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PALAEONTOLOGIA AFRICANA

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

VOLUME 13, 1970

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BERNARD PRICE INSTITUTE FOR PALAEONTOLOGICAL RESEARCH
REPORT OF THE HONORARY DIRECTOR
FOR THE YEAR 1969

The year under review has been one of both consolidation and progress. The decision of the Council for Scientific and Industrial Research to make an annual grant to the University for palaeontological research, outlined in my report for 1968, came into operation at the beginning of the year, replacing the previous arrangement under which it gave financial support to certain individual scientists working within the Institute on specific projects. This ensured a greater degree of collaboration among the staff members, all of whom are now members of the University's organisation and are responsible to the Board of Control, which has been strengthened by the inclusion of an official representative of the C.S.I.R.

STAFF

At the beginning of the year Dr. E. P. Plumstead and Dr. R. J. Davey, until then C.S.I.R. Research Fellows, became full time members of the Institute's staff. Dr. Davey, however, resigned as from the end of August in order to return overseas where opportunities for continuing his specialist studies were more promising than those which southern Africa can offer. Dr. Plumstead, who is in control of palaeobotanical work in the University, had been selected by the Geological Society of South Africa as the du Toit Memorial Lecturer for 1969.

One of the posts of Research Officer which were approved by the University Council in 1968 was filled by the appointment of Mr. B. R. Turner, B.Sc.(Hons.) (Hull) formerly of the staff of the Geological Survey of South Africa, a specialist in sedimentology. The other post was filled by Mr. C. E. Gow, B.Sc.(Hons.) (Cape Town), a vertebrate palaeontologist, formerly on the staff of the South African Museum.

The remainder of the staff of the Institute and the senior bursars prosecuting their studies within it were unchanged during 1969. An additional Honours student, Miss S. Chernin from the Department of Zoology, studied a large labyrinthodont skull from the Luangwa Valley Karroo beds, under the supervision of Dr. Cruickshank.

Tribute should be paid to the zeal displayed by both Dr. Cruickshank and Mr. J. W. Kitching who, in addition to their own research studies, share between them, by mutual arrangement, the burden of the day-to-day management of the Institute's internal problems. Within the University Dr. Cruickshank has attended meetings of the Board of the Faculty of Science and has taken part in discussions on the teaching of palaeontology as part of a degree course incorporating, in addition, archaeology and anatomy. He represents the University on the Board of Governors of the Museums of Man and Science, and is a member of the organising committee for the International Gondwana Symposium which will be held in South Africa in July, 1970. Mr. Kitching is also a member of this committee and will be one of the chief guides on a 12 day excursion through the Karroo which is designed as part of that Symposium. Dr. Plumstead will be chief guide to a post-Symposium excursion.

INTERNATIONAL GONDWANA SYMPOSIUM 1970

This Symposium, under the aegis of the International Union of Geological Sciences and at the invitation of the Government of the Republic of South Africa, will be held during July and the first part of August, 1970. Sessions for lectures and papers will take place in Cape Town and, later, Johannesburg, and there will be two long field excursions. The staff of the Institute will be engaged in various activities connected with both the meetings and the excursions, and their tasks have already commenced. The museum has been equipped with completely new furnishings, and it is anticipated that the Institute's collections, both on exhibition and in store, will be a source of attraction to many of the participants in the Johannesburg meetings. It is hoped to prepare a guide-book to the Museum in time for the Symposium, which will be attended by a number of overseas specialists.

FIELD WORK

Most of the field visits made by Dr. Cruickshank and Dr. Plumstead and Messrs. Kitching, Turner and Gow were undertaken on behalf of the Organising Committee for the Gondwana Symposium for the purpose of acquiring detailed information needed for the preparation of excursion guide-books. Some useful collections were made en route.

Mr. J. Anderson was enabled by the Southern Oil Exploration Corporation (SOEKOR), for whom he is undertaking palynological studies, to spend three months in the continent of Australia where, at several centres, much advanced research on spores and pollen grains in sediments of Permian and Triassic age has been in progress for a number of years. He was enabled to study the material which has led to the establishment of seven zones

in the Permian succession and four zones in the Triassic of that continent. This was made possible by the cordial reception accorded to him by the Australian authorities and palynologists; it is certain that we shall have close co-operation with the Australian experts in this field.

The palaeobotanists on the staff have made a number of field excursions for the collection of study material. These include, under individuals, the following:

Mrs. Anderson—Little Switzerland, the districts of Jamestown and Dordrecht, and Estcourt (for Molteno plants)

Miss Benecke—Vereeniging, Estcourt, and Bergville

Miss Anderson—Weenen, and Estcourt

Miss Dickinson—Hammanskraal quarries (N. of Pretoria).

Mr. B. Maguire, in addition to making further collections of tools at Makapansgat, went with Dr. Heinz of the Medical School on an expedition to study the ecology of the ! Ko Bushmen of Botswana with particular reference to their plant foods. They were accompanied by Miss J. M. Roets, Senior Bursar, also of this department.

For initiation into the mode of occurrence in the field of Karroo vertebrates, Mr. D. Wolfaardt accompanied Mr. Kitching on one of the latter's expeditions.

At Sterkfontein, clearing, hand-sorting and sieving of rubble dumps 1-15 continued throughout the year, according to information supplied by Professor P. V. Tobias. This was essential as a preliminary to further excavation. Blasting was carried out in the West Pit (olim Extension Site) and revealed the presence of some water-worn "foreign" quartzose and quartzite stones.

At Swartkrans Dr. Brain's excavation programme is near completion and laboratory work has yielded a number of additional fossils, including australopithecine remains.

A number of visits were made to Makapansgat in connection with the collecting of specimens for geochronological work. These were made by Prof. L. A. Nicolaysen, Prof. Tobias and Mr. A. Hughes, who were on occasion accompanied by visiting scholars working in the Department of Anatomy.

RESEARCH WORK

It is possible here to give but a brief résumé of the individual investigations that have been in progress in this fundamental branch of the Institute's activities. The full results will appear in the form of published papers in due course.

Dr. A. R. I. Cruickshank has continued his studies on the early Archosaurs, and has completed two papers. One, on *Proterosuchus,* is destined for a symposium which will be held in England in the second half of 1970, to honour Dr. F. R. Parrington, F.R.S. on his retirement from the University of Cambridge. This genus, originally described by Broom from a somewhat imperfect skull, is now considered to include the later-described genus *Chasmatosaurus* Haughton. All the available material, including an almost complete skeleton, has been carefully prepared and studied. The other paper, describing the brain-case of *Euparkeria* from the Upper Beaufort beds, is intended for presentation at the Gondwana Symposium.

A paper of 11 pages, entitled "Reflections on the earliest plant life and its great contribution to the life of to-day", written by Dr. Plumstead, appeared in July as pp.339-349 of the J. Sen Memorial Volume, published in India.

Dr. Plumstead was also engaged in a study of the history of palaeobotanical research in South Africa, on which subject she prepared a paper given before a meeting of the South African Association for the Advancement of Science in July in Pietermaritzburg. She also reviewed the history of fossil plants for the Alex. L. du Toit Memorial Lecture for 1969. This lecture, entitled "Three thousand million years of plant life", was delivered in Johannesburg, Cape Town, Durban and Salisbury, illustrated by numerous lantern slides, and will in due course be published under the aegis of the Geological Society of South Africa.

In the preparation of his M.Sc. thesis, entitled "The distribution of the Karroo vertebrate fauna and its bearing on the zoning of the Beaufort beds of South Africa", Mr. J. W. Kitching has continued his identifications of Karroo fossil reptiles and his consideration of the stratigraphic positions of the localities which yielded them. His work in this field will have a profound effect on our understanding of the areal distribution and the zonal nomenclature of the subdivisions of the Beaufort series.

Other research work on reptilian fossils has been undertaken by Mr. C. E. Gow who, since his appointment, has been engaged on a detailed study of the small skulls and skeletons of the Millerettids, a group of primitive eosuchids. The group contains two morphological forms, typified by the genera *Milleretta* (of which 8 skulls and 1 nearly complete skeleton are available) and *Millerosaurus* (12 skulls, 1 complete skeleton and skeletal fragments).

The skull of *Milleretta* has been found to possess both supratemporal and tabular bones—a new discovery. Acid-prepared skulls will be subjected to X-ray examination.

Since joining the staff, Mr. B. R. Turner has continued his sedimentological studies of the Molteno stage of the Stormberg series which he began while with the Geological Survey of South Africa, and has completed his thesis on the subject for the M.Sc. degree.

Mr. B. Maguire has continued to devote part of his time to the study of stone artefacts found in australopithecine-bearing deposits. He has, for the first time, developed a number of such tools from the refractory Upper Phase I (pink) breccia of the Limeworks deposit (Makapansgat), which have been photographed preparatory to description. He

was associated with Dr. Heinz in an ethnobotanical survey among a group of Bush people living in the Kalahari of Botswana, and considers that these studies have a possible bearing on the ecology of the australopithecines and early hominids.

Breccia recovered from the dumps at Sterkfontein has yielded many crania, jaws, isolated teeth and postcranial skeletal fragments of cercopithecoids and some ungulate remains. Two medical science graduates, Messrs. C. Block and M. Hockman, have completed a provisional inventory of the bones, which include some 300 baboon teeth. Rodent and micro-mammalian remains are being sorted and described by Mr. T. N. Pocock.

From Swartkrans a number of australopithecine remains have been recovered from recently excavated breccia and will be reported in papers being compiled by Dr. C. K. Brain, Dr. J. T. Robinson, Dr. B. G. Campbell, and Mr. R. J. Clarke. These recent discoveries are the property of the University, having been won after the site became its property.

Mr. J. Anderson, employed by Soekor, has been engaged on the examination of spores and pollen from various horizons in the Karroo succession, aimed at the production of a zonal column based on microbotanical remains. At the instance of Soekor, the methods adopted and the progress made by him were examined by Prof. van Zinderen Bakker. His work is still in progress.

Of the research students, three (Mrs. H. Anderson, Miss A. Benecke and Miss S. Dickinson) were engaged in palaeobotanical studies—the first on Molteno plants from the farm Little Switzerland, and the others on Ecca plants from two separate Transvaal localities—Vereeniging and Hammanskraal respectively. Miss J. M. Roets has worked on bone accumulations in Transvaal ape-man-bearing caves with special reference to the bone-collecting habits of both fossil and recent porcupines. Miss S. Chernin, an Honours student, has had as a "project" the reconstruction and description of a large labyrinthodont amphibian skull from Triassic deposits in the Luangwa valley, Zambia. This work has been completed, and will also be presented to the Gondwana Symposium. The palaeobotanical students have been supervised by Dr. Plumstead; the two others by Dr. Cruickshank.

PUBLICATIONS

Volume XII of *Palaeontologia Africana* was published by the Institute in 1969. In addition to the Director's Report for 1968, it contains two papers by Dr. R. J. Davey, and one by each of Dr. G. F. Hart, Mr. R. N. Pienaar, Mr. R. G. Wellbourne (of the Department of Archaeology), and Mr. B. R. Turner. It consists of 204 pages, and contains 21 plates and a number of text-figures.

A paper entitled "A new assemblage of plant fossils from Milorgfjella in Droning Maudland, East Antarctica" by Dr. E. P. Plumstead, including 15 plates, was prepared at the request of the British Antarctic Survey and will be published. Dr. Plumstead also delivered a paper at the July meeting of the South African Association for the Advancement of Science on the History of Palaeobotany in South Africa. She is preparing for publication the full text of the Alex. L. du Toit Memorial Lecture which she delivered at three centres in the Republic and at Salisbury.

Various papers intended for presentation at the Second Gondwana Symposium to be held in 1970 were in the early stages of preparation during the latter part of the year under review.

Several publications have appeared during the course of the year dealing with the results obtained by Professor Dart's research assistant Peter Beaumont. These have been largely concerned with communicating the accurate radio carbon dates for early mining activities investigated in Swaziland and indicate a date of over 40 000 years B.P. for these activities.

TEACHING

As in previous years, senior members of the staff have given courses of lectures to undergraduates in the Departments of Geology and Botany in the University. Instructional seminars and supervision of projects of Honours candidates in Palaeontology are carried on entirely within the Institute.

LIBRARY

Accessions continue at a steady, and ever increasing, rate. The part-time services of Mrs. Edwards were available throughout the year. This has resulted in great progress in the cataloguing of the available material and changes in shelf-arrangement. New shelving has been provided.

ADDITIONS TO AND REARRANGEMENT OF COLLECTIONS

Minor additions to the fossil reptile collections were made during the year as incidental activities while staff members were involved in going over the Excursion routes for the Gondwana Symposium. Dr. Kermack and Dr. Halstead arranged for the Institute to receive small but valuable collections of fossil fish from the Devonian of Scotland and the Welsh Borderlands respectively. These fill gaps in our collection and will be particularly useful for teaching purposes.

Professor Sperber of the University of Alberta kindly donated a small collection of Red River Dinosaur material, largely at the instigation of Professor Tobias.

Considerable additions have been made to the palaeobotanical collections by the Research students. These have already considerably increased our knowledge of the flora of the Molteno stage of the Stormberg and will no doubt also do so for the Ecca.

Palaeoanthropological collecting was limited to the acquisition of a herbarium of plant foods used by the Bushmen, a considerable undertaking.

During the latter part of the year, considerable improvements in the housing of the comparative, recent, mammal material was effected by the University Works Department. This was triggered by the need for a new electricity sub-station to feed the Institute and surrounding buildings, and these installations cut seriously into our limited storage space. As the prepared fossil mammal material is now housed adjacent to the comparative material, this new arrangement will help researchers considerably.

MUSEUM

New Museum cases were delivered at the beginning of the year. The Museum hall has been completely redecorated and equipped with fluorescent lights and new linoleum tiles.

Progress in arranging the new displays was very slow, due largely to the administrative and research commitments of Dr. Cruickshank and Mr. Kitching. The need for specialist technical help in this field is very great.

The collections will however be adequately displayed by the time of the Gondwana Symposium.

OTHER ACCOMMODATION

Last year the attention of the Board was drawn to the need for increased office space in the Institute. The matter was minuted and placed on the Agenda of the Works Department. No concrete developments can be reported nor are plans yet drawn.

However the repainting of the present offices and laboratories has been started and this will be completed in the New Year. We are very grateful to the Maintenance staff for arranging that the work should go to an outside firm for speedy completion.

VISITORS

While the total number of visitors during 1969 was slightly down on the previous year, the range of countries represented by them is in no way reduced.

Notable foreign visitors included Dr. and Mrs. A. W. Gentry and R. J. Clarke of the Centre for Prehistory, Nairobi, Dr. A. Pellat of the Medical School, Salisbury, a group of American Science writers, guests of the Department of Information, Dr. A. Campbell of the Department of Anatomy, Cambridge, Professor C. Howell from Harvard, Dr. L. B. Halstead from Reading, Professor C. Gans from the State University of New York at Buffalo, M. A. Raath of the Queen Victoria Museum, Salisbury, Professor Reyment of the University of Uppsala, Sweden, Drs. Mertens and Koch of West Germany and Drs. Neves and Da Libre from the University of Lourenco Marques.

We also continued to receive a gratifying number of visits from local schools and travellers breaking their journeys in Johannesburg.

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SOME FOSSIL GINKGOPHYTES AND A POSSIBLE VOJNOVSKYALEAN ELEMENT FROM THE GLOSSOPTERIS FLORA OF VEREENIGING, TRANSVAAL

by

S. F. le Roux

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ABSTRACT

A short historical review is given of previously described sites where plant fossils occur in Lower Karroo beds at Vereeniging in the Southern Transvaal. Reference is made to the importance of these sites because of the outstanding discoveries made here in the past. Some new material from the same sites is described and several unusual elements in the *Glossopteris* flora of Vereeniging are recorded for the first time.

Leaves of a plant not previously recorded from Gondwanaland are provisionally described under the term *cf.Nephropsis* on account of a strong resemblance to leaves of the Russian Permian genus *Nephropsis* Zalessky.

The remaining specimens in the assemblage are tentatively placed in the genera *Ginkgoites* Seward and *Psygmophyllum* Schimper respectively. Owing to the paucity of material, type numbers are assigned in certain cases, instead of specific names. Specific identification is attempted, however, in the case of four of the specimens, which are provisionally assigned to *Psygmophyllum kidstoni* Seward.

INTRODUCTION

The fossiliferous Lower Karroo beds occurring at Vereeniging, in the Southern Transvaal, have been for many years a rich source of plant fossils which have shed much light on the nature of the early *Glossopteris* flora in South Africa. A considerable amount of valuable new information concerning this flora became available during the past 25 years as a result of new exposures of fossiliferous deposits. This came about as a consequence of the exploitation of refractory shales by the Vereeniging Brick and Tile Company. These activities started about 25 years ago and were continued for several years. During this time some extensive excavations were made along the northern bank of the Vaal River. The locality is situated about 6 km south of the town on a portion of the original farm Leeuwkuil No. 81, and the excavations concerned are generally known as the "Leeuwkuil Quarries".

During the time when the fossil-bearing deposits were being exposed in these quarries they were intensively exploited by the present author. Collecting was subsequently continued for many years. This eventually led to numerous new discoveries, the most important of which was undoubtedly the discovery of the fructifications of the *Glossopteridae*, which were subsequently described by Dr. Edna Plumstead.

A large collection of plant fossils was built up by the author over a period of many years. The major part of the collection is now lodged in the Bernard Price Institute for Palaeontological Research of the University of the Witwatersrand, Johannesburg. The material which is described in the present paper forms part of the collection and represents the remains of some of the rarer elements of the Vereeniging fossil flora.

NATURE AND RELATIVE STRATIGRAPHIC POSITION

The plant material is preserved in the form of impressions in which there is a complete absence of material suitable for cuticular preparation. The impressions are preserved in fine-grained sediments in which the external morphological features of the specimens are often shown in fine detail.

The fossiliferous layers can be differentiated into distinctly different zones on the basis of colour and texture. These zones occur at specific levels in the sequence of strata overlying the coal in this area. The relative stratigraphic positions of the various specimens under description are described in terms of a previously published description of the different zones as initially exposed (Le Roux, 1963, pp. 1-2).

AGE

The sequence of fossil-bearing beds at Vereeniging forms an integral part of the Coal-measures in this area. These Coal-measures are referred to the Middle Ecca stage of the Karroo system. The general concensus of opinion is that the relative age of the Middle Ecca is Lower Permian. This naturally implies an age lying within very wide limits.

For more exact correlation of the strata, the application of modern methods based on palynology is essential. Investigations of this nature recently carried out by Hart (1966) have led him to the conclusion that the Middle Ecca stage could possibly be of Kungurian age. Further palynological research should be of great value in the elucidation of the question regarding the age of the Middle Ecca. This applies especially to the Vereeniging strata where the occurrence of a peculiar

mixed fossil flora has created some uncertainty regarding the true stratigraphical position of the fossiliferous beds, which are normally included in the Middle Ecca. In a recent discussion of this problem Plumstead (1966, p.6) expresses the opionion that " . . . it is probable that as a result of plant evidence adjustments will have to be made in the classification of the Lower Karroo".

When referring to the age of the Vereeniging fossil plants it is often found convenient to use the term Permo-Carboniferous. This term was derived from the fact that the Vereeniging fossil flora contains elements of both the Permian and Carboniferous periods. This rather vague age designation is of little value, however, when close age determination is demanded.

NAMING AND CLASSIFICATION OF THE FOSSILS

The material which is described in the present paper is of such a nature that the taxonomic position of the plants cannot be determined with any degree of certainty. Some of the specimens are tentatively placed in the genera *Ginkgoites* Seward and *Psygmophyllum* Schimper respectively.

In order to distinguish between the different specimens placed in the genus *Ginkgoites,* it was found to be more satisfactory to assign type numbers rather than specific names. This unusual procedure was also recently adopted by Huard-Moine (1965, p.77) and Plumstead (1967, p.13) in cases where a paucity of material did not justify the institution of a new species.

The remaining material represents impressions of leaves of a plant which has apparently not previously been recorded from Gondwanaland, but which shows a strong resemblance to the Russian Permian genus *Nephropsis* Zalessky. Since there is no conclusive evidence, however, that the new plant was actually generically identical with *Nephropsis* it is thought wiser to describe the specimens concerned provisionally under the term *cf.Nephropsis.*

DESCRIPTION OF THE MATERIAL

GINKGOALES

Genus *GINKGOITES* Seward

The generic name *Ginkgoites* was instituted by Seward (1919, pp.10-11). He motivated the institution of the new name as follows: " . . . In certain instances, for example such leaves as those from the Island of Mull and other Tertiary localities referred to *Ginkgo adiantoides,* there can be no doubt as to the generic identity with the recent species and indeed, so far as concerns form and venation, the Eocene leaves might well belong to *Ginkgo biloba.* On the other hand even in the case of *Ginkgo adiantoides* we lack the confirmatory evidence of flowers and seeds . . .I therefore propose to employ the name *Ginkgoites* for leaves that it is believed belong either to plants generically identical with *Ginkgo* or to very closely allied types . . ."

(A) *Ginkgoites* sp Type A (Plate I, fig. 1 & 1a)

(a) **Material**

Only one specimen is available for study. It is preserved in the form of two counterparts, GK/1 and GK/1a. Specimen GK/1 (Plate I, Figs. 1, 1a) is the more complete of the two counterparts and the description of the plant is therefore mainly based on this specimen.

(b) **Zone**

Buff-coloured silty clay layer (Le Roux, 1963, Plate I, Fig. 2, Layer A, Quarry no. 2).

(c) **Description** (See Plate I, Figs. 1-1a)

The impression is in fine-grained sediment and is that of a single leaf which was evidently torn before preservation. This is clearly indicated by the position of the right-hand lateral lobe.

The original shape of the leaf could have been broadly triangular. The lamina is deeply dissected and divided into 3 primary lobes which converge towards the bases. The lobes have radii of 2,5–3,5 cm and their lateral margins are nearly straight. The lobes are divided into wedge-shaped segments with truncated apices which are repeatedly incised. There is a distinct petiole which is 5 mm long by 2 mm wide. The venation is inconspicuous. Several primary bundles appear to enter each lobe, and by repeated forking give rise to the formation of a number of more or less sub-parallel veins. The veins are spaced about 1 mm apart. The venation is not preserved in sufficient detail to determine whether anastomosis took place or not. The leaf was evidently comparatively thin judging from the faint impression left on the fine-grained sediment. The epidermal features are not preserved and no indication of resin bodies can be detected between the veins.

(d) **Comparisons and discussions**

(i) *General.*

The superficial features of the leaf described here clearly indicate a ginkgoalean origin. The generic identification is based on Dorf's (1958, p.3) modification of a key originally proposed by Florin (1936, p.44) for the identification of ginkgoalean leaves. Any attempt at specific identity would have to be based on the external morphology of a single leaf. Considering the perplexing variability in size and shape of ginkgoalean leaves, this is regarded as an impossible task.

(ii) *Comparisons with Palaeozoic ginkgophytes.*

As far as is known the fossil record of the ginkgophytes beyond the Mesozoic does not include any foliage which could be compared with the new plant from Vereeniging. According to Andrews (1961, p.340) " . . .The most ancient fossil that may with some confidence be attributed to the ginkgophyte line, and which offers some significant clues concerning the evolution of the

living species, is *Trichopitys heteromorpha* from the Lower Permian of Lodeve in southern France.

The latter plant does not show any superficial resemblance to the new plant from Vereeniging, however. Unlike *T. heteromorpha,* the Vereeniging plant shows a remarkable resemblance to the living species. The existence of a plant in Permo-Carboniferous times showing such distinctive ginkgoalean features as *Ginkgoites* sp Type A, is of great phylogenetical interest. It seems to indicate that the earliest ancestors of *Ginkgo biloba* should be sought even farther back in time than was previously thought.

(iii) *Comparisons with Mesozoic ginkgophytes.*

Many of the numerous Mesozoic species show some resemblance to *Ginkgoites* sp Type A. A brief comparison between *G.* sp Type A and similarly deeply lobed leaves from different geological horizons and localities may be of interest.

Of the Mesozoic species the foliage of the widely-spread *Ginkgoites digitata* is certainly the best known. Typical variations in the shapes and sizes of the leaves of this species are illustrated by Seward (1919, Fig. 635, p.17). *G. digitata* is also one of the few species previously recorded from South Africa. It is known to occur in Upper Karroo beds (Upper Triassic) and was first described by du Toit (1927, Text-fig. 16B, p.370).

The lamina of both *G. digitata* and *G.* sp Type A are deeply lobed and the lobes are divided into segments. In the former species the segments are linear oblong with curved margins and obtuse apices. In the latter, however, the segments are wedge-shaped and have straight margins and truncated apices. The petiole of the latter is also much shorter than that of *G. digitata.* The possibility is not excluded, however, that part of the petiole of *G.* Type A was broken off prior to preservation. No marked difference is evident in the venation of the two plants.

The Indian species *G. rajmahalensis* described by Sah & Jain (1965, Text-figs. 3-9, p.156) has, like *G.* sp Type A, deeply incised laminae. Although there seems to be some resemblance between the two plants under discussion as regards their distinctive ginkgoalean features, no close comparison is possible.

Among Triassic species, *G. acosmia* and *G. taeniata,* described by Harris (1935, Fig. 4, p.11 and Fig. 9, p.20) from Greenland, seem to bear some resemblance to the Vereeniging species. This resemblance is of a very superficial nature, however, and consequently it has little or no diagnostic value.

In the Austrian Triassic species *G. lunzenses* described by Kräusel (1943) the leaves were very much larger in size than those of *G.* sp Type A. There is also a marked difference in the mode of division of the laminae of the two plants.

In comparing the leaf of *G.* Type A with those of the Lower Cretaceous species *G. tigrensis* and *G. ticoensis* described by Archangelsky (1965, Plate I, Figs. 1-6, Text-fig. 7, pp.122-128) from Santa Cruz, Argentina, the venation of the latter species appears to be more conspicuous and denser than that of the Vereeniging species.

(iv) *Comparison with* Ginkgo biloba.

The striking resemblance between *Ginkgoites* sp Type A and a leaf of a one year old plant of *Ginkgo biloba* is clearly reflected in Plate I, Figs. 1-2. When the leaves of older specimens of *Ginkgo biloba* are compared with that of *Ginkgoites* sp Type A, the general resemblance becomes less striking, however. This seems to be in agreement with Shaparenko's view (1935, p.5) that primitive characters are more strongly in evidence in the leaves of young ginkgoaceous plants than in older ones. Shaparenko makes an important point in the following statement: "...This matter has to be taken into consideration in describing the fossil *Ginkgo* in order to avoid confusion of the leaf with leaves of other genera and species..."

(d) **Conclusions**

With the meagre evidence available it is impossible to relate *Ginkgoites* sp Type A to any of the known species of this genus. Considering the position of the new plant in time and space, it seems to be more closely related to *Ginkgoites digitata* than to any of the other species with which it has been compared, however.

(B) *Ginkgoites* **sp Type B** (Plate II, figs. 1 & 2.)

(a) **Material**

Two specimens, marked GK/2 and GK/3 respectively, are available for study (Plate II, Figs. 1-2).

(b) **Zone**

Specimen GK/2—Buff-coloured silty clay layer (Le Roux, 1963, Plate I, Fig. 2, Layer A, Quarry No. 2).

Specimen GK/3—Beige-coloured sandy shale layer (Le Roux, 1963, Plate 1, Fig. 1, Layer C, Quarry No. 1).

(c) **Description** (See Plate II, Figs. 1-2)

The leaf is broadest towards the apex. It is distinctly spatulate with the apical portion more or less rhombic in outline. The length of specimen GK/2 is approximately 13 cm and its maximum width is 5,5 cm. The broad distal portion is elongated proximally into a gradually tapering petiole-like structure which is not completely preserved. The distal margins converge to form a bluntly pointed apex. In the case of specimen GK/2 the margin is entire, but there appears to be a median incision in the blade of specimen GK/3. There is no distinct midrib. There are several strong median veins in the proximal half of the leaf. The veins are more or less parallel in the petiolate portion and these veins bifurcate repeatedly, at the same time spreading out fan-wise over the broader

portion of the leaf. Bifurcation was continued up to within 5 mm from the apical margin. Anastomosis of veins appears to have taken place occasionally (see Plate II, Fig. 2).

Generally speaking the two specimens included here under the same name are superficially very similar. There is a distinct difference in the density of the veins, however. In specimen GK/2 there are 13-14 veins per cm but only 6-7 veins per cm in the case of specimen GK/3. At present it is uncertain whether this difference has any important diagnostic value. Two specimens are, therefore, provisionally described together.

(d) **Comparison and discussions**

(i) *General*

In spite of the admittedly meagre evidence available at present, it is believed that the leaves described here were those of a plant related to the genus *Ginkgo.* The specimens are, therefore, assigned to *Ginkgoites* the form genus instituted by Seward (1919, p.11) for extinct members of the Ginkgo family whose epidermal features or other anatomical characters are not preserved.

(ii) *Comparisons with previously recorded ginkgophytic plants with a similar type of foliage.*

Specimen GK/3 described in the present paper (Plate II, Fig. 2) closely resembles a specimen previously recorded from Vereeniging by Plumstead (1961, Plate VIII, Fig. 3, p.548) and which was named *Ginkgoites* sp. Although there is a slight difference in the shapes of the two specimens referred to above, the venation is identical, and it seems probable that the two specimens represent the foliage of a single species. No other South African fossil plant is known which bears any resemblance to *Ginkgoites* sp. Type B.

The foliage of the Devonian plant *Enigmophyton superbum* from Spitsbergen shows some resemblance to the Vereeniging plant in that the leaf also developed from a narrow base into a fan-shaped structure. Unlike the Vereeniging plant the lamina of *E. superbum* is much dissected, however.

The leaf of an American Devonian plant described by Beck (1963, Fig. 1a, p.432) under the name of *Ginkgophyton* sp. has more or less the same shape as that of the Vereeniging plant. A detailed comparison is impossible, however, owing to the fragmentary nature of the leaves described by Beck.

? GINKGOALES

Genus *PSYGMOPHYLLUM* Schimper

This generic name was instituted by Schimper (1870, p.192) for large cuneate leaves of Upper Carboniferous and Permian age. He defined it as follows: "Folia pinnatisecta, pinnis erecto patentibus, e basi valde angustata flabelliformibus, longitudinaliter flabellatim plicatis, plus minus profunde pinnatisectis, vel margine lobatis sen crenatis; nervis plusies dichotomis, erecto-radiatibus. Vernatio foliorum verticaliter involuta".

Seward (1919, p.81) gave the following revised definition of the genus: "The name *Psygmophyllum* is adopted both for entire and deeply divided leaves of larger dimensions than the similar leaflets of fronds included in such genera as *Palaeopteris* and *Adiantites.* Specimens usually occur as detached leaves, but when the leaves are attached to an axis the lamina is usually contracted into a fairly long, decurrent, basal portion. There is no true petiole. The veins spread from the base of the lamina and are repeatedly forked; they may be very numerous in some forms occasionally anastomose, as in *P. flabellatum,* or much farther apart, as in *P. majus* Arb. and *P. brownii* (Daws)."

(A) *Psygmophyllum kidstoni* Seward (Plates III & IV)

(a) **General**

This species was first described from Vereeniging by Seward (1903, Plate XII, Fig. 1, p.93), who defined it as follows: "Vegetative shoots woody, bearing spirally disposed leaves. Leaves wedge-shaped, reaching a length of 13 cm, usually divided by a deep median sinus into two narrow wedge-shaped lobes, truncate distally and tapering gradually to the proximal end of the lamina. Leaves sessile, attached to the axis by a narrow base. The lamina is traversed by numerous spreading and occasionally forked veins following a course parallel to the edge of the leaf. Organs of reproduction unknown."

The specimens described in the present paper came from a different stratigraphical zone from that in which Seward's type specimen was found. Reference was recently made by Plumstead (1961, p.548) to the occurrence of *P. kidstoni* in the new zone mentioned above, but no description was given.

(b) **Material**

The descriptions are based on the following specimens:

PS/1—(Plate III, Fig. 1),

PS/2—(Plate III, Fig. 2),

PS/3 and PS/3a (counterparts) (Plate IV, Figs. 1-1a).

(c) **Zone**

Specimen PS/1-2—Buff-coloured silty clay layer (Le Roux, 1963, Plate, I. Fig. 2, Layer A, Quarry No. 2).

Specimen PS/3-3a—Red ferruginous layer (Le Roux, 1963, Plate I, Fig. 1, Layer B, Quarry No. 1).

(d) **Description of the specimens**

(i) Specimen PS/1 (Plate III, Fig. 1)—This fossil consists of an impression of a strong woody axis bearing spirally arranged leaves. The leaves are rather fragmentary and bear signs of having been damaged prior to preservation (according to Plumstead, 1963, p.148, Plate A, damage of this nature

could have been done by insects). The central terminal leaf, although incomplete, is the best preserved. It is fan-shaped and is divided into two wedge-shaped lobes by a median incision. This leaf has a length of approximately 9 cm and a maximum width of 5 cm. The lamina tapers towards its proximal end and terminates in a decurrent, petiole-like basal portion, which is inserted at an acute angle to the axis. The axis is more or less uniform in width in the region where it is exposed. The specimen described here strongly resembles Seward's type specimen of *Psygmophyllum kidstoni,* and the new specimen is, therefore, referred to the same species.

(ii) Specimen PS/2 (Plate III, Fig. 2). This is a detached leaf having characters similar to those of the leaf described under specimen PS/1. The venation is better preserved in specimen PS/2, however. Three strong veins appear to enter the leaf at the base and by repeated forking produce numerous secondary veins which spread out through the lamina. The veins are approximately 1 mm apart in the region of greatest concentration. The general direction of the veins is more or less parallel to the edge of the leaf. The venation is not distinct enough to determine with certainty whether lateral anastomosis of the veins took place or not. There are several scars in the leaf. They are of the same type as those regarded by Plumstead (1963) to have been produced by insects.

(iii) Specimen PS/3-3a (Plate IV, Figs. 1-1a). This fossil is preserved somewhat differently from the others. Fossilization is due to mineralization, the original organic matter having been completely replaced by red ochre. The red fossil produced stands out in vivid contrast against a lighter background. The lamina is broadly fan-shaped and is divided into two equal lobes by a deep median incision. The lobes are wedge-shaped and truncated distally. The width of each lobe is 6 cm and the radius is about 8 cm. The maximum dimensions inferred for the complete leaf are approximately 11 cm for the width and 10 cm for the length. The lamina tapers proximally and terminates in a petiolate structure which is not completely preserved. Three strong veins enter each lobe and spread across the lobes by repeated dichotomous branching. The veins are about 1 mm apart in the region where they are closest together. The veins run parallel to the lateral margins of the lobes. This specimen is considered to be an exceptionally large leaf of the same identity as the central terminal leaf of specimen PS/1 and is, therefore assigned to *Psygmophyllum kidstoni.*

(B) *Psygmophyllum* sp (Plate V)

(a) **General**

This fossil differs from *P. kidstoni* in respect of its venation and the long petiole-like basal portion. It seems justifiable, therefore, to describe it separately.

(b) **Material**

Only one specimen, PS/4, is available for study.

(c) **Zone**

Beige-coloured sandy shale layer (Le Roux, 1963, Plate I, Fig. 1, Layer C, Quarry No. 1).

(d) **Description of specimen**

The leaf is incomplete and apparently distorted, so that the true shape is unknown. The lamina was evidently torn or lobed and several segments appear to be overlapping. The specimen has a length of 19 cm. It consists of a broad apical portion, 5 cm wide, which is elongated proximally. It is contracted by gradual tapering into a long narrow basal portion which is strongly suggestive of a petiole. The veins are fine, repeatedly forked and lateral anastomosis appears to have taken place. The maximum concentration of the veins is about 12 per cm.

(e) **Comparisons and discussions**

The leaf described above seems to conform to the definition of the genus *Psygmophyllum.* The specimen is, therefore, provisionally placed in this highly artificial genus. No species of this genus is known, however, which shows any resemblance to the fossil described here.

THE UNCERTAIN TAXONOMIC POSITION OF THE GENUS PSYGMOPHYLLUM

Psygmophyllum is essentially a Devonian and Carboniferous genus, but if the identification of certain flabelliform and cuneiform leaves occurring in Permian strata is correct, the range of the genus must be extended into the Permian.

Leaves of the *Psygmophyllum* type have a wide geographical distribution. The classical Gondwana, Cathaysian, Angara and Euramerican floras each contains the genus *Psygmophyllum* as a minor constituent. As pointed out by Seward (1932, p.226), however, it is a disputable question as to whether all the fossils included in *Psygmophyllum* actually belonged to one genus or even to one family.

In spite of the wide-spread occurrence of these leaves, the reproductive organs remain unknown and consequently the true taxonomic position of *Psygmophyllum* cannot be determined with certainty. This has been a most perplexing palaeobotanical problem for nearly a century.

In the present paper the genus is tentatively placed in the Ginkgoales. This is done mainly on the basis of the superficial resemblance of the fossils concerned to ginkgoalean plants. It must be admitted, however, that no valid evidence exists for assuming relationship between *Psygmophyllum* and the Ginkgoales.

? VOJNOVSKYALES

Genus *NEPHROPSIS*-Zalessky

The generic name *Nephropsis* was proposed by Zalessky (1912, p.28, Foot-note) for Permian leaves previously described by Schmalhausen

(1879) and Renault (1888) under the genus *Ginkgo.*

cf. Nephropsis (Plate VI, figs. 1 & 2)

(a) **Material**

Five specimens, marked NP/1-5, are available for study. Specimens NP/1 and NP/4 have counterparts marked NP/1a and NP/4a respectively. Specimens NP/1-2 were selected for illustration because they are the best preserved and show typical variations in characters.

(b) **Zone**

All specimens–Buff-coloured silty clay layer (Le Roux, 1963, Plate I, Fig. 2, Layer A, Quarry No. 2).

(c) **Description** (see Plate VI, Figs. 1-2)

The specimens on which this description is based are very similar to each other and vary only slightly in size and shape. The leaves are bract-like and are flabelliformic to rhomboid in shape. The blade is distally expanded and elongated proximally into a broad stalk-like structure. The expanded distal portion has a width of 20-25 mm and the stalk-like basal portion is approximately 5 mm wide at the point of connexion. The total length of the leaf is 25-32 mm. The lateral margins curve outwards from the base to meet the arched apical margin at an angle. The margin is entire in the case of specimens NP/2, 3 and 5. Shallow incisions are present, however, on each side of the blades of specimens NP/1 and NP/4, thus giving rise to the formation of narrow lateral lobes. The leaves appear to have been of a fleshy nature and were probably much thicker in the central region of the blade than near the peripheral region. Two primary veins enter the leaf at the base. Dichotomous forking of the veins takes place 5 times, dividing up to 3 mm from the distal margin. The densest concentration of the veins is 16-18 per cm. The veins diverge from the base and are strong and prominent in the basal and central regions of the blade, becoming finer and indistinct towards the distal margin.

(d) **Comparisons and discussions**

Plant fossils of the type described here have not previously been recorded from Southern Africa. They do show some resemblance, however, to leaves of *Sphenophyllum,* a genus which is well represented in the Wankie flora of Southern Rhodesia. The venation of the species *Sphenophyllum thonii* Mahr is remarkably similar to that of the new plant. There is also a general resemblance with regard to the shape and size of the leaves of the two plants. The new plant differs from *S. thonii,* however, in the distinctly bract-like nature of the leaves of the former as well as in the stalk-like basal portion and the pronounced curvature of the margins.

The leaves described here are reminiscent of ginkgoalean leaves. They do show some resemblance to the specimens described elsewhere in this paper under the name *Ginkgoites* sp. Type B. The new plant is separated from the Ginkgoales, however, on the basis of the plural nerves entering the leaf as well as on the nature of the branching of the veins.

The specimens under discussion seem to resemble the Russian Permian genus *Nephropsis* Zalessky more closely than any other plant previously described. The new Vereeniging plant conforms to the characteristics of this genus in that it has a transversely elongated blade on a broad stalk-like basal portion and forked veins spreading through the lamina.

The transverse elongation of the leaves is less marked in the new plant than in *Nephropsis integerrima* (Schmal.) Zalessky, the type species of the genus. (Seward's reproductions, 1919, p.78 of Schmalhausen's original figures, 1879, Pl. XVI, Figs. 12-15, were used for comparison because the original publication was not available.) The former plant shows a much closer resemblance to *Nephropsis ubojensis* Schved., figured by Shvedov (1961, Pl. XL, Fig. 1 and Pl. XLI, Fig. 1) than to *N. integerrima* with regard to the distal portions of the leaves. In comparing the Vereeniging plant with Neuburg's figures (1965, Pl. XXIII, Figs. 1-6) of *N. rhomboidea,* similar variations in shape and size seem to occur in both plants. The leaves of the latter are more distinctly rhomboidal, however, than that of the former. There also appears to be a difference in the venation of the two plants.

The occasional lobation of the leaves of the new plant seems to be a distinctive character which has not been observed in any of the known species of *Nephropsis.*

(e) **Conclusions**

In spite of the strong superficial resemblance of the Vereeniging leaves to leaves of the *Nephropsis* type, generic identity can not be inferred in the absence of confirming evidence.

In her description of *Vojnovskya paradoxa,* Neuburg (1955) draws attention to the fact that the foliage leaves associated with this fructification are of the *Nephropsis rhomboidea* type. She points out, however, that all leaves of the *Nephropsis* type cannot be attributed to the Vojnovskyales with certainty. This applies especially to the Vereeniging leaves which are consequently referred to the Vojnovskyales with hesitation.

It seems most remarkable, however, that this new element of the Vereeniging *Glossopteris* flora should show such a close resemblance to an element of the Russian Angara flora. This once again focuses the attention on the unique nature of the Vereeniging fossil flora.

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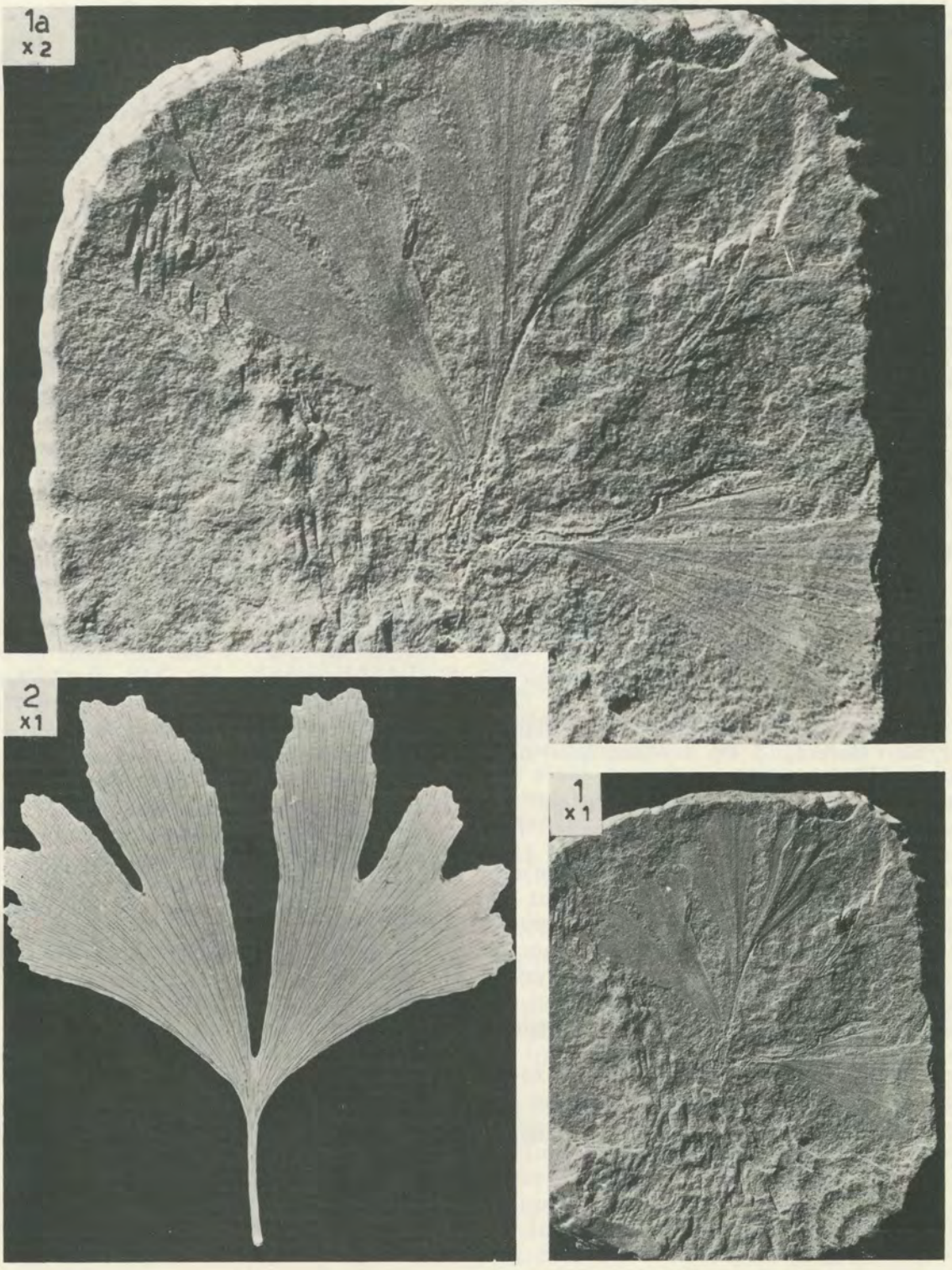


PLATE I

Ginkgoites **sp Type A**

Fig. 1 Foliage leaf, showing shape and lobation of the segments. Specimen GK/1 (Natural size)

Fig. 1(a) The same specimen as shown in Fig. 1 enlarged twice to show more detail of venation.

Ginkgo biloba **Linne**

Fig. 2 Foliage leaf of a one year old plant, showing similarity to leaf illustrated in Fig. 1. (Natural size)



PLATE II

Ginkgoites **sp Type B**

Fig. 1 Almost complete leaf, showing shape and venation. Note entire margin. Specimen GK/2. (Natural size)

Fig. 2 Apical portion of a leaf, showing incision in lamina. Note more open venation as compared with Fig. 1. Arrow indicates a region in which anastomosis of veins appears to have taken place. Specimen GK/3. (Natural size)

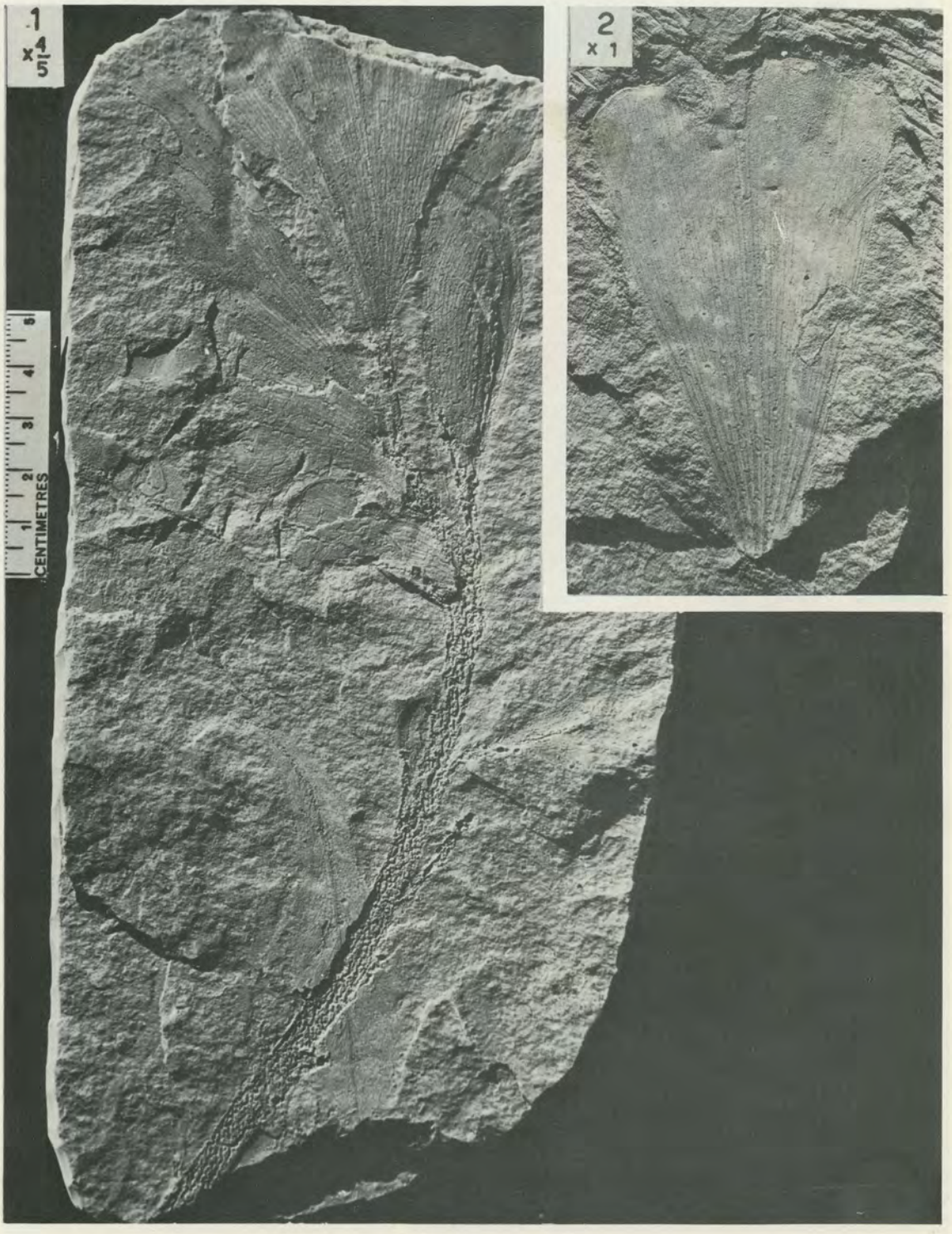
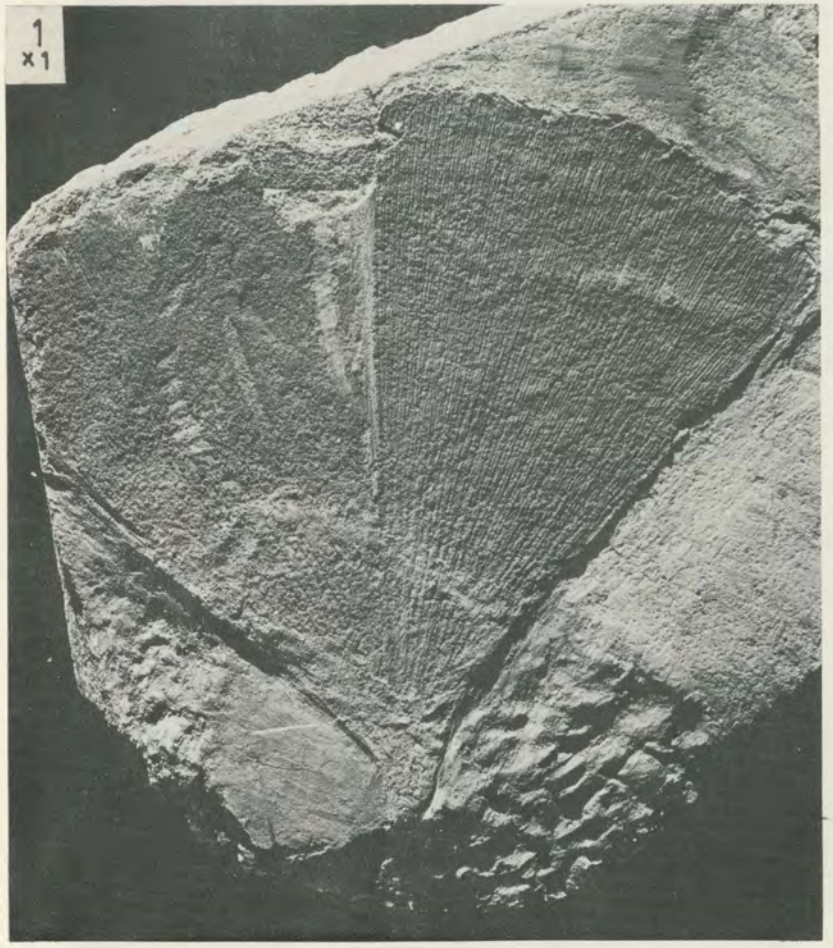


PLATE III

Psygmophyllum kidstoni **Seward**

Fig. 1 Portion of a woody axis with spirally disposed leaves. Note scars presumably produced by insects. Specimen PS/1. (Magnification X 4/5)

Fig. 2 Detached leaf, showing lobation of lamina and dichotomously-branched veins. Specimen PS/2. (Natural size)



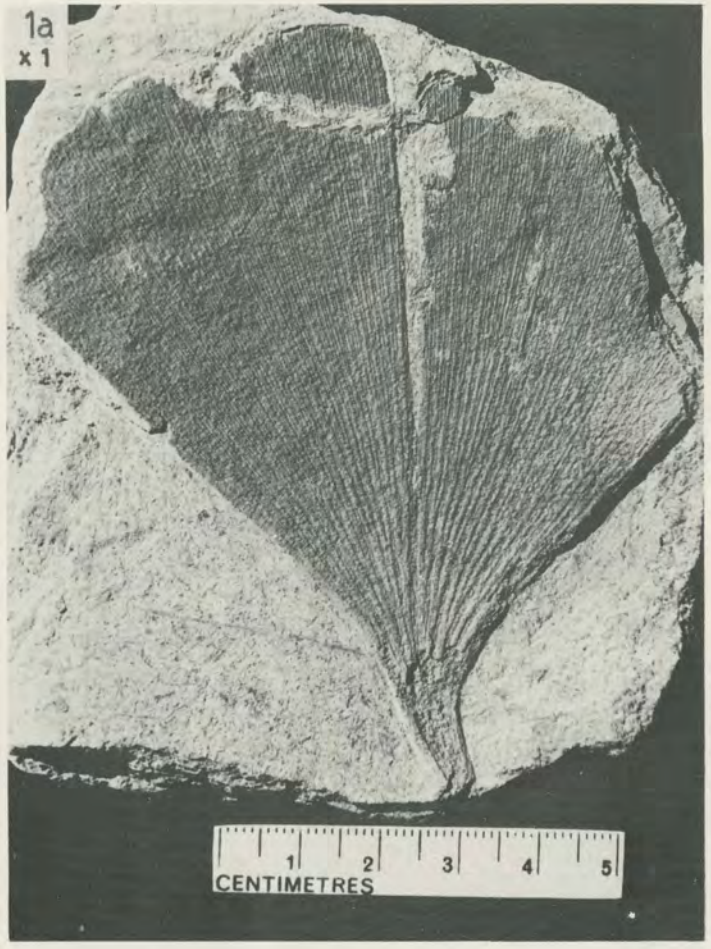


PLATE IV

Psygmophyllum kidstoni **Seward**

Figs. 1-1a Counterparts of an almost complete leaf, showing shape of the lamina and lobes, and details of venation. Specimens PS/3 and PS/3a respectively. (Natural size)

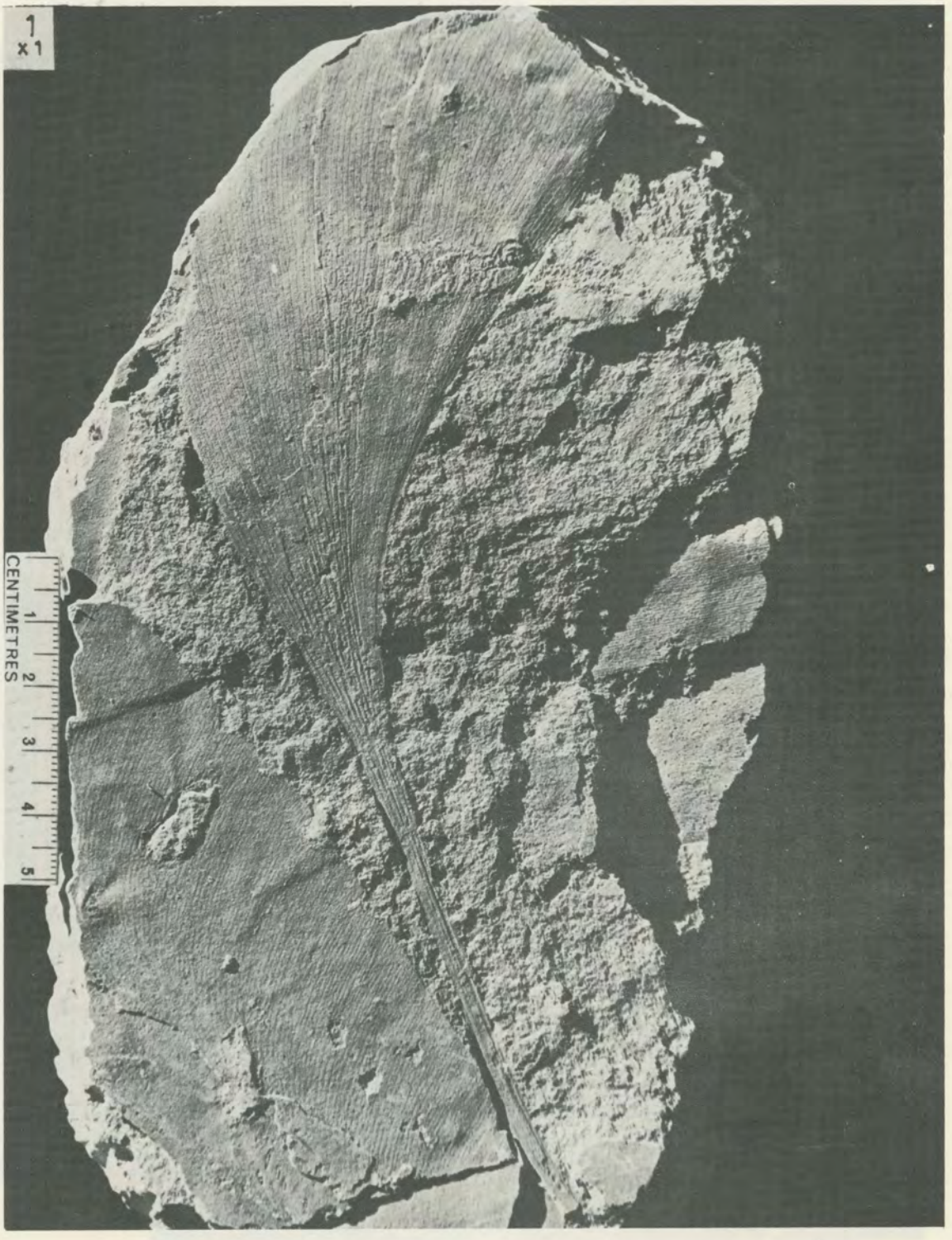
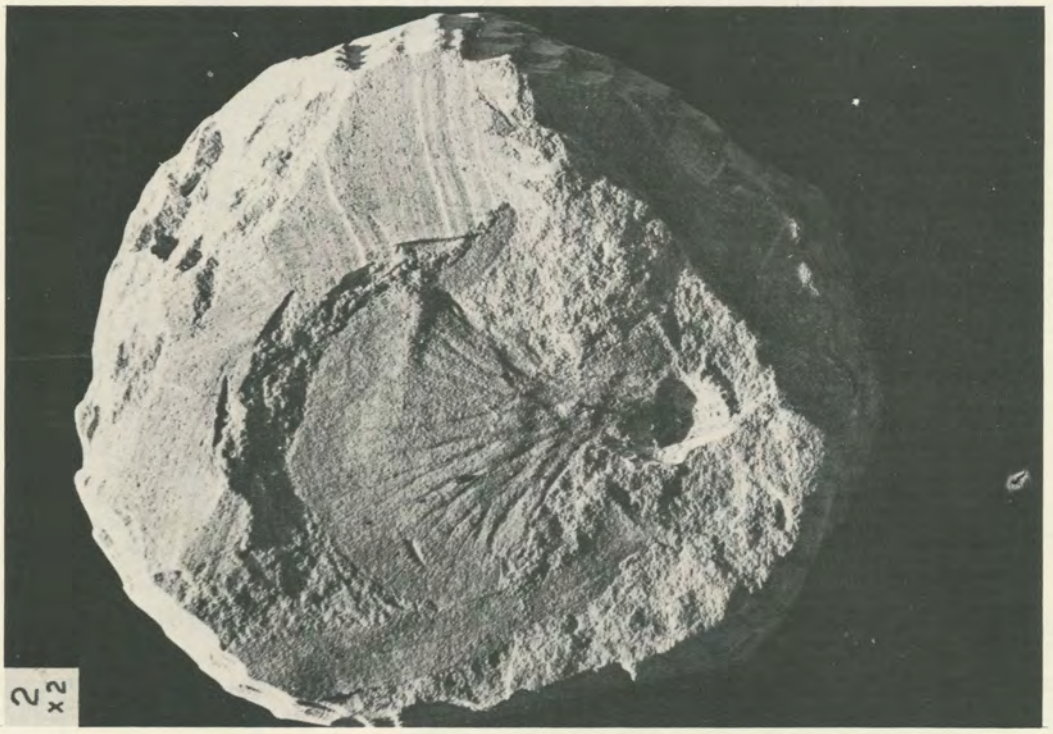


PLATE V

Psygmophyllum sp

Fig. 1 An incomplete leaf, showing the long narrow petiole-like proximal portion and forked veins with lateral connexions. Specimen PS/4. (Natural size)



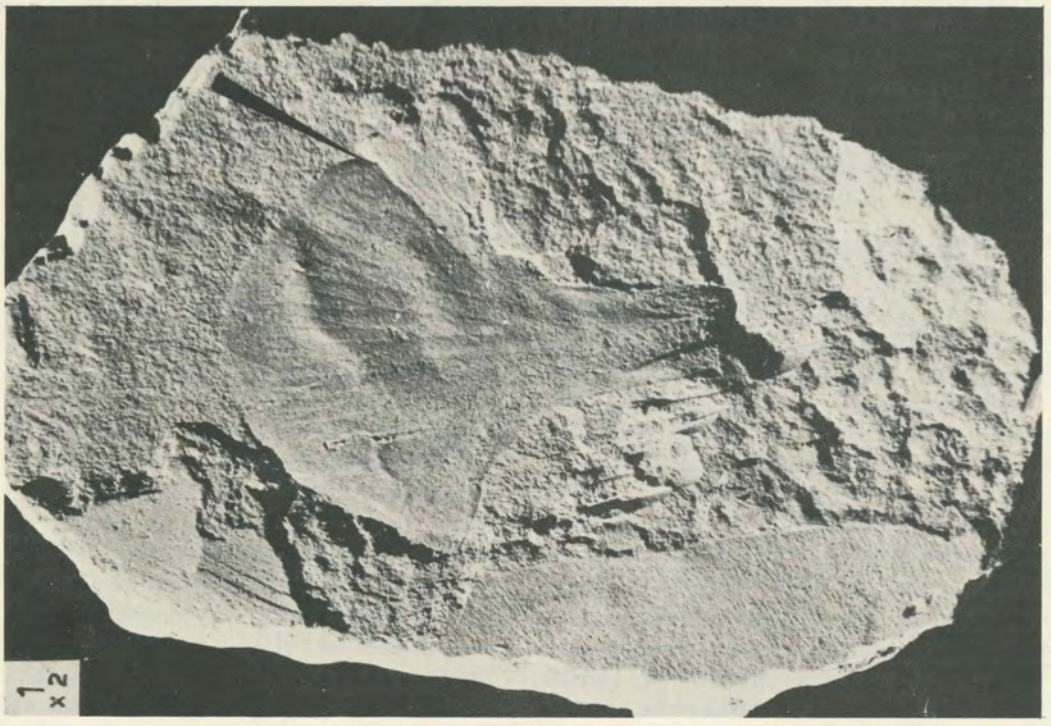


PLATE VI

cf. Nephropsis

Fig. 1 Leaf showing typical shape. Note the broad stalk-like proximal portion and the general bract-like appearance. Arrow indicates incision in the lamina. (Magnification X 2)

Fig. 2 Leaf showing fan-shaped lamina with entire margin. Note strong, repeatedly-forked veins in central and proximal regions of the lamina. (Magnification X 2)

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SKIN STRUCTURE OF SMALL PAREIASAURS
With comments on their taxonomy in the Cistecephalus zone

by

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ABSTRACT

The *Cistecephalus* zone pareiasaurs all show skin armour. The features of this armour are described as found virtually complete in a small pareiasaur, identified here as an about half-grown *Pareiasaurus serridens*. Different in skin structure from this small pareiasaur is the dwarf-form, *Nanoparia pricei*. A few particulars have now been added to the known skin structure of this species. It is suggested that *Cistecephalus* zone pareiasaurs can be referred to 2 principal species: the one is *Pareiasaurus serridens* Owen, to which all the incomplete and variably grown specimens can be assigned such as the genus *Propappus* and some other species from the genera *Pareiasaurus, Anthodon* and *Nanoparia*. The other consists of the single specimen *Nanoparia pricei*. Further affinities are beyond existing evidence to settle.

INTRODUCTION

Through the presence of their armour of dermal ossicles, the pareiasaurs are the only family of Karroo Cotylosaurs in which one may study the structure of the skin. Covering the data up to that time, Boonstra (1934) reviewed and amplified our knowledge of the ossicle pattern. Most of the specimens then available in this country derived from the massive pareiasaurs (*Bradysaurus, Embrithosaurus*) of the *Tapinocephalus* zone in the lower part of the Lower Beaufort beds. A fair number of genera and species were then distinguished, many being based on individual specimens. With more available material, the effects of age, sex, post-mortem deformations of the skull, individual variation and clearer zoning have led Boonstra (1969) to reduce the numbers of valid genera and species from this zone considerably (cf. Broom, 1935).

No such reconsideration has been possible for the less massive and rarer pareiasaurs of the *Cistecephalus* zone in the upper part of the Lower Beaufort beds. As is well known, we are still hampered by types such as *Pareiasaurus serridens* of which the skull has been mislaid, *Pareiasaurus bombidens* in which the jaws were described upside down, *Propappus omocratus* which had no skull to the type specimen, and *Anthodon serrarius*, a small pareiasaur with an imperfect skull; moreover the type material, described nearly a century ago, is housed in the British Museum. Broom (1936b) was eventually prepared to refer Seeley's *Propappus omocratus* to Owen's *Pareiasaurus serridens*, thus cutting down the genera from 3 to 2. In the same year, however, Broom (1936a), described a new pareiasaurian genus from the middle *Cistecephalus* zone. It was the smallest pareiasaurian skull yet found. If it was only an immature specimen Broom suggested a relationship towards *Anthodon gregoryi*, though he preferred to regard it as a miniature form rather than a baby by giving it the generic name of *Nanoparia*, the dwarf pareiasaur. An even smaller skull was added 12 years later from the lower *Cistecephalus* zone as a new species to the same genus (Broom and Robinson, 1948). Facts concerning the genus *Nanoparia* were reconsidered and extended by Brink (1955). In this study Brink gave the only existing account of the dermal ossicles of the smaller of these two pareiasaurs, *Nanoparia pricei*.

MATERIAL

The present study on the dermal armour of small pareiasaurs is based on a hitherto undescribed specimen, kindly loaned to me from the Bernard Price Institute of Palaeontology. Catalogued as *Pareiasaurus* species, specimen No. 548, it was collected at Groot Driefontein, Murraysburg, C.P. by Mr. B. J. Kitching. Horizon: *Cistecephalus* zone. With it I was enabled to compare the type of *Nanoparia pricei* (Broom and Robinson, Cat. No. 6, Bernard Price Institute of Palaeontology).

Identification of BPI Specimen 548. Figs. 1-3 give details of the skull shape, sutures and molar teeth and Table 1 gives comparative skull measurements. Most of the measurements suggest that *Pareiasaurus serridens* is roughly twice the size of this unnamed specimen. There are 3 relative differences: in the latter the maxilla is much shorter, the pineal opening is much farther forward and the cheek development is much less. Holding the maxillary tooth row horizontal, the posterior portion of the skull roof in BPI 548 shows a marked downward shelving, which starts sloping postero-ventrally from a ridge which connects a boss behind the pineal with the two tabular bosses. In this respect it closely resembles the skull shape

of Boonstra's (1934) neotype of *P. serridens*. Of course, if one tips the snout ventrally, the slope is less conspicuous a feature on the occiput (cf. the published side-view of *Anthodon gregoryi*). Table II sets out some of the data on *Cistecephalus* zone pareiasaur skin ossicles. It is clear that the recognised specimens are again about twice the size of the unnamed skull. The body length from snout to pubis here would be approx. 850 mm. Double this in the adult length would at least be about 5½ feet. From the relative scale size it could certainly be more, though this is in keeping with the presumed size of *P. serridens*.

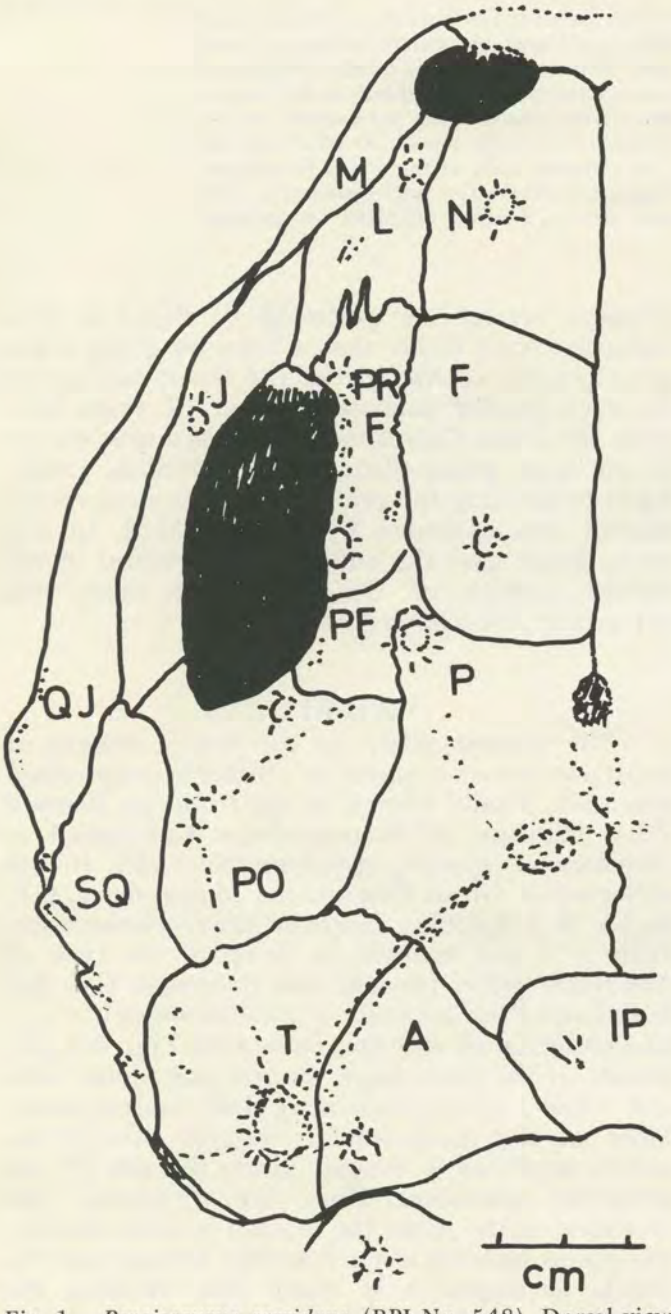


Fig. 1. *Pareiasaurus serridens* (BPI No. 548). Dorsal view with suture and boss patterns. At the occipital margin the single neck scute is shown, which touches the problematic "element A" of Broom, here considered to be a lateral post-parietal or the tabular according to Parrington. See p. 22 for abbreviations.

There therefore seems to be good reason to regard this specimen as an almost half-grown *Pareiasaurus serridens*.

Status of related genera and species.

Pareiasaurus steenkampensis Seeley, 1908 was described on a collection of scutes from Steenkamp's Poort south of Fraserburg. The horizon according to Mr. J. W. Kitching would be in the *Cistecephalus* zone. The scutes look exactly like the scutes from No. 548 except for being twice the size. Boonstra (1934) was convinced that these were not the scutes of *Bradysaurus*. It therefore seems obvious that the status of "Incerta sedis" given by Boonstra to this species can be replaced by synonymy with *P. serridens*.

Pareiasaurus serridens Owen 1876. Richard Owen described this genus and species from a skull cast. The accompanying pelvis with overlying scutes was assigned to the same genus by Watson (1914) after Owen had incorrectly described it as coming from a *Dicynodon*. The scutes described from Boonstra's neotype (1934) are double-sized versions of those in our "unknown" species.

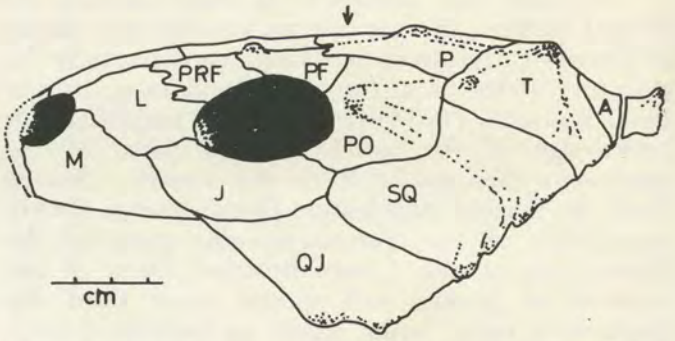


Fig. 2. *Pareiasaurus serridens* (BPI No. 548). Lateral view. To show the contact at the back of the skull between element A and the neck scute, the snout is turned slightly medially, foreshortening the skull length slightly. Arrow at the top indicates the front edge of the pineal opening.

Propappus omocratus Seeley. Watson considered that the scutes of this genus were very like those of *P. serridens*, and Broom (1935) considered on other grounds that Seeley's genus and species was probably synonymous with *P. serridens*. In *Propappus parvus* the scutes are less gross in outline and embellishment. So are those which in this paper we are calling a small *P. serridens*.

Anthodon serrarius Owen. Scutes are undescribed in Owen's account. Boonstra illustrates scutes which could not be distinguished from either *P. serridens* or *Anthodon gregoryi*. However he does describe the boss on the scutes as standing up in a way which sounds like a funnel on a flattish base. This is what we have found in *Nanoparia*.

Anthodon gregoryi Broom 1930. As in the above, the dermal armour is merely alluded to and not fully described or illustrated. The type of this species comes from the *Cistecephalus* zone north

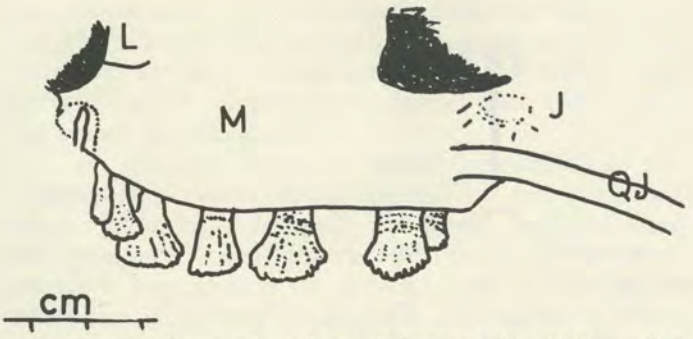


Fig. 3. *Pareiasaurus serridens* (BPI No. 548). Oblique view of left maxilla showing tooth row. The most anterior tooth is seen as a root in the socket under the nasal opening without a crown. Overlap of the teeth is shown, the front edges of the teeth lying medial to the back edge of the next tooth ahead. The seventh tooth space is vacant, making a probable total of 9 cheek teeth.

of Graaff-Reinet (the farm Vlakteplaas near Bethesda Road Station) and is in the American Museum of Natural History. As indicated, this pareiasaur is about three-quarters the size of *P. serridens,* has big heavy cheek plates and a rather short obtuse maxilla. The pineal opening is relatively far back according to skull measurements, but it lies actually behind the frontoparietal suture. Short as Broom's paper is, there are several conflicting statements in it, nor was he happy about the placing of this genus and species. Prepared as I am to consider the unknown specimen BPI No. 548 as a half-grown *Pareiasaurus serridens,* this *A. gregoryi* of Broom would do equally for a $\frac{2}{3}$ grown specimen.

MORPHOLOGY

The Post-Parietal Region The weathered state of the occiput in many specimens has made the region between the tabulars and the parietals difficult to interpret. It is the region where the transverse occipital canal or occipital commissure of the lateral line system would lie—identifiable as such in Stegocephalians (Schmalhausen, 1968), and liable therefore to form centres of ossification in the cranial roof independently of the dermal bone system over the body.

The cotylosaurs clearly show a variable degree of separation or fusion of the two stegocephalian post-parietals leading to 3 possibilities: (a) A median unpaired bone (dermo-supra-occipital, interparietal, post-parietal), (b) a paired bone (post-parietal on either side), (c) a median unpaired plus a paired bone—the situation seen here and described by Broom in *Nanoparia pricei.*

One could call the set of 3 bones between the tabulars and behind the parietals respectively the left and right lateral post-parietal and the median post-parietal. This removes the uncertainty left by Broom (1936) for what he called "element A," to which the name lateral post-parietal seems appropriate.

Broom's "element B," an ossification on the posterior cranial margin seen so far only in *Nanoparia pricei,* lies in our specimen where an inturned piece of the squamosal is seen. If element B does not belong to the squamosal, it can then be a supratemporal, not normally extant here as a separate bone. At this mobile point one would not expect an attachment to the dermal armour, and indeed there is none.

After choosing to interpret the occipital bone pattern as an expression of variability in the interparietal complex, Parrington's (1962) view was brought to my notice. He prefers to regard the interparietal in pareiasaurs as having shrunken to the small oval median bone here described, and the tabular as having slid inward to the occiput, also with some inevitable loss of size. The large prominent bone lateral to this which Broom,

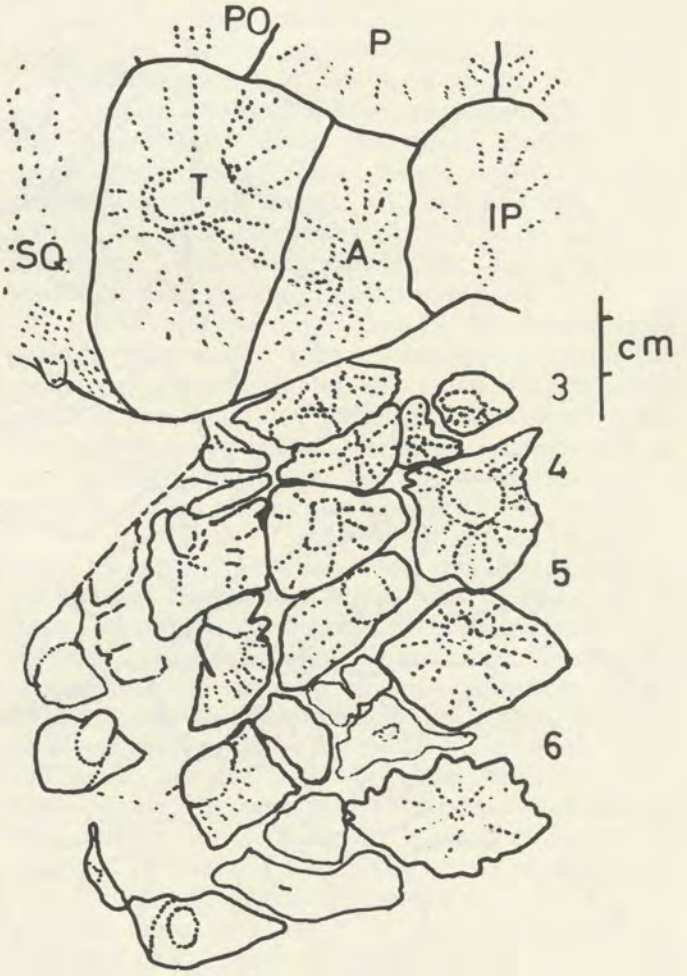


Fig. 4. *Pareiasaurus serridens* (BPI No. 548). The left cervical scutes, dorsal view. It is presumed that the first midline scute overlies the 3rd vertebra (3), and the succeeding transverse rows respectively over cervical 4–6 vertebrae as numbered. The midline row lies opposite the interparietal, the 1st lateral anteroposterior row opposite Broom's "Element A" with which it makes contact, the 2nd lateral anteroposterior row leads back from the tabular and the 4th is roughly in line with the squamosal.

Robinson, Brink and myself preferred to keep as the tabular, normally placed at the paroccipital



Fig. 5 *Pareiasaurus serridens* (BPI No. 548). Scutes over the shoulder girdle, dorsal view. The midline, anterior and posterior ends, are indicated by the heavy arrows. The positions of the scutes overlying the vertebrae 7–11 are numbered as such and the corresponding oblique scute rows spreading from them on either side are indicated by the small tailed and numbered arrows.

prominence in the procolophonids, becomes Parrington's supratemporal; this in turn requires an increase in the nomenclature of the supra- and intertemporal elements in these and other diadectomorph cotylosaurs.

To choose between these possibilities, i.e. fragmenting either the occipital or the temporal bony elements respectively with ensuing size changes, my own interpretation as given here requires less change in relative size of the bony units in question. For want of more decisive evidence, the view which favours less violent changes in the final surface areas and outlines of bone seems for the time being superior. I have therefore allowed it to stand beside Parrington's, knowing that he says "l'identification de l'os temporal unique des Pareiasauriens typiques et des Procolophonides est une problème extremement difficile." A study of comparative suture-line lengths from actual specimens seems to me to be a suitable way of looking at probable trends in bone size over the cranial vault—a pursuit not embarked upon here.

A last possibility remains, viz. a separation of the tabular itself into two ossification centres, one carrying the boss and the other catering for the element A in the occipital declivity.

Skin Structure. The dermal ossicles or scutes are the only guide to the structure of the pareiasaurian skin. It has long been known that the ossicles are closely related in position and number to the underlying vertebrae and ribs. This is also seen in the present specimen, where the last 7 pre-sacral, 4 sacral and one or two caudal vertebrae can be correlated with the overlying scutes.

There are 18 rows of pre-sacral scutes. The exact number of pre-sacral vertebrae is not known in this specimen, but assuming there are 20 as in most pareiasaurs, it means that the first two cervicals are not covered by scute rows.

Referring to Table III, total lengths of scute rows as measured groupwise anteroposteriorly in middorsal line are given in column B where they are measured batch by batch. The numbers of rows per batch is given in column A; column C is equal to B divided by the number of units in A. The same plan is followed in columns D, E and F for the vertebrae, so far as they are exposed. From the table it is clear that the smallest midline scutes at the root of the tail are half the size of the largest ones over the middle of the back, (figures in column C). The figures in the table suggest that the skin (column C) was slightly too small for the underlying vertebral column (column F) which it had to cover. However the fossil shows marked dorsoventral compression making the vertebral column convex ventrally, increasing its apparent length, and the skin is depressed ventrally, decreasing its anteroposterior length somewhat. The ossicles are not more marked over the limb girdles, as is said to be the case for some other species. Perhaps they are at times better preserved over the underlying girdles so as to give this impression.

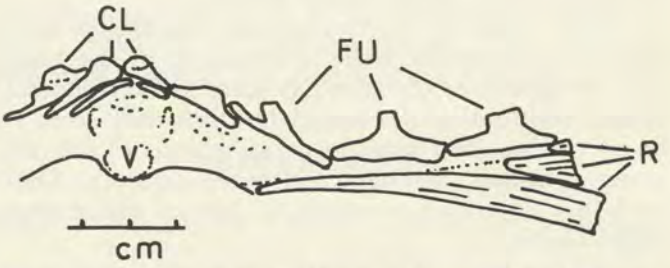


Fig. 6. *Nanoparia pricei.* Fracture through the dorsal wall at the front of the 9th central scute articulating with the 8th oblique row of scutes. Vertical sections through the scutes are shown, indicating funnel-like bosses, overlapping and overriding of scutes and of the rib rows.

The fossilised neck region is dorsoventrally compressed. Round the outsides of the scutes the hemicircumference of the neck at the first scute row is about 130 mm. Scutes are present the whole way round; apart from the dorsal midline scute there are probably four lateral scutes meeting ventrally over the throat. The 2nd and 3rd lateral scutes lie over the side of the neck, and are prominent. They have projecting outer surfaces which increase the outer circumference.

Fig. 4 gives the dorsal view of the cervical scale pattern. One notes a transverse gap between the median post-parietal and the small median scute which is presumed to overlie the 3rd cervical spine. The lateral post-parietal overhangs a scute lying in the 1st lateral position. Through compression the laterally facing scutes also appear in the top view.

In general the formation of distinct bosses is not a prominent feature of this specimen. Many of the cranial bones and scutes rise to blunt elevations, like the summit of a flattish barnacle, but rounded mushroom-like knobs and funnel-like protrusions are virtually absent. Prominent bosses are seen only in the lateral cervical region. There is no direct continuity between the bones of the head and neck, yet the anteroposterior lines of scutes have a general resemblance to the cranial elements. The midline units lie in the median post-parietal axis, the first lateral row in the lateral post-parietal line, the second lateral row in line with the tabular and the third row more or less in line with the scalloped back corner of the squamosal.

Succeeding this, the scute pattern in the dorsal region up to the level of the forelimb is shown in Fig. 5. Here as in the cervical region one recognises a herring bone pattern of scute rows at 45° to the midline: in general the scutes can be attributed to roughly equidistant positions, though the units may be subdivided. This means that two scutes may appear at a site where only one appears at a comparable site elsewhere.

Between the limb girdles, the scutes follow much the same pattern, the rows lying along the curved axes of the ribs. The scutes are largest in

their transverse axis, reaching the maximum sizes quoted in Table II. There appear to be at least 5 lateral scutes in each row (lateral to the median scute) covering the back and flanks.

There can be no doubt that the scutes were also present on the belly. Flattening of the body and disruption of the skin has scattered the ventral, caudal and limb scutes somewhat, but they seem to be of the smallest type in these regions (Table II), being rounded, nodular and more discrete. They probably extended to within 40 mm of the midline if not closer.

At the level of the 16th pre-sacral vertebra an estimate of the transverse hemicircumference of the squeezed body was about 420 mm. Transition to the smaller scute type took place about 220 mm from the dorsal midline.

The principal scutes have a radial structure. Designed like a limpet, they rise externally to a central point which is at times finely rough as if to anchor an overlying cap of horn. The centre may be little elevated or quite flat. From this centre radial undulations or flounce-like ridges diverge which give the edge of the scute a fluted appearance, or a pattern of flat radial arms like a starfish. In these scutes a distinct radial arrangement of bone fibres can also be seen, corresponding to the gross structure. These bony striae often have slit-like lacunae in them filled with matrix. A feature of many scutes is an oval matrix-filled depression on the outer surface like a small oblique cavity, 1-3 mm at the opening. It often lies under the shelter of the central boss. When some of these cave-like depressions were cleaned out they were found to be quite smooth and usually blind. Concerning the direction of its opening, the facing of the hollow area and its position on the scute, no pattern was discovered. They were not related in direction to the bone fibres and appeared more to be an encapsulation in a scute. Minor depressions and pockets were common over scute surfaces as well.

The most prominent part of the scute was not always situated at the centre for radial growth of the bone. An elevation or boss was often quite eccentric relative to the growth centre and situated occasionally at the edge of the scute. Likewise the little pockets or sacs on the scute could even be shared, as it seemed, across adjoining scutes.

The only scutes having prominent knob-like surface elevations were, as noted above, those on the sides of the neck. No scutes were dissected out, but they showed a layered structure, again reminiscent of a barnacle shell.

Besides the scutes with a plainly radial structure there were "secondary" scutes in the rows or parts of the main scutes which merely showed a curling and crinkling structure with depressions and folds. The canals entering these were round, and radial bone structure was not always evident. Their dells were sometimes in continuity with the sac-like cavities of the radial scutes. These same features were recognisable in the cranial bones—a radial structure with a central (e.g. tabular) or eccentric (e.g. lateral post-parietal) prominence, and the lettuce-leaf-like bone without such features (e.g. postfrontal).

Being radial structures arising from growth centres, the resulting junctions between scutes were necessarily of an overall linear and angular type. The junctions were closest over the mid-back but became progressively looser over the sides and ventral surface of the body. Spaces between scutes took several forms—zigzag sutures 1-2 mm across, vertical gaps with scalloped borders, and oblique shelving overlaps with variable and sometimes fairly large spaces between. Cranial suture lines vary of course in the same general way.

Nanoparia pricei **Broom and Robinson.**

The skin and skull structure leaves little doubt that this specimen is quite different from *Pareiasaurus serridens*, although the same may not be said with confidence for *N. luckhoffi*. Thus: (a) Despite the very small size of the animal and its scutes, the development of bosses is striking. There are large mushroom-like bosses, funnel-shaped prominences and blunt thorn-like outgrowths on the skull and scutes. By comparison the skull and scutes of *Pareiasaurus serridens* are rather smooth. (b) The first lateral pair of scutes lying beside the central row touch in the midline behind the central scute and have bosses shaped like a pair of kidneys, one on either side of the midline as illustrated by Brink (1955). The central scutes are just over 14 mm apart, and the vertebrae likewise. The distances change negligibly over the preserved row of 13 scutes. (c) Brink's diagrammatic representation (*loc. cit.*) of the scute pattern suggests a highly improbable gap in the lateral scute rows, which leaves an area uncovered by scutes for some 40-50 mm on either side of the midline series. A little cleaning and an examination of existing fractures in the specimen showed that the scute rows were in fact complete, being merely buried in the matrix above the dorsoventrally flattened rib cage. A section (Fig. 6) shows a complete series, with funnel-like bosses. The medial edge of the scutes lies external to the outer edge of the next most medially placed scute—the opposite of a tile-type of overlap. (d) There is considerable overlap of scale rows and ribs.

One could perhaps make out a case for there being only one species of *Nanoparia*. However, the skin can contribute nothing to this question at present. Broom himself regarded *N. luckhoffi* as possibly a small *Anthodon gregoryi* (= *P. serridens*), which if accepted would leave *N. pricei* as the only species in the genus.

CONCLUSIONS

From a study of the skin in the *Cistecephalus* zone pareiasaurs, the genera *Pareiasaurus* Owen and *Nanoparia* Broom appear to be valid. Being the smaller animal, *Nanoparia* has a more striking

armour; one is reminded that the most striking horny growth of any pareiasaur is that of the small form *Elginia* from Scotland. It seems desirable to place the following into synonymy with *Pareiasaurus serridens: P. steenkampensis, Propappus omocratus* and *Anthodon gregoryi.* The present study could contribute nothing to the placing of other specimens referred to the genus *Anthodon.*

Growth changes as surmised for *P. serridens* comprise a proportional enlargement of the scutes, vertebral column and skull generally, except that the cheeks become disproportionately larger and the skull longer with age. A relatively backward shift of the pineal opening is seen, and the maxillae may come to lodge more cheek teeth.

The structure of the scutes in *P. serridens* indicates the existence of two separate influences in scute structure: these are respectively the ossification centre, presumably dermally determined, and the placing of the boss and the cavities upon the scute surface, presumably epidermally determined. The purpose of the boss is clearly defensive, but the nature of the cavity present on many scutes is uncertain. These excavations have the smoothness that one sees in the bone near the intracranial venous sinuses, but it is hard to guess what such vulnerable cavernous bloodspaces would be doing on the outside of the body. A cutaneous gland pocket is a possibility, though it is unusual to find gland lobule nestling in such a type of bony cavity. More possibly I fancy that all the irregularities are under the control of growth stimuli from a variegated epidermis and do not point to any special organs contained therein.

Although the scute may be subdivided in *P. serridens*, the scutes are so large that no mammal could develop a warm fur coat at the rate of one hair set per scute field. The cotylosaurian scute pattern therefore offers no framework for the suppleness or multiplicity of mammalian hair units.

Finding now that the pareiasaurian scute pattern extended round on to the belly, it becomes easier to derive the turtles from the short bodied dwarf pareiasaurs as Gregory (1946) had proposed when *Elginia* was the only dwarf pareiasaur known. The broad ribs of *Nanoparia pricei* may make a better possible intermediate than the *Tapinocephalus* zone specimens of *Eunotosaurus,* whose claims as an ancestral chelonian have been recently diminished by Cox (1969). In *Eunotosaurus* the presence of dermal armour was shown moreover to be an error of observation, and the ribs exhibit a regional sculpturing which in no way resembles the patterns described here in the pareiasaurian skin or skull.

ACKNOWLEDGMENTS

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ABBREVIATIONS TO ILLUSTRATIONS.

A = Broom's element A.
CL = Central and first lateral scute bosses.
F = Frontal.
FU = Funnel shaped bosses on lateral scute rows.
IP = Interparietal (median).
J = Jugal.
L = Lacrimal.
M = Maxilla.
N = Nasal.
P = Parietal.
PF = Postfrontal.
PO = Postfrontal.
PRF = Prefrontal.
QJ = Quadratojugal.
R = Ribs (3 overlapping sections).
SQ = Squamosal.
V = Vertebral body.

Table I

COMPARATIVE SKULL MEASUREMENTS (mm)

	P. serridens[1]	*A. serrarius*[1]	*A. gregoryi*[2]	*Unknown No. 548*
Median length	318	255	± 240	± 170
Width, greatest	260	135	295	200
Interorbital distance, smallest	180	110	123	78
A-P orbital length	—	—	48	42
Occiput–postr. edge pineal	105	?	34	69
Premaxilla–antr. edge pineal	260	135	± 186	93
Intertabular width	200	110	—	104
Postr. orbit to postr. border cheek	150	124	—	73
Tabular boss to cheek angle	225	175	—	122
Vertical overhang of cheek maxilla border	140	50	—	29
Dentigerous length (maxillary)	180	125	116	± 66
Teeth	14	14	11 "post-canines" ?	10 "post-canines"

[1] After Boonstra [2] After Broom.

Table II

COMPARATIVE SURFACE MEASUREMENTS OF SCUTES

	P. serridens[1]	*Propappus parvus*[1]	*P. omocratus*[1] = *P. serridens*	*Anthodon*[1] *Sp.*	*"Pareiasaurus steenkampensis"*[2]	*Unknown No. 548*
Largest						
Length	67	60	50	64	57	30
Breadth	58	37		45	40	25
Medium						
Length	53	50		54		20
Breadth	45			40		20
Small						
Length	47		± 10		35	10 – 15
Breadth	40				25	8 – 10

[1] After Boonstra [2] After Seeley

Table III

AVERAGE ANTEROPOSTERIOR LENGTHS OF MIDLINE SCUTE ROWS AND VERTEBRAE COMPARED (SPECIMEN No. 548)

Region	*Set of Scute rows rows according to number of underlying vertebra*	*Combined length of of Rows (mm)*	*Average length of scutes over the region (mm)*	*Set of Vertebrae*	*Total length of set (mm)*	*Average length per vertebral body in region (mm)*
Code	A	B	C	D	E	F
Cervical	3 – 6	86	21,5	1 – 6	—	—
Dorsal	7 – 11	116	23,2	7 – 14	—	—
	12 – 16	156	31,2	14 – 16	97	32
	17 – 20	100	25	17 – 20	120	30
Sacral	21 – 24	76	19	21 – 24	100	25
Caudal	25 – 29	75	15	25 – 26	35	17,5

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CONTRIBUTION A LA CONNAISSANCE DES ICTIDORHINIDÉS (GORGONOPSIA)

par

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INTRODUCTION

Le matériel d'Ictidorhinidé disponible est actuellement limité, rappelons-le, à neuf échantillons: sept consistent en un crâne isolé, tandis que les deux autres comportent quelques éléments post-craniens. Ce dixième exemplaire n'apparaît donc pas négligeable, d'autant moins que la plupart des échantillons sont assez mal conservés et qu'en conséquence l'anatomie cranienne de la famille reste encore imprécisée; or cette famille constitue certainement l'une des plus intéressantes des Thériodontes du point de vue de la morphologie évolutive.

Le crâne étudié ici fut découvert par Mr. J. W. Kitching, et nous a été prêté avec l'accord du Gouvernement Sud-Africain. Notre dette de reconnaissance envers l'un et l'autre s'en trouve encore accrue.

DESCRIPTION

Etat du crâne, B.P.I. (F.N.) 3924, Bultfontein, Richmond District, zone à *Cistecephalus*. Il s'agit d'un crâne très écrasé latéralement, et laminé: le côté droit du crâne, jusqu'au bord postérieur de l'orbite, mesure 23 mm de plus que le côté gauche. Il manque la plus grande partie de la fosse temporale droite, et les bords dorsal et postérieur de la fosse temporale gauche ont été érodés; l'arcade zygomatique, totalement absente à gauche, ne persiste à droite que par son extrémité antérieure. Le toit du museau est fort endommagé et le maxillaire droit a subi un décrochement vers le haut par rapport au prémaxillaire, son bord alvéolaire ayant en même temps été abrasé. Les os qui bordent ventralement l'orbite, altéré à droite, n'ont laissé à gauche qu'une empreinte. L'occiput est conservé, à droite, jusqu'au niveau de l'extrémité mésiale de la fosse post-temporale, à gauche jusqu'à l'extrémité latérale de la même fosse. Le condyle occipital a été tronqué à sa racine et les paroccipitaux ne sont présents que par leur tiers médian. Le carré gauche est partiellement conservé. La face ventrale est presque complète, mais la compression a brisé certains éléments dont l'interprétation reste un peu incertaine. Enfin la mandibule s'est maintenue en place, mais tout ce qui se situe postérieurement au dentaire est absent ou incomplet; le bord ventral du dentaire droit est partiellement arasé, le dentaire gauche très abîmé. Les deux incisives supérieures médianes et les deux premières incisives inférieures gauches ont été brisées à la base de la couronne, ainsi que les deux canines supérieures. Les trois premières post-canines inférieures droites sont incomplètes; les post-canines supérieures droites sont entièrement absentes, ainsi que les deux (ou trois) éléments postérieurs gauches en haut, et le ou les éléments postérieurs droits en bas. Enfin la surface osseuse, par endroits bien conservée, est ailleurs intimement mêlée de gangue.

Mesures.

distance entre le bord antérieur des prémaxillaires et le bord postérieur des ailes squamosales
116 (dte) .... 103? (gche) ..... 112,5 (ap. rec.)*
largeur maxima mesurée entre les bords latéraux des arcades zygomatiques
40 ..... 67,5 (ap. rec.)
distance entre le bord antérieur des prémaxillaires et le bord antérieur des orbites
63 (dte) ..... 54 (gche) ..... 59 (ap. rec.)
largeur du museau mesurée aux 2/3 de sa longueur
22 ..... 28,5 (ap. rec.)
hauteur du museau mesurée aux 2/3 de sa longueur
35 ..... 33 (ap. rec.)
largeur inter-orbitaire minima
10 (dte) ..... 11 (gche) ..... 12 (ap. rec.)
largeur inter-temporale mesurée au bord antérieur des fosses temporales
15 (dte) .... 18,5 (ap. rec.)
longueur de l'orbite
39 (dte) ..... 25 (gche) ..... 35 (ap. rec.)
longueur de la fosse temporale
— ..... — ..... 12,5 (ap. rec.
distance entre le bord antérieur des prémaxillaires et le bord antérieur de l'orifice pinéal
94 ..... 94 (ap. rec.)
distance entre le bord postérieur de l'orifice pinéal et la crête nuchale
10 ..... 10 (ap. rec.)
distance entre le bord antérieur des prémaxillaires et le bord antérieur des apophyses transverses ptérygoïdes
70 (dte) ..... 65 (gche) ..... 68 (ap. rec.)
largeur minima de la barre post-orbitaire
5,5 (dte) ..... 5 (gche) ..... 5,25 (ap. rec.)
hauteur minima de la barre sous-orbitaire
— ..... 8 (gche) ..... 7,5 (ap. rec.)

* après reconstitution.

hauteur minima de l'arcade zygomatique
5 (dte) ..... – ..... 5 (ap. rec.)
hauteur du dentaire mesurée derrière les post-canines
– ..... 11 (gche) ..... 11,5 (ap rec.)
longueur du diastème entre I^4 et la canine supérieure
– ..... 7,25 (gche)
diamètre maximum de la canine supérieure
5,5 (dte) ..... 6 (gche)
longueur du diastème entre la canine et Pc^1 supérieures
– ..... 6 (gche)
longueur de la serie post-canine supérieure (5 éléments).
– ..... 10,5 (gche)
Ce crâne a été préparé exclusivement à l'aide d'une aiguille à main.

Généralités.

Les traits les plus marquants de ce crâne en sont la position antéro-dorsale des narines, la convexité du bord ventral du museau, lui-même étroit et élevé; la grande taille des orbites coiffées dorsalement d'un rebord en toit, la petite taille et la position présumée en contrebas des fosses temporales, la situation et la taille de l'orifice pinéal, l'étroitesse inter-orbitaire; la longuer des tubérosités palatales, la position postérieure des apophyses transverses pterygoïdes, l'absence supposée de rostre parasphénoidien ventral et la séparation des deux arêtes ventrales des ptérygoïdes postérieurs; l'absence enfin d'apophyse coronoïde (s. st.) du dentaire, ainsi que la morphologie et la disposition des dents, en particulier des incisives.

Faces dorsale et latérale.

Les narines sont en effet entièrement visibles dorsalement. Elles sont séparées l'une de l'autre par une barre prémaxillaire étroite, dont manque ici le composant gauche; le composant droit est, lui, interrompu un peu en avant du bord postérieur de la narine, de sorte qu'on ne connaît pas l'extension dorsale des prémaxillaires. C'est essentiellement cet os qui constitue le plancher de la narine, qu'un petit orifice arrondi perfore, du côté mésial et assez en arrière. Sous la narine, l'os est bas et légèrement incliné vers l'arrière et le haut. Cette partie antérieure de l'os est perforée d'un ou deux petits orifices vasculaires disposés au-dessus des incisives.

Sur le plancher narial, le prémaxillaire est recouvert latéralement par le septomaxillaire. Entre les deux os persiste une ouverture, qui semble bien se prolonger vers le bas à travers le prémaxillaire. Après avoir pris cet appui ventral sur le prémaxillaire, le septomaxillaire s'élève verticalement en une lame très étroite qui, après courbure vers l'arrière, devait venir s'appuyer dorsalement sur le nasal; mais dans ce cas non plus l'extension dorso-postérieure de l'os n'est pas connue. Ce pilier septomaxillaire émet, dans la narine et assez haut, une lame transversale courte mais profonde antéro-postérieurement; la narine était donc divisée dans sa hauteur en deux compartiments inégaux. En haut et latéralement, le septomaxillaire est séparé du maxillaire par une fosse au fond de laquelle passe un pilier vertical; en avant de celui-ci un orifice aboutit dans la narine;

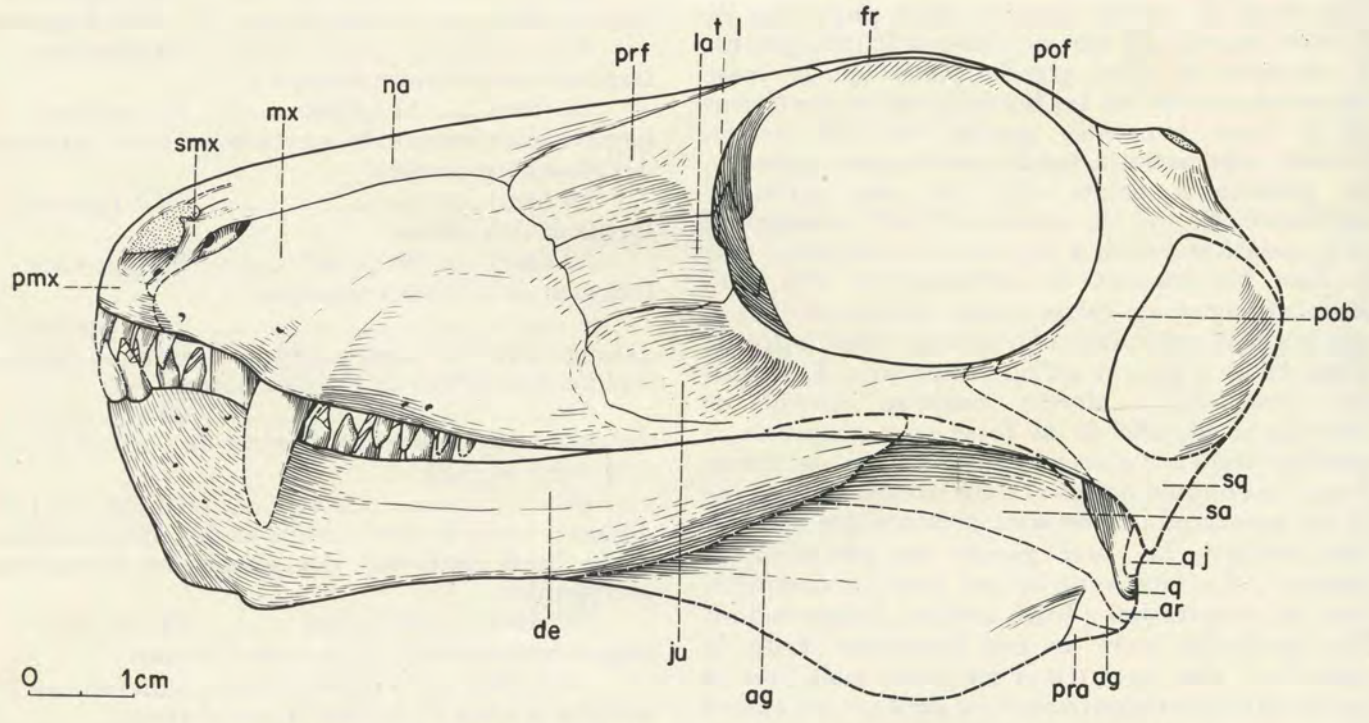


Fig. 1. *Rubidgina* sp., B.P.I.(F.N.) 3924. Crâne, vue latérale gauche (I_1 et I_2 sont celles de droite).

en arrière et en haut un autre orifice orienté vers l'arrière et un peu vers le bas débouchait probablement dans le canal lacrymal. Il semble que ce pilier soit constitué par le septomaxillaire?

Latéro-ventralement le septomaxillaire est à son tour recouvert par le maxillaire qui devait atteindre à l'avant le niveau du bord postérieur de I^3. L'os présente la même forme triangulaire que le museau, son bord dorsal s'élevant doucement vers l'arrière en même temps que son bord ventral s'abaisse, plus fortement d'ailleurs, en décrivant une assez forte convexité dissymétrique. A gauche seulement la limite postérieure de l'os (pointe ventrale exclue) est visible, telle qu'elle est représentée sur la figure 1. Il en résulte un os court, assez bas, le maximum de hauteur se situant presque à son angle postéro-nasal. L'extension postéro-inférieure de l'os n'est pas connue; il ne semble pas qu'elle ait beaucoup dépassé le niveau du rebord orbitaire antérieur. Il n'est pas douteux que l'os était perforé de quelques orifices vasculo-nerveux, mais ceux-ci ne semblent par avoir été très nombreux. L'os présente une légère convexité au niveau de la racine de la canine, apparemment dirigée obliquement vers l'arrière et le haut, et une autre convexité plus forte-mais est-elle naturelle? - en arrière de la première.

Le maxillaire passe en bas et en arrière au jugal. Relativement à la gracilité des autres éléments, le jugal apparaît plus massif, peut-être surtout sous l'orbite où malheureusement ne persiste que son empreinte déformée. On ignore ici encore l'extension postérieure de l'os. La partie intra-orbitaire apparaît peu étendue.

Le lacrymal surmonte le jugal en avant de l'orbite, le contact des deux os étant marqué par une légère concavité. Les deux orifices lacrymaux sont bien délimités l'un de l'autre par une crête transversale, l'orifice dorsal étant plus rond, l'orifice ventral plus allongé et caché, en vue latérale, par un petit éperon du bord orbitaire antérieur. La partie intra-orbitaire du lacrymal, perpendiculaire à la partie latérale de l'os, reste même plus étroite que celle du jugal.

Le lacrymal est à son tour surmonté du préfrontal, à peine plus étendu vers l'avant que le précédent et, semble-t-il, guère étendu non plus sur le rebord orbitaire dorsal. Une côte sépare ses faces dorsale et latérale, et s'épaissit d'avant en arrière pour former un bourrelet au-dessus de l'angle orbitaire antérieur.

Les nasaux sont en très mauvais état; étant donnée la forme du maxillaire, ils ne devaient pas subir de constriction importante avant d'atteindre les préfrontaux. Le niveau du contact fronto-nasal n'est pas certain: il y a bien, légèrement en arrière du rebord orbitaire antérieur, un décrochement osseux qui pourrait correspondre à cette suture; mais celle-ci serait alors située très en arrière.

La delimitation des os du toit cranien (fig. 2) reste sujette à discussion, les sutures n'étant le plus souvent pas nettes, et l'écrasement ayant provoqué des chevauchements osseux ou au contraire des

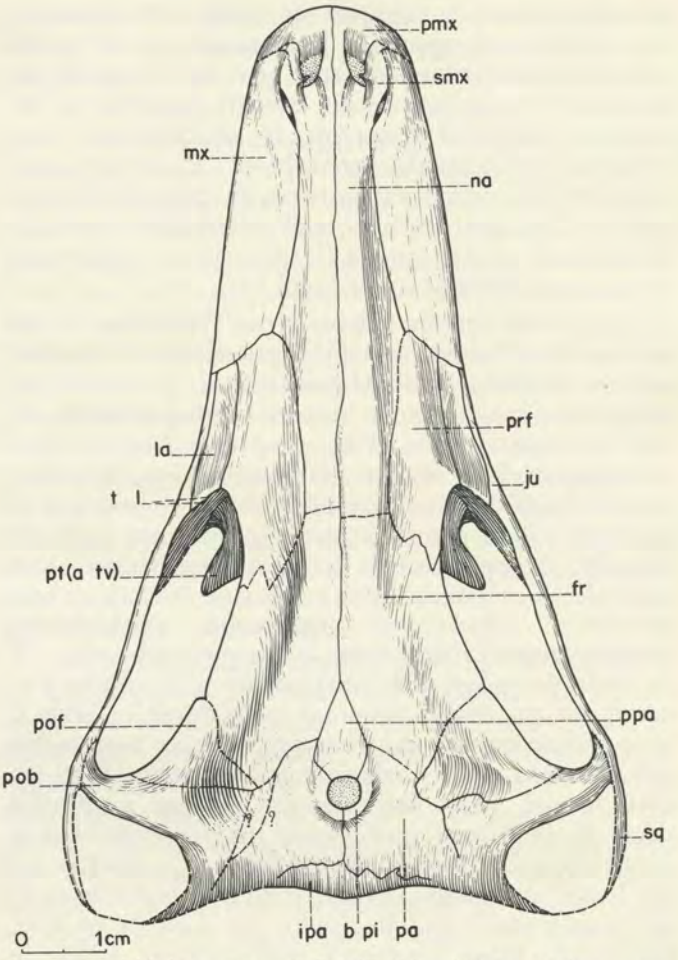


Fig. 2. *Rubidgina* sp., B.P.I.(F.N.) 3924. Crâne, vue dorsale.

déboîtements. La limite postéro-latérale des frontaux en particulier n'a pas été retrouvée avec certitude; il n'apparaît toutefois pas douteux que leur participation au bord sus-orbitaire était importante. Ces os, étroits à l'avant, devaient s'élargir assez considérablement à l'arrière. Par ailleurs, concaves au voisinage de la ligne médiane où ils s'unissent l'un à l'autre en une crête fine, ils se bombaient latéralement en s'épaississant sans doute, puis se terminaient en un bord aigu surplombant les orbites.

Mésialement et à l'arrière, les frontaux se heurtent au prépariétal, petit os triangulaire montant jusqu'au sommet de la bosse pinéale, dont il forme le rebord antérieur.

Il existe à gauche, sur le bord supérieur de l'orbite, une indentation, et il semble bien qu'en avant et en arrière de celle-ci l'os, dont on n'a que l'empreinte, présentait une orientation différente. Il s'agirait donc de la limite latérale du frontal et du postfrontal. Plus en arrière et toujours à gauche, on distingue une portion de suture dirigée longitudinalement, qui doit représenter la partie postérieure de la même limite. Il semble qu'à ce niveau le postfrontal(?) forme un angle aigu et que l'on puisse déceler sur quelques millimètres la partie postéro-dorsale de sa limite latérale, c'est-à-dire de la suture postfrontal-postorbitaire; mais, plus en avant, il est évident que la déformation a

fait se chevaucher ces deux os; après redressement, l'os postfrontal apparaît triangulaire et ne serait pas entré en contact, ou très peu, avec le pariétal. En arrière de la pointe du triangle postfrontal est conservé un petit fragment de postorbitaire sus-temporal remarquablement large; la barre post-orbitaire elle-même est constituée par un élément grêle et l'os, plat en bas, mais triangulaire en haut où sa face postérieure s'élargit, aurait atteint un niveau assez ventral sur le jugal.

A droite, on ne retrouve pas l'indentation du rebord sus-orbitaire signalée à gauche et interprétée comme la limite frontal-postfrontal; plusieurs fissures coupent, dans la région correspondante, le toit sus-orbitaire, et il se peut que l'une d'elles corresponde à la suture antérieure du postfrontal. Ensuite le postfrontal présumé longe longuement la pariétal, avant de se terminer contre un élément déboîté, comportant la barre post-orbitaire, une extension postérieure, une extension mésiale et une antérieure. Barre et extension postérieures appartiennent évidemment à l'os post-orbitaire; s'il en était de même des deux autres extensions, l'os aurait eu un développement considérable. Mais il est possible qu'une suture isole ces deux parties des précédentes; on la distingue en fait assez bien du côté mésial, mais latéralement elle se perd. S'il s'agit de la suture postérieure du postfrontal, l'os aurait ici une forme quadrangulaire et, nous l'avons vu, longerait longuement le pariétal contrairement au "postfronal" gauche; mais il y a eu de ce côté étirement. Pour retrouver une certaine symétrie avec l'autre côté, il faut donc admettre que les côtés antérieur et mésial du "postfrontal" droit correspondent au seul côté mésial du postfrontal gauche; il s'agirait alors d'un os assez développé, triangulaire et descendant quelque peu en avant et latéralement sur la barre post-orbitaire.

Dans ces conditions, le pariétal -dont le départ à partir du prépariétal est très net à gauche-, toucherait d'abord le frontal, contacterait à peine le postfrontal, puis très longuement le post-orbitaire. La limite latérale du pariétal est elle aussi incertaine, en raison des nombreuses fissures qui coupent le toit cranien, mais l'os devait être large et descendait sans doute longuement sur les côtés de l'occiput; au contraire la suture pariétal-interpariétal est bien nette à la limite de la face dorsale et de la face occipitale.

Occiput.

Seule la partie médiane de cette face est conservée à peu près intacte. L'interpariétal en occupe une portion importante: c'est un os à peu près aussi haut que large, convexe en tous sens dans sa moitié supérieure. Dans sa moitié inférieure s'esquisse de chaque côté une fosse profonde, qui se prolonge largement sur le susoccipital tandis qu'une côte médiane prolonge vers le bas la convexité supérieure. Le susoccipital reste bas mésialement, mais on peut se demander s'il n'y avait pas articulation à ce niveau (kinétisme), articulation qui aurait joué au cours de la fossilisation, l'interpariétal recouvrant maintenant en partie le susoccipital. Quoi qu'il en soit, il s'agissait certainement d'un os large, qui aurait atteint latéralement le bord externe des fosses post-temporales. Celles-ci apparaissent plus longues que hautes; le fond en est probablement constitué, du côté mésial, en partie par le susoccipital, en partie par l'opisthotique; l'ouverture latérale est partiellement divisée en deux par une languette osseuse émanée de ce fond mésial.

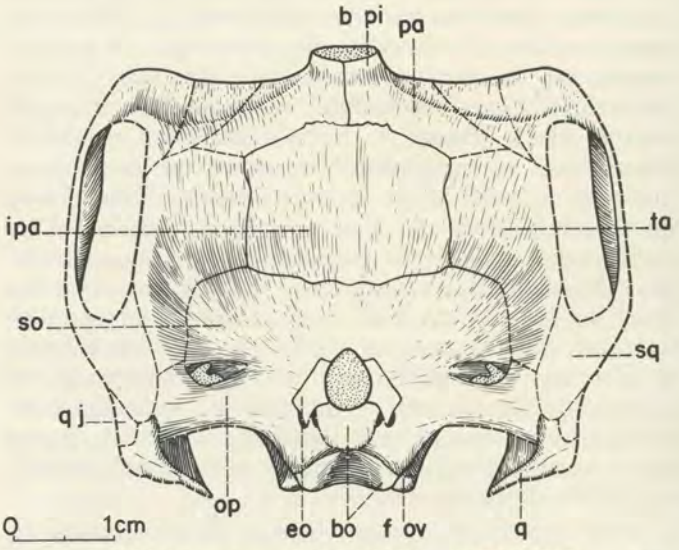


Fig. 3. *Rubidgina* sp., B.P.I.(F.N.) 3924. Crâne, vue postérieure.

De l'opisthotique seule la racine est conservée, à droite comme à gauche. Les exoccipitaux ont été arasés, mais ils sont délimitables; enfin le condyle occipital a été tronqué au ras de l'occiput, Sous le contact exoccipital-basioccipital, on reconnaît le trou condylien, doublé latéro-ventralement par une longue fissure située au voisinage du contact basioccipital-opisthotique. Les tabulaires et les squamosaux sont, à droite comme à gauche, pratiquement absents.

A gauche serait conservé l'os carré, d'ailleurs quelque peu incomplet et consistant essentiellement en une écaille disposée longitudinalement, avec une face latérale convexe et une face mésiale fort concave ventralement, redressée dorsalement (fig. 1 et 3). Il est évident que l'os, s'il a éte quelque peu déplacé, n'a pu subir la rotation nécessaire pour lui donner une orientation transversale comme chez les Gorgonopsidés. Ce carré aurait seulement été quelque peu poussé mésialement à son extrémité ventrale, latéralement et un peu vers l'avant à son extrémité dorsale; mais cette disposition longitudinale serait naturelle. Il manquerait ici le condyle externe, et le quadrato-jugal ne serait pas conservé, le bord postérieur du carré lui-même étant un peu incomplet. Le processus ventral antéro-mésial aurait donné appui à la branche carrée du ptérygoïde, tandis que la concavité mésiale aurait hébergé la tête distale du stapes. Les arguments en faveur de cette interprétation (qui fait de ce carré un os plus proche de celui des Pélycosaures que de celui des Gorgonopsidés) concernent l'aspect du

bord antérieur de l'os, bord qui manifestement se continuait par du cartilage: or on confoit mal un bord latéral de carré gorgonopside cartilagineux, tandis que cela est connu pour le bord antérieur du même os chez les Pélycosaures. D'autre part le bord actuellement postérieur, légèrement arrondi, a certes été abrasé; mais on distingue, à 3 mm environ du bord ventral, une petite indentation qui paraît naturelle et qui pourrait correspondre au passage quadrato-jugal; le carré n'aurait done bien eu qu'une faible extension postérieure et, sans doute, une surface articulaire assez étroite latéromésialement. Ce carré serait actuellement privé de ses contacts avec le aquamosal à l'arrière, avec le ptérygoïde à l'avant.

Face ventrale.

Les choanes étaient allongées et probablement assez étroites. Elles sont séparées l'une de l'autre par le vomer qui se présente, à l'arrière, sous forme d'une courte et fine crête verticale; mais bientôt cette crête se bifurque en même temps qu'elle s'élève. Puis l'os est interrompu accidentellement, mais il semble bien que l'élément que l'on retrouve plus en avant en soit la continuation. Sa forme est alors toute différente, l'os étant convexe de droite

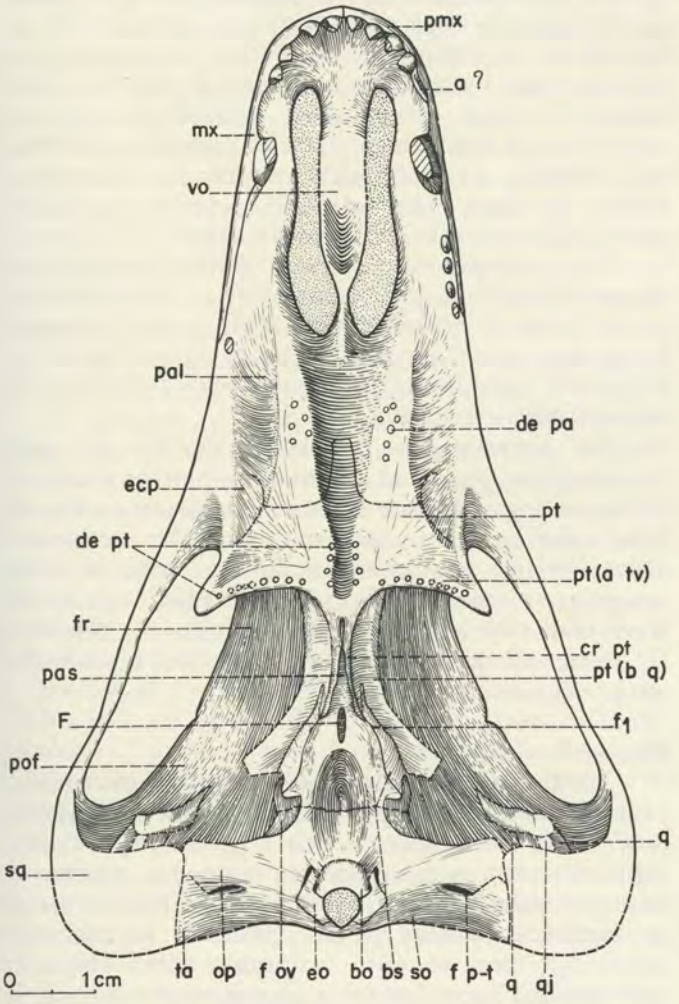


Fig. 4. *Rubidgina* sp., B.P.I.(F.N.) 3924. Crâne, vue ventrale.

à gauche. Le point de contact du vomer avec le prémaxillaire est masqué par les dents antérieures à droite, par la partie palatale du maxillaire à gauche.

Celle-ci aurait été étroite et brève; ce doit en effet en être la limite postérieure que l'on distingue à gauche, au niveau de Pc_3 inférieure. Le palatin qui lui succède devait aussi présenter une partie choanale étroite, et limitée mésialement par un bord aigu; c'est à droite que l'on distingue le mieux cette partie choanale à face ventrale grossièrement horizontale. En arrière des choanes, le palatin descend rapidement pour se terminer par une tubérosité sur le bord ventral de laquelle les dents devaient être disposées en deux rangées; quelques-unes seulement sont actuellement discernables. Entre cette tubérosité et le maxillaire latéralement, la palatin devait se poursuivre vers l'arrière en décrivant une légère concavité; mais l'os est actuellement comprimé et incompletement dégagé à ce niveau. Il en est de même de l'ectoptérygoïde, qui devait être relativement réduit.

La tubérosité ptérygoïde prolonge directement et linéairement la tubérosite palatine; la suture entre les deux os serait assez antérieure dans le fond du sillon palatal, puis elle descendrait obliquement pour atteindre le sommet de la tubérosité. Aucune cavité inter-ptérygoïdienne ne semble séparer les ptérygoïdes à ce niveau. Vers l'arrière, et assez postérieurement en raison de la longueur des choanes et du palais proprement dit, se détachent les apophyses transverses: elles sont élevées, probablement un peu sinueuses à leur bord ventral, et munies d'une rangée de petites dents. Chaque os émet ensuite une longue branche carée, d'abord parallèle à sa symétrique à laquelle elle est mésialement suturée; cette partie antérieure de la branche carrée, légèrement concave, est limitée latéralement par un bord arrondi, tandis qu'elle porte du côté mésial une crête verticale très fine, prolongeant semble-t-il le bord ventral de l'apophyse transverse; cette crête ne s'accole pas à sa symétrique comme chez les Gorgonopsidés mais, en s'élevant légèrement, elle diverge vers l'arrière tout en restant suturée au para-basisphénoïde; elle devait atteindre ainsi à peu près le niveau du trou carotidien. A ce niveau les branches carrées se détachaient de l'axe médian pour rejoindre le carré; mais de cette partie seule la racine est actuellement conservée, au niveau du contact avec la processus basi-ptérygoïden du basisphénoïde. Finalement, la cavité interptérygoïdienne, si elle existait, devait même être plus réduite que chez les Gorgonopsidés.

La suture ptérygoïde-basisphénoïde décrirait le parcours dessiné sur les figures 4 et 5. Dans sa partie médiane, le basisphénoïde est actuellement creusé, an avant de la dépression basilaire, d'une fosse étroite et profonde F, qui ne semble pas s'ouvrir dorsalement; il n'est pas certain que cette cavité soit naturelle: elle n'est pas tout à fait médiane, mais il semblerait que la déformation puisse rendre compte de cette situation et que ses parois soient bien naturelles. De chaque côté de

cette fosse et à la base du processus basiptérygoïde, s'ouvre un gros orifice (f1) orienté vers l'arrière et latéralement; s'il correspond au trou carotidien, il faut remarquer sa situation éloignée de la ligne médiane, comme chez les Gorgonopsidés. En avant et plus ventralement, une fosse profonde et bien délimitée (f2) déprime à gauche le basisphénoïde; mais rien d'équivalent n'est visible à droite, où pourtant l'os est bien conservé; à moins que la dissymétrie ne soit maintenant très importante et que cette fosse soit reportée dans une fente visible plus dorsalement? Enfin, toujours à gauche, plus en avant encore, c'est-à-dire dans le ptérygoïde ou à la limite basisphénoïde-ptérygoïde, mais au même niveau dorsal que le "trou carotidien", une troisième dépression (f3) semble mener à un petit orifice antérieur qui correspondrait, s'il est naturel, au trou vidien signalé par Olson (1944) chez un Cynodonte, et par Tchudinov (1968) chez un Brithopodidé.

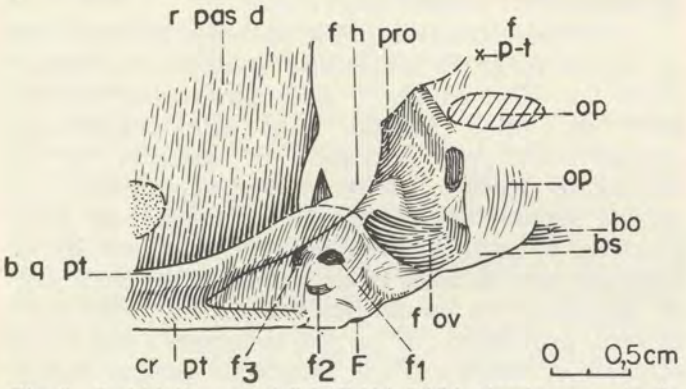


Fig. 5. *Rubidgina* sp., B.P.I.(F.N.) 3924. Partie ventrale de la paroi cérébrale côte gauche. Abreviations p. 38 En outre, x f p-t, niveau de la fosse post-temporale.

En arrière et de chaque côté de la profonde fosse basilaire, l'os émet de larges tubérosités qui bordaient ventralement la fenêtre ovale. Au-dessus de celle-ci, l'os remonte pour rencontrer le prootique, en limitant la fosse hypophysaire.

On ne connaît pas l'importance de la participation parasphénoïdienne à cet axe basicranien; on remarquera seulement qu'aucun rostre ventral ne hérisse actuellement cet axe comme c'est le cas chez les Gorgonopsidés et autres Thériodontes. Au contraire un rostre dorsal élevé, terminé en avant par un bord concave, divise longitudinalement cette région du crâne.

Au fond de la fosse basilaire se dessine le passage au basioccipital. Cet os devait rester assez court; il limitait mésialement et postérieurement la fenêtre ovale. Le condyle occipital, nous l'avons vu, n'est pas conservé.

Du prootique gauche (fig. 5), seule la base a pu être dégagée, et ce jusqu'au niveau de l'échancrure veineuse inférieure; le sommet de l'os se perd malheureusement sous la mandibule. Rien n'est accessible à droite. Toujours à gauche, au-dessus du processus basi-ptérygoïden du basisphénoïde et entre le rostre du parasphénoïde et la fosse hypophysaire, se devine un petit triangle osseux à sommet dorsal, qui ne semble pas faire partie du basisphénoïde; peut-être s'agit-il de la base déportée de l'épiptérygoïde? Aucun autre témoin de cet os n'est conservé.

Mandibule.

Le dentaire, assez élevé à l'avant, formait une symphyse large, sans apophyse mentonnière. Le décrochement actuel du bord ventral au niveau de la canine supérieure est probablement en partie artificiel, mais il y avait sans doute une côte à ce niveau. L'os s'amenuise fortement vers l'arrière pour atteindre son minimum de hauteur juste derrière les postcanines inférieures. Sa hauteur croît à nouveau vers l'arrière, par abaissement du bord ventral à la rencontre de l'angulaire, et par élévation du bord dorsal pour former une "apophyse coronoïde" épaisse, fortement costée, cette côte prolongeant le bord dorsal arrondi de l'os. Le dentaire atteint ainsi, dorsalement et à l'arrière, à peu près le niveau du milieu de l'orbite. De petits foramens vasculaires perforent l'os sur sa partie antéro-ventrale.

Les os postérieurs de la mandibule sont beaucoup moins bien identifiables. L'angulaire s'avance en coin sur la face mésiale de la mandibule et n'apparaît sur le bord ventral qu'au niveau des apophyses transverses ptérygoïdes. La limite postérieure de cet os n'est pas connue; il est toutefois vraisemblable qu'elle se situait au voisinage de l'articulation mandibulaire. Le corps même de l'os et sa lame réfléchie sont mal conservés; la hauteur de cette dernière ne peut être que déduite de celle des apophyses transverses. Enfin la ligne de contact externe angulaire-surangulaire semble avoir été bas située.

Le surangulaire prolonge postérieurement le dentaire, son bord dorsal continuant sans dénivellation le bord dorsal du dentaire, puis s'abaissant fortement vers l'arrière. Ce bord dorsal forme un surplomb vers l'extérieur, en dessous duquel l'os est légèrement concave.

Le préarticulaire ni le coronoïde ne sont discernables. Quant au splénial, on peut le déceler à droite et à gauche sur la face mésiale; mais il reste haut situé sur cette face et n'aurait eu, curieusement, aucune participation au bord ventral de la symphyse mandibulaire, pas plus qu'il ne recouvrait latéralement le bord ventral du dentaire. Il atteignait presque, à l'arrière, le niveau des apophyses transverses.

Denture.

La denture est remarquable à plusieurs égards: premièrement par la morphologie des incisives et leur entrecroisement. La première incisive supérieure est visible à droite comme à gauche; sa base par ailleurs a subi une compression latérale. Il est toutefois évident qu'il s'agissait de dents à base quadrangulaire, le côté antérieur étant étroit et convexe, les faces latérales planes et plus larges, le côté postérieur un peu plus étroit que le côté antérieur.

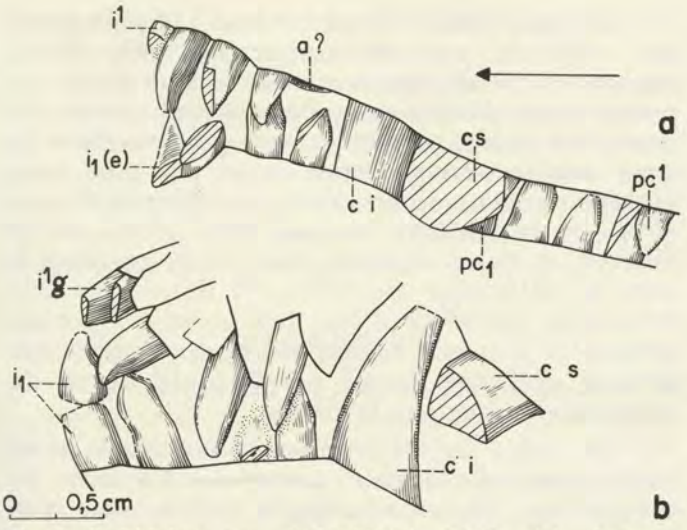


Fig. 6. *Rubidgina* sp., B.P.I.(F.N.) 3924. (a) denture gauche; (b) denture droite inversee.

I^2 supérieure est pratiquement intacte des deux côtés, bien qu'elle soit fendue transversalement à droite. Sa base présente la même forme que I^1 mais, de quadrangulaire, la section transversale devient rapidement triangulaire à sommet lingual. Puis le côté antérieur lui-même se réduit à une grosse côte tandis que les faces latérales convergent pour former la pointe de la dent.

I^3 est presque intacte des deux côtés. La dent est légèrement plus courte à gauche, et les quatre faces y sont moins bien délimitées que sur les précédentes. La face latérale est convexe, la face postérieure, d'abord convexe, devient concave vers la pointe en même temps qu'elle est bordée latéralement, en bas, d'une arête ventrale brève (1 mm) et munie de denticulations. La face linguale de la dent devait être convexe; la face antérieure enfin s'amenuise fort à mi-longueur, si bien que la pointe de la dent forme un crochet.

I^4 présente exactement la même morphologie; elle est seulement nettement plus courte.

Il n'existe pas de cinquième incisive discernable. Les quatre incisives gauches sont très serrées les unes contre les autres, et la seule place possible pour une cinquième incisive serait en arrière de I^4. Il existe en effet immédiatement en arrière de cette dent, et dans la prémaxillaire, une petite cavité allongéea. Mais cette loge, d'une part est très peu profonde et d'autre part semble s'ouvrir vers l'avant et latéralement: son bord mésial en effet ne se prolonge pas par le bord mésial de I^4, mais rejoint le bord latéral de cette dent. Il est difficile de voir là l'alvéole d'une dent, bien que le diastème I^4–C soit actuellement anormalement long. A droite, I^2 et I^3 sont plus éloignées l'une de l'autre, mais ceci provient du déplacement de I^2 et il n'y a pas place de toutes façons pour une incisive intermédiaire. En arrière de I^4 malheureusement, le prémaxillaire est brisé, tandis que le maxillaire a été déporté vers le haut.

Les deux canines supérieures sont brisées très haut. Elles étaient assez larges et devaient s'orienter un peu vers l'avant. Il semble bien n'y avoir qu'une canine supérieure de chaque côté, bien que l'alvéole droit se prolonge sur 3 mm en arrière de la canine.

Cinq mm derrière la canine supérirure gauche viennent 4 postcanines, en arrière desquelles on reconnaît la base d'une cinquième, le tout couvrant 16 mm; puis le bord alvéolaire du maxillaire est altéré. De l'autre côté la seule trace de post-canine visible se situe 18 mm derrière la canine; il est donc vraisemblable que ce crâne portait au moins 6 postcanines supérieures. A gauche, seule la première post-canine est complètement intacte; il ne s'agit pas d'une dent tout à fait simple et conique, puisqu'on y distingue un bord antérieur arrondi et convexe vers l'avant, un bord postérieur plus mince et légèrement concave vers l'arrière d'abord, puis s'étalant pour former une crête couverte de denticulations. Pc^2 et Pc^3 semblent bien avoir présenté les mêmes particularités; Pc^4 est très altérée. Ces dents sont assez espacées les unes des autres.

La position relevée du prémaxillaire fait que, même en occlusion, les premières dents inférieures sont visibles. I_1 inférieure est complètement brisée à gauche; à droite elle persiste en plus grande partie. Il n'est pas douteux que 1_1 comme 1_2, étaient proclives. I_1 droite se situe actuellement entre les deux premières incisives supérieures; I_1 gauche a laissé son empreinte derrière I^2 supérieure gauche. Si l'on tient compte de la déformation, il s'ensuit que I_1 inférieure se situait entre I^1 et I^2 superieures, et aussi labialement qu'elles: il y avait donc entrecroisement. La forme de la dent paraît avoir été très voisine de celle de I^1 supérieure, quadrangulaire à la base, avec toutefois des faces latérales moins planes et une face linguale probablement plus étroite; à son extrémité la dent se termine en crochet tourné lingalement, mais ceci a probablement été artificiellement accentué.

I_2 droite se situe derrière I^2 supérieure droite; 1_2 gauche est brisée à sa base, mais son empreinte recouvre l'espace I^2–I^3 et une partie de I^3 supérieure; il est probable que cette dent se situait entre I^2 et I^3 supérieures. La section de la base de la dent est encore quadrangulaire, mais la dent devient rapidement triangulaire et convexe antérieurement.

I_3 et I_4 sont au contraire mieux visibles à gauche. Ces deux dents sont, elles, nettement linguales par rapport à I^3 et I^4 supérieures à droite, par rapport à I_4 et la partie postérieure du prémaxillaire a gauche. I_3 inférieure évoque, par sa morphologie, Pc^1 supérieure, avec seulement une base plus longue et un collet plus marqué; on y retrouve le bord postérieur tranchant muni de denticulations. Quant à I_4, elle est abîmée à gauche, masquée à droite par I^4 supérieure; elle semble avoit été identique à la précédente. Ce nombre 4 d'incisives inférieures tend à appuyer notre supposition concernant l'existence d'une cinquième incisive supérieure.

La canine inférieure, qui suit immédiatement I_4, s'enfonce, elle aussi, sous le maxillaire; mais elle

est entièrement visible à droite, à la faveur du décrochement de cet os vers le haut. Plus grêle que la canine supérieure, elle passe immédiatement en avant d'elle; elle présente la forme habituelle avec un bord antérieur convexe en tous sens, denticulé sur son deuxième quart ventral, et un bord postérieur tranchant, denticulé sur presque toute sa hauteur. L'alvéole de la canine se prolonge quelque peu en arrière d'elle, mais il n'y a pas d'indication d'une seconde canine.

A droite les postcanines inférieures sont très abîmées; on compte les traces de 5. A gauche elles sont beaucoup mieux conservées, lingualement aux postcanines supérieures; il y en a 7 certaines. Pc_1 suivait des deux côtés à 3 mm environ la canine inférieure; à droite cette dent est brisée; à gauche, elle est presque entièrement masquée par la canine supérieure. Pc_2 est une dent assez longue, à bord antérieur arrondi, à bord postérieur plus tranchant et denticulé, comme Pc^1 supérieure ou I_3 inférieure, mais moins recourbée à son extrémité que cette dernière. Pc_3 présente une forme identique, et il en était sans doute de même des suivantes, dont les bords antérieur et postérieur sont masqués par les postcanines supérieures. Elles ont toutes approximativement la même largeur.

DETERMINATION

Les généralités énumérées au début de la description s'identifient entièrement avec les caractères qui définissent la famille des Ictidorhinidés: la forme convexe du profil supérieur du crâne, avec les fosses temporales situées en contrebas et les narines en position antéro-dorsale; l'élargissement du toit inter-orbitaire postérieur; la disproportion dans le volume relatif des orbites et des fosses temporales; l'accentuation de la bosse pinéale; la position très reculée des apophyses transverses ptérygoïdes; la constitution de la base du crâne; l'absence d'apophyse coronoïde (s. st.) du dentaire et la position basse de l'articulation mandibulaire. Enfin ce n'est que chez les Ictidorhinidés, parmi les Gorgonopsiens, que l'on observe un entrecroisement des incisives antérieures.

C'est précisément cet entrecroisement incisif qui rend aisée la détermination générique de cet échantillon, puisque ce phénomène n'est connu jusqu'ici que dans deux genres, sur les cinq que compte la famille: *Rubidgina* Broom (1943) et *Lemurosaurus* Broom (1940)*. La distinction de l'un par rapport à l'autre se fonde, elle, sur des différences plutôt mineures: la présence ou l'absence de tégument ossifié (?), la largeur inter-orbitaire relative et la longueur des tubérosités dentigères palatales. Or il apparaît qu'ici nous n'avons, pas davantage que sur le type de *Rubidgina,* trace d'un tégument corné, que l'espace inter-orbitaire est même plus étroit que sur ce type, et que les tubérosités palatales ont sur les deux crânes la même forme allongée. Une comparaison plus détaillée s'impose pourtant avant toute identification définitive.

Le crâne décrit ici est environ 1/4 plus grand que celui du type et unique spécimen de *R. angusticeps,* seule espèce connue du genre; mais les proportions, compte-tenu des approximations de leur restauration respective, sont voisines dans les deux cas: le museau serait ici un peu plus long, l'orbite un peu moins vaste, *io.* légèrement plus étroit et le dentaire un peu plus grêle; toutes différences qui pourraient être mises en relation avec la différence de taille, et donc avec une éventuelle différence d'âge. Les fosses temporales présentent la même disproportion par rapport aux orbites, et l'angle formé par le profil dorsal du crâne est sensiblement le même.

Au point de vue osseux, nous avions noté (1970), chez *Rubidgina* comme ici, l'absence de constriction des os nasaux, la brièveté des préfrontaux, la forme triangulaire des postfrontaux (plus petits il est vrai) et leur empiètement sur la barre post-orbitaire, la remontée du prépariétal sur le sommet de la bosse pinéale, la largeur des postorbitaires dorsaux, la faible hauteur du maxillaire et la longueur du lacrymal; il faut toutefois rappeler que ces caractères sont très voisins dans les cinq genres. La face postérieure du crâne de *Rubidgina,* ou ce qui en était préservé, la même orientation que sur le nouvel échantillon. Il scrait intéressant de pouvoir comparer directement les os carrés, car il semble que dans le premier cas cet os présentait une face postérieure plus large; mais peut-être cette largeur a-t-elle été ici sous-estimée.

Sur la face ventrale, et en plus des ressemblances déjà signalées sur le palais, les apophyses transverses occupent la même position relative, mais elles étaient, sur le type, dépourvues de dents. Il ne semblait pas exister davantage de rostre parasphénoïdien ventral. Le dessin de la mandibule paraît avoir été identique dans les deux cas, bien que le dentaire soit, nous l'avons vu, un peu plus grêle ici. On retrouve dans les deux cas le même surplomb du surangulaire dorsal. Malheureusement la face mésiale de la mandibule du type n'est pas connue.

La proclivité des incisives inférieures se retrouve identique sur l'un et l'autre crâne; il y avait donc bien entrecroisement des incisives antérieures sur le type de *Rubidgina angusticeps* comme nous l'avions supposé. Pc_1 inférieure occupe la même position relativement à la canine supérieure. Il semble cependant que la morphologie des postcanines ait été quelque peu différente sur le type, la couronne y ayant une forme plus symétrique; leur nombre était par ailleurs de 9. Mais peut-être ce nombre et cette morphologie correspondent-ils simplement à une série dentaire

* On peut objecter que cet entrecroisement incisif n'était peut-être pas limité à ces deux genres, et que seul l'état actuel des échantillons permet cette distinction. Toutefois, même si l'on admet cette possibilité, on remarque qu'*Hipposaurus* se distingue de tous les autres genres par la taille relativement plus grande des fosses temporales, *Lycaenodon* et *Ictidorhinus* par la position et le relief du palais, ainsi que par la forme du museau particulière à l'un et l'autre genre.

plus précoce? Enfin on ignore pour le type aussi le nombre d'incisives supérieures.

Cette double incertitude concernant le nombre d'incisives, jointe aux quelques différences observées dans les proportions du crâne, les dents ptérygoïdes et le nombre de post-cannines, nous contraignent à laisser en attente la détermination spécifique de ce nouvel échantillon. Nous le désignerons donc *Rubidgina* sp.

REMARQUES

Nous ajouterons ici quelques remarques sur la constitution de la paroi cérébrale et du carré chez les Ictidorhinidés, remarques inspitées par l'examen du crâne d'*Ictidorhinus martinsi,* que nous avons eu la possibilité de dégager davantage.

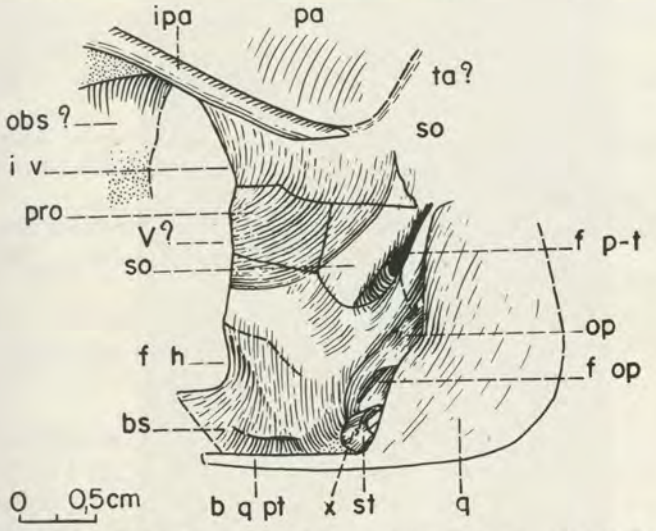


Fig. 7. *Ictidorhinus martinsi,* spécimen-type A.M.N.H. 5526. Paroi cérébrale, côté gauche. Abréviations p. 38. En outre, x, petit foramen (?) sur la face antérieure du stapes.

La paroi cérébrale de *Rubidgina* sp. n'était en effet guère acccessible, mais celle d'*Ictidorhinus* est maintenant observable (fig. 7). Une première constatation est l'étroitesse de la fissure métoptique*: ce caractère a été signalé par Boonstra (1968) chez les Dinocéphales, et par nous (1970) chez les Rubidgéinés (Gorgonopsidés). Les raisons en sont voisines dans le trois cas: extension postérieure et ossification du complexe sphénoïdal, extension antérieure du prootique (liée, chez les Ictidorhinidés et les Dinocéphales, à l'inclinaison vers le bas et l'avant de la face occipitale); mais chez les Ictidorhinidés le prootique est peu ossifié, et il est probable que le nerf V s'échappait en avant de l'os; il y a donc en plus, dans ce cas, confluence des fissures prootique et métoptique, ce qui rend d'autant plus remarquable l'étroitesse de la fissure résultante. Sur cette paroi cérébrale, les sutures sont difficilement délimitables. L'opisthotique, massif, serait recouvert antérieurement et sur les 3/4 de sa longueur par le prootique. Chez *Ictidorhinus* comme chez *Rubidgina,* la face antérieure de l'opisthotique est creusée, au voisinage de son extrémité mésiale, d'une fosse ovale (f op), apparemment assez profonde (davantage chez *Ictidorhinus).* Rien d'équivalent n'est connu chez les Gorgonopsidés, sauf chez *Arctops watsoni* B.P.I. 263, où la fenêtre ovale se prolongeait dans l'opisthotique par une fosse assez profonde. Par ailleurs, Romer et Price (1940) signalent l'existence, sur l'opisthotique de *Dimetrodon,* d'une cavité destinée à loger une partie du processus dorsal et proximal du stapes. L'extrémité proximale du stapes ne paraît pas avoir présenté, ici, d'extension dorsale vers cette fosse de l'opisthotique; mais peut-être s'agissait-il d'un processus dorsal cartilagineux? Le prootique d'*Ictidorhinus* est traversé à mi-longueur par une côte verticale en avant de laquelle l'os plonge mésialement; il devait ventralement participer quelque peu à la paroi de la fosse hypophysaire; mais sa suture avec le basisphénoïde n'est pas visible, pas davantage que l'orifice du nerf VII en avant de la fenêtre ovale. Au-dessus de cette côte, l'os est à peu près plan, incliné seulement légèrement vers la ligne médiane, et son bord antérieur est presque rectiligne: à peine devine-t-on l'incisure veineuse et celle correspondant au passage du nerf V. Pour la suture dorsale du prootique, deux limites semblent discernables, mais la limite supérieure apparaît comme la plus vraisemblable. Postérieurement et dorsalement, le susoccipital succède à l'opisthotique, bordant dorsalement la fenêtre post-temporale. Si c'est bien l'interpariétal qui forme la partie supérieure de la boîte cranienne, la pariétal formerait un ressaut latéral à cet interpariétal, ressaut où peut-être s'attachait l'épiptérygoïde, à moins qu'il ne s'agisse d'une partie du tabulaire? Seule l'extrémité proximale du stapes est conservée, encore sa butée devait-elle être cartilagineuse; l'os amorce une légère torsion, sa concavité antéro-ventrale devenant ventrale. Un minuscule orifice perce sa face antérieure. On ne sait s'il existait ou non un trou stapédial.

Il semble que dans aucun autre groupe de Thérapsides ne soit réalisée cette association d'une paroi cérébrale aussi peu ossifiée avec un complexe sphénethmoidal aussi développé. Il serait intéressant de connaître à cet égard les Eothériodontes.

Le carré d'*Ictidorhinus* est également intéressant. Il s'agit bien, comme chez *Rubidgina* sp., d'un os à orientation longitudinale, avec une face latérale légèrement convexe et une face mésiale fort concave. Mais, quoique ses limites ne soient pas nettes et qu'il ait manifestement été aplati transversalement, sa face postérieure apparaît nettement plus étendue qu'on ne l'avait soupçonné sur B.P.I. 3924, rappelant davantage le carré des Gorgonopsidés; comme chez ceux-ci en effet, les contacts se font davantage avec l'opisthotique (mésialement) qu'avec le ptérygoïde (antérieurement), contrairement à ce que l'on avait cru comprendre chez *Rubidgina* sp. Toutefois le

* Boonstra (1968) écrit au contaire que, un hipposauride de la zone à *Tapinocephalus,* "the sidewall of braincase is widely open between the otic and sphenoidal regions".

recouvrement de cette face postérieure par le squamosal semble avoir été assez réduit, et celui de la face antérieure par le même os inexistant, comme nous l'avions déjà soupçonné chez d'autres ictidorhinides, et contrairement au cas des gorgonopsides où le carré se loge dans une poche du squamosal. Finalement le carré serait ici intermédiaire entre celui sinon des Pélycosaures, du moins de certains Dinocéphales, et celui des Gorgonopsidés; c'est-à-dire que l'os n'aurait pas encore achevé sa migration sur la face postérieure du crâne et qu'il garderait encore une trace de son appartenance au complexe palato-carré.

CONCLUSION

L'intérêt de cette étude est d'accroître quelque peu notre connaissance anatomique encore très fragmentaire des Ictidorhinidés, et peut-être de nous conduire à une réévaluation de cette famille d'une part, de sa signification à l'intérieur des thérapsides d'autre part.

En effet, la comparaison entre deux genres aussi distincts en apparence qu'*Ictidorhinus* et *Rubidgina* nous révèle une similitude plus grande que nous ne l'attendions, non seulement dans les grandes spécialisations, mais jusque dans les détails osseux: forme du toit sus-orbitaire, constitution de la barre post-orbitaire, du septomaxillaire (il apparaît maintenant vraisemblable que est os présentait aussi chez *Ictidorhinus* une lame intra-nariale). Ceci nous conduit à nous demander, premièrement, si *Ictidorhinus* avait bien un museau plus gorgonopside que tous les autres membres de la famille, et si nous ne devrions pas soupçonner l'existence, dans ce genre également, d'incisives antérieures entrecroisées; deuxièmement et en conséquence, si les ictidorhinides, au moins ceux de la zone à *Cistecephalus,* ne se révèleront pas, lorsqu'ils seront mieux connus, plus homogènes que nous ne l'avions précédemment admis. Actuellement toutefois, les particularités de la denture et du vomer restent les deux points de divergence les plus sérieux à l'intérieur de la famille.

Quoi qu'il en soit, cette analyse a confirmé la présence, chez les Ictidorhinidés, de nombreux caractères primitifs, dont certains même n'ont guère dépassé la niveau sphénacodonte: par exemple la petitesse de la fosse temporale et de l'apophyse coronoïde du dentaire, elle-même liée à une faible différenciation de la musculature masticatrice; simultanément se sont développées des spécialisations dont les unes se retrouvent chez les Gorgonopsidés, tels le prépariétal et l'extension du complexe sphénoïdal-, les autres chez les Dinocéphales, tel l'entrecroisement des incisives antérieures. Faut-il en conclure que nous avons là un groupe-charnière situé à la jonction des uns et des autres, et qui témoigne par là même que les Gorgonopsiens, dont ils font toujours partie, se seraient désolidarisés des autres Thériodontes en s'attardant plus longuement sur le tronc sphénacodonte, et en acquérant des spécialisations qui les conduisirent à une impasse?

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Pl. I

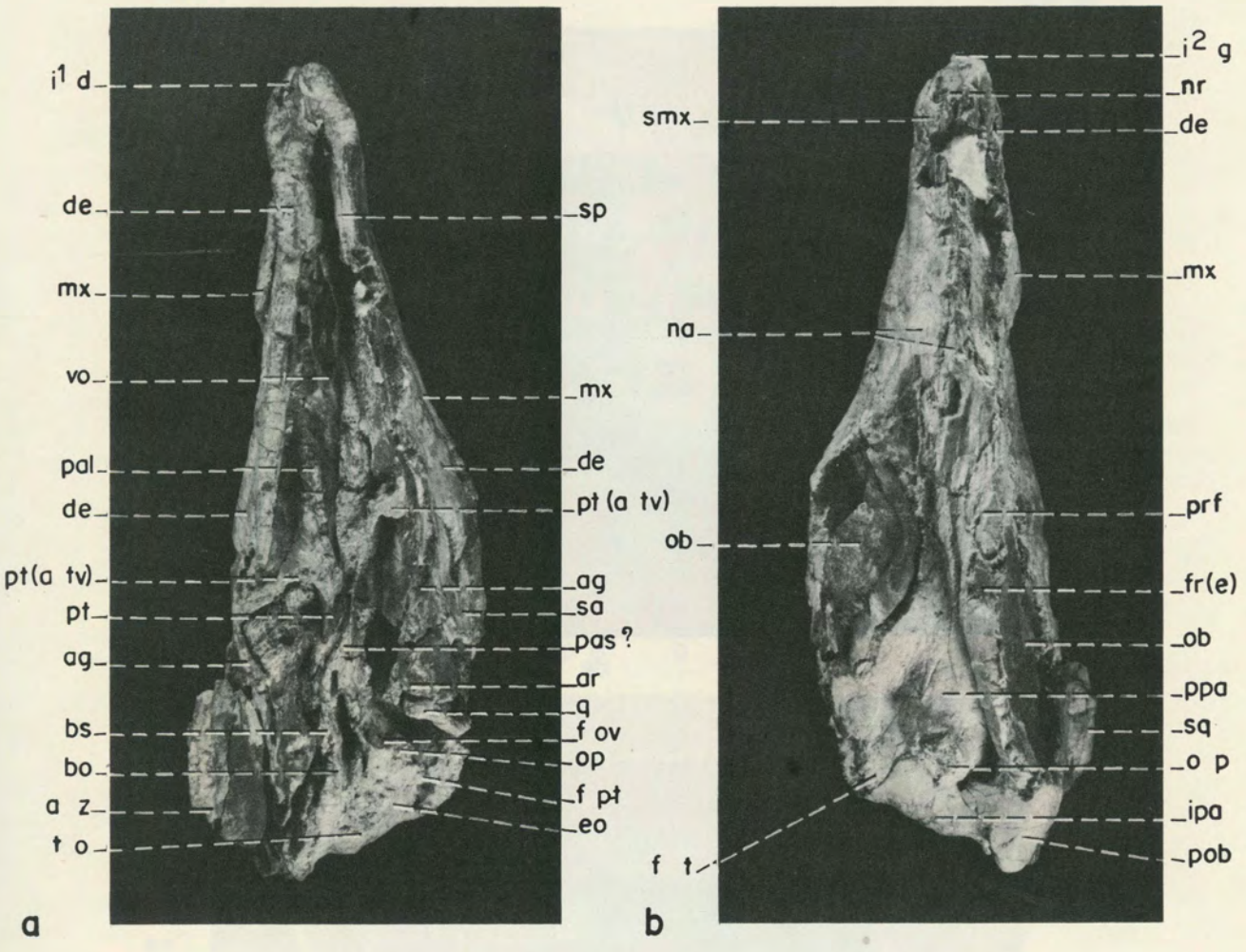


Planche I. *Rubidgina* sp., B.P.I.(F.N.) 3924. G.N. (a) vue ventrale; (b) vue dorsale.

Pl. II

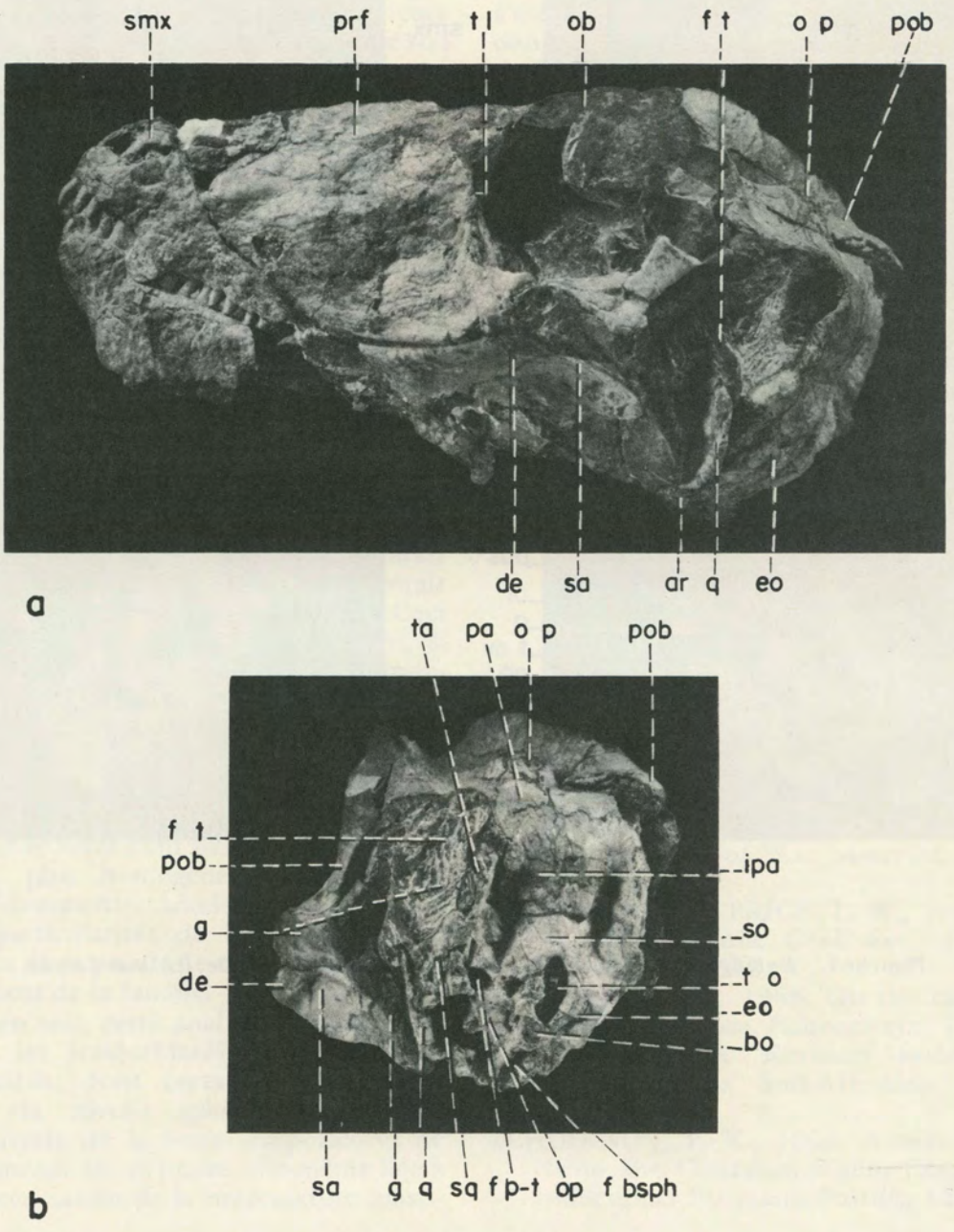


Planche II. *Rubidgina* sp., B.P.I.(F.N.) 3924. G.N. (a) vue latérale gauche; (b) vue postérieure.

Pl. III

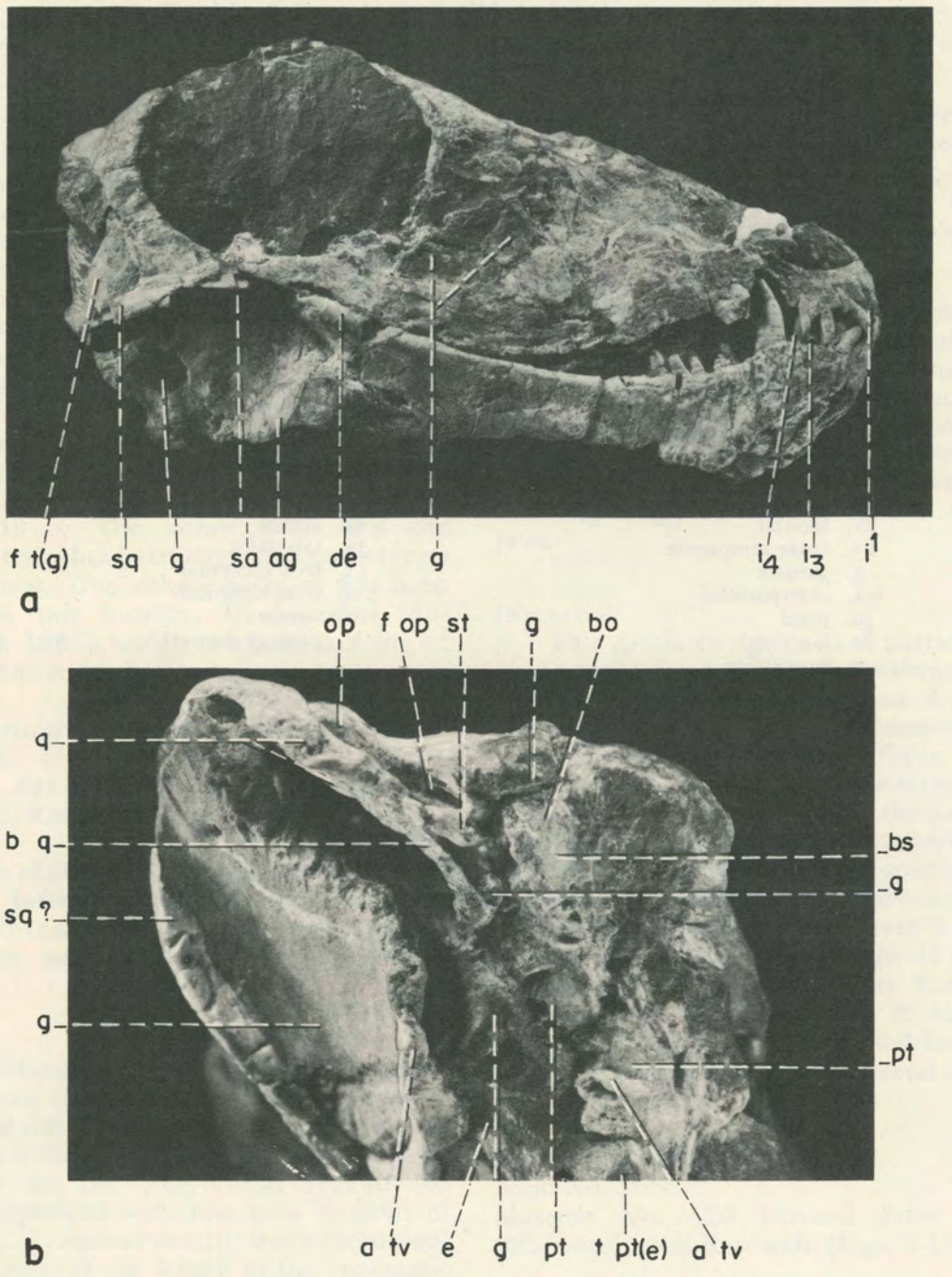


Planche III. (a) *Rubidgina* sp., B.P.I.(F.N.) 3924. Vue latérale droite. G.N.
(b) *Ictidorhinus martinsi*, spécimen-type A.M.N.H. 5526. Vue ventrale, quart postérieur droit. X 2.

Abréviations concernant les figures et les planches.

a, alvéole
ag, angulaire
ar, articulaire
a tv, apophyse transverse du ptérygoïde
a z, arcade zygomatique
bo, basioccipital
b pi, bosse pinéale
b q, branche carrée du ptérygoïde
bs, basisphénoïde
cr pt, crête ptérygoide?
de, dentaire
de pa, dents palatines
de pt, dents ptérygoïdes
e, empreinte
ecp, ectoptérygoïde
eo, exoccipital
f1, fosse, voir texte p. 26, 30
f2, fosse, voir texte p. 30
f3, fosse, voir texte p. 30
F fosse, voir texte p. 29, 30
f bsph, fosse
f h, fosse hypophysaire
f op, fosse
f ov, fenêtre ovale
f p-t, fenêtre post-temporale
fr, frontal
f t, fosse temporale
g, gangue
ipa, interpariétal
ju, jugal
la, lacrymal
mx, maxillaire
na, nasal
nr, narine
ob, orbite
obs, orbitosphénoïde
op, opisthotique
o p, orifice pinéal
pa, pariétal
pal, palatin
pas, parasphénoide
pmx, prémaxillaire
pob, postorbitaire
pof, postfrontal
ppa, prépariétal
pra, préarticulaire
prf, préfontal
pro, prootique
pt, ptérygoide
q, carré
q j, quadrato-jugal
r pas do, rostre parasphénoïde dorsal
sa, surangulaire
smx, septomaxillaire
so, susoccipital
sp, splénial
sq, squamosal
st, stapes
ta, tabulaire
t l, trou lacrymal
t o, trou occipital
vo, vomer
V, passage du nerf V

Palaeont. afr., **13**. 39–45. 1970

PRELIMINARY REPORT ON TWO TRIASSIC DICYNODONTS FROM ZAMBIA.

by

E. A. Crozier.

INTRODUCTION

The purpose of this communication is to establish the presence of a species of Stahleckeriid, hitherto known only from India, in the Zambian Triassic N'tawere Formation and to establish the new specific name of the *Kannemeyeria* specimen also recorded from the same locality.

The skulls and some post-cranial material of these two dicynodonts were collected by Mr. James Kitching from the Luangwa Valley, Zambia in 1961. The material comes from Locality 16, of the Lower Fossiliferous Horizon in the N'tawere Formation. One large skull has been assigned to genus and species *Rechnisaurus cristarhynchus* Roy Chowdhury, 1970. The other skull and the postcranial material has been named *Kannemeyeria latirostris* sp. nov. One other specimen has been described from this locality, *Diademodon rhodesiensis* (Brink 1963), which marks it as being of near *Cynognathus*-zone age.

Rechnisaurus cristarhynchus **Roy Chowdhury**
Field No. 3638.
Museum No. 421 Bernard Price Institute for Palaeontological Research. (Figs. 1-5.)

Material—Large skull, 62 cm long. Badly weathered and distorted. Intertemporal bar, top of occiput, entire right orbital region and most of left zygomatic arch missing. Complete lower jaw, 32 cm long.

Diagnosis.
Skull forms a triangle in dorsal view. Large canine tusks with strong maxillary processes. Wide snout and interorbital region. Mid-nasal ridge and shallow depressions on either side extending from the tip of the snout to the interorbital region. No postfrontal. Preparietal with low boss in front of pineal foramen. Temporal vacuity short and broad. Jugal extends most of the length of the zygomatic arch. Short premaxilla. Septomaxilla forms posterior wall and floor of nostril. Distinct ectopterygoid. A small boss consisting of part of the epipterygoid fused to the pterygoid, behind the pituitary foramen. Palatal surface of the maxilla with three parallel grooves,the central one running into the vomerine ridge. The two anterior ridges meet the ridge around the rim of the premaxilla. Moderate-sized labial fossa at the junction of the maxilla, pterygoid and jugal. Maxilla enters the internal narial passage. Palatine extends the entire length of the pterygoid ramus to meet the maxilla. Interpterygoid space 1,6 cms long, internal nares space 10,4 cms long. Low broad occiput. Deep quadrate fossa on anterior face of occiput.

Lower jaw with massive dentary. Deep central and shallow lateral grooves on dorsal surface of dentary. Surangular with short lateral face. Splenial with mesial face only. Long S-shaped Meckel's fossa. Reflected lamina of the angular meets the horizontal flange of the lateral condyle leaving an oval opening dorsally between the angular and reflected lamina. Long broad shallow condyle allowing longitudinal and lateral movement of the jaws.

Discussion.
This specimen agrees in all particulars with the type except for its size and the shape of the snout. It is thought that the blunt snout of the type (Roy Chowdhury 1970, Figs. 1-3) is due to a fracture or erosion, notwithstanding a definite statement to the contrary by Dr. P. L. Robinson (personal communication). For example, the palatal ridges of the type are not bounded anteriorly by any marked rim, as they are in the specimen here (Fig. 2) and which is the more normal condition.

The specimen described here is important in that it adds a number of details of skull morphology to those already noted by Roy Chowdhury for the type. In particular, it has an almost complete lower jaw, the reflected lamina of which is in a peculiar relation to the lateral condyle of the articular complex.

Kannemeyeria latirostris **sp.nov.**
Field No. 3636.
Museum No. 420 Bernard Price Institute for Palaeontological Research. (Figs. 6-11.)

Material. Small juvenile skull 25,5 cm long. Badly sun-cracked and distorted about a traverse fault. Parietal crest and top of occiput worn away, squamosal wings broken off. Dorso-ventrally flattened. Complete lower jaw, 20 cm long.

Specific Diagnosis.
Skull of Kannemeyeriid type with relatively broad snout. Short premaxilla. Large pineal foramen in a shallow pit below parietal crest. Oval preparietal in

front of it. Postorbitals extend almost the entire length of the intertemporal bar on either side of the parietals. Interparietal with large dorsal face meets the parietals near the end of the intertemporal bar. Zygomatic arches sub-parallel. Short jugal extending from lachrymal to postorbital bar. Frontals form only a short part of dorsal border of orbit. No lateral roof to temporal vacuity on intertemporal bar. Palatal surface of premaxilla with three grooves. The two anterior ridges meet the ridge around the rim of the premaxilla at right angles. The maxillae rise steeply on either side of the premaxilla, and are drawn out into small lateral flanges. Small tusks. No ectopterygoids. Maxillae enter border of internal nares. Medium sized labial fossa. Palatines extend farther anteriorly than the pterygoids. Small interpterygoid space. No tabulars. Large posterior temporal foramen. Small horizontal stapes.

Lower jaw with very short symphysis. Three parallel grooves on dorsal surface. Anterior extension of the angular spliced between the dentary laterally and splenial mesially. Reflected lamina of the angular far back on the shaft of the angular. Long shallow condyle, somewhat restricted laterally. The specific name records the very broad snout region.

Discussion.

This specimen clearly is a member of the genus *Kannemeyeria,* but differs from the other known species in the broadness of the snout, the lack of any marked ridging on the snout and extreme shortness of the symphysis of the dentary. The tusks are more vertically orientated and there are no pronounced horizontal lateral flanges to the maxillae. In addition, it has an extremely low interpterygoid space–internal narial ratio and the interparietal is apparently exposed to a greater extent at the back of the intertemporal bar than might be expected in a species of *Kannemeyeria* (Cruickshank 1970). Some of these differences might be accounted for by reason of its small size and possible youth at death, but as the N'tawere formation is generally accepted as being slightly higher in the succession than the *Cynognathus* zone, a different species of *Kannemeyeria* is not altogether unexpected here.

Additional studies will be carried out on these two specimens and recorded at greater length at another time.

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LIST OF ABBREVIATIONS

A.	Angular
ART	Articular
BO	Basioccipital
bo.t	basioccipital tubera
car.f.	carotid foramen
D	Dentary
ECT	Ectopterygoid
EO	Exoccipital
F	Frontal
f.m.	foramen magnum
f.o.	foramen ovalis
IP	Interparietal
i.pt.v	interpterygoid vacuity
J	Jugal
j.f.	jugular foramen
L	Lacrimal
l.cond.	lateral condyle
l.d.	lacrimal duct
l.f.	labial fossa
m.cond.	median condyle
M.f.	Meckel's fossa
MX	Maxilla
N	Nasal
OP	Opisthotic
P	Parietal
PAL	Palatine
p.b.	pineal boss
p.f.	pineal foramen
pit.f.	pituitary foramen
PMX	Premaxilla
PO	Postorbital
PP	Preparietal
PR.ART	Prearticular
PRF	Prefrontal
PRO	Paraoccipital process of the opisthotic
PSP	Parasphenoid-bassisphenoid complex
PT	Pterygoid
p.te.f.	posterior temporal fenestra
QJ	Quadratojugal
q.f.	quadrate foramen
q.r.pt.	quadrate ramus of pterygoid
SA	Surangular
SO	Supraoccipital
SPL	Splenial
SQ	Squamosal
ST	Stapes
u.c.	Upper canine
V	Vomer
Dots	Matrix
Cross-hatching	Broken bone

ALL SCALES IN CENTIMETRES.

Legends to Text Figures.

Fig. 1. Dorsal view of specimen 3638 as preserved.
Fig. 2. Palatal view of specimen 3638 as preserved.
Fig. 3. Side view of specimen 3638 as preserved.
Fig. 4. Occipital view of specimen 3638 as preserved.
Fig. 5. Left lateral view of lower jaw of specimen 3638 as preserved.
Fig. 6. Dorsal view of specimen 3636 as preserved.
Fig. 7. Palatal view of specimen 3636 as preserved.
Fig. 8. Side view of specimen 3636 as preserved.
Fig. 9. Occipital view of specimen 3636 as preserved.
Fig. 10. Dorsal view of lower jaw, specimen 3636 as preserved.
Fig. 11. Side view of lower jaw, specimen 3636 as preserved.
Figs. 1-5 *Rechnisaurus cristarhynchus* Roy Chowdhury.
Figs. 6-11 *Kannemeyeria latirostris* sp.nov.

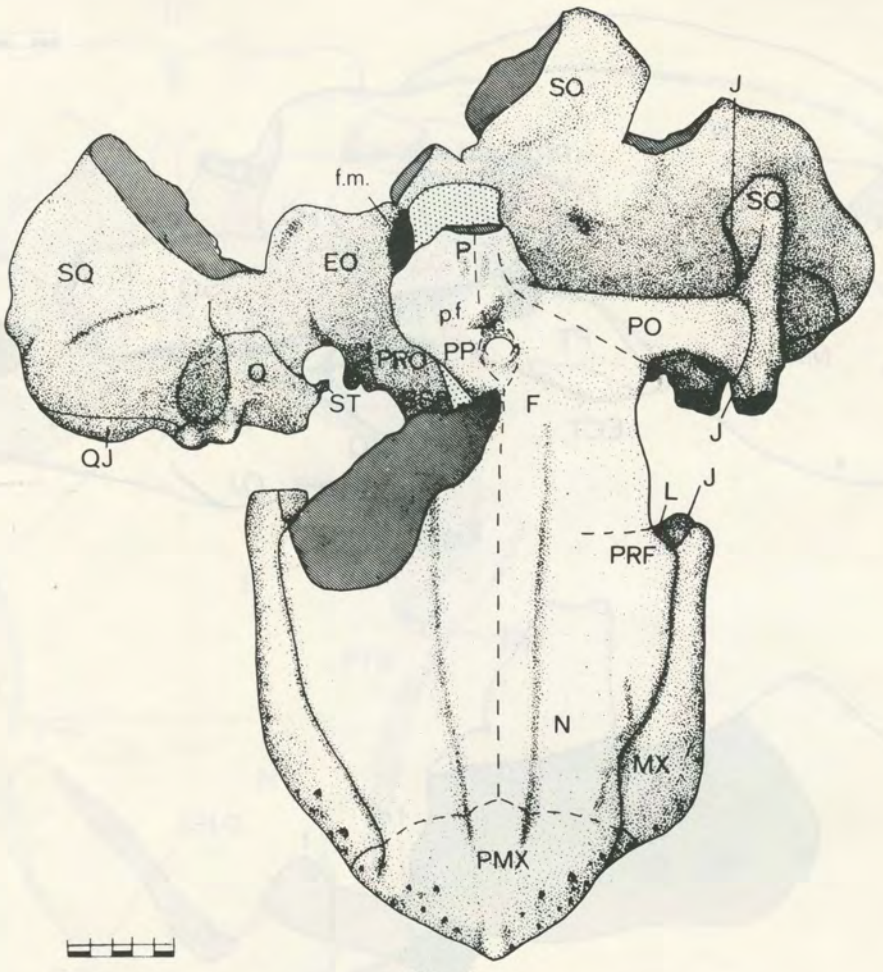

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Fig. 1

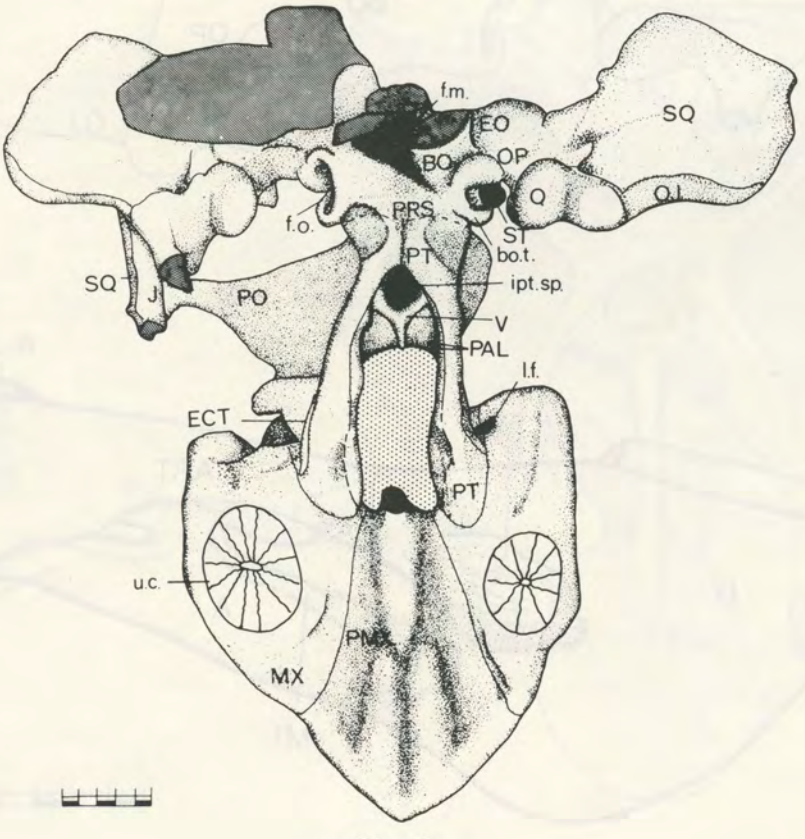

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Fig. 2

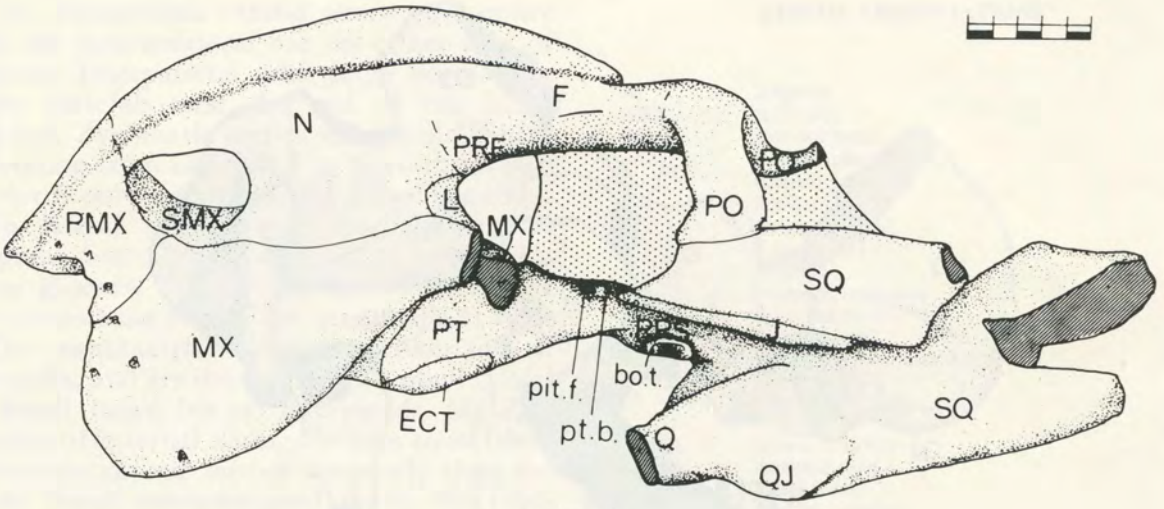


Fig. 3

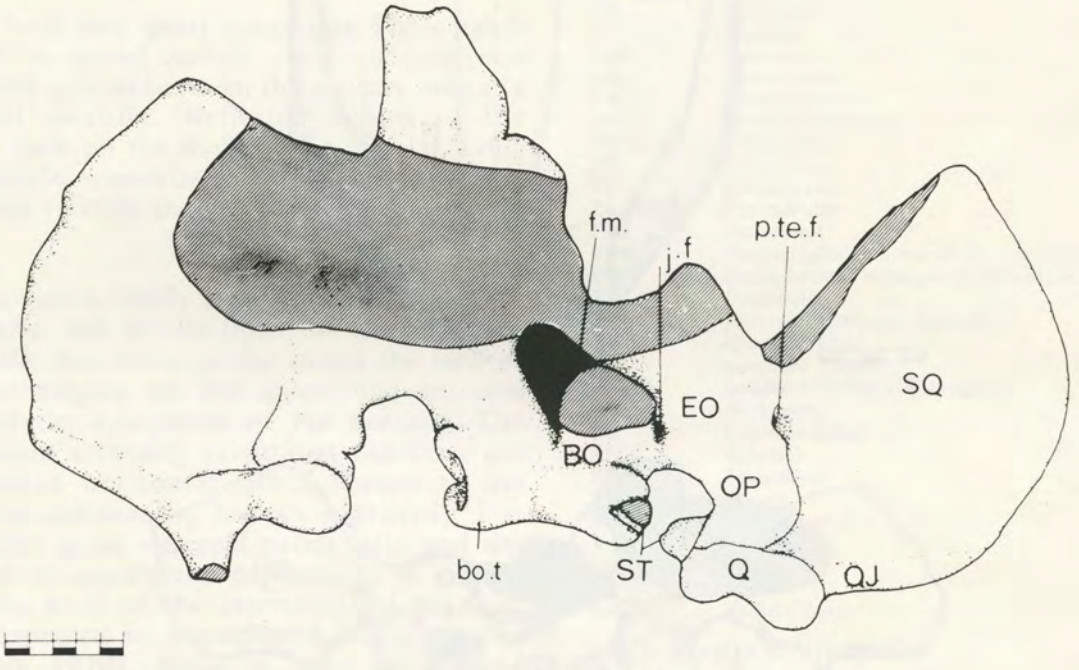


Fig. 4

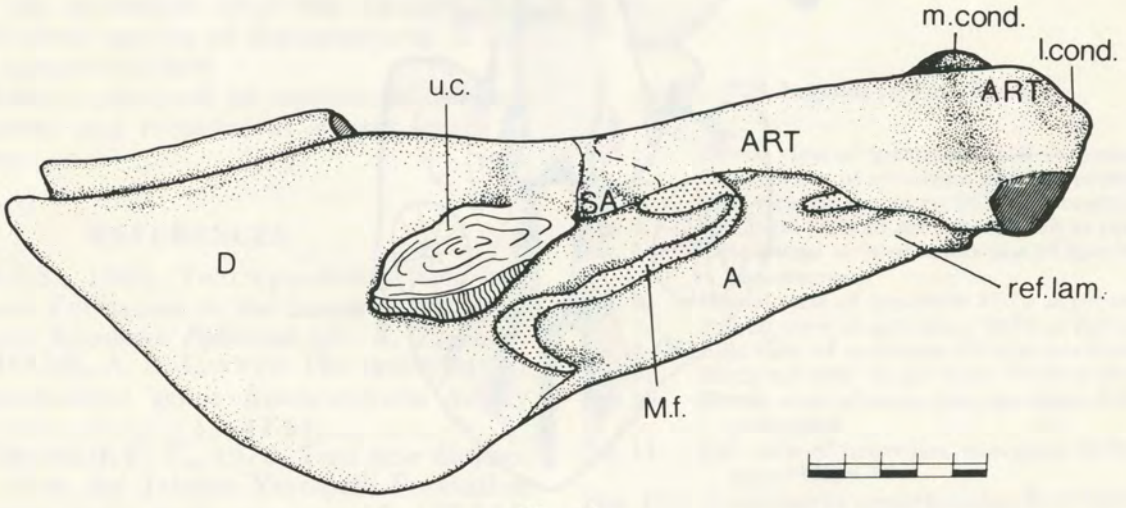


Fig. 5

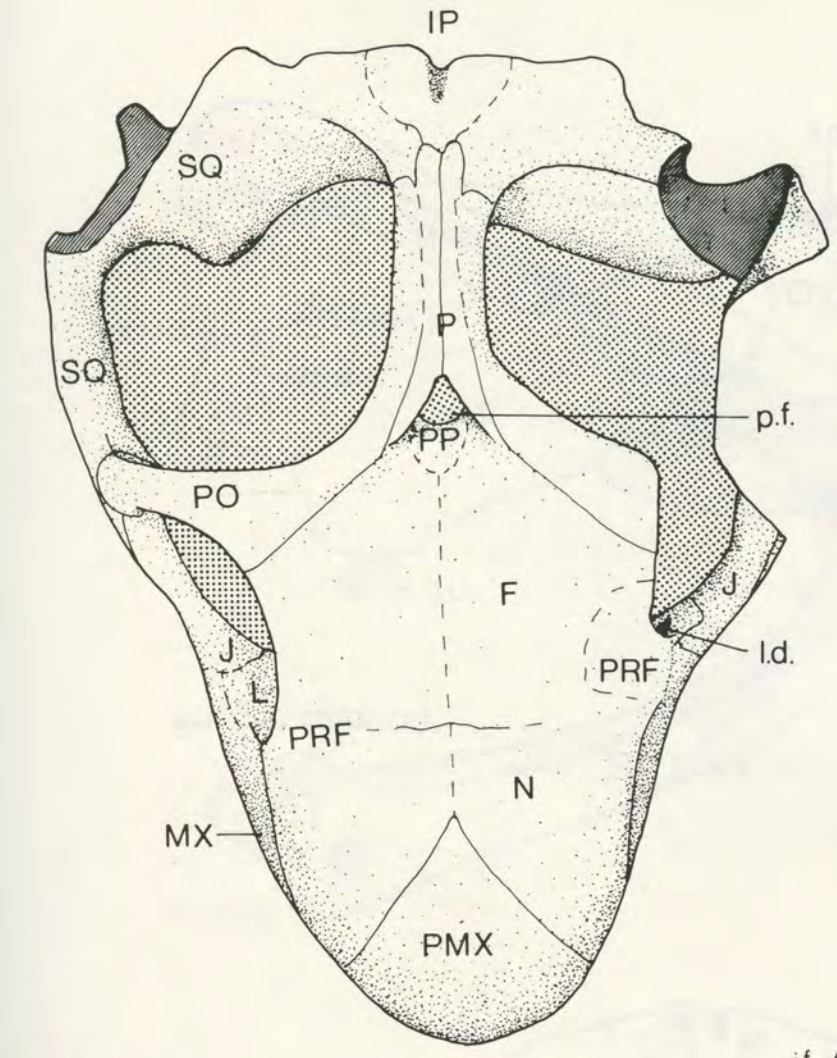

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Fig. 6

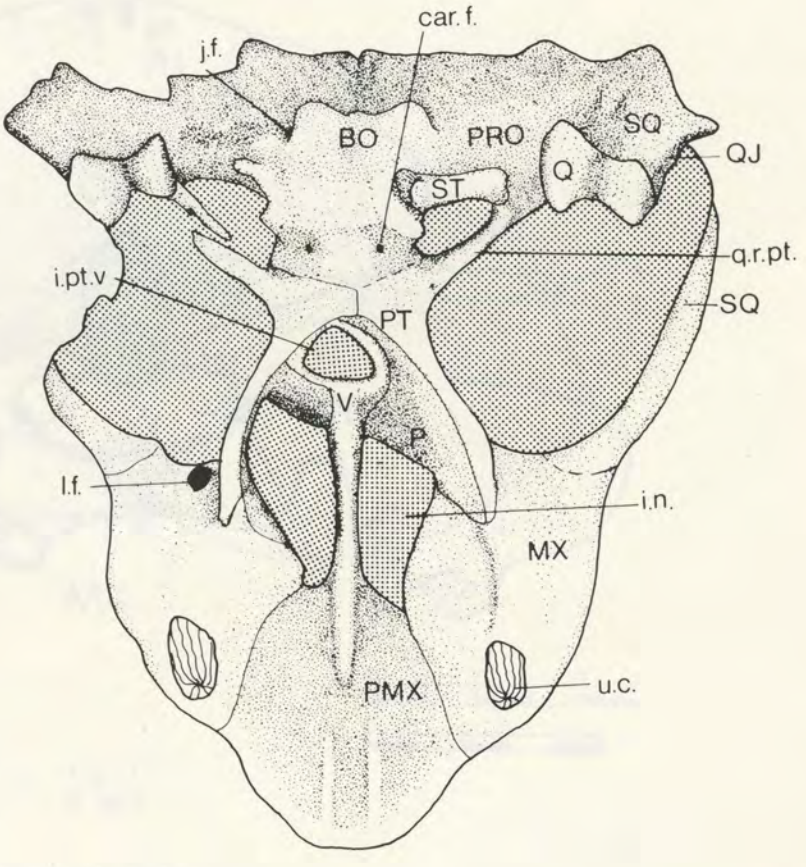

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Fig. 7

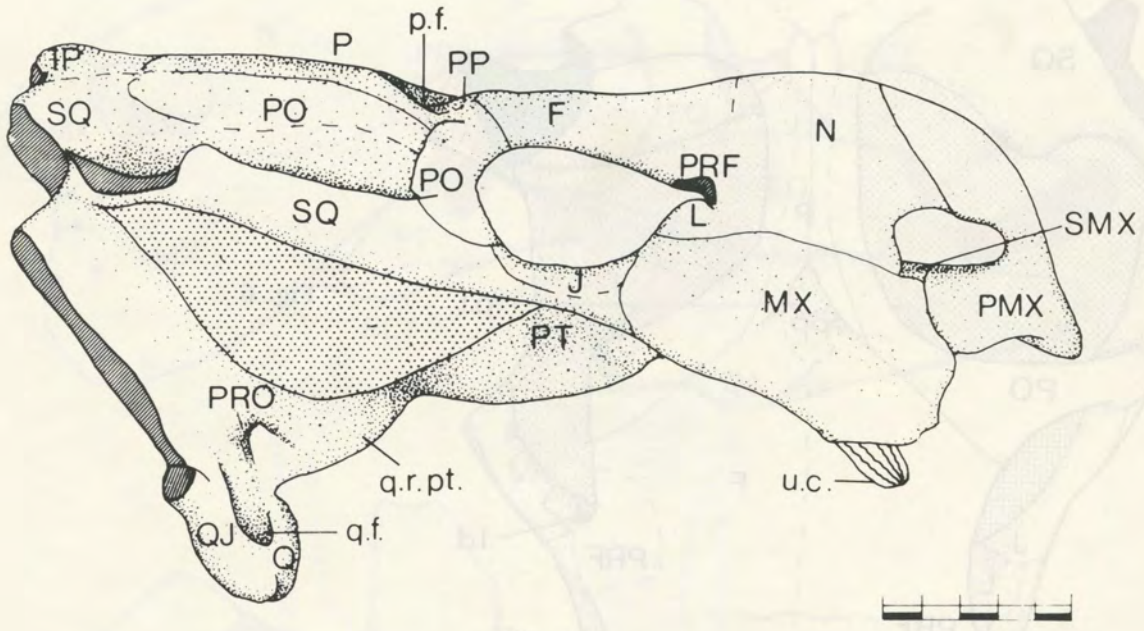

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Fig. 8

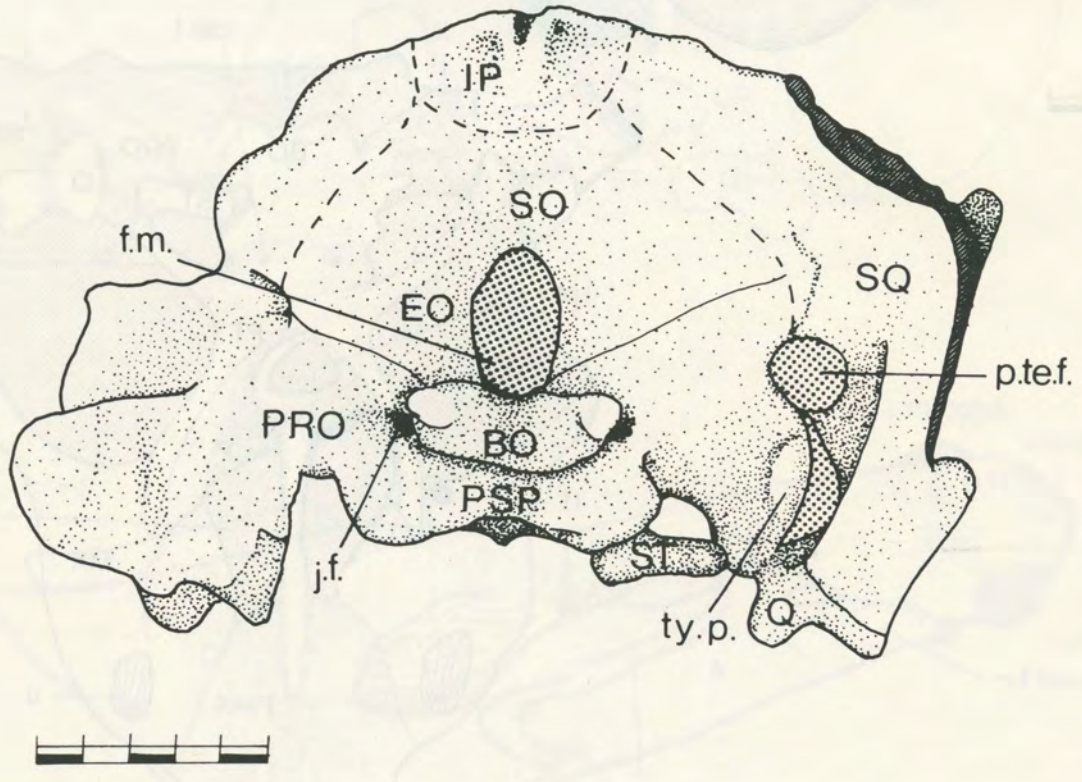

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Fig. 9

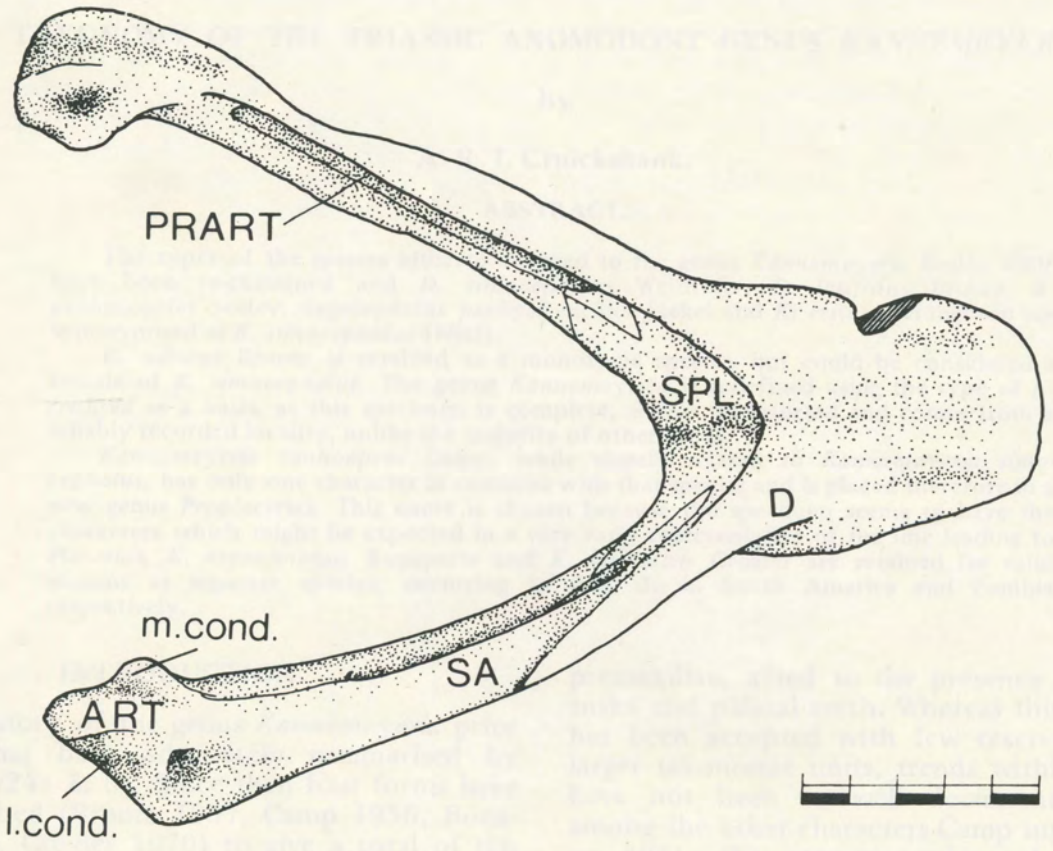

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Fig. 10

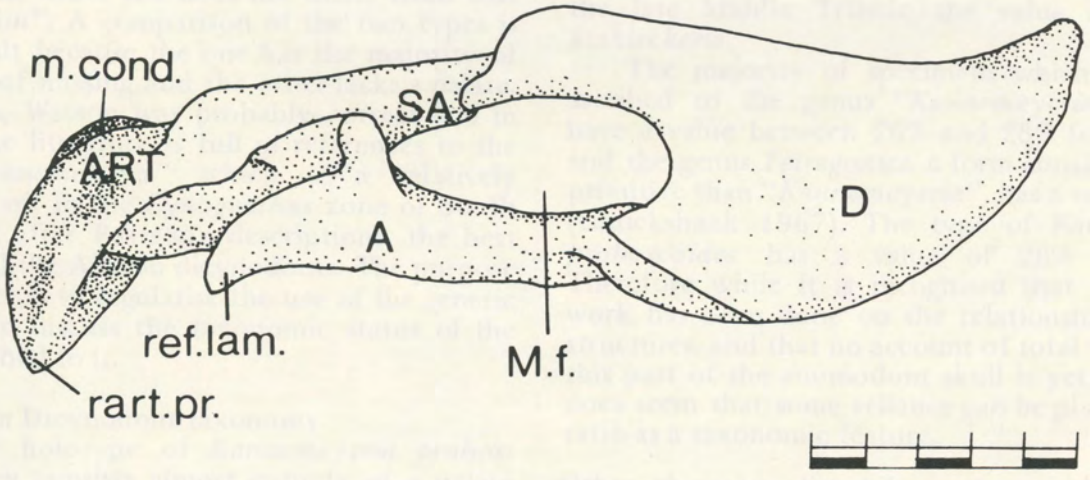

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rart.pr.

Fig. 11

Palaeont. afr., 13. 47–55. 1970

TAXONOMY OF THE TRIASSIC ANOMODONT GENUS *KANNEMEYERIA*.

by

A. R. I. Cruickshank.

ABSTRACT.

The types of the species hitherto assigned to the genus *Kannemeyeria* Seeley 1908 have been re-examined and *D. simocephalus* Weithofer, *D. latifrons* Broom, *K. proboscoides* Seeley, *Sagecephalus pachychynchus* Jaekel and *K. erithrea* Haughton are synonymised as *K. simocephalus* (Weit).

K. wilsoni Broom is retained as a monotypic species, but could be considered a female of *K. simocephalus*. The genus *Kannemeyeria* is redefined using the type of *K. erithrea* as a basis, as this specimen is complete, almost undistorted and comes from a reliably recorded locality, unlike the majority of other types.

Kannemeyeria vanhoepeni Camp, while closely related to *Kannemeyeria simocephalus*, has only one character in common with that species and is placed therefore in a new genus *Proplacerias*. This name is chosen because the specimen seems to have the characters which might be expected in a very early representative of the line leading to *Placerias*. *K. argentinensis* Bonaparte and *K. latirostris* Crozier are retained for valid reasons as separate species, occurring as they do in South America and Zambia respectively.

INTRODUCTION.

The history of the genus *Kannemeyeria* prior to 1924 has been adequately summarised by Pearson (1924a & b). Since then four forms have been described (Broom 1937, Camp 1956, Bonaparte 1966, Crozier 1970) to give a total of ten species attributed at one time or another to the genus (Table 1). However, Watson in 1912 (p. 575) made an error of judgement in equating Seeley's type of *K. proboscoides* with Weithofer's *Dicynodon simocephalus*, stating as he did, *"Kannemeyeria* is a genus founded by H. G. Seeley in 1908 on an imperfect skull of *Dicynodon simocephalus* Weithofer. The genus is easily distinguished from *Dicynodon* and I know three species belonging to it. The lower jaw does not differ from that of *Dicynodon"*. A comparison of the two types is very difficult because the one has the majority of the skull roof missing and the other lacks a palate. Nonetheless, Watson was probably correct and in any case the literature is full of references to the genus *"Kannemeyeria"* which is a relatively common fossil in the *Cynognathus* zone of South Africa, and after Pearson's descriptions, the best known of all the African dicynodonts. The purpose of this paper is to regularise the use of the generic name and to discuss the taxonomic status of the species ascribed to it.

The palate in Dicynodont taxonomy.

As the holotype of *Kannemeyeria proboscoides* Seeley consists almost entirely of a palate (Fig. 1.b) it is necessary to discuss the relevance of palatal characters as taxonomic tools. Toerien (1953; 1955) discussed evolutionary trends in the Anomodontia with particular reference to the palate, and divided them into families on whether or not the palatines had extensive contact with the premaxillae, allied to the presence or absence of tusks and palatal teeth. Whereas this classification has been accepted with few reservations for the larger taxonomic units, trends within the families have not been so well documented. However, among the other characters Camp suggested (1956, p. 323), the structure since defined as the interpterygoid space (Cruickshank 1967) was shown to be very much shorter in Triassic dicynodonts than in their Permian predecessors. There are grounds to believe that the shortening is progressive in time (Cruickshank 1968). Over the Permian-Triassic boundary the interpterygoid space changes from being more than 60% of the length of the internal nares to being markedly less. During the Triassic it seems to become even smaller and by the late Middle Triassic the value is 21% for *Stahleckeria*.

The majority of specimens which have been ascribed to the genus *"Kannemeyeria"* seem to have a value between 26% and 28% for this ratio and the genus *Tetragonias*, a form considered more primitive than *"Kannemeyeria"*, has a value of 32% (Cruickshank 1967). The type of *Kannemeyeria proboscoides* has a value of 26% (Table I). Therefore while it is recognised that insufficient work has been done on the relationship of these structures, and that no account of total variation in this part of the anomodont skull is yet in print, it does seem that some reliance can be placed on this ratio as a taxonomic feature.

Other characters listed by authors as being diagnostic of *Kannemeyeria*.

Weithofer (1881) in describing *D. simocephalus* (Fig. 3c) stressed the presence of the depression between the fronto-nasal and fronto-parietal regions of the skull, the positioning of the large orbit low down on the face and said that the

maxillae were splayed out and that the snout was blunt. He later in the same paper said that the crest was the most highly characteristic feature of the fossil. All these characters are genuine except the splaying of the maxillae, which is due to dorso-ventral crushing, and the blunting of the snout which was due to a break in the premaxilla. He noted a broad ridge running over the snout from the frontals to the premaxilla on the midline which he said was not seen in other dicynodonts. In addition to these, it is clear from an examination of the specimen that there are lateral extensions to the maxillae similar to those described by Broom (1898) for *D. latifrons.*

Dicynodon latifrons Broom 1898 is a specimen smaller than the foregoing and in many ways less satisfactory. For instance it is almost completely unprepared at present. However, it has the narrow crest and the depression between the fronto-parietal and fronto-nasal region described for *D. simocephalus.* There is a marked ridge on the snout and Broom pointed out the presence of the roughened rugose lateral extension to the maxillae.

The tusks were noted as being 13 mm in diameter where they were broken level with the alveolar margins, and seemed to point more forward than downward. Cruickshank (1965) has figured a very small specimen which fits almost exactly the descriptions of the type of *D. latifrons.*

Ptychocynodon pentangulatus Seeley (1904) is a tusk which may or may not be ascribed to the genus *Kannemeyeria* and will not figure again in this paper.

Seeley (1908) described the type of *K. proboscoides* as being an anomodont with a trunk

Table I

SPECIES	AUTHOR	LOCALITY	HORIZON	BRIEF DESCRIPTION
Dicynodon simocephalus No. 8178 Nat. Hist. Mus. Vienna	Weithofer 1888	Probably Dwarsvlei, Aliwal North, C.P. B. R. Turner, Pers. comm.	Cynognathus zone	Right side skull roof. No palate. Snout Broken.
Dicynodon latifrons No. 1192.2. P. E. Mus.	Broom 1898	Burghersdorp, C.P.	Cynognathus Zone	Anterior ¾ of skull. Crushed. Not prepared. Snout broken.
Ptychocynodon pentangulatus	Seeley 1904	Near Burghersdorp	? Cynognathus Zone	Tooth with infolded dentine in root.
Kannemeyeria proboscoides No. 3593 B.M. (NH) London	Seeley 1908	Burghersdorp, C.P.	Cynognathus Zone	Skull lacking parietal region. Snout broken.
Sagecephalus pachyrhyncus No. 3742 B.M. (NH) London	Jaekel 1911	?	? Cynognathus Zone	Badly distorted skull and lower jaw.
Kannemeyeria erithrea No. 3017. South African Mus.	Haughton 1915	Winnaarsbaken Burghersdorp, C.P.	Cynognathus Zone	Good almost undistorted skull, l. jaw & part of skeleton.
Kannemeyeria wilsoni No. 1 East London Museum	Broom 1937	Ravenskloof, portion Q66-14 of farm Hartebeestfontein, Tarkastad, C.P.	Cynognathus Zone	Good skull. Palate damaged. Majority of skeleton.
Kannemeyeria vanhoepeni No. 42916 Mus. of Palaeontology, Berkeley	Camp 1956	Bethel, 16 miles west of Rouxville O.F.S.	Cynognathus Zone	Good skull and l. jaw
Kannemeyeria argentinensis No. PVL. 3465 Institute M. Lillo	Bonaparte 1966	West of Colonia Las Malvinas Dept. San Rafael, Mendoza Prov. Argentine	Upper Puesta Viejo Formation	Good, almost undistorted skull.
Kannemeyeria latirostris No. 3636 B.P.I. for Palaeontological Research	Crozier 1970	Locality 16, Luangwa Valley, Zambia	Ntawere Formation	Good skull & lower jaw, slightly distorted + neck vertebrae.

and very briefly discussed this feature of the specimen without any figures. Therefore a set of stereo photographs is included here to illustrate this specimen for the first time (Fig. 1). As noted, it is almost entirely a palate with a large portion of the naso-frontal region and the left orbit preserved. Nothing exists of the parietal region. It will be noted that the maxillae have lateral flanges, and that the snout has prominent ridges, particularly a heavy median ridge.

Therefore if *"Kannemeyeria"* is an anomodont with a parietal crest as described above for *D. simocephalus* and a strong median ridge on the snout, lateral extensions to the maxillae and an interpterygoid space-internal narial ratio of 26–28%, then all these skulls can reasonably be accommodated in the genus. However, none of them are complete, reliable locality data does not exist for any (Table I) and the whole taxonomic picture is obscured by Watson's statement (1912 p. 575). As noted by Pearson (1924 p. 797) *Sagecephalus pachyrhynchus* (Jaekel 1911) can best be interpreted as the distorted anterior part of a skull of *Kannemeyeria.*

The first specimen to be described from a reliable locality, *K. erithrea* Haughton (1915, 1917) is also the first which is complete and almost undistorted. Haughton figured only the dorsal and lateral views, but as the palate is particularly important in this genus a set of stereo photos of this specimen is included here (Figs. 2, 3a). It will be noted that there is a prominent median ridge on the snout (Fig. 2a, b) and that the maxillae are drawn into roughened shelves lateral to the tusks (Fig. 2a, c). The tusks run in line with the jugal arches until they emerge from their alveoli, when

SKULL OVERALL LENGTH	I PT. SP. / INT. NARES x 100	LARGE ORBIT	PRECANINE REGION	HIGH CREST	NARROW CREST	EXT. EXP. OF INTERPARIETAL ON DORSAL SURFACE	PROM. LONGITUDINAL RIDGE ON SNOUT	PARALLEL OR SUB-PARALLEL ZYG. ARCH	TUSKS IN LINE WITH JUGAL	LABIAL FOSSAE PRESENT	HORIZONTAL LATERAL FLANGES TO MAXILLAE	LOWER JAW.	PRESPINOUS FOSSA	ANTERIOR OF ILIUM
53 cm	–	/	Short	/	/	X	/	/	/	/	/	No reliable association "Normal"?	–	–
30 cm as reconstructed	–	/	–	? /	/	–	? /	? /	/	/	/	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
32.4 cm on palatal midline	26%	/	Short ?	–	–	–	? /	? /	? /	/	/	No reliable ass. "Normal"?	"Large"	"Small"
26 cm as preserved	–	/	Short ?	–	/	–	/	–	/	?	? /	"Normal"	–	–
45 cm	27%	/	Short	/	/	X	/	/	? /	/	/	"Normal"	–	–
52.5 cm	–	/	Short	/	/	X	X	/	? /	?	X	Horizontal tip	"Small"	"Large"
45.5 cm as reconstructed	? 21,6%	X	Long	/	X	/	X	X	X	? X	X	"Normal"	–	–
26 cm	45,4%	/	Short	/	/	X	? /	? /	X	X	X	Incomplete	"Scapula similar to *K. simocephalus*"	"Small"
32 cm as reconstructed	23,2%	/	Short	/	? Type eroded	? X	X	? /	/	/	? X	Very small symphysis	–	–

/ Character present

X Character not present

? Some doubt as to character

– Character not preserved

they turn downwards abruptly. The value for the interpterygoid space-internal narial ratio is 27%. This specimen also has the steeply rising parietal crest and large orbit seen in the other specimens which were sufficiently well preserved to display these features. Therefore in this specimen all the features noted for the others can be clearly seen together and it comes from a reliable locality (Table I).

Kannemeyeria wilsoni Broom (1937) is a special case in that most of the skeleton was collected with the skull (Courtenay-Latimer 1948) and is therefore the most complete of all the *Kannemeyeria* specimens. Broom distinguished it from the previously described species on the grounds that the snout was flatter, i.e. not ridged or was less arched than in *K. simocephalus.* The exact meaning is not clear, but both interpretations fit the specimen. The premaxilla is shorter than in *K. latifrons.* Miss Courtenay-Latimer tells me that when excavated the tusks turned down abruptly at the alveolar margins, but the roots continue the line of the jugal arches. The tusks were very fragile and disintegrated at the time of excavation, but their reconstructions are a true picture of the original state (Fig. 3b). This character would make the specimen similar to *K. erithrea,* but the anterior of the lower jaw differs from other *Kannemeyeria* lower jaws. The scapula has a very much smaller pre-spinous fossa (when compared with Pearson's material) and the ilium has a longer anterior process with a ventral 'hook'.

Taken individually any of these characters would not be significant, but in association they would indicate that this specimen is in fact different from the others. The lack of a heavy ridge on the snout, and absence of flanges on the maxillae might be explained in terms of sexual dimorphism (Cruickshank 1967), but whether this is a female and all the other specimens males will only be decided finally at a later date when much more material is available.

Therefore the specimens of *"Kannemeyeria"* described above fall into two species. One is based on a complex comprising *Dicynodon simocephalus, D. latifrons, Kannemeyeria proboscoides,* and *K. erithrea* and the second is represented at present by one, *K. wilsoni.* For definitions of all generic and specific characters see below. However, mention must be made here of a further three specimens which have been assigned to the genus *"Kannemeyeria".*

The first of these was described by Camp in 1956 as *K.vanhoepeni* (Table I). Of all the characters described for the foregoing specimens of *Kannemeyeria,* it has in common only the high parietal crest. The orbit is much smaller, the tusks do not run in line with the jugal arches, nor are there lateral flanges on the maxillae. The premaxilla is much longer than in the previous specimens, and there is no prominent ridge on the snout. As far as can be estimated, the interpterygoid space-internal narial ratio is about 21%. Thus because this species differs markedly in all the characters but one expected of a member of the genus *Kannemeyeria,* it must be placed in a separate genus of its own (see below).

The second member of this group is a relatively small species described by Bonaparte from the L.Trias of the Argentine as *K. argentinensis.* It seems to have all the characters of the genus, and it differs from the majority of African species only by reason of its downturned tusks, its size and lack of labial fossae. This last point is an important difference but taken by itself ought not to be emphasised when only one specimen of the species is known so far.

The final member of this trio is a newly described species from Zambia (Crozier, 1970) which belongs to the genus *Kannemeyeria.* It is similar in many ways to juvenile specimens of *K. simocephalus.* However, in lacking a strong mid-nasal ridge and having maxillary processes more like that of *K. argentinensis* and a snout region very much wider than any *Kannemeyeria* hitherto described, it is obviously separate. The symphysis of the lower jaw is also remarkably short.

THE GENUS *KANNEMEYERIA* SEELEY 1908.

As the type of *K. erithrea* is the first specimen in the literature to have a reliable locality, and as it is both complete and almost undistorted, it is proposed to re-define the genus in terms of this specimen. The name *Kannemeyeria* must be retained because of the stratigraphical importance placed on this genus and its general use in the literature.

Anomodont therapsida

genus	*Kannemeyeria* Seeley 1908
specimen	*K. erithrea* Haughton 1915 South African Museum No. 3017.
locality	Winnaarsbaken, Burghersdorp, C.P.
horizon	Low, *Cynognathus* zone.

Generic diagnosis: Medium to large-sized skulls, tusks in both sexes. Zygomatic arches parallel or sub-parallel in dorsal view. Parietal crest high and narrow with no extensive exposure of interparietal on dorsal surface. A large orbit dominating the facial region and a relatively short pre-canine region of snout. $\frac{\text{IPT SPACES}}{\text{INT NARES}} \times 100 = 23\text{–}28\%$. Labial fossae may be universally present.

Species:

1. *K. simocephalus* (Weithofer) 1888
   = *Dicynodon latifrons* Broom 1898
   = *Kannemeyeria proboscoides* Seeley 1908
   = *Sagecephalus pachyrhynchus* Jaekel 1911
   = *Kannemeyeria erithrea* Haughton 1915.

Large skull with horizontal flanges on the maxillae and prominent mid-nasal ridge. Tusks run in line with jugal arch, though the tips on emerging may turn sharply downward. Lower jaw with normal

up-turned tip. Prespinous fossa of scapula large and anterior blade of ilium small

2. *K. wilsoni* Broom 1937.

Large skull with no flanges on maxillae and no prominent ridge on snout. Tusks run in line with jugal and the tip turns downward on emerging from maxillae. Lower jaw with anterior end flat. Prespinous fossa on scapula small and anterior blade of ilium large.

3. *K. argentinensis* Bonaparte 1966.

Medium-sized skull with vertical tusks not in line with jugal arches and no flanges on maxillae.

$$\frac{\text{IPT SPACE}}{\text{INT NARES}} \times 100 = 45{,}4\%.$$

a very high value, possibly reflecting its position low in the Triassic succession.

Labial fossae not present in the type, but no other material is yet described and this character may be unique for the type specimen.

4. *K. latirostris* Crozier 1970.

Medium sized skull with sub-vertical tusks and slight flanges on maxillae. No prominent ridge on very broad snout. Tusks roots do curve to run in line with jugal arch. Lower jaw with very short symphysis and up-turned anterior edge.

THE GENUS *PROPLACERIAS* NOV. CRUICKSHANK 1970.

Anomodont Therapsida

genus: *Proplacerias* nov.

holotype: *P. vanhoepeni* (Camp) 1956 (figs. 42c, 43c, d & 50c)
Museum of Palaeontology, University of California, Berkeley, No. 42916.

locality: Bethel farm, 16 miles west of Rouxville, O.F.S.

horizon: *Cynognathus* zone.

Generic diagnosis: See Specific diagnosis.

Specific diagnosis: Large skull, probably tusked in both sexes. Zygomatic arches diverge markedly towards the rear of the skull. Parietal crest high but relatively broad, with extensive exposure of interparietal on dorsal surface. A small orbit placed high on the side of the face, the precanine region of the skull relatively long.

$$\frac{\text{IPT SPACES}}{\text{INT. NARES}} \times 100 = 21\%.$$

Labial fossa doubtfully present. Very small ridge on snout, not extending beyond premaxilla and canines do not follow line of jugal arch.

Discussion on *Proplacerias*, gen.nov.

In all characters here assigned to *Kannemeyeria, Proplacerias* differs markedly except for the overall size of the skull and the high parietal crest (Table I). Cox (1965) has discussed the major trends in Triassic dicynodonts and concludes that they may be divided into two lineages based on whether they were, for instance, browsers or grazers. Camp endeavoured to show that all the Triassic dicynodonts were allied and proposed a lineage which in part led from *Proplacerias* gen. nov., to *Kannemeyeria* and hence to *Placerias* itself. However it seems more reasonable to accept that although *Kannemeyeria* and *Placerias* are closely allied, they represent two different evolutionary trends and that *Proplacerias vanhoepeni* is more likely not to be a direct ancestor of *Kannemeyeria* because of the very marked differences in characters as compared to *Kannemeyeria.* The general shape of the skull and other characters seem to make it a better direct ancestor of *Placerias* and one of the Shansiodontidae still remains a better direct morphological ancestor of *Kannemeyeria* (Cruickshank 1967).

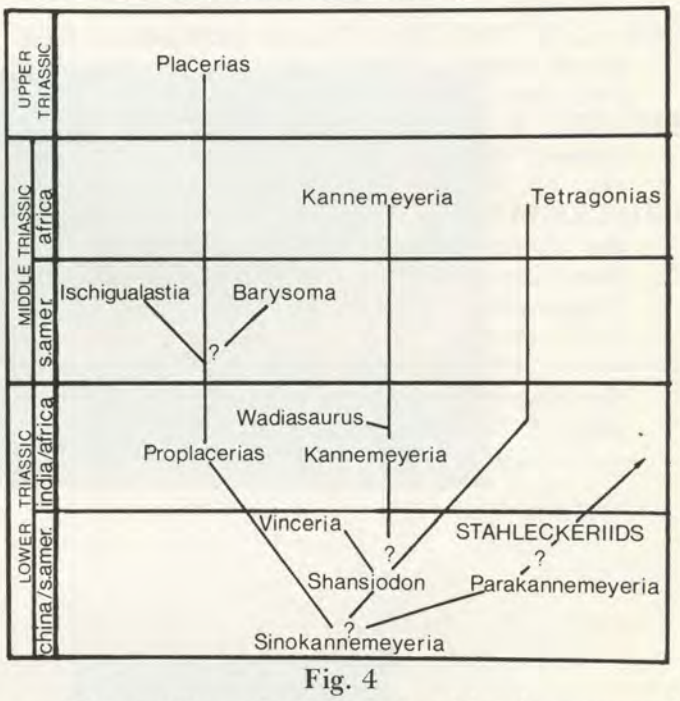


Fig. 4

The outline of the relationships is expressed diagramatically (Fig. 4), the information taken from various authors.

ACKNOWLEDGEMENTS.

With a project like this one which was spread over some years, many people have contributed in several ways towards its well-being.

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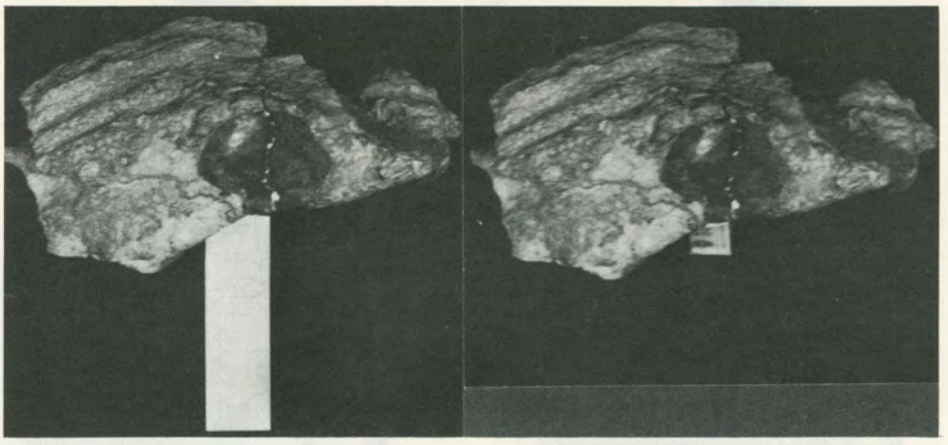
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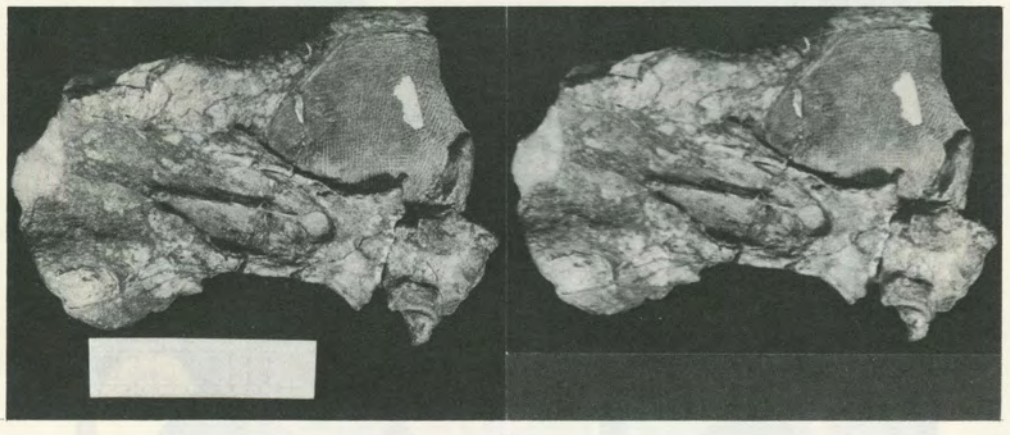
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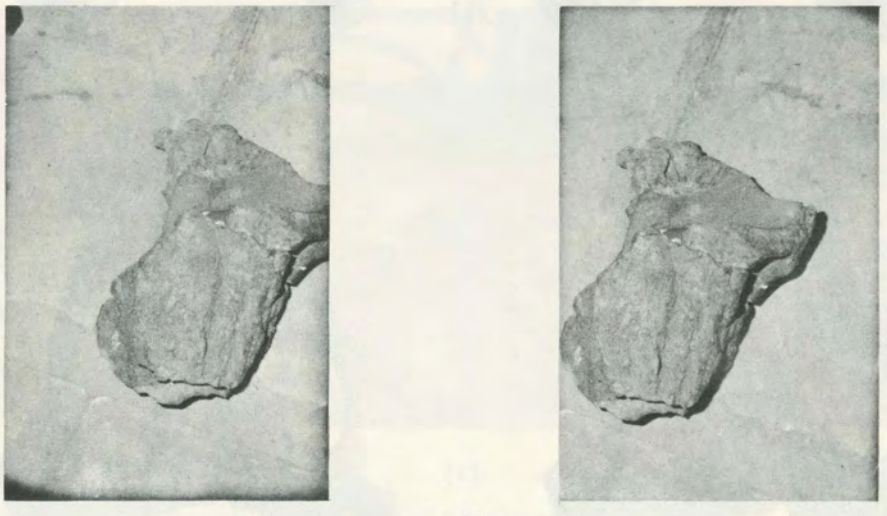
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(a)



(b)



(c)

Fig. 1 (a) Left dorso-lateral view of type of *K. proboscoides* Seeley.
(b) Palatal view of type of *K. proboscoides,* Seeley.
(c) Dorsal view of type of *L. proboscoides Seeley.*
Fig. 1a & b by courtesy of Drs. C. B. Cox, Kings College, London and A. J. Charig, Department of Palaeontology, British Museum (NH).

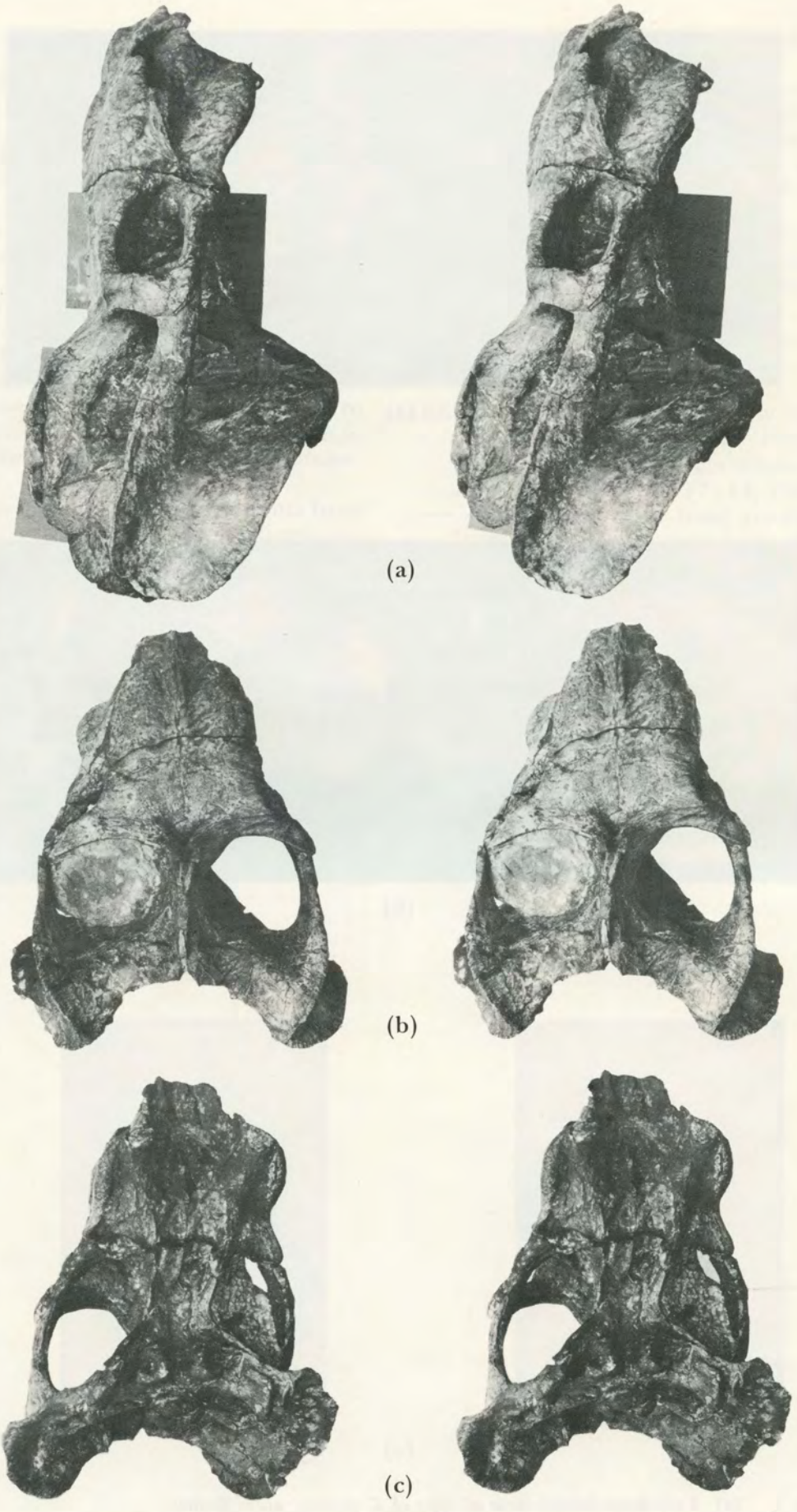
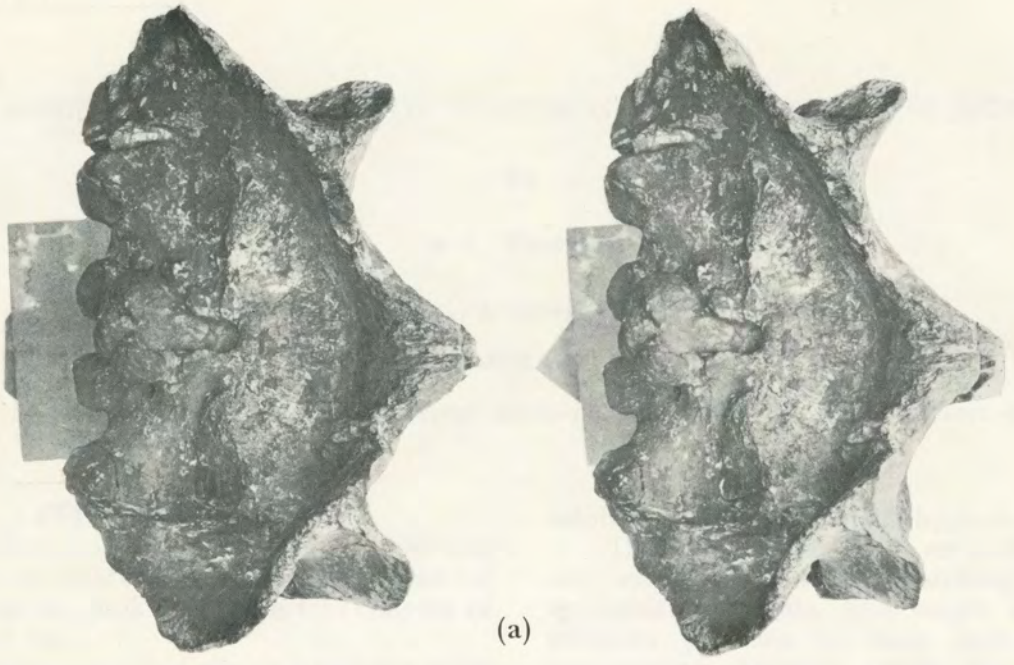


Fig. 2 (a) Right lateral view of type of *K. erithrea* Htn.
(b) Dorsal view of type of *K. erithrea* Htn.
(c) Palatal view of type of *K. erithrea* Htn.



(a)



(b)



(c)

Fig. 3 (a) Occipital view of type of *Kannemeyeria erithrea* Htn.
(b) Three-quarter frontal view of the left side of skull of the type of *K.wilsoni* Broom.
(c) Three-quarter frontal view of right side of skull of the type of *Dicynodon simocephalus* Weit.
Figs. 2a-c & 3a by courtesy of Dr. M. A. Cluver and the Director of the South African Museum, Cape Town. Where scales are not included, overall measurements are given in Table I.

Palaeont. afr., **13.** 57–60. 1970

EPIDERMAL REMNANTS OF *PROTEROSUCHUS VANHOEPENI* (HTN)

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ABSTRACT

Epidermal remnants from *Proterosuchus vanhoepeni* are described. The significance of these findings is briefly discussed.

INTRODUCTION

There is little precise knowledge concerning the stability of epidermal filamentous proteins which make up the bulk of the protein content of the keratinized cell.

Amino acid analyses of the proteins extracted (filaments and embedding matrix) from the stratum corneum show a low percentage of sulphur amino acids, cystine and cysteine (about 2%, usually measured as cysteic acid). Thus the number of disulphide bond-forming residues is low and from this we infer that these proteins are less stable than the proteins extracted from other epidermal structures, which show much higher sulphur content, such as wool. In the latter sulphur-poor filamentous proteins are embedded in a 'stabilizing' sulphur-rich matrix. It has been proposed that the matrix surrounding the filamentous proteins in the keratinized cell of the stratum corneum functions in a similar stabilizing (cross-linking) capacity. This is yet to be proved; a controversy exists as to whether the matrix is sulphur-rich or not (Matoltsy and Matoltsy, 1970).

As the cell enters the final phases of keratinization the cell membrane is stabilized (and resists autolysis) by the addition of a new protein to the inner lamina. This is seen in electron micrographs as a thickening which partially obscures the inner lamina.

Matoltsy and Matoltsy (1966) removed the proteins from the fully keratinized cell (plantar callus) leaving a residue of stabilized cell membranes. Amino acid analysis of this residue showed a relatively high proportion of ½ cystine and proline (the latter is not compatible with α helix formation). This may be the general situation since it is also true for anuran stabilized cell membranes (A. Thornley, unpublished obs., 1971). In addition tritiated cystine injected into rats is transported to the area of the cell membrane in the cell layers immediately below the stratum corneum (Fukuyama and Epstein, 1969). This holds for the Anura as well (A. Thornley, unpublished obs., 1971).

We may therefore be justified in assuming generally that the stability of the modified cell membrane is partially due to the presence of a sulphur-rich (and proline-rich) protein.

This information gives an indication of what one might find when searching for preserved epidermal remnants. One might expect the filamentous proteins to have been destroyed by keratinolytic bacteria, while the stabilized cell membranes may remain partially intact. (The modified cell membrane fragments easily after chemical removal of the filamentous proteins).

The systematic position of *Proterosuchus vanhoepeni* (Htn) (No. C 3016, Nasionale Museum, Bloemfontein) has been examined (Cruickshank, 1971). In his paper Cruickshank mentions that epidermal 'scutes' were observed lying embedded in the matrix (Figure 1). Portions of these 'scutes' were removed, embedded in Epon 812 using standard techniques and sectioned for light and electron microscopy. The results are described here.

METHODS

The rock was suspended in 1% acetic acid in water and the fragments which gradually flaked off collected. Fragments were sorted using a dissecting microscope and the cleanest fixed (?) in 5% glutaraldehyde in 0,1M cacodylate buffer (pH 7,5) for one day. They were then transferred into fresh buffer for one day and subsequently into 1% osmic acid in 0,05M cacodylate buffer (pH 7,5) for 4 hours. After washing in 10% ethanol for one day the samples were dehydrated and embedded in Epon 812 (Luft, 1961). ½ μ sections were cut, stained with toluidine blue (Ito and Winchester, 1963) and examined with the light microscope under oil immersion. EM sections were stained with uranyl acetate and Reynolds lead citrate (Reynolds, 1963).

RESULTS

Light microscopy

A faint blue line of basophilic material was observed under oil immersion over the surface of a layer of uniform crystals. This material had been trapped between the layer of crystals and embedding rock. A further layer was found overlying and

slightly separate from the layer of crystals in two or three samples.

Electron microscopy

The layer of crystals did not show any indications of Haversian systems and therefore the samples were not from scute. The layer of crystals had the dimensions of dermis and may therefore represent the replacement of collagen by ferric (?) salts.

The nature of the material trapped between dermis (?) and rock is shown in figures 2, 3 and 4. The stabilized cell membrane of the stratum corneum appears to have been preserved and there are suggestions of filamentous proteins. The dimensions of these structures are similar to those of other vertebrates (vary from about 60 to 300 Å), but it is unwise to attach too much importance to these sort of data.

More convincing however is the morphology of the material found embedded in the colloidal layer interposed between dermis (?) and rock (Figures 5 and 6). The filamentous proteins (and matrix ?) of the epidermis appear to have been preserved intact. The dimensions of the individual filament cross-sections are within the range reported for these proteins (about 50 to 120 Å).

DISCUSSION

The modified cell membrane remnants are shown packed one layer on top of the other in Figures 3 and 4. This would be indicative of scales, which is not unexpected since *Proterosuchus* has been shown to be a reptile. All known vertebrates, except the Amphibia, have multiple layers of stratum corneum. The latter have one layer, sometimes two. There is insufficient knowledge of these structures to be able to distinguish families of reptiles.

The filamentous structures shown in electron micrograph number 6 are interesting in that they are not associated with modified cell membranes. They must therefore be part of the cell content from layers beneath the stratum corneum; that is, they have not undergone 'keratinization'.

The importance of these studies lies in the fact that they may show that not only is the keratinized cell membrane remarkably stable over millions of years but that the filamentous proteins (and matrix ?) themselves have a unique resistance to breakdown. These developments are obviously important in the evolution of vertebrates.

These observations indicate that ectodermal structures (nails, hairs, scales) may be present in rock samples which contain fossilized vertebrates. The author hopes that this paper will stimulate investigations for and ultrastructural examination of epidermal remnants in palaeontology.

ACKNOWLEDGEMENTS

Photographs were processed by J. Thompson. Material was supplied by Dr. A. R. I. Cruickshank, whose interest in this study is gratefully acknowledged. The author was supported by a Senior Bursary from the University of the Witwatersrand.

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Fig. 1 x 4 Remnants of *Proterosuchus* embedded in mudstone. (Top left)
Fig. 2 x 36 000 Structures with the morphology of thickened membranes (tm) and filamentous proteins (Fp). Dermis (D). (Top right)
Fig. 3 x 90 000 Thickened membranes layered one on top of the other. (Arrows) (Bottom left)
Fig. 4 x 90 000 Thickened membranes layered one on top of the other. (Arrows) (Bottom right)

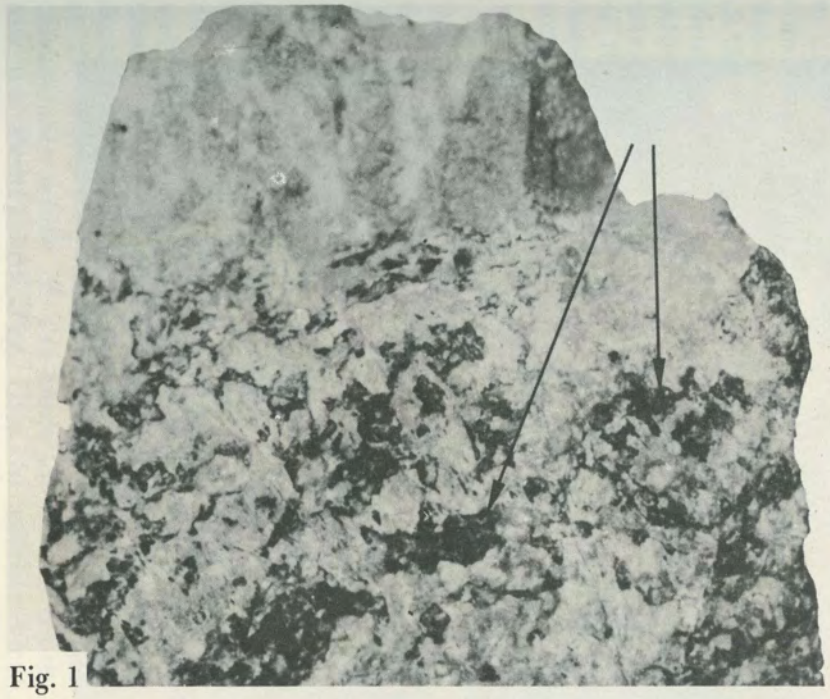


Fig. 1

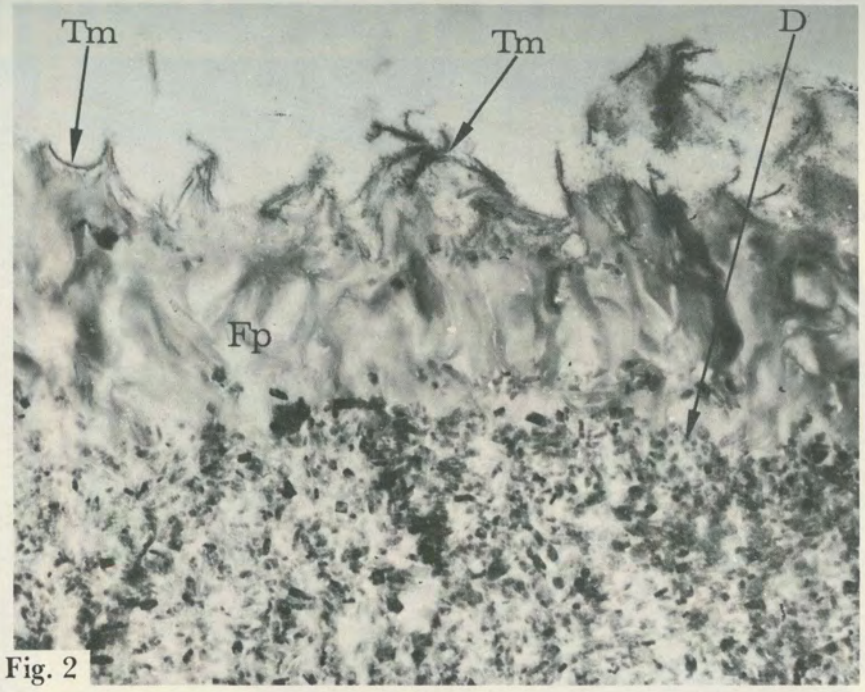


Fig. 2

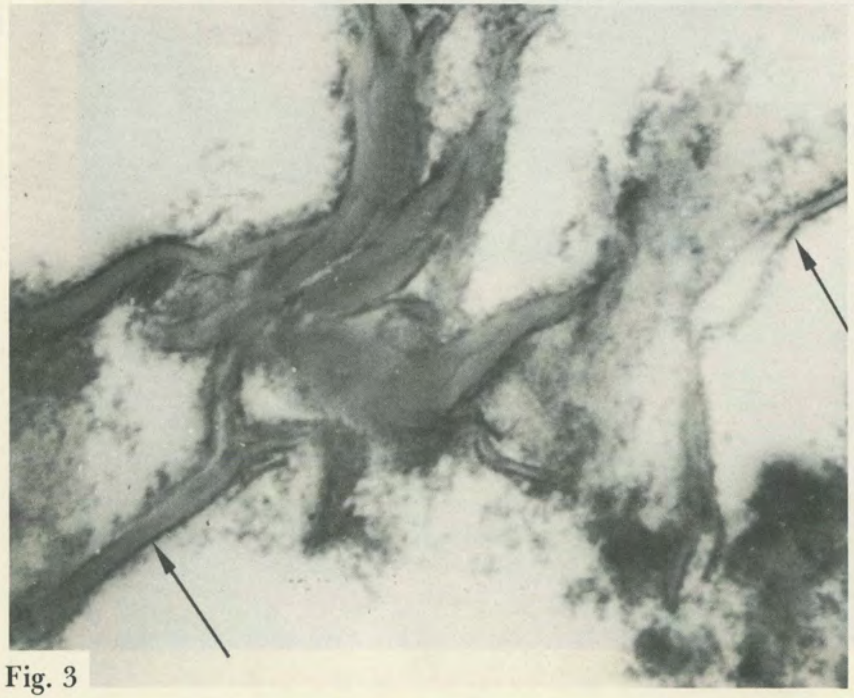


Fig. 3

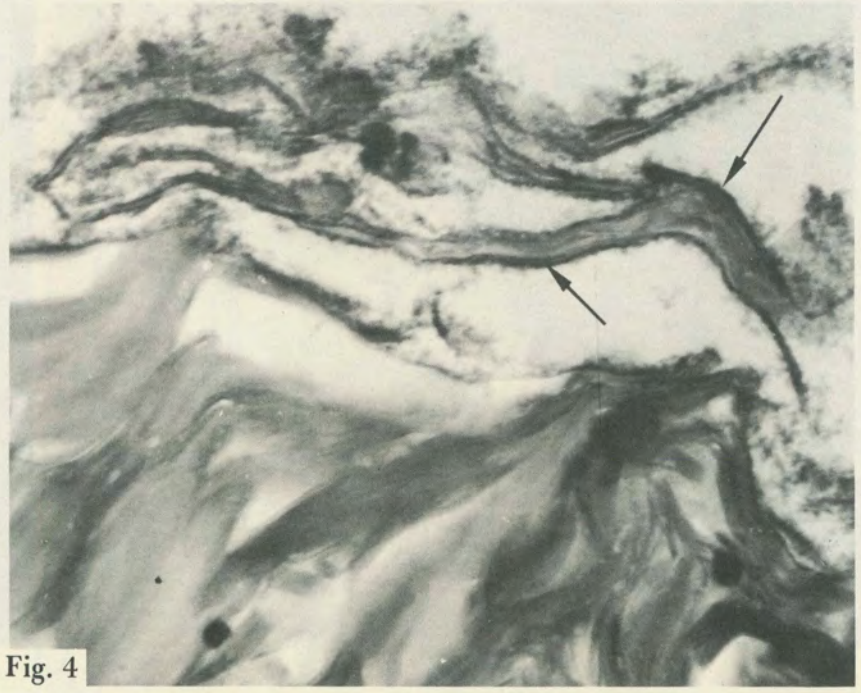


Fig. 4

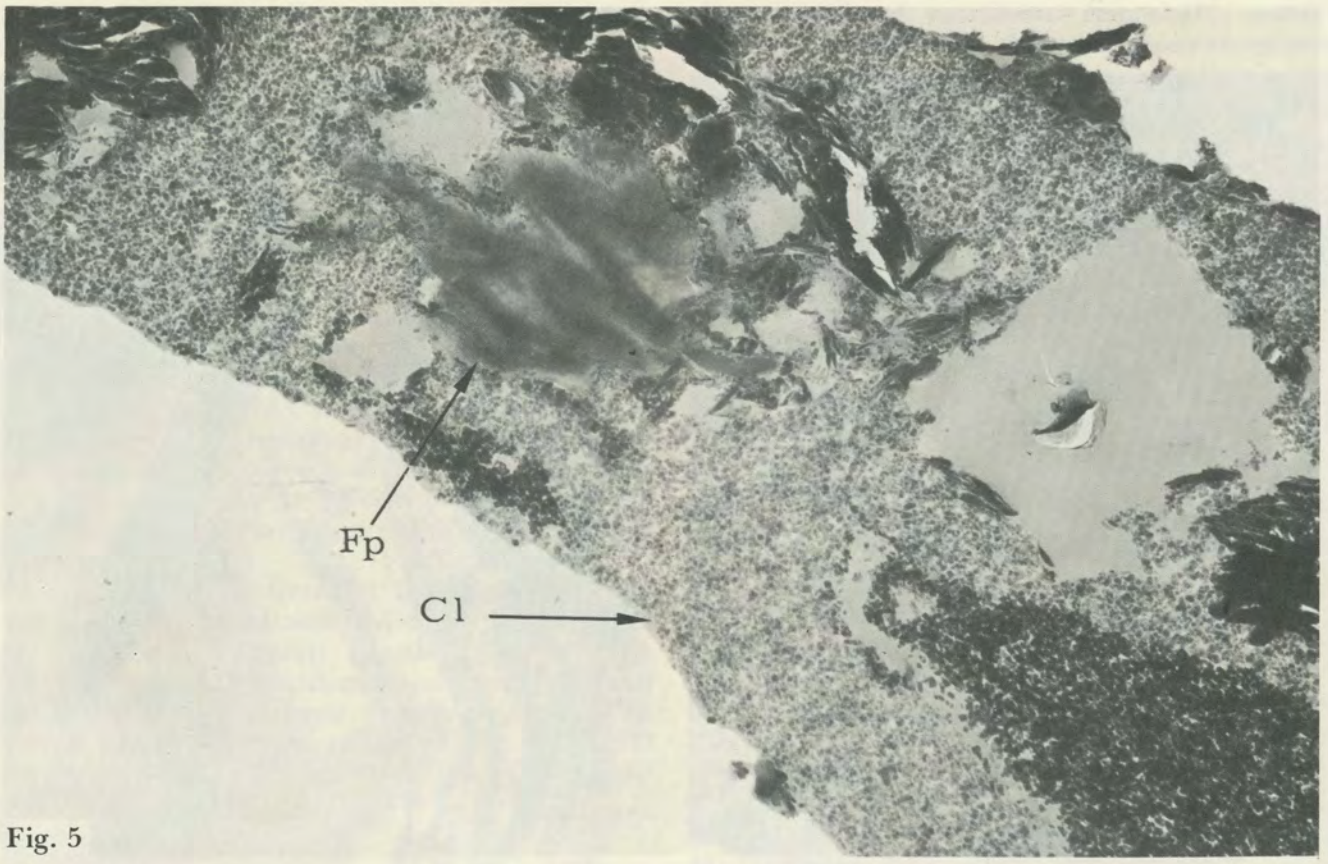


Fig. 5

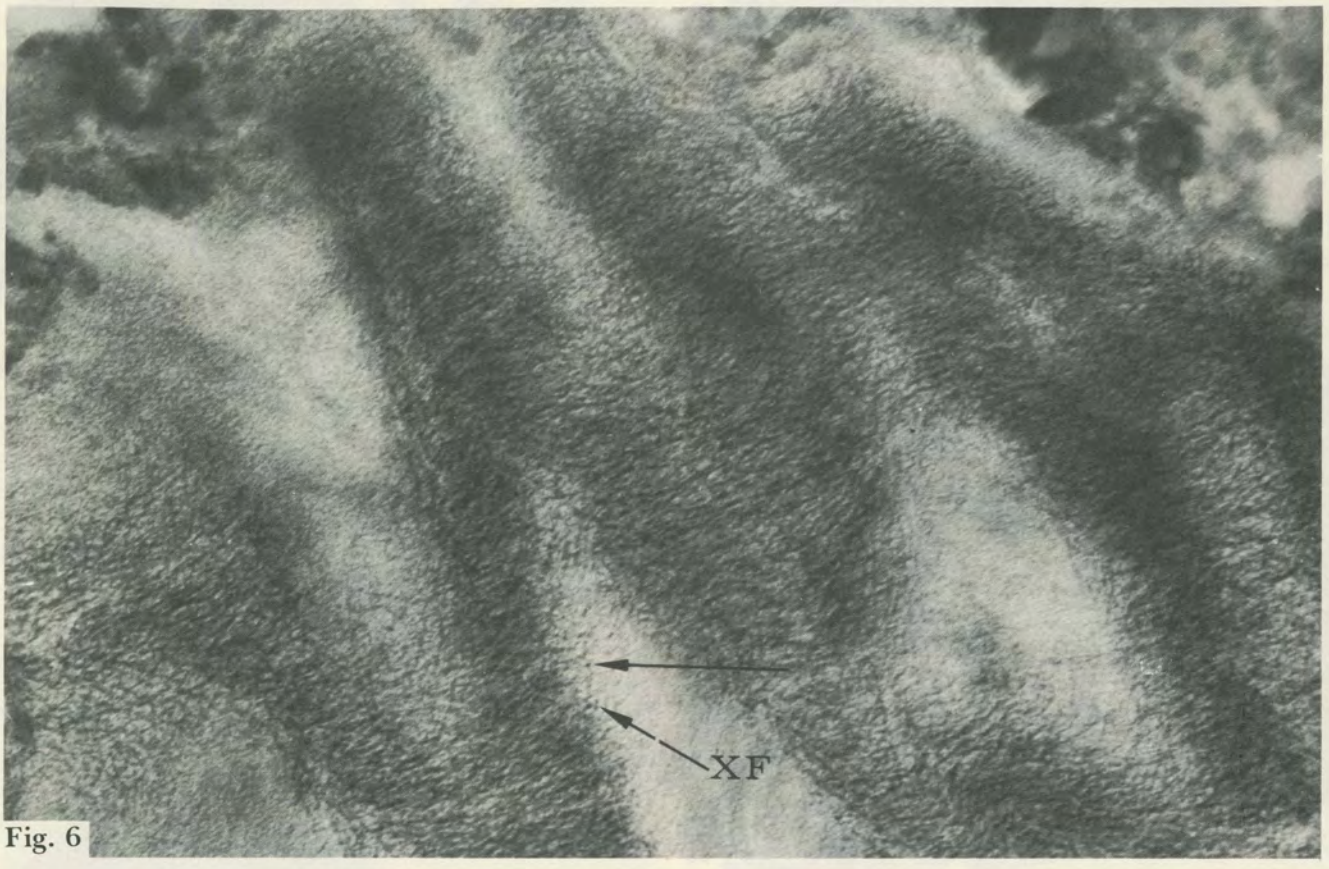


Fig. 6

Fig. 5 x 24 000 Filamentous proteins (Fp) lying within a colloidal layer (Cl). (Top)
Fig. 6 x 83 000 Filamentous proteins. Arrows indicate filaments in cross section (XF). (Bottom)

Palaeont. afr., **13.** 61–62. 1970

THE ANTERIOR OF THE PALATE IN *EUPARKERIA*

by

C. E. Gow

INTRODUCTION

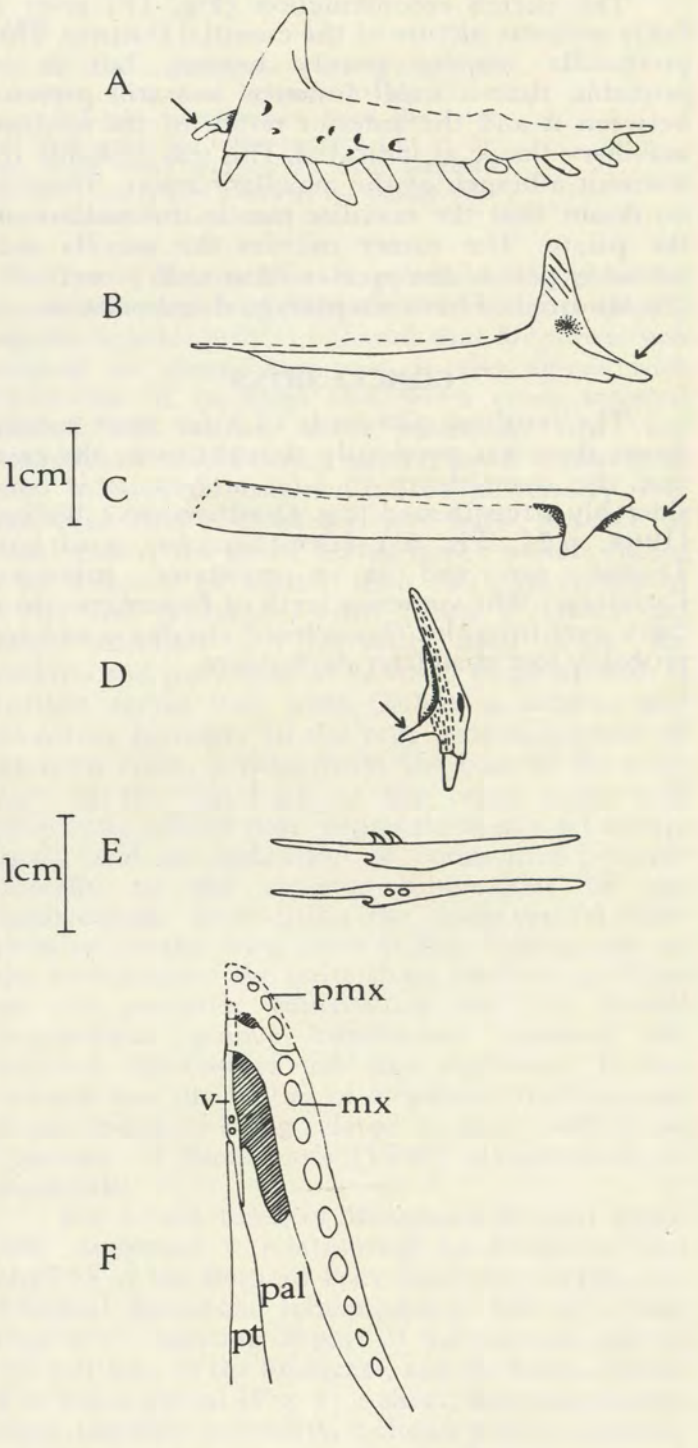
Ewer (1965) has given a careful and comprehensive description of the anatomy of the thecodont *Euparkeria*, but erred if anything on the side of caution in her preparation of the material. This is a commendable approach, but it has meant that certain details remained unknown. Recently Cruickshank (1970) has redescribed and reinterpreted the braincase as being surprisingly primitive. The present author's current interest lies in the origin of the lizards, and this necessarily implies an interest in Archosaur origins. In this regard an important element of the skull is the vomer; this will become apparent when recently completed work on the Millerosauria is published (Gow 1971). The important feature is the nature and disposition of vomerine teeth. Not surprisingly the vomer is not known in detail in any "Eosuchian" or early lepidosaur, as it usually lies hidden by the symphysis of the lower jaws and in any event requires delicate preparation.

In view of the central position of *Euparkeria* in the accepted phylogeny of the Archosaurs it was considered necessary to examine the vomer, and to this end one of the skull blocks listed by Ewer (SAM 6050) was prepared in formic acid. This yielded in addition to the vomers, important new information on the internal structure of the maxillae. The vomer stresses the primitive nature of the animal while the structure of the maxilla considerably strengthens its affinities with later archosaurs.

The maxilla

The important feature of the maxillae is that they have anterior median flanges which meet in the midline of the palate (arrowed in the figure). The lateral view of the left maxilla (Fig. 1A) shows how this flange projects well forward internally beyond the external limit of the maxilla. The lingual view (Fig. 1B) shows the area of attachment of the maxilla to the nasal (hatching) and below this a circular depression (stippled). The apparent discrepancy in depth of the bone between Figs. 1A and B is because lateral and lingual margins have been used respectively. Fig. 1C shows the maxilla in dorsal view. Of interest here are the delicate notch at the anterior tip of the median flange and the considerable width of the bone above the tooth row (cf. Ewer (1965, Fig. 1B)). In anterior view (Fig. 1D) the attachment area of the premaxilla is hatched. Note that this extends along the median flange up to the notch mentioned above.

DESCRIPTIONS (Fig. 1 A-F).



The vomer

Palatal and lateral views of the left vomer are given in Fig. 1E. This is a long narrow element with

considerable depth. It bears two strongly recurved teeth, similar in form and mode of attachment to the rest of the palatal teeth described by Ewer.

THE PALATE RECONSTRUCTED (Fig. 1F).

It is not possible to relate the features described above to Ewer's reconstructions of the skull, as the latter embody several inaccuracies unavoidable at the time. A complete and accurate reconstruction would be a major project and beyond the purpose of this paper.

The sketch reconstruction (Fig. 1F) gives a fairly accurate picture of the essential features. The premaxilla remains poorly known, but it is probable that a small foramen was still present between it and the anterior notch of the median maxillary flange as indicated. This was probably to transmit a branch of the maxillary artery. There is no doubt that the maxillae met in the midline of the palate. The vomer overlies the maxilla and probably part of the premaxilla as well; posteriorly it is sandwiched between pterygoid and palatine.

CONCLUSIONS

The resulting picture is of a far more robust snout than was previously thought to be the case and the resemblance to later archosaurs is considerably strengthened (e.g. *Ornithosuchus*, Walker (1964, p.71, Fig. 6)). (*Ornithosuchus* is of late Triassic age and is a presumed primitive Carnosaur). The vomerine teeth of *Euparkeria* are a carry over from the "Eosuchian" condition and are probably lost in all later Archosaurs.

It is tempting to suggest that a similar state of affairs will be found to exist in the contemporaneous and structurally similar *Erythrosuchus*. In any event the anterior of the palate may prove to be of considerable importance in determining the evolutionary sequence of Early-to-Middle Triassic Archosaurs.

ACKNOWLEDGEMENTS

I am much indebted to the Director of the South African Museum, Cape Town, for the loan of the material here described.

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REVISED CLASSIFICATION FOR *MAKAPANIA BROOMI* WELLS AND COOKE (BOVIDAE, MAMMALIA)

by

A. W. Gentry

British Museum (Natural History)

ABSTRACT

Details of skull morphology, particularly of the basioccipital, show that *Makapania broomi* from the Makapansgat Limeworks Quarry, Transvaal belongs to the tribe Ovibovini, and is very like *Megalovis latifrons* Schaub, best known from the later Villafranchian of Senèze, France. The Ovibovini have only two living species, but in the Pliocene and early Pleistocene they must have been more widespread than hitherto suspected. *Makapania broomi* is the first clear record from Africa south of the Sahara of a fossil member of the Eurasian and North American subfamily Caprinae.

Wells & Cooke (1956: 26-33, Figs. 13-16) described an extinct antelope genus and species *Makapania broomi* from the Limeworks Quarry, Makapansgat, Potgietersrus, South Africa. It was plentifully preserved, and there were associations between horn cores, upper teeth and lower teeth. Wells and Cooke noted the main characters of medium to large size, horn cores inserted just behind the orbits and passing almost directly outwards from the side of the skull, teeth hypsodont, and rather V-shaped lobes medially on the upper molars and laterally on the lowers. They considered that *Makapania* belonged to the tribe Alcelaphini, although clearly a rather unusual member of that tribe.

Having seen more material of *Makapania broomi* than was available at the time Wells and Cooke were working, I believe it to be an ovibovine. The tribe Ovibovini, hitherto known only from Eurasia and North America, contains two living species, the muskox *Ovibos moschatus* (Zimmermann) and the takin *Budorcas taxicolor* Hodgson. It also contains their fossil relatives among which the Chinese *Boopsis sinensis* Teilhard de Chardin (1936) and *Lyrocerus satan* Teilhard de Chardin and Trassaert (1938) are probably early stages in the evolution of the muskox and takin respectively. *Megalovis latifrons* Schaub (1923: 292, Fig. 5; 1943: 281, Figs. 5 & 6) from the Villafranchian of Senèze, France is related to later ovibovines, but perhaps not ancestral to them. There are two Pliocene groups of fossil ovibovines. One contains *Urmiatherium* Rodler from Maragha (northern Iran) and China, the small *Parurmiatherium* Sickenberg from Samos, *Plesiaddax* Schlosser from China and *Tsaidamotherium* Bohlin from China, all with more specialized horn cores than the Pleistocene and living species. A second extinct group contains only *Criotherium* Major from Samos and, as I believe, *Palaeoreas* Gaudry from Samos and Pikermi and Veles in Greece, both with spiralled horn cores but otherwise not very advanced.

The Villafranchian *Megalovis latifrons* is the form with which *Makapania broomi* most closely agrees. Schaub (1923) believed that *Megalovis* was related to sheep. However, it also agrees with Ovibovini in its large size, horn cores inserted behind the orbits, short braincase, not very complicated mid-frontals suture, small supraorbital pits, infraorbital foramen placed posteriorly over the back of P^3, small auditory bulla, absence of basal pillars on molar teeth, upper molars rather long relative to width, with fairly pronounced styles and rounded medial lobes, P^2 remaining large, mandible not markedly deep below the molars, and paraconid of P_4 fused to metaconid. It further agrees well with *Ovibos moschatus* and *Budorcas taxicolor* in the very wide divergence of its horn cores, a ridge from the base of the horn core to the top back of the orbit, fairly well projecting orbital rims, supraorbital pits set widely apart, and an indication of concavities postero-laterally to the anterior tuberosities on the basioccipital. In addition the dorso-ventral compression of the horn cores is like *Ovibos*, and on the basioccipital the quite sharp upstanding ridges on the posterior tuberosities and the central longitudinal groove constricted between the anterior tuberosities are like *Budorcas*. In my opinion any similarities of *Megalovis* to sheep arise from Ovibovini being related to sheep within the Caprinae of Simpsons's (1945) classification of mammals.

The actual fossil of *Makapania broomi* which first suggested a relationship to Ovibovini was M.2793 in the Bernard Price Institute for Palaeontological Research, Johannesburg. This is a skull fragment consisting of part of the frontals, part of the left side of the braincase, and the basioccipital. The basioccipital (Fig. 1) is short, with raised areas close together anteriorly, hollows postero-laterally to these raised areas, and quite bulky posterior tuberosities with a hollow between them which widens towards the rear. The raised areas are in part of the position occupied by the larger and

better defined anterior tuberosities of other bovid basioccipitals, and I shall here call them anterior tuberosities. The basioccipital of M.2793 differs from that of *Megalovis latifrons* in its closer anterior tuberosities, lack of a central longitudinal groove between them, and less upstanding ridged posterior tuberosities. But this is all extremely similar to the basioccipital of *Ovibos* (Fig. 2), and such a pattern can be found in no other bovid. M.2793 differs from Alcelaphini by the triangular rather than quadrangular shape of the basioccipital, and in having no central groove running forwards for the whole length of the bone; in fact, forward of the posterior tuberosities, the centre of the bone is raised between the paired hollows.

Other *Makapania broomi* pieces with basioccipitals, M.555 and M.2935, have less obvious hollows behind the anterior raised areas, but they do show the posteriorly widening valley between the posterior tuberosities and a tendency to high central parts.

M.2793 and M.555 both show a ridge running from the lowest point of the horn base to the nearest part of the orbital rim (Fig. 3); such a ridge is also seen in *Megalovis latifrons* (Schaub 1923, Fig. 5).

M.1024 is the base of a right horn core and the orbit of *Makapania broomi*. The anterior part of the zygomatic arch beneath the orbit is not deepened as it is in Alcelaphini.

When I was able to see the examples of *Megalovis latifrons* in Basle and Paris, I found other impressive similarities to *Makapania broomi*: the wide insertions of the horn cores just behind the orbits, their transverse emergence, the gentle ascent towards the tips, absence of transverse ridges on the horn cores, the short braincase well angled on the facial axis, the extent of the projection of the dorsal parts of the orbital rims, the small localized preorbital fossae, fairly hypsodont teeth, absence of basal pillars, poor to moderate development of styles and ribs between the styles, indentations into the walls of the central cavities of the upper molars, fused paraconid and metaconid on P_4 closing the anterior part of the medial wall, and the mandible not markedly deep below the molar row. Some of these resemblances of *Makapania broomi* to *Megalovis latifrons* are also found in the Alcelaphini, and one might even draw strained parallels with *Connochaetes*. However, such distinctive alcelaphine characters as the rounding of the medial lobes of the upper molars and the lateral lobes of the lowers, the curvature of the entire upper tooth row, and the deep mandibles are absent. Also the median indentation at the back of the palate in *Makapania broomi* is behind the level of the lateral ones, quite unlike Alcelaphini and like *Budorcas* and *Ovibos* although the state of this character is not known in *Megalovis latifrons*.

Differences of *Makapania broomi* from *Megalovis latifrons* are few: longer horn cores, frontals raised between the horn bases, horn cores positioned with their greatest diameter dorso-ventrally in side view instead of antero-posterior, and more of a V shape to the medial lobes of their upper molars and to the lateral lobes of their lowers. Moreover, the raising of the frontals between the horn bases and the position of the longest diameter of the horn bases are similar to the condition found in *Budorcas*.

These morphological similarities of their skulls and dentitions show that *Makapania broomi*, *Megalovis latifrons*, and the living takin and muskox can be taken as quite a neatly defined group of Ovibovini. I shall not here make a prolonged investigation of whether their existing Linnaean names are the best for expressing their relationships; I note only that *Megalovis latifrons* is the closest to *Makapania broomi*.

Megalovis latifrons occurs at European Villafranchian sites other than Senèze, and its nomenclature is tangled like most other mammalian species. The cranium of *Deperetia ardea* from Senèze (Schaub 1923, Fig. 3) is very probably conspecific with the *Megalovis latifrons* fossils from the same site. The skull of *Pliotragus ardeus* from Olténie in Romania (Bolomey 1965, Figs. 1-3) is probably also conspecific. (Kretzoi 1941: 349 had changed the generic name *Deperetia* to *Pliotragus*). It is even possible that this same species includes the original maxilla of *Antilope ardea* Depéret (1884: 252, pl. 8, Fig. 3) from Etouaires, France, in which case a name change might be needed. I shall continue to use *Megalovis latifrons* here. *Hesperoceras merlae* Villalta and Crusafont Pairo (1955: 431, Figs. 1-3) must be at least a closely related form, if not actually conspecific. Finally *Soergelia elizabethae* Schaub (1951: 376, pls. 11, 12) which occurs later in the middle Pleistocene of Süssenborn, Germany, could be a species descended from *Megalovis latifrons*.

The sites from which *Megalovis latifrons* and its synonyms have been published occur through the whole of the Villafranchian according to Heintz (1969) and Kurtén (1963). A horn core, L.7-82, which could belong to *Makapania*, was found below tuff G at Omo, southern Ethiopia in 1968, and is the only possible occurrence of the genus away from the Makapansgat Limeworks Quarry (Fig. 4). According to the dating of lower and higher tuffs in the Omo sequence, this horn core would be aged between 1,8 and 2,6 million years (Howell 1968: 569). This date, together with the time of occurrence in Europe of the genus most closely related to *Makapania*, offer slender indications of the age of Makapansgat Limeworks Quarry.

As interesting as such very tentative indications of a date for the Makapansgat Limeworks fauna is the zoogeographical question of the occurrence of Caprinae in Africa. At the present day the only caprines in Africa are *Capra (Ammotragus) lervia* (Pallas), *Capra nubiana* F. Cuvier and *Capra walie* Rüppell, but only the last in the mountains of Ethiopia is even marginally in the Ethiopian rather than the Palaearctic realm. In the

past various African fossils have been wrongly or doubtfully identified as Caprinae or Caprini, e.g. the Olduvai *Pultiphagonides* Hopwood (see Wells & Cooke 1956: 26, 33 for comment on this), and some other Olduvai fossils (see Leakey 1965: 68). It seems that whatever may ultimately be decided about such questionable fossils, there is now definite evidence of a member of the Ovibovini in subfamily Caprinae in Africa a very long way south of the Palaearctic. The evolutionary problem of how it came to be there is still not solved, but it is certain that in the Pliocene the Ovibovini were more widespread and they can now be regarded as a relict group. Accepting that Caprinae have occurred in Africa, one can question again the tribal affinity of the South African vaal rhebbok, *Pelea capreolus* (Forster), long considered a member of the Reduncini but now recognized as clearly not in that tribe (Roberts 1937: 86, Wells 1967: 100, Gentry 1970: 314). Could it be fairly closely related to goats or to the chamois, *Rupicapra rupicapra* (Linnaeus), despite its geographical isolation from them?

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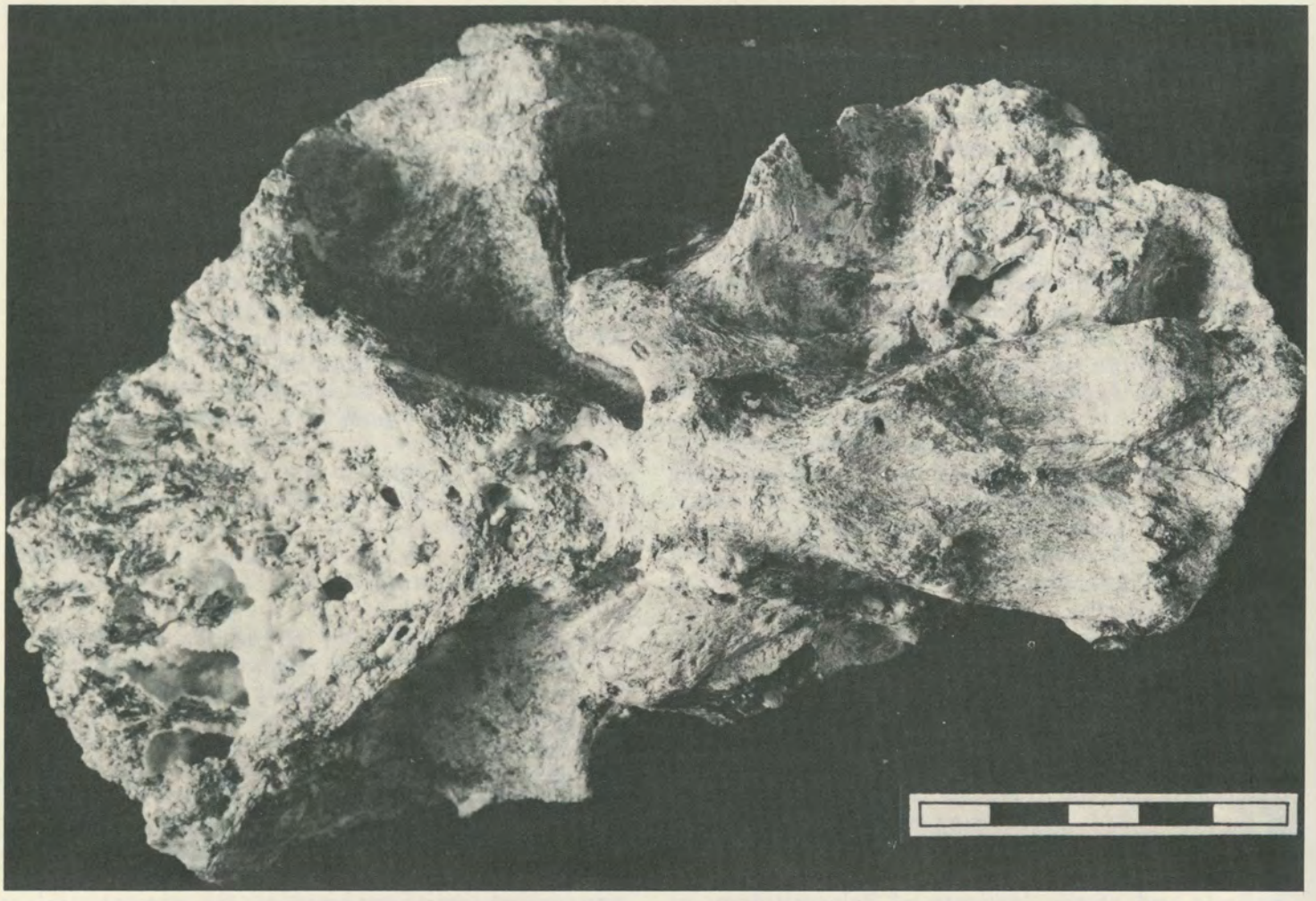




Fig. 1. Basioccipital of skull fragment M.2793 of *Makapania broomi.* The anterior side is to the left. The scale is in centimetres. Top.

Fig. 2. Basioccipital of a muskox, *Ovibos moschatus,* in the British Museum (Natural History), No. 612b. The scale represents 20 mm. Bottom.



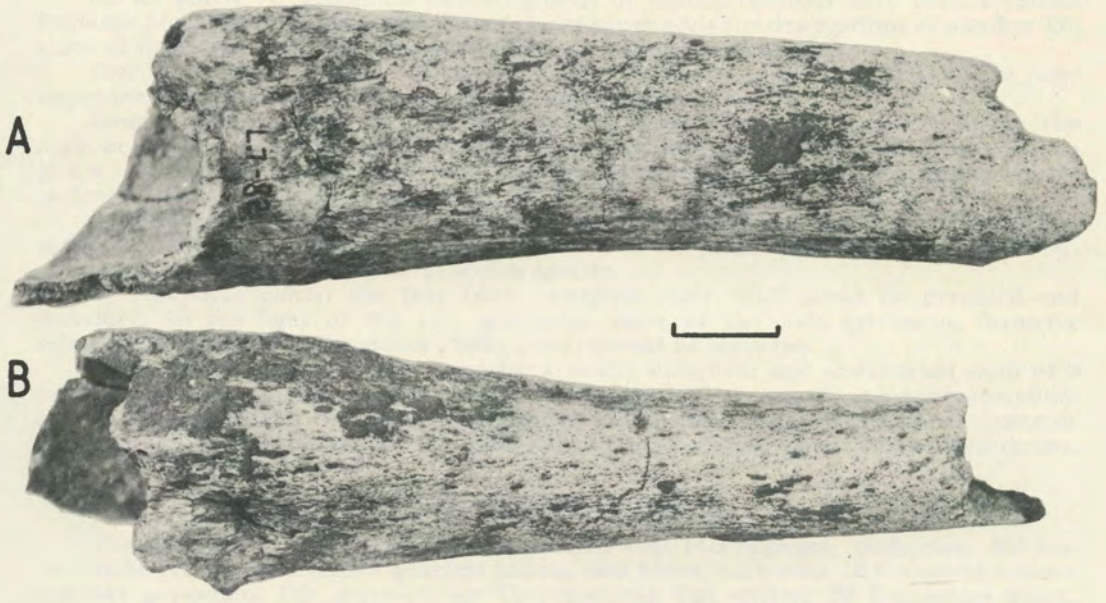


Fig. 3. Lateral view of skull fragment M.2793 of *Makapania broomi*. The anterior side is to the bottom left, and the scale in centimetres. The arrow indicates the ridge from the base of the horn core to the orbit rim.

Fig. 4. Horn core L.7-82 from below tuff G at Omo, Ethiopia. The scale represents 20 mm. The view A is probably ventral, and B is probably anterior.

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NEW FOSSIL CERCOPITHECOIDEA FROM THE LOWER PLEISTOCENE CAVE DEPOSITS OF THE MAKAPANSGAT LIMEWORKS, SOUTH AFRICA

by

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(3) *Parapapio broomi* (M.3056, M.3063, M.3065, M.3067, M.3070, M.3075, M.3082)
(4) *Parapapio whitei* (M.3062, M.3072)
(5) *Simopithecus darti* (M.3071, M.3073, M.3074, M.3083)
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ABSTRACT

So far about 70 specimens of five species of Cercopithecoids have been recorded from the Makapansgat Limeworks. The present paper adds the descriptions of another 20, some of them being the most complete skulls known of these species:

Cercopithecoides williamsi is represented by a nearly complete male skull; its large upper teeth confirm the invalidity of the former species *C. molletti.*

Parapapio jonesi is represented by parts of a young female and two adult males. The male material is the most comprehensive known of this species and made it possible to give a reconstruction of the male skull. Specimen M.2961, described by Freedman (1960) as *Parapapio broomi,* is referred to *P. jonesi.*

Of *Parapapio broomi* 7 new specimens are recorded and described. A fragmentary male skull (M.3065) and a very large mandible (M.3067) most probably belong together, giving a good idea of the male skull of this species.

Of *Parapapio whitei* the first fairly complete male skull could be prepared and described. In the light of the new specimen, some of the male specimens, formerly referred to this species (Freedman 1960; 1965) should be removed.

Simopithecus darti is represented by a nearly complete and undistorted skull of a subadult female, with the mandible being in situ. In addition, a nearly complete mandible of a young male and a fragmentary maxilla of an old male could be described. Some of the teeth of these specimens nearly equal those of *Simopithecus danieli* from Swartkrans.

ZUSAMMENFASSUNG

Von den unterpleistozänen Höhlenbreccien von Makapansgat, Südafrika, die u.a. zahlreiche Australopithecinen geliefert haben, sind bisher auch etwa 70 Cercopithecoidea bekannt geworden. Die gegenwärtige Untersuchung fügt weitere 20 Exemplare hinzu, darunter mehrere nahezu vollständige Schädel, die die Morphologie sämtlicher fünf Arten beträchtlich erweitern.

Cercopithecoides williamsi, ein Colobide, ist durch einen nahezu kompletten männlichen Schädel vertreten. Der Unterkiefer fehlt, aber die oberen Zähne liegen im Grössenbereich der mittlerweile unterdrückten Art *C. molletti.*

Parapapio jonesi ist durch Teile eines jungen Weibchens und zweier erwachsener Männchen repräsentiert. Das männliche Material ist recht vollständig und vermittelt erstmals einen Eindruck von der Schädelmorphologie dieser Art. Exemplar M.2961, das von Freedman (1960) zu *Parapapio broomi* gestellt wurde, gehört wahrscheinlich ebenfalls zu *P. jonesi.*

Von *Parapapio broomi* werden 7 neue Exemplare beschrieben. Ein sehr grosser, aber fragmentarischer männlicher Schädel (M.3065) und eine grosse Mandibel (M.3067), die wahrscheinlich zusammengehören, bilden eine gute Grundlage für eine erste Rekonstruktion des gesamten Schädels.

Von *Parapapio whitei* konnte erstmals ein annähernd kompletter männlicher Schädel gefunden werden. Einige der Exemplare, die von Freedman (1960; 1965) zu dieser Art gestellt wurden, sollten besser wieder daraus entfernt werden.

Simopithecus darti, wahrscheinlich ein naher Verwandter des rezenten *Theropithecus gelada,* ist durch einen nahezu vollständigen Schädel, mit Mandibel in situ, eines subadulten Weibchens vertreten. Es ist das bisher vollständigste Exemplar dieser Fossil-Gattung. Weiterhin wird ein nahezu kompletter Unterkiefer eines jungen Männchens und der obere Zahnbogen eines alten Männchens beschrieben.

Die vorliegenden Funde werden jeweils beschrieben und diskutiert, die metrischen Angaben sind in Tabellen zusammengestellt.

INTRODUCTION

Fossil Cercopithecoids from the Pleistocene cave breccias of South Africa were first mentioned by Haughton (1925). Since that time a large number of additional specimens have been recovered and described by various authors. All material, known before 1957, was examined and restudied by Freedman (1957); at that time about 1 250 specimens were available, about 550 originating from Sterkfontein, 300 from Swartkrans and about 50 to 70 each from Makapansgat, Kromdraai and Cooper's. Odd specimens were known from some other places, listed in Appendix IV A of Freedman (op.cit.). In addition, Freedman (1961; 1965) has described further Cercopithecoids from Makapansgat, Taungs, Bolt's Farm and Witkrans.

From Makapansgat Limeworks so far about 70 specimens of Cercopithecoidea are recorded; the present study adds another odd 20, some of them being the most complete skulls so far known from this site. This material was prepared by the author between March and September 1970 at the Bernard Price Institute for Palaeontological Research, Johannesburg, where these specimens are also housed.

The classification of the living Cercopithecoidea is mainly based on external characteristics and on soft parts (skin and fur colours, morphology of the genitals and intestines), the skull, teeth and other skeletal parts either being considered too uniform or too variable under changing functional conditions (Pocock 1925). This seems to render nearly impossible satisfactory systematics of fossil Cercopithecoidea, consisting, as they do, only of hard parts. Indeed, the classification of these fossil forms is still very problematical. Most of the known material is very fragmentary, mainly consisting of teeth. Therefore, at the present moment, the system of the fossil South African Cercopithecoidea is almost entirely based on tooth characters, or, because of their uniform structure, only on different tooth sizes. Broom (1940), for example, based the classification of the genus *Parapapio* mainly on three categories of molar size, which seemed to emerge from the scant material available to him. But the same author was not able to give a workable differential diagnosis for both the taxa *Parapapio* and *Papio.* At the moment we still lack species definitions for the Pleistocene Cercopithecoidea of South Africa, but Freedman (1957) at least succeeded in establishing fairly satisfying definitions of the 6 genera, known from these deposits. The species, however, are still a kind of working model, reflecting the morphological diversity of the fossil material, but possibly being far from representing natural units.

A comprehensive biological analysis of extant species shows also that small adaptive modifications can form typical patterns which are liable to taxonomic interpretations on the species and genus level (Davis 1964; Maier 1970). A detailed functional analysis of fossil skeletons, combined with palaeoecological considerations, could help to ascertain and to evaluate even small differences between the various forms of fossil Cercopithecoids. In the skull this would apply mainly to the adaptative modifications of the masticatory apparatus, and in the postcranial skeleton to the limb proportions. It becomes evident then that the knowledge of as complete material as possible is of especial importance in such an uniform taxon as the Cercopithecoidea.

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THE STRATIGRAPHY AND LOCALITY OF THE NEW SPECIMENS

As yet little attention has been spent on an exact localization of the fossils found in the South African cave deposits. Most of the material was gained by the activities of the limeworkers and then recovered from the mining dumps. The texture and colour of the matrix sometimes allowed the original locality level to be assessed more or less accurately, but normally only a rough assignment was possible. Fortunately, most of the new Cercopithecoids from Makapansgat to be described below can be exactly localized. In 1963 (according to information by Mr. J. W. Kitching

and Mr. B. Maguire) a large block of 'pink breccia' (Upper Phase I) fell down from the right wall of the limeworker's quarry main entrance, which proved to be particularly rich in Cercopithecoid remains. Probably also, most of the material of the former 'Cercopithecoid dump' was derived from this part of the 'pink breccia'. This area, having yielded Australopithecines as well, therefore seems to be worth a careful and systematic excavation.

Being the main source of the present material, it may be useful to make a few remarks on the sedimentological and palaeontological characteristics of the "Upper Phase I'-breccia of the Makapansgat Limeworks. According to Brain (1958) the Phase I-material is characterized by the mixture of residual cave earth and of surface-derived materials. In the upper parts of the 'Upper Phase I' there is an increasing percentage of surface material to be observed: "The conclusion is that the cave entrance was being progressively enlarged, and admitted larger and larger quantities of surface-derived debris" (Brain 1958; p. 112). Because of the mixed origin of the included sand grains, their morphology and frequency distribution do not allow conclusions as to the climatic conditions.

Therefore we are still bound to make inferences on the nature of the past environment from the fossil fauna. At once, there becomes evident a striking difference in the frequency spectrum of the faunal elements within the different sediment layers: whereas in the lower parts of the Makapansgat deposit ('basal red' and 'Grey breccia') the Bovidae comprise about 90% of the fossil remains, in the 'pink breccia' the Primates dominate with about 80%. There is, however, not much change in the members of the fauna themselves. For example, all of the six forms of Primates (*Cercopithecoides williamsi, Parapapio jonesi, Parapapio broomi, Parapapio whitei, Simopithecus darti* and *Australopithecus africanus*) occur in both the lower and the upper layers. Doubtful is the occurrence of *Parapapio jonesi* in the 'pink breccia' and of the large *Parapapio whitei* in the 'grey breccia'.

Mr. J. W. Kitching was kind enough to compile for this publication a list of the mammals other than Primates, which were so far recorded from the 'pink breccia' of the Makapansgat Limeworks:

Notochoerus sp.
Potamochoeroides sp.
Hippopotamus sp.
Metaschizotherium sp.
Gigantohyrax maguirei
Procavia cf. antiqua
Elephas cf. recki
Oreotragus major
Makapania broomi
Syncerus caffer
Hyaena cf. makapani
Lepus or *Pronolagus*
Hystrix sp.

A more detailed examination most probably would produce some more forms, especially Bovidae, but even now, this variety of mammals seems to indicate a highly diversified surrounding of the ancient cave, reaching from dense forest to savannah-like conditions. Probably the Makapansgat valley had a more or less perennial water course which was accompanied by a gallery forest whereas on the higher levels bush and open grassland persisted. The examination of the microfauna of the Makapansgat deposit, at least some of which came from the 'pink breccia', was indicative of very varied ecological conditions as well (De Graaf 1961).

DESCRIPTION AND DISCUSSION OF THE NEW SPECIMENS

A. Colobidae

(1) *Cercopithecoides williamsi* MOLLETT 1947

This is the only kind of Colobid monkey known from the Pleistocene cave deposits of South Africa. It is referred to the monotypic genus *Cercopithecoides,* which is not yet known from East Africa. In South Africa, however, it is quite common, having been recovered from all of the more important lower and middle Pleistocene sites. There seems to exist a size increase, the forms from the older deposits being slightly smaller than those of the later ones. This led Freedman (1957) to create a new species *C. molletti* for the larger forms from Swartkrans and Graveyard, but subsequent finds closed the size gap, indicating a continuous chronocline (Freedman 1960). At Makapansgat, this species is known from both the 'grey breccia' and the 'pink breccia', the type specimen (M.2038) originating from the latter.

Specimen M.3055 (Figs. 1–4; Tables II–III)

This specimen is a nearly complete and undistorted skull without mandible. Although there is some minor damage, it is the most perfect male skull known so far. It was the only specimen of *Cercopithecoides* found during this recent examination of the Makapansgat breccia. Only a few undetermined Rodent remains were found in the close vicinity of the present skull.

Before fossilization, the incisors and canines, the rostral parts of the nasal bones, the lateral plate of the right pterygoid and the right auditory capsule had been lost or damaged. Some parts of the parietal and occipital, the left temporal, the left jugal arch and the left sphenoid are missing due to post-fossilizational damage. On the left side, an excellently preserved endocranial cast is exposed. The premolars and molars are in very good condition; the last molars being hardly worn and the alveolae of the canines being very large, we can conclude to have the skull of a young adult male.

Cercopithecoides williamsi is a comparatively large Colobid, all living forms from Africa being distinctly smaller. According to Verheyen (1962) the average maximum length of the large *Colobus abyssinicus* is 119 mm, compared with 146 mm in the present specimen. Only some of the Colobids from the Pleistocene of East Africa are still larger (Leakey 1969).

In the present skull, the muzzle length amounts only to about 63% of the length of the braincase; in the type skull this relation is 60%. With the skull orientated on the occlusal plane the muzzle dorsum shows a fairly steep and straight outline, the nasals being comparatively short and elevated. The glabellar region appears to be well developed when seen from the norma lateralis, and it is separated from the vault of the calvaria by a well excavated transverse groove. The calvaria itself shows a well rounded contour, reaching its maximum height at the bregma; this point, however, is scarcely elevated above the supraorbital tori. The nuchal crests are very pronounced, resulting in a dorsally protruding inion, situated at about the level of the meatus acusticus externus. As a consequence, the nuchal plane and the foramen magnum lie at the same level as the alveolar margin, and the condyles being at the same level as the teeth. Many of the extant colobids in comparison exhibit an elevated braincase and a more vertical nuchal plane, as was true for the large and advanced *Paracolobus* from East Africa. The skull proportions of *Cercopithecoides* are very aberrant from the normal colobid-type.

The type skull, when seen from its right side, seems to possess a very flat and elongated braincase, which hardly rises above the eyebrows. This feature was stressed by Mollett (1947) and Freedman (1957), but a close examination reveals that especially this right half of the calvaria was subjected to considerable distortion, the left half showing more normal proportions. In the measurements of the braincase, the new skull resembles the type very closely, the slight differences probably being due to different age and to distortion. The skull M.2999 from the 'grey breccia', in comparison, has a distinctly shorter, higher and broader braincase.

The temporal crests are fairly well marked on the frontals, only to become very faint lines on the parietal bones. The temporal lines do not meet one another medially (minimum distance 16 mm) nor do they reach the nuchal crests; thus the insertion area of the temporalis muscle is very restricted. Unfortunately the inion region shows too much damage to reveal the exact morphology of the nuchal and temporal crests; both are separated, however, by a shallow groove of about 10 mm breadth. Laterally the inferior temporal lines are confluent with the posterior root of the jugal arch, separated from the supramastoid crest by the same groove.

The nuchal plane has a nearly horizontal orientation, not being as steeply sloping as in most of the other Colobidae. Due to some damage, not much of its morphological details can be seen any more. Medially there is a well marked external occipital crest, the condylar fossae are considerably excavated, and they are separated from the anterior condylar canals by transverse bony ridges. These ridges again are separated from the prominent and pointed mastoid processes by very deep and distinct mastoid notches, indicating strong digastric muscles. The occipital condyles form an angle of about 100° with each other. The basilar part of the occipital bone shows a typical median crest between the insertion areas of the prevertebral neck muscles; the spheno-occipital junction is still visible.

The external auditory meatus is separated from the articular fossa and the small postglenoid process by a groove, and it abuts against the mastoid, with which it is fused medially up to the jugular foramen. The carotid foramen lies about 20 mm medial to the lateral margin of the auditory meatus. Just in front of this foramen a very pronounced spine arises, forming the medial wall of the foramen ovale. This spine is compressed more than in the cercopithecids, and it does not include parts of the sphenoid bone. The apex of the petrous temporal ends at the posterior margin of the medial pterygoid plate. The overall length of the tympanic and petrosal bone is about 37 mm; its lateral parts have a transverse orientation, the medial parts lie nearly antero-posteriorly, forming an angle at about the jugular foramen.

The frontal bone possesses a metopic suture right from the nasion to the bregma. The deepness of the ophryonic groove behind the supraorbital tori is about 3 mm medially and about 6 mm laterally in the present specimen; only in some of the female skulls this groove seems to be more pronounced. The supraorbital tori themselves are quite slender, being about 5 mm thick on average, compared with about 10 mm in skull M.2999. The anterior margins of the tori supraorbitales form an obtuse angle of about 137°; this probably is a consequence of an incomplete forward orientation of the orbits, which is also reflected by the broad interorbital region of the Colobidae. At the pterion the frontal bone seems to be excluded from contact with the temporal bone, but the sutures are not clearly visible. The orbits are comparatively large and nearly rounded; in older specimens there seems to occur a certain increase in breadth and a reduction in height, the latter due to the thickening of the supraorbital arcs (Ehara & Seiler 1970).

In *Cercopithecoides* the lacrimo-maxillary suture runs right across the fossa lacrimalis; this arrangement is very typical for the Colobidae (Vogel 1966), whereas in the Cercopithecidae this fossa is entirely framed by the lacrimal bone. The interorbital region is very broad in *Cercopithecoides,* but in both the present specimen and in the type skull the orbitae are not cleaned sufficiently to take accurate measurements. Most probably in all skulls of *Cercopithecoides williamsi* the interorbital breadth is larger than 20 mm. According to Verheyen (1962) the index

$$\frac{\text{Interorbital Breadth} \times 100}{\text{Muzzle length}}$$

is the most valuable characteristic for distinguishing Cercopithecidae and Colobidae. By this criterion *Cercopithecoides* is very distinctly a colobid (s. Verheyen, op.cit.; Graph 22).

The zygomatic bone is comparatively small and gives rise to a slender jugal arch, which does not show a marked lateral expansion, and which lies only slightly below the level of the infraorbital margin. Due to an increased height of the face, in most of the cercopithecids the jugal arch is more lowered in its position. The zygomatic process of the maxilla in the present skull is situated dorsally to the distal half of the second molar. In female skulls and in M.2999 it lies even more rostral, reflecting the shortness of the muzzle. The posterior root of the jugal arch is quite broad and strong, anteriorly forming a high and sharp infratemporal crest. The articular eminence is considerably thickened and slightly oblique, the medial part being more posterior; there is not much transverse concavity.

The lengths of the muzzle and the palate are identical in the present skull and in the type. Probably due to age differences, resulting in an increased growth of the alveolar processes, the height of the face is distinctly larger in the latter. Specimens M.2999 and M.3000 have a somewhat shorter muzzle, but the face height in the former is the same as in the type skull. The infraorbital area in all known skulls is characterized by a small but marked excavation; just below the orbits, the maxilla is pierced by three infraorbital foramina on each side. Otherwise, the maxillae do not show much relief; there is only a faint thickening above the roots of the canines, but no distinct maxillary crests and canine fossae are developed. The nasal bones are damaged distally, but they show an internasal suture and a broad outline, which features are also very typical for both *Cercopithecoides* and most of the Colobidae. Because of the shortness of the nasal bones, the nasal aperture is comparatively long.

A very significant feature of *Cercopithecoides williamsi* is the shortness of its premaxilla, which is wedged between the maxillae and hardly protrudes rostrally. The square outline of the muzzle in dorsal view is mainly due to this transversely cut anterior margin of the premaxilla, and this appearance is stressed by the large canines, causing a wide anterior breadth of the muzzle. The lateral wings of the premaxilla frame the nasal aperture right up to the short nasal bones.

The posterior margin of the hard palate is just at the same level as the distal ends of the last molars. This margin does not have a crest as in M.2999, nor are the posterior palatine foramina as slit-like as in this specimen. The incisive fossa is situated just behind the alveolae of the incisors. The breadth of the hard palate increases from 18 mm at the last molars to 26 mm at the first premolars. The tooth rows are also very close at M^3 (37 mm, measured between the lateral surfaces), then they diverge to a maximum breadth across the mesial half of M^2 (45 mm) and converge to about 41 mm across P^3 and C.

The angle between the palate and the pharyngeal base of the braincase is 126° in the present skull; in the type skull it is 124° and in M.2999 about 122°. This means that the declination of the palate in *Cercopithecoides williamsi* is distinctly larger than in both *Papio* (130°–170°; Frick 1960) and *Parapapio* (see below).

The alveolae of the incisors are very small and rounded, as is to be expected from the small teeth, known from other specimens. The lateral alveolae are slightly larger than the medial ones, which is in accordance with the tooth measurements in M.3000. The morphology of the premaxilla and the incisors is a strong argument for aligning *Cercopithecoides* with the Colobidae. The alveolae of the canines are large and show a triangular outline. The mesial margins have a small bony process, which must have fitted into the mesial groove of the male canines.

The premolars and molars are distinctly smaller than in the similar-sized *Parapapio antiquus* and *P. broomi,* but they resemble those of the smaller species, *Parapapio jonesi.* The molars are square, resulting in Breadth/Length-Indices of about 100. All molars have a reduced breadth across the distal pair of cusps. Tooth P^4 is distinctly larger than the very small P^3; M^1 is the smallest of the molars, whereas M^2 is both the longest and the broadest; but the reduction of the third molar is quite inconspicuous.

The molars exhibit many morphological features, which are typical for the Colobidae: lingually the mesial and the distal cusps are separated by broad V-shaped incisions, as already noticed by Freedman (1957). In the unworn teeth of the present specimen, the lingual cusps (protocone and hypocone)are higher than the buccal ones (paracone and metacone), which is just reverse in the Cercopithecidae. The lingual cusps, however, are worn down faster, resulting in the usual, medially inclined tooth surface of the cercopithecoids. The transverse crests are very high and sharp; in comparison with the Cercopithecidae, these crests in the colobids are conserved over a long span of the lifetime (Welsch, 1967). The mesial and distal foveae are not quite as developed in *Cercopithecoides* and other colobids as they are in many cercopithecids. The occlusal plane possesses a slight antero-posterior convexity in *Cercopithecoides,* a feature which is also more typical for colobids than for cercopithecids.

Conclusions: The new skull of *Cercopithecoides williamsi* most closely resembles the type specimen, which came from the same site. The differences in the shape of the braincase and in the height of the face are due to some distortion and to the greater age at death of the type specimen. The male skull M.2999 from the 'grey breccia' of Makapansgat is altogether more stout and robust, but it does not seem to be opportune at the moment to draw any taxonomic conclusions from these differences.

The present skull, being the most complete male specimen of its taxon, yields much new morphological information, especially on the brain-

case, including its base. The most conspicuous features are the deep mastoid notch, the pronounced klinorrhynchy of the base of the skull and the limited insertion area of the temporal muscle.

Unfortunately, there are not many male upper teeth available for comparison, but the teeth of the present specimen are distinctly larger than all known so far of *Cercopithecoides williamsi,* and, apart from the M^3, even exceed slightly those of the type skull of *C. molletti* (SK551) from Swartkrans. Freedman (1961) therefore was right when again dropping this latter species. The new skull from the Makapansgat Limeworks even renders doubtful the existence of a chronocline (beginning with the Sterkfontein specimens and ending with those from Swartkrans, the specimens from Makapansgat being intermediate), which was established by Freedman (1961) on lower tooth material alone.

Numerous morphological characteristics, of which the most important ones have been mentioned in the descriptive part, make it highly probable that *Cercopithecoides* was a member of the cercopithecoid family Colobidae. This was not always seen clearly in the past: Mollett (1947) discussed similarities of *Cercopithecoides* with *Theropithecus, Simopithecus* and also with *Cercopithecus* and *Macaca.* Robinson (1952) seems to have been the first to recognize the 'semnopithecine' affinities of this form, but Hopwood & Hollyfield (1954) still considered *Cercopithecoides* to be a synonym of *Macaca,* and Freedman (1957; p.246) concluded: "The exact affinities of this species to the living and other living cercopithecoids are not at present clear". In 1961 (p.32) he again stated: "Detailed comparisons with other living and fossil African forms (and possibly Asian types as well) will have to be made in an effort to elucidate the affinities of this genus". As a result of his detailed craniological studies on the smaller African Cercopithecoidea, Verheyen (1962) came to the conclusion, "que *Mesopithecus* et *Cercopithecoides* sont très probablement des représentants des Colobinae" (p.176). Especially valuable criteria for an understanding of the basic differences in the facial skeleton between Cercopithecidae and Colobidae were summarized by Vogel (1966). Although he did not consider *Cercopithecoides* directly, it becomes clear from his paper that this genus shares most of the significant features with the Colobidae. The classification of *Cercopithecoides* within the Colobidae, however, is far from being clear and needs further investigation.

The extant Colobidae are highly specialized arboreal leaf-eaters with complicated stomach adaptations (Kuhn 1964). Most of them have entirely reduced thumbs in adaptation to a semibrachiating locomotion. Therefore, there is a high probability that the fossil *Cercopithecoides williamsi* belonged to the same adaptation type as well, and that this genus consequently would be indicative of densely forested areas in the vicinity of the australopithecine caves. Possibly there existed a kind of tropical fringe forest along the rivers of the nearby valleys, which provided *Cercopithecoides* (and perhaps some of the smaller Cercopithecids like *Parapapio jonesi*) with its habitat.

B. Cercopithecidae

As among the living Cercopithecoidea of Africa, in the Pleistocene deposits of that continent the Cercopithecidae are more numerous and varied than the Colobidae. But whereas today only two genera with three species of Cercopithecidae exist in South Africa, there are so far known five fossil genera and thirteen species of this family. This striking difference in the composition of the Primate fauna, which is also to be observed in several other mammalian orders, probably indicates much more favourable ecological conditions during Pleistocene times. At Makapansgat there have been recovered so far three species of *Parapapio* and *Simopithecus darti,* all of which are represented in the following account. As in Sterkfontein, no true baboons of the genus *Papio* were found at Makapansgat.

(2) *Parapapio jonesi* BROOM, 1940

By tooth dimensions, this species is the smallest of the fossil Cercopithecidae of South Africa. Unfortunately so far only one fairly complete female skull (Sts 565; type) and a few very fragmentary remains of the male muzzle are known of this important species. Important, because it seems to have existed for a comparatively long period and to have been spread also in East Africa (Patterson 1968). It occurs in most of the more important Pleistocene deposits of South Africa, both in the older and in the younger ones.

Specimens M.3057, M.3058, M.3059 (Fig. 5; Tables III–IV)

The following three specimens most certainly belonged to the same animal, and are therefore discussed together. In connection with various postcranial elements (scapula, humerus, radius, etc.) they were found close together in the 'basal red' breccia. M.3057 consists of a small, nearly complete braincase, but the muzzle is broken off just underneath the orbits; no upper teeth are available therefore. M.3058 consists of both corpora of a small mandible, of which all teeth are preserved in very good condition. M_3 is not yet erupted and the second deciduous molars are still present. Judged by the morphology of the canines and the first premolars, which must have been just erupted, the present animal was a young female of about 4 to 5 years (Schultz 1933). M.3059 is a complete set of upper incisors, which lay together just between the braincase and the mandible; stuck into a premaxilla model of plasticene, they fit exactly on the front teeth of the mandible M.3058 (Fig. 5).

As mentioned above, there is only the female type skull known so far, where the braincase shows much damage. The present braincase exhibits much

morphological detail, but is is only a subadult animal with many features not yet fully developed.

The overall length of the present skull was roughly determined by fitting mandible and braincase together; the skull probably was slightly smaller than the type skull, which would be in accordance with the age difference of both specimens. For the same reason the bizygomatic breadth may be smaller in the new female skull. The length of the braincase exceeds that of the type skull, but in the latter the bone cover of the endocranial cast is missing in the occipital region. By the same method as mentioned above, the muzzle length could be roughly estimated at about 58 mm, which is expectedly shorter than in the adult type skull. Indeed, the preserved parts of the facial skeleton, i.e. the upper half of the orbital frame, look still very undeveloped and juvenile. There is, however, a distinct transverse groove behind the weak supraorbital tori and the well pronounced glabella. These features closely resemble those of the type specimen, but are quite unlike, for example, those of *Parapapio antiquus*. The vault of the calvaria rises distinctly above the orbital roof, and it is equally rounded both towards the occipital and towards the lateral sides. The frontal bone shows no sign of a metopic suture. The parietal bones are very extended, whereas the squamae of the temporal bones are rather small, but are in contact with the frontals in the pterion region. The supraoccipital squama reaches far up dorsally, forming a crest-like lambdoid suture with the parietals. The external occipital protuberance (identical with the inion) is well marked and lies about 15 mm below lambda. Both the external occipital crest and the two nuchal lines are only weakly developed. The temporal crests are very small and the temporal lines cannot be seen any more. The insertion area of the temporal muscle obviously was very restricted, however, and it probably did not reach farther backward than to the mastoids, which do not form any prominent processes. The zygomatic processes of the temporal bones are weak and give rise to low supramastoid and infratemporal crests.

Although the temporal fossae are shallow, the minimum interfrontal breadth is narrow in both known skulls. The maximum temporal and the bimastoid breadths are very similar in both specimens. The lateral walls of the calvaria being nearly vertical in female *Parapapio jonesi*, the temporal breadth even may exceed the mastoid breadth, as it does in the present skull. As the squama occipitalis is fairly steep, the occipital part of the braincase is not as lowered as in *Parapapio antiquus*. The external auditory meatus is rather short and it is separated from both the mastoid and the articular fossa by only shallow grooves. At the jugular and the carotid foramina the tympanic plate bends into an antero-posterior direction. The total length between meatus externus and petrous apex is 34 mm. The stout petrosal process is situated medial to the lateral plate of the pterygoid, whereas in *Cercopithecoides* it was just behind. The mandibular nerve pierces this lateral plate by two small foramina.

The foramen magnum and the occipital condyles are rather small in the new specimen, the condylar fossae are well excavated. The postglenoid process is 9 mm wide and 6 mm high, the articular fossa lies just at the same level as the external ear opening and the articular eminence is narrow and concave in transverse direction. Unlike extant baboons, in *Parapapio* this eminence is not very thickened and normally lies at a more dorsal level than the ear capsule.

The mandible, M.3058, is very slender and has an undeveloped sloping symphysial region. There is a mental foramen on each side of the chin, the symphysis itself is pierced by a symphyseal foramen, opening about 5 mm below the incisors. The incisal shelf is short and sloping, reaching backward to about the midst of the first premolars. On the right side the anterior part of the ascending ramus is preserved, showing that it must have been nearly vertical.

The medial incisors are considerably stronger than the lateral ones; both have longish foveae on their lingual aspects. The canines are hardly higher than the unworn incisors. The first premolars possess a comparatively long anterior enamel facet, indicating that the upper canines of female *Parapapio jonesi* are of considerable length, which is confirmed by the data of Freedman (1957). These first premolars show very conspicuous posterior foveae. The second deciduous molars are not yet replaced by the second premolars, but they are very worn. The first permanent molars show considerable wear as well, but the second molars seem to have been erupted not long before the death of this animal.

By the size of its molars, this specimen undoubtedly fits in the species *Parapapio jonesi*, the second molars, together with specimen M.215 from Makapansgat, so far being the smallest of this taxon. The incisors of the present mandible are comparatively large, the canines and first premolars matching the range of *P. jonesi*.

The medial pair of the upper incisors, M.3059, is remarkable for its large size and shovel-like form, whereas the lateral ones are less specialized. If they belong to the present female skull and mandible, which seems very likely, these incisors would indicate a considerable specialization of the frontal dentition in an otherwise quite small and primitive cercopithecid. This enlargement of the medial incisors, which is very significant for the African Papionini, thus would have to be dated back right to the Plio-Pleistocene boundary.

Specimens M.3060 and M.3061 (Figs. 6, 7 & 9; Tables II–IV)

These two specimens most probably also belong together. Both parts lay 5 cm apart from each other in a fine grained brownish breccia, with no other fossils nearby. Next to the mandible

M.3060 an isolated neck vertebra of a cercopithecid was found, (M. 3061 a), which most probably belonged to the same animal as well.

M.3060 is the lower and posterior part of a cercopithecid braincase and the most posterior piece of the right maxilla with M^3 preserved completely. The whole upper half of the braincase and nearly the whole facial skeleton are eroded or blasted away. The fossilized bone of this specimen has a much harder consistency than those found in the ordinary 'pink breccia' and, according to Mr. J. W. Kitching, this specimen could come from the lowest part of the 'Upper Phase I'. Due to their hardness, specimens M.3060 and M.3061 exhibit many morphological details.

M.3061 is a nearly complete and undistorted male mandible, with all teeth well preserved, except the incisors, the right canine and P_3. Both the skull fragment and the mandible seem to fit together exactly, and the last molars of the right side interlock very well. Therefore there are good reasons for assuming that both pieces belonged to the same large male skull of about 170 mm maximum length. The upper last molar of M.3060 lies at the lower border of the observed range of *Parapapio broomi* and slightly above that of *P. jonesi*; however, there are only two male M^3 known of the latter species, both coming from Sterkfontein. The lower teeth of the mandible M.3061 match, however, the range of *Parapapio jonesi*, M_2 and M_3 being shorter than any *P. broomi*. Considering the skull morphology of this and of the specimen M.3051, to be described below, as well, there are good arguments in favour of the present fossil being a big male of *Parapapio jonesi*.

The most interesting feature of the fragmentary braincase M.3060 is its steep and rounded occipital region and the horizontally orientated nuchal plane. Although this region is not known of males of *Parapapio broomi*, it can be gathered from the dorsally expanded calvaria of M.202, M.2961 and M.3065 that this taxon most probably possessed rather a high and pointed inion. The temporal lines of the present specimen meet about 25 mm above the inion under an angle of about 60°. The adjacent temporal crest remains very low, and both lines diverge again 10 mm above the inion, forming a small triangular inion-area, which is bounded occipitally by the low nuchal crest. This marked but low nuchal crest extends laterally into the supramastoid crest and into the posterior root of the zygomatic process of the temporal bone. The preserved zygomatic process of the right side is very strong in this specimen, and it forms a high and sharp infratemporal crest anteriorly. The jugal arch is of considerable strength and it has a height of 13 mm at its anterior end. The zygomatic process of the maxilla starts just behind the last molar, thus indicating a considerable protrusion of the muzzle and the tooth rows, which are also reflected by a 10 mm long alveolar process behind the teeth. The articular eminence is very broad (22 mm) and long, but it is not much elevated; the articular fossa is bound by a strikingly large postglenoid process (breadth 12 mm, height 9 mm) posteriorly.

On the nuchal plane, nearly all of the insertion marks of the neck muscles are clearly visible. Conspicuously deepened are the areas of the musculus rectus capitis posterior just in front of the inferior nuchal lines; consequently these lines and the external occipital crest are to be seen very clearly. The mastoids are not very prominent, but the mastoid notches are quite distinct and the mastoid processes are pointed. The axes of the two occipital condyles meet each other at an angle of about 100°; the whole condylar part is well elevated above the nuchal plane, the basioccipital and the condyles being at about the same level as the tooth rows. In front of the condyles the insertion areas of the longus capitis muscle form deep impressions. The spheno-occipital suture on the steeply ascending pharyngeal face of the base of the braincase is closed; the small part of the hard palate being preserved in the present specimen forms an angle of about 140° with the base of the braincase. The choanal region is laterally bounded by well developed pterygoid plates, the lateral of which is pierced by the mandibular nerve. The auditory capsule (overall length 40 mm) lies more oblique than in the female and is less bent in its middle part.

The completely preserved M^3 of the right side is very broad and conical in its mesial breadth, but shows considerable reduction across the distal cusps. This distal reduction is not as pronounced in the preserved distal half of M^2. Both teeth are considerably worn and exhibit a typical papionine pattern of the enamel loops and of the wear.

The ascending rami of the mandible M.3061 show a backward inclination of about 30°, and they are not very high. The chin region does not show much relief and rises only at an angle of about 50° against the lower border of the corpora. In their outline the corpora of the present specimen are very similiar to those of the mandible 122–66K, described from Kanapoi by Patterson (1968).

The symphysis is not very strong and thickened, with the incisal shelf being comparatively short (24 mm length, reaching backward towards the midst of P_3) and sloping. At the sides of the symphysis and the anterior part of the corpora there are no signs of any mandibular fossae. The oblique lines are very thick and show two well marked tubercles on the lower part of their anterior margin, probably indicating the main insertions of the tendons of the temporalis muscle. Consequently, there exist two very broad grooves behind the last lower molars.

The ascending rami show conspicuous triangular depressions below the coronoid processes, indicating strongly developed deep parts of the masseter muscle. The angle of the mandible is not very pronounced, but is slightly thickened and has

several tubercles at its medial aspect. The condyles are about 18 mm broad and 6 mm long; they are slightly notched at their posterior margin. Although the coronoid processes are slightly higher than the condyles, they are not very well developed and not directed backward; the mandibular notches are very shallow as a result.

All teeth of this specimen are considerably worn, showing that it was a middle-aged male. The dimensions of the first lower premolar fit into *Parapapio jonesi* rather than into *P. broomi.* The length of P_4 is intermediate between the means of these two species, but it does not show the broadening, which is very often to be observed in *Parapapio broomi.* M_1 again is intermediate in length, but in breadth falls nearly below the range of *P. broomi.* M_2 is below the observed length range of male *P. broomi* and matches the length and breadth dimensions of *P. jonesi* fairly well. The length of the systematically important M_3 lies distinctly (with one exception) below that of *P. broomi,* although this being the longest M_3 so far reported for *P. jonesi*; the same is true for the breadth measurements of this tooth.

To conclude, it seems highly probable that the present mandible M.3061 belonged to a comparatively large male of *Parapapio jonesi* rather than to *P. broomi,* but this question would seem to need further statistical testing. Consequently, also the skull fragment M.3060, most probably belonging to this mandible, would have to be referred to *P. jonesi,* and hence would be the first known male braincase of this species.

*Specimen M.3051** (Fig. 8; Tables II–IV)

This specimen consists of a nearly complete, but bilaterally crushed and distorted male skull, embedded in the 'basal red' breccia of the Makapansgat Limeworks. Although most of the upper parts of the skull are missing or dislocated, it provides a fairly good idea of the overall morphology.

The orbital and nasal skeleton is displaced about 40 mm from the maxilla, but the taxonomically important glabellar region is fairly well preserved on the right side. The roof of the calvaria is broken into pieces, most of which are missing; the occipital region, however, is available. The lower part of the muzzle, the jugal arch, the temporal fossae, the outer ear region and the mastoid of the left side, as well as the complete mandible are in situ. Also the occipital condyles and a few upper neck vertebrae are visible. The fossilization of whole corpses seems to be not uncommon in the 'basal red' breccia, and systematic excavations of these layers could provide the very necessary information on the postcranial skeletons of the South African Pleistocene cercopithecoids.

The present specimen, fortunately enough, has complete tooth sets with the exception of the upper incisors. Most of the teeth are, however, not in a position to allow accurate measurements of their breadth. Nevertheless, the size and morphology of the teeth suggest that the present specimen belongs to *Parapapio jonesi* as well, thus being by far the most complete male skull of this species.

The preserved parts of the supraorbital region show clearly that the present specimen is a typical *Parapapio* because the torus supraorbitalis and the glabella are hardly protruding, although they are of some strength. The nasal bone is not sloping steeply between the orbits and there is only a very shallow transverse groove behind the glabella.

The overall length of this specimen is strikingly large when compared with the small teeth, and it coincides fairly well with the estimated length of the specimen M.3060/3061. Although the muzzle must have been quite strong and elongated, it is still distinctly shorter than the braincase; but this is even true for the very elongated *Parapapio whitei* (see below).

The braincase is poorly preserved, mainly its occipital and basal parts being available. The parietals seem to have been of the short and rounded type as in specimen M.3060. They are sloping fairly steeply towards the inion, without forming a conspicuous sagittal crest. The nuchal crests, however, are quite strong, and both these and the temporal lines form a flat and triangular inion region, which lies at a comparatively low level. The nuchal plane is mostly crushed but it most probably had a more broad and rounded outline rather than an elongated and pointed one as in *Parapapio whitei.* Whereas the mastoid of the left side is quite flat, but again shows a distinct notch and process, the condylar part of the occipital bone probably was elevated, the left condyle being situated at the same level as the upper tooth rows. The articular fossa is separated from the auditory meatus by a very high and strong post-glenoid process (10 mm broad, 11 mm high). The anterior part of the jugal arch is of considerable breadth (11 mm) and its anterior root lies above the last molar. In most of these features the present skull exhibits many similarities to M.3060.

The zygomatic bone is strong, and its lateral margin rises at a steep angle, which is very different from that in the male *P. broomi* (M.202). The temporal crest of the frontal is deeply incised behind the orbits, this feature being similiar in the latter species. Together with the well rounded braincase and the comparatively high face, these characteristics would indicate a comparatively strong and steep postorbital part of the temporal muscle.

The left side of the maxilla shows a deep and large canine fossa, dorsally bounded by a sharp maxillary crest. On the right side parts of the muzzle dorsum are exposed, showing a flat area wrinkled with several grooves of the infraorbital nerves and bounded laterally again by a pronoun-

* Prof. P. V. Tobias kindly allowed me to describe this specimen, which is housed in the collection of the Anatomy Department of the Medical School, Johannesburg.

ced maxillary crest. The canine fossa results in exposed anterolateral roots of the first two molars. The premaxilla is partly preserved on the left side; it is much protruded and possesses large alveolae.

The mandible in this specimen is nearly exactly as long as in M.3061, but it has a comparatively higher and steeper ascending ramus. This being a younger male, however, the growing alveolae could have resulted in similar conditions as in the older M.3061. Again, the corpus is quite slender without showing canine fossae or crest formations at the chin region. The strength and shape of the symphysis seems to coincide with that of the mandible M.3061 and with that of Kanapoi. The channel behind the last molars is broad, excavated and laterally bounded by a strong oblique line. The coronoid processes are distinctly higher than the condyles of the mandible; both processes are separated by a shallow mandibular notch. The angle of the mandible is very pronounced in this specimen.

Unfortunately there does not exist much upper tooth material of *Parapapio jonesi* for comparative purposes. The upper canines are very high and slender in the present specimen and in this respect exceed all known canines of *Parapapio broomi*. The dimensions of the two upper premolars are all considerably below the mean values of both male and female *Parapapio broomi* and match very closely those of female *P. jonesi*; in three of these measurements, the values even fall outside the observed range of the males of *Parapapio broomi*. Although the molars of the present specimen are larger than most of the known teeth of *P. jonesi*, they are again distinctly below the mean values of *P. broomi* and below the observed range of the males of this species. The lower teeth of the specimen M.3051 compare very well with those in M.3061, which have been shown to be close to *Parapapio jonesi*.

Specimen M.2961 (see Freedman, 1961)

In 1961 Freedman described and depicted a fairly complete male skull from the 'grey breccia' of Makapansgat, which he referred to *Parapapio broomi*, although he observed numerous morphological differences with the other known skulls of this species. Examination of the new material of *Parapapio jonesi* led to the assumption that this specimen M.2961 could also belong to this species. Unfortunately there are only the last two molars of the right side preserved in this specimen, but in length they fall distinctly below the range of *Parapapio broomi* and are fairly close to the mean values of *P. jonesi*. In the breadths, however, there are more similarities with *P. broomi*. (see Table I)

Due to the lack of the front teeth, there cannot be taken any measurements of the tooth rows; however, the distance between the distal margin of the canine alveolus and the distal margin of M^3 is about 40 mm in M.2961 against 41.5 mm in M.3051, showing that not only the molars but also the premolars must have been very short in specimen M.2961.

TABLE I

		M.2961	$\bar{X}$ *P jonesi* males only	$\bar{X}$ *P broomi* males only
M^2	l	10,4	10,2	11,1
	mb	(12,5)	10,4	11,5
	db	(11,1)	9,6	10,8
M^3	l	(10,3)	10,3	11,2
	mb	11,5	10,9	11,4
	db	9,5	8,5	9,3

In the skull of M.2961 the contours of the braincase are rather different from those in *Parapapio broomi*: it does neither show the elevation just behind the glabella nor the depression thereafter, but it is well rounded all over. The temporal lines meet behind the bregma, but they do not seem to form any conspicuous sagittal crest. As Freedman pointed out already, the glabellar region is quite advanced in the present specimen, the interorbital width is greater and the nasals drop more steeply than in *P. broomi*. There is an internasal suture on the postero-superior 30 mm of the nasal bone. The maxillary crests are well developed, more than in the known specimens of both *Parapapio broomi* and *P. whitei*; they are short, however, and converge anteriorly. The infraorbital margin and the zygomatic bone are shifted forward, similar to the conditions in *P. broomi* (M.202). The canine fossae are shallow in their posterior part; this is different in M.3051, but there is some distortion in this area of the skull. In specimen M.2961, being older than both M.3051 and M.3060, some of the morphological differences may be attributed to age differences. To conclude, it seems probable that this specimen M.2961 is to be referred to *Parapapio jonesi* as well. Together, the three specimens, described here, could give for the first time a fairly complete picture of the male skull of this species; in Fig. 9 a combination of the known features is tried.

Conclusion: For the first time, more or less complete male skulls of *Parapapio jonesi* could be described. Although their teeth belong to the same size category as that of the female type, the size of the skulls is considerably larger, indicating a high degree of sexual dimorphism. The skull of this species does not exhibit, however, the elongated appearance of the males of *Parapapio broomi* and *P. whitei* (see below), but it is more stout and high; the braincase is more rounded and does not show exaggerated crests. The muzzle is comparatively short, but nevertheless possesses more pronounced maxillary crests and canine fossae than those two species.

Even the small female specimen M.3057/3059 has very large and specialized medial incisors; this character is very typical for the papionine Cercopithecidae of Africa, but it is not met with in the closely related Macacini of the Eurasiatic

region or in the African Theropithecini, living sympatric with the Papionini. Apparently, this distinct character evolved very early.

All of the presently described specimens of *Parapapio jonesi* were recovered from either the 'basal red' or the 'grey breccia' of the Makapansgat Limeworks. In the upper parts of this deposit, this species seems to be rare, at least. Nevertheless, this species of the genus *Parapapio* seems to have the widest distribution, both in space and time. As the Colobid *Cercopithecoides williamsi* it occurs in most of the South African deposits, perhaps suggesting a similar habitat for both forms.

(3) *Parapapio broomi* JONES 1937

This type species of the genus *Parapapio* is the best known of this taxon, both in tooth and in skull morphology. It is recorded from Sterkfontein, Makapansgat and Bolt's Farm. In the first two sites, this species seems to be the most abundant Cercopithecoid, and also of the present new material, most of the specimens are to be referred to *Parapapio broomi*. This species is found in the 'grey breccia' and in the 'Upper Phase I' (pink breccia) of Makapansgat Limeworks. In tooth size it is about intermediate between *Parapapio jonesi* and *P. whitei*. All of the new specimens, described here, come from the 'pink Cercopithecoid breccia'.

Specimen M.3056 (Tables II–III) is a fairly complete and undistorted skull, most probably of a female. Before fossilization, the whole occipital bone was broken off exactly along its sutures, both mastoids and auditory capsules being left. Possibly also the missing left jugal arch was lost before fossilization. The premaxilla and the most anterior parts of the maxillae, together with all of the front teeth were lost afterwards. This skull was split during preparation just underneath the orbits, resulting in a battered condition of the upper facial skeleton. The premolars are badly damaged on both sides, and of the molars only the right M^3 is complete. The shortness of the face and the considerable amount of wear of all of the teeth indicate that this was an old female.

Specimen M.3070 (Figs. 10 & 11; Tables II–III) consists of a nearly complete facial skeleton of a very old female. In addition, there are preserved parts of the base of the skull with the outlines of the foramen magnum. Even the premaxilla is fairly complete, but it must have lost its teeth before fossilization. There is a crack along the left maxilla, resulting in a slight distortion of that part of the muzzle and in the loss of the external frame of the left orbit. The whole calvaria is missing from 20 mm behind the glabella. The teeth of the left side are fairly complete, but the canine and the last molar are partly damaged; the last molar is the only complete tooth of the right side.

Specimen M.3082 (Table III) consists of the left half of a female muzzle, comprising premaxilla, maxilla and zygomatic bone. The incisors and the canine are lost, but the alveolar sockets are preserved; that of the canine is so small that it must have belonged to a female. The premolars and molars are complete and without much damage and wear. The remains of this young female *Parapapio broomi* were found a few inches apart from the skull M.3073 of *Simopithecus darti*.

Specimen M.3065 (Fig. 12; Table II) is a very large skull of a male cercopithecoid. It consists of the right half of the facial skeleton (without nasal and premaxillary bones) and of the upper parts of the braincase. Most of the left and basal parts are missing due to prefossilizational damage. The big right canine is partly preserved, but most teeth of the premolar and molar series are very fragmentary, with mostly only the roots left. M^1 exposes a small area of the occlusal surface which is very worn and indicates that this was a very old male. In overall size the present skull even seems to exceed slightly the new skull of a male *Parapapio whitei* (M.3072; see below), but the teeth seem to have been distinctly shorter than in this species. Further, it seems possible that this skull belonged to the very large mandible M.3067, found next to it, which clearly can be aligned with *P. broomi*. Therefore this specimen is tentatively referred to *Parapapio broomi* as well.

Specimen M.3067 (Fig. 13; Table IV) is an extremely long and strong male mandible, of which the right half is nearly complete, whereas on the left side there are preserved only the parts anterior to the first molar. There is some distortion in the symphysial region and, as a consequence, the incisors are missing. The corpus of this mandible is long and high, but it does not have any mandibular fossa; at its rostral end, the chin region slopes backward rising at an angle of about 45° against the lower margin of the corpus. There is only a slight crest formed below the canines, where the mental foramina open. The ascending ramus is inclined backward at about 40° from the vertical axis and it is very broad. The right condyle could be restored in its proper position, and it becomes evident that it does not lie much above the occlusal plane. The coronoid process is lost, and the anterior border of the ascending ramus is more rounded than in *Parapapio jonesi*. Its oblique line is separated by a channel of 10 mm breadth from the posterior alveolar process. Compared with the extraordinary maximum length of the mandible the tooth row appears to be rather small. The molars are very worn and have lost some length due to considerable wear between adjacent teeth. In most tooth measurements the teeth of this specimen are even below the mean values of *Parapapio broomi*, and in all cases fall outside the observed range of *P. whitei*. This striking disproportion coincides with those of the above skull, and a reconstruction (Fig. 14) shows convincingly that this male with the tooth size of a typical *P.*

broomi possessed an extremely elongated muzzle, exceeding even that of *P. whitei.*

Specimen M.3063 (Fig. 13; Table IV) consists mainly of the right half of a female mandible, which is fairly complete, with only the symphysial region and the tip of the coronoid process missing. The left corpus is present as well, but it is badly damaged and without teeth. The ascending ramus is moderately steep and high. The right tooth row is complete from C to M_3, the latter tooth just having been erupted. Some of the anterior teeth show minor damage.

Specimen M.3075 (Table IV) is also a half mandible of a young female, which is broken just at the symphysis, with the left half preserved. The corpus is fairly long and slender, the ascending ramus rising steeply with about 10° backward inclination. The coronoid process is lacking again. The first premolar and the first molar are badly damaged.

Morphological Discussion: The two new female specimens of *Parapapio broomi,* M.3056 and M.3070, together yield a fairly comprehensive picture of the whole skull, which is so far only known from Sterkfontein. The supraorbital arcs and the supraglabellar fossa are scarcely developed in both female skulls. The calvaria rises almost immediately behind the glabella, and it forms a well-rounded vault, dropping rather steeply towards the inion. The postorbital constriction is fairly narrow, but the temporal breadth in the female M.3056 nearly equals that of the male *Parapapio whitei.* The temporal lines probably do not meet medially in the females of this species. As far as can be seen, the nuchal planes lie rather horizontally and the mastoids are moderately developed in both specimens. Due to the considerable breadth of the braincase, the auditory meatus is quite long (in contradiction to Freedman's statement) and oblique. The postglenoid process is quite short in M.3056, and the articular fossa is very much deepened, its floor lying at the same level as the dorsal margin of the outer ear opening. The jugal arch appears to be short and of medium strength in both specimens; its anterior root, starting above the distal half of M^2, is situated much lower than the infraorbital margin.

The facial skeleton is especially well preserved in M.3070, where the muzzle appears to be quite slender and converging anteriorly. Whereas in this specimen the muzzle is more low and elongated, in M.3056 the face is more stout and high, although the missing parts render a comparison difficult. In this latter specimen there are, however, very faint maxillary crests and very shallow canine fossae, but there is still no flattening of the muzzle dorsum. In M.3070, there are only a few furrows of the infraorbital nerves, but otherwise the lateral surfaces of the muzzle slope down in virtually straight lines from the nasal to the alveoles, resulting in a triangular shape of the transverse section. Lateral to the 3 or 4 separate infraorbital foramina there are shallow infraorbital fossae. In both skulls the nasals have a distinct concave contour, especially evident in M.3070, where it is undamaged; here it also shows an internasal suture, but this could also be due to unnatural cracking. In this specimen the nasal aperture is short and ovoid in outline; it is framed by the lateral wings of the premaxillary bones which reach up to the antero-lateral margins of the nasal. The premaxilla is protruding and of rounded outline at its anterior margin. The orbits are comparatively large in both specimens.

The tooth rows are slightly convex laterally, the palate is narrower and deeper in M.3056 than in M.3070. Both specimens also differ considerably in their degree of declination of the palate, which is 43° in M.3056, but only 32° in M.3070. This angle is known, however, to vary very much in extant baboons (Frick, 1960). Although there are considerable age differences between these two specimens, their teeth compare fairly well; both show a reduction of breadth across the distal cusps of M^3. In both, P^4 and M^1 are short, compared with the average of the species, whereas M^3 is comparatively long, but does not fall outside the observed range. The lengths of the tooth rows of M.3070 closely match the averages for *Parapapio broomi.*

Specimen M.3065: There is one fairly complete male skull of *Parapapio broomi* from the 'grey breccia' of Makapansgat (M.202) for comparison. In the shape of the braincase, the glabellar region and the muzzle, there are numerous similarities with M.202, although the new skull seems distinctly more elongated and the whole tooth rows shifted more anteriorly. Altogether, the skull M.202 seems to be about 15 to 20 mm shorter than M.3065, and possibly the time difference between the deposition of the 'grey breccia' and the 'pink breccia' could be responsible for the increased size of the latter. The supraorbital region is hardly developed in this skull, nor is there a transverse groove behind the flattened glabella. Behind the glabella a well marked protuberance of the frontals is present, which was also noticed by Freedman (1957) in his specimens; it reaches its highest point about 35 mm posterior to the glabella. At the bregma the contour line is slightly depressed, then it rises again to form a sagittal crest. Both temporal lines meet 15 mm behind bregma and the starting bony crest seems to indicate that there existed a pronounced sagittal crest and a prominent inion, similar to those seen in M.3072 (see below). This elongated and bulb-like shape of the braincase seems to be very typical for both *Parapapio broomi* and *P. whitei,* but is not met with in the other two species of *Parapapio.*

The muzzle is very elongated in this specimen, but at the same time it is less high than in the equally sized *P. whitei.* The zygomatic bone is very broad and strong; together with the zygomatic

process of the maxilla, the infraorbital wall is shifted forward considerably. The tooth rows lie even more rostrally, so that the zygomatic process starts behind the last molar. Very different from *P. jonesi* and from *P. antiquus* is the absence of any true maxillary crest; as in *P. whitei* there is just a faint and rounded elevation at the exit of the infraorbital foramina, but no crest and canine fossa whatsoever. In this old male, the forward-growth of the alveolar processes (Scott, 1967) was very advanced, as is indicated by the great length of the postmolar alveolus.

Unfortunately there is much damage of the teeth, but their overall length can be determined fairly accurately. The length of the molars seems to fit well that of the males of the few so far described males of *P. whitei,* but as will be shown below, these specimens should mostly be referred to *P. broomi.* The large new male of *P. whitei* (M.3072), found in the same breccia, possesses considerably larger teeth. In addition, Fig. 14 shows that this skull fits well on to the mandible M.3067, which also shows more similarities with *P. broomi* than with *P. whitei.*

There can be no doubt, however, that both *P. broomi* and *P. whitei* are very closely related morphologically, and mainly differ in tooth size. At the moment, there is still a gap between the two size categories, which might well be closed, however, when additional material becomes known.

The mandibles of this species do not need any further discussion. Fig. 13 shows both a male (M.3067) and a female (M.3063) for comparison, with the female even possessing the larger teeth. The immense degree of sexual dimorphism, indicated by the skull material, becomes evident in the mandibles as well. Although hardly pronounced in tooth size, the females are only about 76% of the male skull in length. This observation is in contrast to Freedman's statement that it was less (84 .3%) in *Parapapio broomi* than in *Papio ursinus* (77.4%).

Conclusions: The majority of the specimens from the 'pink breccia' of the Makapansgat Limeworks is to be referred to *Parapapio broomi.* It seems to have been sympatric with *Cercopithecoides, Simopithecus* and *Parapapio whitei.* The presence of *P. jonesi* in this upper layer is doubtful, the best specimens of this taxon all coming from either the 'basal red' or the 'grey breccia'.

The female skulls, though fragmentary, yield a fairly complete picture of the skull morphology of this species, so far best known from Sterkfontein. Both specimens indicate that there was a considerable amount of variation in the shape of the muzzle. The first male skull of *Parapapio broomi* from the 'pink breccia' appears to be of very great length, even exceeding that of *P. whitei.* The orbital region is very unspecialized in this male and the muzzle shows an extreme elongation. As in *P. whitei* there are no distinct maxillary crests and canine fossae.

If this skull is rightly assigned to *P. broomi,* then there existed a considerable sexual dimorphism, the female skulls being only about three quarters as long as those of the males. Apart from the tooth size, *P. broomi* seems to be very similar to *P. whitei,* both being sympatric. However, it is more reasonable at the moment to assume that they were closely related species, which somehow fitted into different ecological niches. Additional material may well fill the gap between the two forms and reveal the existence of one highly variable species.

(4) Parapapio whitei BROOM 1940.

Up till 1957 *Parapapio whitei* was only known from Sterkfontein. In 1961, Freedman referred 6 specimens from Makapansgat to this species, and in 1965 the same author recorded this species from Bolt's Farm and from Taung. As is discussed below, a revision of this species seems to be very necessary, in the light of the new material.

Specimen M.3072. (Fig. 15; Tables II–IV)

This specimen consists of a large male skull with parts of the right mandible in situ. It came from the 'pink breccia' of the Makapansgat Limeworks. There is some damage, both pre- and post-fossilizational. The anterior part of the left jugal arch and the lower parts of the left maxilla and premaxilla together with the left teeth are missing; on the right side the entire jugal arch is broken off, but still indicate a steep and high parietal are removed as well; both supraorbital tori are damaged to some degree. But in general, the remaining parts are fairly complete and undistorted; the whole braincase, including its base, and the right side of the muzzle with all teeth of the right side are present. Of the mandible, the right ascending ramus is completely preserved, whereas the lower and anterior parts of the horizontal ramus are missing; all premolars and molars are complete (except P_3) and in excellent condition. After casting, the lower jaw was separated from the skull.

Specimen M.3062: This is a male mandible, the teeth of which are very large and fit the size of *Parapapio whitei* very well. The incisors and canines were lost before fossilization; the right P_3 most probably was lost afterwards, but it is present on the left side. Apart from the first molars, and the left premolars, the teeth are preserved in good condition; the moderate wear of the last molar indicates a middle-aged male. The posterior margin and the upper half of the ascending ramus are broken off, but still indicate a steep and high ramus, closely comparable with that of M.3072.

Morphological discussion: In 1957, Freedman had practically no male skull and upper teeth material of *Parapapio whitei* available, but there existed about 4 fairly complete mandibles. The molars of the females of this species were

distinguished by their enormous length which lay markedly above the size-range of both sexes of *Parapapio broomi*. In 1961, Freedman described a robust male muzzle from the grey breccia of Makapansgat (M.2962) and in 1965 a complete skull from Bolt's Farm (56785). Although both of these specimens had distinctly shorter teeth, this author referred them to *P. whitei*. Apart from some isolated teeth, only the new skull, however, matches the tooth dimensions of those females mentioned above. It seems improbable that the males had much smaller teeth than the females.

The present skull M.3072 is very much elongated; it resembles the skull M.3065, here referred to *P. broomi*, in many respects, but the face is higher in this specimen. Again, the supraorbital arcs and the glabella are very undeveloped and flat; there is no ophryonic groove whatsoever. Instead there is the same dorsal protuberance of the frontals and the adjacent depression at the bregma as described for *Parapapio broomi*. There is a low and small sagittal crest just behind the bregma. It is probable that the upper temporal lines, which cannot be identified, meet there. The real sagittal crest only starts 20–25 mm behind the bregma; it gradually rises to its maximum height of about 8 mm, which is reached at the external occipital protuberance. Together with the moderately developed nuchal crests there is formed a very pointed and prominent inion. The interfrontal constriction being narrow and the maximum temporal breadth being rather large, the braincase forms an elongated bulb, when seen in norma dorsalis. The length of the braincase nearly equals that of male *Papio ursinus*, the latter possessing only a thicker glabella. The morphology of the braincase of specimen 56785 (see Freedman, 1965; fig. 7) is entirely different from that of both the skulls of *P. broomi* and of *P. whitei*.

Although the muzzle is elongated considerably, it is only about 83% of the braincase length. The interorbital and nasal slope gently between the orbits and form a slightly concave contour. The nasion lies right up at the glabella; the nasal bones form a keel-like crest with a longitudinal suture running down to their rostral margin. Proximally it seems to be a true internasal suture, distally it looks more like a split due to transversal pressure. The orbits themselves are comparatively small, as is the whole upper facial skeleton; this is a very conspicuous difference with both the male skulls, described by Freedman, but it is very similar to the conditions in the males of *Parapapio broomi*. The infraorbital face wall and the strong zygomatic bone again slope anteriorly and laterally, and there is no indication of any canine or infraorbital fossae. The zygomatic process of the maxilla lies dorsally to the mesial half of M^3. The two faint maxillary ridges start at the openings of the 2 or 3 infraorbital foramina and end above the roots of the canines. These ridges cause shallow depressions lateral to the nasal bones.

In dorsal view, the posterior root of the jugal arch seems to be quite narrow, but the broad (22 mm) articular fossa reaches far medially at the underside of the skull; on the right side, a break-section exposes many air cells in the temporal bone lying above the articular area. The postglenoid process is smaller than in the males of *Parapapio jonesi*. The nuchal plane shows a distinct triangular outline, due to the prominent inion. The inion is at a distinctly higher level than in *P. jonesi*; thus the nuchal plane slopes more steeply in *P. whitei*. The foramen magnum is at about the same level as the alveolar border, and it is distinctly elevated above the nuchal plane. The mastoids are still separated by a suture from the occipital bone. They are not very prominent, but show marked processes and notches. As is to be expected in such an elongated skull type, the external auditory meati are long and run obliquely.

The sphenoccipital suture is still visible in this specimen, lying between the posterior margins of the pterygoid fossae. These are quite large and deep; the lateral plates of the pterygoids are of considerable size and height. The palate forms an angle of about 131° against the pharyngeal face of the base of the braincase, showing a considerable declination of 49°. The left alveolar processes are missing, but on the right side they are very steep and high (10 mm).

Of the incisors, the right mesial one is just split in half, but the lateral incisor is fairly complete. Both do not seem to have been very large. The upper canines are slender and not excessively long. The upper two premolars are of considerable size, and they fit the size of some specimens previously referred to *P. whitei*; they do not differ too much from *P. broomi*, but this species is remarkable for the size of its premolars. The length of the first molar by far exceeds those of *P. broomi*, and also for *P. whitei* it is the largest M^1 so far known. Its breadths are within the range of the larger females of this species.

Also the last two molars are only comparable in size with the largest females of *P. whitei*, *Parapapio broomi* and most of the other known skull material having much lower values.

The first premolar of the lower jaw is slightly longer than in males of *P. broomi*; also the second premolar is longer and broader, but matches the size of the previously known specimens of *P. whitei*. The first two lower molars again are enormously elongated and they are distinctly beyond the averages of the known *P. whitei*, not to mention *P. broomi*. The last molar of M.3062, however, is comparatively short for *P. whitei*, although being within the range of this species and being outside that of *P. broomi*. Against that, the M^3 of M.3062 is the largest molar so far recorded for the genus *Parapapio*, and is close to the means of *Papio ursinus*.

Although the mandibles of these two male *Parapapio whitei* are distinctly shorter and less robust than the male M.3067, above referred to *P.*

broomi, their tooth rows are much longer than in this specimen. This would support the view that *P. whitei* is not just a large sized *P. broomi,* but that it was actually a slightly smaller animal, possessing a higher degree of molar enlargement.

Conclusions: The present specimen M.3072 is especially valuable for its completeness and for the fact that both the upper and the lower dentitions are present. It is actually the first male specimen which fits the female type specimen (STS 563). It is slightly larger than this specimen, but that is to be expected of a large male. The skull morphology suggests close relationships with *Parapapio broomi,* which is quite distinct in tooth size, however.

All larger skull remains, referred to this species by Freedman, probably should better be replaced in the light of the new evidence. The large muzzle M.2962 compares fairly well with the large males of *Parapapio broomi,* both in structure and in tooth size. Specimen 56785 from Bolt's Farm is very aberrant in the whole shape of the braincase and of the facial skeleton; the robust build of the circumorbital region even shows some resemblance with the genus *Papio,* as does the outline of the calvaria. In tooth size, however, it matches *P. broomi.* As with the other faunal elements of Bolt's Farm it seems to be quite different from those of both Sterkfontein and Makapansgat.

(5). Simopithecus darti (BROOM & JENSEN) 1946.

This is the largest form of the Cercopithecoidea of Makapansgat, and it was described in 1946 by Broom & Jensen as *Papio darti.* It was only Freedman (1957) who recognised that this species should be aligned with the genus *Simopithecus,* at that time only known from East Africa. At Swartkrans, another, larger *Simopithecus* was found which was put in a new species, *Simopithecus danieli,* by Freedman (1957).

The type specimen (M.201) came from the 'pink breccia' of Makapansgat, but there is also material recorded from the 'grey breccia' of that site. All of the new specimens were found in the 'pink breccia' of the Upper Phase I.

So far only mandible and maxillary fragments, as well as isolated teeth, were known; the new material adds considerably to our knowledge of *Simopithecus darti.* The genus *Simopithecus* has been studied repeatedly within the last decade (Leakey & Whitworth, 1958; Jolly, 1964) and it became highly probable that this form is very similar to the extant *Theropithecus gelada,* and that both are very distinct from the true baboons. This led Jolly (1966) to establish a separate tribe Theropithecini for these two genera. The sister tribe would then be the Papionini, comprising the Mangabeys, Drills and Baboons. These classificatory problems have been discussed at some length by the present author (Maier, 1970).

Specimen M.3073 (Figs. 17–20; Tables II–IV) is the nearly complete skull of a young female, with the third molars not yet erupted. The mandible is in situ, but it is slightly distorted. There is some prefossilizational damage: parts of the right temporal squama with the zygomatic process are missing; the right zygomatic bone is somewhat displaced; the anterior tips of the premaxilla and the chin are damaged and the angle of the left mandible side is broken off. The skull itself is virtually undistorted and shows many new morphological details.

The present skull was associated with numerous postcranial bones which, judged by their size, probably belonged to the same specimen. Just beside the skull a right mandible of *Oreotragus major* and several skull fragments of *Parapapio broomi* (M.3082) were found. The significance of this first complete skull of *Simopithecus darti* is also discussed in a separate paper (Maier, in prep.).

Specimen M.3071 (Fig. 20; Table IV) is a nearly complete mandible of an immature male *Simopithecus.* The incisors are either damaged (right side) or missing (left side) and the canines are not fully erupted; the last molars are still in their crypts, but could be seen by X-ray. The chin shows some damage and the upper parts of the right ascending ramus were damaged before fossilization, whereas the ramus of the left side is complete.

Specimen M.3074 (Table IV) consists of a very fragmentary mandible of an old male of *Simopithecus.* Only parts of the symphysial region and the horizontal corpus of the right side are preserved. Most of the teeth have only their sockets and roots left, but nevertheless give a rough idea of the overall dimensions in an adult male for comparison with the young male M.3071.

Specimen M.3083 (Table III) consists of a fragmentary palate and maxilla with both tooth rows in situ. Only parts of the premaxilla are preserved, and that of the left side is displaced medially. All teeth are very worn and mostly damaged; the canines are large and tusk-like, indicating that the present specimen belonged to a very old male of *Simopithecus darti.* It is the first male palate which is known so far of this species.

Morphological discussion: The most striking difference between the skull of M.3073 and the skulls of *Parapapio* and *Papio* is their different proportioning. Whereas the latter show a marked elongation of the muzzles and braincases, the present specimen is distinguished by its increased height of the skull. The braincase is comparatively rounded, and it is much elevated above the lower facial skeleton and the tooth rows. The proportioning is well reflected by the steep and high ramus ascendens, both in the female and in the male mandible.

Both in tooth and in skull size *Simopithecus darti* is the largest Cercopithecoid from the Makapansgat Limeworks. Most probably, the body size of this species was close to that of the extant *Papio ursinus*; the same is true for the degree of sexual dimorphism.

The supraorbital torus is not very pronounced in this young female skull, but it is still more protruding than in the genus *Parapapio*. The transverse groove behind the torus is comparatively well developed, especially in its lateral parts. 10 mm behind the glabella, the vault of the calvaria rises quite steeply, but is more flattened in the area of the bregma. The parietal part of the calvaria is not sloping steeply, because the inion is situated at a high level. The supraoccipital bone and the lambda are reaching on to the dorsal aspect of the calvaria, the latter lying about 15 mm above the protuberantia externa.

The temporal crests are well pronounced on the anterior part of the frontal, but then become faint lines, which do not meet medially; their minimum distance amounts to about 15 mm. The nuchal crests are only pronounced above the mastoids. The posterior root of the jugal arch is broad and strong, as is the jugal arch itself. The nuchal plane is distinguished by its extreme shortness, which is also responsible for the rounded appearance of the whole braincase. The mastoids are comparatively well pronounced, showing a well-marked notch and process on the left side of the skull. The condylar part of the occipital bone is not as elevated as in some of the skulls of *Parapapio*; the foramen magnum is more or less rounded and of comparatively large size. The choanal and the palatal region is not prepared in the present skull in order to support the brittle bone of which it is made. The postglenoid process is about 9 mm high and the articular fossa and eminence are at the same level as the long auditory meatus. The articular eminence is broad (23 mm) and concave.

Whereas the braincase is not too different from that in many skulls of *Parapapio* (apart from the short occipital region), the muzzle shows more peculiarities. The weakly pronounced glabellar and nasal region drops very steeply between the orbits to give the muzzle dorsum a nearly vertical and concave outline. The nasal itself is long and narrow, without any trace of an internasal suture. The orbits are nearly round and, due to the comparatively weak circumorbital frame, the upper face appears to be quite narrow. This narrowness is underlined by the very high and broad zygomatic bones which give rise to the strong jugal arches. This infraorbital face-wall is nearly vertical, the zygomatic process of the maxilla lying dorsally to M^2. In adult females most probably these features would have been more clearly expressed because the posterior alveolar processes obviously are not yet fully developed in this immature specimen.

There are two faint maxillary ridges, originating at the largest of the infraorbital foramina (about 10 mm below the infraorbital margins), and converging towards the nasal aperture. These maxillary ridges also slope downward, and they are not of the *Papio* or *Parapapio*-type; they resemble much more the maxillary crests of the extant *Theropithecus gelada*. Below these ridges shallow, but well marked, canine fossae are developed. The premaxilla does not protrude much, but its lateral wings, framing the small nasal aperture, reach the lateral sides of the nasal bone. The muzzle breadth across the molars corresponds roughly to that of *Papio* and *Parapapio*, but across the canines and the premolars it is very narrow. The mandible of specimen M.3073 is distinguished by its high and narrow ramus ascendens. The corpus is comparatively narrow and slender; its height decreases anteriorly, and there seems to have existed only a small chin. The lateral surface of the corpus shows some depressions, which are not comparable with true mandibular fossae, however. Behind the second molars, the corpus is thickened due to the large third molar being in its crypt; the same feature is to be observed in the mandible M.3071. The ramus rises at nearly right angles, and it possesses triangular fossae of considerable size and depth. The coronoid process is higher than the condyle, and both are separated by a deeply incised sigmoid notch; the same is true for the male mandible M.3071. The condyle, which is only preserved on the left side, is quite massive, and it is more strongly developed at its medial side; its posterior aspect does not exhibit a deepening, which was observed by Leakey & Whitworth (1958) in several specimens of *Simopithecus oswaldi*. Both the male and the female mandible coincide in the shape of the mandibular condyles.

The teeth are not prepared properly in the skull M.3073, the tooth rows still being in occlusion. On the right side the surface of the molars could be cleaned and they exhibit a surface structure which is typical for the genus *Simopithecus*. The upper incisors are eroded on the left side as are the lower ones on the right; nevertheless the remaining incisors show that the upper medial one is broadened to some degree whereas the lateral incisor and both of the lower ones are quite small and unspecialized. In no case do they protrude as in the Papionini. The upper canines are quite well developed and they exceed the premolars by about 5 mm in height. The lower canines are less conspicuous; the mesial facet of the lower P_3 is of considerable length. The upper premolars are very small whereas the upper molars have a very large size, only encountered in *Simopithecus*, even exceeding that of *Papio ursinus*. The first molar is considerably worn, but the second one is only slightly abraded at its mesio-lingual cusp.

The second lower premolar is about the same size as that of the female *Papio ursinus*. The lower molars are again very elongated in M.3073 exceeding clearly even the males of the extant baboons.

The present specimen yields the first information about the female front teeth (incisors and canines). The upper premolars fit well the female teeth recorded by Freedman, but the first molar is larger than in his specimens. There exists no comparative female material of M^2; in M.3073 it is slightly smaller than in the known males, and it slightly exceeds M.2967 of unknown sex (Freedman, 1961). Inferrring from this specimen, we could expect the unerupted M^3 to be about 17,5 mm long.

In the P^4 there is very conspicuous sexual dimorphism; in the males it obviously is more than 9 mm long, whereas in the females it is only slightly above 8 mm. The specimens M.3027 and M.3035 (Freedman, 1961; Table 20) consequently should be referred to males. Both newly recorded specimens of *Simopithecus darti* show distinctly longer first lower molars than in the specimens recorded by Freedman. The female M.3073 possesses a very large M^2, being longer than any recorded specimen of *S. darti* both male and female. In both the lengths of M_1 and M_2 it is very close to the values recorded for *Simopithecus danieli* from Swartkrans which, however, shows a distinctly larger P_4. The same disproportion between upper premolars and molars seem to be distinctive for *Simopithecus darti* and *S. danieli* as well.

The two male mandibles M.3071 (immature) and M.3074 display interesting age differences. Whereas in the young specimen the chin region is very undeveloped (some parts are missing), the old male shows pronounced crests at the side of the very strong symphysis as is met with in the type mandible (Broom & Jensen, 1946). In the subadult animal, the anterior margin of the corpora is very sloping, whereas old males tend to develop vertical or even protruding chin formations. There is a kind of mandibular fossa in both M.3074, M.201 and M.621, but this is not yet developed in the young specimen.

The height of the ramus ascendens of specimen M.3071 is not as large as in the described female specimen, but the present male must have been distinctly younger. The high vertical ramus of the mandible seems to be very characteristic for the genus *Simopithecus,* although not many complete specimens are known so far. In the giant form *Simopithecus jonathani* from Olduvai Bed IV, this feature attained extreme dimensions (Leakey & Whitworth, 1958).

The incisors of the present mandible (M.3071) are heavily damaged, but they seem to have been high and narrow (the same was observed in the yet undescribed specimen M.3081 of the collection of the Anatomy Department in the University of the Witwatersrand). The just erupting canines and first premolars are very crowded, indicating that there must still take place considerable growth of the symphysial region of the mandible; the same conclusion is suggested by the undeveloped incisal shelf, and by the very large length difference of C–M_3 between M.3071 and M.3074, the latter comparing well with the type specimen.

Although being heavily damaged, specimen M.3083 yields valuable new information on the upper tooth row of the male *Simopithecus darti.* Whereas in the female M.3073 the upper tooth rows seem to converge anteriorly, the new male specimen shows a very square outline of the tooth arch. Both tooth rows run parallel, the breadth between the canines being very large. Although the premaxillae are damaged and distorted, it appears that they were not much protruded; on the left side, the premaxilla still shows the roots of the incisors, which seem to have been small and widely separated. This would underline the broad and square contours of the tooth arch, and make it very well comparable with the male specimens of *Simopithecus oswaldi,* published by Leakey (1943).

The teeth of this specimen being mostly damaged to some degree, they nevertheless provide some measurements of the upper tooth row of male *Simopithecus darti,* about which nothing was known so far. The length dimensions compare fairly well with those in large males of *Papio ursinus,* but the breadth of the tooth arch of *Simopithecus darti* is distinctly larger than in the chacma baboon.

Conclusions: The newly presented material of *Simopithecus darti* comprises the first complete skull of a female, the first fairly complete mandible of a young male and the first, though fragmentary, palate of an adult male. These specimens add considerably to our knowledge of the South African representatives of the genus *Simopithecus.*

Leakey & Whitworth (1958) pointed out that an elevated braincase and a lowered and short face are very typical for the East African forms of *Simopithecus.* The new skull from Makapansgat, although belonging to a subadult female, already shows this increase in the height of the face and the lowering of the tooth rows. This proportioning is reflected by the very high and steep ramus ascendens of the mandible, encountered both in the male and the female.

The functional meaning of the lowering, instead of the protruding, of the tooth rows most probably is the development of a so-called "high linkage" of the mandible. This "high linkage" is very typical for extremely herbivorous and graminivorous mammals; analogous adaptations, for example, are found in the robust form of the australopithecines. Possibly these adaptations of the masticatory apparatus and the peculiar structure of the molars are suggestive of grass-eating, and *Simopithecus* possibly was a dweller of open grassland (Jolly, 1970).

Already Andrews (1916), when he described the first *Simopithecus* from Kanjera, East Africa, saw the close structural connections between this fossil form and the extant *Theropithecus gelada.* This large cercopithecoid is restricted to the higher

levels of the North Ethiopian plateaux, and it is a highly terrestrial and graminivorous animal as well (Starck & Frick, 1958; Crook & Aldrich-Blake, 1968). The close relationship between *Simopithecus* and *Theropithecus* has been confirmed by various authors in recent years, the latter form being considered as the sole remnant of a widespread Pleistocene group of terrestrial cercopithecids.

The South African species of *Simopithecus* seems to be smaller and more primitive than most of the East African ones, belonging to the Lower and Middle Pleistocene. The very primitive structure of the supraorbital region would coincide with an old age for the Makapansgat form, the species of Swartkrans, *S. danieli,* being only slightly advanced. The specializations of the masticatory and tooth apparatus, however, are already highly developed in both *Simopithecus darti* and *S. danieli.* The muzzle shape of the new female skull shows more similarities with *Theropithecus gelada* than with the Middle Pleistocene *S. oswaldi.*

The new material exhibits very large sized molars, more or less fitting the range of the Swartkrans material. Possibly additional finds would close the gap between *Simopithecus darti* and *S. danieli.*

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TABLE II

SKULL MEASUREMENTS OF THE NEWLY DESCRIBED SPECIMENS FROM MAKAPANSGAT

	Cercopithecoides williamsi	*Parapapio jonesi*	*Parapapio jonesi*	*Parapapio jonesi*	*Parapapio broomi*	*Parapapio broomi*	*Parapapio broomi*	*Parapapio whitei*	*Simopithecus darti*
	male M.3055	female M.3057	male M.3060	male M.3051	female M.3056	female M.3070	male M.3065	male M.3072	female M.3073
Max. Length	146	(130)	(165)	(170)	(145)	(143)	(190)	185	161
Basal length	103	–	–	123	–	102	–	132	113
Bizygom. Br.	(98)	(80)	(110)	–	(95)	98	–	110	(105)
Basion-Bregma	62	63	–	–	–	–	–	66	67
Basion-Glabella	78	69	–	–	–	74	–	86	80
Min. Interfront	52	49	–	–	51	(50)	(52)	53	52
Max. Temporal Br.	73	70	74	–	76	–	(76)	77	80
Bimastoid Br.:	81	69	79	–	(77)	–	–	79	–
Inion-Glabella	104	93	–	–	96	–	(115)	115	107
Inion-Basion	49	44	52	55	–	–	–	58	49
For. magnum. Br.	17	14	18	–	–	18	–	17	20
Length	18	17	18	(18)	–	19	–	20	20
Muzzle height pM^3	–	–	–	–	54	–	(49)	61	–
anterior P^3	25	–	–	–	–	15	(27)	24	28
Muzzle Br. ant. M^3	44	–	–	–	51	52	–	–	50
ant. P^3	44	–	–	–	(37)	37	–	–	36
dorsal M^2	47	–	–	–	(38)	(37)	–	44	30
Nasion-Prosthion	66	(58)	–	–	(75)	72	(95)	95	87
Staphylion-Prosth.	57	–	–	68	(60)	61	(65)	78	–
Nasion-Rhinion	–	–	–	–	–	34	–	53	53
Interorbit. Br.	(19)	7	–	–	9	9	(10)	12	12
External Orbit. Br.	80	60	–	–	69	68	(72)	(75)	76
Orbit Height	26	22	–	–	24	23	25	23	26
Orbit Breadth	26	23	–	–	25	25	28	25	26
Nasal Apert Br.	17	–	–	–	–	16	–	20	17
Nasal Apert. L	(30)	–	–	–	–	25	–	36	(27)
Height alveole-Tori	63	–	–	–	64	57	69	71	78
Height alv.- infra orbital margin	34	–	–	(45)	38	33	43	47	50

TABLE III

MEASUREMENTS OF THE UPPER TEETH OF THE NEWLY DESCRIBED SPECIMENS.

				Cercopithecoides	*Parapapio jonesi*			*Parapapio broomi*			*Parapapio whitei*	*Simopithecus darti*	
	Upper teeth			M.3055 right	M.3055 left	female M.3059	male M.3051	M.3056	female M.3070	M.3082	male M.3065	male M.3072	female M.3073	male M.3083
I	1		l	4.7*	4,0*	7,5	–	–	–	–	–	–	8,7	–
			b	5,2*	4,6*	6,5	–	–	–	–	–	–	–	–
			h.	–	–	12,0	–	–	–	–	–	–	(10,5)	–
I	2		l	4,9*	5,0*	5,1*	–	–	–	–	–	–	6,0	–
			b	4,7*	4,5*	5,6	–	–	–	–	–	–	–	–
			h.	–	–	10.0	–	–	–	–	–	–	9,5	–
C			l	13,1*	13,2*		(10,2)	–	(6,5)	–	(12)	(12,0)	8,0	(14)
			b	10,2*	10,7*		(8,2)	–	(6,0)		(8,5)	–	–	12,0
			h	–	–		33,0	–	–		–	–	13,5	–
P	3		1(h)	6,2	(6,2)		7,3	–	–	7,8	–	8,0	(7,8)	–
			l	5,0	(5,2)		6,5	–	(5,5)	6,1	(7,0)	7,5	6,7	(7,0)
			b	6,7	(5,8)		7,1	–	(8,0)	7,9	–	8,4	–	(7,0)
P	4		l	5,7	5,8		6,2	6,0	5,8	6,7	(6,5)	7,0	(7,7)	(7,0)
			b	7,8	(7,1)		7,8	–	8,7	8,7	–	8,9	–	(9,5)
M	1		l	8,9	(9,3)		9,2	8,6	8,9	10,5	(9,5)	11,8	13,2	(10,0)
			mb	8,7	(9,1)	male	(9,2)	(8,5)	9,8	9,9	–	10,7	–	←
			db	8,5	8,5	M.3060	–	–	9,1	9,1	–	9,4	–	–
M	2		l	10,4	10,4	–	10,6	11,1	11,3	11,5	(11,5)	13,3	16,5	(15,0)
			mb	10,1	10,1	–	(11,5)	(11,1)	12,1	12,2	–	12,7	–	(14,0)
			db	8,5	8,5	10,9	–	–	10,5	10,5	–	11,1	–	
M	3		l	10,2	10,2	10,8	10,6	12,5	11,9	11,3	(12,0)	13,8	–	19,0
			mb	9,8	9,8	11,7	(10,5)	11,0	12,2	11,8	–	13,0	–	(14,0)
			db	8,3	8,1	9,2	8,5	8,9	9,2	9,4	–	10,3	–	(12,0)
P	4	–	M3	34,2	34,0		35,9	37,0	(37,0)	38,7	(39,5)	44,3	–	(55)
M	1	–	M3	28,9	29,2		30,3	31,5	(32,0)	33,0	(34,0)	38,0	–	(46,5)
C		–	M3	(50,9)	(50,9)		53,6	–	(49,0)	50,7	(57,0)	62,8	–	(76)

* Alveole measurements

() Values inaccurate due to damage or inaccessibility.

TABLE IV

MEASUREMENTS OF THE LOWER TEETH IN THE NEWLY RECORDED SPECIMENS

Lower Teeth			*Parapapio jonesi* female M.3057	male M.3061	male M.3051	*Parapapio broomi* male M.3067	female M.3063	M.3075	*Parapapio whitei* male M.3062	M.3072	*Simopithecus darti* male M.3071	M.3074	M.3081	female M.3073
I	1	l	5,6	–	5,0	–	–	–	–	–	(7,4)	–	6,9	5,5
		b	5,7	–	–	–	–	–	–	–	(7,0)	–	–	–
		h	10,0	–	8,5	–	–	–	–	–	(12,5)	–	6,0	8,0
I	2	l	(4,7)	–	5,1	–	–	–	–	–	(5,7)	–	6,4	5,0
		b	5,8	–	–	–	–	–	–	–	(7,0)	–	–	–
		h	8,5	–	9,5	–	–	–	–	-	(11,0)	–	5,5	7,5
C		l	4,7	6,7	(5,0)	6,9	(6,5)	–	–	–	(7,5)	(7,5)	(7)	(6,1)
		b	6,7	11,0	(9,5)	10,7	–	–	–	–	(11,0)	(12,5)	13,1	–
		h	(10,0)	17,5	22,0	22,0	12,0	–	–	–	(22,5)	–	(25)	10,5
P	3	1(h)	10,2	14,0	13,9	14,3	10,5	–	18,0	–	17,5	–	24	10,0
		b	4,3	4,6	–	(5,0)	5,9	–	–	6,0	7,3	–	(7,2)	–
P	4	l	7,5*	7,0	6,6	6,8	7,9	7,2	7,4	7,8	9,5	–	8,4	8,2
		mb	5,3											
		b db	5,5	6,3	(6,7)**	7,3	8,2	(8,5)	7,5	7,8	8,4	–	7,7	–
M	1		8,5	8,9	9,2	8,8	10,6	(9,8)	(10,0)	11,4	12,6	–	11,7	12,4
		mb	6,4	6,9	7,4	8,0	8,6	–	–	9,0	9,9	–	(10,5)	–
		db	6,5	7,4	(7,5)**	7,9	8,0	–	–	8,7	10,4	–	(9,8)	–
M	2		9,5	10,7	10,5	10,9	11,8	12,0	12,4	13,2	15,7	–	(13,9)	16,1
		mb	8,3	9,2	9,2	9,8	9,8	10,3	10,6	10,8	12,5	–	–	–
		db	7,9	9,4	9,2	9,3	9,0	–	9,9	10,4	11,6	–	–	–
M	3	1	–	13,7	13,7	15,4	14,4	14,9	17,5	16,1	(22,0)+	(23,5)	(19,8)	–
		mb	–	9,7	9,4	10,6	(9,6)	10,0	11,6	11,0	(13,3)+	–	–	–
		db	–	8,5	(8,0)**	8,8	8,1	8,5	10,0	9,4	(11,5)+	–	–	–
P	4–M3		–	39,9	(41,0)	41,7	44,2	44,0	47,0	48,5	(58,0)+	(60)	(54,6)	–
M	1–M3		–	33,0	(33,8)	35,3	36,5	(36,0)	40,0	40,7	(47,5)+	(51)	–	–
C –	M3		–	62,4	(64,3)	66,5	60,0	–	(68,0)	70,5	(77,5)+	(85)	(87)	–

* deciduous molar
** breadths could not be measured quite exactly
\+ measured from X-ray

TABLE V

Upper Teeth		UPPER TEETH: *Cercopithecoides williamsi* m. & f. n	x̄	*Parapapio jonesi* m n	x̄	*Parapapio jonesi* f n	x̄	*Parapapio broomi* m n	x̄	*Parapapio broomi* f n	x̄	*Parapio whitei* m n	x̄	*Parapio whitei* f n	x̄	LOWER TEETH: *P. jonesi* m. & f. n	x̄	*P. broomi* m. & f. n	x̄	*P. whitei* m. & f. n	x̄
P 3	1 (h)	3	6,0	1	4,3	5	5,4	7	8,0	10	6,6	2	7,7	4	7,4	–	–	–	–	–	–
	b	5	6,2	1	7,5	6	7,1	8	8,0	10	7,4	2	8,3	3	7,9	–	–	–	–	–	–
P 4	l	5	5,6	1	5,6	6	6,0	10	6,6	14	6,4	2	7,0	6	6,9	20	6,8	15	7,2	5	7,7
	b	5	8,0	1	7,7	5	7,7	11	8,9	12	8,4	2	9,2	6	8,7	22	6,7	13	7,1	5	7,1
M 1	l	10	8,5	2	8,3	6	8,7	9	9,9	14	9,6	2	10,0	6	10,7	20	8,6	15	9,3	7	9,7
	mb	4	9,2	1	9,0	5	8,8	9	9,8	12	9,5	2	10,1	5	10,5	17	7,5	12	8,2	5	8,5
	db	3	8,5	1	8,6	5	8,0	6	9,0	10	8,8	–	–	5	9,8	15	7,6	13	8,2	5	8,8
M 2	l	10	9,7	2	10,2	4	10,3	10	11,1	17	11,1	3	12,0	6	12,7	19	10,4	15	11,4	6	12,6
	mb	7	9,9	1	10,4	2	10,5	7	11,5	12	11,1	2	12,3	6	12,4	19	9,3	13	10,1	5	10,6
	db	6	9,1	1	9,6	2	8,9	9	10,8	13	10,1	2	11,0	6	11,4	18	9,0	13	9,7	5	10,5
M 3	l	11	9.6	2	10.3	3	9,6	8	11,2	12	11,0	2	11,7	2	13,3	13	12,7	16	14,7	6	16,4
	mb	7	9,7	2	10,9	3	9,8	8	11,4	11	10,7	3	11,9	1	12,8	11	9,3	11	10,2	5	11,1
	db	5	8,1	2	8,5	3	7,9	7	9,3	10	8,8	2	9,4	1	11,0	12	8,4	14	9,3	5	10,3
P 4 –	M 3	9	31,8	1	32,5	3	33,3	7	37,7	7	36,3	2	39,2	2	39,6	11	37,8	11	41,9	4	45,7
C –	M 3					1	43,1	2	56,0	3	48,6			1	51,7						

Mean values of the known upper and lower teeth of South African Ceropithecoids, mainly according to Freedman. These figures serve for comparison of the newly presented material.



Fig. 1 *Cercopithecoides williamsi* M.3055 seen from the right side. Scale in cm.

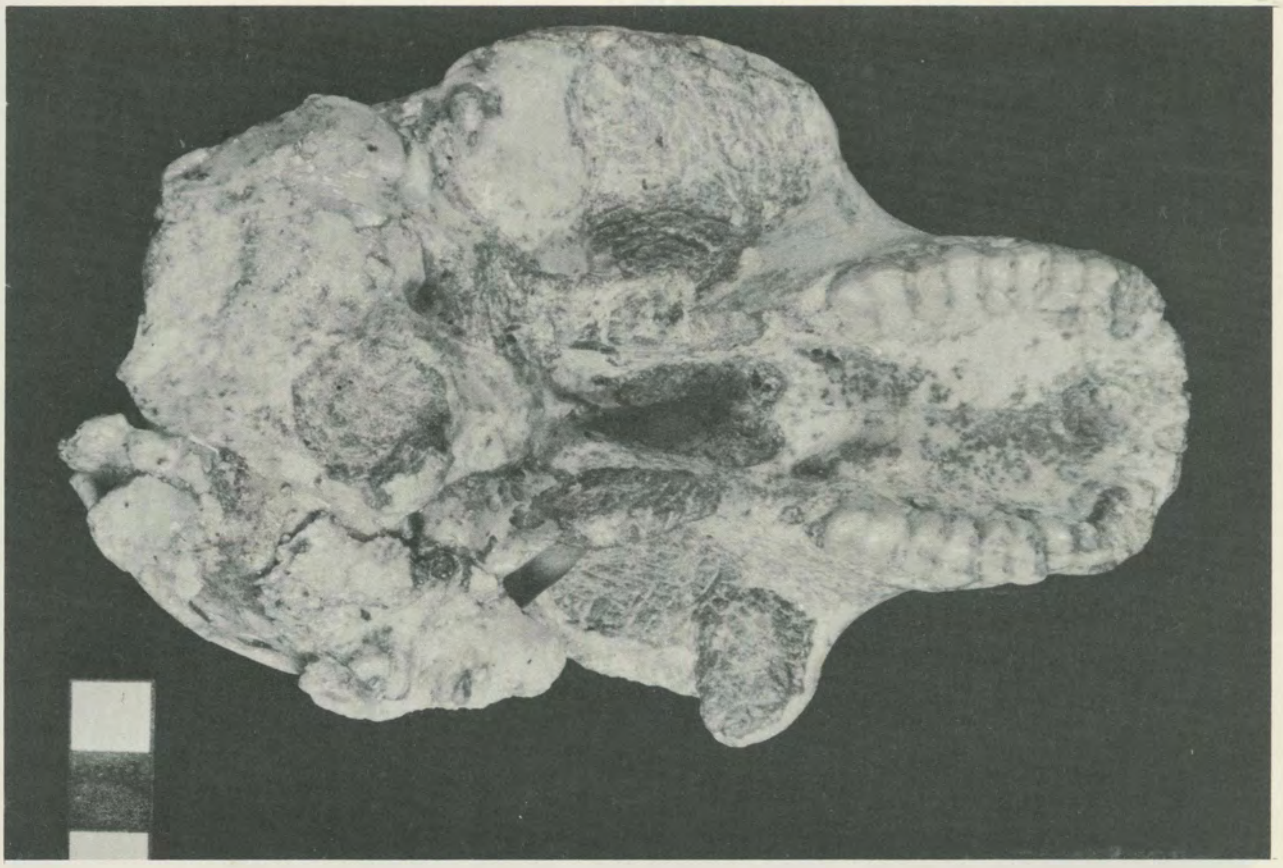


Fig. 2 Basal view of *Cercopithecoides williamsi* M.3055. Note the divergent tooth rows. Scale in cm.



Fig. 3



Fig. 4

Fig. 3 *Cercopithecoides williamsi* M.3055 seen in norma dorsalis. The skull is orientated on the occlusal plane. Scale in cm.

Fig. 4 *Cercopithecoides williamsi* M.3055 seen in norma frontalis. Scale in cm.

Fig. 5 Lower jaw (M.3058) and upper incisors (M.3059) of a young female of *Parapapio jonesi*. Their position is reconstructed. Note the specialized medial incisors. Scale in cm.

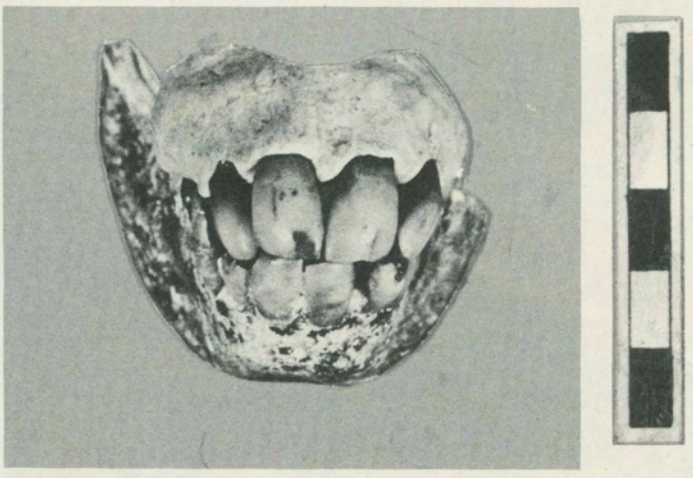


Fig. 5

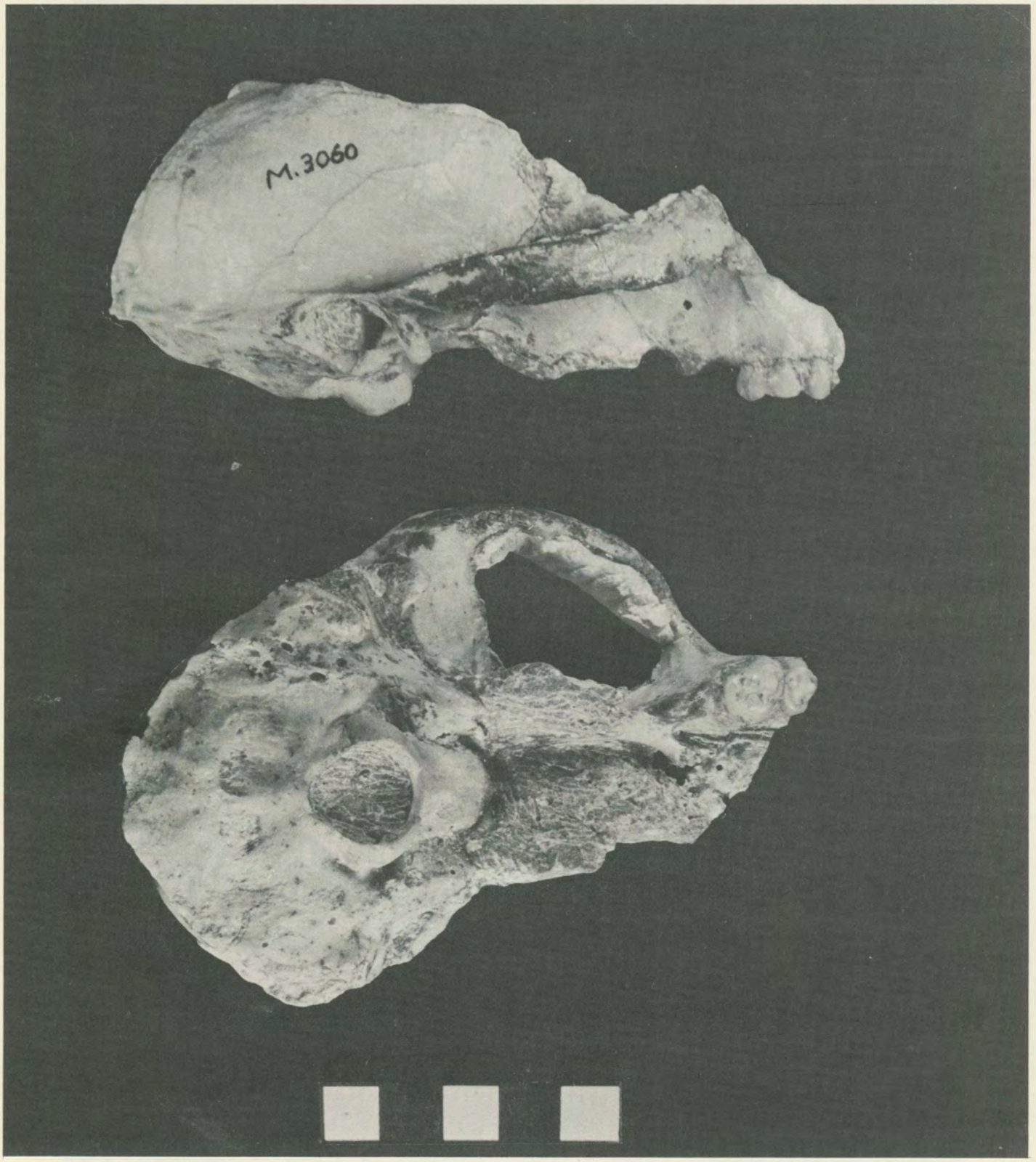


Fig. 6 Specimen M.3060 seen from below and from the right side. Scale in cm.

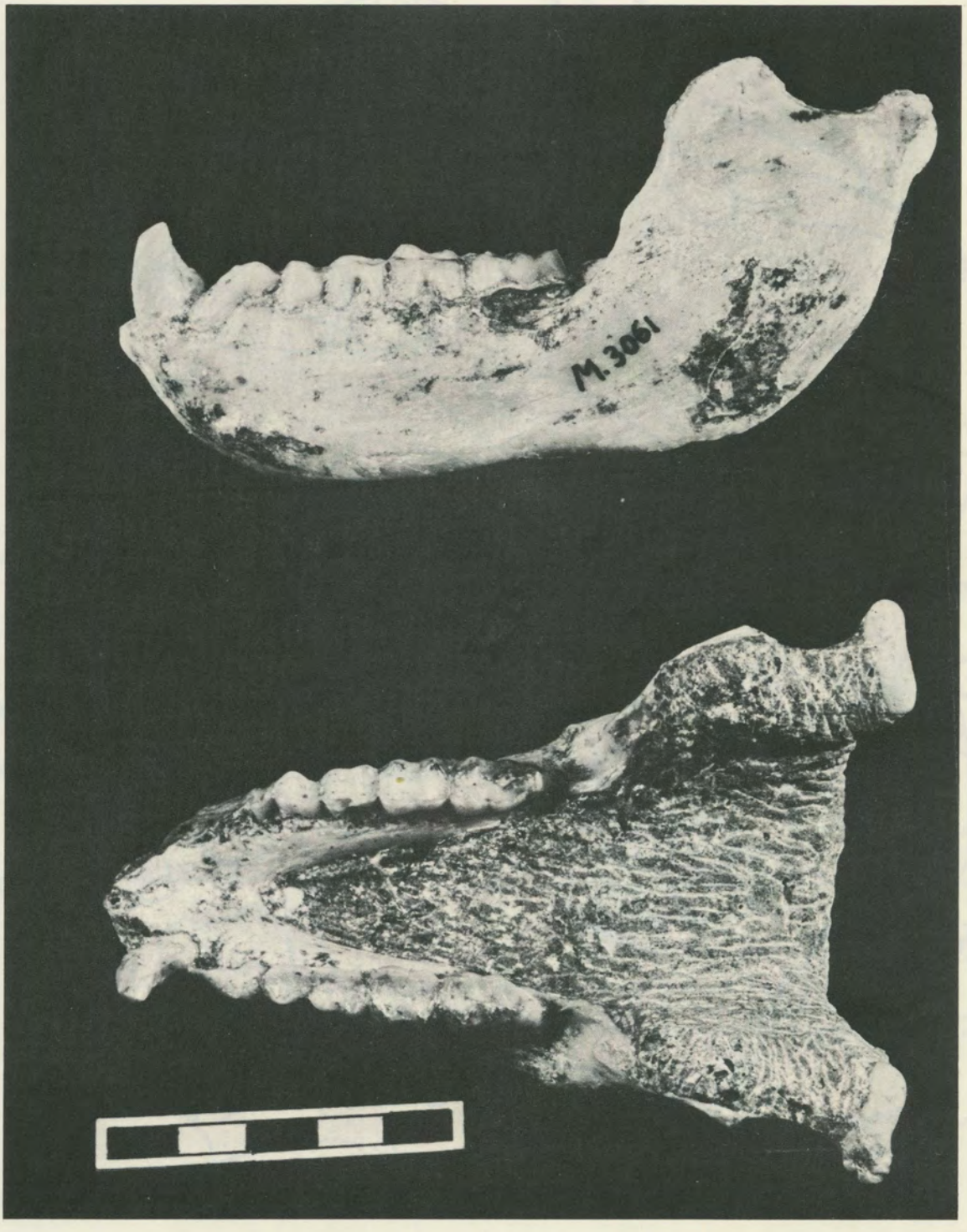


Fig. 7 Specimen M.3061 (*Parapapio jonesi*) from the left side and in occlusal view. Scale in cm.

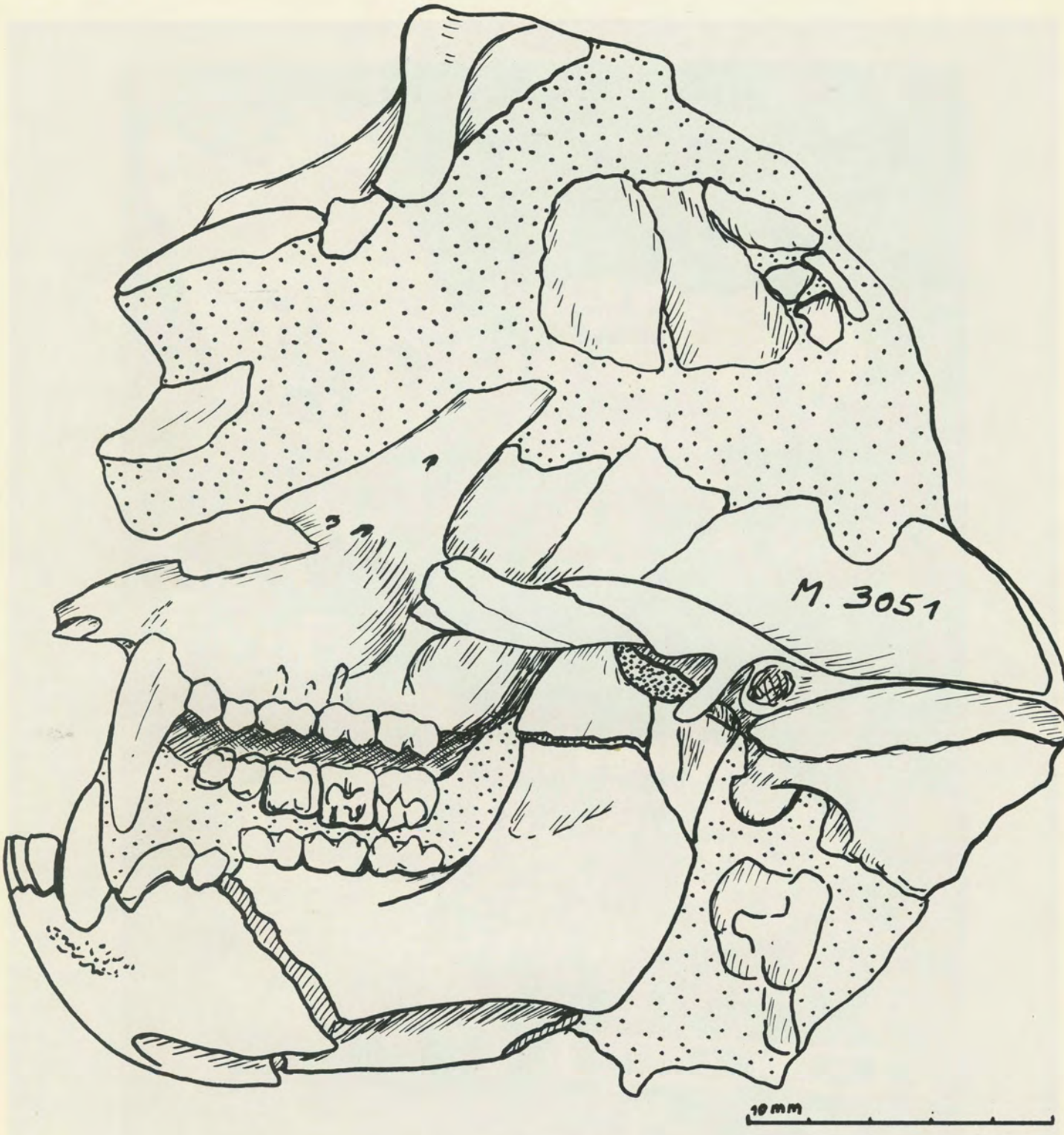


Fig. 8 Male skull of *Parapapio jonesi* (M.3051) from the 'basal red' of the Makapansgat Limeworks. The skull is bilaterally crushed and the upper parts of the skull are displaced.

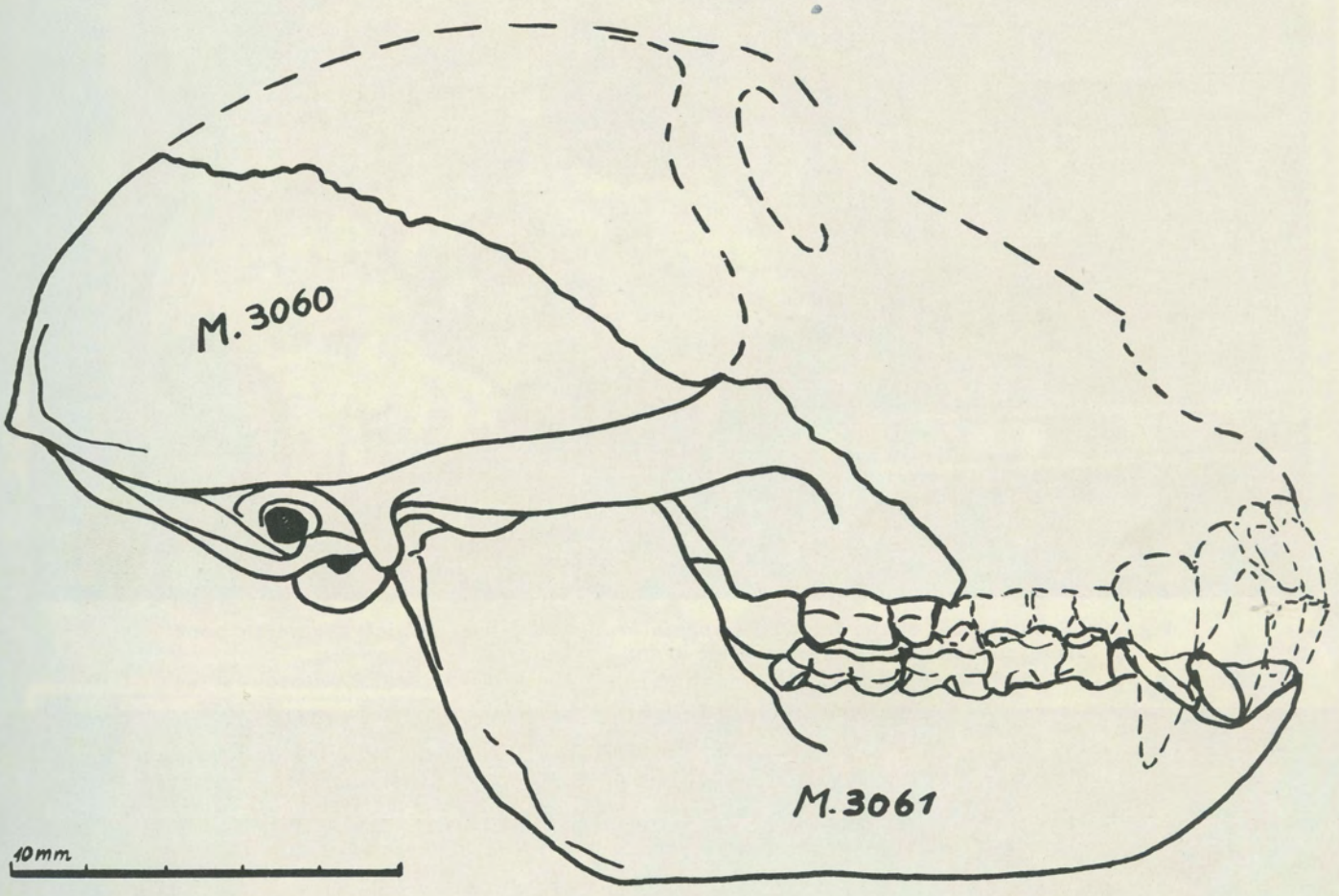


Fig. 9 Reconstruction of the male skull of *Parapapio jonesi* based on the knowledge of several fragmentary specimens. The solid line shows the specimens M.3060 and M.3061, which most probably belong together; the dashed lines are based on the specimens M.2961 and M.3051.



Fig. 10 Frontal view of the female *Parapapio broomi* M.3070. The left zygomatic bone is retouched in dashed lines. Scale in cm.

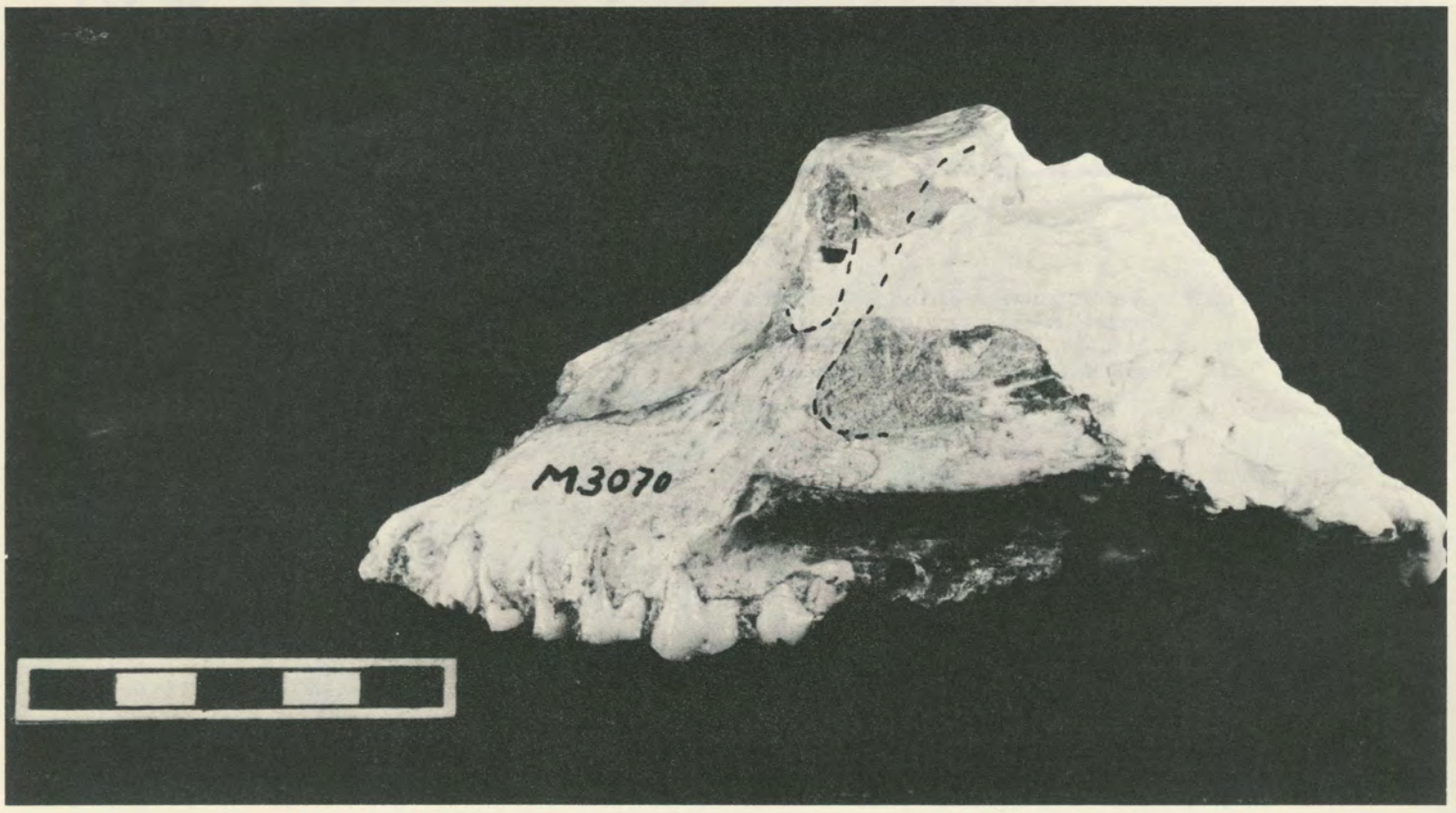


Fig. 11 Lateral view of the female *Parapapio broomi* M.3070. Scale in cm.

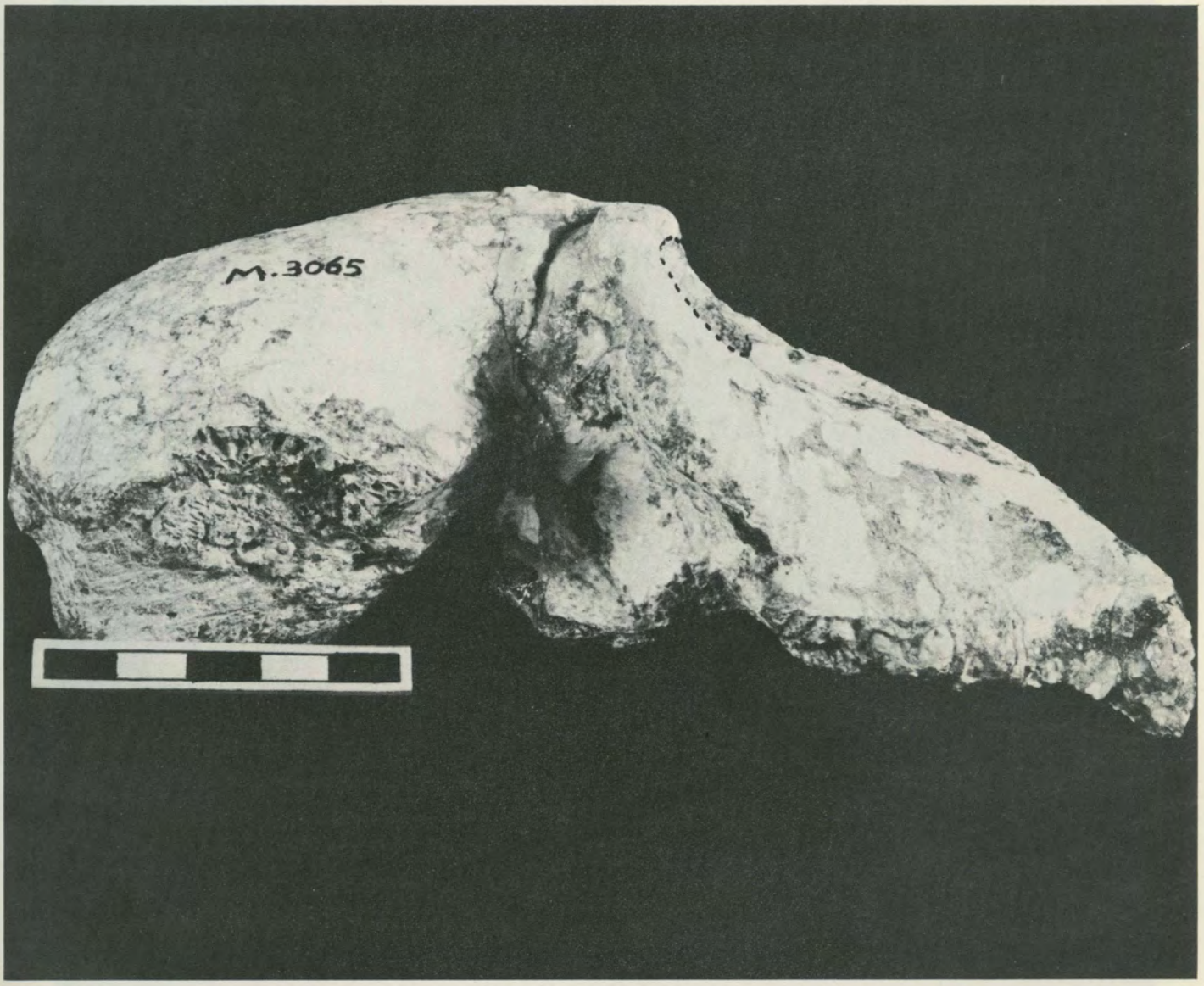


Fig. 12 Lateral view of the incomplete male skull of *Parapapio broomi* M.3065. The posterior and lower parts of the braincase are missing. Scale in cm.

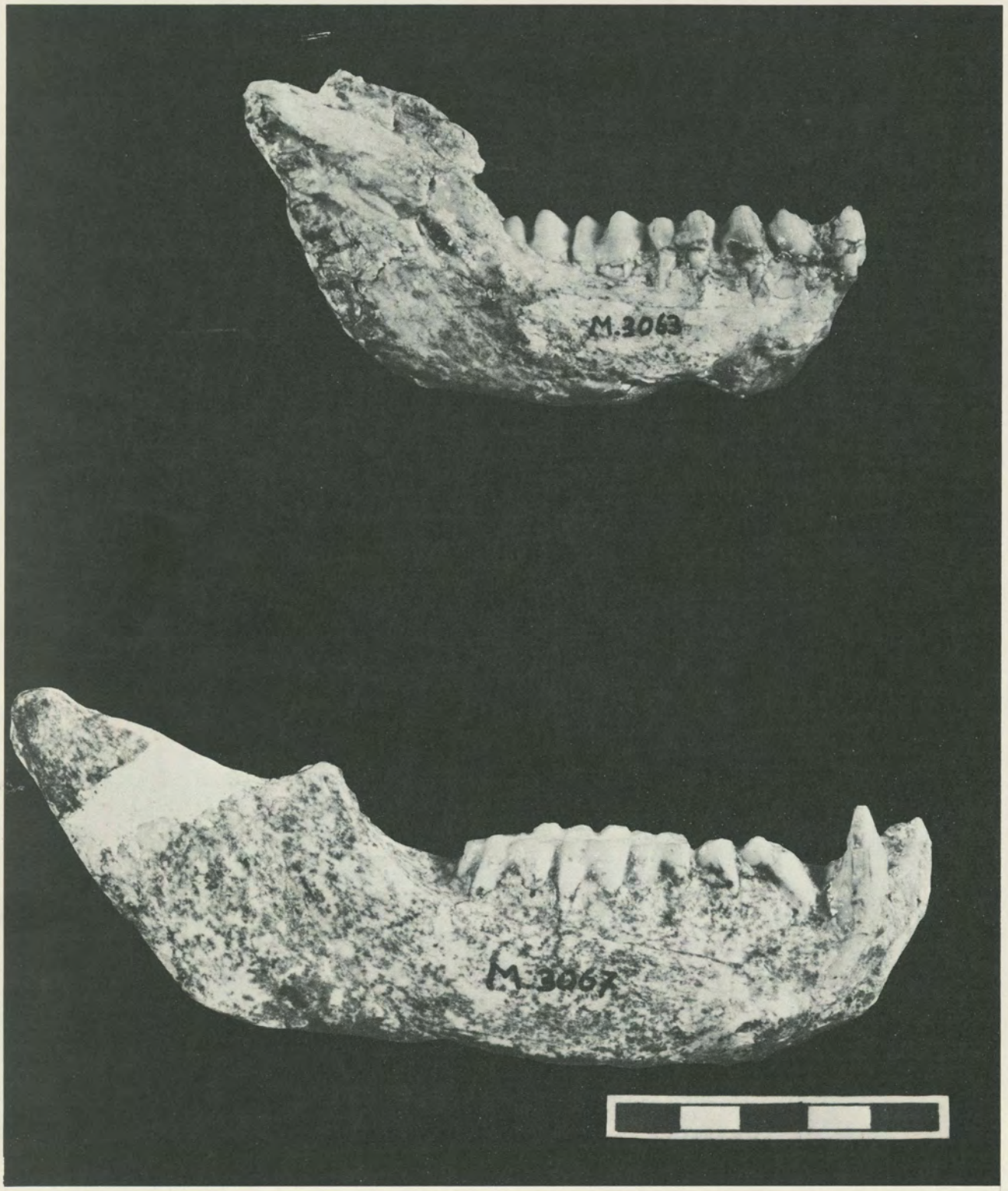


Fig. 13 Male (M.3067) and female (M.3063) mandibles of *Parapapio broomi*. The teeth of the female are even slightly larger than in the male. For both the scale is in cm.

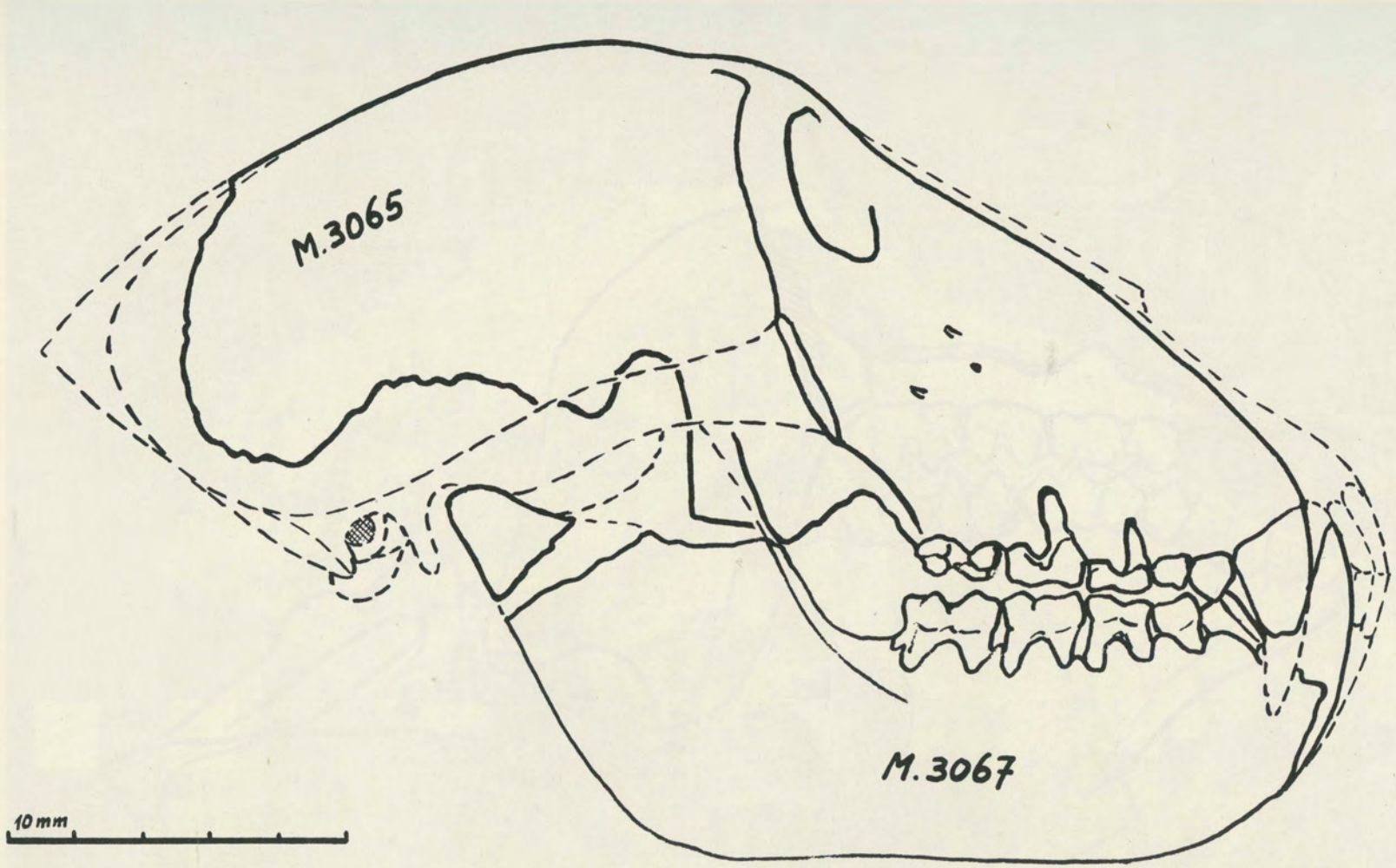


Fig. 14 Reconstruction of the male skull of *Parapapio broomi*. The figure is based on the two specimens M.3065 and M.3067, which most probably belonged to the same animal. The reconstructed parts (dashed lines) are based upon specimen M.3072.

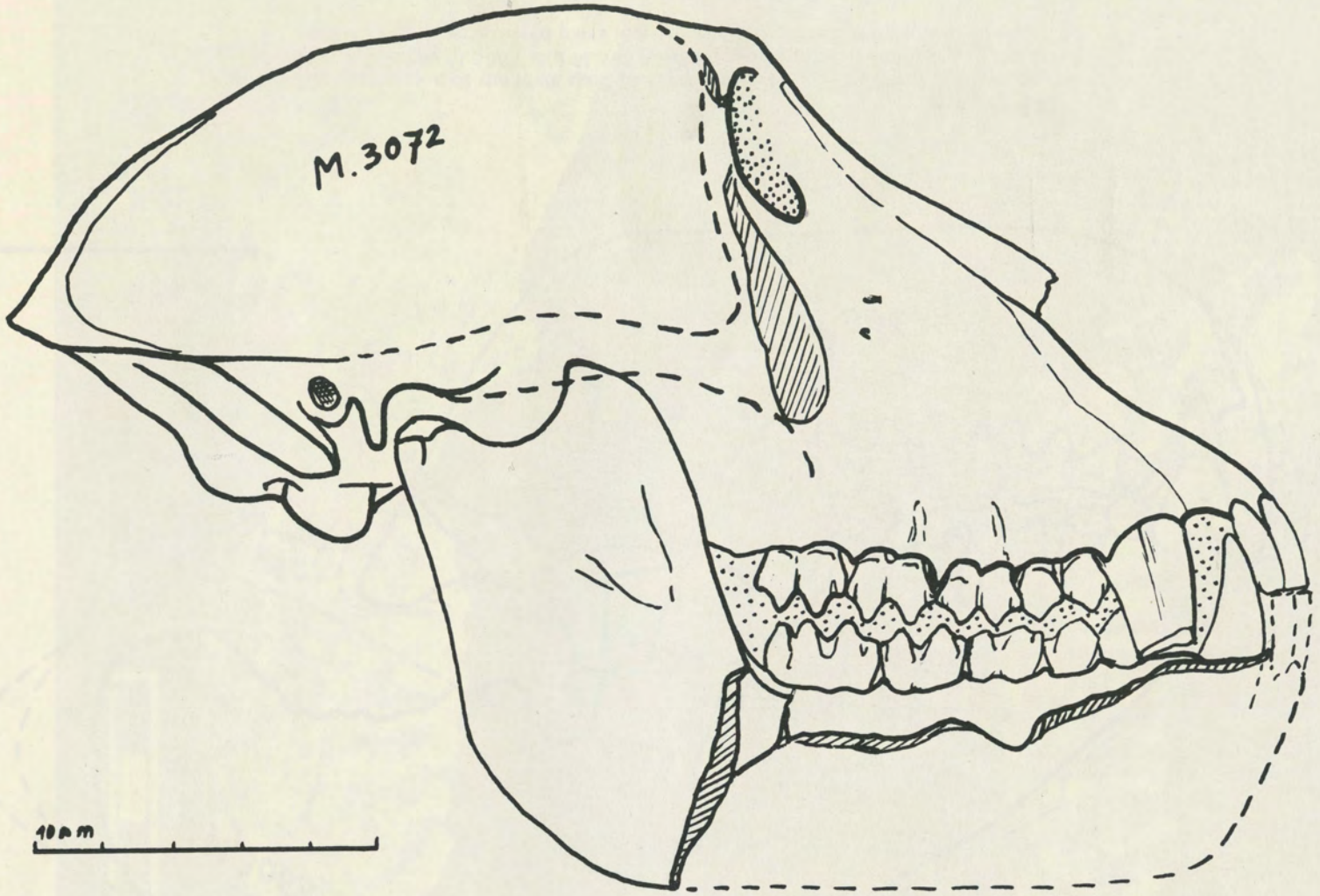


Fig. 15 Male skull of *Parapapio whitei* (M.3072). The solid line shows the preserved parts with the mandible in its original position; the dashed lines are reconstructed. As all of the line drawings, this one is based on a pantograph.

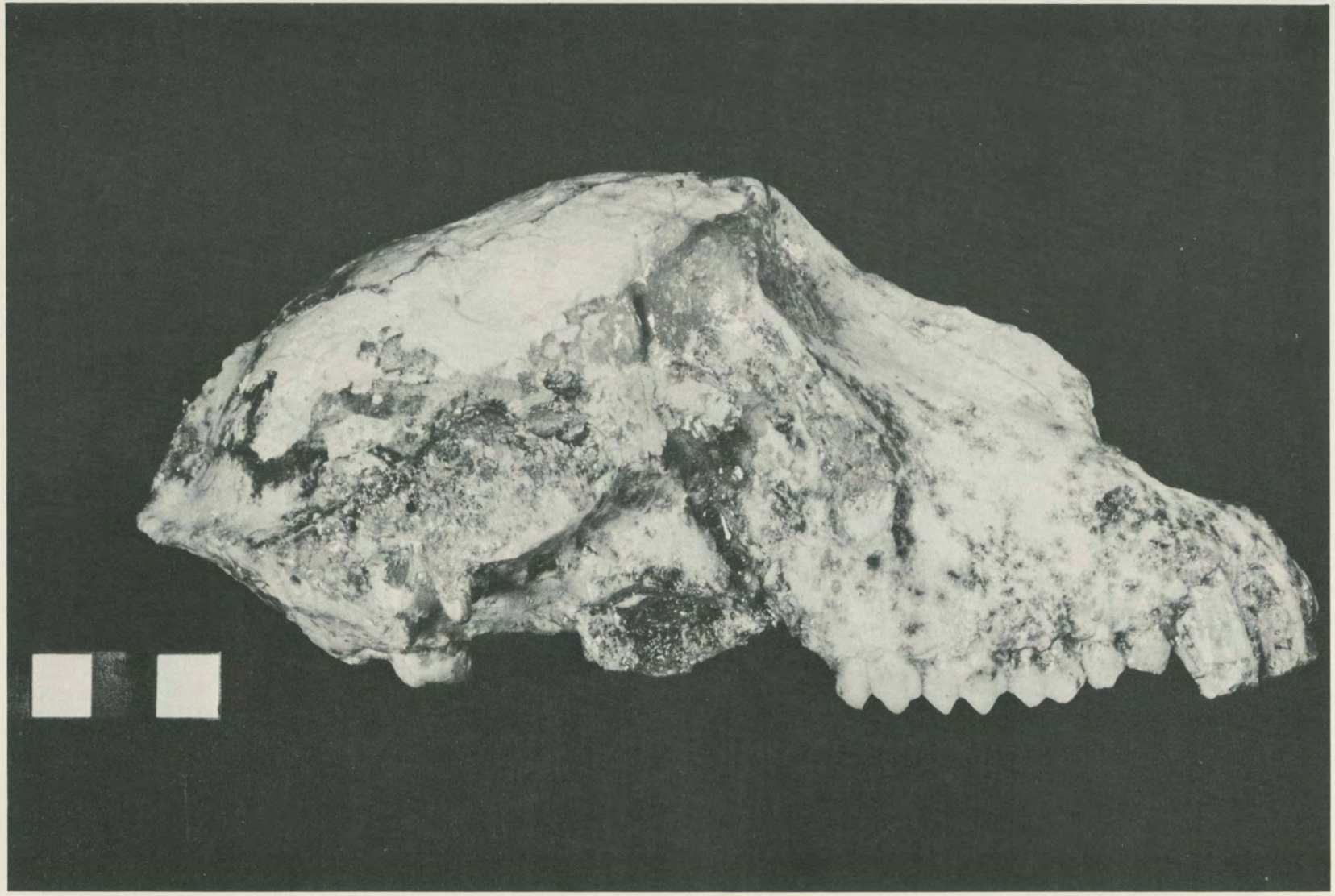


Fig. 16 Male skull M.3072 of *Parapapio whitei* after removal of the mandible. Scale in cm.



Fig. 17 Lateral view of the female skull M.3073 of *Simopithecus darti*. Scale in cm.

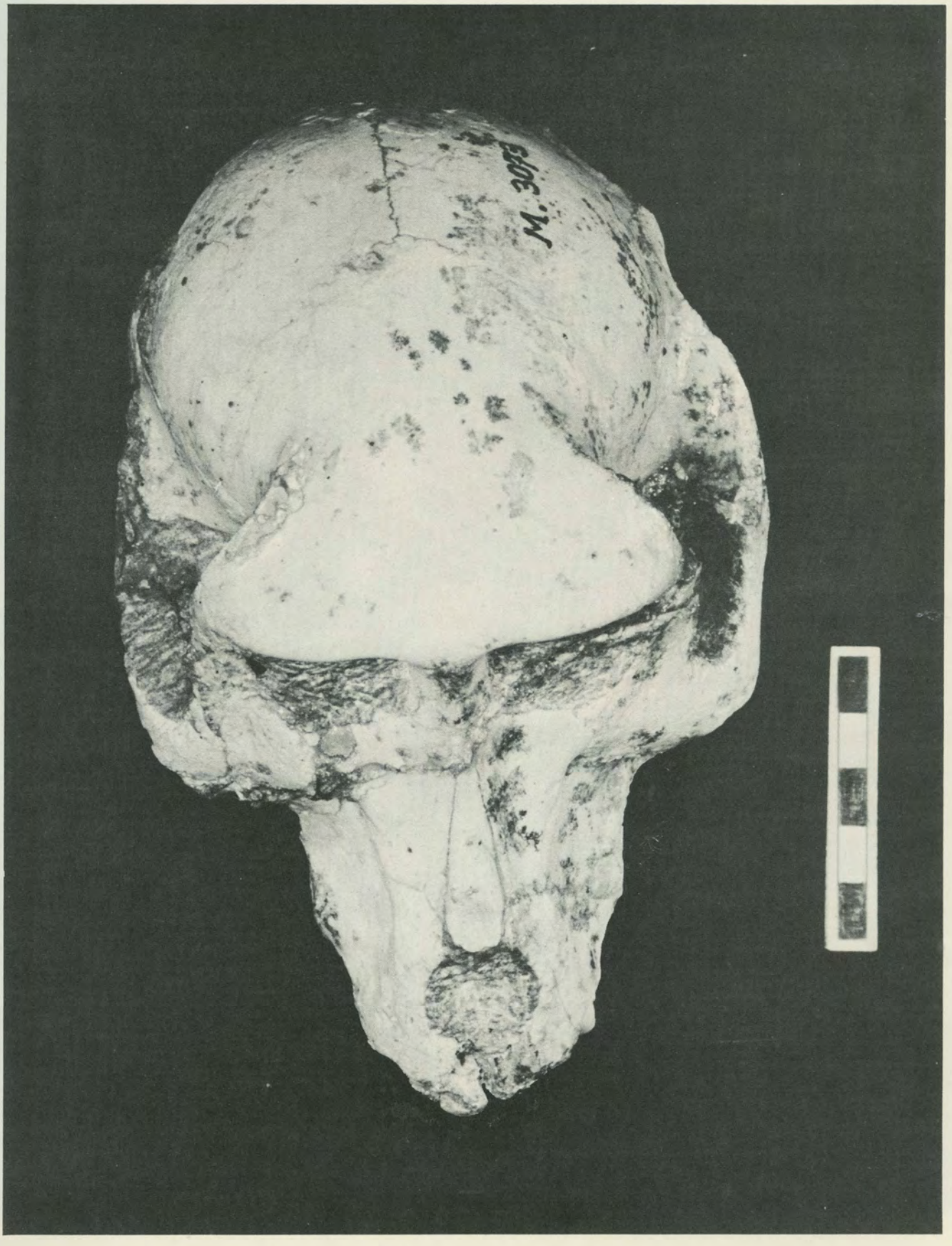


Fig. 18 Antero-dorsal view of the female skull M.3073 of *Simopithecus darti*. Scale in cm.



Fig. 19 Frontal view of the female skull M.3073 of *Simopithecus darti*. Note the slight distortion of the mandible and the comparatively broad medial incisors. Scale in cm.

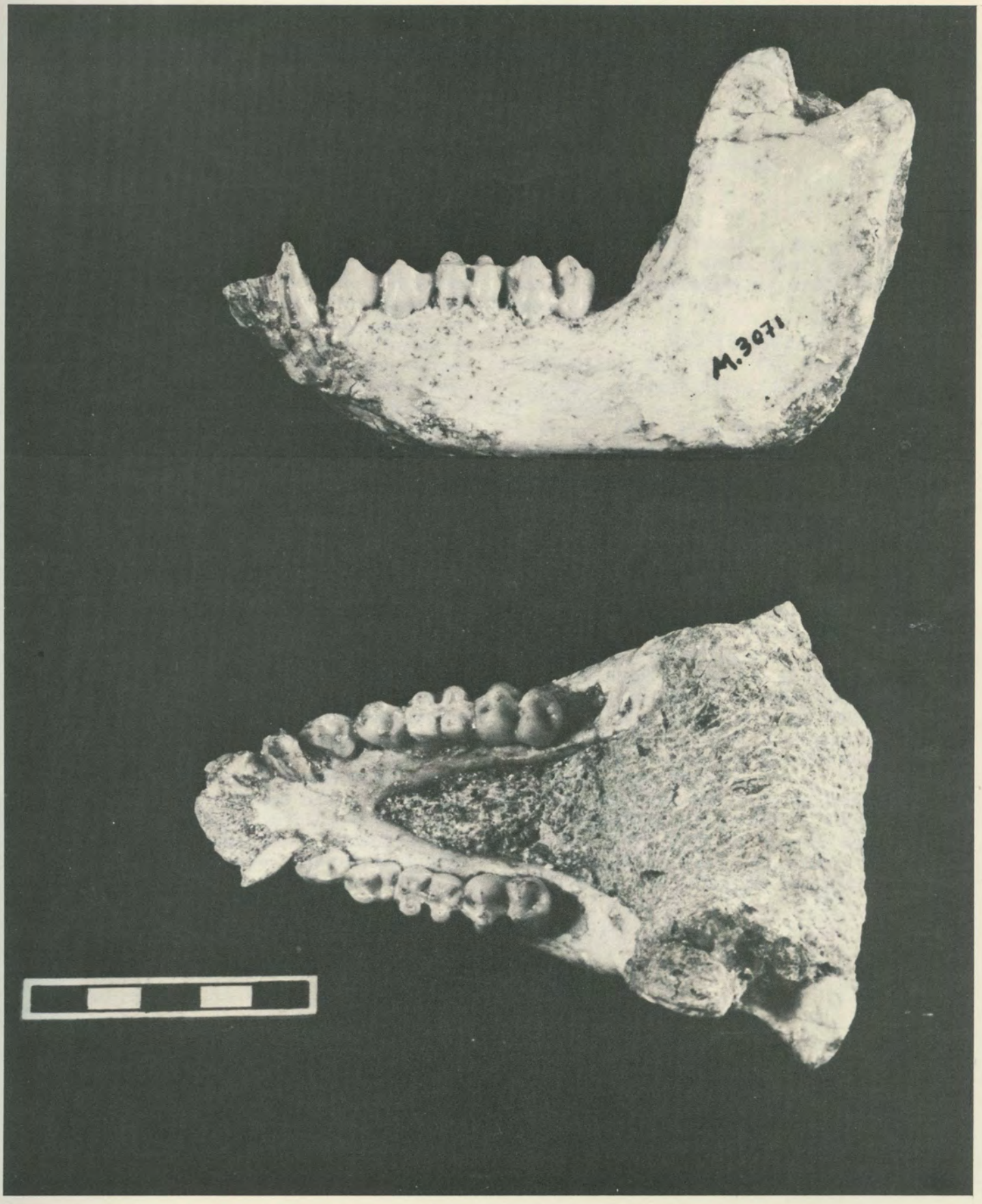


Fig. 20 Lateral and occlusal view of the male mandible M.3071 of *Simopithecus darti*. Note the height of the ascending ramus and the morphology of the molars. Scale in cm.

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A NEW CHECK-LIST OF FOSSIL CERCOPITHECOIDEA OF SOUTH AFRICA

by

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During 1970, the opportunity was afforded me to spend several weeks in South Africa, studying and identifying the cercopithecoid fossils which have been found recently. The new specimens have been recovered, in the main, by Professor P. V. Tobias and Mr. A. R. Hughes at Sterkfontein, and by Dr. C. K. Brain at Swartkrans and Kromdraai; in addition, further specimens have been developed from the Makapansgat breccia at the Bernard Price Institute for Palaeontological Research.

At the request of Professor Tobias, I have compiled a new check-list of the fossil Cercopithecoidea from South African Pleistocene deposits. This list is a revision of the check list published in my monograph of 1957. It is based upon all the papers I am aware of, which have been published since then, as well as the results of my recent visit. The data for the Kromdraai Ape-man Site are tentative: Dr. Brain and I should finish a revision of them soon. We are likewise reviewing the *"Parapapio" coronatus* material and will probably re-assign the specimens to known taxa. The papers in the press by Dr. W. Maier, including that in this issue of *Palaeontologia Africana,* may necessitate one or two revisions.

I should like to thank Professor P. V. Tobias for proposing my visit to South Africa and for the facilities I enjoyed in the Department of Anatomy, University of the Witwatersrand, Johannesburg; and Dr. C. K. Brain for the facilities he kindly made available at the Transvaal Museum, Pretoria. My 1970 visit to South Africa was generously made possible by Grant No. 2402 from the Wenner-Gren Foundation for Anthropological Research.

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SOUTH AFRICAN CERCOPITHECOID FOSSILS BY LOCALTIES

	Taung	Sterkfontein	Makapansgat (limeworks)	Swartkrans	Kromdraai (faunal site)	Kromdraai (ape-man site)	Cooper's	Swartkrans II	Graveyard	Gladysvale	Minnaar's Cave	Bolt's Farm	Skurweberg	Saldanha	'Pretoria'
Parapapio antiquus	X														
P. jonesi	X	X	X	X	X										
P. broomi		X	X									X			
P. whitei	X	X	X									X			
Papio izodi	X														
P. robinsoni				X	X	X	X	X		X		X	X		
P. angusticeps					X	X	X				X				
P. wellsi	X														
P. spelaeus															X
Simopithecus darti			X												
S. danieli				X											
S. hopefieldensis														X	
Dinopithecus ingens				X									X		
Gorgopithecus major					X										
Cercopithecoides williamsi	X	X	X	X		X	X	X	X			X			

Note: Besides the species listed in the above table, Wells (1943) mentions *P. ursinus* from the Wonderwerk Cave, Kuruman, and Peabody (1954) lists "*Papio* (and related baboon genera)" from the *Australopithecus* Cave (lower and upper levels), Black Earth Cave (lower and upper levels,) Witkrans Cave (lower and upper levels) and Iscor—all sites on the Kaap Escarpment. The latter author also lists "? *Cercopithecus* (monkey)" from the upper level of the Black Earth Cave. In addition, Robinson (1952) mentions "a baboon (*Papio*) indistinguishable from the modern chacma baboon" from Graveyard. Robinson's specimens were not available to me, but in view of the new species *P. robinsoni* being so similar to the chacma baboon it would seem probable that his specimens were of this new species. Material probably of *P. ursinus* is described by Freedman (1965) from Witkrans.