PALAEONTOLOGIA AFRICANA

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

VOLUME 14, 1972

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Addendum to Volume 13

The correct address for Mr. S. F. le Roux is: Vereeniging Technical High School, and not as stated in his paper on page 1.

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BERNARD PRICE INSTITUTE FOR PALAEONTOLOGICAL RESEARCH
REPORT OF THE HONORARY DIRECTOR
FOR THE YEAR 1970

INTERNATIONAL SYMPOSIUM ON THE GONDWANA SYSTEM

The scientific highlight of the year was the gathering of Gondwana geologists at the Second International Symposium on the Gondwana System which was held in South Africa in July and the first half of August under the auspices of the International Union of Geological Sciences at the invitation of the Government of the Republic of South Africa. The symposium was attended by about 220 participants, of whom nearly half came from countries lying outside the Republic, among them Australia, India, Germany, Belgium, France, Great Britain, the United States of America, Brazil, Argentine, Gabon, Angola, Zambia and Rhodesia. The retiring General Secretary of I.U.G.S., Dr. W. P. van Leckwijk, honoured the Symposium by his attendance.

Organization was in the hands of a Committee appointed by C.S.I.R., of which Dr. S. H. Haughton was chairman, and Dr. E. P. Plumstead, Dr. A. R. I. Cruickshank, and Mr. J. W. Kitching of the Institute's personnel were members. The committee was responsible for the organization of two long excursions (each of 12 days' duration—one from Cape Town through the Cape Folded Belt and the Great Karroo to Johannesburg, and the other from Johannesburg through the coal-fields of the South-eastern Transvaal and Northern Natal to Zululand and Durban and back) and three shorter excursions; for the preparation and printing of guide-books for these excursions; and for the control of the formal sessions for the reading of papers, which were spread over 5 days at the University of Cape Town and 4 days in the University of the Witwatersrand. During the latter sessions the Institute was visited by a considerable number of the delegates and a visit to Sterkfontein and Swartkrans was arranged.

Preparations for this symposium occupied much of the time of most of the staff during the period January to June. The new cases for the Museum had been installed early in 1969. These had to be furnished with specimens and descriptive labels. Dr. Cruickshank, Dr. Plumstead, Mr. Kitching, Mr. B. R. Turner, and Mr. C. Gow acted as guides on parts of the two long excursions and undertook 'recollection' excursions into the field preparatory to writing the portions of the guide-books for which each was responsible. They, and other members of staff, prepared papers for presentation at the formal sessions, as under:

S. H. Haughton	— Review paper on the Gondwana system in Southern Africa.
E. P. Plumstead	— Plenary paper on Gondwana fossil plants.
A. R. I. Cruickshank	— Early Thecodont Braincases.
A. R. I. Cruickshank & S. Chernin	— A Capitosaurid Amphibian from Upper Luangwa Valley, Zambia.
A. Anderson	— Supposed Fish-trails from Dwyka series, Natal.
J. W. Kitching	— A Review of Beaufort zoning.
B. R. Turner	— Facies of the Molteno cycle.

In addition, Dr. S. H. Haughton delivered an Evening Public Lecture at the University of Cape Town on 'Gondwanaland'.

All these papers have been accepted for publication in the Proceedings of the Symposium, to be printed in South Africa.

Many of the participants in the Symposium with palaeontological interests stayed in, or returned to, Johannesburg after its formal closure in order to study material housed in the Institute. Prominent among these workers may be named Dr. E. Colbert, Dr. N. Hotton III, Dr. B. Hughes, Dr. Pamela Robinson, Dr. A. S. Romer, Dr. J. Bonaparte, and Dr. C. Mendrez who has undertaken special studies on certain Therocephalian forms for the greater part of the year. Dr. H. B. S. Cooke is another of our old friends who came to the Institute and, in spite of an unfortunate and crippling accident sustained on one of the Symposium excursions, delivered a fascinating lecture on recent discoveries in the Tertiary and Quaternary deposits of eastern and north-eastern Africa and their relationships to the allied faunas of southern Africa.

FIELD WORK AND RESEARCH

As stated already, some members of the staff spent time during the early part of the year in visits to the areas in which they had agreed to act as guides to the Symposium excursions, to assure themselves of the accuracy of the daily time-schedules they had previously drawn up, and to open up exposures of sediments and fossils in order to give these a 'fresh' appearance. These visits also resulted in enlarging the collections in the Institute, particularly of plants of Karroo age.

Field collecting has been extended to the Antarctic continent! The discovery, in the

1969–1970 summer, of reptilian bones closely comparable with those known from the Beaufort beds of the Karroo threw new light on the theory of the existence of a single 'Gondwanaland' in Permo-Triassic times. It led the United States authorities to invite Mr. J. W. Kitching—the longest-serving member of the Institute's staff and world-renowned for his ability as a 'fossil-hunter'—to accompany the U.S.A. geological parties in the 1970–1971 expedition to the Trans-Antarctic Mountains. The invitation was accepted; and Mr. Kitching left South Africa for the United States early in October. He has also been invited to visit the Palaeontological Institute at Tucuman, Argentina, with excursions into the neighbouring fossiliferous Karroo equivalents, prior to his return home. Information reaching us indicates that a considerable amount and variety of reptilian material, mostly of equivalent age to the South African *Lystrosaurus* zone, has been discovered and will be transferred to the United States for study.

Another overseas visit was that of Dr. A. R. I. Cruickshank, who had been invited to attend the 18th Symposium of Vertebrate Palaeontology and Comparative Anatomy in Cambridge, England, in September 1970, to which he contributed a paper on the taxonomy and osteology of the genus *Proterosuchus*, including in that genus some species that had originally been assigned to the genus *Chasmatosaurus*. Whilst overseas, he went to Vienna to examine the type skull of the Upper Beaufort anomodont *Kannemeyeria simocephalus* which came from the Aliwal North–Burghersdorp area. The information obtained here is being incorporated in a revision of the family Kannemeyeridae which he is undertaking. In order to re-examine the type of *Kannemeyeria wilsoni* Broom, which is the only reliable associated skeleton of this genus yet known, Dr. Cruickshank visited the East London Museum in which it is housed, in December.

Dr. Cruickshank and Mr. Gow, at the request of the Director of the Transvaal Museum in Pretoria, undertook to assist the Museum by sorting and re-arranging the Museum's Karroo fossil collection. This assistance will be prolonged into 1971.

Mr. C. A. Gow has continued his detailed study of the family Millerettidae, small reptiles from the upper part of the Lower Beaufort beds. The available material belongs partly to the Rubidge collection. It has demanded very meticulous preparation by Mr. Gow in order to display the osteological details in these very small skulls, among which two different genera are recognisable. His M.Sc. thesis will probably be completed by the second half of 1971.

Mr. B. R. Turner continued, in the second half of the year, with field studies of the sedimentological variations in strata assigned to the Molteno series, and only a comparatively small extent of the most southerly outcrops remain unexamined in detail. For work on this series which he had already completed, he was awarded an M.Sc. degree in April, 1970. The full results of the investigations will be submitted by him as a thesis for the Ph.D. degree. Sedimentological studies of this nature are of great value to the palaeontologist in enabling him to envisage the palaeoecology of the animals and plants he is studying; and it is proposed that Mr. Turner's next field of study will be the fossiliferous Upper Beaufort stage, on which the Molteno beds rest over large parts of their outcrop.

Mr. B. Maguire paid a number of visits to Makapansgat and particularly to the Limeworks deposits, during most of which he acted as a guide to parties from the University (one of which included the Deputy Vice-Chancellor and the Registrar) and from the Institute. He has now amassed some 60 000 specimens which he considers to be stone artefacts, but concerning which there are still a few sceptics. He displayed some of these to Dr. Mary Leakey during her visit to the Institute and among them she recognized definite 'utilized' pieces, "although there do not seem to be recognizable tool forms" (M. Leakey in *Nature,* 225, 1118). To some extent, this aspect of Mr. Maguire's studies impinges on the domain of the University's Department of Archaeology but, at the same time, it bears a close relationship to the investigations into the physical nature of the australopithecines and their ecology.

Mrs. H. Anderson continued her work on the plant fossils of the Molteno stage. In addition to visits to various museums in the country—in particular to the South African Museum in Cape Town, where most of the Molteno plants collected by Geological Survey members in the early part of the century are housed, she undertook a field trip to the Elliot district where she collected further material from four separate localities, and prepared it. There are now records from 22 different localities, which have yielded 4 558 plant specimens.

Miss A. Anderson, after presenting her analysis of fish trails from Dwyka deposits in Natal at the Gondwana Symposium, was unfortunately involved in a car accident, the result of which curtailed the time available for study and confined her to laboratory work for the remainder of the year. She began, therefore, the study and classification of fossil seeds from the Vereeniging area as an M.Sc. student.

Miss A. K. Beneke, another M.Sc. candidate, worked on plant megafossils of the Upper Ecca and Lower Beaufort beds of Natal. She made two collecting trips to sites in the Estcourt area and was assisted greatly by Mr. Schaller of Estcourt, whose interest has resulted in the location of a number of previously unknown sites. She has now, for study, 3 372 specimens of plants from these beds.

Yet another candidate for the degree of M.Sc. in palaeobotany is Miss S. J. Dickinson, who is studying a fossil plant assemblage from Hammans-

kraal, north of Pretoria. Since September she has been greatly handicapped by the physical damage sustained in a motor accident and work on her thesis has had to be postponed.

Mrs. R. Falcon, who registered for a higher degree in July, transferred the material on which she had been working in Rhodesia to the Institute. In Rhodesia she had been under the supervision of Professor G. Bond, whom she visited again in August for discussions and to procure samples from a borehole core. The subject of her investigations is "Karroo Palynology in the mid-Zambezi basin, Rhodesia", with special emphasis on the spore content of the Dwyka sediments and their age.

Miss J. M. Roets continued her studies of fossil mammalian skulls from the cave-breccias, paying special attention to the porcupines, for an M.Sc. thesis.

Miss E. A. Crozier, of the Department of Zoology, worked during the year in the Institute on Triassic Anomodonts from Zambia (Upper Luangwa Valley) in preparation for an Honours degree in Zoology. The degree thesis was accepted.

Two scientists in the employ of SOEKOR continued to work in the Institute as candidates for higher degrees, both in the field of palynology. Mr. J. M. Anderson will submit a Ph.D. thesis on "Biostratigraphic palynology of the Permian sediments of the northern Karroo basin of South Africa"; while Mr. I. R. McLachlan, registered as an M.Sc. candidate, is working on the chronostratigraphy of certain Soekor borehole cores based on miospores.

Two overseas palaeontologists have each spent several months in the Institute in detailed studies of certain groups in the collections.

1. Dr. Christiane Mendrez of France has made a comprehensive study of the Therocephalia of the Beaufort series, and in particular the Whaitsiidae, in the course of which she has enhanced the scientific value of specimens in both the Bernard Price Institute and the Rubidge collection by careful preparation, particularly of the skull material.
2. Dr. Wolfgang Meier, of the University of Frankfort, working in collaboration with the University Department of Anatomy, investigated the taxonomy of the Cercopithecoidea found in the cave deposits which include the genera *Simopithecus* and *Parapapio*. His results will appear in the next volume of *Palaeontologia Africana*. Much of the available skull and jaw material was beautifully developed by him, especially to display the dentition.

Under the joint control of Professor P. V. Tobias and Mr. A. R. Hughes work was carried on at the Sterkfontein site during the whole year, with the assistance of an average of 10 African assistants and labourers. Clearing of surface rubble has been completed. Recovery of bones, artefacts and foreign stone has proceeded satisfactorily; a fair sample of bovid teeth and jaws and over 300 cercopithecoid cranial and postcranial remains have been recovered. Rodent material from the surface rubble (overburden) is being studied by Mr. T. N. Pocock, who has also published a description of Pleistocene bird fossils from Kromdraai and Sterkfontein.

At this latter site, the underground cave system is being charted under the supervision of Miss M. E. Marker of the Department of Geography; and the relationship between the breccia outcrops and the underground caves is under investigation, a necessary prelude to the proposed excavations in the consolidated breccia which are planned.

Several on-site conferences of individuals selected by Professor Tobias took place at Sterkfontein during the year and a number of study and inspection visits were made to the Makapansgat limeworks and the Cave of Hearths.

A detailed re-study of the Cave of Hearths hominid mandible was completed by Professor P. V. Tobias, as well as a first study of human radii from the same site. The results will be published in the American Journal of Physical Anthropology.

Professor Tobias participated in the Burg Wartenstein (Austria) Symposium No. 48 on "Functional and Evolutionary Biology of Primates" to which he contributed a paper on "Progress and problems in the study of early man in subsaharan Africa". He also read a paper entitled "Some anatomical lessons from the study of hominid fossils" at the Annual Meeting of the Anatomical Society of Southern Africa, held at Lourenco Marques in May, 1970.

LIBRARY

Throughout the year, Mrs. Edwards was seconded to the Institute by the University Librarian for morning work only. She continued with her task of re-organization and re-arrangement of the books, periodicals, and separates and of incorporating the many additions of which we became possessed by purchase or exchange. To assist particularly in the solving and card-indexing of separates the temporary services of Mrs. Cruickshank were utilized.

ADMINISTRATION AND FINANCE

Although the general administration of the Institute is nominally under the control of the Honorary Director, most of the details have had to be undertaken by the Assistant Director, Dr. A. R. I. Cruickshank. The Board of Control has met twice during the year and has authorized both the estimates of expenditure and the general programme of work submitted to it.

Mr. D. T. Wolfaardt, the Technical Assistant, left the Institute's service at the end of January. The Board approved the conversion of his post to

one of Laboratory Foreman, a post that was filled in June by the appointment of Mr. H. Thackwray, who has taken over much of the minor detail of the administrative work formerly undertaken by Mr. Kitching.

Control of the financial transactions affecting the Institute is in the hands of the University's Financial Department; but mention should be made of our gratitude to the C.S.I.R. for the continuation of the annual grant which it has made in support of the Institute's scientific activities.

BUILDINGS

The increase in numbers of the Institute's permanent staff and of the University's students for higher degrees in palaeontology, together with the ever-increasing size of the collections of both fossil material and of books make for a constantly growing demand on available space. This demand is more urgent at times when the Institute has to find accommodation for visiting scientists for shorter or longer periods.

Realizing this, the University arranged during the year for a consultant to examine the available accommodation in the Douglas Smit Building and to prepare plans for alterations and additions to it which would meet our foreseeable requirements for at least a decade. These plans have been submitted; but no decision has yet been announced concerning their final adoption as a preliminary to operation.

GENERAL

Certain staff members, in addition to supervising work of students working for higher degrees in palaeontology, continue to assist the Department of Geology with undergraduate courses on fossils. Similar assistance to the Department of Botany terminated at the end of 1970, except for Honours courses.

PUBLICATIONS BY STAFF MEMBERS OTHER THAN THOSE LISTED ABOVE

Cruickshank, A. R. I., The Proterosuchian Theocodont in *Studies in Vertebrate evolution* to appear in 1971/72.

Dart, R. A., An anatomist's tribute to F. Mathias Alexander, pp. 1–35, London, The Sheldrake Press.

———, Nuclear Antiquity 1. 'Dating Man'. An interview with N. Eliovson. Nuclear Active, *January 1970*, pp. 12–26.

———, The Bloodstone source of metallurgy *Sociedade Portugesa de Antropologia e Etnologia* 1969, pp. 119–129.

———, Indian Trans-oceanic navigation: its primary place. *Bulletin, Indian Geologists Association*, 2, pp. 75–85.

Davey, R. J., Some dinoflagellate cysts from the Upper Cretaceous of Northern Natal, South Africa. *Palaeontologia Africana* 12, pp. 1–24.

———, The evolution of certain Upper Cretaceous Hystricospheres from South Africa. *Palaeontologia Africana*, 12, pp. 25–52.

Haughton, S. H., What is palaeontology? *S.Afr.J.Sci.* 66, pp. 4–8.

Plumstead, E. P., A review of contributions to the knowledge of Gondwana megaplant fossils and floras of Africa published since 1950. Proceedings of the first I.U.G.S. Symposium on Gondwana Stratigraphy and Palaeontology, 1967. UNESCO, Paris.

———, Reflections on the earliest plant life and its great contribution to the plant life of today. *J. Sen. Memorial Volume*, pp. 339–348.

Turner, B. R., The use of the Indwe Sandstone as a stratigraphic marker in the Molteno stage of the Karroo System. *Palaeontologia Africana*, 12, 203–204.

REPORT OF THE HONORARY DIRECTOR FOR THE YEAR 1971

Following the period of intense activity that marked the Institute's participation in the Second International Symposium on the Gondwana System, held in South Africa from late July to early September, 1970, the year under review can be considered as one of normal operation and growth and of concentration upon the Institute's prime objective of advancing palaeontological knowledge.

It may be appropriate here to consider briefly the rôle that studies such as those undertaken by us play in the research programme of the University of which we form part.

Fossils are more than stones with distinctive shapes and structures. They are the evidence of once-living animals and plants that flourished on land or in the waters of the past. Their remains are preserved in sediments whose nature will reveal the conditions under which entombment was effected. But these conditions of entombment are not necessarily the conditions under which the living animal or plant existed. To ascertain these, at least in part, the fossil itself must be studied in all its parts and be compared with all others found in connection with it in the same sedimentary environment.

For this to be done accurately, large collections are imperative so that statistical studies may be made on characters that have arisen or changed as the result of evolution or of ecological conditions. In the amassing of large collections the vertebrate palaeontologist is at some disadvantage when compared with his colleagues who concentrate on marine invertebrates, on fossil plants, or on microfossils. If he is dealing with the remains of land-dwelling vertebrates his field finds may be but fragments of portions of a skeleton, are likely to be encased in quantities of hard rock matrix, and in very many cases will necessitate long and arduous preparation prior to study. This is certainly true of the vertebrate remains from the Karroo system and from the much more recent cave deposits with which the Institute's vertebrate students are mainly concerned. It is obvious, however, that the larger the collections made from a particular stratigraphic horizon the more detailed and accurate will be our knowledge of the variety of life forms existing at the time of deposition of the beds of that horizon.

What is true for vertebrate fossils is true also for fossil plants. Although the remains that are unearthed are seldom, if ever, of a plant in its entirety, more and more evidence is being accumulated, by the collections and examination of originally woody material, of leaves and leaf impressions, of floral parts, and of spores and pollen, to enable the palaeobotanist to visualize the composition of the plant-life existing in a particular area in a particular period of geologic time. The Institute pays considerable attention to studies in this branch of palaeontology.

The days are past when the palaeontologist was supposed to be satisfied with the bestowal of a generic and specific name on a fossil and with justifying this baptism with a more or less brief reason for his decision. The aim today is mainly biological and ecological, although remaining geological (i.e. historical). The student aims at elucidating the true form of the remains under his consideration, their probable mode of life, their anatomical relationships with geologically earlier, co-existent and later forms, and their exact position in the whole spectrum of the evolution of life on earth. Of course, in view of "the imperfection of the geological record" his aim is never fully achieved. His reward is that he has added to the sum-total of human knowledge by conscientious research.

He must, however, never forget that a fossil is a constituent of the rock in which it is found and that the distinction that is now being stressed in many quarters between lithostratigraphy and biostratigraphy is a somewhat artificial one as far as Phanerozoic sediments are concerned. The fossil may be the remains of an organism that was indigenous to the environment in which the rock material accumulated, or it may have been transported after death into that environment. In either case, the study of the enclosing rock has a bearing on the relationships that existed between the organism and its surroundings, which is why the Institute has sedimentologists working together with its palaeontologists.

The sedimentologist determines the nature of the original mineral constituents of the various types of rocks that together now form a stratigraphical series and the nature of the material that cements them. He draws conclusions regarding the source, or sources, of the constituent parts and, from a study of such phenomena as bedding planes, and other geometric patterns, envisages their mode of transport to their sites of deposition and consolidation. He also studies their post-depositional history. In the case of predominantly non-marine sediments, such as those which make up most of our Karroo system, this line of investigation is particularly important in the deciphering of the history of the area in that span of geological time.

The study of fossils and that of their enclosing rocks thus go hand-in-hand and together they form the basis of the Institute's attempts to add to the knowledge of the land's past history.

STAFF CHANGES

Mr. J. W. Kitching returned from his sponsored collecting and study expedition to the Antarctic and the Argentine at the end of February and resumed his work at the Institute.

At the beginning of the year Mrs. Essers of the University Library staff was appointed as librarian for morning services only by the University Librarian, replacing Mrs. Edwards. In order to maintain the card cataloguing of individual papers in the library accessions, the part-time services of Mrs. Cruickshank were utilized.

Mr. H. O. Thackwray, Laboratory Foreman, was forced to take leave for several weeks in order to undergo a somewhat severe vertebral operation. Fortunately, this was successful and he returned to full-time duty.

Miss Emanuel was appointed as Laboratory Assistant and spent a few weeks learning casting and reproduction techniques at the South African Museum. Her services are proving of considerable value.

Miss Carnell has operated throughout the year as a research assistant to Dr. E. P. Plumstead.

No other staff changes have been made during the year under review.

Reference should be made here to the fact that Mr. Nagel, who worked in the Institute as official photographer for Soekor, decided to resign his position because of an offer to work elsewhere at a higher salary. It had been hoped that he would have been appointed to the Institute's staff in 1972 to fill one of the proposed new posts. At its meeting on 7th September the Board decided that, in order to meet the University's request that it cut its estimated expenditure for 1972, the new posts should not be filled. Mr. Nagel's departure would have affected Soekor's programme badly. The position was saved by a quick response by the Deputy Vice-Chancellor, the Registrar, and the Finance Officer who arranged that monies set aside on the budget for student vacation employment and relief typing could be utilized in order to retain Mr. Nagel's services, Soekor continuing to pay part of the total costs of providing an acceptable salary.

RESEARCH PROJECTS

Despite the many and varied administrative duties which fall to his lot the Assistant Director, Dr. A. R. I. Cruickshank, has almost completed the preparation of a small crocodilian skeleton from the Red Beds which was collected by Mr. C. Gow. He has also prepared a partial Sauropod foot from a Red Bed locality near Fouriesburg, O.F.S. The significance of this specimen lies in its well-preserved ankle and in the superficial resemblance to the foot of the *Cynognathus*-zone Proterosuchian *Erythrosuchus* which may be better understood by comparison with the Red Beds fossil. The Institute's collection of dinosaurian material is relatively poor, and comparison with the greater amount housed in the South African Museum will have to be undertaken.

Since his return to the Institute, the greater part of Mr. J. W. Kitching's time has been spent on the preparation of his M.Sc. thesis, for which the Director is Supervisor. He has completely revised the locality list for *Tapinocephalus*-zone vertebrates and has classified all the types and quoted specimens from each of 141 known fossil localities within the zone. For the remainder of the Lower Beaufort succession, he has adopted a two-zone subdivision—a lower *Cistecephalus*-zone and an upper *Daptocephalus*-zone—and has included in his faunal lists for each the taxonomic changes suggested by Keyser (1969) and Sigogneau (1970) as well as his own notes on certain genera and species. The total number of known vertebrate localities in the now-accepted five bio-zones of the Beaufort series is 581; lists of fossils are given for each of these.

In addition, Mr. Kitching has been analysing mammalian fragments from the Border Cave deposit collected by Mr. P. Beaumont and thus far has examined some 19 000 specimens—less than half of the total number collected. He has also supervised the work of the Bantu preparators, who have completed work on six *Cistecephalus*, two *Daptocephalus*, one *Aulacephalodon* and three *Procolophon* skulls in addition to isolating a large number of mammalian remains from breccia blocks from the Limeworks deposit.

Dr. E. P. Plumstead has been engaged in the compilation of two review papers, one of which is the text of the A. L. du Toit Memorial Lecture which she delivered, in four separate centres, under the auspices of the Geological Society of South Africa in 1969. She has also been preparing a section on Glossopteridophyta for the sixth of nine volumes of the Traité de Palaeobotanique which is being edited by Professor Bourcard of the Université de Paris. A new collection of fossil plants from Antarctica has been studied and reported on for publication in the British Antarctic Journal.

Mr. C. E. Gow completed a study of the reptile family Millerettidae which was submitted to the University and accepted as a thesis for the degree of M.Sc. This thesis has been accepted for publication and will appear in a forthcoming number of the Journal of Zoology. He then proceeded to undertake a detailed study of the genera *Youngina* and *Prolacerta* with a view to elucidating the point of divergence between Archosaurs and Lepidosaurs. This involved months of detailed preparation of the skulls of these two genera and the making of detailed drawings of the specimens. Comparisons have already led to some interesting conclusions of a preliminary nature.

Mr. B. R. Turner completed his mapping of the Molteno strata in the Main Karroo basin of South Africa and Lesotho by the early part of August. For a description of part of his studies he was awarded the degree of M.Sc. by the University.

The results of work in Lesotho prompted preparation of a paper entitled "Revision of the stratigraphic position of Cynodonts from the upper part of the Karroo system in Lesotho" which was submitted to the Geological Magazine for publication. In this it is maintained that certain cynodonts formerly assigned to the Molteno beds were actually found in sediments that form part of the Upper Beaufort succession. A geological map of the whole of the Molteno strata in this main basin is now in preparation.

Mr. B. Maguire has concentrated his attention throughout the year on the preparation of his thesis on Bushmen food plants and their relevance to the ecology of the australopithecines and primitive man, which will be copiously illustrated by photographs. In addition to amassing information from many areas in Botswana and the neighbouring parts of the Transvaal as well as from Makapansgat, he has paid a considerable amount of attention to the primitive lithic artefacts from the Makapansgat breccias, especially from the upper part of the Phase I breccia.

Mrs. H. Anderson has continued throughout the year on her studies of the Molteno flora for a Ph.D. thesis. This has necessitated further field-collecting and visits to various museums in South Africa where types and figured or named specimens of Molteno plants are housed. Many identifications have been made and photographs and drawings prepared, partly with the assistance of Miss Janet Cronjé. An attempt was made to classify the cycads on the basis of cuticles; but, after treatment, the cuticles showed no structure, and correct classification of these cycads remains in abeyance for the present. Save for the *Dicroidium* group, most of the Molteno plant genera appear to be of world-wide occurrence. Much of the literature dealing with them is out-dated and is not available locally; and it is desirable that means should be found to enable this worker to study, at least, related forms housed in various European museums and the relevant literature. Mrs. Anderson's studies have necessitated visits to the South African Museum in Cape Town and the McGregor Museum in Kimberley, at both of which places collections of Molteno plants were examined and photographed, to the Durban Museum (where du Toit's type specimens were located), to the O.F.S. National Museum in Bloemfontein, and to the Geological Survey in Pretoria (in connection with a type specimen).

Miss J. M. Roets has spent much of the year in studies of the fossil porcupine material which forms the subject for her M.Sc. thesis, which is almost ready for presentation. This has involved the study of the gross and detailed morphology of the modern porcupine dentition and of the terminology employed, of the crown enamel pattern, and of the functional aspects of both the modern and fossil dental apparatus. Attempts at the serial sectioning of porcupine teeth were made at the Dental Hospital but lacked a full measure of success. It is of interest to note that, during a period of leave in the winter, Miss Roets gave assistance to Dr. Heinz of the University Medical School in his pioneer Bushman Settlement Scheme in Botswana by teaching a female member of the local ! Ko Bushman band the elements of arithmetic and word recognition. The girl student had been selected as the result of an intelligence test designed by Dr. R. H. Reuning of the National Institute for Personnel Research and, after five weeks of instruction by Miss Roets, could count up to 100, perform simple additions, and recognize about 120 English words.

During this period, Miss Roets also made a further collection of mammalian material—skulls, jaws, palates and bones that had been purposely smashed by Bushmen for the extraction of brain and marrow; this material is of value for comparison with the 'osteodontokeratic' objects yielded by the Makapansgat excavations.

Miss A. Benecke has continued her investigations, under a postgraduate grant, into the plant mega-fossils of the Upper Ecca and Lower Beaufort sediments in Natal. She has paid particular attention to a new site exposed on the double highway near Mooi River which, in addition to a well-preserved and diversified flora, has also yielded the richest insect fauna from any known Permian locality in Southern Africa. A visit overseas enabled Miss Benecke to examine some of Brogniart's type material in Paris and to study Gondwana plant collections at the British Museum and in Cambridge. Her thesis is likely to be completed in 1972.

Miss Ann Anderson, candidate for an M.Sc. degree, has been permitted by the University to transfer her studies to an investigation of South African Palaeozoic trace fossils and their ecological significance. For this purpose she has collected material particularly from beds that have been assigned to the Dwyka series in both the Republic and the Warmbad basin of South West Africa. Haughton and Frommurze reported arthropod tracks from the Warmbad area in 1928 and Martin, in 1970, demonstrated the marine origin of the containing sediments in this basin. Similar tracks have been recovered from particular lithologic facies in the Ecca beds.

After spending several months working in King's College, University of London and at the British Museum and in the Museum of Zoology at Cambridge University, Miss S. Chernin has returned to the Institute to study the skull characteristics of Karroo stereospondylous amphibian fossils, especially those of the Triassic strata, and their nomenclature.

Mrs. R. Falcon is a candidate for the M.Sc. degree, working on the miospore flora of Karroo beds in Rhodesia. Under University instruction, the Institute had to prepare an Honours Equivalent examination for Mrs. Falcon, with Dr. A. S. Brink as External Examiner. This she passed high in the Second Class. She has completed tables and

diagrams of the florizones of her area and has compared the Rhodesian material with miospores typical of Lower and Middle Gondwana assemblages, especially with those of Tanzania and more generally with those of Australia and other parts of Gondwanaland.

Mrs. S. J. Smithies (née Dickinson) married during October and now lives in Pretoria. The car accident of two years ago has physically handicapped her and her attendance at the Institute has been somewhat spasmodic during the year under review. The subject of her investigations, for an M.Sc. degree, is the description of a Permo-Carboniferous plant assemblage from Hammanskraal, north of Pretoria.

Miss Collings is an Honours-in-Zoology student who has been working in the Institute on a Sabre-tooth cat from the Makapansgat Limeworks deposit.

Mr. J. M. Anderson, an employee of Soekor, has worked throughout the year in the Institute as a Ph.D. candidate. His subject is the spores and pollen types obtained from Karroo sediments penetrated by Soekor boreholes in the Karroo Basin. A catalogue of some 150 'species' has been prepared; the different 'species' have been delimited and thousands of photographs have been taken. Tables showing the stratigraphic distribution of the 'species' have been completed.

A collaborative effort by Mrs. H. M. Anderson and Mr. J. M. Anderson resulted in the production of 22 charts, 6 tables and a text entitled "A Preliminary Review of the Biostratigraphy of the Uppermost Permian, Triassic and Lowermost Jurassic of Gondwanaland" which was published by the Institute as a Supplement to Vol. 13 of Palaeontologia Africana.

Mr. I. McLachlan, of Soekor, has been working part-time in the Institute on the preparation of an M.Sc. thesis entitled "The occurrence and significance of inorganic-walled microfossils from the Karroo System in South Africa". Over 500 samples from boreholes that penetrated Upper, Middle and Lower Ecca sediments in the northern part of the Karroo basin have yielded calcareous microfossils that have been studied by means of thin sections, X-ray diffraction, electron-microprobe and wet chemical methods. Some siliceous spicules and small spheres of granular silica have also been observed. In addition phosphate nodules from Upper Dwyka shales have been found to contain arenaceous foraminifera.

Financed by the Anglo-American Corporation and under the direction of Professor R. A. Dart, Mr. P. Beaumont has housed in the Institute the archaeological material obtained by him from 'prehistoric' ore-workings in Swaziland and from caves in the neighbouring areas. The workings are of great interest particularly because they have yielded material on which it has been possible to assess radiometric ages. One locality—Border Cave near Ingwavuma in northern Natal—has yielded the following radio-carbon dates given by Dr. J. Vogel of the C.S.I.R.:

Base of the Iron age	? 2 000 B.P.
Base of the early phase L.S.A.	37 000 B.P. (3 dates)
Base of the terminal phase of M.S.A.	48 000 B.P. (3 dates).

Underlying these dateable horizons there is a full M.S.A. sequence. Samples from this have been sent to the University of California Radio Carbon Laboratory for an attempt at dating by newly devised techniques. The Iron Age levels include glass beads of Asian origin, which indicate a trading connection to the African coast at this early date. Because of the extremely early age for the Iron Age levels, these dates are being re-examined.

The L.S.A. ('Late Stone Age') dates are also among the earliest known for this culture, and contain many interesting artefacts, including a 'tally stick' and a paint palette.

The dates for the terminal M.S.A. ('Middle Stone Age') came from material from a level below that in which there was an infant skeleton of advanced *Homo sapiens sapiens* type. From this it is deduced that modern man occupied South Africa at some undefined period prior to 48000 B.P., a date some 8 000 years older than any previous one. Remarkably well-preserved plants, feathers and insect wings have been found from levels from the present to beyond the present range of Radio-carbon dating.

This site is therefore one of the most important known in Africa and the contents are being analysed by a powerful multi-disciplinary research team which includes members of the Bernard Price Institute.

FIELD WORK AND COLLECTING

During the year under review field work has consisted almost wholly of individual efforts by workers at the Institute undertaken in order to augment the quantity of material available for particular studies, although a few excursions were made for the examination of fossil occurrences reported by outside correspondents or to assist visiting scientists in their studies of fossil occurrences. Assistance of this sort to visiting scientists was given mainly by Messrs. Kitching and Gow, the former of whom also visited the Harrismith, Clarens and Thaba Nchu districts in order to study geological sections for his thesis and, incidentally, collected 14 new reptilian fossils including two almost complete skeletons of *Lystrosaurus*, a skull and partial skeleton of *Myosaurus* and two well-preserved skulls of the rare *Tritylodon*.

Mr. B. R. Turner spent a considerable part of the year in the field completing his mapping of the upper and lower boundaries of the Molteno series. During the course of this he found a number of plant-bearing localities in the vicinities of Molteno, Elliot and Dordrecht from which collections were made, with his assistance, by Mrs. H. Anderson. He

was also able to determine the exact stratigraphical horizon of beds in Lesotho from which cynodont remains had been previously described.

Mrs. H. Anderson also collected Molteno plants from localities along the south-western part of the outcrops of the series and studied the collections of the museums at Cape Town, Kimberley, Bloemfontein, Pretoria and Durban.

Miss A. Benecke, working on Upper Ecca and Lower Beaufort plants, collected from comparatively rich sites near Estcourt and elsewhere in Natal.

Miss A. Anderson, concentrating on the ichnology of the Dwyka and Ecca beds, collected interesting new material from exposures north of the Orange river in the Warmbad district of South West Africa and, with Mr. McLachlan, from Dwyka exposures near Douglas and Kimberley. The preservation of trace fossils is, of course, dependent almost wholly on the nature of the rock outcrop which is independent of its age.

Dr. Plumstead, in the course of a holiday, visited Port St. John's in order to locate the true geological horizon of certain plant-remains that were originally reported as coming from the Table Mountain series of the Cape System. She is satisfied that these plants belong to the Witteberg beds, which form the upper unit of the Cape system and were not obtained from the T.M.S. of the upfaulted block. She has brought to the Institute further material for study. The plants indicate that a revision of the geological map is necessary.

Whilst on leave, Dr. Cruickshank visited the museum and Geological Department of the University in Salisbury, Rhodesia, in order to familiarise himself with current work on Rhodesian dinosaurs.

Field work at Sterkfontein has continued under the control of Professor P. V. Tobias, Professor of Anatomy, and at Swartkrans under that of Dr. C. K. Brain, Director of the Transvaal Museum. Professor Tobias also had some material from Makapansgat transported to his Department, of which no details have as yet been released to the Institute. Mr. Maguire also paid several visits to the Makapansgat sites.

Operations at Swartkrans have been in the hands of Dr. C. K. Brain, Director of the Transvaal Museum, and are financially supported by the Institute. Throughout the year, a labour force of four or five Bantu assistants has been maintained at the cave site, removing the rubble that filled the pit created by earlier workers. This rubble consists of soil in which are embedded artificially broken blocks of cave breccia and of dolomite. The larger pieces of breccia have been hand-sorted and stockpiled for future examination. Removal down to bedrock has revealed the opening to a lower cavern, whose existence had been suspected but not proved; this cavern has undisturbed soil on its floor. With the rubble now removed, the contours of the original cave, which was almost as high as broad, can be delineated.

It has become clear, from studies carried out by Dr. Brain in collaboration with Professor Karl W. Butzer of the University of Chicago, that three breccia units occur at Swartkrans; microfauna from each are being studied in order to clarify habitat conditions of each. Bone samples will be used by Mr. R. Protsch of the University of California in an attempt to obtain age data.

Among the fossils recovered are part of a hominid mandible, a partial skull and endocast of a primate (possibly hominid) and two australopithecine maxillary molars—all of which have been transferred to the Transvaal Museum for study. Other fossils have been stored at the site.

Dr. Brain conducted four groups of University medical students over the site in May and lectured to them on the geology of the site and its fossils. Among other visitors entertained at the site were Professor and Mrs. R. R. Inskeep, Mrs. M. Leakey, Prof. K. W. Butzer, Prof. J. T. Robinson, Mr. R. Clarke, Dr. R. F. Ewer, Dr. T. Partridge and Dr. M. Marker.

Research at the site will be continued in 1972.

At Sterkfontein, field operations under the control of Professor P. V. Tobias continued throughout the year until the early part of December, with the help of ten labourers. Much progress was made with the breaking and sorting of breccia from the old dumps surrounding the west end of the excavation area, resulting in the recovery of much cercopithecoid, some ungulate and some australopithecine material. A new area to the west was cleared of overburden (of which some 64 cubic metres was sieved and sorted). This removal exposed some 71 sq. m of the upper surface of a breccia extending well beyond the expected limits. From this overburden a number of foreign stones and artefacts were recovered, all of which have been catalogued in the Department of Anatomy of the University.

The mapping of breccia exposures in the underground cavern system immediately beneath the fossiliferous quarry has been continued.

Two sets of specimens were despatched to separate laboratories in the University of California for dating, one set including bone from the Lower Phase I breccia at Makapansgat.

Approximately 100 cranial and postcranial fragments of *Parapapio* sp. were recovered from one of the dumps. These were examined by Dr. L. Freedman of the University of Western Australia—who included his identifications in his check-list of cercopithecoids in *Palaeontologia Africana*. Ungulate skull and post-cranial fragments from the same breccia dump are under study by Dr. N. Pocock. In addition, a number of australopithecine fragments have been yielded by examination of the breccia; of these, the most important consist of a partial cranium, in *in situ* breccia, including the palate, several good maxillary teeth, part of the brain-case vault and base, and part of the face—the first important discovery of an australopithecine made in undisturbed breccia at Sterkfontein since the

1957–1958 season. About 20 cm below this find, a crushed mandible with teeth of an older australopithecine individual was unearthed. Another important find was that of four articulated lumbar vertebrae of *Australopithecus*, identified by Dr. F. Ankel, which throw light on the posture of this hominid. An up-to-date review and synthesis of recent views on the taxonomic relations of the australopithecines and a report on the progress of the excavations and discoveries was contributed by Dr. Tobias to a symposium on the occasion of the centenary of Darwin's "Descent of Man" which was organised by the Academia Nazionale dei Lincei, Rome, in October, 1971.

At the Limeworks site in Makapansgat waste material left by the lime-workers was further investigated by a party under the control of Dr. Tobias and Mr. Alun Hughes. Pink breccia, presumably from Brain's Upper Phase I horizon, was sorted and from some 15 or more metric tons of this, bone-bearing parts were transported to the University for study.

TEACHING AND SUPERVISION

Certain members of the permanent staff are called upon to lecture in the University's Departments of Geology and Zoology on palaeontological matters to undergraduate students. Members so used are Dr. Cruickshank, Dr. Plumstead, Mr. Kitching, Mr. Gow and Mrs. H. Anderson.

Honours students and those accepted for M.Sc. theses in palaeontology work under supervision in the Institute. Supervisors appointed by the University in this respect are Dr. Haughton, Dr. Cruickshank, and Dr. Plumstead, the last of whom has had seven higher degree candidates under her control.

LUNCH-HOUR COLLOQUIA

These have been held in the Institute at fairly regular intervals of approximately four weeks. Each colloquium is introduced by an illustrated discourse by a speaker which is succeeded by a discussion.

Our distinguished visitor, Dr. James Hopson of the University of Chicago, was the leader for two of these, one of which was devoted to "Cynodont evolution and the origin of mammals" and the other to "A functional interpretation of the skull crest in duck-billed dinosaurs".

Three other discussions were presented by members of the staff. These were Mr. J. W. Kitching on "Collecting Fossils in Antarctica", Miss J. Roets on "The Takatshwane Bushmen" and Mr. C. Gow on "Millerosaurs and the relationships of early reptiles".

VISITORS

During the year 1971, the Institute had the privilege of assisting the work of a number of visiting scientists; but it was also a pleasure to be able to welcome and entertain Mr. and Mrs. Richard Rubidge and their two sons of Wellwood, Graaff-Reinet. The Wellwood collection of Karroo fossil vertebrates, housed on their farm, is world-famous and the Institute is proud to have an official connection with it. The collection was initiated by the late Dr. S. H. Rubidge, father of the present owner who continues, with his wife, to devote both time and money to its maintenance. Many of its contents have been fully prepared by the Institute for study; and a visit to the Wellwood museum is a *sine qua non* for students of Karroo reptilian fossils.

Professor Bohlin, of Uppsala, spent two days in the Institute studying certain plant fossils.

Dr. and Mrs. Alan Gentry of the British Museum for Natural History came to examine fossil bovid material in the collection.

Mrs. Mary Leakey from the Centre for Prehistory in Nairobi studied our collection of fossil primates.

Professor Swabedissen of Cologne expressed an interest in the wideness of the osteodontokeratic culture housed in the Institute and found the primitive stone tools collected from Makapansgat by Mr. Maguire of very great interest and value.

Dr. James Hopson, of the University of Chicago, spent some three months on an exhaustive and intensive study of cynodont material, during the course of which he visited the museum collections in Cape Town, Wellwood and Pretoria. His results will be embodied in a paper; and some of his conclusions were delivered to the staff in two lunch-hour talks.

Professor Graeme Philip of the University of Sydney paid a short visit, during the course of which he conferred with us on the problem of filling the post of Senior Palaeobotanist which will become vacant on the retirement of Dr. Plumstead from University employment.

Dr. S. Meiring Naudé, retired from the Presidency of the C.S.I.R. and now Scientific Adviser to the Prime Minister, visited the Institute and obtained further knowledge of the scope of the Institute's research activities during a detailed survey of university activities in the field of scientific and technical investigation.

A large party from the Institute for the Study of Man in Africa visited the Institute; and various schools and other groups have been given conducted tours.

PUBLICATIONS

Volume 13 of Palaeontologia Africana appeared and was distributed in the second half of the year. In addition to the Report of the Director for the year 1969, it contained the following papers.

S. F. le Roux. Some fossil Gingophytes and a possible Vojnovskyalean element from the Glossopteris flora of Vereeniging Transvaal.

G. H. Findlay. Skin structure of small Pareiasaurs,

with comments on their taxonomy in the *Cistecephalus* zone.

D. Sigogneau. Contribution à la connaissance des Ictidorhinidés (Gorgonopsia).

E. Crozier. Preliminary report on two Triassic Dicynodonts from Zambia.

A. R. I. Cruickshank. The taxonomy of the Triassic anomodont genus *Kannemeyeria* Seeley 1908.

A. L. Thornley. Epidermal remnants of *Proterosuchus vanhoepeni* (Haughton).

C. E. Gow. The anterior of the palate in *Euparkeria*.

A. W. Gentry. Revised classification for *Makapania broomi* Wells and Cooke (Bovidae, Mammalia).

W. Maier. New fossil Cercopithecoidea from the Lower Pleistocene Cave deposits of the Makapansgat Limeworks, South Africa.

L. Freedman. A new check-list of fossil Cercopithecoidea of South Africa.

As a Supplement to this volume there was issued:

H. M. Anderson and J. M. Anderson: A preliminary review of the biostratigraphy of the Uppermost Permian, Triassic and Lowermost Jurassic of Gondwanaland.

The "Papers and Proceedings of the Second International Gondwana Symposium", issued under the aegis of C.S.I.R. and edited by S. H. Haughton, appeared towards the end of the year in final form. Included in this large volume are the following contributions by members of the Institute.

S. H. Haughton. 1. Review paper on the Gondwana system in Southern Africa. 2. Public Lecture. The Gondwana Symposium.

E. P. Plumstead. Plenary paper. Gondwana plant fossils.

J. W. Kitching. A short review of the Beaufort Zoning in South Africa.

B. R. Turner. Facies analysis of the Molteno sedimentary cycle.

A. R. I. Cruickshank. Early Thecodont braincases.

S. Chernin and A. R. I. Cruickshank. A Capitosaurid amphibian from the Upper Luangwa Valley, Zambia.

A. Anderson. Fish trails from Dwyka shales in Natal.

The July–August number of the Antarctic Journal contained a short article by J. W. Kitching entitled "Palaeontological investigations in the McGregor Glacier Area". He has also been associated with three American colleagues in the preparation of a paper on the stratigraphy and palaeontology of the Shackleton-McGregor Glacier area of the Antarctic.

Dr. E. P. Plumstead has completed the correction of proofs of her A. L. du Toit Memorial Lecture entitled "Three Thousand Million Years of Plant Life", which will be published early in 1972. She prepared a large, fully illustrated, article on the *Glossopteris* flora for an Atlas of Palaeobiogeography edited by Prof. A. Hallam of Oxford and published by Elsevier Publishing Co., Holland; also a large illustrated article on Fossil Plants for the F–G volume of the Standard Encyclopaedia of South Africa, and an illustrated article on Gondwanaland for the same volume.

Among a long list of articles written by P. V. Tobias the following are primarily concerned with material belonging to the Institute.

1. The human skeletal remains from the Cave of Hearths, Makapansgat. *Amer. J. Phys. Anthrop.*, 34, 335–367.

2. Does the form of the inner contour of the mandible distinguish between *Australopithecus* and *Homo*? *Perspectives in Palaeoanthropology: D. Sen. Festschrift Volume* (ed.A.K. Ghosh) 9–17.

In addition, Dr. Tobias has three short articles in Volume III of the Standard Encyclopaedia of Southern Africa and eight others prepared for succeeding volumes. Others dealing with australopithecine and human anatomy are in the press at the moment.

EXTRA-MURAL ACTIVITIES

The Institute has cordial associations with the Museums of Man and Science in Johannesburg, on whose Board of Governors Dr. Cruickshank sits as a representative of the University and of which Dr. A. S. Brink is Director. Dr. Cruickshank is also an elected member of the Council of the Institute for the Study of Man in Africa. Both he and Mr. J. W. Kitching gave broadcast talks, under the chairmanship of Dr. Arthur Bleksley, in the S.A.B.C. programme entitled "Talking Science".

Dr. E. P. Plumstead, who is President of the Subcommission on Gondwana Stratigraphy of the International Union of Geological Sciences, has engaged in a number of extra-mural scientific administrative activities during the year. She has held the following appointments:

Member of the Steering Committee of the Palynological Research Unit of the C.S.I.R. at the University of the Orange Free State.

Member of Council of the South African Association for the Advancement of Science.

Member of Council of the Institute for the Study of Man in Africa.

Member of National Executive of the International Federation of University Woman.

Alternate representative for the Royal Society of South Africa on the Joint Council of Scientific Societies.

Mr. Kitching gave a number of lectures to 2nd year Geology students at the Rand Afrikaans University and some talks to members of the Institute for Adult Education.

In collaboration with Dr. Heinz, Miss Roets prepared a paper entitled "Some problems of communication in health and general education of a community of pre-literate ! Ko Bushmen in south-western Botswana" which she delivered at the Second Rhodesian Science Congress in Umtali, Rhodesia in September.

BUILDING

The plans for alteration of and extensions to the Institute's building that were approved by the Board were accepted by the University Council and operations commenced in November. Fair progress had been made by the end of the year with the new laboratory for Soekor's research workers, the store for Makapansgat material, a new students' darkroom, and the palaeobotany store. Completion of the extensions is expected by the middle of 1972.

It must be stressed that lack of storage space and work facilities during the past year has hampered very considerably the work of the various staff members and research students operating in the Division of Palaeobotany. Although the space problem is expected to be, at least temporarily, solved when the building extensions are completed, there will still remain the urgent need to furnish these extensions with adequate furnishings such as work benches and storage cupboards for the ever-expanding collections.

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SOME MEGASPORES FROM SOUTH AFRICA AND AUSTRALIA

by

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INTRODUCTION

Dr. Plumstead has sent a number of samples from South Africa to us for maceration of the spores from them and for an attempt to determine the horizons from the megaspores only. Other details were not given. In addition to these samples we had some from Australia, and it became very interesting to compare the spores from S. Africa with those from Australia or other Gondwana deposits in India or Brasil.

MATERIAL AND METHOD

The samples from S. Africa are:

G.B. No. 2 109; No. 1. Visible megaspores, President Steyn Gold Mine, Orange Free State, just above tillite;
G.B. No. 2 110; No. 2. Farm Good Hope, Transvaal;
G.B. No. 2 111; No. 3. Visible megaspores, New Schoongezicht Colliery, 14′ above No. 2 seam;
G.B. No. 2 112; No. 4. Salisbury Borehole, 366′, Orange Free State.
G.B. No. 2 113; No. 5. Specimen 8516, Waterberg, Transvaal;
G.B. No. 2 114; No. 6. Visible megaspores, Borehole P 2,555′, Coalbrook Colliery;
G.B. No. 2 115; No. 7. Visible megaspores, Virginia;
G.B. No. 2 116; No. 8. Visible megaspores, St. Helena No. 7 (*Leptophloem australis* zone);
G.B. No. 2 117; No. 9. Tiny Lycopod stems and Lycopod leaves, President Brand, Orange Free State;
G.B. No. 2 118; No. 10. Bubye Coal, Upper Portion, Southern Rhodesia;
G.B. No. 2 134; No. 11. Dundas Seam, above sandstone band, Hlobane, Natal;
G.B. No. 2 135; No. 12. Coking Seam, Hlobane, No. 2, Natal;
G.B. No. 2 136; No. 13. Gus Seam, Coronation area, Hlobane, No. 2, Natal;
G.B. No. 2 137; No. 14. No. 18 Section, Gus Seam, Hlobane, Natal;
G.B. No. 2 138; No. 15. Greenside Colliery, Transvaal.

The samples from Australia are:

G.B. No. 2 068; Greta Coal Measures, Lab. No. 10 729–3/16, Seam Greta, Coll. Pelton, Sub Section D;
G.B. No. 2 069; Upper Coal Measures, Tomago Stage, Lab. No. 9 350–3/16″, Seam Big Ben, Coll. Buchanan, Maitland, Sub Section H;
G.B. No. 2 070; Upper Coal Measures, Newcastle Stage, Lab. No. 7 873 3/16, Seam Young Wallsend, Coll. Stockton Borehole, Sub Section D;
G.B. No. 2 071; Upper Coal Measures, Tomago Stage, Lab. No. 7 399, Seam Liddell, Coll. State Coal Mine, Sub Section K;
G.B. No. 2 072; Greta Coal Measures, Lab. No. 1 993, Seam Homoville, Upper Coll. Hebburn 1, Sub Section B;
G.B. No. 2 073; Upper Coal Measures, Newcastle Stage, Lab. No. 8 587, 3/16, Seam Young Wallsend, Coll. Beston, Sub Section D.

A number of the samples from South Africa consisted of shaly material and in some of them the megaspores were already visible before any maceration treatment had been done. Other samples, No. 10–15, consisted of coal. The samples were macerated with the help of the Zetzche method. At first there appeared to be an important difference between these samples. The first nine numbers needed a maceration time of ¾ hour, and with the exception of No. 2, the residue was composed of a large or a rather large number of very big megaspores. The coaly samples, No. 10–15, needed a maceration time of at least 2 hours or more, and the residue was composed of woody vessels, sometimes with a single remnant of an undeterminable spore, with the exception of No. 14 and especially of No. 15 in which numerous megaspores were noticed. In comparison with the first mentioned specimens these were much smaller and of a quite different character. In consequence of the material it can be said that the coalification of the samples of the last group was too high, or nearly so, by which the spores were attacked by the acid at the same rate as the other components of the coal and were dissolved with them. Experiences of such coals have taught that after

The G.B. numbers are those of the Geol. Bureau at Heerlen, the numbers 1–15 are of Doctor Plumstead.

Mr. H. R. Brown, director Commonwealth Scientific and Industrial Research Organization, Coal Research Section, Australia, has kindly sent some coal samples to us.

maceration practically only woody vessels remain. Indeed a name such as 'Coking Seam' does not give encouragement to expect good results with a spore treatment.

The Australian samples consisted of coal; they needed a maceration time of 4–5 hours or even longer. They contained a good many megaspores, with the exception of No. 2 069 in which only some cuticles could be observed. These Australian megaspores are small or medium in size; the variation in species was small.

The spores were photographed under reflected light, after having been covered with ammonium chloride. By this ornamentations such as ridges, appendages, punctation, etc. were accentuated. A drawback of this method is that small dirt particles on the wall of the spore and even on the cover-glass of an ordinary foraminifera cardboard slide on which the spores were placed during the photographing become visible. Sometimes they are accentuated too much, by which a smooth wall appears to be finely punctuate (Pl. I, fig. 6).

After termination of this manuscript, when description and photography of the spores had been finished, we received a paper of Bharadwaj and Tiwari, 1970, in which they described a method by which they were able to study the internal structure of spores. Some specimens were treated, after maceration, with 5% KOH for about 30 seconds, or longer (2–10 minutes), by which some species became transparent. In some cases a dilute (10%) HNO_3 treatment preceded the alkali treatment. By this the spores became more transparent, the inner body was distinct and bore cushions on its proximal face in some species. Moreover the size increased, sometimes even more than double the original size in the dry condition. We have used this method for three species which we expected to be suitable for this treatment. They are: *T. australis, robus* and *subnitens*. The result was very poor, after a treatment of half an hour they did not become transparent, and the increase in size was inconsiderable. Replacing them, after washing in water, in a strong (75%) HNO_3 the wall became transparent within some minutes. The three species studied did not show cushions on their proximal face.

RELATION BETWEEN THE DIMENSION OF THE SPORES AND THE AGE OF THE DEPOSITS IN WHICH THEY OCCUR.

Studies on megaspores have shewn that spores of the Carboniferous, and especially those of the Lower Carboniferous, are by far the largest (Dijkstra, 1956; Dijkstra and Piérart, 1957, and Dijkstra, 1971). Mesozoic megaspores are distinguishable from the Carboniferous ones, taken collectively, simply on the basis of their smaller size (Chaloner, 1959). He has plotted the mean size of megaspores of various assemblages in a table that shows a general trend of size decreasing from the Carboniferous to the Upper Cretaceous. He has suggested that most of the large Carboniferous megaspores are known to have been borne by arborescent lycopods, whereas two of the smallest Carboniferous megaspores were apparently borne by herbaceous lycopods. It is therefore a plausible hypothesis that the decline in megaspore size may be correlated with the decline in the arborescent lycopods.

Concerning the size of Devonian megaspores a short survey of some investigators of various basins is given. These basins are chosen involuntary. A more extensive survey on Lower Carboniferous and Devonian megaspores is given by Dijkstra, 1971. A repetition in this paper is superfluous.

Arctic: Chaloner, 1959.
Canada: McGregor, 1960, Melville Island.
U.S.A.: Pettitt, 1965, Maine and Perry.
Scotland: Richardson, 1965.
England: Mortimer and Chaloner, 1967.
Ireland: Chaloner, 1968.
Belgium: Piérart, 1964, Roncquières, Brabant.
U.S.S.R.: Nikitin, 1934, Voronesh.

In general it can be said that the Devonian megaspores described from these basins are small or medium in size, and smaller than the largest Lower Carboniferous megaspores.

THE PRESUMABLE AGE OF THE SAMPLES FROM SOUTH AFRICA

Not knowing the exact age of these samples studied from South Africa our provisional conclusion was that the samples 1–9 belong together. Their spores, although of new species, and consequently not comparable with those of Tchad, Egypt, Moscow or other basins, are of very old age, probably belonging to the Lower Carboniferous. This conclusion is influenced by the large diameter of some of them. The other samples, No. 10–15, and especially those of which megaspores could be isolated, are much younger, and their spores are better comparable with species from India, Australia and Brazil. Dr. Plumstead, on being so informed, answered that she would have expected Nos. 1, 4, 7, 8, 9 to be from similar zones, just as 3 and 6 could be also. She expected No. 2 to be different and probably a little younger; 5 and 10 she wanted to check. They are more likely to be typical Gondwana Lower Permian coals. No. 11–14 are Natal coking coals and in this country this usually means that they have been burnt and spores are destroyed; 15 should be the youngest and comparable with India.

THE INFLUENCE OF THE CRUSHING ON THE SHAPE OF THE SPORES

During the study and especially in the description of the spores the question sometimes arose about their original shape. Chaloner, 1953, has discussed the transformation of some spherical and saucer-shaped species after flattening. A thin-walled spherical species normally shows (except for the apical prominence) after flattening a circular outline with one or two tangential folds. If the wall is thicker, a circular disc is produced, without the

formation of any folds. A more or less saucer-shaped spore will show two properties on crushing, which distinguish it from the spherical species. Firstly it has the tendency to settle flat in the matrix before fossilization and, in those cases where it does this, the apex of the spore will appear in the centre of the disc; in a spherical spore the apex might appear anywhere in the disc. Secondly a saucer-shaped spore will occasionally settle on edge, so producing a crumpled and more or less elliptical form when flattened.

Species of which the proximal-distal axis is considerably longer than the transverse axis, for instance the fertile form of *Cystosporites* species and many species belonging to *Lagenicula*, generally fall in a lateral direction in the coalforming swamps and are flattened in this way, by which their apical prominence is clearly distinguishable. If, however, they fall perpendicularly with their distal or proximal axis in the mud, then the prominence is less clearly visible, but lobes built by the triradiate ridges and the arcuate ridge are clearly visible (Pl. IV, fig. 47). Besides the shape of the spore the composition of the sediment may influence the fossil. If they fall in a coarse sandy deposit the grains can cause cavities in the wall of the spore (Pl. IV, fig. 46).

A more interesting deformation in the shape of fossils occurs when the sediment in which they are embedded is shifted by a lateral tectonic pressure. A sample of coal of Spain contained some hundreds of specimens of *Endosporites* (?) *radiatum* (*Triletes karczewski* Zerndt). As is known, this species is triangular, saucer-shaped and its triradiate ridges are of the same length. All the specimens of that Spanish sample were no longer equilateral; one of the ridges was shorter (Dijkstra, 1955, Pl. 41, fig. 28). Besides this species all others of that sample (*T. mamillarius, T. glabratus, T. praetextus*) were deformed in the same way. A very suggestive example of deformation by lateral pressure can be observed in the collection of the Geol. Bureau at Heerlen. It is a petrified stem of 28 cm in length; its diameter is 27 cm. The stem is divided by lateral pressure into four slices that are still connected; the displacement is 36 cm. If parts of such a brittle fossil can be shifted without breaking the tougher wall of a spore may easily be deformed. The triradiate ridges of specimens of the same species may vary in shape, and can be straight or undulate. Probably this is a question of deformation during the fossilization or even long before that process, caused by wrinkling of the ridges during drying of the coat.

DESCRIPTIONS

A. Spores of South Africa

Aphanozonati

Triletes compressus sp. nov.
Pl. I, figs. 1–3; holotype fig. 7.

Spore round-subtriangular in outline, flattened in proximal-distal direction. Diameter 1 320–2 030 μ (the mean of 9 measured specimens being 1 613 μ). Triradiate ridges generally straight, sometimes undulate, 7/8 of the diameter of the spore in length, 30 μ broad, 25 μ high. Arcuate ridges, if distinguishable, 15 μ broad. Where they meet the triradiate ridges the former are curved in the direction of the apex of the spore. Whole coat of the spore more or less reticulate. Reticules 10–25 μ in diameter, on the contact faces stretched in radial direction. Coat about 20 μ thick.

Discussion and comparison. In some respects, especially in shape, this species resembles *T. eregliensis* (Dijkstra, 1952, Westphalian D, Turkey). The coat of the latter is not reticulate, but provided with truncate, obconical papillae. *T. compressus* is more related to *T. patulus* (Dijkstra and Piérart, 1957, Lower Carboniferous of Moscow). The latter is smaller, its diameter varies from 760–990 μ, its coat is finely punctate.

Occurrence: Sample No. 2 111, New Schoongezicht Coll.: No. 2 112, Salisbury Borehole, Orange Free State; No. 2 114, Coalbrook Coll.; No. 2 116, St. Helena No. 7.

Triletes calvus sp. nov.
Pl. I, figs. 4–6; holotype fig. 6

Spore rounded in outline, flattened in proximal-distal direction. Diameter 710–930 μ (the mean of 4 measured specimens being 822 μ). Triradiate ridges straight, 7/8 of the radius of the spore in length, 15 μ broad, 20 μ high. The highest near the apex of the spore. Arcuate ridges not or hardly distinguishable. Whole coat of the spore a little rough to finely reticulate.

Discussion and comparison. This is a species with practically no characteristic ornamentation; its only characteristic property is its long narrow triradiate ridges. *T. patulus* (Dijkstra and Piérart, 1957) is of the same size, but its triradiate ridges are much shorter and wider. The 'tubercles' on the photographs are impurities on the coat of the spore and do not belong to it.

Occurrence: Sample No. 2 111, New Schoongezicht Coll.; No. 2 113, Waterberg, Transvaal.

Triletes inflexus sp. nov.
Pl. I, figs. 7–9; holotype fig. 8

Spore rounded-subtriangular in outline, flattened in proximal-distal direction. Diameter 470–730 μ (the mean being 619 μ, 8 specimens measured). Triradiate ridges straight, exceptionally undulate, nearly as long as the radius of the spore, 30 μ broad, 20–30 μ high, highest near the apex of the spore. Contact faces and arcuate ridges clearly distinguishable. Arcuate ridges 15 μ broad. The distal and the proximal part of the spore (the contact faces excepted) are thickened and swollen. Where the triradiate ridges meet the arcuate ridges the latter are sometimes curved a little in the

direction of the apex of the spore. The wall of the spore is smooth.

Discussion and comparison. The triradiate ridges of this species are wider than those of *T. calvus*. Its contact faces are, with respect to the rest of the coat of the spore, pressed inwards. Probably here the coat is much thinner. The contact faces of *Triangulatisporites membranatus* Butterworth and Spinner, 1967, are relatively smaller, 3/4 of the proximal surface, and their triradiate ridges seem to be narrower.

Occurrence: Sample No. 2 111, New Schoongezicht Colliery; No. 2 112, Salisbury Borehole, Orange Free State; No. 2 117, President Brand.

Triletes densireticulatus sp. nov.
Pl. I, figs. 10–12; Pl. II, figs. 13, 14;
holotype fig. 11.

Spore rounded in outline, generally flattened in proximal-distal direction. Diameter 800–1 180 μ (the mean being 987 μ, 17 specimens measured). Triradiate ridges straight or nearly so, 3/4–7/8 of the radius of the spore in length, 10–15 μ high, 15 μ broad. Arcuate ridges 15 μ broad. Contact faces clearly distinguishable. Where the triradiate ridges meet the arcuate ridges, the latter are curved in the direction of the apex of the spore. Whole wall of the spore, the contact faces included, finely reticulate, diameter of the reticules 5–12 μ.

Discussion and comparison. This species shows some resemblance to *T. compressus*, but the latter is larger, and especially the reticules of the coat are much rougher than the fine ornamentation in *T. compressus*.

Occurrence: Sample No. 2 115, Virginia; No. 2 109, President Steyn Gold Mine, Orange Free State; No. 2 117, President Brand, Orange Free State.

Triletes paucipinnatus sp. nov.
Pl. II, figs. 15–17; holotype fig. 16

Spore round in outline, flattened in proximal-distal direction, Diameter of the spore 730, 580, 570 μ. Triradiate ridges straight, 7/8 of the radius of the spore in length, about 15 μ broad and high. Contact faces scarcely distinguishable, arcuate ridges not visible. Coat of the spore, especially the distal part, rough. Moreover, the contact faces excepted, scarcely covered with appendages. Appendages up to 130 μ long, 5–10 μ broad, their tip spherical-clubshaped. Mutual distance of the appendage varies from 50–100 μ.

Discussion and comparison. As only one complete specimen and two broken ones could be noticed of which most appendages are broken off the shape of the tip of them may be discussable. As far as we know this species is not comparable with any other.

Occurrence: Sample No. 2 113, Waterberg, Transvaal.

(?) *Triletes suspectus* sp. nov.
Pl. II, figs. 18A, 18B; holotype

Spore (?) oval in outline, dimensions 3 400–4 000 μ. Wall on both sides irregularly reticulate. Size of the reticules varies from 50–120 μ.

Discussion. The nature of this object is questionable; probably it is a spore species, belonging to the Aphanozonati. However, triradiate and arcuate ridges, contact faces or other ornamentations could not be noticed. Only one specimen was found.

Occurrence: Sample No. 2 116, St. Helena No. 7.

Triletes transvalensis sp. nov.
Pl. II, figs. 19–22; Pl. III, figs. 23, 24;
holotype fig. 20

Spore rounded-oval in outline, flattened in proximal-distal direction. Diameter of the spore 460–680 μ (the mean being 579 μ, 25 specimens measured). Triradiate arcuate ridges and contact faces not or hardly distinguishable. Whole coat of the spore densely covered with appendages. Appendages staff-shaped, up to 30–50 μ long, blunt-ended, sometimes wedge-shaped or hardly furcate. Mutual distance about 10 μ or less. Here and there fused by a thin, transparent substance. Coat of the spore about 10 μ thick.

Discussion and comparison. The appendages resemble in some respect those of *T. furcatus* Dijkstra, 1955 (= *Gulatriletes vulgatus* Bharadwaj and Tiwari), but the latter are longer and clearly furcate, the diameter of that species larger, the mean being 837 μ. An essential difference, however is that *T. furcatus* has a clearly distinguishable neck-like projection. The processes of *T. surangei* Prem Singg, 1953 (=*Singhisporites surrangei* Bh. and Tiw.), are much longer, as much as 131 μ and their density is not so crowded, and the diameter of that species varies from 643–819 μ. The coat of some *T. transvalensis* specimens is plicate, and shows some ridges that may be the triradiate ridges. This species was abundant in sample No. 2 138 by which the derivation of its name is justified.

Occurrence: Sample No. 2 138, Greenside Colliery, Transvaal.

Triletes subnitens sp. nov.
Pl. III, figs. 25–27; holotype fig. 25

Spore rounded in outline, generally flattened in proximal-distal direction. Diameter 590–820 μ (the mean being 704 μ, 16 specimens measured). Triradiate ridges 5/8 of the radius of the spore, 15 μ broad; arcuate ridges about 10 μ broad. Coat of the whole spore smooth to a little punctate and very thin.

Discussion and comparison. The coat of this species is very thin, sometimes so plicate that the ornamention is not always distinguishable; it is very brittle. The coat of *T. trivedi* Dijkstra, 1955 (= *Talchirella notabilis* Bhard. and Tiw.) is papillate.

The resemblance with *T. nitens* Dijkstra, 1955 (= *Talchirella nitens* Bhard. and Tiw.) is rather great. The diameter of *T. nitens* varies from 450–930 μ (the mean being 695 μ). Its triradiate ridges and generally its arcuate ridges are clearly distinguishable, but that may be caused by a better preservation. The triradiate ridges of *T. nitens* are relatively longer than those of *T. subnitens*. This specis did not show cushions on the proximal face after a treatment with alkali, whereas *Talchirella* species exhibit such objects, according to Bharadwaj and Tiwari.

Occurrence: Sample No. 2 138, Greenside Colliery, Transvaal; No. 2 137, No. 14, No. 8 Section, Gus Seam, Hlobane, Natal.

Triletes irregularis sp. nov.
Pl. III, figs. 28–33; holotype fig. 28

Spore rounded-elliptical or irregular in shape, generally flattened in proximal-distal direction. Diameter 420–580 μ (the mean being 518 μ, 20 specimens measured). Triradiate ridges straight or undulate, 3/4–7/8 of the radius of the spore, 15 μ broad or more. Arcuate ridges not clearly distinguishable. Its coat is smooth and plicate.

Discussion and comparison. T. tchadiensis Dijkstra, 1971, is smaller, 300–460 μ (the mean being 366 μ), even the variety *major* is smaller than *T. irregularis. T. tchadiense* makes a solid impression, its triradiate ridges especially are substantial. It was very abundant and was observed in practically all studied samples of boring Tchad by which a perfect idea of this species could be obtained. These species are not identical. *T. irregularis* is very irregular in shape, it gives an impression of immaturity or abortion. As it was found in the same sample as *T. subnitens*, it may belong to it.

Occurrence: Sample No. 2 138, Greenside Colliery, Transvaal.

Zonales

Triletes capreolatus sp. nov.
Pl. III, figs. 34–38;
holotype fig. 34, cotype fig. 37

Complete spore subtriangular in outline, flattened in proximal-distal direction. Body of the spore rounded 1 610–2 800 μ (the mean being 2 440 μ, 25 specimens measured). Triradiate ridges generally undulate, about 3/4 of the radius of the body of the spore in length, 30–80 μ broad, 25–100 μ high, highest at the apex of the spore. Arcuate ridges 40–60 μ broad. Zone up to 300 μ wide, widest at the contact places of the triradiate ridges with the arcuate ridges. Contact area clearly distinguishable. Coat of the body of the spore rough, finely punctate, 30 μ thick.

Discussion and comparison. Practically all specimens have lost their zone and perispore. Fig. 37 shows a specimen with some remains of the zone; the specimen on fig. 34 is surrounded by its perispore that encloses the whole body of the spore: zone, contact area and triradiate ridges. It is a thick fibrous mass with little structure, it builds a 90 μ wide crest on the triradiate ridges and a shapeless compressed mass in the apex of the spore. The zone is massive; radiating appendages fused by a rim at the periphery of the zone could not be observed. By this this species is not comparable with species such as *T. brasserti, T. rotatus, T. mucronatus,* etc. which are provided with such a zone.

Occurrence: Sample No. 2 113, Waterberg, Transvaal; No. 2 114, Coalbrook Colliery; No. 2 115, Virginia; No. 2 116, St. Helena No. 7, President Brand, Orange Free State.

Triletes lepidus sp. nov.
Pl. IV, figs. 39–41; holotype fig. 39

Spore generally rounded in outline and generally flattened in proximal-distal direction. Diameter of the whole spore, the zone included, 790–1 140 μ (the mean being 960 μ, 8 specimens measured). Triradiate ridges straight, about 300 μ long, 20 μ broad. Arcuate ridges 20 μ broad, not always distinguishable; contact faces clearly visible. Distal area and proximal area, the contact faces excepted, covered with a thick entangled mass of appendages, building at the equator a zone up to 400 μ wide. The individual shape of the appendages is difficult to distinguish, but with some isolated parts of the zone these appendages, running in radial direction, appear to be about 10 μ wide and allied with each other by a transparent substance. The coat of the contact area is rough-striate.

Discussion and comparison. This species is not comparable with species such as *T. brasserti, rotatus, mucronatus*, etc. of which the equatorial zone is composed of a number of radial running appendages that are fused at their periphery, building a rim. By this these species look like a wheel with spokes surrounded by a ring. In some respects it shows some resemblance to *T. furcatus* Dijkstra, 1955 (= *Gulatriletes furcatus* Bharad. and Tiw.), but that species is distinguishable by its neck-like projection. This species most resembles *Triangulatisporites rootsii* Chaloner, 1959, but the dimension of the latter is much smaller (diameter, including the flange, 485–524 μ; the mean being 507 μ and the width of the flange varies from 70–107 μ).

Occurrence: Sample No. 2 138, Greenside Colliery, Transvaal.

Triletes pusillus sp. nov.
Pl. IV, figs. 42A, 42B; holotype

Spore rounded-subtriangular, flattened in proximal-distal direction. Diameter 370–510 μ (the mean being 426 μ, 10 specimens measured). Triradiate ridges straight, 3/4 of the radius of the spore in length, ca. 20 μ broad, the widest in the direction of the periphery. Contact faces clearly

distinguishable, arcuate ridges not obvious. Coat of the spore verrucose, contact faces finely punctuate.

Discussion and comparison. We have treated this species with alkali, but the spore did not become more transparent, an inner body could not be observed, cushions on the proximal face could not be observed, and the increase in size was unimportant. By this a comparison with species belonging to *Srivastavaesporites*, described by Bharadwaj and Tiwari, is difficult. *S. karanpuraensis* looks to be very similar, but its triradiate ridges are tapering towards the ends, which is not the case with *T. pusillus; S. endosporitiferus* has a well-defined inner body and is larger; *S. dijkstrae* is characterized by the absence of well defined contact area; *S. indicus* has an inner body and its triradiate ridges are slightly narrowed towards their ends; *S. utkalensis* has an inner body and is larger and its verrucae are much higher; finally *S. tenuis* and *labiosus* (= *T. tenuis* and *T. labiosus* Dijkstra, 1935) are much larger than *T. pusillus*.

Occurrence: Sample No. 2 138, Greenside Colliery, Transvaal.

Lageniculae

Triletes turnaui sp. nov.
Pl. IV, figs. 43–48; Pl. V, fig. 49? ;
holotype fig. 48

Spore rounded or elliptical in outline, flattened in proximal-distal, lateral, but generally in oblique direction. Diameter 1 080–1 860 μ (the mean being 1 528 μ, 25 specimens measured). Triradiate ridges generally straight, sometimes undulate, 3/4–7/8 of the radius of the spore in length, 30–40 μ broad, highest at the apex of the spore building a pyramidal elevation, about 200 μ in height. Arcuate ridges sometimes clearly distinguishable and about 30 μ wide. Coat of the spore smooth to a little rough, about 15 μ thick.

Discussion and comparison. The pyramidal elevation is not always distinguishable, being best visible in specimens flattened in lateral direction. The surface of the wall of the spore depends moreover on the substratum in which the specimen is embedded. Fig. 46 shows a specimen that was deposited in sandy grains. We do not know a lageniculate species with a smooth wall of these dimensions. Some of the Moscow species (Dijkstra and Piérart, 1957) are very large too, but their wall is covered by a number of appendages.

Derivation of name: after Dr. Elzbieta Turnau of Krakow, who has given me many valuable suggestions during her study stay at Heerlen.

Occurrence: Sample No. 2 109, President Steyn Gold Mine, Orange Free State; No. 2 111, New Schoongezicht Colliery; No. 2 114, Borehole P. 2.555′, Coalbrook Colliery; No. 2 116, St. Helena No. 7; No. 2 117, President Brand, Orange Free State.

Triletes brachytrachelos sp. nov.
Pl. V, figs. 50–55; holotype fig. 50

Spore oval or rounded in outline, flattened in proximal-distal or in lateral direction. Diameter 870–1 940 μ (the mean being 1 429 μ, 30 specimens measured). Triradiate ridges 7/8 of the radius in length, 30 μ broad and up to 200 μ in height, the highest at the apex of the spore, building a neck-line elevation. Arcuate ridges 40 μ wide; where they meet the triradiate ridges triangular lobes are distinguishable, 100 μ in radial, 150 μ in transverse direction. The coat of the spore, the contact faces more or less excepted, rough-reticulate, densely covered with conical appendages, ca. 10 μ in length.

Discussion and comparison. The neck-line elevation is not always visible, its length is up to 700 μ. Some specimens still in a tetrad are covered with a red translucent substance. Probably they are not fully developed specimens. *T. catenulatus* Winslow, 1962, is much smaller (425–740 μ), the shape is different, and the appendages longer. *Biharisporites ocksensis* Chaloner, 1959, has no triangular lobes, its surface is finely granular, or covered with 10 μ high cones. *T. angulatus* Zerndt, 1937, has much larger triangular lobes, its cones vary from 6–24 and its wall is moreover covered with irregularly shaped tubercles. *T. brasiliensis* Dijkstra, 1955, is more comparable, but that species is smaller, its diameter varies from 650–1 610 μ (1 013 μ for the mean), it shows some semi-spherical objects on its wall. *T. punctatus* Trivedi, 1953, is smaller, its diameter is 806 μ long, excluding the neck-like elevation 194 μ in length. Its coat is punctate, the punctae being 12,8 μ in breadth and 11,2 μ in length.

Occurrence: Sample No. 2 114, Coalbrook Colliery; No. 2 115, Virginia; No. 2 116, St. Helena No. 7; No. 2 117, President Brand, Orange Free State.

B. Spores of Australia

Aphanozonati

Triletes australis sp. nov.
Pl. V, figs. 56–59; Pl. VI, figs. 60–62;
holotype fig. 59

Spore rounded in outline, flattened in proximal-distal direction. Diameter 870–1 190 μ (the mean being 1 049 μ, 25 specimens measured). Triradiate ridges generally undulate, sometimes straight, about 1/2 of the radius of the spore in length, 30–40 μ in breadth and up to 30 μ in height. Arcuate ridges not distinguishable. Whole wall of the spore, the contact faces excepted, densely covered with appendages up to 110 μ in length, staff-shaped and furcate at the tip, the bases generally mutually joined by a thin transparent substance. Contact faces covered with very short appendages to punctuate. The coat of the spore is about 10 μ thick.

Discussion and comparison. T. furcatus Dijkstra, 1955 (*Gulatriletes furcatus* Bharadwaj

and Tiwari) has a neck-like projection, its appendages are shorter and its contact faces smooth to sparsely covered with small objects. *T. trivedi* Djikstra, 1955 (*Talchirella notabilis* Bhar. et Tiw.) is smaller (380–780 μ, 630 μ for the mean). Moreover both former species show on the proximal side, after treating with alkali, irregularly arranged pits or cushions along their triradiate mark. These objects could, after alkali treatment, not be observed in *T. australis*. *T. catenulatus* Winslow, 1962, is also much smaller, has an apical projection and its spines are shorter. *Singhisporites radialis* Bharadwaj and Tiwari, 1970, is smaller, 375–508 μ.

Occurrence: Sample No. 2 068, Greta Coal Measures, Colliery Pelton (in great numbers); No. 2 072, Upper Coal Measures, Newcastle Stage, Colliery Stockton; No. 2 073, Greta Coal Measures, Tomago Stage, Colliery State Coal Mine.

Triletes robur sp. nov.
Pl. VI, figs. 63–70; holotype fig. 63

Spore rounded in outline, flattened in proximal-distal direction. Diameter 740–1 240 μ (the mean being 991 μ, 50 specimens measured). Triradiate ridges straight, 3/4 of the radius of the spore in length, 12–15 μ broad, the same in height. Arcuate ridges hardly distinguishable. Coat of the spore, especially the distal part, rough, densely covered with blunt-ended, fleshy papillae, 5–7 μ (up to 15 μ) in length.

Discussion and comparison. The triradiate ridges end at the point of contact with the arcuate ridges. After a treatment with alkali, pits or cushions on the proximal side of the spore could not be observed. We have compared it with *Srivastavaesporites* species Bharadwaj and Tiwari, 1970. However, most of the species described by them are considerably smaller than *T. robur*. It is in dry conditions even larger than some of them in wet condition. *T. labiosus* Dijkstra, 1955, is somewhat larger than *T. robur*, its surface is smooth to finely punctate. Although Pant and Srivastava, having received some specimens of this species from us, could not observe pits or cushions after an alkali treatment, Bharadwaj and Tiwari, 1970, have placed *T. labiosus* in *Srivatavaesporites*.

Occurrence: Sample No. 2 068, Greta Coal Measures, Seam Greta, Colliery Pelton; No. 2 070, Upper Coal Measures, Newcastle Stage, Seam Young Wallsend; No. 2 071, Upper Coal Measures, Tomago Stage, Seam Liddell, Colliery State Coal Mine; No. 2 073, Upper Coal Measures, ? Newcastle Stage, Seam Young Wallsend, Colliery Boston.

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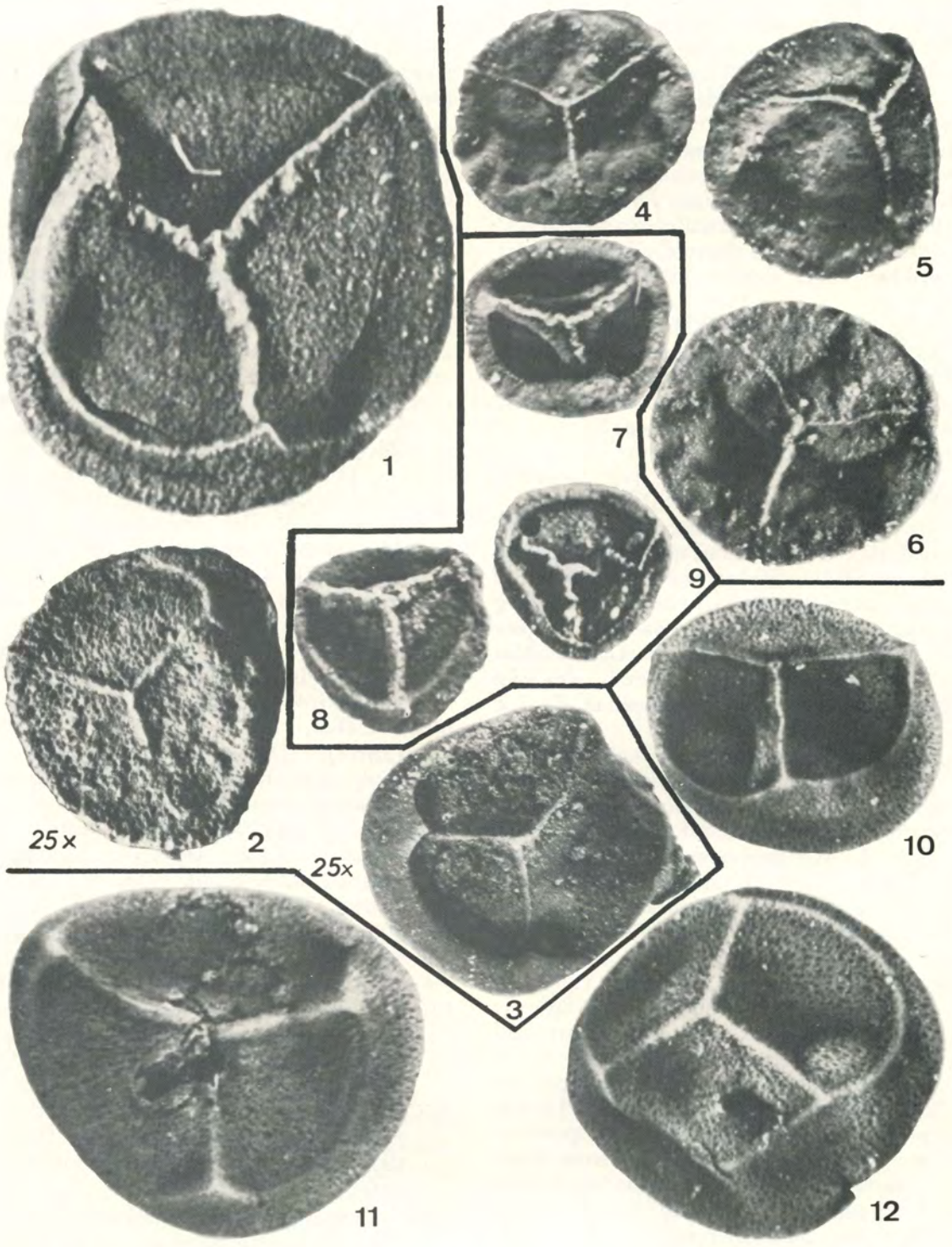


Plate I

Fig. 1 *Triletes compressus* sp. nov., sample No. 2 111—No. 3, S. Africa.
Fig. 2 *Triletes compressus* sp. nov., sample No. 2 116—No. 8, S. Africa.
Fig. 3 *Triletes compressus* sp. nov., sample No. 2 114—No. 6, S. Africa.
Figs. 4—6 *Triletes calvus* sp. nov., sample No. 2 111—No. 3, S. Africa.
Fig. 7 *Triletes inflexus* sp. nov., sample No. 2 111—No. 3, S. Africa.
Figs. 8, 9 *Triletes inflexus* sp. nov., sample No. 2 117—No. 8, S. Africa.
Figs. 10—12 *Triletes densireticulatus* sp. nov., sample No. 2117—No. 9, S. Africa.

The enlargement of all the photographs is 50X, except in some specimens the enlargement is indicated on the plates. The photographs were made by L. R. Funcken.

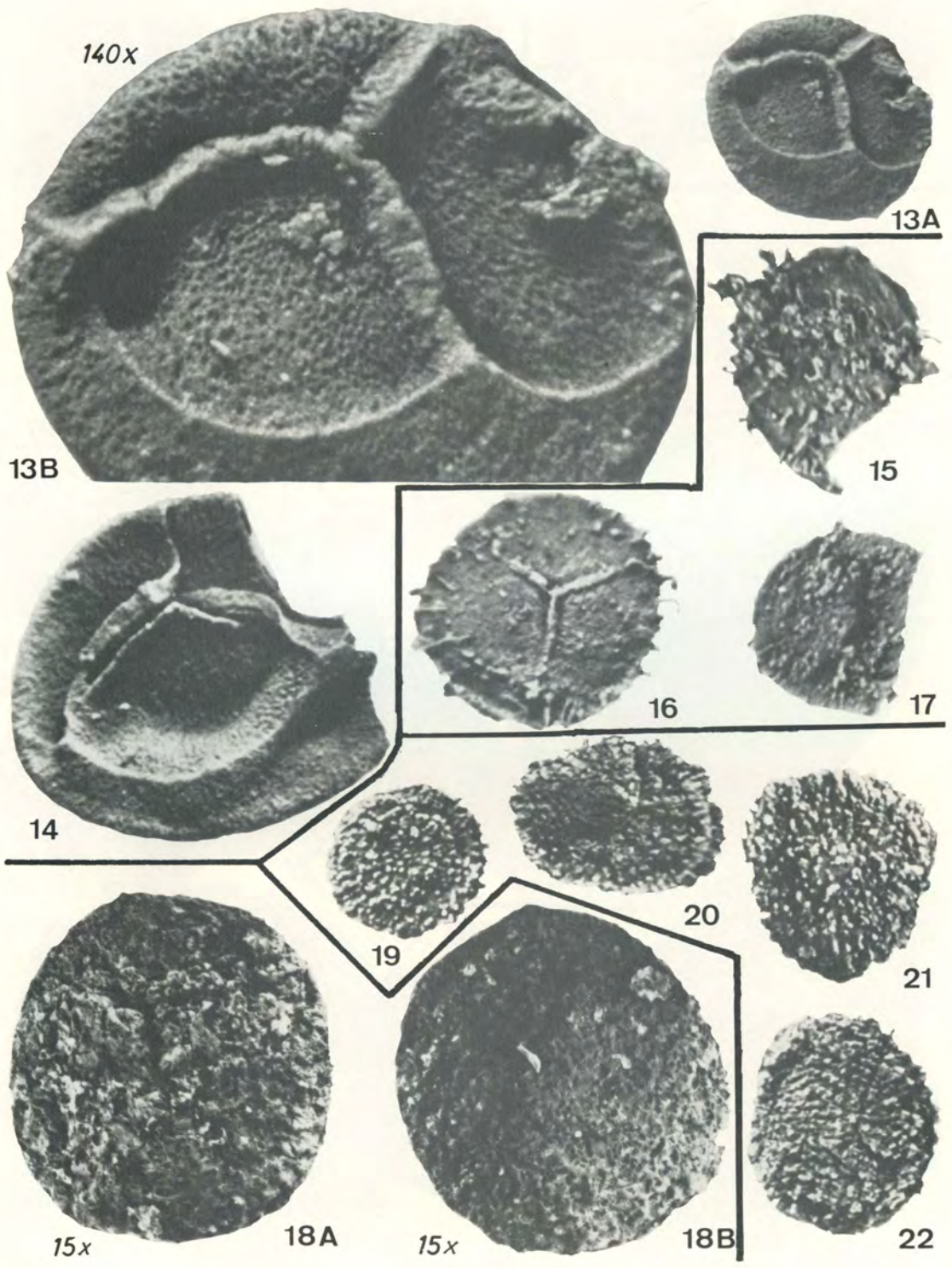


Plate II

Figs. 13A, 13B *Triletes densireticulatus* sp. nov., sample No. 2 109—No. 1, S. Africa.
Fig. 14 *Triletes densireticulatus* sp. nov., sample No. 2 117—No. 9, S. Africa.
Figs. 15—17 *Triletes paucipinnatus* sp. nov., sample No. 2 113—No. 5, S. Africa.
Figs. 18A, 18B (?)*Triletes suspectus* sp. nov., sample No. 2 116—No. 8, S. Africa.
Figs. 19—22 *Triletes transvalensis* sp. nov., sample No. 2 138—No. 15, S. Africa.

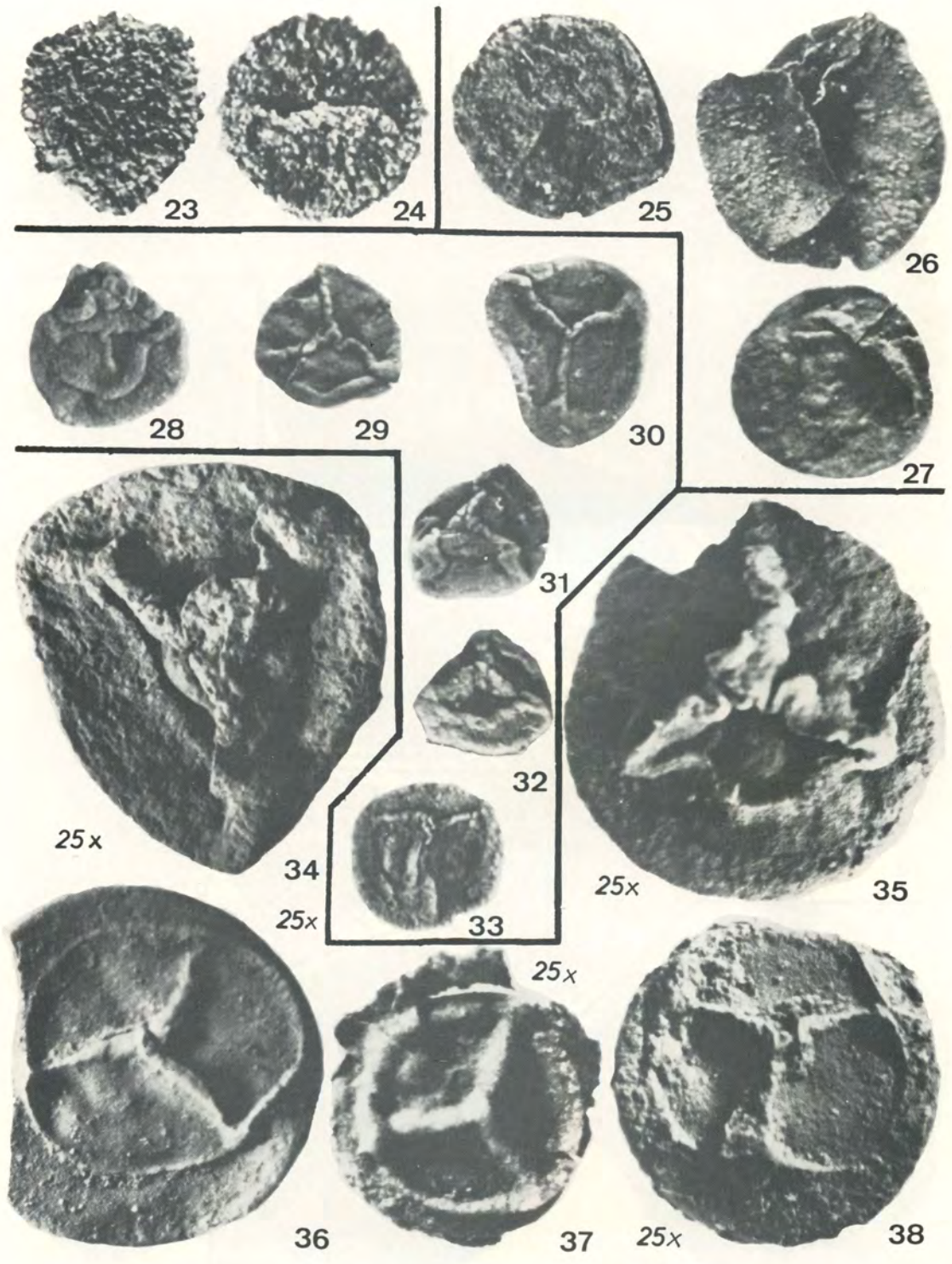


Plate III

Figs. 23, 24 *Triletes transvalensis* sp. nov., sample No. 2 138—No. 15, S. Africa.
Figs. 25, 27 *Triletes subnitens* sp. nov., sample No. 2 138—No. 15, S. Africa.
Fig. 26 *Triletes subnitens* sp. nov., sample No. 2 137—No. 14, S. Africa.
Figs. 28—33 *Triletes irregularis* sp. nov., sample No. 2 138—No. 15, S. Africa.
Figs. 34, 35 *Triletes capreolatus* sp. nov., sample No. 2 116—No. 8, S. Africa.
Figs. 36, 38 *Triletes capreolatus* sp. nov., sample No. 2 114—No. 7, S. Africa.
Fig. 37 *Triletes capreolatus* sp. nov., sample No. 2 115—No. 6, S. Africa.
Fig. 34 Specimen surrounded by its perispore.
Fig. 37 Specimen with remains of its zone.

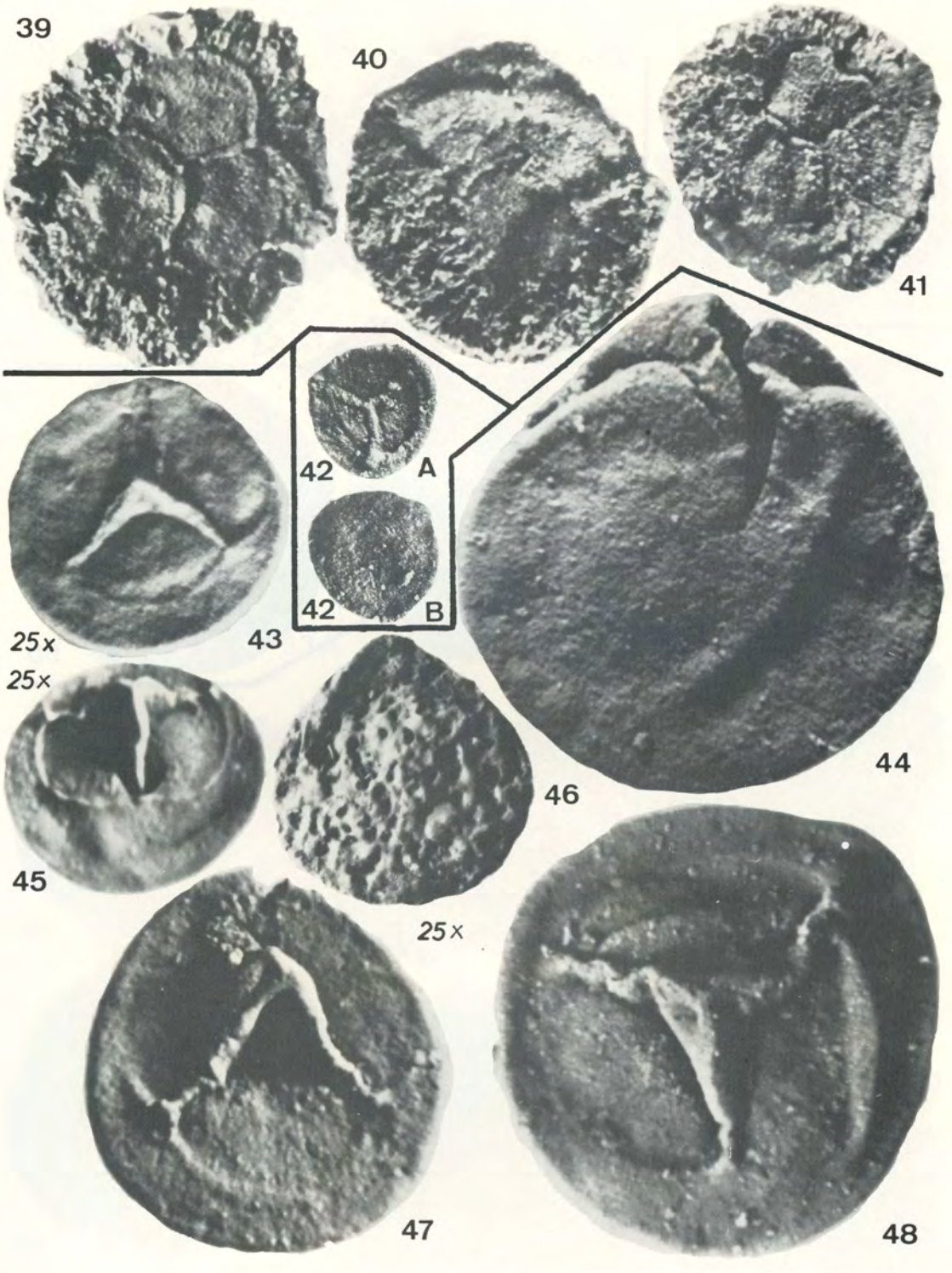


Plate IV

Figs. 39–41 *Triletes lepidus* sp. nov., sample No. 2 138–No. 15, S. Africa.
Figs. 42A, 42B *Triletes pusillus* sp. nov., sample No. 2 138–No. 15, S. Africa.
Figs. 43–45, 47, 48 *Triletes turnaui* sp. nov., sample No. 2 109–No. 1, S. Africa.
Fig. 46 *Triletes turnaui* sp. nov., sample No. 2 116–No. 8, S. Africa. Specimen deposited in sandy grains.

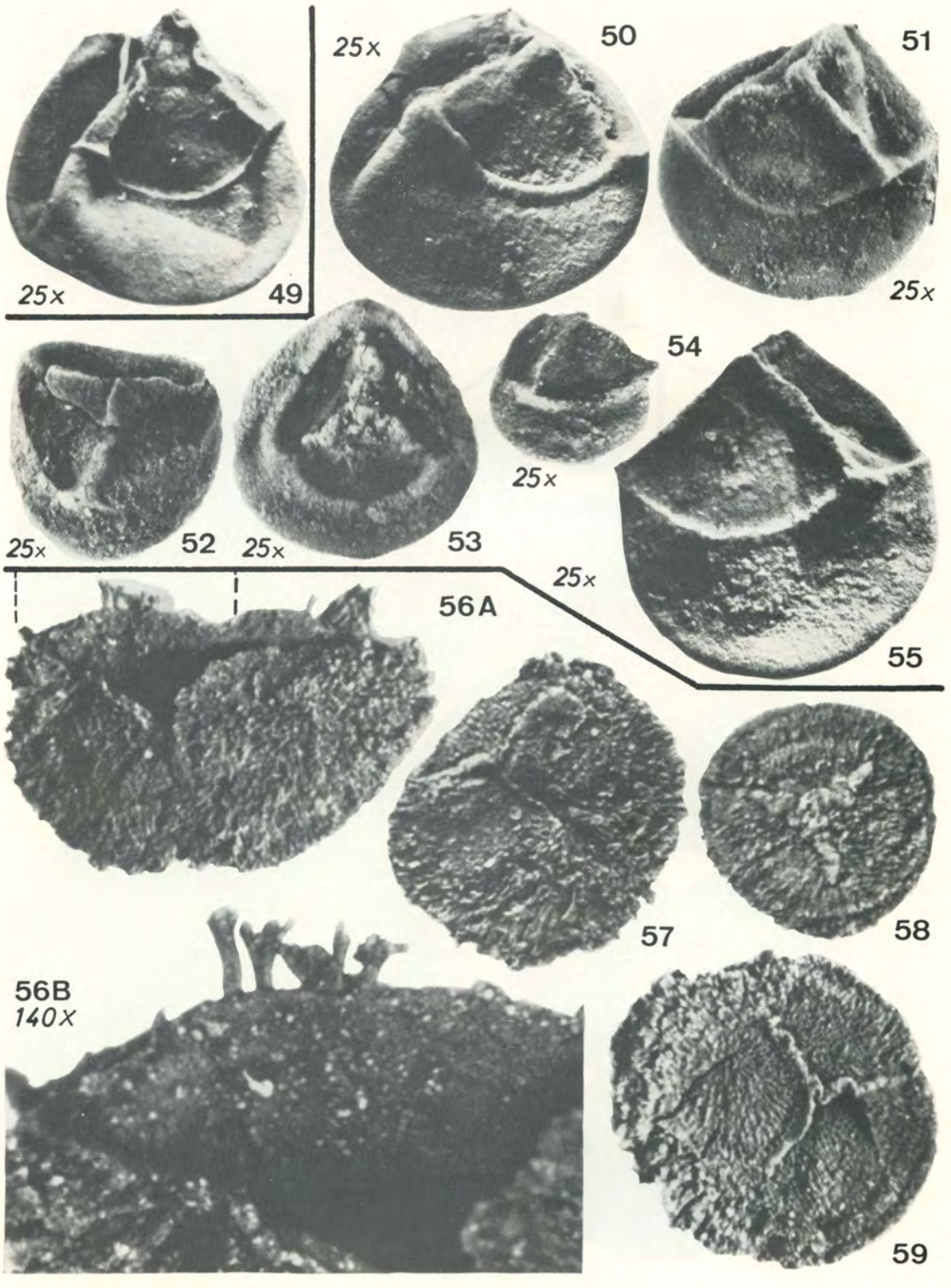


Plate V

Fig. 49 *Triletes* cf. *turnaui*, sample No. 2 111—No. 3, S. Africa.
Figs. 50—55 *Triletes brachytrachelos* sp. nov., sample No. 2 114—No. 6, S. Africa.
Figs. 56—59 *Triletes australis* sp. nov., sample No. 2 073, Australia.

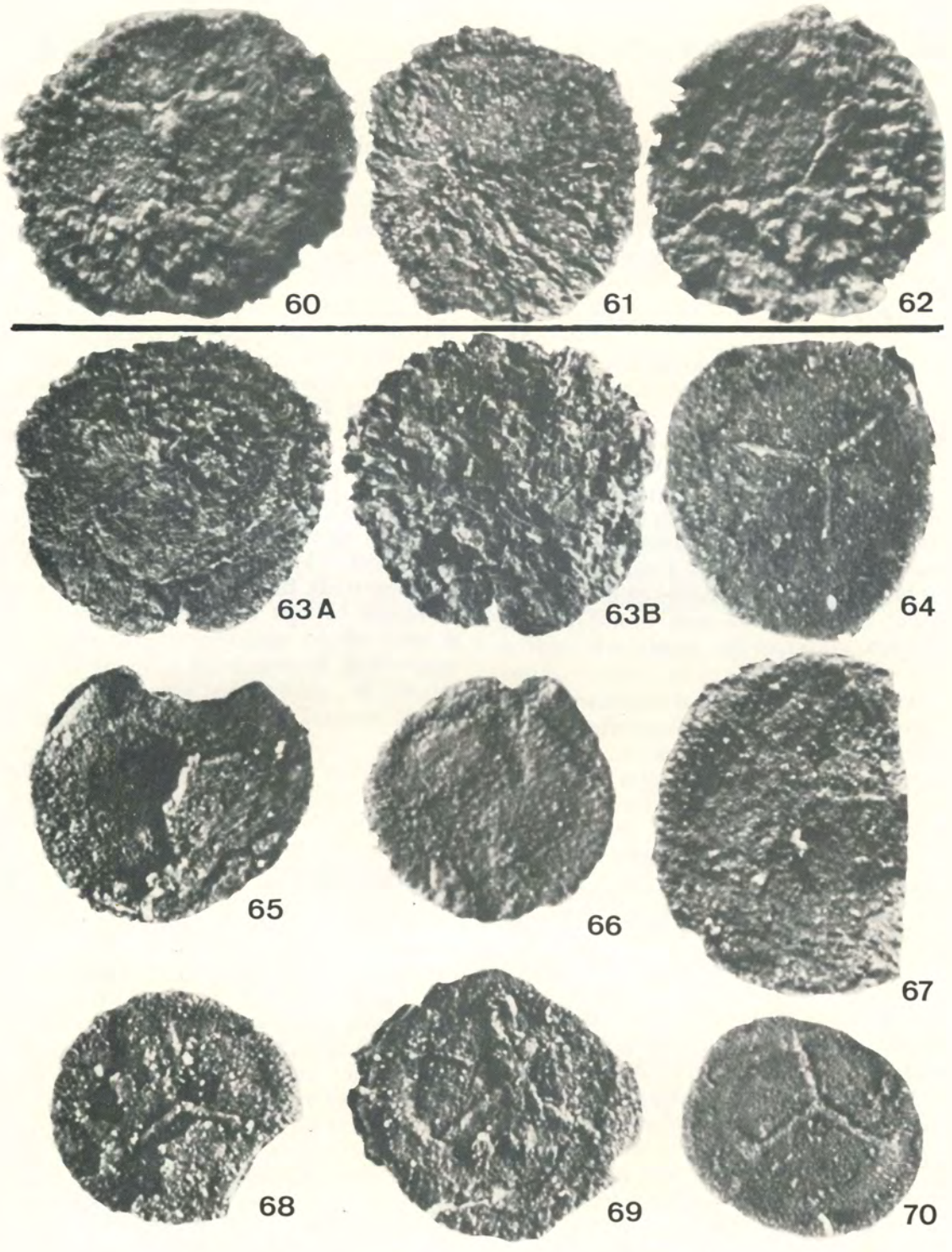


Plate VI

Figs. 60–62 *Triletes australis* sp. nov., sample No. 2 073, Australia.
Figs. 63, 65, 69 *Triletes robur* sp. nov., sample No. 2 070, Australia.
Figs. 64, 66–68, 70 *Triletes robur* sp. nov., sample No. 2 068, Australia.

Palaeont. afr., **14.** 15–16. 1972

A RE-EVALUATION OF THE SYSTEMATICS AND MORPHOLOGY OF CERTAIN ANOMODONT THERAPSIDA

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The cranial morphology of a number of specimens assigned to the genera *Oudenodon, Rhachiocephalus, Aulacephalodon* and *Pelanomodon* was investigated (Keyser, 1969). It was found that the internal morphology and the general structure of the skulls show great agreement. Many of the differences between the genera can be associated with the size of the skull. The main differences between the genera lie in the specialisation of the biting mechanism and in the relative size and shape of the nasal and prefrontal bosses. It is suggested that the genera *Oudenodon* and *Rhachiocephalus* bit off their food with the sides of the horn-covered jaws while the broad-nosed genera *Aulacephalodon* and *Pelanomodon* bit with the transverse anterior tips of the jaws. This difference in the morphology of the jaws is probably indicative of a fundamental dichotomy between the two groups of genera. A similar dichotomy has been suggested for Triassic dicynodonts by Cox (1965).

The skulls of *Oudenodon* and *Rhachiocephalus* have much in common and many of the differences between them can be attributed to differences in the relative sizes of the animals. *Rhachiocephalus* has a large boss surrounding the parietal foramen and a very small fenestra ovalis. The snouts of these two genera are pointed and the lower jaws do not have very pronounced shovel-like tips. These two features indicate that most of the biting took place at the sides of the jaws.

All the available type-specimens of this group of Anomodontia of which *Oudenodon kolbei* is the best known representative, were examined. *Oudenodon baini* Owen (1855) is the type species of the genus. The following South African species are placed in the genus *Oudenodon: Oudenodon baini* Owen, *O. prognathus* Owen, *O. greyi* Owen, *O. brevirostris* Owen, *O. strigiceps* Owen, *O. megalops* Owen, *O. truncatus* Broom, *O. gracilis* Broom, *O. bolorhinus* Broom, *O. kolbei* Broom, *Dicynodon lutriceps* Broom, *D. planus* Broom, *D. platyceps* Broom, *D. halli* Watson, *D. mustonis* Haughton, *D. breviceps* Haughton, *D. cyclops* Haughton, *D. grandis* Haughton, *D. corstorphinei* Broom and Haughton, *Chelyrhynchus lachrymalis* Haughton, *Dicynodon schwarzi* Broom, *D. curtus* Broom, *D. andrewsi* Broom, *D. milletti* Broom, *D. vanderbyli* Broom, *D. wilmanae* Broom, *D. latirostris* Broom, *Oudenodon margaritae* van Hoepen, *O. marlothi* Broili and Schröder, *Dicynodon wellwoodensis* Broom, *D. allani* Broom, *D. maccabei* Broom, *D. glaucops* Broom, *D. moutonae* Broom, *D. brachyrhynchus* Broom, and *D. robertsi* Broom.

The following species from the Upper Madumabisa Mudstone of Zambia are also placed in the genus *Oudenodon*, viz. *Dicynodon luangwaensis* Boonstra, *D. helenae* Boonstra, *D. euryceps* Boonstra and *D. parabreviceps* Boonstra.

Examination of a series of 20 specimens collected in a delimited area north of Graaff-Reinet from *Cistecephalus*-bearing strata showed that the characters used to distinguish the various species are subject to individual variation and deformation. It was found that all the types listed above are within the range of variation exhibited by this series.

Attention is drawn to the fact that all the species previously assigned to *Oudenodon* from the Karroo basin are very similar indeed and that most of the species mentioned above could be synonyms. The Zambian species are possibly all synonymous but differ from the South African species in having broader skulls.

Dicynodon huenei Broili and Schröder (*Oudenodon huenei*), a small species from the *Tapinocephalus* zone of Beaufort West, is tusked, unlike all the species listed above and accordingly will be placed in a new genus, of which a diagnosis will be given in due course.

The genera *Rhachiocephalus, Eocyclops, Neomegacyclops, Platycyclops, Pelorocyclops* and *Kitchingia* appear to be indistinguishable because of similarities in structure which are discussed. The genera were originally distinguished from one another on the structure and relationship of the preparietal, which was found to be highly variable in a group of specimens from a single locality. There is some doubt about this as the variation of the interpterygoid vacuity has not been studied sufficiently.

The skull of *Aulacephalodon* is fairly short and broad. The transverse anterior tip of the short snout is reinforced by anterior longitudinal palatal ridges and ridges on the external surface of the snout. This indicates that most of the biting action of the jaws was restricted to the tips of the jaws. The great widening of the zygomatic arches

posterior to the postorbital bars and the formation of bosses on the zygomatic arches can be attributed to this biting mechanism. It was found that the characters used to distinguish the various species of *Aulacephalodon* depend greatly on the size and consequently the age of the individual.

Because of this, the 16 named species of *Aulacephalodon* are found to be indistinguishable and the possibility that they are all synonyms deserves consideration.

The skull of *Pelanomodon* is very similar to that of *Aulacephalodon* but is tuskless. The similarity is probably the result of the similar biting mechanism. The very large nasal and prefrontal bosses, the presence of two lacrimal foramina in each orbit and the high placement of the orbits and nares in the skull indicate that the animal could have fed amongst vegetation in shallow water.

The taxonomy of the *Pelanomodon*-like anomodonts was investigated. It was found that *Pelanomodon rubidgei* and *P. kitchingi* are probably synonymous. *P. halli* was found to be very different from the above 2 species and very similar to *P. moschops* (Broom). *P. wesselsi* is placed in the genus *Rhachiocephalus*. *Propelanomodon devilliersi* Toerien (1955b) was found to be synonymous with *Dicynodon tylorhinus* Broom. This species should therefore be called *Propelanomodon tylorhinus* (Broom). The genus *Propelanomodon* is related to *Oudenodon* rather than to *Pelanomodon*.

The possibility is that all the genera treated in this paper are descended from a *Robertia broomiana*-like ancestor.

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A NOTE ON THE GENUS *PROPLACERIAS* CRUICKSHANK, 1970.

Since writing the review of the genus *Kannemeyeria* (Cruickshank 1970, pp. 47–55) a cast of the type of *Proplacerias vanhoepeni* (Camp) has been received for examination as part of the programme in the Bernard Price Institute for Palaeontological Research for making types of South African fossils available for study here (Camp 1956, p. 311).

Even a superficial glance at the cast shows that it is unmistakeably a member of the genus *Kannemeyeria*, and probably another specimen of the hitherto monotypic species *K. wilsoni* (Broom 1937). In the review of the genus *Kannemeyeria, K. wilsoni* was recognised as probably being distinct from *K. simocephalus* (Weit.) but the possibility exists that it is the female of *K. simocephalus* (Cruickshank 1970, p. 51).

The side of the skull which is visible in dorsal view in Camp's figures is dorso-ventrally crushed and the orbital border has been extensively re-modelled in plaster of paris. The snout has been pushed backwards and the palate is distorted. Labial fossae are present and the upper surface of the intertemporal bar has been weathered to expose the interparietal in an unnatural manner. The snout does not have a prominent longitudinal ridge, nor are the maxillary flanges as well developed as in *Kannemeyeria simocephalus*. The relevance of the horizontal jaw-tip in the type of *K. wilsoni*, as opposed to the normal, upturned tip in this specimen must be re-assessed.

Therefore as all the distinguishing characters of the genus *Proplacerias* are false, it must be placed into synonymy with the genus *Kannemeyeria* Seeley. Nonetheless, it is clear that the major conclusions reached on p. 51 and in figure 4 (Cruickshank 1970) are still valid and that the evolutionary lines leading to *Placerias* and *Kannemeyeria* are distinct.

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REVISION DU GENRE *PROTOCYNODON* BROOM 1949 ET DISCUSSION DE SA POSITION TAXONOMIQUE

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RESUME

La révision de *Protocynodon pricei* Broom 1949 conduit à placer ce genre parmi les Cynodontia Procynosuchidae. Cette étude complète celle de Broom, (1949); elle a permis, en outre, d'observer le mode de remplacement dentaire et, à la suite d'un dégagement plus poussé, la face interne de la base de l'endocrâne. Le terme de Scaloposauria a été choisi, de préférence à Bauriamorpha, pour regrouper Ictidosuchidae, Scaloposauridae, Bauriidae, Ericiolacertidae, Lycideopsidae, Nanictidopsidae et Silpholestidae. D'autre part, après comparaison entre Scaloposauria et Cynodontia puis entre Procynosuchidae et Silphedestidae, il est suggéré que cette dernière famille soit révisée et placée parmi les Cynodontia, comme l'indiquaient Haughton et Brink, en 1954–et Brink, (1960 a)–,plutôt que parmi les Scaloposauria (Bauriamorpha), comme le suggéraient Watson et Romer en 1956.

SUMMARY

On revision of *Protocynodon pricei* Broom 1949, it is concluded that this genus is to be placed amongst the Cynodontia Procynosuchidae. This study completes that undertaken by Broom (1949); it has also enabled us to observe the tooth replacement and, after further preparation, the internal face of the endocranium basis. In preference to the term Bauriamorpha, Scaloposauria has been chosen to include: Ictidosuchidae, Scaloposauridae, Bauriidae, Ericiolacertidae, Lycideopsidae, Nanictidopsidae and Silpholestidae. In addition, after comparison between Scaloposauria and Cynodontia on one hand, and between Procynosuchidae and Silphedestidae on the other hand, the author suggests that the latter family should be reviewed and placed amongst the Cynodontia, as indicated by Haughton and Brink in 1954, and Brink (1960a), rather than amongst the Bauriamorpha, as suggested by Watson and Romer in 1956.

ZUSAMENFASSUNG

Die Neubearbeitung von *Protocynodon pricei* Broom 1949 bringt es mit sich, diese Gattung den Cynodontia Procynosuchidae zuzuschreiben. Dieselbe, die als eine Ergänzung derjenigen Broom (1949) gilt, liess auch die Zahnersetzungsweise und, infolge einer ausführlicheren Freilegung, die innere Seite der Endokraniumbasis zu beobachten. Die Benennung Scaloposauria, nicht Bauriamorpha, wurde vorgezogen, um Ictidosuchidae, Scaloposauridae, Bauriidae, Ericiolacertidae,

(Editor's Note. The numbered footnotes are listed on pp. 42–43, in order. The figures and plate follow at the end of the paper.)

Lycideopsidae, Nanictidopsidae und Silpholestidae zusammenzustellen. Nach einer Vergleichung der Scaloposauria mit den Cynodontia, ferner der Procynosuchidae mit den Silphedestidae, ist die Verfasserin geneigt zu einer Neubearbeitung dieser letzten Familie. Doch gewissen Merkmalen nach kann dieselbe von jetz ab unter den Cynodontia, wie von Haughton und Brink (1954)–und Brink (1960a)–angegeben wurde, nicht unter den Scaloposauria (Bauriamorpha) (siehe Watson und Romer, 1956), gestellt werden.

INTRODUCTION

Protocynodon pricei Broom 1949, petit spécimen de la zone à *Cistecephalus* a déjà été brièvement décrit par Broom en 1949 qui le considérait (p. 194) comme un Cynodonte primitif. De même, Brink et Haughton, en 1954 (p. 157), font de *Protocynodon* un Cynodonte primitif de la famille des Silphedestidae, avec doute cependant pour ce qui est de l'attribution à cette famille.

Par contre, ce genre a ensuite été classé par Watson et Romer en 1956 (p. 76), dans les Bauriamorpha "*Incertae sedis*". Cette idée fut reprise par Lehman, en 1961 (*in* Traité de Paléontologie de Piveteau, p. 246–270).

Type: Le genre *Protocynodon* n'est représenté que par un crâne très écrasé dorsoventralement et dont la partie ventrale a, de plus, été déplacée vers la gauche par rapport à la partie dorsale. Ce crâne est ainsi plus ou moins réduit à deux faces: l'une dorsolatérale gauche, l'autre ventrolatérale droite. Lorsque nous en avons commencé la révision, le spécimen était encore recouvert d'une couche importante de gangue dans les régions palatale, orbitaires et temporales. Le dégagement de ces dernières montra que les arcades zygomatiques et orbitaires, ainsi que les parois latérales de l'endocrâne, avaient été en grande partie érodées. La région postérieure de l'hémimandibule gauche manque également. Quant à l'hémimandibule droite, à peu près complète, elle est écrasée sur le palais dont elle masque la partie antérieure. La région occipitale aussi est fortement altérée, surtout du côté gauche.

Ce spécimen a été recueilli par S. C. Kitching en octobre 1947, à Ferndale, Graaff-Reinet, province du Cap, Afrique du Sud, dans un niveau de la partie inférieure de la zone à *Cistecephalus*[1].

Le type de *Protocynodon pricei* est conservé au Bernard Price Institute for Palaeontological Research (Johannesburg, Afrique du Sud), sous les numéros: F. 650/M. 16, correspondant respectivement au catalogue de fouille et au catalogue de musée.

Diagnose générique: Cynodonte procynosuchidé de petite taille, à crâne peu large, à museau long et région temporale courte, à orbites moyennes et fosses temporales courtes, à grands frontaux élargis antérieurement, à processus postérieurs des préfrontaux et antérieurs des postorbitaires moyennement larges, à orifice pinéal situé approximativement à mi-longueur du pariétal, à crêtes ptérygoïdiennes orientées parasagittalement, à dentaire moyennement long dont la branche montante, de faible hauteur, est cependant bien individualisée. La lame réfléchie de l'angulaire est à peine détachée du reste de la mandibule; sa surface est encore importante et sinueuse. Le splénial, peu élevé, ne participe pas au bord inférieur de la mandibule.

La formule dentaire supérieure la plus probable est: 5I 2pC 1C 9PC.

DESCRIPTION

Le crâne devait avoir un aspect plus ou moins triangulaire, à narines (*nar.*) allongées antéro-postérieurement (l'allongement a dû, en réalité, être moindre que la déformation du crâne ne le laisse supposer), à orbites moyennement grandes et à fosses temporales assez courtes.

Dimensions: (en mm.)

Longueur maximale du crâne	env. 57,5
Largeur maximale du crâne	env. 33,5
Distance entre le bord antérieur du prémaxillaire et le carré	env. 52
Distance entre le bord antérieur du prémaxillaire et le niveau du bord antérieur de l'orbite	env. 28
Distance entre le bord antérieur du prémaxillaire et le niveau du bord antérieur de la fosse temporale	env. 38,5
Largeur interorbitaire minimale	13,5
Largeur intertemporale minimale	env. 7,5
Longueur des nasaux sur la ligne médiane	23
Largeur postérieure maximale des nasaux	env. 18
Longueur des frontaux sur la ligne médiane	14,5
Largeur de la suture fronto-nasale	env. 11,5
Largeur maximale des frontaux	env. 12,5
Largeur des frontaux d'un point de suture fronto-préfronto-postorbitaire à son symétrique	env. 10,5
Longueur des pariétaux sur la ligne médiane	env. 10,5
Longueur antéorbitaire des préfrontaux	env. 5,5
Longueur des lacrymaux sur la face	env. 8,5
Longueur totale de la dentition maxillaire (en admettant l'existence de deux précanines)	env. 25
Diamètre mésiodistal de la canine principale supérieure	2
Diamètre mésiodistal de la plus grande postcanine supérieure	1,7
Longueur maximale de la mandibule	env. 51,5
Longueur du dentaire	env. 43,5
Hauteur de la branche montante du dentaire	env. 12

Figuration:

Les figures correspondent à des reconstitutions du spécimen. Pour faciliter les comparaisons entre faces latérales de différents genres, c'est la face gauche qui a été représentée, dessinée en partie, par

symétrie, d'après la face droite, mieux conservée. La face externe de la mandibule a été reproduite d'après l'hémimandibule droite tandis que la face interne l'a été suivant l'hémimandibule gauche.

I–CRANE

A. CRANE DERMIQUE

1. Museau et toit cranien

Le museau est moyennement long; la surface en paraît lisse.

Museau

Les prémaxillaires (Pmx)

Le prémaxillaire gauche est érodé tandis que le droit est conservé, sauf à l'extrême pointe du museau. L'extrémité postérieure de la lame médiale est conservée entre les nasaux et est bien développée. L'extension postérolatérale du prémaxillaire est masquée par le maxillaire.

Le nombre des incisives est incertain du fait qu'on ne peut suivre la suture prémaxillaire-maxillaire entre les alvéoles: on observe, à droite, et d'avant en arrière, une dent brisée, quatre dents complètes et, juste avant la canine, une autre dent brisée presque au ras de l'alvéole, située à l'emplacement du "diastème" décrit par Broom (1949, p. 192). Il est possible qu'une incisive manque à l'avant. Il y aurait donc soit 6, soit plutôt 7 dents en avant de la canine (le premier nombre est celui accepté par Broom, (*ibid.*), qui interprète les 6 dents comme étant des incisives et admet l'absence de précanines)[2]. Ces 7 dents correspondent probablement à 6 incisives (= nombre indiqué par Broom) et 1 précanine (= diastème *cf.* Broom), ou à 5 incisives et 2 précanines.

Les septomaxillaires (Smx)

Tandis que le septomaxillaire gauche est très mal conservé, à droite, cet os est en assez bon état. Le septomaxillaire est moyennement long et étroit. Le septum horizontal subsiste partiellement à droite. Le foramen septomaxillaire (*f. smx*), de faibles dimensions, est situé au niveau du bord postérieur de la narine.

Les maxillaires (Mx)

A gauche, la région postérieure du maxillaire est détruite. Au contraire, à droite, le maxillaire est entier. Le maxillaire est bien développé dans sa partie antérieure et recouvre largement le prémaxillaire, bordant latéralement les trois alvéoles qui précèdent la canine. Vers l'arrière, sa hauteur augmente progressivement jusqu'à réduire la surface apparente du nasal à une bande étroite, au niveau de la troisième postcanine, soit approximativement à mi-distance entre le bord postérieur de la narine et le bord antérieur de l'orbite. Ensuite, il y a diminution de la hauteur du maxillaire, progressive au début puis brutale, laissant alors le nasal former une aile atteignant le lacrymal.

Enfin, le maxillaire se prolonge vers l'arrière en s'amincissant. Sa limite postérieure se situe à peu près au niveau du premier tiers de l'orbite. A la base du maxillaire, on observe des orifices, plus ou moins alignés parallèlement au bord inférieur de cet os, pour la sortie des rameaux du V. Au dessus de la canine, un orifice plus important est doublé d'un orifice accessoire un peu inférieur.

Le maxillaire porte onze ou douze dents suivant l'interprétation que l'on donne des deux dents qui précèdent la canine.

Les nasaux (Na)

Les nasaux sont longs, caractère que Broom notait, en 1949, comme typiquement cynodonte. Moyennement larges à l'avant, les nasaux se rétrécissent fortement au tiers de leur longueur pour s'élargir au niveau du deuxième tiers en formant une aile en contact avec le lacrymal[3]—ce contact est une caractéristique apparemment constante des Cynodontes, tandis que toutes les lignées de Thérocéphales *s.l.* (Pristerosauria et Scaloposauria) ont ces deux os plus ou moins largement séparés par le préfrontal et le maxillaire—leur maximum de largeur se situant au niveau du point de rencontre naso-lacrymo-maxillaire. Puis les nasaux se rétrécissent fortement le long de la ligne naso-préfrontale, pour ne présenter au contact des frontaux qu'une largeur à peu près égale à celle qu'ils avaient au premiers tiers de leur longueur. Chaque nasal se termine alors en pointe vers l'arrière. L'ensemble de la suture naso-fronto-préfrontale forme un W dont les nasaux constituent les deux pointes basales.

Les lacrymaux (La)

Le lacrymal gauche est en partie érodé, mais le droit est bien conservé. Broom (1949, p. 192) le considérait comme relativement petit. Il s'étend, vers l'avant, plus loin que le préfrontal, et son contact avec le nasal sépare largement maxillaire et préfrontal (voir note [3]). A droite, l'orifice lacrymal est visible et s'ouvre sur le bord antéro-interne de l'orbite. Une cassure le prolonge en avant.

Toit cranien

Les préfrontaux (Pfr)

Le préfrontal gauche n'est conservé que partiellement tandis que le droit l'est en entier. Si le préfrontal est peu développé vers l'avant, il s'étend largement vers l'arrière entre frontal et postorbitaire pour former avec ce dernier le bord supérieur de l'orbite. Son extrémité postérieure atteint presque le niveau de départ de l'arcade postorbitaire.

Les frontaux (Fr)

Les frontaux forment un ensemble plus long que large; chaque frontal est, comme l'avait remarqué Broom, en 1949 (p. 192), ". . . presque trois fois plus long que large et est séparé de l'orbite par le préfrontal et le postorbitaire jointifs". Leur largeur maximale se situe à l'avant,

peu après la limite naso-frontale. Ils se rétrécissent ensuite doucement, pour s'élargir en formant une pointe latérale entre préfrontal et postorbitaire et diminuer à nouveau jusqu'à leur suture avec les pariétaux. Cette suture est brève comme chez les Thérocéphales *s.l.* et les Cynodontes dans leur ensemble. Les frontaux participent à un peu plus du tiers de la longueur de la région intertemporale.

Les postorbitaires (Ptorb)

Les postorbitaires ne semblent pas avancer à plus du tiers postérieur de l'orbite, tandis que, vers l'arrière, ils s'étalent presque jusqu'à la moitié de la longueur du pariétal, considérée sur la ligne médiane, soit, approximativement, jusqu'au niveau du bord antérieur du foramen pinéal (*f. pi*).

Des deux côtés, les postorbitaires sont brisés, mais, à droite, une empreinte dans la gangue semble montrer que le postorbitaire allait rejoindre le jugal pour former une barre postorbitaire complète.

L'absence de postfrontal, caractère commun aux Scaloposauria et aux Cynodontia, ne peut donc pas ici servir d'argument pour prouver l'appartenance de *Protocynodon* à l'un ou l'autre groupe.

Les pariétaux (Pa)

Les pariétaux sont assez courts, leur longueur correspond environ au cinquième de la longueur de la face supérieure du crâne, prise sur la ligne médiane. Quant à leur largeur, elle semble exagérée du fait de l'écrasement et de l'absence de la région supérieure.

La région supérieure est fortement érodée, n'offrant à l'étude qu'une section dissymétrique où la suture sagittale est visible en arrière du canal pinéal, lui-même situé à peu près à mi-longueur du pariétal. Les grands diamètres de ce canal permettent de supposer que l'orifice pinéal devait être assez important.

Les pariétaux forment la plus grande partie du bord interne et le bord postéro-interne de la fosse temporale, séparant largement postorbitaire (*Ptorb*) et squamosal (*Sq*). Sur le côté droit du pariétal, une gouttière indique, probablement, le trajet de la *vena capitis lateralis (v.c. l)*. Une partie de l'insertion de l'épiptérygoïde (*Ept*) est également visible.

Il est impossible de savoir si le pariétal participait à la face occipitale.

Face occipitale

La face occipitale

La face occipitale est très altérée dans sa région supérieure et latérale gauche. L'angle formé par la face supérieure du crâne et la face occipitale, de même que le degré de concavité de cette dernière ne peuvent être appréciés. A droite, il est cependant possible de distinguer quelques structures:

L'interpariétal (Ipa)

La section de l'interpariétal en vue dorsale et un fragment de ce même os, conservé à droite, montrent qu'il devait être assez large. Sa limite avec le supraoccipital (*Soc*) est, par contre, peu nette et, comme son bord supérieur manque, sa hauteur ne peut être appréciée.

Les tabulaires (Tab)

Le tabulaire droit est bien développé et s'étale largement sur la face occipitale, entourant presque complètement une fosse posttemporale de taille réduite.

2. Joue

Les jugaux (Ju)

Le jugal gauche est brisé. A droite, le jugal s'avance en pointe entre le maxillaire et le lacrymal, jusqu'à la moitié de la longueur extraorbitaire de ce dernier. Il forme le bord externe, peu épais, de l'orbite et envoie verticalement vers le haut un processus; ici, ce processus n'est pas entièrement conservé, mais en raison de la grande largeur de sa base, il devait, sur le spécimen complet, participer de façon importante à la barre postorbitaire.

En arrière, le jugal est également incomplet, mais une empreinte sur la face mésiale de l'apophyse zygomatique du squamosal semble montrer que le jugal doublait entièrement cette barre et atteignait le carré (*Q*). Il semble avoir été plus épais que Broom ne l'a décrit et représenté en 1949 (p. 194 et p. 192, fig. 5).

Les squamosaux (Sq)

Les extrémités antérieures des apophyses zygomatiques des squamosaux sont détruites des deux côtés et on ne peut juger de leur extension.

Le squamosal droit, le mieux conservé, forme sur la face occipitale une aile offrant un large contact avec le tabulaire. En raison d'une cassure, l'encoche pour le carré est accentuée dans sa région supérieure.

Le squamosal forme, en outre, la face postérieure de la fosse temporale.

En 1955a, chez *Ictidosuchops intermedius* (Broom 1938), Crompton décrivit les trois processus du squamosal situés dans la région postérieure de la fosse temporale, comme suit:

Processus 1 ou "processus dorsal" (p. 156).

Processus 2, "invisible en vue dorsale, passe directement vers l'intérieur sous le processus 1, et se présente comme une lamelle osseuse verticale, dont l'extrémité médiale est en contact non sutural avec le prootique" (*ibid.*).

Processus 3, "gît contre la face antérieure du mur antérieur du processus paroccipital" (p. 157).

Ainsi, le processus 1 (processus dorsal) est en contact avec le pariétal, et le processus 2 avec le prootique et le supraoccipital, tandis que le processus 3 est orienté vers le processus carré du ptérygoïde et l'épiptérygoïde.

Dans le cas présent, les processus 1 (*pr. 1*) et 2,

rapprochés par l'écrasement, couvrent en partie le pariétal dans l'angle postéro-interne de cette fosse. Le processus 3 forme la base visible de l'ouverture antérieure de la fosse posttemporale.

Les quadratojugaux (Qj)

Ils sont presque totalement détruits des deux côtés; seul, un petit fragment en forme de baguette s'évasant vers le bas, subsiste à droite dans l'encoche du squamosal.

L'orbite

La forme générale de l'orbite est, en raison de l'écrasement, difficilement appréciable. Elle paraît moyennement grande, plus grande qu'elle n'a été reconstituée par Broom (1949, fig. 5 et 6).

Le bord supérieur de l'orbite est mieux conservé à gauche; il est entièrement formé par le préfrontal et le postorbitaire, ce qui, comme nous l'avons remarqué plus haut, est un caractère de Cynodonte.

La région antérieure de l'orbite est, elle, en meilleur état à droite; elle est essentiellement bordée par le lacrymal, tandis que le bord inférieur l'est par le jugal.

De l'arcade postorbitaire ne subsiste (comme nous l'avons indiqué plus haut p. 22), à droite, qu'un fragment de jugal et une empreinte sur la gangue, l'apophyse postorbitaire du postfrontal étant sectionnée à sa base.

La fosse temporal

La fosse temporale, assez courte par rapport à la longueur totale du crâne, a son bord supérieur formé par le pariétal, recouvert antérieurement par l'aile postérieure du postorbitaire.

A l'avant, une barre orbitaire, probablement complète et formée de l'association postorbitaire-jugal, devait séparer cette fosse de l'orbite. Le jugal faisait également partie du bord inférieur de la fosse temporale, en étant doublé vers l'arrière et l'extérieur par le squamosal. Celui-ci formait à son tour la majeure partie du bord postérieur, laissant à découvert le pariétal dans la région de l'angle postéro-interne.

3. **Plafond buccal**

Toute la région antérieure du plafond buccal est impossible à étudier du fait de l'écrasement de la mandibule sur cette région.

Le vomer (Vo)

De ce fait, il n'y a que la partie postérieure du vomer qui est visible; elle semble assez large.

Les ptérygoïdes (Pt)

Les ptérygoïdes sont incomplètement visibles, masqués à la fois par des fragments de l'hémimandibule droite et par l'hémimandibule gauche. Ils sont séparés par une fosse interptérygoïdienne importante. Sur la ligne médiane, le ptérygoïde envoie vers l'arrière un processus assez puissant dont on peut, en vue supérieure, observer le contact avec le basisphénoïde. Il émet également, vers l'arrière et obliquement, un fort processus carré dont la région postérieure est brisée.

Une crête ptérygoïdienne (*cr. pt*)—ou tubérosité ptérygoïdienne, ou tubérosité dentigère selon les auteurs—oblique, est bien marquée sur le côté gauche. Il semble impossible de voir si elle est entièrement formée par le ptérygoïde ou *pro parte* par celui-ci et le palatin. Elle ne paraît pas porter de dents.

Les palatins (Pal)

Un fragment osseux (*Pal (?)*) est peut-être le témoin de la participation du palatin à un palais secondaire.

La limite entre palatins et ptérygoïdes n'est pas visible en vue ventrale, mais on peut la discerner en vue dorsale, où l'extrémité postérieure des palatins forme une plaque arrondie présentant un large contact avec les ptérygoïdes. Ces rapports osseux sont les mêmes que chez un Procynosuchidé, en bon état de conservation, du Bernard Price Institute (B.P.I. n° : F. 1545, spécimen non encore décrit). De ce fait, il n'y a pas de fosse sousorbitaire.

Les transverses (Tr)

Les limites des transverses, ou ectoptérygoïdes, ne sont visibles ni en vue inférieure ni en vue supérieure.

B. ENDOCRANE

Le basisphénoïde (*Bsph*), comme le reste de la région postérieure de l'endocrâne, est masqué, sur la face ventrale, par les os postérieurs de la mandibule ainsi que par des fragments écrasés de vertèbres. Par contre, en raison même de l'aplatissement du crâne et de la disparition, au cours de la fossilisation, de la paroi latérale gauche de l'endocrâne, il a été possible d'observer la face supérieure de la base endocranienne. Ainsi sont visibles une partie du basioccipital (*Boc*) et le basisphénoïde. Ce dernier envoit latéralement, vers le ptérygoïde, une apophyse étroite, le processus basiptérygoïde (*pr. bpt*) qui, contrairement à ce qui se passe chez les Cynodontes décrits par Parrington, en 1933 et 1935, Rigney, en 1938, et Olson, en 1944, se prolonge assez loin vers l'avant. Au niveau du contact ptérygoïdo-basisphénoïdien, s'ouvre un orifice par lequel passait peut-être la branche palatine du VII.

Le corps du basisphénoïde, évasé à l'avant, se rétrécit ensuite au niveau de l'emplacement des foramens carotidiens internes, pour s'élargir à nouveau vers l'arrière. Ces orifices internes des canaux des carotides internes sont rapprochés de part et d'autre d'une très légère crête médiane qui se prolonge vers l'avant. Olson (1944, p. 97) considère que la selle turcique des Cynodontes est indivise, mais que chez leurs ancêtres, elle devait être partiellement séparée en deux par un septum.

La crête observée chez *Protocynodon* semble

pouvoir être interprétée comme un reste de ce septum.

La selle turcique est peu profonde; sa profondeur est probablement diminuée du fait de l'écrasement du crâne; cependant Olson (1944, p. 68) note que cette fosse est également peu profonde chez les Cynodontes qu'il a étudiés.

En arrière, le basisphénoïde se trouve largement en contact avec le basioccipital. Un mur vertical forme la limite postérieure du basisphénoïde, il n'entre en contact avec le basioccipital que dans sa région ventrale.

Du prootique (*Proot* ?) droit, ne semble subsister qu'un fragment écrasé contre le carré (*Q*) et recouvrant la partie externe du processus 3 du squamosal, Il est possible qu'un os érodé (*Op*?) soit l'opisthotique: celui-ci apparaîtrait alors comme assez massif.

Le carré est abrasé et son allure exacte indéfinissable. Il semble avoir été assez petit, comme le notait Broom (1949, p. 194).

Le reste de la boîte cranienne est complètement écrasé, en partie érodé et masqué par d'autres éléments osseux.

II–MANDIBULE

Malgré le mauvais état du spécimen, la presque totalité de la mandibule a pu être étudiée, la face externe de l'hémimandibule droite et la face interne de l'hémimandibule gauche étant plus ou moins bien conservées.

A. OS DE MEMBRANE

Le dentaire (*De*), moyennement long, ne s'étend que jusqu'à la région antérieure de la fosse temporale. Il ne semble pas suffisamment haut pour avoir dépassé l'arcade zygomatique. La région symphysaire est limitée par un très léger angle mentonnier.

Le bord inférieur s'incurve de façon plus marquée vers l'arrière et un angle très ouvert indique la limite entre la branche horizontale et l'apophyse coronoïde.

La face externe du dentaire gauche semble vierge de toute impression musculaire, tandis que celle du dentaire droit présenterait une esquisse de fossette d'insertion, peut-être homologue de la "fosse massétérienne" (*f. mas*) décrite chez *Diarthrognathus* Crompton 1958, *Leavachia* Broom 1948 et de nombreux autres genres. Cependant, Devillers (1961, p. 394) pense qu'il est douteux que ce soit le masséter qui s'insère dans cette fosse chez *Leavachia* Broom 1948.

La face interne de l'hémimandibule droite est masquée dans sa région antérieure par le dentaire gauche. Une empreinte du splénial (*Spl*) sur le dentaire semble indiquer qu'il participait faiblement à la base de la symphyse. A partir du premier tiers environ de la longueur du dentaire, le splénial occupe la moitié de la hauteur de la branche horizontale tandis que le dentaire forme entièrement les bords supérieur et inférieur de cette branche et en constitue également le quart supérieur et le quart inférieur; ceci probablement au moins pour ce qui est de la partie antérieure de la branche horizontale de la mandibule. Il est possible que dans la partie postérieure, le quart supérieur de cette branche soit occupé par un antécoronoïde (*Acor* ?), si tant est qu'une séparation oblique visible à mi-longueur de cette branche corresponde à un contact dentaire-antécoronoïde et non à une simple fissure de la face interne du dentaire. Chez un Cynodonte procynosuchidé, *Leavachia duvenhagei* Broom 1948 (B.P.I. n°: F.3748/M.357), la présence d'un antécoronoïde a été signalée par Brink (1963 a, p. 71–72, fig. 10). Chez *Leavachia duvenhagei* Broom 1948, l'antécoronoïde occupe la même position et a le même aspect que ce qui est, chez *Protocynodon*, interprété comme un antécoronoïde possible.

L'angulaire (*Ang*), en vue externe, occupe environ un tiers de la longueur totale de la mandibule. L'étalement de la lame réfléchie apparaît moins fort que sur la représentation de Broom (1949, p. 192, fig. 5) et son aspect semble donc moins éloigné de celui de la lame réfléchie de *Leavachia* Broom 1948 comme celle-ci peut être observée, en particulier sur le spécimen n°: F.226–B/M.8–B du Bernard Price Institute for Palaeontological Research. La lame réfléchie de l'angulaire est détachée du reste de l'angulaire et située au niveau de l'angle "goniaque"[4] du dentaire. Cette situation est caractéristique des Cynodontes et très différente de celle observée chez les Thérocéphales. C'est sa sinuosité plutôt que sa taille qui rappelle un peu l'aspect de la lame réfléchie des Thérocéphales. Il faut noter ici que la lame réfléchie de l'angulaire est assez mal connue chez les Cynodontes primitifs, car elle est fréquemment cassée, ce qui limite les possibilités de comparaisons.

Sur la face interne de la mandibule, deux fragments osseux, situés au-dessus du splénial et en avant du préarticulaire, peuvent être interprétés comme appartenant au coronoïde (*Cor*); celui-ci serait alors un petit os ovalaire, à plus petit diamètre antéro-postérieur. Le coronoïde ainsi que le préarticulaire ont été notablement déjetés vers le haut, au cours de la fossilisation.

Le préarticulaire (*Part*) est une baguette haute et mince s'élargissant vers l'arrière pour enrober l'articulaire, dont la forme précise ne peut être connue en raison de l'abrasion de la région postérieure de la mandibule. Le préarticulaire se prolonge ensuite assez loin vers l'arrière.

Le sus angulaire (**Sang**), dont le bord antérieur est situé un peu au-dessus de l'angle formé par les bords supérieur et postérieur de l'apophyse coronoïde, n'est visible que du côté droit et en vue externe. Il est faiblement recourbé et relativement court.

B. OS DE CARTILAGE

L'articulaire (*Art*) est à la fois écrasé et abrasé. Il est ainsi possible de voir l'articulation

carré-articulaire, mais la forme exacte de l'articulaire n'est pas déterminable.

III–DENTITION

A. MORPHOLOGIE DENTAIRE

La mandibule étant en place, la denture supérieure est la seule observable dans son ensemble; elle est assez bien conservée du côté droit mais pratiquement détruite du côté gauche.

Si nous admettons qu'une incisive médiane manque, nous obtenons la formule dentaire probable: cinq (ou six) dents prémaxillaires et douze (ou onze) dents maxillaires, soit 5 incisives, 2 précanines $(pC)^5$, 1 canine et 9 postcanines (PC) ou 6 incisives, 1 précanine, 1 canine et 9 postcanines. Considérant que la première hypothèse est la plus vraisemblable, c'est la terminologie correspondant à celle-ci que nous utiliserons.

Les incisives sont entièrement conservées et, de même que la première (?) précanine, elles sont en forme de crochet à pointe dirigée postérieurement. La base de ces dents, surtout celle de la 1ère (?) précanine, est renflée postérieurement, simulant une sorte de talon.

Il semblerait que la première (?) précanine présente sur sa face vestibulaire des cannelures longitudinales, peu visibles en raison de l'altération de l'émail.

La deuxième (?) précanine est brisée presque au ras de l'alvéole, ce qui permet d'apercevoir deux dents inférieures: la dernière incisive et la canine, celle-ci se trouvant légèrement en avant de la canine supérieure.

La canine est en forme de lame de couteau à double tranchant, le tranchant distal étant plus marqué que le mésial. Elle présente également un renflement basal et postérieur, et sa pointe se recourbe vers l'arrière. Au niveau du renflement basal on observe quelques serrations. La surface vestibulaire est marquée de stries longitudinales délimitant cinq côtes. Ces derniers caractères avaient déjà été notés par Broom (1949, p. 194).

La morphologie des postcanines varie d'avant en arrière, avec un degré de complication croissant jusqu'aux cinquième et sixième postcanines, puis il y a à nouveau simplification pour les dernières dents.

Un léger diastème, entre la canine et la première postcanine visible, correspond soit à la région postérieure de l'alvéole de la canine, jouant lors du remplacement de celle-ci, soit à une postcanine (le nombre total des postcanines serait alors de dix). En raison de la faible longueur du diastème, la première solution nous paraît la plus probable.

La première postcanine visible est caniniforme. Elle est recourbée vers l'arrière et présente sur sa face "labiale" environ cinq côtes.

La deuxième postcanine, cassée, n'apporte aucune indication.

La troisième postcanine, brisée en oblique, semble avoir été molariforme.

La quatrième postcanine, molariforme, présente trois cuspides "labiales" dont l'antérieure et la postérieure, de taille réduite, atteignent sensiblement le même niveau, bien que l'origine de la cuspide antérieure soit plus proche de la racine. La cuspide centrale est par contre très développée. Elle est légèrement dissymétrique, à pointe un peu décalée vers l'arrière.

La cinquième postcanine, qui servit probablement à Broom (1949, p. 194) pour décrire les dents postcanines, est molariforme. Elle possède trois cuspides "labiales" dont la centrale est, de loin, la plus importante. Du côté mésial, un début de cingulum est visible ainsi qu'une cuspide cingulaire. Il en est de même du côté distal. Il y a donc ici au moins cinq cuspides. Mais il n'a pas été possible de voir si la dent était du même type que les postcanines molariformes de *Leavachia* Broom 1948, à nombreuses cuspides cingulaires, ou que celles de *Thrinaxodon* Seeley 1894, plus simples. En effet, les postcanines molariformes de *Thrinaxodon* Seeley 1894 présentent–d'après la description de Crompton (1963)–soit une cuspide cingulaire mésiale et une cuspide cingulaire distale séparées par une surface à peu près lisse, soit des ébauches légères de cuspides cingulaires.

La sixième postcanine présente les deux cuspides "labiales" mésiale et distale. La cuspide médiane est brisée, mais son empreinte reste visible sur la gangue sous-jacente.

La septième postcanine, qui devait être plus petite, est brisée au-dessous du niveau du "collet".

La huitième postcanine, petite, n'a de visible que les trois cuspides "labiales".

Quant à la neuvième, qui semble avoir été de très petite taille, il n'en reste que la base pointant hors de l'alvéole.

B. REMPLACEMENT DENTAIRE

Le remplacement dentaire de type "alterne" est connu tant chez les Scaloposauria, d'après les études de *Scaloposaurus* Owen 1876 par Crompton (1955a) et de *Tetracynodon* Broom et Robinson 1948 par Sigogneau (1963), que chez les Cynodontia, d'après les études de *Thrinaxodon* Seeley 1894, *Parathrinaxodon* Parrington 1936, *Tribolodon* Seeley 1894 par Parrington (1936) et de *Scalenodon* Crompton 1955 par Crompton (1955b). De même l'existence d'ondes de remplacement postéro-antérieures est admise. Il semble que ces dernières puissent être reconnues sur le spécimen étudié. Ce phénomène est moins marqué dans la série précanine que postcanine: l'extrémité du museau et l'incisive médiane manquant, la première dent visible de la série impaire est la troisième incisive: on note alors que la cinquième incisive est de taille légèrement supérieure à cette dernière. La septième dent (ou deuxième précanine) est en cours de remplacement. Dans la série paire, la deuxième incisive est brisée et seule son empreinte suggère qu'elle devait être plus petite que la quatrième incisive. La sixième dent (ou première précanine)

est, comme c'est fréquemment le cas pour les dents immédiatement antérieures aux canines, qu'elles soient incisives ou précanines vraies, plus petite que toutes les dents qui la précèdent. Il est à noter qu'elle devait être mal fixée dans son alvéole, ce qui a permis son déplacement, au cours de la fossilisation. La série impaire postcanine se présente comme suit: une première postcanine, déchaussée et déplacée vers l'avant de l'alvéole pendant la fossilisation, une troisième postcanine en cours d'éruption, une cinquième grande, bien en place, au "collet" situé au-dessus du niveau du bord alvéolaire, une septième postcanine petite et une neuvième extrêmement réduite. La série paire comporte une deuxième postcanine "petite", une quatrième postcanine à éruption non achevée, dont la "couronne" est presque totalement sortie, mais il n'y a pas de "collet" visible. Bien que la sixième postcanine soit incomplète, on peut reconnaître que son "collet" est très nettement au-dessus du niveau de l'alvéole, plus même que pour la cinquième postcanine. La huitième postcanine est, elle, très petite. Ainsi, *Protocynodon* ne fait pas exception à ce qui semble être la règle chez les Cynodontes, à savoir une réduction de taille des dernières postcanines accompagnée de simplification: les postcanines n° 7, 8 et 9 sont ici touchées par cette réduction.

POSITION TAXONOMIQUE
I–PROBLEME DE TERMINOLOGIE: BAURIAMORPHA et SCALOPOSAURIA

Avant d'examiner la position taxonomique de *Protocynodon*, il est nécessaire de faire quelques remarques préliminaires sur la façon dont nous comprenons actuellement la classification des "Bauriamorphes" et celle des Cynodontes primitifs.

L'importance accordée dans les dernières classifications au premier terme–Bauriamorphes– est très variable suivant les auteurs puisque pour Watson et Romer (1956, p. 72–76), l'infra-ordre des Bauriamorpha comporte sept familles, Lycideopsidae, ? Ictidosuchidae, Nanictidopsidae, Silpholestidae, Scaloposauridae, Ericiolacertidae et Bauriidae, tandis que pour Brink (1963a), les Bauriamorpha n'ont valeur que de superfamille correspondant à la seule famille des Bauriidae et qu'une nouvelle superfamille–Ictidosuchoidea– groupe (selon l'auteur, p. 54): "*Scaloposaurus, Ictidosuchops, etc* . . .". Ces deux superfamilles formant alors l'infra-ordre des Scaloposauria.

On note que le terme de Scaloposauria *sensu Brinki* semble recouvrir les mêmes éléments que celui de Bauriamorpha *sensu Watsoni-Romeri*.

Pour comprendre une telle divergence d'opinion, il nous faut remonter aux définitions originelles de ces termes.

En 1917 (p. 171), Watson crée le terme de Bauriamorpha pour remplacer (probablement pour des raisons d'homogénéité de terminologie) celui de Bauridae utilisé en 1914 dans son énumération des Thériodontes et considéré comme un sous-ordre au même titre que Therocephalia, Gorgonopsia et Cynodontia. Les Bauriamorpha sont alors définis (p. 177) comme suit: Thériodontes à courtes fosses temporales séparées par les pariétaux; présence d'un palais secondaire; grandes fosses sous-orbitaires; y sont inclus les genres *Bauria* Broom 1909, *Microgomphodon* Seeley 1895, *Sesamodon* Broom 1896, et *Melinodon* Broom 1905[6].

En 1925, von Huene (p. 60) classe ces mêmes genres ainsi que *Aelurosuchus* Broom 1906 parmi les Cynodontes, tandis qu'il considère comme Thérocéphales (p. 36) *Simorhinella* Broom 1915, *Icticephalus* Broom 1915, *Ictidognathus* Broom 1911 et *Scaloposaurus* Owen 1876.

En 1931, Watson (p. 1192) rappelle qu'il a établi le sous-ordre des Bauriamorpha pour y inclure *Bauria* Broom 1909, *Microgomphodon* Seeley 1895 et *Sesamodon* Broom 1905 et qu'à ces trois genres Haughton[7] a ajouté *Aelurosuchus* Broom 1906, et il précise (p. 1196–97): "Two procedures are possible–to redefine the suborder Bauriamorpha and include in it all the Theriodonts from *Icticephalus* to *Sesamodon*, or to recognize that the family or lineage Scaloposauridae crosses from one suborder to the next in the course of its evolutionary history"–"I am inclined to think the latter treatment more useful and recognize a family Scaloposauridae in the Therocephalia, with *Icticephalus* etc . . . from which the whole suborder Bauriamorpha has arisen . . ." *Ericiolacerta* Watson 1931 est alors inclus dans ce group.

Broom (1932, p. 98) reprend les définitions précédentes et ajoute que les Bauriamorphes possèdent de larges canines, des molaires simples, arrondies et sans cuspides[8], et une formule digitale 2.3.3.3.–ces traits caractérisant alors *Bauria* Broom 1909, *Baurioides* Broom 1925, *Microgomphodon* Seeley 1895, *Microhelodon* Broom 1931, *Aelurosuchus* Broom 1906, *Sesamodon* Broom 1896 et *Melinodon* Broom 1905.

Lorsque Kuhn, en 1937, dans le "*Fossilium Catalogus*" (p. 159), donne la liste des genres appartenant aux Bauriamorpha, celle-ci s'est augmentée, par rapport à la liste de Broom établie en 1932, de trois genres: *Ericiolacerta* Watson 1931 déjà cité par Watson en 1931, *Gomphodontosuchus* von Huene 1928, placé plus tard parmi les Cynodontes Gomphodontosuchidae par Watson et Romer (1956, p. 65) et *Watsoniella* Broili et Schröder 1935.

En 1940, von Huene (p. 312) discutant de l'appartenance d'*Ericiolacerta* Watson 1931 aux Bauriamorphes, utilise ce terme au sens de Watson (1917) en le différenciant nettement des Scaloposauridae, qu'il attache, comme en 1925, aux Thérocéphales, mais contrairement à 1925, il exclut cette fois les Bauriamorphes des Cynodontes. De même en 1948 (p. 80–81), le sous-ordre des Bauriamorpha, individualisé, correspond à la seule famille des "Bauriamorphidae".

En 1953, Boonstra (p. 605) divise le sous-ordre des Therocephalia en deux superfamilles: Pristerosauria et Scaloposauria, cette dernière correspondant aux Scaloposauridae et aux Bauriamorphes *s.s.*, tandis que tous les autres Thérocéphales, y compris les Ictidosuchidae, sont placés dans les Pristerosauria.

Les Scaloposauria sont alors considérés comme caractérisés par une région pariétale large, l'absence de crête pariétale, un arc postorbitaire complet pour les anciennes formes et incomplet pour les récentes, la présence d'un palais secondaire chez quelques formes tardives, l'absence de spécialisation ou le faible développement de la canine, la petitesse ou parfois l'absence de foramen pinéal et l'absence constante de postfrontal.

Trois ans plus tard, von Huene (p. 324) utilise encore le terme de Bauriamorpha au sens de Watson (1917) et laisse les Scaloposauridae dans les Therocephalia qui comportent alors sept familles.

En 1956 également, Attridge (p. 72), comme von Huene, conserve au terme de Bauriamorpha sa valeur primitive, indiquant qu'ils sont "almost certainly the descendants of the early Scaloposaurs".

La même année, Watson et Romer, et Romer seul, reprennent le terme de Bauriamorpha en lui donnant l'importance que l'on sait; en effet, pour Romer (1956, p. 699), les ". . . Early Triassic descendants of this group are frequently termed the Bauriamorpha. But the late and most advanced types are apparently polyphyletic in origin, arising from two or more related Permian families and it is impossible to diagnose them in any fashion so as to contrast them with their Permian relatives. In consequence, all are here included in the Bauriamorpha".

Brink mis à part, tous les auteurs de publications postérieures à 1956 ne tiennent compte que de la classification de Watson et Romer. Il en est ainsi de Crompton (1958, p. 208), puis de Lehman (1961, p. 246 et suiv.) et enfin de Kuhn (1961, p. 70; 1964, p. 311, fig. 8). (Kuhn fait alors dériver des Bauriamorpha les Docodonta et avec doute les Ictidosauria), (1965a, p. 111), (1965b, p. 279, fig. 6 (où les Docodonta sont retirés de la descendance des Bauriamorpha) et p. 281, fig. 7), (1966, p. 136–138). Il en est de même de V'juškov (1964) qui cependant introduit une nuance en créant les "Ictidosuchoidea bauriamorphes", ayant seulement valeur de superfamille (p. 280) et comprenant en outre les Rubidginidae (p. 284). Cox, en 1967 (p. 722–723) suit également la classification de Watson et Romer.

Lorsqu'en 1963a, Brink redéfinit les Scaloposauria, il laisse aux Bauriamorpha la valeur limitée que Watson, en 1917, puis Boonstra, en 1953, leur avaient donnée et laissée, tandis qu'il augmente les Scaloposauria du genre *Ictidosuchops* Broom 1938, "(. . . etc.)". En 1965, il complète cette définition.

Donc, actuellement, les termes Scaloposauria et Bauriamorpha semblent bien recouvrir les mêmes éléments et nous pouvons comparer les définitions que donnent des Bauriamorpha Watson et Romer (1956) et des Scaloposauria Brink (1963 a, 1965).

Un certain nombre de caractères sont indiqués dans l'une et l'autre des définitions et nous notons que la même valeur leur est attribuée par leurs auteurs respectifs. Ainsi les Bauriamorpha, selon Watson et Romer, et les Scaloposauria, selon Brink, possèdent:

- des arcades zygomatiques et postorbitaires faibles, ces dernières pouvant être incomplètes;
- des fosses sous orbitaires de grandes dimensions;
- une fosse inter ptérygoïdienne grande;
- un dentaire faiblement développé postérieurement (Brink), long mais mince (Watson et Romer);
- une crête pariétale moins fine et moins élevée que chez les Therocephalia, absente dans une famille (Brink), formant fréquemment une "lame plate" (Watson et Romer);
- un grand nombre de postcanines;
- de multiples canines (Brink), plusieurs dents maxillaires précanines (Watson et Romer)[9];
- un préarticulaire formant une lame interne, grande, sous l'articulaire (Watson et Romer), des os postdentaires de condition similaire à celle des Thérocéphales (Brink);
- une dentition en général moins hétérodonte que chez les Thérocéphales (Watson et Romer). Une dentition raisonnablement apparentée à celle des Thérocéphales (Brink). La description de Watson et Romer est ici plus précise que celle de Brink, sans être en contradiction avec elle.

Watson et Romer donnent d'autres indications concernant la dentition: la première–canines fréquemment réduites et moins individualisées que chez les Thérocéphales–complète la précédente; quant à la seconde–dents jugales en général petites mais à cuspides–elle n'est valable que pour certains genres.

D'autres caractères ne sont considérés que dans l'une ou l'autre de ces deux classifications. Ainsi pour Watson et Romer, les Bauriamorpha présentent en outre:

- un crâne de construction ordinairement légère;
- une face généralement longue et cylindroïde;
- des foramens vasculaires d'ordinaire présents sur le maxillaire et dont peut faire partie une ouverture largement ouverte vers l'avant, grande ou ébauchée dans la plupart des cas;
- une rangée dentaire maxillaire remarquablement convexe médialement;
- un rameau carré, droit et profond qui se rattache au niveau de la suture entre ptérygoïde et basisphénoïde, par une fine lame à concavité ventrale en général (le bord postérieur de ces lames forme la limite d'un espace considérable au travers duquel est visible la partie antérieure du prootique);

– une tubérosité basicraniale tendant à s'étaler largement;
– un prootique marqué, sur sa face latérale, d'une dépression, dont la paroi médiane présente un orifice débouchant dans la fosse pituitaire, le toit étant horizontal et passant de façon abrupte à la face externe de l'os. Selon Watson et Romer (p. 73), la lame antérieure du prootique forme une partie de la paroi latérale de la boîte cranienne; sa région supérieure –processus dorsal antérieur du périotique, selon Olson (1944, p. 15) et Crompton (1955a, p. 166)–est pratiquement verticale tandis que sa région inférieure –processus ventral antérieur du périotique, *ibid.*– s'incurve très fortement, formant d'abord voûte au-dessus de la base du *cavum epiptericum*, puis se redressant vers le bas, pour redevenir verticale dans un plan parasagittal plus médian que celui de la région supérieure. Cette lame ne se continuant pas vers le bas, en direction du basisphénoide, il existe donc une fenestration de la paroi au niveau de la fosse pituitaire et latéralement à celle-ci;
– un foramen pinéal petit ou absent;
– une fosse temporale relativement petite.

Watson et Romer notent également l'absence de préfrontal chez les Bauriamorpha.

Pour Brink, les autres caractéristiques des Scaloposauria sont:
– des frontaux formant une portion substantielle des bords dorsaux des orbites;
– des alisphénoides (épiptérygoïdes) quelque peu primitifs:
– de grandes fosses sous orbitaires;
– des nasaux généralement peu rétrécis dans leur partie moyenne et peu élargis dans leur partie postérieure;
– l'absence de contact entre lacrymaux et nasaux;
– un palais élémentaire qui peut être mis en rapport (avec celui des Thérocéphales);
– un condyle occipital trilobé de façon caractéristique.

Ces deux dernières listes de caractères sont le plus souvent mentionnées par leurs auteurs respectifs, par comparaison avec les Thérocéphales, et ces définitions, ou coïncident, dans un bon nombre de cas, ou, dans les autres cas, loin de se contredire, se complètent.

Ainsi le terme de Bauriamorpha tel qu'il est utilisé par Watson et Romer, en 1956, et celui de Scaloposauria longuement défini par Brink, en 1965, apparaissent comme synonymes. Il nous faut donc examiner le problème d'antériorité.

Le terme de Bauriamorpha, créé le premier par Watson, en 1917, avait une valeur restreinte que lui conserveront Watson (1931), qui spécifie à cette époque que le sous-ordre des Bauriamorpha est issu de la famille des Scaloposauridae, Broom (1931) et Kuhn (1937), qui y ajoutent seulement quelques genres, Boonstra (1953), von Huene (1956) et Brink (1963 a).

Lorsque Boonstra créa, en 1953, le terme de Scaloposauria, il semble avoir eu la même idée que Watson, en 1931, puisqu'il y place Scaloposauridae et Bauriamorpha.

Ceci avant que Watson et Romer n'augmentent si considérablement la valeur du terme Bauriamorpha que les Scaloposauria Boonstra 1953 s'y trouveraient inclus.

On peut donc résumer les opinions précédentes selon le schéma suivant:

Scaloposauria *Brink*, 1963 a 1965	=	Bauriamorpha *Watson* et *Romer*, 1956	=	Scaloposauria *Boonstra*, 1953 + Ericiolacertidae Ictidosuchidae Lycideopsidae Nanictidopsidae Silpholestidae	=	Bauriamorpha *Watson*, 1917 + Scaloposauridae

Cette intrication de définitions[9] nous fait suggérer de conserver au terme de Bauriamorpha son sens primitif, tel qu'il a été utilisé durant près de quarante ans et d'utiliser le terme de Scaloposauria dans un sens plus général, celui donné par Boonstra (1953), mais élargi par Brink (1963a et 1965). Les Scaloposauria seraient alors définis par la somme de caractéristiques, indiquées par ces auteurs et par Watson et Romer (1956) pour les "Bauriamorpha", et comprendraient les familles que Watson et Romer (*op. cit.*) plaçaient dans les "Bauriamorpha".

II–PROTOCYNODON: SCALOPOSAURE OU CYNODONTE

Nous devons maintenant considérer les traits qui distinguent les Scaloposauria des Cynodontia. En nous basant principalement sur la comparaison entre Scaloposauria et Cynodontia déjà faite par Brink (1963a, p. 54–55) et en complétant essentiellement à l'aide des descriptions de Watson et Romer (respectivement pour les deux groupes, p. 72–73 et p. 61), et de Brink (1960a, p. 149–152), et pour les Scaloposauria seuls à l'aide des études de Brink (1960 b, p. 155–182; 1965, p. 137–138) et pour les Cynodontia à l'aide de celles de Broom (1932, p. 260 et suiv.), Olson (1944, p. 68), Attridge (1956, p. 73–74) et de Brink (1960a, p. 119 et suiv.), nous obtenons, pour les caractères les mieux connus des deux groupes, le tableau suivant:

Scaloposauria	Cynodontia
A) Caractères généraux	
1) *Forme générale du crâne*	
– crâne en général construit lègèrement;	– formes primitives à crâne moins léger que celui des Scaloposauria et formes récentes à crâne assez massif;
2) *Museau*	
– face généralement large et cylindroïde;	– face de longueur variable, présentant généralement un renflement antérieur suivi d'une constriction[11];
– nombreux foramens vasculaires dont un grand dirigé vers l'avant;	– *id.* en général;
3) *Région temporale*	
– étendue, avec la plus grande largeur située postérieurement;	– *id.*;
4) *Région intertemporale*	
– moyennement large;	* – étroite, formée en grande partie par les pariétaux;
– en général peu élevée;	– montrant une élévation progressive;
– crête sagittale ni très élevée, ni très fine, absente dans une famille (Scaloposauridae)[12];	– d'où une crête sagittale relativement étroite (ou très étroite) et formée quasi entièrement par les pariétaux;
5) *Arcades zygomatiques*	
– faibles;	* – de moyennes à très hautes, formées par le jugal et le squamosal, ce dernier allant loin vers l'avant;
6) *Barres postorbitaires*	
– de délicates à incomplètes. Cette dernière disposition est une saisissante caractéristique des Scaloposauridae;	* – toujours présentes, complètes, très larges et puissantes chez de nombreuses formes; incomplètes seulement chez certains Silphedestidae;
7) *Orbites*	
D'aspect très variable dans les deux groupes;	
8) *Fosses temporales*	
– ouverture dirigée latéro-dorsalement;	– ouverture dirigée latéro-dorsalement chez les formes primitives, mais elle est dirigée plus dorsalement que latéralement chez les formes évoluées;
– en genéral relativement petites[13];	– à grande section transversale[13];

9) *Fosses post-temporales*

– grandes;

* – petites et ne formant pas une grande excavation dans la surface postérodorsale des processus paroccipitaux;

10) *Occiput*

– peu élevé;

* – élevé;

– peu profond (peu concave);

* – relativement profond;

– crêtes occipitales basses et peu aiguës;

* – crêtes occipitales bien marquées;

11) *Palais*

– pas de palais secondaire chez les formes primitives, mais en voie de formation ou complet chez les formes tardives;

* – toutes les formes montrent un stade avancé de formation de palais secondaire;

12) *Fosses sousorbitaires*

– grandes;

* – pas de fosses sousorbitaires (sauf chez *Scalopocynodon* Brink 1960, chez lequel elles sont presque complètement closes, *cf.* Brink 1960 a);

13) *Fosse interptérygoïdienne*

– présente et généralement grande;

– absente chez les Procynosuchidae et tous les Cynodontes ultérieurs cf. Brink (1960a, p. 149)[14];

14) *Mandibule*

– surface externe de la mandibule constituée, pour environ les 2/3, par le dentaire;

– surface externe de la mandibule constituée, pour environ les 2/3 chez les Procynosuchidae, les 3/4 ou 5/6 chez les autres Cynodontes primitifs, et dans sa presque totalité chez les Cynodontes évolués, par le dentaire;

B) Caractères propres aux différents os du crâne

1) *Prémaxillaires*

– ne pénètrent pas profondément entre les nasaux;

* – assez forte pénétration des prémaxillaires entre les nasaux;

2) *Maxillaires*

– pas de grand développement de la région moyenne;

– très développés médialement, à la moitié de leur longueur;

– rangée dentaire de légèrement incurvée à remarquablement convexe médialement;

– rangée dentaire à peu près rectiligne chez les formes anciennes, plus incurvée vers la ligne médiane chez les formes récentes;

3) *Nasaux*

– en général, ni très étendus vers l'arrière, ni très "rétrécis";

* – très étendus vers l'arrière, et présentant une constriction médiane très marquée;

4) *Lacrymaux*

– plus courts vers l'avant que les préfrontaux;	* – petits[15] mais dépassent vers l'avant les préfontaux;
– pas de contact entre lacrymaux et nasaux;	* – contact lacrymal–nasal;

5) *Préfrontaux*

– contact préfrontal–maxillaire;	* – pas de contact préfrontal–maxillaire;
– tendent à épaissir la région antéorbitaire;	– région antéorbitaire sans épaississement marqué;
– limités à l'arrière par le frontal;	* – à l'arrière, contact avec le postorbitaire;

6) *Frontaux*

– moyennement larges;	– étroits;
– forment une part importante des bords dorsaux des orbites;	* – exclus des bords dorsaux des orbites par la fusion des préfrontaux avec les postorbitaires;

7) *Postfrontaux*

– absents;	– absents;

8) *Postorbitaires*

– peu développés, que ce soit vers l'avant, l'arrière ou vers l'arcade postorbitaire, en particulier chez les formes les plus récentes;	* – bien développés;
– participent faiblement aux bords latéraux de la région intertemporale;	– participent seulement de façon infinitésimale à la crête sagittale;
– aucun contact entre postorbitaire et squamosal, que ce soit au-dessus de la fosse temporale ou latéralement;	– pas de contact entre postorbitaire et squamosal au-dessus de la fosse temporale[16]; mais parfois contact secondaire établi entre postorbitaire et squamosal pour former une partie de la base de l'arcade orbitaire et de la région antérieure de l'arcade zygomatique;

9) *Prépariétal*

– absent, sauf dans des cas exceptionnels tels que dans celui de *Ictidosuchops baurioides* Broom 1940 (*cf.* Brink, 1960b, p. 179).[17]	– absent;

10) *Pariétal*

– à foramen pinéal petit ou absent;	* – à foramen pinéal présent, "petit"[18] dans les formes anciennes et très petit dans les formes récentes;
– foramen pinéal situé en arrière	– (position du foramen pinéal non indiquée);

11) *Interpariétal*

– en général plus large que haut;	– plus haut que large ou de forme presque carrée pour les spécimens anciens, plus large que haut chez les formes récentes;

12) *Tabulaires*

– faibles tabulaires;

* – grands tabulaires;

13) *Jugal*

– relativement léger, tendant à s'affaiblir;

* – toujours bien développé, tendant à s'accroître;

14) *Squamosal*

– pas de développement particulier de la branche zygomatique;

– tendance à un fort développement de la portion zygomatique;

– sur la face occipitale, squamosal plus en continuité avec le reste de l'occiput que chez les Cynodontes;

– région squamosale nettement individualisée par rapport au reste de l'occiput et à rebord surplombant souvent l'occiput;

– a une faible structure dans la région des carrés;

– région des carrés non particulièrement affaiblie;

15) *Vomer*

– à bord ventral épaissi et à extension horizontale;

* – à bord ventral étroit, en lame;

16) *Transverse*

– large antéro-postérieurement, participe en général au processus transverse;

* – en général réduit, à bord postérieur très éloigné de l'extrémité du processus transverse;

17) *Ptérygoïde*

– processus transverse moyennement allongé;

* – processus transverse très allongé;

– tubérosités dentigères proéminentes;

* – pas de tubérosité dentigère chez les Cynodontes connus;

18) *Complexe basiphénoïde-parasphénoïde*

– quille parasphénoïdienne courte et pointant peu à l'arrière de la fosse interptérygoïdienne;

– quille très réduite;

– rostre en forme de V en section transversale: ce V devient à la fois plus haut et plus large vers l'arrière;

– rostre fortement développé, dorsalement cannelé

– la selle turcique n'est pas profondément creusée et par voie de conséquence, le *dorsum sellae* est peu développé;

id. pour les formes primitives, plus creusée chez les formes récentes;

19) *Epiptérygoïdes*

– en quelque sorte primitifs, assez étroits;

* – larges;

– recouvrement entre épiptérygoïde et prootique;

– large contact avec le prootique;

– sans contact avec le carré;

* – relie le ptérygoïde au carré–condition qui est typiquement mammalienne (Attridge, 1956) –ceci seulement chez les formes evoluées selon Broom (1932);

20) *Prootique*

– passe sous l'épiptérygoïde sans avoir de suture avec lui;

* – présente une large ligne de suture avec l'épiptérygoïde;

21) *Opisthotiques*

– processus paroccipitaux courts et "minces", formant un léger toit pour l'oreille moyenne;	– processus paroccipitaux longs et lourdement construits, formant un léger toit pour l'oreille moyenne;

22) *Carré*

– grand carré;	– petit carré;

23) *Condyle occipital*

– simple;	– double ou commençant à se dédoubler (stades transitoires vers la formation de 2 condyles occipitaux);
– trilobé;	– en forme de croissant;

24) *Stapes*

– présence d'un foramen stapédial;	– présence d'un foramen stapédial;

C) Mandibule

1) *Dentaire*

– dentaire faiblement développé postérieurement;	* – grand[19] à très grand;
– symphyse et branche horizontale formant une courbe continue en général (légère angulation chez les Bauriamorphes *s.s.*);	* – symphyse haute, surtout chez les formes récentes, et marquée d'un "menton" anguleux, presque semblable à celui d'un Gorgonopsien (Brink, 1960 a, p. 147);
– processus coronoïde en voie de développement;	– processus coronoïde en voie de développement chez les formes primitives, très bien individualisé chez les formes tardives;

2) *Eléments postdentaires*

– encore importants;	* – réduits
– lame réfléchie de l'angulaire bien développée;	* – la lame réfléchie de l'angulaire est en général réduite;
– le préarticulaire forme une grande aile interne sous l'articulaire;	– le préarticulaire tend à se réduire;

D) Dents

– dentition en général peu hétérodonte, sauf chez les formes tardives;	– dentition très hétérodonte;
– plusieurs types d'agencement des canines;	– *id.*;
– "canine" fréquemment réduite;	– canine bien individualisée;
– grand nombre de postcanines;	– *id.*;
– postcanines de coniques à cuspidées.	* – les postcanines ont en général dépassé le stade de simple cône. Certains groupes présentent des postcanines complexes.

Dans cette liste, forcément incomplète et susceptible de modifications au fur et à mesure que les groupes considérés seront mieux connus, certains caractères[20] sont tenus pour de bons critères de distinction entre Scaloposauria et Cynodontia.

Ce sont soit des caractères de constance de groupe, qui nous apparaissent donc comme assez "statiques", soit des caractères d'intérêt évolutif évident.

Parmi les caractères statiques, nous distinguons des caractères archaïques tels que:

- présence d'une fosse sousorbitaire (Scaloposauria). Cette fosse, caractéristique des Therocephalia *s.l.* (Pristerosauria et Scaloposauria) ne se retrouve dans aucune autre lignée de Thérapsidés; par contre elle se retrouve dans de nombreux groupes de Sauropsidés. Il nous faut donc admettre que cette fosse est une trace de l'origine commune des deux lignées. Il semble, en effet, difficile d'accepter l'idée que de nombreuses lignées aient acquis, de façon indépendante, une fosse sousorbitaire présentant exactement les mêmes relations;
- fort degré de pénétration des prémaxillaires entre les nasaux (Cynodontia);
- postorbitaire bien développé (Cynodontia);
- assez grande constance du foramen pinéal (Cynodontia);
- occiput élevé et profond (Cynodontia);
- grandes dimensions des tabulaires (Cynodontia);
- processus transverses des ptérygoïdes bien développés (Cynodontia);

des caractères osseux en relation essentiellement avec le développement musculaire:

- grande fosse posttemporale (Scaloposauria);
- étroitesse de la région temporale (ce caractère est dû à la fois à un faible développement cérébral et à un fort développement de la musculature masticatrice (Cynodontia). L'étroitesse de cette région a surtout été notée par les différents auteurs par opposition à la grande largeur intertemporale des Gorgonopsiens et en relation avec la musculature;
- crêtes sagittale et occipitale bien marquées (Cynodontia);

et des caractères, soit en partie sous la dépendance des caractères précédents, soit en partie sous celle de caractères "évolués", mais ne changeant que peu ou pas dans les groupes connus:

- contact entre préfrontal et maxillaire (Scaloposauria) ou entre lacrymal et nasal (Cynodontia);
- participation du frontal au bord supérieur de l'orbite (Scaloposauria) ou bord formé par le préfrontal et le postorbitaire (Cynodontia)[21];

soit indépendants et déjà acquis au moment où nous apparaissent ces groupes tels que le vomer à bord ventral élargi des Scaloposauria, ou étroit des Cynodontia. La différence d'aspect du vomer dans ces deux groupes est intéressante à considérer du point de vue de l'origine des Cynodontes. Pour que les Scaloposauria puissent donner naissance aux Cynodontes, il faudrait en effet que le bord ventral élargi du vomer des premiers, considéré comme primitif, se réduise au point d'avoir l'aspect que nous lui connaissons chez les Cynodontes tels que *Scalopocynodon.* Il semble plutôt que l'élargissement du bord ventral du vomer chez les Scaloposauria et la finesse de celui-ci chez les Cynodontes primitifs, correspondent à des stades "analogues" de deux tendances différentes à l'acquisition d'un palais secondaire. Dans ce cas, les Scaloposauridae connus seraient trop différenciés pour pouvoir donner naissance aux Cynodontes.

Quant aux caractères progressifs, ils correspondent soit à la perte de caractères archaïques, ou en tout cas à leur réduction:

chez les Scaloposauria:

- réduction des barres postorbitaires;
- gracilisation des arcades zygomatiques[22];

et chez les Cynodontia:

- réduction de la région antérieure du préfrontal. Cette réduction laisse ainsi place à l'extension postérieure des nasaux;
- diminution des tubérosités dentigères ptérygoïdiennes et perte de leur rôle dentigère;
- diminution des transverses;
- réduction de la lame réfléchie de l'angulaire et des autres éléments postdentaires;
- réduction du carré;

soit à l'acquisition de caractères nouveaux correspondant à une évolution dans le sens mammalien:

- développement du palais secondaire;
- tendance à l'hétérodontie;

La tendance à l'acquisition de ces deux caractères apparaît dans les deux groupes considérés, mais semble s'y réaliser de façon différente; d'autres ne se trouvent que chez les Cynodontia, ce sont:

- augmentation de la hauteur du maxillaire à mi-longueur et par suite "constriction" apparente des nasaux;
- forme du condyle occipital, tendant à devenir double;
- élargissement de l'épiptérygoïde et acquisition d'une suture avec le prootique;
- tendance à un extrême développement du dentaire;

ou à une spécialisation propre:

- développement des arcades zygomatiques (Cynodontia)[23];
- région symphysaire haute (Cynodontia).

En raison de l'état d'écrasement du spécimen, de nombreux caractères n'ont pu être observés, d'autres sont trop altérés pour que l'on puisse les utiliser avec certitude (telle la largeur intertemporale). Cependant, des régions importantes pour l'étude de la position taxonomique de *Protocynodon* subsistent. Ainsi, on peut noter l'absence de certains caractères, tels que la fosse sousorbitaire, et la présence d'autres,

tels que: prémaxillaires assez longs sur la ligne médiane, présence d'un foramen pinéal, grandes dimensions des tabulaires, petite taille des fosses posttemporales, contact entre nasal et lacrymal, contact préfrontal–postorbitaire éliminant le frontal du bord supérieur de l'orbite, trace de barres postorbitaires bien développées, trace d'arcades zygomatiques non graciles, présence de tubérosités ptérygoïdiennes apparement non dentigères, réduction de la lame réfléchie de l'angulaire, petitesse du carré, grande hauteur du maxillaire dans la région médiane, trace de l'insertion de l'épiptérygoïde sur le pariétal indiquant que cet épiptérygoïde devait être assez large.

Tous ces caractères tendent à faire inclure *Protocynodon* dans les Cynodontia plutôt que dans les Scaloposauria. Ce spécimen présente également un petit septomaxillaire, une hétérodontie marquée, un début de palais secondaire s'étendant assez loin vers l'arrière et un opisthotique assez lourdement construit (si les fragments *Pal* (?) et *Op* (?), planche I, fig. 3, considérés respectivement comme un fragment de palatin et un opisthotique érodé, ont été interprétés avec exactitude).

D'autres caractères tels que la hauteur moyenne de l'arcade zygomatique, le développement peu important de la région antérieure du jugal, la présence d'une fosse interptérygoïdienne, la faible profondeur de la selle turcique et sa division par un léger septum médian, la longueur encore faible du dentaire ainsi que la moyenne hauteur de la symphyse et le développement encore peu marqué du processus coronoïde, la réduction non extrême de la lame réfléchie de l'angulaire et des autres os postdentaires font apparaître *Protocynodon* comme encore primitif; conclusion qui était celle de Broom (1949, p. 194).

III–SITUATION DE PROTOCYNODON PARMI LES CYNODONTES

Les Cynodontes primitifs sont représentés par une seule famille, les Procynosuchidae, selon Watson et Romer (1956, p. 62), et par deux familles, Procynosuchidae et Silphedestidae, selon Haughton et Brink (1954, p. 154 et 157). Ces deux familles sont regroupées par Brink (1963 b, p. 74) avec les Galesauroidea, déjà plus évolués, dans les Procynosuchia. Haughton et Brink (*op. cit.*) situent *Protocynodon* dans les Silphedestidae en indiquant que cette position semble aberrante.

Selon ces derniers auteurs et Brink (1960 a, p. 151–152; 1963 b, p. 74 et 1965, p. 137), ces deux familles de la zone à *Cistecephalus* (un spécimen de Silphedestidae provient cependant de la zone à *Cynognathus* et fut décrit, antérieurement aux classifications de Watson et Romer et de Haughton et Brink, par Brink (1951, p. 340 et fig. 3) peuvent être distinguées par les caractères suivants:

Silphedestidae	**Procynosuchidae**
A) Caractères généraux	
– très petite taille;	– (variation de taille non indiquée);
1) *Région intertemporale*	
– région plutôt large;	– région étroite;
– pas de crête marquée;	– crête proéminente;
2) *Arcades zygomatiques*	
– incomplètes;	– complètes;
3) *Arcades postorbitaires*	
– incomplètes;	– complètes;
4) *Palais*	
– (inconnu)[24]	– palais secondaire en processus de développement: plaques palatales des palatins et des maxillaires ne se recontrant pas toujours sur la ligne médiane;

B) Caractères propres aux différents os du crâne

1) *Nasal et lacrymal*

– pas de contact entre nasal et lacrymal[25];	– contact naso–acrymal;

2) *Squamosal*

– de construction légère dans la région des carrés;	– de construction, dans la région des carrés, assez légère pour les formes primitives, lourde pour les formes tardives;

C) Mandibule

– dentaire long[26];	– dentaire court;
– symphyse dans le prolongement de la branche horizontale formant une courbe régulière à grand rayon[27];	– région symphysaire formant un léger angle avec la branche horizontale;
– processus coronoïde non fortement redressé vers le haut et absence d'angle postéro-ventral;	– processus coronoïde très nettement séparé de la branche horizontale du dentaire mais peu développé;

D) Dents

– nombreuses incisives;	– 6 incisives[28];
– jusqu'a 3 précanines;	– 1 à 2 précanines[29];
– 1 canine;	– 1 canine;
– 8 à 9 postcanines à cuspides distinctes;	– 8 à 11 postcanines, normalement toutes "crénelées" ou tricuspides et pouvant être plus élaborées;
– ?	– remplacement dentaire sur le mode de celui de *Procynosuchus delaharpae* Broom 1937.

Protocynodon, par la présence d'arcades zygomatiques et postorbitaires complètes, d'un contact naso-lacrymal (déjà considéré lors de la comparaison entre Scaloposauria et Cynodontia), d'un dentaire court à léger angle entre la symphyse et la branche horizontale et à processus coronoïde peu développé mais nettement séparé de cette dernière, d'une formule dentaire correspondant à 5 I 2pC 1C 9PC (donc proche de celle de *Leavachia* Broom 1948: 5 I 2pC 1C 10PC) et par son mode de remplacement dentaire, s'intègre dans la famille des Procynosuchidae telle qu'elle est actuellement définie. Par contre, tous les caractères connus de *Protocynodon* l'éloignent des Silphedestidae, famille à laquelle il avait été "provisoirement rapporté bien que ce soit une forme totalement différente", par Haughton et Brink (1954, p. 157), sans en faire une forme plus primitive. Brink (1960 a, p. 152) considère que l'actuelle famille des Silphedestidae "représente plus d'une famille, *Protocynodon* étant un membre de cette branche, une forme qui paraît être structuralement plus primitive, mais qui est plus récente que *Scalopocynodon*".

Quant à cette dernière famille (Silphedestidae), il faut reconnaître qu'elle est assez mal connue. Trois formes, *Silphedestes* Broom 1949, *Silphedocynodon* Brink 1951 et un autre spécimen, que Brink (1951, p. 340) rapproche de *Silphedocynodon* Brink 1951, la composent. Les caractères cités plus haut par opposition avec ceux des Procynosuchidae sont les mêmes que ceux qui, pour une bonne part, ont été utilisés pour distinguer les Scaloposauria des Cynodontia.

Si l'on reprend la description de Broom (1949, p. 188–189), *Silphedestes* Broom 1949 présenterait à la fois des caractères de Scaloposauria (maxillaire long et étroit, nombreuses précanines) et des caractères de Cynodontia (arcade postorbitaire probablement complète et préfrontal ayant un contact avec le postorbitaire, éliminant ainsi le frontal du bord orbitaire). Mais Brink, en 1951, puis en 1954, avec

Haughton, considère que ce spécimen présentait une barre postorbitaire incomplète, ce qui rapproche *Silphedestes* Broom 1949 des Scaloposauria. Broom et Brink ne sont également pas d'accord sur la formule dentaire du spécimen:

$$I\ \frac{5\ (?\ 6)}{4}\quad C\ \frac{5}{7}\quad PC\ \frac{9}{8(?\ 9)}$$ selon le premier,

$$I\ \frac{?\ 7}{7}\quad C\ \frac{4}{4}\quad PC\ \frac{8}{8}$$ selon le second.

Dans les deux cas le grand nombre de "canines" tend à rapprocher encore *Silphedestes* des Scaloposauria.

Silphedocynodon Brink 1951 semble encore plus "scaloposauroïde" en raison d'une possible participation du frontal au bord orbitaire. Quant au troisième spécimen, B.P.I. n°: F.995/M.239, non nommé, il se rapproche de *Silphedocynodon* Brink 1951 par ce caractère, mais présente, d'après la figuration de Brink (1951, p. 340, fig. 3 B), un élargissement postérieur des nasaux. Ces os ont cependant été représentés comme séparés des lacrymaux (*id.*, fig. 3A)[30].

Le dentaire est d'aspect "scaloposauroïde", surtout dans les deux premiers cas, il est incomplet dans le dernier.

La grande majorité des caractères, cités dans la littérature, ont fait conclure à Watson et Romer (1956, p. 75), que "*Silphedocynodon* and *Silphedestes* are not improbably Scaloposaurids, in which both zygomatic and postorbital arches, always slender in this group, have been lost either naturally, in the process of fossilisation or in preparation", tandis que ceux que nous avons observés (*cf.* notes 24 & 25 rapprochent plutôt ces genres des Cynodontes. Brink (1960 a, p. 153) assure que l'absence des barres postorbitaires et zygomatiques est naturelle. L'absence des premières peut alors être considérée comme analogue à celle observée chez les Bauriamorpha *s.s.*, tout aussi bien qu'à celle d'autres Scaloposauria tels que *Scaloposuchus* Broom 1940, *Choerosaurus* Haughton 1929, *Tetracynodon* Broom et Robinson 1948 . . . pour n'en citer que quelques-uns, et à celle du Cynodonte *Scalopocynodon* Brink 1960. Par ailleurs, Brink compare la région temporale des Silphedestidae à celle de *Scalopocynodon* Brink 1960 et en conclut que les Silphedestidae sont bien des Cynodontes.

La révision des spécimens constituant actuellement la famille des Silphedestidae apparaît donc nécessaire avant de conclure à leur appartenance à un groupe ou à l'autre.

Il apparaît également utile d'attirer l'attention sur le terme de "Silpholestoidea", superfamille créée par Brink (1963 b, p. 73–74) pour inclure *Scalopocynodon* Brink 1960 (ainsi que les Silphedestidae, semble–t–il). Il s'agit probablement d'une faute de typographie (pour "Silphedestoidea"[31]), car la famille des Silpholestidae, créée par Watson et Romer (1956, p. 74) pour *Ictidodraco* Broom et Robinson 1948, *Scaloporhinus* Boonstra 1953, *Silphoictidoides* von Huene 1950, *Silpholestes* Broom 1948 et *Tetracynodon* Broom et Robinson 1948, n'a aucune raison d'être incluse dans les Cynodontes. En effet, Signogneau (1963, p. 34) considère que certains spécimens de Silpholestidae doivent être intégrés à la famille des Scaloposauridae, une révision pouvant peut-être même conduire à y adjoindre tous les Silpholestidae.

Cependant, la superfamille des "Silphedestoidea" paraît mal définie, car tous les caractères que Brink cite comme étant communs à *Scalopocynodon* Brink 1960 et aux "Silphedestidae" sont des caractères de Scaloposauria, ainsi que nous l'avons vu plus haut. Et, de plus, si l'on considère la liste des caractères communs à *Scalopocynodon* Brink 1960 et aux "Silphedestoidae" et celle des caractères qui les différencient, indiquées par Brink (1960 a, p. 151–152), nous constatons que la dernière (paragraphes C et E) est deux fois plus longue que la première (paragraphe D) et, qu'en outre, elle comporte des caractères évolutifs importants pour la distinction de familles. Les différences sont donc plus importantes que les ressemblances.

IV–SITUATION DE PROTOCYNODON PARMI LES PROCYNOSUCHIDAE

Alors que Haughton et Brink (1954, p. 154–156) indiquent cinq genres sud-africains (*Galecranium* Broom 1948, *Galeophrys* Broom 1948, *Leavachia* Broom 1948, *Paracynosuchus* Broom 1940 et *Procynosuchus* Broom 1937) pouvant être inclus dans la famille des Procynosuchidae, Watson et Romer (1956, p. 62–63) leur adjoignent: un genre sud-africain, *Nanictosaurus* Broom 1936–*Nanictosuchus* Broom 1936 lui étant considéré comme synonyme, tandis que Haughton et Brink placent ces deux genres, maintenus séparés, parmi les Galesauridae–un spécimen est-africain, *Parathrinaxodon* Parrington 1936, et deux genres russes, *Dvinia* Amalitzky 1922 et *Permocynodon* Sushkin 1929. A cette liste, Mendrez (1966–67, p. 432) ajoute *Cyrbasiodon*.

Les Procynosuchidae étrangers à l'Afrique du Sud connus actuellement sont très différents des espèces autochtones: *Permocynodon* Sushkin 1929[32] d'U.R.S.S., est à la fois plus évolué et moins spécialisé que ces dernières. D'une part, il est plus évolué en raison de la présence d'une longue boîte cranienne, d'un palais secondaire complètement fermé, d'un dentaire très développé vers l'arrière–à grand processus coronoïde, à petite apophyse goniaque–, d'une lame réfléchie de l'angulaire, ou *lobus tympanicus* selon Sushkin (1929, p. 808), très réduite–ce qui est en contradiction avec la description de Lehman (1961, p. 162)–, et très détachée du reste de la

mandibule. D'autre part, il est moins spécialisé en raison de la présence d'un squamosal encore bas, et d'une barre postorbitaire peu épaisse. Ces deux derniers caractères seuls sont presque identiques chez *Permocynodon* Sushkin 1929 et *Protocynodon*. *Permocynodon* Sushkin 1929 possède en outre une symphyse mandibulaire dite en forme de "cuillère" qui semble lui être propre. Sa formule dentaire supérieure serait: 4 (ou 6) I lC 2M. *Dvinia* Amalitzky 1922 est uniquement représenté par quelques fragments qui ne peuvent servir ici à une comparaison.

Parathrinaxodon Parrington 1936, décrit par Parrington (1936, p. 132 et suiv., fig. 7 à 9), du Tanganyika, présente des barres sousorbitaires qui s'écartent largement; le spécimen aurait 6 I, et pas de précanine. Outre le palais secondaire bien fermé, il se rapproche de *Thrinaxodon* Seeley 1894 selon Parrington (1936, p. 136), et de *Permocynodon* Sushkin 1929 par de nombreux caractères.

Parmi les Procynosuchidae sud-africains, *Leavachia* Broom 1948 est le genre le mieux connu. Les différentes espèces de ce genre ont été décrites successivement par Broom (1948, p. 618–627, fig. 35–43), Broom et Robinson–sous le nom d'*Aelurodraco microps* (1948, p. 29–33, fig. 1 et 4; la figure 4 est sous-titrée *Whaitsia pricei, in errore*)–, Brink et Kitching (1951, p. 342–347, fig. 1–2), Brink et Kitching (1953, p. 314, fig. 1 et 2) et Brink (1963, p. 57–75, fig. 10–11). Il nous a, en outre, été possible d'observer certains spécimens au B.P.I. for Palaeontological Research, Johannesburg. De même, *Procynosuchus* Broom 1937 a été longuement décrit par Broom en 1937 (p. 314–315, fig. 14) et en 1938 (p. 279–287, fig. 1 à 7) puis par von Huene (1950, p. 124–125, fig. 59) et enfin par Brink et Kitching (1953, p. 314 et 316). Par contre, la description des autres genres est sommaire, ce qui, en plus du mauvais état de conservation de *Protocynodon*, limite les possibilités de comparaison. *Galecranium* Broom 1948 a été l'objet de deux brèves études, l'une de Broom (1948, p. 628–629, fig. 44A et B), l'autre de Brink et Kitching (1953, p. 314); quant à *Galeophrys* Broom 1948 et *Paracynosuchus* Broom 1940, ils ne sont connus que grâce à une note chacun; le premier genre a été créé par Broom en 1948 (p. 627–628, fig. 44 C et D), et le second par le même auteur en 1940 (p. 73, fig. 2 A et B). Enfin, *Cyrbasiodon* Broom 1931, représenté seulement par un maxillaire portant quatorze dents, a été décrit brièvement par Broom, en 1931 (p. 163–164) et en 1932 (p. 77, fig. 23 I à N) et l'aspect de ses dents rappelé par Mendrez (1966–67, p. 430–432, fig. A 1 à 3).

Protocynodon diffère de *Leavachia* Broom 1948, de *Galecranium* Broom 1948, et de *Galeophrys* Broom 1948, par un crâne relativement étroit, par un museau relativement long et une région temporale courte, ce qui le rapprocherait plutôt de *Paracynosuchus* Broom 1940 et de *Procynosuchus* Broom 1937.

De même, les orbites de *Protocynodon* paraissent nettement plus grandes que celles de *Leavachia* Broom 1948, de *Galecranium* Broom 1948 et de *Galeophrys* Broom 1948, légèrement plus grandes que celles de *Procynosuchus* Broom 1937 mais toutefois moins que celles de *Paracynosuchus* Broom 1940.

Le septomaxillaire de *Protocynodon* est étroit comme chez *Leavachia* Broom 1948, *Galecranium* Broom 1948 et *Procynosuchus* Broom 1937 (il n'est pas figuré chez les autres formes).

Le maxillaire de *Protocynodon* s'affine vers l'avant, comme chez *Leavachia* Broom 1948, *Galecranium* Broom 1948 et *Procynosuchus* Broom 1937, mais diffère de celui de *Cyrbasiodon* Broom 1931 dont la partie antérieure paraît tronquée. Cette région est endommagée chez *Galeophrys* Broom 1948 et semble l'être également chez *Paracynosuchus* Broom 1940, d'après la reconstruction de Broom (1940, fig. 2 B).

La grande surface des frontaux lui est particulière, mais le fait que la plus grande largeur de l'ensemble de ces os soit antérieure et que la suture fronto-nasale soit longue et en forme de W rapproche *Protocynodon* de *Galecranium* Broom 1948 et de *Galeophrys* Broom 1948.

Le préfrontal semble être moins réduit à l'avant chez *Protocynodon* que chez les autres genres.

L'ensemble préfrontal-postorbitaire est, au niveau des orbites, moins large que chez tous les autres Procynosuchidae d'Afrique du Sud.

L'orifice pinéal est à peu près à mi-longueur du pariétal, prise sur la ligne médiane, comme chez *Paracynosuchus* Broom 1940, alors que sa position est plus antérieure chez les autres genres. Les rapports entre les limites de l'orifice pinéal et le bord postérieur du postorbitaire sont, de ce fait, différents. Mais il ne semble pas qu'il faille accorder une grande importance à ce caractère.

Les crêtes ptérygoïdiennes sont orientées parasagittalement chez *Protocynodon* tandis que chez *Leavachia* Broom 1948 elles apparaissent obliques, leur région antérieure s'écartant de la ligne sagittale.

Les tabulaires semblent ne pas former la totalité du bord de la fosse posttemporale. Mais, d'une part, cette interprétation n'est pas certaine en raison du mauvais état de conservation de cette région et, d'autre part, il n'est pas sûr que ce caractère soit un bon critère intergénérique. En effet chez *Leavachia* Broom 1948, il a été possible d'observer deux types de dispositions de cette région: *Leavachia microps* (Broom et Robinson) 1948 (B.P.I.n°.F.226-B/M.8-B) présente une fosse posttemporale dont a peine les deux tiers sont bordés par le tabulaire tandis que cet os forme la totalité du bord de la fosse posttemporale chez *Leavachia duvenhagei* Broom 1948 (B.P. I. n°: F. 3748/M.357).

Le dentaire de *Protocynodon* est un peu plus long que celui de *Leavachia* Broom 1948 et nettement plus court que celui de *Paracynosuchus*

Broom 1940. La branche montante est moins élevée mais mieux individualisée que chez *Leavachia* Broom 1948.

La lame réfléchie de l'angulaire est moins détachée du reste de la mandibule que chez *Leavachia* Broom 1948; sa surface semble à la fois plus grande et plus sinueuse. Chez les autres Procynosuchidae, la surface de la lame réfléchie est réduite et très légèrement ondulée.

Le splénial est, chez *Protocynodon*, de bien moindre largeur que chez *Leavachia* Broom 1948; d'autre part, il ne participe pas au bord inférieur de la mandibule.

Si on tente de comparer la formule dentaire la plus probable de *Protocynodon* (5I 2pC IC 9PC) à celle des autres Procynosuchidae sud-africains—*Procynosuchus* Broom 1937, *Paracynosuchus* Broom 1940, *Leavachia* Broom 1948, *Galecranium* Broom 1948, *Galeophrys* Broom 1948 et *Cyrbasiodon* Broom 1931—, on constate que, chez ceux-ci, l'unanimité est loin d'être faite au sujet du nombre des dents, et en particulier de celles antérieures à la canine vraie, qu'elles soient incisives ou précanines. On peut résumer l'opinion des différents auteurs selon le schéma suivant (schéma dans lequel, pour faciliter les comparaisons, la nomenclature dentaire utilisée par ces auteurs a été modifiée en fonction de la distinction entre précanines—ou canines antérieures cf. Broom—, et canine vraie—ou canine principale, *ibid.*:

Procynosuchus Broom 1937	5–6 I	1 pC	1 C	10	PC	Broom, R. (1937, p. 315)
	6 I	1 pC	1 C	10	PC	*P. delaharpae* Broom, R. (1938) . . . . (p. 281)
	sans doute					
	6 I	1 pC	1 C	10 10	PC à gauche PC à droite	*P. rubidgei* Broom, R. (1938) . . . . (p. 285, fig. 5)
	6 I	1 pC	1 C	10	PC	Broom, R. (1948, p. 629)
	5 I	2 pC	1 C	10	PC	Brink, A. S. & Kitching, J. W., *P. rubidgei* (1953, p. 316)
	5 I	1 pC	1 C	10	PC	Haughton, S. H. & Brink, A. S. (1954, p. 156)
	5 I	2 pC	1 C	10	PC	Brink, A. S. (1963 b, p. 66)
Paracynosuchus Broom 1940	I	1 pC	1 C	7	PC	Broom, R. (1940, p. 73)
	perdues					
	5 ? I	1 pC	1 C	7	PC	Haughton, S. H. & Brink, A. S. (1954, p. 156)
Leavachia Broom 1948	6 I	2 pC	1 C	8	PC	Broom, R. (1948, p. 620 & 629)
	id.	*id.*	*id.*		*id.*	Brink, A. S. & Kitching, J. W. (1951, p. 342)
	5 I			8	PC	Brink, A. S. & Kitching, J. W. (1953, p. 313)
	5 I	2 pC	1 C	8	PC	Haughton, S. H. & Brink, A. S. (1954, p. 155)
	5 I	2 pC	1 C	10 environ, du fait de la variation de ce nombre selon l'âge.	PC	Brink, A. S., (1963 b, p. 59)
Galeophrys Broom 1948	6 I	2 pC	1 C	9	PC	Broom, R. (1948, p. 628 & 629)
	id.	*id.*	*id.*		*id.*	Brink, A. S. & Kitching, J. W. (1951, p. 342, 343 & 346)
	id.	*id.*	*id.*		*id.*	Haughton, S. H. & Brink, A. S. (1954, p. 155)

Galecranium Broom 1948	6 I	2 pC	1 C 11 PC	Broom, R. (1948, p. 629)
	pratiquement certaines mais les 4 premières sont perdues			
	5 I	2 pC	1 C 11 PC	Brink, A. S. & Kitching, J. W. (1953, p. 314)
	(5?) 6 I	2 pC	1 C 11 PC	Haughton, S. H. & Brink, A. S. (1954, p. 154)
Cyrbasiodon Broom 1931	–	–	(1?)C 11(12?) PC	Broom, R. (1931, p. 164)
	–	–	11 dents, mais deux sont probablement perdues	Broom, R. (1932, p. 77)
	–	3 pC	1 C 10 PC	Mendrez, C. H. (1966–67, p. 430)

Tandis que les Procynosuchidae non sud-africains–*Dvinia* Amalitzky 1922, *Permocynodon* Sushkin 1929 et *Parathrinaxodon* Parrington 1936–paraissent former un groupe caractérisé par l'absence de précanine, il semble que, malgré les incertitudes qui règnent au sujet des formules dentaires des genres sud-africains, on puisse répartir ces derniers en trois groupes. Le premier groupe–formé par *Procynosuchus* Broom 1937 et *Paracynosuchus* Broom 1940–ne possède qu'une précanine, selon l'avis le plus général. Le second–formé par *Leavachia* Broom 1948, *Galeophrys* Broom 1948 et *Galecranium* Broom 1948–possède deux précanines. Enfin, le troisième, représenté par un seul genre–*Cyrbasiodon* Broom 1931–possède trois précanines. Par la présence probable de deux précanines, *Protocynodon* serait à rapprocher du second groupe. Le nombre de ses postcanines, entrant dans la marge de variation du groupe, ne s'oppose pas à cette suggestion.

Il n'est pas impossible qu'au cours de l'évolution des Procynosuchidae, le nombre de leurs précanines diminue de trois à zéro, la canine vraie devenant alors–comme chez les mammifères–la première dent maxillaire. Cependant, les relations entre les quatre groupes cités ci-dessus et leurs positions stratigraphiques respectives, tout comme leur anatomie, sont bien trop mal connues, pour permettre de conclure à une filiation, plutôt qu'à une simple variation.

Brink et Kitching (1951, p. 343) considéraient que le nombre de postcanines changeait avec l'âge, mais que le nombre d'incisives et de canines (*s.l.*) pouvait servir à distinguer différents genres. Si le nombre de canines–ou plutôt de précanines–semble contribuer à établir une discrimination, le nombre d'incisives ne paraît guère utilisable comme caractère distinctif. En effet, à l'intérieur d'un même genre, et ce pour tous les genres de Procynosuchidae autres que *Galeophrys* Broom 1948, le nombre des incisives varie selon les auteurs. Seule une révision de cette famille permettra donc de reconnaître ou non une valeur discriminative à ce caractère.

L'ensemble des caractères cités plus haut, tout particulièrement les grandes dimensions des frontaux et de la lame réfléchie de l'angulaire, font qu'à ce jour *Protocynodon* peut être considéré comme un genre distinct des autres Procynosuchidae.

CONCLUSIONS

Au cours de cette nouvelle étude de *Protocynodon*, dont le type est l'unique spécimen connu, nous avons été amené à conclure qu'il s'agissait d'un Cynodonte et non pas d'un Scaloposaure. L'appartenance de *Protocynodon* aux Procynosuchidae plutôt qu'aux Silphedestidae semble également indiscutable. A l'intérieur de la famille des Procynosuchidae, *Protocynodon* apparaît actuellement comme un genre valable. Une comparaison plus poussée avec les autres Procynosuchidae ne sera possible que lorsque l'étude de ces derniers sera complétée et le degré de variabilité de certains caractères, et par suite leur valeur discriminative, connus.[33]

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NOTES

[1] Cf. Brink et Haughton, (1954, p. 194); ceci est confirmé par une information *in litteris* 2/2/1968 de Kitching, J. W. et infirmerait l'assertion de Broom, (1949, p. 192), indiquant que le spécimen avait été trouvé à Elim, Burghersdorp district par Ben Kitching.

[2] *Précanines*: dents situées sur le maxillaire à l'avant de la canine vraie; tandis que cette dernière est longue et en forme de croc, les précanines sont le plus souvent de taille réduite et incisiformes.

[3] L'observation du contact entre nasal et lacrymal est ici en contradiction avec l'observation de Broom, qui (p. 192, fig. 5) représente au contraire un contact entre préfrontal et maxillaire. Ceci a déjà été discuté dans une précedente note (Mendrez, 1966–67, p. 432, fig. B).

[4] *Angle goniaque*: angle postéro-inférieur du dentaire formé par le bord ventral de la branche horizontale et le bord postérieur de la branche montante.

[5] *Précanines*: cf. définition ci dessus.[2]

[6] Il faut remarquer que (p. 183), dans un tableau illustrant la phylogénie des reptiles primitifs, Watson, emploie le mot "Bauriasauria" pour, apparemment, regrouper Bauridae et *Pachygenelus* Watson 1913, mais il ne semble ni le définir ni l'utiliser ailleurs: ce serait donc un *nomen nudum*

[7] 1922, p. 306.

[8] Il est maintenant notoire que cette description des molaires n'est plus valable, mais, en 1932, seule la face "labiale" des dents avait été étudiée.

[9] Brink considère comme "*canines*" la dent plus ou moins caniniforme et toutes les dents qui la précèdent sur le maxillaire, tandis que Watson et Romer réservent ce nom à la seule dent maxillaire caniniforme.

[10] Intrication qui a conduit Lessertisseur et Sigogneau, en 1965 à préciser, dans le tableau de la p. 96, que le terme de Bauriamorpha était employé à la fois au sens strict et au sens large.

[11] Ceci est à peine esquissé dans les familles primitives, mais très accentué dans les autres.

[12] Brink, (1965) ne précise pas s'il inclut les Nanictidopsidae et les Silpholestidae dans la famille des Scalopsauridae bien que l'impression en soit donnée par son texte.

[13] En réalité la fosse temporale semble avoir un aspect assez variable à l'intérieur de chaque groupe.

[14] Des études postérieures du même auteur (1963 b) montrent que cette fosse existe chez les Procynosuchidae.

[15] Considérés comme tels, sauf par Broom, (1932), mais très grands chez un nouveau spécimen de *Notictosaurus luckhoffi* Broom 1936 (B.P.I., n°: F.3892), Cynodonte galesauridé étudié par Brink en 1965 (p. 113). Le degré de variabilité du lacrymal chez les Cynodontes serait à préciser. Broom (1932) considère que le lacrymal des Cynodontes est toujours bien développé sur la face. Cette apparence semble souvent être plus en relation avec la réduction de la région antérieure du préfrontal qu'avec une élongation du lacrymal.

[16] Il semble qu'il y ait une contradiction partielle à ce sujet entre Watson et Romer (1956, p. 61) pour qui les postorbitaires "... do not meet the squamosals above the temporal fenestrae" et Attridge (1956, p. 73) selon lequel "Postorbital and squamosal meet in most genera". Il faut probablement comprendre qu'il s'agit dans cette dernière citation du contact secondaire entre postorbitaire et squamosal.

[17] De toute facon, Brink (même référence) conclut: "... (the) preparietal, a feature which has proved in the past to have no diagnostic value whatsoever".

[18] Moins cependant que celui des Scaloposauria.

[19] De faible développement cependant chez les formes primitives.

[20] Marqués d'un astérisque dans le tableau comparatif.

[21] Caractères apparemment constants chez les Thérocéphales et les Cynodontes; variables chez les Gorgonopsiens (communication personnelle de Sigogneau) parmi lesquels des spécimens de grande taille présentent un contact préfronto-postorbitaire, tandis que de petits spécimens possèdent un frontal participant au bord susorbitaire.

[22] L'aspect des arcades zygomatiques aurait donc dans les deux groupes une valeur évolutive différente.

[23] Voir note[22].

[24] La partie postérieure du palais est cependant visible et paraît être de type Cynodonte chez *Silphedestes* Broom 1949. (Ceci a été confirmé récemment par Battail, communication orale, janvier 1969).

[25] Cependant le spécimen B.P.I. n°: F.995/M. 239, considéré par Brink comme proche de *Silphedocynodon* Brink 1951, présente ce contact de façon très nette. Il semble qu'il en soit de même chez *Silphedestes* Broom 1949. Cette région est moins bien conservée chez le type de *Silphedocynodon* Brink 1951.

[26] et[27] Et d'après les figures 1–2–3 p. 338, 339 et 340 (*in* Brink 1951).

[28] Mais *Leavachia* Broom 1948 possède 5 incisives (Brink, 1963 b, p. 61, fig. 10).

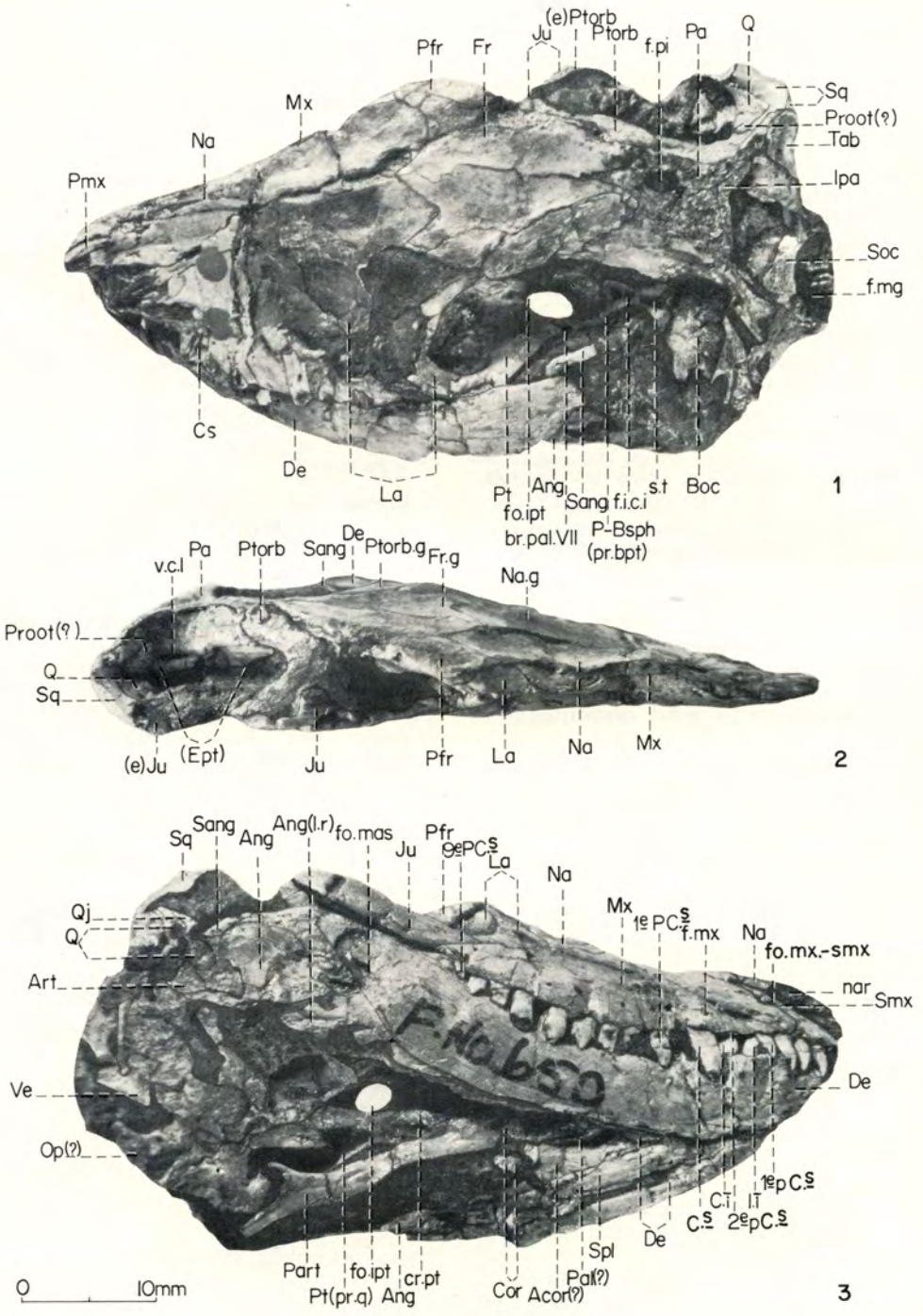
[29] Selon Parrington (1936, fig. 8, p. 134), *Parathrinaxodon* Parrington 1936 ne possède pas de précanine, et Mendrez, (1966–1967, p. 430) a observé la présence de trois précanines chez *Cyrbasiodon boycei* Broom 1931.

[30] Voir note[25].

[31] Emendation proposée.

[32] Sushkin (1929, p. 804–808, fig. 1 à 4; la fig. 2 est sens dessus dessous). *Ibid.* (1935, p. 49–52, pl. 1).

[33] Tandis que cet article était sous presse, Kitching (dans une communication orale du 4/2/1972) indiquait qu' "il était arrivé aux mêmes conclusions dans ses notes de terrain et sa liste de localités de fossiles du Karroo (1963, non publié) et que Hopson et lui-même à la suite de leur révision des Procynosuchidae (1971, sous presse) considéraient le spécimen étudié ci-dessus comme étant un jeune *Procynosuchus*".



PLANCHE

Protocynodon pricei Broom 1949

Fig. 1 — face dorsolatérale gauche
Fig. 2 — vue "latérale" droite
Fig. 3 — face ventrolatérale droite

Acor(?),	antécoronoïde (?);
Ang,	angulaire;
Ang (l.r),	angulaire (lame réfléchie);
Art,	articulaire;
Boc,	basioccipital;
br.pal. VII,	passage (?) de la branche palatine du VII;
Cs̄,	canine supérieure;
Cī,	canine inférieure;
Cor,	coronoïde;
cr.pt,	crête ptérygoïdienne;
De,	dentaire;
(e)Ju,	empreinte du jugal;
(Ept),	limites d'insertion de l'épiptérygoïde;
(e)Ptorb,	empreinte du postorbitaire;
f.i.c.i,	foramen interne de la carotide interne (= foramen antérieur du canal de la carotide interne);
f.mg,	foramen magnum;
f.mx,	foramen maxillaire;
f.pi,	foramen pinéal;
fo.mx.-smx,	fosse maxillo-septomaxillaire;
fo.ipt,	fosse interptérygoïdienne;
fo.mas,	fosse massétérienne;
Fr,	frontal;
Fr.g,	frontal gauche;
Iī,	dernière incisive inférieure;
Ipa,	interpariétal;
Ju,	jugal;
La,	lacrymal;
Mx,	maxillaire;
Na,	nasal;
Na.g,	nasal gauche;
nar,	narine;
Op(?),	opisthotique (?);
Pa,	pariétal;
Pal(?),	palatin (?);
Part,	préarticulaire;
P–Bsph (pr.bpt),	complexe parabasisphénoïde (processus basiptérygoïde);
1ère pCs̄,	première précanine supérieure;
2ème pCs̄,	deuxième précanine supérieure;
1ère PCs̄,	première postcanine supérieure;
9ème PCs̄,	neuvième postcanine supérieure;
Pfr,	préfrontal;
Pmx,	prémaxillaire;
Proot?,	prootique ?;
Pt,	ptérygoïde;
Pt (pr.q),	ptérygoïde (processus carré);
Ptorb,	postorbitaire;
Ptorb.g,	postorbitaire gauche;
Q,	carré;
Qj,	quadratojugal;
Sang,	susangulaire;
Smx,	septomaxillaire;
Soc,	supraoccipital;
Spl,	splénial;
Sq,	squamosal;
s.t,	selle turcique;
Tab,	tabulaire;
Ve,	vertèbre;
v.c.l,	gouttière de la veine *capitis lateralis*.

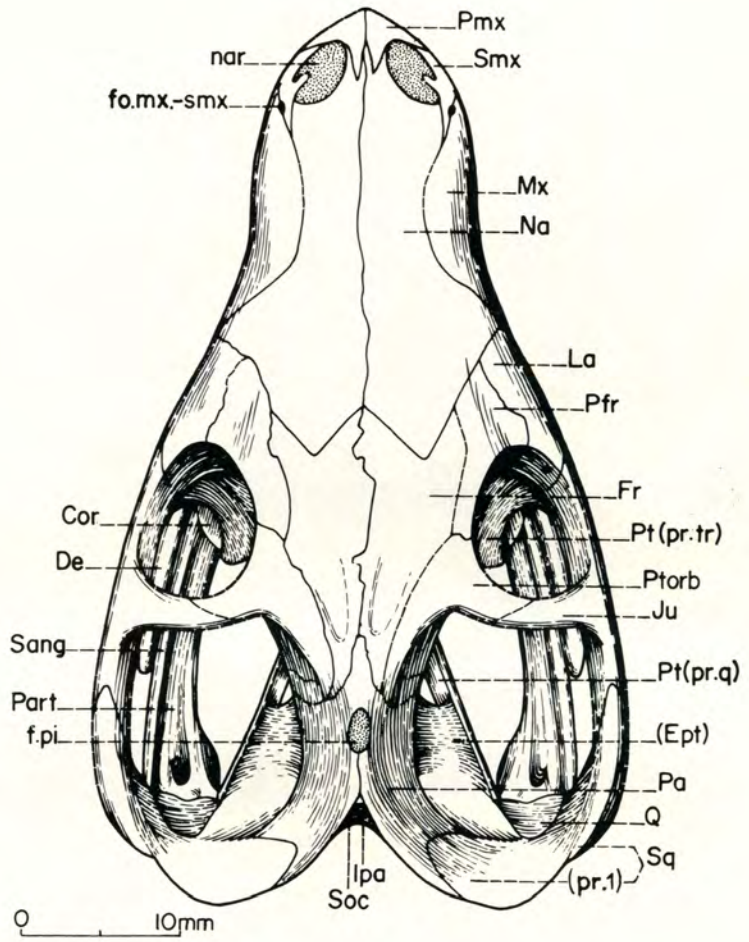


Fig. 1 – *Protocynodon pricei* Broom 1949: reconstitution du crâne en vue dorsale (x 2)

Cor,	coronoïde;
De,	dentaire;
(Ept),	emplacement de l'épiptérygoïde;
f.pi,	foramen pinéal;
Fr,	frontal;
fo.mx.-smx,	fosse maxillo-septomaxillaire;
Ipa,	interpariétal;
Ju,	jugal;
La,	lacrymal;
Mx,	maxillaire;
Na,	nasal;
nar,	narine;
Pa,	pariétal;
Part,	préarticulaire;
Pfr,	préfrontal;
Pmx,	prémaxillaire;
Pt (pr.q),	ptérygoïde (processus carré);
Pt (pr.tr),	ptérygoïde (processus transverse);
Ptorb,	postorbitaire;
Q,	carré;
Sang,	susangulaire;
Smx,	septomaxillaire;
Soc,	supraoccipital;
Sq,	squamosal, (*pr.1*, processus dorsal);

.....: limite du fragment osseux restant
---------: limite de l'os reconstitué } *(postorbitaire)*

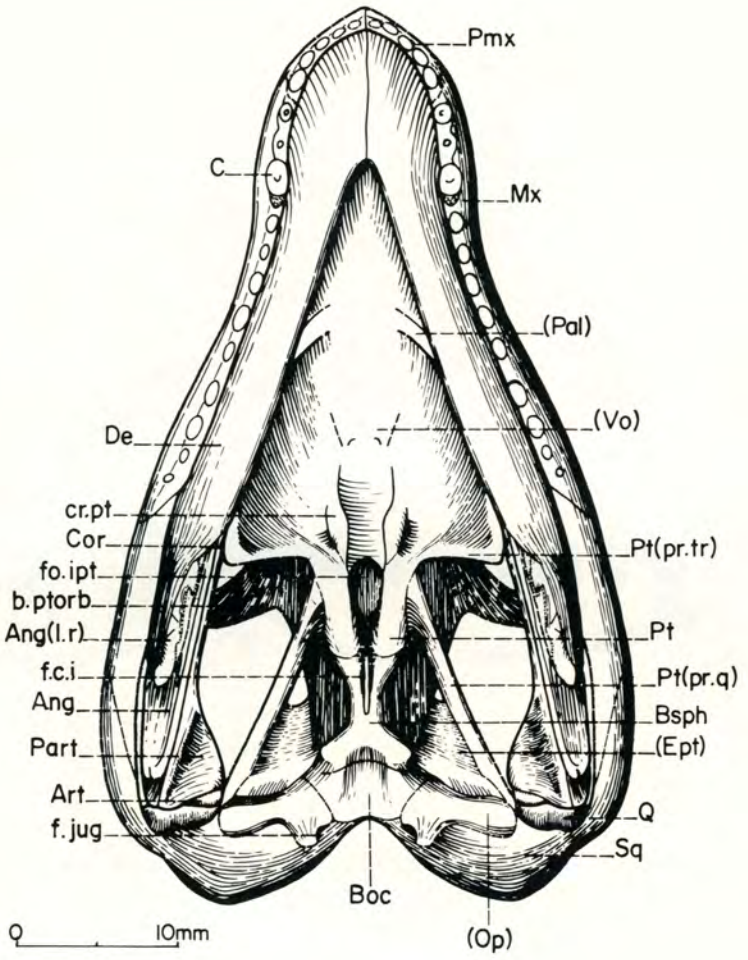


Fig. 2 – *Protocynodon pricei* Broom 1949: reconstitution du crâne en vue ventrale (x2)

Ang,	angulaire;
Ang (l.r),	angulaire (lame réfléchie);
Art,	articulaire;
b.ptorb,	barre postorbitaire;
Bsph,	basisphénoïde;
Boc,	basioccipital;
C,	canine;
Cor,	coronoïde;
cr.pt,	crête ptérygoïdienne;
De,	dentaire;
(Ept),	emplacement de l'épiptérygoïde;
f.c.i,	foramen de la carotide interne;
fo.ipt,	fosse interptérygoïdienne;
(f.jug),	foramen jugulaire;
Mx,	maxillaire.
(Op),	opisthotique;
(Pal),	palatin;
Part,	préarticulaire;
Pmx,	prémaxillaire;
Pt,	ptérygoïde;
Pt(pr.q),	ptérygoïde (processus carré);
Pt(pr.tr),	ptérygoïde (processus transverse);
Q,	carré;
Sq,	squamosal, (*pr.1*, processus dorsal);
(Vo),	vomer;

.....: *limite du fragment osseux restant*
---: *limite de l'os reconstitué.*
} *(lame réfléchie de l'angulaire)*

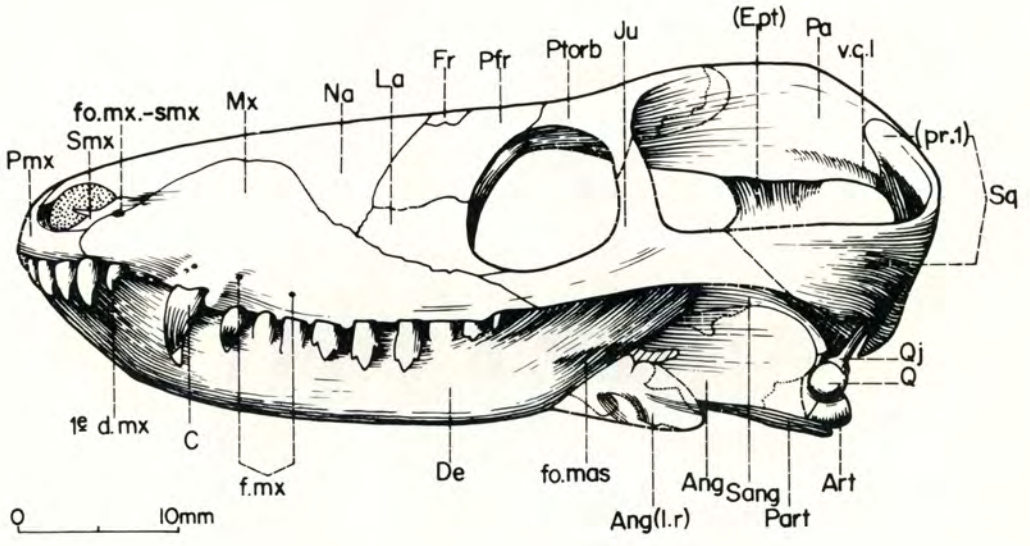


Fig. 3 — *Protocynodon pricei* Broom 1949: reconstitution du crâne en vue latérale (x 2)

Ang,	angulaire;
Ang (l.r),	angulaire (lame réfléchie);
Art,	articulaire;
De,	dentaire;
1ère d.mx,	première dent maxillaire;
fo.mas,	fosse massétérienne;
f.mx,	foramen maxillaire;
Fr,	frontal;
fo.mx.–smx,	fosse maxillo–septomaxillaire;
(Ept),	épiptérygoïde;
Ju,	jugal;
La,	lacrymal;
Mx,	maxillaire;
Na,	nasal;
Pa,	pariétal;
Part,	préarticulaire;
Pfr,	préfrontal;
Pmx,	prémaxillaire;
Ptorb,	postorbitaire;
Q,	carré;
Qj,	quadratojugal;
Sang,	susangulaire;
Smx,	septomaxillaire;
Sq,	squamosal;
v.c.l,	gouttière de la veine *capitis lateralis;*

.....: *limite du fragment osseux restant*
--------: *limite de l'os reconstitué* } *(angulaire et postorbitaire)*

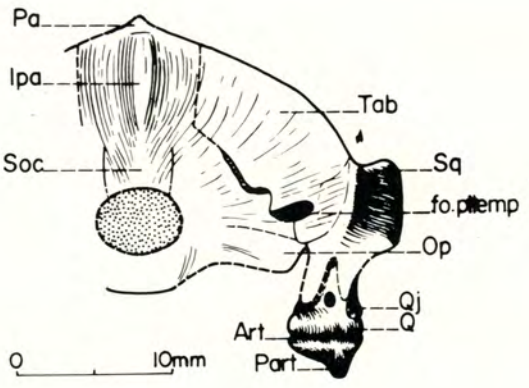


Fig. 4 — *Protocynodon pricei* Broom 1949: reconstitution du crâne en vue occipitale (x2)

Art,	articulaire;
fo.pttemp,	fosse posttemporale;
Ipa,	interpariétal;
Op,	opisthotique;
Pa,	pariétal;
Part,	préarticulaire;
Q,	carré;
Qj,	quadratojugal;
Soc,	supraoccipital;
Sq,	squamosal;
Tab,	tabulaire.

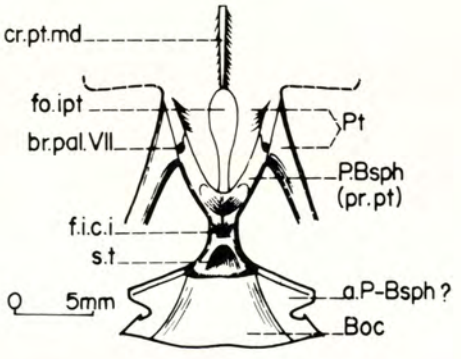


Fig. 5 — *Protocynodon pricei* Broom 1949: reconstitution de la face dorsale de la base de l'endocrâne (x 2)

a.P–Bsph ?,	aile du complexe parasphénoide–basisphénoïde ? ;
Boc,	basioccipital;
br.pal. VII,	passage (?) de la branche palatine du VII;
cr.pt.md,	crête ptérygoïdienne médiodorsale;
f.i.c.i,	foramen interne de la carotide interne (= foramen antérieur du canal de la carotide interne);
fo.ipt,	fosse interptérygoïdienne;
P–Bsph (pr.bpt),	complexe parashénoïde–basisphénoïde (processus basiptérygoïde);
Pt,	ptérygoïde;
s.t,	selle turcique.

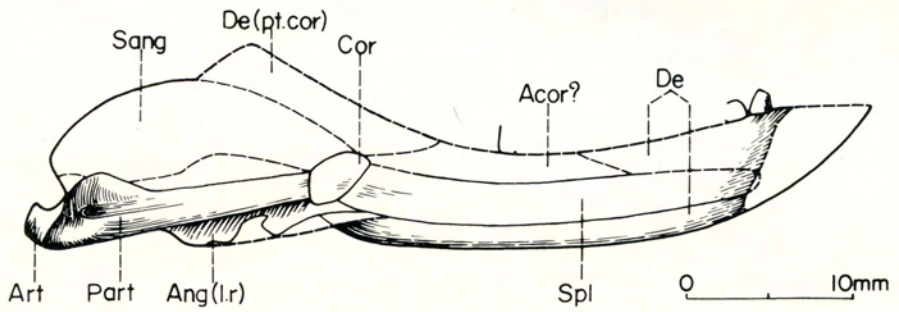


Fig. 6 — *Protocynodon pricei* Broom 1949: reconstitution de la mandibule en vue mésiale (x 2)

Acor?,	antécoronoïde? ;
Ang (l.r),	angulaire (lame réfléchie);
Art,	articulaire;
Cor,	coronoïde;
De,	dentaire;
De (pr.cor),	dentaire (processus coronoïde);
Part,	préarticulaire;
Sang,	susangulaire;
Spl,	splénial.

Palaeont. afr., **14.** 51–69. 1972

ON *CYRBASIODON BOYCEI*, BROOM 1931, (CYNODONTIA PROCYNOSUCHIDAE), FROM SOUTH AFRICA

by

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ABSTRACT

The revision of the type of *Cyrbasiodon boycei* has led the author to conclude that the maxilla, which constitutes this type, bears fourteen teeth corresponding to a complete maxillary series: 3 precanines, 1 canine and 10 postcanines. The general pattern of the teeth and the aspect of a remnant of secondary palate agree with those of the Cynodontia Procynosuchidae. Within this family, *Cyrbasiodon* can be favourably compared with the genera *Leavachia* and *Parathrinaxodon*. However, because of the anterior breadth of the palatal process of the maxilla, the different number of precanines, and of a slight difference in the canine's ornamentation, it seems preferable to maintain *Cyrbasiodon* as a separate genus, until the variations of the other Procynosuchidae are better known. The comparison of the tooth pattern of the Procynosuchidae with that of *Diarthrognathus* has shown strong similarities leading to the conclusion that the tooth pattern of the former foreshadows that of the latter.

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INTRODUCTION

The type of *Cyrbasiodon boycei* has been subject to discussion as to the locality where it has been found, the horizon of the locality and its taxonomical position within the therapsids.

Genus *Cyrbasiodon* Broom 1931.

Diagnosis: rather large procynosuchid maxilla bearing 3 precanines, 1 canine and 10 postcanines, differing from the closest genera *Leavachia* and *Parathrinaxodon* in the less developed palatal process of the maxilla, in the number of precanines and in the presence of serrations on both anterior and posterior edges of the canine. (This poor diagnosis will perhaps not stand when the Procynosuchidae are better known.)

Type species:

Cyrbasiodon boycei Broom 1931.

Species *C. boycei* Broom 1931.

Derivation of name: in honour of Mr. David Boyce, preparator of the Durban Museum, who discovered the specimen (cf. Broom 1931, p. 163–164).

Material: only the holotype.

Holotype: nearly complete left maxilla bearing fourteen teeth corresponding to the dental formula: 3 pC, 1 C, 10 PC. The postcanines are well differentiated into caniniform and molariform teeth. This holotype is in the Durban Museum (no museum number), Natal, South Africa.

Locality: uncertain;

"at Bezuidenhout's Pass, Natal", according to Broom (1931, p. 164);

"at Bergville", according to the same author (1932, p. 77). Bezuidenhout's Pass is in the Bergville district and this may be why Broom indicates in 1932 "at Bergville". But the town Bergville is situated approximately 18 miles (= approx. 29 kilometers) away from Bezuidenhout's Pass.

Horizon: uncertain;

Bezuidenhout's Pass is in the *Cistecephalus*-zone according to Broom (1931, p. 164) but in the *Lystrosaurus*-zone according to Kitching (*in litteris*, 19-1-1968). The latter author mentions in that locality the occurrence of *Thrinaxodon*, *Lystrosaurus* and *Lydekkerina* and concludes that the "specimen, if the locality is correct, came from the *Lystrosaurus*-zone."

Near the town Bergville, the *Daptocephalus*-zone occurs. (The *Daptocephalus*-zone corresponds to the upper part of the classical *Cistecephalus*-zone, (cf. Kitching 1970, p. 309–310).)

Diagnosis: C. boycei is the only known species.

Taxonomical position: see page 55.

The specimen was incompletely prepared when kindly lent to the Bernard Price

Institute for Palaeontological Research by the Natal Museum. It then showed only eleven teeth, those described by Broom, in 1931 (p. 164). In this publication Broom suggests that "probably a small canine is lost in front and the complete dentition is probably eight premolars and four molars". In 1932 (p. 77), Broom indicates that "the maxilla . . . has eleven teeth but probably two are lost". After further development, it appears that no teeth are missing. The maxilla bears fourteen teeth: 3 precanines, 1 canine and 10 postcanines.

In 1966 (1967, p. 430) Mendrez proposed the following table, slightly modified, of equivalences between these two formulae:

According to Broom, 1931					Premolars							Molars				
		1	2		3	4	5		6	7	8	9	10	11
According to Mendrez, 1966	1	2	3	4	5	6	7	8	9	10	11	12	13	14
					can.	?	?	Molariform						
	Precanines			C	Postcanines									

C: canine; can: caniniform

Figures: The palatal view of *Cyrbasiodon* (fig. 2, 8 and 9) has been reconstructed, taking into account the anterior part of the medial edge of the maxilla, and what is thought to be a fragment of the palatine. The orientation of the maxilla and its distance from the mid-line have been calculated to allow space for a premaxilla bearing the procynosuchid number of incisors (5 or 6). This latter condition and the outer contour of the precanine part of the maxilla are responsible for the standing of *Cyrbasiodon's* maxilla slightly farther away from the mid-line than that of *Leavachia.* The position of teeth has been corrected.

DESCRIPTION

I–MAXILLA

The left maxilla (Text-fig. 1–2 and Plate I) which constitutes the type of *Cyrbasiodon boycei* is nearly complete; only the upper part of the facial plate and the median part of the palatal process *(Mx (pr. palat.))* are missing.

Its outer surface (Text-fig. 1 and Plate IA) is smooth and presents anteriorly a few openings for the cutaneous ramifications of the deep ophthalmic division of the trigeminal nerve, *VI (f. mx)*.

The inner part of the maxilla (Text-fig. 2) is characterised by two features: an anterior contact surface for the premaxilla and a fragment of palatal process. The contact surface (*c. s. Pmx*), in front of the first precanine shows that the maxilla overlapped the premaxilla for about 4 mm. The fragment of palatal process (*Mx (pr. palat.)*), Text-fig. 2 and Plate IB, increases regularly as far as the level of the second postcanine and then slowly decreases up to the second last postcanine. The maximal breadth of this fragment is about 6,3 mm. The presence of a palatal process suggests that the possessor of such a maxilla had a secondary bony palate, as noted by Broom in 1931 (p. 164, "There is a little doubt there is a secondary palate") and again in 1932 (p. 77, "There is some indication that the genus had a secondary palate"). The bony palate of *Cyrbasiodon* was probably imperfect because of the relatively short breadth of this process compared with the total length of the maxilla. In palatal view, the *sulcus alveolaris interiors (s. a. i*, Text-fig. 2) for the dental lamina and the pits for the replacing teeth are clearly visible.

II–DENTITION

Nomenclature: The classical nomenclature in Mammals and that for Reptiles, adopted by Edmund (1969, p. 119) are as follows:

mesial = inner (incisors) = anterior (molars)
distal = outer (incisors) = posterior (molars)
lingual = posterior (incisors) = inner (molars)
labial (incisors) / buccal (molars) = vestibular (= anterior (incisors) / = outer (molars))

The former terminology will be used here for all the maxillary teeth, with the usual equivalence given for the molars for:

length = mesio-distal (= longitudinal) diameter;
breadth = bucco-lingual (= vestibulo-lingual = transversal) diameter.

A. Precanines (Text-fig. 3)

The three precanines are characterised by their small size as compared with the postcanines.

1. First precanine, (= first maxillary tooth, not quoted by Broom, Text-fig. 3(1a- 1c- 1d).

The first precanine was completely embedded in shale when the specimen was

borrowed from the Durban Museum. This tooth is sectorial in being thick in the centre but sharp-edged mesially and distally. The tip curves strongly inwards and slightly backwards. The bucco-lingual diameter increases greatly towards the base; this is due mainly to a lingual swelling. As the distal part is slightly overlapped by the second precanine, it is impossible to appreciate its exact shape. The lingual surface is not perfectly smooth but extremely feebly grooved and ridged.

2. Second precanine (= second maxillary tooth, tooth number one according to Broom, Text-fig. 3 (2a- 2c- 2d)).

The second precanine is both larger and broader than the first, but has nearly the same general pattern. However, the tip is less curved lingually and the bucco-lingual diameter does not increase markedly towards the base. As the distal side is visible, it is possible to notice the presence of a very small heel.

3. Third precanine (= third maxillary tooth, tooth number two according to Broom, Text-fig. 3 (3a- 3b- 3c- 3d- 3e)).

The third precanine is small, more or less conical and with a bucco-lingual diameter slightly smaller than the mesio-distal. The point curves slightly inwards. It is impossible to observe any detail of the damaged surface.

B. **Canine** (= fourth maxillary tooth, tooth not quoted by Broom, Text-fig. 4).

The canine was formerly completely covered with matrix. It is just erupting and the point barely reaches the alveolar border. Although the exact bucco-lingual diameter is impossible to measure, one notices that it is considerably smaller than the mesio-distal. The mesial and distal edges are equally sharp. The tip is smooth, but the remainder of the cutting edges are serrated. The lingual surface, the only one which it is possible to examine, shows four prominent smooth ridges.

C. **Postcanines** (Text-fig. 5, 6 and 7).

Ten very well differentiated postcanines are present. The anterior ones have a simple shape; the intervening ones have a complicated pattern; and the smaller posterior one, though looking like the intervening ones, is more rudimentary.

1. First postcanine (= fifth maxillary tooth, tooth number three according to Broom, Text-fig. 5 (1a- 1b- 1c- 1d- 1e)).

The first postcanine is 'caniniform', much resembling the second precanine. It is elliptic in section with strongly pronounced sharp mesial and distal edges. (The main cusp of the other postcanines, when preserved, has sharp but not so pronounced edges.) The distal edge is marked by small serrations and is followed by a bulge or heel. The tip is directed inward and backward. The buccal surface as well as the lingual surface are marked by fine grooves.

2. Second postcanine (= sixth maxillary tooth, tooth number four according to Broom, Text-fig. 5 (2a- 2b- 2c)).

The second postcanine is broken, but the lower part of the crown and the small heel are present. This tooth, when complete, must have had the same pattern as the first postcanine.

3. Third postcanine (= seventh maxillary tooth, tooth number five according to Broom, Text-fig. 5 (3a- 3b- 3c- 3e)).

The third postcanine is also broken, but at a lower level than the second postcanine. The part which is left is more elongated mesio-distally than the former tooth; it does not show any start of cingulum, but some slight marks of tiny cusps suggests that the shape of this third postcanine was perhaps intermediate between that of the caniniform preceding tooth and that of the molariform following ones.

4. Fourth postcanine (= eighth maxillary tooth, not mentioned by Broom).

The fourth postcanine is an erupting tooth still deeply enclosed in the socket. Only the main cusp, the distal cusp and two distal cingular cusps could be shown. However, this is enough to make one notice that the fourth postcanine is 'molariform'.

5. Fifth postcanine (= ninth maxillary tooth, tooth number six according to Broom, Text-fig. 6 (1a- 1b- 1c- 1d- 1e)).

The fifth postcanine is nearly cylindrical with subequal bucco-lingual and mesio-distal diameters. The crown is relatively high and the neck slightly indicated. Seen in lateral (= buccal) view, it appears tricuspidate with a small cusp preceding and following the main strong cusp. The distal edge of the latter is serrated. The tip is slightly directed inward and the lingual surface presents some small grooves and ridges. On the lingual side of the tooth, a well developed cingulum bears four cusps of different size. The first buccal cusp and the first cingular one are separated by a small cingular crest. The second cingular cusp is more important than the first, itself bigger than the fourth; the third is very small.

6. Sixth postcanine (tenth maxillary tooth,

tooth number seven according to Broom, Text-fig. 6 (2a- 2b- 2c)).

The sixth postcanine is an erupting tooth which resembles the fifth in being tricuspidate in lateral view, with a small cusp on either side of the main strong one—the main cusp (of which the distal edge is serrated as in the former tooth), the distal cusp and only the tip of the mesial cusp are visible out of the socket. The cingulum is here more complex than in the fifth postcanine, showing four well developed cusps—of which the second is bigger than the third, itself more important than the subequal first and fourth—followed by a small crest and two rudimentary cusps.

7. Seventh postcanine (eleventh maxillary tooth, tooth number eight according to Broom, Text-fig. 6 (3a- 3b- 3c)).

The seventh postcanine is a large tooth with the mesio-distal diameter of the crown larger than that of the root, and with a clear neck. As in the preceding teeth, there are three buccal cusps; the tip of the main one is broken off. In addition, there are four cingular cusps: three important ones—of which the second is bigger than the third, itself more developed than the first—followed by a small crest and a tiny cusp.

8. Eighth postcanine (twelfth maxillary tooth, tooth number nine according to Broom, Text-fig. 7 (1a- 1b- 1c- 1d- 1e)).

The eighth postcanine has a very well marked neck and presents, as the others, three buccal cusps, of which the main one is the central. The distal edge of this cusp being damaged, only the beginning of the serrations is visible near the tip. The second in size is the distal, behind which part of the cingulum is visible in lateral view. This cingulum is the most complicated of those observed on *Cyrbasiodon*'s postcanines: it presents six well formed cusps—which are quoted here according to decreasing size: third, fourth, first, fifth, sixth and second—and a seventh rudiment-

Table of measurements of the maxillary teeth of *Cyrbasiodon boycei* (in mm)

number of the tooth on the maxilla	Interpretation	ϕ v – l		ϕ m – d		h. crown	h. out of the alveola	h. of the main cusp.
		neck	max. crown	neck	max. crown			
1	Precanine						3,0	–
2	Precanine						4,5	–
3	Precanine						2,7	–
4	Canine	–	–	–	–	–	(–)	–
5	caniniform postcanine	–	2,1	2,1	2,2	2,4	3,8	–
6	? postcanine	2,1	2,1	2,0	2,3	–	–	–
7	? postcanine	2,0	–	2,2	2,5	–	–	–
8	molariform postcanine	–	–	–	–	–	(–)	–
9	molariform postcanine	2,0	2,1	2,2	2,3	3,2	5,0	1,8
10	molariform postcanine	–	2,3	–	2,4	–	1,8	1,8
11	molariform postcanine	2,1	2,2	2,1	2,6	(3,0)	(4,0)	–
12	molariform postcanine	2,0	2,3	2,2	2,6	2,8	3,0	1,3
13	molariform postcanine	1,7	1,9	1,9	2,1	–	–	–
14	molariform postcanine	1,5	1,5	1,8	1,9	–	–	–

h= height
ϕ m – d = mesio-distal diameter
ϕ v – l = vestibulo-lingual diameter
(–) = inside the alveola
( ) = measure reconstructed
max. crown = maximal diameter of the crown

ary one at the foot of the distal buccal cusp. The third cusp presents mesially and distally a small cusp.

9. Ninth postcanine (thirteenth maxillary tooth, tooth number ten according to Broom, Text-fig. 7 (2a- 2b- 2c)).

The ninth postcanine shows a crown well delimited by a neck, but as it is broken at a fairly low level, no detail of the cusp pattern is available.

10. Tenth postcanine (fourteenth maxillary tooth, tooth number eleven according to Broom, Text-fig. 7 (3a- 3b- 3c- 3d- 3e)).

The tenth postcanine is a small rudimentary tooth, of which the main cusp is partly broken. Apart from the main cusp, only the distal cingular one is well developed; the mesial one and the cingulum are rudimentary.

III—INSERTION OF THE TEETH IN THE SOCKETS AND TOOTH-REPLACEMENT

As stated above, the removal of the matrix has permitted the author to observe the pits for the replacing teeth and the *sulcus alveolaris interior* (= longitudinal groove) which, according to Crompton, 1962, p. 238, "probably supported the dental lamina", and *ibid.*, 1963 b, p. 481. The pits are lingual and distal to the corresponding sockets.

A. Precanines

The first precanine is small, with its lingual pit not completely closed and still communicating with the socket. The second precanine is high, with a closed socket and a separated small pit lingually to it. The third one is small, without any visible lingual pit, and appears to be older than the first precanine. However, the second precanine appears to be the oldest as the process of its replacement has already started.

B. Canine

The canine is in process of eruption, and has not yet emerged from its socket, but its tip is not far from the edge of this socket. This latter is wide open and still connected to the longitudinal groove by the remnant of the pit.

C. Postcanines

The first postcanine is still young: it is nearly completely grown but there is still a remainder of its pit on the lingual side. The second postcanine is a well grown tooth with alveolar bone up to the neck. A new pit is situated lingually to it. The third postcanine is also a mature tooth, loose in its socket and moved forward during the process of fossilisation; there is a disto-lingual pit to it. The fourth one is in process of replacement; the new tooth is still lingual to the socket, inside the pit. The fifth postcanine is a very old tooth, not far from falling out; it is fairly loose and its crown has reached a much more ventral level than any of the others; there is a very wide pit disto-lingually to it. The sixth postcanine is a young erupting tooth with only half of the crown out of the socket—this latter being still connected to the *sulcus* by means of an open pit. The seventh postcanine is a well grown tooth with an important pit. The eighth one is a nearly mature tooth without pit. The ninth postcanine, though small in size, seems to have been well grown, with a new lingual pit larger than that of the seventh postcanine. The tenth is a small tooth with its socket still connected to the groove by the remainder of its pit.

The alternation within the postcanine row is clearly noticeable here. The odd series, as a whole, is older than the even. The teeth of the odd series are all grown and they all, but the first, present a new pit for a replacing tooth. The even series has some of its members still in the sockets or only just protruding. The sequence within each series has been summarised by Romer, in 1961, p. 23: "If in either odd or even series we pick out an empty alveolus or young tooth and proceed backward, we find that successive teeth are more and more mature, and then show resorption preliminary to being shed; following this, we may find another alveolus or young tooth, and repeat the sequence . . .". This is peculiarly easy to observe within the even series: after the second old postcanine, the fourth postcanine is still in the socket, the sixth postcanine half erupted and the eighth is completely so, the tenth postcanine is again a new tooth, but more mature than the fourth. In the odd series, the first postcanine is younger than the third, itself younger than the fifth; then the sequence is repeated as the seventh postcanine is younger than the ninth and both are younger than the fifth. Some teeth of both series were in use simultaneously, probably in the caniniform set as well as in the molariform set.

In each odd or even series, the more mature teeth are the back ones, so the situation corresponds to a "back to front sequence of tooth eruption". This agrees with Crompton's quotation (1962, p. 239) of the existence of a wave of replacement passing "from back to front along each alternately numbered series" in "early *Cistecephalus*-zone cynodonts" (Crompton, unpublished MS.) and other early therapsids (Romer and Price 1940).

DISCUSSION

I—HISTORY

The taxonomical position of *Cyrbasiodon boycei*, as quoted above (cf. p. 51) and in a former publication (Mendrez, 1967, p. 430—432), varies according to the different authors.

Broom, 1931, p. 164, considers *Cyrbasiodon* as "most probably a primitive cynodont", but later (1932, p. 77) as "possibly belonging to the Scaloposauridae".

Parrington, in 1936 (p. 137) suggests that it is "probably a related form" to *Parathrinaxodon proops*, a cynodont.

Von Huene (1940, p. 257) places *Cyrbasiodon* amongst the cynodonts.

In 1949, Broom (p. 189) adopted a position intermediate to those of 1931 and 1932, in regarding *Cyrbasiodon* as a "cynodontoid therocephalian".

In the "Bibliographical list of Reptilia from the Karroo beds of Africa", Haughton and Brink (1954, p. 142–143) place *Cyrbasiodon* within the Scaloposauridae but specify that it is "doubtfully a scaloposaurid".

Crompton (1955, p. 162) thinks that *Cyrbasiodon* can possibly be included in the Scaloposauridae–group C, because of its cusped postcanine teeth.

In 1956, Watson and Romer, in a "Classification of therapsid reptiles" place it in the family Ericiolacertidae.

Lehman (1961, p. 259) keeps this taxonomical position but remarks that: "the appartenance of this fossil to the Ericiolacertidae and even to the bauriamorphs is doubtful".

In 1961 (p. 43) Romer noted that *Cyrbasiodon* is presumably related to *Ericiolacerta.*

In 1966 (1967, p. 432) Mendrez places it amongst the Cynodontia Procynosuchidae and quotes that it can be favourably compared to *Leavachia* on the grounds of the aspect of the secondary palate and of the morphology of the teeth.

II–COMPARISON WITH OTHER PROCYNOSUCHIDS

The other procynosuchids which, for the moment, appear closest to *Cyrbasiodon* are *Leavachia* and *Parathrinaxodon.*

Leavachia: the different specimens of *Leavachia* all come from the *Cistecephalus*-zone of South Africa (from the top of that zone according to Kitching, personal communication, February 1966, now called *Daptocephalus*-zone cf. Kitching 1970). *Leavachia* is considered to be a Cynodont Procynosuchid by Watson and Romer (1956, p. 62–63) as well as by Haughton and Brink (1954, p. 155) and this is followed in later classifications. (Specimens from the collection of the Bernard Price Institute for Palaeontological Research, Johannesburg, the Rubidge collection, Graaff-Reinet, and the collection of the National Museum, Bloemfontein, South Africa.)

Parathrinaxodon: the type and only known specimen comes from the Lower Bone Bed (K6 of Songea Series) of Stockley site B 19, or Kawinga formation cf. Charig 1963, Ruhuhu Valley, Tanzania. The Lower Bone Bed is usually considered equivalent to the *Cistecephalus*-zone of South Africa. (Accidentally, von Huene, 1950, p. 131, places *Parathrinaxodon* amongst the Manda Beds fossils, which has been considered by Haughton, 1932, p. 668, and Stockley, 1932, p. 618, as equivalent to the Molteno Beds of South Africa.) (Collection of University Museum of Zoology, Cambridge, England.)

A. Secondary bony palate

In lateral view, the general pattern of the maxilla, as described above, agrees with that of *Leavachia* (cf. Brink, 1963, fig. 10) with a maximum height almost reached before mid-length and a long slope of its posterior edge. In *Parathrinaxodon,* the maximum height is reached only at mid-length and the posterior slope is more abrupt (cf. Parrington, 1936, fig. 7A). However incomplete, the palatal process of *Cyrbasiodon*'s maxilla (Text-fig. 2, 8) matches quite well with that of *Leavachia* (Text-fig. 9), the difference lying in the more narrow anterior part of *Cyrbasiodon*'s palatal process. This would correspond to a palate more open anteriorly. If a separate fragment of bone *(fra. Pal* Text-fig. 2) has been correctly interpreted, the posterior part of *Cyrbasiodon*'s bony palate was nearly as closed as that of *Leavachia.* The situation in *Parathrinaxodon* is very similar to this, though the palate is almost completely closed. It is interesting to note that the closed part of the palate is the posterior and that a 'slit' remains at the level of the canines and the first postcanines: in the process of closing the palate, the known procynosuchids appear to proceed from back to front. (See also p. 58).

B. Teeth

1. Morphology and number.

The number and pattern of *Cyrbasiodon*'s teeth integrate themselves also in the "*Leavachia-Parathrinaxodon* context".

As far as the number of maxillary teeth are concerned, the only difference lies in the number of precanines: three in *Cyrbasiodon,* two in *Leavachia,* none in *Parathrinaxodon.*

The pattern of the teeth is also very similar, as can be seen for precanines (*Cyrbasiodon,* Text-fig. 3, *Leavachia* Text-fig. 10), anterior postcanines (*Cyrbasiodon* Text-fig. 5, *Leavachia* Text-fig. 11 (1–2) and *Parathrinaxodon* in Parrington 1936, fig. 9A) and posterior postcanines (*Cyrbasiodon* Text-fig. 6 and 7, *Leavachia* Text-fig. 11 (3) and 12 and *Parathrinaxodon* in Parrington 1936, fig. 9 B–C–D). In both former genera the precanines are simple, unicuspidate and can present a small posterior 'heel'. The anterior postcanines are also simple, unicuspidate, but present a stronger heel. It is interesting to note that the second postcanine of a small *Leavachia* is more

complicated than that of bigger specimens; it is molariform as are the postcanines in the small specimen B.P.I. No. F.1559/M.354, Text-fig. 12(1a–b), but is caniniform in the bigger specimens, B.P.I. No. F 226A/M.8A, Text-fig. 11(1). This confirms that in procynosuchids the pattern of an identically placed postcanine varies with the generation to which it belongs, but more specimens are needed before comparing the tooth replacement of procynosuchids to that of *Thrinaxodon* described by Osborn J. W. in 1970 (pers. comm.). These features as well as a serrated posterior edge (*Cyrbasiodon* Text-fig. 5 (1a- b- c- d- e), *Leavachia* first right postcanine of R.C. No. 92 and No. 304) can also be observed on *Parathrinaxodon*: "they are slightly compressed and spear-shaped with a single cusp, the posterior border swelling out and having a crenulated edge running down towards the tip" (Parrington, 1936, p. 135). The posterior postcanines are more complicated, usually tricuspidate in lateral view, but sometimes part of the cingulum is visible too (*Cyrbasiodon* Text-fig. 7 (lb.), *Leavachia* Text-fig. 12 (7b)), as one cusp is intermediate between the cingular set proper and the buccal row. These postcanines are "bounded medially, well below the level of the main cusps, by a cingulum bearing a series of smaller cusps" (Romer, 1961, p. 43)[1]. "The number and size of the cingular cusps vary with the situation of the postcanine on the maxilla" and probably also "with the generation to which it belongs" (Mendrez, 1966, p. 432). The main cusp is ornamented, with slight grooves and ridges (*Cyrbasiodon* Text-fig. 6 and 7, *Leavachia* Text-fig. 12 (1a–1b)) and serrations on the distal edge (*Cyrbasiodon* Text-fig. 6 and 7, *Leavachia* Text-fig. 12 (lb). On a posterior postcanine of *Parathrinaxodon*, "in outer view are seen the remains of a large central cusp with a small accessory cusp on either side. Internally there is a cingulum which carries a small accessory cusp anteriorly and apparently also a second accessory cusp posteriorly, but this latter was broken off and left in the matrix when the crown was removed" (Parrington *op. cit.* p. 135). Between the places of these two cusps, the cingulum is broken, so that the probable other cingular cusps cannot be observed.

In section, the canines of these three genera appear flattened buccolingually. Further comparison is impossible at the moment: *Cyrbasiodon's* canine presents serrations on both anterior and posterior edges (Text-fig. 4); we do not know yet of any serrations on *Leavachia*'s canines, but this might be due to their bad state of preservation. The right canine (the left is missing) of *Parathrinaxodon* is "oval in shape" (Parrington *op. cit,* p. 135) but, as it is "badly damaged", its structure is unknown.

2. Replacement.

Crompton's assertion of the existence of a wave of replacement passing "from back to front along each alternate numbered series" in "early *Cistecephalus*-zone cynodonts" has been quoted above and the specimens of *Leavachia* and *Cyrbasiodon* fit in that description. Even and odd series have been also recognised in *Parathrinaxodon* (Parrington *op. cit.*, p. 135) but the back to front replacement has not been quoted because of the bad preservation of the tooth rows.

CONCLUSION

At present, *Cyrbasiodon* seems to fit fairly well with what is known of the procynosuchids. The comparison with *Leavachia* and *Parathrinaxodon* leads to the table on p. 58.

We are faced with the following alternatives: either the breadth of the palatal process of the maxilla and the number of precanines vary within a genus and then *Cyrbasiodon* could be included in the genus *Leavachia* as suggested in an earlier paper (Mendrez 1966, p. 432); or these two elements are stable within the same genus and then *Cyrbasiodon* differs from *Leavachia* in retaining characters which appear more primitive such as a more open secondary palate and a higher number of precanines. If the second element of the alternative is to be retained, *Cyrbasiodon, Leavachia* and *Parathrinaxodon* would show different stages of evolution of procynosuchids; *Parathrinaxodon* presenting more mammal-like characteristics: the secondary palate nearly completely closed and the canine being the first tooth of the maxilla. However, filiation between these three genera is out of the question as they appear, for the moment, contemporary; the most primitive

[1] This description, which appears to apply to the lower postcanines of procynosuchids (cf. Eloff, 1970, fig. 17 A, eighth right lower postcanine of Bloemfontein National Museum No. C.27) as well as to the upper ones, does fit also these of the ictidosaurian *Diarthrognathus.* There is a striking resemblance between the pattern of procynosuchid postcanines and that of those of *Diarthrognathus* (cf. paratype in Bloemfontein National Museum No. C.249, first right lower postcanine–personal observation–and posterior lower postcanines in Crompton (1963a, Plate I fig. C). Behind the distal buccal cusp of the first right lower postcanine, part of the cingulum is visible in lateral view, as on the eighth postcanine of *Cyrbasiodon* (Text-fig. 7 (lb)) and the sixth right postcanine of *Leavachia* (Text-fig. 12 (7b)); however, that tooth shows, on the medial and main buccal cusps, wear-facets which have not been observed in procynosuchids.

		Cyrbasiodon South Africa *Daptocephalus* or *Lystrosaurus* Zone	*Leavachia* South Africa Upper part of *Cistecephalus s. l.* =*Daptocephalus* Zone	*Parathrinaxodon* East Africa Lower Bone Bed (= Kawinga Formation) of Tanzania = ? *Cistecephalus* Zone *s.s.*
Palatal processes of Maxilla	anterior part	fairly well apart	closer than in *Cyrbasiodon*, but still separated from the vomer by a slit on each side.	only separated by a median narrow slit.
	posterior part	fairly close	fairly close	joined
Teeth	precanines	3	2	0
	canine	1	1	1
	postcanines	10	7 to 12	11

one—*Cyrbasiodon*—might even be more recent (cf. Kitching, *op. cit. in* p. 51).

These three genera have their secondary palate more closed posteriorly than anteriorly: the process of closing the palate seems to have been in the known procynosuchids from back to front. In the opposite, the therocephalians appear to have a secondary palate progressing from front to back. Some (the whaitsiids) even have a secondary bony palate at the level of the canine and later strengthen the posterior part of the primary palate.

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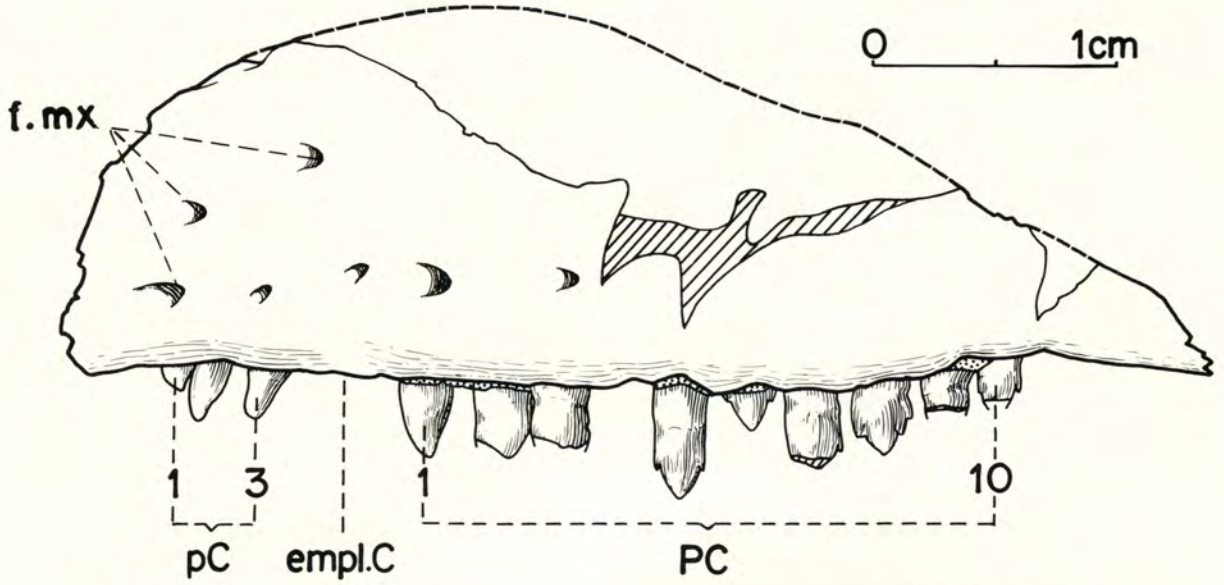
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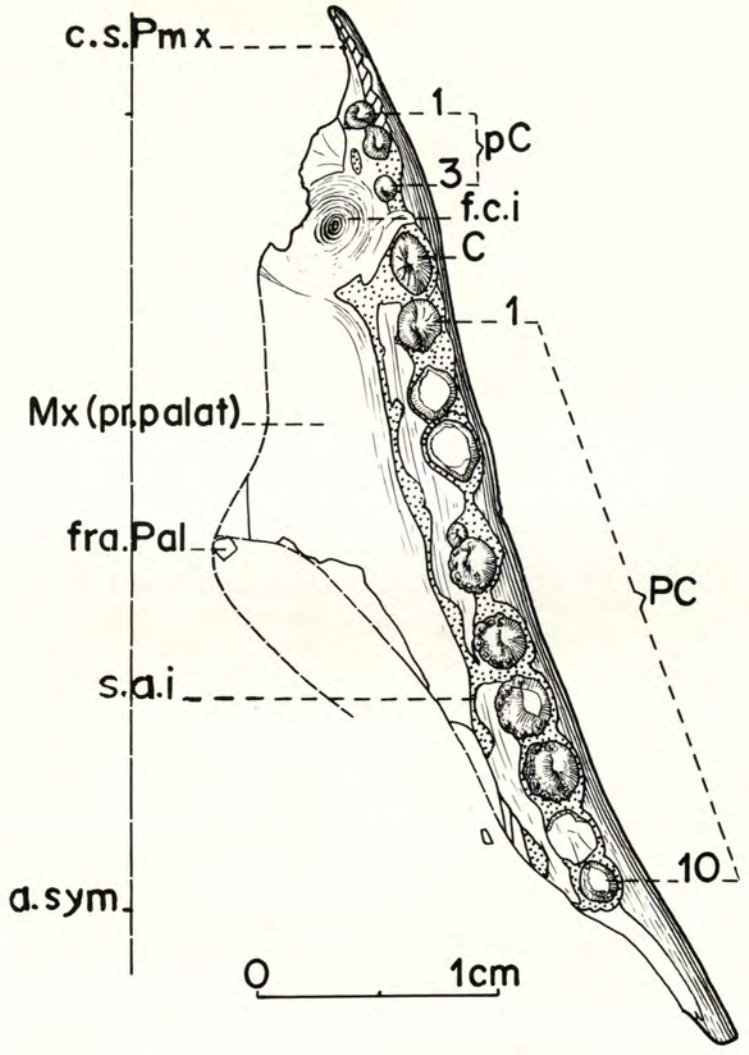
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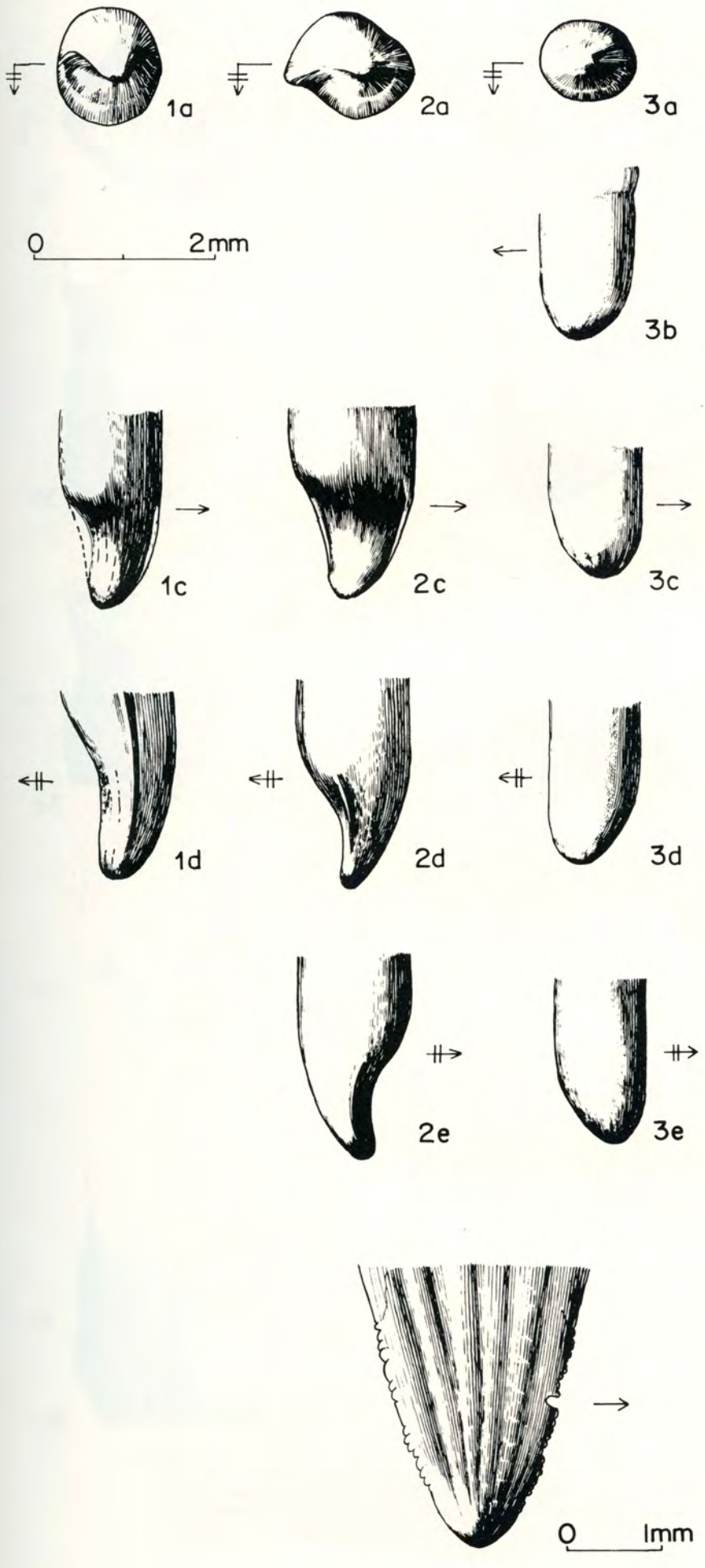
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Text-fig. 1. *Cyrbasiodon boycei*—Lateral view of left maxilla (X 3). *empl. C*, emplacement of the canine; *f. mx*, maxillary foramina; *PC*, postcanines; *pC*, precanines.



Text-fig. 2. *Cyrbasiodon boycei*—Ventral view of left maxilla (X 3). *a. sym.* axis of symmetry; *C*, canine; *c. s. Pmx*, contact surface on the maxilla for the premaxilla; *f. c. i*, fossa for the lower canine; *fra. Pal*, fragment of palatine; *Mx (pr. palat)*, palatal process of the maxilla; *PC*, postcanines; *pC*, precanines; *s. a. i*, *sulcus alveolaris interior*.

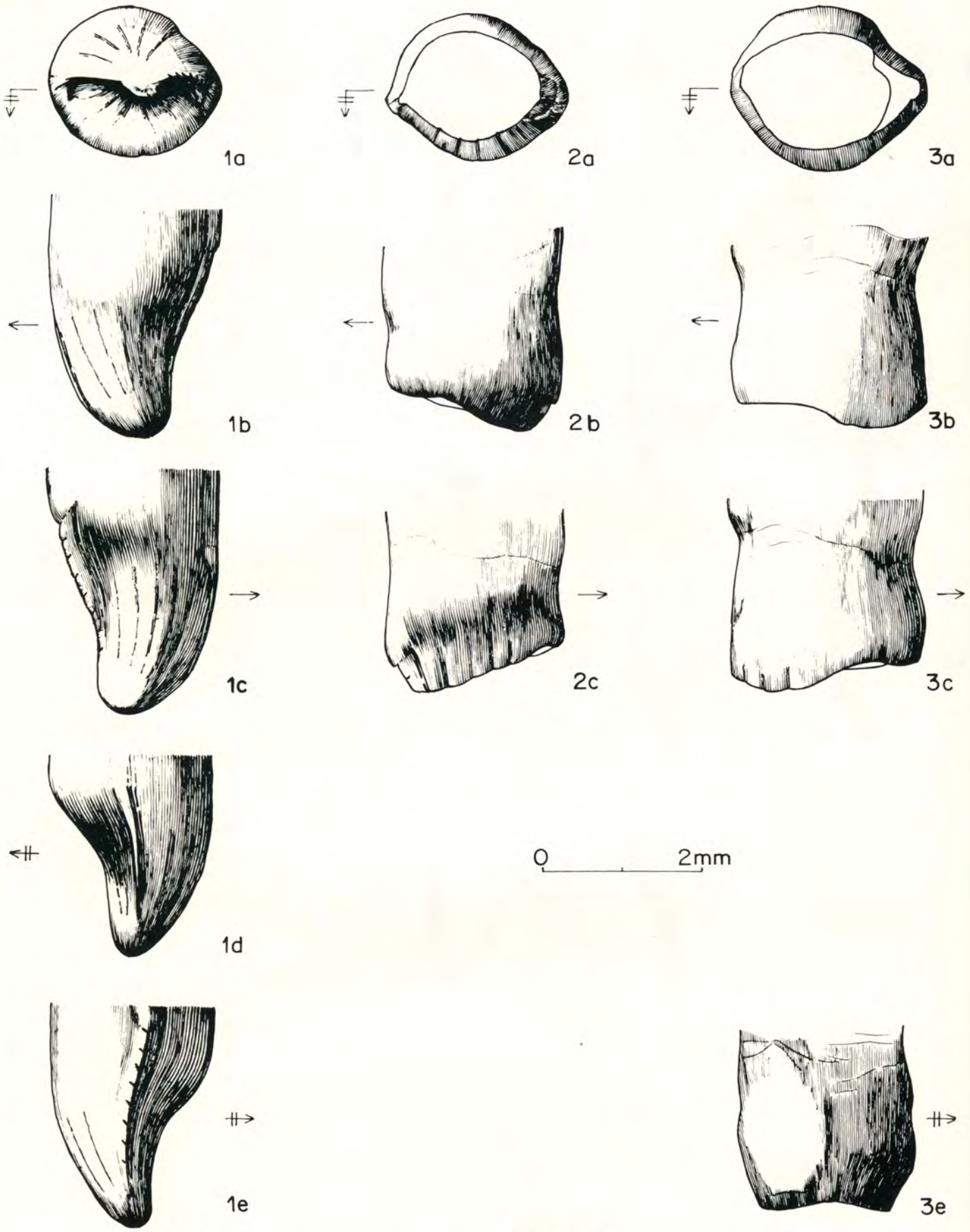


Text-fig. 3.

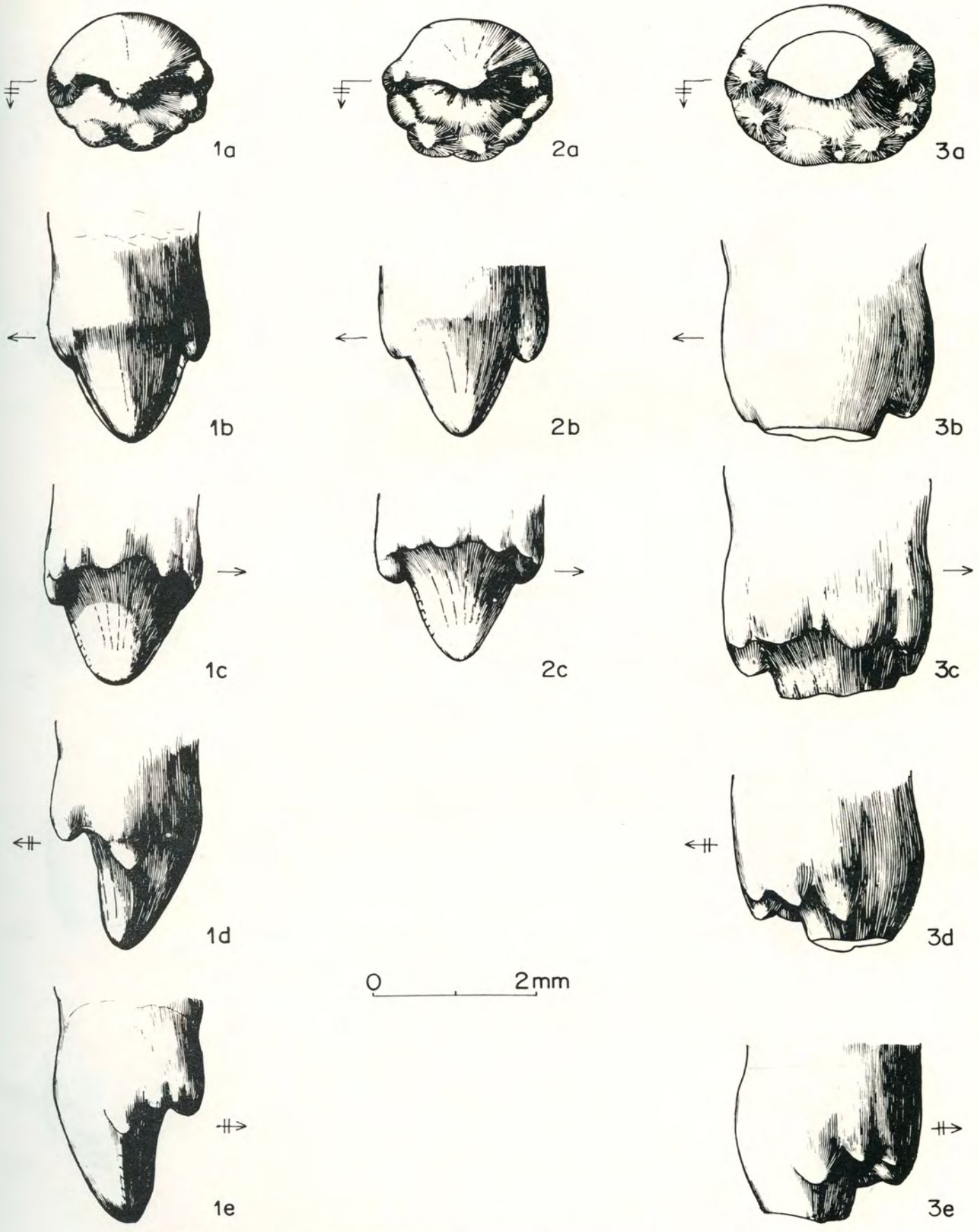
Cyrbasiodon boycei—precanines (X 14). 1, first precanine = first maxillary tooth, not quoted by Broom; 2, second precanine = second maxillary tooth = tooth number 1 according to Broom; 3, third precanine = third maxillary tooth = tooth number 2 according to Broom. *a*, occlusal face; *b*, buccal face; *c*, lingual face; *d*, mesial face; *e*, distal face.

Text-fig. 4.

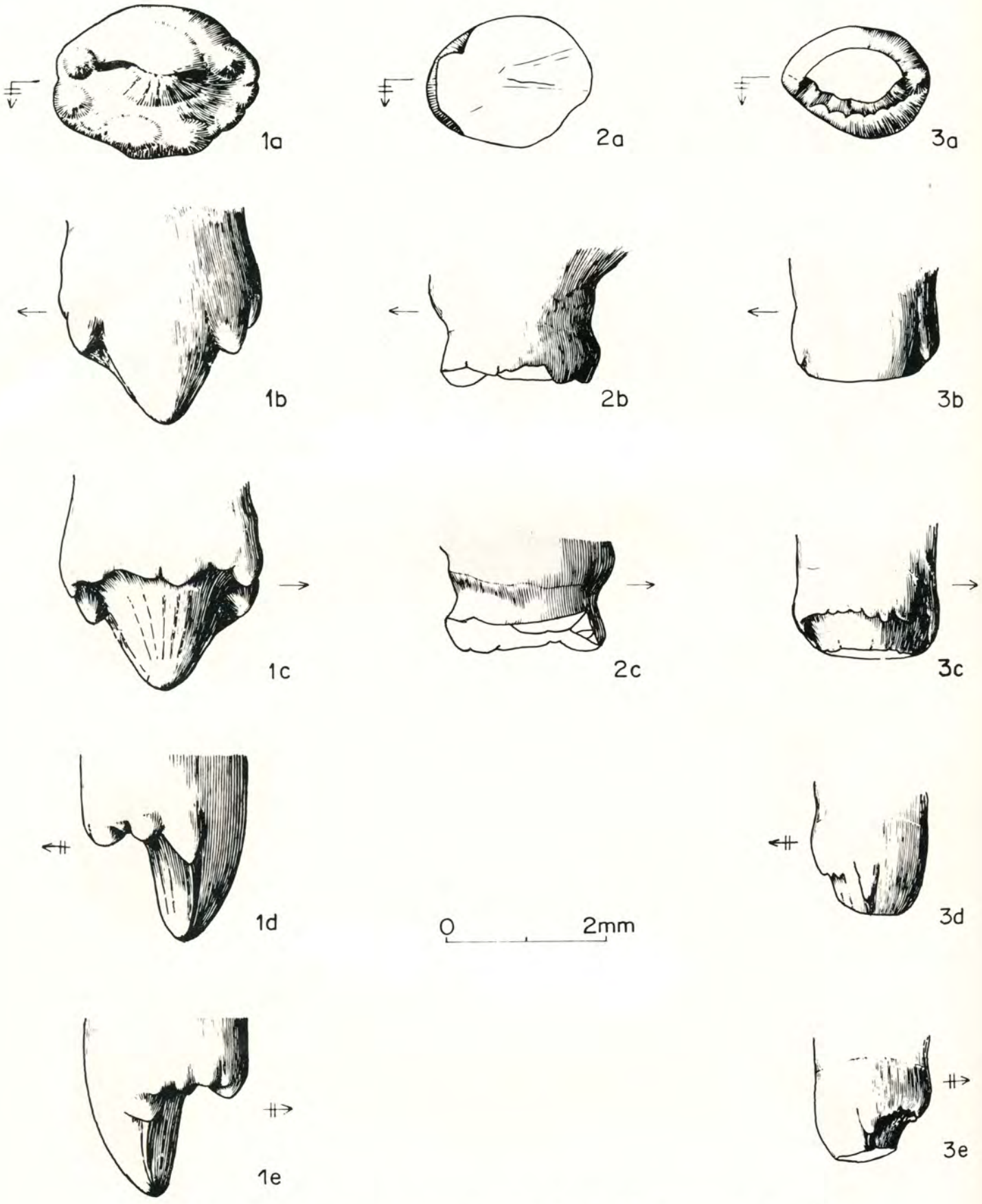
Cyrbasiodon boycei—canine (X 14) = fourth maxillary tooth, not quoted by Broom. Lingual face.



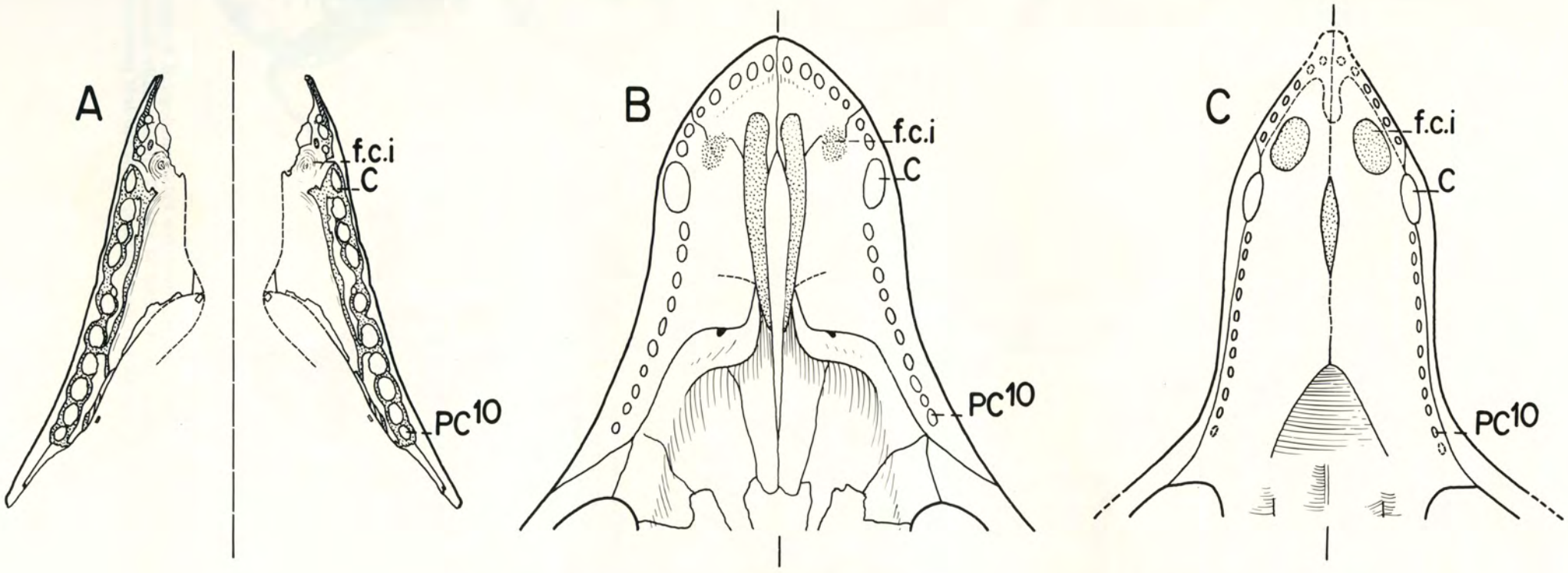
Text-fig. 5. *Cyrbasiodon boycei*—postcanines (X 14). 1, first postcanine = fifth maxillary tooth = tooth number 3 according to Broom; 2, second postcanine = sixth maxillary tooth = tooth number 4 according to Broom; 3, third postcanine = seventh maxillary tooth = tooth number 5 according to Broom; *a*, occlusal face; *b*, buccal face; *c*, lingual face; *d*, mesial face; *e*, distal face.



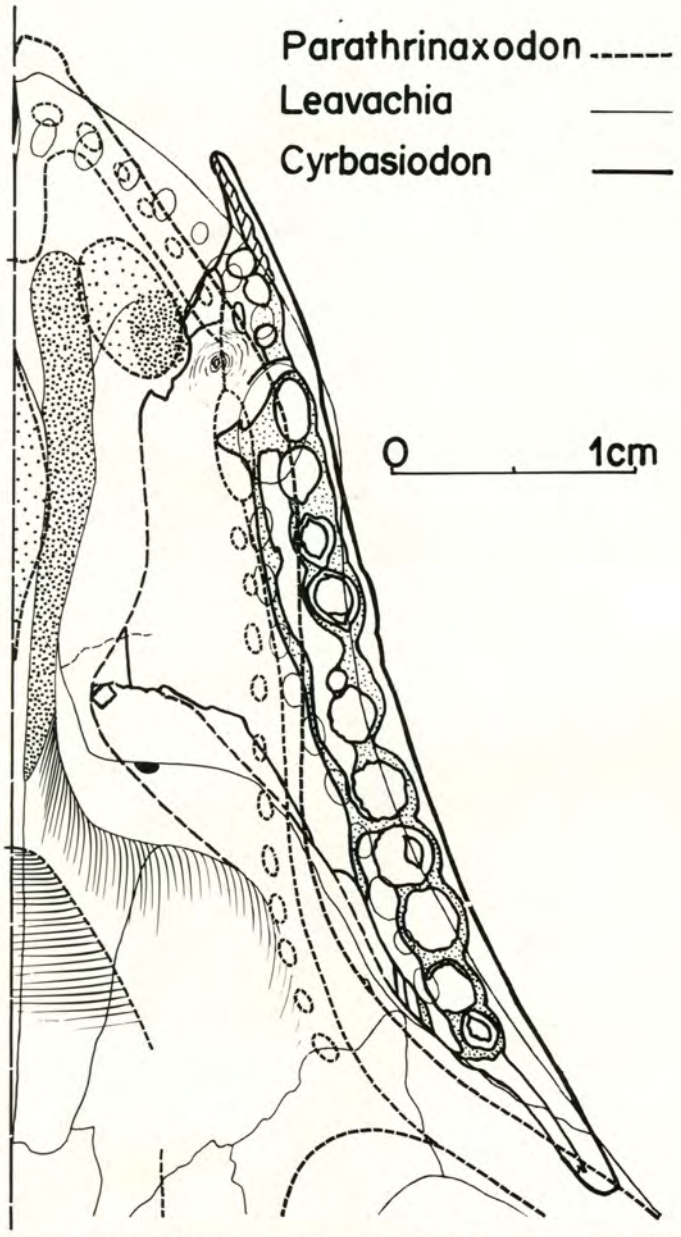
Text-fig. 6. *Cyrbasiodon boycei*—postcanines (X 14). 1, fifth postcanine = ninth maxillary tooth = tooth number 6 according to Broom; 2, sixth postcanine = tenth maxillary tooth = tooth number 7 according to Broom; 3, seventh postcanine = eleventh maxillary tooth = tooth number 8 according to Broom; *a*, occlusal face; *b*, buccal face; *c*, lingual face; *d*, mesial face; *e*, distal face.



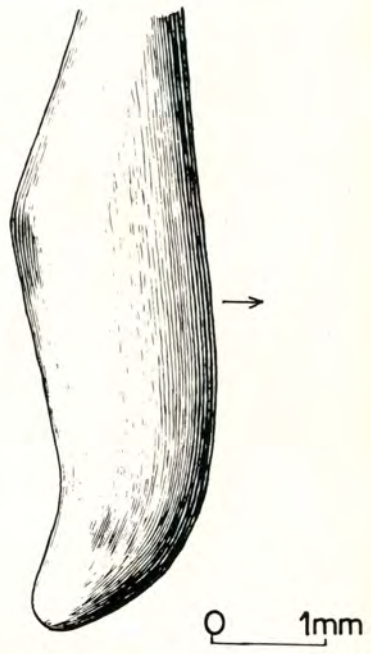
Text-fig. 7. *Cyrbasiodon boycei*—postcanines (X 14). 1, eighth postcanine = twelfth maxillary tooth = tooth number 9 according to Broom; 2, ninth postcanine = thirteenth maxillary tooth = tooth number 10 according to Broom; 3, tenth postcanine = fourteenth maxillary tooth = tooth number 11 according to Broom; *a*, occlusal face; *b*, buccal face; *c*, lingual face; *d*, mesial face; *e*, distal face.



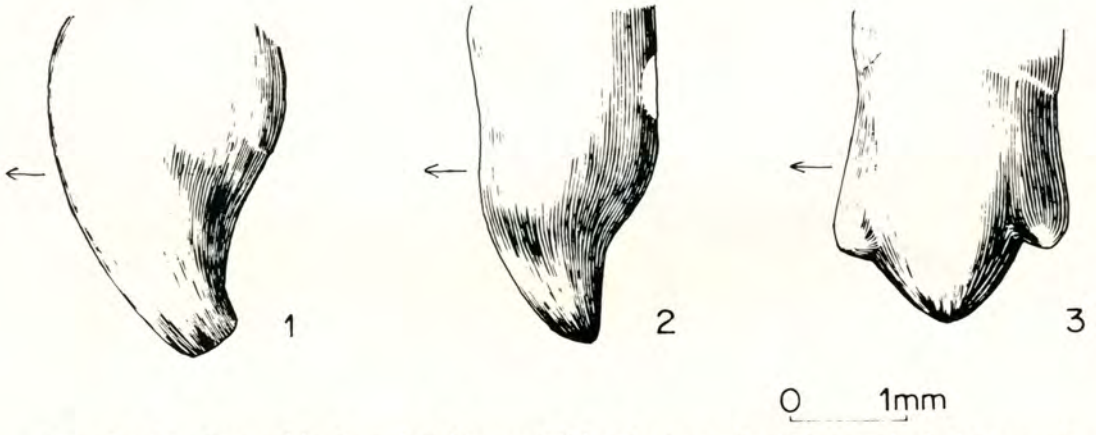
Text-fig. 8. *A, Cyrbasiodon; B, Leavachia; C, Parathrinaxodon;* ventral views of palate (no proper scale). *Leavachia* (Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa, no. F.3748/M.357) after Brink, 1963, fig. 10B. *Parathrinaxodon* (University Museum of Zoology, Cambridge, England) after Parrington, 1936, fig. 8.



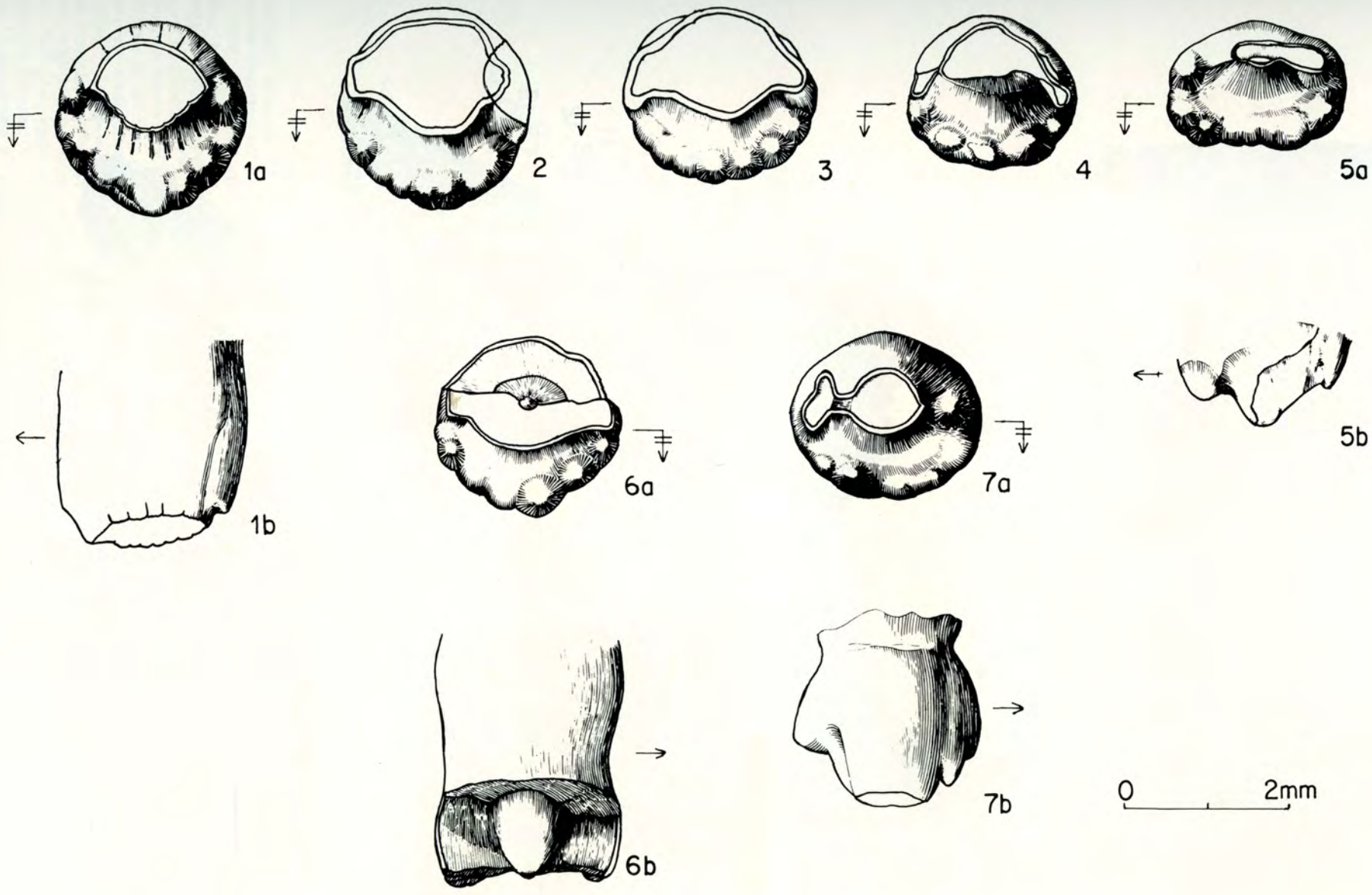
Text-fig. 9. Heavy continuous line, *Cyrbasiodon;* light continuous line, *Leavachia;* dashed line, *Parathrinaxodon*; Superposition of ventral views of palates (*Cyrbasiodon's* palate X 3; other palates brought to same size.) Specimens as in Text-fig. 8.



Text-fig. 10. *Leavachia* (Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa, no. F.591/M.234) third right precanine, buccal face (X 14).



Text-fig. 11. *Leavachia.* 1 and 3 (Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa, no. F.226B/M.8B); 2 (same collection no. F.226A/M.8A); 1 and 2, second left postcanines; 3, eighth left postcanine. (X 14).



Text-fig. 12. *Leavachia*, postcanines (X 14). (Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa, no. F.1559/M.354); 1, second left postcanine; 2, third left postcanine; 3, fourth left postcanine; 4, sixth left postcanine; 5, seventh left postcanine; 6, second right postcanine; 7, sixth right postcanine; *a*, occlusal face; *b*, buccal face.

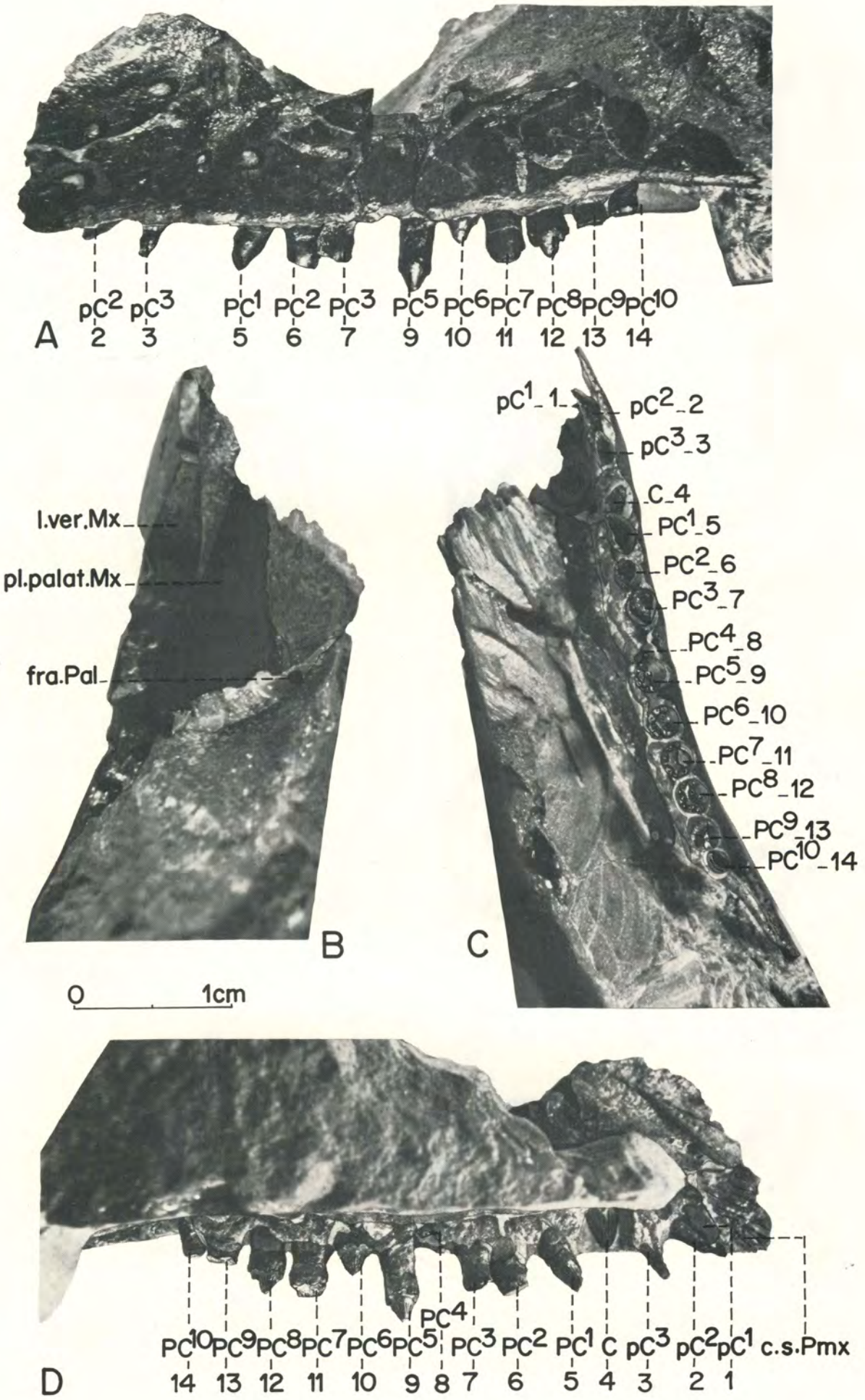

pC2 pC3 PC1 PC2 PC3 PC5 PC6 PC7 PC8 PC9 PC10
A 2 3 5 6 7 9 10 11 12 13 14
l.ver.Mx
pl.palat.Mx
fra.Pal
B
pC1_1
pC2_2
pC3_3
C_4
PC1_5
PC2_6
PC3_7
PC4_8
PC5_9
PC6_10
PC7_11
PC8_12
PC9_13
PC10_14
C
0 1cm
PC4
PC10 PC9 PC8 PC7 PC6 PC5 PC3 PC2 PC1 C pC3 pC2 pC1 c.s.Pmx
D 14 13 12 11 10 9 8 7 6 5 4 3 2 1

PLATE I

Cyrbasiodon boycei–Daptocephalus-zone of Bergville or *Lystrosaurus*-zone (not *Cistecephalus*-zone) of Bezuidenhout's Pass (South Africa), left maxilla (X. 2.7); *A*, lateral view; *B*, dorsal view; *C*, ventral view; *D*, medial view; *C–4*, canine = fourth maxillary tooth; *c. s. Pmx*, contact surface on the maxilla for the premaxilla; *fra. Pal*, fragment of palatine; PC^1*–5*, first postcanine = fifth maxillary tooth = tooth number 3 according to Broom; PC^2*–6*, second postcanine = sixth maxillary tooth = tooth number 4 according to Broom; PC^3*–7*, third postcanine = seventh maxillary tooth = tooth number 5 according to Broom; PC^4*–8*, fourth postcanine = eighth maxillary tooth; PC^5*–9*, fifth postcanine = ninth maxillary tooth = tooth number 6 according to Broom; PC^6*–10*, sixth postcanine = tenth maxillary tooth = tooth number 7 according to Broom; PC^7*–11*, seventh postcanine = eleventh maxillary tooth = tooth number 8 according to Broom; PC^8*–12*, eighth postcanine = twelfth maxillary tooth = tooth number 9 according to Broom; PC^9*–13*, ninth postcanine = thirteenth maxillary tooth = tooth number 10 according to Broom; PC^{10}*–14*, tenth postcanine = fourteenth maxillary tooth = tooth number 11 according to Broom; pC^1*–1*, first precanine = first maxillary tooth; pC^2*–2*, second precanine = second maxillary tooth = tooth number 1 according to Broom; pC^3*–3*, third precanine = third maxillary tooth = tooth number 2 according to Broom; *pr. palat. Mx*, palatine process of the maxilla.

Palaeont. afr., **14**. 71–85. 1972

A REVISED CLASSIFICATION OF CYNODONTS (REPTILIA; THERAPSIDA)

by

* James A. Hopson and †James W. Kitching

INTRODUCTION

Cynodonts are very advanced mammal-like reptiles of the Permo-Triassic which are of special interest to evolutionists because they gave rise to the Class Mammalia during Middle or Late Triassic time. Cynodonts have been known from strata of Early Triassic age in South Africa for over one hundred years, and numerous specimens have been collected and described. In recent years the record of cynodonts has been extended into earlier and later time zones, not only in southern Africa, but in East Africa, South America, Russia, China, and, most recently, in North America. Much of the material from outside of Africa has not yet been fully described.

Approximately 125 species of cynodonts (including ictidosaurs and tritylodonts, herein considered to be cynodonts) have been named. Of these, however, only a very small handful has been adequately characterized so that any one species can be reliably distinguished from all others. As a result of the taxonomic confusion which prevails in the Cynodontia, our knowledge of the patterns of evolution within the group is based on detailed knowledge of a few species.

The stimulus for the present revised classification of cynodonts was an extended research visit to the Bernard Price Institute for Palaeontological Research by the senior author in late 1971. The purpose of the visit was to study primitive cynodonts, but all available cynodont material in this and many other South African museums was examined.†† The junior author has also studied most of the cynodont material in South Africa as part of a revision of the stratigraphy and vertebrate fauna of the Beaufort Series. Many of the taxonomic conclusions independently reached by the two authors have proven to be identical, though based in great part on different evidence. Because of the large amount of overlap in our work, we have decided to publish our taxonomic conclusions as a joint report, reserving for separate future papers the presentation of the detailed evidence upon which these conclusions are based. For the sake of completeness, the senior author has reviewed the non-South African cynodonts, though many of the taxonomic judgments on these forms are less securely based than are the judgments on the South African cynodonts. The revision of the family Tritylodontidae is based on the senior author's unpublished studies.

We wish to thank the following colleagues for access to unpublished information which has been incorporated into this paper: Dr. J. F. Bonaparte, Fundacion Miguel Lillo, Tucumán, Argentina; Dr. A. W. Crompton, Museum of Comparative Zoology, Harvard University; and Mr. J. W. A. van Heerden, National Museum, Bloemfontein.

Several aspects of this classification require comment. In deciding whether to consider a generic or specific name to be valid, we have taken the position that the burden of proof is on the describer to convince us that the named taxon is distinct from earlier-named taxa. Where there is a reasonably high probability that two named taxa are synonymous, we have usually synonymized them, even though the evidence for their identity is not conclusive. We have done this because: (1) the cynodonts have been excessively split (as, in fact, have most therapsid groups), so that our first priority seemed to be the reduction of the confusing welter of inadequately-characterized genera and species to fewer, more adequately defined taxa; (2) many of the type specimens are fragmentary and poorly-preserved so that diagnostic characters are lacking; (3) where locality and stratigraphic data are available, it is evident that an excessive number of closely-related species have been named from very limited geographic areas and from within very narrow stratigraphic intervals. In those cases where taxa based on inadequate types could be reasonably synonymized with adequately-characterized species, we did so, but where inadequate types could not be so allocated we have chosen to declare the names on which they are based to be *nomina vana*.

The higher-level classification adopted here differs substantially from that used in most earlier classifications (e.g., Watson and Romer, 1956; Romer, 1966; Lehman, 1961; but see Haughton and Brink, 1954). We have abandoned separate infraordinal rank for the "Ictidosauria" (i.e., Tritheledontidae) and Tritylodontidae; instead they are listed as families within the Infraorder Cynodontia. These groups are clearly cynodont derivatives and we believe that their positions as

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†† This research was supported by a grant from the National Science Foundation.

advanced end-members of two major adaptive lines within the cynodont radiation are best indicated by incorporating them within the Cynodontia. Their respective positions as the culmination of the carnivorous and herbivorous rami of the cynodonts has been expressed in the classification by dividing the infraorder into two main groups at the level of superfamily. For the carnivorous group, we have adopted Brink's (1963) term *Cynognathoidea*; for the herbivorous group, we have chosen to use Simpson's (1928) term *Tritylodontoidea*. These choices were determined by: (1) familiarity of the root genera, *Cynognathus* and *Tritylodon* and (2) the fact that these genera represent extremes of specialization within their respective groups. The resulting classification, we believe, possesses the advantage of expressing both phyletic relationships and adaptive trends better than those classifications which place the cynodonts and their therapsid descendants in three infraorders (Cynodontia, Ictidosauria, and Tritylodontia). A similar sort of reclassification of other therapsid groups, notably of the therocephalian-bauriamorph assemblage, is also overdue.

INFRAORDER CYNODONTIA

SUPERFAMILY CYNOGNATHOIDEA Brink 1963.

Cynodonts in which the posterior postcanine teeth usually possess three or more cusps aligned in an anteroposterior row; a narrow lingual cingulum bearing several small cusps is frequently present, but only rarely is the cingulum expanded to form a broad lingual shelf; canines are usually well-developed; incisors are usually small and unspecialized. Most members are carnivorous. Included are primitive cynodonts of the Permian and earliest Triassic and all carnivorous cynodonts of the later Triassic.

FAMILY PROCYNOSUCHIDAE Broom 1948.

Includes: Silphedestidae Haughton and Brink 1954; Dviniidae Tatarinov 1968 a.

Primitive cynodonts with five or more incisors, small "precanine" maxillary teeth in front of the enlarged canine, and posterior postcanine teeth with a prominent lingual cingulum; the dentary is small, with a low coronoid process, no angle, and with the masseteric fossa restricted to the posterodorsal portion of the bone; palatal plates of the maxillae and palatines do not meet at the midline so that the secondary palate is incomplete; interpterygoidal vacuities usually present; ribs normal, lacking plate-like expansions.

Horizon: Upper Permian: *Daptocephalus* Zone, Beaufort Series, of South Africa; Zone IV of Russia; Kawinga Formation of Tanzania.

Genus *PROCYNOSUCHUS* Broom 1937.

Synonyms: ? *Cyrbasiodon* Broom 1931; *Paracynosuchus* Broom 1940a; *Mygalesaurus* Broom 1942; *Aelurodraco* Broom and Robinson 1948b; *Leavachia* Broom 1948; *Galeophrys* Broom 1948; *Galecranium* Broom 1948; *Silphedestes* Broom 1949; *Protocynodon* Broom 1949; *Silphedocynodon* Brink 1951; *Scalopocynodon* Brink 1961.

PROCYNOSUCHUS DELAHARPEAE Broom 1937.

Synonyms: ? *Cyrbasiodon boycei* Broom 1931; *Procynosuchus rubidgei* Broom 1938; *Paracynosuchus rubidgei* Broom 1940a; *Nanictosuchus melinodon* Broom 1940a; *Nanictosaurus robustus* Broom 1940b; *Mygalesaurus platyceps* Broom 1942; *Aelurodraco microps* Broom and Robinson 1948b; *Leavachia duvenhagei* Broom 1948; *Galeophrys kitchingi* Broom 1948; *Galecranium liorhynchus* Broom 1948; *Silphedestes polyodon* Broom 1949; *Protocynodon pricei* Broom 1949; *Silphedocynodon gymnotemporalis* Brink 1951; *Leavachia microps* Brink and Kitching 1951a; *Leavachia gracilis* Brink and Kitching 1951a; *Scalopocynodon gracilis* Brink 1961.

Horizon: Upper Permian: *Daptocephalus* Zone of South Africa.

Remarks: Many genera and species have been based on juvenile specimens of *Procynosuchus*, including all forms placed in the Family Silphedestidae by Haughton and Brink (1954). *Cyrbasiodon boycei* is probably synonymous with *P.*

delaharpeae, but in view of the poor quality of the type specimen of the former species, we have chosen to retain the latter well-established name. (See paper by Mendrez in this volume, p. 51).

Genus *DVINIA* Amalitzky 1922.

Synonyms: *Permocynodon* Woodward 1932.

DVINIA PRIMA Amalitzky 1922.

Synonyms: *Permocynodon sushkini* Woodward 1932.

Horizon: Upper Permian: Upper Tatarian deposits of Arkhangel'sk region, Russia.

Genus *PARATHRINAXODON* Parrington 1936.

PARATHRINAXODON PROOPS Parrington 1936.

Horizon: Upper Permian: Kawinga Formation of the Ruhuhu Valley, Tanzania.

PROCYNOSUCHIDAE incertae sedis:

Genus *NANOCYNODON* Tatarinov 1968b.

NANOCYNODON SEDUCTUS Tatarinov 1968b.

Horizon: Upper Permian: Upper Tatarian of Russia.

Remarks: Tatarinov placed this species in the Galesauridae, but it is more likely a juvenile procynosuchid.

FAMILY GALESAURIDAE Lydekker 1890.

Includes: Nythosauridae Watson 1917; Cynosuchidae Haughton 1924a; Cynosauridae Haughton and Brink 1954; Thrinaxodontidae Watson and Romer 1956.

Moderately advanced cynodonts with four upper and three lower incisors, no "precanine" maxillary teeth, and posterior postcanines with internal cingulum moderately developed or absent; dentary with well-developed coronoid process, incipiently-developed angular region, and masseteric fossa extending to lower border of the bone; postdentary elements slightly reduced in height from procynosuchid condition; palatal plates of the maxillae and palatines may or may not meet at the midline; interpterygoidal vacuities present only in juveniles; thoracic and lumbar ribs with plate-like expansions.

Horizon: Upper Permian to Lower Triassic: Beaufort Series (Upper *Daptocephalus* Zone to *Cynognathus* Zone, most abundant in *Lystrosaurus* Zone) of South Africa; Fremouw Formation of Antarctica.

Genus *CYNOSAURUS* Schmidt 1927.

Synonyms: *Cynosuchus* Owen 1876; *Cynosuchoides* Broom 1931; *Nanictosaurus* Broom 1936; *Mygalesuchus* Broom 1942; *Baurocynodon* Brink 1951.

CYNOSAURUS SUPPOSTUS (Owen 1876).

Synonyms: *Cynosuchus suppostus* Owen 1876; *Cynosuchus whaitsi* Haughton 1918; *Cynosaurus suppostus,* Schmidt 1927; *Cynosuchoides whaitsi* Broom 1931; *Nanictosaurus kitchingi* Broom 1936; *Mygalesuchus peggyae* Broom 1942; *Baurocynodon gracilis* Brink 1951.

Horizon: Upper Permian: Upper *Daptocephalus* Zone of South Africa.

Remarks: This is the only undoubted galesaurid from the Permian. The last three synonyms are based on small juvenile specimens.

Genus *GALESAURUS* Owen 1859.

Synonyms: *Glochinodon* van Hoepen 1916; *Glochinodontoides* Haughton 1924b.

GALESAURUS PLANICEPS Owen 1859.

Synonyms: *Glochinodon detinens* van Hoepen 1916; *Glochinodontoides gracilis* Haughton 1924b; *Notictosaurus gracilis* Broom and Robinson 1948a; *Notictosaurus trigonocephalus* Brink and Kitching 1951b.

Horizon: Lower Triassic: *Lystrosaurus* Zone of South Africa.

Remarks: Small, immature specimens have usually been

referred to the genus *Galesaurus*, large, mature specimens to *Glochinodontoides*.

Genus *THRINAXODON* Seeley 1894a.

Synonyms: ? *Nythosaurus* Owen 1876; *Ictidopsis* Broom 1912a; *Notictosaurus* Broom 1936; *Micrictodon* Broom 1937.

THRINAXODON LIORHINUS Seeley 1894a.

Synonyms: ? Nythosaurus larvatus Owen 1876, *Ictidopsis elegans* Broom 1912a; *Ictidopsis formosa* van Hoepen 1916; *Thrinaxodon putterilli* Broom 1932; *Notictosaurus luckhoffi* Broom 1936; *Micrictodon marionae* Broom 1937.

Horizon: Lower Triassic: *Lystrosaurus* Zone of South Africa; Fremouw Formation of Antarctica.

Remarks: *Nythosaurus larvatus* Owen is based on the natural mould of a skull bearing impressions of the postcanine teeth. It is probably synonymous with either *Thrinaxodon liorhinus* or *Platycraniellus elegans*. We consider it to be indeterminate at present, and retain Seeley's name for this best-known species of cynodont.

Genus *PLATYCRANIELLUS* van Hoepen 1917.

Synonyms: *Platycranion* van Hoepen 1916; *Platycranium* van Hoepen 1917.

PLATYCRANIELLUS ELEGANS (van Hoepen 1916).

Synonyms: *Platycranion elegans* van Hoepen 1916; *Platycraniellus elegans* van Hoepen 1917.

Horizon: Lower Triassic: *Lystrosaurus* Zone of South Africa.

Remarks: This species is known with certainty from the type only which comes from Harrismith, Orange Free State. A second specimen referred to this species by Brink (1954) is a *Galesaurus*.

Genus *TRIBOLODON* Seeley 1894a.

TRIBOLODON FRERENSIS Seeley 1894a.

Horizon: Lower Triassic: *Cynognathus* Zone of South Africa.

Remarks: This is the youngest species referable with certainty to the Galesauridae. Though frequently classified as a cynognathid, it is a typical galesaurid in its known features.

FAMILY CYNOGNATHIDAE Watson 1917.

Includes: Karromysidae Haughton 1924a.

Advanced carnivorous cynodonts of large size, with elongated facial region and short temporal region; zygomatic arch, postorbital bar, and occipital plate of the squamosal very broad and heavy; occipital portion of the squamosal not emarginated dorsally (as in other advanced cynodonts); dentary very large, with broad posterodorsally-directed coronoid process and distinct angle; postdentary jaw elements greatly reduced in dorsoventral dimension to form a sturdy rod; surangular forms accessory articulation with the squamosal; posterior cheek teeth laterally compressed, with three to six(?) cusps aligned anteroposteriorly, and lacking cingulum cusps except in very young individuals; lumbar ribs with overlapping expansions.

Horizon: Lower Triassic: *Cynognathus* Zone of South Africa and Lesotho (reference to Middle Triassic Molteno Beds of Lesotho is incorrect. Turner: in press); Puesto Viejo Formation of Argentina.

Genus *CYNOGNATHUS* Seeley 1895b.

Synonyms: *Karoomys* Broom 1903b; *Lycognathus* Broom 1913b; *Lycochampsa* Broom 1915b; *Cynidiognathus* Haughton 1922; *Lycaenognathus* Broom 1925; *Cynogomphius* Broom 1932; *Cistecynodon* Brink and Kitching 1953.

CYNOGNATHUS CRATERONOTUS Seeley 1895b.

Synonyms: *Cynognathus berryi* Seeley 1895b; *Cynognathus platyceps* Seeley 1895b; *Karoomys browni* Broom 1903b; *Nythosaurus browni* Broom 1912a; *Lycognathus ferox*

Broom 1913b; *Lycochampsa ferox* Broom 1915b; *Cynidiognathus longiceps* Haughton 1922; *Cynidiognathus broomi* Haughton 1922; *Lycaenognathus platyceps* Broom 1925; *Lycaenognathus kannemeyeri* Broom 1931; *Cynogomphius berryi* Broom 1932; *Cynidiognathus merenskyi* Broili and Schröder 1935b; *Cistecynodon parvus* Brink and Kitching 1953; *Cynognathus minor* Bonaparte 1967a.

Horizon: Same as for family.

Remarks: Generic and specific distinctions within the Cynognathidae have been based on characters which vary with age (tooth number and morphology, skull proportions) and are influenced by postmortem deformation. It seems best to us to recognize but a single species, pending a thorough revision of the family. *Karoomys, Cistecynodon*, and *Nythosaurus browni* are based on tiny juveniles of *Cynognathus*.

FAMILY CHINIQUODONTIDAE von Huene 1936.

Advanced carnivorous cynodonts of small to large size, in which secondary palate extends nearly to or beyond the posterior end of the tooth row (in contradistinction to all other families—except the Tritheledontidae— in which the secondary palate ends well in front of the last tooth) ; occipital portion of the squamosal emarginated dorsally; dentary very large, contacting the squamosal in at least one species; postdentary elements reduced to a narrow rod; surangular contacts the squamosal; postcanines vary greatly in morphology, in some species are sectorial with small or no cingulum cusps, in others have broad lingual shelves which contact similar shelves in the occluding dentition; this family probably contains the immediate ancestors of mammals.

Horizon: Middle and Upper Triassic: Middle Triassic Chañares Formation of Argentina, Manda Formation of Tanzania; Middle or Upper Triassic Santa Maria Formation of Brazil; Upper Triassic Ischigualasto Formation of Argentina.

Genus *CHINIQUODON* von Huene 1936.

CHINIQUODON THEOTONICUS von Huene 1936.

Horizon: Middle and Upper Triassic: Middle Triassic Chañares Formation of Argentina; Middle or Upper Triassic Santa Maria Formation of Brazil; Upper Triassic Ischigualasto Formation of Argentina.

Remarks: This species is poorly understood; possibly some of the specimens referred to it from the Chañares and Ischigualasto formations do not belong here.

Genus *BELESODON* von Huene 1936.

BELESODON MAGNIFICUS von Huene 1936.

Horizon: Middle or Upper Triassic: Santa Maria Formation of Brazil.

Remarks: *Belesodon* is not clearly separable from *Chiniquodon* except on the basis of features which may merely reflect ontogenetic differences. However, because important features of the postcanine dentition are not known for either genus, we prefer to maintain them as distinct for the present.

Genus *ALEODON* Crompton 1955.

ALEODON BRACHYRAMPHUS Crompton 1955.

Horizon: Middle Triassic: Manda Formation of Tanzania.

Remarks: Undescribed specimens being studied by Crompton indicate that this species is a chiniquodontid, the only one known from Africa.

Genus *PROBELESODON* Romer 1969.

PROBELESODON LEWISI Romer 1969.

Horizon: Middle Triassic: Chañares Formation of Argentina.

Genus *PROBAINOGNATHUS* Romer 1970.

PROBAINOGNATHUS JENSENI Romer 1970.

Horizon: Middle Triassic: Chañares Formation of Argentina.

Remarks: This species possesses a contact between dentary and squamosal bones, generally considered one of the principal diagnostic characters of mammals. Despite previous remarks to the contrary (Barghusen and Hopson, 1970), *Probainognathus* is probably very close to the line which gave rise to the Class Mammalia.

FAMILY TRITHELEDONTIDAE Broom 1912b.

Includes: Ictidosauridae Young 1947; Diarthrognathidae Crompton 1958.

Very advanced carnivorous cynodonts of small size in which incisors number two above and below; in some species the upper postcanines (and probably the lowers as well) have a transversely-oriented cutting edge, in others the uppers have an oblique and the lowers a longitudinal cutting edge; secondary palate very long (as in the Chiniquodontidae); postorbital bar absent; dentary contacts the squamosal at least in some.

Horizon: Upper Triassic: Stormberg Series (Red Beds and Cave Sandstone) of South Africa and Lesotho; Los Colorados Formation of Argentina (Bonaparte, personal communication).

Genus *TRITHELEDON* Broom 1912b.

TRITHELEDON RICONOI Broom 1912b.

Horizon: Upper Triassic: Red Beds of South Africa.

Remarks: Crompton (in Hopson and Crompton, 1969) has restudied the type and only specimen and has determined its close affinities with *Pachygenelus* and *"Diarthrognathus"*. For this reason, we use the family name Tritheledontidae Broom 1912 for all of the forms called "ictidosaurs".

Genus *PACHYGENELUS* Watson 1913.

Synonyms: *Diarthrognathus* Crompton 1958.

PACHYGENELUS MONUS Watson 1913.

Synonyms: *Diarthrognathus broomi* Crompton 1958.

Horizon: Upper Triassic: Red Beds and Cave Sandstone of South Africa and Lesotho.

Remarks: *Diarthrognathus broomi* is based on two juvenile specimens which are probably, though not certainly, referable to *P. monus*. Although a specific distinction may prove to be valid, it is doubtful that generic differences exist.

SUPERFAMILY TRITYLODONTOIDEA Simpson 1928 (New rank, erected as suborder). Cynodonts of omnivorous or herbivorous habits in which some or all of the postcanine teeth have transversely-widened crowns which meet in complex occlusion; dentary very large with large coronoid process and distinct angular region often with a true angular process; postdentary elements reduced to narrow rod; surangular contacts squamosal; occipital portion of the squamosal emarginated dorsally; lumbar ribs primitively with overlapping expansions, but rib specializations lost in later forms.

FAMILY DIADEMODONTIDAE Haughton 1924a.

Includes: Gomphognathidae Broom 1903a; Traversodontidae von Huene 1936; Gomphodontosuchidae Watson and Romer 1956; Trirachodontidae Romer 1967.

Primitive to advanced cynodonts of omnivorous to herbivorous habits in which canines are not lost, postcanine teeth are single-rooted and upper postcanines are much wider than long; postorbital bar and prefrontal and postorbital bones present; lumbar ribs with overlapping expansions except in very advanced forms.

Horizon: Lower to Upper Triassic: Lower Triassic *Cynognathus* Zone of South Africa, Puesto Viejo Formation of Argentina; Lower or Middle Triassic "*Sinokannemeyeria* Fauna Beds" of Shansi, China;

Middle Triassic Las Cabras and Chañares formations of Argentina, Ntawere Formation of Zambia, and Manda Formation of Tanzania; Middle or Upper Triassic Santa Maria Formation of Brazil, and Potrerillos Formation of Argentina; Upper Triassic Ischigualasto Formation of Argentina, and Newark Group of Nova Scotia, Canada.

SUBFAMILY DIADEMODONTINAE New Rank.

Includes: Eudiademodontinae Lehman 1961; Gomphodontoinae Lehman 1961.

Primitive omnivorous or herbivorous diademodontids in which the postcanine dentition consists of an anterior series of simple pointed teeth, a middle series of transversely-expanded "molariform" teeth, and a posterior series grading from "sub-molariform" to sectorial; upper "molariform" teeth wider than long with a large outer cusp and one or two smaller inner cusps connected by a centrally-located transverse ridge; lower "molariform" teeth nearly circular in crown view with large outer and inner cusps joined by a centrally-located transverse ridge; lumbar ribs with broad overlapping expansions.

Genus *DIADEMODON* Seeley 1894b.

Synonyms: ? *Cynochampsa* Owen 1859; *Gomphognathus* Seeley 1895a; *Octagomphus* Broom 1919; *Cyclogomphodon* Broom 1919; *Protacmon* Watson 1920; *Sysphinctostoma* Broili and Schröder 1936; *Gomphodontoides* Brink and Kitching 1951b; *Cragievarus* Brink 1965.

DIADEMODON TETRAGONUS Seeley 1894b.

Synonyms: ? *Cynochampsa laniaria* Owen 1859; *Diademodon mastacus* Seeley 1894b; *Diademodon browni* Seeley 1894b; *Gomphognathus kannemeyeri* Seeley 1895a; *Gomphognathus polyphagus* Seeley 1895a; *Diademodon entomophonus* Seeley 1908; *Gomphognathus minor* Broom 1911; *Diademodon platyrhinus* Broom 1913a; *Trirachodon browni* Broom 1915a; *Cyclogomphodon platyrhinus* Broom 1919; *Octagomphus woodi* Broom 1919; *Protacmon brachyrhinus* Watson 1920; *Gomphognathus grossarthi* Broili and Schröder 1935a; *Gomphognathus broomi* Broili and Schröder 1935a; *Sysphinctostoma smithi* Broili and Schröder 1936; *Protacmon reubsameni* Broom 1950; *Sysphinctostoma gracilis* Broom 1950; *Gomphodontoides megalops* Brink and Kitching 1951b; *Diademodon parringtoni* Brink 1955; *Diademodon laticeps* Brink 1955; *Diademodon rhodesiensis* Brink 1963; *Cragievarus kitchingi* Brink 1965.

Horizon: Lower Triassic to Middle Triassic: Lower Triassic *Cynognathus* Zone of South Africa; Middle Triassic Ntawere Formation of Zambia.

Remarks: The named species of African diademodontines have been based on dental differences and variations in skull sizes and proportions which can be attributed to ontogenetic variation and, perhaps, sexual dimorphism, as well as to postmortem distortion. In the absence of valid criteria for distinguishing species of *Diademodon*, we prefer to recognize a single species. The earliest named diademodontine, *Cynochampsa laniaria,* is based on a fragmentary snout lacking postcanine teeth; we prefer to consider it a *nomen vanum*.

DIADEMODONTINAE incertae sedis:

Genus *ORDOSIODON* Young 1961.

ORDOSIODON LINCHEYUENSIS Young 1961.

Horizon: Lower or Middle Triassic: Beds approximately equivalent to *Cynognathus* Zone of Shansi, China.

Remarks: This species is based on a small dentary probably of juvenile diademodontine.

SUBFAMILY TRIRACHODONTINAE New Rank.
Primitive omnivorous or herbivorous diademodontids in which the postcanine dentition consists of transversely-expanded "molariform" teeth, plus one or two sectorial teeth at the posterior end of the tooth row (simple anterior teeth and "sub-molariform" posterior teeth are lacking); upper and lower "molariforms" of similar morphology, crowns with three main cusps in a transverse row across the centre of the tooth with cusps connected by ridges, margins of the crowns with continuous rim of small cingulum cusps; lumbar ribs with broad overlapping expansions.

Genus *TRIRACHODON* Seeley 1894b.
Synonyms: *Trirachodontoides* Broom 1932; *Inusitatodon* Brink and Kitching 1953.
TRIRACHODON BERRYI Seeley 1894b.
Synonyms: *Trirachodon kannemeyeri* Seeley 1895a; *Trirachodon minor* Broom 1905; *Trirachodontoides berryi* Broom 1932; *Inusitatodon smithi* Brink and Kitching 1953.
Horizon: Lower Triassic: *Cynognathus* Zone of South Africa.
Remarks: The named species are based on dental and size characteristics which change ontogenetically.

Genus *CRICODON* Crompton 1955.
CRICODON METABOLUS Crompton 1955.
Horizon: Middle Triassic: Manda Formation of Tanzania.

TRIRACHODONTINAE incertae sedis:
Genus *SINOGNATHUS* Young 1959.
SINOGNATHUS GRACILIS Young 1959.
Horizon: Lower or Middle Triassic: "*Sinokannemeyeria* Fauna Beds" of Shansi, China.
Remarks: Young believed this form to be a galesaurid, but it is clearly more advanced and appears to have "molariform" postcanine teeth of diademodontid, especially triracho-dontine, appearance.

SUBFAMILY TRAVERSODONTINAE Lehman 1961.
Includes: Gomphodontosuchinae Lehman 1961.
Advanced herbivorous diademodontids in which the postcanine dentition consists of transversely-expanded "molariform" teeth, with one or two sectorial teeth occurring only in certain ontogenetic stages of the more primitive species; upper postcanines with three main cusps in a transverse row behind the centre of the crown, with the outer cusp being the largest and possessing a vertical shear surface on its inner face, and with a small to very large basin in the central portion of the crown; lower· postcanines with two main cusps oriented more or less transversely on the anterior half of the crown and a basined "heel" on the posterior half of the crown, with the outer cusp possessing a vertical shear surface on its outer face; lower canine reduced in advanced forms; lumbar ribs with broad overlapping expansions in early members, but these become progressively reduced and ultimately lost in advanced members of the group.

Genus *TRAVERSODON* von Huene 1936.
TRAVERSODON STAHLECKERI von Huene 1936.
Synonyms: ? *Traversodon major* von Huene 1936.
Horizon: Middle or Upper Triassic: Santa Maria Formation of Brazil.
Remarks: ? *Traversodon major* is based on fragments which differ from *T. stahleckeri* only in size.

Genus *GOMPHODONTOSUCHUS* von Huene 1928.
GOMPHODONTOSUCHUS BRASILIENSIS von Huene 1928.
Horizon: Middle or Upper Triassic: Santa Maria Formation of Brazil.

Genus *PASCUALGNATHUS* Bonaparte 1966.
PASCUALGNATHUS POLANSKII Bonaparte 1966.
Horizon: Lower Triassic: Puesto Viejo Formation of Argentina.
Remarks: The earliest and most primitive traversodontine, it shows many resemblances to *Diademodon* indicating a diademodontine origin of traversodontines.

Genus *ANDESCYNODON* Bonaparte 1967b.
ANDESCYNODON MENDOZENSIS Bonaparte 1967b.
Horizon: Middle Triassic: Las Cabras Formation of Argentina.
Remarks: A primitive traversodontine, slightly more advanced than *Pascualgnathus.*

Genus *SCALENODON* Crompton 1955.
SCALENODON ANGUSTIFRONS (Parrington 1946).
Synonyms: *Trirachodon angustifrons* Parrington 1946; *Scalenodon angustifrons* Crompton 1955.
Horizon: Middle Triassic: Manda Formation of Tanzania.

Genus *LUANGWA* Brink 1963.
LUANGWA DRYSDALLI Brink 1963.
Horizon: Middle Triassic: Ntawere Formation of Zambia.
Remarks: Although its postcanine morphology is not adequately known, this species seems to be distinct.

Genus *MASSETOGNATHUS* Romer 1967.
MASSETOGNATHUS PASCUALI Romer 1967.
Synonyms: *Massetognathus teruggii* Romer 1967.
Horizon: Middle Triassic: Chañares Formation of Argentina.
Remarks: The type skull of *M. teruggii* differs from that of *M. pascuali* in no significant features other than size. It is here considered to be an old individual of the latter species.

Genus *EXAERETODON* Cabrera 1943.
Synonyms: *Theropsis* Cabrera 1943; *Proexaeretodon* Bonaparte 1963b.
EXAERETODON ARGENTINUS (Cabrera 1943).
Synonyms: *Belesodon? argentinus* Cabrera 1943; *Exaeretodon frenguellii* Cabrera 1943; *Theropsis robusta* Cabrera 1943; *Exaeretodon argentinus* Bonaparte 1962; *Proexaeretodon vincei* Bonaparte 1963b.
Horizon: Upper Triassic: Ischigualasto Formation of Argentina.
Remarks: With the exception of the following form, all Ischigualasto traversodontines can be accommodated in a single species for which the name *E. argentinus* has page priority.

Genus *ISCHIGNATHUS* Bonaparte 1963a.
ISCHIGNATHUS SUDAMERICANUS Bonaparte 1963a.
Horizon: Upper Triassic: Ischigualasto Formation of Argentina.
Remarks: This species is similar to, but apparently distinct from, *Exaeretodon.*

Genus *SCALENODONTOIDES* Crompton and Ellenberger 1957.
SCALENODONTOIDES MACRODONTES Crompton and Ellenberger 1957.
Horizon: Upper Triassic: Lower part of the Red Beds, Stormberg Series, of Lesotho.
Remarks: The type specimen was said to be from the Molteno Beds, but Crompton (in Cox 1969) and Turner (in press) have since determined that it is from the overlying Red Beds. *Scalenodontoides* is very similar to *Exaeretodon* and the two may prove to be identical.

TRAVERSODONTINAE incertae sedis:

Genus *THEROPSODON* von Huene 1950.

THEROPSODON NJALILUS von Huene 1950 *nomen vanum*.

Horizon: Middle Triassic: Manda Formation of Tanzania.

Remarks: This form is based on a complete but poorly preserved skull with lower jaws in place. Because several other genera and species of traversodontines, mostly undescribed, are now known from the Manda Formation and are differentiated primarily on the basis of postcanine morphology, which is not readily available in the type specimen of *T. njalilus*, we believe it is best to consider it a *nomen vanum*.

Genus *COLBERTOSAURUS* Minoprio 1957.

Synonym: *Colbertia* Minoprio 1954.

COLBERTOSAURUS MURALIS (Minoprio 1954).

Synonyms: *Colbertia muralis* Minoprio 1954; *Colbertosaurus muralis* Minoprio 1957.

Horizon: Middle or Upper Triassic: Potrerillos Formation of Argentina.

Remarks: This species is inadequately known, being based on a fragmentary dentary. Bonaparte (1966) compares it to the traversodontines *Andescynodon* and *Pascualgnathus*.

FAMILY TRITYLODONTIDAE Cope 1884.

Includes: Bienotheriidae Young 1940.

Very advanced herbivorous cynodonts in which one pair of upper and lower incisors is greatly enlarged, canines are absent, and multiple-rooted postcanine teeth bear three (upper) or two (lower) longitudinal rows of crescentic cusps; postorbital bar and prefrontal and postorbital bones absent; lumbar ribs lack overlapping expansions.

Horizon: Upper Triassic to Middle Jurassic: Upper Triassic Red Beds and Cave Sandstone, Stormberg Series, of South Africa and Lesotho; Lufeng Series of Yunnan, China; Los Colorados Formation of Argentina; Kayenta Formation of the United States; Rhaetic of Germany; Lower Jurassic fissures of England; Middle Jurassic Stonesfield Slate of England.

Genus *TRITYLODON* Owen 1884.

Synonyms: *Likhoelia* Ginsburg 1961; *Tritylodontoideus* Fourie 1962.

TRITYLODON LONGAEVUS Owen 1884.

Synonyms: *Likhoelia ellenbergeri* Ginsburg 1961; ? *Tritylodontoideus maximus* Fourie 1962; ? *Tritylodontoides maximus* Fourie 1963;

Horizon: Upper Triassic: Red Beds and Cave Sandstone, Stormberg Series, of South Africa and Lesotho.

Remarks: The generic name *Tritylodon* should be restricted to southern African forms and should not be applied to isolated teeth from the Rhaeto-Lias of Europe (see *Tritylodon fraasi* below), as the latter are, in fact, generically indeterminate. *Likhoelia* is based on a juvenile specimen of *T. longaevus*. Kitching (ms.) believes *Tritylodontoideus* to be a large *T. longaevus*.

Genus *BIENOTHERIUM* Young 1940.

BIENOTHERIUM YUNNANENSE Young 1940.

Synonyms: *Bienotherium elegans* Young 1940.

Horizon: Upper Triassic: Lower Lufeng Series of Yunnan, China.

Remarks: *B. elegans* is based on an immature *B. yunnanense*.

BIENOTHERIUM MAGNUM Chow 1962.

Horizon: Upper Triassic: Lower Lufeng Series of Yunnan, China.

Remarks: *B. magnum* is recognized as a distinct species because

it comes from a higher horizon than *B. yunnanense* and is much larger.

Genus *LUFENGIA* Chow and Hu 1959.

LUFENGIA MINOR (Young 1947).

Synonyms: *Bienotherium minor* Young 1947; *Lufengia delicata* Chow and Hu 1959; *Lufengia minor* new combination.

Horizon: Upper Triassic: Lower Lufeng Series of Yunnan, China.

Remarks: Hopson (ms.) believes *B. minor* Young pertains to the genus *Lufengia*.

Genus *OLIGOKYPHUS* Hennig 1922.

Synonyms: *Mucrotherium* E. von Heune 1933 *Uniserium* E. von Huene 1933.

OLIGOKYPHUS TRISERIALIS Hennig 1922.

Synonyms: *Oligokyphus biserialis* Hennig 1922; *Mucrotherium cingulatum* E. von Huene 1933; *Uniserium enigmaticum* E. von Huene 1933.

Horizon: Lower Jurassic: Liassic Bonebed of Germany.

OLIGOKYPHUS MAJOR Kühne 1956.

Synonyms: *Oligokyphus minor* Kühne 1956.

Horizon: Lower Jurassic: Lower Lias Fissures of Somerset, England.

Remarks: Kühne described two size groups of *Oligokyphus* from a single fissure to which he gave separate names. We believe it more likely that the groups represent male and female of a single species for which the name *O. major* has priority.

Genus *STEREOGNATHUS* Charlesworth 1855.

STEREOGNATHUS OOLITICUS Charlesworth 1855.

Horizon: Middle Jurassic: Stonesfield slate of Oxfordshire, England.

Remarks: This is the latest known therapsid reptile.

TRITYLODONTIDAE OF UNCERTAIN TAXONOMIC POSITION

TRITYLODON FRAASI Lydekker 1887 *nomen vanum*

Synonyms: *"Triglyphus"* O.Fraas 1866; *Tritylodon fraasi* Lydekker 1887; *Triglyphus fraasi* Hennig 1922.

Horizon: Rhaeto-Liassic Bonebed of Wurttemberg, Germany.

Remarks: The type and only specimen of this species, an isolated upper postcanine tooth, is lost. Because its crown pattern is identical to that of several genera of tritylodontids, it is not diagnostic and is best regarded as a *nomen vanum*.

CHALEPOTHERIUM PLIENINGERI (Ameghino 1903) *nomen vanum.*

Synonyms: *Microlestes plieningeri* Ameghino 1903; *Chalepotherium plieningeri* Simpson 1928.

Horizon: Rhaeto-Liassic Bonebed of Wurttemberg, Germany.

Remarks: The type and only specimen of this species consists of a damaged upper postcanine tooth which is not diagnostic as to genus or species; therefore, *C. plieningeri* is a *nomen vanum.*

CYNODONTIA incertae sedis:

Genus MICROHELODON Broom 1931.

MICROHELODON EUMERUS (Seeley 1895a) *nomen vanum.*

Synonyms: *Microgomphodon eumerus* Seeley 1895a; *Microhelodon eumerus* Broom 1931.

Horizon: Lower Triassic: *Cynognathus* Zone of South Africa.

Remarks: The type and only specimen is a damaged snout which may pertain to a bauriamorph or to a cynodont. Seeley associated a cynodont skeleton with the type, but

Broom (1931) and Brink (1955) consider this association to be incorrect.

Genus *ARCHAEODON* von Huene 1925.
ARCHAEODON REUNINGI von Huene 1925.
Horizon: Upper Triassic? : "Youngest Stormberg" equivalent? of South-West Africa.
Remarks: The type and only specimen is an isolated tooth with divided roots, but lacking the crown. It does not appear to be referable to the Tritylodontidae and is unlike any known Triassic mammal. We question the correctness of the reported Triassic age.

Genus *DROMATHERIUM* Emmons 1857.
DROMATHERIUM SYLVESTRE Emmons 1857.
Horizon: Upper Triassic: Cumnock Formation, Newark Group, of North Carolina, United States.
Remarks: This incomplete dentary with damaged postcanine teeth may belong to a cynodont or to a mammal. Its affinities are at present indeterminate.

Genus *MICROCONODON* Osborn 1886.
Synonyms: *Tytthoconus* Palmer 1903.
MICROCONODON TENUIROSTRIS Osborn 1886.
Synonyms: *Tytthoconus tenuirostris* Palmer 1903.
Horizon: Upper Triassic: Cumnock Formation, Newark Group, of North Carolina, United States.
Remarks: This tiny dentary is possibly a mammal, or it may be a cynodont, most likely a chiniquodontid, close to the reptile-mammal class boundary.

Genus *KUNMINIA* Young 1947.
KUNMINIA MINIMA Young 1947 *nomen vanum.*
Horizon: Upper Triassic: Lower Lufeng Series of Yunnan, China.
Remarks: This poorly-preserved little skull may be that of a mammal, possibly the same as *Morganucodon oehleri* from the same beds. The specimen as now known is indeterminate and the name is best considered a *nomen vanum.*

Genus *TRICUSPES* E. von Huene 1933.
TRICUSPES TUBINGENSIS E. von Huene 1933.
Horizon: Lower Jurassic: Liassic Bonebed of Germany.
Remarks: This isolated tooth may pertain to a cynodont, to a mammal, or to some unknown reptilian type.

Genus *EORAETIA* Dietrich 1937.
EORAETIA SIEGERTI Dietrich 1937.
Horizon: Upper Triassic or Lower Jurassic: Rhaeto-Lias of Halberstadt, Germany.
Remarks: The affinities of this isolated ulna are uncertain.

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A NEW SPECIES OF MACHAERODONT FROM MAKAPANSGAT

by

G. E. Collings

ABSTRACT

The skull and associated mandible belonging to a new species of machaerodont, *Megantereon problematicus* Collings is described. The specimen came from the lowermost horizon of banded and contaminated travertines at the Makapansgat Limeworks. An estimate of its relationship with other sabre tooth cats is given.

CLASSIFICATION

Class – Mammalia
Order – Carnivora
Sub-order – Fissipedia
Infra-order – Aeluroidea
Family – Felidae
Sub-family – Machaerodontinae
Genus – *Megantereon* Croizer and Jobert
Species – *Megantereon problematicus* nov.

DIAGNOSIS

A large *Megantereon*, whose carnassials are longer and narrower than any previously described species of this genus. The carnassial width to length ratio is 1 : 3, as opposed to all other described *Megantereon* species, which have a carnassial width to length ratio not exceeding 1 : 2.

INTRODUCTION

The Pliocene/Pleistocene sabre tooth cats are an assemblage of unrelated genera, which are assumed to have radiated from an earlier Oligocene felid stock, represented by *Dinictis* and *Hoplophoneus* (Matthew 1910). Both of these showed machaerodont tendencies, but it was probably the comparatively unspecialised *Dinictis* which led to the varied group of later sabre tooths, as well as the modern felids. The Pleistocene sabre tooths can be separated into a number of groups, each following slightly different lines of machaerodont modification. *Megantereon* and *Smilodon* are superficially very similar, and may be said to have been the most specialised of the Pleistocene sabre tooths. However, on closer analysis, they appear quite unrelated, and could be examples of parallel evolution. *Megantereon*, *Machaerodus* and *Therailurus* belonged to the Old World, and seem to have co-existed in the same habitats, while *Smilodon*, so far, has only been found in the New World.

DESCRIPTION

The specimen, No. M.8280 of the Bernard Price Institute for Palaeontological Research, is the incomplete skull and mandible of a large machaerodont belonging to the genus *Megantereon* (Figs. 1, 2, and 3). It was recovered by Mr. J. W. Kitching, in 1958, from the layer of banded and contaminated travertines at the site of the so-called "Ancient Entrance" at the Makapansgat Limeworks. These impure travertines are immediately overlain by the 'basal red breccia' (calcified red mud of Brain–1958) which is, in turn, succeeded by the relatively thin layer of exceedingly bone-rich grey breccia. The skull is considerably distorted, having been subject to lateral compression during fossilization, and a great deal of the cranium is missing. The teeth and mandible however are perfectly preserved, and enable an accurate diagnosis of the genus and species.

The preserved features of the skull, such as the small coronoid process and the specialisation of the teeth, are in agreement with those of the genus *Megantereon*. However, specimen M.8280 is defined as a new species of *Megantereon* on the basis of certain dental characters, which have not been observed in other machaerodonts previously described. The general proportions of the lower carnassials in all other species of *Megantereon* are about twice the width to the length, whilst in specimen M.8280, the length is approximately three times the width. A comparison of its teeth measurements with those of some other *Megantereon* species and the South African sabre tooth cats is given in Table 1.

A brief description of the dentition now follows (Figs. 1–7). The upper canines are much flattened laterally, crenulated, moderately long, but only slightly curved; P^3 is much reduced; P^4 has a vestigial protocone and a well developed parastyle; M^1 is small and rounded. The mandible has a deep symphysis, a mental crest and a mental process; the coronoid process is much reduced. The lower canines are comparatively small and raised above the level of the cheek teeth; P_3 is much reduced; P_4 has well developed accessory cusps; M_1 has a vestigial metaconid.

DISCUSSION

The inner surface of both upper and lower tooth rows had been worn extensively to form a continuous oblique shearing plane and the individual cusps had been obliterated to form one

longitudinal ridge. This indicates that the animal was old at the time of death. Observations on the teeth revealed that the animal also suffered from some dental defects. The right upper canine has a greater antero-posterior length than the left one and this seems to be the result of a genetic abnormality. This caused it to shear unnaturally against the lower canine in jaw closure and may have contributed to differential wear on both sides of the cheek teeth.

P_3 and P_4 on the left side had been broken in life, and the left P^3, which opposes P_3, is also broken (compare Figs. 5 and 6). This may have influenced the animal to use the right side more while masticating, as the right teeth appear more worn than the left.

The geological age of specimen M.8280 is estimated as Lower Pleistocene. The fossil fauna of Makapansgat shows a similarity with the oldest horizon of the Omo beds in East Africa. These have been dated by the Potassium–Argon method as 4,1 million years old, with the youngest horizon being 1,4 million years old (Cooke 1970, pers. comm.). This makes the Omo beds older than the European Villafranchian with which it was previously thought they corresponded. However, in view of the extremely specialised dentition of *Megantereon problematicus* it is more likely that the Makapansgat fossil fauna accumulated somewhat later, at an age that corresponds to the accepted Lower Pleistocene. Although the European species of *Megantereon* are regarded as Lower Pleistocene (Stirton 1951), there are descriptions of other species from the Upper Pliocene of India (Pilgrim 1932, Colbert 1935), and from the Lower Pliocene of China (Young 1935, Teilhard de Chardin 1939, Chang 1957) which gives this genus a long range in time. It is quite possible that an African species could have evolved independently from a Pliocene group and reached a high degree of specialisation by Lower Pleistocene times.

SUMMARY

1. The skull of a machaerodont from the Makapansgat Limeworks is described.
2. It is ascribed to a new species, *Megantereon problematicus* Collings, on the basis of its unique dental pattern.
3. A determination of the age of the deposit is estimated as probably Lower Pleistocene.

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Explanations to text figures

Fig. 1 Right lateral view of skull M.8280.
Fig. 2 Palatal view of skull M.8280.
Fig. 3 Outer view of right mandible M.8280.
Fig. 4 Inner view of left mandible M.8280.
Fig. 5 Inner view of right cheek teeth M.8280.
Fig. 6 Outer view of left cheek teeth M.8280.
Fig. 7 Dorsal view of lower jaw. Distortion corrected. M.8280.

Key to Abbreviations

al.	alveolus
ant. acc. csp.	anterior accesory cusp
cor. proc.	coronoid process
con.	condyle
eam.	external auditory meatus
fr.	frontal
g.	glenoid
iof.	infra-orbital foramen
j.	jugal
m.	maxilla
man. for.	mandibular foramen
man. sym.	mandibular symphysis
men. cr.	mental crest
men. for.	mental foramen
men. proc.	mental process
meta.	metacone
o.	orbit
p.	parietal
pal.	palatine
para.	paracone
parad.	paraconid
parast.	parastyle
proto.	protocone
protod.	protoconid
pt. lac. for.	posterior lacerate foramen
pt. pal. for.	posterior palatal foramen
s.	squamosal
tb.	typanic bulla

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TABLE I*

A comparison of dentitions of some *Megantereon* spp. from Asia and Europe with South African machaerodonts

		Therailurus barlowi (Ewer)	*Therailurus piveteaui* Ewer	*Machaerodus transvaalensis* Broom	*Megantereon whitei* Broom	*Megantereon gracilis* Broom	*Megantereon problematicus* Collings	*Megantereon eurynodon* Ewer	*Megantereon falconeri* Pommel	*Megantereon palaeindicus* (Bose)	*Megantereon praecox* Pilgrim	*Megantereon inexpectatus* Teilhard	*Megantereon nihowanensis* Teilhard & Piveteau	Isolated canine associated with *M. nihowanensis*	*Megantereon megantereon* Croizet & Jobert
Upper Canines	crown height	57,0	±43,0	60,0	–	–	55,8	74,0	–	–	–	–	–	50,0	80,0
	ant. post.	24,3	20,0	23,9	–	–	34,3	25,5	–	–	–	25,0	–	31,0	22,2
	trans.	15,0	12,0	12,7	–	–	14,0	12,8	–	–	–	10,0	–	13,0	–
p^3	ant. post.	18,4	19,4	–	–	–	10,8	12,0	12,5	–	–	16,0	18,0	–	–
	trans.	8,8	8,9	–	–	–	5,7	5,4	6,3	–	–	7,0	–	–	–
p^4	ant. post.	36,9	40,0	–	–	–	53,2	30,2	33,0	–	13,0	35,0	25,0	–	29,5
	trans.	14,5	12,0	–	–	–	8,9	10,6	12,3	–	13,5	13,0	11,0	–	13,5
M^1	ant. post.	5,9	4,0	–	–	–	5,7	4,2	4,5	–	–	5,0	–	–	–
	trans.	?	?	–	–	–	–	7,8	8,0	–	–	10,0	–	–	–
Diastema length		9,8	5,5	–	–	–	12,8	–	15,5	–	–	–	–	–	?
Lower Canines	crown height	26,5	–	–	–	–	21,6	12,1	–	–	–	–	24,0	–	–
	ant. post.	6,7	–	–	–	–	14,9	8,2	–	–	–	–	11,0	–	–
	trans.	12,5	–	–	–	–	10,7	–	–	–	–	–	6,5	–	–
P_3	ant. post.	12,9	–	–	–	–	13,0	6,3	8,0	–	–	–	8,7	–	–
	trans.	6,7	–	–	–	–	7,0	–	6,3	–	–	–	–	–	–
P_4	ant. post.	12,8	–	–	–	12,4	22,6	17,0	21,0	23,5	–	–	21,5	–	–
	trans.	10,3	–	–	–	6,8	9,9	–	12,5	11,0	–	–	–	–	–
M_1	ant. post.	25,9	–	–	19,6	19,2	34,0	19,8	26,0	20,0	–	–	–	–	22,0
	trans.	13,5	–	–	9,4	8,5	12,0	9,2	13,0	10,0	–	–	–	–	–
Diastema length		30,4	–	–	–	–	45,5	–	–	34,5	–	–	–	–	–

*Data from various authors.

Fig. 1

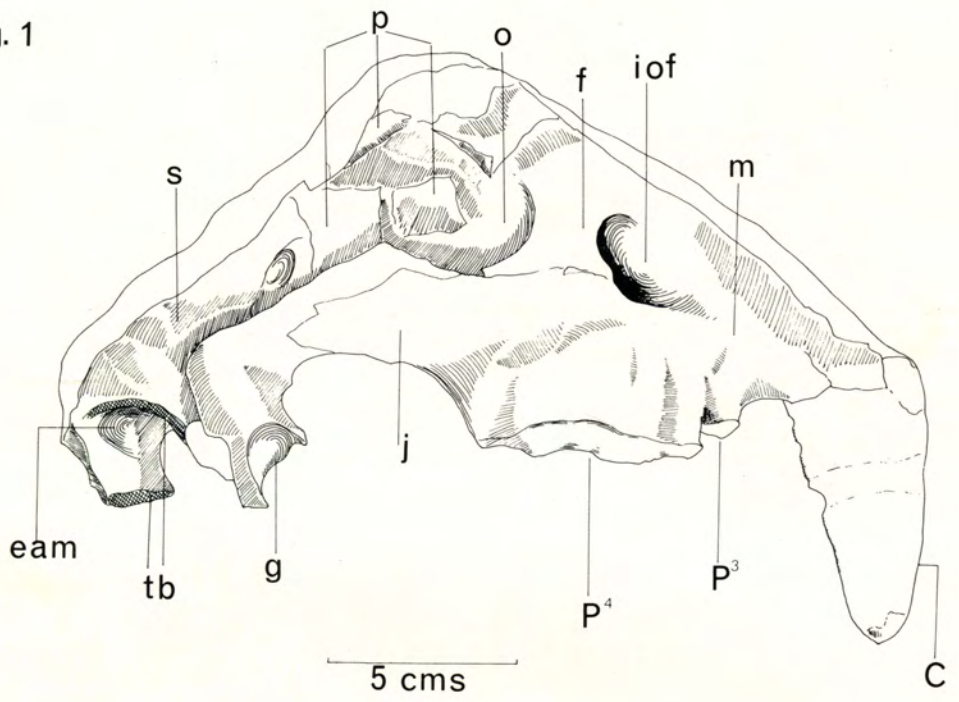

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Fig. 2

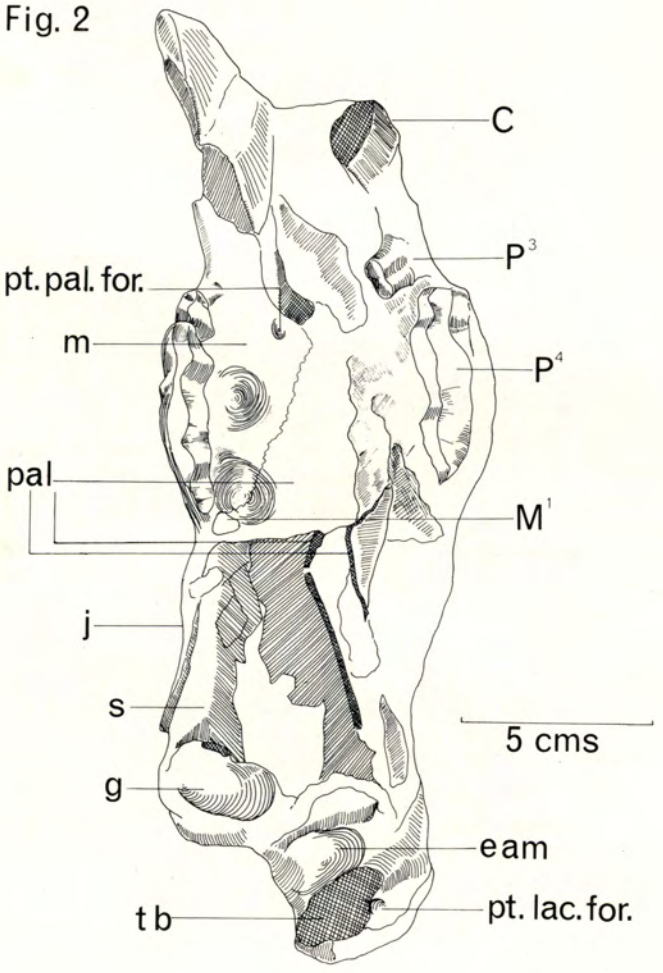

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Fig. 3

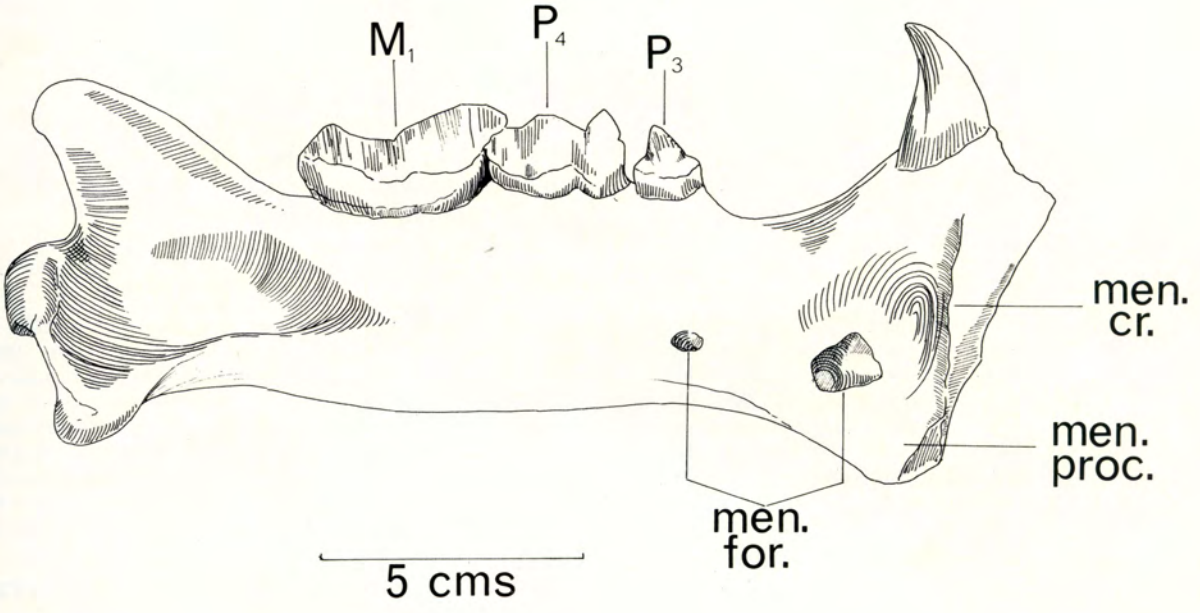

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Fig. 4

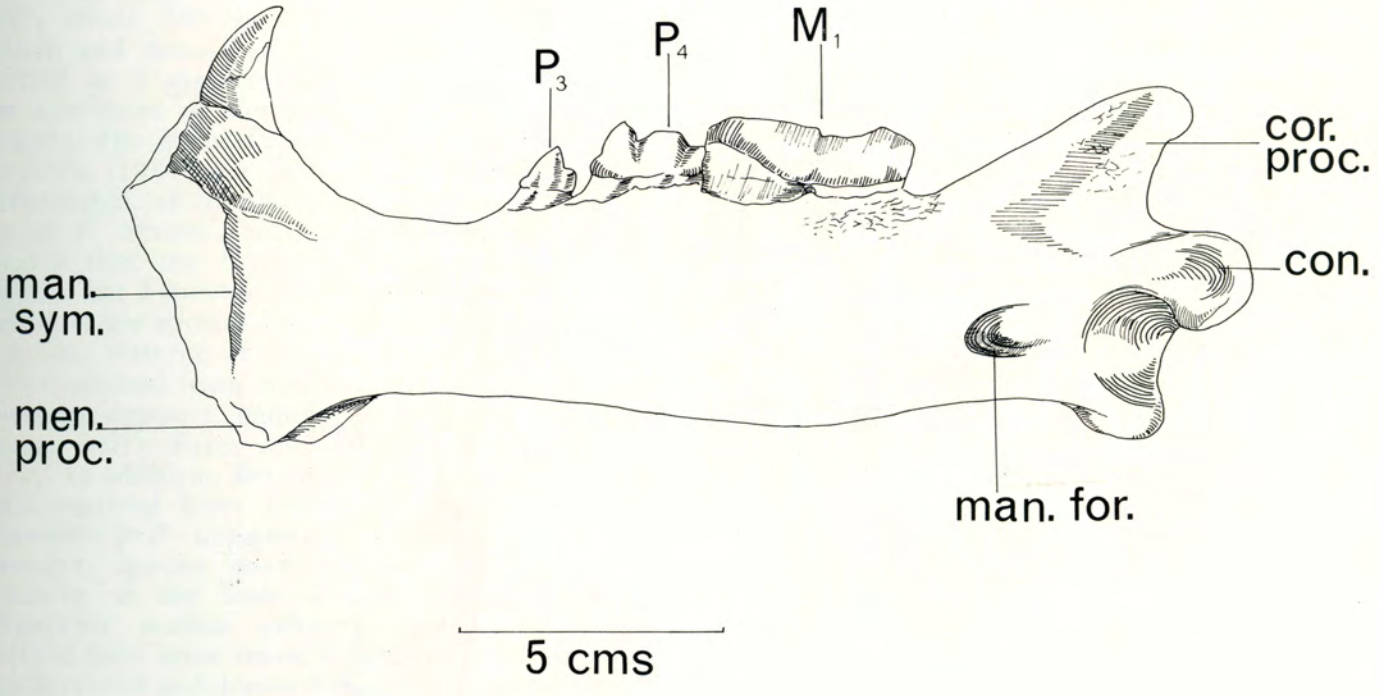

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Fig. 5

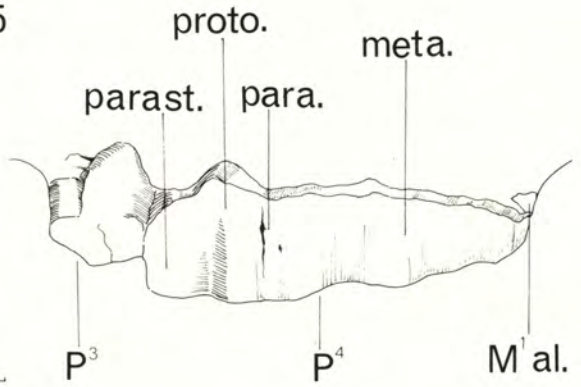
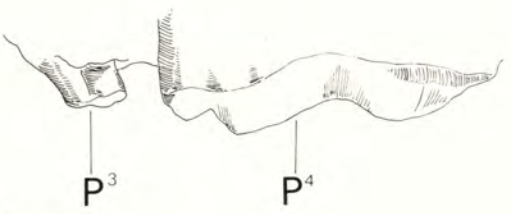
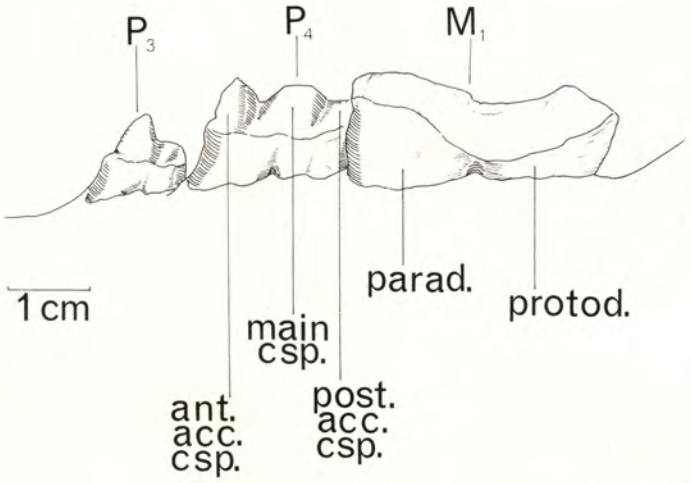


Fig. 6





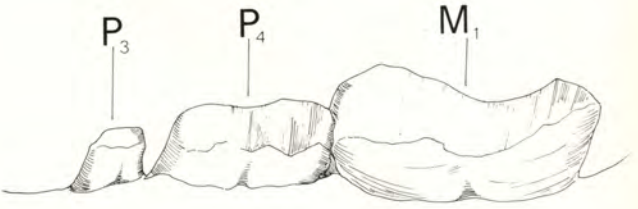
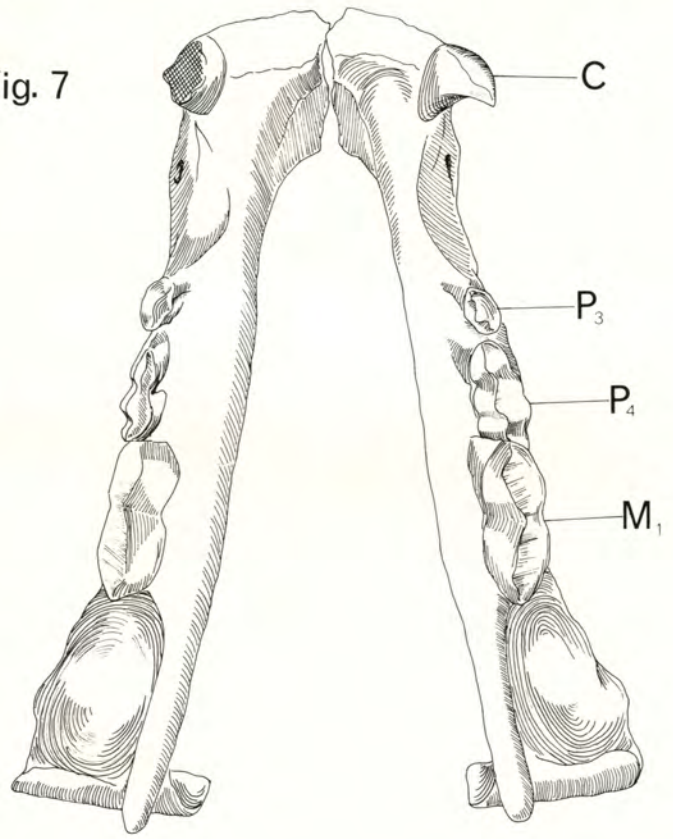


Fig. 7



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THE *PARAPAPIO* SPECIES OF STERKFONTEIN, TRANSVAAL, SOUTH AFRICA

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ABSTRACT

The premolar and molar dimensions of the *Parapapio* specimens hitherto described from the South African lower Pleistocene deposits at Sterkfontein have been re-examined. The relatively minor sexual dimorphism in these teeth (except P3 length) was confirmed. 103 new cercopithecoid specimens from Sterkfontein were tentatively assigned to the 3 previously described *Parapapio* spp. from that site. The new and old samples of each species were compared and then pooled. Analysis of this new enlarged sample, and also the newly available distribution data of *Parapapio* from other South African deposits, both tend to support the validity of *3 Parapapio* spp., *P. jonesi, P. broomi* and *P. whitei*, at Sterkfontein.

INTRODUCTION

The South African lower Pleistocene limestone deposits have yielded, over the years, a very considerable number of fossil cercopithecoid specimens. In the most recent review of the material recovered (Freedman, 1957), about 1 250 specimens were examined and, since then, several additional significant groups of specimens have been reported (Freedman, 1960, 1961 & 1965). From this material a total of 6 genera, including 14 species, have been described.

Of this large and varied cercopithecoid assemblage, about 600 specimens come from Sterkfontein and almost all of the material has been referred to 3 species of the genus *Parapapio*. (A few specimens of *Cercopithecoides williamsi* are present). The genus *Parapapio* was first described by Jones (1937) for a batch of specimens from Sterkfontein, all of which he included in the type species *P. broomi*. Subsequently, Broom (1940) decided that the Sterkfontein material included not one but 3 species of *Parapapio* and he named a slightly larger species *P. whitei*, and a smaller one, *P. jonesi*. Material of these 3 species has now also been described from various other South African limestone deposits, namely Swartkrans, Makapan, Taung, Bolt's Farm and Kromdraai (Freedman, 1970). In addition, Broom (1940) re-studied some *Papio* material from Taung and transferred it to *Parapapio* (= *P. antiquus*). Although the various *Parapapio* species were originally differentiated primarily on the basis of dental size variations, subsequent studies utilising more and better material have since revealed a number of morphological cranial and dental differences between the 4 described species. The present study will, however, only be concerned with dental metrical features.

Recent work at Sterkfontein (Tobias and Hughes, 1969) has brought to light a further good sample of cercopithecoid specimens. The present paper is concerned with re-examining statistically the specific validity of the 3 *Parapapio* species at Sterkfontein in terms of the premolar and molar teeth, assessing the newly recovered material and putting on record the premolar and molar size statistics for the total samples now available of each of the 3 *Parapapio* species from this site.

MATERIALS AND METHODS

The Sterkfontein material of *Parapapio* previously described by Freedman (1957) was used for the initial analyses of this study. The new material available from Sterkfontein included a total of 565 specimens of which 103 (Appendix 1–3) were used in the later dental metrical analyses. The area from which the new material came is listed as STW, D13, 1969–1970 (Tobias & Hughes, 1969). This area is a rubble dump near the East Pit and consisted of "large masses of blasted-out breccia" resulting from the early lime working. The material is rich in bone; a considerable variety of mammals and other vertebrates are represented (Tobias & Hughes, 1969).

The system of measurements used in this study follows Freedman (1957). Breadth measurements are mesial (bm) and distal (bd); length is maximum (l). Measurements in brackets (Appenddix) are approximate due to damage. Measurements were taken to the nearest 0,1 mm but mean values are given to 2 decimal places. Where only one decimal place is given in the tables for a 'mean value' only a single observation was available.

ANALYSIS

A large amount of *Parapapio* material from Sterkfontein is now available. However, only a small proportion of those specimens can be assigned with certainty to a specific sex and species. Further, because of the fragmentary nature of the specimens, insufficient numbers are available in such groups for multivariate analyses of, say,

P3–M3 or even M1–M3 of either the upper or the lower jaw. Even when analyses of particular single teeth for such comparisons are attempted, most sample sizes are still statistically small.

(a) Sexual Dimorphism.

Fortunately, one of the features of the genus *Parapapio* is the very small statistical size difference between the sexes in the premolars (except P3 length) and the molars. To examine the possibility of pooling the sexes in the comparisons contemplated, it was therefore decided to compare the dimensions of these teeth in the two sexes by "t" tests. Where only a single specimen of one sex was available for a particular comparison, a modified "t" test (Simpson, Roe & Lewontin, 1960, p. 183) was used. For this initial study only the previously described and sexed material (Freedman, 1957) was utilised.

Tables 1A and 1B show the results of this analysis. Of the 71 "t" tests performed, in the upper dentition only 5 tests were significant at or above the 5% level and in the lower teeth 9 tests revealed this level of significance. Inadequate male samples of *P. whitei* severely limited the number of upper dentition tests possible but the lower teeth comparisons in this taxon confirm the very low degree of dental sexual dimorphism in the genus. It will be noted that, possibly because of the small sample sizes, in 6/14 *P. broomi* lower dimensions, 4/13 *P. jonesi* upper dimensions and 11/16 *P. whitei* measurements, the female mean figure is actually larger than that of the male. This finding is surprising in view of the larger overall size of the male cranium as compared with that of the female in all of the comparisons hitherto possible (Freedman, 1957 and 1965).

From the results of the analysis of metrical sexual dimorphism in the premolar–molar dentition of the 3 *Parapapio* spp., it would seem that pooling of data from the 2 sexes for inter-specific comparisons can be validated except, as expected, for P3 l(h).

(b) Comparison of the 3 *Parapapio* spp. at Sterkfontein.

Still using the previously described material only, a comparison was next made of the premolar and molar dimensions of the 3 *Parapapio* spp. from Sterkfontein, using pooled male and female data. The results are shown in Tables 2A and 2B and "t" tests are again used to assess the comparisons. Of the 39 tests on upper tooth dimensions, 31 are significant at the 5% level or higher; using only the molars, 26/27 tests were significant. In the lower tooth comparisons, of the 42 "t" tests performed, 31 were significant at the 5% level or better; in the molars, 27/30 tests were significant. The *P. whitei–P. broomi* comparisons of the lower teeth include the fewest number of significant "t" test results, but even here, 7/10 molar dimensions differ at the 5% level or higher. For each dimension in both the upper and lower teeth the pattern is consistently: *P. whitei* >*P. broomi* >*P. jonesi*.

(c) Comparison of the new and old samples of each of the 3 *Parapapio* spp. from Sterkfontein.

The 103 newly excavated *Parapapio* specimens from Sterkfontein used in this study include only a very few fairly complete cranial and mandibular specimens (Plates 1 and 2); most of the specimens are only single teeth or small groups of teeth. All of these specimens were tentatively classified on the assumption of 3 progressively larger species being present. (In the Appendix they are listed under individual tooth types as *P. jonesi, P. broomi* and *P. whitei*). Assignment was essentially subjective and based on overall size and apparent size discontinuities. The 3 groups resulting (= sample I) were then compared by "t" tests with the earlier sample (Freedman, 1957) from the same site (= sample II). Of the 31 upper tooth comparisons made (Table 3A), only 3 tests (2 of these in *P. whitei*) were significant at the 5% level or higher; in the 32 lower tooth comparisons (Table 3B), again only 3 significant differences (all in *P. jonesi*) were found. Because of the paucity of material of *P. whitei,* only P^3, P^4, M^1 and M_3 could be compared. Of the 11 tests on these *P. whitei* teeth, 2 were significant, 1 at the 0,01% level and the other at 0,001% level. Comparing the various mean values for samples I and II for all 3 species, in the upper teeth the new sample mean values were greater than those of the old sample in all but 7 of the 31 instances; in the lower teeth, the new sample mean was greater than the old in only 11 out of the 32 comparisons made.

(d) Statistical summary of the dimensions of the upper and lower premolar and molar dimensions of the *Parapapio* spp. from Sterkfontein.

Tables 4A and B are derived from the combined old and new samples. The numbers of specimens of *P. whitei* are mostly still small but the *P. broomi* and *P. jonesi* samples are now mostly over 10 and half of the samples include over 20 individual measurements. An oddity is the fact that the numbers of *P. broomi* specimens in the various categories are about double those of *P. jonesi* in the upper teeth, whilst in the lower teeth the *P. jonesi* numbers are mostly greater. It is not at present clear whether these differences could be due to chance effects or to misassignments. The coefficients of variation (C.V.) and the standard deviations (S.D.) are, for the most part, reasonable, except for P3 l(h). These dimensions (and those of the canines) exhibit sexual dimorphism and hence high standard deviations and coefficients of variation are to be expected when the 2 sexes are lumped. The other high values for these statistics are for certain upper tooth dimensions (e.g. P^3 b, P^4 l and M^1 l) of *P. whitei.* Sample sizes are small here and the high values result from single rather large specimens.

(e) Size-frequency distribution of M_3 of *Parapapio* spp. from Sterkfontein.

To investigate further the *Parapapio* specimens from Sterkfontein, it was decided to re-examine one of the major diagnostic criteria hitherto used for classifying this material. For this purpose the M_3 tooth was selected. This tooth was chosen as the hypoconulid makes identification certain, whereas with the other molars there is often some uncertainty as to the position of the tooth in the toothrow, and damaged roots may even make an upper-lower tooth distinction difficult. Further, for this tooth a good sample of over 50 specimens was available. This sample includes the previously described material (Freedman, 1957), which had only been utilized if the sex could be determined, and the new batch of specimens (Appendix) in which every available specimen was measured.

Figure 1 is a histogram of M_3 l for 48 specimens of these 2 batches of *Parapapio* specimens from Sterkfontein. With no selection or subdivision the distribution is obviously bimodal and possibly trimodal. When 2 dimensions of M_3 (mesial breadth, bm, and maximum length, l) are plotted for the 41 available specimens (Fig. 2), there is an apparent cluster below about 10,5 mm breadth and 13,5 mm length, and another less clear group above about 11,0 mm breadth and 16,0 mm length. For making the second subdivision, a cut off at about 16,0 mm appears clear; for the breadth, 11,0 mm seems the logical point on the basis of overall tooth size, as a lower cut off would include teeth very much shorter and hence unreasonably much smaller in overall size. Subdivisions at these two length-breadth positions result in 3 groups which correspond with the 3 species postulated for this material.

The separation of the 3 species using the breadth and length of M_3 becomes more obvious if the 2 dimensions are combined into indices (Table 5). Two indices have been used; the robustness value, bm x l, and the crown module, $(bm + l)/_2$ (Goose, 1963). For the robustness values there is only overlap between *P. jonesi* and *P. broomi*. This overlap is due to a single large tooth, a male *P. jonesi* (STS. 258); the next largest tooth in *P. jonesi* has a robustness value of only 123,69. For the crown module ranges there is no actual overlap but the same single large male *P. jonesi* tooth just equals the lowest *P. broomi* figure.

DISCUSSION

It has been previously noted (Freedman, 1957) that the overall ranges for each dimension (by sex) of the pooled *Parapapio* material from Sterkfontein (i.e. of all 3 species together) appear to be too great for a single species, when a modern cercopithecoid species (*Papio ursinus*) is used as a standard. The possibility was also considered that the whole of the *Parapapio* material might represent a simple, temporal size increase, as the Sterkfontein material is generally believed to have accumulated over a considerable time. However, during excavation of the site there was no apparent evidence of such a size increase up through the deposit (Robinson—personal communication).

Analysis of the distribution of the *Parapapio* material from the other South African limestone deposits where this genus has been found also tends to discount the possibility that the Sterkfontein *Parapapio* material represents a chronocline. Thus, examination of Table 6 shows that only at Sterkfontein and Makapan are all three *Parapapio* species present. These are, however, the only 2 sites from which reasonable numbers are available and it is also interesting to note that the 3 species are present at these sites in very similar proportions. (The value of *chi square* obtained on comparing these two distributions is 1 803 with 2 degrees of freedom, which is well below the 5% level of significance). Although numbers are small at the other sites, it is noteworthy that at Taung only *P. jonesi* and *P. whitei* have been recovered, whilst from Bolt's Farm only *P. broomi* and *P. whitei*. Of special interest is the fact that only *P. jonesi* has been found at both Swartkrans and Kromdraai, which are both of more recent age than Sterkfontein and Makapan (Brain, 1958). These latter findings all take on added significance when one recalls that *P. broomi* is by far the most common form at both Sterkfontein and Makapan, whilst *P. whitei* is the least common.

Maier (1970) has recently described twenty important new specimens from Makapan which he refers to the 5 previously described species from that site. Of this very good material, he refers 6 specimens to *P. jonesi*, 7 to *P. broomi* and 2 to *P. whitei*. He also suggests that, on the basis of this new material, several previously described *Parapapio* specimens from Makapan require reclassification. Maier gives very full anatomical descriptions of the new specimens and is able to extend considerably our morphological knowledge of the populations of these 3 species at that site. However, although detailed measurements of the various specimens are included, he has not attempted any detailed metrical comparisons. It would seem that a full statistical re-assessment of the 69 *Parapapio* specimens now known from Makapan (similar to that made here for Sterkfontein) would be extremely valuable. The two populations could then be compared both morphologically and metrically and, hopefully, would resolve a number of the presently contentious aspects.

The analyses made earlier, and also the above considerations, all seem to support the probability that the Sterkfontein *Parapapio* material represents 3 species and the scanty cranial evidence available also tends to support this same hypothesis (Freedman, 1957 and 1965). A recent study by Swindler, McCoy and Hornbeck (1966) is also of interest in this connection, as these authors have shown that, on dental metrical data alone, two extant cercopithecoid species, *Papio ursinus* and *Papio anubis*,

show very considerable overlap for all dental dimensions studied.

From the foregoing analysis and review, it would then seem that 3 species of increasing size, *P. jonesi, P. broomi* and *P. whitei*, still best account for the *Parapapio* material hitherto described from Sterkfontein.

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TABLE 1 A

STATISTICAL COMPARISON OF THE MALE AND FEMALE UPPER PREMOLAR AND MOLAR TEETH IN EACH OF THE 3 *PARAPAPIO* SPP. FROM STERKFONTEIN (in mm)

Species	Statistics	P^3		P^4		M^1			M^2			M^3		
		b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	l
P. broomi	Male	8,15	8,33	8,94	6,63	9,90	9,03	9,95	11,47	10,87	11,38	11,34	9,04	11,34
	Female	7,33	6,49	8,32	6,47	9,52	8,77	9,63	10,86	10,11	10,98	10,53	8,77	11,09
	"t"	** 4,02	* 2,54	* 2,16	1,19	1,86	0,76	1,35	1,62	*** 4,41	1,58	2,01	0,70	0,76
	d.f.	12	13	16	15	14	10	15	9	12	15	9	9	10
P. jonesi	Male	7,5	4,3	7,7	5,6	9,00	8,60	8,30	10,40	9,60	10,15	10,85	8,45	10,25
	Female	7,05	5,38	7,70	6,03	8,77	7,83	8,87	10,45	8,85	10,13	9,80	7,87	9,63
	"t"	1,15	0,73	0,00	2,71	1,75	1,29	0,88	0,12	1,24	0,03	3,21*	1,29	1,45
	d.f.	3#	2#	2#	3#	2	2	4	1	1	3	3	3	3
P. whitei	Male	–	–	8,6	6,7	–	–	10,4	–	–	–	–	–	–
	Female	7,87	7,42	8,78	6,90	10,57	10,00	10,56	12,83	11,82	12,72	12,80	11,35	12,77
	"t"	–	–	0,44	0,23	–	–	0,29	–	–	–	–	–	–
	d.f.	–	–	4#	4#	–	–	4#	–	–	–	–	–	–

"t" test significance levels: * = 0,05, ** = 0,01, *** = 0,001
modified "t" test (Simpson, Roe & Lewontin, 1960, p. 183)

TABLE 1 B

STATISTICAL COMPARISON OF THE MALE AND FEMALE LOWER PREMOLAR AND MOLAR TEETH IN EACH OF THE 3 *PARAPAPIO* SPP. FROM STERKFONTEIN (in mm)

Species	Statistics	P_3		P_4		M_1			M_2			M_3			
		b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	bh	l
P. broomi	Male	6,00	14,5	7,15	7,75	7,97	8,03	9,80	10,15	9,93	11,33	10,05	9,10	5,95	14,83
	Female	5,50	8,37	6,98	7,14	8,27	8,34	9,09	9,93	9,43	11,56	10,13	9,30	6,77	14,71
	"t"	1,60	*** 5,60	0,53	1,74	0,79	0,74	1,32	0,41	1,10	0,53	0,17	0,44	1,51	0,29
	d.f.	8	8	6	8	6	6	8	7	7	9	5	8	3	10
P. jonesi	Male	5,45	14,95	7,01	7,05	8,08	8,08	9,10	9,64	9,54	10,78	9,50	8,67	4,60	13,2
	Female	4,90	8,69	6,50	6,66	7,36	7,47	8,42	9,31	9,02	10,39	9,20	8,35	5,04	12,82
	"t"	** 3,13	*** 9,00	2,10	* 2,32	*** 5,07	** 4,25	1,78	1,51	* 2,38	2,04	1,03	0,88	1,10	1,41
	d.f.	12	12	15	13	10	9	13	12	11	13	6	7	4	7
P. whitei	Male	5,53	16,4	7,05	7,80	8,30	8,65	9,38	10,65	10,70	12,13	11,10	10,23	6,5	16,17
	Female	5,77	11,33	7,20	7,60	8,67	8,87	10,17	10,63	10,30	12,97	11,00	10,40	–	16,67
	"t"	1,12	2,40	0,26	0,41	1,04	1,13	** 5,01	0,08	1,70	* 2,91	0,67	0,39	–	1,34
	d.f.	4	2 #	3	3	3	3	5	3	3	4	3	3	–	4

"t" test significance levels: * = 0,05, ** = 0,01, *** = 0,001
modified "t" test (Simpson, Roe & Lewontin, 1960, p. 183)

TABLE 2 A

STATISTICAL COMPARISON OF THE UPPER PREMOLAR AND MOLAR TEETH (in mm) OF *PARAPAPIO* SPP. FROM STERKFONTEIN (DATA FROM FREEDMAN, 1957)

Species		P^3		P^4		M^1			M^2			M^3		
		b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	l
P. broomi: Mean		7,64	7,23	8,59	6,54	9,64	8,81	9,65	11,23	10,49	11,12	10,90	8,89	11,19
P. jonesi: Mean		7,10	5,28	7,66	5,90	8,74	8,07	8,62	10,16	9,12	10,14	10,22	8,10	9,88
P. whitei: Mean		7,87	7,42	8,75	6,87	10,57	10,00	10,53	12,83	11,82	12,72	12,80	11,35	12,77
P. broomi vs *P. jonesi*	"t"	2,06	2,08	** 2,98	*** 3,92	*** 5,58	** 3,08	*** 4,78	** 3,26	*** 5,53	*** 3,60	1,62	* 2,28	*** 4,20
	d.f.	19	17	21	20	24	19	28	18	20	20	14	14	15
P. jonesi vs *P. whitei*	"t"	* 2,70	1,35	*** 6,21	* 2,48	*** 9,43	*** 6,21	*** 5,40	*** 8,96	*** 6,95	*** 6,91	** 4,71	*** 7,52	** 5,13
	d.f.	6	6	9	9	9	10	10	9	9	9	5	5	6
P. whitei vs *P. broomi*	"t"	0,65	0,19	0,52	1,55	*** 4,28	*** 4,60	** 3,55	*** 5,12	*** 4,87	*** 5,76	** 3,26	*** 4,83	** 3,61
	d.f.	17	17	22	21	21	17	24	19	21	21	11	11	13

"t" test significance levels: * = 0,05, ** = 0,01, *** = 0,001

TABLE 2 B

STATISTICAL COMPARISON OF THE LOWER PREMOLAR AND MOLAR TEETH (in mm) OF *PARAPAPIO* SPP. FROM STERKFONTEIN (DATA FROM FREEDMAN, 1957)

Species		P_3		P_4		M_1			M_2			M_3			
		b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	bh	l
P. broomi: Mean		5,63	11,16	7,06	7,23	8,20	8,24	9,31	10,07	9,72	11,42	10,19	9,30	6,22	14,72
P. jonesi: Mean		5,07	10,78	6,77	6,82	7,51	7,59	8,61	9,29	9,02	10,42	9,30	8,40	4,95	12,71
P. whitei: Mean		5,65	12,60	7,14	7,68	8,52	8,78	9,71	10,64	10,46	12,55	11,06	10,30	6,50	16,42
P. broomi vs *P. jonesi*	"t"	***3,77	0,32	1,68	**2,85	***4,22	***3,88	**3,01	***3,92	**3,10	***5,97	***4,73	***4,95	***4,96	***8,31
	d.f.	31	31	31	33	27	26	33	30	29	32	20	24	15	27
P. jonesi vs *P. whitei*	"t"	**3,20	1,02	1,44	***4,44	***4,91	***6,07	***3,98	***5,31	***4,88	***9,92	***11,00	***8,17	***5,06	***12,01
	d.f.	23	20	23	23	20	18	25	22	21	23	14	15	8	17
P. whitei vs *P. broomi*	"t"	0,12	0,74	0,36	1,99	1,33	*2,46	1,39	*2,20	*2,56	***4,25	**3,56	***4,14	0,58	***5,96
	d.f.	18	17	16	18	15	16	20	16	16	19	14	17	9	20

"t" test significance levels: * = 0,05, ** = 0,01, *** = 0,001

TABLE 3 A

COMPARISON OF THE UPPER PREMOLAR AND MOLAR TEETH (in mm) OF TWO SAMPLES OF 3 SPECIES OF *PARAPAPIO* FROM STERKFONTEIN (I = NEW SAMPLE; II = 1957 SAMPLE)

Species	Statistics	P^3		P^4		M^1			M^2			M^3		
		b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	l
P. jonesi	M (I)	–	–	7,87	5,95	8,55	8,10	8,93	10,44	9,26	10,50	9,85	8,86	10,00
	M(II)	7,10	5,28	7,77	6,11	8,74	8,07	8,62	10,16	9,12	10,13	10,08	8,07	9,85
	"t"	–	–	0,67	0,42	0,64	0,06	0,73	1,05	0,62	1,61	0,71	2,99 *	0,70
	d.f.	–	–	8	8	7	7	11	8	8	12	10	9	11
P. broomi	M(I)	7,70	7,80	8,45	6,75	9,82	8,92	9,95	11,43	10,50	11,21	10,60	8,92	10,87
	M(II)	7,65	7,16	8,60	6,54	9,64	8,81	9,65	11,23	10,49	11,18	10,98	9,09	11,21
	"t"	0,21	0,85	0,55	1,19	1,00	0,47	1,19	0,62	0,05	0,15	0,98	0,45	1,16
	d.f.	20	19	24	23	23	18	24	19	22	26	19	18	20
P. whitei	M(I)	9,5	8,4	9,93	7,90	11,1	10,7	13,2	–	–	–	–	–	–
	M(II)	7,87	7,42	8,75	6,87	10,57	10,08	10,53	12,83	11,82	12,72	12,80	11,35	12,72
	"t"	3,74	0,39	5,44 ***	1,67	1,16	1,07	5,43 **	–	–	–	–	–	–
	d.f.	2	3	7	6	3	4	5	–	–	–	–	–	–

"t" test significance levels: * = 0,05, ** = 0,01, *** = 0,001

TABLE 3 B

COMPARISON OF THE LOWER PREMOLAR AND MOLAR TEETH (in mm) OF TWO SAMPLES OF 3 SPECIES OF *PARAPAPIO* FROM STERKFONTEIN (I = NEW SAMPLE; II = 1957 SAMPLE)

Species	Statistics	P_3		P_4		M_1			M_2			M_3			
		b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	bh	l
P. jonesi	M(I)	5,15	14,55	6,17	6,97	7,23	7,40	9,18	8,70	8,28	10,44	8,99	7,92	5,00	12,75
	M(II)	5,07	10,78	6,69	6,82	7,51	7,59	8,61	9,29	9,02	10,42	9,30	8,40	4,95	12,71
	"t"	0,25	1,58	1,76	0,76	1,09	0,73	1,62	2,72 *	3,31 **	0,11	1,91	2,35 *	0,26	0,17
	d.f.	19	18	24	22	18	16	23	26	25	27	16	18	13	19
P. broomi	M(I)	4,8	15,0	7,0	7,1	7,97	8,03	9,87	9,20	9,00	11,40	9,82	8,96	6,22	14,52
	M(II)	5,63	11,16	7,06	7,23	8,20	8,24	9,31	10,00	9,72	11,42	10,19	9,30	6,22	14,72
	"t"	1,92	1,04	0,15	0,27	0,78	0,72	1,28	2,09	1,63	0,05	1,67	1,75	0,02	0,92
	d.f.	13	14	12	14	13	14	16	13	13	15	21	24	18	26
P. whitei	M(I)	–	–	–	–	–	–	–	–	–	–	11,4	10,4	6,1	15,3
	M(II)	5,65	12,60	7,14	7,68	8,52	8,78	9,71	10,64	10,46	12,55	11,06	10,30	6,50	16,42
	"t"	–	–	–	–	–	–	–	–	–	–	2,05	0,22	0,77	2,10
	d.f.	–	–	–	–	–	–	–	–	–	–	4	4	1	5

"t" test significance levels: * = 0,05; ** = 0,01, *** = 0,001

TABLE 4 A

STATISTICAL SUMMARY OF THE DIMENSIONS OF THE UPPER PREMOLAR AND MOLAR TEETH (in mm) OF *PARAPAPIO* SPP. FROM STERKFONTEIN

Species	Statis-tics	P^3		P^4		M^1			M^2			M^3		
		b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	l
P. jonesi	M	7,10	5,28	7,80	6,08	8,70	8,08	8,69	10,30	9,19	10,29	9,97	8,43	9,93
	N	5	4	10	10	9	9	13	10	10	14	12	11	13
	S.D.	0,31	1,63	0,20	0,46	0,36	0,55	0,64	0,42	0,34	0,46	0,55	0,58	0,38
	C.V.	4,4	30,9	2,6	7,6	4,1	6,8	7,3	4,1	3,8	4,4	5,5	6,9	3,8
P. broomi	M	7,66	7,31	8,57	6,59	9,68	8,84	9,72	11,29	10,49	11,19	10,87	9,05	11,12
	N	22	21	26	25	25	20	26	21	24	28	21	20	22
	S.D.	0,48	1,46	0,58	0,38	0,37	0,43	0,54	0,68	0,51	0,56	0,80	0,70	0,61
	C.V.	6,2	20,0	6,7	5,8	3,9	4,9	5,5	6,0	4,8	5,0	7,4	7,7	5,5
P. whitei	M	8,28	7,62	9,14	7,13	10,68	10,18	10,91	12,83	11,82	12,72	12,80	11,35	12,77
	N	4	5	9	8	5	6	7	6	6	6	2	2	3
	S.D.	0,87	1,97	0,66	0,85	0,42	0,54	1,09	0,55	0,77	0,65	–	–	– –
	C.V.	10,5	25,9	7,2	11,9	4,0	5,2	10,0	4,3	6,5	5,1	–	–	– –

TABLE 4 B

STATISTICAL SUMMARY OF THE DIMENSIONS OF THE LOWER PREMOLAR AND MOLAR TEETH (in mm) OF *PARAPAPIO* SPP. FROM STERKFONTEIN

Species	Statis-tics	P_3		P_4		M_1			M_2			M_3			
		b	l(h)	b	l	bm	bd	l	bm	bd	l	bm	bd	bh	l
P. jonesi	M	5,08	11,16	6,61	6,85	7,47	7,56	8,72	9,10	8,77	10,43	9,18	8,21	4,97	12,73
	N	21	20	26	24	20	18	25	28	27	29	18	20	15	21
	S.D.	0,40	3,33	0,56	0,38	0,40	0,41	0,73	0,60	0,65	0,42	0,36	0,49	0,35	0,54
	C.V.	7,8	29,8	8,5	5,6	5,4	5,4	8,3	6,5	7,4	4,1	4,0	6,0	7,1	4,3
P. broomi	M	5,57	11,40	7,06	7,22	8,15	8,20	9,40	9,95	9,62	11,42	10,00	9,14	6,22	14,63
	N	15	16	14	16	15	16	18	15	15	17	23	26	20	28
	S.D.	0,46	3,59	0,39	0,44	0,46	0,44	0,70	0,60	0,62	0,52	0,55	0,51	0,53	0,57
	C.V.	8,2	31,5	5,5	6,2	5,6	5,4	7,4	6,1	6,4	4,6	5,5	5,6	8,5	3,9
P. whitei	M	5,65	12,60	7,14	7,68	8,52	8,78	9,71	10,64	10,46	12,55	11,12	10,32	6,37	16,26
	N	6	4	5	5	5	5	7	5	5	6	6	6	3	7
	S.D.	0,23	2,80	0,45	0,37	0,39	0,22	0,46	0,21	0,31	0,55	0,19	0,38	0,38	0,62
	C.V.	4,1	22,2	6,3	4,8	4,6	2,5	4,7	2,0	3,0	4,4	1,7	3,6	5,9	3,8

TABLE 5
OBSERVED RANGES FOR TWO INDICES (ROBUSTNESS VALUE & CROWN MODULE) FOR 41 M_3 TEETH OF THE 3 *PARAPAPIO* SPP. FROM STERKFONTEIN

Index	*P. jonesi* (N = 15)	*P. broomi* (N = 20)	*P. whitei* (N = 6)
Robustness value	103,32 – 130,00	126,00 – 166,92	172,05 – 184,80
Crown module	10,35 – 11,50	11,50 – 13,15	13,30 – 13,85

TABLE 6
NUMBER OF SPECIMENS OF *PARAPAPIO* DESCRIBED FROM VARIOUS SOUTH AFRICAN LIMESTONE DEPOSITS

Species	Taung	Sterkfontein	Makapan* (limeworks)	Swartkrans	Kromdraai (faunal site)	Bolt's Farm
P. jonesi	1	25	15	3	2	0
P. broomi	0	43	34	0	0	5
P. whitei	3	14	5	0	0	2

* Excluding Maier (1970)

APPENDIX 1

MEASUREMENTS (in mm) OF NEW *PARAPAPIO* MATERIAL FROM STERKFONTEIN
1. SPECIMENS TENTATIVELY ASSIGNED TO *P. JONESI*

(a) Upper teeth

Spec. No.	P^3 b	P^3 l(h)
STW 18	8,1	7,5

Spec. No.	P^4 b	P^4 l(h)
STW 18	–	7,0
23	7,8	–
27	8,0	6,1
77	7,8	5,8

Spec. No.	M^1 bm	M^1 bd	M^1 l
STW 18	–	–	9,3
23	9,1	8,6	9,6
53	8,0	7,6	7,9

Spec. No.	M^2 bm	M^2 bd	M^2 l
STW 18	11,1	9,6	11,0
20	10,2	9,4	10,7
23	10,3	9,0	10,6
24	–	–	10,2
27	10,6	9,3	10,4
34	10,0	9,0	10,1

Spec. No.	M^3 bm	M^3 bd	M^3 l
STW 18	10,5	–	10,4
20	9,7	8,2	10,0
24	–	–	9,8
27	9,9	8,2	10,1
49	10,0	9,0	10,3
50	10,1	9,0	9,8
72	9,4	9,0	9,6
81	9,4	9,1	10,1

(b) Lower teeth

Spec. No.	P_3 b	P_3 l(h)
STW 3	5,2	15,4
57	5,1	13,7

Spec. No.	P^4 b	P^4 l(h)
STW 3	6,2	7,2
9	6,2	6,5
46	6,3	7,1
78	6,0	7,1

Spec. No.	M_1 bm	M_1 bd	M_1 l
STW 3	(7,6)	(7,9)	10,0
9	–	–	8,4
22	(7,0)	(7,2)	8,3
46	–	–	9,2
82	7,1	7,1	10,0

Spec. No.	M_2 bm	M_2 bd	M_2 l
STW 3	8,8	8,3	11,2
9	8,9	7,9	10,1
11	(9,3)	8,8	10,4
15	8,8	8,6	11,0
22	8,6	8,0	10,1
33	9,1	–	10,3
46	–	8,5	9,8
51	7,8	8,0	10,2
64	9,0	8,4	10,8
65	8,0	8,0	10,5

Spec. No.	M_3 bm	M_3 bd	M_3 bh	M_3 l
STW 3	8,8	7,5	4,8	13,0
9	8,9	7,6	4,6	12,5
11	–	8,4	5,0	12,8
22	9,0	8,1	–	12,6
33	9,1	7,7	4,6	13,0
43	9,2	8,1	5,4	13,0
53	9,5	8,6	5,2	12,6
56	8,4	7,4	5,4	12,3

APPENDIX 2

MEASUREMENTS (in mm) OF NEW *PARAPAPIO* MATERIAL FROM STERKFONTEIN (continued)
2. SPECIMENS TENTATIVELY ASSIGNED TO *P. BROOMI*

(a) Upper teeth

Spec. No.	P^3 b	P^3 l(h)
STW 10	7,2	7,4
14	7,7	5,9
58	7,6	9,0
84	8,2	8,6

Spec. No.	P^4 b	P^4 l(h)
STW 10	8,5	7,2
12	8,7	5,9
14	8,6	7,5
58	8,5	6,6
84	7,9	6,1
2	8,5	7,2

Spec. No.	M^1 bm	M^1 bd	M^1 l
STW 2	10,1	9,1	10,3
6	9,6	8,5	10,3
10	9,7	9,1	10,5
58	9,5	9,0	9,5
67	10,0	8,8	9,5
74	10,1	9,0	9,6

Spec. No.	M^2 bm	M^2 bd	M^2 l
STW 2	11,9	11,2	12,1
10	11,4	10,3	11,4
12	11,0	10,1	10,5
14	11,2	9,9	11,1
25	–	10,4	11,2
58	12,1	11,2	11,7
63	10,5	10,2	10,5
67	12,4	11,4	12,1

Spec. No.	M^3 bm	M^3 bd	M^3 l
STW 12	(11,5)	9,0	10,7
58	10,8	9,0	11,2
30	9,3	–	11,7
73	11,0	9,4	10,7
87	11,1	9,0	10,8

APPENDIX 3

MEASUREMENTS (in mm) OF NEW *PARAPAPIO* MATERIAL FROM STERKFONTEIN (continued)

2. SPECIMENS TENTATIVELY ASSIGNED TO *P. BROOMI* (continued)

(b) Lower teeth

Spec. No.	P_3 b	P_3 l(h)
STW 70	4,8	15,0

Spec. No.	P_4 b	P_4 l(h)
STW 1	7,0	7,1

Spec. No.	M_1 bm	M_1 bd	M_1 l
STW 61	8,3	8,3	10,4
83	7,5	7,7	9,2
1	(8,1)	(8,1)	10,0

Spec. No.	M_2 bm	M_2 bd	M_2 l
STW 1	9,5	9,0	11,0
69	8,9	8,9	11,7
83	9,5	9,1	11,1

Spec. No.	M_3 bm	M_3 bd	M_3 bh	M_3 l
STW 1	9,8	8,7	5,8	14,1
8	9,6	8,6	5,9	14,8
13	11,0	9,4	–	14,7
17	9,5	8,2	6,5	13,8
32	10,4	8,8	6,0	14,2
37	10,1	9,7	6,0	14,5
38	10,2	9,8	7,0	14,6
40	9,3	8,3	6,0	14,7

Spec. No.	M_3 (contd.) bm	M_3 (contd.) bd	M_3 (contd.) bh	M_3 (contd.) l
STW 41	9,4	9,0	5,9	14,6
42	9,9	9,4	6,8	15,6
47	9,5	8,7	6,8	14,8
83	9,2	8,9	5,7	13,8

3. SPECIMENS TENTATIVELY ASSIGNED TO *P. WHITEI*

(a) Upper teeth

Spec. No.	P^3 b	P^3 l(h)
STW 21	9,5	8,4

Spec. No.	P^4 b	P^4 l(h)
STW 31	10,1	–
35	10,0	8,6
21	9,7	7,2

Spec. No.	M^1 bm	M^1 bd	M^1 l
STW 21	(11,1)	(10,7)	13,2

M^2 Nil

M^3 Nil

(b) Lower teeth

P_3	M_1
Nil	Nil
P_4	M_2
Nil	Nil

Spec. No.	M_3 bm	M_3 bd	M_3 bh	M_3 l
STW 36	11,4	10,4	6,1	15,3

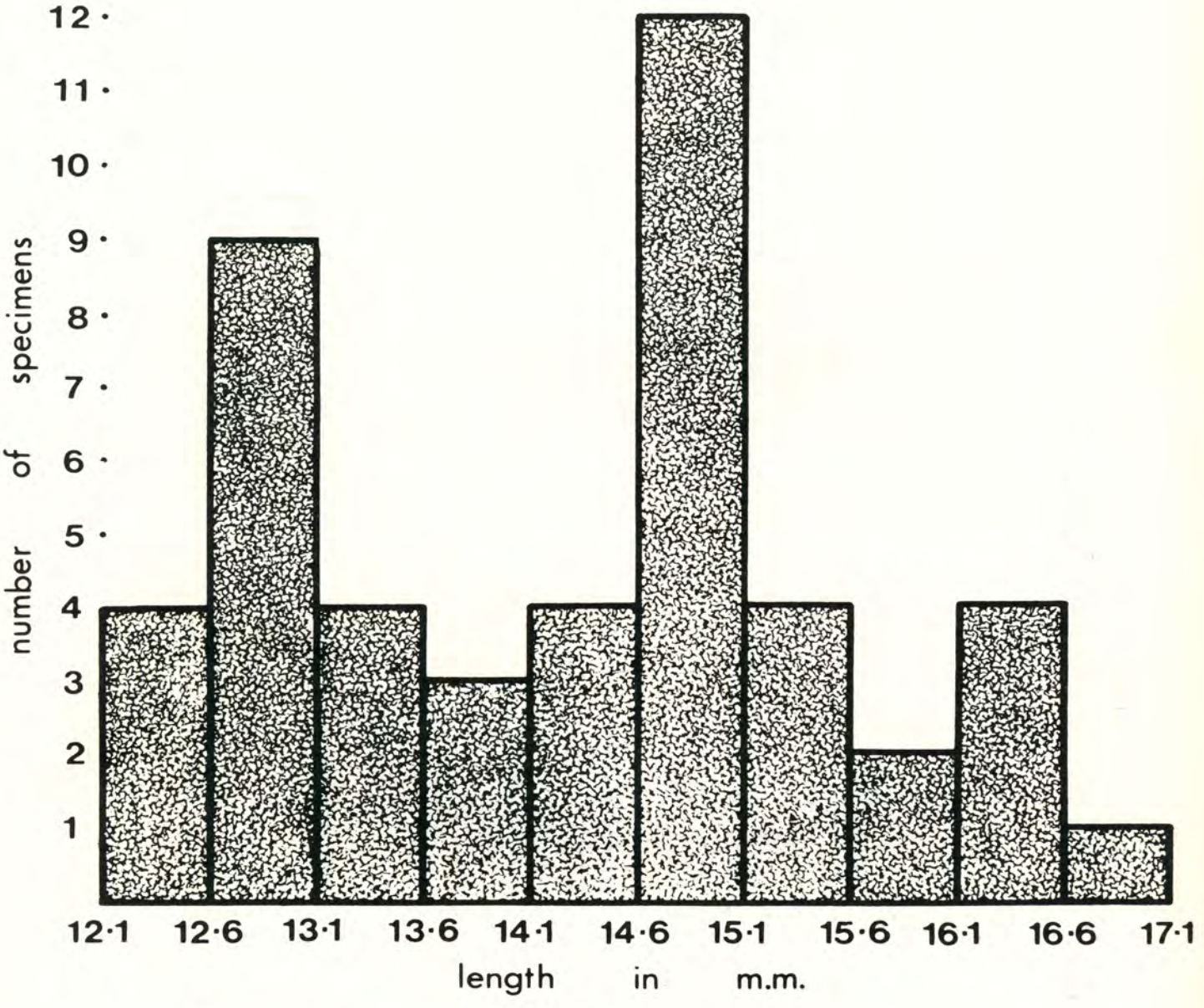


Fig. 1. Histogram of the length (l) of 48 specimens of M_3 of *Parapapio* spp. from Sterkfontein.

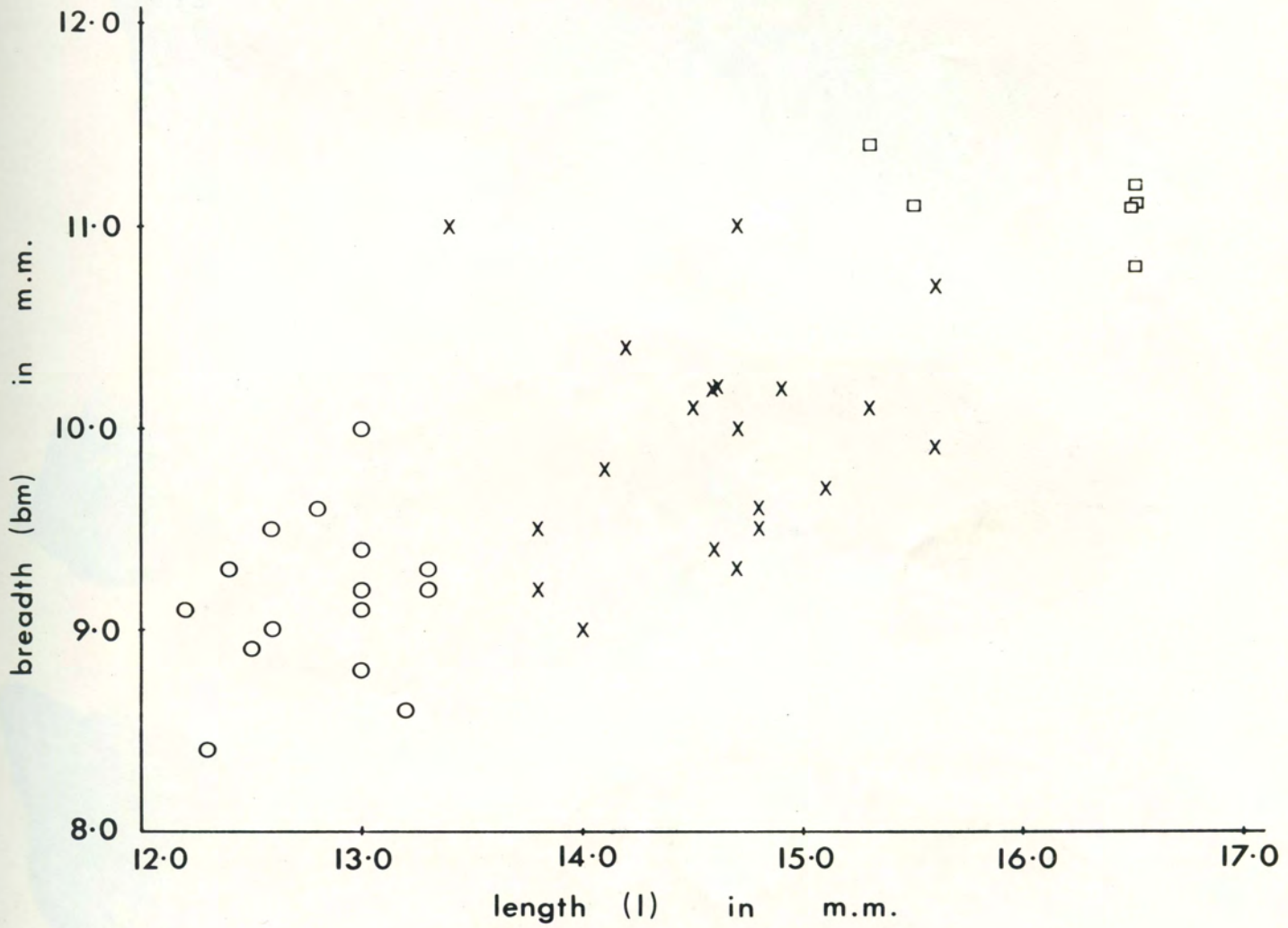


Fig. 2. Scattergram of the length (l) and mesial breadth (bm) of 41 specimens of M_3 of *Parapapio* spp. from Sterkfontein. ○—*P. jonesi*; ×—*P. broomi*; □—*P. whitei*.



Plate 1 From above downwards, dorsal, lateral and ventral views of *P. broomi* female cranium (STW 12).

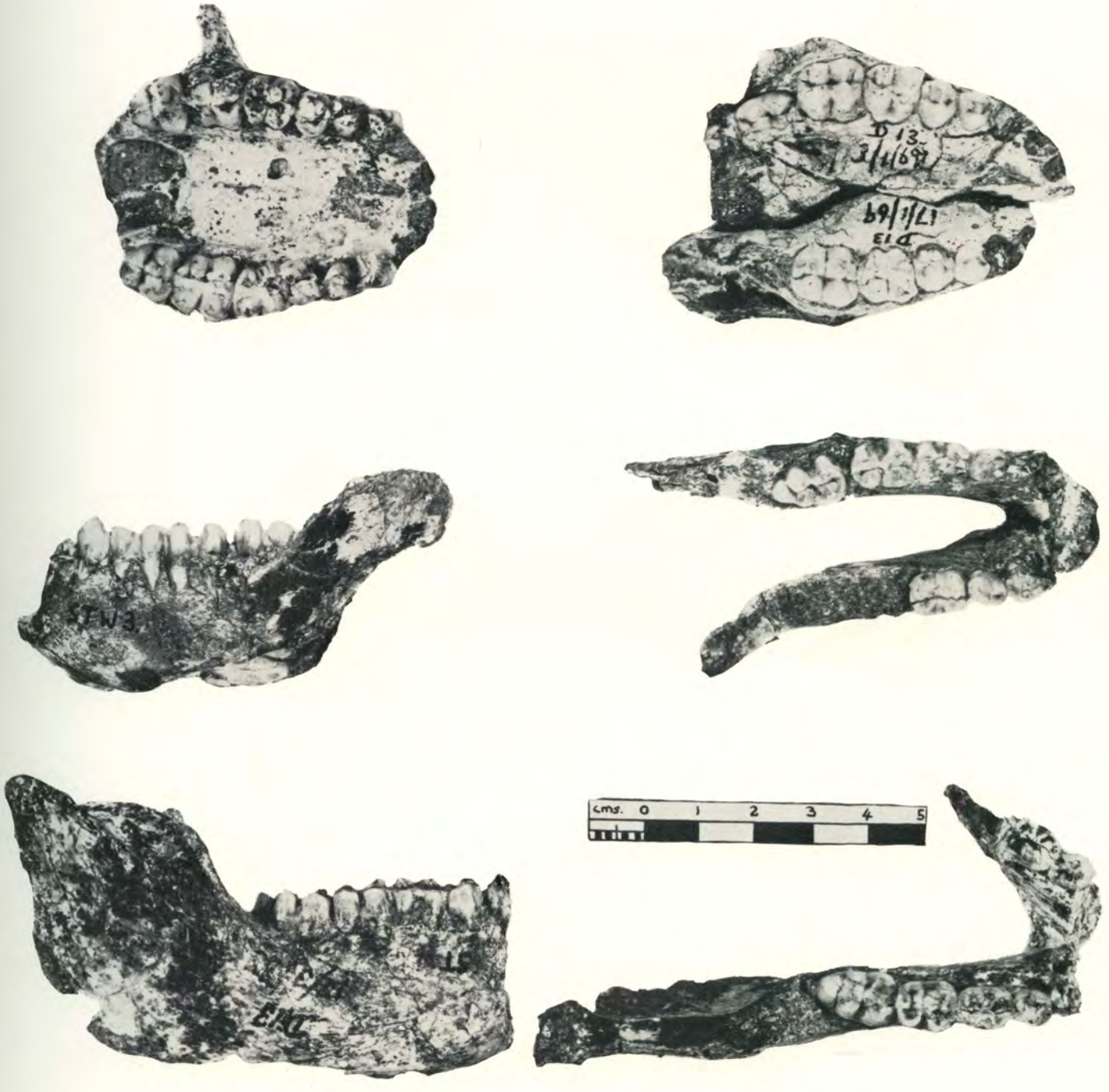


Plate 2 Top: Palates of *P. broomi* females (left, STW 58; right, STW 10)
Centre: Lateral and occlusal views of *P. jonesi* male mandible (STW 3).
Bottom: Lateral and occlusal views of *P. broomi* ? female mandible (STW 1).