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PALAEONTOLOGIA AFRICANA

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

VOLUME 16, 1973

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1972

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Addendum:
Add. On p. 17 of volume 14: "By A. R. I. Cruickshank".

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BERNARD PRICE INSTITUTE FOR PALAEONTOLOGICAL RESEARCH
UNIVERSITY OF THE WITWATERSRAND, JOHANNESBURG
REPORT OF THE HONORARY DIRECTOR
FOR THE YEAR 1972

The year under review has been, for the staff of the Institute, one of partial frustration because of the somewhat extensive alterations and additions to the buildings which continued uninterruptedly from early in January until the middle of December. Some of the offices were temporarily uninhabitable; and almost the whole of the collections were, at some time or another, subjected to temporary moves from one locale to another previous to reaching what, it is hoped, will be their final storage places. However, these "trials and tribulations" are almost at an end. Staff members and research students are now satisfactorily housed and now able to work and think without the external noise, dirt, and inconvenience that the presence of builders always entails. Tribute must be paid to all of them for the manner in which they contributed to the safe keeping of the invaluable collections possessed by the Institute. Certain additional furnishings and equipment are still needed; but we have every confidence that these will be supplied.

STAFF CHANGES

Dr. E. P. Plumstead, having terminated her official position as a member of the University staff, consented to serve the Institute as an Honorary Research Fellow in Palaeobotany. Her successor as Senior Research Officer, appointed by the University, is Dr. Hans Tralau of Stockholm who was expected to assume duty in the Institute late in 1972, but has not yet arrived. Dr. Plumstead kindly consented, pending his assumption of duty, to keep a watchful eye on the progress of the three Ph.D. candidates and four M.Sc. candidates who are working on palaeobotanical theses and for whom she was appointed supervisor at the beginning of their studies. In the case of one of the Ph.D. candidates she requested permission from the University to be relieved of the duties of supervisor.

Miss E. Barrett resigned from the post of Secretary and was replaced on 1st June by Mrs. S. J. Holloway.

Owing to her husband's transfer, Mrs. Essers had to resign from the post of part-time Librarian. Fortunately, we were able to replace her by Mrs. Edwards, who had previously worked with us.

Mr. P. Nagel was appointed as a temporary laboratory assistant while undertaking part-time photographic work on behalf of Soekor which contributed towards his salary.

Soekor appointed two women laboratory assistants to help their research officers stationed in the Institute. One, Miss Moran, was appointed in September; the other, Miss C. Serbon, in November.

Dr. Plumstead's assistant, Miss Carnell, left in September and has not yet been replaced.

Mrs. E. A. Nesbitt returned to the Institute in August in order to complete her M.Sc. thesis on Pareiasaurs.

RESEARCH WORK

1. The Assistant Director, Dr. A. R. I. Cruickshank, had most of his time taken up with day-to-day administrative matters, lecturing in the Department of Geology and supervision of research students. However, he began a study of the foot structure of early Archosaurs by assembling a series of feet belonging to *Proterosuchus, Erythrosuchus, Euparkeria, Massospondylus* and an unnamed crocodile from the Red beds. He wrote a short paper on Gorgonopsian mode of life for the $S_2 A_3$, and a paper on *Kannemeyeria* which will appear in *Palaeontologia Africana*. He paid a visit to Rhodesia and accompanied Mr. M. A. Raath, of the Rhodesian National Museums, on a collecting trip to the Chitake River in the Zambezi valley, which was very productive of Forest Sandstone fossils.
2. Mr. J. W. Kitching completed his massive thesis entitled "On the Distribution of the Karroo Vertebrate Fauna with Special Reference to certain Genera and the Bearing of this Distribution on the Zoning of the Beaufort Beds". This is an outstanding contribution and, at the request of the supervisor, the University authorities agreed to raise its status to that of a Ph.D. thesis. Mr. Kitching also continued, somewhat spasmodically, his study of the fossil bone material from the Border Cave deposits, which have been excavated by Mr. P. Beaumont. Thus far he has sorted and identified a total of 57 040 fragments.
3. Dr. E. P. Plumstead examined lycopod fossils discovered at Port St. Johns and paid two visits to the area with a view to revision of the stratigraphy and structure of the region which the fossil discoveries will entail. She has continued with the overall study and summary of the characters of the *Glossopteris* flora, in preparation for a section in Vol. VI of the "Traité de Palaeobotanique" which will be published in Paris.

   Dr. Plumstead attended, by invitation, the NATO Advanced Study Institute meeting at

Newcastle-upon-Tyne, England, which was a Symposium on Continental Drift, Sea Floor Spreading and Plate Tectonics, and was held in April. There she read a paper entitled "The enigmatic *Glossopteris* Flora and Uniformitarianism", and took the chair at one of the sessions.

Several of her papers, written in 1972, await publication in various journals and are likely to be available for distribution in 1973.

4. Mr. C. W. Gow has continued, under adverse conditions, with the detailed preparation of specimens and their examination in connection with his studies of the genera *Prolacerta* and *Youngina* as a basis for a discussion of the origins of Lepidosaurs and Archosaurs. Since these studies were commenced, the Institute has been acting as a centre of work for Dr. R. L. Carroll of McGill University, Montreal, whose interests parallel very closely those of Mr. Gow and who has examined much of the available material.

   Mr. Gow also secured for the Institute the Putterill collection of Karroo vertebrate material, a fact that is recorded with pleasure.
5. Mr. B. R. Turner has been engaged throughout the year on the preparation of his doctoral thesis on the stratigraphy and sedimentary history of the Molteno beds in the Karroo basin of South Africa and Lesotho. Descriptive accounts of the cyclic nature of the sedimentation were completed. The interpretation of the information is now being assessed quantitatively; variables disclosed by the study are being tested through various mathematical approaches which, it is believed, will yield important results, justifying the time spent on them. In the enlarged building, Mr. Turner has a fully-equipped sedimentological laboratory.
6. Mr. B. Maguire has had certain other duties to perform which have, to a considerable extent, interfered with the preparation of his thesis which deals with the plant-life of the Kalahari and its relationship to the life-habits of the Bush people and their possible ancestors. He has also continued his study of the large collection of chipped stones—which he and some other workers consider to be artefacts—which has come from the beds excavated at the Makapansgat sites. It is hoped that his thesis will be completed during the coming year.
7. Miss J. Roets, who has been accepted by the University as a candidate for the Ph.D. degree, has had—like all staff members—her research work seriously interrupted by the unusually heavy departmental commitments, especially those associated with the transfer of the large collections of fossil and recent mammal bones to the new accommodation prepared for them. Her thesis is concerned primarily with the morphology and classification of the porcupine genus *Hystrix*, which was described in 1758 and to which, since that date, more than 80 separate species have been assigned, of which 15 are fossil, the earliest appearing in the Late Miocene. Her studies have involved consideration of the acceptability of individual morphological characters for specific determinations, and the investigation of porcupine lairs with a view to elucidating the rate of bone accumulation therein and the proportion of gnawed bones in the débris. She hopes to complete her thesis within the first quarter of the coming year.
8. Mr. P. Beaumont operates in the Institute under a special arrangement originally made between the Anglo American Corporation and Professor R. A. Dart for the study of the work of early Man in Southern Africa. Work at the various sites examined by him has been wholly subsidised by the Corporation; the Institute provides him with office accommodation and storage space. At the request of the Corporation, an advisory Committee was established early in 1972; on this the Institute is represented by 3 members, one of whom—the Honorary Director—acts as chairman. Most of the work during the year under review has been connected with the results of excavations at the Border Cave, where the lowest layers of the fossil-bearing sediments (which include well-preserved animal hair fragments) have been assigned a minimum age of 35 000 years B.C. Some of the conclusions reached have been published; but there remains much to be elucidated and it is hoped that the necessary financial arrangements to allow Mr. Beaumont to continue his studies will be made. Collaboration with Mr. A. Boshier, of the Johannesburg Museums of Man and Science, has been maintained throughout the year; and age determinations have been undertaken by Dr. J. Vogel of the National Physics Laboratories of the C.S.I.R.
9. Mrs. H. Anderson has made considerable progress with her thesis on the fossil plants of the Molteno beds, which is now in an advanced stage of preparation. She undertook further collecting trips in connection with it.
10. Two of Soekor's scientists—Mr. J. Anderson and Mr. I. R. McLachlan—are registered with the University as higher degree candidates and have accommodation in the Institute for this purpose. In return for its annual financial contribution, the Institute houses a laboratory and preparation room for Soekor, which now employs four scientists on micropalaeontological work, two European lady assistants, and one male Bantu laboratory assistant in the accommodation thus provided. Mr. Anderson has spread his net rather widely. Although his thesis is entitled "Biostratigraphic palynology of the Permian sediments of the Northern Karroo basin of South Africa" he has considered it essential to compile charts and a

world map dealing with the geographic distribution, with reference to ammonite stages, and the ages and correlations of Permian (and in part Triassic) plant-bearing strata of the world.

Mr. McLachlan has selected for his thesis the title "The Occurrence and Significance of Inorganic-Shelled Microfossils in the Karroo System in South Africa". He has, during the year, processed 530 samples from 9 borehole sections in the northern and north-western parts of the Karroo basin and has, together with Miss A. Anderson, collected material from outcrops particularly in the Orange River valley area from Douglas downwards. Sites in Dwyka deposits in the Douglas area have yielded foraminifera, and a possible conodont and radiolaria particularly in nodules and limestone bands. Sponge spicules of a variety of shapes have been found not only in the Douglas rocks of Dwyka age but also in nodules in Ecca beds in the Welkom area and near Hopetown. Although acanthomorphite acritarchs have been recorded from a number of sites in the northern Karroo, they have not thus far been found in the material examined by Mr. McLachlan.

11. Miss Ann Anderson, a research student, continued her work on South African trace fossils of Palaeozoic age and their ecological significance. Sixteen arthropod walking-trail sites of Dwyka and Ecca age have been studied in the field for sedimentological and stratigraphic evidence. Variations within a single "ichnospecies" are being illustrated by means of photographs and line drawings.
12. Miss S. Chernin completed her M.Sc. research programme on "Capitosaurid amphibians from the Upper Luangwa Valley, Zambia" and has submitted the paper for examination. She has begun a comprehensive review of the Southern African fossil Amphibia.
13. Mrs. R. M. S. Falcon has finished and handed in her thesis on the palynology of the Rhodesian Dwyka sediments. Owing to her husband's transfer, she left for England in July. Still registered as a Ph.D. candidate at the University, she has arranged to undertake research work under Dr. D. Chaloner at Birkbeck College, London, while resident in England.
14. Mrs. E. A. Nesbitt is studying the cranial anatomy of Pareiasauridae from the Beaufort series, with special emphasis on the anatomy of the brain-case and the systematics of the family. The immediate objective is the preparation of an M.Sc. thesis.
15. Miss G. E. Collings is an M.Sc. candidate working on the preparation and identification of post-cranial skeletal parts of sabre-tooth cats (Machaerodonts) occurring in breccias from Makapansgat. Comparisons are being made with material from other parts of the world.
16. Mrs. A. K. Malleson is engaged on a description of plant megafossils of the Upper Ecca and Lower Beaufort series, and particularly on material from the Mooi River site near Estcourt, Natal. Much of the material shows reproductive structures, and some 66 insect wings or fragments thereof are present on the slabs from Mooi River.
17. Mr. R. Randall has worked throughout the year, as an Honours B.Sc. student, on two projects—fossil plants from Cedara, and the Hyenidae from the Makapansgat deposits.
18. Dr. C. Mendrez, of Paris, made the Institute her headquarters during the first half of the year, continuing her studies for her doctoral thesis for our University. She examined relevant material in Cape Town, Wellwood, Bloemfontein and Kimberley. While working in the last-named centre, the contents of her car were rifled and she lost practically the whole of her manuscript notes, some of the illustrations for her thesis, and most of her personal possessions, of which no trace has been found. She proposes to return to the Institute in 1973.

FIELD WORK

No prolonged field trips were undertaken during the year under review. Some short trips were made to individual localities for specific collecting purposes in connection with individual research projects. Dr. Cruickshank accompanied two field excursions organized under the auspices of the Geology Department of the University—one consisting of a small party of Honours students who spent 3 days collecting fossil plants at Cedara, and the other lasting 10 days in Natal on which he explained the geological features of the dongas at Harrismith, the Bergville road quarry, and the Cretaceous outcrops at the Umzamba river mouth. On this excursion he was assisted by Mrs. H. Anderson. Mention has already been made of his visit to Rhodesia. He and Mr. C. Gow examined Boon's cave in the Dolomite between Tarleton and Rustenburg, at the request of the owner who wishes to commercialise it. They concluded that the talus screen below a swallow-hole deserves excavation.

Mr. Kitching spent a week in the field, visiting Wellwood in order to return certain specimens to that collection and collecting 20 reptilian skulls from localities in the Graaff-Reinet, Aliwal North and Rouxville districts, of which two *Cynognathus* zone procolophonids (cf. *Myocephalus crassidens*) were the most exciting. Mention should be made here, with gratitude, of the donation to the Institute by Mr. B. J. Kitching of 25 fossil reptilian specimens from the Middelburg and Bethulie districts from the *Lystrosaurus* zone beds. Among them are an almost complete skull and skeleton of *Thrinaxodon* and skulls tentatively assigned to the

genera *Galesaurus, Owenetta ?* , cf. *Oliveria, Scalopo-saurus* and *Lystrosaurus.*

Excavatory work at Sterkfontein has continued throughout the year under the control of Professor P. V. Tobias and his assistant, Mr. A. Hughes. The presence of African labourers on the site and their housing on this University property has rendered necessary the discussion of various sanitary and administrative matters, in which Dr. Cruickshank has participated.

Mr. Maguire has on several occasions acted as a guide to the Makapansgat deposits for parties organized by the University or by one or other of the national societies whose annual meetings were being held in Johannesburg or Pretoria. In this task he was assisted by Miss Roets.

Dr. C. K. Brain, Director of the Transvaal Museum, has continued his excavatory work and collecting at the Swartkrans site, which is now University property. The collections made during the year will, after study and description, be transferred ultimately to the Institute.

UNIVERSITY JUBILEE YEAR

The 50th anniversary of the University's foundation was celebrated during the year under review. Among the many functions was an exhibition which lasted a week and coincided with the annual meeting of the $S_2 A_3$. To this the Institute contributed a stand which dealt with all the aspects of its scientific work (including Karroo vertebrates from South Africa and the Antarctic, fossil plants from the Karroo, and the geology and fossils of the Makapansgat and Border Cave areas). The exhibit was arranged by Mr. Maguire, Mrs. H. Anderson, Miss J. Roets and Miss Emanuel, who were on duty for the week from July 3—11 to explain the import of the exhibits to visitors and donors.

It may be noted that a similar exhibit was arranged by the same staff members on a request from the Museums of Man and Science, in connection with that body's "launch day" appeal for funds.

CO-OPERATION WITH THE GEOLOGY DEPARTMENT

As in past years, most of the palaeontological instruction by lectures and practical work in this Department of the University has been in the hands of members of the Institute's staff—Dr. Cruickshank, Mr. Gow, Mr. Maguire, Mrs. H. Anderson and Miss J. Roets. Supervision of post B.Sc. candidates in palaeontology is carried out in the Institute.

The Institute is also represented on the University Committee of Directors of Research Institutes and on the Board of the Faculty of Science.

VISITORS

Although the semi-chaos created by the building operations hampered hospitality and ready access to the collections, a number of overseas and local palaeontologists visited the Institute for study during the year. Among them were Drs. Eck, Smart, Maglio and Marshall from the U.S.A., who were interested in mammalian remains from Makapansgat, Dr. R. W. Alf from the U.S.A., Dr. Day from Britain, Dr. Walker from Kenya, Dr. Every from New Zealand, and Dr. M. Clason of Holland who examined the osteodonto-keratic material first described by Professor Dart. Periodic visits were made by Dr. A. W. Keyser of the Geological Survey of Pretoria, who is specializing in fossil reptilia from the Beaufort beds.

LIBRARY

At the end of May, Mrs. Edwards returned as part-time Librarian, replacing Mrs. Essers. As a result of the building alterations the appearance of the Library has been transformed, so that it has a brighter and more spacious look. The steel catalogue drawers have been replaced by a new wooden cabinet donated by the University Library, who also provided adequate seating accommodation in the form of chairs and small tables. A new map cabinet is an urgent requisite, as is the provision of an additional bookcase and some additional shelving.

Annual circulation figures almost doubled during 1972. The cataloguing of the reprint and small pamphlet collection (numbering over 8 000 at the end of the year) was completed and a start has been made on the analysis of sets of monographs-in-series. Thanks are due to the University Librarian for the transfer to the Institute of a set of Monographs of the Palaeontological Society.

A considerable amount of binding of serial publications has been carried out by the University Binder to whom our thanks are due.

Lists of additions, together with photocopies of the contents pages of the more important journals, are being circulated each month to the staff members and to the staff of the Department of Geology.

PUBLICATIONS

Volume 14 of *Palaeontologia Africana* was issued towards the end of the year. It contains the following articles:

S. J. Dijkstra. Some Megaspores from South Africa and Australia.

A. W. Keyser. A Re-Evaluation of the Systematics and Morphology of certain Anomodont Therapsida.

A. R. I. Cruickshank. A note on the Genus *Proplacerias* Cruickshank, (1970).

Ch. H. Mendrez. Revision du Genre *Protocynodon* Broom 1949 et Discussion de Sa Position Taxonomique.

Ch. H. Mendrez. On *Cyrbasiodon Boycei*, Broom 1931, (Cynodontia Procynosuchidae), from South Africa.

James A. Hopson and James W. Kitching. A revised classification of Cynodonts (Reptilia; Therapsida).

G. E. Collings. A new species of Machaerodont from Makapansgat.

L. Freedman and N. S. Stenhouse. The *Parapapio* species of Sterkfontein, Transvaal, South Africa.

It has been decided, in order to accelerate the rate of distribution among fellow-workers of papers written by Institute staff, to produce subsequent volumes of *Palaeontologia Africana* in parts. The first part of Volume 15 is in the printers' hands, in part; it will contain 4 papers. It is also intended to supplement the work by issuing a Memoir Series to accommodate important long dissertations, of which the first will be Mr. Kitching's doctoral thesis.

A number of papers, based on Institute material, written by workers at the Institute were submitted for publication by other bodies. Among those which appeared in print during 1972 were the following:

A. R. I. Cruickshank

1. The Proterosuchian thecodonts. *In:* Studies in vertebrate evolution, Eds. K. A. Joysey and T. S. Kemp, Edinburgh, Oliver and Boyd, 89–119.
2. Diapsid reptiles. *Standard Encyclopaedia of Southern Africa,* V (5), 14–17.

E. P. Plumstead

1. Fossil Plants. *Standard Encyclopaedia of Southern Africa*, V(5), 2–11.
2. Gondwanaland. *Standard Encyclopaedia of Southern Africa*, V(5), 258–266.
3. Fossil Floras and latitudes. (Précis of paper presented at the I.U.G.S. Symposium on Continental Drift, Montevideo). *Trans. Amer. Geophysical Union,* LIII(2).
4. Three thousand million years of plant life in Africa: Eleventh Alex L. du Toit Memorial Lecture. Annexure to *Trans. Geol. Soc. S. Afr.,* LXII, 1–72, 26 plates.
5. The mystery of moving continents–a South African point of view. *South African International* (South Africa Foundation), III(2), 101–111.

J. W. Kitching, J. W. Collinson, D. H. Elliott and E. H. Colbert.

Lystrosaurus zone (Triassic) fauna from Antarctica. *Science, N.Y.,* 175, 524–527.

C. E. Gow

The osteology and relationships of the Millerettidae (Reptilia: Cotylosauria). *J. Zool. Lond.,* 167, 219–264.

B. R. Turner

1. Silica diagenesis in the Molteno sandstone. *Trans. Geol. Soc. S. Afr.,* 75, 55–70.
2. Revision of the stratigraphic position of cynodonts from the upper part of the Karroo (Gondwana) system in Lesotho. *Geol. Mag.,* 109, 349–360.

C. H. Mendrez

On the skull of *Regisaurus jacobi*, a new genus and species of Bauriamorpha Watson and Romer 1956 (= Scaloposauria Boonstra 1953) from the Lystrosaurus zone of South Africa. *In:* Studies in Vertebrate Evolution, Eds. K. A. Joysey & T. S. Kemp, Edinburgh, Oliver & Boyd, 191–212.

R. M. S. Falcon

A preliminary account of the palynology of the Lower Karroo succession in the mid-Zambezi basin. *Bull. Geol. Survey, Rhodesia*, No. 70.

E. A. Nesbitt and G. H. Bond

Fossil chelonians from the Gokwe Formation, Rhodesia. *Arnoldia,* 5(37), 1–7.

P. V. Tobias

1. The Distribution of Cranial Capacity Values Among Living Hominoids. *Proc. 3rd Int. Congr. Primat*, Zurich 1970, 1, 18–35. 1971.
2. The men who came before Malawian History. *In:* The Early History of Malawi, Ed. B. Pachai, Longman Group, London, 1–16. 1972.
3. Progress and Problems in the Study of Early Man in Sub-Saharan Africa. *In*: The Functional and Evolutionary Biology of Primates, Ed. Russell Tuttle, Chicago/New York, Aldine-Atherton. xxii + 487 pp. Chapter 3. 63–93. 1972.
4. Recent Human Biological Studies in Southern Africa, with special reference to Negroes and Khoisans. *Trans. Roy. Soc. S. Afr.*, 40(3), 109–133. 1972.
5. "Dished Faces", Brain Size and Early Hominids. *Nature, Lond.*, 239, (5373), 468–469. 1972.
6. Darwin, "Descent" and Disease. *Trans. Roy. Soc. S. Afr.*, 40(4), 239–260. 1972.

ANGLO AMERICAN SWAZILAND PROJECT

P. B. Beaumont and A. K. Boshier

Some comments on recent findings at Border Cave, Northern Natal. *S. Afr. J. Sci.,* 68, 22–24.

P. B. Beaumont and J. C. Vogel

On a new radiocarbon chronology for Africa south of the Equator. *African Studies*, 31, 65–89 and 155–182.

A. K. Boshier and P. B. Beaumont

Mining in Southern Africa and the emergence of modern man. *Optima,* 22, 2–12.

J. C. Vogel and P. B. Beaumont

Revised radiocarbon chronology for the Stone Age in South Africa. *Nature*, 237, 50–51.

Palaeont. afr., **16.** 1–15. 1973

A NEW TRIASSIC VERTEBRATE FAUNA FROM SOUTH WEST AFRICA

by

A. W. Keyser

*Geological Survey, Private Bag X112, Pretoria**

ABSTRACT

A new fauna of mammal-like reptiles is described from a continental sequence of sediments in South West Africa hitherto known as the Etjo Beds. These include representatives of the Anomodontia (two new forms and one known from the Karroo basin), Bauriamorpha, (one specimen comparable with a known form), Cynodontia (one new form and two known from the Karroo basin) and one small eriopoid amphibian. On the basis of this faunal assemblage it can be shown that there is a disconformity between the upper Plateau Sandstone Formation containing traces of Dinosaurs of possible Carnian–Norian age and a lower Omingonde Mudstone Formation with this new fauna, of essentially Upper Beaufort (Scythian/Anisian) age. The two formations are distinguished on lithological grounds. The Triassic sequence in the neighbouring Doros area is thought to be equivalent to the Plateau Sandstone Formation.

INTRODUCTION

The Karroo formations of South West Africa consist mainly of epicontinental sediments which range in age from Permian to Triassic. Triassic sediments have been found only in the northern part of the territory where they are known as the Etjo Sandstone (Fig. 1) (Table I). Lower Karroo sediments (Dwyka and Ecca) are poorly developed in the north and are absent from the area that was investigated in the Otjiwarongo district where the best outcrops occur. Palaeontologically, the Lower and Middle units of the Beaufort series have not as yet been recognized in the territory.

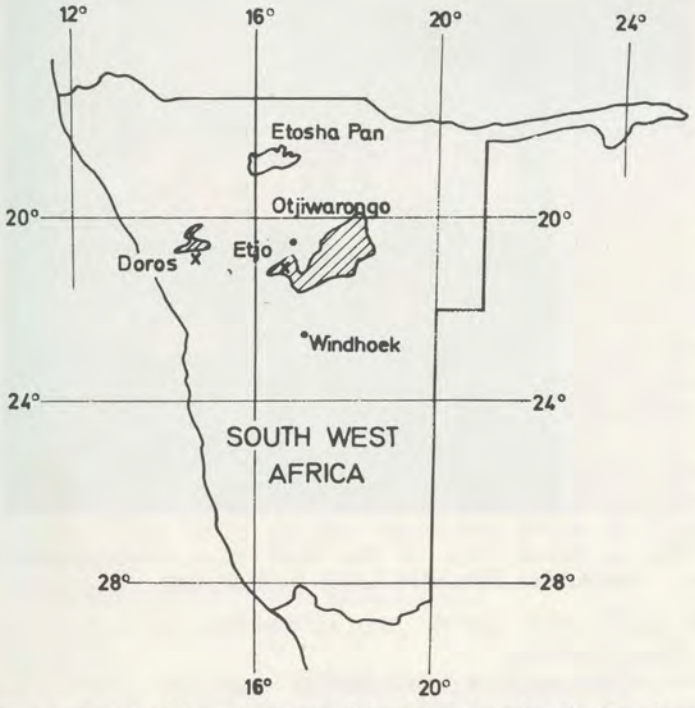


Fig. 1. Map of South West Africa showing the distribution of Triassic sedimentary rocks (Shaded).

The succession in the Otjiwarongo district consists of a basal conglomerate, felspathic grit and arkose followed by an alternation of red and green shales, siltstones, sandstones and grit, the whole being overlain by a thick layer of sandstone, referred to as the Plateau Sandstone by Gevers (1936). The beds below this sandstone are known as the Lower Etjo Beds (Gevers, 1936). The Plateau Sandstone has been described as being of aeolian origin. On Etjo Mountain this conclusion can no longer be drawn, the dune cross-beds that characterise aeolian sandstone deposits were not observable, while trough cross-bedding is common at Etjo and in the Waterberg. The Plateau Sandstone is correlated with the Cave Sandstone of the South African Karroo basin. The Lower Etjo Beds are correlated with the Red Bed and Molteno stages of the Karroo sequence in South Africa (Gevers, 1936).

The Karroo strata in South West Africa have hitherto yielded very few fossils with the exception of the common occurrence of *Mesosaurus* in the Dwyka of the southern part of the territory (see McLachlan and Anderson, 1973 for a review of the occurrence of the genus in S.W.A.). The Triassic beds in the northern part have been regarded as being almost unfossiliferous because very few fossils had been found there prior to 1972. Tracks of a Saurischian dinosaur and another, smaller quadrupedal animal were discovered by Elmenhorst and described by Von Huene (1925a). These are from the farm Otjihaenemaperero immediately north of the farm Etjo Nord. The tracks occur in the Plateau Sandstone. Gevers (1936) mentions that Gröpel discovered a cast of a skull on the farm Breitenbach near Grootfontein in

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1926. This was identified as a "Karroo reptile" by Strömer von Reichenbach (quoted Gevers, 1936).

Von Huene (1925b) described a "mammalian molar" with two roots found by Reuning in the vicinity of Doros, in the Southern Kaokoveld. In the author's opinion this tooth is more likely to be that of one of the larger Triassic cynodonts in which postcanine teeth with two roots are now known to occur.

Fragmentary remains of *Mesosaurus* have also been described from this area by Reuning and Von Huene (1925). These are from a lower horizon of Dwyka age.

The author recently had the opportunity to visit the Doros area as well as the main outcrops of the Etjo Sandstone near Otjiwarongo. The strata at Doros and in the valley of the Huab River appear to have been deposited in a separate basin from the much larger occurrence in the Otjiwarongo district. Some poorly preserved fish remains were collected from a thick bed of friable red shale immediately beneath the "main sandstone bed" which is overlain by the lowermost lava flow in the area. This locality is about 6 km north of Doros. A lumbar vertebra of a dinosaur was seen at the same locality, but could not be collected because of the extreme hardness of the baked shale next to a dolerite dyke. The occurrence of dinosaur remains is indicative of a Red Beds/Cave Sandstone (Upper Triassic) age. The *Mesosaurus* locality could not be found.

The Triassic Etjo Beds occur in an elongated basin with a north-east to south-west strike. This basin extends from near Omaruru to the Okavango River. The greater part of the outcrop is covered by wind-blown Kalahari sands. In the south the sediments lie unconformably on a basement of crystalline rocks of the Damara System and its associated intruded granites. The northern boundary of the outcrop in the Otjiwarongo area is formed by the great Waterberg thrust fault which has elevated the rocks of the Fundamental Complex to the level of the Etjo Beds.

The best outcrops of the Etjo Beds are at the type locality on the farm Etjo Nord.

Etjo Mountain consists of a narrow plateau of Plateau Sandstone which is about 15 km long with an east-west orientation. The edges of the plateau are a series of steep cliffs. The lower slopes are made up of sandstone, grit and shale of the Lower Etjo Beds. Although the slopes are mainly covered in sandstone scree, good outcrops of shale occur in the steeper ravines and slopes.

Vertebrate fossils are found mainly in the argillaceous sediments, but some specimens were recovered from the grit beds. Lime-rich nodules are common in the shales and sandy shales. The sandstone and grit beds tend to be lenticular and individual strata cannot be followed for any distance. On the north-western buttress of the mountain the lower parts of the slopes consist of a large body of grit and conglomerate which probably represents a large erosion channel. There are horizons at which sandstone and siltstone beds are more abundant, and which can be used as markers for subdividing the Lower Etjo Beds on Etjo Mountain. There is no certainty that this subdivision will be usable over the rest of the basin in which these beds were deposited as the outcrop of the Lower Etjo Beds is very poor in other places. The whole succession of the Lower Etjo Beds is fossiliferous and scraps of bone were seen in all the rock types represented.

There are a large number of small chloritized dolerite dykes to be seen on all the large outcrops of sediment on the slopes of the mountain.

Twenty-five specimens of fossil vertebrates were collected from the Lower Etjo Beds on Etjo Mountain, the significant ones of which will be described here to amplify the preliminary announcement (Keyser, 1973). Fuller treatment of the fauna will appear in due course.

SYSTEMATIC DESCRIPTIONS

Class Amphibia (Fig. 2)

A small skull of an eriopoid amphibian resembling *Micropholis* was collected below the lower arenaceous horizon on the northern slopes of Etjo Mountain.

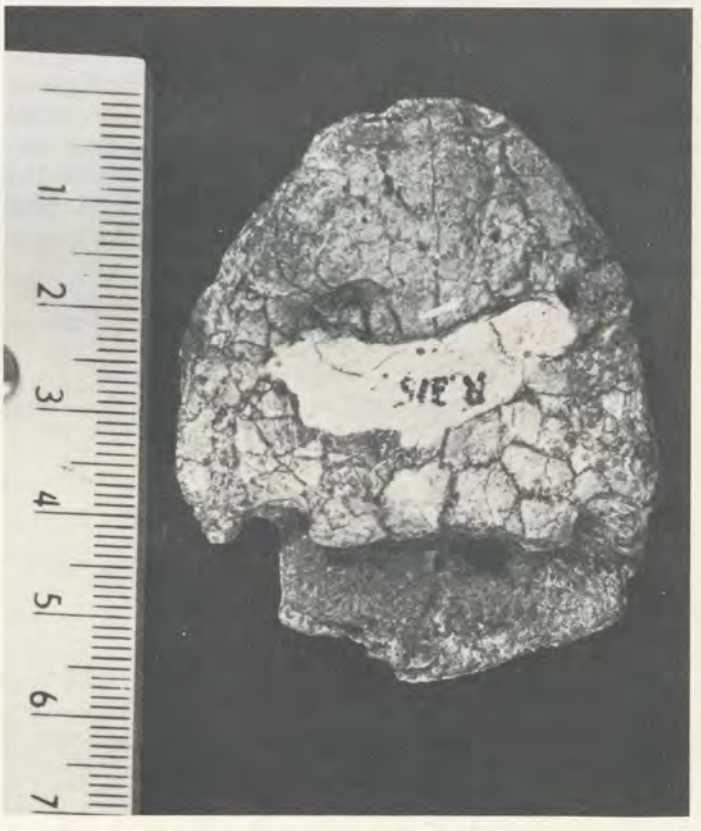


Fig. 2. Dorsal view of the skull of a small eriopoid amphibian. Specimen R315. Scale in mm.

Class Reptilia

Infraorder Anomodontia

Suborder Dicynodontia

Family Kannemeyeridae

Kannemeyeria simocephalus (Weithofer) (Fig. 3)

A large well-preserved skull that had lost its stapes and quadrates prior to burial. The specimen is a large individual with very large caniniform processes and exceedingly wide lateral flanges. The median longitudinal ridge on the anterior and dorsal surfaces of the premaxilla is very prominent. These features could perhaps be used to distinguish this specimen from the species occurring in the Karroo basin of South Africa. However, as the range of variation of these features is not known for the Lower Etjo palaeodeme, it is not at present possible to decide if there is, in fact, a significant difference.



Fig. 3. Anterodorsal view of large skull of *Kannemeyeria simocephalus* (Weithofer). Specimen R313. Scale in mm.

The genus has been described from the *Cynognathus* zone of the Beaufort series of South Africa, the Manda Formation of Tanzania and the Puesto Viejo Formation of Mendoza, Argentina. (Weithofer, 1888; Cruickshank, 1965, 1970; Bonaparte, 1966.)

This specimen was recovered between the lower and middle arenaceous horizons of the Lower Etjo Beds on the northern slope of Etjo Mountain.

Family Stahleckeridae, Cox, 1965.

Dolichuranus primaevus gen. et sp. nov. (Figs. 4 and 13)

Holotype: specimen R334. Skull and partial skeleton in the collections of the Geological Survey, R.S.A.

Type locality: Southern slopes of a hill north of Etjo Mountain, from an horizon below the lowermost arenaceous horizon.

Diagnosis: Large dicynodont. Skull overall length about 370 mm with large tusks. Greatest skull width across the occiput. The snout tapers anteriorly, but the tip is square, and blunt. The temporal fossae and intertemporal bar are short. The postorbitals extend along the intertemporal bar to the level of the posterior margin of the temporal fossae. The secondary palate is very extensive and extends backwards past the middle of the skull. The interpterygoid vacuity is small and is situated at the back of the choanal depression. The margins of this vacuity are raised. A prominent tubercle is found on the pterygoid immediately in front of the footplate of the epipterygoid. The premaxilla extends backwards to the level of the anterior margins of the orbits.

Discussion: This new genus is very similar to *Dinodontosaurus turpior* as characterized by Cox (1965). The most noticeable difference is that the intertemporal bar and temporal fossae are longer in *Dolichuranus* and that the postorbitals are much longer in the new form.

In Dinodontosaurus the postorbitals do not extend back farther than the posterior margin of the parietal foramen in any of the specimens that the



Fig. 4 (a)



Fig. 4 (b)

author has seen. This feature is used as one of the main distinguishing features of the genus by Cox (1965). The new form is morphologically intermediate between the Upper Permian genus *Daptocephalus* and the Upper Triassic genus *Dinodontosaurus*. It is possibly more advanced than the Anisian genus *Tetagonias* (Cruickshank, 1967) from the Manda Formation of Tanzania because it has a far more extensive secondary palate. There is a marked resemblance in overall shape to *Kannemeyeria latirostris* Crozier (1970). It differs however in the more extensive secondary palate, which may not have been preserved in Crozier's specimen which in any case is very much smaller. In the author's opinion Crozier's species belongs in this new genus and should therefore be referred to as *Dolichuranus latirostris* (Crozier).

Family Shansiodontidae, Cox, 1965.
Rhopalorhinus etionensis gen. et sp. nov. (Figs. 5 and 14)
Holotype: R320 in the collections of the Geological Survey, R.S.A.
Type locality: Northern slopes of Etjo Mountain between the upper and lower arenaceous horizons of the Lower Etjo Beds.
Diagnosis: Large dicynodont. Skull length overall about 350–400 mm, with prominent nasal bosses and a narrow intertemporal crest. The labial fossae

Fig. 4. Holotype of *Dolichuranus primaevus* gen. et sp. nov. Specimen R334.
(a) Dorsal view.
(b) Ventral view.
(c) Left lateral view.



Fig. 4 (c)

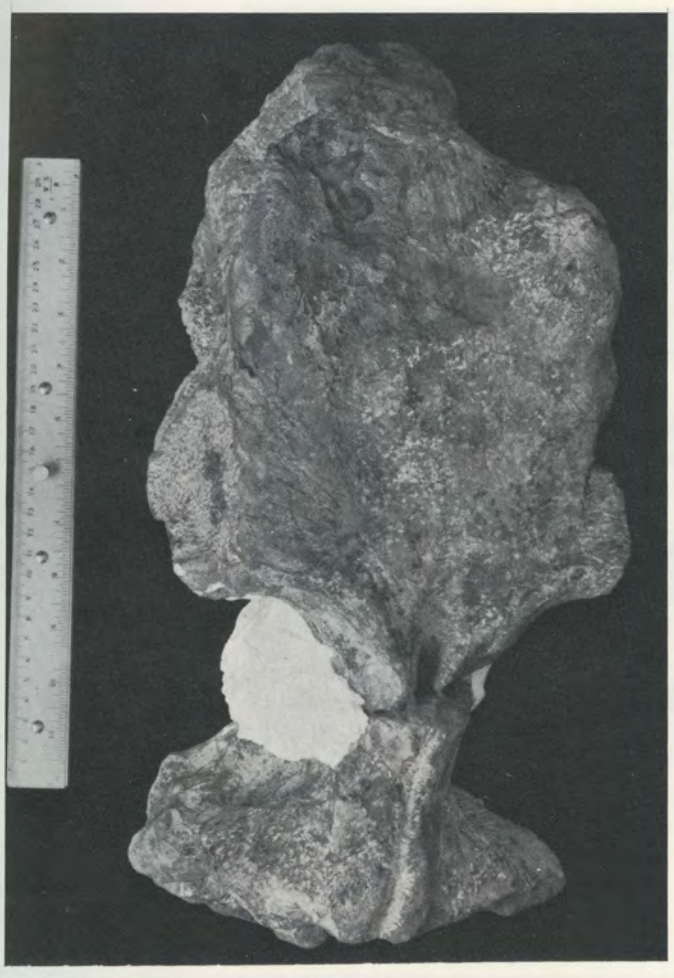


Fig. 5 (a)

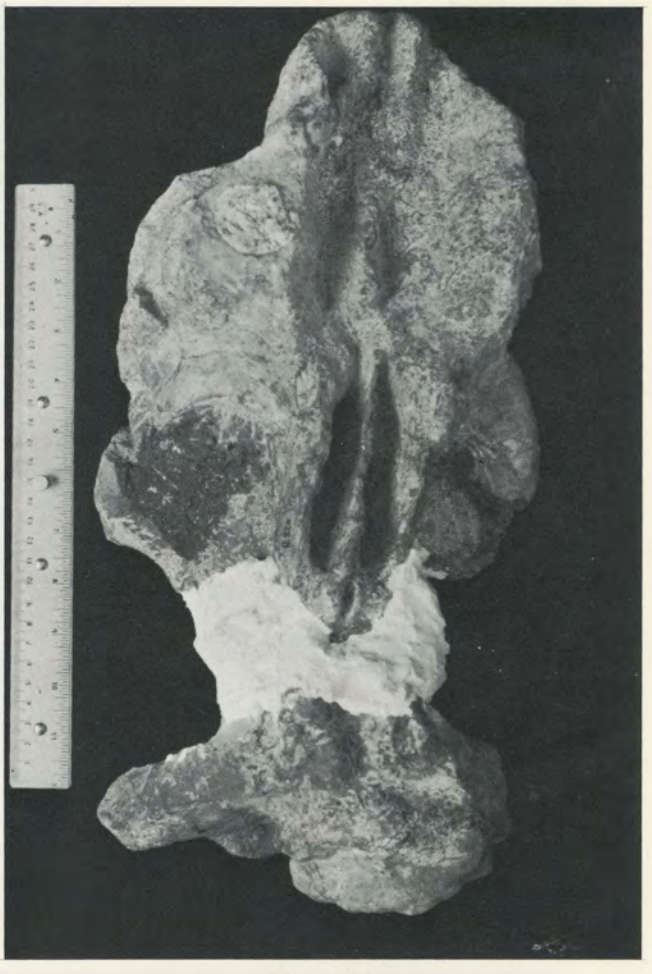


Fig. 5 (b)

Fig. 5.
(a) Dorsal view of type of *Rhopalorhinus etionensis* gen. et sp. nov. Specimen R320.
(b) Ventral view of type of *R. etionensis* gen. et sp. nov. Specimen R320.
(c) Lateral view of type of *R. etionensis* gen. et sp. nov. Specimen R320. Arrow indicates level of interpterygoid space.

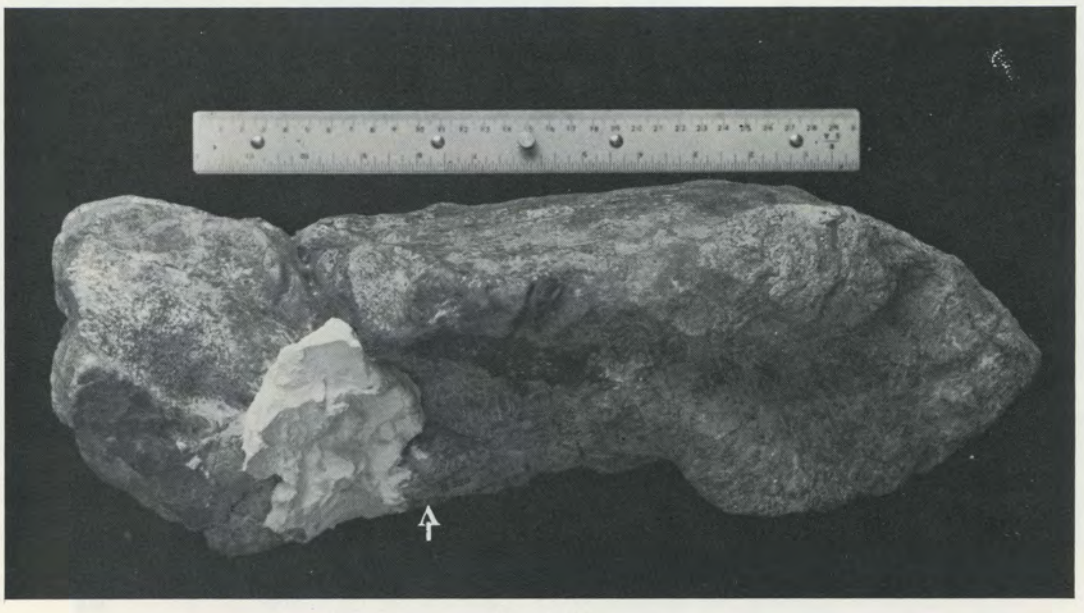


Fig. 5 (c)

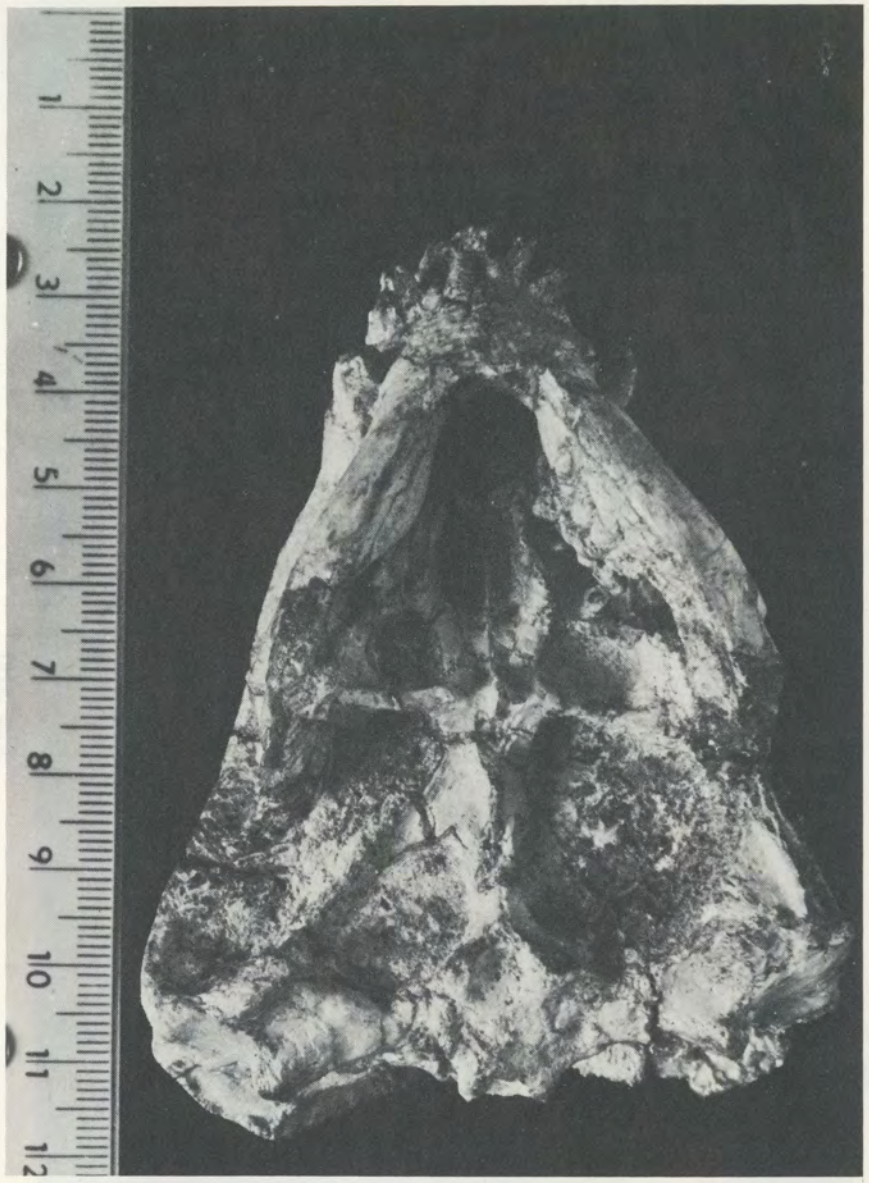


Fig. 6 (a)

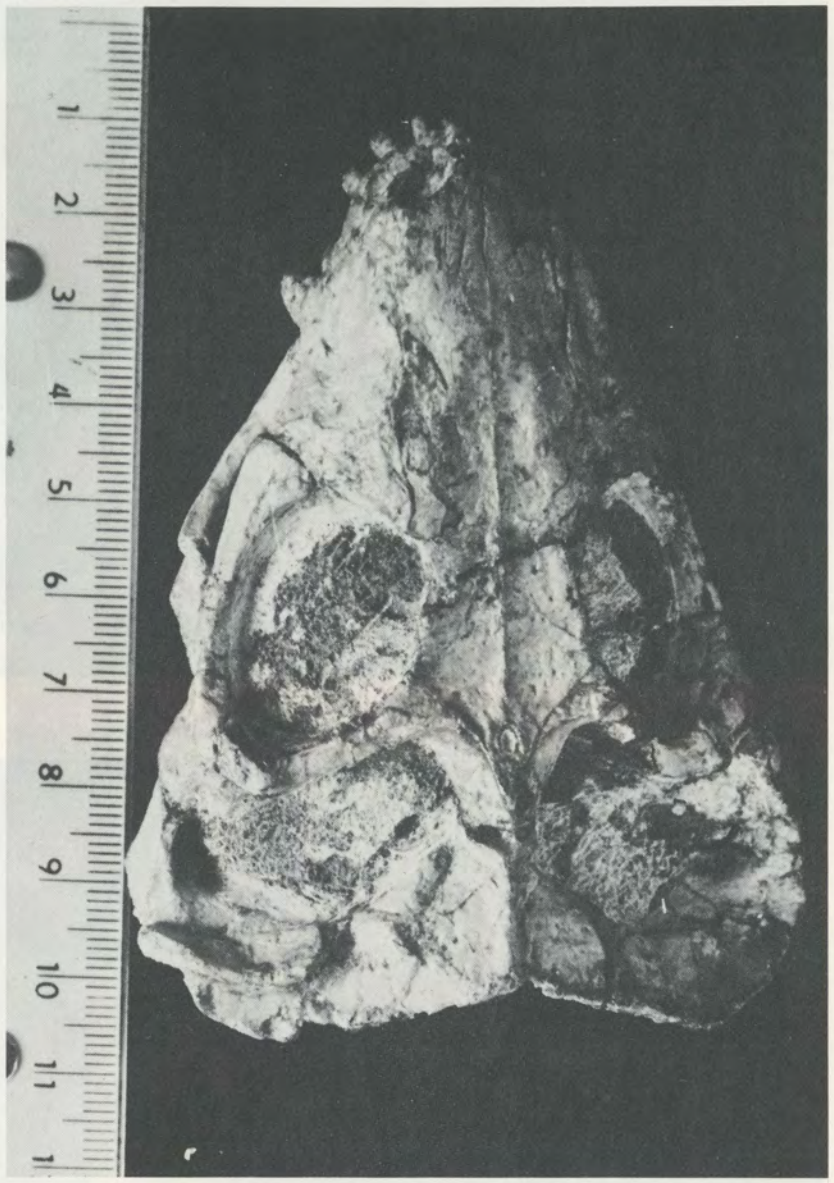


Fig. 6 (b)

Fig. 6.
(a) Dorsal view of *Sesamodon*-like bauriamorph. Specimen R337. Scale in mm.
(b) Ventral view of same.

are very small, and the interpterygoid space very small with raised flap-like margins that are visible in lateral view. The interpterygoid space is placed outside the choanal depression and immediately posterior to it. The premaxilla is long and the beak narrow. The postorbital reaches the squamosal on the intertemporal bar. The tusks are large.

Discussion: This new genus differs from most other Triassic dicynodont genera in the possession of prominent nasal bosses. The only exceptions to this are *Rhinodicynodon* (Kalandadze, 1970) and *Elephantosaurus* (Vjuschkov, 1969) from Cisuralia in Russia. From the former it differs in having an even longer snout and being very much larger. The postorbitals are very much longer than in *Rhinodicynodon* and the snout is also differently shaped. Very little is known about *Elphantosaurus*. The specimens probably belong to the family Shansiodontidae (Cox, 1965) as is evidenced by the broad snout and nasal bosses and in that the intertemporal bar does not form a very prominent raised crest.

Infraorder Bauriamorpha

A small skull resembling *Sesamodon browni* Broom (1905) (Fig. 6) was discovered above the uppermost arenaceous horizon on the western buttress of Etjo Mountain, in the Lower Etjo Beds.

There are five upper postcanine teeth (*Sesamodon browni* has 7). The first upper postcanine is blunt and has a flat crown. In *Sesamodon* this tooth is pointed. The interpterygoid space is very long.

The postorbital arches are complete. There is a small parietal foramen placed anterior to the posterior margins of the orbits. There is no preparietal.

Unfortunately the type of *Sesamodon* is so poorly known that it is at present impossible to identify the new specimen from the available descriptions.

A large reflected lamina of an obviously much larger specimen was found at the same horizon. If it be assumed that this latter specimen is a *Bauria*-like form, then its skull length must have been 280 mm overall.

Infraorder Cynodontia

Family Cynognathidae

A small lower jaw resembling that of *Cynognathus*, associated with an occiput and brain-case was found below the lowest arenaceous horizon on Etjo Mountain (Fig. 7). The symphysis is very long and there are only two incisors on each side. Both canines are lost. The postcanine teeth are poorly preserved, but are clearly sectorial. The available material is inadequate for a more specific determination.



Fig. 7. Dorsolateral view of a lower jaw and braincase of a small cynognathid cynodont. Specimen R314. Scale in mm.

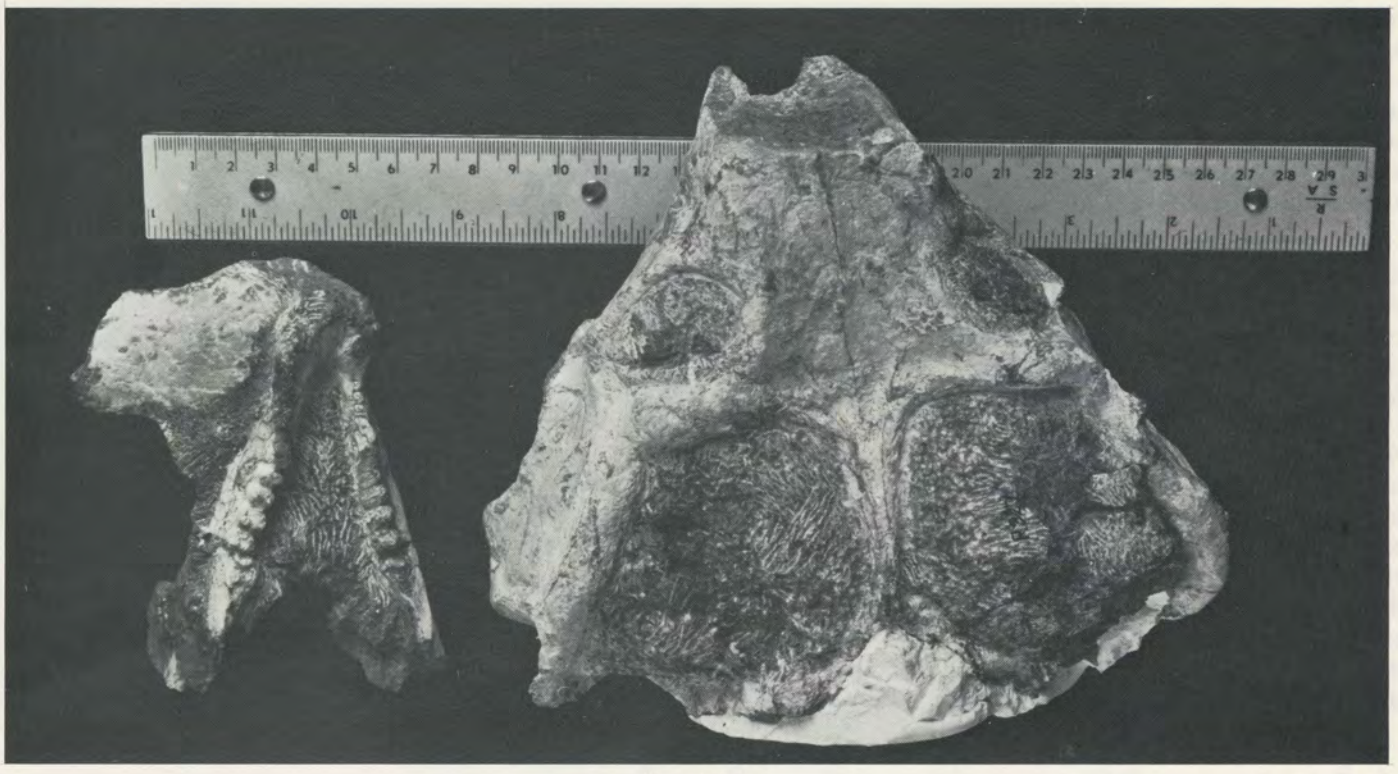


Fig. 8 (a)

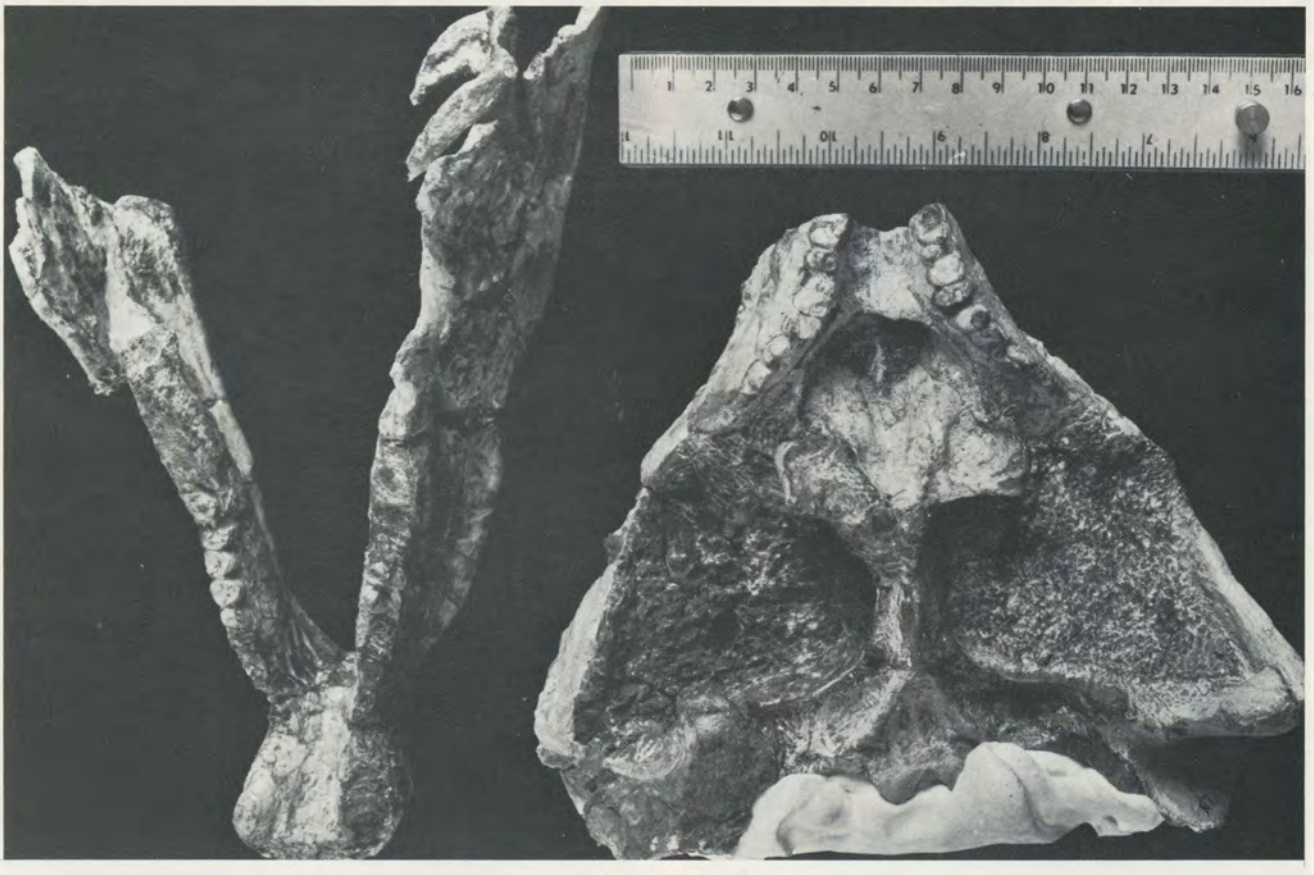


Fig. 8 (b)

Fig. 8.
(a) Dorsal view of a skull of *Diademodon tetragonus* Seeley (right) and a lower jaw of another specimen (left). Specimen R327 and R335.
(b) Ventral view of the same skull (right) and yet another lower jaw (left). Specimen R321. The small element on the inside of the left ramus of this lower jaw is probably a hyoid.

Family Diademodontidae

Diademodon tetragonus Seeley (Fig. 8)

This material was derived from the nodule-bearing shale-beds between the two arenaceous horizons. It consists of the posterior two-thirds of an adult skull with some postcranial elements and two adult lower jaws. The material has not as yet been fully prepared, but exhibits no characters which can be used to distinguish it from *Diademodon tetragonus*. Differences may however appear when the specimens are fully prepared.

Titanogomphodon crassus gen. et sp. nov. (Figs. 9 and 10)

Holotype: Badly preserved and crushed posterior part of a large skull, R322, in the collection of the Geological Survey, R.S.A.

Type locality: Northern slope of Etjo Mountain in a grit bed, in the upper arenaceous horizon.

Diagnosis: Very large gomphodont cynodont with small orbits and one tubercle on the anterior and three tubercles on the dorsal orbital margins. A relatively large parietal foramen is present. The distal end of the postorbital arch has a boss-like thickening. The secondary palate is short and does not reach back to the last gomphodont postcanine, which is peg-like and has a blunt point. It is ellipsoidal in section, with the long axis of the ellipse orientated parallel to the sides of the jaw. The last three postcanines appear to be of similar sectorial types but their long axes swing round, so that the fourth from last postcanine is transversely orientated. These posterior sectorial teeth are preceded anteriorly by large crushing molariform teeth. These teeth are also ellipsoidal in section, and are transversely orientated. They display large lingual and labial cusps placed near the anterior margin of the crown and connected by a transverse ridge. Behind this ridge a basin is present which slopes towards the back of the crowns. The raised sides of the basin coincide with the lateral margins of the tooth. A small cusp occurs on the labial margin posterior to the main labial cusp. There is a sharp ridge on the anteriorly-sloping front of the crowns anterior to the transverse ridge that connects the main cusps. Small additional cusps occur on the posterior margins of the crown. The rest of the postcanine series is not known.

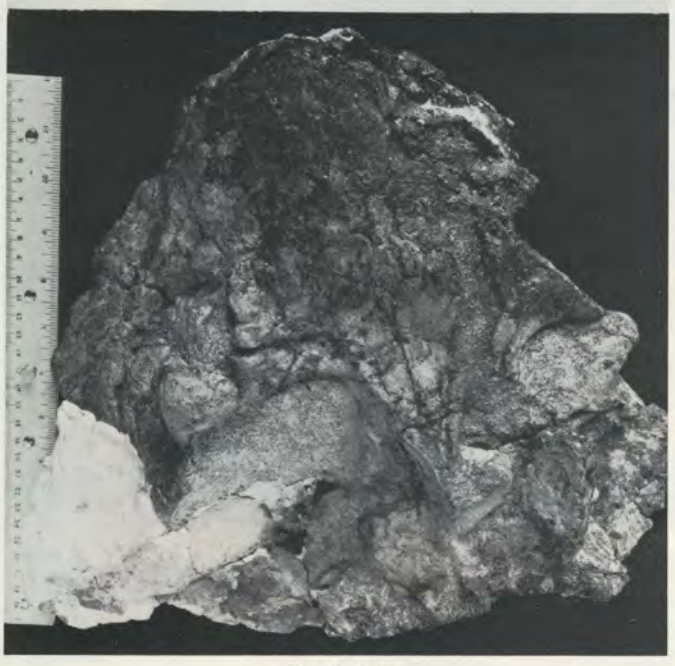


Fig. 9 (a)



Fig. 9 (b)

Fig. 9.
(a) Dorsal view of Holotype of *Titanogomphodon crassus* gen. et sp. nov.
(b) The same. Ventral view.

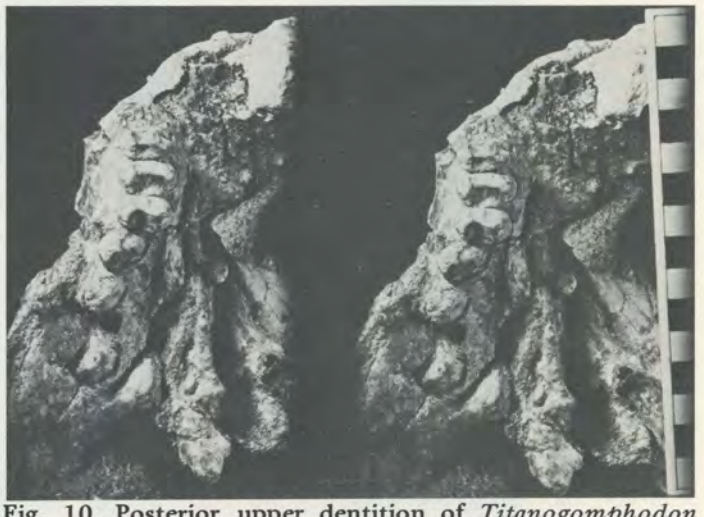


Fig. 10. Posterior upper dentition of *Titanogomphodon crassus* gen. et sp. nov. Anterior of skull at top of page. Specimen R322. Scale in centimetres.

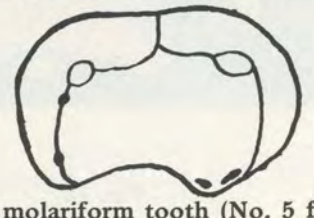


Fig. 11. Upper molariform tooth (No. 5 from the back of the tooth row). Occlusal view. Front side at the top of the page.

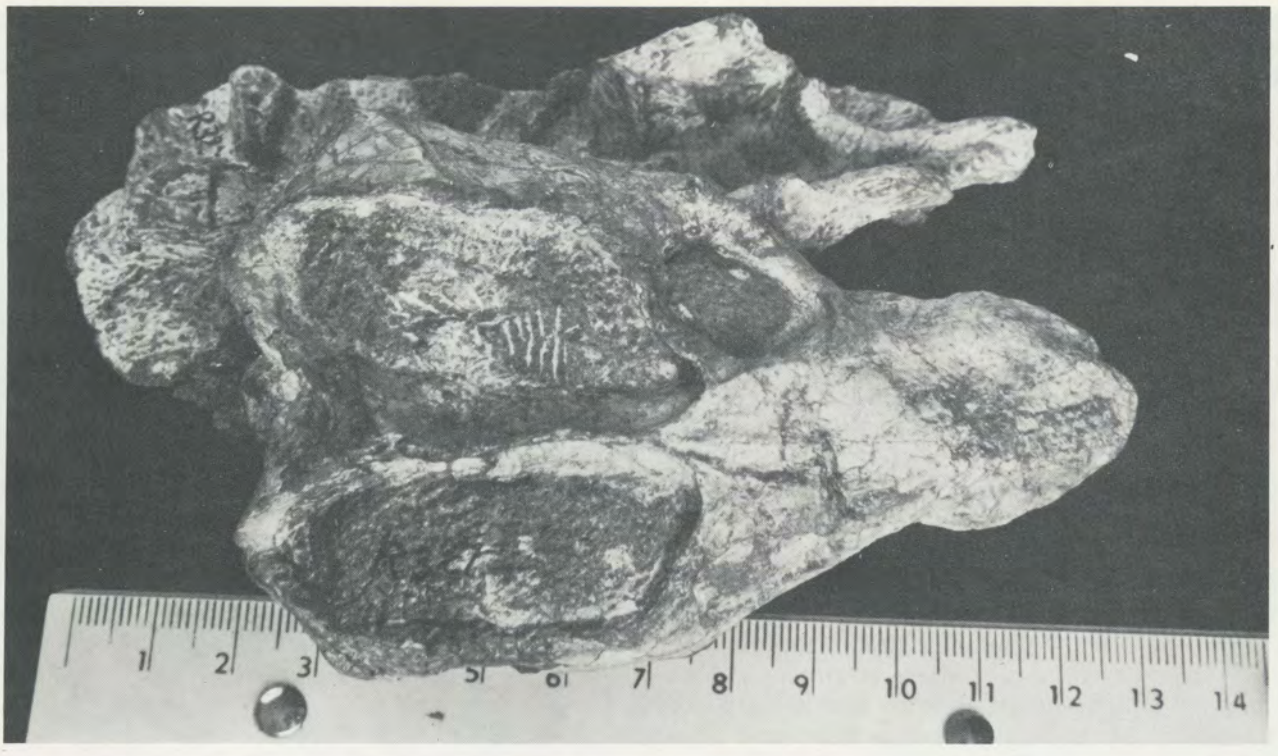


Fig. 12 (a)



Fig. 12 (b)

Fig. 12.
(a) Dorsal view of skull of *Trirachodon* sp. Specimen R327.
(b) Ventrolateral view of same.

Discussion: If reconstructed to have more or less the same proportions as *Diademodon* the skull of this species could have been about 430 mm long, which is very much larger than in any known species of *Diademodon.*

This specimen is placed in the subfamily Diademodontinae (Hopson and Kitching, 1972) as there is no indication of a central cusp in any of the available molariform teeth. It shows agreement with the Traversodontinae in the anterior placement of the transverse ridge between the cusps and in the development of a secondary basin in the crowns of the molariform teeth. *Titanogomphodon* therefore appears to be an advanced diademodontid that developed convergently with the traversodont cynodonts.

Trirachodon sp. (Fig. 12)

A complete but poorly preserved skull with much of the postcranial skeleton was found above the lower arenaceous horizon on the western buttress of Etjo Mountain. The bone surface is badly cracked and the matrix does not part from the bone easily. It is clearly very similar to *T. berryi* Seeley, but has apparently no parietal foramen and the intertemporal crest is very much narrower. The skull differs from all of the described specimens of the genus in having a large diastema in both the upper and lower jaws. There appear to be only six postcanine teeth in the maxilla. This specimen is much smaller than *Cricodon metabolus* Crompton (1955) from the Manda Formation.

THE AGE OF THE FAUNA

The fauna of the Lower Etjo Beds contains five genera that are also encountered in the *Cynognathus* zone of the Beaufort series of the Karroo System in the Republic of South Africa. Two specimens of these five genera could be identified specifically with forms from the Karroo Basin viz. *Kannemeyeria simocephalus* and *Diademodon tetragonus.* It is not unlikely that the small cynognathid cynodont, the bauriamorphs and the trirachodontid from the Lower Etjo Beds are also *Cynognathus* zone forms.

This therefore indicates that these strata could be at least as old as the *Cynognathus* zone of South Africa and the Puesto Viejo Formation of Argentina. It is assumed by several workers that the age of the *Cynognathus* zone fauna is equivalent to that of the upper Scythian of Europe, where strata of this age are mainly of marine origin, and the assignment of a Lower Triassic age to the *Cynognathus* zone is based on a comparison of the amphibian fauna of the R.S.A. with European forms (du Toit, 1954).

However the presence of an advanced Cynodont (*Titanogomphodon* gen. nov.) and of several advanced dicynodonts is indicative of a slightly younger age. *Kannemeyeria* also occurs in the Manda Formation of Tanzania (Cruickshank, 1965), which is generally assumed to be of Anisian age. This formation also contains a traversodont cynodont and the dicynodont *Tetragonias njalilus* (Crompton, 1955; Cruickshank, 1967). The latter is very similar to *Dolichuranus* described here.

The Ntawere Formation of Zambia has a fauna of diademodontid and traversodontid cynodonts (Brink, 1963), a species of *Dolichuranus* (Crozier, 1970) and a form referred to the genus *Rechnisaurus* (Crozier, 1970) which was previously known from the Yerapalli Formation of India. Additionally some amphibian material recently described (Chernin and Cruickshank, 1970) indicates that the Ntawere Formation can be contemporaneous with the Manda Formation.

The cynodonts and dicynodonts described here from the Lower Etjo Beds are manifestly more primitive than the forms from the Upper

Table 1

The Chronostratigraphic relationships of Triassic Rocks in S.W.A.

SOUTH AFRICA		Doros and the Huab Valley	Otjiwarongo area after Gevers (1936)	Otjiwarongo area new proposal	Stage	Period
STORMBERG SERIES	*Cave Sandstone Stage* aeolian sandstone	aeolian sandstone	*Plateau Sandstone* aeolian? sandstone	Plateau Sandstone Formation sandstone	Carnian, Norian	Triassic
	Red Beds Stage red sandstone, shale and siltstone	Red shale and aeolian sandstone	Lower Etjo Beds: red shale, sandstone, grit and conglomerate			
	Molteno Stage grit, sandstone, grey shale and coal	? Sandstone and Shale	Lower Etjo Beds: Lowermost part of Lower Etjo Beds grit, conglomerate, arkose	disconformity *Omingonde Mudstone Formation* red shale, sandstone, arkose, grit and conglomerate	Ladinian Anisian	
BEAUFORT SERIES			absent	absent	Scythian	
ECCA SERIES			absent	absent		
DWYKA SERIES		Shale, diamictite, limestone and sandstone	absent	absent		Permian

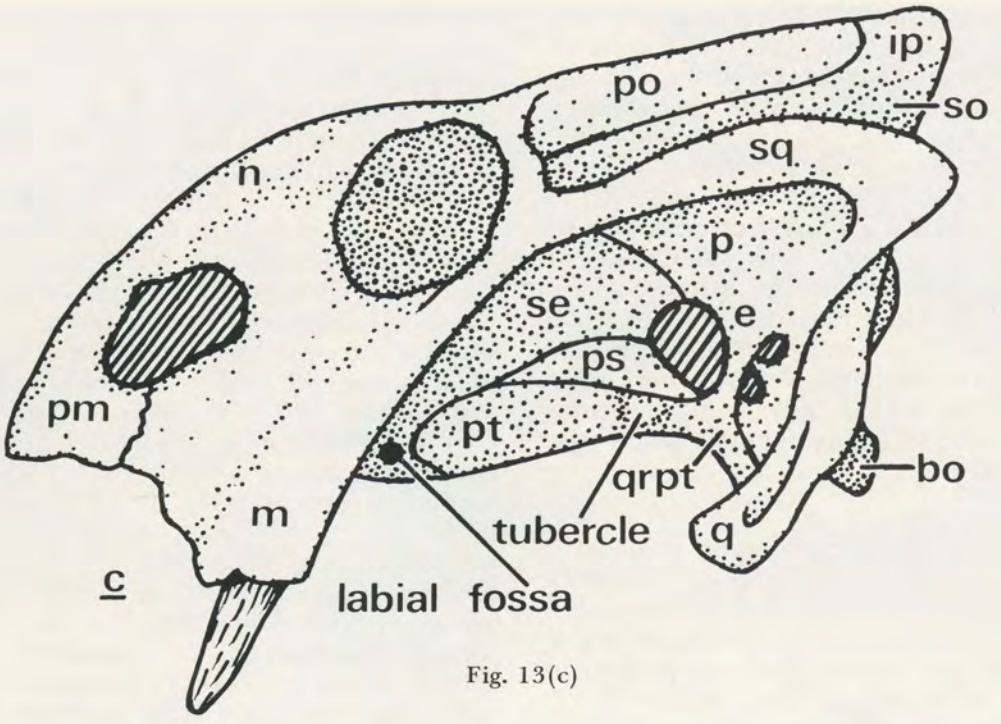


Fig. 13(c)

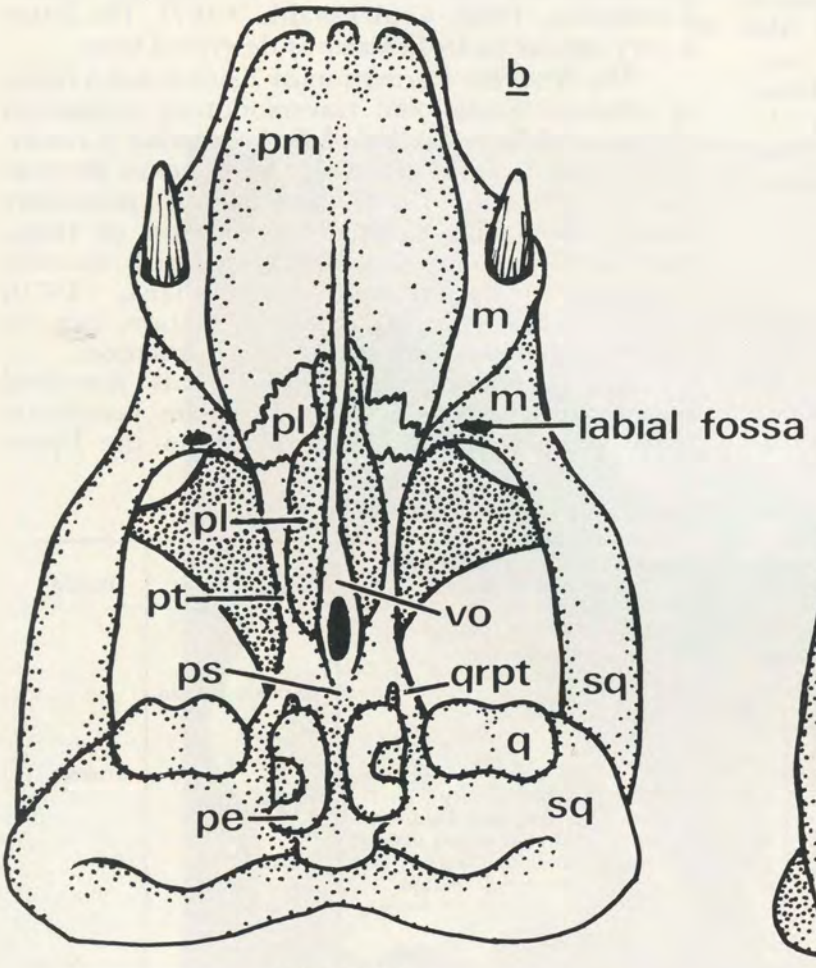


Fig. 13 (b)

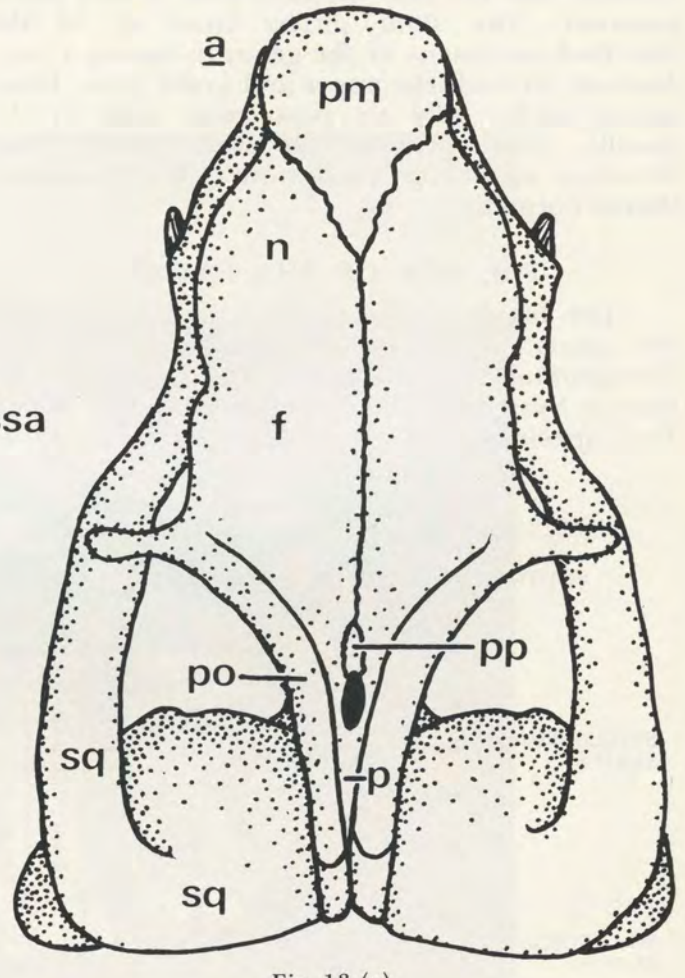


Fig. 13 (a)

Fig. 13.
(a) Dorsal,
(b) Ventral, and
(c) Lateral view of *Dolichuranus primaevus* gen. et sp. nov. (X ⅓)

Triassic Ischichuca, Ischigualasto and Santa Maria Formations of South America. There are as yet no records of either traversodont or chiniquodont cynodonts in the Lower Etjo Beds, which indicates that they are probably slightly older than the Manda and Ntawere Formations which do contain traversodonts. The dicynodonts of the Lower Etjo Beds are however as highly developed as those of the Manda and Ntawere Formations. Therefore for the present it seems best to correlate the Lower Etjo Beds with the lower part of the Molteno stage of the Stormberg series of South Africa (Table 1).

There is no apparent obvious stratigraphic break in the Karroo System in the area around Molteno in the Eastern Cape Province of South Africa as is the case farther to the north and it would therefore appear that the Molteno Stage extends from the Scythian (?) *Cynognathus* zone to the Carnian (?) Red Beds Stage of the Stormberg Series. This would indicate that the Molteno Stage occupies virtually the whole of the Middle Triassic, assuming that the *Cynognathus* zone is not younger than Lower Triassic in age.

The trackways in the Plateau Sandstone at Otjihaenemoperero are possibly those of a saurischian, which indicates a Carnian or Norian age. According to Colbert (1963) saurischians did not appear until the Upper Triassic. This would then show that the upper part of the Middle Triassic is absent in the succession on Etjo Mountain.

As has been pointed out by several authors (e.g. Sill, 1969) the use of stage names from the European stratigraphic column is as yet premature for the Gondwanaland "Formations" of the Southern Hemisphere. From the above discussion it would seem that the Lower Etjo Beds are probably younger than the *Cynognathus* zone (? Upper Scythian) of South Africa and older than the Manda Formation (? Anisian) of Tanzania. It is therefore clear that the Lower Etjo Beds are either uppermost Scythian or Lower Anisian in age, if the correlation of the *Cynognathus* zone and the Manda Formation with the alpine succession is correct.

As has been pointed out earlier, a disconformity separates the Plateau Sandstone and the Lower Etjo Beds. Additionally, the Plateau Sandstone has been shown to contain trackways probably made by Upper Triassic Saurischians and it has been concluded that a large part of the Middle Trias is missing from the succession in the Otjiwarongo district. This adds to the desirability of regarding the Lower Etjo Beds as a separate formation from the Plateau Sandstone on lithological grounds.

As the name Etjo Sandstone is commonly used to designate Upper Karroo sediments throughout South West Africa, it would be preferable not to use it as a formation name here. The name Omingonde Mudstone Formation is suggested, from the farm of the same name in the Otjiwarongo district, as a designation for those strata hitherto called the Lower Etjo Beds. The best outcrops occur on the western buttress of Etjo Mountain on this farm which may be designated as stratotype. The name Plateau Sandstone Formation is proposed here for those strata above the Omingonde Mudstone Formation. The stratotype being along the same section as the Omingonde Formation. The formal proposal of the new stratigraphic names and the designations of stratotypes has been submitted to the South African Committee for Stratigraphy.

The upper part of the Karroo succession in the area between Doros and the Huab River consists of red shale and aeolian sandstone with an intercalation of lava. As has been pointed out earlier, the Plateau Sandstone is not obviously aeolian and the red shale below it at Etjo is of Middle or Lower Triassic age. The red shale near Doros is of Upper Triassic age, as indicated by the presence of a dinosaur vertebra in it.

In common with current usage, the upper part of the Karroo succession in the Doros area is also commonly referred to as the "Etjo Sandstone". Although there are several outcrops of Karroo strata between Doros and the main occurrence in the Etjo area e.g. at the Erongo Mountains, at a locality south of the Okonjenje Igneous Complex and at the Petrified Forest in the southern Kaokoveld, it is however quite clear that the sedimentation and age of the strata at Doros are quite different from that at Etjo Mountain and that the Upper Karroo sequence in the area between Doros and the Huab Valley should be referred to by another formational name.

ACKNOWLEDGEMENTS

I am indebted to Mr. H. Preuss for many kindnesses during my stay at Etjo and to Drs. S. H. Haughton, A. R. I. Cruickshank and J. W. Kitching and Messrs. B. R. Turner and P. J. Rossouw for critically reading the manuscript and much valuable advice.

Miss Ruth Emanuel re-drew figures 13 and 14 for publication.

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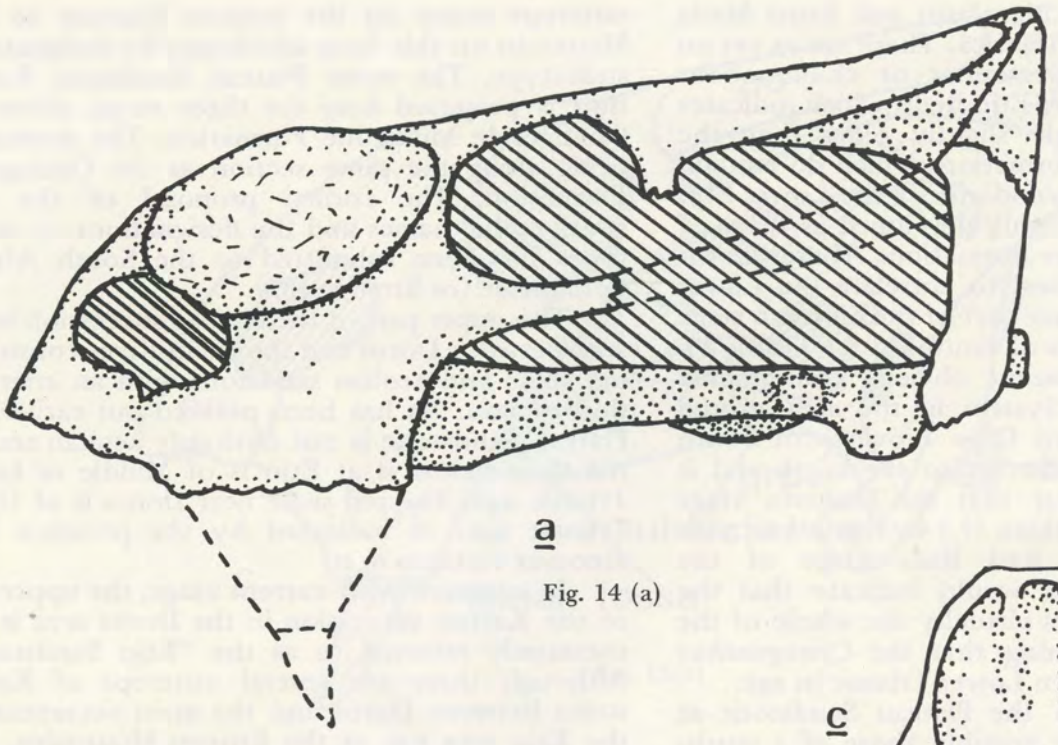


Fig. 14 (a)

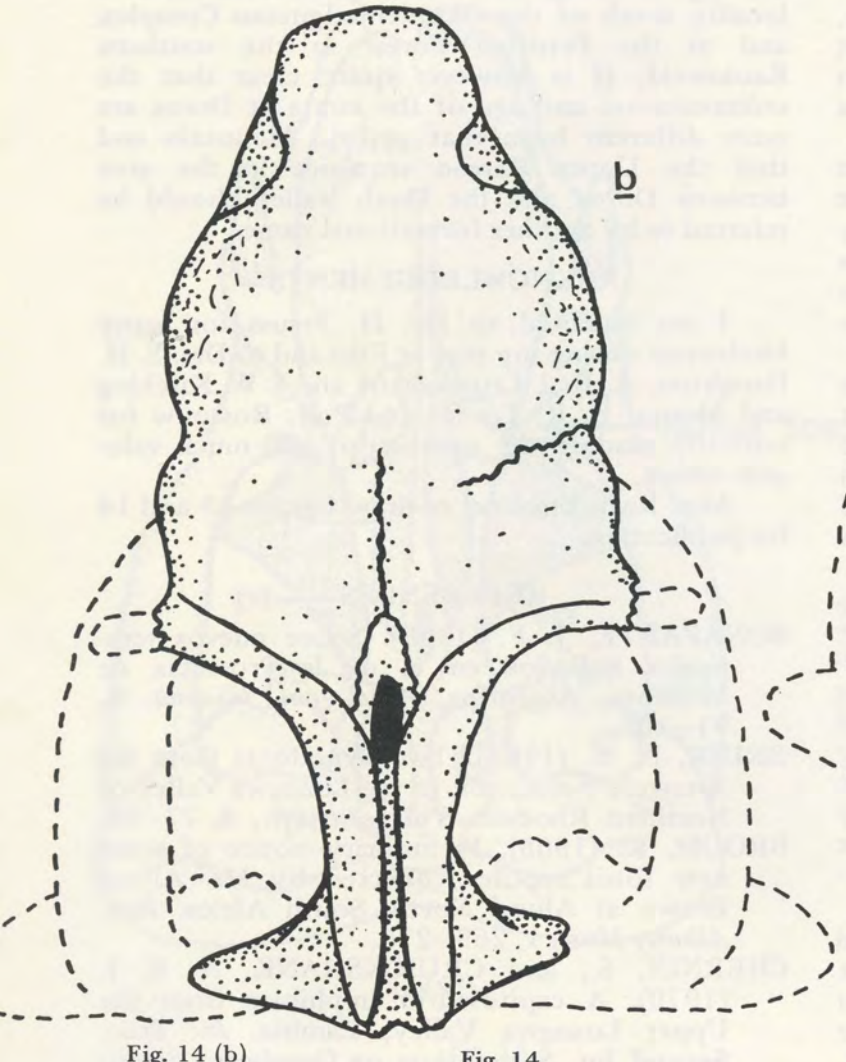


Fig. 14 (b)

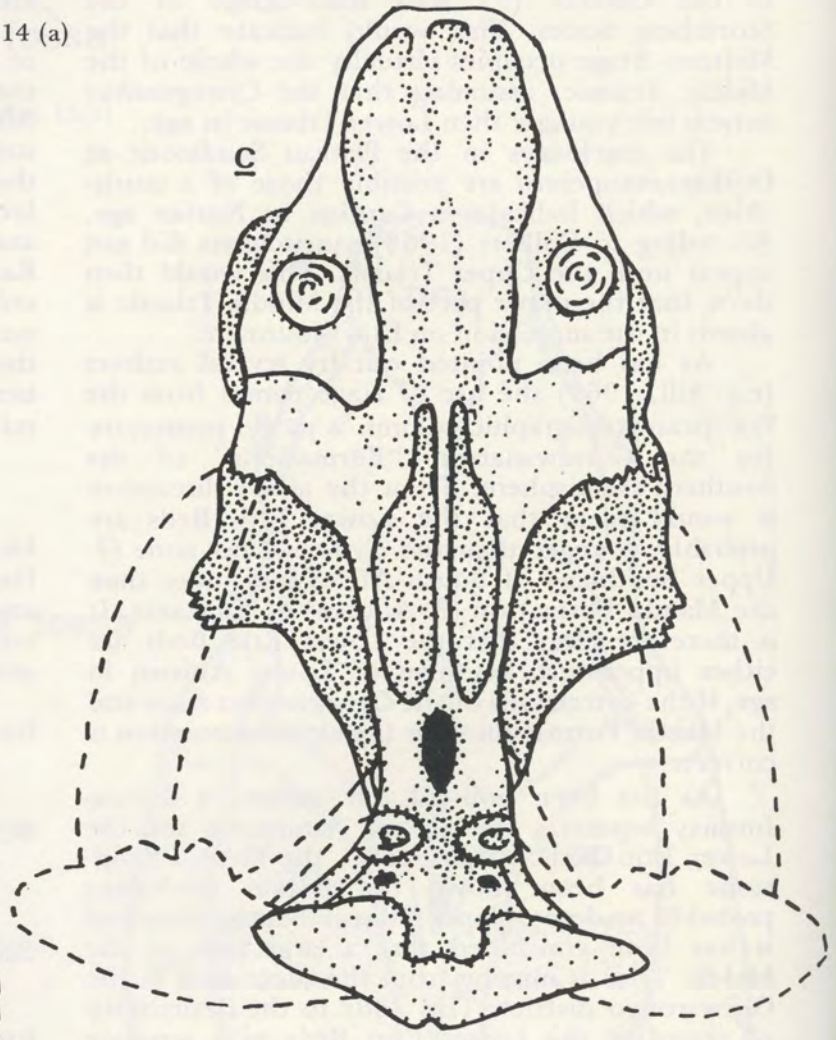


Fig. 14 (c)

Fig. 14.
(a) Lateral,
(b) Dorsal and
(c) Ventral view of *Rhopalorhinus etionensis* gen. et sp. nov. (X $\frac{1}{3}$)

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Palaeont. afr., **16.** 17–23. 1973

BRIEF SYNTHESIS OF PRESENT INFORMATION ON THE GEOGRAPHICAL AND STRATIGRAPHICAL DISTRIBUTION OF FOSSIL FISH WITHIN THE STORMBERG SERIES, SOUTH AFRICA

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ABSTRACT

A list is given of all specimens of *Semionotus capensis* Smith Woodward in South African collections. In addition a recent discovery of fish comparable with *S. capensis* in the Molteno Beds is recorded. This is the first true record of vertebrate life in this stage of the Stormberg Series, and if the identification can be confirmed, extends the record of this species in South Africa quite considerably.

INTRODUCTION

In the fossil record the family Semionotidae, to which is assigned the genus *Semionotus* Agassiz, 1832, is known from early Triassic to late Jurassic. The wide-spread genus *Semionotus*, the type species being *Semionotus bergeri* Agassiz, occurs in European Keuper Sandstone of Coburg and Thuringia (Zittel, 1932), as well as the Bunter (Lower Triassic), Muschelkalk, Rhaetic (Upper Triassic), the Trias of Connecticut Valley and New Jersey of the United States, Madagascar and South Africa. Hills (1958) considers that the semionotid *Corunegenys bowralensis* Wade, from Bowral (Upper Triassic, Australia), is very close to *Semionotus capensis* Smith Woodward, 1888.

STRATIGRAPHY

The Stormberg Series was reviewed (Anderson and Anderson, 1970) and correlated in age as follows:

Drakensberg Lavas
Cave Sandstone Formation } —Lower Jurassic
Red Beds Formation—Uppermost Triassic
Molteno Formation—Lower Upper Triassic

(Note: The use of Formation names is at variance with the present stratigraphic names which are based on the old dual system of stratigraphic classification. Acceptance of these new names awaits the findings of the South African Committee of Stratigraphy.)

The following quote (Beukes, 1970, pp. 326–7) is of importance in helping to ascertain the stratigraphic origin of most *Semionotus capensis* records:

> "The sedimentary structures and properties of the rocks of the Red Beds are indicative of a warm climate with seasonal rain storms during deposition. Furthermore these properties, together with a change of heavy-limbed fossils of dinosaurs in the lower strata to lightly-built cursorial types in the upper strata (Haughton, 1924), are evidence in favour of an increasing aridity in climatic conditions during deposition of this stage (Haughton, 1969, p. 367). This gradual change in climate resulted in the uneven contact between the Red Beds and Cave Sandstone stage as indicated by lenses of Red Beds in Cave Sandstone and *vice versa*. They also indicate that aeolian sand gradually encroached upon this area and that at one stage deposition of Red Beds and Cave Sandstone took place simultaneously."

In the Bethlehem-Kestell area Van Eeden (1937) found that, as stated above, the dividing line between the Red Beds and Cave Sandstone is not sharply defined. As this is adjacent to the Senekal-Ficksburg area, which is so rich in well-preserved specimens of *Semionotus capensis*, it would be reasonable to associate these fish fossils with the transition beds, and would account for the record of Anderson and Anderson (loc. cit.) of freshwater fish fossils from both the Upper Red Beds and Lower Cave Sandstone stages.

As there has been disagreement as to whether or not vertebrate remains are known from the Molteno Formation the new record of *Semionotus* cf. *capensis*, discussed below, is thus of importance. This appears to be the first record of vertebrates definitely coming from the Molteno Formation.

FOSSIL FISH

(a) *Cave Sandstone and Red Beds*

In spite of the numerous records of *Semionotus capensis* quoted below there is little information available regarding the exact localities or horizon from which the specimens came. The most detailed description is that of the type locality itself (Smith Woodward, 1888). The fish fossils were found in rocks in caves at the base of a precipice on Farm Weltevreden between Senekal and Ficksburg. The rocks at the base of the precipice were described as consisting of a belt of ribbon

sandstone which, when worked down, showed a beautiful ribbon pattern of varying colours—red, white, yellow and light buff.

Stockley (1947) quoting Du Toit (1904) states: "Above Palmietfontein the Telle River runs between cliffs of Cave Sandstone from two hundred to two hundred and fifty feet in thickness. I am informed by the Rev. D. F. Ellenberger, of the Masitise Mission Station, that at a point close to the Telle River, four miles from Masitise, many fish fossils were obtained from the Sandstone. These fish remains, I believe, have been presented to the museum at Maseru."

The fossils mentioned by Stockley (loc. cit.) have not been discovered. There is no Museum at Maseru but I have been informed by Dr. L. G. S. Smits of the University of Botswana, Lesotho and Swaziland, that a slab with fossil fish is in the small museum at the Training College at Morija, but it is not known whether these are from the Masitise Mission or Quthing. Gardiner (*in litt.*) has informed me that he has seen fragments of *Semionotus capensis* from the Cave Sandstone of the Likhoele Hills near Mafeteng.

In the museums of the Republic of South Africa *Semionotus capensis* is well represented in fish fossil collections. These have been examined and all, many with numerous fish in an excellent state of preservation, are preserved in sandstone. In the absence of any detailed localities being available these are taken as coming from the transition between Red Beds and Cave Sandstone. The following is a list of the specimens of *S. capensis* examined:

National Museum, Bloemfontein:
C.2842: Wittebergen between Bethlehem and Fouriesburg, no exact locality recorded.
C.292: 24 km west of Senekal, Mr. Collins, 1926.
C.2827: Daskop, Ficksburg, Mrs. J. F. Wiesner.
C.2606: Stafford Hill, 1,5 km north-east of Ficksburg, G. Liquori.
C.286: Driefontein, 40 km east-north-east of Senekal, C. Barrett, 1924.
C.2821: Schutters Draai, near Ficksburg, C. Stevens.
C.1079: No locality, just Orange Free State.
No number: Witteberg, M. J. Keyter.

McGregor Memorial Museum, Kimberley:
428: Ficksburg, Orange Free State.
No number: Two slabs with excellent specimens from Ficksburg, Orange Free State.

Natal Museum, Pietermaritzburg:
741: Ficksburg, Orange Free State.
821: Ficksburg, Orange Free State.
822: No Locality recorded.

Museum and Snake Park, Port Elizabeth:
1201B: Orange Free State, no locality.
1201C: Basutoland Border, no locality, F. C. Bengstedt.
1201E: Orange Free State, no locality.

South African Museum, Cape Town:
K436: Clocolan, Orange Free State, P. J. Lange.
2781: Narime (?) Vale, Senekal, Orange Free State.
1065: Ficksburg, Sir H. de Villiers.
No details: Two slabs with good specimens.

Transvaal Museum, Pretoria:
2829(209): Two slabs from Ficksburg.
2830(210): One small block, Rouxville, Orange Free State.

Albany Museum, Grahamstown:
477: Two slabs from National Museum, Bloemfontein, recorded as coming from Senekal, Orange Free State.

University of Lesotho, Botswana and Swaziland, Roma, Lesotho:
No number: One slab presented by C. F. Jacot Guillarmod, from a quarry at Excelsior, Orange Free State. Slab could not be traced.

Although it is stated by Anderson and Anderson (loc. cit.) that in the lower zone of the Cave Sandstone, where *Semionotus capensis* occurs, occurrences of freshwater fishes are rare, it should be noted that slabs of sandstone from the Senekal and Ficksburg Districts with fish fossil remains indicate that there was a considerable concentration of fishes at the time of preservation. No other fossil remains or fish species have been discovered in those particular slabs quoted above, but Forey and Gardiner (1973, Volume 15) have described a new redfieldid fish from the Likhoele Hills near Mafeteng (Cave Sandstone), Lesotho.

Haughton (1924, pp. 338–341) has discussed *Semionotus capensis* as well as an unidentified incomplete small fish preserved in a piece of shale taken from near the base of Cave Sandstone, Siberia, Wodehouse, Cape Province. The long-based anal fin distinguishes this species from *Semionotus capensis*. Unfortunately the specimen is not available at present for examination and comparison with what appears to be similar material from two other sites.

One of these is Sutherlands Quarry, Biggarsberg, Natal, from which two incomplete specimens, Registered No. N.M. 21, Natal Museum, Pietermaritzburg, were described as representing an "Unidentified Palaeoniscid Fish" by Smith Woodward (1893). These fish remains are preserved in sandstone referred, at that time, by Mr. Draper

to the "Molteno Beds, 150 feet above the main coal seam". As Biggarsberg lies well within the Ecca Series the possibility of locating the exact site, Sutherlands Quarry, is being investigated.

The other site is near a coal mine, Stormberg, Cape Province, where fish fossil 1201 D Port Elizabeth Museum (see Figure 5) was discovered. This is also an incomplete fish which resembles greatly the two specimens from Biggarsberg. As it comes from near a coal mine it could possibly be from the Molteno Stage, this being the only formation with well-developed coal seams in the area. Unfortunately the exact horizon and locality from which this fossil came are unknown. This species, with a long-based anal fin and scale markings similar to the Biggarsberg material, and the fish discussed by Haughton (loc. cit.), is the same average size as *Semionotus capensis* but is neither a semionotid nor redfieldid. Kodachrome photographs of important features of this fossil have been sent to Gardiner who has informed me (*in litt.*, 1972) that after comparison with Triassic fish fauna material in the British Museum he has come to the conclusion that the Stormberg fish represents a new form. Further material is required before a detailed description can be published.

(b) *Molteno Stage*

Up to early 1971 no fish fossils from the Molteno Beds were known for certain. The Stormberg fossil referred to above appears to have been overlooked, and the Biggarsberg fossil shelved due to a suspected discrepancy in stratigraphic interpretations. Then an interesting discovery, confirmed again in January this year, was made by Mrs. Heidi Anderson, of the Bernard Price Institute for Palaeontology, who found impressions of fish amongst some of her specimens whilst she was collecting plant fossils on the Farm Denwood, Bird's River, near Dordrecht. [B.P.I. collection C-Dt.II. 355, 750a, b; 752a, b (fin only). Spp. 355 and 750 are substantially complete except for the head (Figs. 1 and 2).].

Stratigraphy:

The stratigraphy is obscured in this area by the "Bird's River Dolerite Complex" (P. Booth, 1971, M.Sc. thesis, Rhodes University). The Molteno Stage is about 230 metres thick in this area and the fossiliferous kaolinitic shales appear to lie close to the top (pers. comm. B. Turner, 1972). The kaolinitic shales have been tilted by the dolerite to 13 degrees from the horizontal and are exposed over a large area along the back of the dam.

Associated fossils:

This is an excellent plant fossil locality with a *Dicroidium* flora, the most common leaf being *Baiera* sp. and to a lesser degree *Dicroidium*, *Lepidopteris*, *Phoenicopsis*, *Ginkgo*, *Taeniopteris*, *Yabeiella* and various reproductive structures. A number of insect wings including 5 Ephemeroptera, 1 Meganioptera, 8 Odonata, 1 Plecoptera, 1 Protoorhoptera, 1 Orthoptera, 13 Blattodea, 7 Homoptera, 3 Coleoptera, 1 Megaloptera (E. Riek in press and preparation) have also been found.

Specimens of the fish impressions were sent to the Albany Museum and these were identified as either closely related to, or conspecific with, *Semionotus capensis* Woodward. Full details and a photograph, (Figures 1 and 2) were sent to Gardiner who confirmed the identification. In his letter Gardiner drew attention to the similarity of the Bird's River specimens to those of the Likhoele Hills, Lesotho. Figures 3 and 4 are of *Semionotus capensis* near Senekal, these are preserved in Cave Sandstone. The Bird's River specimens are incomplete, but the anal, dorsal and caudal regions are sufficiently complete to separate this species from the Stormberg and Biggarsberg species discussed above, as well as the redfieldid from Lesotho.

This discovery of *Semionotus* cf. *capensis*, where the horizon can be determined and described with certainty as near the top of the Molteno, is of considerable interest in being the first vertebrates definitely from it. The material available is poorly preserved and, if future collecting proves the identification of this fish to be correct, the period of existence of *Semionotus capensis* in South Africa will have to be extended considerably.

ACKNOWLEDGEMENTS

I am grateful to Mrs. H. Anderson of the Bernard Price Institute for Palaeontology, University of the Witwatersrand, for supplying me with such interesting material from Bird's River, as well as extensive data included in this paper. Professor H. Eales, Department of Geology, Rhodes University, kindly examined the rock in which the specimens of *Semionotus capensis* in the Albany Museum are preserved. I am indebted to Dr. B. Gardiner of the Queen Elizabeth College, London, for his valuable collaboration in the identification of fish fossil material. I am also indebted to the Directors of the museums mentioned above who so kindly made fish fossil material available to me for examination.

The study of the fish fossils of southern Africa is part of a research programme sponsored by the C.S.I.R., Pretoria.

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Figure 1
Semionotus cf. *capensis* from Farm Denwood, Bird's River, E. Cape. C–Dt. II 355. B.P.I.

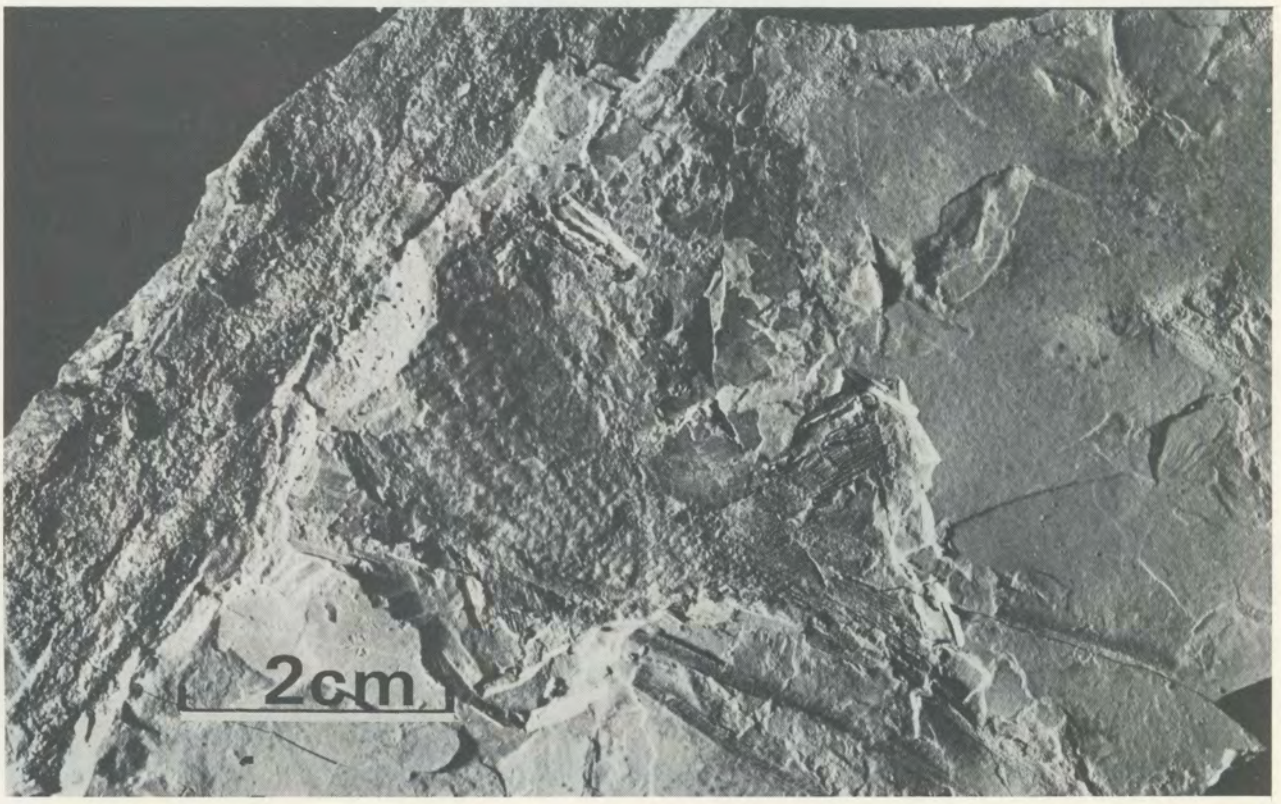


Figure 2
Semionotus cf. *capensis* from Farm Denwood, Bird's River, E. Cape. C–Dt. II 750a.

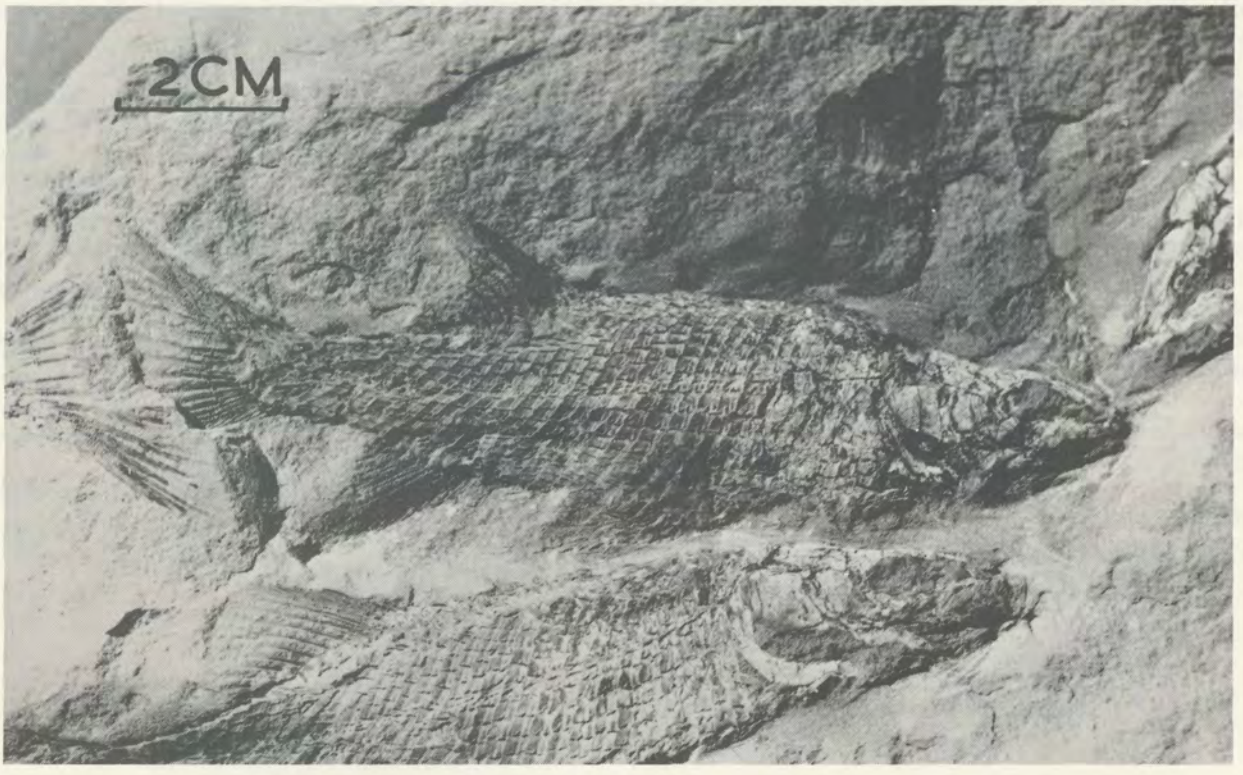


Figure 3
Semionotus capensis. Cave Sandstone, Ficksburg. McGregor Memorial Museum No. 428.

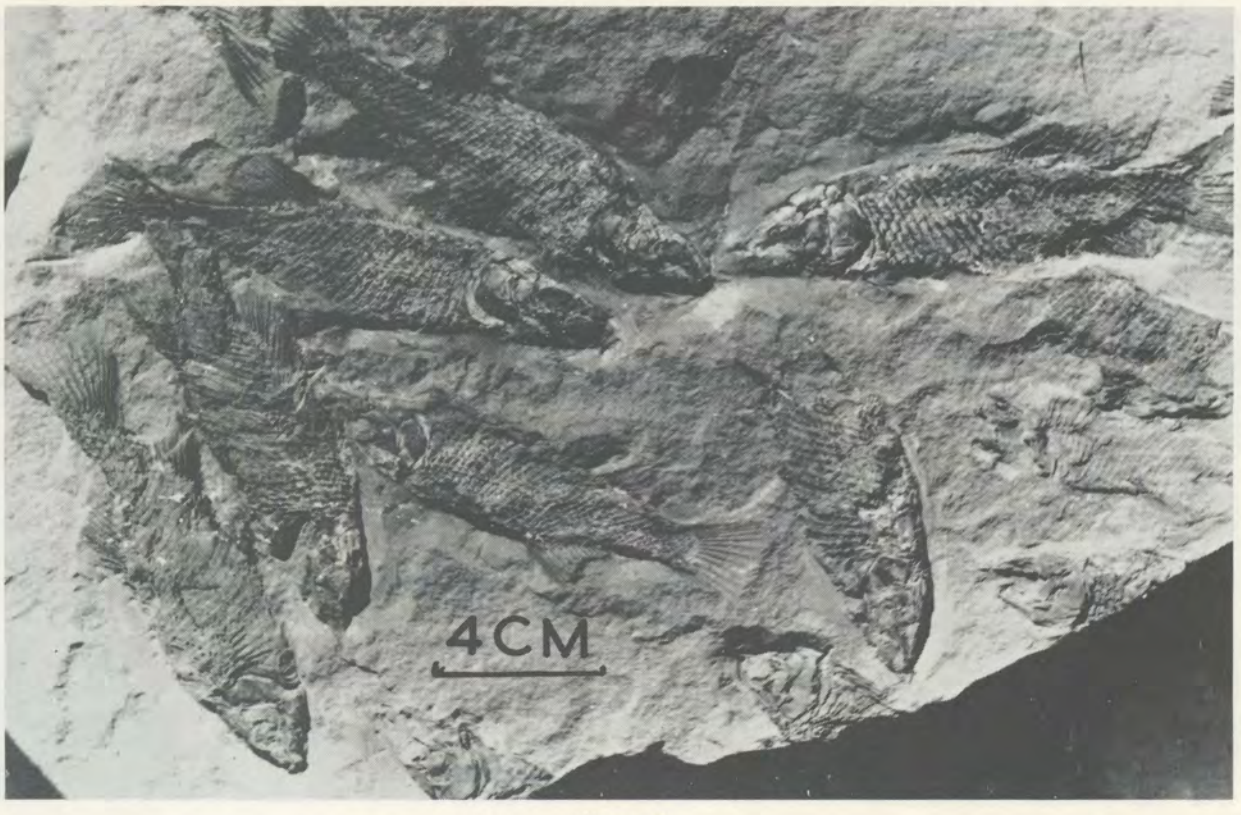


Figure 4
Semionotus capensis. Cave Sandstone. Ficksburg. McGregor Memorial Museum No. 428.

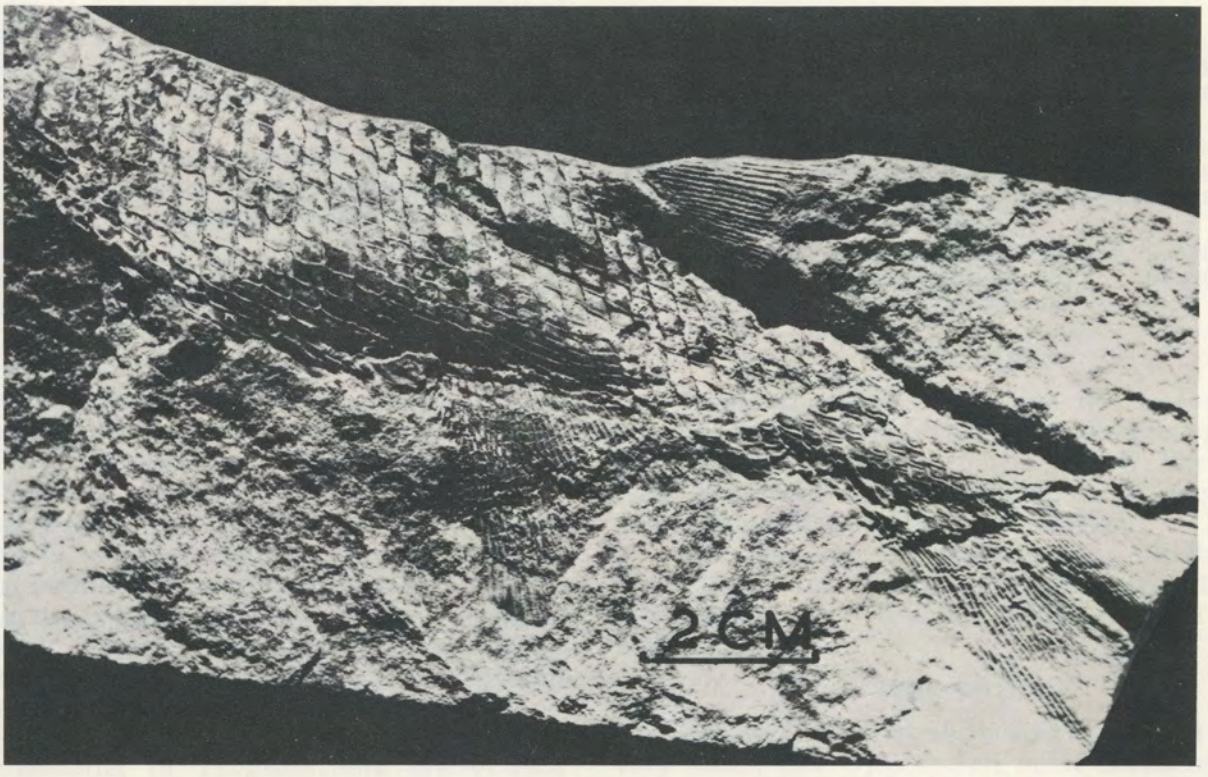


Figure 5
Fish fossil from Stormberg, Cape Province. Port Elizabeth Museum No. 1201 D.

Palaeont. afr., **16.** 25–35. 1973

A RE-EVALUATION OF THE GENUS *TROPIDOSTOMA* SEELEY

by

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ABSTRACT

The type specimens of *Cteniosaurus platyceps* Broom, *Dicynodon acutirostris* Broom, and *Dicynodon validus* Broom were re-examined and were found to be very similar in a number of features rarely encountered in other Anomodontia. The skull of the type of *Cteniosaurus platyceps* is described in some detail. It is concluded that the above species must be considered to be junior synonyms of *Tropidostoma microtrema* (Seeley).

INTRODUCTION

The genus *Cteniosaurus* was first introduced by Broom (1935, pp. 66–67, Fig. 7) to accommodate forms resembling *Tropidostoma microtrema* (Seeley) with more "molars" which are serrated both in front and behind. Since the appearance of the first descriptions no further work has been done on the genus and no other specimens have been referred to it to the author's knowledge.

While examining the type specimens of anomodontia in the Transvaal Museum, Pretoria, the author came across the type material of *Cteniosaurus platyceps* Broom. This was completely unprepared and in the condition in which it was collected in the field and subsequently described by Broom in 1935. No preparation whatever had been done on the specimens.

It was decided to subject the specimens to preparation in order to ascertain the affinities of the genus within the Endothiodontidae and to study the cranial morphology of the genus in greater detail. The type specimens of *Dicynodon acutirostris* Broom and *Dicynodon validus* Broom were prepared for comparison.

Later the author had the opportunity to study the type material of *Tropidostoma microtrema* (Seeley) as well as a large number of other specimens referred to this species in the British Museum (Natural History).

The morphological description is based on the following:

MATERIAL

Catalogue No.	Diagnosis	Locality
T.M. 249	Skull lacking left zygomatic arch. Holotype of *Cteniosaurus platyceps* Broom.	Leeukloof, Beaufort West
T.M. 383	Anterior half of skull. Paratype of *Cteniosaurus platyceps* Broom.	Leeukloof, Beaufort West
T.M. 384	Posterior half of skull. Paratype of *Cteniosaurus platyceps* Broom. It is possible that it belongs to the same skull as T.M. 383.	Leeukloof, Beaufort West
T.M. 385	Crushed skull lacking quadrates and tip of the snout. Paratype of *Cteniosaurus platyceps* Broom.	Leeukloof, Beaufort West
T.M. 387	Crushed skull lacking occiput and zygomatic arches. Paratype of *Cteniosaurus platyceps* Broom.	Leeukloof, Beaufort West
T.M. 250	Laterally crushed anterior half of skull. Holotype of *Dicynodon acutirostris* Broom.	Leeukloof, Beaufort West
T.M. 252	Distorted anterior half of skull and mandible. Holotype of *Dicynodon validus* Broom.	Leeukloof, Beaufort West

TECHNIQUE

Preparation was done by the conventional mechanical methods. The more detailed preparation was done with a dental mallet. The matrix does not react with hydrochloric or acetic acid precluding the use of acid preparation.

The drawings are based mainly on the holotype of *Cteniosaurus platyceps* Broom, additional information was obtained from the rest of the material.

THE SKULL

The skull is fairly short and broad and appears very much like *Oudenodon baini* Owen on superficial examination (Plate V). The intertemporal region is wider than in most other Anomodontia. The external nares are small and placed high up in the snout. The dorsal part of the premaxilla on the surface of the snout extends far posteriorly, unlike the condition in most other *Cistecephalus* Zone dicynodonts.

The palatines form a very important part of the secondary palate and are as extensive as in *Compsodon helmoedi* van Hoepen.

THE SNOUT AND SKULL-ROOF

The premaxillae (Figs. 1, 2 and 3) are completely fused and tend to separate the nasals anteriorly extending posteriorly to the level of the posterior margins of the external nares. This latter feature is rare in *Cistecephalus* Zone dicynodonts. There is a prominent median and two less

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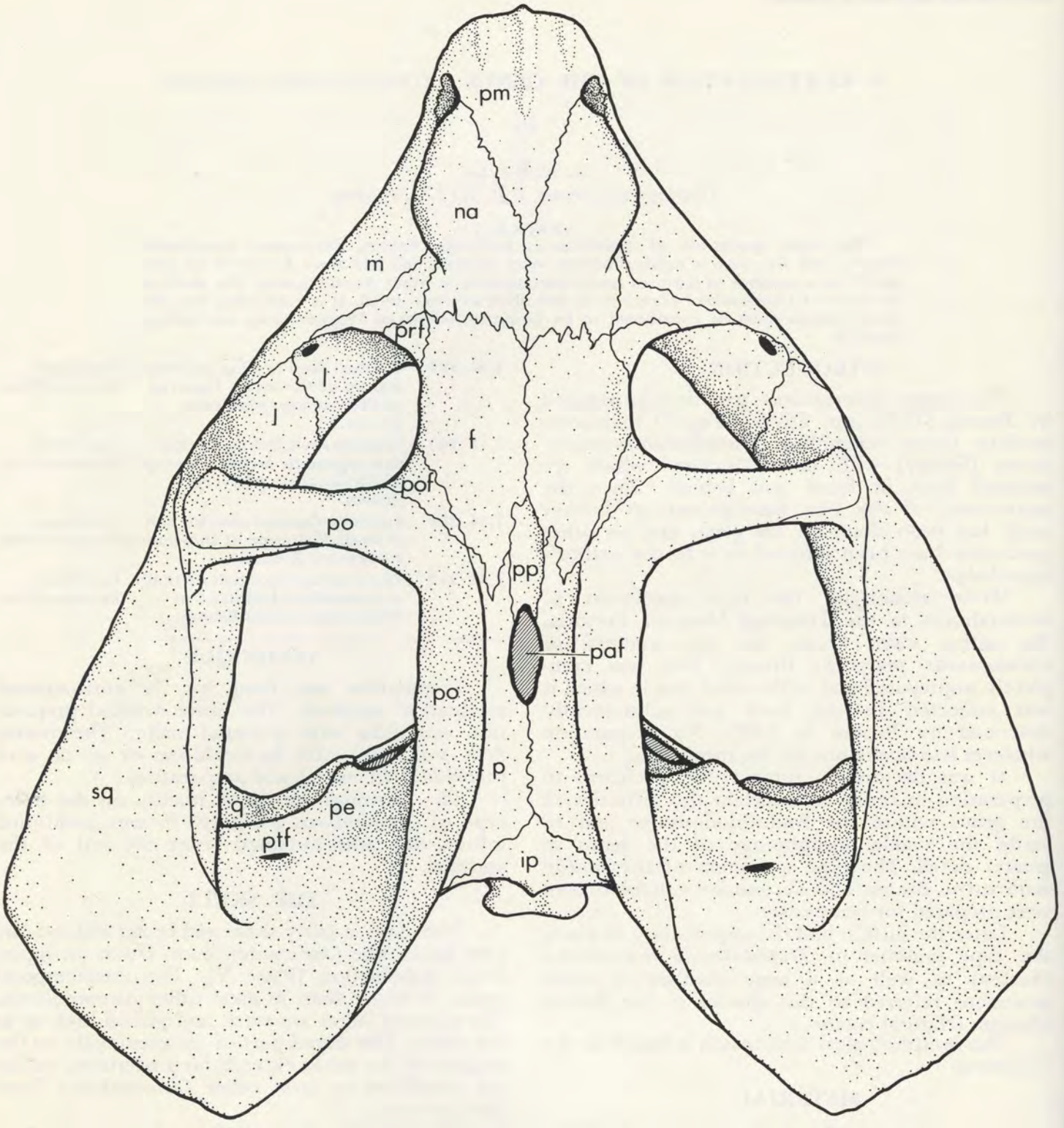


Fig. 1 Reconstruction of the dorsal view of *Tropidostoma microtrema* (Seeley) (about natural size). Abbreviations in this and subsequent figures after Romer "Osteology of the Reptiles".

prominent lateral external longitudinal ridges on the antero-dorsal surface of the snout.

On the palatal surface the premaxillae exhibit the usual two anterior and one posterior median palatal ridges. Posteriorly the premaxillae are in sutural contact with the palatines and the vomer anterior to the anterior margins of the choanal slits. Laterally they form straight sutures with the maxillae.

The septomaxillae lie in depressions surrounding the nares externi, which they bound ventrally and posteriorly. They form sutures with the premaxillae, maxillae and lachrymals.

The maxillae (Figs. 1, 2 and 3) are the only tooth-bearing elements in the skull. They constitute an important part of the sides of the snout and form prominent caniniform processes that bore tusks in some specimens. One of the

paratypes, T.M. 383, displays a large socket on its right caniniform process. The occurrence of post-canines is highly variable in the type material. The holotype of *Cteniosaurus* and specimen T.M. 383 show no trace of post-canines in the maxillae. Specimen T.M. 387 has a single large root of a post-canine on the alveolar margin posterior to the caniniform process. Specimen T.M. 385 has post-canines on each maxilla. In this specimen the post-canines are placed medial to the alveolar border on the palatal part of the maxilla postero-medial to the caniniform process. On the right side there are two post-canines and a socket of a third. On the left there is one post-canine and a socket of a second. In this specimen the post-canines are arranged in clusters and not in rows. A similar range of variation was observed in the British Museum specimens of *Tropidostoma microtrema* (Seeley). In the anterior part of the zygomatic arch, the maxilla extends posteriorly to the level of the postorbital arch.

The nasals form the posterior halves of the dorsal margins of the nares externi where they are thickened to form small nasal bosses. Anteriorly they are separated by the posterior dorsal process of the premaxillae. This development of the premaxillae results in relatively short nasal bones.

The prefrontals (Figs. 1 and 2) are slightly thickened, but do not form such prominent bosses as in *Oudenodon*.

The frontals form the dorsal margins of the orbits where they are slightly raised but not to the same extent as in *Oudenodon*.

The postfrontals (Fig. 1) separate the frontals from the parietals, seemingly as, superficial, triangular-shaped bones, visible on the dorsal surface.

The preparietal (Fig. 1) is a small lanceolate bone that constitutes the anterior margin of the parietal foramen. The shape of this bone is highly variable in the type series. It is long and narrow in the holotype and very broad in specimen T.M. 385. In specimen T.M. 383 the preparietal is situated entirely in front of the parietal foramen and does not take part in the formation of the anterior margin of the parietal foramen.

The postorbitals extend posteriorly to meet the squamosals at the posteromedial corners of the temporal fossae.

The parietals form two longitudinal plates posterior to the parietal foramen on their ventral sides. These plates are fused with the expanded dorsal extremities of the epipterygoids.

The interparietal (Figs. 1 and 4) is visible in the dorsal view of all the types except T.M. 384.

The jugals (Figs. 1, 2 and 3) form the medial parts of the zygomatic arches and extend posteriorly to near the posterior margins of the temporal fossae.

The squamosals (Figs. 1, 2, 3 and 4) extend anteriorly to the level of the middle of the orbits.

The tabulars (Fig. 4) are small plate-like bones that lie on the sides of the interparietal and overlap the squamosals.

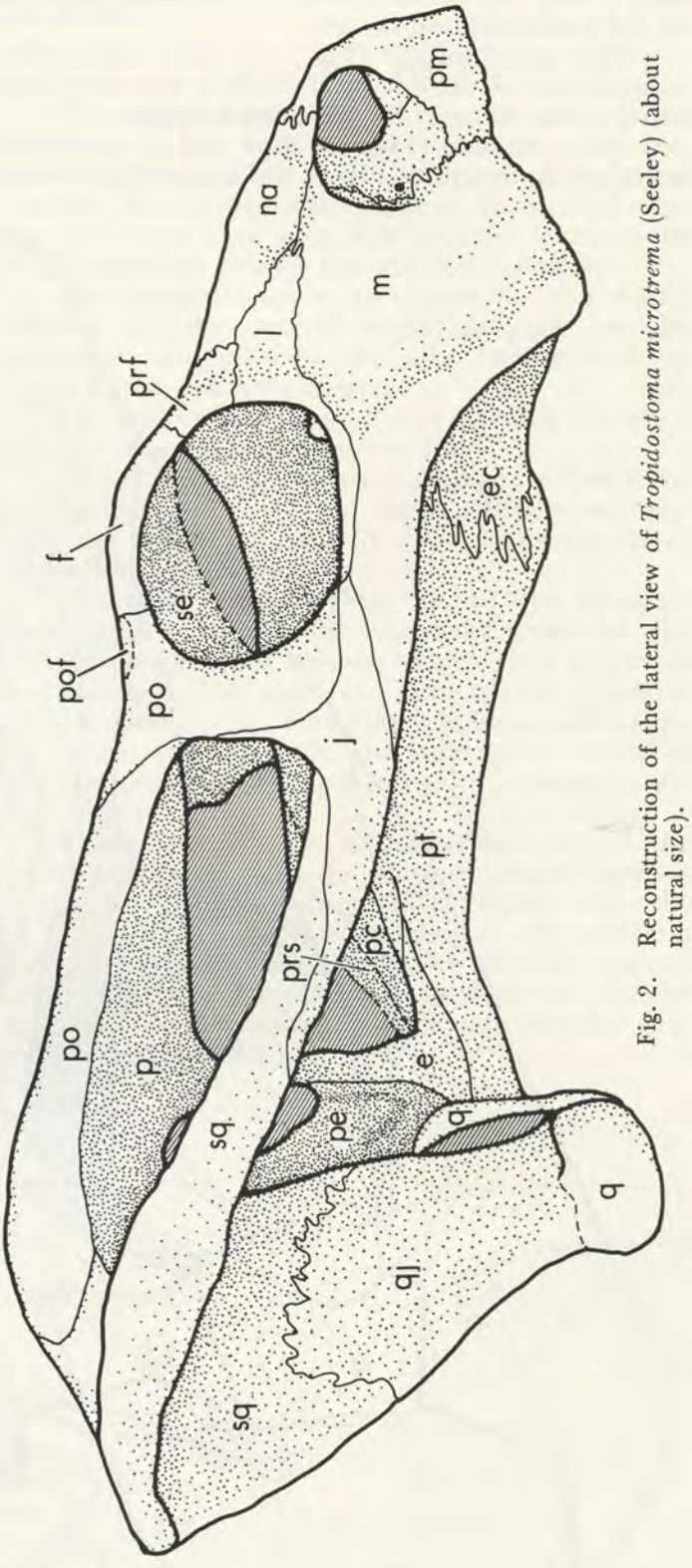


Fig. 2. Reconstruction of the lateral view of *Tropidostoma microtrema* (Seeley) (about natural size).

THE OCCIPITAL AND OTIC REGIONS

These regions do not show any unusual specialisations and the structure does not differ appreciably from any of the other medium-sized anomodonts of the *Cistecephalus* Zone.

The supraoccipital (Fig. 4) extends between the post-temporal fossae and constitutes the dorsal half of the margins of the foramen magnum. It only forms the dorsal halves of the medial margins of the post-temporal fossae.

The exoccipitals (Fig. 4) form the lateral tuberosities of the occipital condyle and meet each other in the floor of the foramen magnum.

The periotics (Figs. 1, 2, 3 and 4) constitute most of the lateral walls of the brain-case. On the occipital surface the periotics form the greater part of the medial and the ventral margins of the post-temporal fossae. The paroccipital processes that extend laterally to meet the squamosals in the suspensoria are fairly massive. Where the distal extremity of the paroccipital process meets the squamosal, a ridge is formed. This ridge is termed the tympanic process by Cox (1959, p. 9) and the opisthotic process by Barry (1967, p. 145). There are very prominent venous grooves on the antero-

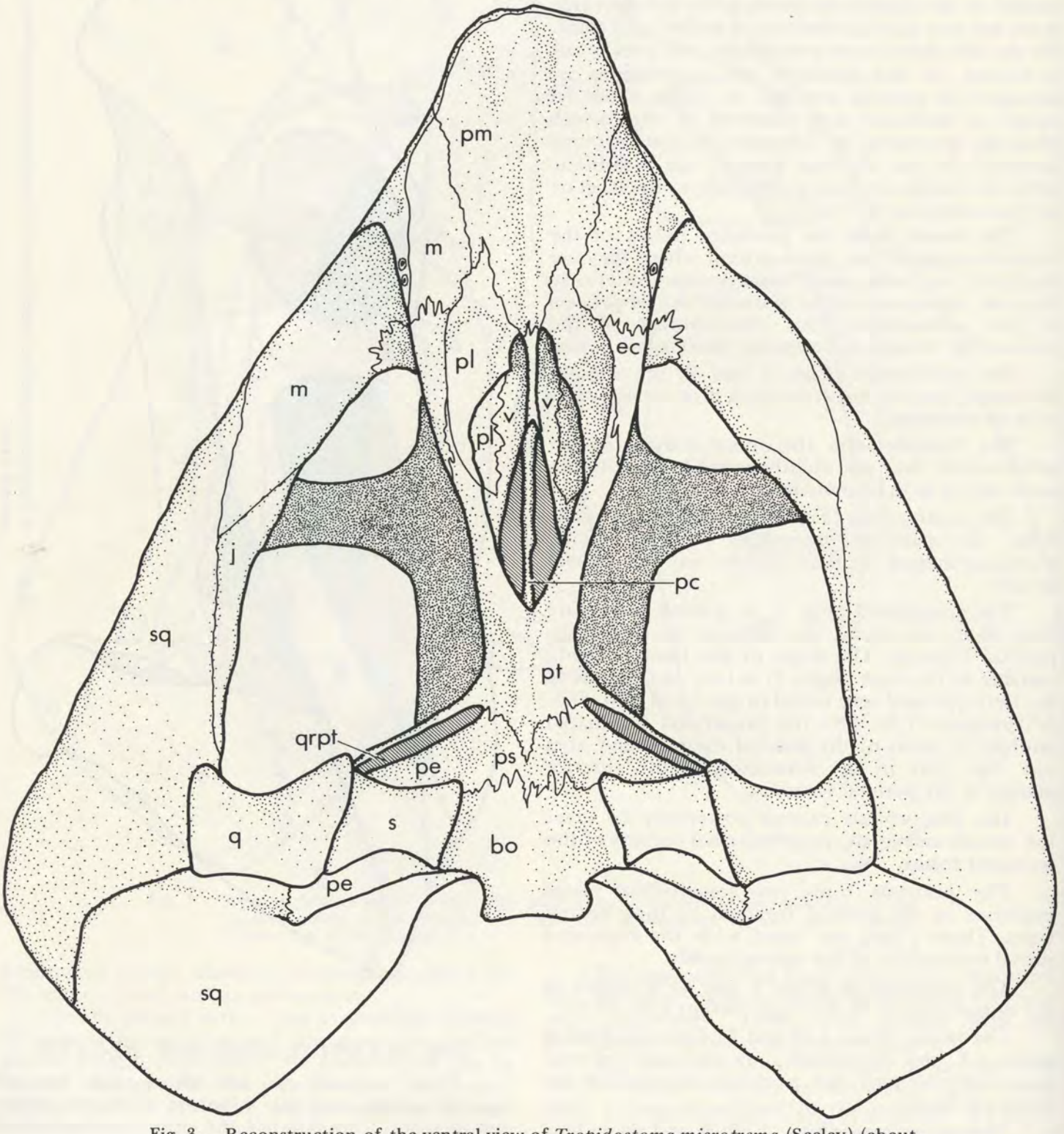


Fig. 3. Reconstruction of the ventral view of *Tropidostoma microtrema* (Seeley) (about natural size).

lateral face of the periotic. These grooves connect the post-temporal fossae with the pterygo-quadrate foramina ventrally and the notch between the supraoccipital and the periotic dorsally. The periotic appears to form most of the margins of the fenestrae ovales. The fenestrae are small and circular and are situated at the posterior extremity of a flat surface for articulation with the stapes.

The basioccipital (Figs. 3 and 4) is indistinguishably fused with the basisphenoid. Sutures between the basisphenoid and the periotics can be seen ventral to the jugular foramina. Anteriorly the basioccipital is overlapped by the parasphenoid which covers the basioccipital basisphenoid contact.

The proximal end of the stapes is larger than the distal end. The distal ends are closely appressed to the quadrates.

THE BASIS CRANII

The basisphenoid cannot be studied satisfactorily in the material at hand as little of it can be seen in a prepared specimen. Ventrally it is covered by the parasphenoid and the pterygoids and dorsolaterally by the periotics. The exact relationship of the cultriform process to the vomer and the elements of the sphenethmoid region are uncertain due to the crushing of all the specimens, but the cultriform process appears to reach the level of the posterior part of the nasal cavity.

The sphenethmoid (Fig. 2) consists of two separate ossifications. The posterior element consists of a thin vertical plate of bone that stands on the dorsal surface of the cultriform process dorsal to the interpterygoid vacuity. The anterior element consists of a vertical median plate that divides dorsally to form two wings that lie against the frontals. There is general agreement that the wings are the orbitosphenoids. The median vertical part is termed the presphenoid by Agnew (1958, p. 94) and septosphenoid by Boonstra (1968, p. 260) and Barry (1967, p. 149). No foramina for the passage of the optical nerves were seen in the orbitosphenoids.

THE PALATE

The quadrates (Fig. 1, 2, 3 and 4) of *Cteniosaurus* are very similar to those of *Oudenodon baini* Owen. As in the latter genus the lateral condyle is more prominent that the medial one. The quadrates have a smaller articular facet on the dorsal processes than is found in *Oudenodon*.

The quadratojugals are fused to the dorsal surfaces of the lateral condylar parts of the quadrates and extend dorsally to form interdigitated sutures with the jugals.

The pterygoids (Figs. 2 and 3) have the usual configuration found in Anomodontia.

The ectopterygoids are interdigitated with the pterygoids posteriorly and the maxillae anteriorly. They are of similar size to the ectopterygoids of *Oudenodon baini* Owen.

The epipterygoids (Fig. 2) are thin elongate plates that connect the quadrate rami of the pterygoids with the ventral longitudinal plates of the parietals. The quadrate rami of the epipterygoids do not extend along the quadrate rami of the pterygoids and are short. The anterior extremity of the foot-plate of the epipterygoid is fused to the basisphenoid.

The palatines form an important part of the secondary palate and are more extensive than in most other anomodontia. They form both the lateral and the anterior margins of the anterior choanal slits and have extensive sutural contact with the premaxillae. Near the posterior end of the choanal slits the palatines develop tubercles that project ventromedially.

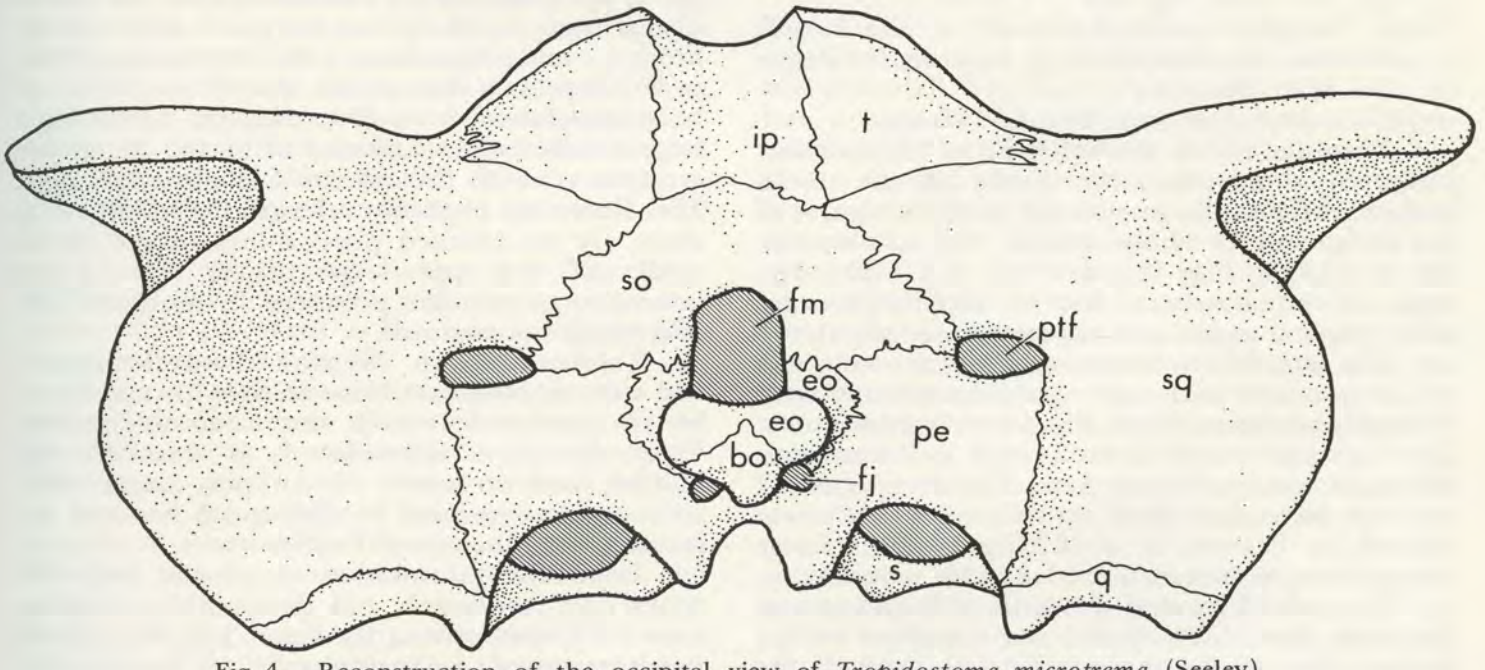


Fig. 4. Reconstruction of the occipital view of *Tropidostoma microtrema* (Seeley) (about natural size).

The suture between the vomers and the premaxilla (Fig. 3) occurs at the level of the anterior margins of the choanal slits. The interpterygoid vacuity is long and extends anteriorly for two thirds of the length of the choanal depression. The margins of the vacuity are raised to a greater extent than in *Daptocephalus.*

THE LOWER JAW

Broom (1953, p. 67) described some "molars" found in the lower jaw of the holotype. Unfortunately, the parts of the specimen containing the teeth are lost. Part of the ramus of a mandible lies against the occipital surface of the holotype. Unfortunately, it is so weathered that no features can be distinguished. There is no other lower jaw material available at present.

COMPARISON OF THE SKULL WITH *TROPIDOSTOMA MICROTREMA* (SEELEY)

(Plates I and II)

Dicynodon microtrema Seeley (1889, pp. 228–232, Pl. 11)
Dicynodon (Tropidostoma) duni Seeley (1889, pp. 232–236, Pl. 12)
Tropidostoma microtrema (Seeley) (Broom, 1915, pp. 355–361, Figs. 3–4)
Tropidostoma microtrema (Seeley) (Broom, 1932, pp. 209–211, Fig. 69C–D)
Tropidostoma microtrema (Seeley) (van Hoepen 1934, pp. 71–74, Fig. 9)
Tropidostoma microtrema (Seeley) (Broili and Schröder, 1935, pp. 239–241, Fig. 9)
Tropidostoma microtrema (Seeley) (Watson, 1948, pp. 855–857, Figs. 13–14)
Tropidostoma microtrema (Seeley) (Haughton and Brink, 1954, p. 67)
Tropidostoma microtrema (Seeley) (Watson, 1960, pp. 131–308, Fig. 10)
Type: Occipital part of a skull in the British Museum (Natural History), London. Catalogue No. 868. (Plate I)
Type Locality: Tafelberg, Beaufort West.

Examination of the holotype of *Cteniosaurus platyceps* shows that the bones of the dorsal surface of the skull agree closely with the figures of the dorsal surface of the skull of *Tropidostoma* by Broom (1915, Fig. 3 and 1932, Fig. 69D). The type of *Cteniosaurus* has a slightly broader intertemporal region and a more pointed snout.

The lateral view of the snout of the holotype of *Cteniosaurus platyceps* agrees remarkably with Watson's specimen (1948, Fig. 9) of *Tropidostoma.* The high placement of the nostril in the snout is the most notable feature here. The dorsal view of the specimen described by Watson (1948) was figured by Pearson in 1924 (Fig. 8). This figure shows the structure of the floor of the nasal cavity.

The palatal view of the skull of *Tropidostoma* has been figured by all the above authors except Seeley. One of the most striking features of the palatal view is the long interpterygoid vacuity with its raised margins. Such structure of the interpterygoid vacuity is rare among anomodonts. The vacuity of the specimen figured by Watson (1948, Fig. 13) is relatively shorter than in the specimens figured by the other authors. The length of the vacuity is variable in the types of *Cteniosaurus.* In specimen T.M. 383 it is almost as short as in Watson's specimen. The British Museum specimens from Tafelberg, Beaufort West show a similar range of variation.

Another very noticeable feature is the large part that the palatines play in the formation of the secondary palates of both *Cteniosaurus* and *Tropidostoma.* The palatines usually form the anterior margins of the anterior choanal slits in *Cteniosaurus.* This feature is, however, subject to some variation. In specimen T.M. 383 the anterior margin of the left choanal slit is formed by the premaxilla while the one on the right side is bounded by the palatine. A similar condition is figured by Broili and Schröder (1935, Fig. 9) in a specimen identified as *Tropidostoma microtrema.* In the specimen of *Tropidostoma* figured by Watson (1948, Fig. 13) the palatines appear to form the anterior margins of the anterior choanal slits. In the palate figured by Broom (1915, Fig. 3 and 1932, Fig. 69D) there is extensive contact between the palatines and premaxilla, but the palatines do not form the anterior margins of the choanal slits.

The ectopterygoids of both genera are extensively developed to meet the jugals on the medial sides of the anterior roots of the zygomatic arches.

The dentition is highly variable in the type series of *Cteniosaurus platyceps* as has been shown in the first part of this paper in the section dealing with the maxilla. The dentition of *Tropidostoma* is also highly variable and the post-canines are absent in mature specimens (Broom, 1915, p. 358 and 1932, pp. 209–211). This could also be the case in *Cteniosaurus* as there are no post-canines in the holotype and in specimen T.M. 383. Broom (1935, p. 67) expresses the opinion that *Cteniosaurus* can be distinguished from *Tropidostoma* by having a large number of molars and in having the molars serrated on both the anterior and posterior edges. This statement probably refers to the lower jaw, as there are no serrated post-canines in any of the skulls of the type series. There is only one unbroken post-canine preserved in specimen T.M. 385 which is unserrated.

Toerien (1953, p. 75) showed that the number and structure of post-canine teeth is too variable to be of taxonomic use in the Endothiodontidae. From the above discussion it is clear that the number and structure of the post-canine teeth alone cannot be used to distinguish between the genera *Cteniosaurus* and *Tropidostoma.*

From the information obtainable from the types of *Cteniosaurus* and the published descriptions of *Tropidostoma,* specimen T.M. 383, one of the type series of *Cteniosaurus,* can be placed in either of the two genera because the left palatine

does not form the anterior margin of the left anterior choanal slit while the right one does!

The evidence at present available to the author points to close affinity between the two species. It is therefore desirable to place both species in the same genus i.e. *Tropidostoma.*

Although the present facts do not permit a distinction being made between the two species, there is still insufficient information at hand to prove conclusively that they are synonyms. Studies on the variation of additional specimens from both the type localities are necessary to decide this point. Present evidence however suggests that the name *Cteniosaurus platyceps* Broom is a junior synonym of *Tropidostoma microtrema* (Seeley).

COMPARISON OF THE SKULL WITH *DICYNODON ACUTIROSTRIS* BROOM
(Plate III)

Dicynodon acutirostris Broom (1935, pp. 71–72, Fig. 12)

Dicynodon acutirostris Broom (Haughton and Brink, 1954, p. 72)

Type: Anterior half of skull in the Transvaal Museum, Pretoria. Catalogue No. T.M. 250. (Plate III)

Type Locality: Leeukloof, Beaufort West.

The type is laterally compressed and the flange of the right maxilla is bent over the palatal surface. This was not evident in the unprepared state in which it was described originally. The snout was therefore broader than is shown in Broom's figure (1935, Fig. 12).

There is a striking similarity between the holotype of *Dicynodon acutirostris* and the type series of *Cteniosaurus platyceps*. This similarity is notable in both general shape and in a number of details that are of taxonomic importance and which are rare in other Anomodontia. It is also notable that the type locality of both these species is given as Leeufontein, Beaufort West.

The palatines of *Dicynodon acutirostris* form the anterior margins of the anterior choanal slits. As far as the author could ascertain this feature only occurs in this species, in *Cteniosaurus platyceps* and in *Compsodon helmoedi* van Hoepen.

Another uncommon feature that *Dicynodon acutirostris* has in common with the type series of *Cteniosaurus platyceps* is the long interpterygoid vacuity with raised margins.

Other unusual characters shared by the two species are the great posterior extent of the premaxilla on the dorsal surface of the skull, the presence of small nasal bosses situated behind the level of the middle of the nares externi, the presence of raised orbital margins, the presence of tubercles on the alveolar margins behind the caniniform processes, the fusion of the septomaxilla with the maxilla, the wide contact between the jugal and the ectopterygoid at the anterior root of the zygomatic arch, the dorsal position of the nares externi in the snout and the presence of tubercles on the medial surface of the palatine at the posterior extremity of the anterior choanal slits.

The characters enumerated above are of rare occurrence in other Anomodontia and indicate affinity between the two species. This view is strengthened by the fact that the type locality of both species is the same.

Broom (1935, p. 72) compared the type with various species of *Dicynodon* but not with *Cteniosaurus* described in the same paper. The reason for this is that the type of *Dicynodon acutirostris* is laterally crushed and therefore appears to have a much higher snout than any specimen in the type series. The resemblance between the types could only be noted after preparation. There is no sign of teeth in either the holotype of *Cteniosaurus platyceps* or that of *Dicynodon acutirostris*. As specimens of *Tropidostoma* tend to lose all post-canine teeth and are often tuskless (Broom, 1915, p. 358 and 1932 p. 211), the absence of teeth in a larger specimen is of no value as a distinguishing feature.

The present evidence indicates that the name *Dicynodon acutirostris* should become a junior synonym of *Tropidostoma microtrema* (Seeley) when further material from the type locality is studied.

COMPARISON OF THE SKULL WITH *DICYNODON VALIDUS* BROOM
(Plate IV)

Dicynodon validus Broom 1935 (pp. 70–71, Fig. 11)

Dicynodon validus Broom (Haughton and Brink, 1954, p. 85)

Type: Anterior third of skull and lower jaw in the Transvaal Museum, Pretoria. Catalogue No. 252. (Plate IV)

Type Locality: Leeukloof, Beaufort West.

The holotype of this species is badly crushed and distorted. The enormous tusks are broken off, but a cast of the left tusk is preserved in the matrix. The skull is greatly deformed and a line drawn through the anterior margins of the orbits makes an angle of 30 degrees with the long axis of the skull. The intertemporal region is turned upwards. This was certainly not the case in the living animal as is evinced by a fracture at the point where the intertemporal bar turns dorsally. This fracture occurred prior to the lithification of the mudstone in which the specimen is preserved and was not visible when the specimen was originally described as it was covered by matrix. This upturning of the intertemporal bar was considered to be the main distinguishing feature of the new species by Broom (1935, p. 71).

Because of the deformation the specimen has undergone many of the sutures are obliterated. The palatal region is particularly difficult to interpret.

The specimen has a number of rare features that agree with the type series of *Cteniosaurus*

platyceps. The nares externi are small and placed high up in the snout. There are nasal bosses that are situated posterior to the level of the middle of the nares externi. The septomaxilla is fused to the other surrounding elements in a similar fashion. The dorsal margins of the orbits are slightly raised. The palatines appear to form the anterior margins of the anterior choanal slits, but there is some doubt about this interpretation because of the many cracks in this part of the skull.

The specimen differs from the type series of *Cteniosaurus platyceps* by being much larger than any specimen in the series, by having large tusks and a more robust build. It differs from the type of *Dicynodon acutirostris* by having tusks and being larger.

From the above it appears that the differences between the three species could be due to difference in size and consequently in age. The type of *Dicynodon validus* Broom is, however, such a poor specimen that no definite conclusion can be reached.

CONCLUSIONS

If one assumes that the holotype of *Cteniosaurus platyceps* Broom is a medium sized specimen, it appears that the types of *Dicynodon acutirostris* Broom and *Dicynodon validus* Broom are what one would expect a large individual of *Cteniosaurus platyceps* Broom to look like. When the specimens studied for this paper are arranged according to size the specimens have the appearance of being a growth series. As arranged, the series of skulls display a number of trends associated with an increase in size. Firstly, there is the tendency to a reduction in the number of post-canine teeth. Secondly, there is an increase in the size of the nasal bosses. Thirdly, the orbital margins tend to become more raised in the larger specimens and fourthly, there is a tendency for the bones in the snout to become more massive. By speculative extrapolation of the series of skulls to find a theoretical young specimen, one could arrive at a small skull with a wide intertemporal region, an oudenodont type of palate and a fair number of post-canine teeth. Such a specimen would conform to Toerien's (1953, p. 110) definition of the genus *Emydops*. It is, therefore, likely that a young specimen of *Tropidostoma microtrema* (Seeley), would be referred to some species of *Emydops*. A species of the latter genus, *Emydops microdon* (Broom) (1935, p. 382), has been described from Leeufontein. There are however no intermediate specimens between this species and the type series of *Tropidostoma platyceps* (Broom) and present evidence indicates that they are separate species.

The great similarity that exists between the species *Cteniosaurus platyceps* Broom, *Dicynodon acutirostris* Broom, *Dicynodon validus* Broom and *Tropidostoma microtrema* (Seeley) could mean that the resemblance between them is more then superficial and that they are synonyms.

The genus *Tropidostoma* can be derived from an *Emydops*-like form by an increase in size and in the extent of the palatine in the secondary palate and a decrease in the width of the intertemporal region. The skull of *Tripidostoma* shows some very advanced features such as a more extensive secondary palate than found in any other anomodont and the development of nasal bosses while retaining a primitive endothiodont dentition. The genus *Tropidostoma* cannot be regarded as a transition between the families Endothiodontidae and Cryptodontidae because of the secondary palate in this genus is even further developed than in the most advanced Cryptodontidae like *Oudenodon* and *Rhachiocephalus*. The genus *Tropidostoma* therefore appears to be a specialized side branch of a line of *Emydops*-like endothiodonts leading towards the Cryptodontidae.

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Plate I
Dorsal view of the type of *Tropidostoma microtrema* (Seeley).

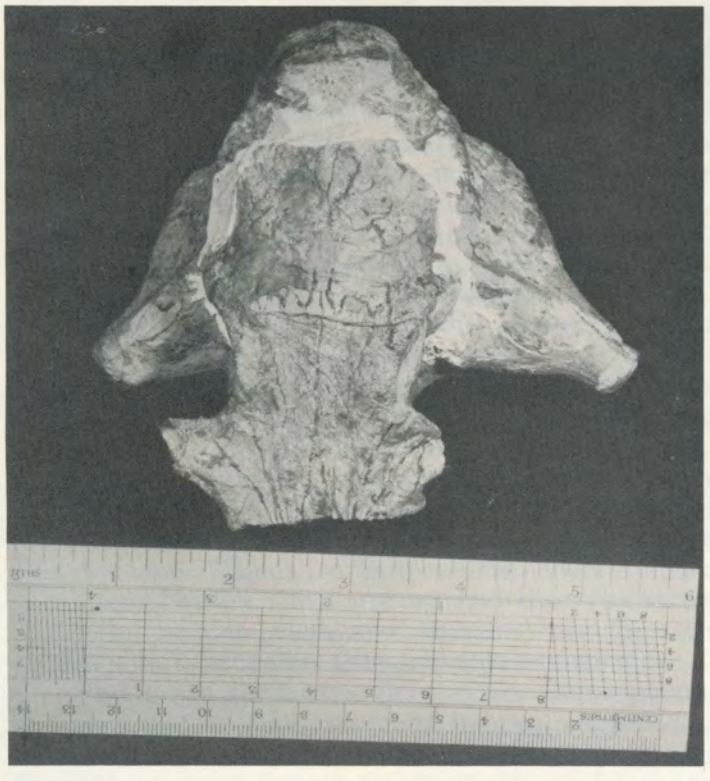


Plate II
Dorsal view of the snout of *Tropidostoma microtrema* B.M.N.H. 860.



Plate III
Dorsal view of the type of *Dicynodon acutirostris* Broom.

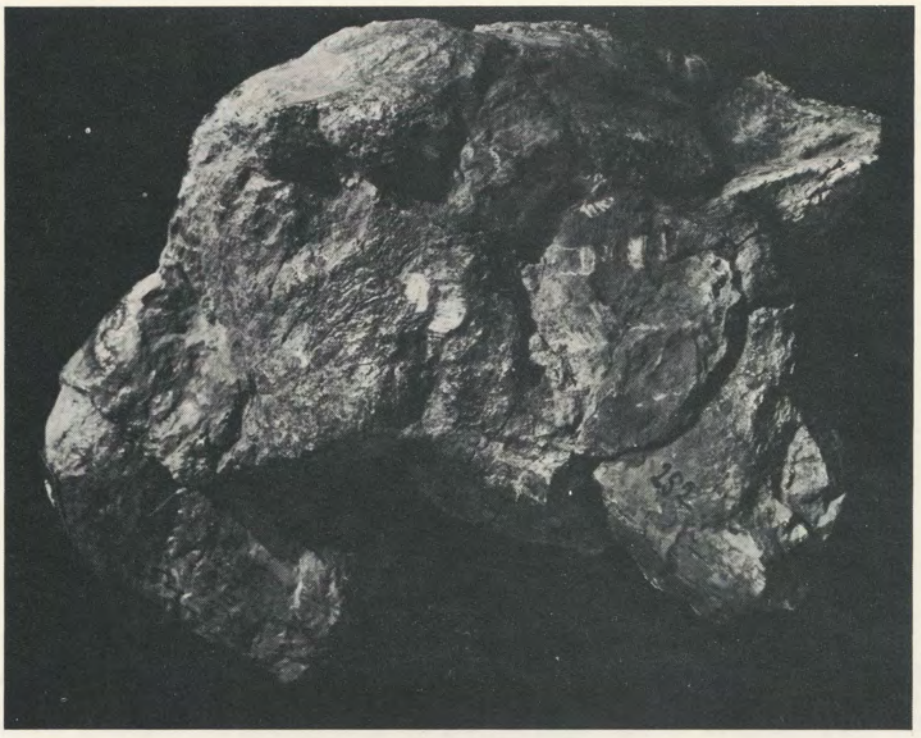


Plate IV
Lateral view of the type of *Dicynodon validus* Broom max. length of skull 172 mm.

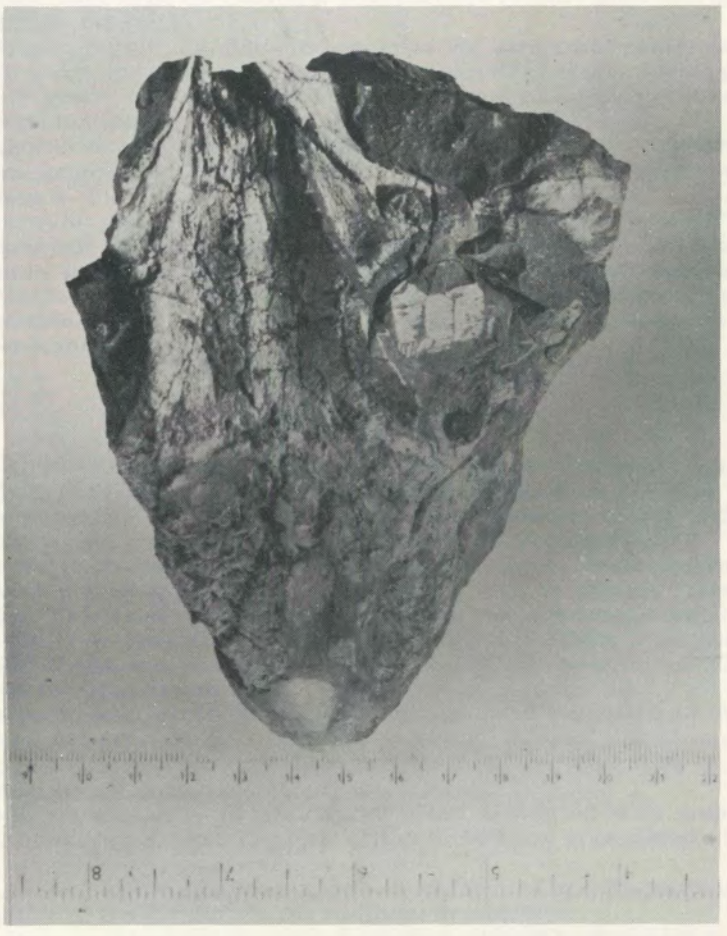


Plate V
Dorsal view of the type of *Cteniosaurus platyceps* Broom max. length of skull 190 mm.

Palaeont. afr., **16.** 37–58. 1973

PALEOXYLOLOGIE DU GONDWANA AFRICAIN: ETUDE ET AFFINITES DU GENRE *AUSTRALOXYLON*

par

Janine Marguerier

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RÉSUMÉ

Les bois fossiles étudiés ont été collectés dans les formations du Gondwana africain et plus particulièrement dans les séries du Karroo du Mozambique et de l'Ecca au Natal.

L'auteur considère les problèmes posés par ces plans ligneux et leurs espèces affines désignés improprement sous le nom de genre *Dadoxylon*.

Une étude comparative montre que ce type de structure de la flore gondwanienne présente une association de caractères anatomiques bien précis: caractères primitifs évoquant les plans ligneux des Cordaïtes de la province euraméricaine (ponctuations radiales araucariennes plurisériées, oculipores araucarioides); caractères particuliers s'éloignant de la disposition araucarienne classique (ponctuations radiales abiétinéennes accompagnées éventuellement de crassules, ponctuations radiales disposées en groupes ou suivant 2 files radiales espacées).

Aussi, l'auteur propose de désigner ce type de structure limitée au seul bois secondaire par le genre de forme *Australoxylon*. Au sein de cet ensemble de plans ligneux se rapportant à ce genre, on peut distinguer deux groupes suivant le pourcentage plus ou moins élevé de ponctuations radiales abiétinéennes.

Les plans ligneux de ce type souvent associés à des formations médullaires sont alors désignés par des genres de forme définis en fonction de la structure de la région médullaire (tableau n° 2).

Le genre *Australoxylon* regroupe un certain nombre d'espèces formant un ensemble cohérent qui s'épanouit au Permien dans l'hémisphère austral (tableaux n° 1 et 2).

Ces structures se rencontrent généralement dans des formations ayant livré des empreintes de Cordaïtophytes se rapportant au genre *Noeggerathiopsis*. Aussi, le genre *Australoxylon* semblerait donc correspondre à la structure de certaines Cordaïtophytes de la Flore Gondwanienne.

ABSTRACT

The fossil woods studied were collected in the African Gondwana formations and more particularly in the Karroo series of Mozambique and the Ecca of Natal.

The author considers the problems set by these ligneous plants and their allied species, previously wrongly ascribed to the generic name of *Dadoxylon*.

A comparative study shows that this type of Gondwana floral structure shows an association of very precise anatomical characteristics, such as primary features recalling the woods of the Cordaïtales of the Euramerican province (araucarian radial multiseriate pits, araucarian field pits), peculiar characteristics which differ from the classic araucarian disposition (radial abietinean pits occasionally provided with rims of Sahnio, radial pits set in groups or in two spaced radial files).

The author proposes to refer to this type of structure, restricted to the secondary wood, under the form-type of *Australoxylon* gen. nov. Among this group of ligneous plants referring to that genus we may distinguish two groups, according to the more or less high percentage of the radial abietinean punctuations.

The ligneous arrangements of this type, often associated with some medullary formations, are therefore indicated by types of a definite form in relation to the structure of the pith.

The genus *Australoxylon* comprises a certain number of species forming a coherent whole representative of the Permian in the southern hemisphere.

These structures are generally found in formations which have yielded impressions of Cordaïtophytes connected with the genus *Noeggerathiopsis*. The genus *Australoxylon* would thus seem to correspond in structure to some Cordaïtales from the Gondwanian flora.

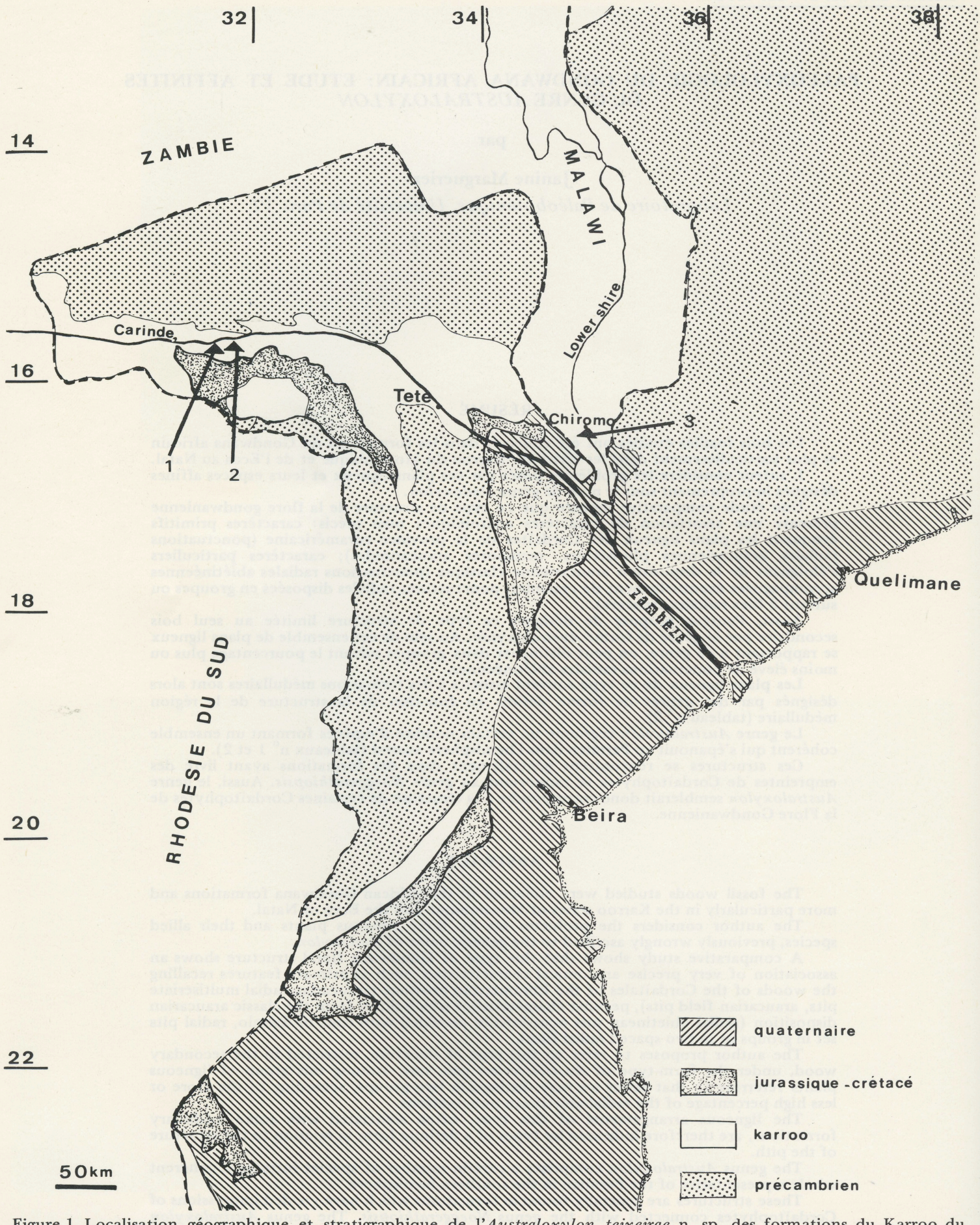


Figure 1. Localisation géographique et stratigraphique de l'*Australoxylon teixeirae* n. sp. des formations du Karroo du Mozambique (gisement des bois fossiles numéros 4 875 et 4 876 indiqué par le triangle n° 1). Gisement d'une espèce affine des formations du Karroo du Mozambique: *Dadoxylon nicoli* da Silva, Baretto et de Carvalho (triangle n° 2). Gisement d'une autre espèce affine des formations du Karroo du Malawi: *Dadoxylon nicoli* (Seward, 1919) Walton, 1956 échantillons A et B (triangle n° 3).

INTRODUCTION

L'étude de ces structures a été effectuée suivant la technique habituelle. De plus, certaines lames minces ont été observées après coloration à la safranine chrysoïdine ou au bleu de toluïdine.

Une partie des échantillons qui font l'objet de ce travail nous a été communiquée par Monsieur le Professeur Teixeira. Ils proviennent des couches de charbon du Bassin de Tete dans le Mozambique et ont été récoltés à une vingtaine de kilomètres de Carinde. Ces formations correspondent du point de vue stratigraphique à celles de l'Ecca de l'Afrique du Sud. La seule étude paléoxylologique dans cette région est de Henriques da Silva, Barreto et Brito de Carvalho en 1967. Elle concerne la structure de *Dadoxylon nicoli* Seward (pp. 37–59).

GYMNOSPERMEAE

Australoxylon teixeirae nov. gen. n. sp.

Holotype: Collection Boureau n° 4875.
Syntype: Collection Boureau n° 4876.
Bassin de Tete. Route de Carinde–Màgòe (21 km. à l'est de Carinde).
Laboratoire de Paléobotanique, Université de Paris VI.

Etude Anatomique

Nos bois fossiles se présentent sous la forme de secteurs ligneux de couleur beige mesurant 5 cm de hauteur et 10 x 10 cm de section. Il s'agit de bois homoxylés pycnoxyliques dépourvus de canaux sécréteurs verticaux et de parenchyme ligneux vertical.

Lame Mince Transversale. (Pl. 1, fig. 2–3; Pl. II, fig. 1).

Fibres-trachéides

Les zones annuelles sont bien marquées et d'épaisseur relativement constante (8 mm à 9 mm en moyenne). Le passage du bois initial au bois final est progressif.

Le bois final est peu développé, constitué de 3 à 6 assises de fibres-trachéides dont la section transversale est rectangulaire à quadrangulaire. Les fibres-trachéides au nombre de 400–450 par mm^2 sont disposées en files radiales opposées et parfois alternes.

Le diamètre radial des fibres-trachéides du bois initial est compris entre 25 et 60 μ (diamètre radial moyen: 40–50 μ), le diamètre tangentiel varie de 25 à 60 μ (diamètre tangentiel moyen: 45–50 μ). Dans le bois final, le diamètre radial se situe entre 9 et 25 μ (diamètre radial moyen: 16–20 μ), le diamètre tangentiel est compris entre 18 et 46 μ (diamètre tangentiel moyen: 40 μ). L'épaisseur des parois est d'environ 4 μ. Les méats sont absents.

Rayons ligneux

Les rayons ligneux de 18–25 μ de largeur moyenne sont généralement unisériés et séparés par 1 à 10 fibres-trachéides (le plus souvent 1 à 5).

Lame Mince Tangentielle. (Pl. I, fig. 1–5 et fig. 2 et 3 du texte).

Rayons ligneux

Ils sont en général unisériés (52%), assez souvent bisériés (48%) sur 2 à 9 cellules. Une étude statistique portant sur le nombre des cellules couchées des rayons a montré que celui-ci varie de 1 à 36 cellules et peut atteindre exceptionnellement 60 cellules (Figure 2).

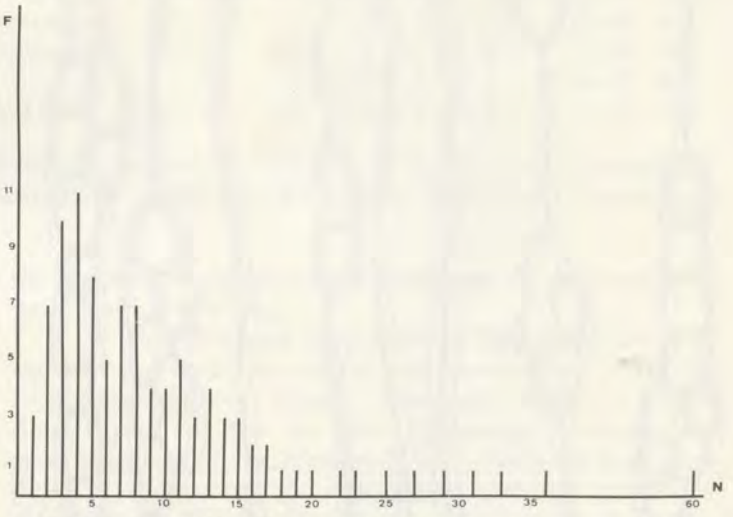


Figure 2. *Australoxylon teixeirae* nov. gen. n. sp., Histogramme montrant la variation du nombre des cellules couchées formant la hauteur des rayons. (F): fréquence. (N): hauteur des cellules.

Nombre de cellules:	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 60.
Fréquence:	3, 7, 10, 11, 8, 5, 7, 7, 4, 4, 5, 3, 4, 3, 3, 2, 2, 1, 1, 1, 0, 1, 1, 0, 1, 0, 1, 0, 1, 0, 1, 0, 1, 0, 1, 0, 0, 1, 1.

Les rayons ligneux sont peu nombreux; la densité est de 8 au mm horizontal tangentiel; elle est comprise entre 18 et 20 au mm^2. La section tangentielle des cellules couchées est nettement rectangulaire (Pl. I, fig. 1 et 5). La hauteur moyenne varie de 16 à 50 μ (hauteur moyenne: 25–35 μ), la largeur se situe entre 12 et 40 μ (12 μ au niveau des rayons bisériés) et la largeur moyenne est voisine de 18–25 μ. Le rapport hauteur/largeur des cellules est compris entre 100/40 et 100/90. Le rapport moyen est de 100/65.

Fibres-trachéides

Elles présentent occasionnellement des petites ponctuations contiguës, circulaires (11 μ de diamètre), à lumen circulaire (3 μ).

Lame Mince Radiale. (Pl. II, fig. 4; Pl. III, fig. 1, 2, 4; Pl. IV, fig. 3, 4, 5; Pl. V, fig. 1, 2, 3 et fig. 4 du texte.)

Fibres-trachéides

Les sections radiales nous permettent

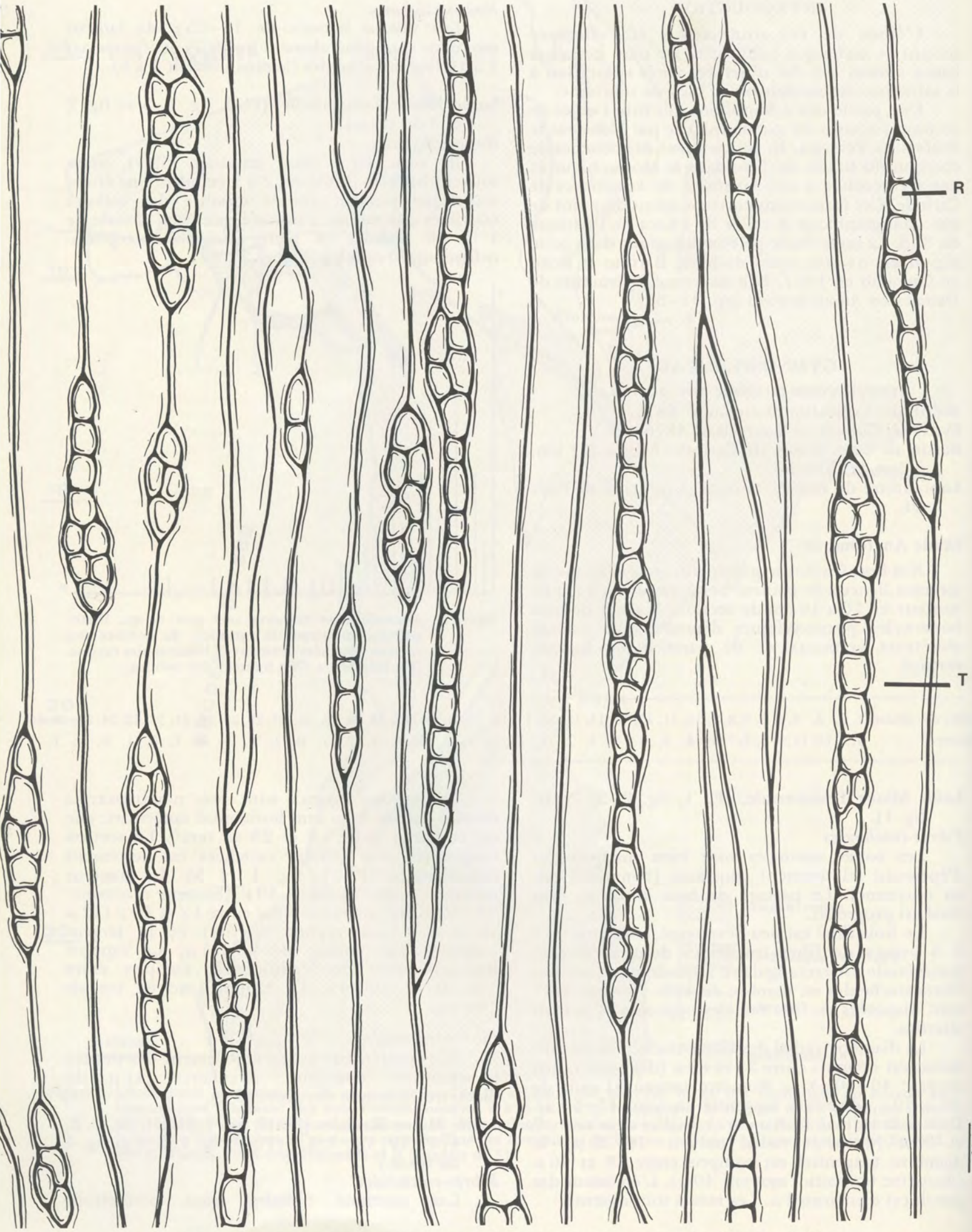


Figure 3. *Australoxylon teixeirae* nov. gen. n. sp., Section tangentielle: fibres-trachéides (T), rayons ligneux (R) et nombreuses terminaisons des fibres-trachéides.

d'observer les différentes formes et dispositions des ponctuations suivantes:

Ponctuations unisériées, circulaires, espacées. 19% (fig. 3).
Ponctuations unisériées, contiguës, légèrement écrasées: 1%.
Ponctuations bisériées, alternes, hexagonales: 9%.
Ponctuations trisériées, alternes, hexagonales: 9% (Pl. III, fig. 4).
Ponctuations localement trisériées, opposées: 2%.
Ponctuations disposées suivant 2 files radiales indépendantes et espacées les unes des autres dans le sens horizontal: 17% (Pl. III, fig. 2).
Groupes de 2 ponctuations opposées, circulaires, distants les uns des autres: 27% (Pl. III, fig. 1 et 4 et fig. 4 du texte).
Groupes de 3, 4, 5 ponctuations opposées, circulaires, distants les uns des autres: 16% (Pl. III, fig. 1 et 4 et fig. 4 du texte).

Données numériques concernant les ponctuations radiales (mesures effectuées en μ).

Nombre de séries, forme et disposition des ponctuations	Ep	L	h	l	h^1	l^1	m	Σ
I sériées, circulaires espacées, lumen elliptique oblique	5	43	15	13	6	3	10–10	0,86
I sériées, circulaires, contiguës, lumen circulaire	5	40	12	12	6	6	9–9	0
2 sériées alternes, lumen elliptique, horizontal	6	54	11	13	6	4	8–8	0,84
3 sériées alternes, lumen circulaire	6	60	11	12	4	4	6–6	0,91
2 sériées en 2 files indépendantes, lumen elliptique, horizontal	5	50	10	10	7	4	8–8	0
Groupe de 2 ponctuations opposées, lumen elliptique oblique	4	44	14	13	7	3	5–5	0
Groupe de 4 ponctuations opposées, lumen circulaire . . .	5	44	12	12	6	6	4–6	0
I sériées, circulaires, espacées, lumen circulaire (bois final) .	6	28	12	12	3	3	2–2	0

Ep: épaisseur de la paroi des fibres. L: Largeur des fibres-trachéides. h: hauteur de la ponctuation radiale. l: largeur de la ponctuation radiale. h^1 : grand axe du lumen. l^1 : petit axe du lumen. m: largeur des marges latérales. Σ : coefficient d'écrasement.

Ces différents types de ponctuations radiales ne sont pas distribués de manière quelconque; leur répartition semble en relation avec le calibre des éléments vasculaires: prédominance de ponctuations unisériées, circulaires, espacées, et de groupes de ponctuations en paires opposées au voisinage du bois final (Pl. V, fig. 1).

De nombreuses dispositions de ponctuations radiales peuvent coexister sur une même paroi de fibres-trachéides. Nous pouvons citer à titre d'exemple le cas le plus fréquent: passage de ponctuations disposées en 2 files radiales indépendantes, espacées, à des ponctuations trisériées alternes (Pl. III, fig. 2).

Signalons que les ponctuations radiales sont généralement de faibles dimensions (12 et 13 μ de diamètre) et présentent toujours un grand lumen plus ou moins circulaire (6 μ). Ces caractères anatomiques ainsi que la présence de groupes de ponctuations distants les uns des autres (5 et 20 μ) et de files radiales indépendantes semblent constants et spécifiques de ce plan ligneux.

On aperçoit très souvent les terminaisons tronquées et arrondies des fibres-trachéides (Pl. V, fig. 2).

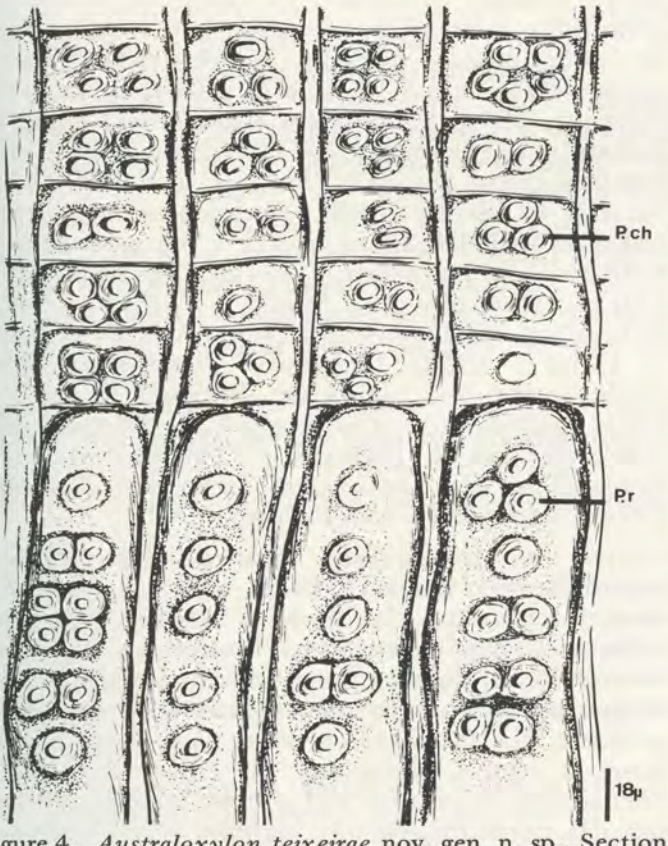


Figure 4. *Australoxylon teixeirae* nov. gen. n. sp., Section radiale: ponctuations radiales (P.r) et ponctuations de champs (P. ch) caractéristiques.

Rayons ligneux

Les parois horizontales et verticales des cellules couchées sont lisses, minces et rectilignes (Pl. V, fig. 3). Les sections des cellules sont généralement rectangulaires. Leur hauteur est assez élevée (50–18 μ), elle est en général de 25–35 μ. La longueur est comprise entre 110 et 240 μ, la valeur la plus fréquente étant de 180 μ.

Ponctuations de champs

Les champs de croisement sont garnis de ponctuations au nombre de 1 à 10, semi-aréolées, disposées généralement en rangées horizontales. Celles-ci s'apparentent au type araucarioïde. Elles sont rondes ou ovales lorsqu'elles sont peu nom-

breuses et présentent des contours hexagonaux dans le cas où le nombre est plus élevé. Leurs dimension est voisine de celle des ponctuations radiales (11 μ). Leur lumen est toujours large, circulaire ou elliptique, allongé soit horizontalement, soit obliquement à 45° (8 x 6 μ) (Pl. IV, fig. 3, 4, 5).

Données numériques concernant les champs de croisement et les ponctuations de champs (mesures effectuées en μ).

Nombre, type, disposition des ponctuations de champs	H	L	h	l	h^1	l^1
1 ponctuation au centre du champ, lumen elliptique oblique	32	34	13	11	10	6
2 ponctuations araucarioïdes, les unes au dessus des autres, lumen elliptique oblique	28	40	14	11	10	4
3 ponctuations araucarioïdes disposées en quinconce, lumen elliptique horizontal	30	41	13	10	8	6
4 ponctuations araucarioïdes suivant 2 rangées horizontales, lumen elliptique, oblique	32	42	11	10	10	6
7 ponctuations araucarioïdes, disposées en groupe, lumen elliptique horizontal	36	64	11	11	8	4
7 ponctuations araucarioïdes disposées en 2 rangées verticales, lumen elliptique oblique	42	40	10	10	5	3
3 ponctuations araucarioïdes suivant I rangée verticale, lumen elliptique oblique, (bois final)	36	26	10	8	9	6

H: hauteur des champs de croisement. L: largeur des champs de croisement. h: hauteur de la ponctuation de champs. l: largeur de la ponctuation de champs. h^1 : grand axe du lumen. 1^1 : petit axe du lumen.

AFFINITES

Le bois fossile que nous venons de décrire est caractérisé par la présence:

de zones annuelles distinctes. (Passage progressif bois initial–final)
d'oculipores araucarioïdes.
de ponctuations radiales araucariennes, abiétinéennes et d'un type assez particulier (groupes de ponctuations distants les uns des autres).

Une comparaison avec les formes affines de l'hémisphère austral nous montre que les structures voisines ont été réunies jusqu'à présent dans le genre de forme *Dadoxylon*. Nous ne pouvons maintenir cette nomenclature pour de telles structures qui ne correspondent pas à la définition du genre (Endlicher, 1847, p. 298).

L'ensemble de ces caractères anatomiques si particuliers nous paraissent suffisants pour justifier la création d'un nouveau nom de genre *Australoxylon* qui regroupe ces structures de bois secondaire des territoires à flore de Gondwana.

Il convient, maintenant de préciser les affinités que présentent notre échantillon avec les espèces relativement bien décrites et figurées de l'hémisphère sud.

La présence de ponctuations radiales essentiellement araucariennes nous permet d'éloigner un grand nombre d'espèces.

Dadoxylon lukugense Grambast, 1960 du Permien du Congo Belge; *Dadoxylon rangei* Kräusel, 1928; *Dadoxylon porosum* Kräusel, 1928; *Dadoxylon sclerosum* Walton, 1925; *Solenoxylon wissi* Kräusel, 1956; *Solenoxylon kursi* Kräusel, 1956; *Solenoxylon oberholzeri* Kräusel, 1956; *Lobatoxylon kaokense* Kräusel, 1956 du sud-ouest africain; *Dadoxylon nummularium* White, 1908; *Dadoxylon meridionale* White, 1908; *Dadoxylon butiense* Rau, 1933; *Dadoxylon derbyi* Oliveira, 1936; *Trigonomyelon pedroi* (Zeiller, 1896) Walton, 1925 du Brésil et *Dadoxylon indicum* Holden, 1917; *Dadoxylon parenchymosum* Maithy, 1963; *Dadoxylon gondwanense* Maithy, 1964; *Dadoxylon jamudhiense* Maheshwari, 1964; *Dadoxylon jamuriense* Maheshwari, 1965.

Nous ne retenons pas les espèces présentant un certain nombre de caractères communs avec notre échantillon mais un pourcentage encore trop élevé de ponctuations radiales araucariennes: *Polysolenoxylon withei* (Maniero, 1944) Kräusel & Dolianiti, 1958; *Solenopitys paulistana* Kräusel & Dolianiti, *1958*; Dadoxylon lafoniense *Halle, 1912*; *Barakaroxylon jhariense* (Surange & Sahni, 1956) Surange & Maithy, 1962; *Dadoxylon nighanense* Maheswari, 1964; *Barakaroxylon monocanalosum* Kulkarni, 1969; *Damudoxylon waltoni* Maheswari, 1967; *Kaokoxylon zalesky* (Sahni, 1933) Maheswari, 1961, *Barakaroxylon kraeuseli* Surange & Maithy, 1962; *Dadoxylon parbeliense* Rao, 1935; *Indoxylon canalosum* Surange & Maithy, 1963; *Trigonomyelon raniganje* Maheshwari, 1966; *Dadoxylon nicoli* (Seward, *1919*) Walton, *1956* (échantillon D); *Dadoxylon farleyense* Walkom, 1928; *Dadoxylon allanii* Kräusel, 1962.

Notre échantillon montre des affinités certaines avec les différentes espèces regroupées dans les tableaux. Le premier tableau réunit les caractères des échantillons limités au seul bois secondaire et le deuxième tableau les différentes diagnoses des bois fossiles dont le bois secondaire présente des analogies certaines avec notre bois et dont la région médullaire est conservée et bien décrite; ces structures ont été en général définies par des noms de genre en rapport avec l'anatomie de la moelle (*Barakaroxylon, Kaokoxylon, Trigonomyelon*).

Un rapprochement étroit doit être signalé avec *Dadoxylon* sp. Warren, 1912 du Permien inférieur du Natal (échantillon n° 11), *Dadoxylon arberi* (Seward, 1917) Walton 1925 du Beaufort inférieur de la province du Cap et plus particulièrement avec *Dadoxylon duartei* Japiassu 1970 du Permien Permien des Iles Falklands (oopores douteux), *Dadoxylon duartei* Japiassu, 1970 du Permien supérieur du Brésil (Pl. I, II, présence douteuse du parenchyme ligneux vertical), *Dadoxylon bengalense* Holden 1917, *Dadoxylon kharkhariense Maithy* 1964 (p. 91, fig. 3) du Permien inférieur des Indes, *Dadoxylon nicoli* (Seward, 1919) G. H. da Silva, L. S. Barreto & L. H. B. de Carbalho, 1967 du Permien inférieur du Mozambique (Pl. II, III, IV). Toutefois une assimilation complète ne peut être faite avec ces espèces car les descriptions sont en général trop sommaires. Il convient de donner une appellation spécifique nouvelle à ce bois fossile; nous le dédions à Mr. le Professeur Teixeira qui nous l'a transmis.

DIAGNOSE

Australoxylon nov. gen.

Zones d' accroissements distinctes.

Section transversale quadrangulaire des fibres-trachéides.

Fibres-trachéides à terminaisons arrondies et plus ou moins tronquées.

Ponctuations radiales de 3 types:

araucariennes: unisériées, contiguës, plus ou moins écrasées et plurisériées alternes.

abiétinéennes: unisériées circulaires espacées, bisériées opposées et trisériées localement opposées.

dispositions particulières: files radiales indépendantes, espacées de ponctuations circulaires. Groupes de 2–3–4–5 de ponctuations distants les uns des autres.

Ponctuations de petite taille ($< 15\ \mu$) à lumen large plus ou moins circulaire.

Ponctuations radiales et groupes de ponctuations limités dans certains cas par des crassules.

Ponctuations de champs en général en assez grand nombre: oculipores araucarioïdes à large lumen et dont le diamètre est légèrement inférieur à celui des ponctuations radiales.

Rayons ligneux homogènes de hauteur moyenne (1–20 cellules), généralement unisériés ou localement bisériés, relativement peu nombreux. Cellules couchées des rayons ligneux à parois horizontales ou verticales minces et lisses, assez hautes.

Australoxylon teixeirae nov. gen. n. sp.

Bois secondaire homoxylé, pycnoxylique.

Parenchyme ligneux vertical et canaux sécréteurs absents.

Zones d'accroissement distinctes: 8–9 mm d'épaisseur.

Fibres-trachéides à section transversale nettement quadrangulaire.

Bois initial: diamètre radial moyen (40–50 μ), diamètre tangentiel moyen (45–50 μ). Bois final: diamètre radial moyen (16–20 μ) diamètre tangentiel moyen (40 μ).

Densité des fibres-trachéides: 450–500 par mm^2.

Ponctuations radiales: unisériées, circulaires, espacées: 19%; unisériées, contiguës, légèrement écrasées: 1%; bisériées, alternes, hexagonales; 9%; trisériées, alternes, hexagonales: 9%; localement trisériées, opposées: 2%; disposées suivant 2 files radiales indépendantes et espacées: 17%. Groupes de 2 ponctuations opposées, circulaires: 27%, Groupes de 3, 4, 5 ponctuations circulaires: 16%.

Ponctuations radiales de petite taille, circulaires, (12–13 μ) à grand lumen circulaire (6 μ).

Rayons ligneux homogènes, généralement unisériés (52%), localement bisériés (48%) sur 1 à 2 cellules en moyenne. Hauteur de 1 à 36 cellules (valeur moyenne: 2 à 16).

Hauteur moyenne des cellules (25–35 μ). Rapport hauteur/largeur: 100/65. Densité des rayons ligneux: 18–20 par mm^2.

Parois-des cellules couchées des rayons ligneux horizontales, rectilignes, lisses et minces et terminales lisses et verticales. Longueur moyenne des cellules: 180 μ.

Ponctuations de champs: 1–10 le plus souvent 4–6. Oculipores araucarioïdes (11 μ) à lumen large, elliptique oblique, (8 x 6 μ).

Ponctuations tangentielles occasionnelles (11 μ).

Localité: District de Tete. Route de Carinde-Màgoè (21 km à l'Est de Carinde).

Etage: Ecca (Permien inférieur).

Notre travail concerne maintenant des échantillons transmis par le Professeur Fabre et provenant des formations de l'Ecca au Natal. Celles-ci ont livré une flore typiquement gondwanienne à *Glossopteris* et des structures conservées dont certaines ont fait l'objet d'études (Warren, 1912; p. 345–380).

Australoxylon natalense nov. gen. n. sp.

Holotype: Collection Boureau n° 4105.

Syntype: Collection Boureau n° 4106.

Laboratoire de Paléobotanique, Université de Paris VI.

(The localities given for these specimens are La Mercy and Dogs Back respectively. No further information available–Ed.)

Etude Anatomique

Notre échantillon correspond à un secteur ligneux de couleur brune mesurant 5 cm de haut et 10 x 8 cm de section. Il s'agit d'un bois homoxylé pycnoxylique dépourvu de canaux sécréteurs verticaux et de parenchyme ligneux vertical.

Lame Mince Transversale (P. II, fig. 3).

Fibres-trachéides

On note la présence de zones d'accroissement d'épaisseur variable (5 mm, 7 mm, 8 mm, 1 cm) accompagnées quelquefois de faux cernes peu marqués. Le passage du bois initial au bois final est très progressif. Le bois final est plus ou moins développé, constitué de 4 à 12 assises de fibres-trachéides disposées en files radiales alternes et très souvent opposées. La section transversale des fibres-trachéides est quadrangulaire à rectangulaire. Les méats sont absents. On distingue très souvent des zones de compression au niveau des éléments vasculaires du bois initial situées au voisinage de la ligne limitante. Celles-ci se renouvellent périodiquement au sein de chaque zone d'accroissement. De telles structures semblent fréquentes dans les plans ligneux caractéristiques de la flore du Gondwana et ont été signalées et figurées par de nombreux auteurs (Arber, 1904, p. 193, fig. 41; Warren 1912, p. 361, fig. 3).

Exemples de mesures de quelques fibres-trachéides:

bois initial. Diamètre radial: 40–80 μ (éléments de grand calibre au niveau de la ligne limitante (Pl. II, fig. 3); diamètre radial moyen: 45–50 μ.
Diamètre tangentiel: 30–60 μ, diamètre tangentiel moyen: 45 μ.

bois final. Diamètre radial 10–30 μ, diamètre radial moyen: 16–20 μ; diamètre tangentiel: 16–45 μ, diamètre tangentiel moyen: 35 μ.

Epaisseur de la paroi des fibres-trachéides: 4 μ.

Densité des fibres-trachéides: 400–500 par mm^2.

Rayons ligneux

Les rayons ligneux sont généralement unisériés et séparent des files radiales des fibres-trachéides de 1 à 10, le plus souvent 1 à 7.

Lame Mince Tangentielle (Pl. I, fig. 4; Pl. II, fig. 2 et fig. 5 et 6 du texte).

Rayons ligneux

Les rayons ligneux sont le plus souvent unisériés (56%) et localement bisériés (44%) sur 1 à 6 cellules, (le plus souvent 1 cellule) (Pl. I, fig. 4; Pl. II, fig. 2).

La hauteur des rayons varie de 1 à 31 cellules (exceptionnellement 40) avec une valeur moyenne de 2 à 15 cellules.

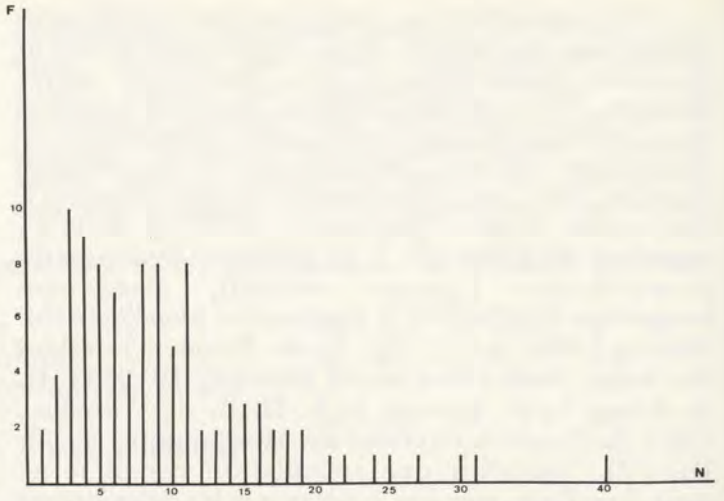


Figure 5. *Australoxylon natalense* nov. gen. n. sp., Histogramme montrant la variation du nombre des cellules couchées formant la hauteur des rayons. (F): fréquence. (N): nombre de cellules.

La structure de ce bois est peu dense, les rayons sont en effet peu nombreux: densité moyenne de 6 par mm horizontal tangentiel et de 15 par mm^2. Les cellules couchées présente une section tangentielle nettement rectangulaire. La hauteur est comprise entre 15 et 35 μ (hauteur moyenne: 26 μ). La largeur est faible, elle va de 6 à 25 μ (largeur moyenne: 15–20 μ). Le rapport hauteur/largeur se situe entre 100/35 et 100/90, le rapport le plus fréquent étant de 100/60.

Fibres-trachéides

Elles sont dépourvues de ponctuations tangentielles.

Lame Mince Radiale. (Pl. III, fig. 3; Pl. IV, fig. 1, 2; Pl. V, fig. 4; Pl. VI, fig. 1, 2, 4, 5 et fig. 7 du texte).

Fibres-trachéides

L'examen des sections radiales nous permet de distinguer les différentes dispositions suivantes:

Ponctuations unisériées circulaires espacées: 19% (Pl. VI, fig. 4).

Ponctuations unisériées contiguës plus ou moins écrasées: 2% (Fig. 7 du texte).

Ponctuations bisériées alternes: 5%.

Ponctuations bisériées opposées: 6% (Pl. VI, fig. 5).

Ponctuations localement trisériées alternes: 6%.

Ponctuations localement trisériées opposées: 9% (Pl. VI, fig. 2, 5 et fig. 7 du texte).

Ponctuations localement quadrisériées alternes: 1% (fig. 7 du texte).

Ponctuations disposées en 2 files radiales indépendantes espacées: 16% (Pl. IV, fig. 1; Pl. VI, fig. 5 et fig. 7 du texte).

Nombre de cellules:	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 40.
Fréquence:	2, 4, 10, 9, 8, 7, 4, 8, 8, 5, 8, 2, 2, 3, 3, 3, 2, 2, 2, 0, 1, 1, 0, 1, 1, 0, 1, 0, 0, 1, 1, 0, 1.

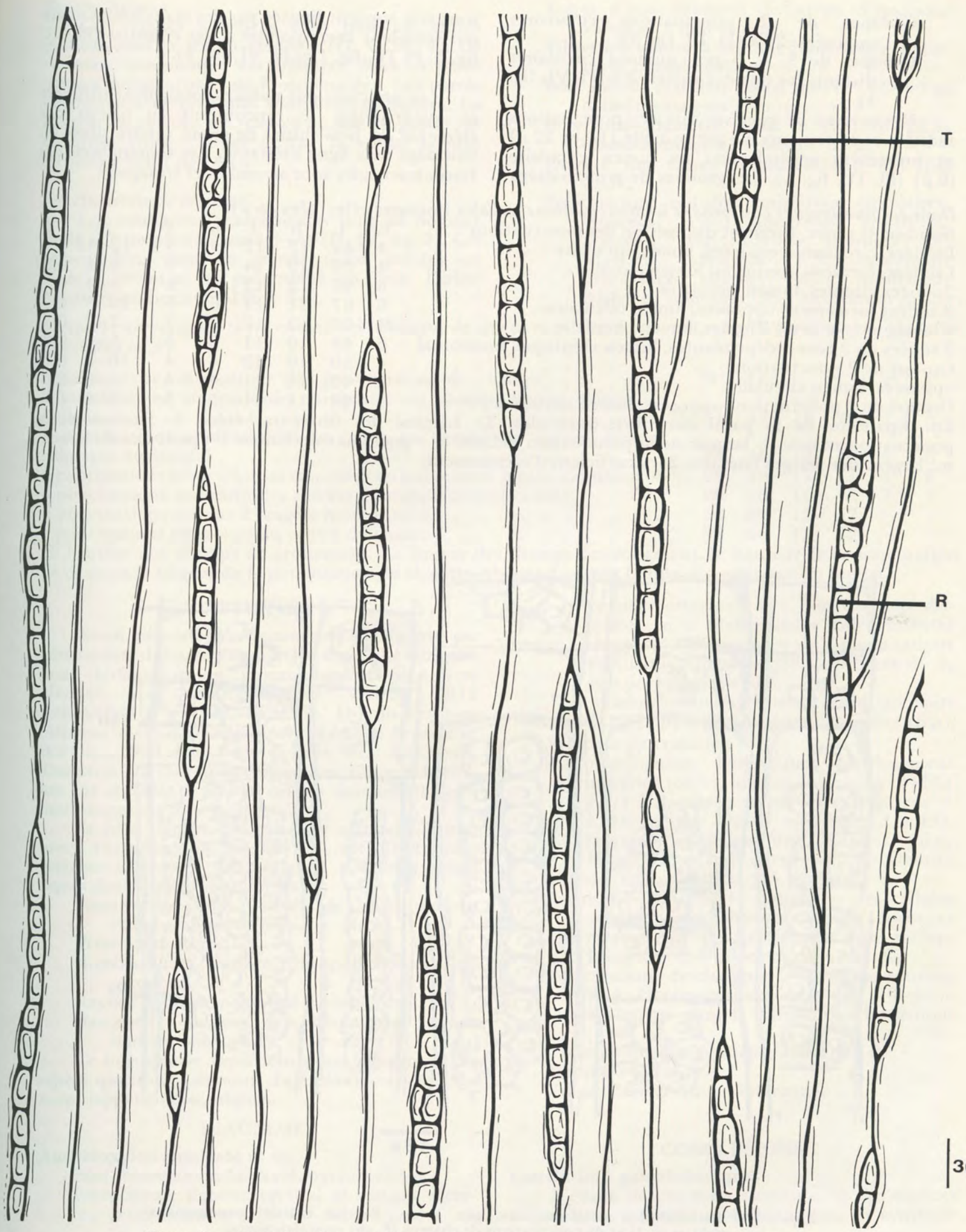


Figure 6. *Australoxylon natalense* nov. gen. n. sp., Section tangentielle: fibres-trachéides (T) et rayons ligneux (R).

Groupes de 2 ponctuations circulaires opposées: 28% (Pl. III, fig. 3).
Groupes de 3, 4, 5 ponctuations circulaires distants les uns des autres: 8% (Pl. VI, fig. 1).

Il convient de préciser que ces ponctuations radiales sont toujours de petite taille (11 et 12 μ) et présentent généralement un lumen circulaire (6 μ) (Pl. IV, fig. 1). Les groupes de ponctuations sont très souvent limités par des traits horizontaux qui semblent correspondre à des crassules (Pl. III, fig. 3; Pl. IV, fig. 1 et Pl. VI, fig. 5).

Les ponctuations radiales localement trisériées et quadrisériées se rencontrent au niveau des éléments du bois initial de grand calibre situés au voisinage dela ligne limitante. Les terminaisons des fibres-trachéides sont arrondies et tronquées.

Données numériques concernant les ponctuations radiales (mesures effectuées en μ).

Nombre de séries, forme et disposition des ponctuations	Ep	L	h	l	h^1	l^1	m	Σ
I sériées, circulaires, espacées, lumen circulaire	4	44	12	12	5	5	12–12	0
I sériées, écrasées, contiguës, lumen circulaire	4	30	12	14	5	5	4–4	0,87
2 sériées alternes, lumen circulaire	6	46	12	12	5	5	5–4	0
3 sériées localement opposées, lumen circulaire	6	67	11	11	6	6	10–8	0
4 localement sériées, alternes, lumen circulaire	4	60	12	12	7	7	2–2	0
2 sériées en 2 files indépendantes, lumen elliptique, horizontal	6	48	10	11	6	5	5–4	0,99
Groupe de 2 ponctuations	4	50	10	12	4	4	10–8	0,75
opposées, lumen circulaire	4	42	11	11	4	4	6–6	0
Groupe de 4 ponctuations opposées, lumen circulaire	5	48	11	11	5	5	7–6	0

Ep: Epaisseur de la paroi des fibres-trachéides. L: Largeur des fibres-trachéides. h: hauteur de la ponctuation radiale. l: largeur de la ponctuation radiale. h^1 : grand axe du lumen. l^1 : petit axe du lumen. m: largeur des marges latérales. Σ : coefficient d'écrasement.

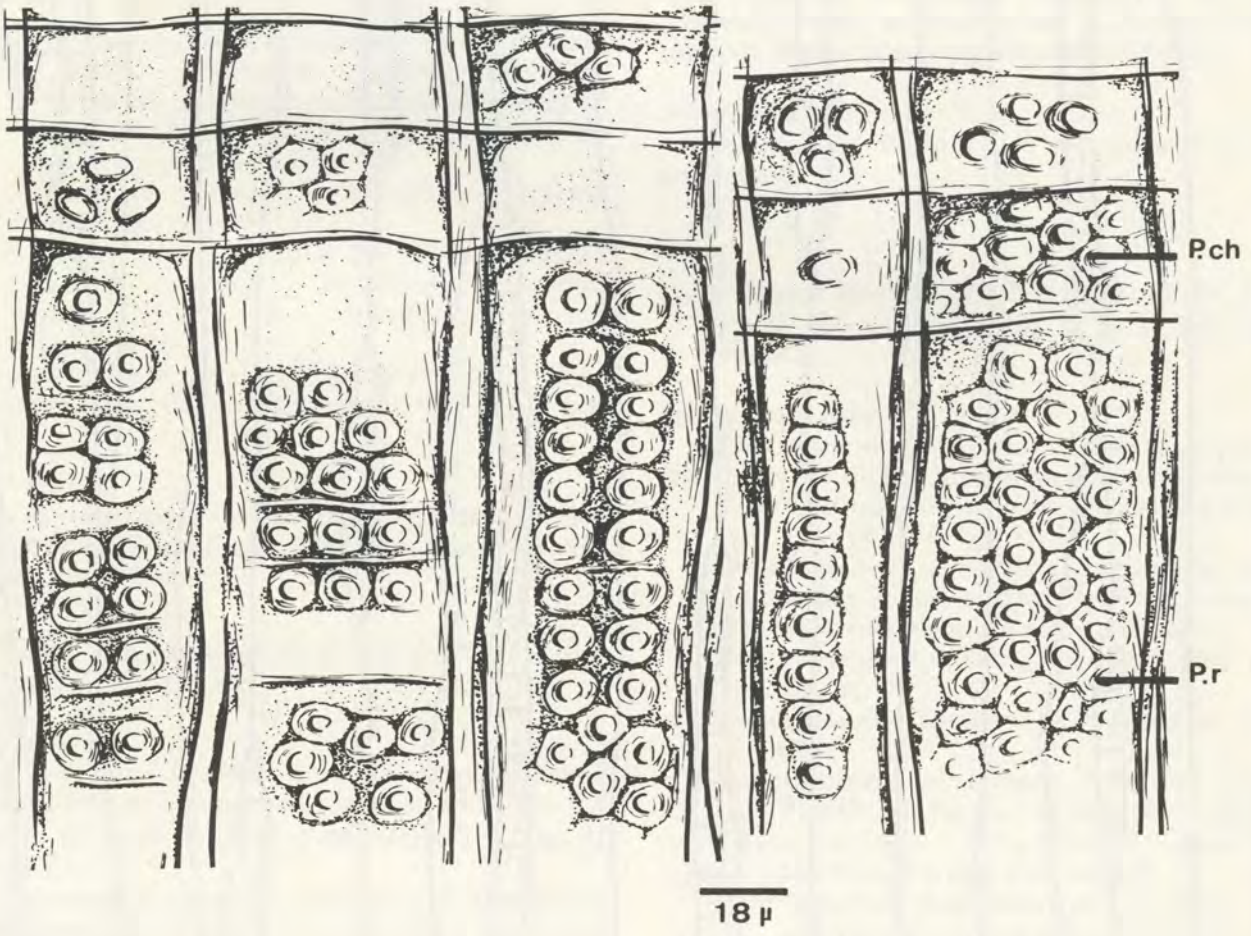


Figure 7. *Australoxylon natalense* nov. gen. n. sp., Section radiale: ponctuations radiales (P. r) et de ponctuations de champs (P. ch) caractéristiques.

Rayons ligneux

Les cellules couchées sont plus ou moins renflées dans la région médiane (Pl. V, fig. 4). Ce caractère anatomique est fréquent dans les plans ligneux mézozoïques de Protopinacées. Les parois horizontales et verticales sont lisses et minces. La hauteur moyenne est de 26 μ. La longueur est comprise entre 150 et 220 μ, la valeur la plus fréquente étant de 180 μ.

Ponctuations de champs

Les oculipores araucarioïdes sont au nombre de la à 7 (le plus souvent 3–4) (Pl. IV, fig. 2). Ces ponctuations sont de grande taille, rondes ou ovales (10–11 μ) et présentent un large lumen circulaire ou horizontal (6 x 7 μ).

Zones d'accroissement distinctes, d'épaisseur variable: 5 mm–1 cm.

Fibres-trachéides à section transversale nettement quadrangulaire.

Bois initial–diamètre radial moyen: 45–50 μ; diamètre tangentiel moyen: 45 μ.

Bois final–diamètre radial moyen: 16–20 μ; diamètre tangentiel moyen: 35 μ.

Densité des fibres-trachéides: 450–600 par mm^2.

Ponctuations radiales: unisériées, circulaires, espacées: 19%; unisériées, contiguës, écrasées: 2%; bisériées alternes: 5%; bisériées opposées: 6%; localement trisériées alternes: 6%; localement trisériées opposées: 9%; localement quadrisériées alternes: 1%; ponctuations disposées en 2 files radiales indépendantes espacées: 16%; groupes de 2 ponctuations circulaires opposées: 28%; groupes de 3, 4, 5 ponctuations: 8%.

Ponctuations radiales de petite taille, circulaire (11–12 μ) à grand lumen circulaire (6 μ).

Présence de crassules.

Rayons ligneux homogènes, généralement unisériés (56%), localement bisériés (44%) sur 1 à 2 cellules en moyenne. Hauteur: 1 à 31 cellules (valeur moyenne: 2 à 15). Hauteur moyenne des cellules: 26 μ. Rapport hauteur/largeur: 100/60. Densité des rayons ligneux: 15 par mm^2.

Parois horizontales et terminales des cellules couchées des rayons ligneux lisses et minces. Cellules renflées en leur milieu. Longueur moyenne des cellules: 18 μ.

Ponctuations de champs: 1–7, le plus souvent 3–4. Oculipores araucarioïdes: 10–11 μ à lumen large, elliptique, horizontal (6 x 7 μ).

Ponctuations tangentielles absentes.

Localité: Natal.

Etage: Ecca (Permien inférieur).

Données numériques concernant les champs de croisement et les ponctuations de champs (mesures effectuées en μ).

Nombre, type, disposition des ponctuations de champs	H	L	h	l	g^1	l^1
2 ponctuations araucarioïdes au centre du champ, lumen elliptique oblique	34	42	10	10	7	5
3 ponctuations araucarioïdes les unes au dessus des autres, lumen elliptique horizontal	26	48	12	10	8	6
4 ponctuations araucarioïdes disposées en quinconce, lumen circulaire	28	40	11	11	8	8
4 ponctuations araucarioïdes suivant 2 rangs, lumen circulaire	28	50	10	10	7	7
6 ponctuations suivant 2 rangées horizontales	30	60	12	12	–	–
7 ponctuations en groupe au centre du champ	32	60	12	12	–	–

H: hauteur des champs de croisement. L: largeur des champs de croisement. h: hauteur de la ponctuation de champs. l: largeur de la ponctuation de champs. h^1 grand axe du lumen. l^1 : petit axe du lumen.

AFFINITES

Nous procédons comme précédemment par élimination. L'étude compartive des deux tableaux nous indique qu'un rapprochement peut être effectué avec *Dadoxylon sp.* Warren, 1912 (échantillon n° 11, p. 353, fig. 1b) du Permien inférieur du Natal et *Dadoxylon bakeri* Seward et Walton, 1923 du Permien des Iles Falklands. Toutefois, la correspondance avec notre échantillon est difficile à établir car les documents dont nous disposons sont trop limités.

Ce plan ligneux présente quelques similitudes avec *Australoxylon teixeira* n. sp. Cependant, certains caractères anatomiques semblent spécifiques dans l'échantillon du Natal:

Pourcentage plus élevé de ponctuations radiales abiétinéennes.

Présence de crassules.

Nombre plus restreint de ponctuations de champs.

Rayons ligneux en général moins hauts.

Hauteur et largeur des cellules des rayons ligneux plus faibles.

Ce bois fossile appartient donc à une nouvelle espèce que nous nommons *Australoxylon natalense* n. sp. rappelant son origine.

DIAGNOSE

Australoxylon natalense n. sp.

Bois secondaire homoxylé, pycnoxylique.

Parenchyme ligneux vertical et canaux sécréteurs absents.

CONCLUSIONS

Conclusions paléobotaniques

L'étude de ces deux structures et des espèces affines nous a permis de faire un essai de synthèse

sur l'anatomie de certains plans ligneux caractéristiques de la flore du Gondwana.

En effet, ces bois fossiles montrent des caractères anatomiques très particuliers qui n'ont jamais été observés jusqu'à présent dans aucun bois fossile homoxylé, justifiant ainsi l'appellation générique dont ils sont l'objet. Ces structures sont encore désignées par le nom de genre *Dadoxylon* sans tenir compte de la définition initiale. Ce genre de forme prend alors une signification trop large et perd toute valeur taxonomique (Kräusel & Dolianiti, 1958, p. 128). Nous avons donc établi le genre de forme *Australoxylon* qui s'applique à un certain nombre de plans ligneux gondwanien (voir plus haut, 197), regroupés en partie dans le tableau 1. Ce type de bois secondaire homoxylé se trouve quelquefois associé à des formations médullaires hétérogènes (genres *Trigonomyelon*, Walton, 1925, *Kaokoxylon* Kräusel, 1956; *Barakaroxylon* Surrange & Maithy: tableau n° 2).

Ces structures forment ainsi un ensemble cohérent présentant des caractères précis et stables.

Caractères primitifs qui évoquent les plans ligneux des Cordaïtes de la province euraméricaine:

Section transversale quadrangulaire des fibres-trachéides, ponctuations radiales pluriséries, oculipores araucarioïdes (présence douteuse de ponctuations simples signalée dans les diagnoses: tableau 2).

Caractères relativement plus évolués:

Ponctuations radiales abiétinéennes, présence de crassules dans certains cas, zones d'accroissement distinctes, faux cernes.

Caractères particuliers au genre Australoxylon:

Ponctuations radiales disposées en groupes ou en files radiales espacées, circulaires, de petit diamètre (10—12 μ) à grand lumen plus ou moins circulaire (5—7 μ). Oculipores dont les dimensions sont à pau près équivalentes à celles des ponctuations radiales à lumen large plus ou moins elliptique oblique (Walton, 1925, p. 3, 4, 7. Pl. I). Signalons en outre la présence relativement constante de rayons ligneux de hauteur moyenne généralement unisériés, localement bisériés, principalement sur 1 cellule, la hauteur importante des cellules couchées, le passage progressif du bois final au bois initial dans une zone d'accroissement et la terminaison tronquée et arrondie des fibres-trachéides.

Au sein de cet ensemble de plans ligneux se rapportant au genre *Australoxylon*, on peut reconnaître différents groupes de structures bien définies en fonction du type des ponctuations radiales.

GROUPE I: *Ponctuations radiales araucariennes prédominantes. Polysolenoxylon withei* (Maniero, 1944) Kräusel & Dolianiti, 1958; *Solenopitys paulistana* Kräusel & Dolianiti, 1958: couches d'Irati (Permien inférieur) du Brésil; *Dadoxylon lafoniense* Halle, 1912; *Dadoxylon* cf. *augustum* Halle, 1912: Permien des Iles Falklands; *Dadoxylon nicoli* (Seward 1919) Walton, 1956 (échantillon D): Permien du Malawi; *Barakaroxylon jhariense* (Surange & Sahni, 1956) Surange & Maithy, 1962; *Barakaroxylon monocanalosum* Kulkarni, 1969; *Indoxylon canalosum* Surange & Maithy, 1963: Permien inférieur des Indes; *Dadoxylon nighanense* Maheshwari, 1964, *Damudoxylon waltoni* Maheshwari, 1967: Permien supérieur des Indes; *Dadoxylon australe* Arber, 1905; *Dadoxylon farleyense* Walkom, 1928: Permien d'Australie (New South Wales); *Dadoxylon daintreeii* (Chapman, 1908) Maithy, 1968: Permien d'Australie (Queensland); *Dadoxylon allanii* Kräusel, 1962: Permien de l'Antarctique.

GROUPE II: *Dadoxylon duartei* Japiassu, 1970: Formation Morrow Pelado (Permien supérieur) du Brésil; *Dadoxylon bakeri* Seward & Walton, 1923: Permien des Iles Falklands; *Dadoxylon sp.* Warren, 1912 (échantillon n° 11), *Australoxylon natalense* nov. gen. n. sp.: formation de l'Ecca au Natal; *Dadoxylon arberi* (Seward, 1917) Walton, 1925: formation du Beaufort de la province du Cap; *Dadoxylon arberi* (Seward, 1917) Kräusel, 1928: formation du Karroo du Sud-Ouest Africain; *Dadoxylon nicoli* (Seward, 1917) Walton, 1956 (échantillons A, B, C): Permien du Malawi; *Dadoxylon nicoli* G. H. da Silva, L. S. Barreto & L. H. B. de Carvalho, 1967; *Australoxylon teixeirae* nov. gen. n. sp.: Permien inférieur du Mozambique; *Dadoxylon bengalense* Holden, 1917; *Dadoxylon kharkhariense* Maithy, 1964; *Dadoxylon barakarense* Surange & Saxena, 1957: Permien inférieur des Indes; *Trigonomyelon raniganje* Maheswari, 1966: Permien supérieur des Indes; *Dadoxylon arberi* Sahni & Singh, 1926: Permien d'Australie (New South Wales).

Il est souvent délicat de préciser à quel groupe appartiennent certains plans ligneux, les données biométriques et les figurations étant souvent insuffisantes. De plus, quelques bois fossiles sont des espèces intermédiaires où coexistent des ponctuations araucariennes et des ponctuations spécifiques du genre *Australoxylon* en pourcentage plus ou moins équivalent.

Nous pouvons citer à titre d'exemple; *Barakaroxylon kraeuseli* Surange & Maithy, 1962 du Permien inférieur des Indes; *Dadoxylon parbeliense* Rao, 1935; *Kaokoxylon zalessky* (Sahni, 1933) Maheshwari, 1961 du Permien supérieur des Indes.

Ces structures du Gondwana dont les ponctuations radiales s'éloignent de la disposition araucarienne et abiétinéenne classique ont été, nous semble t'il, à tort rapprochées des plans ligneux mésozoïques de Protopinacées; en effet, la disposition et la forme des ponctuations radiales des bois mixtes est quelque peu différente: les ponctuations sont en général de plus grande taille et le lumen est petit. Dans le cas des ponctuations

opposées, les files radiales sont généralement contiguës (Pl. VI, fig. 6). Certains caractères anatomiques du genre *Australoxylon* rappelleraient plutôt ceux que l'on rencontre dans les structures de Progymnospermes appartenant au genre *Callixylon*. Les ponctuations radiales sont dans ce cas de petite taille, circulaires ou hexagonales, disposées en groupes distants les uns des autres, quelquefois séparés par des crassules (Boureau, 1970, p. 441, fig. 348).

Il convient également de souligner certaines similitudes ou convergences de forme entre le genre *Australoxylon* et le plan radial de certaines Glossoptéridophytes; *Glossopteris srivastavai* (Srivastava, 1954) Surange & Maheshwari, 1960 (Pl. I, fig. 2, 3, 4, 5). Cependant, il est difficile d'établir des affinités précises car ce groupe est encore assez mal connu quant à l'anatomie de ses représentants.

Il en est de même pour le genre *Novoguineoxylon* du Jurassique? de la Nouvelle-Guinée Hollandaise (Boureau, 1955, Pl. L, LI, LII). Ce plan ligneux présente une structure qui s'apparente à la fois à celle des Cycadophytes et au genre *Australoxylon* (petites ponctuations radiales opposées ou groupes de deux ponctuations opposées: Pl. VI, fig. 3).

Conclusions stratigraphiques

Ces bois fossiles peuvent apporter des précisions intéressantes du point de vue stratigraphique. En effet, ils sont en général localisés dans des formations géologiques d'âge précis: *Brésil*—Couches d'Irati (Permien inférieur), Formations Morro Pelado (Permien supérieur). *Iles Falklands*—Lafonian Sandstone (Permien inférieur), Choiseul Sound (Permien supérieur). *Province du Cap*—Partie supérieure du Beaufort inférieur (Permien inférieur). *Natal*—Ecca supérieur et Beaufort inférieur (Permien inférieur). *Mozambique*—Ecca supérieur (Permien inférieur). *Malawi*—Coal Shale Group: Ecca supérieur (Permien inférieur). *Indes*—Séries de Damuda: Barakar stage (Permien inférieur), Raniganj stage (Permien supérieur). *Australie*—Newcastle Coal Measures (Permien).

La répartition verticale de ces structures est donc limitée. Leur présence peut indiquer un âge probable allant du Permien inférieur au Permien supérieur (généralement à la base du Permien supérieur).

Conclusions taxonomiques

Ce petit inventaire des structures du bois secondaire du type *Australoxylon* de l'hémisphère sud ne permet pas de formuler des conclusions de caractère absolu quant à la position systématique de ces plans ligneux. Toutefois, nous pensons comme le présume Arnold qu'ils peuvent appartenir à une entité systématique particulière; on remarque que ces bois fossiles proviennent en général de formations ayant livré une flore assez particulière. Citons, à titre d'exemple, quelques associations caractéristiques:

Iles Falklands—genres *Gangamopteris, Phyllotheca, Glossopteris Desmiophylum, Dadoxylon lafoniense, Dadoxylon cf. angustum, Dadoxylon bakeri* (Adie, 1952, p. 390).

Mozambique—Schistes du Bassin de Tete: genres *Glossopteris, Schizoneura, Vertebraria, Noeggerathiopsis, Dadoxylon nicoli, Australoxylon teixeirae* (Borges, 1952, p. 237.)

Natal et Transvaal—formations de l'Ecca moyen: *Gangamopteris, Glossopteris, Noeggerathiopsis, Lepidodendron, Phyllotheca, Schizoneura, Sigillaria; Dadoxylon sp., Dadoxylon arberi* (Du Toit, 1926, p. 274).

Malawi—Coal Shale Group: genres *Glossopteris, Gangamopteris, Vertebraria, Noeggerathiopsis, Dadoxylon nicoli,* Sphénophytes (Walton, 1956, p. 169).

Indes—Barakar stage: genres *Glossopteris, Gangamopteris, Vertebraria, Schizoneura, Phyllotheca, Noeggerathiopsis, Sphenopteris, Pseudoctenis, Taeniopteris, Barakaria, Rhipidopsis, Sphenophyllum, Angiopteridium, Cyathea, Rhabdotaenia, Dictyopteridium, Voltzia, Samaropsis* (Surange, 1966, p. 55—68).

Australie—Queensland: genres *Glossopteris, Gangamopteris, Vertebraria, Noeggerathiopsis, Phyllotheca, Sphenopteris, Dadoxylon arberi,* (Hill, 1952, p. 42).

Ces formations semblent donc caractérisées par la coexistence des trois groupes de végétaux fossiles suivants: Glossopteridophytes (genres *Glossopteris, Gangamopteris, Vertebraria*), Cordaidophytes (genre *Noeggerathiopsis*) et structures du type *Australoxylon (Dadoxylon lafoniense, cf. angustum, nicoli, arberi, Australoxylon teixeirae, natalense).* Arber (1905, p. 191), Sahni & Singh (1926, p. 103—104) et Arnold (1968, p. 350) présument que ces structures pourraient correspondrent à celles de Gymnospermes (*Noeggerathiopsis*). Zeiller signale également à propos de l'étude de *Dadoxylon pedroï*: "On a à faire à une plante plus ou moins affine aux Cordaïtes telle peut-être que *Noeggerathiopsis* ou *Euryphylum*, mais on ne peut malheureusement faire à cet égard que de simples conjectures". L'investigation d'un matériel plus abondant serait nécessaire et pourrait confirmer cette position systématique.

Conclusions paléoécologiques

Ces structures du Gondwana possèdent toujours des zones d'accroissement. Celles-ci sont plus rares que dans les bois de la même époque de la Province euraméricaine. On peut se rallier au point de vue de L. Grambast (1960) qui propose l'explication suivante: "On peut penser que les Gymnospermes des territoires à flore du Gondwana, soumis au stimulus des périodes climatiques différenciées ont naturellement évolué plus vite que celles des régions septentrionales qui se sont développées dans un milieu beaucoup plus homogène".

Cette étude analytique permet de préciser quelque peu nos connaissances anatomiques encore trop fragmentaires des structures gondwaniennes. Des mises au point ultérieures devront nécessairement être faites à la suite de déterminations de nouvelles espèces et de regroupement de certaines d'entre elles.

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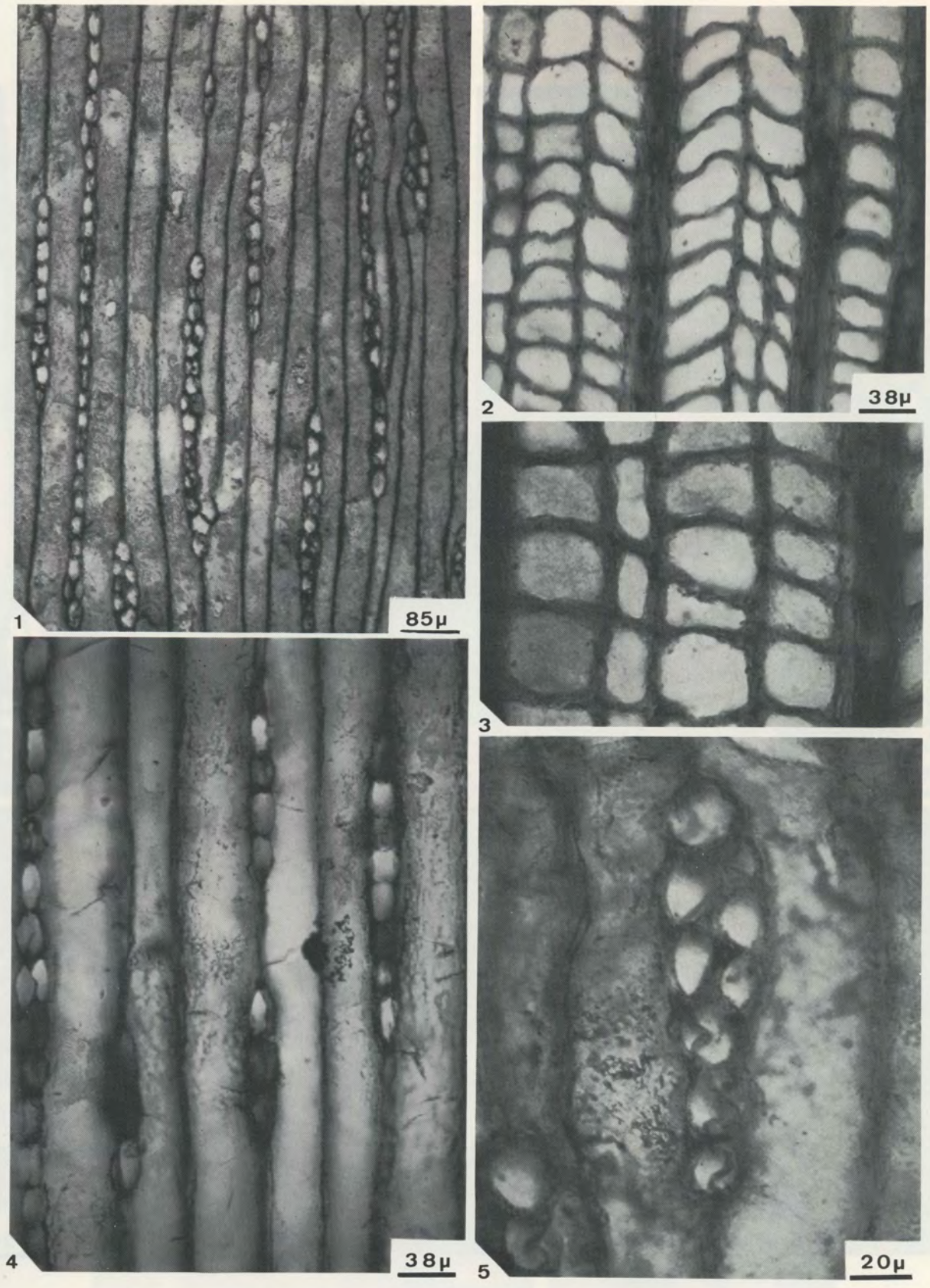


PLANCHE I

Figure 1. *Australoxylon teixeirae* nov. gen. n. sp., Section tangentielle.
Figure 2. *Australoxylon teixeirae* nov. gen. n. sp., Section transversale.
Figure 3. *Australoxylon teixeirae* nov. gen. n. sp., Section transversale: section quadrangulaire des fibres-trachéides.
Figure 4. *Australoxylon natalense* nov. gen. n. sp., Section tangentielle.
Figure 5. *Australoxylon teixeirae* nov. gen. n. sp., Coloration: chrysoïdine, Section tangentielle: détail d'un rayon ligneux localement bisérié.
Figures 3 et 5 à la même échelle

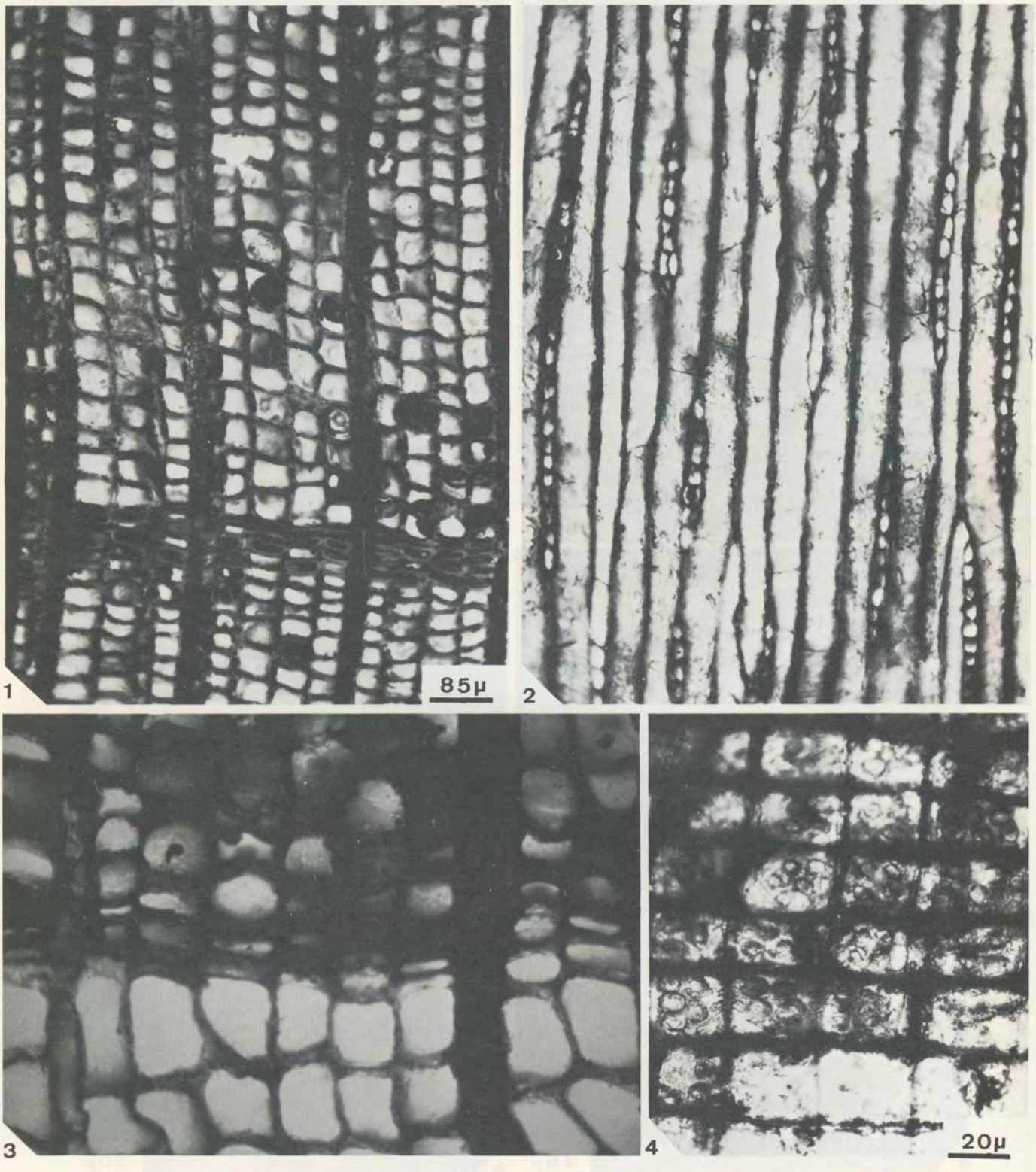


PLANCHE II

Figure 1. *Australoxylon teixeirae* nov. gen. n. sp., Section transversale: zone d'accroissement et faux cerne.

Figure 2. *Australoxylon natalense* nov. gen. n. sp., Section tangentielle: rayons ligneux unisériés et localement bisériés.

Figure 3. *Australoxylon natalense* nov. gen. n. sp., Section transversale: région de la ligne limitante.

Figure 4. *Australoxylon teixeirae* nov. gen. n. sp., Section radiale: cellules couchées des rayons ligneux et ponctuations de champs.

Figures 1, 2 à la même échelle et figures 3, 4 à la même échelle.

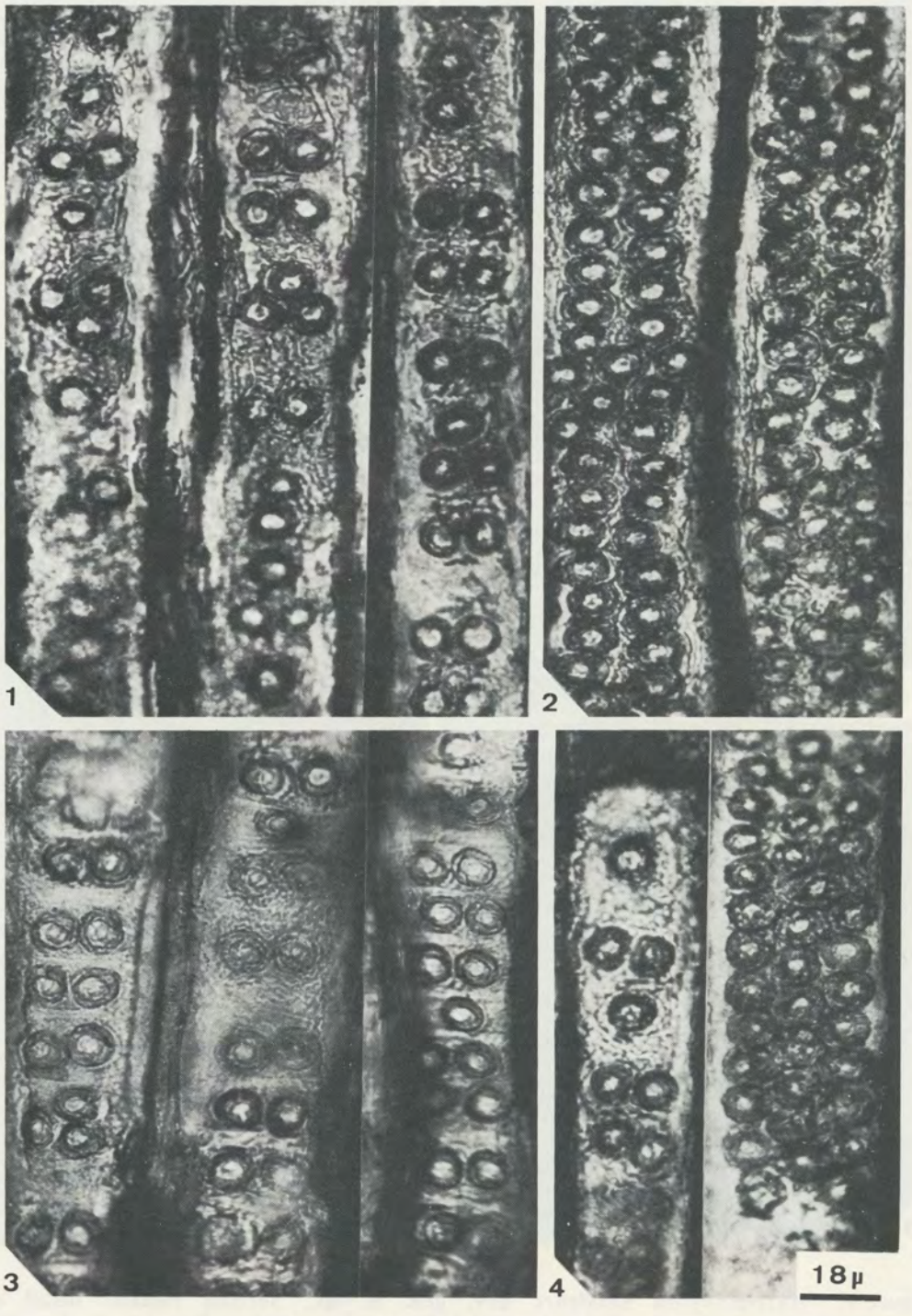


PLANCHE III

Figures 1, 2 et 4. *Australoxylon teixeirae* nov. gen. n. sp., Section radiale: différentes dispositions des ponctuations radiales.

Figure 3. *Australoxylon natalense* nov. gen. n. sp., Section radiale: ponctuations radiales et crassules?

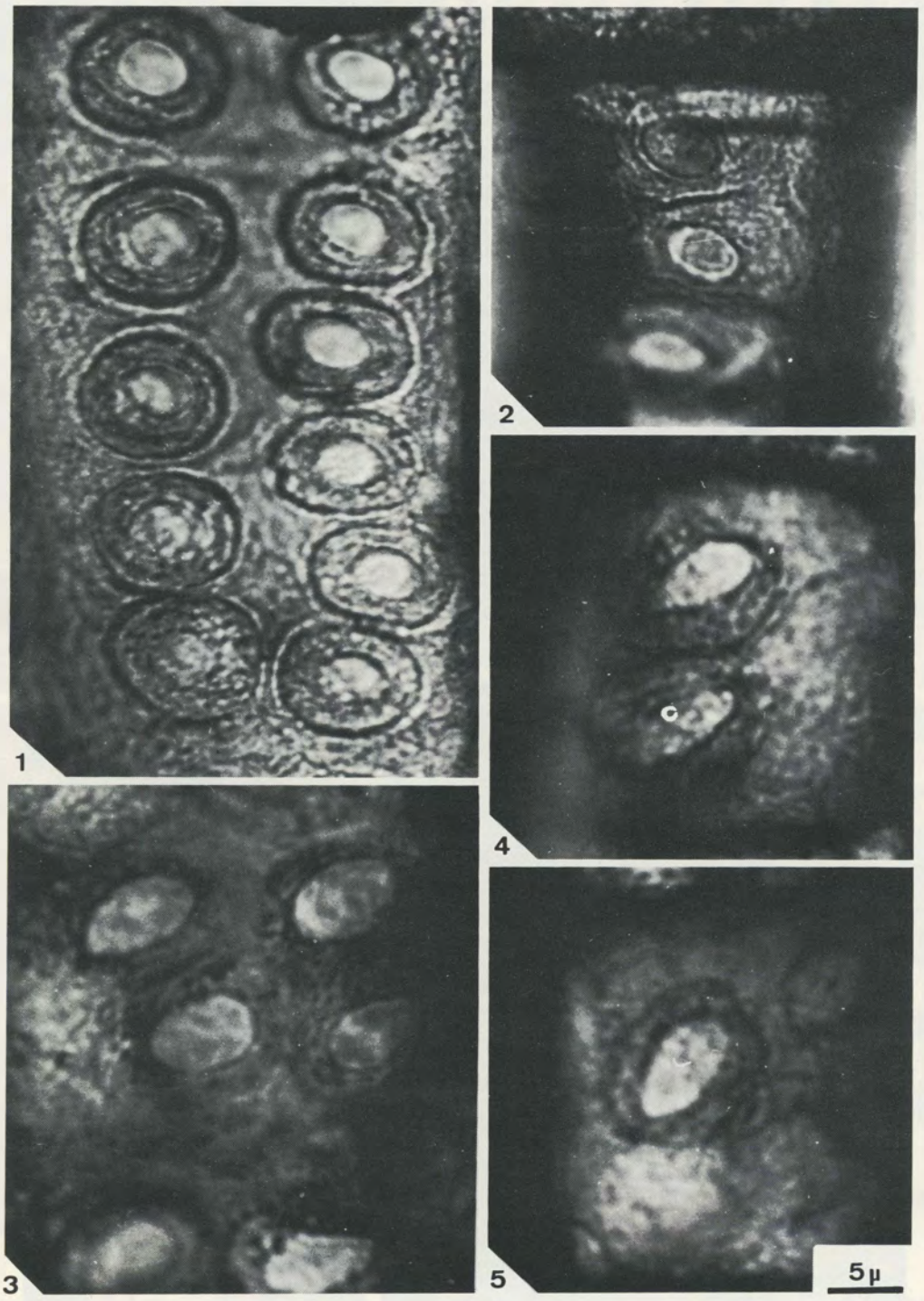


PLANCHE IV

Figure 1. *Australoxylon natalense* nov. gen. n. sp., Section radiale: détail des ponctuations radiales caractéristiques de ce plan ligneux et du genre *Australoxylon*.

Figure 2. *Australoxylon natalense* nov. gen. n. sp., Section radiale: détail des ponctuations de champs araucarioïdes.

Figures 3, 4 et 5. *Australoxylon teixeirae* nov. gen. n. sp., Section radiale: détail des ponctuations de champs.

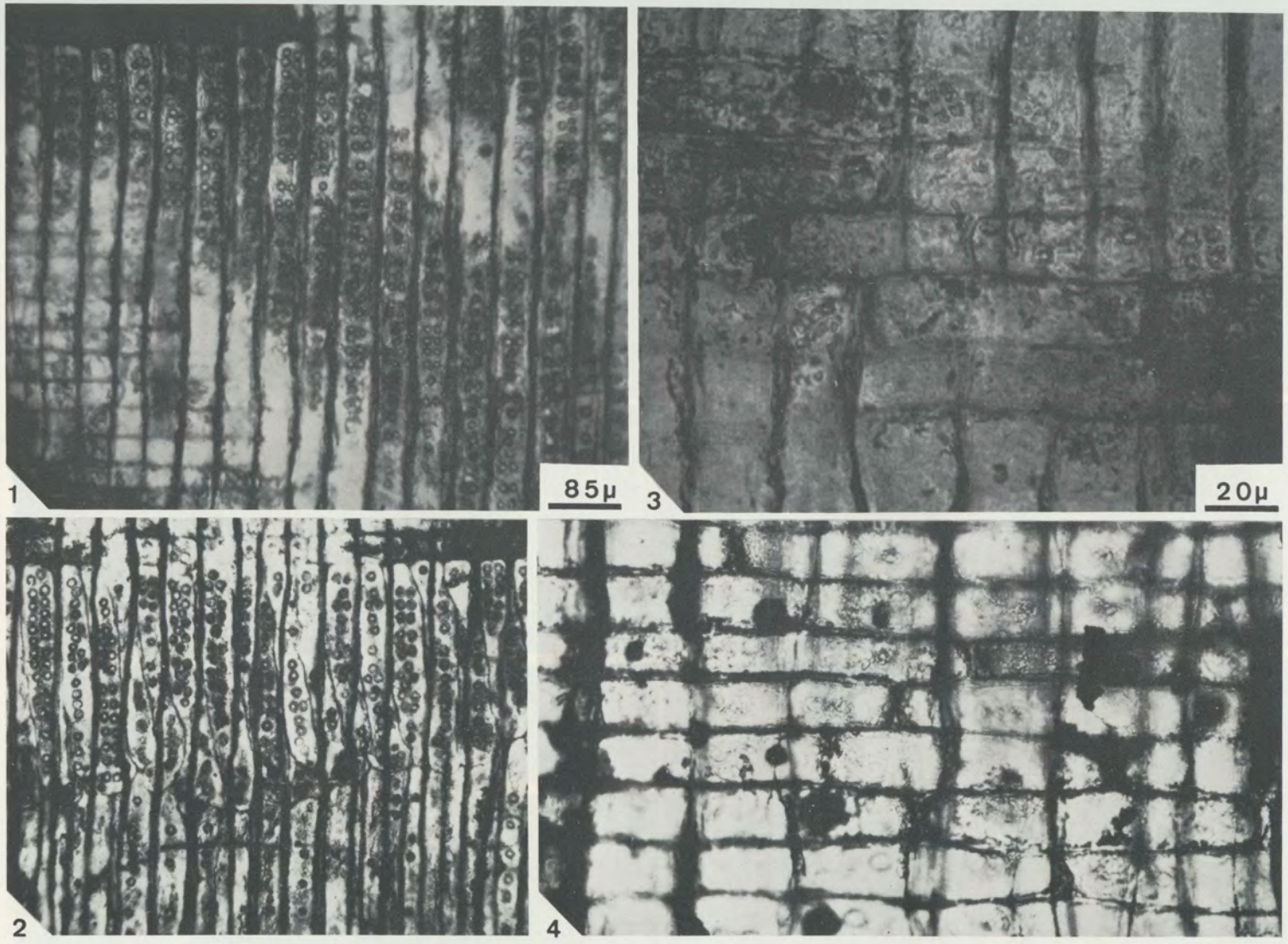


PLANCHE V

Figures 1 et 2. *Australoxylon teixeirae* nov. gen. n. sp., Sections radiales: vues d'ensemble. Remarquez la terminaison tronquée des fibres-tracheides.

Figure 3. *Australoxylon teixeirae* nov. gen. n. sp., Section radiale: cellules couchées des rayons ligneux.

Figure 4. *Australoxylon natalense* nov. gen. n. sp., Section radiale: cellules couchées des rayons ligneux.

Figures 1, 2 à la même échelle et figures 3, 4 à la même échelle.

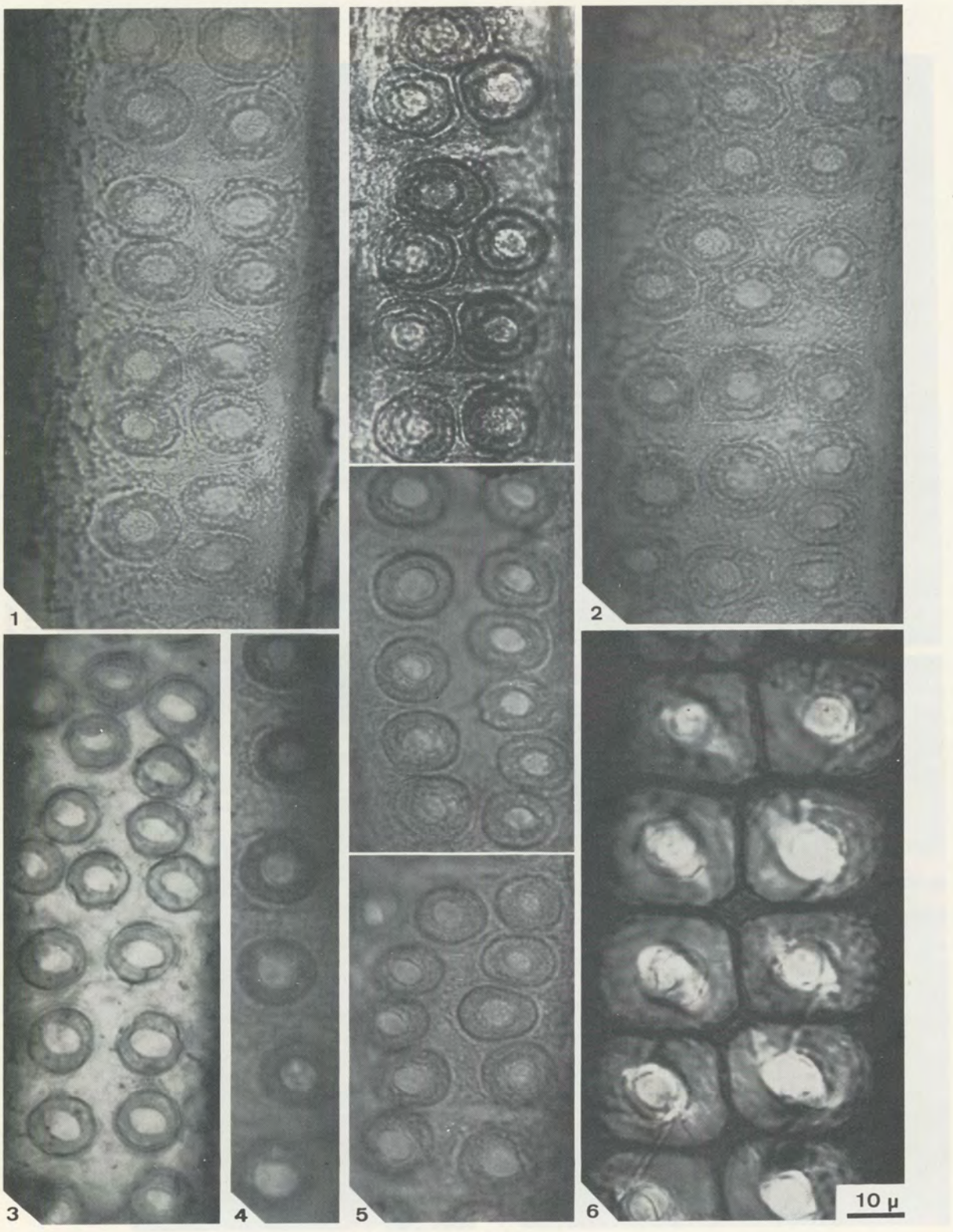


PLANCHE VI

Figures 1, 2, 4 et 5. *Australoxylon natalense* nov. gen. n. sp., Section radiale: différentes dispositions des ponctuations radiales, présence éventuelle de crassules.

Figure 3. *Novoguineoxylon lacunosum* Boureau 1965. Section radiale: ponctuations radiales caractéristiques.

Figure 6. *Protopodocarpoxylon orientale* Vozenin-Serra 1969. Section radiale: ponctuations radiales mixtes.

Palaeont. afr., **16**. 59–83. 1973

THE BIOSTRATIGRAPHY OF THE PERMIAN AND TRIASSIC

Part 2 (Charts 23–35)—A Preliminary Review of the Distribution of Permian and Triassic Strata in Time and Space

by

J. M. Anderson

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1. INTRODUCTORY NOTE

The charts presented here (i.e. charts 23–35) are intended to form part of a series with those (i.e. charts 1–22) compiled by H. M. Anderson and J. M. Anderson as a supplement to Palaeontologia Africana, Volume 13, 1970 (see bibliography). Charts 1–22 were presented under the title "A preliminary review of the biostratigraphy of the uppermost Permian, Triassic and lowermost Jurassic of Gondwanaland". Further charts are to follow and will be numbered from 36 onwards.

The overall series of charts will henceforth be entitled—"The biostratigraphy of the Permian and Triassic". Charts 1–22 form *Part 1* of the series; charts 23–35 form *Part 2*. Parts 3, 4, 5 etc. will deal in turn with particular aspects of the flora and fauna. The tetrapod vertebrates, insects and macroflora will most likely be studied first.

The work completed to date was carried out under the auspices of Southern Oil Exploration Corporation (SOEKOR) and the University of the Witwatersrand. J. M. Anderson was employed from January 1971 to the present at the Bernard Institute for Palaeontology, Witwatersrand University, as a research officer, with the help of a substantial grant from SOEKOR and from April 1970 to March 1973 as a geologist/palynologist on the permanent SOEKOR staff. H. M. Anderson has been employed as a junior research officer from January 1971 to the present at the Bernard Price Institute for Palaeontology, Witwatersrand University.

2. THE AIM OF THE OVERALL PROJECT

The aim is to discover the evolving story of life and landscape during the 90 odd million years of the Permian and Triassic, and to appreciate the interdependence of the patterns of evolution of the plants, animals, climate and landscape.

In order to attain this understanding it is intended to compile—

(i) Separate phylogenetic charts (all to the same scale—½ cm equals 1 million years) for each major plant and animal group (e.g. the macroflora, microflora, tetrapod vertebrates, insects, ammonites).

(ii) A series of fairly detailed palaeogeographic maps, each representing a single "Standard Stage" or "Substage" of the Permian and Triassic.

2.1. Compilation of Initial Data on Major Plant and Animal Groups

There follows a brief account of the envisaged approach to compiling the initial data (prior to drawing up the palaeogeographic maps and phylogenetic charts) for each particular plant or animal group. Each group will be dealt with in the same manner. Imagine, therefore, that the following account applies, say, to the tetrapod vertebrates.

(i) A correlation chart (drawn to the same scale as the eventual phylogenetic chart) including all known productive horizons—formations, members, zones etc., will be compiled (see chart 5 in Anderson and Anderson, 1970).

(ii) A series of geological maps (as in chart 26) covering each productive area will be drawn up to indicate, as far as is possible, each known collecting locality. The position of these areas will be indicated on a reduced simplified world map of the Permian and Triassic (see chart 26).

(iii) A brief account of the general productivity (considering both quantity and quality of material) of the formation, member or zone, will be given. This falls into two parts:
  (a) The estimated potential productivity of the unit;
  (b) The comprehensiveness of the collections presently available.

(iv) For each productive unit a comprehensive, fully classified list of the available material (down to species where possible) will be given. (See charts 1 to 4 of Anderson and Anderson, 1970.) The list will be arranged in phylogenetic order according to the most recent, most reliable systematics available. Each species, genus (or larger taxa where necessary) will be commented on as regards—
  (a) The vintage and reliability of the taxonomy available;
  (b) The number of specimens available. In cases where the material is common, the relative abundance will be given;
  (c) The number of localities from which the material is known;
  (d) The state of preservation of the material.

(v) A brief but comprehensive account of the known flora and fauna of the unit will be given.

(vi) For each productive unit a brief geological account will be given, e.g. isopach map, facies map, current directions etc.

(vii) For each productive unit a brief palaeogeographic assessment will be made.

2.2. The Phylogenetic Charts

These charts will be drawn up more or less as was chart 5 in Anderson and Anderson (1970).

The degree to which the phylogenetic chart will reflect the true picture will depend on several factors—

(i) The accuracy of the correlation chart incorporating each productive horizon (formation etc.) (see section 5 of text for elaboration on the approach taken in the compilation of a correlation chart).

(ii) The state of the systematics and taxonomy available.
(iii) The comprehensiveness of the collections available from each productive horizon (formation etc.).
(iv) The degree to which a theoretically fully comprehensive collection from a productive horizon (formation etc.) actually reflects the true composition of the flora or fauna existing in the area at the time.
(v) The degree to which a full set of comprehensive collections from each existing productive horizon (formation etc.) of the same age throughout the world would reflect the true composition of the flora and fauna of the world at the time.

The reliability of the correlations, systematics and the comprehensiveness of the collections will vary greatly from horizon to horizon. These factors must be clearly recognized when compiling or studying any phylogenetic chart. Certain portions of any such chart will necessarily be based on very shaky correlations, rudimentary systematics and inadequate collections, whilst others will be based on excellent data. The charts will need to be updated at fairly regular intervals.

In studying the phylogenetic charts it will also be very important to have a realistic awareness of points (iv) and (v) above. Very briefly it may be stated, however, that the apparent lack of diversity of plant and animal life during the Permian and Triassic (see Anderson and Anderson, 1970) and the often marked similarity between assemblages of the same age from widely separated areas in the world suggest that the phylogenetic charts could eventually present a fairly reliable reflection of the true story.

3. THE PURPOSE OF THE PRESENT SET OF CHARTS

It is necessary to review the presently available data ragarding the distribution of Permian and Triassic strata in time and space. It is the aim in the present text and set of charts to attempt this.

The world map (chart 23), showing the known distribution of Permian and Triassic strata, is considered a desirable prerequisite to an understanding of the palaeogeography of the time. The general relationship between the various depositional areas—the geosynclinal troughs, the shelf seas, the intra-cratonic basins, the restricted valley deposits—become simpler to comprehend.

The distribution of known productive localities for any particular animal or plant group for the time-span being considered can be plotted (as in chart 26 for example—"Maps showing the known distribution of Dzhulfian, Changhsingian and Griesbachian ammonoid faunas") in relation to known Permian and Triassic strata.

The remaining charts (24—35) are all directed towards an attempt to compile meaningful, time-oriented correlation charts of the Permian and Triassic strata. Rigorous definition and international usage of "Standard Reference Stages", "Substages" and "Ammonite Zones"; the application of absolute age data and the consideration of rates and continuity of deposition and compaction of sediments are all considered vital in an attempt to compile a correlation chart which is to be used as a base for subsequent phylogenetic studies. See section 5 for further comment on the application of these aspects, dwelt on in charts 24 to 34, to the compilation of chart 35 (Correlation of World Permian strata).

It will be noted that most attention is paid to the "Reference Stages" and correlation of Permian strata and far less to the Triassic. Tozer (1967 and 1971) (see bibliography) has dealt at length with the proposal of "Standard Reference Stages", "Substages" and "Ammonite Zones", based on strata in Western and Arctic Canada, for the Triassic System. His proposals are accepted in this paper with further discussion offered only with regard to the lowest Triassic Stage, i.e. Griesbachian. No extensive correlation chart of Triassic strata is given here. However, study of charts 5 and 21 of Anderson and Anderson (1970) and charts 29 and 31 of this paper partially fills this need.

4. NOTES ON THE PERMIAN SYSTEM: "STANDARD REFERENCE STAGES", "SUBSTAGES" AND "AMMONITE ZONES"; LOWER AND UPPER BOUNDARIES

4.1. Brief historical sketch of the development of the present concept of the Permian System and its stages in the type area, i.e. The southern Urals and Russian platform

Dunbar *et al.* (1960, p. 1765—6) wrote "The Permian rocks on which the system was founded occupy a vast structural basin west of the Ural Mountains, measuring about 700 miles from west to east and 1 000 miles from north to south. This region is divisible into two major structural elements, the Russian platform and the Uralian geosyncline. Over the broad platform the Carboniferous and Permian strata are nearly horizontal and of moderate thickness, but as they pass eastwards into the geosyncline the Permian rocks thicken greatly and undergo rapid facies changes. It was here, along the western border of the Ural Mountains that the Permian System was established".

Murchison visited this region during the summer of 1840 and 1841 and proposed and defined the Permian System in 1841 and 1845. The original Permian System, as conceived by Murchison, comprised only the rocks now included in the Kungurian, Kazanian, and Tatarian Stages.

In 1874 Karpinsky proposed and defined the Artinskian Stage. In a monograph on the ammonites of this stage Karpinsky, in 1889, proposed that the stage should be included in the Permian. This suggestion gained almost immediate recognition. "Thus the base of the Permian was

lowered in its type region to the base of the Artinskian".

"In the original statement in which Karpinsky proposed the Artinskian Stage and described its type section, he referred to a basal calcareous unit in the Orenburg region as the Sakmarian limestone, named for exposures along the Sakmara River".

"In a comprehensive restudy of this region Ruzhentsev (1936) proposed to subdivide the original Artinskian into two stages, restricting the name Artinskian to the upper and using the name Sakmarian for the lower . . .".

In 1937 Ruzhentsev referred to the basal Sakmarian as the Assel horizon. In 1950 these beds were elevated to the rank of a "Substage" of the Sakmarian Stage and in 1951 Ruzhentsev proposed that the Asselian should be recognised as a stage (see Ruzhentsev, 1954, p. 1).

4.2. **The "Standard Reference Stages" and "Substages" of the Permian System** (See Charts 24, 29 and 31.)

Unlike the Carboniferous, Triassic and Jurassic Systems, where the succession of "Standard Reference Stages" occurs in each case in a more or less coherent area (see Chart 31), the Permian presents a difficult case. The type area for the Permian along the western flank of the Urals does not provide an unbroken sequence of marine ammonite-bearing strata throughout the Permian. Only the Lower Permian "Reference Stages" are based on the southern Urals sequence. The Upper Permian "Reference Stages" have to be sought elsewhere.

The sequence of "Standard Reference Stages" used in this paper (see Charts 24, 29 and 31) is built up from three different areas—

(i) The Asselian, Sakmarian and Artinskian Stages (with five substages) of the Lower Permian—typified by strata in the southern Urals (USSR).

(ii) The Guadalupian Stage (with four substages—Roadian, Wordian, Capitanian and Amarassian) comprising the lower half of the Upper Permian—typified by strata in western Texas and northern Mexico.

(iii) The Dzhulfian and Changhsingian Stages of the upper half of the Upper Permian—typified by strata in the Trans-Caucasus (USSR) and northern Iran.

4.2.1. *The Asselian, Sakmarian and Artinskian Stages of the Lower Permian—typified by strata in the southern Urals (USSR).* (See Charts 24 and 25 for details.)

In contrast, particularly to the upper half of the Upper Permian, a fair degree of unanimity exists regarding the useage of "Standard Reference Stages" of the Lower Permian. The well exposed highly fossiliferous marine strata of the southern Urals clearly present the most useful "Standard Reference" sequence for this period. Of this fact, few authors in the last decade or so would throw any doubt. Some difference of opinion does exist however as to the stage breakdown of the sequence. These differences are made clear in the following summary of "Standard Stage" preferences indicated in a number of significant papers dating from 1961.

(i) *Glenister and Furnish* (1961, p. 678–684, t. 2) in a paper on "The Permian ammonoids of Australia", recognised three stages—the Asselian, Sakmarian and Artinskian, typified by strata in the southern Urals. In the Artinskian they recognised two substages—the Aktastinian and Baigendzhinian.

(ii) *Nassichuk, Furnish and Glenister* (1965, p. 2–4, t.1) in a paper on "The Permian Ammonoids of Arctic Canada", recognised the same three stages—the Asselian, Sakmarian and Artinskian, typified by strata in the southern Urals. However, in this paper three substages were recognised in the Artinskian—the Aktastinian, Baigendzhinian and a third unnamed substage typified by the Basal Word Limestone of the Glass Mountains, western Texas. This third substage they include in the Artinskian of the Lower Permian, rather than the Guadalupian of the Upper Permian, since they regarded its ammonite and brachiopod faunas as more closely related to the former. They write—"In these two groups of fossils there are such strong relationships with those found in the underlying Leonard Formation [the U.S.A. equivalent of the Artinskian] that this stratigraphic unit should logically be regarded as uppermost Lower Permian rather than basal Guadalupian as commonly assigned. Under our definition this time boundary corresponds to the extinction in two of the most characteristic Lower Permian ammonoid elements: the Perrinitidae and Metalegoceratidae".

(iii) *Ruzhentsev and Sarýcheva* (1965, p. 88–90, t. 13) in a paper on "The development and change of marine organisms at the Palaeozoic-Mesozoic boundary" wrote "there is good agreement about the subdivision of the Lower Permian section. Recent data, summed up by Glenister and Furnish (1961), indicate that the Lower Permian deposits can and should be divided into three stages, Asselian, Sakmarian and Artinskian". They wrote further as regards the necessity for international recognition and usage of a sequence of "Standard Reference Stages" for the Permian . . . "further study of the Permian deposits of the globe is only possible if we accept a unified scale".

(iv) *Smith* (1964, p. 211–214) in his chapter "The Permian Period" in "The Phanerozoic Time-scale" writes—"For the purpose of erecting a Permian time-scale the standard section adopted is that of the type-area of the Russian platform and southern Urals". He recognised three stages within the Lower Permian—the Sakmarian, Artinskian and Kungurian.

(v) *Chao* (1965, correlation table) in a paper on "The Permian ammonoid–bearing formations

of south China", referred to the Russian platform and southern Urals as the "Standard Reference". He recognised three stages within the Lower Permian—the Sakmarian, Artinskian and Kungurian.

(vi) *McKee et al.* (1967) in their comprehensive correlation chart of the Permian strata of the United States referred to the Russian platform and southern Urals as the "Standard Reference". They recognised three stages within the Lower Permian—the Sakmarian, Artinskian and Kungurian.

(vii) *Dickins* (1969) in his comprehensive correlation chart of the Permian strata of Australia referred to the Russian platform and southern Urals as the "Standard Reference". He recognised three stages within the Lower Permian—the Sakmarian, Artinskian and Kungurian.

Comments and résumé of "Reference Stages" used in this paper.

(a) All the authors listed above recognise the southern Urals as the "Standard Reference Section" for the Lower Permian.

(b) Glenister and Furnish (1961) and Ruzhentsev and Sarýcheva (1965) recognise three "Standard Reference Stages" within the Lower Permian—the Asselian, Sakmarian and Artinskian.

(c) Nassichuk, Furnish and Glenister (1965) recognised the same three "Standard Stages" but refer an additional substage (typified by the Basal Word Limestone of the Glass Mountains, western Texas) to the uppermost Artinskian. In the present paper this substage is referred to the base of the Guadalupian Stage (see notes on Guadalupian Stage below).

(d) Smith (1964), Chao (1965), McKee *et al.* (1967) and Dickins (1969) all recognise the Sakmarian, Artinskian and Kungurian as the "Standard Reference Stages" of the Lower Permian.

(e) The present paper follows Glenister and Furnish (1961) and Ruzhentsev and Sarýcheva (1965) in referring to the Asselian, Sakmarian and Artinskian Stages as "Standard" for the Lower Permian. No particular reason is known why the authors in note (d) dismiss the Asselian. The Kungurian by virtue of its very limited marine fauna is of little use as a basic reference.

4.2.2. *The Guadalupian Stage (with four substages—Roadian, Wordian, Capitanian and Amarassian) comprising the lower half of the Upper Permian—typified by strata in western Texas and northern Mexico.* (See Chart 24 for details.)

The lower half of the Upper Permian is well represented by marine ammonite-bearing strata in western Texas and northern Mexico. Excellent highly fossiliferous strata (with ammonites) covering this period are exposed in three areas—the Guadalupe Mountains at the northern end of the Delaware Basin in western Texas; the Glass Mountains at the southern end of the same basin; and in Val de Las Delicias, Coahuila Province, northern Mexico. Prior to 1965 only two stages, the Wordian and Capitanian, were recognised in these strata. Since then:

(i) *Nassichuk, Furnish and Glenister* (1965, p. 2—4, t. 1) suggested that an additional stage, comprising the basal limestone of the Word Formation, should probably be recognised. No formal name was proposed. They suggested that the included ammonite fauna was more similar to that in the upper Leonardian Series than that in the lower Guadalupian Series, and that the stage should therefore be regarded as uppermost Lower Permian rather than lowermost Upper Permian. They note that ". . . there is little ammonoid evidence for detailed correlation of the American sections with those of the late Artinskian in the Urals, although certain species in the upper Leonard Formation appear to be younger phylogenetically".

(ii) *Spinosa, Furnish and Glenister* (1970, p. 730—31) recognised a distinctive fauna in the uppermost part of the Guadalupian Series as developed in Val de Las Delicias, Coahuila Province, northern Mexico. They note that "Collectively, this fauna is similar to that designated as the Amarassi 'faunal element' [which] . . . represents the youngest Permian on Timor". They refer to these uppermost Guadalupian strata as Amarassian. They do not actually define the Amarassian as a distinct stage or substage of the Guadalupian.

(iii) *Furnish and Glenister* (1970, p. 154—155, t.1) list a chronological sequence of "Reference Stages" for the upper part of the Permian in which they include the Roadian (represented by the basal limestone of the Word Formation and its faunas) and the Amarassian (represented by the faunas mentioned above from Coahuila and Timor). This appears to be the first occasion on which the Roadian and Amarassian have been introduced as stages. Although they do not officially define them, they mention that "Furnish and Glenister are preparing a manuscript to elaborate on the names . . .".

Comments and résumé of "Reference Stage and Substages" used in this paper.

(a) In the present paper I have recognised the Guadalupian Stage (typified by strata in the western Texas/northern Mexico region) as being divisible into four substages—Roadian, Wordian, Capitanian and Amarassian.

(b) The term Amarassian (based on strata in

Timor) is used here, purely provisionally, as a means of referring to the uppermost substage recognised, but as yet unnamed, in the Guadalupian of the western Texas/northern Mexico region. It would be preferable for all four substages to be defined and named in this region. In Charts 24, 29 and 35 I have bracketed Amarassian to indicate that its use is a provisional convenience.

(c) The evidence, although not particularly clear, suggests that time gaps (included as two million years on Charts 24, 29 and 35) occur between the top of the Artinskian and the base of the Roadian, and between the top of the Amarassian and the base of the Dzhulfian.

4.2.3. *The Dzhulfian and Changhsingian Stages of the upper half of the Upper Permian—typified by strata in the Trans-Causasus (USSR) and northern Iran—(See Charts 24 and 27 for details.)*

A great diversity of opinion persists in the most recent literature in regard to the recognition of "Standard Reference Stages" for the post-Guadalupian Permian. This is clearly a reflection of the incomplete nature of the information presently available.

The following are the most relevant conclusions arrived at by a series of authors from 1961 to 1972 and I will conclude with my own assessment of what appear to be the most useful available "Standard Reference Stages" for the period in question.

(i) *Glenister and Furnish* (1961, p. 684, t. 2), according to Spinosa *et al.* (1970, p. 730), formally defined the Dzhulfian Stage as a ". . . post-Guadalupian standard for the uppermost Permian". The Dzhulfian Stage (based on the Trans-Caucasus) was taken to represent the whole of post-Guadalupian Permian. The stage as proposed by Glenister and Furnish presumably coincides with the ammonite-bearing upper three beds of the Dzhulfian Stage as defined in detail by Ruzhentsev and Sarýcheva (1965) (see below). The Chhidru beds of the Salt Range, the Kuling Shales of the Himalayas, the Wuchiaping Formation of southern China, the Ankitokazo fauna of Madagascar, the Foldvik Creek Formation of east central Greenland, were all considered equivalents of the Dzhulfian Stage of the Trans-Caucasus, with *Cyclolobus*, although rare, taken as "the best index fossil".

(ii) *Ruzhentsev and Sarycheva* (1965, t. 14 and p. 18–20), regarded the Dzhulfian Stage as occupying the whole period between the upper limit of the Guadalupian and the end of the Permian. They defined the stage in detail with reference to the type-section at Dorasham 2, Dzhul'fa Gorge, in the Trans-Caucasus (see Chart 26). They divided the stage into a series of five beds, the lower two being characterised particularly by fusulinids and brachiopods respectively with no known ammonites; the upper three bearing numerous ammonite specimens.

(iii) *Chao* (1965, p. 1825 and correlation charts) suggested that the *Tompophiceras–Paratirolites* sequence of beds which succeed the Dzhulfian Stage in the Trans-Caucasus (Ruzhentsev and Sarýcheva (1965, p. 20–21) had placed these beds in the lowermost Triassic) should be included in the uppermost Permian and correlated them with the Changhsing Formation of south China on ammonite evidence. Chao referred to the Kazanian and Tatarian as his "Standard Reference Stages"; the Changhsing Formation of south China and the *Tompophiceras–Paratirolites* beds of the Trans-Caucasus he equated with the Tatarian; the Wuchiaping Formation of south China, the Chhidruan Stage of the Salt Range and the Dzhulfian Stage of the Trans-Caucasus he equated with the Kazanian.

(iv) *Furnish* (1966) recognised two Permian stages above the Guadalupian, i.e. the Chhidruan followed by the Dzhulfian with the Chhidruan divided into two substages, the Godthaabian and the Jabian. He writes (p. 266)—"On a somewhat informal basis, the term 'Neopermian' is employed for that segment of geologic time in which the genus *Cyclolobus* is known to have existed. The Chidruan Stage, typified by Salt Range strata is the primary reference, but the genus has been reported to occur in the next younger Dzhulfian Stage. Godthaabian Substage (early Chidruan) is defined on the basis of an evolutionary step in the genus *Cyclolobus*. Jabian Substage is then applied to the late Chidruan in the type area. Only the term Godthaabian is new in a time-rock sense; it is derived from Godthaab (Good Hope) Gulf near the East Greenland *Cyclolobus* localities."

His Chidruan (Chhidruan) Stage was represented apparently by the upper three (ammonite-bearing) beds of the Dzhulfian stage as defined by Ruzhentsev and Sarýcheva 1965 (see above). Furnish did not have this Russian work available to him at the time of writing.

(v) *Stepanov et al.* (1969, fig. 6) and *Taraz* (1969, text and figs.), following Ruzhentsev and Sarýcheva (1965), considered the *Tompophiceras–Paratirolites* beds to be lowermost Triassic and had the Dzhulfian Stage occupying the whole period between the end of the Guadalupian and the end of the Permian.

(vi) *Tozer* (1969, t. 2 and p. 349–350) followed Chao (1965) in including the *Tompophiceras–Paratirolites* beds of the Trans-Caucasus in uppermost Permian. He writes that it is apparent ". . . that there is no satisfactorily defined stratigraphical term, based on a marine

sequence, to accommodate the youngest Permian rocks . . . For the time being, it is probably best to follow Chao (1965, p. 1824), and Waterhouse (1967) who use the term Tatarian, despite the fact that the typical Tatarian based almost entirely on red continental deposits, does not constitute a satisfactory standard stage".

(vii) *Furnish and Glenister* (1970, p. 154–155, t. 1) write—"There is little unanimity of opinion regarding Permian stage names, particularly in the upper portion of the system . . . New data within the last few years suggest relationships for the post-Guadalupe sequence not visualized previously (Furnish, 1966)." They recognised three stages between the top of the Guadalupian and the end of the Permian, i.e. the Araksian (typified by strata in the Trans-Caucasus), followed by the Chhidruan (typified by strata in the Salt Range) and the Changhsingian (typified by strata in south China). They include the three stages in the Dzhulfian Series. The Araksian and Changhsingian Stages were introduced for the first time, but were not formally defined; this was deferred for a manuscript presently in preparation by them.

The Araksian stage they write—" . . . is thought to be largely synonymous with Godthaabian (Furnish, 1966) from East Greenland, but it is introduced because it now has the advantage of a diverse fauna in sequence". The Araksian Stage is presumably intended to correspond with (and to replace) the Dzhulfian Stage of the Trans-Caucasus as defined by Rezhentsev and Sarýcheva (1965).

The Chhidruan Stage I assume is still intended (as in Furnish, 1966) to be typified by the whole of the Chhidru Formation of the Salt Range.

The Changhsingian Stage is presumably intended (as in Furnish, 1966) to be typified by the Changhsing Formation as presented in Chao (1965), and to be equivalent to the *Tompophiceras–Paratirolites* beds of the Trans-Caucasus as defined by Ruzhentsev and Sarýcheva (1965).

(viii) *Tozer* (1971, p. 453–454) offered a number of critical comments on the Araksian, Chhidruan and Changhsingian sequence of stages as proposed by Furnish and Glenister (1970), but made no attempt to present an alternative scheme. He feels that the "Standard Reference Stages" for the post-Guadalupian Permian should, as far as is possible, be typified by strata comprising a single section and suggests the well known Trans-Caucasus for this purpose. He writes– "Having Araksian and the Changhsingian equivalent defined in the same section would also focus attention on a major problem– The position of the Chhidruan stage in relation to Araksian [i.e. Dzhulfian] and Changhsingian. Furnish and Glenister place the Chhidruan between the other two, because Chhidruan cyclolobids are believed to be more advanced than Araksian. But this begs another question: how is the Chhidruan represented at Dzhulfa (in the Trans-Caucasus)? By an unconformity or non sequence? Furnish and Glenister do not provide the answer, but in the context of proposing a sequence of three stages to cover latest Permian time, as they have done, should not this question have been considered? "

(ix) *Waterhouse* (1972, p. 159) also offered critical comment on the Araksian, Chhidruan and Changhsingian sequence of stages proposed by Furnish and Glenister (1970). He writes—"If one plots several sequences in which Capitan and/or Chhidru faunas are known—such as those in the Glass Mountains, Guadalupe Mountains, Coahuila–Mexico, Kolyma River in eastern Siberia, Japan (several areas), China (several areas), eastern and western Australia, New Zealand, Armenia, Iran, Salt Range, and Cambodia—he will be immediately struck by the fact that not a single section shows both the Capitanian and Chhidruan stages. If one is present, the other is absent; nowhere do they occur together. The reason is obvious—they are one and the same stage. Each has a characteristic ammonoid genus, *Timorites* and *Cyclolobus*. These two genera inhabited different geographic realms of the same age . . . They were contemporaneous."

He notes also that the Chhidruan and Dzhulfian (Araksian) seem to be "mutually exclusive", but then continues to write: "In not one sequence does the Chhidruan fauna follow a Djulfian fauna, including the name or type areas of Djulfa, Chhidru-Salt Range, and Changhsing! By contrast, the rival interpretation can point to several successions, firmly correlated by various faunal and stratigraphic data, in which the Chhidruan fauna is followed by the lower Djulfian Fauna, (e.g. Waterhouse, 1969)".

Comments and résumé of "Reference Stages" used in this paper.

(a) *The time relationship between the Araksian (Dzhulfian) and Chhidruan Stages as proposed by Furnish and Glenister (1970)*

(N.B.) Under this heading I shall refer to the Dzhulfian Stage—as defined by Ruzhentsev and Sarýcheva (1965)—rather than the Araksian Stage, since the two appear to be synonymous, and the Dzhulfian has priority).

It is interesting to follow the evolution of thought concerning this question in the three papers—Glenister and Furnish (1961); Furnish (1966); and Furnish and Glenister (1970). In the first paper the faunas of the two stages

TABLE 1. THE KNOWN DISTRIBUTION OF THE GENUS CYCLOLOBUS (Excluding *C. persulcatus*)

		C. oldhami	*C. walkeri*	*C. teicherti*
Known *Cyclolobus* material of the Chhidruan Stage (typified by the Chhidru Formation of the Salt Range).	Salt Range	7 specimens	6 specimens	1 specimen
	Spiti area of Himalayas	2 specimens	30 specimens	–
	E. Kumaon of Himalayas	1 specimen	2 specimens	–
	Madagascar	–	> 150 specimens	–

		C. kullingi
Known *Cyclolobus* material of the Dzhulfian Stage (typified by strata in the Trans-Caucasus (USSR) and northern Iran	Trans-Caucasus (USSR)	1 specimen
	N. Iran	1 specimen
	C. Iran	1 specimen
	E. C. Greenland	several specimens

were considered to be of the same age, in the second the Chhidruan fauna was considered to be the older, and in the third the Dzhulfian fauna was considered to be the older.

Furnish and Glenister (1970) write—"To a large degree, an understanding of age relationships in the Upper Permian is based upon ammonoid faunas. A phylogenetic sequence of cyclolobids constitutes the primary reference, although there are a number of other less diagnostic families ranging through this portion of the system".

The above table presents the known distribution of the species within the genus *Cyclolobus*. (nb. *C. persulcatus*, which occurs in the Amarassian Stage of Timor, and is the most primitive known species within the genus, is not included.) The arrangement of species is according to Furnish and Glenister (1970), and constitutes the latest revision of the genus. See Chart 27 for further details.

C. kullingi is regarded by Furnish and Glenister (1970) as more primitive than *C. oldhami* and *C. walkeri*. *C. teicherti* (known from only one specimen) is considered by them to be closely related to *C. kullingi* and even more so to *C. persulcatus*, the Amarassian form from Timor.

Of the 19 other ammonite genera (see table on Chart 27) known from the eight areas listed above as representing the Dzhulfian and Chhidruan Stages, only two, *Stacheoceras* and *Medlicottia* are common to both stages. Very few specimens of these two genera are available and I am aware of no detail suggesting whether or not the Dzhulfian Stage representatives are indicative of an earlier stage in development than those from the Chhidruan Stage.

Of the remaining genera, *Popanoceras, Episageceras, Xenodiscus* and *Xenaspis* occur exclusively in the Chhidruan; whilst *Pseudogastrioceras* and 10 genera of the family Araxoceratidae occur exclusively in the Dzhulfian. Those genera exclusive to the Chhidruan are all known from Guadalupian or pre-Guadalupian strata.

The differing peculiarities of generic distribution between the Dzhulfian and Chhidruan Stages appear to be far more indicative of ecological rather than age differences. The differences exhibited by the included *Cyclolobus* species do not appear to provide concrete evidence that the Dzhulfian is older than the Chhidruan as tentatively suggested by Furnish and Glenister (1970). *C. kullingi*, even if shown to exhibit primitive characteristics, could easily represent a conservative offshoot from the main evolutionary line. It would appear that the associated invertebrate faunas of the two stages cannot be invoked to solve the problem.

Until such time as further information suggests evidence to the contrary, I prefer to regard the Dzhulfian and Chhidruan stages as contemporary, and since the Dzhulfian has priority, it is favoured in the present paper. Also, the latest Permian stage (see below) occurs in sequence with the Dzhulfian in its type area, but is not present in the Salt Range, the type area of the Chhidruan Stage.

(b) *The time relationship between the Dzhulfian and the underlying Amarassian.*

Spinosa *et al.* (1970), write—"A problem in relating the Dzhulfian to the underlying Guadalupian has involved failure to recognize the ancestry of the dominant Dzhulfian ammonoid [family], the Araxoceratidae . . . in older strata. This problem has been resolved with the discovery of an ancestral araxoceratid, *Eoaraxoceras ruzhencevi* Spinosa, Furnish and Glenister . . . in the uppermost Guadalupian (Amarassian) . . . beds of the Valle de Las Delicias, Coahuila, Mexico. Recognition of this Mexican occurrence appears to provide the link between the Paraceltitinae, which characterize the Guadalupian, and the advanced Dzhulfian araxoceratids". The Dzhulfian Stage of the Trans-Caucasus moreover contains, according to Spinosa *et al.*, representatives of other genera, e.g. *Pseudogastrioceras, Stacheoceras* and *Cyclolobus* which can

all be related to ancestral forms in the Guadalupian of western Texas, northern Mexico and Timor.

Waterhouse (1972) (see earlier), on the other hand, considers the Chhidruan Stage (and apparently also the Dzhulfian Stage) to be equivalent to the "Capitanian Stage". In arriving at this assessment he had apparently not yet had the Spinosa *et al.* (1970) paper available to him.

In the "Standard Reference Stages" (see Charts 29 and 35) I have taken Spinosa *et al.* (1970) to be correct.

Moreover, as in the case between the top of the Changhsingian and the base of the Triassic, it seems most reasonable to presume that some time gap exists between the end of the Amarassian Stage (typified by strata in northern Mexico) and the base of the Dzhulfian Stage (typified by strata in the Trans-Caucasus). It is most unlikely that the one follows on immediately after the other.

(c) *The Changhsingian Stage.*

Following Chao (1965), Tozer (1969), Furnish and Glenister (1970), the *Tompophiceras–Paratirolites* beds of the Trans-Caucasus (and northern and central Iran) and the equivalent Changhsingian Stage of southern China are considered to be uppermost Permian, rather than lowermost Triassic. The *Tompophiceras–Paratirolites* beds overlie the type Dzhulfian Stage strata in the Trans-Caucasus and would constitute an obvious "Standard Reference" for the uppermost Permian stage, as suggested by Tozer (1971). However, no stage name has, as yet, been coined for this sequence of beds, and I have used for provisional convenience the term Changhsingian as the only partially suitable name available. In Charts 29 and 35 I have bracketed Changhsingian to indicate that its use is purely a matter of convenience.

(d) *The time relationship between the Changhsingian and the overlying Griesbachian (the lowest Triassic stage)*

(See notes on Chart 29 elaborating on this point).

(e) *Résumé of "Reference Stages" used in this paper.*

The Trans-Caucasus (USSR) and the closely adjacent northern Iran sections provide the most useful known post-Guadalupian Permian sequence for use as a "Standard Reference" for this period. The two stages recognised within this sequence of strata, i.e. the Dzhulfian followed by an unnamed stage equivalent to the Changhsingian Stage of South China, are taken to be the "Standard Stages". The unnamed stage is referred to in Charts 29 and 35 as (Changhsingian). In the text to the charts and in the general text the brackets are discarded.

Time gaps of unknown duration are considered, in this paper, to occur between the Dzhulfian and the underlying Amarassian and between the Changhsingian and the overlying Griesbachian. These time gaps are included in Charts 24, 29 and 35 as occupying two million and one million years respectively.

4.3. The "Standard Reference Ammonite Zones" of the Permian System

"The pre-eminence of ammonites as zonal marker fossils for local and world-wide correlations is undisputed. No other organisms enable the Upper Paleozoic and Mesozoic systems to be classified and correlated in anything like such detail. This usefulness is due to their rapidity of evolution, with wealth of forms changing rapidly up the stratal column, their wide distribution and comparative indifference to facies, and usually their ease of recognition, even in the field without the use of the microscope or laborious techniques".–Arkell (1957, p. L 124).

This view, apparently, does not ride entirely undisputed. Waterhouse (1972, p. 160) in conclusion to a discussion on the "Reference Stages" of the Middle to Upper Permian writes for instance " . . . it does not mean that ammonoids have to be abandoned as time indices for the Middle and Upper Permian, however. They are certainly as useful as Fusulinacea, and, where present, as accurate as brachiopods, and obviously just as open to misinterpretation". Ammonites first appear in the Lower Devonian and die out at the end of the Cretaceous. The diversity attained by them within the Devonian, Carboniferous and Permian is relatively limited (see Table 2). A marked increase in the number of genera is met with in the Triassic, Jurassic and Cretaceous. The number of recognisable "Ammonite Zones" per system is more or less directly proportional to the number of genera occurring. Miller *et al.* (1957, p. L 24) in the *Treatise on Invertebrate Paleontology* record only five "Ammonite Zones" in the Permian whereas Arkell (1957, p. L 125) in the same volume records 58 for the Jurassic. For the Permian therefore each zone occupied nine million years on average, whereas in the Jurassic each zone occupied only a little over one million years. The situation in which a nine million year resolution of 'Ammonite Zones' for the Permian is the best achievable does not augur well for meaningful world-wide correlation within this system. A lot has been written, however, on the ammonites of the Permian since 1957 and now 11 "Reference Stages" and/or "Substages" can be recognised. Ruzhentsev and Sarýcheva (1965) recognise seven "Ammonite Zones" within the upper two stages (see Chart 24). Zonal schemes have not been devised for the lower

TABLE 2. NUMBER of AMMONITE FAMILIES, GENERA & REFERENCE ZONES RECOGNIZED IN THE DEVONIAN to CRETACEOUS.

AGE IN MILLIONS of YEARS	GEOLOGICAL SYSTEM	APPROX. NUMBER of FAMILIES + GENERA	NUMBER OF REFERENCE AMMONITE ZONES	DURATION IN MILLIONS OF YEARS	REFERENCES
65	CRETACEOUS	47 fams. 530 gen.	36 zones	70	Arkell '57, p. L 128 (genera) Teichert '67, fig 20 (families)
135	JURASSIC	40 fams. 650 gen.	58 zones	75	Arkell '57, p. L 128 (genera) Teichert '67, fig 20 (families)
210	TRIASSIC	72 fams. 395 gen.	34 zones	45	Tozer '71
255	PERMIAN	16 fams. 70 gen.	(5 zones)	45	Miller et al '57; p. L 24, L29-L79 (genera) Chart 24 of this paper (families)
300	CARBONIFEROUS	15 fams. 70 gen.	11 zones	60	Miller et al '57; p. L 24, L29-L79.
360	DEVONIAN	19 fams. 80 gen.	8 zones	35	Miller et al '57; p. L 24, L29-L79.
395					

nine stages (and/or substages) and considering the fairly low diversity of genera occurring, such zones would possibly not be more finely resolved than the stages.

4.4. **The Carboniferous/Permian boundary**

4.4.1. *Brief description of certain aspects of Carboniferous strata in the Northern Hemisphere (based on Francis and Woodland 1964, p. 221–226).*

(The notes presented here are intended to accompany Table 3, and are included for general reference in the discussion on the Carboniferous/Permian boundary.)

North-west Europe (Stephanian).

"The Stephanian Stage . . . is confined almost entirely to isolated intermontane 'limnic' basins which extend intermittently from central France to Czechoslovakia". Plant beds are abundant.

Russia (general Carboniferous).

"In the *Moscow basin* the Carboniferous rocks consist almost entirely of marine limestones and dolomites of shallow water facies. In the *Urals* the sequence is very varied: on the western slopes marine limestones predominate as in the Moscow basin, though the facies in general appears to be of deeper-water type; traced eastwards considerable parts of the limestone sequence are replaced by rapid interdigitation with marine clastic deposits, interbedded locally with much volcanic materials; coals occur only locally among the lower deposits".

In the *Donetz Basin* red beds of continental facies containing plant remains apparently predominate in the Carboniferous. Limestones containing marine faunas interdigitate with these red beds.

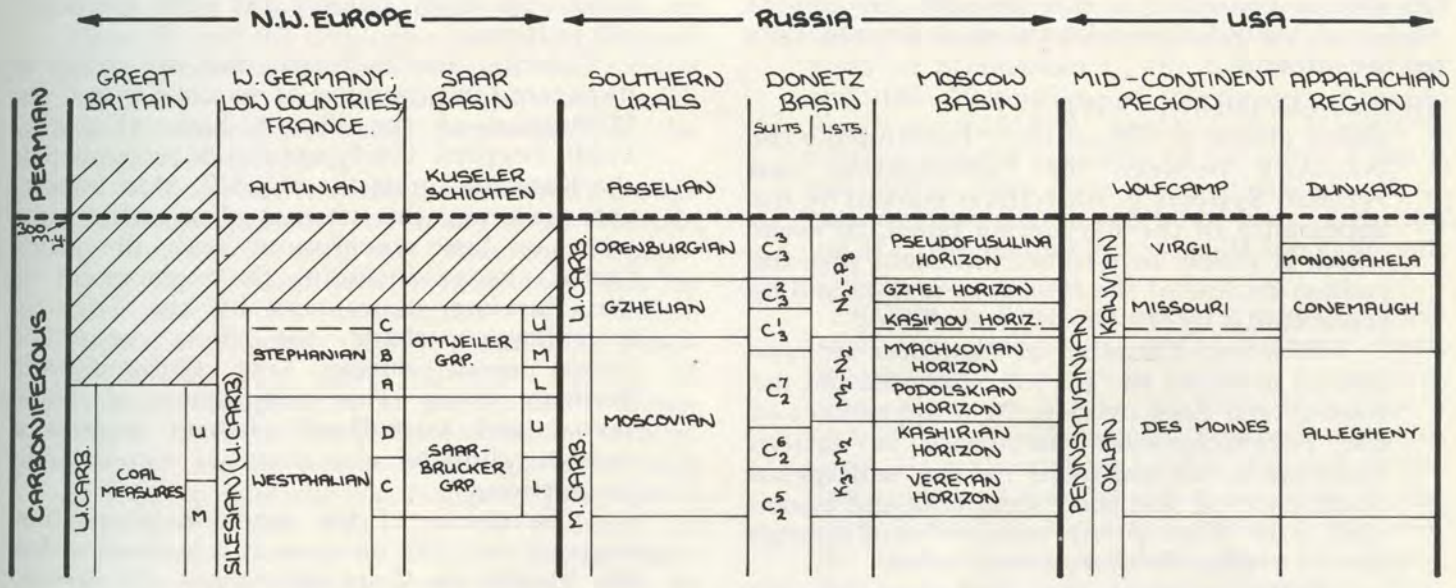
U.S.A. (Pennsylvanian).

In the *Appalachian* region the Pennsylvanian sequence is very similar to the U. Carboniferous in north-west Europe. "It is a cyclic coal-bearing non-marine sequence . . ." Correlations with Europe are based on the floras. In the *Mid-continent* region marine sequences occur in the Pennsylvanian. "Foraminifera are widespread in the marine limestones. In the beds above the Atoka in particular the fusulinid fauna is remarkably similar to that of Russia". Interdigitation of plant and marine facies allows correlation with the Appalachian section. See also notes by Helby (1969) quoted later in the section regarding the Permian/Carboniferous boundary as recognised in Australia.

4.4.2. *The Carboniferous/Permian boundary as recognised in the Northern Hemisphere continents.*

Smith (1964, p. 214–215) writes that the Carboniferous/Permian boundary is taken " . . . at the base of the zone of the fusuline, *Pseudoschwagerina (Schwagerina)* as originally proposed by Beede and Kniker (1924) and since adopted by the geological surveys of the USSR and the USA, by the Geological Society of America's Permian Subcommittee, by comparable Soviet committees (e.g. Stepanov *et al.*, 1962) and by leading authorities on the Permian from many countries. This horizon has been chosen because (a) in the view of most authors it marks the major break in marine faunas taken as a whole; (b) in many parts of the world it directly succeeds an unconformity or non-sequence and; (c) the faunal assemblage of the zone as a whole is so distinctive as to make it easily recognized. A minority view favoured by some Russian and most Chinese authors is that the base of the Permian should be taken at the top of

TABLE 3. THE UPPER HALF OF THE CARBONIFEROUS SYSTEM IN THE NORTHERN HEMISPHERE



Based on: Francis & Woodland (1964, T.1)
Helby (1969, p 69-71)

Key: ---- The Carboniferous/Permian boundary as recognized by Francis & Woodland (1964, T.1), & adhered to in this paper.

— — — The position of the Carboniferous/Permian boundary as recognized by Helby (1969, p 69-71).

the zone of *Pseudoschwagerina* because they consider that it is at this horizon that the major evolutionary break in fusulines occurs."

"Recognition of the Permian-Carboniferous transition in continental sequences is more difficult, but by widely accepted convention [recommended by the Congress for the Advancement of Studies of the Geology and Stratigraphy of the Carboniferous (at Heerlen, 1952)—see Helby, 1969, p. 70] it is taken at the base of the lowest beds containing the plant *Callipteris conferta* Brongniart."

"Since very few sequences contain interdigitations of typical marine and continental beds much controversy has centred on the time relationship between the respective index-fossils. Fomichev (1960), however, has shown that in the Donetz basin [where interdigitation of marine beds with fusulinids and continental beds with plants does occur (see Francis and Woodland, 1964, p. 223—224] *Callipteris conferta* appears much earlier than *Pseudoschwagerina*."

According to Francis and Woodland (1964, p. 223—224) this difference between the first appearance of *Callipteris conferta* and *Pseudoschwagerina* " . . . may be as much as 1 900 metres. This apparent difference may be due to accidents of collection or preservation, but there is no gainsaying the fact that there is almost insurmountable difficulty in correlating the continental facies of one area with the marine facies of another."

Ruzhentsev (1954, p. 4) writes—"The boundary between the Carboniferous and Permian according to the vertical distribution of the ammonoids, and also in terms of the other groups in the fauna, should be drawn between the Orenburg and Assel Stages [of the southern Urals] . . . No new data will be able to alter this conclusion, to which the majority of investigators have come—the conclusion that the Assel deposits belong to the Permian System . . . The ammonites of the Assel Stage are undoubtedly more closely related to those of the Sakmar Stage than to those of the Orenburg."

As far as I can ascertain (see Ruzhentsev, 1954, p. 1 and Dunbar *et al.*, 1960, p. 1766) the boundary between the Carboniferous and Permian, i.e. between the Orenburgian and Asselian Stages, as defined according to the ammonoids (see above and Chart 24) in the southern Urals is taken to coincide with the base of the Zone of *Pseudoschwagerina*. How exactly this is so I have no means of knowing from the literature available to me.

The definition of the "Standard Reference Stages and Substages" of the Permian is based on ammonites. Surely the Carboniferous/Permian boundary should be defined likewise and not on a different group of organisms, i.e. the fusulinids, as is presently the most internationally accepted custom. It is apparent that an exact definition of the boundary, based on the ammonite faunas of the southern Urals, should be instituted.

4.4.3. *The Carboniferous/Permian boundary as recognised in the Gondwana continents.*

Locating, with confidence, the correct position of the Carboniferous/Permian boundary in the Gondwana countries is not possible on present evidence. Australia provides the most hopeful data for the attempt.

(i) *Australia* (Helby, 1969).

Helby (1969, p. 70) writes: "Traditionally the boundary between the Carboniferous and Permian Systems in Australia is marked by the appearance of the *Eurydesma* fauna, an event which is widely held to be coincident with the sudden decline of the *Rhacopteris* flora and its replacement by the *Glossopteris* flora."

However, a number of sequences are now known in which the *Eurydesma* fauna and the *Rhacopteris* flora overlap. "The appearance of the *Potonieisporites* microflora in eastern Australia is accompanied by the widespread occurrence of glacigene sediments and associated with *Rhacopteris* remains" and appears also to overlap the *Eurydesma* fauna.

Helby suggests that the base of this microflora (hitherto regarded as the uppermost Carboniferous microflora in Australia) ". . . is the closest available approximation to and most convenient location for the top of the Carboniferous System in Australia."

Helby's discussion regarding the relationships between the most significant biological changes in Australia and Euramerica near the Carboniferous/Permian boundary runs as follows:

"If problems of terminology are to be avoided, the location of the Carboniferous/Permian boundary in Australia should be based on an adequate definition of both the top of the Carboniferous type section and the base of the Permian type section. In brief, the top of the Stephanian C—the uppermost division of the Stephanian in the St. Etienne and Saar Basins—defines the top of the Carboniferous System, and, consequently, the base of the Permian System, in Western Europe. To alleviate the considerable problems concerning delineation of this boundary, the Congress for the Advancement of Studies of the Geology and Stratigraphy of the Carboniferous (at Heerlen, 1952) recommended that the top of the Carboniferous be drawn below the lowest occurrence of the gymnosperm *Callipteris conferta* Sternberg."

"A distinct lithological change from coal measure to red beds can be seen in the central portions of the Stephanian C, accompanied by a marked floral change from a typical Stephanian flora to a flora with a distinct Autunian aspect (Cignoux, 1955, p. 200). In a study of the palynostratigraphy across the presently recognised Carboniferous/Permian boundary in the Pfalz Basin, a northern extension of the Saar Basin, Helby (1966) demonstrated the presence of a major microfloral change within the Breitenbach Formation (Stephanian C), characterised by the decline of dominant *Lycospora* and the rise to prominence of *Potonieisporites, Illinites* and other spermatophyte forms."

"Helby also indicated that this change is duplicated in a number of sections within the Missourian of the Illinois Basin (Kosanke, 1950; Peppers, 1964) and can be recognised in the Kassimovian of the U.S.S.R. More important, however, this change of microflora was more or less synchronous with the major faunal change—including the replacement of the *Fusulina* microfauna by the *Triticites* microfauna—perhaps the most important faunal event during Late Carboniferous/Permian times. This coincidence of major faunal and microfloral changes suggests a sudden climatic alteration of considerable proportions."

"Synthesis of the available information suggests that the changes at a horizon within the Stephanian C are expressions of a drastic, widespread change in the earth's climatic patterns. Numerous changes in the style of sedimentation at this particular horizon complement the theory. A similar pattern can be recognised in Australia, where the major floral event of the Upper Carboniferous/Permian sequence is represented by the sudden decline of the *Grandispora* microflora and its replacement by the *Potonieisporites* microflora, an event which appears to be intimately associated with the widespread development of glacigene sediments in eastern Australia. Of further interest is the appearance in abundance of *Potonieisporites* and other spermatophyte pollen, both in the Euramerican and Australian regions. It appears reasonable to suggest that the changes described above are virtually synchronous. Physical evidence supporting this hypothesis is provided by the apparent parallelism of this horizon with the line marking the base of the Kiaman Magnetic Interval."

Helby's suggestion that the base of the *Potonieisporites* microflora ". . . is the closest available approximation to and most convenient location for the top of the Carboniferous System in Australia. . ." means that he is advocating a fairly considerable downward displacement of the Carboniferous/Permian boundary in the various reference sections in Russia, Europe and U.S.A.

In view of the discussion held earlier in this section (4.4.2.) his suggestion would probably not be widely acceptable.

(ii) *Australia and remainder of Gondwanaland.* (This paper).

(N.B. References and detail regarding the microfloral data discussed below are given in Anderson, 1973, Ph.D Thesis in preparation).

Unlike the remainder of Gondwanaland, excellent marine invertebrate faunas occur commonly in Australian Permian strata. Ammonite faunas of Tastubian to Roadian age occur (the location of these are shown on Chart 35 and the fauna given on Chart 30) and these provide a reasonably sound basis for the correlation of strata, within this range, with the "Standard Reference Sequences" of the Northern Hemisphere.

None of the remaining invertebrate groups provide, at present, any really good evidence for correlations with the "Reference Sequences". The foraminifera, for instance, can be used safely for correlation only within Australia (Crespin, 1958). Fusulinids, stratigraphically the most important group of Permian foraminifera in the Northern Hemisphere, are unknown in the Australian Permian.

The marine faunas of the glacigene beds of Western Australia (i.e. Nangetty Fm., Lyons Grp. and Grant Fm.) are all included in invertebrate Zone A by Dickins (1969). Since the Holmwood Shale (Perth Basin) with its Tastubian age ammonoids is placed in the upper part of Zone A by Dickins (1969), we may presume the glacigene beds to be not much older (unless Zone A represents a longer time period than later zones). I have included the Holmwood Shale (in Chart 35) as upper Tastubian and the glacigene beds as lower Tastubian.

The microflora of the Nangetty Fm. (Perth Basin—Microbaculispora Assemblage Zone of Segroves, 1970) and the Grant Fm. (Canning Basin) appear to be equivalent. I am aware of no published work on the microflora of the Lyons Group (Carnarvon Basin). The Microbaculispora Assemblage is only subtly different from the Quadrisporites Assemblage (in the lower part of which occurs the Holmwood Shale), further evidence to suggest that no long time interval separates the glacigene beds from the Tastubian.

The Microbaculispora Assemblage Zone of Western Australia can be fairly confidently correlated with microfloral Stage 2 of eastern Australia, also associated with glacigene beds. It occurs in the Boonderoo beds of the Galilee Basin, the Merrimelia Fm. of the Cooper Basin and the glacigene beds of Victoria.

Thus there apparently occurred in Australia widespread deposition of glacigene deposits during the lower Tastubian. These deposits, and younger Permian deposits in areas where the glacigene beds do not occur, rest most frequently with unconformity on L. Carboniferous or older rocks. In certain areas in eastern Australia (e.g. the Joe Joe Fm. of the Galilee Basin and western Springsure Shelf; and the Seaham Fm. of the Lower Hunter Valley—Sydney Basin) glacigene beds, apparently of uppermost Carboniferous age were deposited. These constitute microfloral Stage 1 of Evans (1967), i.e. the *Potonieisporites* microflora discussed by Helby (1969) (see above). This microflora Helby takes to be the time equivalent of microfloras in the upper parts of Stephanian C, the Kasimov Horizon and the Missourian of north-west Europe, Russia and U.S.A. respectively. If this is correct and the correlations shown in Table 3 are correct, then these lower glacigene beds of eastern Australia would be of lower Gzhelian age (i.e. the second-last stage of the Carboniferous).

Thus in Australia there appears to have been two pulses of glacial activity (each occupying very probably less than a ½ million years—see notes on Dwyka Tillite in Section 5 of text), one occurring in the lower Gzhelian some 10 million years before the end of the Carboniferous and the other occurring in the lower Tastubian some five million years after the start of the Permian. The first pulse appears to have been of less widespread effect than the second.

Taking into consideration the remaining Gondwana countries (particularly those areas included in Chart 35), throughout there occur glacigene strata at the base of an essentially Permian/Triassic sequence. These strata rest for the greater part with strong angular unconformity on Precambrian strata or Basement Granite. For the remainder (i.e. the southern and south-eastern extremities of the Karroo Basin of South Africa; the Transantarctic Mountains; and the Parana Basin of South America) they apparently rest unconformably on beds of Devonian and earlier Palaeozoic age. (At places in the Southernmost Karroo Basin the lithological evidence suggests a break in sedimentation between the strata of the Witteberg beds of the Cape 'Supergroup' and the overlying Dwyka Tillite. The former is thought to be Devonian or possibly L. Carboniferous in age on uncertain palaeontological evidence (Anderson, 1973).

The microfloras of these glacigene beds are (considering those areas where they are fairly well known, e.g. northern Karroo Basin of South Africa; Middle Zambezi Valley of Rhodesia; Parana Basin of South America; India) essentially the same and can be matched with the Stage 2 microflora of eastern Australia and the Microbaculisporites Assemblage Zone of the Perth Basin of Western Australia, i.e. with the second pulse of glacial activity in Australia.

Present data thus seem to suggest that the bulk of the glacigene strata throughout Gondwanaland are of essentially the same age. The exceptions are the uppermost Carboniferous glacial period in eastern Australia (discussed previously) and the Carboniferous

alpine glaciation of South America (discussed below).

Along the Andean Mountain belt of Bolivia and Argentina numerous scattered small outcrops (often connected in subsurface to form relatively small basins—see Chart 23) of Upper Palaeozoic strata display evidence of glacial activity. These areas are not included in the correlation chart (i.e. Chart 35).

Frakes and Crowell (1969, p. 1007, see also Figure 3), write—"Glacial activity is recorded in rocks of Early Middle and Late Carboniferous and Early Permian (?) age in Argentina and Bolivia . . . Direct evidence for glaciation in the . . . Andean basins consists of a single striated floor and common striated clasts in diamictites and associated strata. Many Andean diamictites are intercalated in sequences which contain marine invertebrate fossils and turbidites . . . Ice centers apparently developed in rugged highlands within the Andean orogenic belt. Alpine or piedmont glaciers, or both, flowed downward onto narrow shelves, and till then moved into the marine portions of the basins by mudflow and sliding. The continental portions of the basins lay generally eastward of the marine areas and a topographically mature terrane still farther east was affected only slightly by glaciation, presumably because it was distant from glacial centers and lay at a relatively low elevation."

The overall history of glaciation in the Carboniferous and Permian of Gondwanaland thus possibly reads as follows:

(a) Alpine and piedmont type glaciation occurred in the rugged highlands of the Andean orogenic belt (of Bolivia and Argentina) intermittently throughout the Carboniferous.

(b) A relatively minor pulse of glaciation (of less than 500 000 years duration, and of fairly restricted nature) affected several areas in eastern Australia some 10 million years before the close of the Carboniferous.

(c) A major period of glaciation, possibly reminiscent of the Pleistocene glacial epoch, lasting up to 500 000 years and affecting the whole of Gondwanaland occurred some five million years after the start of Permian.

The attempt to locate the Carboniferous/Permian boundary in Gondwanaland has clearly become an attempt to date the ubiquitous glacial deposits. The major proportion of these appear to fall within the Permian and to rest with distinct unconformity on Lower Carboniferous and older rocks.

4.5. The Permian/Triassic boundary

See notes on Chart 29 for discussion on the Permian/Triassic boundary. Nothing further is added here.

5. DISCUSSION ON THE PERMIAN CORRELATION CHART (Chart 35).

A good proportion of the information in Charts 24–34 is directed towards an attempt to compile a meaningful correlation table (Chart 35) representing the true time-relationships between Permian strata distributed throughout the world.

The following factors are considered vital to an attempt to compile a correlation chart to be used as a base for subsequent phylogenetic studies:

(i) The choice of "Standard Reference Stages", "Substages" and "Ammonite Zones" and the definition of the lower and upper boundaries of the Permian System. (See 5.1 below.)

(ii) The application of absolute age data. (See 5.2 below.)

(iii) The consideration of all available palaeontological and lithological data. (See 5.3 below.)

(iv) The consideration of rates and continuity of deposition, and of compaction of sediments. (See 5.4 below.)

5.1. The choice of "Standard Reference Stages", "Substages" and "Ammonite Zones" and the definition of the lower and upper boundaries of the Permian System

Considerable controversy exists in the literature as to what should constitute the "Standard Reference Stages", "Substages", and "Ammonite Zones"; and the lower and upper boundaries of the Permian System. I have thus been obliged to make my own judgements. (See Charts 24 to 30 and section 4 of text.)

The "Standard Reference Sequence" used is by no means ideal since it is necessary to compile it from three sections from three different areas, i.e. the Lower Permian from the southern Urals; the lower half of the Upper Permian from western Texas and northern Mexico; and the upper half of the Upper Permian from the Trans-Caucasus (USSR). The exact time relationships between these three sections are not clear, but there appear to exist time intervals between them. The duration of these intervals cannot, on present evidence, be confidently estimated, but since it is necessary to indicate them on the correlation chart, I have taken them to occupy two million years each. There appears likewise to be a break in time between the top of the Changhsingian Stage and the base of the Triassic. I have taken it to occupy one million years. There is, as far as I can gather, no evidence for a break between the lowermost Permian and uppermost Carboniferous as defined in the southern Urals.

Further questions exist: Did there not occur time breaks within each of the three sequences combined to form the "Standard Reference", and if so how long were they? What was the true relative time duration of each "Stage" and "Substage"? As I have drawn Chart 35, most of the "Substages", plus those "Stages" which have not been further subdivided, are each taken to occupy

the same period of time, i.e. four million years. The Amarassian and Roadian "Substages" have each been taken to occupy two million years.

It must be accepted that the presently used foundation for world Permian correlations is shaky and subject to possible need for substantial alterations.

5.2. **The application of absolute age data** (See Charts 31—33).

The data presently available is very limited and is of use only in forming a rough provisional guide to the age of the start and finish of the Permian System and hence to its duration, i.e. ± 45 million years. No ages can be applied to any of the "Reference Stages" and certainly no direct use of absolute age data can be made in the correlation of Permian strata.

5.3. **The consideration of all available palaeontological and lithological data**

I have attempted to indicate on Chart 35, for each formation, member etc., the palaeontological content (other than the microfloras) on which the correlations are based. Microfloras have been used extensively, particular in the case of the Gondwana countries, in correlations, but because of the difficulty experienced in gathering comprehensive data (relating to which strata yield good assemblages, poor assemblages or no assemblages at all) I have not attempted to indicate such information. A similar problem exists in the case of marine deposits of the U.S.A. I have not been able to gather adequately comprehensive data as to which portions of which sections are marine (with or without ammonites), weakly marine or non-marine and have therefore indicated only certain of this information (see Chart 35 for notes).

New and improved palaeontological data will continually become available and will necessitate a continual need for revision of the correlation chart.

In the case of barren or palaeontologically unstudied strata correlation has to be attempted where possible on lithological characteristics alone. This is reasonable where the succession in adjacent or even widely separated basins is similar and where certain horizons in one or other of the basins are barren or unstudied.

5.4. **Rates and continuity of deposition; compaction of sediments**

These factors need to be seriously considered when compiling a time-oriented correlation chart. Unfortunately, at the present time, only rough conclusions can be drawn from our state of knowledge concerning recent and present rates of deposition, continuity in sedimentation and compaction of sediments (see Chart 34). A brief discussion follows, taking the strata of the Karroo Basin of South Africa as an example of the manner in which I have attempted to apply the available information (see map on Chart 35 for location of areas discussed and Anderson (1973) for derivation of information included in this section).

Upper Ecca (of the Welkom and Ladybrand —marked LA on chart 35/areas.

General Thickness: ± 250 m.

Sediment type and environment of deposition: The Upper Ecca sediments represent a single, apparently unbroken transgressive-regressive sequence from delta-front (sandy to clayey silts) to pro-delta (silty clays) and back to delta-front deposits. The pro-delta sediments occupy some 5/6 of the total sequence. The sediments fine steadily from the top and bottom to the middle of the succession. The Middle Ecca below and the Tapinocephalus Zone equivalent above represent the delta-plain and alluvial-plain facies of the same cycle. The Upper Ecca sediments of the area under discussion were deposited in a shallow shelf sea (apparently non-marine) deepening gradually to the south-east and in all likelihood never reaching more than 50—100 m in depth.

No time break, of any significance, in the succession from the Middle Ecca through the Upper Ecca into the Tapinocephalus Zone equivalent is suggested from a study of the included microfloral assemblages.

Possible maximum depth of burial in past: ± 2 000 m (N.B. this figure is a direct estimate of the thickness of strata that have possibly been removed by erosion and is not based on diagenetic evidence).

Porosity: 10—12% in Welkom area, steadily decreasing to 2—4% in Ladybrand area.

Original clay content: Unknown.

Present clay content: Mixed layer illite—montmorillonite, and kaolinite most abundant; chlorite and true illite generally less abundant; true montmorillonite very rare.

Calculations on duration of sedimentation:

The only rates of deposition figures available in the table on Chart 34 which can possibly be applied to the Upper Ecca are those of 7 and 5 cm/1 000 years for sandy and silty clays of the upper continental slope and silty clays of the lower continental slope, respectively, of the Gulf of Mexico. Just what Kukal (1971) is referring to as the upper and lower continental slopes and just how nearly applicable these situations are to the Upper Ecca I cannot be sure. It would be most desirable to have numerous figures available on recent and present delta-front and pro-delta deposition.

At a rate of 6 cm/1 000 years, 60 m would be deposited in one million years (assuming no compaction occurred, i.e. that the porosity remained what it was at the original sediment surface: ± 80%).

General compacted thickness of Upper Ecca: 250 m.

Average primary porosity: 7%.

Original porosity at sediment surface: 80%.

If we assume that the reduction to 7% porosity was a result purely of compaction, then the present sediment thickness is ± 1/5 what it would have been assuming no compaction had occurred. Thickness of Upper Ecca (assuming no compaction) would then be: 1 250 m (nb. it is not necessary to compensate for montmorillonite—see notes on compaction of shales and muds on Chart 34—since for any porosity under about 15% the sediment would be ± 1/5 thickness of the uncompacted sediment).

At a rate of 60 m/one million years, the duration of Upper Ecca sedimentation would be in the order of 21 million years.

On Chart 35 the period between the Middle Ecca and the Tapinocephalus Zone equivalent is 13½ million years. (The positions on the Chart of the Middle Ecca and Tapinocephalus Zones are based on general world-wide palaeontological correlations.)

I have concluded, on the above calculation and on palynological evidence that no hiatus of any time significance occurred during Middle Ecca to Tapinocephalus Zone equivalent sedimentation.

The theoretically calculated 21 million years does not coincide exactly with the possible maximum of 13½ million years available on Chart 35. It would be remarkable if it did, considering the provisional nature of the correlation chart and the urgent need for more data on recent and present rates of deposition.

Middle Ecca. (In those areas of the northern Karroo where it is preceded and succeeded by normal Lower and Upper Ecca deposits.)
Thickness: Variable from 15 to 300 m.
Sediment type and environment of deposition: Typical sandstones, siltstones, shales and coals of deltaic and alluvial-plain sequences.
Porosity of sandstones: ± 12% in Welkom area grading down to ± 6% in Ladybrand (LA) area.
Duration of Middle Ecca sedimentation: Sediments accumulate far more rapidly in delta-plains than in shallow shelf seas (see table on Chart 34). It would be impossible, on presently available information, to calculate very precisely the duration of Middle Ecca sedimentation, but assuming there had been no major breaks in sedimentation it would probably have been well within one million years. However, on palynological evidence at least one major break appears to be present. I have exaggerated the probable duration of the Middle Ecca on Chart 35 for the sake of clarity.

Lower Ecca (of the Ladybrand (LA) area, and elsewhere in the northern Karroo).

Lower Ecca sediments and their inferred environment of deposition are much the same as those of the Upper Ecca. Without repeating the above calculation, it is possible to conclude that the Lower Ecca in its normal development occupies the full period between the Dwyka Tillite and the Middle Ecca.

Dwyka Tillite (of the northern Karroo area).

If the Pleistocene glaciation can be taken as a guide, the Dwyka Tillite, consisting of a very variable thickness of tillites, varves, sandstones, siltstones etc. deposited on an irregular glacially eroded basement, was most likely deposited in under one million years. The Pleistocene glacial period according to synthesis of all the most recent data (Evans in PTS '71) endured for ± 400 000 years. I have included the Dwyka Tillite (and supposed equivalents throughout Gondwanaland) on chart 35 as occupying two million years, rather than the possibly more likely ½ million years, to avoid cramping.

The tetrapod-bearing zones of the Beaufort Series (whole of Karroo Basin considered).

I am aware of no figures on rates of deposition of recent or present sediments which may offer a guide to the duration of the various zones of the Beaufort Series.

However, a consideration of the vertebrate assemblage known from each successive zone suggests the occurrence of definite time-intervals between them (except perhaps between the Cistecephalus and Daptocephalus Zones). Considerable advances in the general evolutionary status of the overall assemblage of each successive zone are evident. On the other hand, no evidence of evolutionary change is evident within the scope of any particular zone. Since only 15—20 million years are available for accommodating four zones it would appear most likely that each was of relatively short duration.

In Chart 35 I have included each as occupying two million years. This very likely represents an over-exaggeration.

5.5. Explanation of the variable emphasis directed towards the treatment of the various countries in the Permian correlation chart

Particular emphasis has been placed on the attempt to correlate strata of Gondwanaland with strata in the Northern Hemisphere.

As regards the Northern Hemisphere, all those sections including the important marine strata (particularly ammonite-bearing strata) and vertebrate-bearing strata have been included.

As regard Gondwanaland, most attention has been paid to Australia and southern Africa. Fairly comprehensive coverage of these areas has been attempted. For India, Antarctica and South America only a single section has been given in each case—the most complete and representative for that country (continent).

The reason for the emphasis placed on Australia is that marine strata are far more common than in any other Gondwana region. Ammonite-bearing beds of Tastubian to Roadian age occur and it is these that provide the essential

basis for the correlation of Gondwana strata with the Northern Hemisphere (see Chart 30).

Southern Africa has been emphasised for two reasons. Firstly, virtually all known tetrapod vertebrate-bearing beds of the upper 2/5 or so of the Gondwana Permian occur in this region (particularly in the Karroo Basin of South Africa). These provide some basis for correlation with the tetrapod zones of the Russian platform. Secondly, my particular field of specialization involves the elucidation of the Permian microfloral sequence in South Africa. It is via this microflora that correlation is achieved with Australia and hence indirectly with the Northern Hemisphere.

5.6. Concluding remarks on the Permian correlation chart

I have attempted to take into consideration all available information in the compilation of this chart. It must be appreciated, however, that any correlation chart can, at best, only be as good as the available information. A very great deal of data must still be forthcoming before any such chart can be confidently regarded as accurately reflecting the true sequence of events that occurred.

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Linda Botha, Marietjie Botha, Elsme Immelman (all SOEKOR staff) and my sister-in-law Evelyn Schwytzer typed the initial drafts of the text. Mable du Plessis typed the final draft of the text and Sharyn Holloway typed the bibliography: to all of them many thanks.

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9. NOTES ADDED AT PROOF STAGE

Note 1

TEICHERT, C. April 1973 (letter). The University of Kansas, Paleontological Institute, Department of Geology, Lawrence, Kansas 66044, U.S.A.

Teichert has brought to my attention four very recent papers (which are unfortunately not yet available to me) relevant to the discussion on the Permian-Triassic boundary. Three of these were presented at the Permian-Triassic conference in Calgary, Alberta, 1971, the proceedings of which have now been published as vol. 20, No. 4 (December, 1972) of the Bulletin of Canadian Petroleum Geology. Two of the three conference papers were by Kummel and Teichert on the Permian-Triassic boundary of East Greenland and in the Tethys area, and the third by Kummel on lower Scythian faunas. The fourth reference is a major work (250 pages and numerous plates) on the Permian-Triassic boundary in North-western Iran (Kuh-e-Ali Bashi), to be published later this year in the Bulletin of the Museum of Comparative Zoology, Harvard University. Teichert writes that it "... will be the first fully palaeontologically documented discussion of the section in that area. Among other things we show that the ammonoid zonation introduced by the Russians for the 'Changhsingian' interval is based in part on erroneously identified genera and has to be greatly modified."

Note 2 (see Charts 29 and 35)

The Zaluch Group of the Salt Range should be extended to include the Chhidru Formation.

Note 3 (see Charts 28 and 29)

KUMMEL, B. (1972). The Lower Triassic (Scythian) Ammonoid *Otoceras. Bull. Mus. comp. Zool. Harv.*, 143(6), 365–417.

(a) Kummel recognises only one species, with two subspecies, within the genus *Otoceras* i.e. *Otoceras woodwardi woodwardi* (restricted to the Himalayan region) and *Otoceras woodwardi boreale* (restricted to the Arctic region).

(b) Kummel finds the Griesbachian Stage (of the Sverdrup Basin) and its four-fold ammonoid zonation proposed by Tozer unacceptable as a standard for international correlation. Teichert (1973, letter) agrees with Kummel. The disparity of views currently held is a reflection of the incomplete state of the information available. Further material and taxonomic studies will undoubtedly smooth out the problems.

Note 4 (refer to Chart 35).

McLACHLAN, I. R. and ANDERSON, Ann (1973) (see bibliography). McLachlan, I. R. 1973 (pers. comm.). Bernard Price Institute for Palaeontological Research, Witwatersrand University, Johannesburg.

The marine strata indicated for the Kalahari Basin and the Warmbad Basin (both in South West Africa) should be shifted down and included in the uppermost part of the glacial Dwyka Tillite equivalents. A marine horizon of equivalent age occurs in the uppermost sections of the Dwyka Tillite over at least the Southern two-thirds of the South African Karroo Basin.

An unconformity is thought to occur between the Nossob Sandstone and the 'Eurydesma Beds' in the Kalahari Basin.

10. ERRATA Referring to Part 1. (i.e. Charts 1–22 and accompanying text).

Page 4 References.
Add "(See chart 8)" after "Balme (1968)"

Chart 1 (a) Third last paragraph, bottom right hand corner.
Add "(See chart 8)" after "Gyronitan zone".
(b) Last paragraph, bottom right hand corner.
Replace "Bed 3 of Madagascar" by "Bed 5 of Madagascar".
(c) See note (nb.) in Cistecephalus zone title block.
Replace "actually included there" by "indicated in the correlation section thereof".
(d) Cynognathus zone: See notes referring to Euparkeria capensis.
Replace "bipedal" by "semi-bipedal".
Replace "hybernation" by "aestivation".
(e) Cynognathus zone. Invertebrate fauna.
Replace "millipedes" by "millepedes".
(f) Lystrosaurus zone; See notes referring to Myosaurus gracilis.
Replace "mouse sized" by "rat sized".

Chart 2 Red Beds; See notes referring to Hypsilophodontidae.
Replace "Both forms are the order of 4 inches long" by "The skulls of both forms are the order of 4 inches in length".

Chart 3 South America; Ischichuca Fm.
Replace "Masetognathus" by "Massetognathus".

Chart 5 (a) Add "Germ (Rhaet)" in the list indicating the geographic and stratigraphic distribution of the Tritylodontidae.
(b) Stratigraphic columns. China.

Delete West and South; switch Yunnan with Shansi and Sinkiang at heads of columns.

Chart 9 5th paragraph of explanatory notes.
Delete "at present" from first line.

Chart 20 (a) Madagascar; Sakamena Group; Bed 5.
Add "(See chart 8)" after "Gyronitan zone".
(b) Southern Africa; Middle Zambesi Valley etc.; Palaeontology; Ripple Marked Flags.
Delete "No descriptions . . . presented, but" in second sentence.

Add at end of second sentence "Descriptive work on the flora is confined to two very brief and poorly illustrated papers—i.e. Seward, A.C. 1921 (See Bibliography)
and Walton, J. 1926; Additions to our knowledge of the fossil flora of the Somabula Beds, Southern Rhodesia. *Trans. geol. Soc. S. Afr.* 29: 137–140.

Chart 21 (a) See note (c) beneath key.
Replace "both plants and invertebrates occur" by "both plants and vertebrates occur".
(b) Drakensberg lavas. Replace "dolerite feeders" by "Karroo dolerites (possible feeders)".

Palaeont. afr., **16.** 85–86. 1973

BOOK REVIEW, by S. H. Haughton

Findlay, G. H. Dr. Robert Broom, F. R. S. Palaeontologist and Physician/1866–1951. A biography, appreciation and bibliography. A. A. Balkema/Cape Town/1972.

This book, of 208 pages and 57 illustrations, is priced at R7,50. It is prefaced by a 5-page appreciation of the subject written by Raymond A. Dart, the anatomist of the University of the Witwatersrand who startled the world in 1924 by his description of the "man-ape" *Australopithecus* represented by a juvenile skull and lower jaw found in the limestone deposits of Taungs, C. P.

Dr. Findlay has divided his account of his subject into two parts and has added a chronology and a bibliography, the latter consisting of 456 entries written from the year 1885 until the final one in 1952. Of this number, 37 have Broom listed as a co-author, but in the senior capacity. By far the greater number consist of descriptions of the anatomy of vertebrate fossils and of living vertebrates (amphibia, reptilia, mammals, and hominids); but some are of a more theoretical nature, and four of them are of interest to the philatelist.

Part 1 of Findlay's book is entitled "Biography"; part 2 "Science and the Man". Broom's life extended from his birth in Paisley in Scotland in 1866 to his death in Pretoria in 1951 and appears to have been governed throughout by a sense of superiority over most of his fellow scientists, and an objection to remaining chained to any one environment for any considerable time. The author's first paragraph in Chapter I is of some significance: "Robert Broom liked working out his family heritage. Alas, it was a bleak one—made up of six generations of Scotsmen setting their faces against poverty and tuberculosis, reinforced from time to time by stern calls to religion." Robert himself suffered from ill-health during his early years, so that his early schooling was of a sporadic character; but fresh air, away from Glasgow, at the week-ends and during the summer holidays worked wonders, opened his eyes and mind to the wonders of Nature, and developed a thirst for first-hand knowledge.

Four years at Hutcheson's Grammar School in Glasgow were followed by three years as an unpaid laboratory assistant in the Chemistry Department of Glasgow University. At the age of 17, Broom enrolled as a student of science and medicine at Glasgow, where he appears to have been something of a "lone wolf", unorthodox, and with something approaching contempt in his mind for most of those giving instruction. One man, however, appears to have exerted a great influence on this young student—John Young, Under-Curator of the Hunterian Museum, who introduced Broom to practical palaeontology and taught him the use of the microtome for preparing microscopic sections. In the Medical School, Broom found Cleland, the anatomist, of interest and was guided by the clinical accuracy displayed by Gairdner; but "the only branch of clinical work for which Broom immediately developed a liking was midwifery". For this, in his final medical examination in 1889, Broom carried off the William Hunter medal. This led him, after registration as a medical practitioner, to work for some months at the Glasgow Maternity Hospital, before shifting to the Royal Infirmary.

Then followed a period of "wanderlust". Two voyages as a ship's doctor to North America and back in 1891 were followed by emigration to Australia in 1892 after becoming affianced to his sweetheart Mary Baillie. First to Queensland, where he had little medical work to do, spent many hours collecting plants and animals of all sorts, found an interest in the aborigines and their detailed knowledge of the wild life of the region, and was laid prostrate for weeks by a bad attack of typhoid fever. Thence, in 1893, he migrated to New South Wales where he was joined by and married to Mary Baillie. In this State he remained until 1896, doing medical work at a succession of centres but concentrating for the most part on the "study of Nature", both living and fossil, and completing his M.D. thesis. In May, 1896, the Brooms sailed for England, and Broom made there his first acquaintance with Karroo vertebrate fossils from South Africa. Here was a study to which he considered he could contribute to morphological knowledge; so in January 1897 they sailed for South Africa which country was to be "home" for Robert until his death on April 6, 1951.

Chapters III to IX of Part I of this book are devoted to a fairly detailed account of Broom's doings and movements during these 54 years, with many quotations from diaries and letters which give ample evidence of Broom's self-confidence and, in some cases, the contempt he felt for any worker in his chosen fields who did not agree with his views or his actions. He described the staff members of the South African Museum at Cape Town—of whom Dr. Louis Péringuey was the Director and the present reviewer a member—as "jealous nonentities".

Settling in the town of Douglas, on the Vaal river, in 1918 Broom began to take an interest in the physical characteristics of the various non-European groups that lived in the area—Bushmen, Korannas, Hottentots—and made a collection of skulls and skeletons, some from "very old graves", which he studied intensively. His methods were not always in strict accordance with the law; but his studies led him to the conclusion that the Bushman and the Koranna were the two fundamental types in the area and that the Hottentot was a cross between the two. He admitted that these views were not universally accepted but "I think the world will ultimately agree with my solution in the main". During his years at Douglas, Dart's account of the discovery in the Taungs breccias of the skull and lower jaw of a young "man-ape", *Australopithecus*, burst upon the world and was received with scorn by highly-placed anatomists in Europe;

but Broom vigorously supported Dart's conclusions—and his own discoveries made from 1936 onwards fully substantiated the stand taken by them.

Through the influence of General J. C. Smuts and the Hon. J. H. Hofmeyr, stimulated by Professor Dart, Broom was appointed as a temporary "assistant for Palaeontology and Physical Anthropology" at the Transvaal Museum, in Pretoria, in 1934, a post that he occupied until his death. It was here, in addition to writing many descriptions of what he considered to be new genera and species of mammal-like reptiles of Karroo age, that he contributed so much to the discovery, recovery, and description of the humanoid remains found in deposits in caves in the dolomites of the Transvaal, in particular those from the Sterkfontein area (including Kromdraai). The chapters of the book dealing with these seventeen years are of intense interest. They, and the others, display a man of endless industry and immense powers of observation.

In Chapter XI the author attempts an evaluation of "the Man and His Thoughts". In a review of a book such as this, it is not desirable to enlarge on the author's findings. Suffice it to say that the author has depicted the simple nature of his subject's attitude towards his fellow-workers in the same fields of study—admirable fellows if they agreed with his conclusions, but pompous or ignorant nonentities if they did not so agree. There can be no doubt that Broom's mind was an extremely active one and that he saw that the essential preliminary to the postulation of a hypothesis was the possession of facts. But facts of themselves were to him useless unless they could be co-ordinated into a coherent whole; and the attainment of this coherent whole was his objective in the two fields of study in which he spent most of his scientific life—the origin of mammals and the origin of Man. Read this chapter more than once—it is revealing.

The book ends with a short chapter entitled "Broom's Contribution to the Origin of Man" (which does not exactly express its contents), followed by a Chronology and a Bibliography. Of the works listed 64 appeared during the years that he was associated with the Transvaal Museum.

Readers of this book will agree that it is a fitting tribute to an outstanding scientific personality who made South Africa his home and who did much to enhance its importance in the field of vertebrate palaeontology, an importance that is now recognized on a world-wide scale.

NOTES FOR THE GUIDANCE OF AUTHORS

GENERAL. The increase in size and scope of the journal during the last two years has emphasised the need for a greater degree of consistency in the style of manuscripts submitted for publication. The suggestions to authors given here is an attempt to ensure consistency and avoid unnecessary delays in publication. Authors are urged to follow these suggestions when preparing papers and especially where changes in the general style of the journal have been introduced. These are not only aimed at consistency but to help speed up editorial work and cut down publication time. For general style requirements and layout of papers authors should consult recent issues of the journal. *Palaeontologia Africana* is published annually in separate parts; the number of parts being largely determined by the number of contributions. In this way rapid publication of research material is assured. All aspects of palaeontological research are published and contributions from other related branches of the earth sciences are also welcome. There is no subscription rate although separate parts or volumes may be purchased. Free exchange with other institutes is encouraged and information about this can be obtained from the editors.

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