones, B and C, C and D, E and F, F and G. A further four are possible. These numerical assemblage breaks illustrated are not necessarily the delineations of discrete and separate assemblage zones. The scale depicting the order of importance of the breaks must be taken into account when assessing the comparisons of the actual visual assemblage zones and numerical assemblage zones, and where the major microfloral vegetational changes occur.

To summarise, the shaded half matrix illustrates a major microflora below 664 ft, a transitional zone between 646 ft and 580 ft, and a series of minor microfloras overlapping one another above 556 ft. The degree to which each assemblage zone varies can be defined numerically.

The Simpson coefficient ("total common species to number of species in poorer sample") allows for the comparison of assemblages poor in variety with very rich ones. This prevents the masking of poor samples and serves the useful purpose of dividing the two major floral assemblage zones (NAZ I and II). Thereafter the focal point of the numerical assemblage zones appears to be those samples bearing the richest species variation. Adjacent to these groups of high similarity are samples less varied in content which may exhibit clear and distinct affinity to one group, or a shared affinity to several. By this means large-scale sub-zones and microfloral breaks or overlapping of sub-zones are made obvious.

Simpson's coefficient would therefore seem to be adequate at delineating major assemblages to these zones no matter how poor the species variation. In terms of correlating a random or unknown sample numerically, this coefficient would indicate the major assemblage zone or zones to which it may be most closely compared. Thereafter a more stratigraphically limited comparison within the zone or zones may be made using such methods as the Jaccard coefficient (Sokal and Sneath, 1963). This method has been used, but for the sake of brevity is not included here. Both coefficients adequately illustrate the presence of the previously defined visual assemblage zones and the breaks between them in varying degrees of importance.

### (b) Agglomerative Techniques in Classification

Cluster analyses are agglomerative techniques based on high similarity coefficients for the purpose of delineating or grouping similar individuals. *Single Linkage clustering* is one of many methods of clustering. It is initiated by grouping together individuals with the highest related similarity; thereafter by lowering gradually the coefficient value of admission, more members are admitted into the cluster. The single linkage is the means whereby an individual or group of individuals (cluster) are joined. Sokal and Sneath (1963, p. 180) discuss the single linkage methods at length.

If an individual or cluster joins a second cluster on the basis of equal similarity between one member in each, then the inferred group similarity may be too generalised a concept and many members may in fact be quite removed from each other. Similarly, one individual or cluster, when representing a transition microflora, may at the same level of similarity be required to join two separate other clusters not related to each other (except having this common element). This "overlapping" effect is a disadvantage and transitional or repetitive cycles are therefore difficult to illustrate. Where this has occurred (primarily in the youngest floras) a method of cross-hatching has been adopted in this paper.

Further formulae and methods of recalculation have been devised (Sneath, *in* Sokal and Sneath, 1963, p. 181) to overcome this problem, but for the purpose of this paper only the initial single-linkage methods have been employed to test their possible validity, and for confirmation of other methods of zone delineation. In order to test two aspects, the Simpson coefficient values have been applied to samples arranged in stratigraphic order (i.e. *stratigraphically aligned*), whilst the Sokal coefficient values have been used to illustrate the clustering of *randomly distributed* samples.

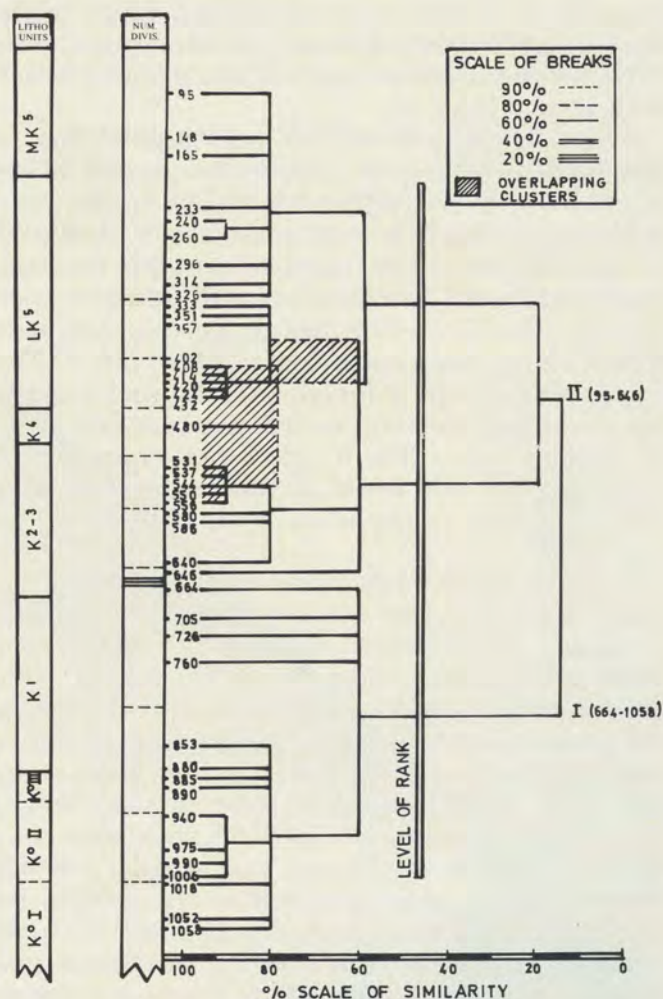


Figure 4. Agglomerative clustering based on the Simpson coefficient samples in stratigraphic sequence.



(a) *Stratigraphically-aligned assemblage clusters*

Single linkage clustering of sample assemblages placed in stratigraphic sequence is illustrated in Figure 4 and the coefficient used is the qualitative one of Simpson. The sample assemblages are placed relative to their depth in the borehole core with an adjacent log indicating the lithological units. The levels at which the clusters join represent the values of similarity which have been obtained using the Simpson coefficient and are therefore taken from the same half matrix of values as the *shaded* half matrix. The scale of similarity is again divided into five units representing 0–100% similarity.

Assemblages with the highest degree of similarity are initially joined, e.g. 90%, followed at a lower level by those sample assemblages with the next highest similarity coefficient value, e.g. 80%. Assemblages, or clusters, which compare with one or more individuals in another cluster are also joined, indicating a generalised grouping or overlapping but in these cases cross-hatching indicates the span of time involved.

The results are shown in Figure 4. There are four clusters at the highest level of similarity (90%) followed by four further clustered groups corresponding to those seen at the 80% level in Figure 2. One transition zone exists at this level between 544 ft and 408 ft and another one between 408 ft and 420 ft at the next level.

The basic *level of rank* has been drawn between 60% and 40% on the scale of similarity. This level was selected to illustrate as simply as possible the clustering of all assemblages into three major groups or floras with the younger two overlapping. The major break occurs between the lower two floras, i.e. between samples 646 and 664. This break agrees with other results already seen in the half matrix. The clusters of Simpson are generalised, wider embracing stratigraphically, and most significant at one level (80%, a relatively low degree of similarity). This clustering and series of breaks agrees with those of the half matrix, but adds a *two-dimensional* aspect of magnitude to the breaks.

(b) *Randomly distributed clusters*

Single linkage clustering by means of randomly distributed assemblages is illustrated in Figure 5. Sokal's coefficient was used in this technique, to test once more the validity of sample groupings based on both a different coefficient and method of clustering. The values are plotted on a scale of dissimilarity indicating the greater the coefficient value the larger the dissimilarity between assemblages. For the purposes of unbiased comparison, the assemblages are numbered (see Figure 6).

The method of progressive addition involves the linking together of random sample assemblages bearing the lowest dissimilarity values, and thereafter admitting usually singly assemblages with progressively increasing dissimilarity.

The initial groupings of related assemblages oc-

curs at a level of 2.8 and progresses by single linkage admittance of one or more clusters up the scale of dissimilarity. *Level of rank* is arbitrarily taken as being 4.4. Above this, at level 4.7, three entities emerge, one random assemblage (21) and two large and distinct clustered microfloral groups stratigraphically separated with a large break above assemblage 28. At the basic rank level, two major clusters and five single assemblages join. The two major assemblage groups represent (1) one biostratigraphic entity, NAZ I (assemblages 29–34 inclusive, or 664–1 058 ft), and (2) one near biostratigraphic entity, NAZ II (1–27, or 95–640 ft), excluding assemblages 21, 22, 23 and 27 which have been regarded elsewhere as a separate group. Assemblage 28 is quite unique and stands alone, joining above the basic rank level to the NAZ I. This assemblage has previously been illustrated as representing a lone transition position, but eventually joining the upper limit of NAZ I at a low level of similarity. The two largest breaks therefore occur below and above assemblage 28. Breaks between these assemblages are regarded as similar to one another but marginal to the major NAZ II.

Within the two large assemblage groups, NAZ I and NAZ II, seen at basic level or rank, smaller groups of equally clustered assemblages show the existence of mutually related floras, the most notable of which in NAZ I is assemblage 35–43, inclusive, i.e. 885–1 058 ft, (i.e. VAZ A and B, found in the Dwyka interglacial sediments). Lower orders of dissimilarity occur in adjacent assemblages which agrees with the transitional nature of NAZ C.

In NAZ II, grouping of assemblages is more random and shows a reorganisation of stratigraphic levels in an attempt to show similarity groupings. At 4.2 a large number of assemblages and clusters join showing a broad constant level of dissimilarity. Sub-groups below this do, however, possess assemblages almost adjacent to one another and linked progressively up the stratigraphic column with minor readjustments in the stratigraphic order.

Sub-division at level 4.0 shows low dissimilarity (high similarity) between assemblages 2, 3 and 4 and 11, 12, followed closely by assemblage 7, then 8 and 9, thereby forming a group of assemblages 2, 3, 4, 7, 8, 9, 11 and 12 leaving out assemblages 1, 5 and 6 which are separately grouped together. Such separation may be related to reworking of older sediments bearing similar assemblages, or by cyclic repetition of a similar climate and ecological environment. Further sub-groupings are illustrated at 4.0, with one significant group, 25 and 26, at 3.3. These assemblages are shown to be associated again in ordination classification.

Where assemblages are linked closely, but in fact are not adjacent to one another stratigraphically, the possibility of similarity caused by reworking of sediments or climatic oscillations must be considered carefully. These linkages, although relatively infrequent, may therefore be due to a number of



FIG. 5.

SINGLE LINKAGE CLUSTERING BASES ON THE SOKAL COEFFICIENT -  
RANDOM SAMPLES JOINED (PROGRESSIVE ADDITION).

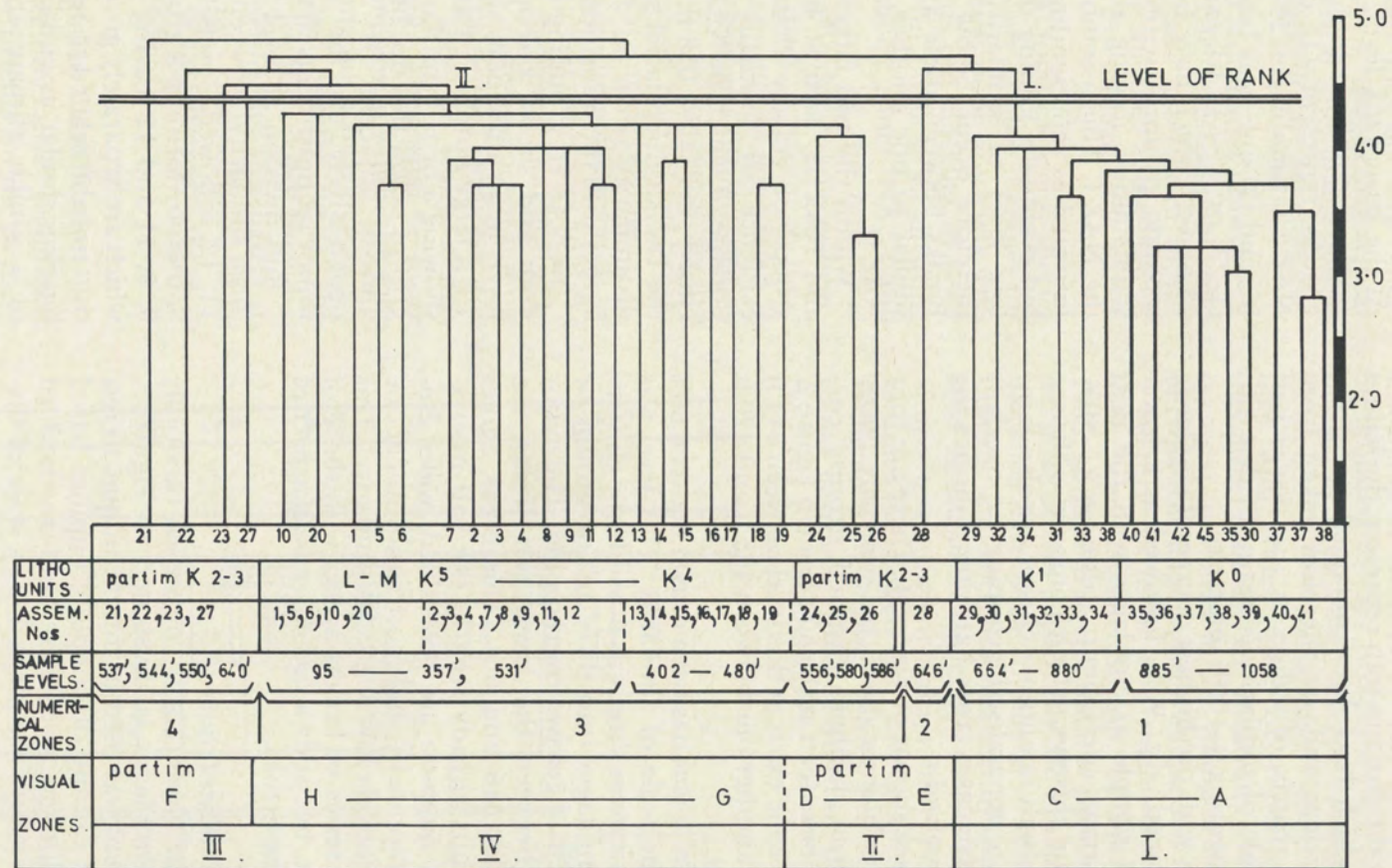


Figure 5. Single linkage clustering bases on the Sokal coefficient — random samples joined (progressive addition).



factors which must be taken into consideration in the final interpretation of this method of analysis.

### (c) Summary

A summary of the assemblage boundaries using agglomerative sub-division may be seen in Figure 6.

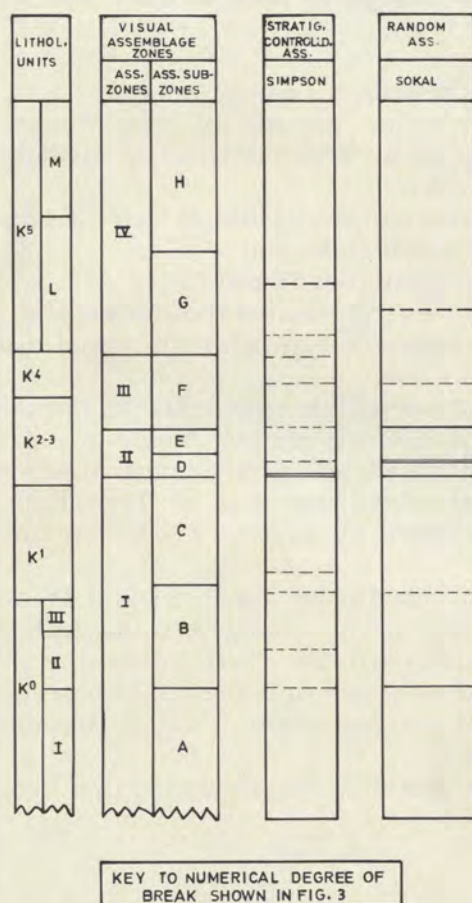


Figure 6. Agglomerative sub-division: single linkage clustering.

#### (1) Stratigraphic distribution of assemblages

The primary advantage of stratigraphically controlled clustering methods is that it allows for quick checking as to the natural groupings of the samples within the lithostratigraphic context and within a two-dimensional background. The disadvantages involve the difficulty in illustrating the distributed affinities of transitional assemblages to the major floras.

In comparison with the visual assemblage zones, the delineations of assemblage sub-zones A–H are moderately well defined by the Simpson coefficient. Further detailed definition of the sub-zones are deemed potentially possible using more refined methods in the future.

#### (2) Random distribution of assemblages

Sokal's linear coefficient used in single linkage clustering of random assemblages shows good stratigraphic grouping of similar assemblages. The four major groups seen at a standard rank level of 4.4 virtually coincide with the four major assemblage zones obtained by visual means. Breaks

between these zones are noted with varying importance in the stratigraphically aligned cluster analyses. Further sub-divisions in the younger zones (above 28) are based on minor groupings of stratigraphically disorientated assemblages which may show affinity to each other due to cyclic factors as discussed previously. This re-arrangement of the assemblages is not possible as is clearly illustrated in earlier methods.

The advantage of this method is the unbiased approach to clustering, based solely on numerical levels of dissimilarity. The distinct numerical assemblage zonal breaks seen here confirm more positively the major natural visual groupings already proposed. The slightly disorientated minor groups of assemblages seen above 28 may well prove useful in ecological studies.

On summarising the agglomerative techniques of sub-division, emphasis must be placed on the random distribution method (Sokal coefficient). This gives (1) an unbiased, two-dimensional grouping of similar assemblages at high levels of dissimilarity; (2) it surpasses the clumsy nature of illustrating transitional assemblages (as in stratigraphic methods); and (3) natural groupings of randomly distributed low-level dissimilarity groups may allow for the study of palaeogeographical or palaeoecological factors common to all of them. This method warrants further study.

The advantages of the stratigraphically aligned agglomerative procedures are based on the natural microfloral changes up the stratigraphic column which may be correlated with lithological factors. This method may only be used over long time intervals, involving thick sequences. Narrow stratigraphic limits would cause undue overlapping and difficulty in the clustering of similar randomly distributed assemblages.

In terms of comparison with the visual assemblage groups, the Sokal and Simpson coefficients illustrated by these agglomerative techniques both confirm the boundaries of the major assemblage zones and most sub-zone delineations (with the possibility of even further divisions).

### SPATIAL ORDINATION — A METHOD OF NON-HIERARCHICAL CLASSIFICATION

The spatial relationships between compared assemblages requires a coefficient of distance based on linear geometrical theories. For this method of classification, termed spatial ordination or clustering, Sokal's coefficient was chosen (see Methods of Analysis).

Two methods of illustrating spatial grouping amongst similar assemblages are employed:

- (1) — Single axis ordination, and
- (2) — Spatial or double axis ordination.

#### (a) Single axis ordination

This is a simple graphical method or ordination based on the relationships of all assemblages to two







FIG. 8. — SINGLE AXIS ORDINATION — REFERENCE SAMPLES 1:39 (95 : 990') (DISSIMILARITY VALUE  $D_{jk} = 8.3$ )

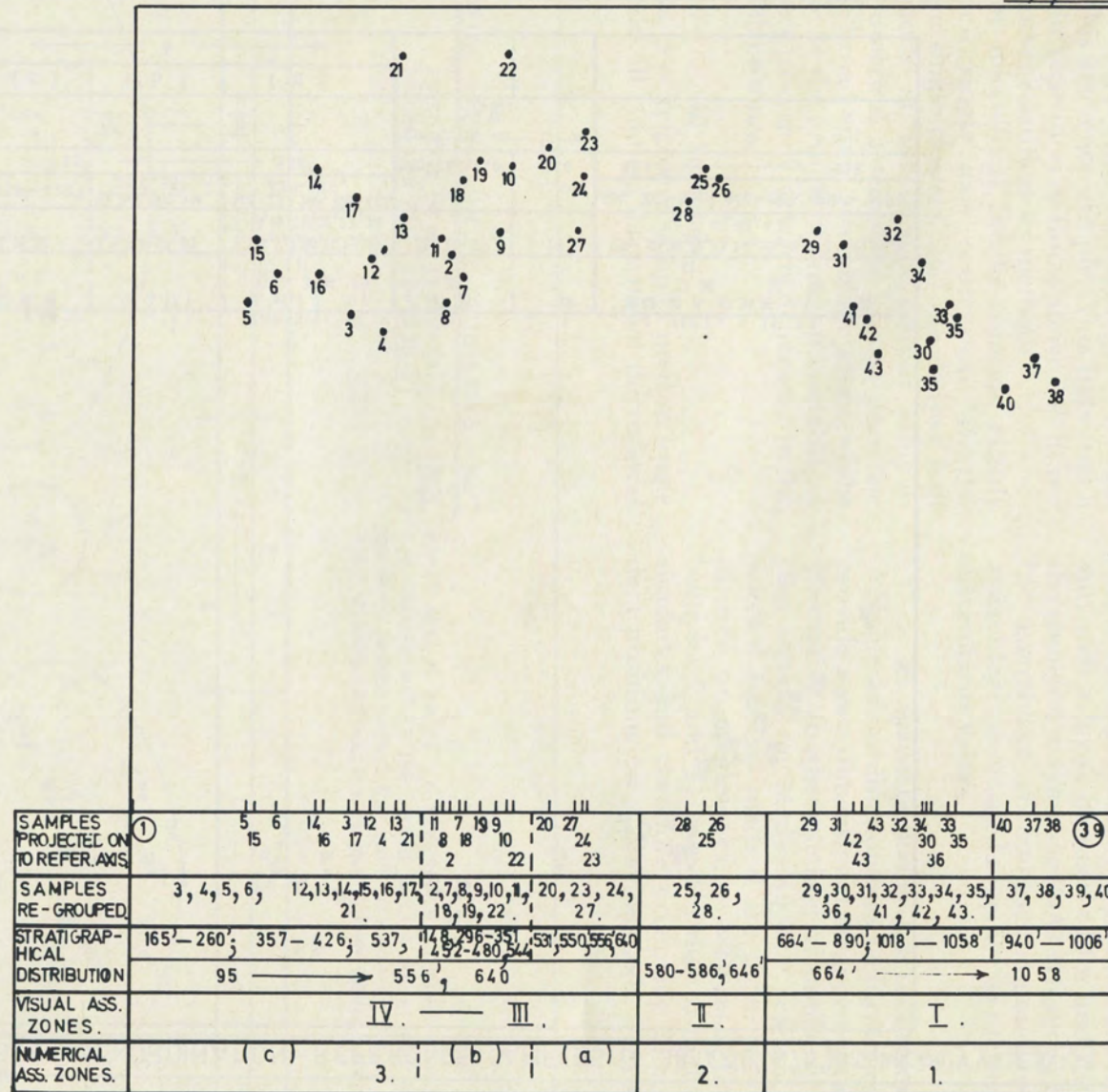


Figure 8. Single axis ordination — reference samples 1:39 (95 : 990') (dissimilarity value  $D_{jk} = 8.3$ ).



period of time at least three distinct floras were seen to have occurred with marked breaks between them.

(b) *Reference samples 14 and 38 — Figure 9*

These reference samples, bearing abundant species variation in both, show most clearly six demarkated assemblage groups. The major breaks occur between samples 24 and 25, between 27 and

28, and between 28 and 29, and below 646 ft with minor breaks occurring between three assemblage groups above sample 24. The latter three, unlike the first three, are adjacent.

The numerical groups 1, 2 and 3 are stratigraphically clearly divided and represent the Visual Assemblage Sub-zones A, B and C (=NAZ I); VAZ D (=NAZ II) and VAZ E (=NAZ III). Above

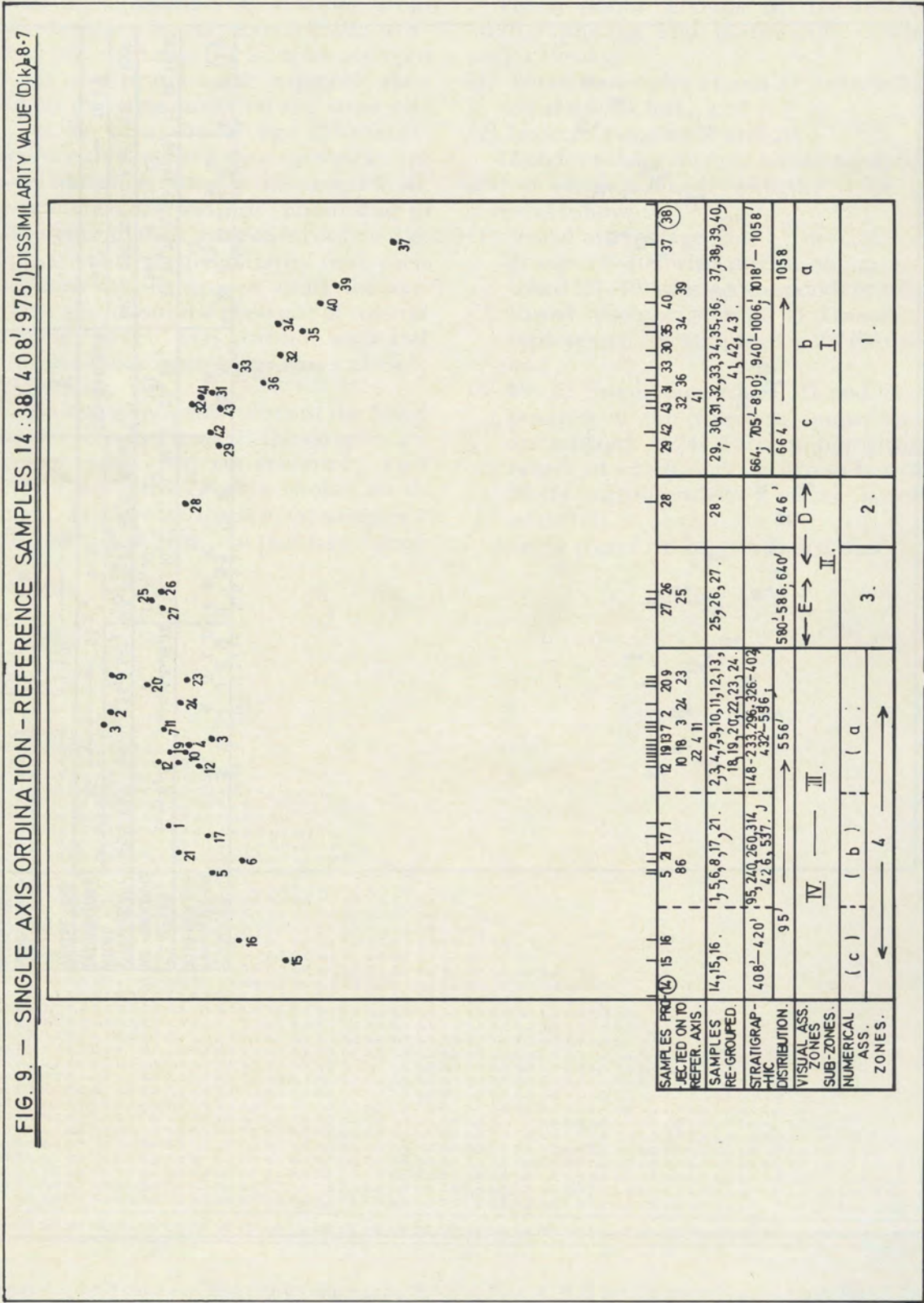


Figure 9. Single axis ordination — reference samples 14:38(408':975') (dissimilarity value Djk) = 8,7.



sample 24 (556 ft) the assemblages are randomly arranged in three groups of proportional dissimilarity relative to the reference assemblages. NAZ (C) with samples 14–16 are stratigraphically adjacent and very similar, whilst groups (a) and (b) possess assemblages older and younger than those in (c) falling into two marked groups of dissimilarity. When stratigraphically divided into concentric bands of dissimilarity above and below assemblage NAZ (c), the random assemblages fall into similar associated assemblage groupings to those of the single linkage clusters, indicating progressive dissimilarity of floras away from this reference sample. This indicated a potential cyclic repetition of floras above 586 ft, not indicated in other classificatory methods.

Two major microfloral breaks coincide exactly with the first single axis ordination (a), the agglomerative single clusters, and the divisive half matrix methods of sub-division. From samples 25–40 the numerical assemblage groups correlate well with the broad visual assemblage zones, whilst above sample 24 the groups of random assemblages form a distinct pattern not clearly delineated in the visual assemblage zones.

#### (b) Summary

The two pairs of reference samples used in single axis ordination all confirm three major microfloral

zones with large-scale breaks between samples 24 and 25 (i.e. 556 ft and 580 ft) and between samples 28 and 29 (i.e. 646 ft and 664 ft).

Three of the major visual assemblage units are thus well defined with visual assemblage zones III and IV apparently absorbed into the youngest numerical zone. Below the oldest microfloral break an assemblage occurs which has the possibility of further sub-division with different reference samples.

In the middle numerical assemblage zone, two further stratigraphically separated assemblages occur, with a break between 640 ft and 646 ft, whilst the youngest major zone (NAZ III) shows four possible assemblage groupings composed of random assemblages associated together by means of similar dissimilarity values.

#### (c) Spatial or double-axis ordination

Single axis ordination may be further extended to provide a two-dimensional arrangement of samples illustrating another method of similarity grouping. (See section on Methods.) The reference samples selected for this method are those previously ordinated on single axes, as well as a further pair (samples 7 and 11) selected due to high degree of similarity and therefore occupying almost coincident positions on a previous axis. This single axis

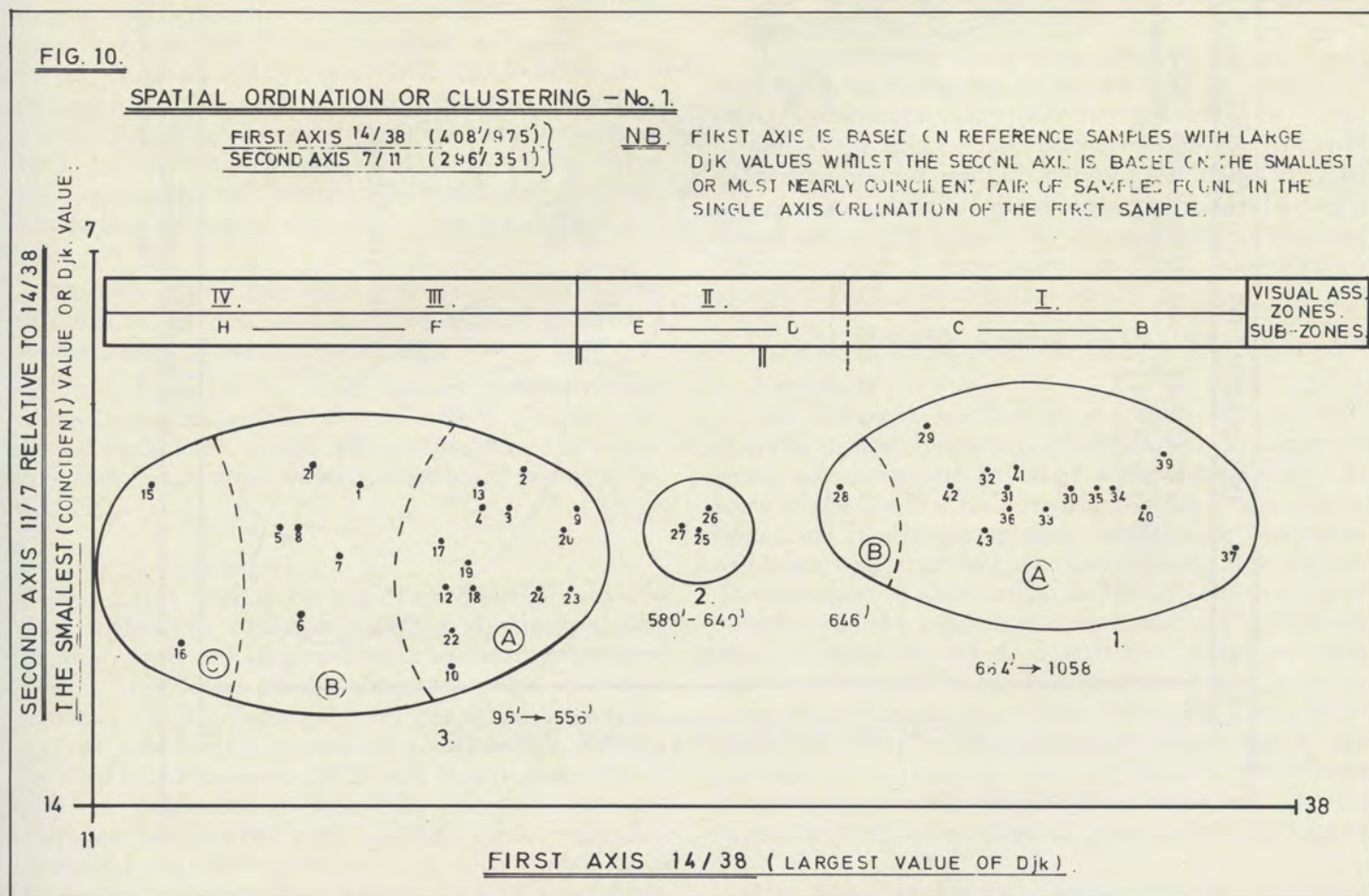


Figure 10. Spatial ordination or clustering — No. 1.



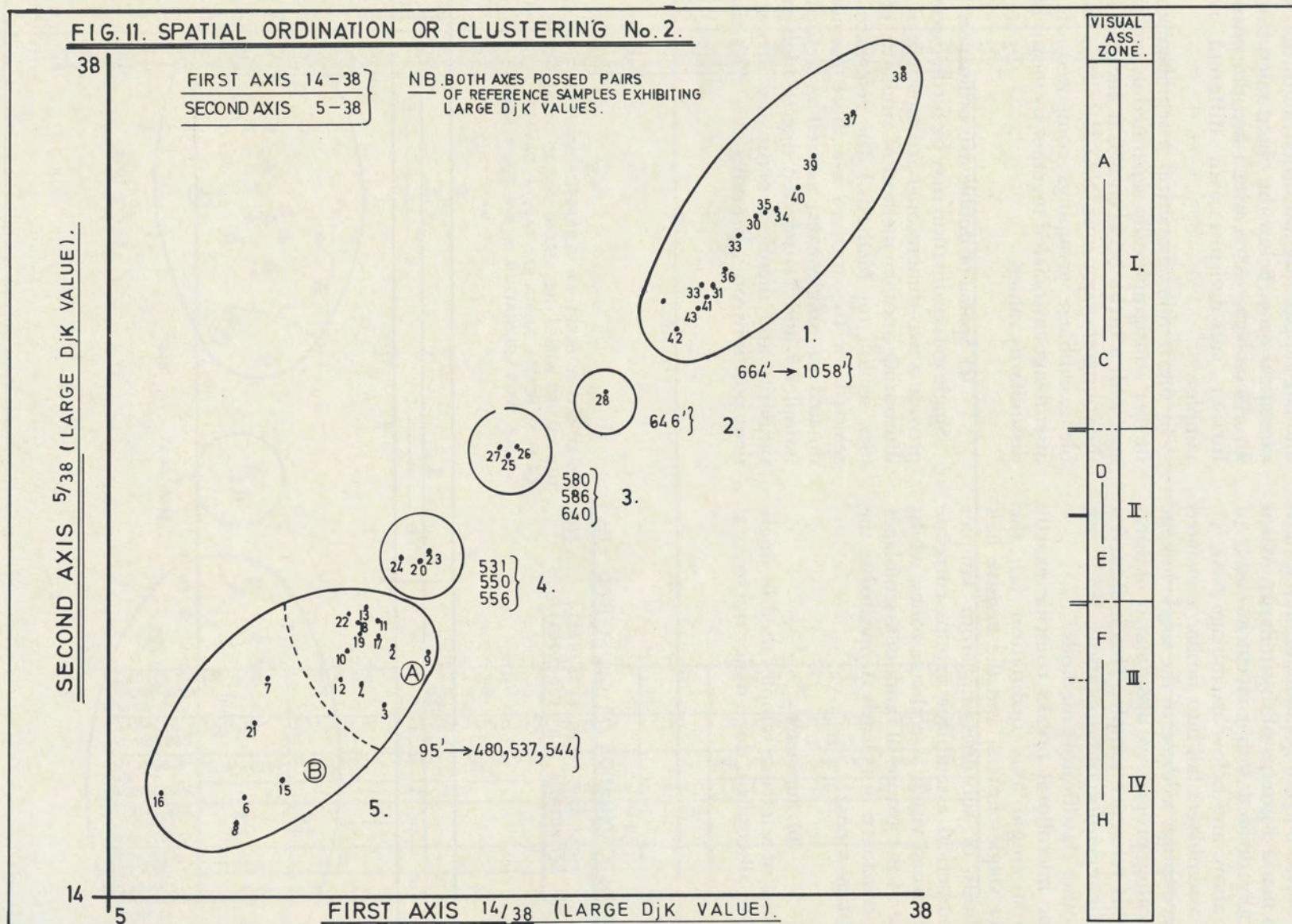


Figure 11. Spatial ordination or clustering — No. 2.



ordination is not illustrated here. The purpose in choosing such wide ranging reference samples is to illustrate the maximum possible variations relative to these.

In both examples of spatial ordination the results of two single axes ordinations are arranged as co-ordinates, with each sample assemblage then located relative to both axes, and perpendicular to points on those axes.

- (1) *Spatial ordination number 1* (Figure 10) shows the result of clustering or ordination of samples based on reference samples 7 and 11, and 14 and 38. Reference pair 7 and 11 were chosen as the closest coincident pair of samples, and therefore the most similar relative to reference samples 14 and 38 on a single axis ordination not shown here.
- (2) *Spatial ordination number 2* (Figure 11) was constructed using reference samples 14 and 38, and 5 and 38. Both axes possess pairs of reference samples exhibiting large dissimilarity values. This variation from no. 1 was attempted in order to explore the possibility of any further microfloral patterns.

## Results

### (a) *Spatial ordination no. 1*

Three broad microfloral assemblage groups are clearly visible, each stratigraphically divided from the other two. NAZ I is comprised of assemblages 28–43, NAZ II, 25–27, and NAZ III, 1–24. Within groups I and III two further sub-divisions based on a transitional or marginal position may be seen — NAZ I—28, from 29–43; and NAZ III — three groups of randomly assorted assemblages which are not stratigraphically aligned, except for 14, 15 and 16.

The two major microfloral breaks occur between samples 24 and 25, and between 27 and 28, with a further break between 28 and 29.

The major breaks and numerical assemblage zones thus grouped are closely similar to those obtained in Sokal's single axis ordination, and coincide well with three visual assemblage zones I, II, and III + IV.

### (b) *Spatial clustering No. 2*

Five major microfloral zones are distinctly clear in this ordination diagram; all are stratigraphically divided, with the largest breaks occurring between 24–25, 27–28 and 28–29. One minor break occurs between 19–20. In comparison to spatial cluster no. 1 more emphasis is placed on the more prominent form of break between 28/29 and assemblages 20, 23 and 24 represent a transition assembly to the youngest major flora 1–19, (21 and 22 are regarded as weak links). The groups of random assemblages in numerical assemblage Zone 5 are similar to those already shown by other methods.

## (d) Summary

### (Figure 12)

The clustered groups of assemblages in these two sets of spatial ordination graphs shows a convincing degree of clustering separated by significant breaks. Three major numerical assemblage zones are obvious (with a possible fourth) which are comprised of stratigraphically adjacent samples in the borehole core. They may therefore be termed biostratigraphic units. Major breaks occur between assemblages 24/25, 27/28 and 28/29.

Minor variations occur, for example, in:

- (1) assemblages 14, 15 and 16. These are stratigraphically grouped together in single ordination No. 1, and not so evidently in No. 2. This small biostratigraphic unit occurs at the base of visual assemblage zone G.
- (2) assemblages 1–24 are divided into three sub-groups showing repetitive floras as seen already in single ordinations No. 1 and 2, but with slightly different magnitudes. Assemblages 25–27 coincide in both. The older assemblages 29 to 40 are potentially further sub-divided into two, varying again in degree of magnitude.
- (3) one sample assemblage, 28, is spatially equidistant from both adjacent assemblage groups showing a separate, transitional microflora. In spatial ordination No. 1, this assemblage is a sub-group (B) in NAZ I, but it is sufficiently distant to warrant its own sub-group in spatial ordination No. 2.

This method of illustrating numerical division is successful, showing the positions and groupings of the assemblages into distinct clusters in two-dimensional space. The numerical zones coincide with the broad visual assemblage zones in all respects with the exception of the boundary between visual sub-zones G and H. These methods warrant further study, especially in the "associated assemblages" of assemblages 1–24.

## SUMMARY AND CONCLUSIONS

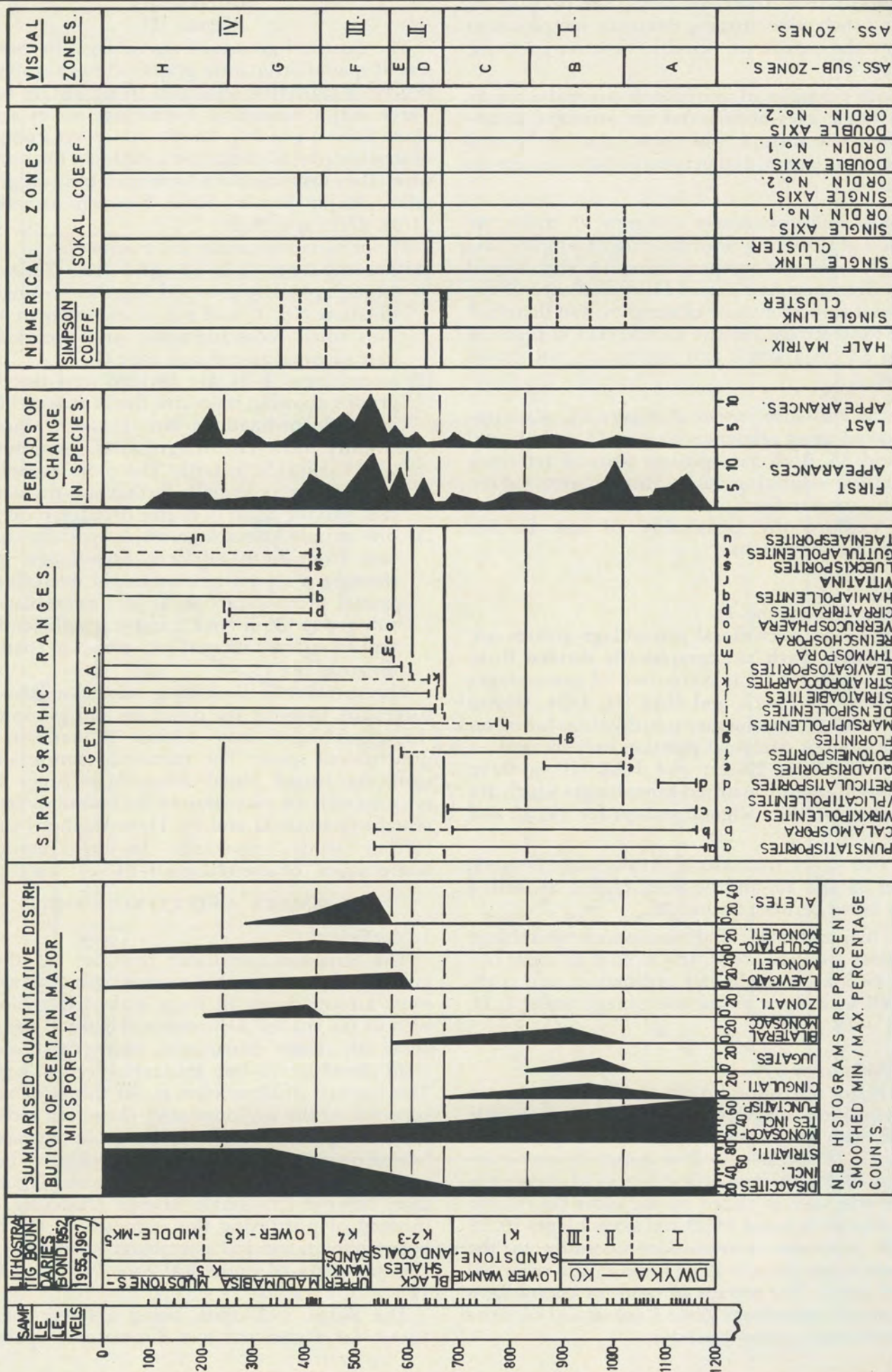
### 1. *Coefficients*

The Simpson coefficient provides for the up-grading of poorly stocked assemblages. This appears most advantageous in large scale subdivision. As seen in the shaded half-matrix (Figure 2) the major floras are clearly demarcated, whilst the *relationships of all assemblages* to one another is seen at a glance. This method of illustration is, for this same reason, superior to the agglomerative clustering technique seen in Figure 4. Here, similar groupings are seen but transitional floras and assemblages bearing complex relationships are not indicated. The advantage, however, in single linkage clustering is the method of portraying the *magnitude* of the breaks between the numerical assemblage zones at a glance. (See summary of numerical zone breaks in Figure 12.)

The Sokal coefficient, being a linear measure, allows for a one and two dimensional spatial or-



FIG. 12. — SUMMARY OF SUBDIVISION OF THE MATABOLA FLATS CORE





dination of similar assemblages and ease in clustering of randomly distributed assemblages. Furthermore it shows more clearly the existence of recurrent or repetitive floras within the assemblage group 1–24 not clearly seen elsewhere.

## 2. Parameters

Despite all possible combinations of the presence/absence data (i.e. positive and negative matches, common or common to only one sample; linear and non-linear coefficients; agglomerative, divisive and non-hierarchical techniques of illustration; and spatial ordinations employing various parameters such as maximum time or maximum quantitative values), it appears that the major floral zones always occur distinctly and with considerable definition.

The conclusion drawn is that the floral changes are of sufficient magnitude to mask almost all variations that occur in numerical techniques such as these.

## 3. Correlations

In comparison with the (visual) palynological biostratigraphic zones and sub-zones of Falcon (1975) (see Figure 12), the major *numerical* zones appear to conform to the major *visual* zones, with the major numerical breaks occurring during deposition of the Black Shales and coals ( $K^{2-3}$ ). Minor breaks in the Dwyka ( $K^0$ ) Lower Wankie Sandstone ( $K^1$ ) Flora are consistent with floral changes during and immediately after a period of glaciation, whilst a minimum of changes are noted during the deposition of the youngest sediments, the Madumabisa Mudstones ( $LK^5$ ,  $MK^5$ ).

The major points at which first-appearances and last-appearances of species occur, together with selected quantitative and qualitative data obtained visually (Falcon, 1975), are illustrated in conjunction with the boundaries of the numerical assemblages in Figure 12. In comparing the biozones erected by Hart and Fiehler (1971) in Tanzania and those illustrated here (based on species ranges and frequency data), it becomes obvious that the major change seen by Hart in his transition zone (based on points of inflection for the regression equations of *Cordaitina* and *Protohaploxypinus*) appears to be equivalent to that seen as the major numerical break between

assemblage zones I and II in the basal Black Shales and Coals.

## 4. Sub-division

In terms of sub-dividing a single stratigraphic sequence into practical delineated assemblage zones, it is concluded here that visual methods (analysing qualitative and quantitative data for various ranks of miospore taxa) are equally reliable to numerical methods (processing only presence/absence data of all species) when both forms of analyses are taken as a whole. This bears out the conclusions previously reached by Gordon and Birks (1972) in Quaternary palaeoecology.

Visual methods are easier, quicker and more direct to process than the numerical methods (when computer facilities are limited), but they possess the disadvantage of subjective bias. Numerical methods are essentially objective, unbiased and well defined, allowing for a further advantage, that of two-dimensional projection of assemblages into groups where magnitude of the floral change is measured. Repetition of similar microfloral assemblages at random stratigraphic levels, i.e. cyclic or repetitive assemblages, is also better illustrated by numerical methods. This may allow for certain palaeoecological, climatic or depositional (reworking) influences to be studied.

At present, visual methods of microfloral analysis are prevalent in Gondwana palynological studies but it is hoped that this paper, along with Hart and Fiehler (1971) and Christopher and Hart (1971), may serve to introduce numerical methods for further development in detailed stratigraphic analysis. This may be particularly so when a broader and more universal systematic scheme has been accepted, and numerical methods based on more reliable and well-circumscribed taxa have been further refined and thereafter projected on to a more sophisticated computer basis.

## ACKNOWLEDGEMENTS

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# A REVIEW OF THE BRYOPHYTA FROM THE UPPER TRIASSIC MOLTEÑO FORMATION, KARROO BASIN, SOUTH AFRICA

by

Heidi M. Anderson

## ABSTRACT

The Bryophyta from the Upper Triassic, Molteno Formation, Karroo Basin, South Africa are reviewed. Two species of liverworts, *Marchantites cyathodoides* (Townrow) comb. nov., *M. tennantii* sp. nov. (with possible fertile structures), and one species of moss, *Muscites guescelini* Townrow (with impressions of antheridia) are described. A single specimen is referred to *Thallites* sp. A. A total of 49 specimens are available, 11 from Townrow's collection and 38 from the present collection. These are derived from a total of six separate localities.

## INTRODUCTION

The occurrence of bryophytes in the Molteno Formation follows the pattern of sparse representation established for other floras. Since the detailed account of one moss and one liverwort species by Townrow (1959) the Molteno material rates amongst the better known fossil bryophyte records. The present review has been necessitated by the recent additions resulting from an extended collecting programme.

The fossil record of pre-Tertiary Bryophyta is very limited (Lundblad, 1954; Jovet-Ast, 1967; Lacey, 1969). The earliest known bryophyte material is recorded from the Upper Devonian (Grambast and Lacey, 1967). By Upper Carboniferous times the Hepaticopsida (liverworts) and Bryopsida (mosses) are known as two well differentiated groups.

It is important to remember that the classification of living genera and species depends largely on microscopic details of the gametophyte and sporophyte. These details are mostly absent in fossil material, which makes the classification of fossil bryophytes unsatisfactory and they are thus largely placed in form genera.

On rare occasions well preserved material has allowed careful study and comparison with modern bryophytes. Such examples are *Naiadita* (Hepaticopsida) described by Harris (1939) from the Rhaetic of England, *Ricciopsis* (Hepaticopsida) described by Lundblad (1954) from the Rhaeto-Liassic of Sweden, and various moss genera belonging to the Sphagnales and Bryales described by Neuberg (1960) from the Permian of Russia. The Molteno forms described by Townrow (1959) also fall into this category.

## BRYOPHYTA OCCURRENCE

The occurrence of Bryophyta in the Triassic of Gondwanaland is briefly considered. Besides the four

species (total of 49 specimens) reviewed in this paper from the Molteno, there are only two further records known to the author:

*Marchantites cyathodoides* — Townrow, 1959, p. 3;

Brookvale plant bed, Hawkesbury Sandstone, Sydney Basin, Australia; Middle Triassic (1 specimen).

*Thallites* sp. — Jain and Delevoryas, 1967, p. 565;

Minas de Petroleo, Cacheuta Basin, Argentina; Upper Triassic (2 specimens on one slab).

This apparent paucity of bryophytes from the Triassic of Gondwanaland (excluding the Molteno) is most likely a reflection of the need for more intensive collecting.

## MATERIAL

The only Molteno bryophyte material described to date derives from the Upper Umkomaas locality (Townrow, 1959). In the present paper additional material (38 specimens) is recorded and described from Upper Umkomaas and a further five localities (Table 1). This constitutes the sum of the available specimens resulting from an extensive collecting programme from 42 localities (Anderson, 1974). The bryophytes were mainly obtained from localities where comprehensive collecting has been undertaken, i.e. Little Switzerland, Upper Umkomaas and Dordrecht II (more than a thousand specimens overall have been catalogued from each). The majority of Bryophyta derive from Dordrecht II (21 specimens). This is due both to the abundance of the material that has been quarried and to the clarity of the impressions which render the small specimens more recognisable. The bryophyte specimens from the present collection are housed at the Bernard Price Institute for Palaeontological Research, Witwatersrand University.



Table 1  
Molteno Bryophyta

Note: Townrow (1959) collection is indicated by the figures in brackets

| Locality           | Hepaticopsida                    |                               | Bryopsida                  | ?Bryophyta             |
|--------------------|----------------------------------|-------------------------------|----------------------------|------------------------|
|                    | <i>Marchantites cyathodoides</i> | <i>Marchantites tennantii</i> | <i>Muscites guescelini</i> | <i>Thallites</i> sp. A |
| Little Switzerland | 2                                |                               | 4                          |                        |
| Upper Umkomaas     | 3 (4)                            |                               | 3 (7)                      |                        |
| Sani Pass          |                                  |                               | 1                          |                        |
| Dordrecht II       |                                  | 2                             | 21                         |                        |
| Molteno I          |                                  |                               |                            | 1                      |
| Vineyard I         |                                  |                               | 1                          |                        |

### EXPLANATIONS TO ILLUSTRATIONS

The photography of certain specimens was difficult as they consist of black compressions set in a black matrix. Generally the best results for these were obtained by photography under Xylol. Equipment used included a 35 mm camera with macrolens and bellow attachment, a Zeiss stereo microscope with camera adaptor, and an Aristophan camera. All the specimens are firstly illustrated natural size and backed up by various magnifications indicated on the photographs (i.e. 1 ×, 5 ×, etc.). The specimens are catalogued both according to a collecting number (indicated by locality code and number) and a publication number (indicated by BPI (Pal) PB 104–124, 152–156). These are indicated on the photographs by a pair of numbers: the upper being the collecting number and the lower the publication number.

The line drawing (Figure 1) represents a composite reconstruction based on the part and counterpart of the holotype of *Marchantites tennantii*. The drawing was made by direct trace from photographs and the details checked under binocular microscope.

### CLASSIFICATION

Where possible the classification used in the most recent comprehensive review of the fossil Bryophyta (Jovet-Ast, 1967) has been followed. Certain anomalies were, however, encountered.

The form genus *Hepaticites* was placed in the order Jungermanniales under "Genres Incertae Sedis" by Jovet-Ast (1967). Following this, *H. cyathodoides* Townrow would fall in the Jungermanniales. This is contrary to Townrow (1959) and Lacey (1969). Townrow suggested a strong affinity to the Marchantiales and Lacey regarded it as the earliest acceptable record of this order. Walton (1925) furthermore suggested that only those fossil liverworts which bore undoubted affinities to the Marchantiaceae should be included in genus *Marchantites*. As some of the Molteno forms show such affinities they are classified in the genus *Marchan-*

*tites* rather than in the more general form genus *Hepaticites*.

The genus *Thallites* Walton 1925 was placed in the family Marchantiaceae by Jovet-Ast (1967) which is incorrect when Walton's (1925) original diagnosis is considered: "Fossils in which the plant body is of a thalloid form, as may be found in the Algae, Bryophyta, or sometimes in higher groups; but possessing no characters by which they may be assigned to any one of these groups to the exclusion of all the others". According to this definition it is doubtful whether *Thallites* may even be included in the Bryophyta.

The genus *Muscites* Brongniart 1929 was placed under "Bryophyta Incertae Sedis" by Jovet-Ast (1967). As this genus is a form genus for fossil mosses it is here suggested that it should rather be placed under the class Bryopsida as Incertae Sedis.

The Molteno species are classified below. As the fossil species are incompletely known, it has been thought advisable not to place them in families.

Phylum: Bryophyta Schimper 1879.

Class: Hepaticopsida Rothmaler 1951.

Order: Marchantiales Engler 1892.

Genus: *Marchantites* (Brongniart, 1849) Walton 1925.

Species: *M. cyathodoides* (Townrow, 1959) comb. nov. *M. tennantii* sp. nov.

Class: Bryopsida Rothmaler 1951.

Order: Incertae sedis.

Genus: *Muscites* Brongniart 1829.

Species: *M. guescelini* Townrow 1959.

Phylum: (possibly allied to the Bryophyta)

Genus: *Thallites* Walton 1925.

*Thallites* sp. A.

*Marchantites cyathodoides* (Townrow) comb. nov.

Plate I, Figures 1–10.

Type material: Holotype — Townrow, 1959, Plate IA, number 13929, housed in the South African Museum, Cape Town. Locality: Upper Umkomaas, Natal. Molteno Formation.

Molteno material:

(a) Locality: Little Switzerland.

Slabs: PB 104 (N-L.Sw. 1046) PB 106 (N-L.Sw. 383).

preservation: compressions.

(b) Locality: Upper Umkomaas.

Slabs: Townrow (1959) collection now consisting of microscope slides, 13927–13930 (South African Museum, Cape Town). PB 107 (N-U.U. 1158) PB 108 (N-U.U. 1018), PB 109 (N-U.U. 1157).

Preservation: compressions.

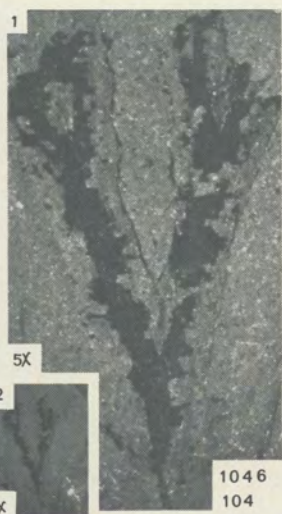
Diagnosis: Townrow, 1959, page 2.

Discussion: Townrow (1959) preferred to place the species in the non-committal genus *Hepaticites* and to indicate its similarity with the extant liverwort *Cyathodium* in his choice of the specific name *cyathodoides*. It is here felt that this species can safely be placed in the genus *Marchantites* (Brongniart) Walton. The prostrate forked thallus, a conspicuous midrib, rhizoides, possible air chambers and central scales all indicate an affinity with the Marchantiaceae.

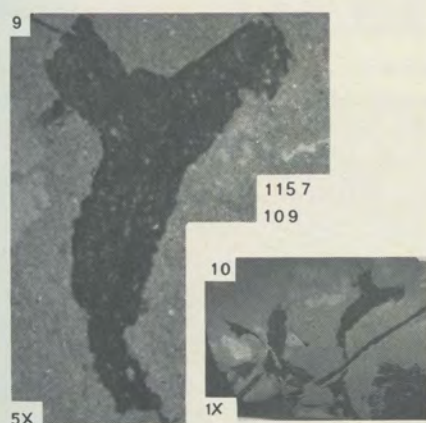
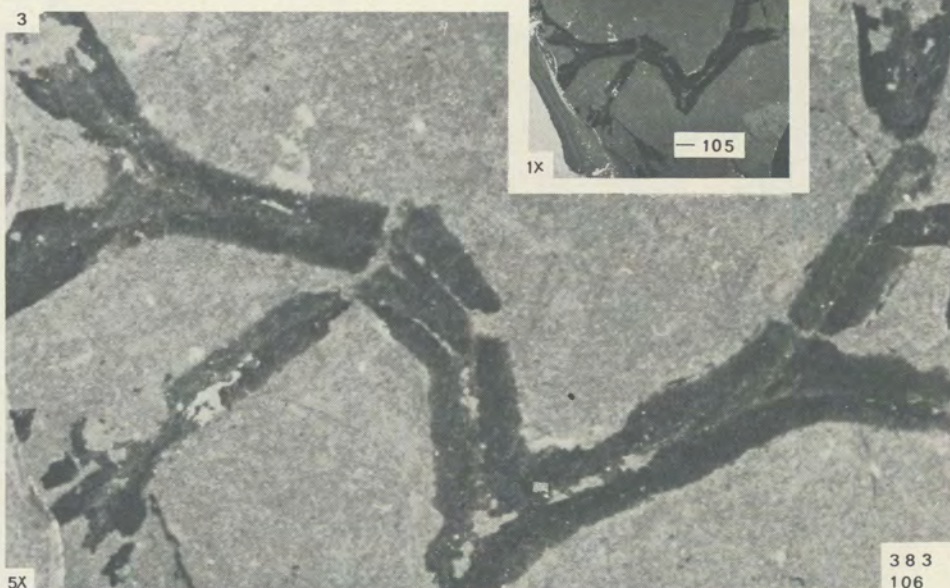


## PLATE I

## MARCHANTITES CYATHODOIDES



Little Switzerland N—L.Sw.



Upper Umkomaas N—U.U.

## THALLITES SPA







Figure 1. *Marchantites tennantii*, a composite reconstruction based on the part and counterpart of the holotype (PB 111).

In view of Townrow's (1959) detailed microscopic study none of the new specimens (all compressions) have been macerated. The most complete specimen available, i.e. from Little Switzerland (Plate I, Figures 3 and 4) shows a three-fold dichotomy but no true apex. Two clear apices are present (Plate I, Figures 5 and 6) amongst the Upper Umkomaas specimens. The portions of thalli shown in Plate I, Figures 8 and 7 have probably been derived from the same parent plant.

Townrow (1959) recorded five specimens but only four are available at the South African Museum, Cape Town. The whereabouts of the remaining specimen is unknown.

*Marchantites tennantii* sp. nov.

Plate I, Figures 1–11; Figure 1.

*Type material*: Holotype PB 111 (C-Dt.II 1035a, b). *Locality*: Dordrecht II (Birds River), Eastern Cape. Molteno Formation. The species is named in gratitude to the family Tennant on whose farm the locality is situated.

*Molteno material*: The specimen listed above and PB 112 (C-Dt.II 275'y) which is provisionally referred to this species. Both specimens are preserved as impressions.

*Diagnosis*: Plant thalloid, dichotomising every 4 to 8 mm, thallus lobes diverging at between  $50^{\circ}$  to  $70^{\circ}$ , margin partially undulating, width 2,5 to 4 mm. Midrib conspicuous, 1 mm wide, extending almost to apex, bearing an imprint, probably caused by ventral scales. Lateral wings of thallus 0,75 to 1,5 mm wide, bearing a clear imprint of polygonal areas; these occur in rows arching from midrib to about  $30^{\circ}$  to meet the margin at  $80^{\circ}$ . Rhizoids and internal structure unknown.

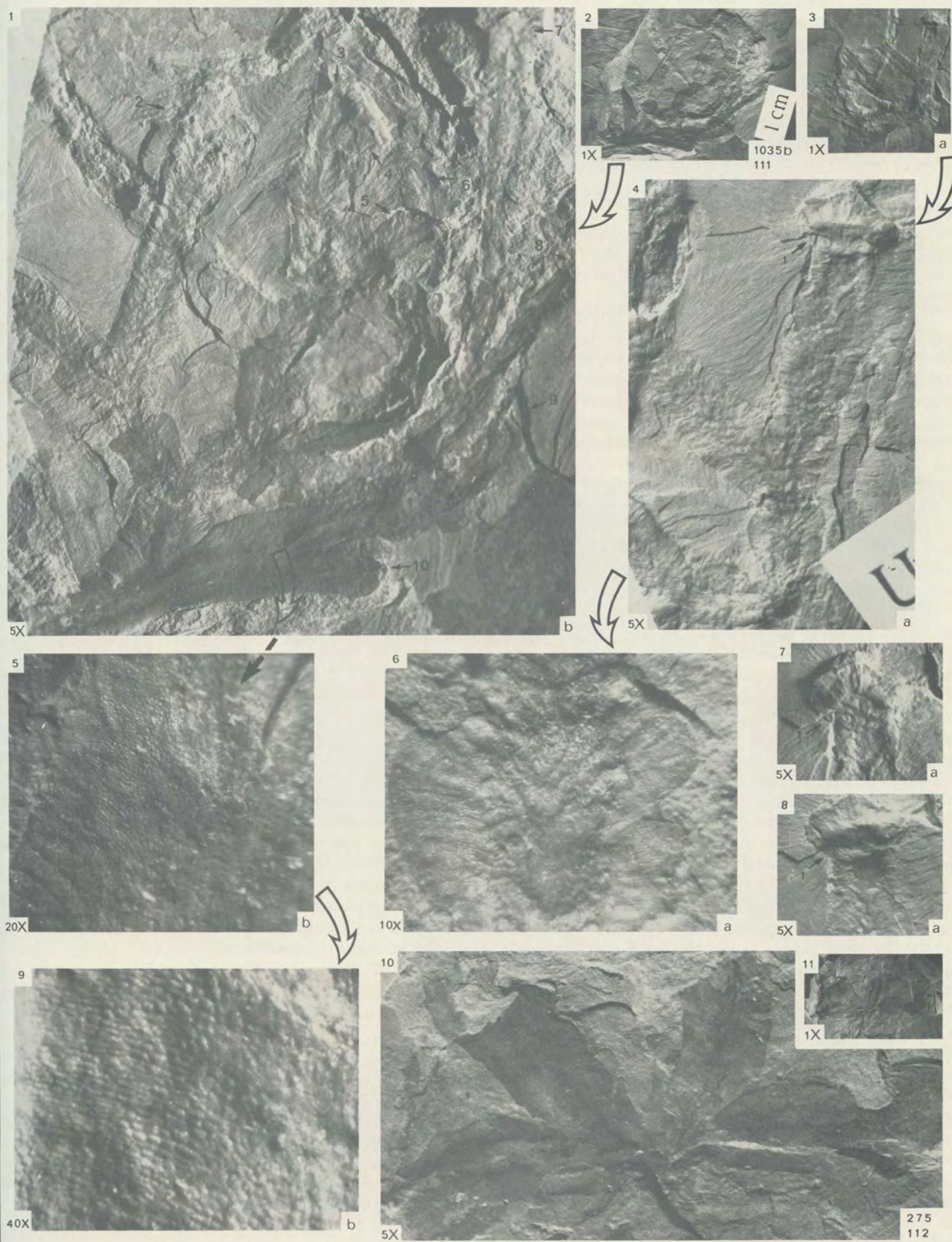
*Discussion*: This species can safely be placed in the order Marchantiales (Watson, 1975, pers. comm.). It has thus been placed in the genus *Marchantites* rather than the noncommittal genus *Hepaticites* because it has a prostrate forked thallus, a conspicuous midrib, polygonal areas and probable ventral scales. The species is unfortunately not suitably preserved for study of the internal structures, e.g. air chambers. This lack of detail makes a meaningful comparison with modern genera and species impossible.

The holotype (Plate II, Figures 1–9) is a very clearly preserved impression. The thallus bears an imprint of apparent cellular structures. These are referred to as



## MARCHANTITES TENNANTII

Dordrecht II C-Dt II





polygonal areas (Plate II, Figures 5 and 9) as there is no evidence that they represent individual cells. Similar polygonal areas (multicellular) are common in the modern Marchantiaceae. Watson (1957, pers. comm.) noted that the size and pattern of the polygonal areas of the holotype was much in accord with that found in several modern liverworts of the order Marchantiales, e.g. *Reboulia hemispherica*.

In an effort to obtain further structural details (e.g. to check the existence of a pore in the polygonal areas) a latex pull was made from the holotype and examined by SEM (Chaloner and Gay, 1972). Besides obtaining a greater magnification of the grooves demarcating the polygonal areas, no details were visible. The sediment encrusting the liverwort at the time of deposition was apparently sufficiently fine to carry the impressions of polygonal outlines, but not any of the more detailed structures.

The part and counterpart of the holotype both appear to represent the dorsal side only of the liverwort (Plate II, Figures 1 to 3). No rhizoids have been found and the presence of ventral scales is inferred from the irregular nature of the midrib region. Townrow (1959) also regarded the specimens of *M. cyathodoides* as preserved dorsal side up and was able to demonstrate this by making balsam transfers. Based on this he suggested that they were preserved *in situ*.

The wings of the thallus appear to be very thin and are probably only a few cells thick. The distinct curved lines on the wings (Plate II, Figures 5 and 6) probably indicate that the thallus wings were slightly corrugated. The latter feature occurs in certain extant species.

Of particular interest are certain apices (numbered in clockwise direction on Figure 1) in this liverwort. The first apex (see also Plate II, Figures 4, 7 and 8) shows a slight depression from which arises a distinctly elevated portion of thallus which is here interpreted as possibly representing an immature archegoniophore or antheridiophore. Certain apices (numbers 6 and 7) do not show this complexity of structure but show instead a gradual weakening of the midrib and continuation of the lateral wings to form a relatively unbroken curve at the apex. Another possibility is that apices numbers 1 and 2 show the initials of a dichotomous branch, as is clearly seen closely behind apices numbers 3 and 4. It is uncertain whether number 5 is a true apex or a broken portion of the thallus. At the points numbered 8–10 the thallus appears to continue. However, to avoid damaging the specimen these areas were not further exposed. At all the other points (numbers 1–7) every effort was made to clear the covering rock.

As this specimen consists only of an impression there is no way of checking microscopically whether certain of these apices actually represent archegoniophores or antheridiophores. Such structures have been specially noted, however, because the known fossil record of pre-Tertiary liverworts, with apparently only one exception, *Naiadita lanceolata* Harris (1939) from the Rhaetic of South West England, is devoid of fertile structures. Good fertile structures occur (gemmae cups and antheridiophores) in fossil liverworts from the Eocene

of France, e.g. *Marchantites sezannensis* and *Marchantia munieri* Jovet-Ast (1967).

This species is close to *M. cyathodoides* which Townrow (1959) has compared with other similar liverworts, fossil and modern. The species is distinguished from *M. cyathodoides* by the somewhat wavy thallus margin (as opposed to a smooth one) and in the greater width of the thallus (4 mm in contrast to 2 mm). The absence of internal structure in this species rules out a comparison of microscopic characters. This species also shows a resemblance to *Thallites barwoni* (Medwell) Lundblad 1955 recorded from Victoria, Australia by Medwell (1954). However, *T. barwoni* has a thallus margin regularly dentate and the size is about twice as large as the Molteno specimen.

#### *Muscites guescilini* Townrow 1959

##### Plates III–V

*Type material:* Holotype — Townrow, 1959, Plate IC, number 13931, housed in the South African Museum, Cape Town. Locality: Upper Umkomaas, Natal. Molteno Formation.

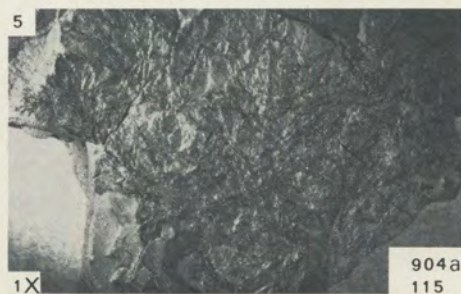
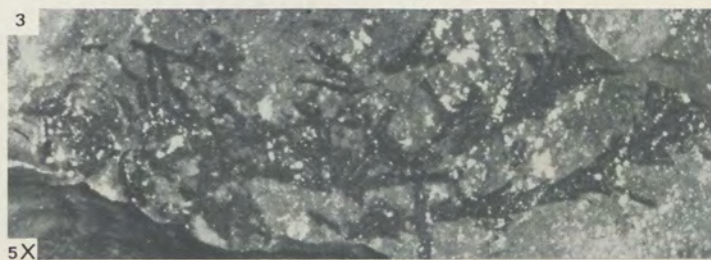
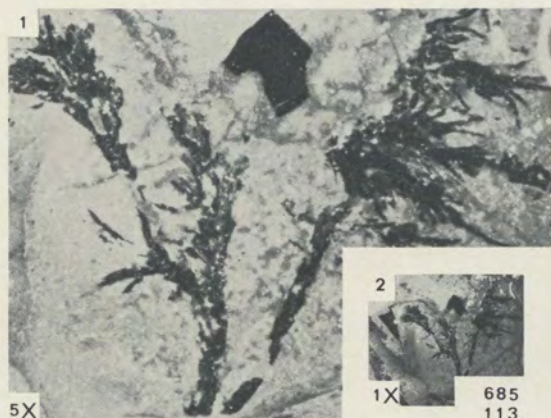
##### *Molteno material:*

- (a) Locality: Little Switzerland.  
Slabs: PB 105 (N-L.Sw. 383), PB 113 (N-L.Sw. 685), PB 114 (N-L.Sw. 821), PB 115 (N-L.Sw. 904 a–h).  
Preservation: compressions.
- (b) Locality: Upper Umkomaas.  
Slabs: Townrow (1959) collection consisting of microscope slides, 13931–13936, 14070, South African Museum, Cape Town: PB 116 (N-U.U. 1156), PB 117 (N-U.U. 1160), PB 118 (N-U.U. 1161a, b).
- (c) Locality: Sani Pass.  
Slab: PB 119 (N-S.P. 191a, b).  
Preservation: compression.
- (d) Locality: Dordrecht II.  
Slabs: PB 120 (C-Dt.II 687), PB 121 (C-Dt.II 1040a, b), PB 122 (C-Dt.II 286), PB 123 (C-Dt.II 691c), PB 124 (C-Dt.II 457a, b), PB 152 (C-Dt.II 1037), PB 153 (C-Dt.II 285a, b), PB 154 (C-Dt.II 456a, b), PB 155 (C-Dt.II 1038), PB 156 (C-Dt.II 1033). Unfigured specimens are C-Dt.II 283–4, 458, 485, 1029–1032, 1034, 1036, 1039, 1093.  
Preservation: impressions.
- (e) Locality: Vineyard I.  
Slab: C-Vy.I 163a, b (not figured).  
Preservation: impression.

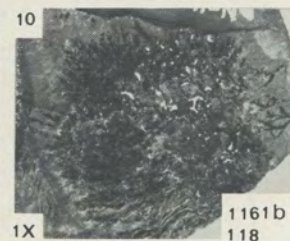
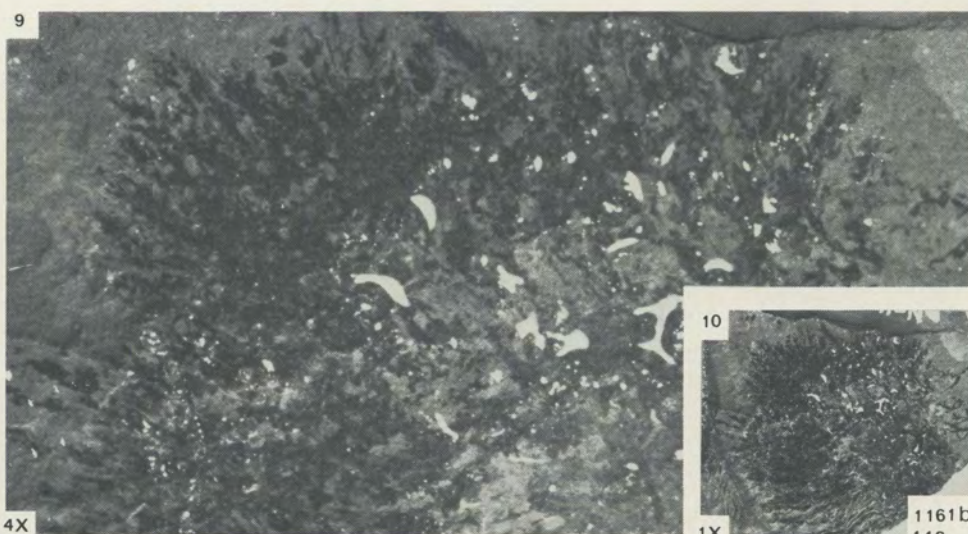
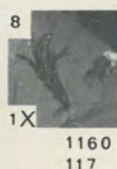
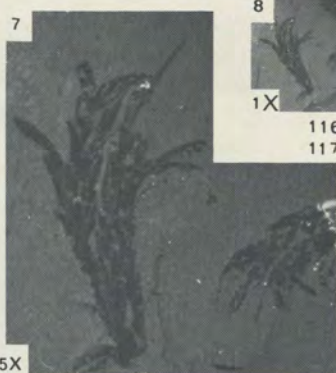
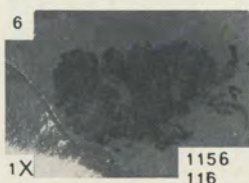
*Diagnosis:* Townrow, 1959, p. 12.

*Discussion:* Townrow (1959) based this species on material from Upper Umkomaas. He recorded 15 specimens, 12 of which were made into balsam transfers. Seven specimens are housed in the South African Museum, Cape Town. A note by Townrow accompanying the specimens records that the specimen illustrated in Figure 2E disintegrated while being mounted and no longer exists. What has become of the remaining seven specimens is not known. Further material is here noted from the type locality and from an additional four localities.



MUSCITES GUESCELINI

Little Switzerland N—L.Sw.

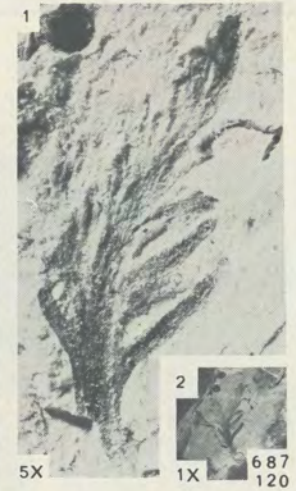
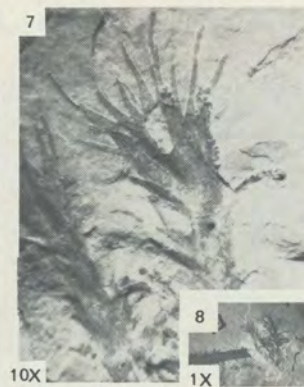
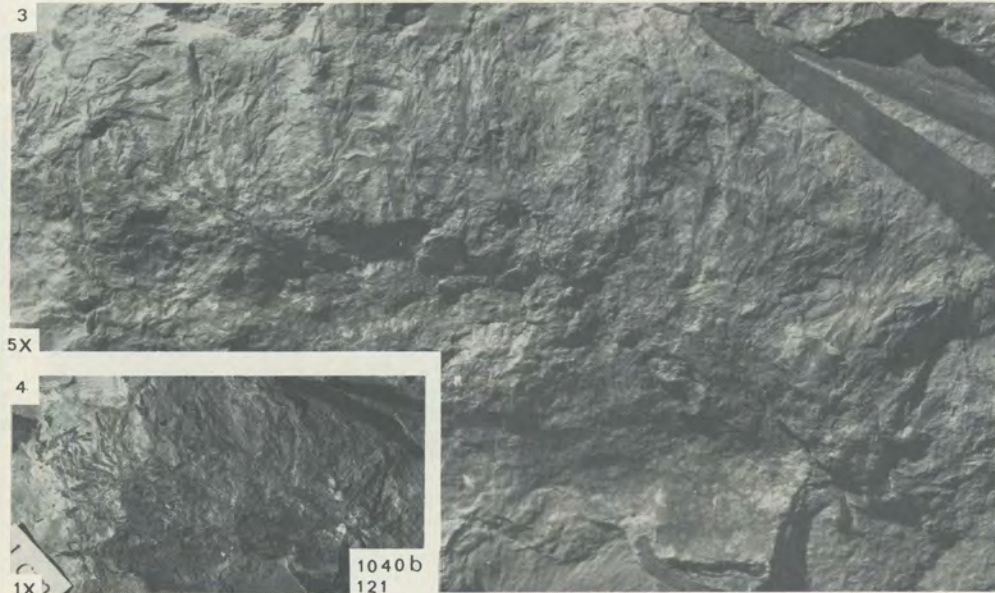


Upper Umkomaas N—U.U.



Sani Pass N—S.P.

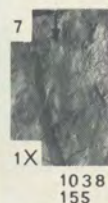
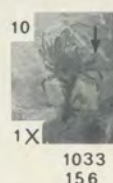
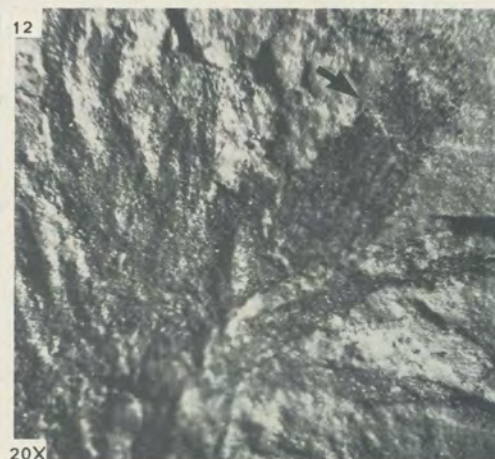
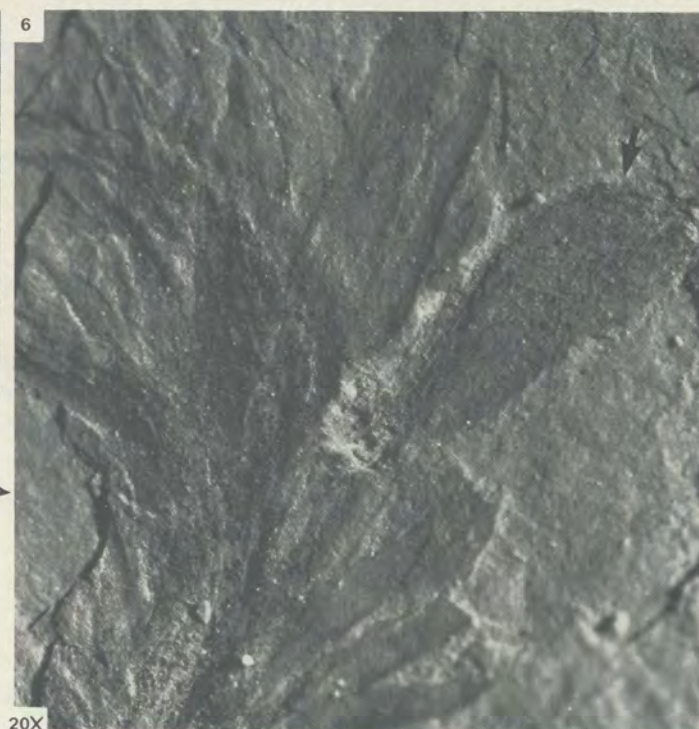
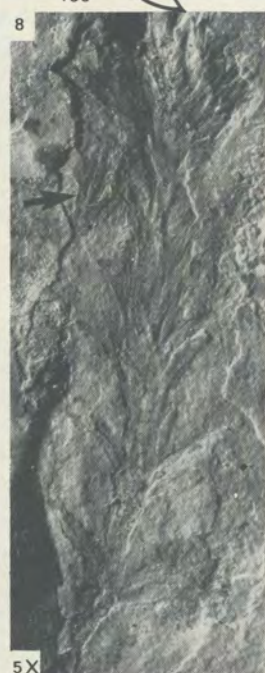


MUSCITES GUESCELINI

Dordrecht II C-Dt II



## MUSCITES GUESCELINI

285a  
153456a  
1541038  
1551033  
156

Dordrecht II C-Dt. II



As Townrow (1959) has made a very detailed microscopic study of the species, no attempt has been made to repeat this.

The majority of the new material comes from Dordrecht II and this, like the rest, is closely comparable to *M. guescelini*. The leaves are borne spirally, vary from 1–2 mm in length and have no nerve (Plate IV, Figures 5 and 7). Townrow (op. cit.) noted that leaves became more oblong apically. Certain tips show distinctly elongated leaves (Plate IV, Figure 7) while leaves of a more oblong nature also occur (Plate IV, Figure 9). Townrow (op. cit.) noted that leaf shape varied considerably in his specimens.

The new material includes eight moss cushions (clusters) which were probably preserved *in situ*. The best examples are from Upper Umkomaas (Plate III, Figures 9 and 10) and Dordrecht II (Plate IV, Figures 4 and 6). In each of these the radiating branches of the gametophyte are clearly visible. In the moss cushions (Plate III, Figures 5, 6 and 9) the leaves are not clearly preserved and these fossils appear to have been partially eroded by water action. This probably occurred recently, when the fossiliferous horizon became exposed to water seepage. In contrast to these, the moss cushion from Dordrecht II shows some extremely well preserved leaves (Plate IV, Figures 3 and 5). Some good branched specimens also occur from Little Switzerland (Plate III, Figure 1) and Dordrecht II (Plate IV, Figures 9 and 11).

Of particular interest are certain probable fertile structures encountered at the Dordrecht II locality. These have all been figured, while of the remaining material from Dordrecht II (total 17 specimens) only a selection has been illustrated. A probable fertile structure enclosed by numerous (5?) leaves and possibly attached by a short stalk to the stem of one of the branches of a small moss cluster occurs (Plate V, Figures 1, 2 and 3). This inference is drawn from the fact that in modern mosses the fertile structures are usually provided with some protection.

The remaining structures all resemble moss antheridia.

The extant antheridium "is a delicate sac enclosing antherozoid mother cells and, ultimately, male

gametes. In form it varies from subglobose, through ovoid to ellipsoid; the wall of the sac is almost always one layer of cells and the whole structure is borne on a stalk of varying length" (Watson 1964). The probable moss antheridia here recorded are 1.5 to 2 mm long and thus similar in size to those of modern *Polytrichum commune* which are 1.5 mm in length. Two of these appear to be attached near the apical portion of a stem (Plate V, Figures 6 and 11), while the third lies apparently detached near the apex of a stem (Plate V, Figure 8). The best preserved specimen shows faint striations indicating cell structure (Plate V, Figure 6). Similar striations also occur in another specimen (Plate V, Figure 12). On the remaining specimen fairly deep grooves are visible (Plate V, Figure 9).

#### *Thallites* sp. A

Plate I, Figures 11 and 12

*Molteno material:*

Locality: Molteno I.

Slab: PB 110 (C-Mo.I 33'x').

Preservation: impression.

*Discussion:* The slab shows two similar specimens alongside one another (Plate I, Figure 11) aligned in the same direction. The central dark midrib area and the transparent wing (Plate I, Figure 12) indicate that it may be a liverwort; but in the absence of further details, e.g. rhizoids, its affinity remains obscure. Since only a single specimen is available no specific name is appended.

#### ACKNOWLEDGEMENTS

This paper is dedicated to Dr. Edna Plumstead who introduced me to palaeobotany. I am grateful to Dr. E. V. Watson, Reading University, England for useful taxonomic suggestions regarding the new liverwort described herein. I would like to thank Family Tennant who gave so much aid and hospitality while collecting at Dordrecht II, the Monuments Commission and Forestry Department for necessary permits, and the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand for facilities. For photographic assistance I am grateful to Mr. Thompson, Zoology Department, University of the Witwatersrand; National Institute of Metallurgy; Mrs. Adele Romanowski and Dr. R. Ellis, Botanical Research Institute. Finally a special thank you to my husband, family and friends who have helped and encouraged me in so many ways and made this work possible.

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# THE PLANT RECORD IN THE DWYKA AND ECCA SERIES (PERMIAN) OF THE SOUTH-WESTERN HALF OF THE GREAT KARROO BASIN, SOUTH AFRICA

by

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## ABSTRACT

There is a different relationship between the Dwyka and Eccla Series deposits in two geographically distinct areas of the Great Karroo Basin: in the south-west the White Band terminates the Upper Dwyka Shales, which conformably separate the Dwyka Tillite Stage from the Eccla Series, while in the north-east the Eccla Series, including the Coal Measures, rests directly on the Dwyka glacial deposits or pre-Karroo basement. The stratigraphic correlation of the sequence in the two areas is uncertain as the White Band and Coal Measures sandstones nowhere occur in the same section. The floras from the north-east have been widely described and illustrated; not so those from the south-west. The available information, part of it new, and representative illustrations are presented in this article. The material is too poor to merit formal taxonomic definition, but some general comparisons are possible. The genera *Gangamopteris* and *Noeggerathiopsis* are characteristic of the "*Glossopteris* flora" in the Coal Measures in the north-east; they also occur in the glacial deposits in the south-west. This could be cited in support of isochronous accumulation of the sediments in question. Against this, there is some evidence indicating that *Gangamopteris* may persist above the White Band into the Eccla Series in the south-west. The advanced "*Glossopteris* floras" from the Upper Eccla Stages and overlying Beaufort Series in the two halves of the basin appear to be alike. A single incomplete specimen of an "advanced" *Glossopteris* leaf has been found incongruously in the White Band equivalent in South West Africa. It is concluded that reliable correlation between the various Lower Karroo sequences cannot be based on the existing megaplant record.

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## INTRODUCTION

In the early literature, the strata of the Dwyka and Eccla Series\* in the Cape Province were collectively referred to the "Lower Karroo" (Schenck, 1888; Molengraaff, 1898). We revert to this use of the term, employing it for the Dwyka and Eccla deposits throughout the Great Karroo Basin, because it emphasizes the uncertainty of the basinwide stratigraphic relationship between the two Series. In the south-western portion of the basin the glacial deposits grade upwards into the Upper Dwyka Shales, which terminate with the White Band and are conformably overlain by the Eccla Series Shales. In the north-eastern portion the White Band has not been recognised, and

the entire non-glacial sequence is placed in the Eccla Series. The so-called Middle Eccla Coal Measures are developed only in the north-east. Correlation between the non-glacial successions in the two portions of the basin is open to speculation as no single section is known to contain both the White Band, classically

\* Although the established terminology (Haughton, 1969) of "Series" and "Stage" denotes a chronostratigraphic framework, the subdivision of the Karroo strata has been based largely on lithological criteria. The South African Committee for Stratigraphy is currently revising the nomenclature (*Trans. geol. Soc. S. Afr.*, 1971), but the revised code has not yet been formally applied to the Lower Karroo strata (which are of Permian age, according to J. M. Anderson, 1973). For this reason we follow the old nomenclature in this article. It should be appreciated, however, that no time connotation is implied.



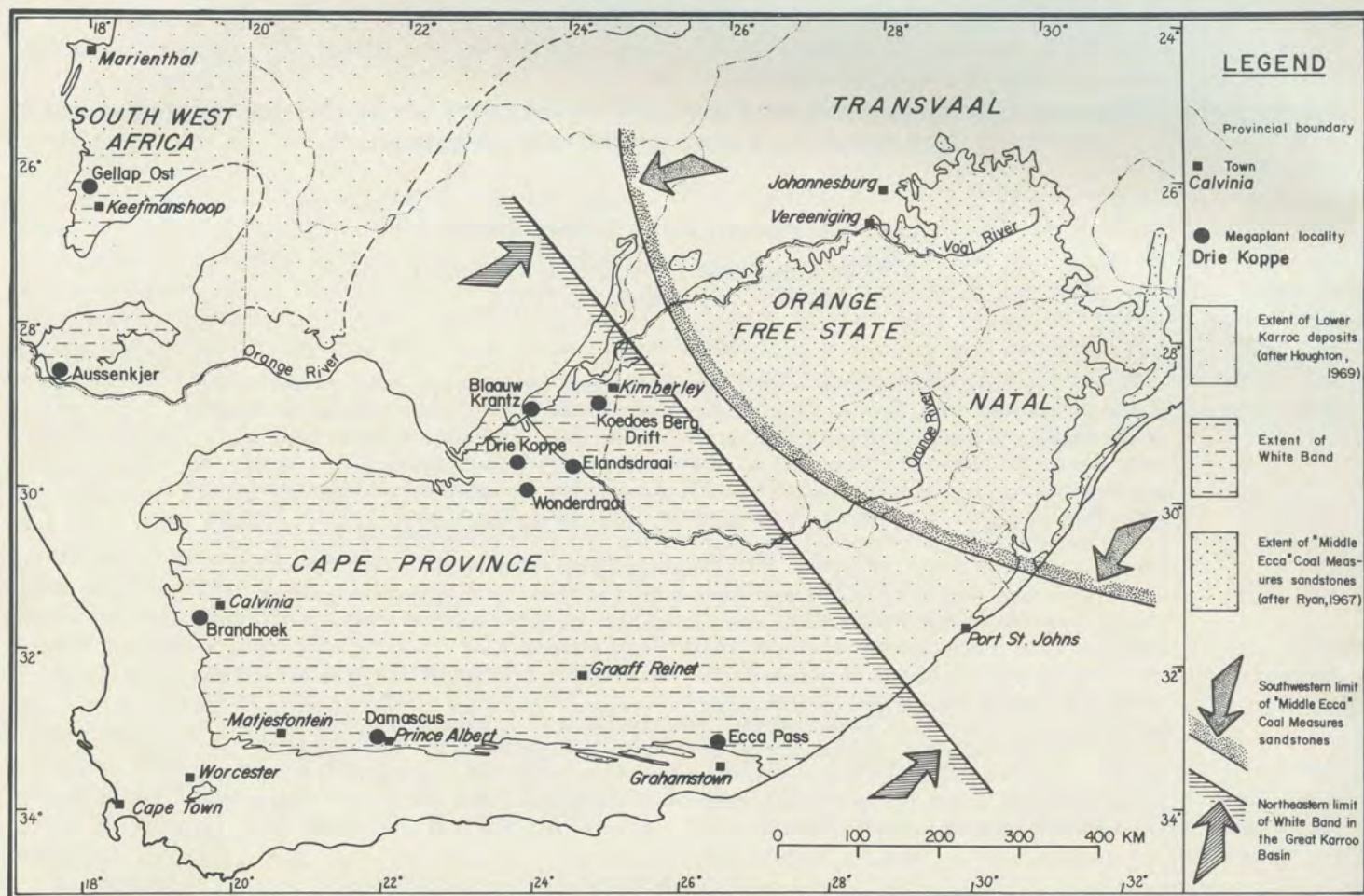


Figure 1. Map of southern Africa showing Lower Karroo megaplant localities in the areas where the White Band is present.

developed in the south-west, and the farthest extension of the sandstones associated with the Coal Measures in the north-east (Figure 1).

Dr. Plumstead has described the "Middle Eccla" Coal Measures in several publications (1957; 1958b; 1961; 1966a), and has contributed to the understanding of the component flora in her classic papers on *Glossopteris* and *Gangamopteris* fructifications (1952; 1956a, b; 1958a; 1962a). Other studies include those of Zeiller (1896), Arber (1905), Seward (1903; 1907), Leslie (1921), Du Toit (1932), Le Roux (1963; 1970; 1975) and Kovács-Endrödy (1974). In contrast, the floras from the south-western portion of the basin have received scant attention, although fossil leaves and other vegetable matter from the south-west were mentioned by several of the pioneering geologists. Feistmantel (1889) and Seward (1903; 1907) described some of the material.

It is the purpose of the present article to update the record of the Lower Karroo floras in the south-western portion of the Great Karroo Basin and to collate the available information. This is undertaken to facilitate comparison with the floras in the north-east.

#### GANGAMOPTERIS AND GLOSSOPTERIS LEAF FORMS

Although we do not present any formal systematic descriptions, it is nevertheless necessary to define the scope of our usage of the generic terms *Gangamopteris* and *Glossopteris*, applied to the ubiquitous Late

Paleozoic tongue-shaped leaves of Gondwanaland. We follow tradition in referring to those leaves without a definite midrib as *Gangamopteris* and to those with one as *Glossopteris* (cf. Seward, 1941; Andrews, 1961). The two forms are gradational, and the distinction between them is not always obvious. In both forms the secondary venation, on the lamina, is reticulate.

The two forms are essentially contemporaneous, but *Gangamopteris* is a little more primitive than *Glossopteris*: it is relatively more abundant in the earlier deposits and it disappears well before *Glossopteris*, which survives into the Triassic (Seward, 1941; Du Toit, 1954; Plumstead, 1967; 1972). In the later "*Glossopteris* floras" the individual leaves are generally smaller than in the earlier ones (Plumstead, 1966b). The later floras are also more monotonous in that they contain fewer non-*Glossopteris* elements (Du Toit, 1954; Plumstead, 1969).

#### MEGAPLANT OCCURRENCES IN THE SOUTH- WESTERN LOWER KARROO STRATA

The lithological succession and the stratigraphic positions of the megaplants are summarised in Figure 2 and their geographical locations are indicated in Figure 1.

##### Dwyka Tillite Stage

Massive diamictite is an unlikely medium for the preservation of fossil leaves, but Du Toit managed to find two occurrences in the south-western Karroo out-



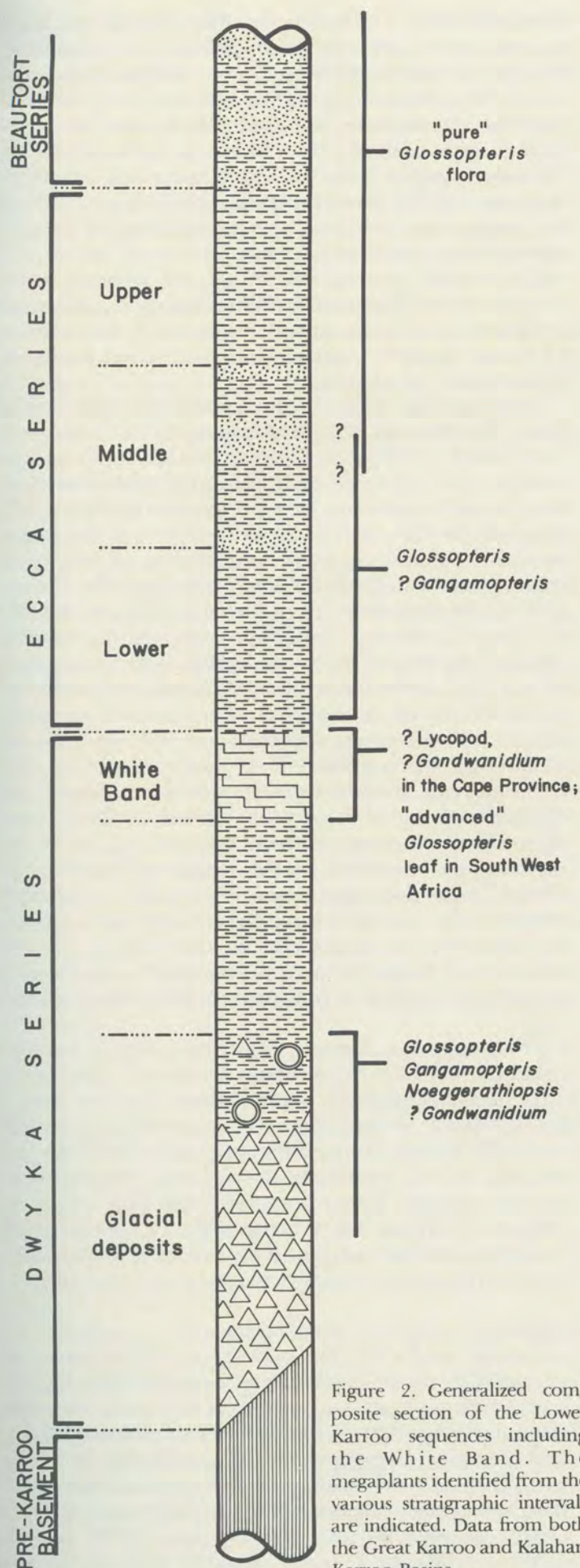


Figure 2. Generalized composite section of the Lower Karroo sequences including the White Band. The megaplants identified from the various stratigraphic intervals are indicated. Data from both the Great Karroo and Kalahari Karroo Basins.

crops. In 1907 (p. 182) he reported that "At Wonderdraai near Strydenberg [ $\pm 23^{\circ}42'E, 30^{\circ}00'S$ ], . . . wedged in between boulders of rhyolite, were found some fragments of an uncrushed but carbonised plant stem and a portion of a frond of *Gangamopteris*". This was referred to again by Rogers and Du Toit (1909, p. 193). Later Plumstead (1969, Pl. VII, Figure 1) recognised a scrap of *Glossopteris* on Du Toit's original specimen, which is now housed in the South African Museum, Cape Town (catalogue no. K.1135). In his second reference to plant fossils in the massive glacial deposits Du Toit (1929, p. 244) observed that "a pseudo-boulder of quartzite from the tillite at Matjesfontein [ $\pm 20^{\circ}43'E, 33^{\circ}13'S$ ] in the Cape yielded a poor specimen of either a *Cordaites* or a *Psymophyllum*". From his tentative identification it would appear that the specimen had non-reticulate, parallel, venation as in *Noeggerathiopsis* (Plumstead, 1964, p. 306).

The final retreat of the glaciers was accompanied by a marine incursion into the Great Karroo Basin (McLachlan and Anderson, 1973a). Fossil wood occurs in abundance with the fish and invertebrates preserved in these glaciomarine deposits (op. cit., Figures 10 and 11). The fossils are usually enclosed in calcareous concretions which provided protection from compression and other damage during diagenesis. This mode of preservation is reminiscent of the northern hemisphere Carboniferous coal balls (Francis, 1961; Schopf, 1975) and the similar occurrences recently described from Antarctica (Schopf, 1970; 1971) and Australia (Gould, 1973) in the southern hemisphere Permian. In the Karroo Basin, however, the plant material was transported into the marine depositional environment; unlike coal balls, the Karroo concretions are not the result of marine inundation of a megafloal community and its debris *in situ*. Hundreds of concretions from the Early Permian glaciomarine horizon in the Great Karroo Basin (see McLachlan and Anderson, 1973b) have been examined, but only one from Blaauw Krantz locality ( $23^{\circ}58'E; 29^{\circ}01'S$ ) on the Riet River, 125 km west-south-west of Kimberley, has yielded any leaves. They have reticulate venation (Figure 5) and no definite midrib, and are therefore referred to the form-genus *Gangamopteris*. Within the flattened ellipsoidal concretion all the leaves have a generally similar orientation (Figure 4): they apparently all originate from the single twig lying along the axis of the concretion (Figure 6).

In 1906 (p. 120) Du Toit recorded that "A fragment of what appears to be a *gangamopteris* was found at Koodoes Berg Drift [ $24^{\circ}29'E; 28^{\circ}57'S$ ] on the Riet River, in a shale containing a few glaciated boulders". This locality is a short distance upstream from the aforementioned Blaauw Krantz locality, and it is probably in the same horizon, although his leaf fragment does not occur in a concretion. Examination of the specimen (Figure 3) reveals that the preserved scrap of foliage is not of the tip of a leaf with evenly spreading venation: there appears to be a midrib running almost parallel with the intact margin, in which case the fragment should be referred to *Glossopteris* or *Gondwanidium* rather than to *Gangamopteris*. The wide spread of the vena-



tion is more compatible with *Gondwanidium* than with *Glossopteris*.

### Upper Dwyka Shales Stage

Rogers and Schwarz (1899, p. 89), Du Toit (1906, pp. 119–120), Hälbich (1958, p. 124) and others have recorded indeterminate plant fossils from the Upper Dwyka Shales. McLachlan and Anderson (1973b, p. 418) expressed the opinion, referring particularly to the White Band, that the frequently mentioned “plant remains” are likely to be intrasediment horizontal burrows. Such burrows abound at some levels, but genuine plant material is also definitely present elsewhere.

Unidentified fossil wood has been reported from the Upper Dwyka Shales in general by Woodward (1965, p. 48), and from the White Band near Prince Albert in particular by Haughton *et al.* (1953, p. 23) and Rossouw *et al.* (1964, p. 32). Mr. R. D. F. Oosthuizen of the farm Zwartskraal in this vicinity is in possession of a tree trunk 60 cm in diameter from the White Band in a quarry at Prince Albert.

Seward (1907, p. 484) described a fragment of the lycopod stem *Lepidodendron australe* from a borehole at Élandsdraai ( $\pm 24^{\circ}15'E$ ;  $29^{\circ}40'S$ ) south of Kimberley. Du Toit (1907, p. 182; 1926, p. 215; 1954, p. 280) considered the enclosing shale to be from the Upper Dwyka Stage. We found another specimen south of Kimberley also having a somewhat doubtful stratigraphic position. It is from a shale quarry immediately east of the “Drie Koppe” hills ( $23^{\circ}38'E$ ;  $29^{\circ}41'S$ ). Both the surface topography and the Karroo strata in the area are almost horizontal, which renders the interpretation of the stratigraphic position of isolated outcrops difficult as the relative position of the White Band cannot be readily determined. On the 1:1 000 000 Geological Map of the Republic of South Africa (1970) both localities fall well within the Dwyka Series. No more detailed map is available. The leafy fragment on the recently found specimen from Drie Koppe is itself somewhat contentious. The venation is not reticulate as in *Gangamopteris* and *Glossopteris*; it is parallel, spreading slightly, reminiscent of *Noeggerathiopsis* (Figure 11). The outline of the fragment is generally leaf-like, but there is lamina preserved on each of two, or maybe more, superimposed levels. The puzzling feature is that the direction of the parallel venation is not quite constant. If there is only a single leaf involved, it must have been furled so that its long margins overlapped; if there is more than one leaf represented, it is possible that it was a shoot tip in which the individual leaves had not yet spread apart.

Schwarz (1912, pp. 151–152) noted that “In the Upper Dwyka Shales there have been found in Kimberley and Calvinia a number of remains of a little reptile *Mesosaurus*, while *Glossopteris* occurs sparingly”. This could be a reference to *Glossopteris* in the White Band. Du Toit (1926, p. 215; 1954, p. 279) certainly listed *Glossopteris* sp. from the White Band near Kimberley. Engelbrecht (1961, p. 109) reiterated the report, but he did not confirm the occurrence in his detailed description of the geology of an area in the

vicinity (1973). Unfortunately the original specimen cannot be traced: it is in neither the Alexander McGregor Memorial Museum in Kimberley nor the South African Museum in Cape Town, where most of Du Toit's collections are currently housed (A. J. B. Humphreys and M. A. Cluver, pers. comm.). We recently found a scrap of leaf lamina with reticulate venation on the farm Damascus ( $21^{\circ}57'E$ ;  $33^{\circ}13'S$ ), 3 km west of Prince Albert. The intact margin is strongly curved, and there is evidence of the existence of a midrib on the opposite side (Figure 13). If the specimen is part of a *Glossopteris* leaf the overall shape would appear to have been unusually squat. It seems more probable that it is a single pinnule of a leaf similar to the fern-like *Gondwanidium*.

Another interesting specimen was found in the White Band by Mr. R. D. F. Oosthuizen on the farm Brandhoek ( $\pm 19^{\circ}32'E$ ;  $31^{\circ}36'S$ ), 25 km south-west of Calvinia. It is a twice dichotomising twig apparently covered in short spiny “leaves” or bracts (Figure 12). Towards the base almost the entire width of the twig is occupied by eight or more vertical rows of nearly circular “scars” and the “leaves” may even be absent; towards the three free tips of the twig a thin central axis or “stem” becomes apparent, although the overall width of the twig (“leaves” included) continues to taper evenly. The central axis occupies about one eighth of the width of each of the terminal branches. The closely set “leaves” diverge at approximately  $45^{\circ}$ . The free tips of the twig are rounded. There is the suggestion of a line of circular bodies between successive “leaves” on the left hand side of the terminal branch on the extreme right. The diameter of these circular bodies is approximately one third of the length of the adjacent “leaves”. The detail is too poorly preserved to establish whether any of the terminal branches were indeed fruiting cones or not. Detail in the “leaf scars” and elsewhere is likewise absent, so the identity of the twig as lycopod, conifer or bryophyte must remain conjectural.

Even more enigmatic are the “fucoid straps” collected from the White Band by Mr. B. Oelofsen of Stellenbosch University. Some of these “fucoids” have a blocky surface texture (Figure 17), superficially reminiscent of *Vertebraria* roots; others are almost smooth. The smooth variety frequently has a blunt rounded end, and occasionally there is a coarse, apparently reticulate, “venation” (Figure 16). Whether these Problematica are in fact of vegetable origin is not certain. Even if they are, their identity remains obscure.

### Ecce Series

Rogers and Du Toit (1909, p. 199) listed the equisetalian stems *Schizoneura* sp. and *Phyllothea* sp., the seed *Cardiocarpus* sp. and the leaves *Glossopteris browniana* Brongt., *Gangamopteris cyclopteroides* var. *attenuata* Feistm. and *Cordaites* (*Noeggerathiopsis*) *hislopi* Bunb. from the Ecce Series in the Cape Province. Equisetalian stems had been previously recorded by Rogers and Schwarz (1902, p. 109), Rogers and Du Toit (1903, p. 30), Schwarz (1905, p. 289) and Seward (1903, p. 79) and



then by Rogers (1925, p. 19). The *Cardiocarpus* seeds were found in an Ecce outlier near Worcester station in the south-western Cape Province by Schwarz (1905, pp. 288–289) and named by Seward, apparently in an unpublished communication. An example of a possibly similar seed was recently found in the Lower Ecce Stage west of Grahamstown by Mr. C. S. Kingsley (Figure 10).

Along with the *Cardiocarpus* seeds, Schwarz (loc. cit.) found “many fragmentary kinds of *Gangamopteris* and *Glossopteris*” near Worcester, as well as some *Phyllothea* from another locality in the vicinity. Seward (1903) described at least some of this material. He provided an illustration of a scrap of lamina which he identified as being probably *Glossopteris browniana* Brongn. var. *indica*. He also recognised “One small and very obscure fragment . . . [which] is no doubt a fragment of *Gangamopteris*; it agrees closely with Feistmantel’s (1889) figure of *G. cyclopteroides* var. *attenuata*”.

Feistmantel (1889) described and figured *Gangamopteris cyclopteroides* var. *attenuata* Feistm. and *Noeggerathiopsis hislopi* Feistm. from the “Kimberley Shales”. The specimens were supplied by Moulle (1885, p. 41). Although the local “Kimberley Shales” are part of the basinwide Ecce Series (Corstorphine, 1899, p. 24), Moulle did not actually specify in his book that the leaves were indeed from the Kimberley Shales as such: he merely recorded the occurrence of the leaves in his description of the rock sequence at Kimberley and in the Orange Free State. The leaves are mentioned in the sub-section in which he defined the change into the “Upper Karroo” Stormberg Series at the top of the stratigraphic column. This tends to imply an origin from the Beaufort Series which intervenes between the Ecce and Stormberg Series. Another, more likely, possibility is that the leaves might have been collected from the Ecce Series substantially north of Kimberley, beyond the limit of the White Band; they certainly are reminiscent of the typical Coal Measures leaves found at Vereeniging on the northern border of the Orange Free State.

The third species of leaf, *Glossopteris browniana* Brongn., which was identified by Feistmantel (1889) from the south-western portion of the Great Karroo Basin, has a somewhat more precise geographic location: the material was provided by Dunn (1886, p. 11) from Camdeboo, south-east of Graaff-Reinet. It is not clear from the original description whether the specimen(s) came from the upper Ecce or the overlying Beaufort Series, but the distinction is not particularly significant as in that area very similar *Glossopteris* leaves occur in both Series.

*Glossopteris* in the Ecce Series has been mentioned quite frequently in the geological descriptions of the south and western Cape Province (Rogers and Schwarz, 1902, p. 109; Rogers and Du Toit, 1903, p. 30; Du Toit, 1926, p. 274; Schwarz, 1905, p. 288; Rogers, 1925, p. 19; Mountain, 1946, p. 22; Haughton *et al.*, 1953, p. 28), and one fragment, not including the midrib, was illustrated by Seward (1903, Pl. XIII, Figure 1). There are fewer reports of *Gangamopteris* from the south-west portion of the Great Karroo Basin

(Rogers and Du Toit, 1903, p. 30; Schwarz, 1905, p. 288, *vide ante*) and no illustrated example. In his current detailed investigation of the Ecce Series in the eastern Cape Province, Mr. C. S. Kingsley of Port Elizabeth University has, to date, seen only *Glossopteris* (Figures 7–9), no *Gangamopteris*. He reports that in his study area recognisable leaves occur in the Middle and Upper Stages of the Ecce Series but not in the Lower Stage (which includes the Upper Dwyka Shales and White Band) (pers. comm., Ph.D. in prep.). Kingsley’s observations corroborate the assessment made by Haughton *et al.* (1953, p. 28).

Silicified wood has been widely reported from the Ecce Series in the south-western portion of the Great Karroo Basin (Schenck, 1888, p. 230; Rogers and Schwarz, 1902, p. 109; Rogers and Du Toit, 1903, p. 29; Du Toit, 1907, p. 183; 1926, p. 274; Rogers, 1925, p. 19; Mountain, 1946, p. 22; Rossouw *et al.*, 1964, pp. 35, 37). None of it appears to have been formally described, although it is frequently colloquially referred to *Dadoxylon* sp.

## COMPARABLE MEGAFLORES FROM SOUTH WEST AFRICA AND SOUTH AMERICA

The characteristic fossil reptile genus *Mesosaurus* which occurs in the White Band of the south-western portion of the Great Karroo Basin also occurs in South West Africa and South America (Du Toit, 1954, pp. 335, 354). It is generally taken to indicate approximately simultaneous accumulation of the entombing sediments. As such, at least a superficial comparison of the south-western Lower Karroo megaflores with those close above and below the *Mesosaurus* zone elsewhere is indicated.

Rigby (1970) reviewed the plant fossils from the relevant strata of the Parana Basin in Brazil, South America. His species list shows that the flora in the Guatá Subgroup underlying the White Band equivalent Irati Formation is more diverse than in the Estrada Nova Formation overlying it, with five *Gangamopteris* spp. in the former and only two in the latter. From within the Irati Formation itself he listed three species of wood (Kräusel and Dolianiti, 1958), but no leaves. However, according to Bigarella and Salamuni (1967, p. 66), Pinto (1955) found a *Glossopteris* leaf in strata which Machado and Castanho (1956) assigned to the Irati Formation. From Argentina, Harrington (1967, pp. 998–999) recorded an horizon containing *Glossopteris*, *Gangamopteris* and *Noeggerathiopsis* species, which is both under- and overlain by *Eurydesma* beds. The lamellibranch genus *Eurydesma* is characteristic of the latter stages of the Paleozoic glaciation throughout the former Gondwanaland (Dickins, 1961).

The salient comparison between the fossil plants on either side of the Atlantic Ocean dates back to Du Toit, 1926, p. 278:

“The Rio Bonito Group [now a Formation within the Guatá Subgroup] contain coals and have yielded an abundant flora including *Gangamopteris*, *Glossopteris*, *Lepidodendron*, *Sigillaria*, etc., strikingly like



that of the [north-eastern] Ecra Series.

It should be noted though that in South America this plant-bearing stage lies below the zone of *Mesosaurus* . . ."

Coals are also developed below the *Mesosaurus* horizon in the Kalahari Karroo Basin of South West Africa (see Figure 1) (Martin, 1953). A catalogue of the associated plants is not available, but Kräusel (1956) did describe three genera and species of silicified wood from the Upper Dwyka Shales near Marienthal and Keetmanshoop. These are generically different from those he described from the Irati Formation in South America, and from that apparently identified by Seward from the Ecra series in the Great Karroo Basin (Du Toit, 1926, p. 274).

Mr. B. Oelofsen of Stellenbosch University recently found portion of a *Glossopteris* sp. leaf in the *Mesosaurus*-bearing strata in the Kalahari Karroo Basin while he was collecting specimens of the little reptile. The leaf is from the farm Gellap Ost ( $\pm 18^{\circ}00'E$ ;  $26^{\circ}30'S$ ) north-west of Keetmanshoop. It has a distinct midrib, and the secondary veins run nearly perpendicular to the midrib (Figure 14). These features are indicative of an "advanced" form of *Glossopteris* (Kovács-Endrödy, pers. comm.)

Mr. Oelofsen also found what appears to be a plant impression in the White Band on the farm Aussenkjer ( $\pm 17^{\circ}30'E$ ;  $28^{\circ}30'S$ ) in the Warmbad Basin. Superficially it is leaflike, being bilaterally symmetrical with a longitudinal median ridge (Figure 15). The median ridge occupies approximately one tenth of the total width, 18 mm, of the impression. There is, however, no evidence of secondary venation. Instead there are regular rows of raised dots running obliquely across the impression; they are uninterrupted by the median longitudinal ridge. The rows of dots and the individual dots in each row are both approximately 5 mm apart. The outer margins of the impression appear to be irregularly indented, but this is probably the result of fracture along the margins during parting. Neither base nor tip of the structure is present. Interpretation is problematic. The raised dots might feasibly have been fern sori, but the absence of venation in the lamina tends to detract from interpretation of the structure as a leaf. Another possibility is that the structure is a flattened fleshy stem or reproductive cone which had a firm central column and firm protuberances on its outer surface. This suggestion is not entirely satisfactory either as the arrangement of the dots is too completely regular to represent protuberances from both surfaces of the perfectly two-dimensional "compression".

#### MEGAFLORAL SUCCESSION IN THE NORTH-EASTERN PORTION OF THE GREAT KARROO BASIN

Dr. Plumstead (1966a, b; 1967; 1969; 1973) has outlined the megaplant succession from the north-eastern portion of the Great Karroo Basin. The following is a brief summary of her zonation. In boreholes in the northern Orange Free State she recognised a pre-

*Glossopteris* zone, containing lycopods only, in the transition beds between the Dwyka Tillite Stage and the overlying Middle Ecra Stage. Apparently above this, in other boreholes farther north, she distinguished a proto-*Glossopteris* zone containing moss and various leaves, the majority of which resemble *Gangamopteris*. Although examples with occasional reticulation are encountered infrequently, the venation generally shows bifurcation only, no reticulation. These two basal zones are interbedded with "fluvioglacial" deposits, but the evidence for direct glacial deposition has not been unequivocally established. Leslie (1921, p. xxiii) reported what he considered to be undoubted evidence of plant fossils in the actual glacial conglomerate exposed near Vereeniging: he found well-preserved *Gangamopteris* leaves in a shale 7.5 cm from the basement between large erratic boulders lying on the pre-Karroo surface. That particular outcrop is no longer in existence, but when Nel and Jansen (1957, p. 28) mapped the area in detail they observed that the "conglomerate, which occurs in places at the base of the Karroo beds, . . . has the character of an ordinary, coarse conglomerate rather than a boulder-clay or tillite". The inference is that Leslie's nearly 300 mm long *Gangamopteris* leaves (some of which are illustrated by Plumstead, 1969, Pl. VII 2, 3, 4) at least are not necessarily representative of the Dwyka glacial flora in the north-east. They are probably merely part of the non-glacial Middle Ecra Coal Measures zone, albeit an early part. The flora of this mixed *Glossopteris* zone contains a variety of leaf forms (e.g. *Gondwanidium*, *Noeggerathiopsis*) besides *Gangamopteris* and *Glossopteris*. The final Palaeozoic *Glossopteris* zone, firmly established in the Beaufort Series, is marked by an overwhelming preponderance of *Glossopteris*, without any *Gangamopteris* or *Noeggerathiopsis* being involved.

#### STRATIGRAPHIC OCCURRENCE OF GANGAMOPTERIS AND GLOSSOPTERIS IN THE TWO PORTIONS OF THE GREAT KARROO BASIN

In the Middle Ecra Stage in the north-eastern portion of the Great Karroo Basin fossil leaves are beautifully preserved *en masse* at some localities (e.g. Vereeniging, described by Leslie, 1921). With the possible exception of the Upper Ecra Stages, similar banks of leaves have not yet been reported from the Lower Karroo strata in the south-western portion of the Basin. The explanation probably lies in the differing depositional conditions which prevailed in the two areas. In the north-east the leaves appear to have accumulated in quiet lake or marsh environments, within or not too distant from the thriving *Glossopteris* forests; in the south-west leaves occur only sporadically in more remote offshore deposits (Ryan, 1967). Whatever the cause, it does seem that only strenuous effort and good fortune will yield plant collections adequate for reliable definition of the floras in the south-western Lower Karroo deposits. A detailed comparison between the floras of the north-eastern and south-western portions



of the Great Karroo Basin is therefore not feasible at this stage. Some generalisations are nevertheless possible:

1. In the south-western portion of the Basin and in South America (Harrington, 1967) both *Gangamopteris* and *Glossopteris* occur in Dwyka glacial deposits; in the north-eastern portion there are no confirmed records of these leaves in unambiguous glacial deposits.
2. *Gangamopteris* sp. leaves are characteristic of the Middle Ecça Stage in the north-east. In the south-west these leaves certainly occur below the White Band, less certainly above it, although they have been reported from both above and below the White Band equivalent in South America (Mendes, 1967; Rocha-Campos, 1967; Rigby, 1970).
3. The record in the Lower and Middle Ecça Stages in the south-west is very poor. By the Upper Ecça Stage only *Glossopteris* leaves, no *Gangamopteris*, are present. This seems also to be the case in the north-east (Plumstead, 1966b, p. 8).

#### CORRELATION BETWEEN THE SOUTH-WESTERN AND NORTH-EASTERN PORTIONS OF THE GREAT KARROO BASIN

There has been controversy about the correlatives of the so-called "Middle Ecça" Coal Measures of the Transvaal and Natal, in the north-eastern portion of the Great Karroo Basin, ever since their discovery towards the end of the last century. The early correlations suggested by Dunn (1886) and Draper (1897) were naturally with the Molteno Stage of the Stormberg Series because these are the only strata in the Cape Province characterized by any marked development of coal. When it was appreciated that the floras in the Transvaal and Natal Coal Measures were clearly older than those in the Molteno coal horizons (Feistmantel, 1889; Seward, 1897), Dunn (1898; 1900) argued in favour of correlation of the former with the Ecça Series in the Cape Province. This conclusion was accepted by Corstorphine (1903; Hatch and Corstorphine, 1905), but not by Molengraaff (1904), who preferred to correlate the Transvaal Coal Measures with the Beaufort Series in the Cape Province. Each author cited fossil plants in support of his preferred correlation. Mellor (1906) discussed this anomaly, regretting that practically all the fossils available as evidence are plant remains. He established that the Coal Measures strata contained no evidence of contemporaneous glacial activity, and decided that correlation with the Beaufort Series was most likely. Du Toit reviewed the situation in 1918. He (p. xx) pointed out that the varied Ecça sediments in the southern Cape Province graded into an argillaceous facies in the northern Cape Province, and that the Coal Measures in Natal graded southwards into a similar argillaceous facies. This correlation has been followed in most subsequent texts (Du Toit, 1926; Haughton, 1969; Rust, 1973; Cooper, 1974; A. M. Anderson, 1975). Unfortunately the Ecça deposits in the southern Cape Province do not link directly with those along the

east coast as that corner of the Great Karroo Basin is truncated by the Indian Ocean. It is in that critical interval that the White Band disappears. Early observers (Rogers and Schwarz, 1901; Du Toit, 1920; 1946) reported the occurrence of strata reminiscent of the White Band directly overlying the massive Tillite Stage near Port St. Johns. However, the gray Upper Dwyka Shales which underlie the White Band in the remainder of the Cape Province are missing, and the characteristic White Band fossils (the reptile *Mesosaurus* and *Notocaris* sp. crustaceans) have not yet been found in that area. It therefore seems best to regard the existence of White Band at the northern side of the truncation with reservation. This renders the traditional correlation of the argillaceous Ecça facies in the Northern Cape with similar facies in Natal somewhat less tenable. The currently more fashionable theory is that the so-called Middle Ecça Coal Measures in the north-east were isochronous, not with the Ecça Series in the south-west, but with some part of the Dwyka Series (Kent, 1938; Van Eeden, 1961, 1973; Plumstead, 1962b; McLachlan and Anderson, 1973a; J. M. Anderson, 1973). Unfortunately the outcrops along the north-western edge of the Basin are too poor to provide a decisive solution; nor is there a borehole anywhere in the Basin known to have intersected both Coal Measures sandstones and unequivocal White Band.

We return, in slightly different context, to Mellor's (1906) lament that the megaplants are too ill-understood to provide much indication one way or the other: in the intervening seventy years there has been little improvement in the definition of the Lower Karroo megaflores of the Cape Province, covering the south-western portion of the Great Karroo Basin. At least it is clear now that the Beaufort Series, with its more advanced "pure" *Glossopteris* flora, overlies the Ecça Series in the north-east and that a similarly advanced flora occurs in the Upper Ecça Stage and Beaufort Series in the south-west: correlation of the Coal Measures with the Beaufort Series thus needs no longer to be considered seriously. The present controversy centres on the option of correlation with the Dwyka or Ecça Series in the south-west. At the generic level, plants (*Gangamopteris*, *Noeggerathiopsis*) characteristic of the "Middle Ecça" Coal Measures in the north-east were certainly established during the Dwyka glaciation in the south-west, but there is some indication that they may have persisted above the White Band into the Ecça series as well. If so, it is possible that within the timespan represented, given suitable environmental conditions at any locality, coals with closely similar floral composition might equally well have accumulated either before or after White Band formation. There is a further complication: presently available information does not preclude the possibility that the White Band and *Mesosaurus* may be diachronous. The presence of "advanced" *Glossopteris* in the *Mesosaurus* horizon in South West Africa could be taken to indicate correlation with the Upper Ecça Stages or Beaufort Series in the Great Karroo Basin. However, no reliance can be placed on a single, incomplete leaf, particularly as similar "advanced" forms also occur in the



Middle Ecca Coal Measures sequence (cf. Plumstead, 1956a, Pl. 6) where the "primitive" *Gangamopteris* is still abundant.

It must be regretfully concluded that, with the currently available evidence, megaplants contribute little towards the resolution of the correlation controversy outlined above.

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## EXPLANATION OF ILLUSTRATIONS

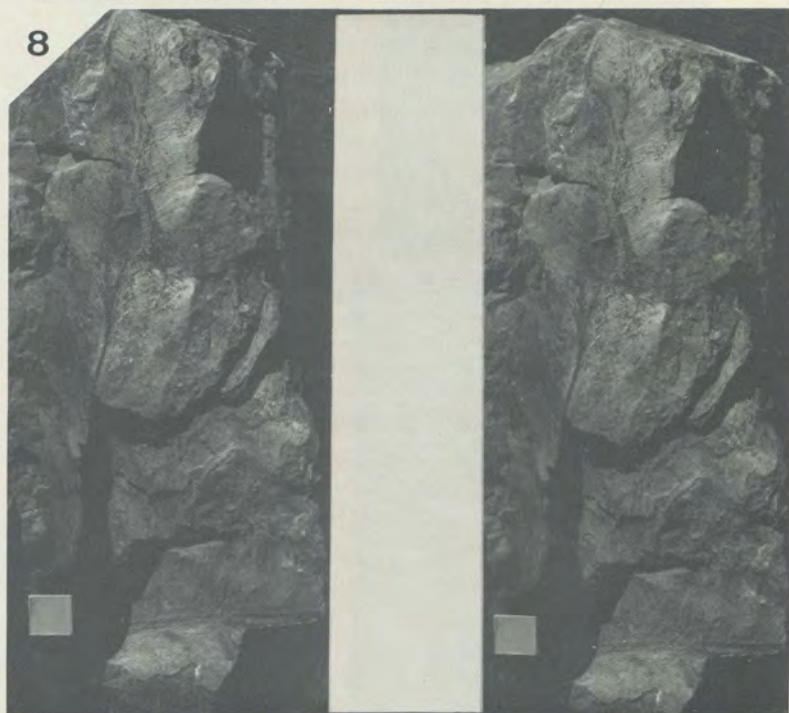
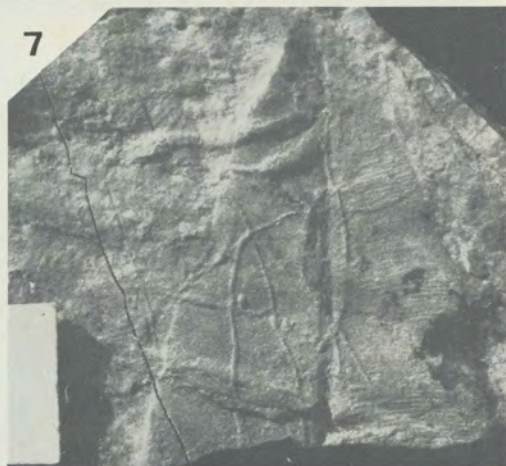
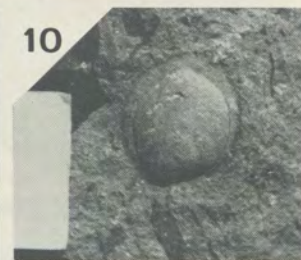
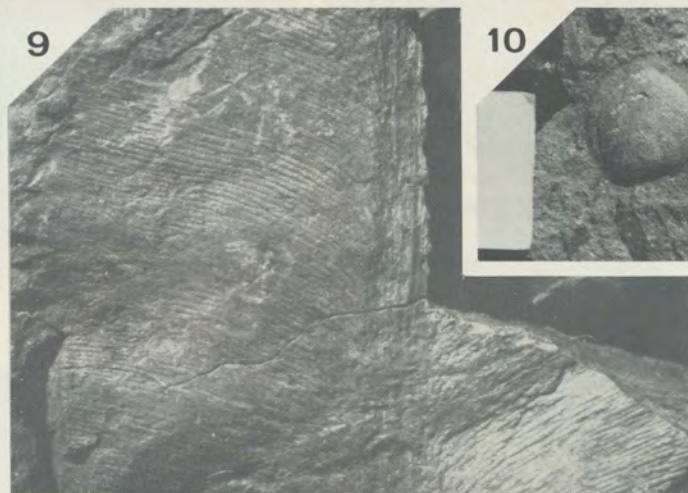
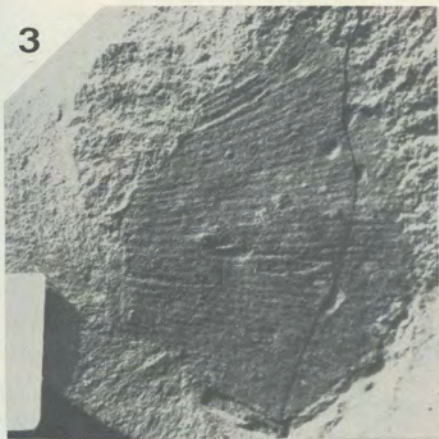
### PLATE I

- Figure 3. Scrap of lamina found by Du Toit (1906) in shale near the top of the Dwyka Tillite Stage at Koodoes Berg Drift. The leaf appears to have torn along the midrib on the left. The venation lineation spreads towards the margin on the right. Even if the margin on the right is not intact, the spread of the venation is too wide to conform with the typical elongate *Glossopteris* leaf form; it is more likely that the fragment is one pinnule from a *Gondwanidium*-like frond. ( $\times 2$ , South African Museum specimen number K1136.)
- Figure 4. Stereopair of the concretion containing leaves from Blaauw Krantz locality. It has been split open along the widest section of the flattened concretion. ( $\times 0.5$ , Bernard Price Institute, B.K. 7.)
- Figure 5. Detail of reticulate venation and ill-defined midrib from one of the *Gangamopteris* leaves in the Blaauw Krantz concretion ( $\times 2$ .)
- Figure 6. Polished section, perpendicular to the section shown in Figure 4, of the Blaauw Krantz concretion. The dark rimmed oval feature in the top right hand quadrant of the picture is a stem in which the cellular structure is preserved. The smooth curving line at the bottom of the picture is the outer surface of the concretion. The sinuous hair-fine lines between it and the stem are leaves in cross section ( $\times 1$ .)
- Figure 7. Tip of *Glossopteris* leaf from the Middle Eccla Stage at Eccla Pass, north of Grahamstown. It has a persistent midrib and the secondary veins leave it at a wide angle. The meandering lines crossing the leaf are intrasediment burrows. ( $\times 2$ , C. S. Kingsley, field specimen number 70/7/1.)
- Figure 8. Stereopair of two *Glossopteris* leaves from the Upper Eccla Stage at Eccla Pass, north of Grahamstown. ( $\times 0.5$ , C. S. Kingsley, field specimen number 75/63/1.)
- Figure 9. Detail of the midrib and reticulate secondary venation of one of the leaves shown in Figure 8 ( $\times 2$ .)
- Figure 10. Well-preserved seed from the Lower Eccla on the farm Bosfontein, west of Grahamstown. The body of the seed has a peaked apex (pointing towards the top of the page in the photograph). A marginal flange, probably a wing, surrounds the body of the seed. It is widest towards the apex and absent at the base where the seed was attached to the parent plant. ( $\times 2$ , C. S. Kingsley.)

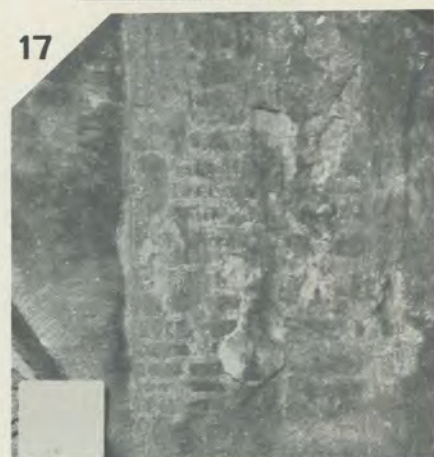
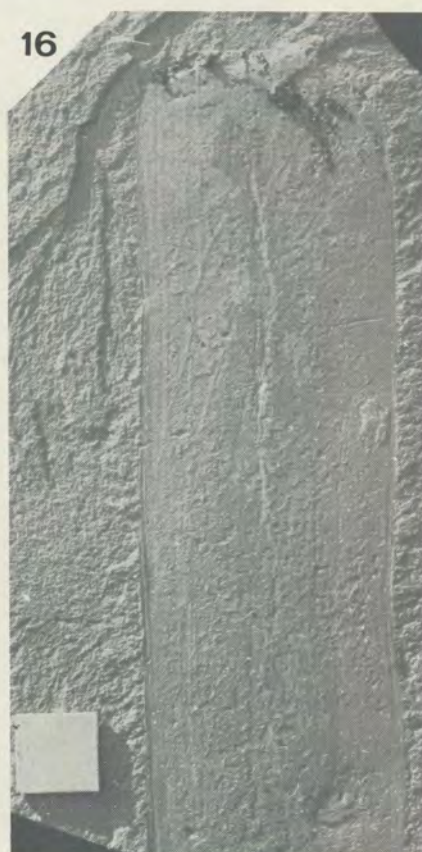
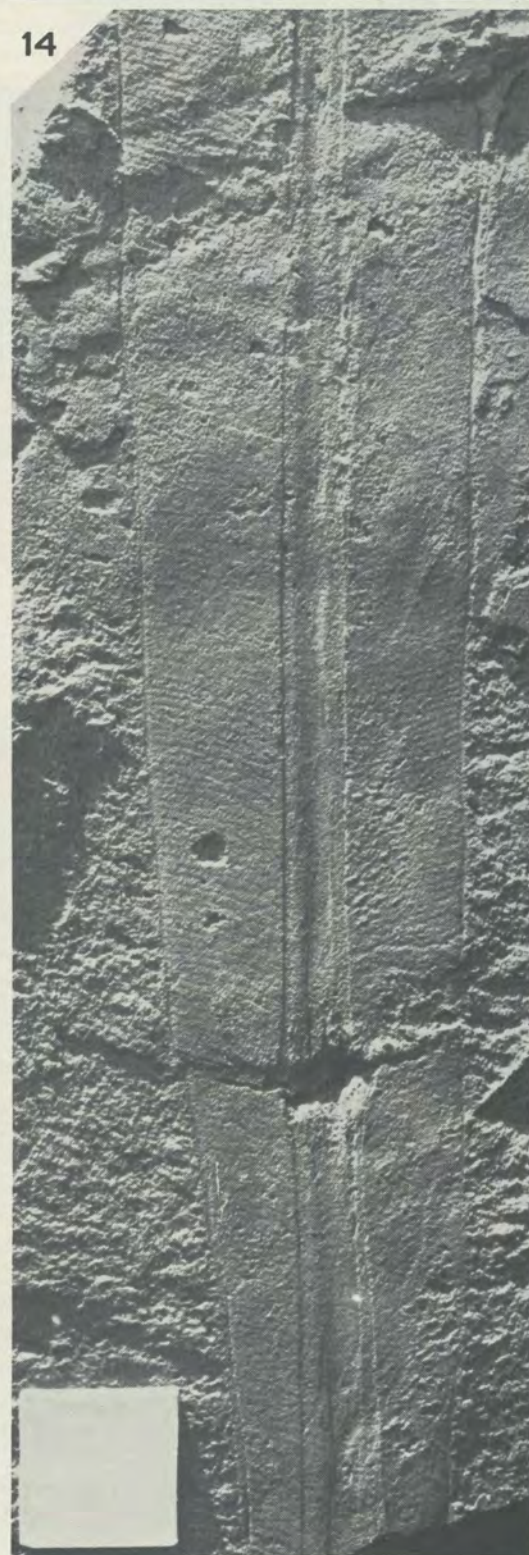
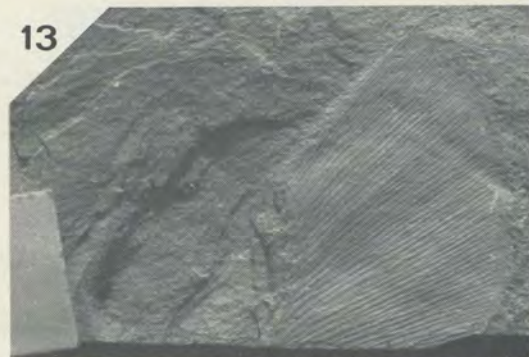
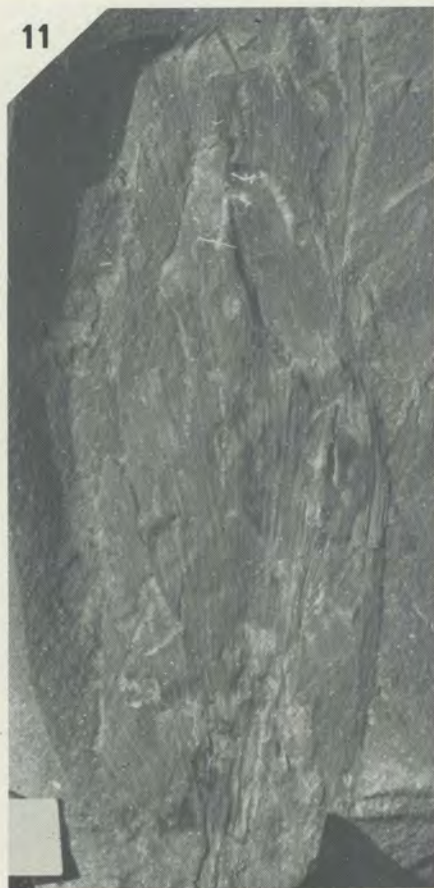
### PLATE II

- Figure 11. Leaf-like impression with spreading venation from Drie Koppe, probably from the Upper Dwyka Shales. ( $\times 1$ , Bernard Price Institute, D.K. 1.)
- Figure 12. Dichotomising leafy twig from the White Band at Brandhoek. ( $\times 1$ , R. D. F. Oosthuizen, specimen number G 38.)
- Figure 13. *Gondwanidium*-like pinnule from the White Band on the farm Damascus. The reticulate venation spreads from the torn edge on the left towards the smooth curving intact margin on the right. ( $\times 2$ , Bernard Price Institute, Da. 1.)
- Figure 14. Basal portion of "advanced" *Glossopteris* leaf from the *Mesosaurus* horizon on Gellap Ost in South West Africa. The midrib is well defined. ( $\times 2$ , B. Oelofsen, field collection number USS 6/4/4.)
- Figure 15. Problematic structure from the White Band on Aussenkjer in southern South West Africa. ( $\times 1$ , B. Oelofsen, field collection number USS 6/6/2.)
- Figure 16. Problematic "fucoid strap" from the White Band near Calvinia. The tip, near the top of the picture, is bluntly rounded. There is a suggestion of a coarse reticulate venation towards the top/left. ( $\times 1$ , B. Oelofsen, field collection number USS 1/10/4.)
- Figure 17. Problematic "fucoid strap", with "blocky" surface texture, from the White Band near Calvinia. ( $\times 1$ , B. Oelofsen, field collection number USS 1/7/4.)











## PRELIMINARY REPORT ON EQUISETALEAN PLANTS FROM LIDGETTON, NATAL

by

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## ABSTRACT

Fossils of *Equisetum*-like plants from a site near Lidgetton, Natal, South Africa (29°26'S, 30°07'E) are described. These comprise rhizomes bearing roots, stems of varying width showing external and some internal structure (especially nodal markings and vasculature), and ultimate branchlets bearing leaf whorls. No reproductive organs were found. A tentative decision is reached that they are parts of plants of a single genus, perhaps even a single species, and that relationship is closest to *Equisetites* Sternberg.

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## INTRODUCTION

Prior to 1929 macroscopic plant remains were taken from accessible parts of a bed of shale exposed in a small stream at Lidgetton about 35 kilometres north-west of Pietermaritzburg at 29°26'S, 30°07'E. According to Thomas (1958), to whom the plant remains were sent, they were of two main types: firstly a series of leaves and leaf-like organs of various sizes, including shorter scale-leaves without a midrib, all referable to the form genus *Glossopteris*, and secondly "... parts of equisetalean plants, stems, pith-casts, branches and leaves." Of these last named fossils this author wrote

"These may belong to the form called by Du Toit (1927, p. 315) *Neocalamites carreri* Zeiller, but, from the more abundant material present in this collection, it is clear that the plant differed very considerably from the species described by Zeiller."

The equisetalean fossils enumerated by Du Toit (1927) were from Molteno beds near Dordrecht, Cape Province and near Fletcherville, East Griqualand and thus were of Triassic age and younger than the Lower Beaufort specimens from Lidgetton. The first of the Molteno plants (Du Toit no. 833) was a short section of flattened stem showing a node with attached leaf sheath that ended in 18 short free teeth each only 2 mm long. This was tentatively compared with *Equisetites platyodon* Schönlein and Schenck, 1865, from the Middle Keuper

of Germany, which had about the same number of free leaf teeth at a node. Two other specimens (Du Toit nos. 8329 and 5806) were referred to *Neocalamites carreri* Zeiller. These showed (no. 8329) a node with external stem surface carrying a leaf whorl consisting of about 60 free leaves, at least 5 cm long in some cases, that broadened and overlapped basally (visible internally were narrow longitudinal ridges and the under surface of a nodal diaphragm), and (no. 5806) the exterior of a portion of stem with the shallow fluted internodal surface traversed by extremely fine striations and with about 18 leaf scars situated immediately beneath each of the two nodal lines present. Other specimens from Duart Castle, Hlatimbe Valley, Natal, were striated moulds with the ridges and grooves continuous in their course from one internode to the next, a feature regarded as characteristic of *Neocalamites*.

Thomas (1958) made no other reference to the "equisetalean plants" from Lidgetton, neither describing them further nor contrasting them with the Triassic plants described by Du Toit (1927). Plumstead (1969, Pl. XVI, 1) referred ribbed and jointed Permian stems superficially similar to many from Lidgetton to *Paracalamites* Zalesky (1927). In so doing she followed Rigby (1966), who proposed that unidentifiable stem fragments from Lower Gondwana deposits frequently referred to as *Phyllothea* sp. or *Schizoneura* sp. should be described as *Paracalamites*. According to Zalesky, the



stems referable to the form genus *Paracalamites* have ribs of the pith cast opposite at each node. Townrow (1955) in an amended diagnosis of *Phyllothea* adopted a maximum diameter of "up to 2 cm" for main stems. Many of the stems from Lidgetton exceed this size, Dix (1974) having recorded widths up to 4 cm. Thus, at present, there is no clarity as to the name, or names, if more than one type is represented there, that should be applied to the parts of equisetalean plants at the Lidgetton site.

The purpose of this paper is to record, in the form of a preliminary report, the more important structural features and range of variation of these equisetalean specimens. It may also be possible to come to some conclusion as to whether one, or more, taxa are present and to refer a tentative name, or names, to these.

## MATERIAL AND METHODS

The bulk material collected in the field has yielded hand specimens that will be housed in the Natal Museum, Pietermaritzburg. The plants occur as impressions and incrustations or as what have been previously interpreted as pith casts, all of which sometimes show cellular patterns, occasionally with great clarity. In a later paper this cellular detail will be studied more closely and the carbon that remains in many of the incrustations will be treated in an endeavour to make cuticular preparations.

The present paper deals mainly with macroscopic plant parts which have been studied under a binocular microscope with strong low-angle unilateral illumination from a Tiyoda 8,8V 5A focusing bench light.

## THE PLANT PARTS

### Stems

Portions of stems of varying lengths (from a few mm up to 24 cm) and widths (from 2 mm to 6,8 cm), all comprising short nodes alternating regularly with shorter or longer, ribbed and furrowed internodes, lie side by side or occasionally cross one another in the matrix. Up to seven, usually all of approximately the same size range, may occur on a single hand specimen. Generally only the narrow stems carry whorls of leaves and thus can be immediately orientated in relation to base and apex. The wider stems that appear to lack leaves do not all exhibit similar superficial markings and thus need careful interpretation if external surfaces are to be correctly distinguished from internal casts, and distal and proximal ends accurately recognized. An attempt has been made to sort the equisetalean stem fossils into types and to interpret these. A summary of the more important findings follows.

### *Stems thought to exhibit external features*

#### (i) *Stems that appear to carry roots.* (Figures 1, 5)

Four stems from 2,0–5,5 cm in width show the presence of a dense cluster of dichotomously branching, non-articulated, smooth surfaced outgrowths laterally from a node or from two successive nodes. The form and position of the outgrowths and the angles at which

they lie to the stems suggest that they are roots — richly branched roots as would be in keeping with plants growing in water. A number of other stems, some wider, some narrower, show aggregations of similar outgrowths in close proximity.

If these outgrowths are roots, then the stems bearing them were probably below the surface of the substrate and thus should be interpreted as rhizomes. The markings they carry must be those of the external rhizome surface since, if they were pith casts, root attachment would not be visible. That these stems are rhizomes is supported further by the next stem category.

#### (ii) *Stems that exceed 4 cm in width.* (Figures 1, 2)

Of 57 stems measured, 14 were 4 cm or more in width (limits 4,0–6,8 cm: mean 5,3 cm). These widest stems comprised internodes (length limits 16,5–42,0 mm: mean 25,8 mm) with the nodes giving the impression of being numerous and closely placed because of the width of the stems. Many of the stems were curved, not straight. This curvature, together with the apparent shortness of the internodes, suggests the stems were not aerial and thus probably were rhizomes. None of these wide stems showed the presence of whorls of leaves. Nodal markings were clearly defined and more or less uniform and will be considered later.

#### (iii) *Stems from 0,5 to 3,9 cm in width.* (Figure 13)

Of the remaining 43 stems, 37 fell within 1,0–3,9: mean 2,1 cm in width, while 6 were between 1,0 and 0,5: mean 0,75 cm in width. These stems of intermediate width had internodes that appeared longer than those of the widest stems (length limits 5–43 mm: mean 19,7 mm) (ratio of node length: node width for stems of intermediate width 10:1; for wide stems 5:1). These stems were mostly straight or only very slightly curved, which is suggestive of aerial growth. Because of their narrower width they gave the fallacious impression that their internodes were longer than were those of the widest stems. They also lacked intact leaf whorls, but there are some specimens in which basal fragments of a sheath might be present, while a very few show evidence of a few free leaf segments lying close to the stem and possibly still attached to the sheath which, in turn, is fused to the stem. The nodes, especially in the case of the incrustations, were mostly clearly defined but any markings were usually less definite and detailed and thus more difficult to interpret than those of the wider stems.

#### (iv) *Stems less than 0,5 cm in width.* (Figure 18)

Fragments of stems, under 0,5 cm in width are frequent in the matrix. Lengths of from under a centimetre to up to about 10 cm occur. These obviously exhibit features of external form, for a leaf whorl is present at every node. This means that no nodal markings are visible. Each leaf whorl is narrowest at the node where it is attached, and gradually widens to the mouth of the leaf sheath from where free leaf segments curve upwards and usually inwards. Thus the fused bases of each leaf whorl form an enveloping cup-like leaf-sheath



round an internode. The sheath, because of its greater width at the mouth, stands away slightly from the internode and thus gives a characteristic form to the stem as a whole. Usually only few leaf segments are present on each sheath, a majority of these probably having been lost before, or during, fossilization.

Twelve of these narrow stem portions were measured. The parameters obtained are summarized as follows:

- (a) Overall stem length: limits 2–7,5 cm: mean 4,0 cm.
- (b) Leaf sheath length: limits 5–7,5 mm: mean 6,5 mm; (measured from narrowest point of the stem — the node — to the mouth of the sheath).
- (c) Leaf sheath width at point of attachment to stem: limits 1,3–3,0 mm: mean 2,4 mm;
- (d) Leaf sheath width at mouth: limits 2,7–4,0 mm: mean 3,6 mm.

The maximum number of leaves visible at any single node was seven, which number appeared to span, without any break, the diameter of a flattened narrow stem, thus suggesting the total number of leaves at a node was probably about fourteen.

(v) *Nodal markings.* (Figures 6, 7, 9, 14, 23, 28, 29)

On all the stems considered so far, the nodal markings appear to be of the same general pattern, but the details vary according to the quality of the fossil and whether this is an impression or an incrustation, from stem to stem, node to node on the same stem, and sometimes from one side of a node to the other.

Where the nodal markings are seen from what appears to be the external stem surface they consist of two parallel horizontal lines that extend across the stem and demarcate the depth of the nodal area. Between these lines are a series of evenly placed, more or less oval, or arched, flat or slightly depressed scars. In the best specimens each scar carries at one end a small, often slightly raised, sometimes flat or depressed, mark. Each oval scar is separated from the one to left and right of it by a narrow vertical furrow or depression, the shoulders of which are raised to form two slightly raised ridges that border the furrow. Usually the furrows that separate the oval scars extend from the nodal area on to one of the adjacent internodes more pronouncedly than on to the other. It is on the two raised ridges that border each of these furrows that cellular texture (usually isodiametric or slightly oblong cells) is sometimes visible. The internode that does not show the more pronounced furrows is usually almost smooth, but may sometimes show faint cellular markings also.

It seems that these nodal markings are exposed when the leaf-sheath of fused leaf bases is lost. Each oval scar appears to be the area of attachment of a leaf, and the raised mark within it the position at which a vascular strand entered the leaf. It is difficult to be certain whether these vascular scars were basal or apical on the scar. By consideration of other stem markings it seems reasonable to conclude that the internode with more pronounced furrows and ridges was likely to have been

the meristematic base of the internode above the node that, in the living plant, was covered and protected by the fused bases of the leaves. The lower of the two parallel lines demarcating the area of the node is likely thus to represent the lower line of attachment of the leaf whorl, and the more or less smooth appearance of the internode below probably results from the continuity during development of this internode and the leaf sheath. If this interpretation is accepted then the vascular scars are situated at the upper ends of the leaf scars. This then permits orientation of most of the fossil stem fragments and allows more valid comparisons to be made between them. In some cases the impressions appear to show nodal structure from the inner surface. Here the nodal markings are less clear and thus more difficult to interpret.

(vi) *Branch scars.* (Figure 12)

In a few stem fragments, one or two depressed areas elliptic to almost circular in outline occur above or below a node. When more than one is present they lie in the same horizontal line and are suggestive of scars left where branches have emerged. If the interpretation of nodal markings suggested above is followed, these branch scars lie above the node, which is not, however, in keeping with the branching of extant equisetalean stems, where, when the leaf whorl is removed, the branch scars lie on the line of the nodal plate. Nor do they agree with the photograph shown by Lacey and Huard-Moine, 1966 (Pl. 1, 5.) in which a branch stem appears attached directly at a node. So far no branches that clearly show attachment to larger stems have been seen among the fossils from Lidgetton.

(vii) *Stem ridges.* (Figure 13)

The number of ridges on the internodal portions of the stem fragments varies widely, and counts from 6–44 have been made. In counting it is often difficult to interpret ridges with accuracy. As might be anticipated, ridge number appears to relate to stem width, the widest rhizomal (?) portions carrying the most ridges.

The ridges of one stem internode generally appear to alternate with those of the internodes above and below, but it is difficult to interpret their courses accurately. At this stage it is best to state that there is often alternation, but there may be variation.

(viii) *Uncertain features.* (Figures 11, 26, 27)

One specimen, a fragment of stem 3,5 cm in length, 0,6 cm in width, clearly ridged and furrowed and with part of a node evident, carries a number of narrowly elliptic, slightly depressed scars orientated with their longitudinal axes parallel with the ridging of the stem. Immediately above the node these scars lie in a horizontal row, but on the internode they are scattered: 25 scars are present in all. Each has a fine raised line running down the longitudinal axis of symmetry. Some appear to be reversed in relation to others. It may be that these are the marks of attachment of the dichotomously branched, non-articulated, smooth surfaced outgrowths so frequent in the matrix that have been interpreted as roots, but this is



far too uncertain to be suggested except very tentatively. That they represent points of attachment of fertile units is almost as unlikely, since in the equisetalean plants both reproductive branches, and sporangiophores, are usually whorled and at nodes.

Seven stem fragments (length limits 13–30 mm; mean 21 mm; max. width limits 7–15 mm; mean 11 mm) appear to represent the apices of what must have been actively growing stems, for in each case the tip is overarched by a “brush” of fine leaves arising from successive nodes that are closely placed with only short internodes between them. In each of three specimens, 5, 5 and 6 nodes could be detected from the base upwards before the closely packed leaves obliterated the outlines. The clearest of these nodes were measured and were successively 3,5; 2,5; 2,5 mm long and 3,0; 3,5; 3,7 mm wide. The leaves are similar to those of the narrow stems described under (iv) above.

#### *Stems thought to exhibit internal features*

##### (i) *In the longitudinal plane.* (Figures 10, 20, 21, 22, also 2)

Many stem fragments were sorted from the stems that have been considered so far because of differences in the nature of the nodes and the markings present at these nodes. This new group comprises stems all of which fall within the length and width ranges described above. They were not grouped into the same size ranges, however, since this did not seem useful.

These stem fossils consist of a series of vertical parallel ribs that run the length of an internode and which are separated from one another by an equivalent number of long narrow areas occupied by matrix. At each node the ribs link to form a continuous transverse band approximately the same depth as the nodes in the fossils dealt with above, before continuing again as ribs through the next successive internode. There is no alternation of ribs from one internode to the next; instead they follow in the same line. Occasionally, however, two adjacent ribs become confluent in the next internode, thus reducing the overall number. The nodes do not exhibit markings of the kind represented in stems grouped above. Instead the ribs often show fine longitudinal striations some of which, at a node, turn almost horizontally, before turning again to pass out into the adjacent rib of the next internode, while others continue through the node without altering direction. Some specimens, in addition to these fine striations, show imprints of oblong cells on the flanks of the ridges. These are the only markings represented.

These fossils are interpreted as follows. Presumably as burial of the plant fragments takes place, the stems are flattened. During and prior to this process, partial or complete infilling of the central pith cavity must occur. This central cavity, with collapse, if not decay, of the lining cells (presumably parenchymatous tissue), must have an inner ridged and furrowed form similar to that of the outer stem surface. After fossilization and subsequent exposure, shearing of the shale must take place through the tissue of the stem at a point that either exposes the inner stem surface adjacent to the pith cavi-

ty or, more likely, that passes through the tissue of the stem itself, thus exposing as fine lines the course of the cells through internode and node.

##### (ii) *In the transverse plane.* (Figures 16, 17)

In frequent association with the equisetalean stem fragments are circular plates showing a uniform and usually well defined pattern of small isodiametric cells. These plates are either flat, slightly convex, or occasionally just concave. Usually they are complete, sometimes they lack a central area, occasionally only a sector is visible. Thirty complete discs were located and measured: ten more were sufficiently complete for measurement to be possible. The size range of these forty discs was from 5,0–16,0 mm: mean 9,4 mm in diameter. Two specimens were found in which a disc of this kind formed the transverse plate at a stem node (see Figure 15 for one of these). They are interpreted as being the transverse nodal diaphragms that became detached from the stems with partial decay or damage. This interpretation appears to be supported by the finding of three specimens in which two diaphragms occurred at different levels in the matrix, the one partly covering the other. One specimen consists of two diaphragms, separate from one another, lying close together (Figure 16). Another specimen comprises a portion of a stem, partially broken up, with seven diaphragms associated with it: these occur in two groups of two (in each of which the plates partially overlay one another) and three isolated, partially hidden units.

#### **Leaves** (Figures 4, 18, 24, 25)

The free leaf segments on both the narrow stems and the stem apices appear to be of the same type. They are from 5–10 mm in length and taper gradually to an acute apex from a base about one millimetre in width. With the exception of one isolated leaf sheath in which the free segments are well spread from one another, each showing clearly what appears to be a central unbranched midvein (not illustrated), all free leaf segments appear to be without defined veins. The margins are entire and unspecialized. The apparent absence of veins from the leaf segments needs explanation in view of the marks on the leaf scars that are interpreted as vascular scars. It is possible the vascular traces terminated soon after entering the leaf sheath and did not continue into the leaf segments.

#### **Roots** (Figures 3, 30)

Structures that have been interpreted as roots (see (i) p. 44) were smooth-surfaced and completely lacked nodes and internodes. Fragments are extremely frequent and are scattered throughout much of the matrix. They are least common in those specimens that carry straight lengths of stem interpreted as being aerial in growth. Some portions as much as 6 cm in length and 3 mm in width, narrowing gradually towards the tip, are present. These branch frequently and irregularly along their length, the angle of each branch being usually less than 90° (often  $\pm 45^\circ$ ) to the main axis.



These branches re-branch repeatedly, the ultimate or penultimate forkings always being dichotomous. There is no evidence whatever of appendages having been borne upon these structures, nor have wider, more robust branches that could have been major axes of a smooth-stemmed plant been found.

#### COMPARISON OF STRUCTURAL FEATURES OF EQUISETALEAN PLANT FOSSILS WITH THOSE OF AN EXTANT SPECIES OF *EQUISETUM*

In Southern Africa one species of articulate is extant. This is *Equisetum ramosissimum* Desf., a perennial herb with an underground rhizome dark brown in colour and erect, straight aerial stems that carry, at each node, a whorl of leaves, the bases of which are fused marginally to sheath the stem while the free segments are elongate, filiform, early drying and thus readily broken off. When the elongate apices do break, they leave minute fragments attached to the sheath that are sometimes erroneously interpreted as representing the full leaf length.

By comparison of features of this plant with those of the equisetalean fossils from Lidgetton, it is not intended to imply that relationship exists between them, apart from the fact that all fall within the division Sphenopsida. It seemed possible that by study of a living species of *Equisetum*, some information relevant to the interpretation of structural features of the fossils might be obtained.

The following points have emerged:

- (i) Plants of *Equisetum ramosissimum* growing in 30–40 cm of water above a muddy substrate produced many adventitious roots. These roots were smooth and showed no evidence of the ridges and furrows that characterized the stem internodes. Branches to these roots were frequent, and irregularly placed. The ultimate divisions were difficult to trace but did not appear dichotomous. Main roots were developed in a circle from below a stem node, never along the internodes.
- (ii) When a leaf whorl was removed from an aerial stem, a narrow zone of markings somewhat similar to those on the fossil stems considered above, but much more faintly marked, was revealed. The leaf whorl did not abscise cleanly and some epidermal tissue from the internode below was removed with it (Figure 34). The vascular traces appeared to enter the leaves high on the nodal scar.
- (iii) On older parts of the living rhizome the leaf whorls were almost entirely decayed away leaving an irregular ledge at the node: on younger parts the leaf whorls were intact.
- (iv) Internodes of the rhizome were far less obviously ridged and furrowed than were internodes of the aerial stems.
- (v) Nodal diaphragms carried isodiametric cellular markings.

#### DISCUSSION

The parts of equisetalean fossil plants described in this paper have been interpreted as large leafless rhizomes carrying well branched roots; portions of leafless, unbranched, narrower stems that presumably were aerial; apices of these stems that carried simple linear leaves from the nodes, each leaf possibly with a single midvein but usually appearing to lack venation; fragments of narrow stems (presumably ultimate branchlets of larger stems) with a whorl of leaves of the simple type described above at each node, these leaves being fused by their bases into a cup-like sheath that enveloped the stem, but stood away from it at the widened mouth; fragments of stems broken in half, or possibly in tangential section, to reveal the internal anastomoses of the conducting tissues; finally, displaced nodal diaphragms.

Two diaphragms have been found in position (each at the node of an isolated stem fragment), and roots appear to be in direct connection with stem nodes, but apart from these instances, no evidence of direct relationship of plant parts has been obtained. At the same time no discordant evidence exists to suggest that these parts may not, in life, have been united into organisms of one kind, possibly a single species, almost certainly a single genus.

Despite careful searching, no indications whatever of reproductive organs have been detected. Groups of sporangia of the *Arberiella* type are not infrequent in the matrix but these must have been detached from scale-leaves of *Eretmonia*, since scale-leaves bearing sporangia are occasionally present.

The equisetalean vegetative fragments alone are, however, sufficiently characteristic to attempt identification. The large size of some of the rhizomes suggests a reasonable duration of growth for these. Presumably the plants of which they formed part were perennial. This is further supported by anatomical evidence obtained from acetate "pulls", one of which (Figure 19) shows what is almost certainly secondary conducting tissue in a fragment of stem that was sectioned transversely.

Broad comparison of the fossils with plants of an extant species of *Equisetum* suggests that the Lidgetton fragments probably came from plants constructed on the same general pattern as is *Equisetum*, but which were very much larger and which underwent secondary thickening. Many of the widest stems were probably rhizomes developed under water. This might afford explanation of why leaf whorls are completely lacking from the wider stems (rhizomes), whereas they are present on the slender branchlets. The wide stems must have attained their size over a reasonably long period of growth. Thus, firstly, the internodes must have become fixed in length, the meristematic zone at the internodal base, by this time, having probably lost the capacity for cell division. Secondly, after so long a period in water, and with increase in rhizome width, the leaf whorl probably fragmented and decayed away, leaving the nodal markings clearly defined.



The Lidgetton stems relate closely to leafless sphenopsid stems of Middle to Upper Ecca age from Wankie, Rhodesia that were described, but not assigned to any particular genus, by Lacey and Huard-Moine (1966). These authors commented that in their stems the longitudinal striations appeared to alternate at the nodes. They ascribed this to possible twisting of the specimen before compression. Some evidence for alternation of striations (ridges) from one internode to the next has been obtained from the Lidgetton fossils, so possibly this is characteristic of these plants and not the result of twisting. If so, it is another point of relationship with *Equisetum*.

*Paracalamites* is a form genus to which the isolated stem fragments from Lidgetton could be referred. However, there seems little to be gained by this, for there appears to be confusion as to the path of the ridges through the nodes in stems referred to it, for Rigby (1966) states:

"Zalessky erected this genus [*Paracalamites*] in 1932 [sic] to include Permian articulate stems and rhizomes having the ribs of the pith cast opposite at each node, as in *Asterocalamites*, not alternating."

Later Rigby continues:

"From *Paracalamites* sp. described below it is thought that ribs dichotomise and recombine with adjacent ribs at nodes rather than dichotomise and recombine with themselves as in *Asterocalamites* . . ."

He then goes on to describe the specimen as follows:

"Ribbing is distinct in only a few places. It is opposite at nodes on both the inner and outer surfaces."

There is some slight resemblance to *Stellotheca robusta* (Feistmantel) Surange and Prakash in the cup-like base to the leaf whorl (Rigby, 1966, p. 48), but there the relationship ends.

Perhaps one of the most valuable contributions that will be derived from study of the Lidgetton sphenopsids will prove to be the better understanding of nodal markings and nodal and internodal structures that these fossils provide. With such information available, re-study of Du Toit's (1927) Triassic sphenopsids

should be undertaken. Comparisons should also be made against the types of already established genera and species. In this way definite conclusions may be possible as to whether the Lidgetton fossils are distinctive and worthy of description as new, as appears to be the case at present, or whether they should be referred to a genus and species, or perhaps to genera and species, already established. There seems little doubt that the affinities of these Lidgetton specimens lie with Equisetales rather than with Sphenophyllales, and with Equisetaceae rather than with Calamitaceae. It is tempting to take this further and to suggest the relationship lies with *Equisetites*, for Andrews, (1961, pp. 274-5) makes the following statements that suggest this possibility:

"Stem impressions of *Equisetites* are distinguished from the calamitean plants partly by the fusion of the leaves into a sheath, and if the assumption that they are closely allied to *Equisetum* is correct, they attained an appreciably greater size than the living species." [of *Equisetum*].

"There are a few intriguing suggestions that plants closely akin to *Equisetum* did live in the late Paleozoic."

*Equisetum ramosissimum* comes in late summer to autumn. The strobili do not persist on the plants into spring. It may be that disruption of the Lidgetton plants prior to fossilization took place at a season when cones were not present. Nevertheless the matrix must be carefully studied for evidence of spores that could relate to the distinctive elater-bearing spores of living *Equisetum* species.

#### ACKNOWLEDGEMENTS

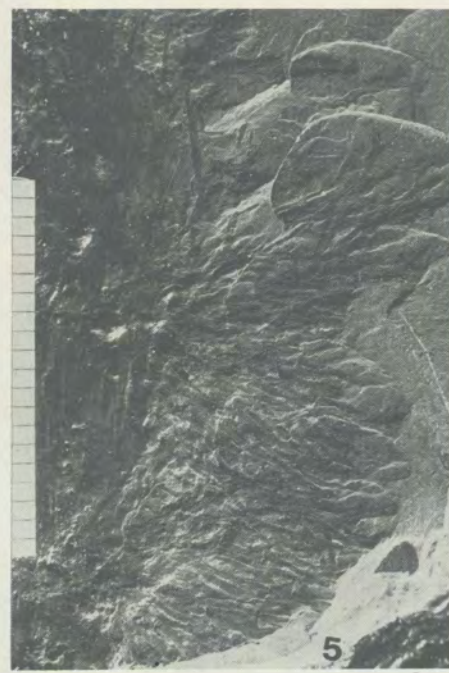
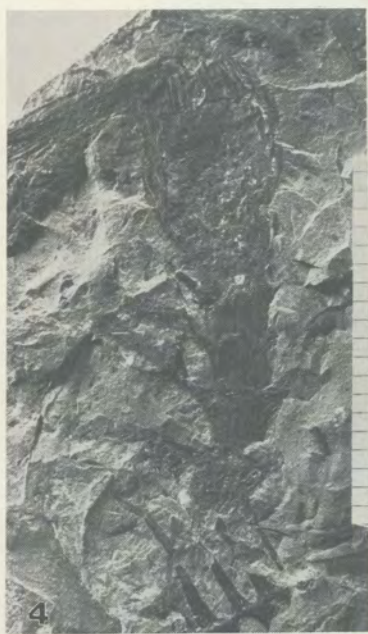
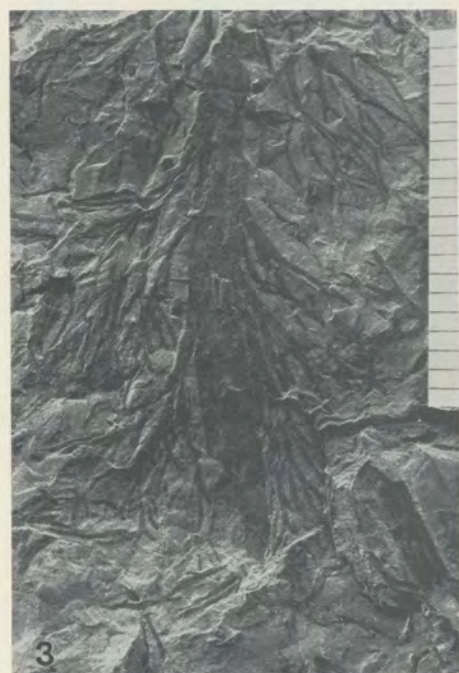
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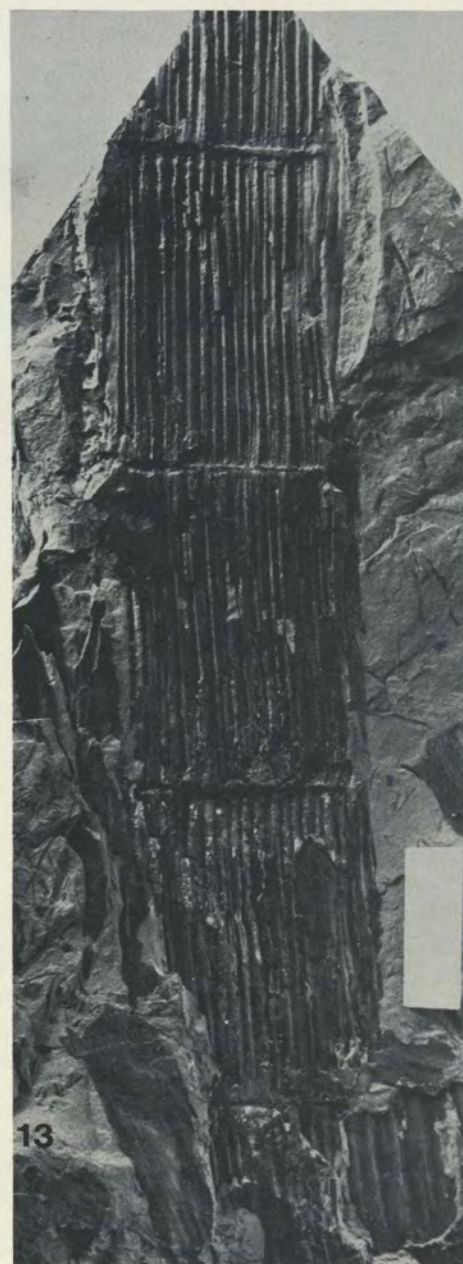
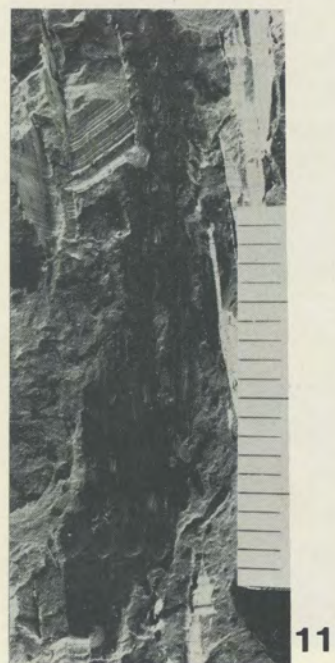
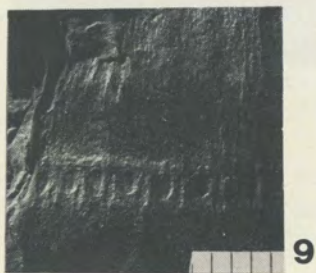
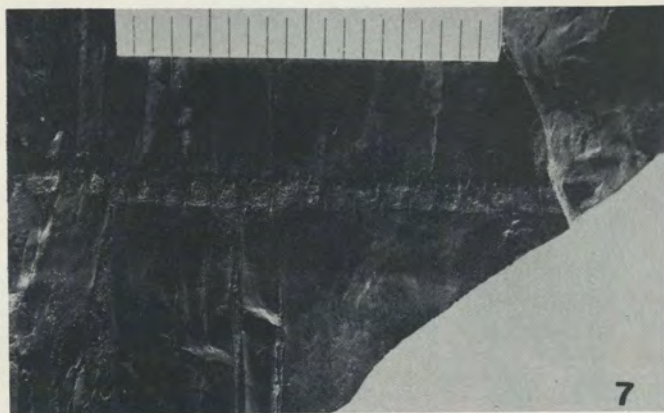


# PLATE I

Equisetalean plant fossils from Lidgetton (thought to be orientated as in life: except where otherwise stated stems are interpreted as being in external view).

- Figure 1. Portion of rhizome (?) showing, at left, apparent attachment of well branched, smooth, adventitious rootlets.
- Figure 2. Impression of another portion of rhizome, showing nodal markings seen from the internal surface. (Note that towards the top of the photograph the impression is overlain by sediment carrying vascular tissue — carbon present as a thin layer in which fine longitudinal markings that alternate with adjacent ribs at the node, may be discerned.)
- Figure 3. Portion of a root with lateral roots (note frequency of dichotomous branchings).
- Figure 4. Stem apex (note overarching leaves and below a series of nodes and internodes).
- Figure 5. Portion of rhizome (?) showing two successive nodes with adventitious rootlets developed from these.







**PLATE II**

Equisetalean plant fossils from Lidgetton (thought to be orientated as in life: except where otherwise stated, stems are interpreted as being in external view).

Figure 6. Stem fragment showing nodal markings at three successive nodes.

Figure 7. Stem fragment showing detail of nodal markings (note what are thought to be leaf scars, each with a vascular bundle scar (?) towards the top).

Figure 8. This fossil is tentatively interpreted as ribs of two successive internodes with the furrows between the ribs somewhat infilled. (But the node is narrow and without characteristic markings.) Such fossils have previously sometimes been interpreted as a stem node with an attached whorl of leaves which are free from one another, but this is thought to be incorrect.

Figure 9. Another stem fragment showing nodal markings.

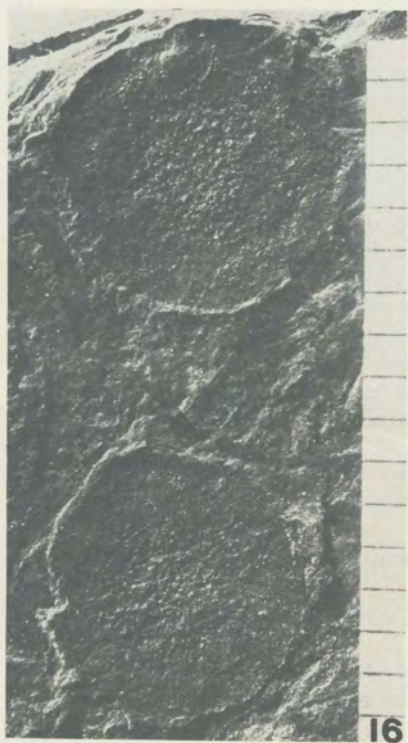
Figure 10. This fossil is thought to represent an internal cast or tangential section of a stem fragment. Ribs of successive internodes are linked by nodes which show a horizontal extension of tissue, and the occasional confluence of ribs. Markings associated with nodes as seen in external view are lacking.

Figure 11. Fragment of stem showing, at the base, four leaf scars of a node, and above, a series of scattered narrow-elliptic scars, some of which appear reversed in relation to the others.

Figure 12. Stem fragment showing a node with (above in the photograph) three (or four ?) elliptical or rounded depressions that are tentatively interpreted as branch scars.

Figure 13. A length of stem showing three whole and two parts of ridged and furrowed internodes that are separated by nodes, the markings of which are poorly defined: leaf whorls appear to be entirely lacking (carbon is present over some internodes).





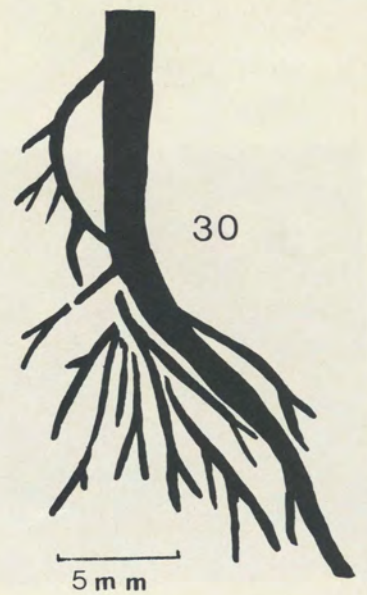
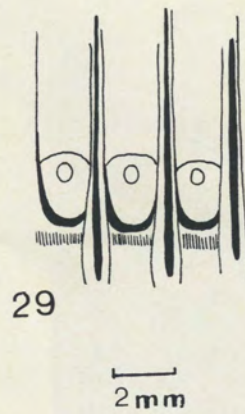
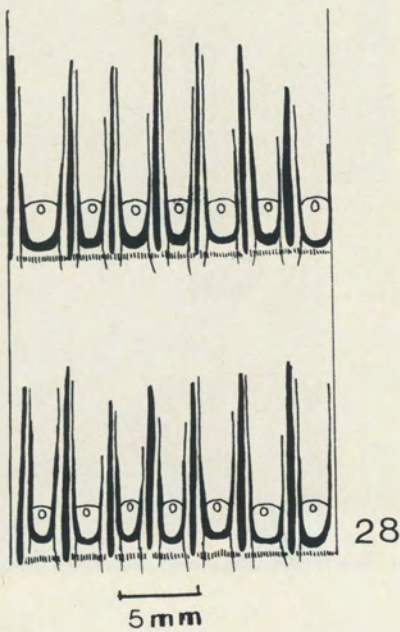
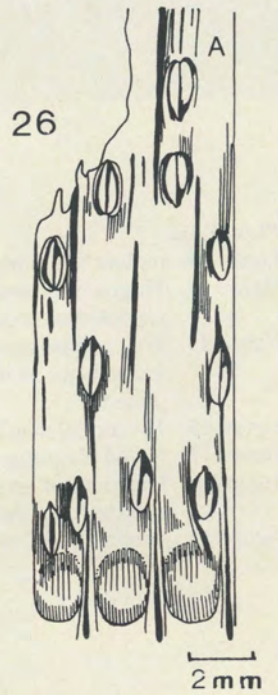
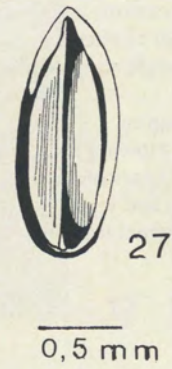
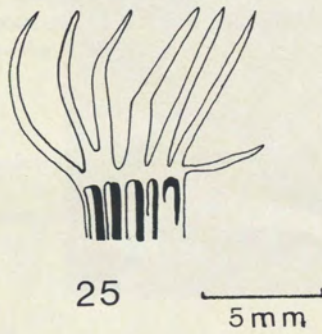
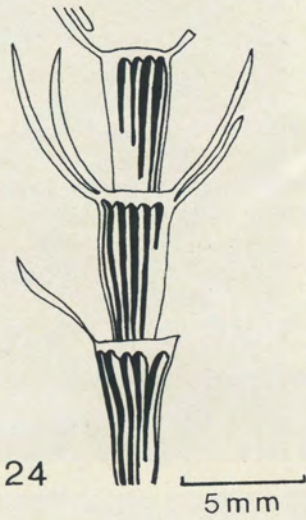
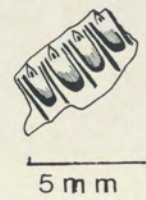
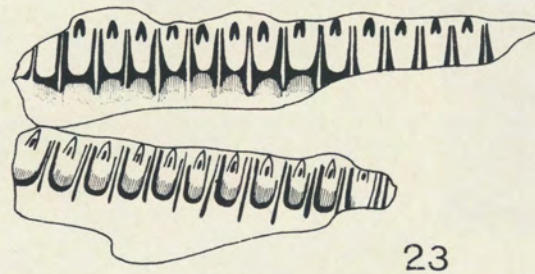
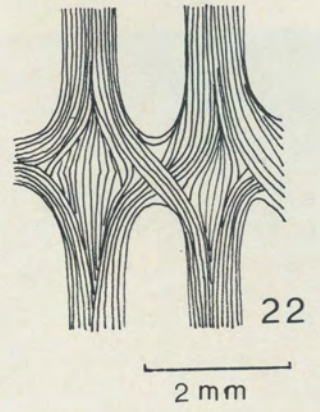
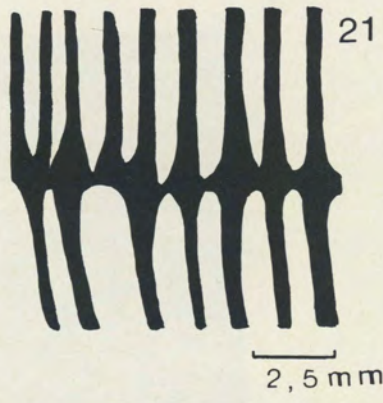


**PLATE III**

Equisetalean plant fossils from Lidgetton.

- Figure 14. Fragment of stem broken above node and infilled with matrix. The nodal markings are clear and depressions in the front face are represented as projections in the internal surface behind (seen above in the photograph).
- Figure 15. Fragmented stem or rhizome showing portion of a nodal diaphragm and ribs of two successive internodes with intervening node splayed out as though compressed from above (compare Du Toit no. 8329, 1927, where a similar structure is differently interpreted).
- Figure 16. Two nodal diaphragms.
- Figure 17. Nodal diaphragm showing cellular markings.
- Figure 18. Fragment of aerial branchlet showing three (possibly four) leaf whorls that are each wider at the mouth than the base. From the mouths free, linear, leaf segments arise.
- Figure 19. Acetate "pull" of etched transverse section of portion of stem (note cells in radial rows, presumably tracheids of secondary xylem).



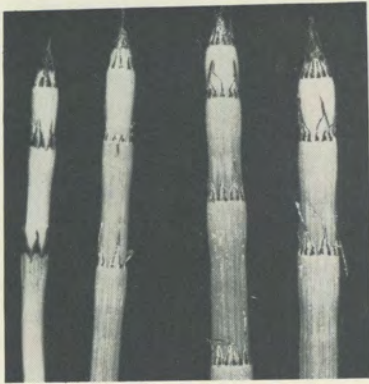




**PLATE IV.**

- Figure 20. Representation of course of ribs in fossil illustrated in Plate II, Figure 10. (Note occasional confluence of ribs at node.)
- Figure 21. Enlargement of node seen in Figure 20.
- Figure 22. Further enlargement of node showing the course of the fine striations visible in the carbon present.
- Figure 23. Representation of node illustrated in Plate III, Figure 14.
- Figure 24. Representation of portion of narrow branchlet illustrated in Plate III, Figure 18.
- Figure 25. Representation of a portion of a leaf whorl, showing fused leaf sheath and free leaf segments.
- Figure 26. Representation of the portion of stem illustrated in Plate II, Figure 11. (Note reversal of scars at A.)
- Figure 27. Enlargement of a single scar illustrated in Figure 26.
- Figure 28. Representation of nodal markings (external view).
- Figure 29. Enlargement of nodal markings shown in Figure 28. (The dark vertical lines represent depressions, the white areas adjacent to them raised shoulders: between each depression is a leaf scar with a vascular scar asymmetrically placed.)
- Figure 30. Representation of a portion of a root. (Note the numerous dichotomous branchings.)



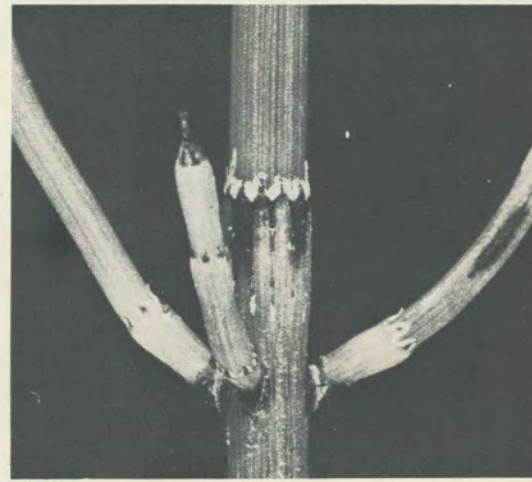


31

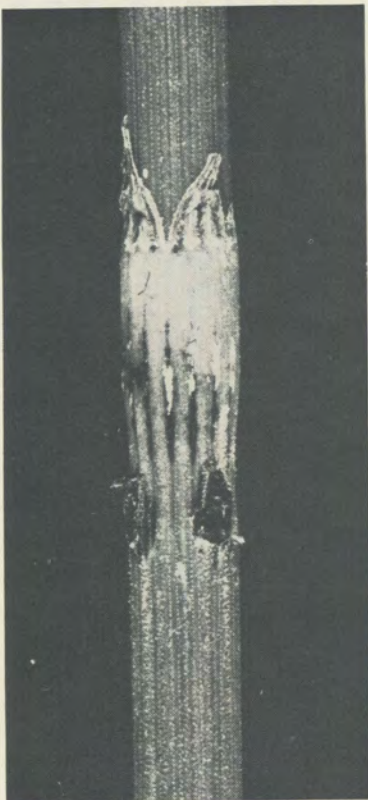
31, 36 — 5 mm

37 — 3 mm

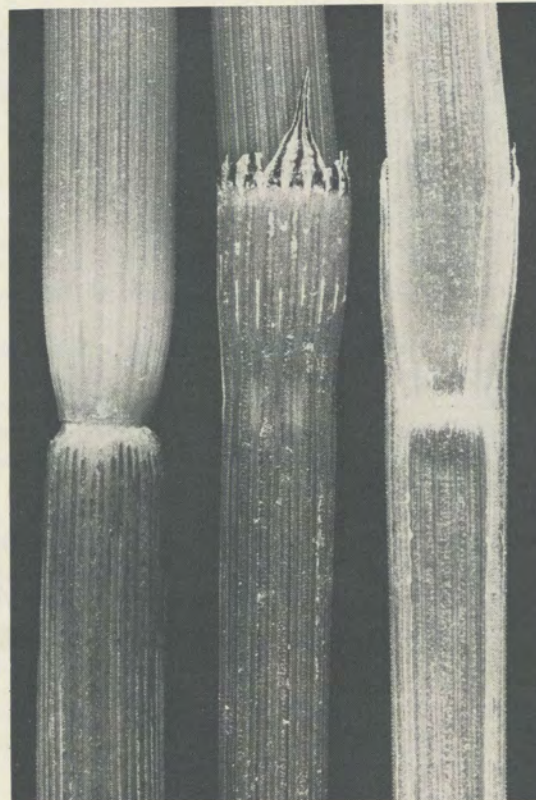
32-35 — 2 mm



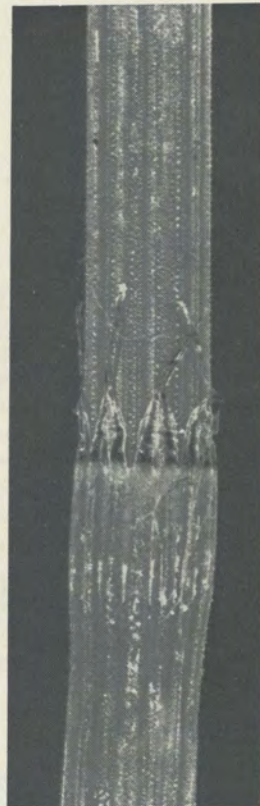
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33



34



35



36



37



**PLATE V**

*Equisetum ramosissimum* Desf.

Figure 31. Stem apices.

Figure 32. Portion of stem showing node with whorled lateral branches.

Figure 33. Portion of stem showing node with branch scars.

Figure 34. Stem nodes: left, with leaf whorl removed (note that fragments of internodal epidermis have come away with the leaf whorl); centre, with leaf whorl intact; right, in longitudinal section showing relative positions of nodal diaphragm and leaf whorl.

Figure 35. Stem node with leaf whorl showing long, dry attenuate apices to leaves.

Figure 36. Portion of rhizome showing leaf whorls and adventitious roots developed from the nodes (note the absence of clearly defined ridges and furrows).

Figure 37. Enlargement of portion of rhizome shown in Figure 6 (note branching of adventitious roots as they leave the rhizome).



## ON SOME "NORTHERN" ELEMENTS IN THE LOWER GONDWANA FLORA OF VEREENIGING, TRANSVAAL

by

S. F. le Roux†

## ABSTRACT

A small assemblage of plant elements from the Lower Permian of Vereeniging, in the southern Transvaal, is described here. The assemblage is constituted of form-genera normally only found in the palaeofloristic regions of the northern hemisphere. The genera concerned are: *Pecopteris* (*Asterotheca*), *Cladophlebis*, *Sphenophyllum* and *Psymphyllum*. The intermingling of these "Northern" elements with the *Glossopteris* flora of Vereeniging serves to illustrate the mixed nature of this flora. Reference is made to similar mixed Gondwana floras elsewhere in Africa and also in South America.

## INTRODUCTION

The specimens described in this paper represent plants belonging to genera of the northern hemisphere. Hence they are frequently referred to as "Northern" elements. Their occurrence at Vereeniging is of special interest since such elements are not characteristic of the Lower Gondwana flora of this locality. The genera concerned are: *Pecopteris* (*Asterotheca*), *Cladophlebis*, *Sphenophyllum* and *Psymphyllum*.

The type material consists of impressions in a fine-grained matrix and no organic matter remains. Identification is consequently based on external morphology only. The plant remains come from a rich fossiliferous horizon in the Lower Permian Coal-measures of Vereeniging. The stratum concerned is composed of a soft laminated clay which is exposed at Leeuwkuil, a famous site situated about 6 km south of the town. The specimens concerned come from a zone known as Layer A, Quarry No. 2, Leeuwkuil (Le Roux, 1963). The material is now housed in the museum of the Bernard Price Institute for Palaeontological Research at the University of the Witwatersrand, Johannesburg.

## DESCRIPTION OF MATERIAL

## PTEROPSIDA OF UNCERTAIN SYSTEMATIC POSITION

Genus *Pecopteris* Brongniart

This genus includes plants with fern-like foliage which may show similarity in gross morphological features in sterile fronds. In the absence of reproductive organs it is impossible to establish the natural affinities of such plants, however. Some pecopterids are known to have borne seeds and were therefore probably pteridospermous plants. On the other hand some species bore marattiaceous sporangia and are referred to the genus *Asterotheca*. Where both sterile and fertile

fronds are known to occur on the same plant the two genera are combined in the name *Pecopteris* (*Asterotheca*), with the genus *Pecopteris* taking priority according to the rules of nomenclature.

*Pecopteris* (*Asterotheca*) *singeri* Archangelsky

Plate I, Figures 1, 2 and 3

This species was originally described from the Lower Permian of Argentina by Archangelsky (1958). A more detailed description was subsequently given by Archangelsky and De la Sota (1960). More recently a plant from Wankie, Rhodesia, was referred to this species by Huard-Moine (1964) and Lacey and Huard-Moine (1966).

## Material

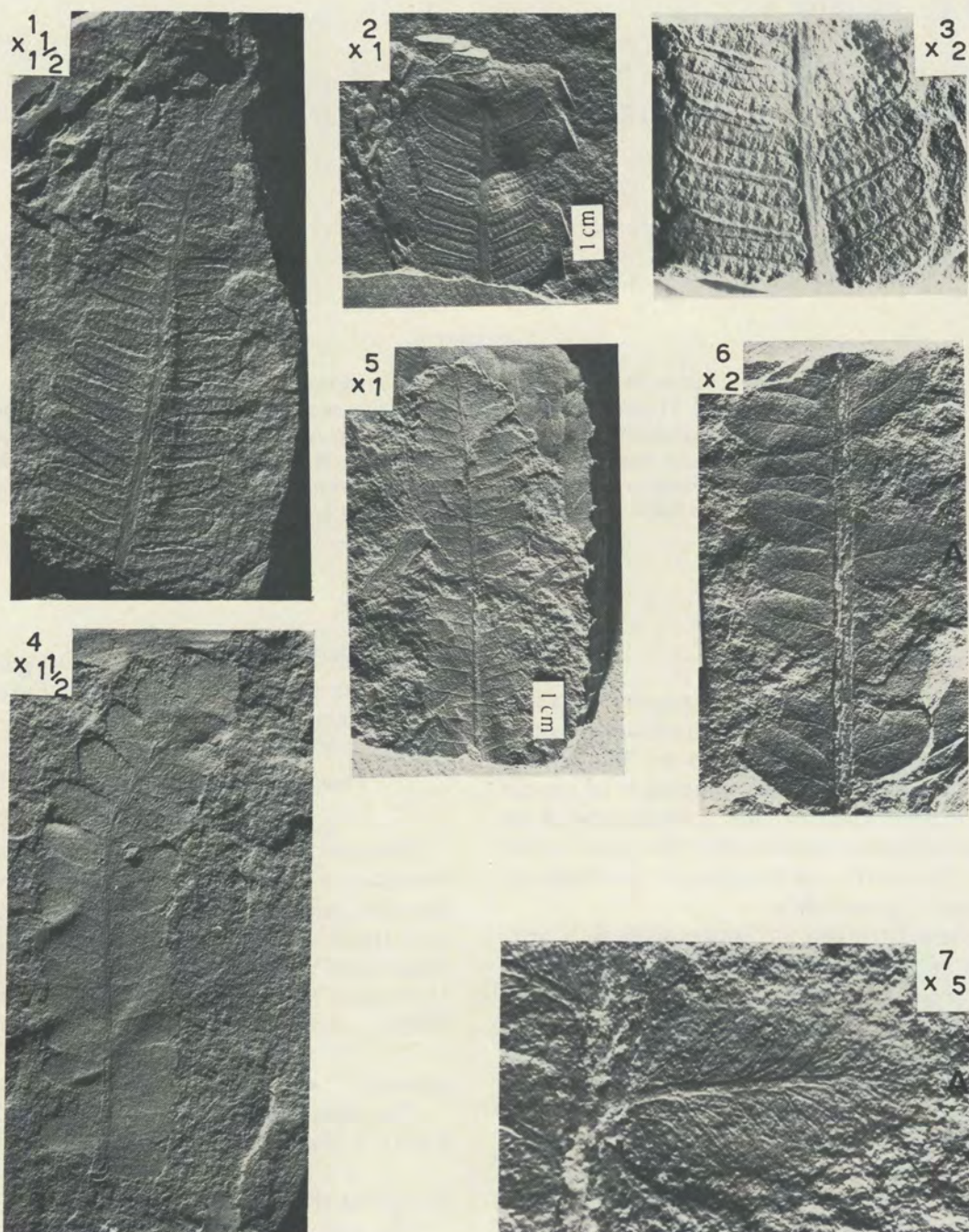
The specimens available for study are marked: PAS/1–3 (Figures 1, 2 and 3), PAS/4, 5 (not figured).

## Description (Figures 1–3)

The pinna is acuminate pointed and terminates in an elongated wedge-shaped lobe. The pinnules are obtusely pointed and are attached by the whole broad base to the rachis of the pinna. The pinnules are alternately placed and inserted at an angle of approximately 70 degrees to the rachis, which has a width of 1.5 mm at its maximum. Opposite rows of pinnules are sometimes of unequal length. The maximum length of a pinnule is 13 mm and the width at the base is 5 mm. The pinnules are slightly decurrent. The margins are more or less parallel in the apical region, but slightly curved near the base. There is a strong median vein traversing the pinnule. Closely-spaced synangia are borne along the margins of the pinnules on either side of the median vein. The synangia are oval to sub-circular in shape, numbering 9–10 on either side; each synangium having a diameter of 1–2 mm. The nature of sterile pinnules is unknown at present.

†Deceased 2 August, 1976





# **PLATE I**

*Pecopteris (Asterotheca) singeri* Archangelsky.

Figure 1. Apical portion of a fertile pinna showing broad base of pinnules and prominent median vein. (Magnification X  $1\frac{1}{2}$ .)

Figure 2. Fragment of a fertile pinna showing the arrangement of the sori on the pinnules. (Natural size.)

Figure 3. The same specimen as shown in Figure 2 enlarged twice to show more detail of the sori.

*Pecopteris (Asterotheca) cf. plumsteadiae* Huard-Moine.

Figure 4. Apical portion of a sterile pinna showing flexuous nature of the pinna and obtusely pointed apex. (Magnification X  $1\frac{1}{2}$ .)

Figure 5. Portion of a sterile pinna showing slightly decurrent median veins, forked secondary veins and parallel sides of the pinnules. (Natural size.)

*Cladophlebis cf. nebbensis* Brongniart.

Figure 6. Portion of a sterile pinna showing shape and arrangement of the pinnules (Magnification X 2.)

Figure 7. The pinnule at "A" in Figure 6 magnified 5 times to show the venation.



### Comparisons and discussions

A close comparison is possible between the new plant and a fertile pecopterid from Wankie, referred to *Pecopteris (Asterotheca) singeri* Archangelsky by Huard-Moine (1964) and Lacey and Huard-Moine (1966). With the exception of a small difference in the size of the pinnae of the two plants, they seem to be identical in other respects. The same remarks seem valid when comparing the Vereeniging plant with the Argentinian type material described by Archangelsky (1958) and Archangelsky and De la Sota (1960). Unfortunately a comparison with regard to sterile pinnules has not been possible owing to the lack of such specimens in the case of the Vereeniging plant. In view of the strikingly close resemblance between the fertile pinnules of the latter and those of *Pecopteris (Asterotheca) singeri* there seems to be little doubt that the two plants are specifically identical.

*Pecopteris (Asterotheca) plumsteadiae* Huard-Moine

This species was first described from Wankie by Huard-Moine (1964).

*Pecopteris (Asterotheca) cf. plumsteadiae* Huard-Moine

Figures 4 and 5

### Material

The specimens available for study are: PAP/1,2 (Figures 4 and 5), PAP/3 (not figured).

*Description* (Based on sterile pinnae only. See Plate I, Figures 4 and 5).

The pinna is flexuous and terminates rather abruptly in a bluntly-pointed lobe. The pinnules have rounded apices and parallel sides. The pinnules are alternately placed and attached nearly at right angles to the rachis. The maximum size of a pinnule is 10 mm long and 4 mm wide. The primary vein is slightly decurrent and the secondary veins are given off obliquely from it. The veins fork once and there are normally 5 secondary veins on either side of the median vein.

### Comparisons and discussions

The superficial features of the plant described here seem to be very similar to those of a new pecopterid described from Wankie by Huard-Moine (1964). Since no fertile specimens are available of the Vereeniging plant, a closer comparison between the two plants concerned is not possible. Under the circumstances it is therefore proposed to refer the new plant provisionally to the Wankie species.

Genus *Cladophlebis* Brongniart

Some fragmentary remains of a fern-like plant, found in Lower Gondwana (Middle-Ecca) sandstone near Vereeniging, were first recorded by Seward and Leslie (1908), who identified the plant as *Callipteridium* sp, but at the same time remarked that it closely resembled *Cladophlebis roylei* Arber. Recently Plumstead (1961, 1966a, 1969) mentioned that the genus was represented in the Vereeniging flora. No examples of

such plants were figured or described, however, by the latter author.

*Cladophlebis cf. nebbensis* Brongniart

Figures 6 and 7

### Material

The specimens available for study are marked: CLA/1 (Figure 6); CLA/2 (not figured).

*Description* (Figures 6 and 7)

The pinnules are obtusely pointed and placed alternately at a wide angle to the strong rachis of the pinna. The margins are entire and nearly parallel. The pinnules are 7–9 mm long and 3–5 mm wide, and are attached by the whole width of the base. The primary vein is slightly decurrent and terminates before reaching the extreme end of the pinnule. The secondary veins are given off obliquely and fork once.

### Comparisons and discussions

The specimen figured here is a portion of a sterile pinna which shows a very strong resemblance to a plant recorded from Wankie, Rhodesia, and described by Walton (1929) as *Cladophlebis* sp. Supplementary material from the same locality was subsequently referred to *C. cf. nebbensis* Brongniart by Huard-Moine (1964) and Lacey and Huard-Moine (1966). The Vereeniging plant is found to be identical to the Wankie species with respect to gross morphology and it is therefore proposed to apply the same specific name to the former plant.

## SPHENOPHYLLALES

Genus *Sphenophyllum* Brongniart

Plants belonging to this genus form a minor constituent in the Vereeniging fossil flora. The occurrence of such plants in this flora was mentioned by Plumstead (1961, 1966a, 1966b) but no actual specimens were described.

The scanty remains of a single species is described here for the first time.

*Sphenophyllum cf. thonii* Mahr

Plate II, Figures 8, 9, 10

### Material

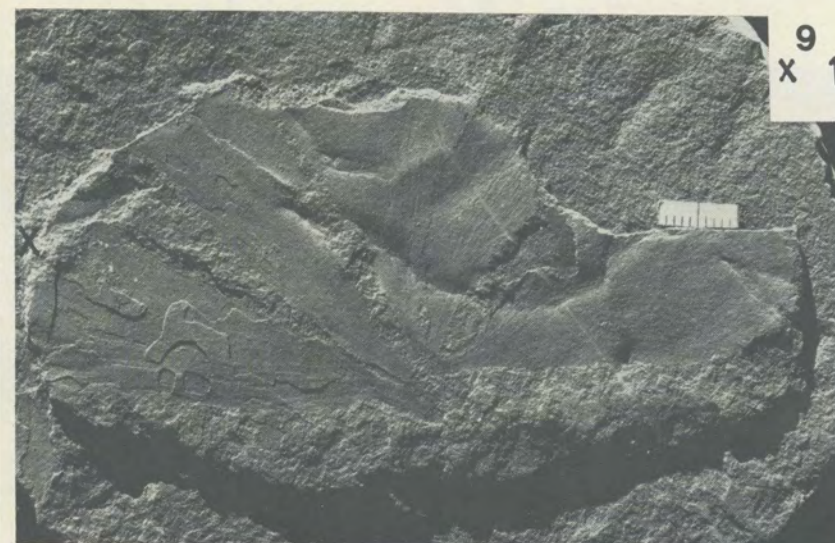
The following specimens are available for study: SPHY/1 (Figure 10), SPHY/2 and SPHY/2a (counterparts — Figures 8 and 9).

*Description* (Figures 8–10)

*Specimen I* (Figure 10)

This specimen shows a portion of a shoot with two incomplete whorls of leaves spread out in one plane and attached to a slender axis having a diameter of 2 mm. The leaves are triangular in shape with the lateral margins more or less straight and the distal margin slightly curved. The lateral margins are entire and the corners are rounded. The leaves are 15 mm wide at the





# **PLATE II**

*Sphenophyllum* cf. *thonii* Mahr.

Figures 8 and 9. Counterparts showing a detached whorl of 5 leaves with indications of forked veins on some leaves. Note remnants of a sixth leaf superimposed on the leaf at "X". (Natural size.)

Figure 10. Two incomplete whorls of leaves on a portion of stem. Note the typical verticillate arrangement of the wedge-shaped leaves, and slender stem. (Natural size.)



apices and the overall length is 25 mm. The venation is obscure and cannot be made out.

#### *Specimens 2 and 2a* (Figures 8 and 9)

This fossil is preserved in two counterparts, showing a whorl of 5 leaves with indications of a possible sixth leaf overlying one of the outer leaves. The leaves are wedge-shaped and have a maximum width of 20 mm and a length of 50 mm. The nerves are very indistinct but two primary veins appear to enter the leaves at the base and by repeated forking produce many secondary veins spreading out fan-wise throughout the leaves.

#### *Comparisons and discussions*

The poor preservation of the specimen figured (Figure 10), does not permit a close comparison with any known species of *Sphenophyllum*. Considering the shape and size of the leaves there seems to be a resemblance to *S. thonii* var. *minor* Sterzel, a Cathaysian element recorded by Halle (1927) from the Shihotse flora of China. A similar comparison can be drawn between the Vereeniging plant and a similar species recorded from Wankie (Walton, 1929). Subsequent investigations of the Wankie flora by Huard-Moine (1965) and Lacey and Huard-Moine (1966) led these authors to the conclusion that there was little justification for Sterzel's institution of the varietal species *S. thonii* var. *minor*, and this name was consequently abandoned for the Wankie species in favour of *S. thonii* Mahr.

On the strength of the above conclusion the Vereeniging specimen is tentatively referred to *S. cf. thonii* Mahr.

The specimens in Figures 8 and 9 show some resemblance to *Benlightfootia mackii*, an element in the Wankie flora recorded by Lacey and Huard-Moine (1966). The characteristic notching of the leaves of that plant is completely absent in the Vereeniging specimen, however. The fossil is believed to represent a detached whorl of leaves which was possibly derived from a larger specimen of the same species of plant as that shown in Figure 10. It is, therefore, tentatively included in this description with some hesitation.

### ? GINKGOALES

#### Genus *Psygmyphyllum* Schimper

This genus was previously recorded from Vereeniging (Seward, 1903; Le Roux, 1970). Additional information concerning the genus was recently revealed by a new discovery. It is thought appropriate to include the description of this supplementary material in the present paper since *Psygmyphyllum* is essentially also a northern hemisphere genus.

#### *Psygmyphyllum kidstoni* Seward

Plate III, Figures 11 and 12

#### *Material*

The following specimens are available for study: PS/4 and PS/4a (counterparts — Figures 11 and 12).

#### *Description* (Figures 11 and 12)

The specimens described here represent counterparts showing a portion of a shoot bearing simple leaves on a very stout axis having a maximum width of 15 mm. The leaves are cuneate and the lamina is contracted into a long basal portion resembling a petiole. The leaves appear to be spirally arranged on the axis. The laminae are torn, making it difficult to determine the exact shape and degree of original lobing. The venation is badly preserved, but the veins can be seen to spread out from the base of the laminae and are repeatedly forked. No lateral anastomosis can be detected.

#### *Discussion and comparisons*

Compared with *P. kidstoni* the axis of the new specimen is much broader than that of Seward's type specimen. Furthermore the leaves of the latter are longer, more elongated and more distinctly lobed than those of the new specimen. It is believed that the difference between the two specimens could be due to the possibility that the type specimen was derived from the terminal end of a foliage shoot while the new specimen apparently represents a basal portion of a shoot of the same species of plant. An isolated, wedge-shaped leaf was previously recorded from Vereeniging (Le Roux, 1970) and at the time of its description was provisionally referred to *P. kidstoni*. The close resemblance of this leaf to those of the new specimen suggests a mutual parent plant and the latter is, therefore, referred to *P. kidstoni*.

### CONCLUSIONS AND DISCUSSION

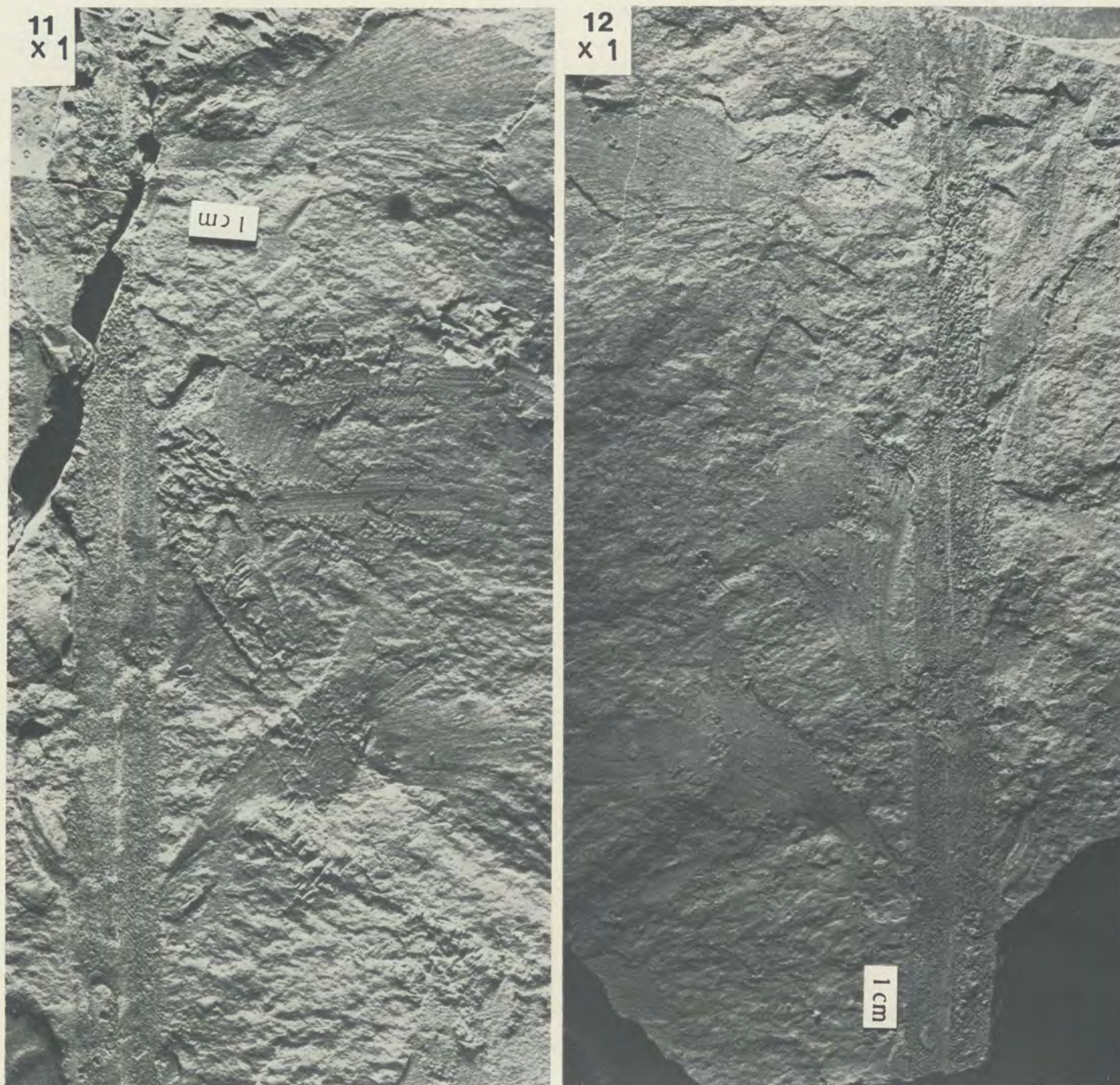
The intermingling of the *Glossopteris* flora of Vereeniging with northern elements has been known for some time (Le Roux, 1949). Recently Plumstead (1961, 1966a, 1969) discussed the significance of this fact in the light of recent discoveries at Vereeniging. Since she did not describe any of these elements the present description of an assemblage of such plants must be regarded as an attempt to fill this gap partly.

Similar examples of mixed floras are known to occur elsewhere in Africa and have been recorded by Walton (1929), Lacey and Huard-Moine (1966) and Teixeira (1950).

In South America Archangelsky (1958) and Archangelsky and De la Sota (1960) recorded northern elements intermingling with the Gondwana flora of Santa Cruz. Subsequently Arrondo (1972) gave a comprehensive list of plants recorded from the Golandrana formation of Santa Cruz, reflecting the large number of northern elements present in the Gondwana flora of Argentina.

The significance of northern elements in the Gondwana flora has been the subject of much discussion and has recently been summarised by Archangelsky (1967) in his discussion on the Permian flora of Argentina.





### PLATE III

*Psygmothylum kidstoni* Seward.

Figures 11 and 12. Portion of a foliage shoot showing strong woody axis and cuneate leaves in counterparts. (Natural size.)

### ACKNOWLEDGEMENTS

The author is very greatly indebted to Mrs. Heidi Anderson who made the photographs for the plates (except Figures 1 and 4 and Figures 8 and 9), and also for her invaluable assistance in other

respects.

Grateful thanks are also due to the management of the Rand Water Board for permission to collect on their property.

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## NOTES ON SOME GLOSSOPTERIS SPECIES FROM HAMMANSKRAAL (TRANSVAAL)\*

by

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## ABSTRACT

The study of *Glossopteris* began with the mistake that two half fronds were glued together as one and that specimen was chosen as the holotype of one of the first *Glossopteris* ever described, *Glossopteris browniana* var. *indica* Bngn. The mistake led to confusion and even to distrust of the possibility of identifying *Glossopteris* species on frond impressions only. As most of the *Glossopteris* remains are such, and the literature from Brongniart onwards is mainly based on them, the frond morphography is bound to be the starting point of the classification. The present paper shows that (a) with the examination of greater numbers of specimens, it is possible to select the specific characters and to learn the individual variations and (b) identifications can only be based on the original descriptions and figures of the taxa.

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## INTRODUCTION

"Possibly it (*Glossopteris*) suffered more than any other common plant fossil in classification." Plumstead (1962), in Fossil Floras of Antarctica.

This sentence expresses a thought of which all palaeobotanists who have ever worked on Gondwanaland material were conscious. Many attempts were made to solve and clear the perplexity in the taxonomy of the *Glossopteridaceae*.

In 1965 Maheshwari summarised the problems and stressed that "the natural thing is to devise a classification based on the morphographic character" as "most of the Lower Gondwana fossils occur more frequently as (leaf) impressions". He gave directives for more precise circumscriptions of species.

Supporting Maheshwari, I add some particulars to the method and problems in the systematic studies of *Glossopteris* and illustrate them with examples. According to him the main reason for the confusion was "a complete lack of accepted criteria" on which to base the classification.

Another reason is that in the descriptions different authors do not always use the same expressions in the same meaning or the accompanying illustrations are not clear. In the last century the drawings were sometimes incorrect (Feismantel: "an evil which is not always under the control of the author", 1881b, Pl. XXXII A). Nowadays on the photographs the fine veins are sometimes blurred and unaccompanied by drawings. "Wenn spätere Autoren an etwa fehlenden Details der Abbildungen der Arbeiten von 1804 und 1820 Anstoss nahmen, so konnten sie nicht ahnen, das 150 Jahre später oft wesentlich weniger Details zeigende Abbildungen gegeben werden." (Remy, 1966, p. 4). The terms of morphographic characters and the method of description have to be standardized. Both photographs and accurate drawings should accompany the description (see Remy, 1966; Dilcher, 1974).

The main cause of the controversy is, however, that usually the authors did not refer to the original descriptions and figures of the species in their identifications.

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They used second or even later descriptions and in doing so they often added mistakes to those already existing.

If a considerable number of frond impressions are examined, it becomes clear that certain of them consistently display the same characters. These characters can be called specific characters, and the fronds of which they are typical represent a species. In this case the species is not an artificial taxon, although our knowledge is limited to the fronds of the plant assigned to such a species.

The specific characters are determined, preserved and inherited by genes. The morphological characters of any individual are reflections of a specific genetic composition. If constant and distinguishing characters can be found on any organ of plants, including the morphography of fronds, they follow the same genetic rule.

As most of the literature from Brongniart onwards is mainly based on frond impressions, their morphography is bound to be the starting point of the classification. Only knowing a species well as fronds can research proceed for further details of the classification.

When we find cuticles on fronds or fructifications and seeds attached to them, our knowledge of the species concerned improves, and we get closer to the reconstruction of a once-living organism. If taxonomy does not serve this goal, it has missed its essential purpose. It is possible that accumulating knowledge on the genus *Glossopteris* will lead to the separation of several groups of species on generic level. The species, however, will always remain the basis of any classification.

Unfortunately the ICBN is extremely vague when dealing with rules to be applied in palaeobotany. Its Article 3, Note 1, reads: "fossil plants are usually based on fragmentary specimens, and since the connection between these specimens can only rarely be proved, organ-genera and form-genera are distinguished as taxa within which species may be recognised and given names according to this Code." It does not give any directives as to which rules are applicable when "rare" connections are found. Do the newly described parts or organs take the name of the already known part, or should new form-genus names be created for them? When a fructification is attached to a frond, undoubtedly they were parts of the same individual plant. My opinion is that parts with proved connection can bear only one name, following the rule of priority.

Article 59 of ICBN unfortunately lumps fossil plants and fungi in one. The text, however, deals with fungi only with two or more states in their life cycle, and says: "The correct name of all states which are states of any one species is the earliest legitimate name typified by the perfect state." As vascular plants, and Glossopteridaceae with them, have no perfect or imperfect state, Article 59 is not applicable to them. The correct name of all organ names, once the connection between them is proved, is the earliest legitimate name.

Take as an example *Glossopteris taeniopteroides* Feistmantel, which in the Hammanskraal flora is

represented by fronds without fructifications, fructifications without fronds, or many of both attached one to the other. If any of them is found at other localities without great alteration, attached or not, for a clearer view of the evolution and of the correlation they have to be called *G. taeniopteroides*. For this reason all similar fructifications, once attached to fronds, should be assigned to *Glossopteris*.

Maheshwari writes about "the difficulties encountered in determination of transitional forms". "The problem arises that, when a variation is presumed in a character, how are we to know its range?"

In my recent study I have chosen species as examples to show how easily one can be misled following the later literature and neglecting the original author; examining a great number of fronds, I selected the constant specific characters that coincide with the author's species and tried to show individual variations. As in living plants, the size of the fronds and the density of the venation is and was subject to environmental effects. If the great number of fronds indicated autumnal leaf-fall, all are about the same age and the small ones are not younger. They were situated on the trees or shrubs where the lack of humidity or sunshine or both restricted them in their growth.

Attention was paid to possible differences on the upper and lower surfaces of the fronds. It was seen that they differ and not in the same way in all the examined species. This difference in the two surfaces could possibly be the reason why Brongniart (1830, p. 223) wrote of *Glossopteris browniana* (including at that time *Glossopteris indica*) "nervulis basi obliquis reticulatis, apice tantum simplicibus vel furcatis", examining an upper surface, where the anastomoses are fewer and not so well marked.

Finally I would stress that there is not one character which can be used with the same importance in all the species. For example, the pattern of the meshes in *Glossopteris indica* Schimper and *Glossopteris communis* Feistmantel is the main and most constant character, but in *Glossopteris taeniopteroides* Feistm. it changes from specimen to specimen. The characters for each species must be worked out by examining great numbers of fronds. Only at the beginning with the first species was it permissible to describe them from one or a few specimens, but today, having dozens of *Glossopteris* specific names, one could be led to re-describing an already named species.

#### THE GENUS *GLOSSOPTERIS* AT HAMMANSKRAAL

I selected *G. communis* Feistmantel and *G. taeniopteroides* Feistmantel for my study as they have been misunderstood many times, mixed with other species and often mentioned under wrong names. *G. taeniopteroides* seems to be a very important species, in some floras the dominant one, e.g. in Hammanskraal.

My study is not a revision. I cite from the vast literature only authors with whom it is interesting to compare the original descriptions and who have had a



misleading effect. I cite always the authors of the species, especially as some of their papers are not easily available, and to show how the description of a species changed as, e.g. when *G. taeniopteroides* was later mentioned as *G. indica* Schimper.

As both *G. communis* and *G. taeniopteroides* were synonymised by Arber as *G. indica*, I start with the history of *G. indica*. It is not the first time that the confusion between *G. indica* and *G. communis* has been discussed (e.g. Srivastava, 1956, p. 5; Plumstead, 1962, p. 38; Rigby, 1966, p. 130) but here I investigate matters not previously mentioned.

Brongniart (1830, p. 223) divided *Glossopteris browniana* into two varieties:

Var. *Australasica*: foliis minoribus subspathulatis obtusis.

Var. *Indica*: foliis majoribus lanceolatis acutiusculis.

Fortunately with these short descriptions he gave often criticised but quite useful figures. On them the difference of the two varieties is obvious; the more or less equal meshes of the var. *australasica* and the short, broad meshes near to the midrib on var. *indica*.

The Figure 2 on Pl. 62 of Brongniart (1830) shows that the holotype of *G. browniana* var. *indica* is not one whole frond, but is broken in the middle. Following the outline of the two parts, they would meet properly, but the midribs do not, as it was indicated by the artist with dotted line. By courtesy of Prof. Lehman of the Paris Museum, I received the photograph of the holotype. On that it is clearly visible that the base and top parts are not of the same frond, moreover not of the same species. The artist drew the same type of venation on both parts, which is true only on the lower part (Pl. VI).

When Schimper (1869, Vol. I, p. 645) raised the two varieties to species rank, his description of *G. indica* was in accordance with the drawing and the base of the holotype. Unfortunately he gave no figures.

Lectotype: the basal half of the type specimen of *Glossopteris browniana* var. *indica* Brongniart, No. 506, Museum d'histoire naturelle, Paris.

The lectotype designation seems to be necessary because the specimen is wrongly combined from halves of two different species, the basal half agreeing with Schimper's description (1869, Vol. I, p. 645).

The study of *Glossopteris* started with the mistake that two specimens were glued together as one which was chosen as the holotype of one of the first *Glossopteris* fronds ever described. The mistake led to confusion and even to distrust of the possibility to identify *Glossopteris* species based only on frond impressions.

Zeiller was the one who studied Brongniart's type material and pictured them (1896, p. 367, Figures 11 and 12). He noticed the difference in the venation of the two parts and figured both of them. Figure 11 is from the lowest part of the base and Figure 12 seems to be the lowest part of the upper half. On Figure 11, the two or three shorter meshes near to the midrib are well figured, which is the main character of *G. indica*.

If one puts Figure 12 and Feistmantel's Figure 1a of *G. taeniopteroides* (1878) beside each other, there is no doubt that the venation is the same.

In 1902 Zeiller returned to the question of *G. indica* and discussed it at some length. He gave excellent photographs of fronds which are similar to his drawing of Figure 12 and the upper half of the holotype. On p. 11, with Figure 3, Pl. III, Zeiller wrote that the specimen had so few anastomoses that one would even think one was dealing with a *Taeniopteris*. "Je ne serais pas surpris que le *Gloss. taeniopteroides* Feistmantel, . . . ne fut autre chose qu'une forme de *Gloss. indica* assimilable à celle de la Pl. III, Fig. 3, 3a." The Plate III, Figure 3 really illustrates a *G. taeniopteroides*, as do all his figures except Plate II, Figure 2 — named as *G. indica*. After Zeiller's article for a long time *G. taeniopteroides* was mentioned as *G. indica* (e.g. Halle, 1912; Walton, 1929), which probably would not have happened if the students of the floras had read Schimper.

Bunbury (1861, p. 368) was not sure that the two varieties were distinct. He found the venation "essentially the same", in shape and venation "many shades of variation". Nevertheless his Figure 4, Plate VIII is in accordance with Brongniart's. It is interesting to compare the figure of *G. indica* illustrated by Bunbury (Figure 4) and *G. stricta* Bunbury in Arber's book (1905). Arber was at that time confused by Zeiller and he saw the slabs with Bunbury's types. Moreover he writes (Arber, 1905, p. 77): "This species (i.e. *G. stricta*) is distinguished from *G. indica* . . . by the contrast in the size and shape of the meshes bordering on the midrib with those of the rest of the lamina." The frond on Plate IV, Figure 1, is certainly more similar to *G. indica* than to *G. stricta*.

When Schimper (1869, p. 645) raised the two varieties to species rank, he gave the following descriptions of *G. indica*: "fronde subsequipedali, e basi augusta late stipitata pedentim latiore et in medio 5–6 centim. lata, apicem versus sensim augustiore, lanceolato-acuminata; acuta, raro mutica, rachi lata dorso convexa pluries sulcata, supra late canaliculata, areolis secus rachim positae abbreviatae, latiusculis, caeteris hexagono- en parallelogrammo-elongatis, angustis." In French he states: "Cette espèce se distingue du *Gl. Browniana* par . . . les mailles près du rachis plus larges."

In 1876 Feistmantel found fronds which were similar in shape to *G. indica* but of different venation. He named them *G. communis* and described them as (p. 375): "Fronde simplici, variante, sed plerumque speciosa, integerrima, ovato-oblonga, apice elongata-acuminata, basi attenuata in rachidem decurrente, rachide crassa usque ad apicem currente, nervis omnibus anastomosantibus, retia oblonga, augustissima formantibus." "The frond is simple, oblong-oval, the apex oblongly acuminate (as in *Glossopteris indica*, Schimp., while it is obtuse in *Glossopteris browniana*, Bgt.); at base the frond is attenuate, running down into the rachis; the rachis thick, reaching to the apex; the secondary veins all of pretty equal thickness, all anastomosing; the areoles are all pretty equally oblong and very narrow (while in *Glossopt. indica* they are more polygonal and larger next to the rachis), reaching to the margin." The single figure (Plate XXI, Figure 5), is good enough to



give, together with the description, the main characteristics of the species.

The confusion started when Feistmantel, using for the second time the name *G. communis*, wrote: "It is oblongly, sometimes, however, more obtusely, acuminate at the apex." (1879, p. 16.) On Plate XVII, Figure 2 the "top portion" shows a quite obtuse apex. In the Flora of the Damuda-Panchet Div., p. 98 we find: "the apical portion slightly prolonged, and the apex itself as a rule pointed". Here he gave more figures of the species than ever before or after. This is the paper to which almost all authors turned to compare their specimens to *G. communis* and where Feistmantel under one name figured more species. It is not necessary here to go into more details, as Zeiller (1902) dedicated pages to criticising this work, unfortunately in such a way that he did more harm than good.

The name *G. communis* was out of use for many years; because of a wrong definition *G. indica* was not recognised and instead of it *G. taeniopteroides* Feistmantel was named as such.

In the Flora of Western Bengal (1886), p. 26, Feistmantel had some doubts "... the specimen was not quite distinct, so that doubts might have been entertained about its nature, had anybody chosen to do so." But "at present I figure several specimens about which there is no doubt whatever, that they belong to *Glossopteris communis*." The given figures are of fragments. In the "plant-bearing beds of Eastern Australia and Tasmania" (1890) p. 124, we read "the apical portion prolonged and the apex generally pointed".

Feistmantel was an excellent taxonomist and his mistake is understandable. He worked with floras of a great number of fossils. He was the one who laid the fundamentals for all the palaeobotanists working on Gondwanaland material. His task was enormous.

In 1908 (Permo-Carboniferous ... p. 115), Seward and Leslie submitted a drawing and a description of specimens collected from Vereeniging to Zeiller who designated them as *G. angustifolia* var. *taeniopteroides*. Seward noticed the similarity between those and *G. indica* sensu Zeiller. It is indeed the same species.

Halle (1912) figures more specimens as *G. indica*. One of them "in general, forms with dense venation and parallel, comparatively rarely anastomosing secondary veins, seem to be predominant among the Falkland-material of this species." (Page 169.) In Plate 7, Figures 4 and 4a, he shows a "specimen which may be best referred to as *G. indica* ... The venation presents some peculiarities, however, which make its attribution to that species a somewhat doubtful step. ... Close to the midrib the areoles are fairly large and open; at a greater distance from it, they rapidly become narrower, and the marginal part of the lamina is characterised by very dense sub-parallel secondary veins, forming only few anastomoses". The predominant species is *G. taeniopteroides* and the one with the peculiar venation is *G. indica*.

Seward and Walton on fossil plants from the Falkland

Islands (1923, p. 322): "The enlarged piece of lamina reproduced in Fig. 13, Pl. XXI, differs from most of the specimens in the very small number of lateral anastomoses between the lateral veins, a feature shared by some of the leaves of *G. indica* from Antarctica named *G. indica* var. *Wilsoni* and by specimens described by Zeiller (1902, Pl. III, Fig. 3, 3a) from the Lower Gondwana rocks of India." It is *G. taeniopteroides*.

Walton (1929, p. 70) reports *G. indica* from Southern Rhodesia. "This common species is probably the dominant fossil in the flora represented in the collection." Figure 19 shows a *G. taeniopteroides*.

*Glossopteris occidentalis* White (1908) from South Brazil and *Rhabdotaenia waginae* Rigby (1966) from Western Australia belong also to *G. taeniopteroides* Feistmantel.

Seward (1897, p. 321) wrote about a specimen from Vereeniging: "possibly a fragment of *Gangamopteris*. This form of leaf bears a close resemblance to those named by Feistmantel *Glossopteris damudica*, which is difficult to distinguish from his *G. communis* (*Browniana* var. *indica*). Compare also *G. ampla* Dana." The Plate XXII, Figure 1, is an apex of *ampla* Dana. Seward here touched on a problem which was mentioned many times: whether *Gangamopteris* as a genus exists at all? Later he discussed the question (1905, p. 2) more profoundly and came to the conclusion that the absence of the midrib has no great taxonomic importance. The mentioned *Glossopteris* species are represented at Hamanskraal and they are well distinguished. *G. ampla* Dana (1849, p. 717): "Frond very large and broad ovate, entire, undulate, apex obtuse. Midrib very stout and broad,  $\frac{3}{4}$  to 1 inch at base, and slender towards apex. Venation close, narrow, reticulate. Near the margin for nearly an inch, veins very much subdivided; more closely crowded, and scarcely reticulate." Rigby (1966) on Plate 34, Figure 41, figured the type specimen. *G. damudica* Feistmantel (1881b, p. 105): "Fronde latissima, obovata, apice obtuse an emarginate; rhachide crassa, nervus secundariis angulo subrecto ex rhachide egredientibus, retia rhachidem versus breviora, trigonalia an polygonalis, latiuscula, marginem versus oblonge-polygonalia, augusta formantibus."

McCoy at first neither noticed nor figured the anastomoses in the median part. Moreover (1847), he wrote "all the nerves dichotomise at irregular intervals, and those of the sides occasionally anastomose and are connected by a few transverse bars". When he described the genus *Gangamopteris* (1874) he marked anastomoses in the middle part near the base (Figure 3a).

McCoy (1874, p. 11): "Gen. Char. ... no midrib; veins coarsely reticulate, many arising from the base, branching as they diverge towards the margin, and frequently anastomosing to form an irregular polygonal network. The gigantic ferns constituting the genus *Gangamopteris* were originally described by me in a paper in the Annals of Natural History for 1847, from a single terminal leaflet having the form and netted neuration of the narrow varieties of *Glossopteris* Brow-



niana, but which I pointed out as generically distinct from wanting the midrib." This description is adaptable to *Glossopteris browniana*, the first described *Glossopteris* species, as was noticed by Zeiller (1896, p. 364). This is true of *G. ampla* Dana, if one looks at the upper surface of a frond. Often it is difficult to decide whether in the middle the parallel veins or a bundle of veins can be called a midrib, and thus whether it is a *Glossopteris* or a *Gangamopteris*.

With careful and close examination one can follow the secondary veins into the "midrib" in many *Glossopteris* fronds, in which case the midrib is nothing else but a bundle of veins, actually the same vein being first in the middle and then turning towards the margin.

Plumstead (1958, p. 65): "an *Ottokaria* type of fructification being characteristic of two leaf genera, *Gangamopteris* and *Glossopteris*". Does this not show that we deal with one genus only?

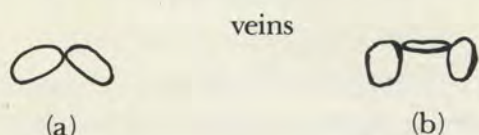
The genus *Gangamopteris* is more typical in the Lower Gondwana formations. It seems that the evolutionary tendency progressed in one taxon from the equally spread venation through the always more dense parallel veins in the middle to the real midrib. A revision of the species from this respect could shed more light on the correlation. A decision of the generic status of *Gangamopteris* needs further research.

Fructifications were reported as borne not only on the petiole but on the midrib of the fronds. The seeds of *G. communis* Fstm. were attached to the median vein bundle. On one frond of *G. pseudocommunis* Kovács more seeds and at least two big protecting leaves were found in connection with the median vein bundle.

Before dealing with the detailed descriptions of the species, I wish to explain my observations connected with the venation.

It depends on the preservation whether the median parallel veins are clearly seen or are only a groove or the impression of a strong vein in the middle.

Splitting the slabs it was possible to examine the counterparts. The pattern of the venation in various species differed often on the two counterparts and not in the same way. In some specimens, on one surface the number of anastomoses was less than on the other. I discussed the matter with Mr. R. Ellis of the Botanical Research Institute. We agreed on the possibility that the veins do not actually join by the anastomoses. There are two ways of forming anastomoses — both can be seen, e.g. on a well-preserved *G. browniana* Bngn. impression. One is when the veins touch one another, and the other is when there is a connecting vein as a bridge between them. If the cross section of a frond was as it is shown on Figures a and b, then there would be more anastomoses on one surface and less on the other.



As the plant remains from Hammanskraal were impressions or badly preserved carbonaceous crusts, it was impossible to prove the cause of the difference in the two surfaces.

Another way in which the two surfaces differ is shown in *G. pseudocommunis* Kovács. Here on one surface the venation is well seen with anastomoses, the other displaying only the cuticle with fine lines. That surface was described as genus *Rubidgea* by Tate (1867) (Kovács, 1977 in press). Some impressions are not merely on one surface. Depending on how preservation was effected, some specimens display the characters of both surfaces. On *G. pseudocommunis* Kovács, e.g. on the "*Glossopteris*" surface there are sometimes "*Rubidgea*" patches, or the other way round, or between the veins there are fine lines running independently of the venation.

In describing the shapes, I have followed Dilcher (1974, pp. 18–20). In the descriptions I give the maximum width of the fronds.

#### *Glossopteris browniana* Bngn. 1828

##### Plate IVe; Figures 1a and 1b

*G. Browniana* Brongniart, 1828, Prodr. Hist. Veget. foss., p. 54.

*G. Browniana* var. *australasica* Brongniart, 1830, Hist. Veget. foss., p. 223, Plate 62, figs. 1 and 1a.

*G. Browniana* Brongniart, in Schimper, 1869, Traité Paléont. vég., 1, pp. 645–46.

Brongniart's description: "G. foliis lanceolatis vel subspathulatis obtusis (1–2 pollicibus latis); nervo medio valido superne canaliculato; nervulis basi obliquis reticulatis, apice tantum simplicibus vel furcatis, marginique subperpendicularibus, vix. obliquis. var. *Australasia* foliis minoribus subspathulatis obtusis." Schimper's description: "fronde minore, rarissime pedali, plerumque longitudine inter centim. 6 et 10 ludente, apicem versus repente angustata, nunquam acute lanceolata, mutica, saepe rotundata, areolis rachi proximis longioribus, plantae junioris elongato-, an-sioris spathulato-lingulata." Brongniart's figure, see Figure 1a. Frond oblanceolate, narrow elliptic. Length 3.5–12 cm, width 1–4 cm. Apex suddenly contracted, varying, often obtuse; base attenuate.

Parallel veins occupy the whole width of the base; as the blade begins to broaden, in the first mm, the outer veins bifurcate, the inner branch runs parallel with the median veins, the outer branch turns aside; they bifurcate repeatedly. The bifurcating veins approaching each other give the impression of anastomoses, or nearby veins are connected by a short one, forming polygonal meshes. The meshes are better seen on the lower surface (on impression where the veins are incised); on the upper surface (on impression where the veins are raised), the veins run less frequently near to each other to meet, and thereby the number of anastomoses is fewer.

The parallel median veins are not always apparent, due to the preservation; sometimes they look like a

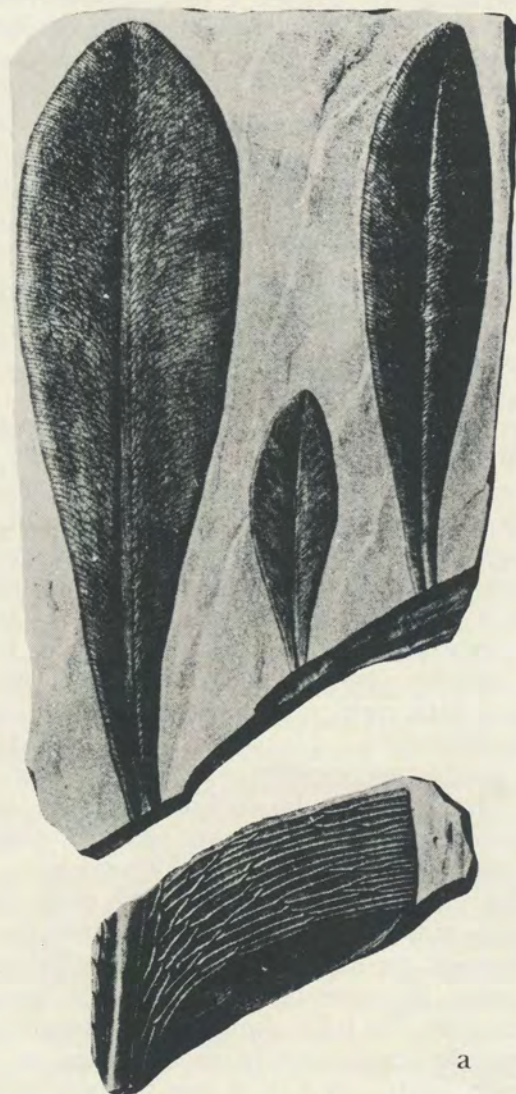


striated midrib, or there is only a groove in the middle. Some middle veins reach the apex without turning aside.

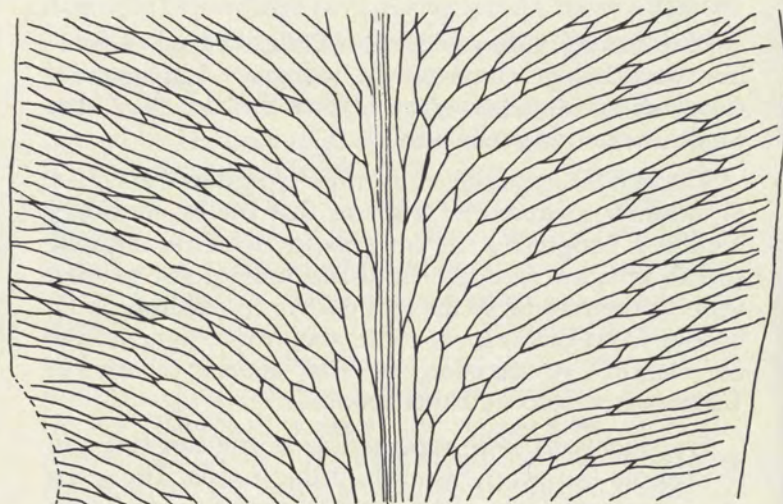
The first meshes form with the median veins a more acute angle than those following. The meshes are polygonal; all are about the same size.

Number of examined specimens: 33.

Comparison: Between *G. browniana* Bngn. and *G. indica* Sch. (Figure 2). In extreme cases the shape and size can be similar, but usually *G. indica* is larger. The apex of *G. indica* is always acute, but *G. browniana* has usually an obtuse apex but sometimes acute. The main



a



b

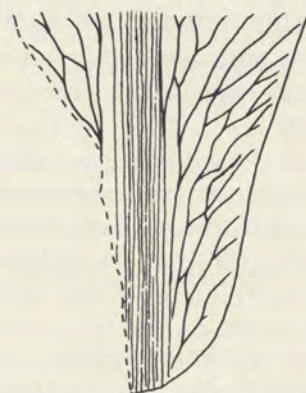


Figure 1. (a) Brongniart's original drawing of *Glossopteris Browniana* var. *australasia* from Hist. Végét. foss., Plate 62, Figures 1 and 1a. 1830.

(b) *Glossopteris browniana* Bngn. Portions of the frond (Catalogue no. H.I. 15) showing the obtuse apex, the parallel veins in the middle and the polygonal meshes, the attenuate base. x2 approx.

specific difference is in the venation. The meshes of *G. browniana* Bngn. are polygonal all over, usually the longest near the middle. Because of the polygonal shape of the meshes, the veins nowhere run parallel. In *G. indica* Sch. the middle meshes are usually broader and shorter than the rest, but always shorter. They are oblong nearer to the margin, where the veins are parallel.

*Glossopteris ampla* Dana 1849

Plate 1a; Figures 3a, 3b, 3c, 13 and 20.



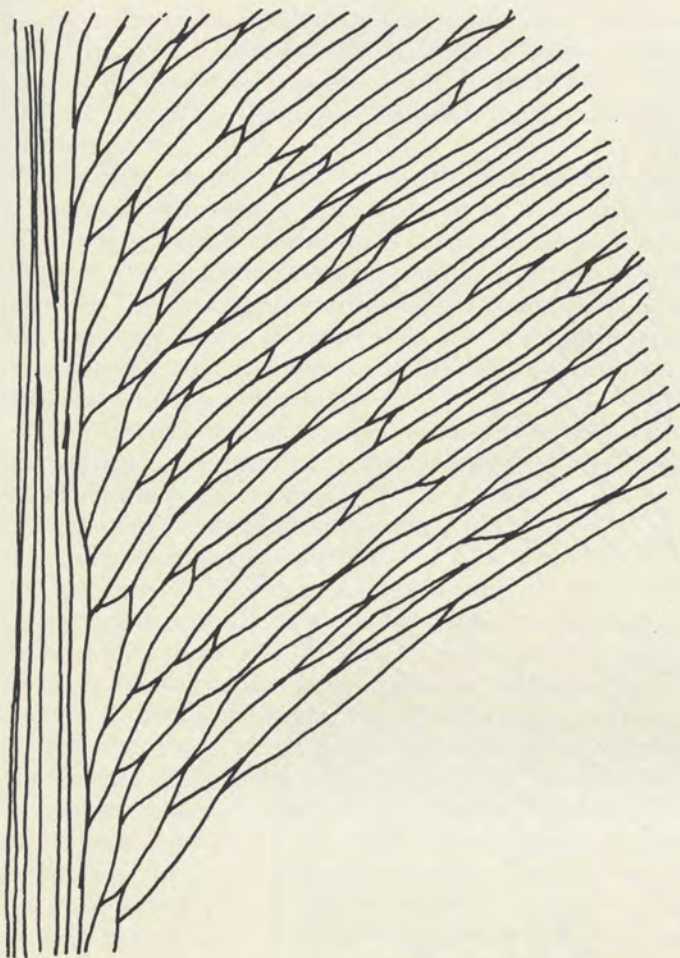


Figure 2. *Glossopteris indica* Schimper. Portion of the frond (Catalogue no. H.I. 74). The side veins are parallel except near to the middle, where the meshes are broader and shorter. x3.

*G. ampla* Dana, 1849, in Wilkes' U.S. Exped., Vol. 10, p. 717, Figures 1a and 1b.

There is nothing to add to the original description of Dana, which is quoted on page 70. The specimens examined agree in all details with the original description. Under the name *G. ampla* Dana Arber (1905, p. 78, Figure 20) gave a description and figure of *G. damudica* Fstm. and synonymised *G. damudica*. The two species were re-established (Archangelsky, 1957; Plumstead, 1962). The difference in the venation of these two species is impressive. The veins of *G. ampla* Dana pass from the middle with a long curve, forming very long and narrow meshes, which are more or less the same all over the blade. The first meshes of *G. damudica* Fstm. next to the median veins are triangular; then the veins turn at almost a right angle to the margin, and are parallel; the meshes are never so long as in *G. ampla* Dana.

Number of examined specimens: 99.

*Glossopteris indica* Sch. 1869

Plate Ia; Figures 2, 4, 5 and 21.

*G. Browniana* var. *indica* Brongniart, 1830. Hist. Veget. foss., p. 223, Plate 62, Figure 2.

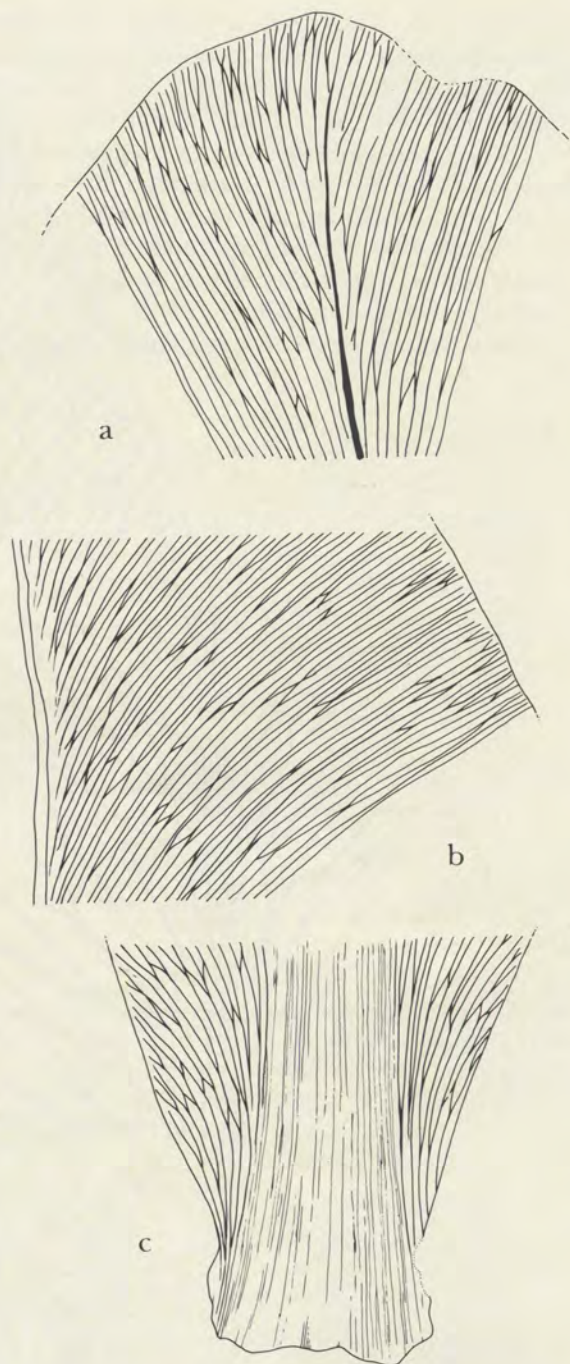


Figure 3. *Glossopteris ampla* Dana. (a) The obtuse apex of the specimen H.I. 134; (b) The portion of the frond no. H.I. 25 showing the long, narrow, equal sized meshes; (c) The base of the specimen no. H.I. 245 with the broad middle part. x1,5 approx.

*G. indica* Schimper, 1869, Traité Paléont. veg. 1, p. 645.

Brongniart's and Schimper's descriptions are given on page 69. Brongniart's figure Plate VI.

Frond narrow elliptic, tapering to the base and apex, apex always acute.

Length usually more than 20 cm; according to some fragments it can exceed 30 cm. Width 3–7 cm.

In the middle the veins are parallel, but due to the preservation this is not always obvious. Sometimes they are overlain by a layer, which in connection with *G.*



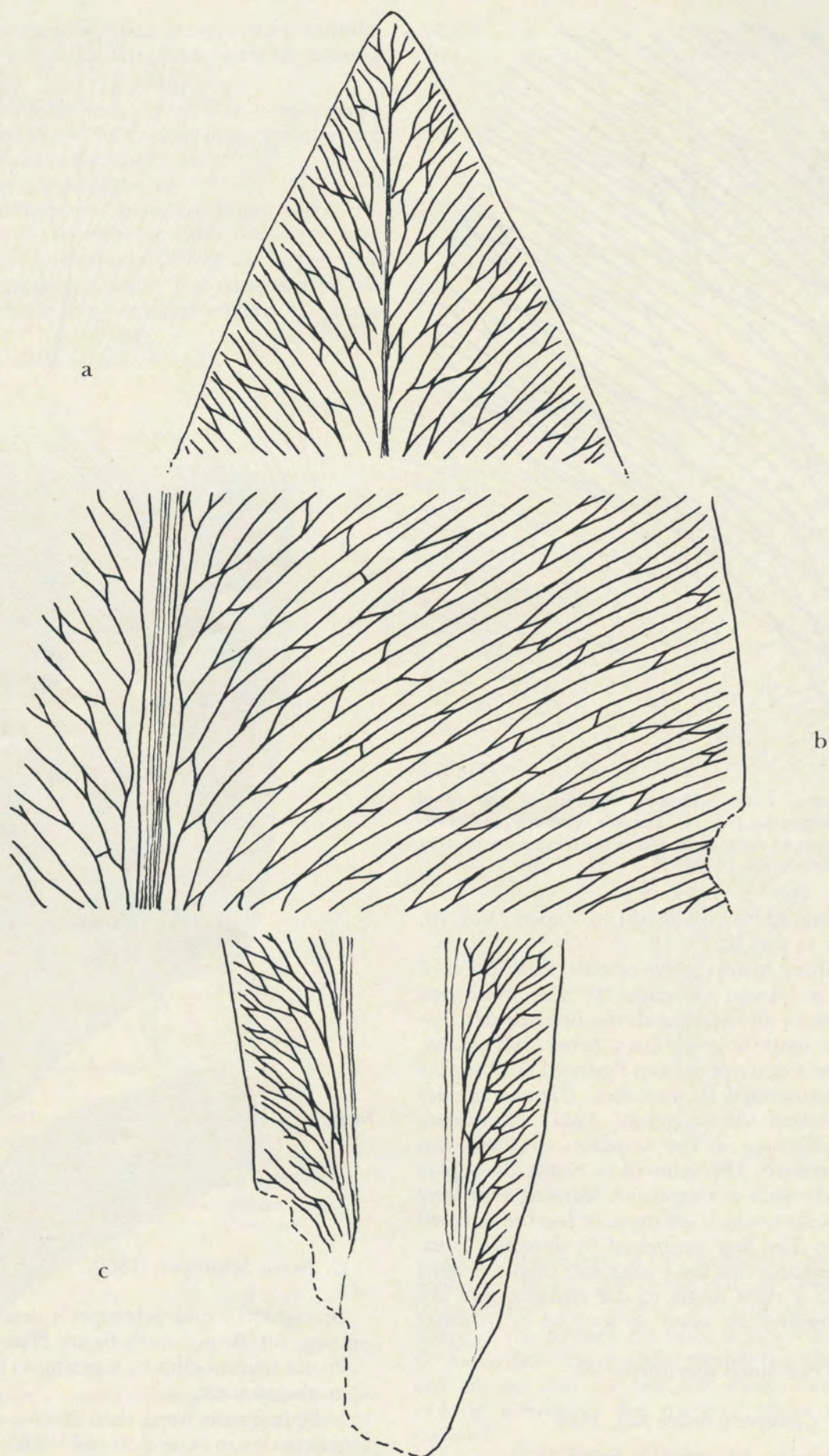


Figure 4. *Glossopteris indica* Schimper. (a and b) The acute apex and the middle portion of the specimen no. H.I. 38 a; (c) The base of the specimen no. H.I. 28 a. x3.



*communis* Fstm. was called by Feistmantel the "peculiar cell structure". I am not able to decide whether it was a part of the frond or was the result of the preservation. One or two of the median veins reach the apex without turning aside.

The first meshes formed by the lateral veins are polygonal, with two or three rows at an acute angle to the median line; then the veins turn at a more oblique angle to the margin, forming parallel, narrow oblong meshes. The first meshes are usually broader and in all cases shorter than the others. At the apex and at the base the difference between the first and the following meshes is not always striking.

On the upper surface the venation is very faint; anastomoses are seen near the middle and few in the parallel-running side veins.

Number of examined specimens: 103.

Comparison (Figures 5, 6 and 7).

The veins of *G. browniana* Bngn. and *G. indica* Sch. start from the middle at an acute angle, then turn to the margin at a more oblique angle; those of *G. communis* Fstm. have about the same direction, but are slightly curved. *G. browniana* Bngn. has relatively big polygonal, *G. communis* Fstm. very narrow oblong meshes. The inner meshes of *G. indica* Bngn. border the median veins in two or three rows, and differ from the meshes of the more lateral parallel veins. The first meshes of *G. communis* Fstm. in shape, size and direction are more or less the same as the rest.

The shape of *G. indica* Sch. is elliptic, of *G. taeniopteroides* Fstm. oblanceolate. The apex of *G. indica* is always acute, that of *G. taeniopteroides* always obtuse or rounded. The veins of *G. indica* change their course after the first meshes, in which the anastomoses are always well marked. The secondary veins of *G. taeniopteroides* (Figure 8) after bifurcation follow the same direction, anastomoses are few and irregular. When there are meshes, they are all oblong and narrow, with no difference between the median and marginal meshes.

To differentiate *G. indica* Sch. from *G. damudica* Dana (Figure 9) can be difficult when the apex is missing, as in both species the venation with two kinds of meshes is typical; moreover the veins, except near the median line, are parallel. The meshes bordering the median bundle of veins, however, differ; in *G. indica* they are in two or three rows, oblong-polygonal and form an acute angle with the median veins; in *G. damudica* the meshes of the first row are long and parallel with the middle, and the meshes of the second row are triangular, trapezoid.

*Glossopteris communis* Fstm. 1876

Plate Ib; Figures 7, 10a, b, c and 11.

*G. communis* Feistmantel, 1876. Jl. asiat. Soc. Beng. 45, 2, 4, p. 375, Plate 21, Figure 5.

For Feistmantel's description see p. 69 and figure see Text fig. 11d.

Frond is narrow or very narrow elliptic, apex always acute, gradually tapering towards the apex and base.

Length 10–20 cm; width 2,5–7 cm. The veins are parallel in the middle, which is not always well visible, as they are often covered by the "peculiar cell structure" (Feistmantel, 1881b, p. 98). The vein bundle reaches the apex, gradually thinning.

The veins emanating from the median bundle arch moderately and reach the margin almost in the same course. The meshes are oblong, very narrow and more or less of the same size and shape on the whole blade. The venation is very dense, and crowded to such an extent that the veins are not clearly distinguished.

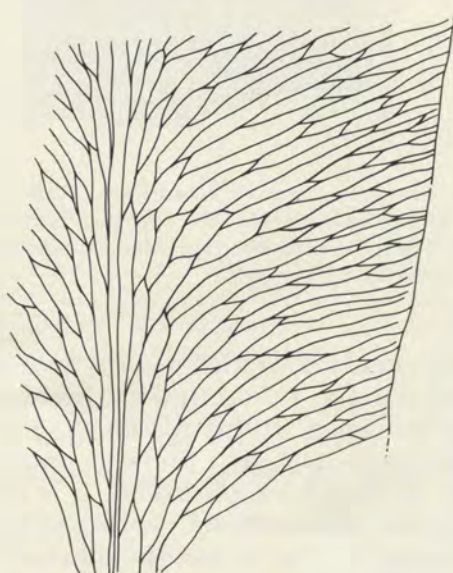


Figure 5. *Glossopteris browniana* Bngn. Portion of the frond (Catalogue no. H.I. 15) to show the veins starting from the middle at an acute angle, then turning to the margin at a more oblique angle. The meshes are all polygonal.  $\times 1,5$  approx.

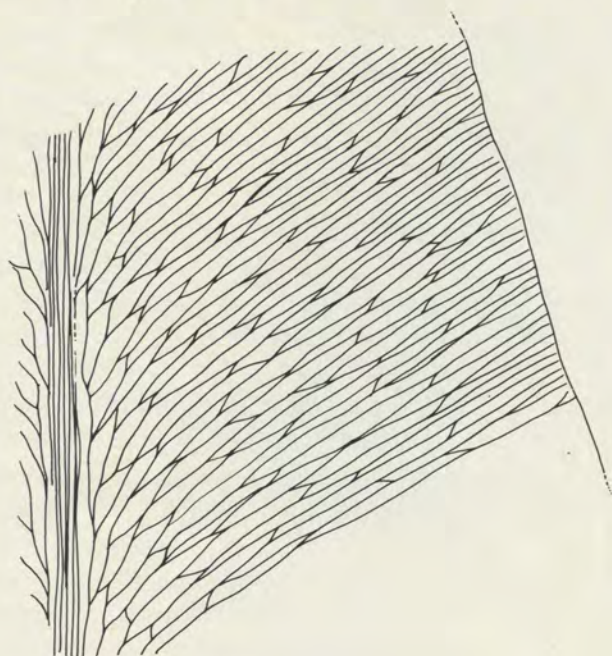


Figure 6. *Glossopteris indica* Schimper. Portion of the frond (Catalogue no. H.I. 174). Two or three inner meshes border the median veins and differ from the long meshes of the lateral parallel veins.  $\times 3$  approx.



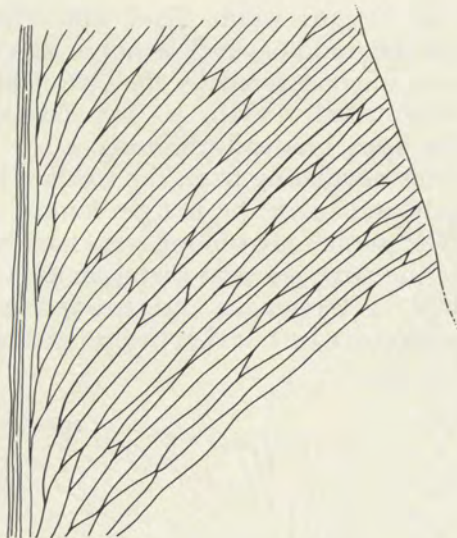


Figure 7. *Glossopteris communis* Feistmantel. Portion of the frond (Catalogue no. H.I. 67). The slightly curved veins have about the same direction. All the meshes are narrow and oblong. x1,5 approx.

A seed attached to the median vein bundle was described (Kovács, 1974a), and the frond is now identified as belonging to this species. Re-examining the same specimen (H.I. 74), knowing more about the venation of the *Glossopteris* fronds, it is certain that a number of the middle veins supported the megasporophyll. The remainder followed their course in the middle of the leaf. That is why the bundle of veins suddenly becomes narrower above the seed.

Number of examined specimens: 199.

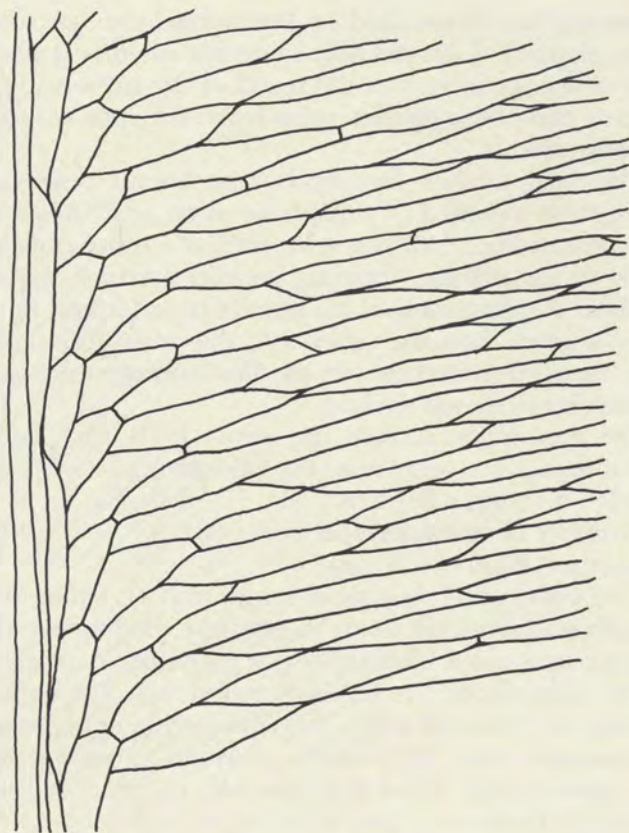


Figure 9. *Glossopteris damudica* Fstm. Portion of the frond (Catalogue no. H.I. 126). The first long meshes are parallel with the middle, the next meshes are more or less triangular, trapezoid, then the veins form polygonal, and finally oblong, parallel meshes, running to the margin almost at right angle. x2,5 approx.

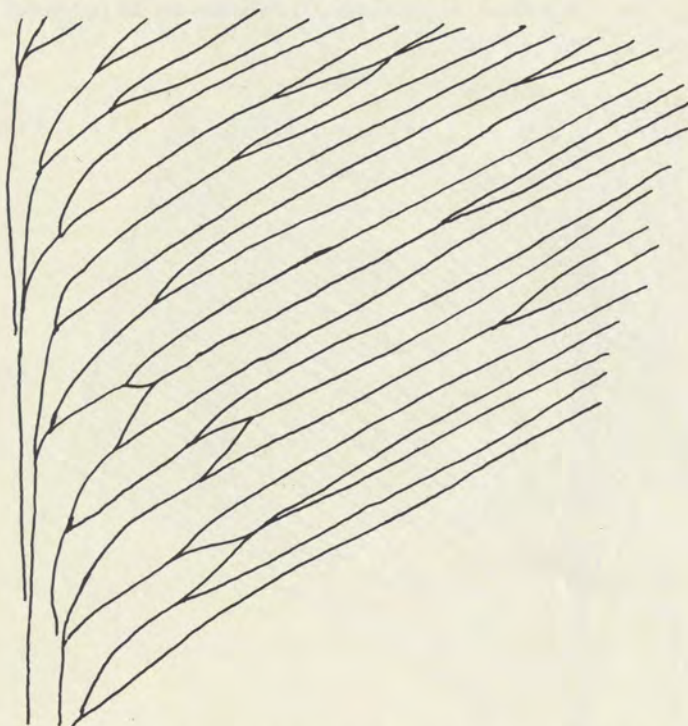


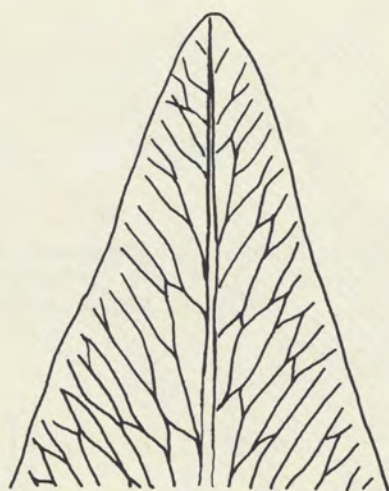
Figure 8. *Glossopteris taeniopteroides* Fstm. Portion of the frond (Catalogue no. H.I. 27a). The veins after bifurcation follow the same direction, anastomoses are few and irregular. 2,5 approx.

#### Comparison

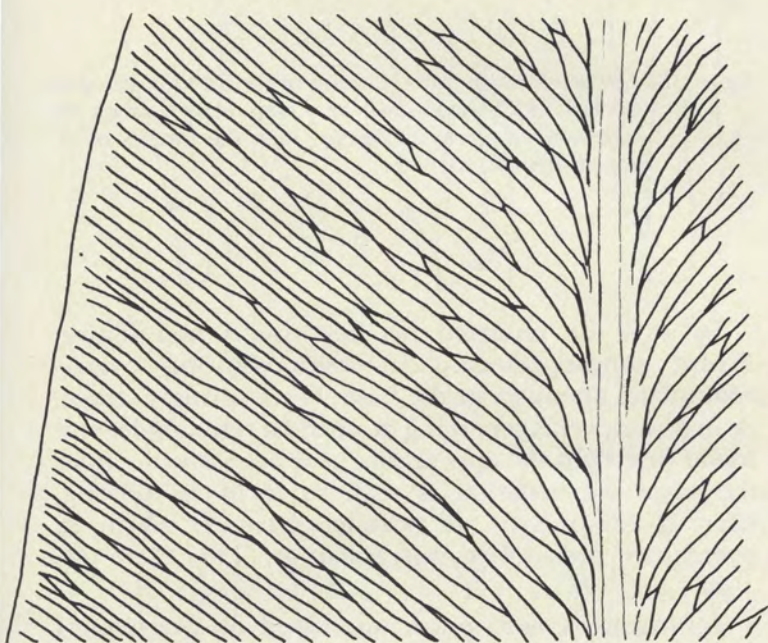
Feistmantel, describing *G. communis*, figured fronds with obtuse apices (1879, Plate 17, fig. 2; 1881, Plate 37A, fig. 4, Plate 38A, fig. 1). At Hammanskraal both *G. communis* Fstm. and the species with obtuse apex have been found. *G. communis* differs from the species, which I named as *G. pseudocommunis*, not only in the shape of the apex, but in venation. The veins of *G. communis* Fstm. curve a little, forming very narrow crowded meshes. The veins are more or less straight (Figure 11). The veins of *G. pseudocommunis* Kovács arch forming prominently arcuate venation with bending meshes (Figure 12). A few of the median parallel veins always reach the apex in *G. communis*. The median veins near the apex sometimes spread out fan-like in *G. pseudocommunis*. On the upper surface *G. pseudocommunis* has the "Rubidgea" feature, but the two surfaces of *G. communis* do not differ significantly.

*G. communis* differs from *G. ampla* in shape and venation. *G. communis* has an acute apex, *G. ampla* obtuse, rounded or emarginated. The base of *G. communis* tapers gradually, that of *G. ampla* abruptly. The veins of *G. ampla* form very long bending meshes (Figure 13). The meshes of *G. communis* are shorter and straighter.

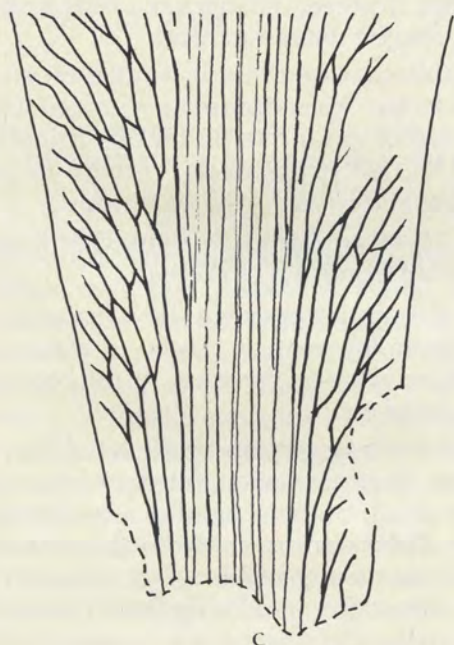




a



b



c



d

Figure 10. *Glossopteris communis* Fstm. (a) The acute apex of the specimen no. H. I. 28 (a); (b) Portion of the frond (Catalogue no. H.I. 137). The meshes are oblong, narrow and more or less of the same size and shape; (c) The gradually tapering base of the specimen H.I. 39. x3 (d) Feistmantel's original drawing (1876).

*Glossopteris taeniopteroides* Fstm. 1878

Plate IIe; Plate IIIa, b and c; Plate IVa; Figures 14, 15, 16 and 17

*G. taeniopteroides* Feistmantel, 1878, Palaeontographica, Nachtr. 3,3, p. 92, Plate 9, Figures 1 and 1a.

*G. indica* Schimper, in Zeiller, 1902, Mem. Geol. Surv. India, N.S. 2, 1, pp. 8–13, Plate 1, Figures 1–5, Plate 2, Figures 1, 3 and 4 Plate 3, Figures 1, 3.

*G. angustifolia* Bngn. var. *taeniopteroides* Seward and Leslie, 1908, Quart. J. Geol. Soc. London. 64, p. 113, Text Figures 2 and 3, Plate 9, Figure 2.

*G. occidentalis* White, 1908, Co. Est. Minas Carvas Pedra Brazil. Rio de J. Pt. 1. p. 511–3–5–7. Plate VII, Figures 1–4 and 4a.

*G. indica* Schimper, in Halle, 1912, Bull. Geol. Instn. Univ. Uppsala, 11, p. 169.

*G. indica* Schimper cf. var. *Wilsoni* Seward, in Seward-Walton, 1923, Quart. J. Geol. Soc. Lond. 79, p. 322, Plate 21, Figure 13.

*G. indica* Schimper in Walton, 1929, Bull. geol. Surv. S. Rhod. 15, 2, p. 70, Plate C, Figure 19.

*Rhabdotaenia waginae* Rigby, 1966, Palaeontographica 118, B. p. 135, Plate 34, Figure 43; Plate 35, Figure 56; Plate 36, Figure 57.

Feistmantel's description: Fronde simplici speciosa, oblonge-ovate-spathulata, ad basem attenuata; rhachide valida, lineata, nervis secundariis sub angula subrecto egredientibus, primo aspectu nervationi Taeniopteridis simulantibus, sub lente retia oblonga, angusta, oblique-acute-parallelo gramma aut indistincte polygonalia exhibentibus.



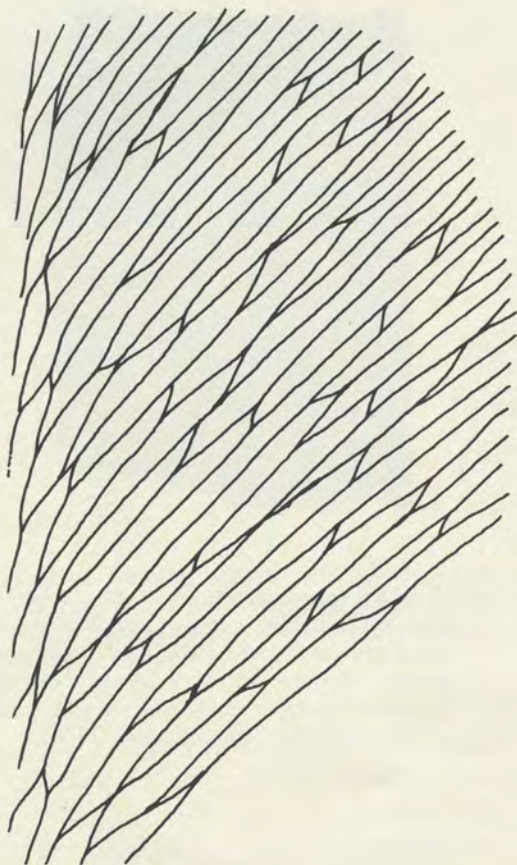


Figure 11. *Glossopteris communis* Fstm. Portion of the frond (Catalogue no. H.I. 67). The veins are more or less straight. x3.

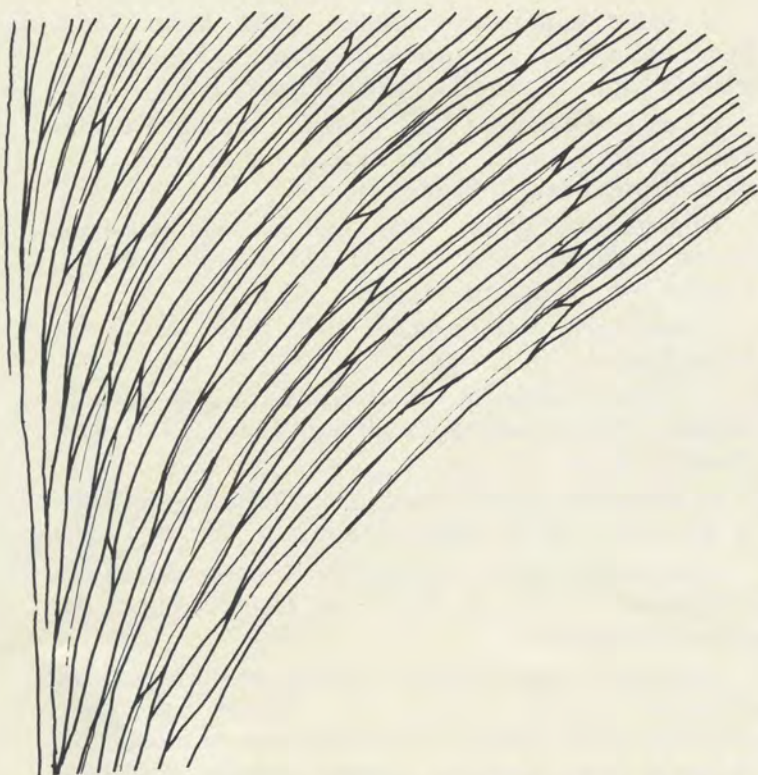


Figure 12. *Glossopteris pseudocommunis* Kovács. Portion of the frond (Catalogue no. H.I. 171). Arcuate venation with bending meshes, with fine lines between the veins. x3.

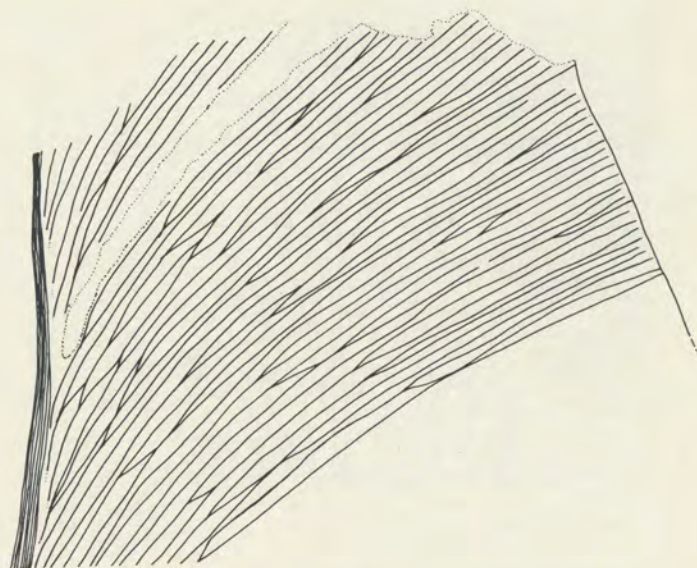


Figure 13. *Glossopteris ampla* Dana. Portion of the frond (Catalogue no H.I. 25). Venation with very long meshes, which are narrower relatively to the size than the meshes of *G. pseudocommunis*. x3.

In 1890 he repeated his description and figure: Frond simple, elegant in form, oblong ovato-spathulate, attenuate at the base; costa strongly striate, or grooved; veins emerging at nearly a right angle, giving at first sight the appearance of a *Taeniopteris*. Under the glass the venation is seen to form an oblong, narrow, obliquely-acute parallel network, which in sometimes indistinctly polygonal (p. 128, Plate 18, figs. 1 and 1a).

Feistmantel's description was based on one typical fragment. The venation, as it was determined, is characteristic in the one specimen. The number of anastomoses, however, changes not only from frond to frond, but also on the same frond.

Frond oblanceolate or narrow oblanceolate, the fertile fronds lyrate. Apex obtuse or rounded. (Figure 14.) Base cuneate or on the fertile fronds roundly hastate. (Figure 15.) All transitional forms between the oblanceolate and lyrate form can be found.

Length 15–30 cm, width 3–7 cm. One fragment was of a very small frond, 1,5 cm broad.

Midrib strong. It appears to be a real unit, i.e. not a bundle of parallel veins. It can be as wide as 7 mm at the base, narrowing to the apex. At the base it occupies a third of the blade.

In respect of anastomosis of the secondary venation, some veins anastomose regularly, some once and others not at all, but run parallel towards the margin. The angle of the veins varies from almost a right angle to 35°. The constant character of the venation is that the secondary veins after branching from the midrib bifurcate and run parallel towards the margin.



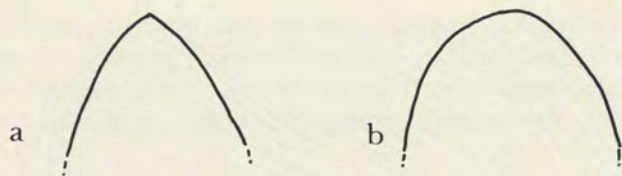


Figure 14. *Glossopteris taeniopteroides* Fstm. (a) The obtuse apex of the specimen no. H.I. 76; (b) The rounded apex of the specimen no. H.I. 298. x1.

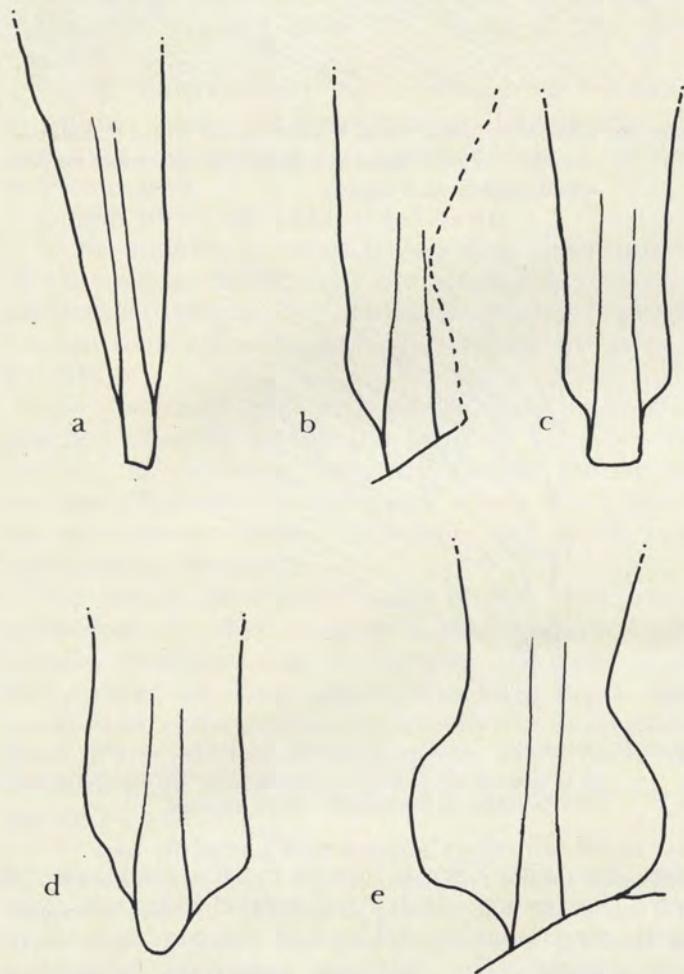


Figure 15. *Glossopteris taeniopteroides* Fstm. The variation of the base from cuneate to roundly hastate. Catalogue nos: (a) H.I. 150; (b) H.I. 17; (c) H.I. 17; (d) H.I. 21; (e) H.I. 76. x1.

The reproductive organ is attached to the petiole. It is a strobilus with two protective leaves. Bannerjee (1969) reported the female fructification from Bihar, India. The seeds were prepared out of an attached fertile body. According to his description ("arranged in linear rows . . .") "sessile seeds are attached to the median axis . . .") and his photographs it seems not impossible that the seeds were on the midrib, and covered by a strong veil.

The fructifications from Hammanskraal, mentioned here, are probably pollen-bearing organs, though Dr. Stapleton of the Geological Survey, Pretoria, found no pollen in them.

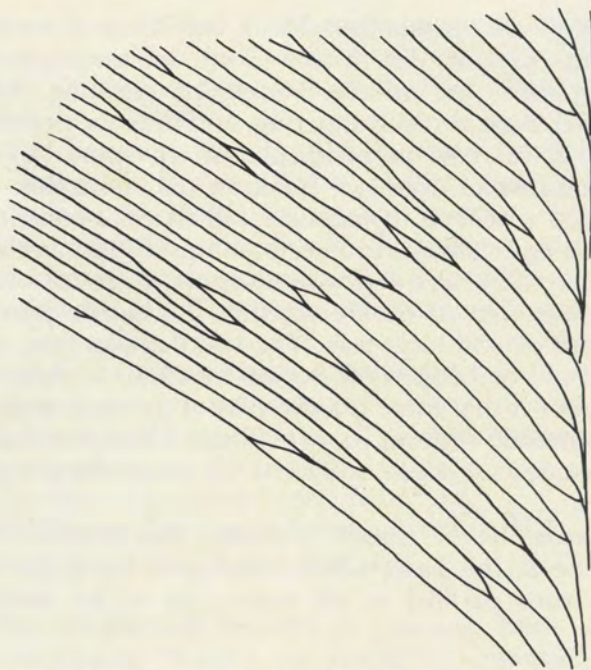


Figure 16. *Glossopteris taeniopteroides* Fstm. Portion of the frond (Catalogue no. H.I. 21). x2 approx.

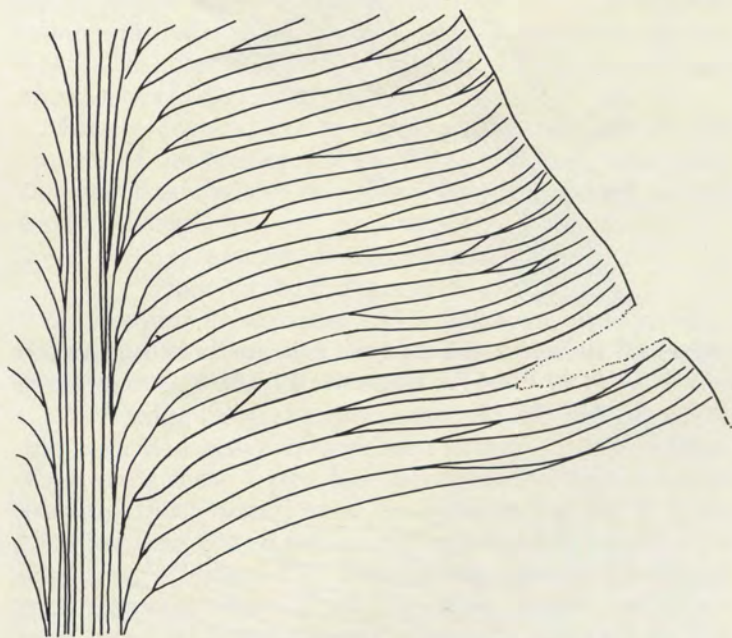


Figure 17. *Glossopteris taeniopteroides* Fstm. Portion of the frond (Catalogue no. H.I. 160) showing venation. x2 approx.

Number of examined specimens: 558.

The bifurcating parallel veins with few irregular anastomoses is such a typical character that the species is easily recognisable even on fragments.

*Glossopteris damudica* Fstm. 1881

Plate IVb, c and d; Figures 9, 18 and 19.

*G. damudica* Feistmantel, 1879. *Palaeont. indica*, ser. 12, 3, 1, p. 17.

*G. damudica* Feistmantel, 1881, *Palaeont. indica*, Ser. 12, 3, 3, p. 105, Plates 30A, 1-2; 31A, 1-3; 32A, 1; 40A, 6.



A whole frond was found with excellently preserved venation. Length with petiole 15 cm, maximum width 3,5 cm above the middle. Petiole 1,5 cm long. Apex rounded. Base abruptly tapering, and near the petiole it ends with narrow perpendicular sharp spurs (Figure 18). Feistmantel does not mention the spurs, but the discussed specimen in venation and shape is consistent with his description. Another base was also found with the same characters, but without spurs. I was unable to detect any sign to decide whether the base originally was with or without spurs. The spurs are so fine, that they could be broken off during fossilisation. Another possibility is that there is a diversity at the base, as in *G. taeniopteroides*. Without more evidence I have not found the hastate base alone sufficient for establishing a new species.

**Venation:** In the middle the veins run parallel. The first one at the base, which bifurcates, has a branch which runs parallel as the outermost of the median

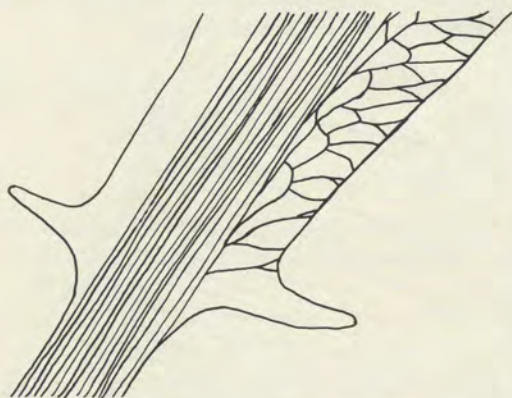


Figure 18. *Glossopteris damudica* Fstm. Enlargement of basal portion of the frond (Catalogue no. H.I. 126) to show the spurs.  $\times 1,6$  approx.

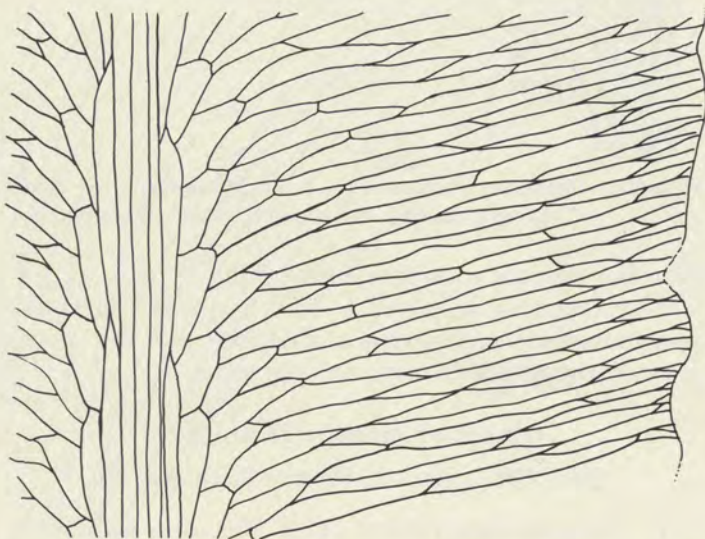


Figure 19. *Glossopteris damudica* Fstm. Portion of the frond (Catalogue no. H.I. 126) to show venation. The meshes near to the median veins are triangular, then polygonal, finally oblong.  $\times 2$  approx.

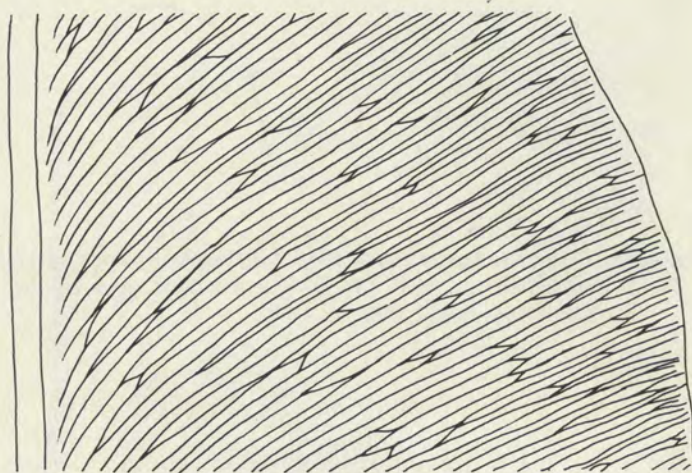


Figure 20. *Glossopteris ampla* Dana. Portion of the frond (Catalogue no. H.I. 170) to show the long, narrow, more or less equal meshes.  $\times 2,5$  approx.

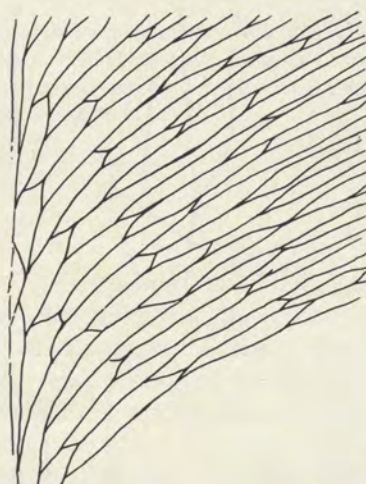


Figure 21. *Glossopteris indica* Schimper. Portion of the frond (Catalogue no. H.I. 27a) showing the oblong-polygonal meshes near to the middle.  $\times 2,25$  approx.

veins. The other branch runs to the margin above the spur. The branch which runs parallel bifurcates twice again; the branching veins reach the margin without anastomosing. The following outermost bifurcating veins form a network in which the first long meshes are parallel with the middle, the next meshes are more or less triangular, trapezoid, then the veins form polygonal, and finally longer oblong parallel meshes, running to the margin almost at right angles. The direction of the venation is more or less the same from the base to the apex. (Figure 19.)

Number of examined specimens: 11.

For comparisons see *G. ampla* Dana and *G. indica* Sch. (Figures 20 and 21). It is not difficult to distinguish *G. damudica* from *G. communis*. *G. communis* has equal meshes.

Another frond was found with hastate base. The apex was missing. The venation showed the typical *Glossopteris* feature, but the fragment was not sufficient for identification. The base is similar to that described by Lacey, Van Dijk and Gordon-Gray (1974) as *Belemnopteris elongata*. Feistmantel established the genus



*Belemnopteris* for broad arrowhead shaped fossils with three chief veins. I am of the opinion that these fronds with hastate base have a closer resemblance to the genus *Glossopteris* than to the genus *Belemnopteris*.

*Glossopteris pseudocommunis* n. sp.

Plate IIa, b, c and d; Figures 12, 22, 23, 24, 25 and 26.

*G. communis* Feistmantel (pars) 1879, 1881 Palaeont. indica Ser. 12, 3, 1 (Suppl.) Plate 31, Figure 4. Palaeont. indica, Ser. 12, 3, 1, Plate 17, Figure 2; 1881, Palaeont. indica, Ser. 12, 3, 3, Plate 17A, Figure 4, Plate 38A, Figure 1.

Frond oblanceolate. Apex obtuse or rounded, sometimes acute, but never pointed (Figure 22). The base long and tapering into a petiole about 4 cm long and 7 mm wide.

Length 10–28 cm, width 1, 4–5, 5 cm.

In the middle the veins are parallel. Unfortunately on the only specimen where the petiole was preserved, the base is overlapped by another frond, but where the median veins are seen again, they appear the same as the petiole.

The outermost veins arch steeply from the median bundle, bifurcate repeatedly, forming long bending meshes. As the veins leave the median bundle this becomes thinner. Near the apex it is only a thin line or the veins spread fan-like. The veins arch evenly from the middle to the margin.

The size of the meshes varies on the same frond. Sometimes the bifurcating veins anastomose near the middle, sometimes near the margin; thus some of the first meshes are short, others very long. Some veins anastomose at the margin, but usually they end without joining. The number of anastomoses on the half blade is two or three, sometimes only one. (Figures 23, 24, 25 and 26.)

The two surfaces differ intensely. On the lower surface (where the veins are incised) the above described venation is seen. On the upper surface there are fine lines arching from the middle (Figures 25 and 26) without anastomosing. That surface was described by Tate as genus *Rubidgea*. On an impression either one surface of a frond or both can be seen. There are impressions of *Glossopteris* venation covered at some places with "*Rubidgea*" patches. On other impressions the "*Rubidgea*" surface is interrupted irregularly by typical anastomosing and stronger *Glossopteris* veins. Often the

two surfaces are seen on the same impression, when the lines of the "*Rubidgea*" surface run between the actual veins. These lines were named by Pant (1956, p. 130, Figure 1A) as fibres.

On specimen No. H. II.57b, there are more *G. pseudocommunis* fronds. On one of them there are three seeds in a row beside the median bundle. Two more seeds are on the other side of the median bundle but they seem to be dislocated, and one seed fell out when splitting the slab. There are carbonaceous fragments of two protecting fronds and the impression of one of them. As the preservation is rather poor and only one specimen was found further discussion about the female reproductive organ of *G. pseudocommunis* would be premature.

Number of examined specimens: 138.

Holotype: Geological Survey, Pretoria, H.I. 103a.

Paratypes: H.I. 29, H.I. 150, H.I. 172, H.I. 195, H.I. 216.

For comparison between *G. communis* Fstm. and *G. pseudocommunis* Kovács see under *G. communis*, page 76.

In extreme cases big *G. pseudocommunis* fronds can have the same size as smaller *G. ampla* fronds. The base of *G. ampla* tapers abruptly, the base of *G. pseudocommunis* gradually. The meshes of *G. pseudocommunis* are always broader relatively to the size of the frond than the meshes of *G. ampla*.

Finally, I would like to report a rare species from the quarry of the Marico Mineral Co. (Pty) Ltd., which lies 3,5 km from where the previously mentioned fossils were collected.

*Glossopteris divergens* Fstm. 1881

Plate Va, b, c; Figures 27 and 28.

*G. divergens* Feistmantel 1881. Palaeont. indica, Ser. 12., 3,3, p. 104, Plate 28A, Figures 3 and 4; Plate Va, b, c. Text Figures 27 and 28.

"To judge from the specimens the leaf was obovate; the midrib appears to have been strong; . . . The secondary veins show a peculiar arrangement; in the lower portion their direction is downwards; in the middle they are horizontal; and in the upper portion they pass upwards" (Figure 27) "exhibiting thus a diverging arrangement, while in all the other species the veins pass more or less obliquely upwards, especially in the basal portion of the leaf. The veins form anastomoses, the meshes being short close to the midrib, and becoming oblong towards the margin, but being pretty broad throughout." (Figure 28) (Feistmantel, 1881, p. 104.)

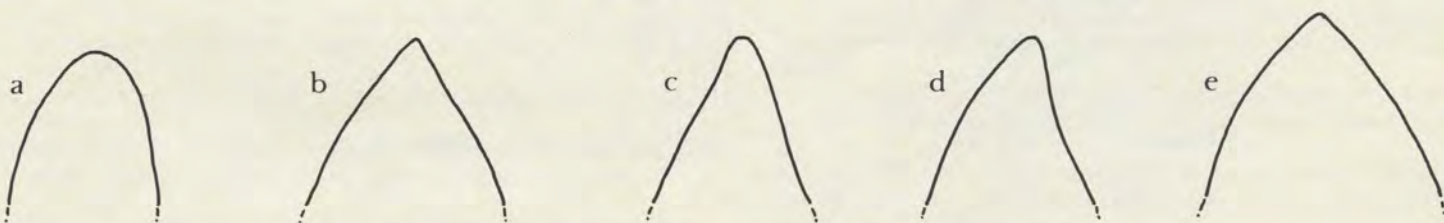


Figure 22. *Glossopteris pseudocommunis* Kovács. The variation of the apex. Catalogue nos. (a) H.I. 192; (b) H.I. 151; (c) H.I. 216; (d) H.I. 74; (e) H.I. 50. x1.



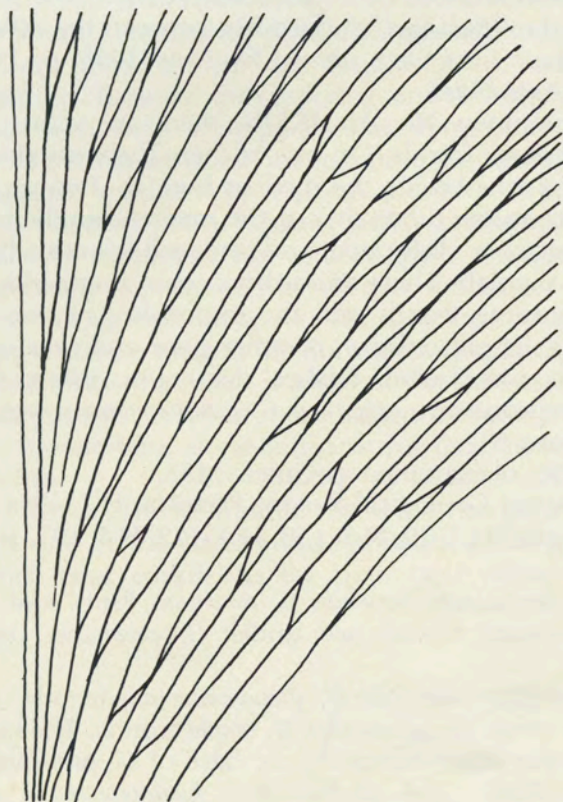


Figure 23

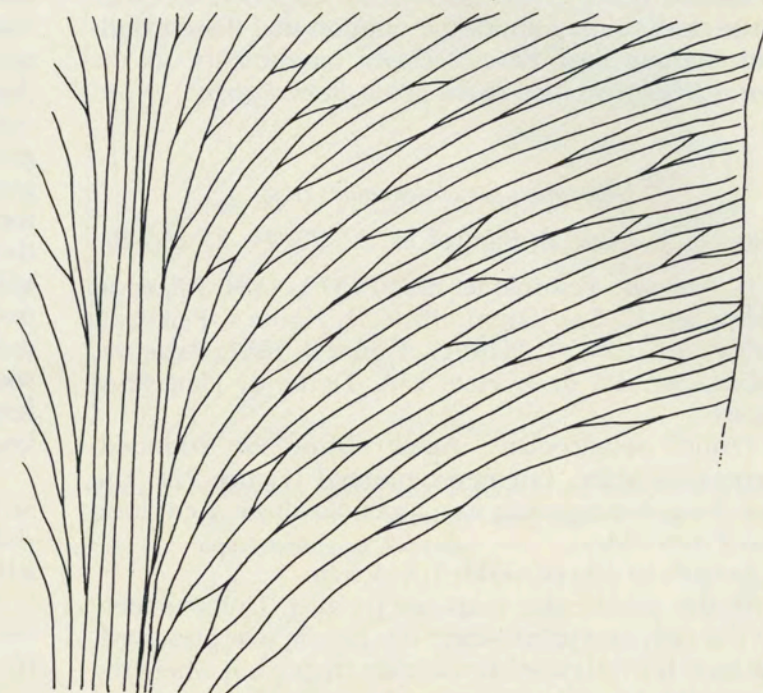


Figure 24

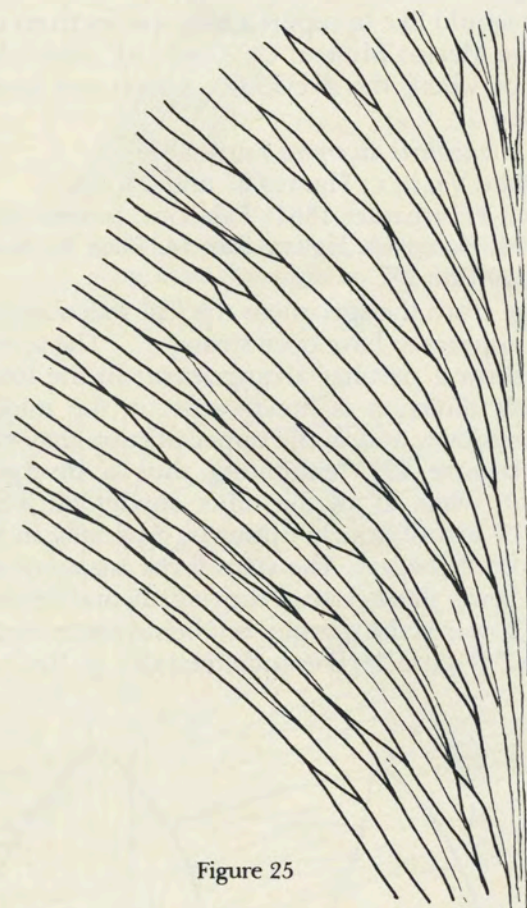


Figure 25

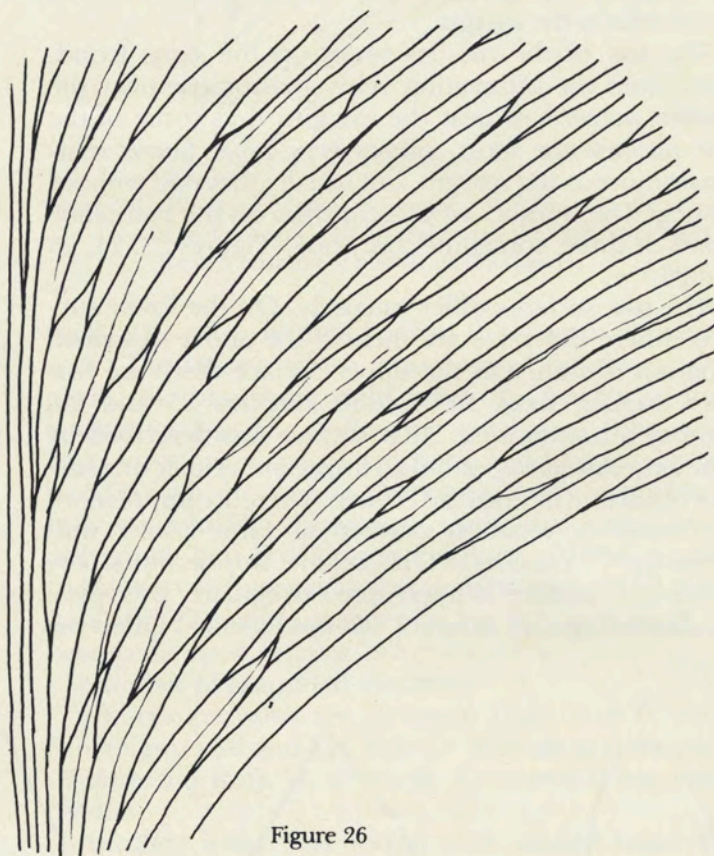


Figure 26

Figures 23–26. *Glossopteris pseudocommunis* Kovács Figure 23. Catalogue no. H.I. 76; Figure 24. Catalogue no. H.I. 175; Figure 25. Catalogue no. H.I. 27a; Figure 26. Catalogue no. H.I. 27a. Showing venation.  $\times 2,5$  approx.



Fifteen fragments were found. One base and three apices were preserved. They were large fronds, some of them 10 cm broad. No one fragment was sufficient to judge the length and shape. Two apices were obtuse and one rounded, emarginated. The base was truncate.

The fronds have no midrib, but parallel veins in the middle. Otherwise the venation is as described by Feistmantel (1881).

Srivastava (1956, p. 4) described the cuticle of an incomplete specimen, which he identified as *G. cf. divergens* Fstm. His photographs do not exhibit the

characters mentioned by Feistmantel, i.e. the divergent course of the veins and the short meshes close to the middle line.

#### ACKNOWLEDGEMENTS

Thanks are due to Dr. J. F. Enslin, the Director of the Geological Survey, Pretoria, and to Dr. A. W. Keyser, the chief geologist of the Palaeontological Department for permission to publish this paper. I am grateful to Dr. S. H. Haughton for critical examination of the manuscript, to Dr. B. de Winter and to Mr. R. Ellis for many discussions of botanical questions. To talk over the taxonomical problems with Dr. S. Endrödy-Younga was a great help. The figures were drawn by Mrs. R. Fregona, who with her critical observations helped to improve the descriptions. I am thankful to Dr. C. R. Hill, British Museum, for checking Pant's holotypes of *G. fibrosa* and *G. hispida*, to Prof. Dr. J. P. Lehman, Museum, Paris, for sending the photograph of the holotype of *G. indica*, to Dr. S. Endrödy-Younga for making the photographs, to Mr. J. J. Brits for allowing me to collect on his farm, to Prof. Dr. W. Remy, to the Plant-systematic Institute of E. L. University, Budapest, and others for sending the copies of the original literature.

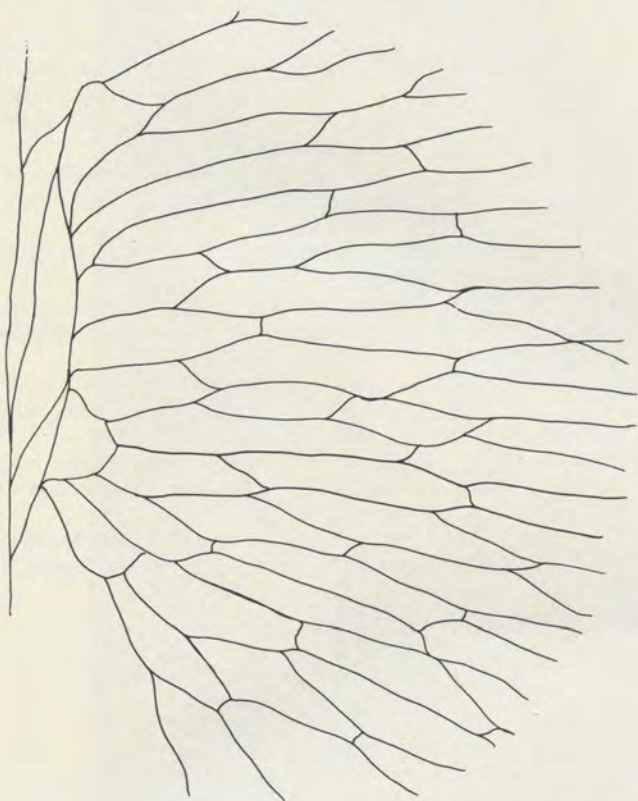


Figure 27. *Glossopteris divergens* Fstm. Portion of the frond (M.II. 65) showing the divergent course of the veins. x2 approx.

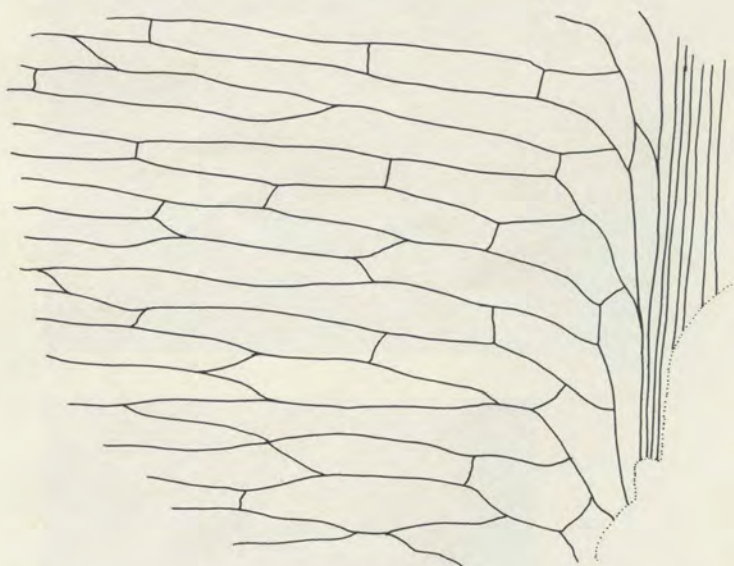


Figure 28. *Glossopteris divergens* Fstm. Portion of the frond (M.II.68) showing the short meshes near to the parallel middle veins. x2 approx.

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## PLATE I

Ia



Ib



## PLATE I

- (a) *Glossopteris ampla* Dana. Catalogue no. H.I. 171.  
 (b) *Glossopteris communis* Feistmantel, apex. Catalogue no. H.I. 67.  
 (c) *Glossopteris indica* Schimper, apex. Catalogue no. H.I. 102.

Ic





II a



II c

## PLATE II



II b



II c



II d



**PLATE II**

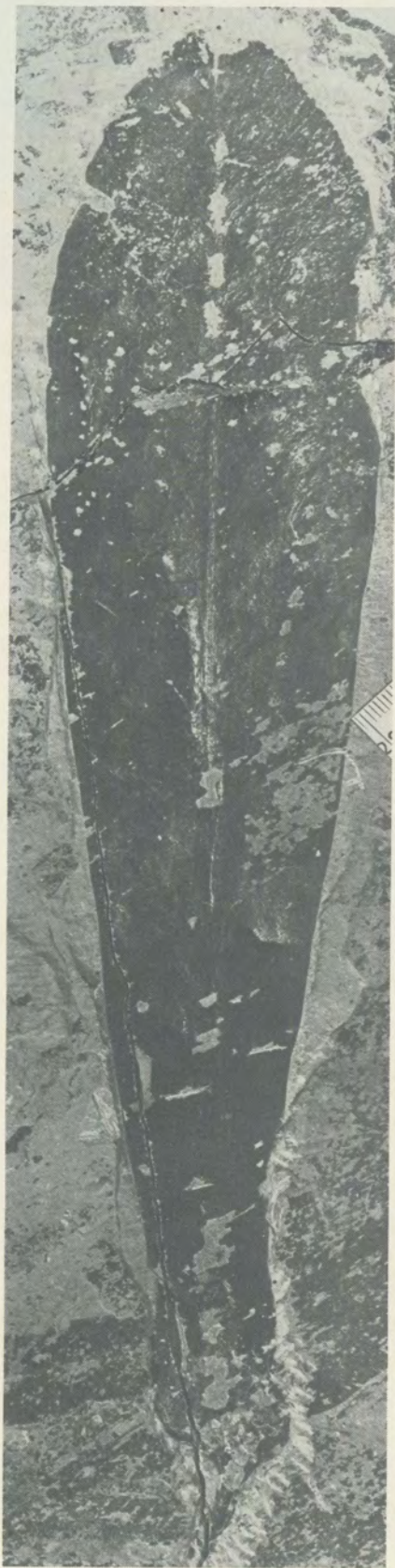
- (a) *Glossopteris pseudocommunis* Kovács paratypes, one apex, one base with petiole, an almost whole leaf, x1. Catalogue no. H.I. 29.
- (b) *Glossopteris pseudocommunis* Kovács, Holotype with the "Rubidgea" surface, Catalogue no. H.I. 103a.
- (c) *Glossopteris pseudocommunis* Kovács, Holotype, counterpart of H.I. 103a. Catalogue no. H.I. 103b.
- (d) *Glossopteris pseudocommunis* Kovács paratype with "fibres". Catalogue no. H.I. 172.
- (e) *Glossopteris taeniopteroides* Feistmantel, apex. Catalogue no. H.I. 150.



III b

## PLATE III

III a



III c



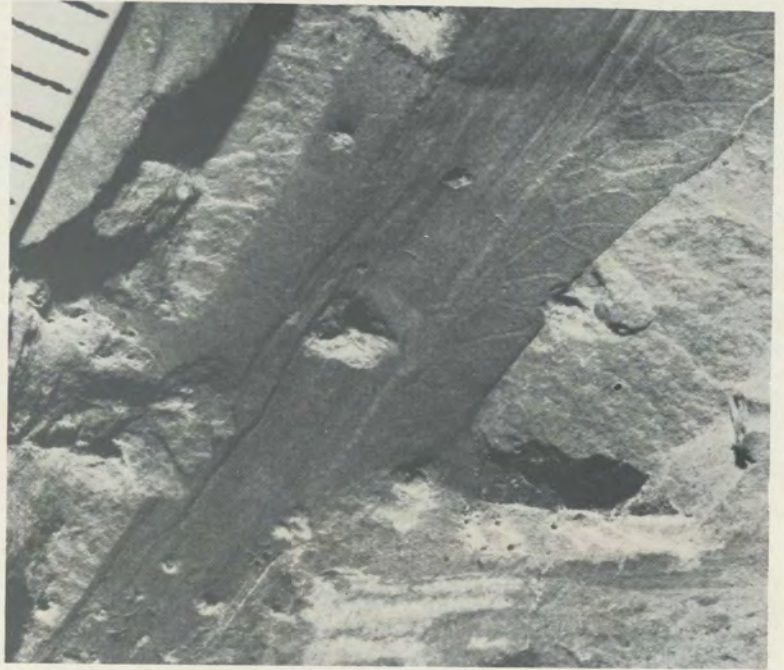
**PLATE III**

- (a) *Glossopteris taeniopteroides* Feistmantel. Catalogue no. H.II. 57a.
- (b) *Glossopteris taeniopteroides* Feistmantel, apex, x2. Catalogue no. H.II. 160.
- (c) *Glossopteris taeniopteroides* Feistmantel, two bases, one with fructification. Catalogue no. H.I. 4a.

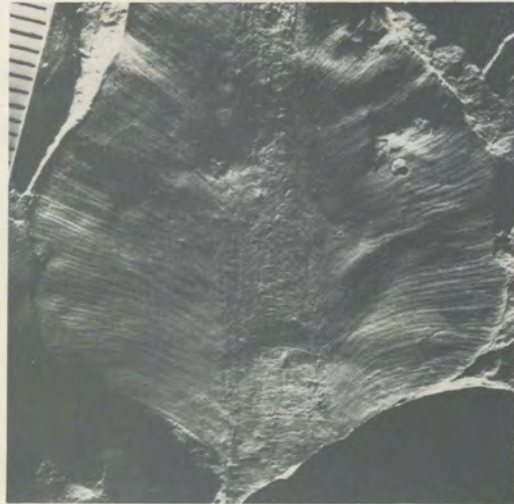




IV b



IV c



IV a



IV d



IV e

PLATE IV



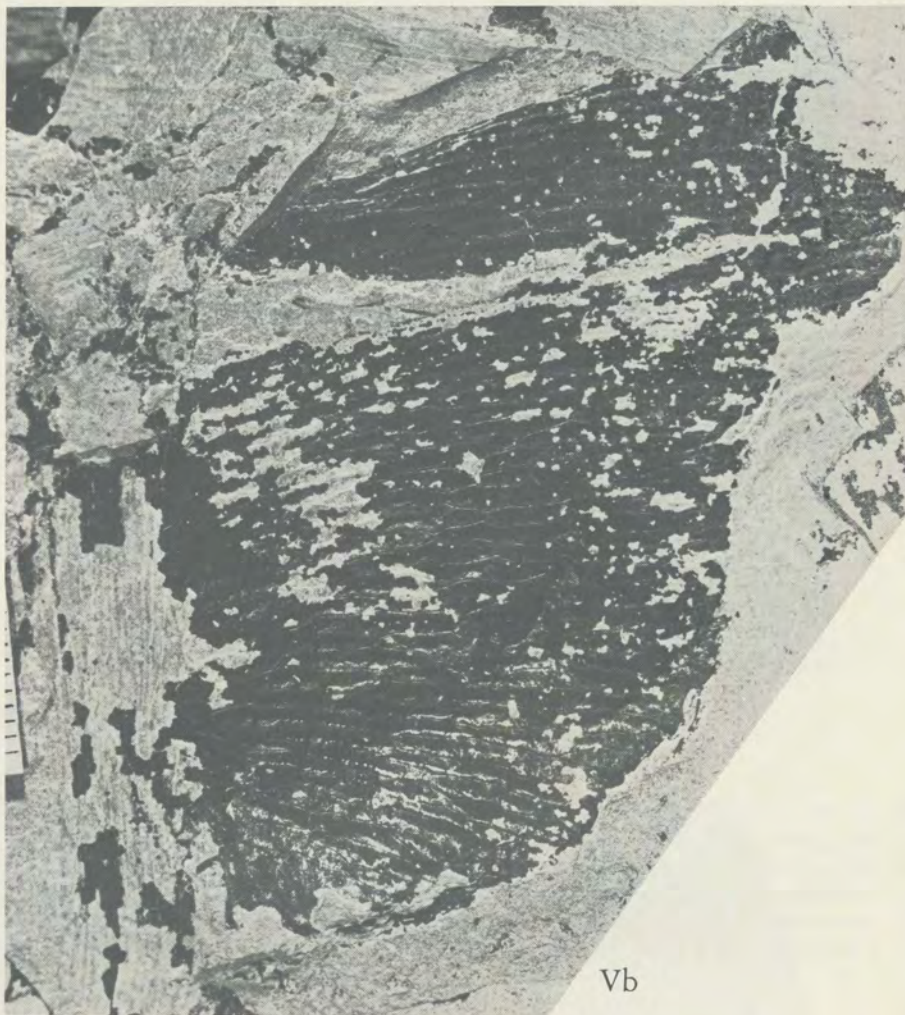
**PLATE IV**

- (a) *Glossopteris taeniopteroides* Feismantel, lyrate base. Catalogue no. H.I. 16.
- (b) *Glossopteris damudica* Feismantel. Catalogue no. H.I. 126.
- (c) *Glossopteris damudica* Feismantel, enlargement, showing "spurs". Catalogue no. H.I. 126.
- (d) *Glossopteris damudica* Feismantel. Catalogue no. H.II. 174.
- (e) *Glossopteris browniana* Brongniart, x2. Catalogue no. H.I. 15.



## PLATE V

Va



Vb



Vc



**PLATE V**

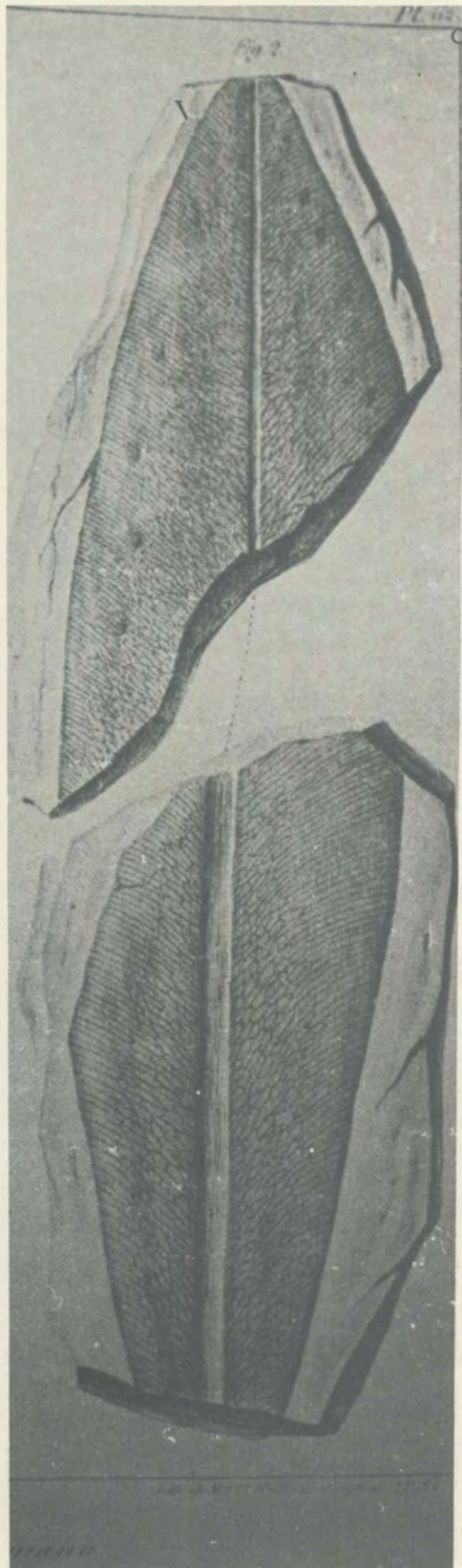
- (a) *Glossopteris divergens* Feistmantel, fragment with base. Catalogue no. M.II. 66.
- (b) *Glossopteris divergens* Feistmantel, base. Catalogue no. MII. 65.
- (c) *Glossopteris divergens* Feistmantel. Catalogue no. M.II. 67.



## PLATE VI

VIa

VIb





**PLATE VI**

(a) Holotype of *Glossopteris browniana* var. *indica* Brongniart, xl. No. 506, Muséum d'histoire naturelle, Paris, and (b) its drawing from: Brongniart, Hist. Végét. foss. 1830, Plate 67, Figure 2.



# SEVERAL NEW FORMS OF GLOSSOPTERIS FRUCTIFICATIONS FROM THE BEAUFORT DAPTOCEPHALUS-ZONE (UPPER PERMIAN) OF NATAL, SOUTH AFRICA

by

Anna K. Benecke

## ABSTRACT

Fertile material, consisting of 27 specimens showing 29 fructifications from Mooi River and 46 specimens showing 98 fructifications from the Loskop site, is described. An emended generic diagnosis of *Dictyopteridium* is given; specimens belonging to *D. sporiferum* Feistmantel and *D. flabellatum* sp. nov. are described, as well as *Fetura* gen. nov. including *F. natalensis* comb. nov. and *Scopus* gen. nov. containing *S. gibbosus*, *S. confertus*, *S. didiscus* and *S. obscurus* spp. nov.

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## INTRODUCTION

The history of the fructifications associated with the *Glossopteris* flora is a chequered one, particularly that of the fossils ascribed to *Dictyopteridium sporiferum* Feistmantel. Originally *D. sporiferum* was assigned to the ferns (Feistmantel, 1881), then it was described as a fleshy rhizome with caducous hairs by Zeiller (1902) and now it is generally accepted as being the fructification of one of the species of the form-genus *Glossopteris*. With a change in the grouping of the fructifications the interpretations of their morphological structures have also varied. The round markings were interpreted as sori (Feistmantel, 1881), as marks left by rootlets (Zeiller, 1902), as seed cushions (Harris, in Plumstead, 1952) and as non-specific sacs (Rigby, 1971). At the same time the gross morphology has varied from a flat leaflet (Feistmantel, 1881), a round rootlet (Zeiller, 1902), a flattened reproductive structure (Maheshwari, 1965) and a cone without protection (Surange and Chandra, 1974); the last authors in 1975 consider it as a cone with protec-

tion on one side, the protective body being referred to as a "fertile scale", which is somewhat confusing as it is in fact a sterile scale and usually referred to as a protective scale or half. Similarly, venation reported by Feistmantel (1881) was refuted by Zeiller (1902), re-reported by Maheshwari (1965), again refuted by Surange and Chandra (1973) who in 1974 agreed that they too could detect venation but ascribed it to wrinkling between the seed cushions and not to venation.

From this short history it can be seen that there is great uncertainty about the fructifications ascribed to *Dictyopteridium sporiferum*. If the function of the morphological structures were better understood, more accurate descriptions could be made and the probable morphology of the whole fructification would become evident. From the available evidence it may be taken that *D. sporiferum* is a female fructification, since Surange and Chandra (1973) figure areas on *D. sporiferum* specimens which show seed-like structures. Whether there are any male parts on the structure has not been proven.



The type of preservation probably plays a large part in the current confusion. Information has been taken from casts and moulds, compressions and impressions and possibly replacements. Each of these methods of preservation can give a different picture. Originally this may confuse the issue, but ultimately it should assist in an accurate reconstruction of the whole fructification, each form of preservation supplying additional information.

Rigby (1962a) drew up a schematic line of evolution for the *Glossopteris* fructifications. He does not include *Dictyopteridium*, possibly not recognizing it as a *Glossopteridalean* fructification. At present there is still no irrefutable proof of the association but *Dictyopteridium* is accepted as being one of the *Glossopteris* fructifications (Plumstead, 1958).

Rigby (1961) reported *Glossopteris* fructifications from New South Wales (Illawarra Coal Measures) which he classified as *Scutum thomasi* Plumstead, and some which were left unclassified. The remainder of the flora from that horizon is similar to that of the Raniganj stage of India, and not to the South African *Ecca*. Unfortunately there are no figures provided so to comment is difficult, but it might be possible that some of these fructifications are similar to the new ones described below from the *Daptocephalus* zone.

Two of the fructifications under discussion are referable to *D. sporiferum* and a new species, *D. flabellatum*, is instituted for specimens closely allied to *D. sporiferum*. A monospecific genus, *Fetura*, including *Plumsteadia natalensis* Lacey *et al.* 1975 is instituted for a form mainly represented from Mooi River. The remainder of the specimens are included in the new genus, *Scopus*, in four new species, where the apparent anomaly of four different types of fructification occurring on a single variety of *Glossopteris* leaf arises. This anomaly will only be resolved when the morphology is more perfectly understood. That these four "morphological species" merely show developmental differences of mature and immature forms is not thought likely as no intermediate examples have been found, and simple enlargement of the organs, i.e. growth, could not account for the change in appearance between one form and another. Whether male and female forms are here demonstrated, or possibly even some form of vegetative reproduction, is not now discussed. Only confusion arises from efforts of precisely determining morphological features that do not lend themselves to definition at this stage; the application of precise names implies specific functions for which there is no evidence at present. Thus knobs, sacs and bulges are left rather vague terms that do not imply any function nor do they imply inclusion into any specific group of plants.

## DESCRIPTION OF THE FOSSIL SITES

Two of the eighteen localities falling within the Lower Beaufort *Dactylocephalus* zone (Kitching, 1972) from which collections of fossil plants have been made yield

ed fructifications described below, namely the Loskop and the Mooi River National Road sites in Natal.

The Loskop material, coded N-Lk, was collected on the banks of the Little Tugela River, five kilometres beyond the Loskop railway siding on provincial road R35 between Estcourt and Bergville, just above the Courton bridge and the Soolaer monument. A small hill was used as a quarry for road metal, exposing a rich fossil horizon beneath a fairly substantial sandstone layer. The exposed fossil layer measured more than 200 metres long and continued into the hillside, and was approximately one metre thick. It is a diversified flora typical of the *Daptocephalus* zone *Glossopteris* floras, as listed below. Large quantities of fossilized material are so densely packed as to make it difficult to work in places. Many of the specimens described below were obtained from one large block, 80 × 50 × 20 cm. Unfortunately it was a loose block so it is not known which was the upper surface. This may have been relevant as *Dictyopteridium flabellatum* sp. nov. and the specimens belonging to the new genus, *Scopus*, appear to have been in separate layers, and establishing the embedding order might have thrown some light on their possible functions, such as a spring shedding of male (pollen) organs and summer-autumn mature fruit fall. Specimens similar to those from the large block were found scattered throughout the site, too infrequently to establish a geochronological succession.

The Mooi River National Road locality, coded N-MN, is on the N3 freeway on the first road cutting a few hundred metres beyond the bridge over Grantleigh stream after Mooi River towards Estcourt. The large collecting platform exposed during road excavations was destroyed subsequently by further road work, thus the fossiliferous horizon is now inaccessible in the hill side. The collection represents a varied but typical *Daptocephalus* zone *Glossopteris* flora as listed below. The preservation of some specimens is good but many show loss of detail due to *in situ* weathering. The matrix often has fine fissures running diagonally across the specimens. In a few instances these could be mistaken for venation. There is an abundance of fossils at the site but usually the specimens lie singly, hence associations (real or imagined) are difficult to determine.

A list of the genera found at the two sites is as follows:

### Loskop

*Sphenophyllum*  
*Sphenopteris*  
*Phyllothea*  
Ribbed stems  
*Noeggerathiopsis*  
Scale leaves  
*Glossopteris*  
Diverse seeds  
Diverse fructifications  
Wood  
*Vertebraria*  
Insect wing

### Mooi River

*Sphenophyllum*  
*Sphenopteris*  
*Phyllothea*  
*Noeggerathiopsis*  
Scale leaves  
*Glossopteris*  
Diverse seeds  
Diverse fructifications  
Wood  
Insect wings  
Bivalve



The material is now housed at the Bernard Price Institute for Palaeontological Research of the University of the Witwatersrand, Johannesburg.

#### Note on measurements

Measurements taken of all specimens which are more or less complete, or which illustrate a feature particularly well, have been considered and the range for a particular feature is given. Many of the dimensions are not considered diagnostic *per se*, and hence the figure has been given as approximate, making provision for dimensions outside the present observed range to be included.

Wing width is measured from the point where any surface pattern of the fructification ceases to occur and a structureless tissue follows to the margin.

Stalk length is taken from a point where the natural curve of the base of the fructification would cut across the upper end of the stalk.

The material was investigated under a binocular microscope with the light at a very low angle of incidence.

The numbers given in this paper to holotypes, paratypes and figured specimens are those which are written in ink on the individual specimens. This is because, at present, the fossil-plant collection in the Institute has not yet been systematically catalogued and enumerated. The numbers given in brackets (e.g. PB 005a) are those which are intended to be given in a contemplated catalogue of illustrated specimens.

### DESCRIPTION OF MATERIAL

Genus *Dictyopteridium* Feismantel 1881

*Dictyopteridium sporiferum* Feismantel

Figures 1, 4, 5, 6

Type species: *Dictyopteridium sporiferum* Feismantel 1881. Fossil Floras of the Gondwana System, Vol. III, pt. II, Plate 23A, Figures 4–6, 14. Figures 4 and 5 refigured by Surange and Chandra (1973), Plate 1, Figures 1 and 5.

#### List of figured specimens

*Lectotype*: Refigured in Surange and Chandra (1973), Plate 1, Figure 1, specimen No. G.S.I. 5210 which is Feismantel's specimen on Plate 23A, Figure 4 (1881).

Zeiller (1902), Plate 4, Figure 8, refigured by Surange and Chandra (1973), Plate 1, Figure 6.

Arber (1905), Figure 51, refiguring of Zeiller (1902).

Walkom (1922), Plate 9, Figure 48.

Rigby (1962b), Plate XI, Figure 4.

Saksena (1962), Plate 2, Figure 17.

Maheshwari (1965), Plate 1, Figures 3 and 4.

Surange and Chandra (1973), Plate 1, Figures 2 and 3.

Surange and Chandra (1974), Plate 2, Figure 3.

Holmes (1974), Plate 8, Figure 14.

Surange and Chandra (1975), Plate 8, Figure 20 (counterpart of 1974 specimen).

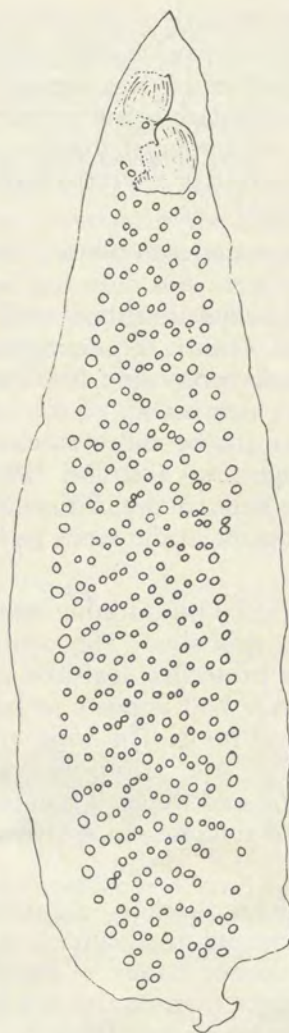


Figure 1. A complete specimen of *Dictyopteridium sporiferum* showing seeds exposed at the tip, the randomly distributed discs (knobs not shown), the wing and the stalk.

### Description and comparison

From all the specimens comprising this collection only two are referable to *Dictyopteridium sporiferum* Feismantel: a complete specimen from Mooi River, N-MN 895 (PB 002) (Figures 1, 5 and 6), and a tip on the reverse side of N-Lk 410 (PB 001) from Loskop (Figure 4). The complete specimen is lanceolate tending to oblong-lanceolate tapering from the upper half. Tip acute, base truncate, short stalk present. There is a very narrow wing around the whole of the raised central area. The surface of the central area appears to have been fleshy and smooth except for randomly distributed slightly recessed structures or discs. The discs are small convexly flattened bodies of about 0.5 mm diameter, with slightly pitted surfaces compared with the smooth surface of the surrounding area. Each disc shows centrally a very faint secondary protuberance or knob, approximately 0.15 mm in diameter or a third that of the disc (Figure 4). Figure 2a shows an envisaged surface cross section of *D. sporiferum*. The mode of attachment of the compound disc to the surface of the central area is not known. In view of the fact that no missing or misplaced discs were observed, the at-



tachment is shown as fairly solid, although there is no proof that the discs were not further undercut and thus more tenuously attached to the main surface. The discs are arranged more regularly along the margin of the raised central portion and are very slightly larger than the rest. There does not appear to be any other difference between the central and lateral discs.

At the tip (Figures 5, 6) the covering layer comprising the smooth fleshy area with discs has been torn away and two flattened bodies that show seed-like striations have been exposed. On the remaining area there is no indication of underlying seed-like bodies, further suggesting a fleshy consistency of the covering layers. These seeds appear to be more rounded than those figured by Surange and Chandra (1973). The discs could hardly have been seed cushions as Surange and Chandra (1973) suggest as the seeds lie below the surface of these discs.

There is no evidence of a double nature to the two fructifications here described. The counterpart which may have shown a protective 'leaf-like' structure is not preserved. The fertile half appears to have been a bilaterally symmetrical body. The wing appears to be a uniform structure, not composed of projecting ovuliferous scales or seed wings. It is in organic connection with the raised central area splaying out along its sides.

The specimen from Loskop (Figure 4) shows the same surface structuring and patterning as that from Mooi River. The double nature of the disc and knob arrangement is clearer than on the first specimen. The wing area is poorly preserved. There is no evidence of underlying seeds. The fructification lies at a slight angle to the mid-rib of an underlying *Glossopteris* leaf with open reticulate venation, that opens out to nearly right angles at the margin. Whether there ever was any connection between this leaf and the fructification can only be surmised, but the alignment of the fructification with the mid-rib is suggestive of such an association.

The two specimens described above are comparable with those given in the list of figured specimens. These, under the present system of classification, are all referable to *Dictyopteridium sporiferum* Feistmantel, which appears to be a rather rare form of fructification.

Surange (1966) reports *D. sporiferum* from the Talchir Coalfield, Barakar stage, Damuda series, and the Karanpura coalfield, Raniganj coalfield and South Rewa Basin from the Raniganj stage, Damuda series, India. The Australian specimens come from the Illawarra Coal Measures (Holmes, 1974) and the Baralaba Coal Measures (Walkom, 1922).

White (1962) reported fertile material which was interpreted as a gradation of normal *Glossopteris angustifolia* leaves through a male stage which would correspond to *Dictyopteridium sporiferum*, and finally to a female stage. The progressive modification of the leaves to increased fertility is supported with schematic line drawings. In the text it is mentioned that all stages are observed in the fossil form. White (1963) figured the

stages (Plate 22, Figures 1–5) including all in the new species *Lidgettonia australis* with no further mention of a similarity of the male stage to *Dictyopteridium sporiferum* Feistmantel. This appears a more satisfactory interpretation as the figure (Plate 22, Figure 5, White, 1963) does not show the discs associated with *Dictyopteridium*. On Plate 24, Figure 12, White (1963) figures a fragment of *D. sporiferum* which if correctly determined shows a very large wing.

Plumstead (1972) reports the occurrence of *D. sporiferum* from a borehole sunk at Somkele. The figures (Plate 5, Figures 1, 2) show leaf-like structures with protuberances that do not fall within the present limits of the genus *Dictyopteridium* but possibly resemble more White's (1962) material discussed above.

Total length: 43 mm; Stalk length: 2 mm; Diameter discs: 0.5 mm; breadth: 12 mm; Stalk breadth: 1 mm; Diameter knobs: 0.15 mm; Wing width: 2 mm.

Disc density approximately 150–172 discs/10 mm<sup>2</sup>.

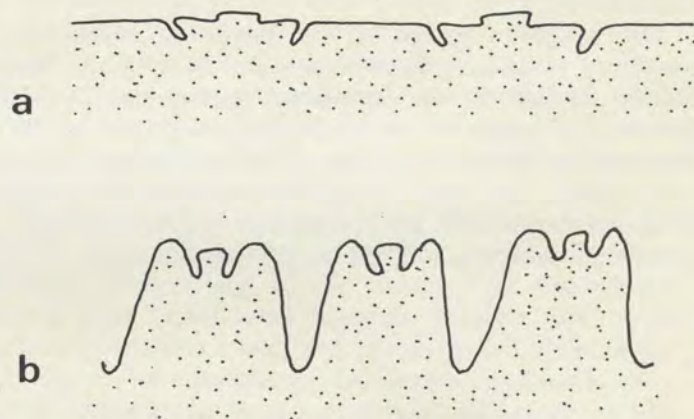


Figure 2. Envisaged cross section of (a) the compound, slightly recessed discs of *Dictyopteridium*; (b) the sacs indented to accommodate the simple discs of *Fetura*.

Thanks must be expressed to Surange and Chandra (1973) for publishing photographs of Feistmantel's 1881 original specimens and also of Zeiller's 1902 specimen. It is hoped that this example will be followed by others who have access to type specimens that have been inadequately figured in the past.

#### *Dictyopteridium flabellatum* sp. nov.

Figures 7–24 and 88

Holotype N-Lk 424 (PM 005a), counterpart N-Lk 360 (PB 005b), Figures 9, 10.

Paratypes N-Lk 406 (2) and counterpart (PB 011a, b), Figures 19, 20, 21, N-Lk (PB 008) Figures 13, 14.

#### *Specific diagnoses*

Fructification double, bi-laterally symmetrical, oblong-lanceolate; tip acute, base truncate gathering into stalk area; from several entry points at base an acute dichotomous vein-like pattern in high relief of grooves with swollen areas between them curving out-



wards at approximately 15°, swelling further to form an ordered array of elongated sac-like swellings along the margin, which form an escarpment ending in a wing; over the entire central raised portion on swollen areas between grooves are randomly scattered discs with knobs, not recessed into depressions. Protective half has reverse relief of fertile half, wing area tends to be broader.

#### Name derivation

Flabellatum (L) = fan shaped. Dichotomizing grooves show fan-shaped pattern.

Total length: 34–35 mm; breadth 5–14 mm: Stalk when present: length 1.5–3 mm; breadth 2 mm: Wing width: 0–2 mm.

Disc diameter approximately 0.4–0.5 mm.

Knob diameter approximately 0.15–0.2 mm.

Swollen marginal bulges approximately 8–10/10 mm.

Disc density approximately 80–175/10 mm<sup>2</sup>.

#### Type locality

Five kilometres past Loskop railway siding, above the Soosilaer Monument on the Little Tugela River, Natal. *Daptocephalus* zone, Upper Permian.

### Description and comparison

There is no direct evidence that the dichotomizing grooves are veins as no vein structure is visible. The vein was possibly embedded in a fleshy surface with the tissue above the vein being less fleshy and hence forming a groove. The randomly scattered discs with knobs are clearly visible on the swollen ridges in Figure 14. Figures 19 and 20 show the wing area which tends to be broader on the protective half than on the fertile half. Figures 22–24 show two fructifications lying close together. By projecting their bases it appears that the two specimens joined basally. It is proposed that the specimen closest to the scale in Figure 24 (and enlarged in Figure 22) is the fertile head while the other specimen in Figure 24 (and enlarged in Figure 23) is the protective half of what was originally one reproductive body. Maheshwari (1965) figured a specimen (Plate 1, Figure 2) of *D. sporiferum* which shows the same arrangements for the two halves.

Figure 12 is a slightly laterally compressed specimen that shows the lateral sacs from an “escarpment” view. In well-preserved specimens the marginal swellings show no particular surface patterning (Figures 15, 18, 20). In Figure 8 the margin is poorly preserved (partial rotting before preservation?). On the upper side of the illustration are a series of five solid round bodies in the place of the marginal swellings. These round bodies show no particular structure that could assign to them a special function, but their order and position appears significant. Figure 9 has a portion of the high relief surface missing on the left-hand side revealing a row of about eight flat oblong areas lying side on (enlarged in Figure 88) their long axis at right angles to the margin, thus not corresponding with the orientation of swollen sacs on the upper surface. These flat areas are clearly

striated. They do not show any particular thickness, nor do they appear to be seeds. The stalk-like structure to the inside of these striated bodies is on a lower level and is probably not part of the fructification. At the very tip a small area is also missing (still attached to top of Figure 10), revealing a similarly faintly striated area below it. How to reconcile the round structure from Figure 8 with that of the striated areas in Figure 9 is not clear.

The tip of the specimen shown in Figure 9 broke off (arrowed), showing a cross sectional view of the specimen. From this it appeared that on the left-hand side the main surface folded over, continuing as the lower striated surface. The details on the right-hand side were obscure. It is thus not clear whether the cross section is as shown in Figure 3a or 3b.

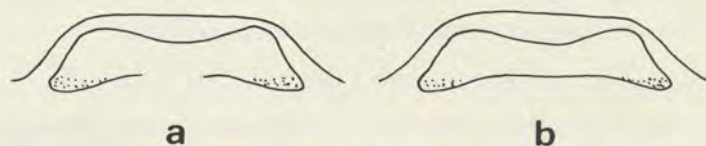


Figure 3. Possible cross section of *D. flabellatum* with an overlying protective cover; (a) an open, folded over structure, and (b) a closed structure.

With the tenuous evidence on hand 3a is favoured.

These fructifications are not found closely associated with any leaves. All the specimens to date come from Loskop.

It is suggested that the Maheshwari (1965, Plate 1, Figure 5) specimen may be included in this group due to the vein-like relief shown on the Canada balsam transfer. Without being shown what the specimen looked like before a transfer preparation was made, it is difficult to assess whether the vein-like relief was in fact not visible on the upper surface, so the interpretation, that it represents the “other” (i.e. lower? reverse?) surface only, is not clear. The observation by Maheshwari (loc. cit.) that the “scars” (discs) are not present on the ridged and grooved surface is not in accordance with the evidence as noted in *D. flabellatum* where the discs with knobs are found randomly distributed on the ridges. Thus the inclusion of Maheshwari’s (1965, Figure 5) specimen into this group is tentative.

In the present collection there are enough specimens showing consistent distinguishing features to warrant the institution of a new species. The general shape of the fructification, and more particularly the details of the discs with knobs bring together the two species under *Dictyopteridium*. *D. sporiferum* is recognized as a female fructification; thus the possibility exists that *D. flabellatum* is its male counterpart, although there is no direct evidence to support this.

The position of the genus *Isodictyopteridium* Rigby 1972 is unclear. Without seeing Walkom’s 1922 specimen the opinion of Surange and Chandra (1974) is accepted that *Isodictyopteridium* should be merged with *Dictyopteridium* again. The specimens figured by Holmes (1974) and included in *Isodictyopteridium* are strange in



showing a thick central strand; however, Maheshwari, (1965, Plate 1, Figures 1–2) shows a similar strand. Figures 11 and 12 (Holmes, op. cit.) do not show a clear surface, but Figure 13 (Holmes, op. cit.) could possibly belong to *D. sporiferum*.

Some confusion appears to have arisen about the surface structure of *Dictyopteridium*. The actual fructification or fertile half has discs with knobs while the counterpart shows a pitted surface — the negative image of the fertile half. The pitted surface is clearer on a reverse mirror image of the fertile half and less clear though still discernible on the inner surface of the protective half.

Following on the discussions of both *D. sporiferum* and *D. flabellatum* it is felt that the most recent diagnosis for the genus as given by Surange and Chandra (1973) needs revision.

#### Genus *Dictyopteridium* Feistmantel 1881

Diagnosis Surange and Chandra, 1973, p. 128

A pedicellate female fructification of linear-lanceolate shape about 3.5 cm long and 1 cm broad; the cone axis or receptacle covered over with round to oval seed cushions or seeds, seed cushions or seeds crowded on the cone axis in close spirals, seeds arranged on two margins in regular rows, one below the other; seed small, oval with obtusely pointed neck and round or concave chalazal end.

Emended diagnosis: *Dictyopteridium* Feistmantel 1881

Fructification bi-partite, bi-laterally symmetrical, lanceolate to oblong-lanceolate, tip acute, base truncate, short stalk present; very narrow wing surrounds raised central portion; randomly scattered discs with knobs attached to outer surface over central area of fertile half, protective half usually shows reverse relief of fertile half on inner side, with a broader wing area around the outside.

Genus *Fetura* gen. nov.

Type species *Fetura natalensis* comb. nov.

#### Generic diagnosis

Bi-partite, stalked fructifications consisting of leaf-like protective part and fertile head composed of sacs with depressions to accommodate simple discs. Sacs ordered along the margin; very narrow wing surrounds fertile head. Fructification attached to a *Glossopteris* leaf.

*Derivation of name:* *Fetura* (L) = breeding, bringing forth of young.

*Fetura natalensis* comb. nov.

Figures 25–41

*Synonymy:* *Plumsteadia natalensis* Lacey et al., 1975. Figures on p. 397.

#### Specific diagnosis

Fructifications bi-partite, lanceolate oblong, tip obtuse to acute, base truncate ending in a squat stalk; cen-

tral head of fertile half covered with randomly distributed sub-circular sacs, touching at their bases, free higher up, sac top depressed to accommodate disc shaped structure; sacs radiating out from upper end of stalk poorly defined, elongated, lacking the depressions with discs in most cases; sacs along margin regimented, tending to be elongated with the long axis of the sac at approximate right angles to the main axis of the fructification, depression on the inner end to accommodate disc; disc size more or less constant on both central and lateral sacs; narrow wing sometimes visible; protective half of fructification leaf-like, has little relief over entire surface, only slight depressions to accommodate sacs from fertile half, venation-like striations sometimes visible; fructification attached to mid-rib of a *Glossopteris* leaf, towards base of lamina.

Total length: 13–25 (29)\* mm. Wing width: 0–3 mm; breadth: 4–10 mm. Stalk length: 1.5–2 mm; breadth: 1–2.5 mm.

Disc diameter approximately 0.2–0.4 mm.

Central sac diameter approximately 0.6–0.8 mm.

Lateral sac length approximately 1.0–2.5 mm.

Lateral sac width approximately 0.8–1.5 mm.

Central sac density approximately 104–175 sacs/10 mm<sup>2</sup>.

Lateral sacs 10–14 sacs/10 mm.

Many of these dimensions are not considered diagnostic and hence the figure has been given as approximate, making provision for dimensions outside the present observed range to be included.

#### Type locality

Mooi River National Road, road cutting a few hundred metres after Grantleigh Spruit Bridge on the N3, shortly after Mooi River on the way to Estcourt. *Daptocephalus* zone. Upper Permian.

#### Description and comparison

The central head of the fertile half of the fructifications referable to *F. natalensis* is covered with more or less randomly distributed roundish sacs (Figure 36) which are touching at the base, sometimes crowding one another and are free higher up. The sac tops are depressed to accommodate a simple disc-shaped structure (Figure 35). On the sac top a rim is formed, surrounding the depression, which can give the impression of a circular structure (the rim) round a central body (the disc). Many of the descriptions of this phenomenon give the impression of “compound discs” as in *Dictyopteridium*, where the disc with knob has a similar concentric appearance, of a totally different origin.

The sacs radiating out from the upper end of a short stalk are poorly defined; they are elongated and lacking a depression with disc in most cases. The sacs along the margin are regimented and tend to be elongated with the long axis of the sac at approximate right angles to the main axis of the fructification (Figure 27). The

\* refers to specimens figured 30 and 31, see below.



lateral sacs have a depression on the inner end to accommodate the discs. The disc size is more or less constant on the central and lateral sacs. A narrow wing is sometimes visible, apparently the undifferentiated continuation of the lateral sacs (Figure 32). In size it is just larger than the thickness of the central head. Figure 37 shows an abnormally large wing at the tip but has a few ill-defined sacs with discs, and is thus placed in this group. The protective half of the fructification has little relief over its entire surface, showing only slight depressions to accommodate the sacs from the fertile half (Figures 25 and 30). It appears to have venation which on closer inspection shows no vein detail either dichotomising or anastomosing. It may be fine venation or an accident of preservation. Figure 26, being the fertile half does not show this venation-like pattern. Figures 28 and 29 are interpreted as showing the fructifications covered by the protective half, the general sac lay-out corresponding with the other specimens of the species, but all disc detail obscured. Figure 29 shows one of the few specimens from Loskop placed in this group which is predominantly represented by samples from Mooi River.

The specimen shown in Figure 38 has been retained in *F. natalensis* as the poorly defined sacs show discs, although it superficially resembles *Scopus gibbosus* forms.

*F. natalensis* has simple discs unlike the *Dictyopteridium* species which have compound discs. Figure 2b shows an envisaged cross section of a *Fetura* sac with disc, the actual mode of attachment is not known and the internal configuration of the sac is not known, although it may have been a hollow sac with inclusions. The sac appears to have been a soft structure judging from the radiating tension gathers round the recessed disc (an upholstery button effect) visible on Figure 26 on the seventh sac from the bottom right hand side (arrowed). Most sacs do show this effect under a microscope. On the same specimen the ninth sac down, top right (arrowed), shows the only observed sac with a missing disc. The sac appears hollow and deflated. The shedding of discs does not seem to be the normal occurrence, as all the other sacs show the discs firmly in place.

The specimens figured in Figures 30 and 31 are counterparts showing two different surfaces of protective and fertile halves respectively. Figure 31 shows very poorly defined sacs and discs but a few are visible on the right hand side thus placing it under *Fetura*. At 29 mm length it is 4 mm larger than the largest Mooi River specimen. It is thus provisionally placed in this group. Figures 33 and 41 (counterparts) are poorly preserved but the sacs along the margin make them referable to *Fetura*. They show a possible triple structure with two protective halves and a central fleshy, fertile portion. The triple structure may be an illusion caused by the tearing of the fleshy portion. These specimens may be immature examples.

Figure 34 shows a fragment of a typical *F. natalensis* lying in alignment with the mid-rib of a *Glossopteris* leaf. Where the fructification is missing there is a clear

convex impression on the lamina, with lateral sacs well defined. The lamina is not altered beneath the fructification, the veins clearly following their natural course from the well-defined mid-rib. The manner in which the lamina has been moulded suggests that the fructification must be a rigid structure. It is puzzling that the mould is convex, suggesting a concave back surface for these fructifications. A more substantial fructification could have been imagined which would have left a straight or even slightly concave impression on the lamina. The supporting tissue might be in this case merely a thin rigid leaf-like or bract-like structure forming a base for the sacs which are borne only on the upper surface, the thickness of the fructification being the thickness of the sacs. This interpretation could also hold for the type specimen of *Plumsteadia microsacca* Rigby, 1962b, Plate XI, Figure 5. However, the original interpretation given was that there is an adnate organ (the convex mould area) "developed from expansion and rupture of the mid-rib" (op. cit., p. 344). The mid-rib in Figure 34 is so clear that it cannot be described as expanded or ruptured. The mid-rib is not so clear in Rigby's (1962b) figured Australian specimen.

The *Fetura* specimens are most similar to the *Cistella*, *Plumsteadia* and *Scutum* groups. The type specimens for *Cistella* Plumstead and *Scutum* Plumstead were re-examined. The sac details are difficult to observe in the material preserved from Vereeniging, which includes these type specimens, as the grain size of the matrix begins to obscure the fine detail. The sacs on the *Scutum* species show depressions, with some mass in the depressions; whether these are comparable to the discs on *Fetura* is difficult to assess. However, the very large fluted wing of the *Scutum* group excludes *Fetura* from *Scutum*, *Fetura* only having a very narrow wing or 'wing-like' area. *Cistella* and *Plumsteadia* have no wing. The sac details of *Fetura* are different from those described by Rigby (1971, Figures 2a-c) for *Plumsteadia*, where they are described as being unexploded and exploded sacs in the course of developmental ripening. There is no reference to discs on these sacs nor do the figures show any such structures. Amongst all the sacs on the *Fetura* specimens only one showed a missing disc (Figure 26) and the resultant structure could hardly be referred to as an exploded sac as the edge of the depression is smooth.

*Plumsteadia* Rigby 1962b has been redefined (Rigby 1969, paper not available). The Rigby 1971 definition is very different from the first one and is meant to absorb *Cistella*. The limits of the genus *Plumsteadia* have become confused and at this stage it would appear that *Cistella* is not synonymous with *Plumsteadia*. *Cistella* Plumstead 1958 is a genus instituted for fructifications from the Lower Gondwana horizons (Ecca series in South Africa). *Cistella stricta* does not show indented sacs with discs but *C. waltonii* has an arrangement of sacs similar to the *Fetura* arrangement of regimented sacs along the margin and random sacs in the centre. The *C. waltonii* sacs have a central cavity, somewhat larger and deeper than the depression on a *Fetura* sac; there does not appear to be a disc in the cavity.



The *Daptocephalus* zone plants are very much younger than the *Ecce* plants and, although they are still referred to as a "*Glossopteris* flora", they differ from the lower flora and thus if specimens show slight differences a new genus should be instituted rather than stretching the generic bounds over such long time intervals.

Lacey *et al.* (1975) placed identical specimens, collected from the same locality (Mooi River) in the genus *Plumsteadia* which for differences in sac and disc arrangement is unacceptable (see above). In their diagnosis of *Fetura natalensis* (= *Plumsteadia natalensis*) sp. nov. there is no mention of a protective half to the fructification, nor of a short stalk. The presence of a wing is problematical; there is definitely a lateral area below the escarpment, formed by the lateral sacs, that is undifferentiated and very wing-like. It is not seen on all specimens, nor often on both sides of the fructification, and is very narrow. Whether it is referred to as 'wing-like' or as a 'wing' does not alter the fact that some such structure is visible on many, though not all, specimens. Lacey *et al.* (1975) separate *Dictyopteridium sporiferum* and *F. natalensis* on the basis of *D. sporiferum* being a cone (radially symmetrical) and *F. natalensis* "a flattened bifacial organ" (p. 399). The two genera are separable on the disc detail and the compound nature of *F. natalensis* — many sacs forming the fertile head. The specific name of *multiplex* was to have been used for these specimens. The comparison of *F. natalensis* with *Hirsutum dutoitides* Plumstead by Lacey *et al.* (1975) is not as close as they would suggest as the sacs on *H. dutoitides* do not have a regimentation as they do in *Fetura*.

The sac and disc differences between *Fetura* and both *Cistella* and *Plumsteadia* are considered diagnostic. None of the existing genera of fructifications can comfortably accommodate *Fetura natalensis*, thus a new genus is proposed.

*Scopus* gen. nov.

Type species *Scopus gibbosus* nov.

#### Generic diagnosis

Fructification usually bi-partite, consisting of a protective leaf-like organ and a bi-laterally to radially symmetrical compound reproductive structure; stalked, attached to the petiole of a particular species of *Glossopteris* leaf.

#### Derivation of name

*Scopus* (L) = a mark set up to shoot at; referring to several different types of fructification occurring on a single leaf type, and the comment this is likely to elicit.

*Scopus gibbosus* sp. nov.

Figures 42–45, 55–81, 85, 94

Holotype N-Lk 316 a and b, Figures 42 and 43 (PB 026) a and b.

Paratypes N-Lk 318, Figure 73 (PB 051).

N-Lk 370 a and b, Figures 72 and 71 (PN 050) a and b.

N-Lk 315a, PTO Figure 56 (PB 035).

#### Specific Diagnosis

Fructification bi-partite, rather narrowly deltoid ovate to lanceolate and oblong; tip acute to rounded obtuse, base sub-cordate or truncate, stalk present; fertile head winged, with centrally random, rounded or flattened bulges under a thin covering layer; protective half has same shape range as fertile half, winged, shows various degrees of being keeled along central axis.

Total length: 20–38 mm; breadth: 5–14 mm. Stalk length: 0–7.5 mm; breadth: 1.5–4 mm. Wing width: 0–3.5 mm.

Bulge size approximately 1–1.5 mm.

Distance between bulges approximately 2 mm.

Bulge density approximately 36–44 bulges/10 mm<sup>2</sup>.

#### Type locality

Five kilometres past Loskop railway siding, above the Sooi laer Monument on the Little Tugela River, Natal. *Daptocephalus* zone, Upper Permian.

#### Derivation of name

*Gibbosus* (L) = bulgy, referring to the central head showing bulges covered by a thin integument.

#### Description and comparison

The fructification consists of two separable portions ranging in shape from rather narrowly deltoid ovate to lanceolate and oblong. The tip is acute to rounded obtuse, the base sub-cordate to truncate with a thick stalk more or less centrally attached to the base. With the protective half removed the winged (Figures 71, 72) or unwinged (Figure 66) fleshy head shows random rounded (Figure 59) or flattened bulges (Figures 75–77) under a thin covering layer over the central portion. The protective half has the same shape range as the main body. It is preserved as either a convex (outer surface) or concave (inner surface) structure, winged especially towards the tip (Figure 57): it may be keeled along the whole length of the main axis (Figure 63), only towards the tip (Figure 56) or not at all (Figure 57). The protective half appears to have been a fairly rigid structure and when both halves are preserved the stalk tends to be continuous with the protective half (Figures 57, 65 and 72), while the fertile half shows a break (Figure 71) or a tenuous attachment to the petiole of a *Glossopteris* leaf (Figure 55). The fructification attachment to the petiole appears to be almost immediately below the end of the lamina; this point is obscured by the overlying fructification, thus the exact mode of attachment is not clear. The fructification is free of the lamina as it lies at various angles to the mid-rib. With the protective cover lying over the fertile half all relief of bulges is obscured (Figure 63). Both halves range from more or less bi-lateral symmetry to definite asymmetry. In some instances the fructification is preserved in such a way as to suggest a leaf folded over along the mid-rib, enclosing the bulges within the folded area (Figures 74, 78, 79). The specimens showing this tendency are provisionally grouped under *S. gibbosus* as



there is insufficient evidence to separate them; they are not found associated with any *Glossopteris* leaf, and the stalk in Figure 74 is longer and thinner than usual, but the bulges appear to correspond to the general design of the species.

The *S. gibbosus* in Figure 64 is more laterally compressed than the other specimens. It shows that the structure tends to be bi-laterally symmetrical rather than cylindrical as was proposed by Surange and Chandra (1973) where *Dictyopteridium sporiferum* is described as "cone-like". The same authors in 1975 proposed that *Scutum* and allied fructifications have a lenticular shape.

The fertile half of *S. gibbosus* is nearly always preserved as a convex structure, though it may lie flat. If a wing is present it forms an escarpment off the sides of the raised portion. The cell pattern suggests that the surface of the covering layer and the wing are continuous. The wing is composed of large cells. The covering layer over the raised central head appears to be a fairly thin structureless layer (Figures 44, 59) which nevertheless obscures the detail of the bulges beneath, only showing them as bulgy rounded or overlapping flattened areas (possibly a developmental feature?). In two instances the layer has been torn away or damaged, exposing the bulges (Figures 73, 76, 77). In both the bulges are round flattened structures (tightly overlapping in Figures 76 and 77) suggestive of seeds, though not showing any of the characteristic striations frequently found on seeds. No evidence of a micropylar end or any other structure can be distinguished. In some examples there appears to be evidence of a third structure, a second protective part lying beneath the fleshy head (Figures 44, 45). Towards the tip (Figure 44) a fleshy portion has broken away, exposing a further layer. Similarly Figure 71 shows a portion missing from the base and another structure below it. These areas may be impressions of the reverse side of the head but they seem too definite for impressions and might thus be structures in their own right.

The wing in some examples (Figures 58, 67) tends to fold under the head on one side while being exposed on the other; in other examples it is visible at the tip and folds under the head just over halfway towards the base.

The specimen in Figure 43 shows a finely striated area on the torn part of the fructification (not visible on the photograph). Figure 94 shows a similarly striated "scale leaf" which is the only free-lying one observed. Whether this is merely a coincidence of similar striations on different structures or whether such small scale leaves are associated with the fructifications cannot be assessed, as these are the only two examples found.

The specimen in Figure 62 shows relatively little surface detail, but enough to suggest that it is not a protective half obscuring the fertile part, but rather the covering layer being fleshier than usual, or the bulges not well developed.

Figure 63 shows the only fructification associated with a cordate based leaf in this collection. From the keeled appearance of the specimen it is interpreted as

being the protective cover over the fleshy portion. The fact that it is on a slightly different leaf does not warrant separation from the group at this stage.

From Mooi River the specimen (Figure 80) does not show the features of the other groups but displays random bulges which places the specimen within the *S. gibbosus* group, although it is not quite typical. With this as the only Mooi River example there is not strong evidence for *S. gibbosus* occurring at that site.

The positioning of these fructifications is so consistently in alignment with the mid-rib of the leaf on the petiole that they must be in the original position, although actual organic connections cannot be demonstrated (Figures 42, 43, 58, 61, 62, 63, 69, 70, 73).

There are no examples of the fleshy, fertile and protective parts lying adjacent to one another. The specimens shown in Figures 55 and 56 are the closest to this, although certainly not touching, being a few centimetres apart on the same rock surface.

Surange and Chandra (1973, Plate 1, Figure 7) show a specimen that could be a protective half belonging to this category rather than to *Dictyopteridium sporiferum*, although no fertile halves of anything resembling *S. gibbosus* have been reported from India.

#### Description of the *Glossopteris* leaf variety to which the *Scopus* fructifications are attached

They are medium sized ob-lanceolate leaves with an acute tip, the lamina gradually merging into the petiole. There is a strong mid-rib, the lateral veins leave the mid-rib at a very acute angle and open near the centre of the leaf half to an angle of approximately 45°, the vein islands are distinct, elongated, the veins dichotomizing and anastomosing from three to five times between the mid-rib and margin, there are approximately eleven vein endings per 10 mm at the margin. Before a general revision of the Lower Beaufort (*Daptocephalus* zone) *Glossopteris* leaves is available, this leaf will remain as *Glossopteris* species. Figure 70 shows a fairly small but almost complete leaf specimen with the tip of a *S. gibbosus* on the bottom left.

#### *Scopus confertus* sp. nov.

Figures 46–54

Holotype N-Lk 315 a and b, Figures 46 and 47 (PB 028) a and b.

#### *Specific diagnosis*

Fructification bi-partite, narrowly oblong, apex subtruncate, base truncate; in some cases stout projections randomly radiate off the central body; short stalk present attaching fructification to petiole of a *Glossopteris* leaf; central head covered with tightly packed, randomly placed, oblong swollen bodies; protective half leaf-like.

Total length: 6–14 plus mm; breadth: 3–4 mm. Stalk length: 1.5 mm; breadth: 1 mm. Stout projection length: 1.5–2 mm.



*Type locality*

Five kilometres past Loskop railway siding, above the Soolaer Monument on the Little Tugela River, Natal. *Daptocephalus* zone, Upper Permian.

*Derivation of name*

*Confertus* (L) = crowded; referring to the oblong swollen bodies tightly packed over the fertile head.

**Description and comparison**

These narrowly oblong fructifications probably had a radially symmetrical fertile half; as in various specimens belonging to this group the preservation shows a three dimensional remain (Figures 46, 50, 52, 54). A short stalk attaches the fructification to the petiole of a *Glossopteris* leaf a small distance below the ending of the lamina (organic connection visible in Figures 46 and 47). The function of the stout projections radiating off parts of the central body is not known. The fact that only one specimen (Figures 46, 47) shows these projections suggests that they may have been of a transient nature, being shed at a later developmental stage. The mode of attachment of the projections to the central axis is not visible; they appear to have come out between the tightly packed swollen bodies that cover the central head. The nature and function of the oblong swollen bodies is not clear. They appear to be individually attached to the central axis, and do not have any encasing tissue. The sacs are distorted due to overcrowding, and they do not give the impression of being very resistant bodies, as in most cases there appears to have been some form of tissue disintegration before preservation; thus only the specimen figured in 46 and 47 show the complete sacs.

The protective half is visible in two instances (Figures 51, 54). Figure 51 shows a flattish leaf-like structure in possible organic connection with the continuation of the leaf mid-rib (probably on the petiole). Whether this connection is real or apparent is not clear as the stalk may only be closely appressed or adnate to the petiole. In Figure 54 the fleshy portion is lying on the protective half in a depression with a wing-like area spreading out on a level with the fleshy head (upper left of figure).

The specimen figured 48 and 49 is slightly different from the others, the oblong bodies appearing more swollen and overlapping but it appears to fit best into the *S. confertus* group and is thus included.

Figure 50 shows a fructification on the right hand side of a good specimen of the *Glossopteris* leaf variety to which the *Scopus* fructifications are attached. The leaves appear to be the same and yet *S. gibbosus* and *S. confertus* are two morphologically distinctive units with no intermediate specimens having been found; thus two morphological species or form-species are proposed. Whether they represent male and female reproductive units of the same plant or whether the differences are developmental with the intermediary forms not yet discovered is unclear. There is no evidence particularly to recommend either theory.

*Scopus didiscus* sp. nov.

Figures 69, 81–84, 93, 94

Holotype N-Lk 317 a, Figure 81 (PB 056).

Paratype N-Lk 369 a (5), Figure 83 (PB 062).

*Specific Diagnosis*

Fructifications double, quadrato-orbiculate, base slightly contracted, central area strongly obtuse-cuneate convex to almost flat; fluted wing-like area may surround central area, showing radially divergent from the central area dichotomizing vein-like striations.

Total length: 11–15 mm; breadth: 9–13 mm: Wing width: 0–3 mm.

Vein-like endings along margin approximately 14/10 mm.

*Type locality*

Five kilometres past Loskop railway siding, above the Soolaer Monument on the Little Tugela River, Natal. *Daptocephalus* zone, Upper Permian.

*Derivation of name*

*Didiscus* (L) = two plates, referring to the two apparently rigid concavo-convex disc-shaped bodies facing one another, forming a central cavity.

**Description and comparison**

The double disc-like fructification usually presents a convex view. The raised central area is strongly obtuse-cuneate convex (Figure 81) to almost flat (Figure 82(9)). There may be a fluted wing-like area surrounding the convex portion (Figure 81) or it may be absent (Figure 82(7)). Coming off the central area, more or less radially, are dichotomizing striations superficially vein-like but not showing any definite vein structure. The two halves of the fructification appear to be fairly firmly attached, as in three specimens they have remained together in spite of a gap allowing considerable sediment infill (Figures 81, 83, 84). No other structure appears to be preserved between these two halves.

Superficially Figure 82(9) appears to have a relatively long stalk. This is probably the petiole continuation from the leaf with which it is aligned, although it might be an adnate stalk. This specimen connects *S. didiscus* with the same type of *Glossopteris* leaf as the other *Scopus* fructifications, the positioning and alignment being the same; the other specimens do not show a stalk, merely a contracting of the base.

The specimens give the impression of being thin but rigid structures. The specimens are in close association with *S. gibbosus* and *S. obscurus*. The structure was possibly protective in function; whether it contained any of the other *Scopus* species cannot be deduced from the material on hand. The only fructifications to fall within the size range of the central cavity are the *S. confertus* forms; they, however, have their own protective halves, which do not resemble *S. didiscus* at all, and thus it seems unlikely that they should be connected.



There appeared to be a mass fall of *S. didiscus* as seen in Figures 93 and 94, whether this was seasonal or a freak of nature is not known.

*Scopus obscurus* sp. nov.

Figures 86, 87, 89–94

Holotype N-Lk 222 a and b, Figures 89, 91, 92 (PB 072) a and b.

Paratypes N-Lk 315 a and c, Figure 87 (PB 071). N-Lk 369 b (2), Figures 86 and 90 (PB 059).

#### *Specific diagnosis*

Fructifications thin, appearing fleshy, quadrato-oblong, tip obtuse to apiculate, base truncate with short stalk; slightly swollen “sacs” sometimes developed at approximately right angles to margin, giving a gently fluted appearance; if “sacs” absent structureless appearance results.

Total length: 15–22 mm; breadth: 11–13 mm. Stalk length: 4 mm; width: 1 mm.

Sacs at margin if present approximately 9/10 mm.

Sac width: 0,8–1,1 mm; length approximately: 1,5 mm.

#### *Type locality*

Five kilometres past Loskop railway siding, above the Sooiiaer Monument on the Little Tugela River, Natal. *Daptocephalus* zone, Upper Permian.

#### *Derivation of name*

Obscurus (L) = showing little detail, obscure.

#### **Description and comparison**

These fructifications do not appear to have a closely associated protective cover as do the other *Scopus* forms. Whether there ever was such a cover remains to be discovered. The fructifications appear to have been thinly fleshy, particularly the specimens that show little structuring (Figure 86); whether that is a developmental feature, tending to a more structured, rigid, mature form is not known. Figure 90 is an enlargement of Figure 86 and shows large surface cells, forming faint radiating striations.

Figure 86 shows the structureless form while Figure 89 shows a specimen with very well developed and perfectly aligned sacs. Figure 87 shows an intermediate stage with sacs developed towards the top only. Whether these sacs were ever hollow structures is difficult to determine, as in the preserved form they appear to be fairly flat.

The specimen in Figures 91 and 92 shows the organic connection between the stalk and leaf petiole, the cell patterning can be followed through. It is interesting to note that in Figure 91 the leaf petiole bearing the fructification continues and joins a small stalk that appears to fork off a thin branch.

The specimen figured in 87 has the actual organic connection of the fructification and the petiole broken, but the positioning of the fructification on the leaf petiole implies the original position.

These fructifications occur in close proximity to *S. didiscus* but it is doubtful whether they form a unit together; the overall dimensions of the two are different, *S. obscurus* being larger than *S. didiscus*.

The *Glossopteris* leaf to which these fructifications are attached is the same as for the other *Scopus* species.

This *S. obscurus* is a small group. Originally it was thought that the difference in appearance from *S. didiscus* could have been due to an accident of preservation, but with even the cell pattern surviving fossilisation the preservation was probably good and hence these have been separated from *S. didiscus*. What were thought to have been intermediary forms are specimens of *S. didiscus* which tend to have the more flaccid appearance of *S. obscurus* but they have the radiating, dichotomising vein-like striations typical of the *S. didiscus*.

These specimens all came from Loskop.

#### **SUMMARY AND CONCLUSION**

“There are no clear indications of the original nature of any of these structures save the stalk nor of their morphological category. There can be little doubt of the vegetable origin of the fossil, and it seems highly probable that it was connected with the reproduction of the plant on which it grew” (Thomas, 1921, p. 287).

After more than fifty years one cannot with much certainty say more than this!

If the specific designation of fossil plants is to have any meaning it must represent a definable unit, hence four names have been given to separate the four morphological forms of the *Scopus* group, although they appear to belong to the same form of *Glossopteris* leaf. Thus in this case “species” does not imply a breeding unit but merely a recognisable morphological form, i.e. a form species. A future amalgamation of these four form species into a “real” species (a breeding unit) can only take place once the roles of each form in the reproductive cycle of the plant have been understood.

The interpretation of the simple discs of *Fetura* and the compound discs, discs with knobs, of *Dictyopteridium* is difficult. That they are seed cushions (Surange and Chandra, 1974) is not acceptable as the seeds are below the surface bearing the compound discs; thus the knob cannot be the area of vascular bundles as was suggested by Surange and Chandra (1975), nor is it in this case likely to be the place of the attachment of the stigma or the base of the style (Plumstead, 1956 and Varama, 1963), although the slight pitting on the surface of the discs as compared with the smooth surface which covers the rest of the fructification is reminiscent of a stigma. The relevance of the pitting is not clear. In *Fetura natalensis* the discs top a definite sac, thus occurring in a predetermined position, which is not the case in *Dictyopteridium sporiferum* or *D. flabellatum*. That these discs are only a surface embellishment does not seem a very satisfactory explanation either, as they show some consistency in positioning, either along the margin of *Dictyopteridium* (although the central area has



a random distribution of discs) or on the sacs in *Fetura*.

Walton (in Plumstead, 1952, p. 332) puts forward the idea of a cone or strobilus with appendages that would form the wing for the fossil form of *Scutum*, with the same principle applying to similar types of fructifications. Surange and Maheshwari (1970) accept this organisation, putting forward the idea that the scales which overlap on the central head area break off when the specimen is split showing a "protective" counterpart that is not the same as the main fructification. This idea is neither acceptable for wing formation nor as an explanation of the origin of the protective half. The wing area could not have such a uniform appearance if it were composed of closely appressed scales, nor could there always be such a clean break as to leave no trace of the scale on the fertile half. The counterpart would have to show some sign, even if only in the cell pattern, that it had a composite nature, which is not the case. Likewise the margin of this counterpart could not be entire, which it is, if it consisted of a torn-off agglomeration of scales. This theory could also not explain how there is sometimes a reverse mirror image on the counterparts when the protective cover is not preserved, as this would imply that the scale leaves would fall off completely in some instances and not at all in others, with no intermediate stages possible.

Surange and Maheshwari (1970) also put forward that the "false, irregular venation-like design which is generally seen on the counterpart could result from seepage of sediment in the small crevices between the overlapping scales". The faint venation-like pattern seen on the protective half can certainly not be described as "normal" type *Glossopteris* venation (Surange and Chandra, 1975) if its origins were due to overlapping scales. From evidence of the specimens on hand and

due to the difficulty of explaining the double nature of the fructification with compound cover, the wing appears to be a uniform structure, continuous with the central head.

Sen (1955) and Surange and Chandra (1974) suggest that the protective half falls away to expose the fertile half for fertilisation, which would account for the large number of unattached "scale leaves" found in this type of deposit. However, the large number of "scale leaves" found in the deposits under discussion are not of the same shape or size as the "fertile halves" and are thus probably totally independent of the fructification, rather representing the protection of growing points. This suggested deciduous habit of the protective half would be a most inconsistent feature as fructifications with the protective half attached are also found, in which the seeds have been totally shed according to Surange and Chandra's (1973) interpretation of discs being seed cushions. The protective half of these fructifications would appear to be more persistent than suggested by the above authors. It probably protected the whole fructification rather than the seeds directly as the seeds are protected by the covering layer.

Archangelsky and Bonetti (1963) and Arrondo (1972) show different types of *Glossopteris* fructifications from South America which throw no further light on the local specimens. The fructification reported by Lambrecht, Lacey and Smith (1973) from the Law Glacier area, Central Antarctica is so poorly preserved as to make comparison difficult, but it does not appear to have any resemblance to the South African specimens.

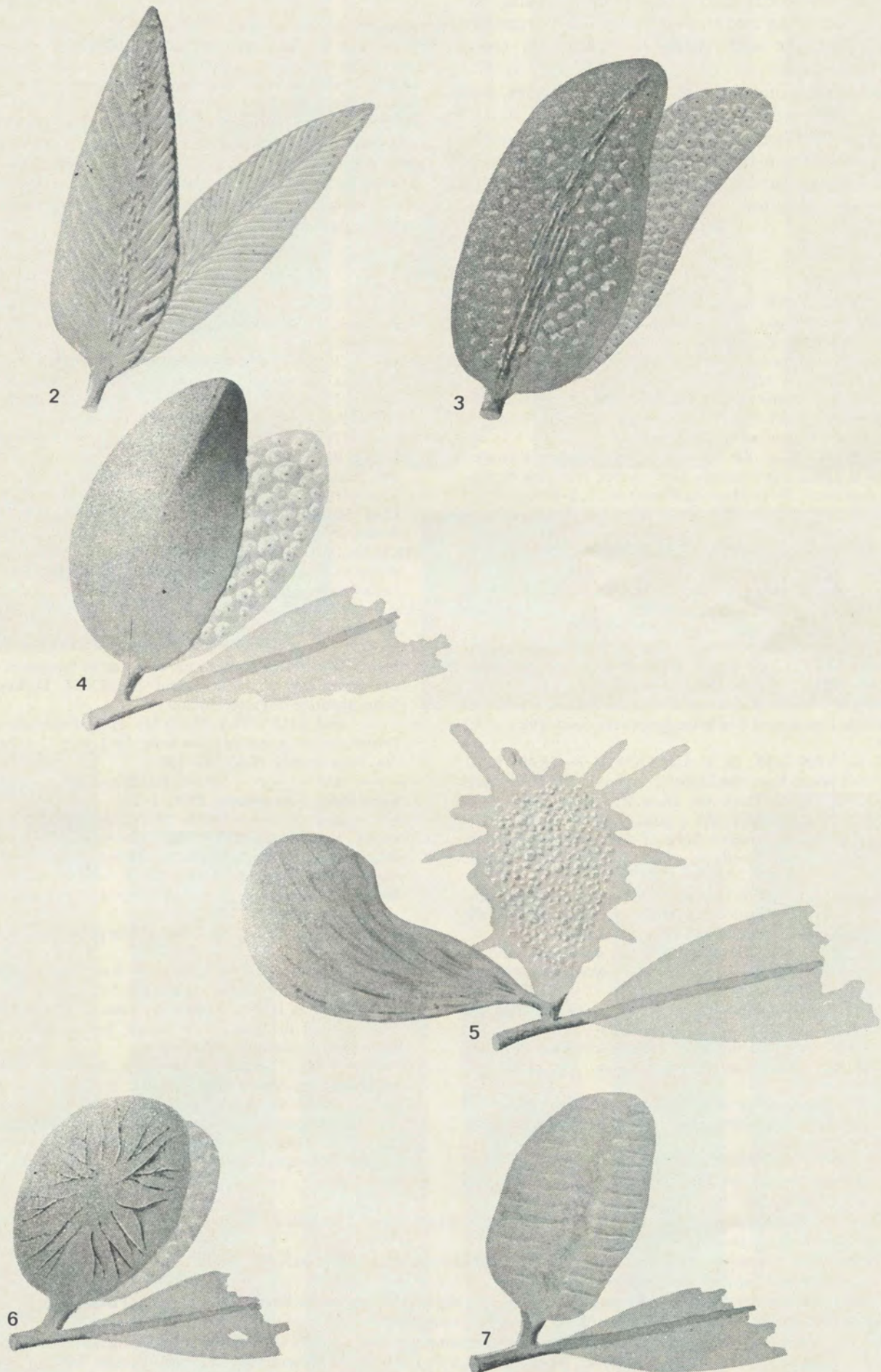
Taking into account the difficulty of adequately describing these fructifications without using terminology which implies inclusion in a definite plant group, resultant impressions are necessarily vague,

TABLE I  
Tabular classification of the Fructifications

| Species                             | Overall shape                                   | Tip                 | Base                    | Wing     | Surface relief                                                                          | Disc detail                                       |
|-------------------------------------|-------------------------------------------------|---------------------|-------------------------|----------|-----------------------------------------------------------------------------------------|---------------------------------------------------|
| 1. <i>Dictopteridium sporiferum</i> | lanceolate oblong-lanceolate                    | acute               | truncate                | 2 mm     | Smooth, fleshy surface with depressions accommodating discs                             | Discs with knobs, larger along margin             |
| 2. <i>D. flabellatum</i>            | narrowly oblong lanceolate                      | acute               | truncate                | 0-2 mm   | High relief of grooves and ridges. Discs on ridge not in depressions                    | Random discs with knobs                           |
| 3. <i>Fetura natalensis</i>         | lanceolate oblong                               | obtuse to acute     | truncate                | 0-1 mm   | Sacs touching at base, depressed tips accommodating discs. Lateral sacs elongated       | Discs simple, same size over whole fructification |
| 4. <i>Scopus gibbosus</i>           | narrowly deltoid ovate to lanceolate and oblong | acute rarely obtuse | sub-cordate to truncate | 0-3,5 mm | Thin undifferentiated layer overlying bulges                                            | —                                                 |
| 5. <i>S. confertus</i>              | narrowly oblong                                 | sub-truncate        | truncate                | —        | Random oblong swollen bodies tightly packed                                             | —                                                 |
| 6. <i>S. didiscus</i>               | quadrato-orbiculate                             | —                   | obtusely cuneate        | 0-3 mm   | Dichotomising vein-like pattern radiating off central area                              | —                                                 |
| 7. <i>S. obscurus</i>               | quadrato-oblong                                 | obtuse to apiculate | truncate                | —        | Sac-like areas at right angles to central axis along margin, some show no detail at all | —                                                 |

For reconstructions of Nos 2-7 see opposite page.





Note. The pits on the bulges in 4 above are an error in reconstruction and should not have been inserted.



which expose the fructifications to much theorising. No certain function being ascribed to most of the structures makes comparisons with other fructifications mentioned in literature all the more difficult as the specimens are very often not very clear themselves, and the figures even less clear.

An attempt has been made here merely to describe the structure of these fructifications as they appear in this collection; the actual interpretations will be left to persons more specialised in the field of comparative morphology.

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Figure 4. *Dictyopteridium sporiferum* showing the randomly distributed compound discs with knobs, in possible association with the *Glossopteris* leaf behind it. x 5 N-Lk 410 PTO (PB 001).

Figure 5. *D. sporiferum* with seeds visible at the tip under the disc bearing surface. x 2 N-MN 895 (PB 002).

Figure 6. Enlargement of Figure 5 to show seed details. x5.

Figure 7. The broadest specimen of *D. flabellatum* showing typical ridges and marginal swellings. x 2 N-Lk 478a (PB 003).

Figure 8. *D. flabellatum*, the poorly preserved margin discloses five round bodies in place of the marginal swellings. x 5 N-Lk 398 (PB 004).

Figures 9 and 10. Holotype *Dictyopteridium flabellatum* sp. nov. showing the random discs and knobs on the swollen areas between grooves and the ordered array of swollen sac-like endings. Figure 9 on left shows the striated bodies under the torn-away surface. The arrow indicates the breaking point. x 2 N-Lk 424 and N-Lk 360 (PB 005 a, b).

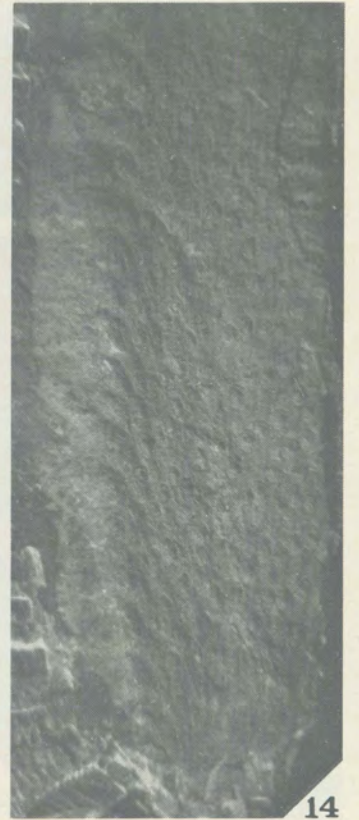
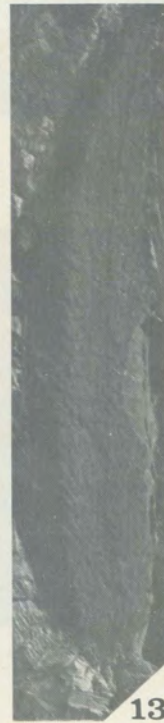
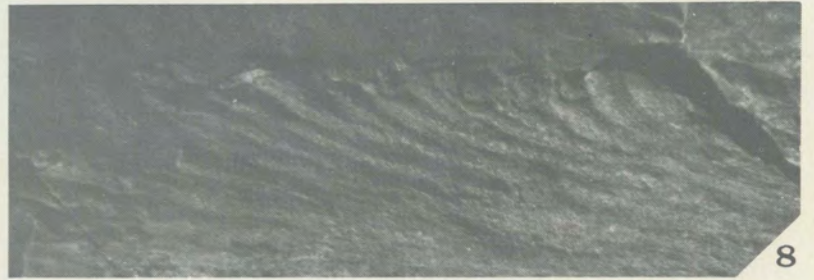
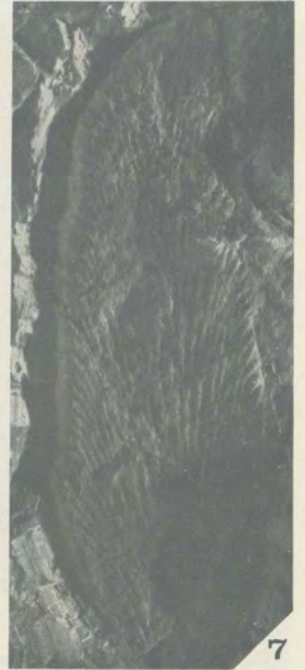
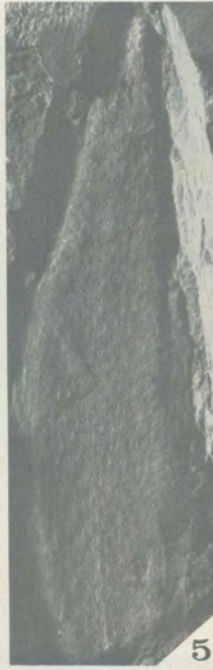
Figure 11. *D. flabellatum* showing dichotomising grooves. N-Lk 31b x 2 (PB 006).

Figure 12. Lateral compression shows sac-like swelling on *D. flabellatum* forming an escarpment ending in a small wing. x 2 N-Lk 322a (PB 007).

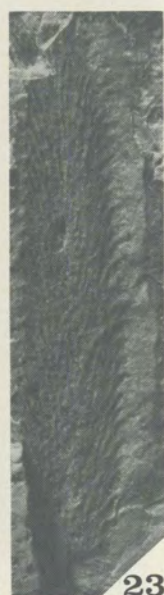
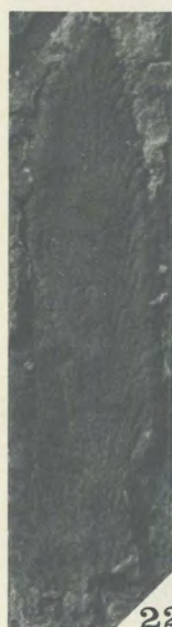
Figure 13. Paratype. An almost complete specimen of *D. flabellatum* showing a short stalk and tip. x 2 N-Lk 410 (PB 008).

Figure 14. Enlargement of above. Detail of discs with knobs. x 5 N-Lk 410 (PB 008).





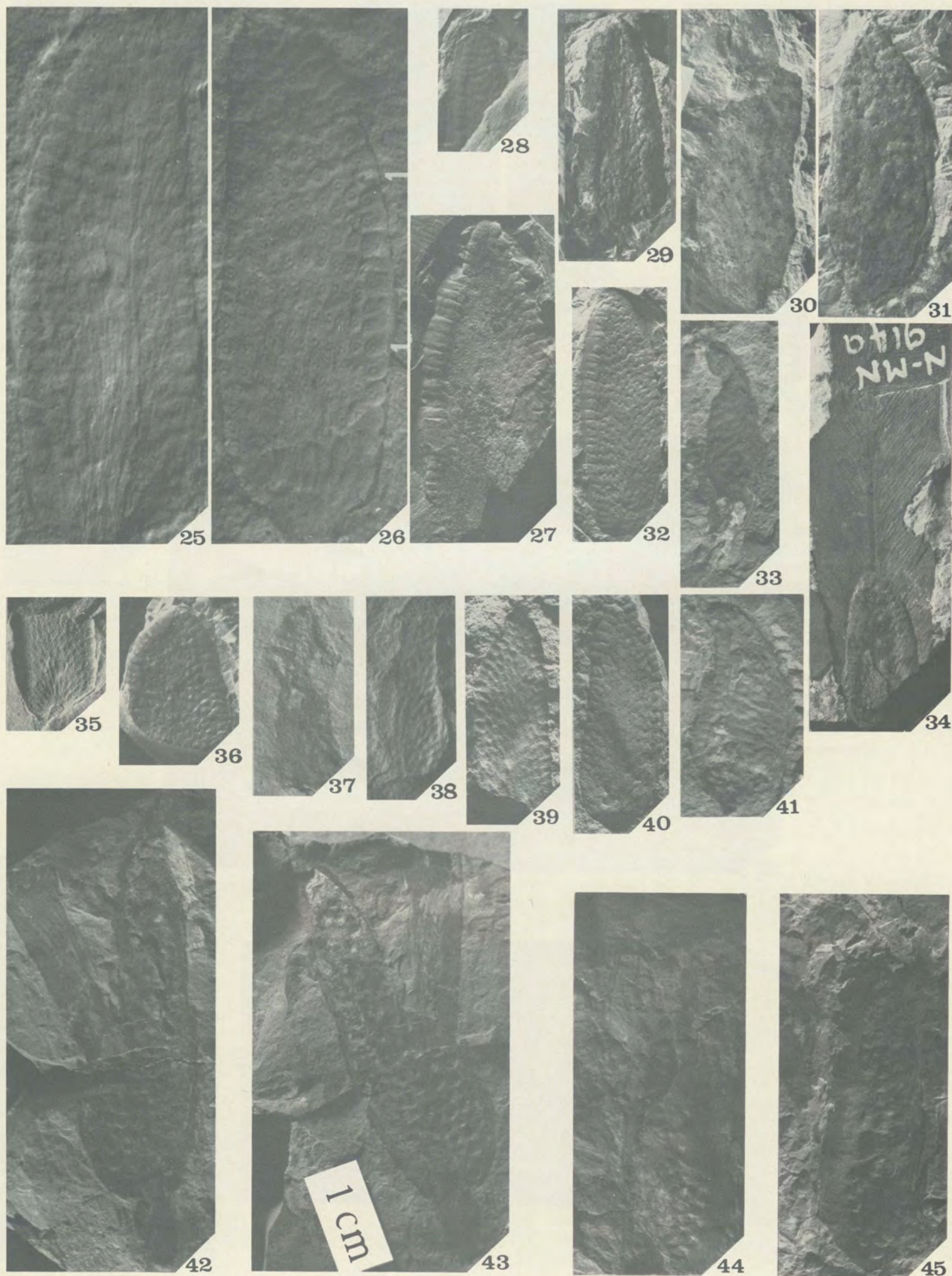






- Figures 15 and 16. Fertile and protective halves of *D. flabellatum*. One of the largest specimens. Enlargement of Figure 21 (1). x 2 N-Lk 406a and c (PB 009 a, and c).
- Figures 17 and 18. Protective and fertile halves of *D. flabellatum*. Figure 17 shows the slight depressions over its surface to accommodate the discs of the fertile half. Figure 18 shows particularly well developed lateral swollen ends. x 2 N-Lk 407 and N-Lk 406 (4) (PB 010 a, b).
- Figures 19 and 20. *D. Flabellatum* paratype. Protective and fertile halves, both showing a clear wing, the protective half shows a clear reverse image of the grooves and ridges. x 2 N-Lk 406b and N-Lk 406a (2) (PB 011 b and a).
- Figure 21. The parent block of Figures 15–20, to show the relative position of the fructifications to each other. Parallel with and to the left of the centimetre measure is a very poorly preserved specimen (3). x 1 N-Lk 406a (PB 009–011).
- Figures 22 and 23. Fertile protective half of *D. flabellatum* possibly of one fructification. The fertile half does not show a wing while the protective half has a clear wing. x 2 N-Lk 411a (PB 012).
- Figure 24. The parent block of Figures 22 and 23 to show the spatial relationship between the two halves of what may have been one fructification. x 1 N-Lk 411a (PB 012).





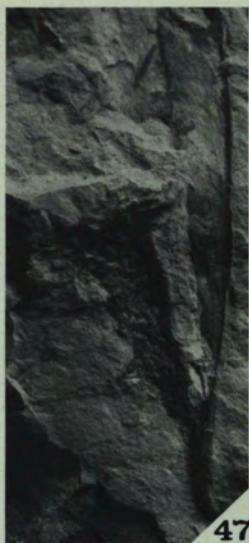


- Figure 25. Holotype *Fetura natalensis* comb. nov., the protective half showing the venation-like striations and only faint reverse relief of the counterpart. x 5 N-MN 909a (PB 013a).
- Figure 26. Holotype *Fetura natalensis*, the fertile half showing sacs with simple knobs; the sacs are ordered along the margins and arranged at random centrally; a short stalk is visible. The seventh sac from bottom right (arrowed) shows the upholstery button effect, and on the same side the ninth sac down (arrowed) is missing the disc, giving a deflated impression. x 5 N-MN 909b (PB 013b).
- Figure 27. Tip of *F. natalensis* with particularly well developed lateral sacs and poorly developed central sacs. x 2 N-MN 901 (PB 014).
- Figure 28. From the arrangement of the lateral and central sacs the specimen is interpreted as *F. natalensis* seen with the protective cover over the fertile half, thus the disc details are obscured. x 2 N-MN 913a (PB 015).
- Figure 29. Same interpretation as for Figure 28. This specimen is from Loskop (as is that from Figures 30 and 31) and is provisionally placed in the *F. natalensis* group. x 2 N-Lk 39b (PB 016).
- Figures 30 and 31. *F. natalensis*, protective and fertile halves. Discs and sacs poorly defined but recognisable. x 2 N-Lk 416 N-Lk 329 (PB 017a, b).
- Figure 32. *F. natalensis*; the wing appears to be undifferentiated continuation of the lateral sacs. There is no evidence of a compound nature to this wing as no sediment infill is visible between sac endings. x 2 N-MN 906 (PB 018).
- Figures 33 and 41. *F. natalensis* possibly showing a triple structure, (41) being the fertile half with what could be another protective part lying beneath it, (33) is the clear protective part. x 2 N-MN 890 and N-MN 904 (PB 019a, b).
- Figure 34. Fragment of *F. natalensis* in alignment with a *Glossopteris* leaf showing convex impression moulded on the lamina by the reverse side of the fructification. x 2 N-MN 914a (PB 020).
- Figure 35. Very clear discs depressed into sacs can give a double ring effect to *F. natalensis* which is quite different from the compound discs of *Dictyopteridium*. Here the outer ring is formed by the curved edge of the sac round the depression containing the disc which forms the inner ring. x 2 N-MN 915a (PB 021).
- Figure 36. A broad tip of *F. natalensis*. x 2 N-MN 897 (PB 022).
- Figure 37. Specimen with abnormally large wing on left tip and ill defined sacs. Provisionally placed in *F. natalensis*. x 2 N-MN 899 (PB 023).
- Figure 38. *F. natalensis* that could be mistaken for *S. gibbosus*, but has poorly defined sacs and discs. x 2 N-MN 892 (PB 024).
- Figures 39 and 40. Protective and fertile halves of *F. natalensis*. x 2 N-MN 960 a and b (PB 025a, b).
- Figure 41. See Figure 33.
- Figures 42 and 43. Holotype *Scopus gibbosus* torn in such a way as to reveal the protective half behind the fleshy fructification (42). The attachment to the petiole of a *Glossopteris* leaf is not clear, the two structures apparently merging. x 2 N-Lk 316a and b (PB 026a, b).
- Figures 44 and 45. A specimen of *S. gibbosus* which shows a possible second protective half lying beneath the fertile head, visible at the tip of (44) where the bulgy mass has broken away. x 2 N-Lk 384a and b (PB 027a, b).





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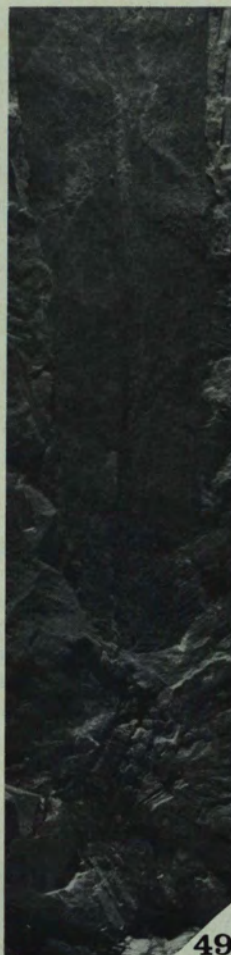
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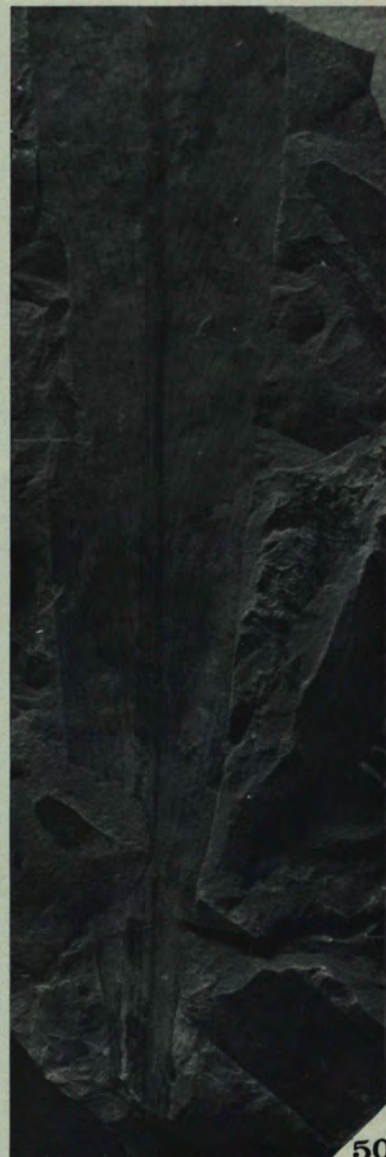
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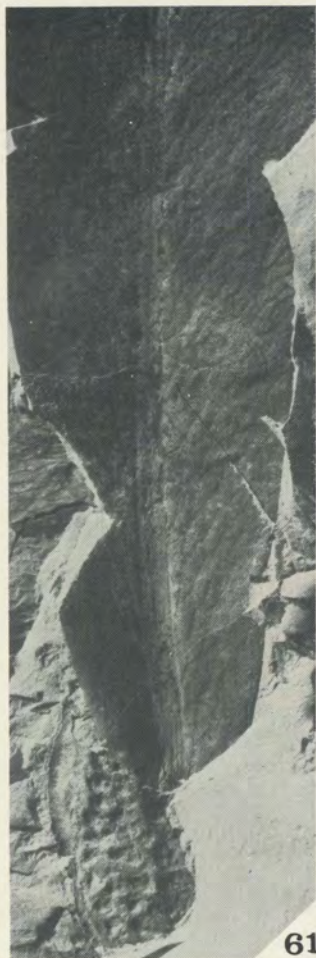


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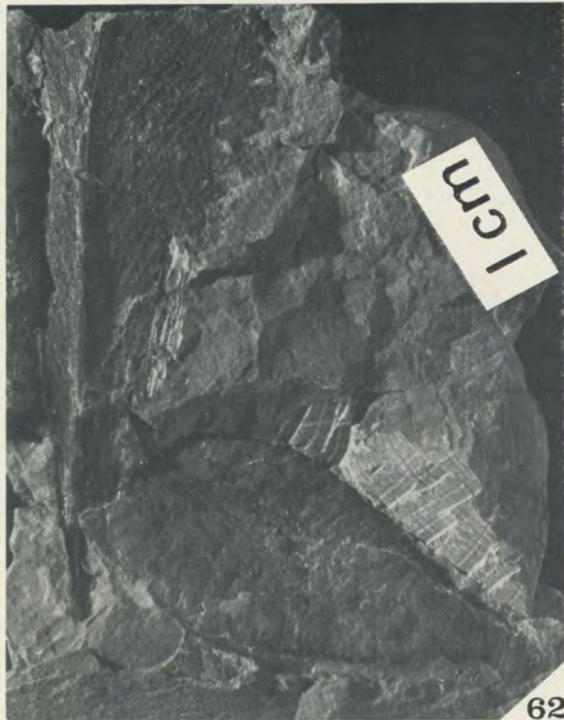


- Figures 46 and 47. Holotype *Scopus confertus*. The organic connection of the fructification onto the petiole of a *Glossopteris* leaf is clearly visible. Stout projections of unknown function radiate out at irregular intervals from what was probably a radially symmetrical body, the surface of which is covered with tightly packed, swollen, oblong bodies. x 2 N-Lk 315b and a (PB 028b, a).
- Figures 48 and 49. The swollen, overlapping, oblong bodies are larger and of slightly fleshier appearance than those of the Holotype, but the overall size, position on the petiole and shape of the fructification places it within *S. confertus*. x 5 and x 2 N-Lk 315 PTO (PB 029).
- Figure 50. A *S. confertus* next to right hand side of a good *Glossopteris* leaf specimen of the *Scopus* type. x 2 N-Lk 217 (PB 030).
- Figure 51. Leaf-like protective half of *S. confertus* attached (?) to the petiole of a *Glossopteris* leaf. x 2 N-Lk 359 PTO (PB 031).
- Figures 52 and 53. *S. confertus* counterparts showing a sub-truncate tip of a cylindrical body, closely associated with a *Glossopteris* leaf though dislodged from the petiole. x 2 N-Lk 306a and b (PB 032a, b).
- Figure 54. The cylindrical fertile half lies in a depression in the protective half, which forms a wing visible on the upper left. x 2 N-Lk 316a (PB 033) *S. confertus*.
- Figure 55. The fertile part of a *S. gibbosus* in alignment with the mid-rib of a *Glossopteris* leaf. The protective half figured in 56 is lying close by on the same rock surface. x 2 N-Lk 315a PTO (PB 034).
- Figure 56. A Paratype of *S. gibbosus*, a protective half, stalked and keeled at the tip. x 2 N-Lk 315a PTO (PB 035).
- Figure 57. Stalked, concave inner surface of a protective half of *S. gibbosus*. Not keeled, winged at the tip. At attachment of stalk with protective half a ridge is seen, probably to accommodate the fertile half. Mode of attachment of the fertile half to protective half not known, possibly a gradual fusion of cells as no abscission lay is visible. x 2 N-Lk 293b (PB 036).
- Figure 58. *S. gibbosus* in alignment with mid-rib of *Glossopteris* leaf. Wing is clear on the right hand side and folded under the fructification on the left (see Figure 67). x 2 N-Lk 314 (PB 037).
- Figure 59. *S. gibbosus* with well-rounded bulges. x 2 N-Lk 373a (PB 038).
- Figure 60. *S. gibbosus* showing a large wing round the central head. x 2 N-Lk 244 PTO (PB 039).

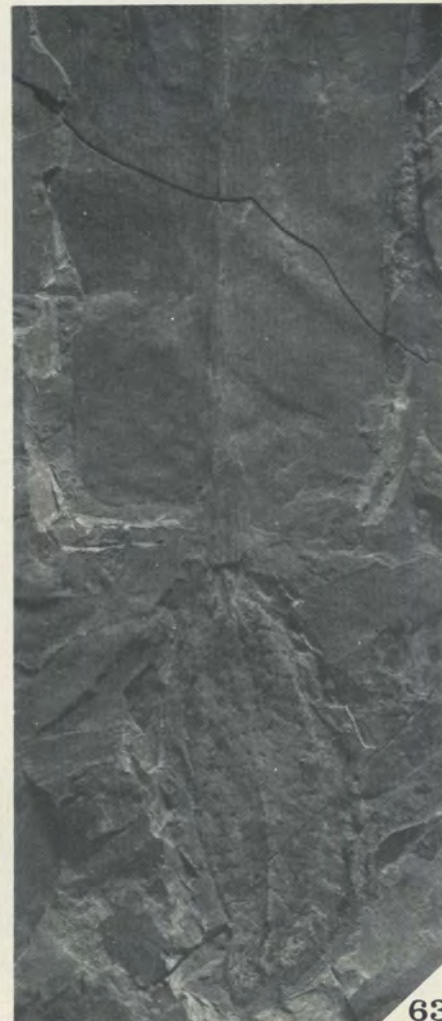




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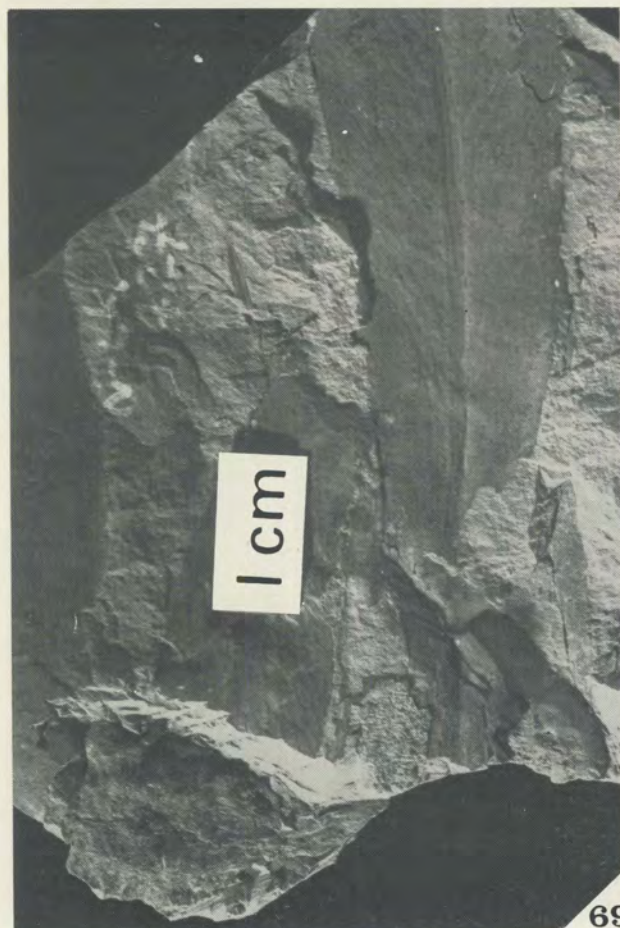
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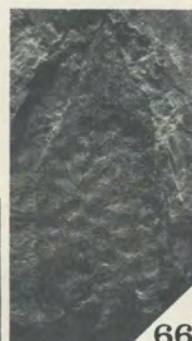
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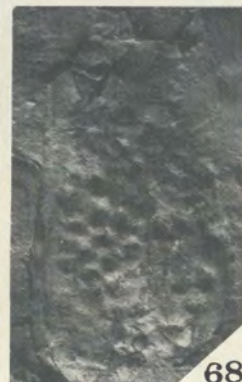
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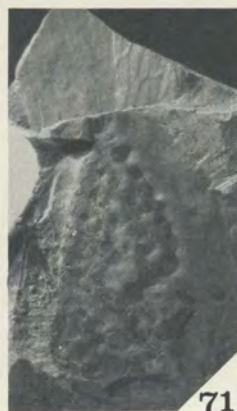
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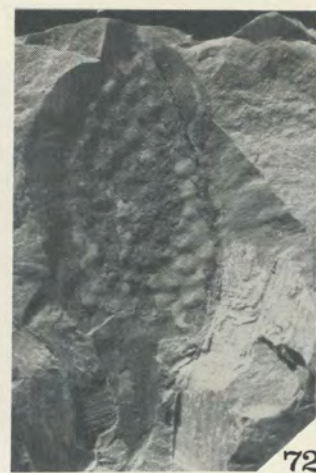
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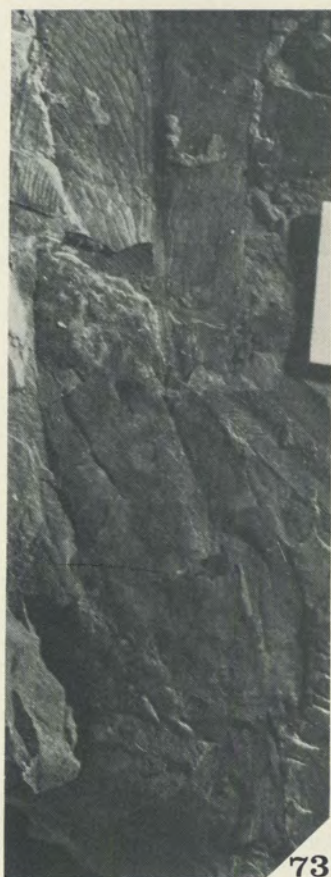


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- Figure 61. *S. gibbosus* in alignment with mid-rib of *Glossopteris* leaf. x 2 N-Lk 294 (PB 040).
- Figure 62. The fleshier than usual appearance of this *G. gibbosus* obscures the bulges, it does not appear to be covered by the protective half. Probably attached to the *Glossopteris* leaf. x 2 N-Lk 313 (PB 041).
- Figure 63. *S. gibbosus* which is covered by a protective half which is keeled along the whole length, obscuring the bulges of the fertile half. This is the only fructification associated with a cordate based *Glossopteris* leaf. x 2 N-Lk 232 (PB 042).
- Figure 64. A slightly laterally compressed *S. gibbosus* showing that the structure could not have been radially symmetrical. x 2 N-Lk 300a (PB 043).
- Figure 65. Protective half of *S. gibbosus* with clear stalk. x 2 N-Lk 298b (PB 044).
- Figure 66. An unwinged fertile head of *S. gibbosus*. x 2 N-Lk 295b (PB 045).
- Figure 67. *S. gibbosus* with wing clear on left hand side and folded under head on the right. x 2 N-Lk 309 (PB 046).
- Figure 68. A broad fertile head of *S. gibbosus*. x 2 N-Lk 315a (PB 047a) (see Figure 85 for enlargement).
- Figure 69. A *S. gibbosus* with large wing at the right base of a *Glossopteris* leaf; in lower left corner is a *S. didiscus*. x 2 N-Lk 427 (PB 048).
- Figure 70. Tip of a *S. gibbosus* visible at the left base of a small almost complete *Glossopteris* leaf. x 2 N-Lk 310a (PB 049).
- Figures 71 and 72. A paratype of *S. gibbosus*, fertile and protective half, strongly winged. Figure 72 shows a slight break at the top of the stalk which may have been the point of attachment of the fertile half. Figure 71 is the fertile half, it has a small portion missing at the base revealing a possible second protective part beneath it; it is aligned with a fragment of *Glossopteris* leaf. x 2 N-Lk 370b and a (PB 050b, a).

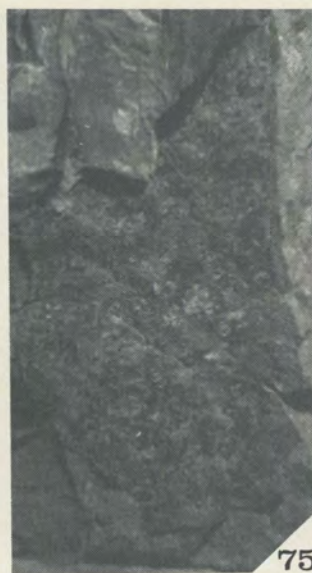




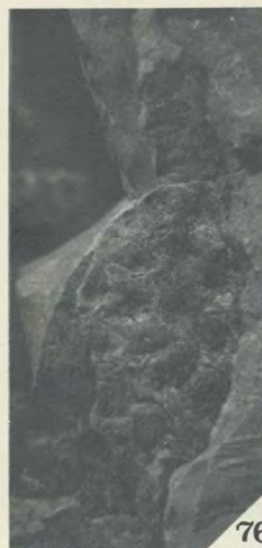
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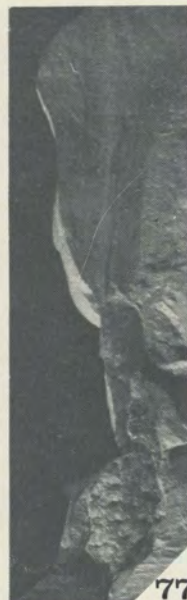
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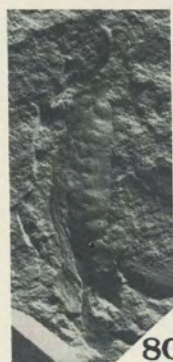
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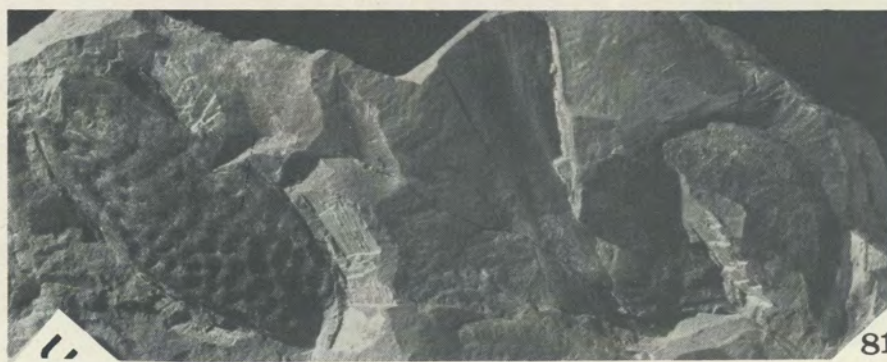
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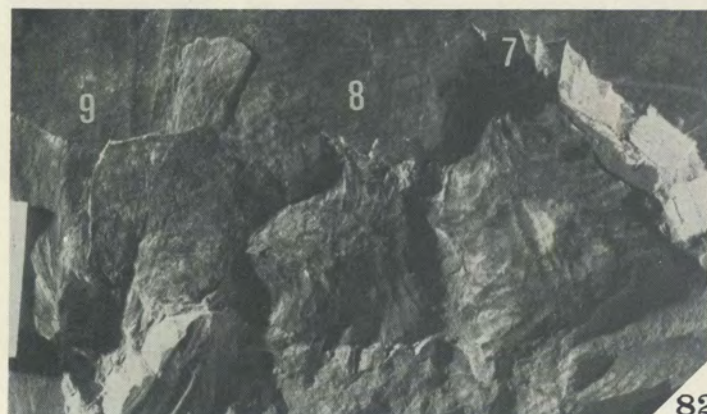
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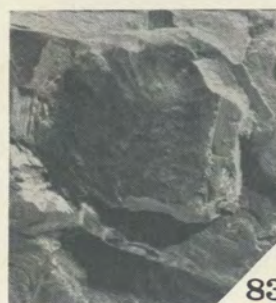
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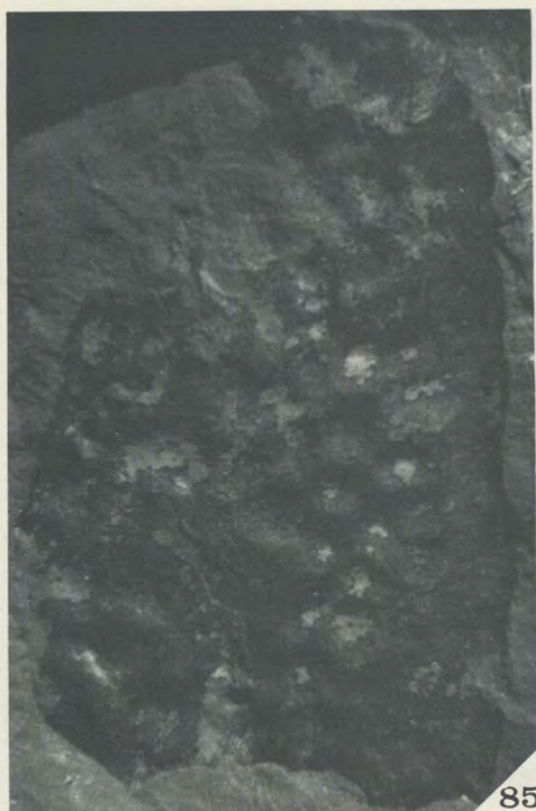


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- Figure 73. *S. gibbosus* attached to the petiole of a *Glossopteris* leaf. Structureless covering layer obscuring the bulges on the main head, damaged at the base showing round, flattened structure. x 2 N-Lk 318 (PB 051).
- Figure 74. *S. gibbosus* appears to be folded along central axis to enclose the fertile body, long stalk present. x 2 N-Lk 293a (PB 052).
- Figures 75 and 76. Protective and fertile halves of *S. gibbosus* with the covering layer removed in Figure 76 showing overlapping flattened bulges suggestive of seeds but not showing seed-like markings or structures. Fructification associated with a *Glossopteris* leaf. x5 N-Lk 293 a and b (PB 053 a, b).
- Figure 77. A x 2 of Figure 76.
- Figures 78 and 79. *S. gibbosus*, the central fructifications in the plates appear to be folded along the central axis, the two outer ones are more usual specimens. x 2 N-Lk 296a, b (PB 054a, b).
- Figure 80. The fertile part of *S. gibbosus* appears to be lying on the protective part, the bulges do not show any details hence inclusion into this group. x 2 N-MN 908 (PB 055).
- Figure 81. Holotype *Scopus didiscus* showing double nature of fructification associated with base of a *Glossopteris* leaf. Strongly convex upper surface, and fluted wing-like area clearly visible on right. Sediment infill between two halves visible where top part has broken away, exposing other half of fructification, lying near to a typical *S. gibbosus*. x 2 N-Lk 317a (PB 056).
- Figure 82. Three specimens of *S. didiscus*, left to right: (9) an almost flat specimen that appears stalked probably due to alignment with a *Glossopteris* petiole; (8) the central one shows typical convex aspect and a good wing area; (7) while the one on the right is convex with no wing area showing. x 2 N-Lk 369a (9), (8) and (7) (PB 066, 065, 064).
- Figure 83. *S. didiscus* paratype; the double nature is not clearly illustrated in the figure, but the sediment along the right hand side of the shown disc is the infill between the two halves. x 2 N-Lk 369a (5) (PB 062).
- Figure 84. *S. didiscus* showing double nature of fructification with sediment infill. x 2 N-Lk 244 (PB 057).







- Figure 85. Enlargement of counterpart of *S. gibbosus* as figured in 68, showing cell pattern. x 5 N-Lk 315c (PB 047c).
- Figures 86 and 90. Paratype *S. obscurus* in its structureless form. It has a relatively fleshy appearance. Figure 90 shows the cell pattern. x 2, x 5 369b (2) (PB 059).
- Figure 87. Paratype *S. obscurus*, the organic attachment between fructification and petiole broken, but obviously in original position on leaf petiole. On the upper half of the specimen faint indications of the "sacs" are visible, as well as clear cell pattern. x 5 N-Lk 315c (PB 071).
- Figure 88. Enlargement of a portion of *Dictyopteridium flabellatum* from Figure 9, showing the detail of the striated sac-like bodies which are exposed where the covering layer has torn away. x 5 N-Lk 424 (PB 005a).
- Figure 89. Enlargement of Figure 92 showing stalk and petiole junction, clear "sacs" and a good cell pattern.
- Figure 90. See Figure 86.
- Figures 91 and 92. Holotype of *Scopus* showing sac-like marginal areas at right angles to central axis. Organic attachment of fructification to leaf petiole, which in turn joins a small twig, is seen in Figure 92. This is the structured form of the species. x2 N-Lk 222a and b (PB 072a, b).



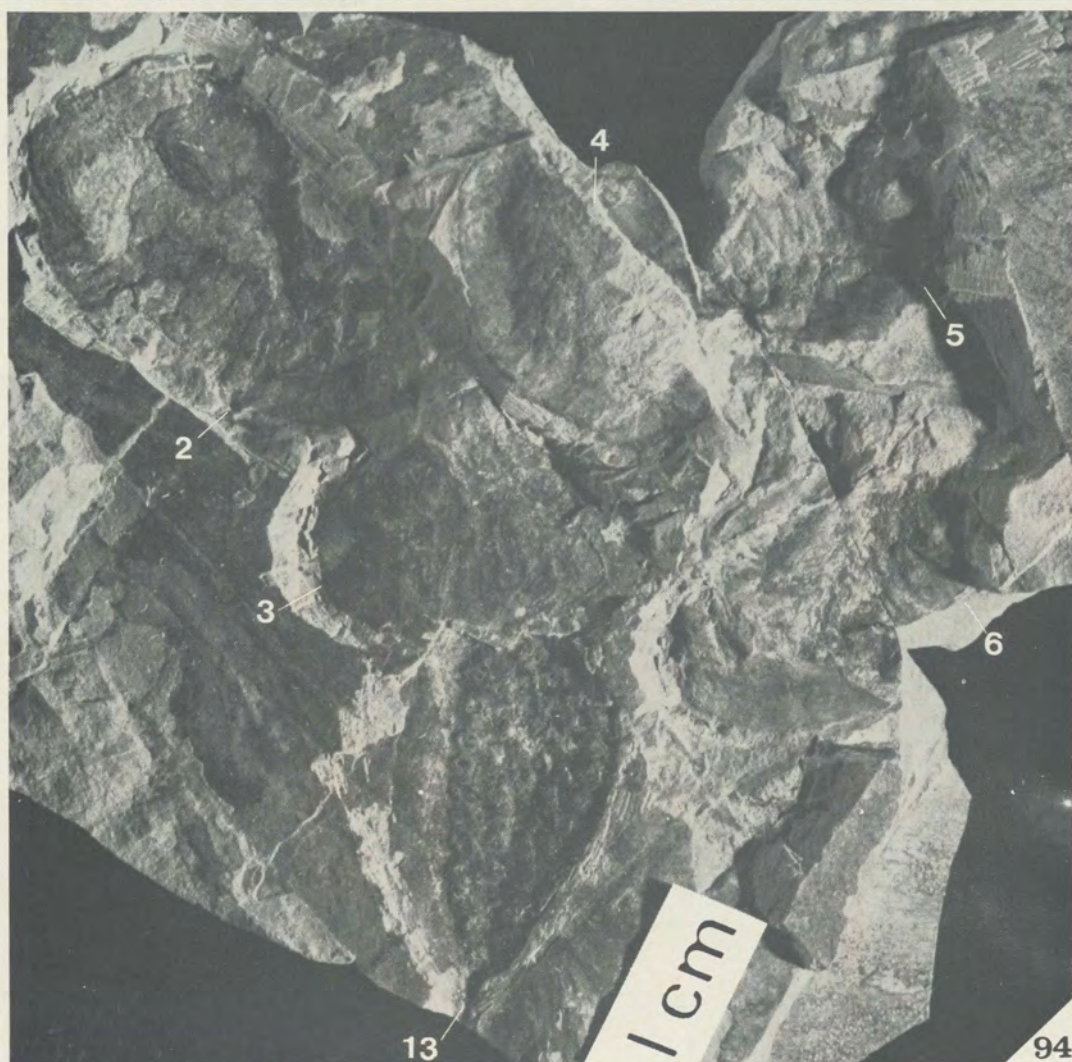
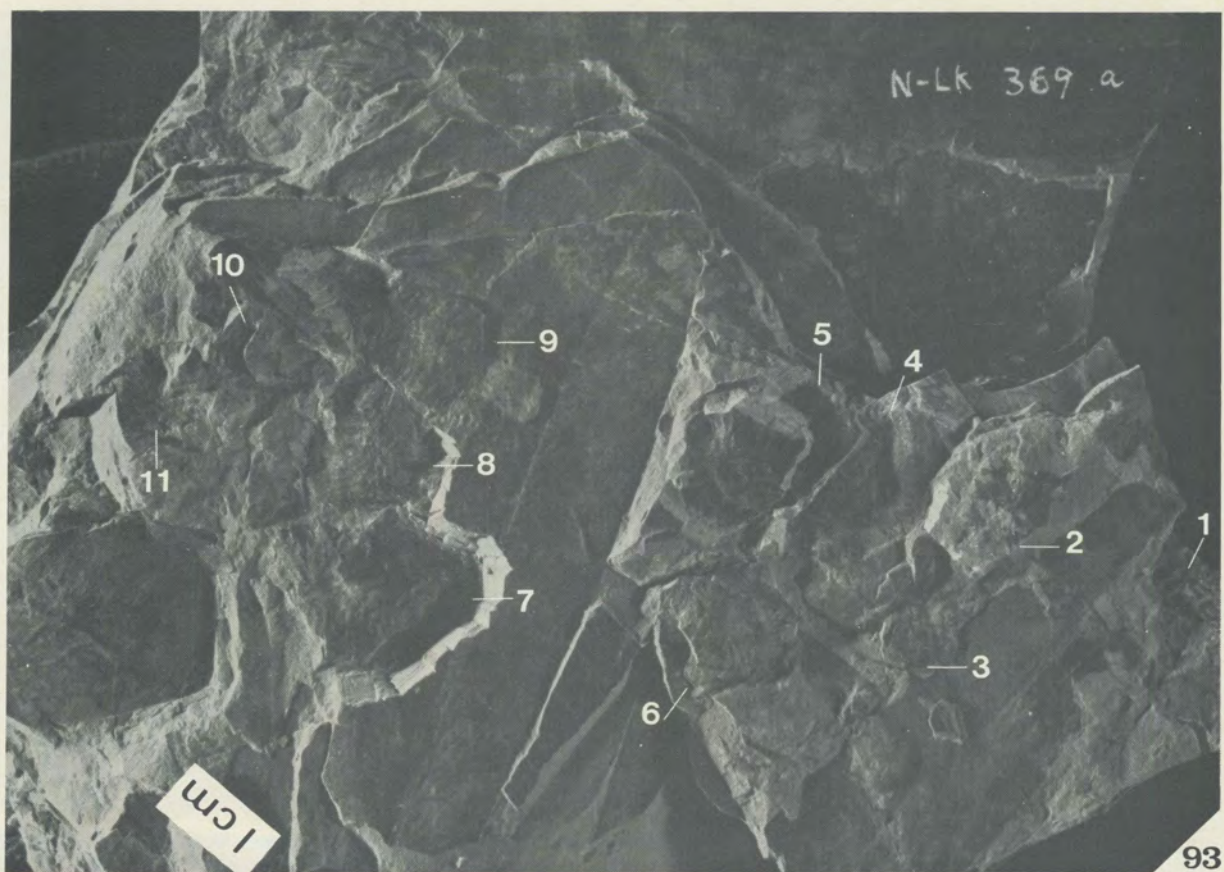




Figure 93. The parent block of many of the specimens to show the spatial arrangement of the fructifications, one to the other.

c. x 1 N-Lk 369a

- (1) *S. gibbosus* (PB 058)
- (2) *S. obscurus* paratype (PB 059)
- (3) *S. didiscus* (PB 060)
- (4) *S. obscurus* (PB 061)
- (5) *S. didiscus* paratype (PB 062)
- (6) *S. didiscus* (PB 063)
- (7) *S. didiscus* (PB 064)
- (8) *S. didiscus* (PB 065)
- (9) *S. didiscus* (PB 066)
- (10) *S. didiscus* (PB 067)
- (11) *S. didiscus* (PB 068)

Figure 94. The counterpart of the lower right portion of Figure 93. The white figures refer to the same fructification as on Figure 93. x  $2\frac{1}{2}$  N-Lk 369b.

- (13) *S. gibbosus* (PB 070).

Just below (6) lies a scale leaf showing faint venation patterns and a finely striated surface.



# ON THE ANATOMY OF *DADOXYLON ARBERI* SEWARD WITH SOME REMARKS ON THE PHYLOGENETICAL TENDENCIES OF ITS TRACHEID PITS

by

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## ABSTRACT

A well preserved specimen of *Dadoxylon arberi* Seward has been discovered in the Beaufort Series (Upper Karroo System) of the Empangeni district in Natal, South Africa. The species is characterized by the tracheid pits which are araucaroid in the multiseriate condition, but which are more often circular and separately arranged or appear in stellate groups. The cross field pits tend to be aligned in horizontal pairs.

*Dadoxylon arberi* shows a relationship with several species of the recent Araucariaceae. Its resemblance to other Gondwana woods from other Southern Hemisphere countries suggests a great uniformity in the elements of the coniferous flora of that time.

It is suggested that *Dadoxylon arberi* represents an intermediate form between the Araucariaceae and Podocarpaceae. The reduction in the seriation of the tracheid pits and a drifting thereof seems to stand in close correlation with the formation of annual rings.

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## *DADOXYLON* ENDLICHER

### Diagnosis

Annual rings present, not clear or absent; rays mostly uniseriate from 1–30 or more cells high, horizontal walls thin and smooth; radial tracheid pits uni- to multiseriate; alternate, contiguous, hexagonal; cross field with simple or bordered pits, contiguous or separate; resin tracheids sometimes present; wood parenchyma absent or weakly present (Seward, 1919; Warren, 1912).

### Nomenclature

There has always been much confusion about the usage of the names *Dadoxylon* Endlicher and *Araucarioxylon* Kraus for fossil araucaroid wood. Araucaroid wood was first described by Witham (1833) and the name

*Pinites* Witham was given. But the name was a homonym for the name *Pinites* Lindley and Hutton which was based on another type. Goeppert (1842) then proposed the name *Araucarites* Goeppert which was, however, preoccupied by the name *Araucarites* Presl used for a cone impression. Endlicher (1847) proposed the name *Dadoxylon* Endlicher to solve the problem. Kraus (1872), however, instituted the name *Araucarioxylon* Kraus as a synonym for *Dadoxylon*.

Both names were afterwards used with some authors using *Dadoxylon* for Paleozoic woods and *Araucarioxylon* for Mesozoic and younger woods. Gothan (1905) criticised the habit on the basis of the inaccuracy of the geological ages of some specimens and some localities. According to Gothan (1905), Grand'Eury coined the name *Cordaioxylon* Grand'Eury for the wood of the Cordaitales. Seward (1919) proposed that the names *Cor-*



*daioxylon* and *Araucarioxylon* should be written in brackets after *Dadoxylon* and *Araucarioxylon* in order to distinguish between the woods of the Cordaitales and araucaroid Coniferales. Gothan (1905) indicated that it is impossible to distinguish between the secondary wood of the Cordaitales and araucaroid Coniferales. This, together with the fact that the geological borders of the two taxa overlap, makes it impossible to refer a wood specimen to any of the two taxa.

According to the rule of priority the name *Dadoxylon* is the correct name and must be applied to both araucaroid Coniferales and Cordaitales woods.

### DADOXYLON ARBERI SEWARD

Figures 1–8

#### Diagnosis

Annual rings present; rays uniseriate, sometimes biseriate in the middle; radial walls of tracheids with uni- to tri-seriate, exceptionally with tetraseriate pits, triseriate and tetraseriate pits araucaroid, biseriate pits araucaroid but more often circular, separate, or contiguous, alternate, opposite or subopposite, rows sometimes separated by a small passage, uniseriate pits circular, contiguous or separate, stellate groups often present; cross field with from 1–9 simple, circular or ovoid, separate pits which tend to build horizontal pairs; wood parenchyma absent.

#### Nomenclature

The name *Dadoxylon australe* Arber was proposed by Arber (1905) for an araucaroid fossil wood specimen from the *Glossopteris* flora of Australia. He was at that time, however, ignorant of the existence of the earlier homonym *Dadoxylon australe* Crie which was based on another type. To overcome the problem Seward (1917) proposed the name *D. nicolai* Seward, but the name *Araucarioxylon nicolai* Carruthers already existed and because *Dadoxylon* and *Araucarioxylon* are synonyms, the name *Dadoxylon nicolai* was illegitimate (Walton, 1925). Later on Seward (1919) proposed the name *Dadoxylon arberi* Seward, but Walton (1956), in contradiction to his earlier (Walton, 1925) reference to the illegitimacy of *D. nicolai*, used the name again. Sahni and Singh (1926) suggested that *D. bakeri* Seward and Walton (1923) shows a great resemblance to *D. arberi* and Walton (1956), although with some hesitation, made it synonymous with *D. arberi*. Sahni and Singh (1926) also pointed out that there is a great resemblance between *D. arberi* and the secondary wood of *Araucarioxylon daintreei* Chapman and concluded that the two plants are identical. Kräusel (1928), however, suggested that Sahni and Singh's specimen of *D. arberi* from the Newcastle Series in Australia differs sufficiently from the holotype of Arber to be placed into a new species. This suggestion was followed by Sahni (1933) who gave it the name *Dadoxylon kräuseli* Sahni.

### Anatomy of the specimen from the Beaufort Series of the Empangeni District, Natal

*Cross section* (Figures 1 and 2)

The annual rings are very clear. Shearing zones occur in which the tracheids follow the typical oblique course for a short distance (Figure 2). The lumina of the tracheids in these zones are filled with a dark substance and this makes the shearing zones observable with the naked eye as dark tangential bands. The tracheids in the shearing zones are greatly deformed. According to Warren (1912) shearing zones are formed in the wider and weaker early wood tracheids in which a better circulation of water than in the narrower late wood tracheids makes them easily infiltratable by iron oxide. Great lateral pressure exerted on the wood at the time of petrification caused a shift in the alignment of the weaker zone.

The lumina of the normal tracheids in the early wood are more or less rectangular, while the radial diameter of the late wood tracheids is much smaller than that of the early wood. The diameter of the tracheids thus varies from 34–47 (–67)  $\mu\text{m}$  tangentially and from 18–46 (–57)  $\mu\text{m}$  radially. The tracheid walls are about 3  $\mu\text{m}$  in thickness. There are from 2 to 8 tracheid rows between each two consecutive rays. There is no sign of wood parenchyma.

*Tangential section* (Section 3)

The walls of the tracheids are smooth. The rays are uniseriate except for here and there where a ray is biseriate in the middle. The height of the rays varies from 1–18 (–25) cells. The cells appear angular or oval in the middle of a ray, while the upper and lower cells are nearly circular or acute. The individual cells are from 21–28 (32)  $\mu\text{m}$  high and from 12–20 (–26)  $\mu\text{m}$  wide.

*Radial section* (Figures 4–8)

The radial tracheid pits show a great variety in arrangement. The pits are uni- to triseriate or they are arranged in stellate groups of 3 to 5 pits. The pits are either araucaroid or appear separate. The latter condition dominates. The uniseriate pits are circular and may stand separate (Figure 6) or appear in solid chains (middle of Figure 3). The pit aperture of the uniseriate pits tends to be obliquely oval. The biseriate pits are araucaroid (Figure 5), but more often they are circular to faintly oval, contiguous or nearly separate. The arrangement is alternate or subopposite (Figure 4). Opposite separate biseriate pits occur in combination with stellate groups (Figure 7). Two of the pits of a stellate group are opposite or subopposite with a single median pit at the top or at the bottom of the group. The pits in the stellate groups are always separate. Triseriate pits are of rare occurrence, but if so arranged they are always araucaroid. This arrangement seems to be restricted to the wider tracheids and towards the ends of the tracheids. The ends of the tracheid walls are more often transverse than oblique. The diameter of the tracheid pits varies from 7–14  $\mu\text{m}$  in the tangential direction and from 7–10  $\mu\text{m}$  in the longitudinal direc-



tion. The pit apertures of the uniseriate pits, as mentioned above, tend to be obliquely oval, but in the multiseriate and stellate groups the apertures are more or less horizontally oval to circular. The pit aperture, however, never reaches beyond the border of the pit (typically araucaroid).

Both the radial and tangential walls of the ray cells are thin and smooth and are about 1.0–1.5  $\mu\text{m}$  in thickness. The number of cross field pits varies from 2–4, sometimes 5, pits, but mostly there are 4 pits which are aligned in horizontal pairs (Figure 8). The pits are obliquely oval and it cannot be established whether they are simple or bordered (apparently they are bordered with wide, oblique oval apertures). The diameter of the pits (or their apertures) varies from 5–7  $\mu\text{m}$ .

### COMPARISON WITH RECENT WOOD TYPES

The general structure resembles that of the Araucariaceae, a family which is restricted in its geographical distribution to the Southern Hemisphere, but which has no representatives in South Africa. The absence of wood parenchyma makes *Dadoxylon arberi* more closely related to *Araucaria* Juss. than to *Agathis* Salisb. According to Greguss (1955) the horizontal alignment of the cross field pits is typical of the Araucariaceae. The number of cross field pits is more or less the same as that of *Araucaria klinkii* Lauterb., *A. rulei* F. v.M., *A. beccari* Warb., *A. humboldtiensis* Buch and *A. mülleri* Brongn. and Gris. Stellate groups of tracheid pits also occur in *A. columnaris* (Forst.) Hook. as well as in *A. montana* Brongn. and Gris. (Greguss, 1955). The tracheid pit rows are also separated by a small passage in *A. columnaris*.

### COMPARISON WITH OTHER GONDWANA WOOD TYPES

Several wood specimens from various Gondwana floras have been brought into connection with *Dadoxylon arberi*. In South Africa this species has been described from other localities. Arber (1910) points out that a wood specimen from the Karroo System from the Ladysmith district, Natal, only deviates from *D. arberi* in having nearly constant uniseriate pits. The variation in the arrangement of the tracheid pits is, however, a diagnostic feature of this species and this cancels out any relationship on the species level. The second species described by Warren (1912) from the Upper Karroo System shows a remarkable resemblance to *D. arberi*, especially as far as the number and arrangement of the cross field pits are concerned. The seriation of the tracheid pits of Warren's specimen is the same as in *D. arberi*, but it, however, lacks stellate groups. Interesting enough, shearing zones are also present in some of the other specimens described by Warren.

Walton (1925) described various specimens from the Karroo System of the Cape Province which he identified as *Dadoxylon arberi*. Stellate tracheid groups of pits as well as separate, uniseriate pits are quite evident in

his specimen. The biseriate pits are also separated by a small passage in some instances (Walton, 1925, Plate 1, Figure 3). The tracheid pits are, however, sometimes arranged in four rows. The cross field shows up to 9 circular to elliptical apparently simple pits. Walton (1956) also described specimens of this species from the Karroo System of Malawi whose anatomical measurements and further details are more or less the same as the Empangeni specimen.

From the Upper Newcastle Series (= Lower Beaufort Series) of New South Wales, Australia, Sahni and Singh (1926) described various specimens of *Dadoxylon arberi*. Their specimens do not, however, show stellate groups. They noticed a resemblance between their specimens and the secondary wood of *Araucarioxylon daintreei* Chapman and suggested that the two names are synonyms, but that their specimens do, however, stand closer to the South African species of *D. arberi* described by Walton (1925). Sahni followed a suggestion made by Kräusel (1928) that his specimens differ sufficiently enough from both *D. arberi* and *Araucarioxylon daintreei* to be placed into a new species and renamed it *Dadoxylon Kräuseli* Sahni. Walton (1956) must have been ignorant of this fact and still placed the New South Wales specimens in synonymy with *D. arberi* (his *D. nicolai*).

Rao (1936) noticed the resemblance of a wood specimen from the Indian Glossopteris Flora with *Dadoxylon arberi*, but instituted the name *Dadoxylon parbeliense* Rao for it. The only real difference lies in the absence of stellate tracheid groups in Rao's specimen and Rao added: "But perhaps *D. arberi* itself has to be split up into a number of species in view of its wide distribution and the number of incompletely known woods included in it".

Nearly the same variation in tracheid pitting occurs in *Dadoxylon deccani* Shukla (1938). This specimen shows a stronger tendency towards a drifting of the tracheid pits and the rays are up to 49 cells in height. The characteristics of the cross field resembles that of *D. arberi*. A reinvestigation might prove that this specimen should be taken up into *D. arberi*.

Surange and Maithy (1962) instituted a new form genus, *Indoxylon* Surange and Maithy which is characterized by a passage separating the pit rows. This condition is here, however, much more accentuated than in *D. arberi*. *Indoxylon canalosum* Surange and Maithy resembles *D. arberi* as far as the characteristics of the rays and the number of cross field pits are concerned. It is, however, felt that this species falls within the generic limits of *Dadoxylon*.

*Dadoxylon jamudhiense* Maheshwari from the Upper Permian of India only differs from *D. arberi* in having about 45 per cent of its rays biseriate. The tendency towards a drifting of the tracheid pits and the from 1–4 cross field pits, which are arranged in horizontal pairs, shows a very close relationship to *D. arberi*. The height of the rays, namely from 1–18 cells, confirms this.

The anatomical features of *Dadoxylon ampense* Sah and Jain from the Jurassic Period of India are similar to those



of *Dadoxylon arberi*. The only essential difference lies in the presence of resin tracheids (Sah and Jain, 1964). The same authors described *D. mandroense* which stands even more closely to *D. arberi*. The tracheid pits are uni-triseriate and show the same variation in pattern. It also has the same number of pits in the cross fields of the late wood, while there are from 4–12 pits in the cross fields of the early wood.

*Dadoxylon arberi* also shows a relationship with a Gondwana wood from Brazil. This is implied by Kräusel and Dolianiti (1958) who, in a table of comparison, place *Dadoxylon roxoi* Kräusel and Dolianiti opposite *D. arberi*.

## PHYLOGENETICAL CONSIDERATIONS AND CONCLUSION

*Dadoxylon arberi* and other Gondwana araucaroid woods exhibit a variety of arrangement of their tracheid pits. The typical araucaroid pattern in the triseriate and terraseriate pits (Walton, 1925) and to a lesser extent in the biseriate pits has been retained. There is a great tendency towards a looser arrangement of the pits in both the horizontal and vertical planes. There also exists a tendency towards a change from the alternate to the opposite arrangement. Another prominent feature is the reduction in the seriation of the pits.

The question arises whether this mixed arrangement of the tracheid pits is of any phylogenetic significance. Gothan (1907) was the first to claim that an intermediate type of pitting exists between the araucaroid and abietoid types. According to Eckhold (1921) the change from the araucaroid to the abietoid type started in the Triassic and that while the araucaroid type was declining towards the end of the Mesozoic, the abietoid made its appearance and occurred generally towards the end of that era. The change was brought about by a phylogenetic drifting ("Wandlung") of the densely packed araucaroid pits which has led to a looser arrangement. According to Eckhold the change followed two possible pathways. The one pathway is illustrated by the formation of stellate groups and the other by a reduction in seriation. *Dadoxylon brandlingii* Lindley and Hutton from as early as the Carboniferous Period shows this tendency towards a reduction in seriation and drifting of the pits — a similar condition which prevails in *D. arberi*. The opposite arrangement of the pits is considered by Henes (1959) to represent either a tendency to revert to an ancestral condition which would support Jeffrey's (1903) theory that the abietoid type is the original type, or the introduction of a new phylogenetic trend. Henes (1959) also observed a reduction in seriation, vertical drifting and formation of groups of the tracheid pits in *Eristophyton beinertianum* Zalesky, also from the Carboniferous Period, and claims that the reduction of the pits on the radial walls of the tracheids can also be observed in *Callixylon* Zalesky of the Devonian Period. Sahni and Singh (1926) also saw in the stellate groups of pits in *D. arberi* a resemblance with *Callixylon* and that the affinity between

the wood types is also illustrated by the end-to-end arrangement of the tracheids.

According to Walton (1925) the transition from the multiseriate araucaroid to the separate and sometimes even opposite pits of *Dadoxylon arberi* supports the idea that the araucaroid type was the original type and that the abietoid type has been derived from it. The transitional wood types are all placed into the Protopinaceae by Kräusel (1919). The most primitive form genus of the Protopinaceae is *Protopodocarpoxylon* Eckhold. It resembles the Araucariaceae, but has the transitional type of tracheid pitting and is characterized by its podocarpoid cross field pits. Like the Araucariaceae the ray cell walls are thin and smooth, a feature which still prevails in all the living members of the Podocarpaceae (Greguss, 1955).

The Coniferales are only represented by their three most primitive families in the Southern Hemisphere, viz. Araucariaceae, Podocarpaceae and Cupressaceae. Only the latter two are presented in South Africa. The Podocarpaceae occur as early as the Cretaceous Period in the geological history of South Africa (Schultze-Motel, 1966). Here it is represented by the form genera *Podocarpoxylon* Gothan and *Phyllocladoxylon* Gothan. If *Dadoxylon arberi* is compared with *Podocarpoxylon umzambense* Schultze-Motel from the Upper Cretaceous Period, a great resemblance in the arrangement of the tracheid pits becomes apparent. The pits of the latter stand separate or may be contiguous in exceptional cases. Furthermore, the pits are uniseriate and are often arranged in horizontal pairs ("Zwilling-stüpfel"). Rarely stellate groups, each of which consists of three pits, occur. The typical araucaroid pattern is totally absent. In *P. angustiradiatum* Schultze-Motel from the same horizon the araucaroid pattern still prevails. Greguss (1955) considers *Podocarpoxylon* Gothan of the Triassic Period to be one of the precursors of the Podocarpaceae which, in their turn, he derives from the Araucariaceae. *Dadoxylon arberi* could thus have played an important role in the evolution of the Podocarpaceae.

It has been held by several authors in the past that there is a close correlation between tracheid size and the seriation of the pits in their walls (Henes, 1959; Bailey and Faull, 1934). The Mesozoic Coniferales more often contain annual rings than the Cordaitales. They also show a stronger tendency towards a reduction in the seriation of the tracheid pits together with a drifting thereof. Gothan (1907) noticed that the horizontal and tangential ray cell walls of *Protocedroxylon transiens* (Gothan) Eckhold (= *Cedroxylon transiens* Gothan) contain abietoid pits, while the early wood contains araucaroid pits and the late wood separate pits which are sometimes arranged in stellate groups ("Sterngruppen" of Gothan). This correlates with the observations made by Bailey (1933) in certain *Cedrus* spp. Here the abietoid type of pitting dominates by far the araucaroid in young stems, while the araucaroid and abietoid types occur mixed in old slow-growing stems. In the latter case, however, the araucaroid type is more restricted towards the wide early wood tracheids,



while the abietoid type is confined to the transitional zone between the proto- and metaxylem as well as in the narrower late wood tracheids. Bailey and Faull (1934) also demonstrated that the pits are larger and more numerous in large tracheids with thin walls and decrease in size and number as the tracheids become smaller and thick-walled in *Sequoia sempervirens*.

Bailey (1925) proposed that the circular type of bordered pit was not an original feature of the transitional zone between the proto- and the metaxylem, but that this type of pit had worked back into the transitional zone and even into the protoxylem which has led to the elimination of the original typical scalariform and transitional pitting of the Cordaitales. It seems that the more efficient abietoid type of pit became established in woods with annual rings and that once they became established they have shifted to the earlier stages of the ontogenetical stages.

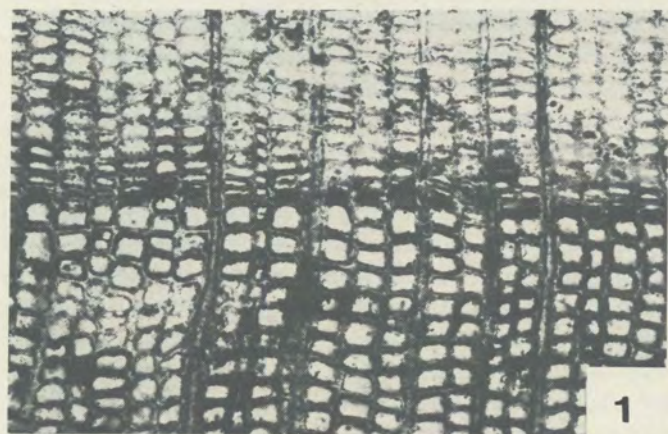
The Araucariaceae have tracheids which are more angular in shape than the other families of the Coniferales. This is also the case in the majority of the *Dadoxylon* spp. It is only where annual rings are formed that the tracheid diameter decreases, especially in the radial direction. The lateral contact surface between the

wide thin-walled tracheids is larger than that of the thick-walled tracheids with a smaller radial diameter. The relatively larger contact surface of the early wood tracheids facilitates a higher seriation or, in other words, more numerous pits. The reduction in contact surface brought about a reduction in seriation. Another factor which could have played a role in the reduction in seriation was the rounding up of the tracheids which also decreased the lateral contact surface between adjacent tracheids and has led to the pits being confined to the median part of the radial wall. The reduction in seriation consequently affected the form and structure of the bordered pits. Where the lateral transport of water and minerals took place through a larger number of pits in the araucaroid type, the same function had to be performed by a lesser number of pits. With this restriction placed on the lateral flow by the reduction in the number of pits the problem had to be overcome by an enlargement of the size of the apertures which led to the evolution of the abietoid type of bordered pit where the aperture reaches beyond the border of the pit in contrast to the smaller aperture of the araucaroid type of pit.

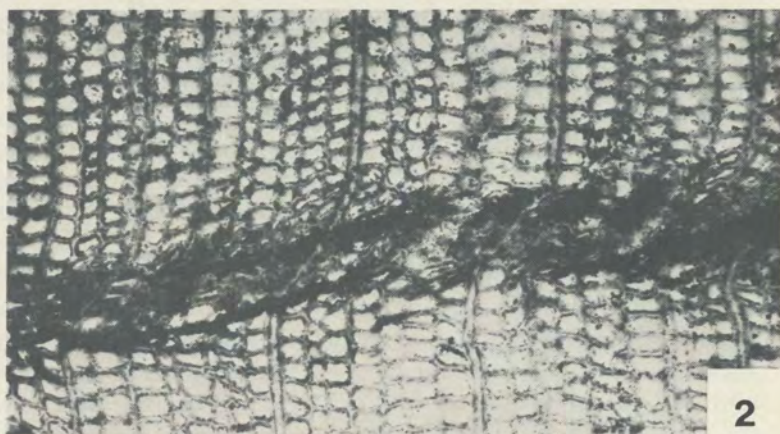
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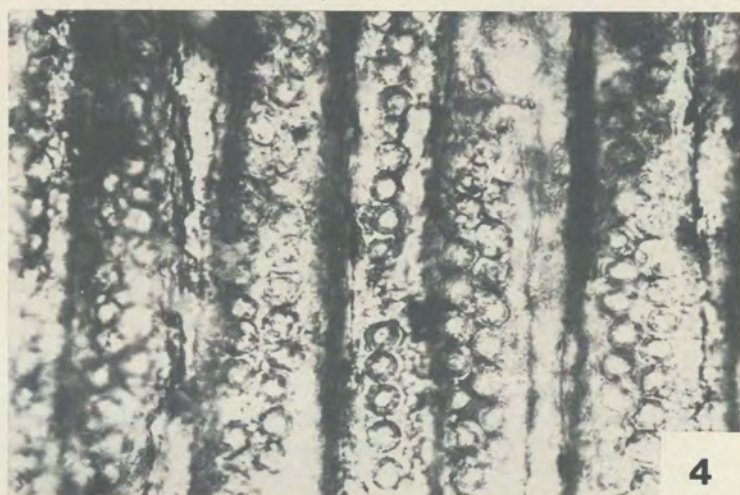
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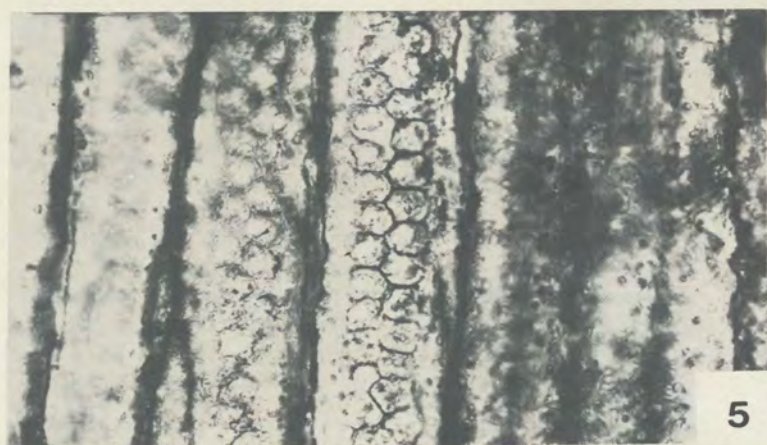
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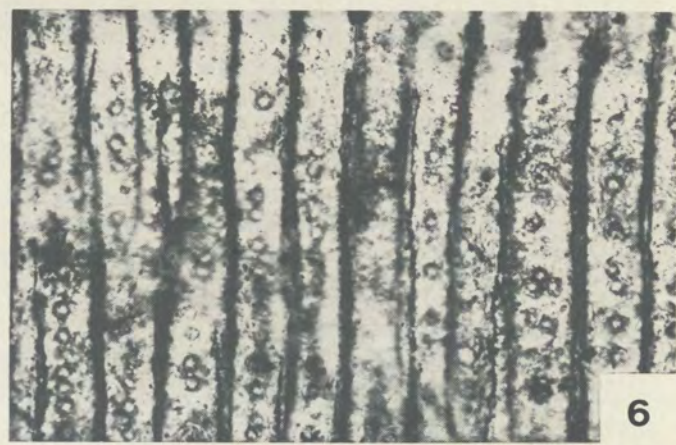
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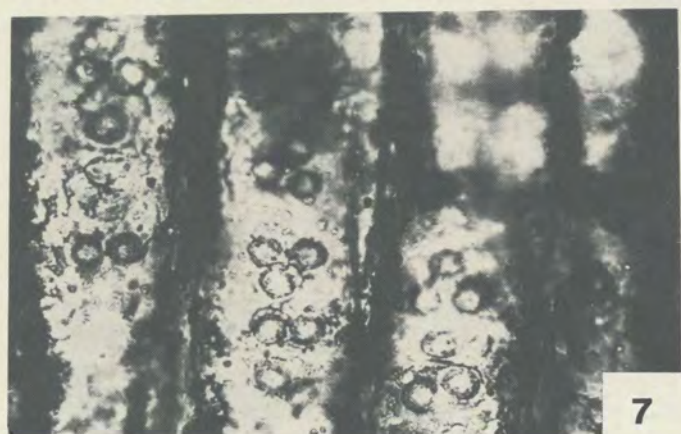
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- Figure 1. Cross section; early and late wood;  $\times 40$ .  
Figure 2. Cross section; shearing zone;  $\times 40$ .  
Figure 3. Tangential section; uniseriate rays;  $\times 40$ .  
Figure 4. Radial section; uniseriate, contiguous, circular pits with obliquely oval apertures (at bottom); circular, subopposite pits, separated by small passage (on left hand side);  $\times 300$ .  
Figure 5. Radial section; biseriate, araucaroid pits;  $\times 300$ .  
Figure 6. Radial section; uniseriate, separate, pits; stellate group on right hand side;  $\times 80$ .  
Figure 7. Radial section; stellate groups; opposite pits on left hand side;  $\times 300$ .  
Figure 8. Radial section; obliquely oval cross field pits (or apertures) arranged in horizontal pairs;  $\times 300$ .



A NEW SPECIES OF *DAMMAROXYLON* SCHULTZE-MOTEL, *D. NATALENSE* SP. NOV.  
FROM THE CRETACEOUS OF NATAL, SOUTH AFRICA\*

by

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ABSTRACT

In the Cretaceous rocks of the M'hlosinga district, Zululand, Natal a new species of the form genus *Dammaroxylon* Schultze-Motel, *D. natalense* sp. nov., has been discovered. New evidence regarding the structure of the marginal ray parenchyma cells has been obtained. The conclusion is reached that *Dammaroxylon* could possibly take an intermediate phylogenetic position between the Araucariaceae and Podocarpaceae.

SYSTEMATIC PALAEOBOTANY

Class GYMNOSPERMAE

Order CONIFERALES

Family ARAUCARIACEAE

Genus *DAMMAROXYLON* SCHULTZE-MOTEL 1966

Type species: *Dammaroxylon africanum* Schultze-Motel

Discussion

The non-committal name *Dadoxylon* Endlicher has been used for secondary araucaroid fossil wood types since before the turn of the century. An enormous number of species has been ascribed to it. It includes woods of both the Paleozoic and the Mesozoic as well as from the Cordaitales and the Coniferales. Various authors have attempted to split the taxon, but without any success. Hence *Dadoxylon* has become a "collecting box". Kräusel and Range (1928) suggested that anatomical structural modifications in secondary wood should be looked for, on the basis of which new genera should be instituted. Border cells (=marginal ray parenchyma cells) were first observed by Greguss (1955) in recent wood and he suggested that these structures are important for the identification of wood types. Schultze-Motel (1966) discovered border cells in araucaroid fossil wood and used it as a basis for distinguishing *Dammaroxylon* from *Dadoxylon*.

*Dammaroxylon natalense* sp. nov.

Plate I, Figures 1–17; Table 1

*Holotype*: Dept. of Botany, University of the North, Pietersburg. Slides E4a–e; Plate 1, Figures 1–17.

*Locality*: M'hlosinga district, Zululand, Natal.

*Age*: Cretaceous.

*Derivation of name*: The plant is named after the province of Natal in which it has been discovered.

Diagnosis

Secondary wood with annual rings; rays uniseriate, 1–7(–14) cells high; border cells undulate regularly or irregularly, shape varies from conical and tongue- to bladder-shaped, border cells double layered in some instances; radial tracheid pits constantly uniseriate, contiguous or separate, circular or horizontally slightly flattened; cross field pits 2–6(–12), circular or oval, bordered, pit apertures circular, pits aligned in horizontal pairs or rows or scattered, contiguous or separate; wood parenchyma absent.

ANATOMY OF THE FOSSIL WOOD

*Cross section* (Plate I, Figures 1 and 4): Annual rings are present (Figure 4). The tracheids are well preserved and are mostly circular or oval in shape (Figure 1). The radial diameter of the tracheids varies from 21–34(–46)  $\mu\text{m}$ , while the tangential diameter varies from 16–35(–39)  $\mu\text{m}$ . The tracheid walls are from 3–8(–12)  $\mu\text{m}$  in thickness.† There are from 4–13 rows of tracheids between each two consecutive rays. Wood parenchyma is absent.

*Tangential section* (Plate I, Figures 2, 6, 7, 9 and 10): The tracheid walls are smooth (devoid of pits). The rays are constantly uniseriate (Figure 2) and 1–7(–14) cells high. The shape of the ray cells is oval to rectangular. The height of these cells varies from 18–27(–36)  $\mu\text{m}$  while their width varies from 9–12(–18)  $\mu\text{m}$ . The ray cell walls measure 2–3(–5)  $\mu\text{m}$  in thickness. The rays are bordered above and below by border cells which vary in shape from conical (Figure 10) and tongue- (Figure 9) to bladder-shaped (Figure 6). In some instances the

\* Partly based on an M.Sc. thesis submitted to the University of Pretoria.

† Measurements of cell walls are that of both walls.



border cells appear on top of one another on the one side of the ray (Figure 7). The height of the border cells varies from 3–15(–30)  $\mu\text{m}$ .

*Radial section (Plate I, Figures 3, 5, 8 and 11–17):* The tracheid pits are constantly uniseriate (Figure 3) and mainly circular, although they appear slightly flattened horizontally in some instances. The pits stand contiguous or separate. They vary from 12–17(–20)  $\mu\text{m}$  in height and from 15–18(–20)  $\mu\text{m}$  in width. The horizontal and tangential walls of the ray cells are thin and smooth (Figures 12 and 13) and measure 2–3(–5)  $\mu\text{m}$  in thickness. The rays are bordered above and below by border cells (Figure 16), the outer walls of which undulate regularly (Figure 11) or irregularly (Figure 5). The border cells at the top and at the bottom of the same ray may differ in height (Figure 16). A small secondary triangular cell appears in some instances on top of the border cells (Figure 8). The border cells are normally higher where they are in contact with the tracheid walls (Figures 11 and 16). The outer walls of these cells are thin. Their walls do not seem to contain any pits. Some border cells show 'septa' (Figure 17). Trabeculae occur in some of the tracheids (Figure 14). The cross fields usually show 2 to 6 pits (Figures 12, 13 and 15), but there may be as many as 12 pits per field. The pit apertures are circular (Figure 17). When less than six pits occur in a cross field, they are usually large, separate and scattered (Figure 13). When more than six pits occur in a cross field they are contiguous and aligned in horizontal rows (Figures 12 and 15). The cross field pits measure 4–6(–7)  $\mu\text{m}$  in diameter.

TABLE 1

The most important anatomical measurements of *Dammroxylon natalensis* sp. nov.

| TRACHEIDS                |                          |
|--------------------------|--------------------------|
| Radial                   | 21–34(–46) $\mu\text{m}$ |
| Tangential               | 16–35(–39) $\mu\text{m}$ |
| Wall thickness (double)  | 3– 8(–12) $\mu\text{m}$  |
| Pits: height             | 12–17(–20) $\mu\text{m}$ |
| width                    | 15–18(–20) $\mu\text{m}$ |
| RAYS                     |                          |
| Height (in cells)        | 1– 7(–14)                |
| Height of cells          | 18–27(–36) $\mu\text{m}$ |
| Width of cells           | 9–12(–18) $\mu\text{m}$  |
| Wall thickness (double)  | 2– 3(– 5) $\mu\text{m}$  |
| Cross field pits: number | 2– 6(–12)                |
| diameter                 | 4– 6(– 7) $\mu\text{m}$  |
| Border cells: height     | 3–15(–30) $\mu\text{m}$  |

### Comparison with other fossil wood types

The presence of border cells identifies the specimen with *Dammroxylon*. It differs essentially from the type species, *D. africanum* Schultze-Motel, as well as from the only other species, *D. umzambense* Schultze-Motel, to be placed in a separate species. The rays of *D. africanum* are 1–16(–20) cells high while the tracheid pits are uni-

seriately or biseriately arranged. The new species resembles *D. africanum* as far as the number and arrangement of the cross field pits are concerned. The type species furthermore contains wood parenchyma. Schultze-Motel's (1966) second species, *D. umzambense*, also differs from the new species in that it has a tendency to form biseriate pits while the cross field shows 1–4 pits. Wood parenchyma may also be present in this species. Both Schultze-Motel's species are from the Upper Cretaceous of the Umzamba Beds of East Pondoland. They both lack annual rings, but shearing zones are present which, according to Warren (1912), is indicative of the differentiation of the wood into early and late wood.

The new species can also be compared with *Dadoxylon jamuriense* Maheshwari H. K., an element of the Indian Glossopteris flora (Maheshwari, 1965). Maheshwari, however, only refers to the border cells of his species as a wavy wall running along the long axis of the ray cells. This species should rather be known as *Dammroxylon jamuriense* (Maheshwari H. K.) nov. comb.

The only other wood type in which border cells are present is *Araucariocaulon breveradiatum* Lignier (1907). Although Lignier's illustration (Figure 36) clearly shows the border cells, he does not pay any attention to it in his description. Seward (1919) reproduced the same illustration, but he also did not refer to the border cells. Seward, however, described the fossil as "... an aberrant type the position of which is by no means clear". It is felt that this wood type should also be included under *Dammroxylon* under the name *D. breveradiatum* (Lignier) nov. comb.

### Further remarks on the nature of the border cells

Border cells were first observed by Greguss (1955) in the Araucariaceae and he described them as follows: "Marginal ray parenchyma cells: cells on the upper or lower margin of a ray, commonly different in structure from the inner ray cells and therefore important in identification." According to him these cells lack cross walls and pits, but they have a wall structure similar to that of the ray cells. They form part of the rays and are independent of the tracheid end walls. In *Ginkgo biloba* L. the end walls of the tracheids are thickened where they are in contact with the ray cells and give the impression of border cells (Greguss, 1955). Pool (1922) described border cells as intercellular spaces between the fibre tracheids and medullary rays which form "connecting frames" on the radial walls of the ray cells. Greguss (1957) also described border cells in the Podocarpaceae.

The ontogenetic origin of border cells has as yet not been investigated. Greguss (1970) states that they are "meristematic" and he describes them as "... probably cambial or more nearly monopleuric cambial (in) nature produced by the division of the so-called medullary ray cells proper". They should rather be interpreted as derivatives of the cambial ray initials than being cambial in nature. Also, the meristematic potentiality is limited to the ray initials and is not a characteristic of the derivatives thereof. They can rather



be described as undeveloped derivatives of the ray initials. The secondary border cell may represent a derivative of a ray initial which did not develop further in the radial direction.

## DISCUSSION AND CONCLUSION

*Dammaroxylon* seems to be limited to the Cretaceous rocks which occur along the East Coast of South Africa. The araucaroid structural pattern is exemplified by the tracheid pitting and the tendency towards horizontal alignment of the cross field pits. The ray cell walls are in the primitive, thin-walled primary stage. There are, however, indications of its abietinean affinities. This is shown by the rounded off shape of the tracheary lumen which is accompanied by a reduction in seriation of the tracheid pits.

The known species of *Dammaroxylon* can be arranged in a phylogenetical series. The most primitive of the

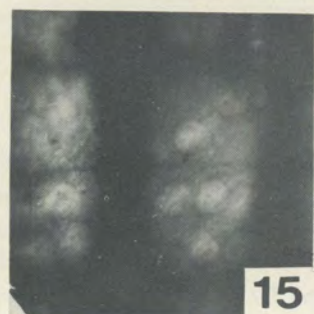
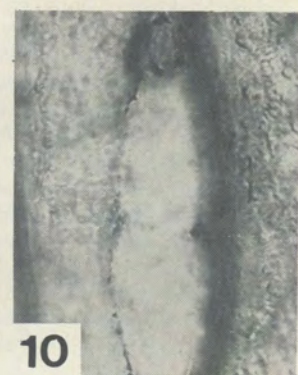
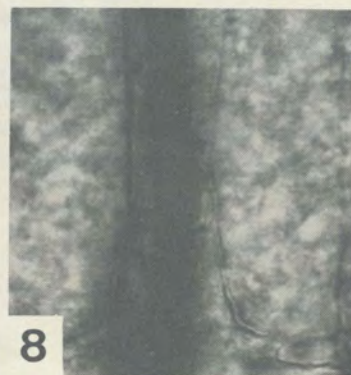
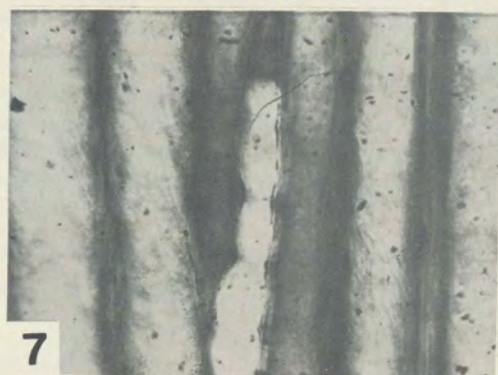
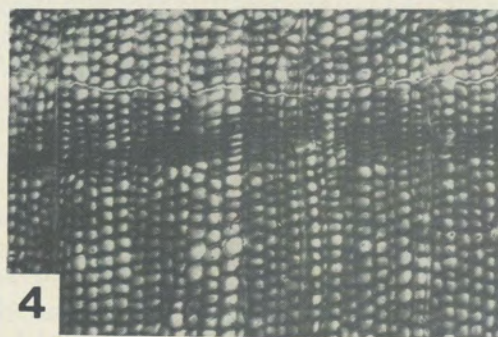
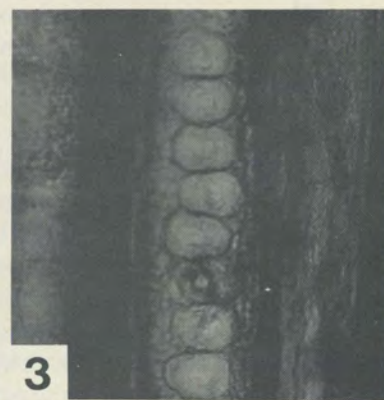
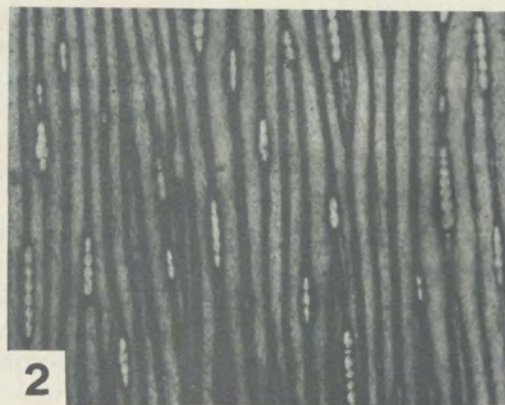
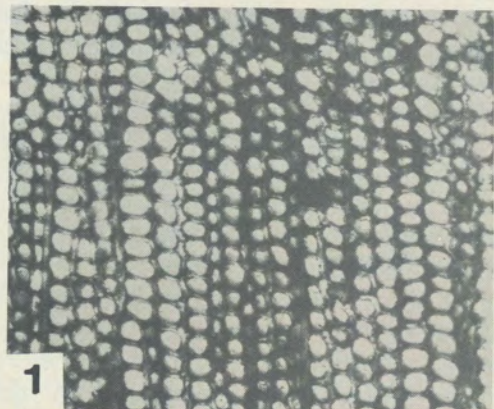
series is *D. africanum* where the tracheid pits are typically araucaroid and always contiguous. *D. umzambense* has progressed a step farther and the tracheid pits are more often uniseriate, but still contiguous and seldom biseriate. In *D. natalense* the greatest reduction is found where the pits are constantly uniseriate. Furthermore, the series show a reduction in the number of cross field pits together with an enlargement thereof. The pits sometimes occur scattered in the field which is a deviation from the normal araucaroid pattern.

The presence of border cells in recent taxa is at this stage still problematic. The ontogenetic origin and general occurrence thereof still remain to be discovered by further investigation — especially in the Araucariaceae and Podocarpaceae. The fact that these cells have been discovered in both these taxa is indicative of a phylogenetic relationship and *Dammaroxylon* could take an intermediate position between the two taxa.

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**PLATE**

- Figure 1. Cross section; circular tracheids;  $\times 80$ .
- Figure 2. Tangential section; uniseriate rays;  $\times 80$ .
- Figure 3. Radial section; uniseriate, contiguous, circular tracheids;  $\times 400$ .
- Figure 4. Cross section; early and late wood;  $\times 40$ .
- Figure 5. Radial section; irregularly undulating border cells;  $\times 400$ .
- Figure 6. Tangential section; bladder-shaped border cell;  $\times 800$ .
- Figure 7. Tangential section; two border cells on top of one another;  $\times 300$ .
- Figure 8. Radial section; secondary, triangular cell on top of border cells;  $\times 800$ .
- Figure 9. Tangential section; tongue-shaped border cell;  $\times 800$ .
- Figure 10. Tangential section; conical border cell;  $\times 800$ .
- Figure 11. Radial section; regularly undulating border cells;  $\times 800$ .
- Figure 12. Radial section; contiguous cross field pits aligned in horizontal rows; smooth end wall of ray cell;  $\times 600$ .
- Figure 13. Radial section; small number of separate cross field pits; smooth horizontal walls of ray cells;  $\times 300$ .
- Figure 14. Radial section; trabecula in tracheid;  $\times 300$ .
- Figure 15. Radial section; cross field pits in horizontal rows with tendency to be separate;  $\times 300$ .
- Figure 16. Radial section; border cells on top and at bottom of ray differ in height;  $\times 300$ .
- Figure 17. Radial section; border cell with "septum"; cross field pits with faint circular aperture;  $\times 500$ .



## AN ENTOMOBRYID COLLEMBOLAN (HEXAPODA: COLLEMBOLA) FROM THE LOWER PERMIAN OF SOUTHERN AFRICA

by

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## ABSTRACT

*Permobrya mirabilis* gen. et sp. nov., recorded from carbonaceous shales of the Middle Ecca of southern Africa, is a rather large entomobryid collembolan. The specimen, preserved in lateral view, is complete except for the dentes and mucrones of the furcula and details of the claws which are not visible in the shale matrix. The species is surprisingly similar to Recent Collembola.

## INTRODUCTION

Collembola are such fragile animals that they are rarely preserved as fossils, except in amber. *Rhyniella praecursor* Hirst and Mulik 1926 from the Middle Devonian Rhynie Cherts of Scotland is the only recorded Palaeozoic species that is almost certainly a collembolan. Tillyard (1928) was of the opinion that the species was a collemboloid hexapod but until the segmentation of the abdomen is known he refrained from placing the species definitely in the Collembola. From a study of additional specimens in which head, thorax and basal segments of the abdomen are preserved Scourfield (1940) concluded that *Rhyniella praecursor* was a true Collembolan that combined podurid and entomobryid characters.

An almost complete collembolan was discovered by the writer in carbonaceous shales of Middle Ecca age at Hammanskraal, near Pretoria, southern Africa. The specimen and counterpart were recovered from fragments of a slab of rock damaged in transit through the mails. This sample had been sent for detailed study of an insect nymph discovered by Dr. Éva Kovács-Endrödy during a study of the plant fossils in the shales.

The collembolan is clearly preserved in lateral view to show most of the diagnostic characters of the Entomobryidae: only the structure of the pronotum, details of the tarsal claw and the structure of the dentes and mucrones are unknown. The species combines characters of a number of Recent genera. There are no characters unique to the fossil species.

## Order Collembola

## Family Entomobryidae

*Diagnosis*

Most of the thoracic and abdominal segments distinctly defined. Pronotum completely hairless, often concealed under the mesonotum. Body scaled or with at least dense ciliated club-shaped setae. Segment 4 of abdomen usually much longer than segment 3. Furcula always well developed.

The family has a world-wide distribution. The species are often amongst the largest of the Collembola, with length up to 10 mm.

A species from the Lower Permian of southern Africa is referred to the family.

Genus *Permobrya* gen. nov.

*Type species. Permobrya mirabilis* sp. nov.

*Diagnosis*

It is not possible to give a valid generic diagnosis because Recent genera are defined largely on the dentes, mucrones and claws and the structure of these parts is not known in the fossil. However, the genus is similar in general appearance to *Lepidosira* and *Lepidocyrtus* except that the legs are rather short and stout, the eyes are not distinctly defined (or preserved) and the fourth antennal segment is annulated. In this last character the genus resembles *Mesira* and *Lepidocyrtoides*.

Although the structure of the dentes, mucrones and claws is not known, the presence of scales on the body and the long fourth abdominal segment leaves no doubt that the genus is correctly referred to the Entomobryidae.

*Permobrya mirabilis* sp. nov.

Figures 1—4

*Type*

HI 248 a, b, in Geological Survey, Pretoria.

*Type locality*

North-western corner of the farm Haakdoornfontein 119 JR, 7.25 km almost due south of Hammanskraal, near Pretoria, Africa, in carbonaceous shale of Middle Ecca age.

*Description*

Lateral view of whole animal. Length without furcula c. 4.5 mm. Outline of head, viewed from in front, vague. Antennae both preserved, inserted close together, one mostly overlying the head, the other fully exposed and distinct. Antennae 4-segmented, all



segments long, increasing regularly in length, terminal segment slightly more than twice as long as first, distinctly wider than basal segments as preserved and annulated, with 7 or 8 annuli. Mesonotum distinctly sclerotised, lateral margin obscured by overlying antenna. Metanotum slightly shorter than mesonotum, lateral margin apparently convex. First two segments of abdomen very short, each about half as long as metanotum, and extending laterally only as far as metanotum. Segment 3 about as long as 1 and 2 combined, lateral margin ill-defined. Segment 4 large, as long as basal three segments combined, sclerotisation apparently extending to ventral margin of the body as preserved. Apical segment or segments about as long as high. Furcula distinct but only manubrium preserved: manubrium long and stout, almost as long as terminal segment of abdomen. Ventral tube distinct, about twice

as long as wide. Two legs preserved, one apparently a hind leg, the other possibly a fore leg, with proportions differing in the two legs. Combined coxa plus trochanter of (fore?) leg about as long as femur. Tibio-tarsus somewhat shorter and narrower than femur. From the irregular outline of the dorsal margin of the body it would appear that the body was covered with scales.

*Note.* It is surprising that this species of such great age should resemble Recent Collembola so closely.

#### ACKNOWLEDGEMENTS

I am grateful to John Green for the photographs and Dr. Éva Kovács-Endrödy for the opportunity to study the insects from this Middle Ecca horizon, without which this outstanding hexapod would not have been discovered.

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Figures 1–4. *Permobrya mirabilis*. 1 and 3: Untouched photographs. 2 and 4: Retouched photographs.

(For overall size, see text page 141.)



## FOSSIL INSECTS FROM THE MIDDLE ECCA (LOWER PERMIAN) OF SOUTHERN AFRICA

by

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## ABSTRACT

Three insects are recorded from carbonaceous shales of Middle Ecca age from Hammanskraal, near Pretoria. *Thaumtophora pronotalis* gen. et sp. nov., is an aquatic nymph of the Paraplecoptera showing lateral abdominal gills. *Sysciophlebia kovacsae* sp. nov. is a tegmen of a spiloblatinid cockroach. The third specimen is a small protopsyllidiid nymph. Only three insects of greater age are known from southern Africa.

## INTRODUCTION

Most of the Palaeozoic insects known from southern Africa are recorded from the Middle Beaufort Series of Upper Permian age (Riek, 1973, 1974 and in press). Only three insects of greater age are known from this region, the blattodean *Rhodesiomylacris bondi* (Zeuner, 1955) from the Lower Beaufort, the paraplecopteron (?) *Boutakovia salei* (Pruvost, 1934) from the base of the Ecca, and the paraplecopteron *Hadentomoides dwykensis* (Riek, 1974) from the top of the Dwyka Series and probably of late Upper Carboniferous age.

Three insects are recorded in this paper from carbonaceous shales of the Middle Ecca. A collembolan is also recorded from the same sediments (Riek, this volume). The insects were collected by Dr. Éva Kovács-Endrödy, at Hammanskraal, near Pretoria, during her study of the plant fossils. The insects consist of two nymphs and the fore wing of a cockroach. All are of considerable interest. The blattodean fore wing is referred to the Spiloblatinidae, a family typical of the late Upper Carboniferous. One moderately-sized nymph is referred to the Paraplecoptera on the large paratergal processes on the pronotum and the presence of lateral abdominal gills. The second very small nymph, with a body length of 5 mm, is referred to the Protopsyllidiidae (Homoptera).

## SYSTEMATICS

## Order Blattodea

## Family Spiloblatinidae

The family is characterized by the well developed Sc, extending at least to the middle of the wing, combined with the loss of the archdictyon. It is sometimes difficult to distinguish between Spiloblatinidae and some Poroblatinidae in which Sc is also well developed, but in the latter family the stem of Sc tends to be straight and not subparallel to the costal margin as in Spiloblatinidae.

The family is recorded mainly from the latter part of the Upper Carboniferous. A species from the Lower Permian of southern Africa is referred to the family and placed in a known genus.

Genus *Sysciophlebia* Handlirsch

*Sysciophlebia* Handlirsch 1906

Type species: *Blattina euglyptica* Germar 1851

## Diagnosis

CuA sigmoidally curved and subparallel to caudal margin distally, and distal branches simple. Sc extending well towards apex of wing. Rs with branches tending to form a forward pectinate series.

The genus is recorded for the Upper Carboniferous of North America, Europe and Russia. A species from the Lower Permian of southern Africa is referred to the genus and compared with the type species, *euglyptica*, from the Upper Carboniferous of Europe.

*Sysciophlebia kovacsae* sp. nov.

Figure 1

## Etymology

The species is named for Dr. Éva Kovács-Endrödy who discovered this and the other fossil insects, incidental to her studies of the plant fossils.

## Type

H.T. 201, in Geological Survey, Pretoria.

## Type locality

North-western corner of the farm Haakdoornfontein 119 JR, 7.25 km almost due south of Hammanskraal, near Pretoria. Middle Ecca.

## Description

Fore wing (tegmen) complete except for clavus, base and part of apex. Length as preserved 21 mm in-



dicating a wing length of 23 mm. Sc extending to apical third of wing. Costal veinlets mostly simple, occasionally 2-branched towards wing base. R slightly sigmoidal towards base, 3-branched, branching about level with apex of clavus. Rs with 5 forward branches to wing margin, ending slightly above middle of apex. M parallel to R at base, first branching not preserved but apparently slightly after the origin of Rs. M with six branches, to wing apex. CuA appearing to arise as a forward branch of CuP near wing base. CuA sigmoidally curved, subparallel to hind margin distally, branching before the origin of Rs, with 11 or more branches to the posterior margin, distal branches simple, pectinate, first branch very deeply forked, second branch forked. CuP strongly curved to wing margin. Clavus not preserved.

*Notes.* The species can be compared closely with the type species *euglyptica* which, itself, varies somewhat in venation, especially in the branching of R and arrangement of the branches of Rs which sometimes appear more dichotomic than forwardly pectinate. The new species differs from *euglyptica* in the very deep forking of the first and second branches of CuA and the more abrupt forward origin of the stem of CuA.

### Order Paraplecoptera

The Paraplecoptera is a large, very diverse, widely distributed order that made its first appearance in the Upper Carboniferous of North America, Europe and Russia, was abundant in the Permian of Russia, Moravia, North America and southern Africa, and apparently persisted to the Triassic of Siberia, Australia and Japan. The Paraplecoptera is most probably the ancestral group of all Neoptera.

The Paraplecoptera, Protoblattodea and Protorthoptera are recognised by me as being sufficiently distinct to warrant separate ordinal status. A few of the species at present referred to the Paraplecoptera may subsequently require re-allocation to other orders when more details of the morphology are known. The order Paraplecoptera is used in a broad sense to embrace those insects in which the me-

dian field of the fore wing is usually independent of the cubital field and the most posterior branch of CuA is not set off as a distinct vein (Cun or CuA2). The Protoperlaria are included in the Paraplecoptera. The order Protorthoptera embraces those "orthopteroids" in which there is partial fusion between MP and CuA and development of a distinct CuA2 but which, unlike Orthoptera *s. str.*, have numerous irregular branches to MA. The order Protoblattodea embraces those species in which there is a distinct clavus in the fore wing and partial fusion between MP and CuA. There will always be difficulty in the placement of some wings because, as in Recent Orthoptera, it is possible that the oblique branch of M fusing with CuA may assume a transverse alignment and appear similar to a cross vein.

The presumed nymphs of several species of Paraplecoptera have been described. The best documented are the presumed nymphs of the Lemmatophoridae (Carpenter, 1935) from the Upper Permian of Kansas. These nymphs, which are almost certainly correctly placed, are said to have gills, laterally, on the first nine abdominal segments. Although there may be some doubt about the structure and number of these processes as interpreted by Carpenter, the nymphs are very similar to those of Recent Plecoptera, and all Plecoptera nymphs are aquatic with the exception of a very few apomorphic species of Gripopterygidae. Carpenter illustrates the gills as inserted over the whole lateral margin of the segment, and thus reminiscent of a pleural lobe to the segment, whereas gills are normally inserted at or close to the postero-lateral margin of the segment. Thus, gill 9 as interpreted by Carpenter would more probably be gill 8 protruding caudally from its insertion postero-laterally on segment 8. This would mean only eight pairs of gills. However, Carpenter illustrates nine such processes on each side of the abdomen of each of the two types of nymphs occurring in the Lower Permian of Kansas illustrated by him.

*Kaltanympa thysanuriformis* (Sharov, 1957) from the Lower Permian of Kuzbass was referred to the Paraplecoptera. This generalised nymph has few



Figure 1. *Sysciophlebia kovacsae* sp. nov. Holotype.



distinctive attributes but it differs from other paraplecopteran nymphs in the apparent small size of the head.

The supposed crustacean, *Pygocephalus cf cooperi* of Dix and Pringle (1930), from the Upper Carboniferous of England, interpreted as the abdomen of a blattodean nymph by Rolfe (1967) is, in all probability, the abdomen of an aquatic nymph of the Paraplecoptera. There is a striking similarity between the terminalia of this nymph and female nymphs of some Recent Plecoptera. The lateral dark areas on the abdomen very probably represent lateral gills.

A nymph from the Lower Permian of southern Africa is referred to the Paraplecoptera. Lateral abdominal gills are presented on at least the basal six segments.

This nymph differs noticeably from the numerous nymphs referred to the Protoperlaria (= Paraplecoptera in part) (Carpenter, 1935) not only in the development of paratergal lobes on the pronotum but also in wing bud development and number of gills. Carpenter stated that gills are present on segments 1–9 in the nymphs from the Lower Permian of Kansas, whereas, at most, they occur on segments 1–8 (known only from 1–6 but lateral margins of segments 7 and 8 obscured) in the present nymph. Paratergal lobes are not developed in the Kansan nymphs and the wing buds were not clearly differentiated from the central part of the nota.

With reference to the paraplecopteran nymphs from the Lower Permian of Kansas, Carpenter (1935) stated "when we compare the Kansas permian nymphs with those of Recent Perlarians, we find at once such similarity that it is difficult to detect the differences which we might expect in view of the great age of the fossils". The nymphs were referred to the Paraplecoptera and not the Plecoptera because of the absence of adult Plecoptera and the abundance of adult Paraplecoptera supported by the abundance of nymphs.

The present nymph can be referred to the Paraplecoptera with just as much assurance because of the development of distinct paratergal processes on the pronotum and their similarity to the same structures in adult Paraplecoptera. Paratergal processes are absent or indistinct in both adult and nymphal Plecoptera.

The nymph is named to facilitate future reference to the specimen. It is difficult to differentiate between generic and specific characters. However, the form of the paratergal processes and the form of the tarsal segmentation are probably of generic significance. Family placement is left in abeyance until the fauna from this horizon is better known.

Genus *Thaumatothorax* gen. nov.

Type species: *Thaumatothorax pronotalis* sp. nov.

#### Diagnosis

Pronotum produced to large, convexly margined, sculptured, paratergal processes. Tarsi 3-segmented, first tarsomere short and quadrate.

*Thaumatothorax pronotalis* sp. nov.

Figures 2–3

#### Type

H.T. 248, in Geological Survey, Pretoria.

#### Type locality

North-western corner of the farm Haakdoornfontein 119 JR, 7,25 km almost due south of Hamanskraal, near Pretoria. Middle Ecca.

#### Description

*Nymph.* Immature, but with distinct wing-pads, nymph complete except for head and anterior part of pronotum. Length as preserved 13 mm, without the cerci, indicating a body length of 18 mm. Pronotum broader than mesonotum, with distinct paratergal processes, lateral margin of process markedly convex. Processes sculptured with irregular grooves, processes apparently thicker than central disc of pronotum. Mesonotum and metanotum slightly broader than long, without obvious sculpture or differentiated areas, the median ecdysial suture line distinct on metanotum, and with distinct postero-laterally directed wing-buds. The wing-buds are widely separated, especially on mesonotum, and the posterior margin of the wing rudiment is broadly free. Abdomen 10-segmented, segment 1 short and visible only at meson (covered laterally by hind wing-bud). Segment 2 short, segments 3–9 subequal, longer than segment 2, segment 10 about as long as segment 9, rounded postero-laterally. At least abdominal segments 1–6 with small lateral gills inserted close to the lateral margin posteriorly. (Lateral margins of segments 7 and 8 not exposed, segment 9 without gill.) Gills not distinctly defined but apparently short, finger-like and annulated. Cerci not fully preserved and with some margins indefinite, segmentation not distinct, preserved portion about as long as width of abdomen. The dark area between the bases of the cerci apparently represented an extrusion from the anus. Hind leg preserved, viewed posteriorly, stout. Coxa about as long as broad at base, tapering to apex. Trochanter triangular. Femur very broad, with a longitudinal carina towards lower margin (? representing the margin of the lower groove into which the tibia folds). Tibia slightly longer than femur but only about half as wide, lower margin with at least six stout spines from middle to apex. Tarsus short and stout, 3-segmented, first tarsomere short, quadrate, second transverse, third distinctly longer than first two combined.

Except for the large lobes on the pronotum, the nymph can be compared closely with the nymphs of Plecoptera, especially Eustheniidae which the nymph resembles even in the structure of the gills. It is not known whether lateral abdominal gills were present on segments 7 and 8 as the lateral margins are obscured. They were not present on segment 9 but were present on segments 1–6. In Eustheniidae, gills are present on segments 1–5 (*Stenoperla*) or 1–6 (most genera). The broad flattened hind leg of the fossil nymph differs





Figures 2 and 3. *Thaumtophora pronotalis* gen. et sp. nov. Holotype. 2. Untouched. 3. Retouched.  
(For size of specimens see text)

from that of the Eustheniidae mainly in the development of a distinct series of stout spines on the distal half of the lower margin of the tibia. The 3-segmented tarsus differs only in detail.

There are no characters of the nymph with the exception of the paratergal lobes on which it should not be referred to the Plecoptera. However, on this character the nymph is referred to the Paraplecoptera.

**Order Hemiptera**  
**Suborder Homoptera**  
**Family Protopsyllidiidae**

The family is recorded from the Upper Permian and Triassic of Australia, the Upper Triassic and Jurassic of Asia, and the Triassic of southern Africa. Nymphal exuviae have been recorded from all three regions. The Lower Permian nymph (H.I. 150a) resembles those previously described as far as can be ascertained from the somewhat imperfect preservation.

**ACKNOWLEDGEMENTS**

I wish to thank Dr. Éva Kovács-Endrödy and the Director of the Geological Survey of South Africa for the opportunity to study these most interesting early fossil insects. The photographs were prepared by John Green of CSIRO, Canberra.

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## AN UNUSUAL MAYFLY (INSECTA: EPHEMEROPTERA) FROM THE TRIASSIC OF SOUTH AFRICA

by

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## ABSTRACT

An unusual mayfly from the Upper Triassic near Dordrecht in the Cape Province of South Africa is described as *Xenophlebia optata* gen. et sp. nov., and is ascribed to a new family, the Xenophlebiidae, as its sole representative.

## INTRODUCTION

The classification of Recent Ephemeroptera is based, to a considerable extent, on structures other than the wings of the adults. However, the major groups (subfamilies and higher categories) of Recent Ephemeroptera can be defined on differences in venation, with the possible exception of a few Baetoidea (Ametropodidae and Metretopodidae) in which it is also necessary to know the structure of the adult tarsi, or the structure of the head of the nymph, to distinguish them from Heptageniidae.

The major trend in the wings of Ephemeroptera has been reduction in the size of the hind wing. The known Permian species and some early Mesozoic ones had a hind wing that was as long as and slightly broader than the fore wing. Reduction has culminated in the complete loss of the hind wing in the more specialised Recent species of a number of phyletic lines. In the initial stages of reduction of the hind wing, a complementary tornus, or obtuse angle, formed on the hind margin of the fore wing at a point about level with the apex of the hind wing. The tornus is situated between the two branches of the cubitus, except in the Baetiscidae. Even though the hind wing is relatively large in the Baetiscidae, which retain a very primitive wing venation, the tornus is in the anal field. The Baetiscidae is the only family in which CuA and CuP are subparallel and connected by simple cross veins for all or most of their length. In all other mayflies, the tornus, when present, is between the branches of Cu. As the hind wing is reduced, there is a greater complementary reduction in the length of CuP as compared with CuA so that the length of the wing margin occupied by the cubital field increases up to a point, and then remains relatively constant.

When the hind wing is very reduced or absent, the tornus is lost, and the hind margin of the fore wing is rounded, and slightly to markedly widened in the cubito-anal field. The base of the wing is markedly widened in Caenidae, Baetidae and Tricorythidae but it is not widened in Leptophlebiidae. The hind wings are not markedly reduced (or absent) in other Ephemeroptera. At no stage in the sequence of reduction do the two main branches of the cubitus become re-oriented and subparallel to one another as they are

in the Permian Mithodotidae and Recent Baetiscidae.

However, the fossil species under review from the Upper Triassic of southern Africa has a very reduced cubito-anal area, and the two branches of Cu are close and subparallel (and connected by a simple cross vein or veins). The tornus is lost but the wing is not widened at base. The cubito-anal field is markedly reduced and occupies only a minute area at the base of the wing.

Reduction in venation resulting in a long relatively narrow wing with a minute cubito-anal field (and a large MP field) had been unknown in any phyletic line, either fossil or Recent.

This very unusual mayfly, of which only the wing, almost certainly a fore wing, is known, is referred to a new superfamily without recognisable close phyletic relationship to any known Ephemeroptera.

## SYSTEMATICS

## SUPERFAMILY XENOPHLEBIOIDEA

superfam. nov.

*Diagnosis*

*Wing.* Stem of Cu distinct to wing base, as in Permian Ephemeroptera, branching into CuA and CuP more basally than the thickened stem of the anal field. Basal thickened stem of anal field curved upwards, mainly at the cross connection between 1A and CuP; stem more similar to that in Recent than in Permian species. Rs appearing to arise as a forward branch of MA, and MP arising very close to the wing base, before the separation of Rs + MA from the stem of R, as in Recent Ephemeroptera. Bullae present, on Sc and the upper branch of Rs. Posterior branch of MP arising close to base, not deflected towards CuA close to its origin from the stem of MP, but more or less straight throughout its length.

*Notes.* The basal origins of the main veins are partly as in Recent Ephemeroptera and partly as in the Permian Proterismatidae and Mithodotidae. The more or less straight posterior branch of MP is similar to that in Baetoidea, Heptagenioidea and Leptophlebioidea, as distinct from Ephemerioidea, but the triad is developed very close to the wing base, as in Ephemerioidea. The absence of cubital intercalary veins may be due entirely to the very marked reduction in the cubito-anal field of



the wing, and may not relate the group to the Baetiscidae in which this area of the wing is fully developed.

The absence of a tornus indicates that the hind wing was absent or minute, at least in the one known species. However, development of the hind wing is variable in Recent Ephemeroptera.

The superfamily represents a line of development distinct from any that lead to the Recent Ephemeroptera, in which such a marked reduction in the cubito-anal field is unknown.

One included family, from the Upper Triassic of southern Africa.

#### FAMILY XENOPHLEBIIDAE fam. nov.

##### Diagnosis

*Wing.* MP forming a simple triad, or at most with a tendency towards attached marginal intercalary veins. Without intercalary veins between MP and CuA. Without cubital intercalary veins (CuA and CuP connected by a simple cross vein or veins). CuP straight. Rs arising from close to wing base. Cross venation well developed. Wing without short marginal intercalaries.

One included genus.

Genus *Xenophlebia* gen. nov.

##### Etymology

Xenos = stranger, and phleps = vein, from the very unusual venation.

##### Type species

*Xenophlebia optata* sp. nov.

##### Diagnosis

*Wing.* Almost certainly fore wing: hind wing almost certainly absent. Tornus absent. Cubito-anal area minute. Triad on MA arising about middle of vein. Rs forking moderately close to origin, but about level with triad on MA. CuA and CuP very short, connected by only a basad cross vein. Three distinct anal veins, all minute, simple. MP with convex middle branch forking close to wing margin (possibly a variable character). Cross veins complete over whole wing, simple, except in part, close to margin. Cross veins simple in pterostigmatic area. Bulla on upper branch of Rs very close to origin of branch.

*Xenophlebia optata* sp. nov.

(Figures 1-3)

##### Type

C-Dt II 752 a, b and paratypes 754 a, b and 755 a, b, in Bernard Price Institute.

##### Type locality

Bird's River, Dordrecht, Eastern Cape Province. Molteno Formation. Upper Triassic.

##### Description

In Recent Ephemeroptera specific characters are recognised mainly in the terminalia which are unknown for the species.

##### Holotype

Fore wing, complete. Length *c.* 21 mm. Cross veins not appreciably closer in the pterostigmatic area than more basally and, thus, pterostigma not defined. Triad on MP arising from basal fork in vein. Bulla on upper branch of Rs at the level of the first cross vein to the basad triad. Short cross connection from CuA near its base to the stem of M before separation of MP. 1A very widely separated from CuP, with a strong cross connection appearing as an upward continuation of the stem of A. Only three anal veins, simple, the third very short.

C-Dt II 754 a, b is a complete wing, slightly weathered and therefore the impression is pale but venation distinct, including basal swellings of the veins. Costal margin thickened at base. Humeral vein simple, humeral space not widened but rather long.

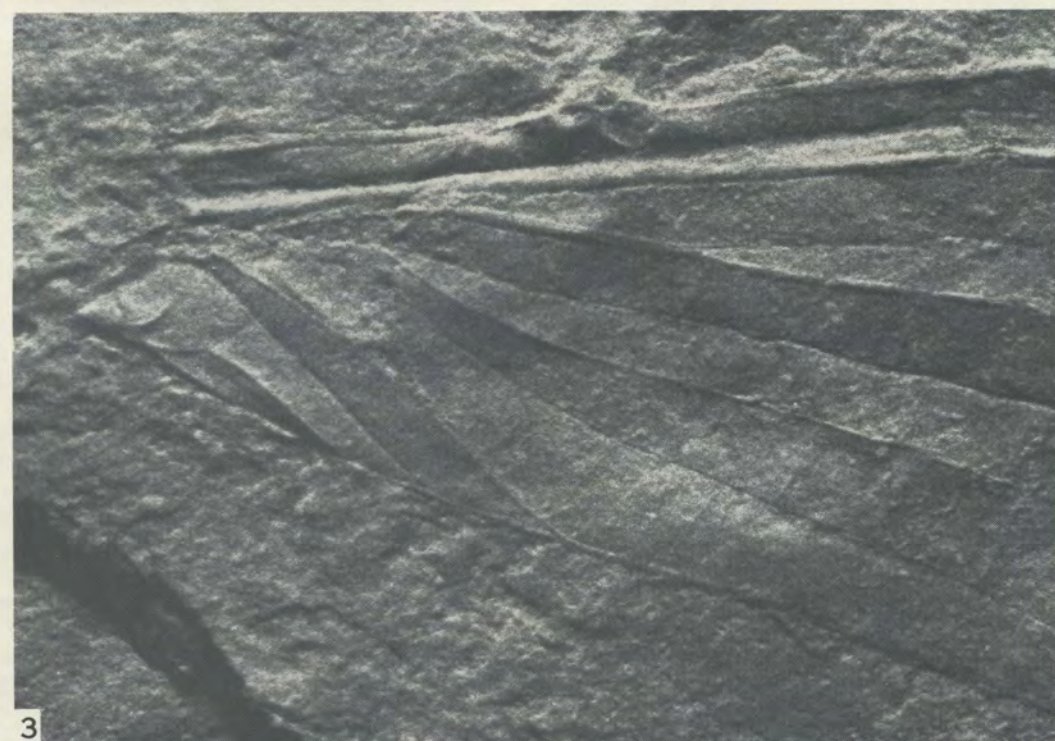
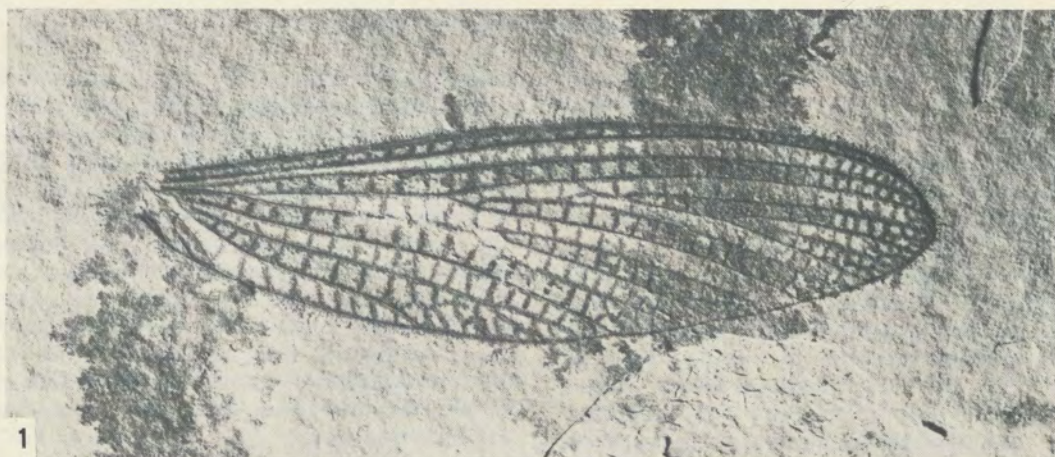
C-Dt II 755 a, b is the distal half of a wing from the bullae to apex. This wing is very slightly larger than the other two wings.

*Note.* The venation of the almost perfectly preserved holotype wing is accentuated by mineral staining.

#### ACKNOWLEDGEMENTS

I am grateful to John Green, CSIRO, Canberra for the photographs.





Figures 1–3. *Xenophlebia optata* gen. et sp. nov. 1. C-Dt II 752 a, reversed. 2. C-Dt II 754 b. 3. C-Dt II 754b. Base of wing enlarged.  
(For size of specimens, see text.)



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