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PALAEONTOLOGIA AFRICANA

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

VOLUME XI 1968

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REPORT OF THE HONORARY DIRECTOR FOR THE REMAINDER OF THE YEAR 1967

This report covers the period from April 1st 1967 to the end of that calendar year, in order that its terminal date shall coincide with that of the financial year.

It should be stressed at the outset that the term "palaeontological research", which forms part of the Institute's title, has in modern times a wider significance than it had for earlier geologists. While it still entails the collection, preparation, and study of fossils with the object of deciding the genera and species to which they can be attributed, it is becoming more and more *de rigueur* to accept that they are the remains of once-living animals and plants, and to endeavour to deduce from all the available evidence their modes of life. That is why we in the Institute welcome as co-workers the scientists who are endeavouring to elucidate, by field and laboratory studies, the conditions and the environments in which the fossil-bearing sediments were deposited.

Staff

During the period under review the staff was enriched by the coming of Dr A. R. I. Cruickshank, who arrived from Edinburgh on October 19th and assumed duty on that day as Assistant to the Honorary Director and Scientific Officer. Dr Cruickshank's special studies will be concerned with the vertebrates of Karroo age, a continuation in a field with which he has been familiar for some years. As Assistant to the Honorary Director, a good proportion of the administrative work of the Institute falls to be done by him; and he has speedily familiarized himself with this aspect of his duties.

Other welcome additions to the permanent staff are Miss J. Kallenbach, who became typist in April 1967, and Mr D. Wolfaardt who assumed duty as a technical assistant at the end of the year.

It is pleasing to report that the longest-serving member of the staff, Mr J. W. Kitching, has been accepted by the University as a candidate for the degree of M.Sc., for which he will submit a thesis entitled "On the distribution of the Karroo vertebrate fauna with special reference to certain genera and the bearing of this distribution on the zoning of the Beaufort beds". The preparation of this thesis is now in hand. Mr Kitching has had to shoulder most of the day-to-day supervisory work during the period under review, a task he has performed with his customary efficiency.

Dr E. P. Plumstead and Dr R. J. Davey, both C.S.I.R. Fellows, have continued their valued work at the Institute. The former, as President of the International Subcommission on Gondwana stratigraphy, attended a symposium held in the Argentine and Brazil. She also attended a symposium on Continental Drift at Montevideo, organized under the joint auspices of I.U.G.S. and U.N.E.S.C.O.

With the consent of the Government of South Africa she issued, at the Argentine meeting, an invitation to hold a Gondwana symposium in the Republic in 1970, an invitation which was cordially accepted. An organizing committee for this symposium has been established by C.S.I.R. Dr Davey has acted, inter alia, as an adviser to S.O.E.K.O.R.; this Corporation has agreed to the appointment, as from the beginning of 1968, of Mr J. Anderson as a palynologist, working on their behalf, on the staff of the Institute and to subsidize the Institute for this work.

Professor Dart's assistants, Messrs. B. Maguire and P. Beaumont, have continued to work at the Institute, as have the two subsidized sedimentary geologists Messrs P. Ryan and T. Stratten. Mr A. Keyser, of the Geological Survey staff, is preparing a thesis on certain anomodont reptiles, and has made considerable use of the facilities which we have placed at his disposal.

Publications

During the period under review, Volume X of Palaeontologia Africana was issued and distributed. The major part of this volume consists of Dr Plumstead's description of the fossil plants of the Cape system (Palaeozoic), in the preparation of which she examined almost every specimen available in collections in South Africa. The paper is illustrated by 25 photographic plates. Financial contributions to the cost of this volume made by C.S.I.R. and by the Geological Survey of South Africa are gratefully acknowledged.

The preparation of Volume XI is in hand.

Research Work

A. *Palaeoanthropology*

Until his departure for the United States of America in August to occupy a chair in Philadelphia, the work of Messrs Maguire and Beaumont was supervised by Emeritus Professor R. A. Dart. Mr Maguire had completed, by July, his analysis of more than 16,000 suspected chert artefacts found in the surface soil overlying the australopithecine pink breccias at the Makapansgat Limeworks site and presented his findings on these very primitive worked cherts at the S_2A_3 meeting in Pretoria. During two visits to Makapansgat he collected some 200 artefacts from the Phase 2 breccia. He is continuing with an examination of quartzite and vein-quartz artefacts from soils above the breccias and of the stone artefacts from the solution cavities which penetrate the surface of these breccias. The collection under study consists of approximately 40,000 pieces.

Mr Beaumont has continued with the investigations into the pre-European mining industry in Swaziland which he has been undertaking with the support of the Anglo American Corporation.

Plans have been drawn by Professor P. V. Tobias and a band of co-workers for a further detailed attack on the problems posed by the famous site at Sterkfontein which is under the control of the University of the Witwatersrand,

whose Council has charged the Board of Control of this Institute with its supervision. These plans include new excavations within a defined area—now surrounded by a security fence. Preliminary clearing of rubble has begun, and from this rubble some 380 artefacts, some with adherent breccia, had been recovered by the end of August. From the rubble there have also been extracted bone-bearing breccia and rodent bones in addition to the artefacts of various cultures (early Acheulean, MSA, and LSA); all have been labelled and stored. The direct responsibility for the field activities rests on Mr A. R. Hughes, Supervisor of Laboratories of the University's Department of Anatomy. The main objects of the renewed studies are to ascertain the full extent of the cave deposit, to throw further light on the stratigraphy of the breccias, to obtain (if possible) absolute radioactive dating of the deposits, and to increase the knowledge of the fauna.

B. *Karroo Fossil Reptiles*

Since his arrival at the Institute Dr Cruickshank has begun a study of the diapsid genus *Chasmatosaurus* and of its relationship to the later form *Erythrosuchus*. He has prepared certain specimens by removal of matrix; among them is an almost complete foot thought to belong to the second of these genera. The study was, of course, merely in its preparatory stages at the end of 1967.

Mr A. Keyser, of the Geological Survey staff, has made considerable use of the Institute's facilities and collections, including specimens from the Rubidge collection, in preparation for a doctoral thesis on the skull characters of certain Anomodont genera. Much of the material that he has handled has been further developed in order to display features in which he is particularly interested for comparative purposes.

As an initial step in the preparation of his thesis Mr J. W. Kitching has compiled a record on cards of the exact locality of each of the known and identified reptiles from the Karroo beds in South Africa and has pictorially represented this information on an extensive wall-map formed of sheets of the Topocadastral maps on the scale of 1:250,000. He has begun the compilation of a detailed chart which will show the zonal distribution of the known genera. There can be no doubt that this study will lead to a revised zonification of the Beaufort series.

We have received a typescript copy (in two volumes, one consisting of photographs) of the thesis submitted in Paris by Dr D. Sigogneau. The thesis deals with the classification and anatomy of the Gorgonopsia and is based almost entirely on studies which she undertook in the Institute over a period of nearly two years. The contents of the thesis, which is in French, are very detailed; but the conclusions are of such importance that we hope to be able to publish an extended summary in *Palaeontologia Africana*.

C. *Micropalaeontology*

Dr R. J. Davey has undertaken work on Cretaceous microplankton occurring in borehole core material from Zululand. He has paid particular attention

to three genera of hystricospheres and their genetic relationships and has shown that by the systematic change of certain variables an evolutionary series has been produced, possibly as a result of the adaptation of the organisms to environment. He considers that the evolutionary stages can be correlated with positions in the Upper Cretaceous sedimentary sequence. In this work the Institute's Zeiss photomicroscope has proved of great value. Dr Davey has spent some time in revising his Ph.D. thesis on non-calcareous microplankton from the Cenomanian of England, France and North America, which will be published by the British Museum (Natural History) in 1968. He has also supervised the preparation of palynological material from borehole cores submitted by S.O.E.K.O.R.

D. *Palaeobotany*

Dr Plumstead has continued her studies of fossil plants from various parts of Africa and has examined material from a new area of Antarctica sent to her by the British Antarctic Survey. Borehole cores from Somkele, Zululand, sent by the Geological Survey, yielded excellent samples of two plants, one of which is new to South Africa, while specimens from the deepened Sambokkraal borehole near Merweville, C.P., sent by S.O.E.K.O.R., yielded a new species. Two visits to the Orange Free State yielded specimens from a new shaft on St Helena G.M. and from a number of borehole cores. Collections of plant fossils were recorded from the Ulco Limeworks and from the area of the Verwoerd dam.

For publication, Dr Plumstead prepared "A Review of Contributions to the Knowledge of Gondwana mega-plant fossils in Africa published since 1950" which was presented at the Gondwana Symposium in Argentina in October 1967, of which she was President, and "Fossil Floras and Latitudes" which was presented at the Continental Drift Symposium in Uruguay in the same month.

Mr J. Anderson, an M.Sc. student, worked on Triassic fossil plants which he had collected from the Oliviershoek Pass area in Natal.

E. *Sedimentology*

Throughout the period under review Mr T. Stratten and Mr P. J. Ryan continued work at the Institute. The former is making a detailed study of the Dwyka series of the Karroo basin; the latter almost completed his description of the sedimentology of the Ecca series of the same basin, which he has presented as a Ph.D. thesis to the University of the Witwatersrand. The detailed work of both investigators has an important bearing on the understanding of the ecological conditions under which plant and animal life flourished in the region in Lower Karroo times.

Teaching

The institution by the University of an Honours B.Sc. course in Palaeontology necessitates the regularization of formal instruction and the extension, in a limited degree, of the assistance that, for some years past, has been given by members of the Institute.

As a part-time lecturer attached to the Department of Geology, Dr Plumstead has given courses in Palaeobotany and in the Geology and Petrology of Coal to 2nd, 3rd and 4th year students, while Mr Kitching has been called upon to give talks on Karroo vertebrates and Karroo stratigraphy to undergraduates.

For the year 1968, Regulations bearing upon the Honours B.Sc. in Palaeontology have been drawn up and submitted to the University for approval. If adopted, they will necessitate close liaison between the Institute's staff and the Professor of Anatomy and his staff.

GONYAULACYSTA PARORTHOCERAS

A New Species of DINOFLAGELLATE CYST

by Roger J. Davey

Introduction

Davey (1968 in press) emends the species *Gonyaulacysta orthoceras* Eisenack and also transfers it to the genus *Cribroperidinium* Neale and Sarjeant. By emending Eisenack's species the specimens described by Sarjeant (1966) as *G. orthoceras*, from the Lower Cretaceous of England, must now be excluded from this species. Hence, a new species is here erected to accommodate them.

Systematic description

Gonyaulacysta parorthoceras sp. nov.

1966 *Gonyaulacysta orthoceras* (Eisenack); Sarjeant: 121, pl. 14, figs. 5, 6; text-fig. 29

DIAGNOSIS: Shell ovoidal with strong, tapering apical horn accounting for about one-fifth to one-quarter of overall length. Shell wall of moderate thickness, granular to tuberculate. Tabulation 4′, 1a, 6″, ?6c, 7‴, 1p, 1⁗; crests low bearing small spinelets. Cingulum strongly spiral, of moderate breadth: sulcus broad and extending to antapex.

HOLOTYPE: B.M. (N.H.) slide V.51730, specimen 3. Speeton Clay, Shell West Heslerton Borehole No. 1, West Heslerton, Yorks, at 19.25 metres depth. Lower Cretaceous (Upper Barremian).

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TOOTH STRUCTURE IN *Rhizodus hibberti* AG., A RHIPIDISTIAN FISH

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Abstract

The structure of the large laniary teeth of the Lower Carboniferous rhipidistian fish *Rhizodu hibberti* Ag. is interpreted in terms of a new theory of tooth development. The structure of these teeth is found to correspond almost exactly to that of the synchronomorial scale as defined by Örvig (1951) and Stensio (1961; 1962). These labyrinthodont teeth are thus shown to be composed of many tooth primordia, and are not a single unit of dentine. Some isolated *Rhizodus* teeth are described in which the entire labyrinthodont structure is missing, leaving an empty space inside the tooth. From this, a non-mechanical tooth removal mechanism is postulated.

Introduction

New interpretations of vertebrate hard tissues (bone, dentine and enamel) have been made by Örvig (1951) and Stensio (1961; 1962). The former reviewed the characteristics of the various types of dentine and introduced into his discussion a new theory on which to base descriptions of teeth and scales. This is termed the "Lepidomorial Theory". The lepidomorial theory proposes that each tooth or scale in any vertebrate is composed in general of several lepidomoria or units of dentine. Lepidomoria can be combined in two basic ways, to give what are known as either adesmic or monodesmic teeth or scales. Stensio (1961; 1962) elaborated the lepidomorial theory and introduced the terms 'cyclomorial' and 'synchronomorial' to describe the state of affairs if more than one generation of lepidomoria were involved in tooth or scale formation. In the adesmic or cyclomorial state the lepidomoria lay down hard tissue before the papillae have time to fuse and in the monodesmic or synchronomorial scale the opposite holds good (figs. 1 & 2).

Synchronomorial scales thus contain at an early stage one large compound pulp cavity. It is surrounded by a thin layer of mantle dentine which bulges outward into vertical ridges, marking the position of the individual lepidomorial crowns. Between these ridges, the mantle dentine projects inwards into the pulp cavity as comparatively low intrapulpar crests. These crests represent the vestiges of the mantle dentine in the lepidomorial crowns where the latter fused together. During further development they grow inward and join, thus forming several partition walls which divide the embryonic monodesmic pulp cavity into secondary lepidomorial units. Circumvascular dentine is gradually developed on the partition walls so that the interior of the crown is almost completely filled with hard tissue (fig. 2c).

Running through the simple pulp cavities of the lepidomoria of Palaeozoic elasmobranchs was a vascular loop. It entered the scale by means of a neck canal and left through a basal canal (fig. 1). These canals persist in considerable numbers in the composite scales of these fish and must be correlated with the vascular canals of Williamson as seen in ganoid scales (fig. 4). Dentinal tubules in each lepidomorial unit or crown issue from the upper part of each ascending vascular canal of Williamson.

Örvig (1951) concludes that all hard tissues in the vertebrates are related and laid down by cells which, although differing in any one animal, have a common ancestry. Thus bone, dentine and enamel are closely related tissues. Enamel is further differentiated into that belonging to the lower vertebrates and that belonging to the mammals. In the former it is of mesodermal origin and in the latter it is of ectodermal origin (Kvam 1946; Poole 1956a & b; Scott & Symons 1964). As opposed to many earlier authors (e.g. Widdowson 1928) Örvig recognises only three types of dentine in the lower vertebrates. These he calls osteodentine, tubular dentine and orthodentine.

Osteodentine is composed of dentinal osteons (modified primary osteons as opposed to Haversian systems proper) and an interstitial bony substance which may or may not contain bone cells. The bony substance arises first as trabeculae in the pulp tissue and the dentinal osteons are then deposited on the trabeculae without any resorption of the hard tissue. Before the formation of the dentinal osteons the intervascular trabeculae are lined with cells, frequently osteocyte-like, which during the process of deposition of the dentinal osteons modify into true odontoblasts.

Tubular dentine, as defined by Moy-Thomas (1939b), is composed of dentinal osteons with an interstitial enamel-like substance. However, Poole (1956a & b) regards this sort of enamel as being similar to dentine and thus tubular dentine may be only a variety of orthodentine.

Orthodentine consists of an outer layer of pallial (mantle) dentine and an inner layer of circumvascular (circumpulpar) dentine. The latter consists of large dentinal osteons, either lining vascular cavities in the teeth or the whole pulp cavity. The mantle dentine is pierced by odontoblast processes and may be very thin. Vasodentine (Tomes) is regarded as a variety of orthodentine showing

secondary loss of odontoblasts and the incorporation of blood capillaries in the dentine.

It is not known which type of dentine is the oldest. Örvig (1951) considers that teeth originally consisted of an outer layer of mantle dentine with an inner mass of osteodentine. In the majority of cases the osteodentine has been lost and the teeth are thus formed from orthodentine. Tarlo (1963; 1964) and Örvig (1965) discuss the nature of "aspidin", an acellular bone-like tissue found in Ordovician ostracoderms. In support of his earlier work, Örvig considers it to be secondarily acellular, whereas Tarlo concludes that the condition is primitive, seeing that it is the oldest vertebrate hard tissue known.

Bystrow (1938; 1939; 1942) has described the structure of teeth and dermal bones of osteolepid and dipnoan fish and labyrinthodont amphibia. This present publication is the first to describe the well-known labyrinthine tooth structure of Rhipidistians in terms of the lepidomorial theory. The similarity of the labyrinthodont tooth to the synchronomorial scale is notable (figs. 2 & 3). In addition, tooth replacement phenomena are described here which agree with those illustrated by Bystrow, but which do not agree with the usually accepted patterns.

Material and Method

The specimens used in the descriptions are from the unregistered collection of the Royal Scottish Museum, except for the tooth sectioned longitudinally (figs. 5 & 6). This latter specimen is from the Hugh Miller collection and has the number E. (Nat. Hist.) 352.

The techniques used in preparing the teeth for study were small variations of standard rock-section cutting. An attempt to make serial transverse sections of one tooth was only partially successful. The apparatus used for this attempt was a screw slot-cutter with a reinforcing washer. However it tended to shatter both the tooth and itself if the specimen was not held absolutely rigid.

Description of Material

The fish from which the teeth came is classified by Romer (1966, p. 361) as follows: order Crossopterygii, sub-order Rhipidistia and family Rhizodontidae. *Rhizodus* is common in the Lower Carboniferous of both Europe and North America. In general the fish of this family have slender bodies, paired fins with short obtuse lobes and cycloid scales. In some forms there is a heterocercal tail and the backbone has ring-like centra (*Rhizodopsis*), while in others the tail is diphycercal and the notochord is unconstricted (Moy-Thomas 1939a). Hugh Miller, quoted by Barkas (1875), estimated that some individuals of *Rhizodus* must have measured at least 40 feet overall although the only complete specimen recorded was 9 feet long (Stock 1880).

Two sorts of tooth occur on the mandibles of *Rhizodus*: a fringe of denticles 1.5–2.0 cms. high on the dentary and a shorter series of very much larger teeth on shelves of bone (coronoids) inside the dentary (fig. 5). Each shelf of bone supporting laniary teeth has room for two, only one of which is normally fully erupted (Pander 1860, Tab. 10 & 11). The external appearance of both types of teeth is identical, except for their size. The height of the large laniary teeth on a mandible 25 cm. long diminishes from 6 cm. at the front to just over 2 cm. at the back. There were four functional laniary teeth on this mandible, one laniary tooth in the process of being shed, and seven denticles. In other specimens the number of denticles is very much greater, and it is thought that this low number is aberrant.

The laniary teeth are slender cones which curve backwards and inwards. They are oval in cross section with the long axis roughly parallel to the jaw and the oval may be drawn out into one or two fine cutting edges. The basal third of the crown is cut by deep grooves and the whole crown is covered in fine striae.

The laniary teeth of *Rhizodus* have the same macrostructure as the synchronomorial scale described by Örvig (1951). Distally there are no intrapulpar crests dividing the pulp cavity and on the exterior there is a moderately thick layer of enamel. Towards the root intrapulpar crests develop and finally a rather complicated infolding of the dentine is seen (the 'Plicidentine' of Tomes) (fig. 3c–d). The enamel layer thins off towards the neck of the tooth. Also, in the grooves, it is thinner than normal.

Smart (personal communication) suggests that the packing together of the lepidomorial units typical of 'Plicidentine' would make an extremely strong, yet light structure designed to withstand heavy shocks. It is known that the majority of fish and aquatic arthropods of the Carboniferous were heavily armoured and a strong piercing tooth would be essential to these predacious Rhipidistians.

In longitudinal section the ascending vascular canals of Williamson are clearly seen. These gradually fuse to form the single monodesmic pulp cavity (fig. 6). No neck canals of Williamson are present. The ascending vascular canals of Williamson connect directly with the vascular spaces in the jaw and the cell spaces become visible as the dentine becomes more bone-like. Eventually the cell spaces take the form of true osteocytes, in a similar manner to those of bone of attachment.

Typically, odontoblast spaces are not found in orthodentine. However, in the teeth of this specimen of *R. hibberti* they occurred frequently in the dentine lining the pulp cavity. They measure about 7μ by 2μ. The dentinal tubes are about 1μ in width, and the "growth lines" of the circumpulpar dentine coincide with the point where they branch. (In fact it is not a branching, but a fusion of the inwardly migrating odontoblasts which causes these rings to appear (fig. 7).)

No other cell spaces are present in the dentine, but near the exterior of the tooth a granular layer containing many cell-like spaces is seen. This may be similar to the 'Granular layer of Tomes' as found in mammals, but in position is

more akin to the regions of globular dentine described by Bystrow in *Osteolepis* and other labyrinthodonts. It is however not nearly so extensive as in these other animals.

The teeth of *Rhizodus* are thecodont and are held in the jaw with a well developed bone of attachment. Basally and radially this bone of attachment passes into true bone with cell spaces, and is distinct from the dentine at all levels except the lowest. Bone of attachment is seen in the crevices on the exterior of the tooth. As the grooves widen towards the base of the crown, this bone of attachment tends to cover more and more of the outer surface until at the level of the jaw it surrounds the entire crown. Where enamel is present, bone of attachment always overlies it. In the lower basal sections there are some spaces between the trabeculae of bone of attachment rather bigger than normal. These spaces may mark regions where bone has not been formed, or, having been formed, is in the process of being resorbed prior to the tooth being shed (fig. 3d) (see also under Discussion).

Cell spaces do not occur in the bone of attachment except near the base of the tooth and where it merges into the bone of the jaw. At first these cell spaces are compact with few processes and measure approximately 30μ by 8μ. Their long axes are parallel to the trabeculae. Towards the jaw their shape gradually changes and more processes are seen. The cells here measure 40μ by 5μ (Roux 1942).

Bone of attachment presents rather higher birefringence in polarised light than does dentine and a more even colour than ordinary bone. This is possibly due to the presence of smaller crystallites more constantly orientated and coincides with the idea that bone of attachment was being constantly removed and relaid while the tooth erupted.

Resorption of tooth tissue is known to occur in most vertebrates from the outside initiated through mechanical stimulus. Whereas this probably occurred in *Rhizodus*, there is also evidence that dentine was resorbed through the pulp cavity. Transverse sections of an isolated tooth found in rock, and especially those sections from the base of this tooth, show a marked difference from the corresponding sections of teeth still attached to jaws (fig. 9a & b). In the latter all structures associated with the labyrinthodont pattern are seen, but in the former most of the dentine has been removed and all that remains is the outermost layer. Bone of attachment shows signs of erosion, but enamel seems to be untouched. The complete jaw referred to on page 6 has a pair of laniary teeth with their roots contiguous. If, as is most likely, one of these teeth is replacing the other, then signs of dentine removal are to be expected on the side of the older tooth, nearest the replacing one. No evidence of this can be seen.

In figure 3d it will be noticed that alongside the fully functional tooth there lies remnants of another. The matter is discussed below.

Discussion

The interpretation of the labyrinthodont tooth given in this paper, using Örvig's descriptions of the synchronomorial scale as a basis, gives an entirely new

orientation to one of the best known features of the Palaeozoic fish and amphibia. A consideration of the generalised synchronomorial scale shows that the equivalent of many generations of tooth material fuse to form a single tooth. This is the state of affairs seen in the labyrinthodont tooth of *Rhizodus hibberti* of the Lower Carboniferous.

Under Tomes' classification the dentine in labyrinthodont teeth was known as 'Plicidentine'. It can now be interpreted more accurately as a variety of orthodentine, with an outer layer of mantle dentine and an inner layer of circumvascular dentine (Örvig 1951, pp. 347–359). Mantle dentine is characterised by the presence of odontoblast processes; it is of even structure and does not have the concentric lines similar to growth rings that circumvascular dentine has (figs. 7 & 8). Therefore it would appear to represent an initial rapid deposition of hard tissue and would be expected to predominate in the tip of the tooth. As far as can be ascertained this is so.

A granular layer similar to that in the dentine is seen in the enamel, becoming more marked towards the tip. At the same time the layer in the dentine becomes reduced (fig. 8). The presence of this layer in the enamel can be explained if this enamel is formed by the dentine organ and is subjected to similar influences as the dentine during development. Therefore the enamel is probably mesodermal in origin.

In postulating that the dentine of these teeth was removed under control of a non-mechanical system, rather than in the more normal way, the following facts must be examined. Firstly, each shelf of bone supporting the laniary teeth has room for only two, and, of which, it seems normal that only one was functional at any one time. On the lower jaw of *Rhizodus* referred to on page 6, a pair of teeth lie side by side. There is no evidence of erosion where they are in contact, which would be expected if mechanical stimulus was the normal method of removing the older tooth. Secondly, transverse sections of adjacent tooth sockets show remnants of dentine with labyrinthodont structure lying round the edge of the empty socket and other sections of isolated (presumably shed) teeth identified as belonging to *Rhizodus*, reveal that all internal dentine is absent. These observations suggest that the dentine is removed from the interior before the tooth is shed. Any mechanism responsible for dentine resorption could also trigger off the eruption of the other tooth of the pair.

It could be postulated that the isolated teeth with no labyrinthodont structures present were in fact newly erupted teeth broken away from the pair as a natural hazard of life. However in figure 9b it will be seen that the remnants of dentine and enamel are in general only slightly thinner than the walls of the tooth in figure 9a. The dissociated nature of the fragments can be explained only if the supporting structures in the centre of the tooth had been eroded from the inside. Newly erupted teeth figured by Bystrow (1938) for *Benthosuchus* always have the labyrinthodont structures thinly developed, as are the tooth walls themselves. They are much thinner than the tooth wall in figure 9b.

Bystrow (1942) discusses the pattern of dermal bone growth in *Dipterus*

with reference to Westoll-lines. In sections of dermal bones he shows resorption spaces occurring within the hard tissues and, in other publications (1938; 1939), he shows similar resorption spaces in the bases of teeth of *Benthosuchus*, *Glyptolepis*, *Holoptychius* and *Eusthenopteron*. Regarding the Westoll-lines, Jarvik (1948) agrees that they must represent growth stages, and Bystrow's analysis of their nature must lead to the conclusion that some cyclical mechanism of dentine resorption from within the tooth must have operated in these vertebrates.

In some mammals milk teeth are shed even if the permanent tooth-germ is excised (Oberstzyn 1963). Therefore it seems possible that replacement teeth do not need to erupt from directly below the functional tooth and that the basal dentine can be removed by some process other than mechanical stimulus.

Acknowledgments

The descriptions of the laniary teeth of *Rhizodus hibberti* in this paper were carried out as part of the requirements for the degree of B.Sc. (Hons.) in Zoology in Edinburgh University. I am very grateful to Dr C. D. Waterson of the Royal Scottish Museum for the loan of the material, to Mr G. F. Friend for supervising the work, and the technical staff of both the Geology and Zoology Departments for the time and trouble taken helping to cut the sections and take the photographs. The Cambridgeshire Education Authority supplied a very generous grant during the course of the year. Dr R. Sprinz and Dr Alun Maddy kindly read this paper in manuscript and made many valuable suggestions for its improvement. Mr G. M. Burnett undertook the onerous task of translating the German texts, for which I am very grateful.

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EXPLANATION OF TEXT FIGURES

Fig. 1. The mode of formation of Cyclomorial scales. From Örvig, 1951.
(a) Vertical section of the primordial lepidomorium, consisting of a dentine crown and a bony base.
(b) A more advanced stage of development. The hard tissues of the second lepidomorium have begun to form.
(c) Two lepidomoria in the final stages of development.
lpca—lepidomorial pulp cavity; cr—crown of primordial lepidomorium; ve—vessels entering the pulp cavity through both the neck and basal canals of Williamson; bp—basal plate of the primordial lepidomorium; can. W. n.—neck canal of Williamson; p. ldu'—papilla of soft tissue of the first areal zone of growth; ldup-ldu'—crowns of the primordial and second lepidomorium respectively; bpa—basal plate of the Cyclomorial scale; can. W. b—basal canal of Williamson; bp'—basal plate of the second lepidomorium.

Fig. 2. The mode of formation of a Synchronomorial scale. From Örvig, 1951.
(a) Horizontal section of the crown at early stage of development. A thin layer of mantle dentine has formed round the embryonic synchronomorial pulp cavity.
(b) More mantle dentine has formed, and the intrapulpar crests have grown out to form partition walls.
(c) Formation of dentinal osteons within the secondary lepidomorial pulp cavities formed in stage two.
pd—pallial (mantle) dentine; ipcr—intrapulpar crests; v. sp.—secondary lepidomorial pulp cavities; v. can—vascular canals; osd—dentinal osteons; empca—embryonic monodesmic pulp cavity.

Fig. 3. Transverse sections of laniary tooth of *Rhizodus hibberti* Ag.
Unregistered collection Royal Scottish Museum. See also Fig. 5.
(a) 2 cm. from apex.
(b) 2.26 cm. from apex.
(c) 2.46 cm. from apex.
(d) 4.11 cm. from apex.
Pc—main pulp cavity; ipcr—intrapulpar crests; ce—cutting edge of tooth; Sp—large spaces between tooth and jaw-bone; Od—dentine of functional tooth; Od'—dentine of alternate tooth; Ba—bone of attachment; Bj—bone of jaw. Lines represent 1 cm.

Fig. 4. Vertical section of ganoid scale to show ascending canals of Williamson (can. W), but no neck canals. From Örvig, 1951.

Fig. 5 Tooth of *Rhizodus hibberti* Ag. prior to being sectioned transversely. See also Fig. 3. Unregistered collection, Royal Scottish Museum. Bj—bone of jaw; Sh—shale in which tooth and jaw remnant is embedded. Line represents 1 cm.

Fig. 6. Longitudinal section of incomplete laniary tooth of *R. hibberti*. Registered number E (nat. hist.) 352. Hugh Miller collection, Royal Scottish Museum.
Pc—main pulp cavity; Ba—bone of attachment; Bb—basal bony region of tooth; Bj—bone of jaw; can. W—ascending canal of Williamson; V. can. J—vascular canals of the jaw. Line is 1 cm. long.

Fig. 7. Orthodentine in laniary tooth of *R. hibberti*, showing mantle dentine (pd) and circumvascular dentine (Cpd). The latter with "growth rings" caused by synchronous fusion of inwardly migrating odontoblasts (Gr). Ba—bone of attachment. Line is 1 mm. long.

Fig. 8. High power view of figure 3b. to show granular layer in both dentine and enamel.
e—enamel; gr. e—granular layer in enamel; gr. d—granular layer in dentine; pd—mantle dentine. Line is 50μ long.

Fig. 9. Transverse sections of *Rhizodus* teeth at equivalent levels.
(a) Section of tooth immediately above level of jaw-bone. c.f. fig. 3c.
(*b*) Basal section of isolated tooth with dentine missing from interior of tooth. Distortion of tooth caused by pressure of overlying sediment.
Od-dentine.

Fig. 1

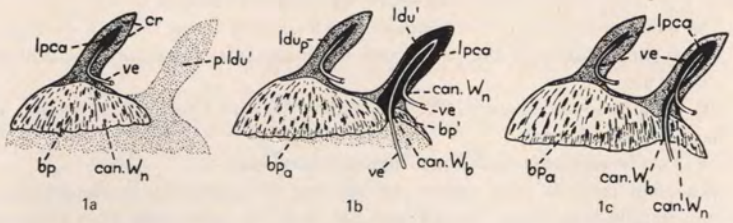


Fig. 2

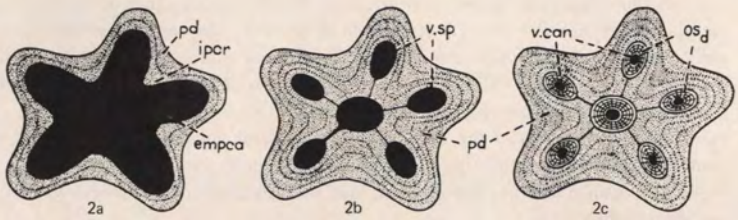


Fig. 3

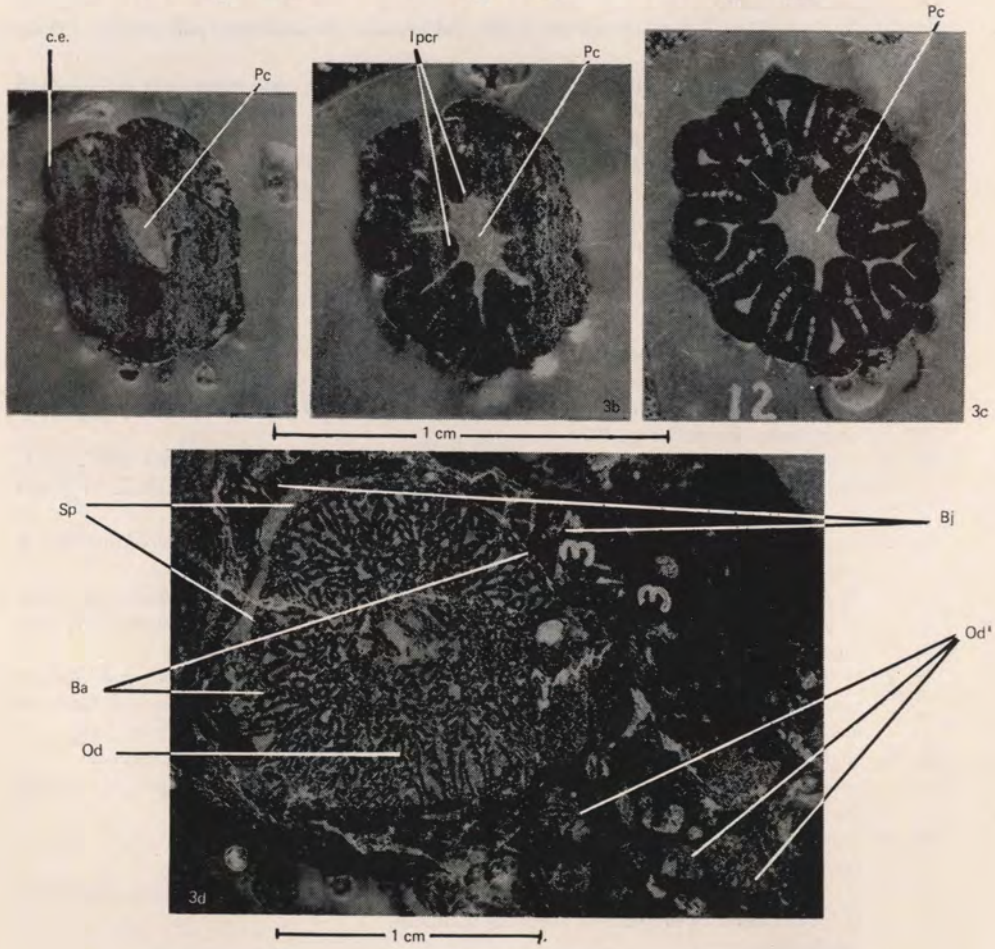


Fig. 4

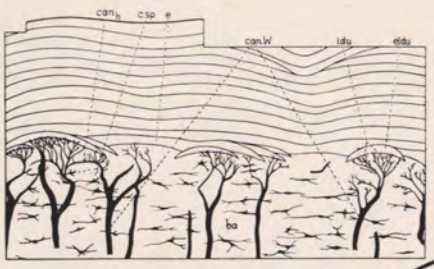




Fig. 5



Fig. 6

Fig. 7



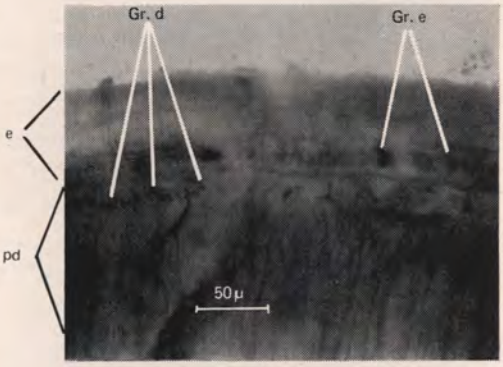
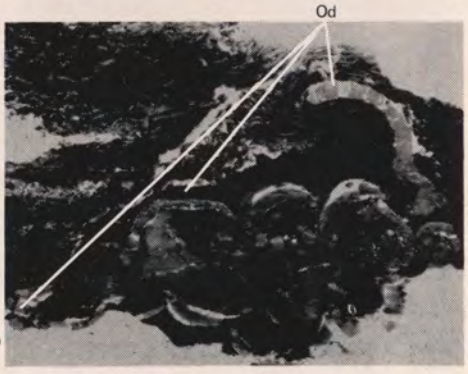


Fig. 8

Fig. 9





ON THE STRUCTURE OF THE SKIN IN *URANOCENTRODON (RHINESUCHUS) SENEKALENSIS*, VAN HOEPEN

By G. H. Findlay

In the famous collection of fossil remains of the labyrinthodont *Uranocentrodon*, housed since 1911 in the Transvaal Museum, the bony skin armour from the ventral surface of the body of at least six individuals has been preserved. In spite of this lavish quantity of material only a few notes on the osseous skin structure were included in van Hoepen's (1915) description, and all later papers have passed it by almost completely.

The two most recent contributions with full bibliographies on the skeleton of *Uranocentrodon* are those of Romer (1947) and Watson (1962).

Most of the sandstone slabs from the *Lystrosaurus* (basal Triassic) zone of Senekal which contain this skin material have been grouped together for many years in a large closed display case. Three slabs apparently unconnected with each other had not been cemented into the display and were separately available at the Museum for detailed study. They proved to belong together, and fitted to yield a strip of armour some 25 inches long down the ventral midline and in places up to 4 inches broad on one or other side of the midline. On these portions the present study is mainly based. They had been presented to the museum by the Municipality of Senekal after the main collection had been purchased.

The complete skeleton of *Uranocentrodon* in the National Museum, Bloemfontein, has a length between the limb girdles of some 40 inches, clearly covered by ventral armour which extends laterally to a maximum of 5–6 inches from the midline. From these measurements, it may be concluded that the study material available which comprised this 25 inch strip gave a fairly extensive view of the skin structure, pending opportunities to compare it in detail with the rest of the collection.

Orientation of Specimens

The dermal ossicles in *Uranocentrodon* form an inverted-V or chevron pattern, with the point of the chevron lying in the ventral midline directed like an arrowpoint towards the head end of the animal. In the specimen studied the bilaterally diverging lines of bones meet at an angle of 60° at the anterior end of the specimen falling to 50° over the slenderer parts farther back. The angles of divergence from the midline itself decline therefore from 30° to 25° respectively.

Mostly it was the internal aspect of the skin armour which showed uppermost on the stone slabs from Senekal. In some cases the skin had obviously slipped out of line with the vertebral column and was clearly indented from above by displaced parts of the axial skeleton.

Because the ossicles overlap one another, it is their medial ends which are seen on the internal surface of the armour, and their lateral ends on the external surface. Therefore if the free ends of the ossicles point towards the midline, it is the internal surface which is being examined. By establishing the midline, the direction of divergence and the pointing directions of the free ends of the ossicles, one can orientate the specimen in all planes. Confirmation may be obtained from the position and orientation of the vertebral column where present.

When the midline is not visible on the specimen, as is the case in some of the slabs collected at Senekal, the morphology of the individual bony ossicles must be used to determine the facing of the specimen.

Anatomy of the Typical Dermal Ossicle

The dermal ossicles may be considered as belonging to two regional types: those which lie away from the ventral midline, comprising up to 8 clear rows in our material, and those which abut on the midline itself, limited naturally to a single row contributed from either side.

The *laterally placed ossicle* (Fig. 1), seen from the internal or dorsal aspect, has a smoothly pointed flame-shaped medial end (G). Its lateral end (C) after narrowing somewhat, exhibits a thin saucer-like expansion with a slight anterior deflection. These ends are frequently broken off in the specimens. Such an ossicle measures about 35 mm. from end to end. Although both ends taper, the ossicles measure about 5–6 mm. across at the centre where they are broadest. The most conspicuous feature of the ossicles, and indeed the only feature to work from if the ends are missing, is a conical buttress (F) running along the posterior edge of the ossicle. This cone (Fig. 1F) has its apex near the posterior edge of the spoon or saucer-like lateral end of the ossicle where it is about 1 mm. broad, and it swells evenly in thickness to a breadth of 2–3 mm. just medial to the midpoint of the ossicle. Here the buttress flattens out over the posterior part of the flame-shaped medial end of the ossicle.

This buttress converts the dorsal aspect of the ossicle into a grooved or gutter-like channel (E). In the gutter-like part of the ossicle, two structures are clearly housed. One is the next most lateral ossicle of the same row, whose flame-shaped medial end lies about 8 mm. away from the inner tip of the ossicle in which it lies (Fig. 1). The posterior edge of the overlying ossicle impinges on the anterior facing of the conical buttress, while its anterior edge abuts on or overrides the buttresses in the next headward row of ossicles (Fig. 1). The second group of structures which lie in the guttered surface of the internal aspect of the scale are the grooves and foramina presumably for nerves and vessels. These lie tucked in the angle formed where the ossicle rises up to form the buttress. Here they would be sheltered from and protected by the overlying ossicle (Fig. 5).

The medial or flame-shaped end of the ossicle shows on its inner aspect a number of grooves suggesting muscular, ligamentous or tendinous attachments passing horizontally forward, interspersed with vascular grooves and foramina.

The external aspect of the dermal armour could not be directly studied in plan view, but sections cut through one of the slabs at right angles to the line of the laterally placed ossicles showed the following features. The outer surface was saw-toothed in cross-section (Fig. 2), the ossicles having roughly the shape of angle irons with the angle pointing to the outer surface of the animal. The pattern was occasionally ratchet-like, with the short slope of the ratchet formed by the posterior buttress of the scale.

The *midline ossicles* differ in having broadly expanded medial ends (Fig. 3) by contrast with the tapering flame-shaped medial ends of the laterally placed ossicles. These ends lie along the midline, each overlapping alternately with the one from the opposite side. The expanded end of each ossicle can be divided into two areas: an anterior portion which points forward and dorsally, and exhibits the markings of vessels and ligaments, and a posterior portion, which continues laterally into the end of the ossicle buttress, and is flattened or hollowed out dorsally over the midline to receive the ventral surface of the next most caudal ossicle from the opposite side.

The ossicles whose medial ends form the midline differ somewhat in shape according to their position. Those placed farthest forward are squarish with a straight anterior edge at right angles to the midline. They also give the impression of being tilted from the horizontal, so that their posterior edges would point backwards and downwards on the outside of the body along the midline. Farther back the midline scales are flatter and less massive, and have the shape of miniature mutton chops which lie without tilting on a level with the rest of the scales (Fig. 4).

Construction of the Armour

As the ossicles in succeeding rows are of roughly equal length, their lateral ends lie in a straight line which is more or less parallel to the ventral midline. In any particular row of ossicles the next most lateral ossicle reaches the exterior aspect of the armour in the following manner. The anterior edge of any ossicle touches the buttress of the more headward ossicle but diverges from this edge of contact at point A, Fig. 1, as it tapers laterally. An angle of divergence of some 10°–15° is formed (Fig. 1), and through this cleft along the anterior free margin of the ossicle the body of the next ossicle escapes laterally, being partly held behind in the cavity of the outer end of the more medial ossicle. This supporting cavity lies roughly in line with the 10°–15° point of divergence at the front edge of the ossicle so supported. A double imprint is therefore sometimes seen on the matrix here—that of the oblique divergence of the more medial scale, and the groove formed by the ridged outer surface of the escaping lateral scale.

The arrangement described ensures that no external portion of the armour could be displaced in any direction on its own without hinging on another part of the armour for movement and support.

Significance of the Ventral Armour

The armour which clothes the entire ventral surface of *Uranocentrodon* between the limbs would probably function as a protector of the internal organs from even and uneven pressures on the ground, and at the same time be of some mechanical use when the animal was either lying at rest or walking. The special structure of the armour suggests that it may well have served several such functions.

For example, the posterior buttress of the ossicle structure would counteract denting from the outside. It would also resist and transmit forward and backward pressures in the rows of ossicles. The inverted V–shaped arrangement of the ossicle rows, the backward and downward projections of the midline ossicles and the tougher posterior edge of the external aspect of the lateral ossicles are all features which make one think of the gripping tread of a motor tyre. Such a tread would principally prevent a backwardly slipping movement, and the slanting rows of scales would check a sideways slip in either direction. This arrangement would be useful for crawling up or lying on a sloping bank. Furthermore, it is perhaps worth pointing out that in walking on its widely separated limbs, the *Uranocentrodon* probably also exhibited fish-like undulations of the spine for which the inverted V–pattern would be useful. In a forward swerve to the right, the left hand ossicle rows would slide the longest distance with their ridges lying in line with the direction of movement. This would minimise friction. The right hand rows would at the same time move a comparatively short distance obliquely to the line of movement. The friction on the right side would actually be greater, but would be offset by the shortest sliding distance and the possibility that the simultaneous stride on the foot of this side would raise this part of the body somewhat off the ground.

Nature of the Epidermal Covering

It seems rather unlikely that the bony armour just described was either naked or projected even partly through the epidermal surface. A tough overlying dermis with a thick epidermal covering would adequately transmit the surface distortions to the underlying bony shield—and this is the arrangement seen over other sculptured and ossicular dermal bones in living amphibia.

There is an interesting possibility that the epidermis over the bony ridges was capped by a horny layer just as is the case in certain fresh-water fish. Van Hoepen was able to follow the ventral armour in some of his *Uranocentrodon* specimens round to the dorsum of the fossilised remains, where he found the ossicles gradually replaced by reddish brown non-bony rings which he took to be horny scales. This seems indeed to be the most likely interpretation.

Having found small bright red powdery patches near the outer surface of the scales while cleaning the present specimen, it seemed worth considering if this could also represent keratin. Because of the high sulphur content of keratin Dr S. H. Haughton suggested the following mechanism to me—conversion of ferruginous mud to ferrous sulphide at the sites of decomposing keratin with

subsequent conversion of the ferrous sulphide to haematite. This would give the site of keratin deposits a reddish tint after all traces of keratin had disappeared.

The perforated centres of the horny rings described by van Hoepen, which are still clearly seen in his mounted exhibit, would possibly have been the sites of glandular openings on the surface.

Bloodvessels and nerves to the ventral body surface could reach it from the dorsum and sides of the body, and also to a small extent from channels which perforate the ossicles or escape between the outer free ends of the ossicles.

Comparison with other South African Labyrinthodonts

Of the South African stereospondylous labyrinthodonts, skin scutes have been described only by Kitching (1957) for *Laidleria*. Mr Kitching had nevertheless observed their presence in *Lydekkerina* as well, and lent me a specimen for study. The ossicles in this specimen were scanty and disarranged, but the best developed examples were about 6 mm. long and 1 mm. broad—a length to width ratio of 1:6 exactly as in *Uranocentrodon*, and there was a slight suggestion of the finer structural features such as the posterior buttress, the flame-shaped medial and the rocker-like lateral end. The ossicles of *Lydekkerina* were one-sixth the length of those in *Uranocentrodon* (6 mm. as compared with 35 mm.). This size difference was about equal to the ratios in total body length between *Lydekkerina* and *Uranocentrodon*, respectively (15 inches and 6–7 feet).

Reports from elsewhere allow limited comparisons. The closest resemblances are towards *Onchiodon (Sclerocephalus) labyrinthica* as described by Credner in 1893. In this case the scales are of somewhat similar construction with a length of 15 mm. for an animal 1.3 metres long.

Summary

The structural and functional features of the dermal armour of the ventral body surface of *Uranocentrodon* are discussed, chiefly based on one specimen acquired by the Transvaal Museum after the first examples had been described.

Acknowledgments

My thanks are due to Dr C. K. Brain, Dept. of Palaeontology, Transvaal Museum, for loan of the specimens, and to the C.S.I.R. Photobiology Group, whose facilities were used in making this study.

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EXPLANATION OF TEXT FIGURES

Fig. 1. Semi-diagrammatic reconstruction of four dermal ossicles on ventral body surface of *Uranocentrodon*. Dorsal facing (i.e. internal surface). A—point of lateral divergence from buttress of next most headward scale. B—point of medial divergence of next most tailward scale. C—kidney-shaped lateral end of scale. E—neuro-vascular groove. F—posterior buttress, enlarging medially. G—flame-shaped medial end. θ—point of escape to the outside from the most lateral ossicle in each row. Total length from tip of C to tip of G about 37 mm.

Fig. 2. Section through five complete ossicle rows, middle row defective. Ventral surface below, embedded in sandstone matrix. Anterior end to left. Photograph shows angle-iron-like or ratchet-like construction of ossicles, with posterior buttress showing as a thickening making up the right-hand portion of the ossicle. Section also shows manner by which anterior (left) border of scale approaches posterior border of buttress by means of a sharp edge at the middle of the buttress.

Fig. 3. Midline portion of midline ossicle seen from dorsal aspect. Dish-like area of bone with extension to posterior buttress on the left. Straight anterior edge defective. Overlying distal scale belonging to right-hand scale removed.

Fig. 4. Midline view farther back than figure 3. Flame-shaped medial ends of left-hand ossicle rows running obliquely up from left. Emerging from beneath them the dilated midline ossicle row (damaged), resembling inner end of mutton chop in shape. Overlapping ossicles alternately from right side not shown.

Fig. 5. Dorsal view of left-side ossicle row showing in centre the lateral end (to the left) of one ossicle rising up from C to point A (as in figure 1) with the posterior conical buttress (with small gap in it) on its lower or posterior edge. The buttresses of other ossicles show the tendency to broaden towards the right (midline).

Fig. 1

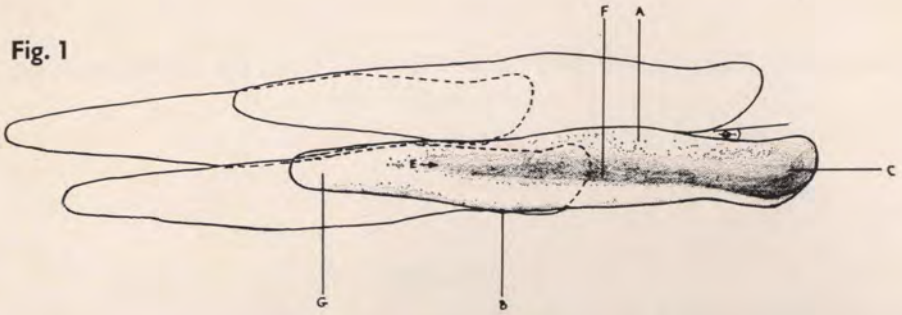

Fig. 3



Fig. 5



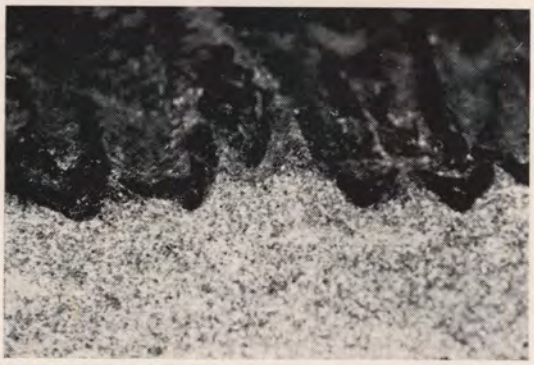

Fig. 2



Fig. 4

C

A COMPARISON OF THE PALATES OF PERMIAN AND TRIASSIC DICYNODONTS

By A. R. I. Cruickshank

Abstract

Whilst comparing the skulls of some Triassic dicynodonts with Permian members of the family, it was noted that the interpterygoid space in the former is consistently smaller than in the latter (Cruickshank 1965: 1967). In analysing this difference further, the palates of a series of Permian and Triassic dicynodonts were examined, either directly or from published diagrams. From graphs drawn using the various measurements taken from the palates, the geological age of the specimens can be deduced as can their estimated lengths, if fragmentary.

The Dicynodont Palate—General Measurements

It is possible to divide the dicynodont palate into four main regions, here termed "mouth", "internal nares", "interpterygoid space" and "brain-case" (fig. 1). The lengths of these regions, measured on the mid-line of the palate were plotted on two series of graphs (figs. 2–6). The table of measurements can be seen in Cruickshank (1962).

From figure 2 it can be seen that when the lengths of the internal nares and the interpterygoid spaces are compared, then in general, the interpterygoid space of the Permian forms is greater than 60% of the length of its internal nares, whereas the value for the Triassic forms is always less than 60%. It is considered that this is significant because dicynodonts are the dominant fossil group in the terrestrial deposits of "Gondwanaland" and they thus might be used as stratigraphic markers where the more commonly used macrofossils are missing.

Other measurements were also plotted to see if there were other similar relationships between the parts of the palate and these are described below.

The length of the "mouth" when plotted against the total length of the specimen shows in general a linear relationship between the two parameters and no distinction between Permian and Triassic forms is seen. The "mouth" being about 30% of the total length of the specimen, except in the case of those over 400 mm, where the value drops below this (fig. 3a). Where the length of the "mouth" is expressed as a percentage of the total median basal length of the skull, no distinction can be drawn between Permian and Triassic forms once more (fig. 3b). In general this conclusion holds good for all the graphs where the parts of the palate are expressed as percentages of the whole skull length. However with increased knowledge of the dicynodonts and using proper statistical techniques, perhaps some points of interest may emerge from these graphs (figs. 3b, 4b, 5b, 6b).

When the length of the "internal nares" is plotted against total median basal length of the skull, a tendency can be seen for the Permian and Triassic forms to separate out (fig. 4a). The lengths of the "internal nares" of the Triassic dicynodonts ranges between 20–23% of the whole, whereas those of the Permian dicynodonts range between 13–15% of the whole. However, no conclusions can be drawn from this graph for skulls of less than 150 mm overall length.

A measure which might be of value is to compare the length of the interpterygoid space with the whole skull (fig. 5a). The interpterygoid space of Permian dicynodonts in the 0–150 mm range is always more than 12% of the whole skull length. Even above 300 mm overall length the interpterygoid space is never less than 8% of the whole. On the other hand the majority of Triassic dicynodonts seem to have an interpterygoid space less than 8% of the whole length of the skull, and only one has a value greater than 12%.

The length of the "braincase" (fig. 6a) seems to bear a linear relationship to the rest of the skull in much the same way as the mouth does, except that there seems to be less deviation from the straight line. This measure may be of use in estimating the overall length of fragmentary specimens.

Discussion

This type of analysis is best done with many more specimens than were available in this instance. Thus no attempt has been made to apply other than the most empirical of interpretations to the graphs.

In addition, no account has been taken here of the Upper Permian genus *Cistecephalus*. This genus has no interpterygoid space, the area being filled with a part of the parasphenoid rostrum (Keyser, in press). Thus no place could be found for it in this or similar analyses. However *Cistecephalus* is already a most important zone-fossil of the South African Karroo beds, even if it is aberrant in the palatal region.

Cruickshank (1967, p. 201) has already discussed the evolutionary mechanisms which may have caused the noticeable difference between the length of the interpterygoid spaces in Permian and Triassic dicynodonts. As far as this paper is concerned it should be noted (fig. 2) that there seems to be a correlation between the horizons of the specimens measured and their position on that graph. For instance a group of three larger dicynodonts (*Daptocephalus leoniceps* (Owen)) straddles the 60% line and towards the lower end of the size range a number of *Lystrosaurus* specimens are close to, but still on the "Triassic" side of the line. *Daptocephalus* (Ewer 1961) is a form characteristic of the uppermost Permian in South Africa and *Lystrosaurus* is the zone-fossil of the succeeding beds, which are of Lower Triassic age. The other forms marked on the graph range through the Lower to Middle Triassic, and end on the far right with *Stahleckeria* (von Huene 1942) an upper Middle Triassic form.

Thus it seems possible to separate Permian and Triassic dicynodonts on the

one palatal character with confidence, but whether these can be assigned to a distinct horizon within the era on these grounds is uncertain at present.

I would like to express my thanks to Dr F. R. Parrington, F.R.S., of the University Museum of Zoology, Cambridge for his help and encouragement while I was his research student. Dr K. A. Joysey helped considerably with the interpretation of the graphs. Financial assistance was given by the University of Edinburgh and the D.S.I.R.

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EXPLANATION OF TEXT FIGURES

Fig. 1. A. Diagrammatic representation of dicynodont palate to show the regions discussed in this paper.

B. Generalised diagram to show the region around the interpterygoid space in Triassic dicynodonts.

C. The same for Permian dicynodonts.

ECT—Ectopterygoid; PAL—Palatine; PMX—Premaxilla; PSP—Parasphenoid; PT—Pterygoid; V—Vomer.

ipt.sp.—interpterygoid space; ipt.vac.—interpterygoid vacuity; lab.fos.—labial fossa.

a—"mouth"; b—"internal nares"; c—"interpterygoid space"; d—"braincase".

Fig. 2. Graph to show the relationship between the internal nares (b) and the interpterygoid space (c). All measurements in mm.

Fig. 3. A. Graph to show the relationship between the mouth (a) and the total (median basal) length. All measurements in mm.

B. Graph to show the relationship between the mouth expressed as a percentage of the total (median basal) length, and the total (median basal) length.

Fig. 4. A. Graph to show the relationship between the internal nares (b) and the total (median basal) length. All measurements in mm.

B. Graph to show the relationship between the internal nares expressed as a percentage of the total (median basal) length, and the total (median basal) length.

Fig. 5. A. Graph to show the relationship between the interpterygoid space (c) and the total (median basal) length. All measurements in mm.

B. Graph to show the relationship between the interpterygoid space expressed as a percentage of the total (median basal) length, and the total (median basal) length.

Fig. 6. A. Graph to show the relationship between the braincase (d) and the total (median basal) length. All measurements in mm.

B. Graph to show the relationship between the braincase expressed as a percentage of the total (median basal) length, and the total (median basal) length.

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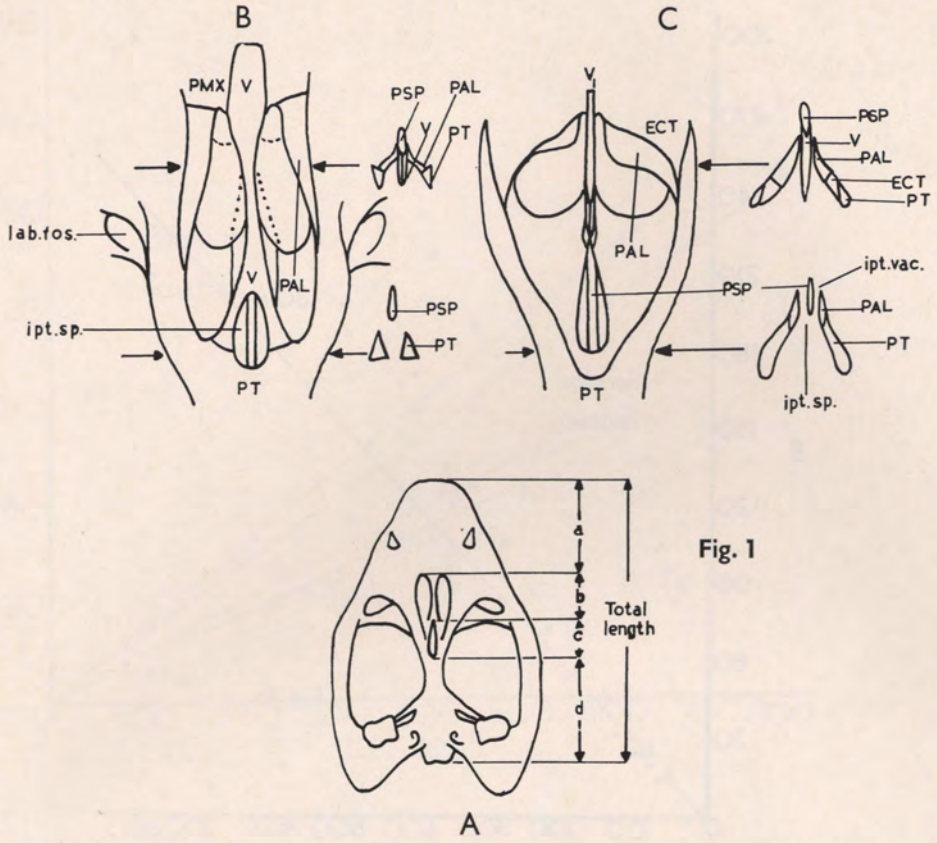
B. Graph to show the relationship between the braincase expressed as a percentage of the total (median basal) length, and the total (median basal) length.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a
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Total length
A

Fig. 1

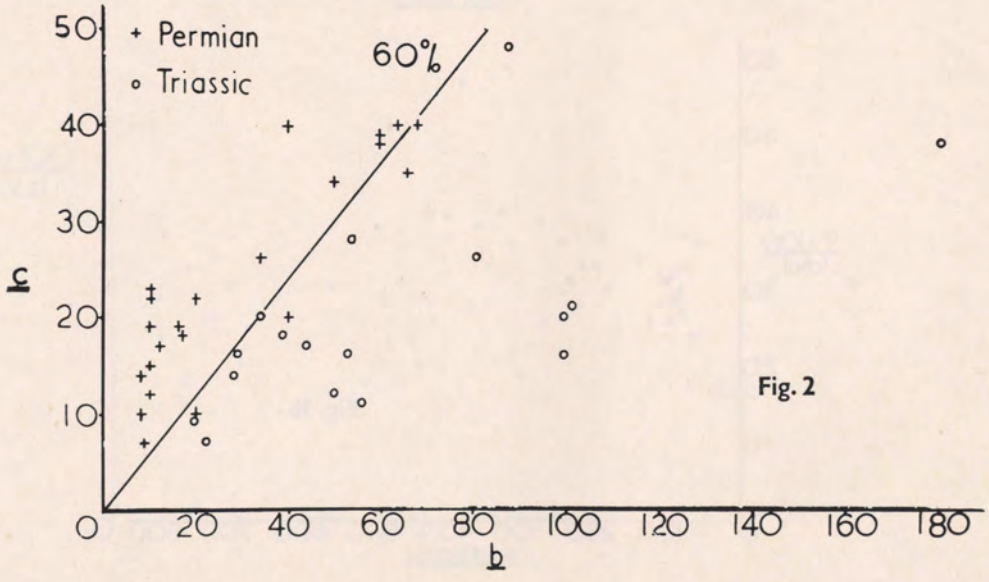
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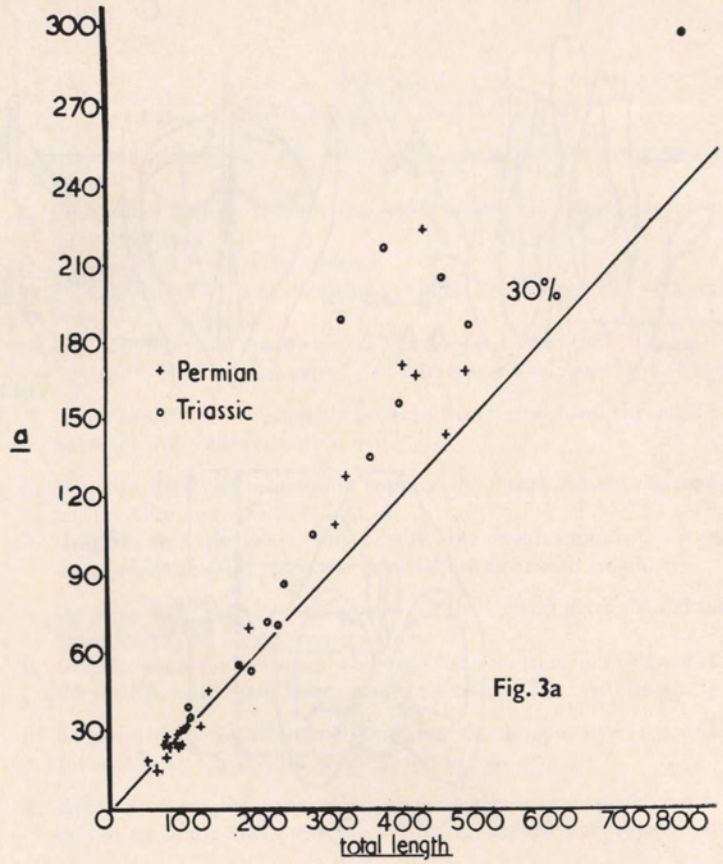
Fig. 2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total length

Fig. 3a

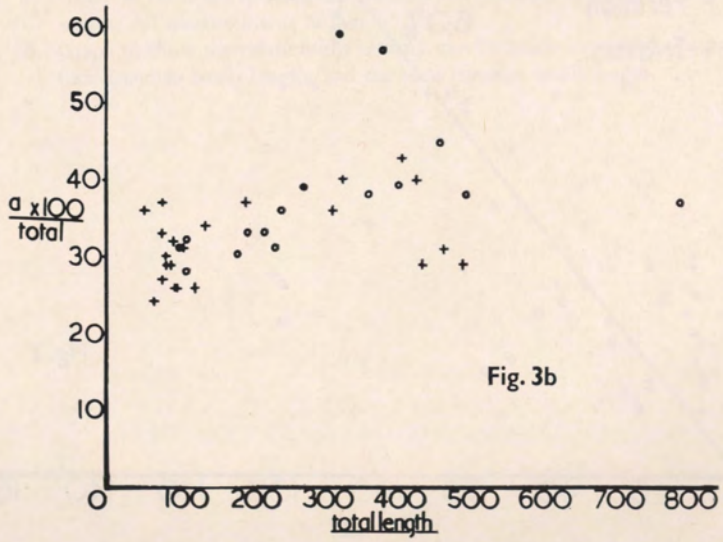
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Fig. 3b

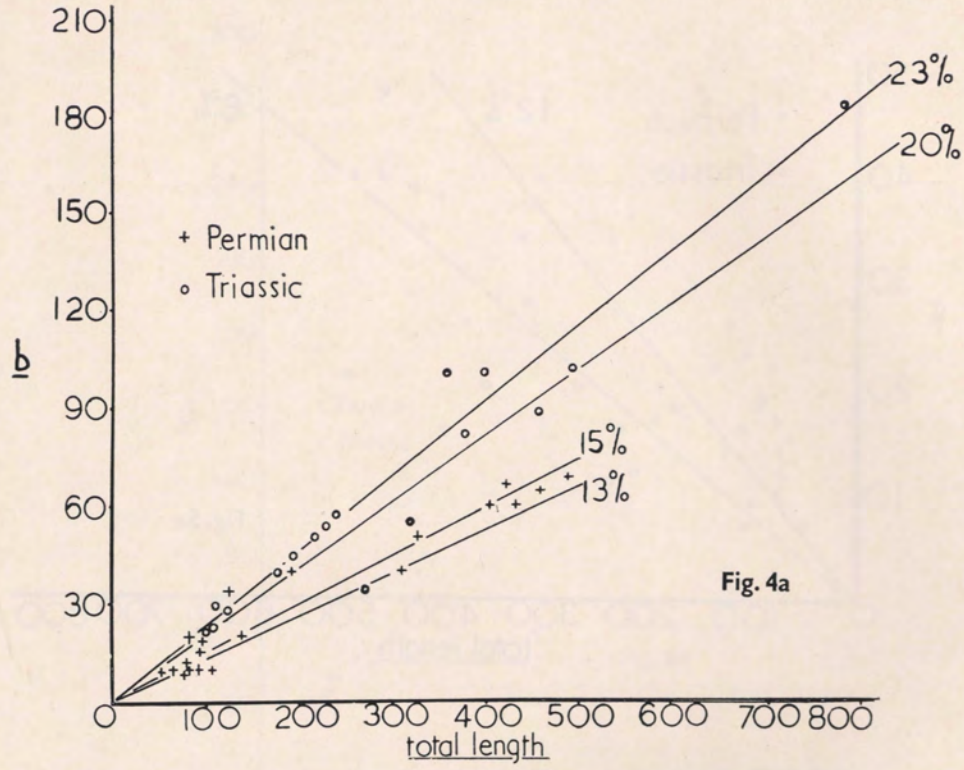
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Fig. 4a

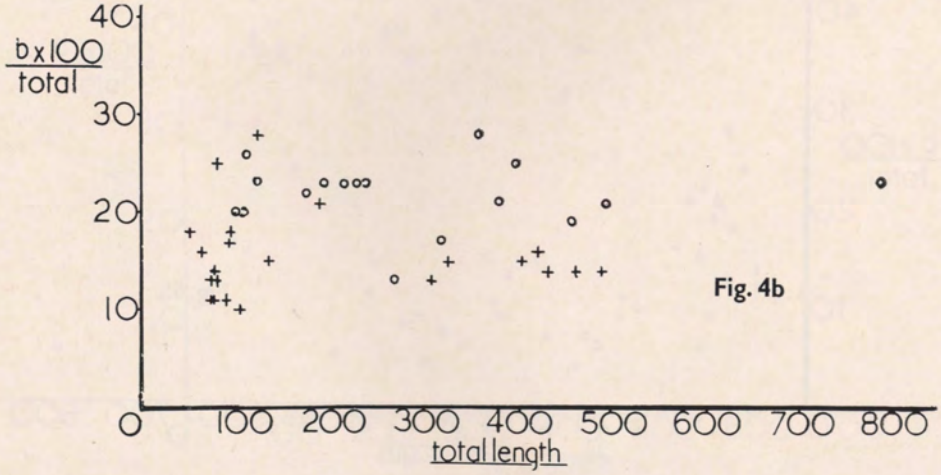
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Fig. 4b

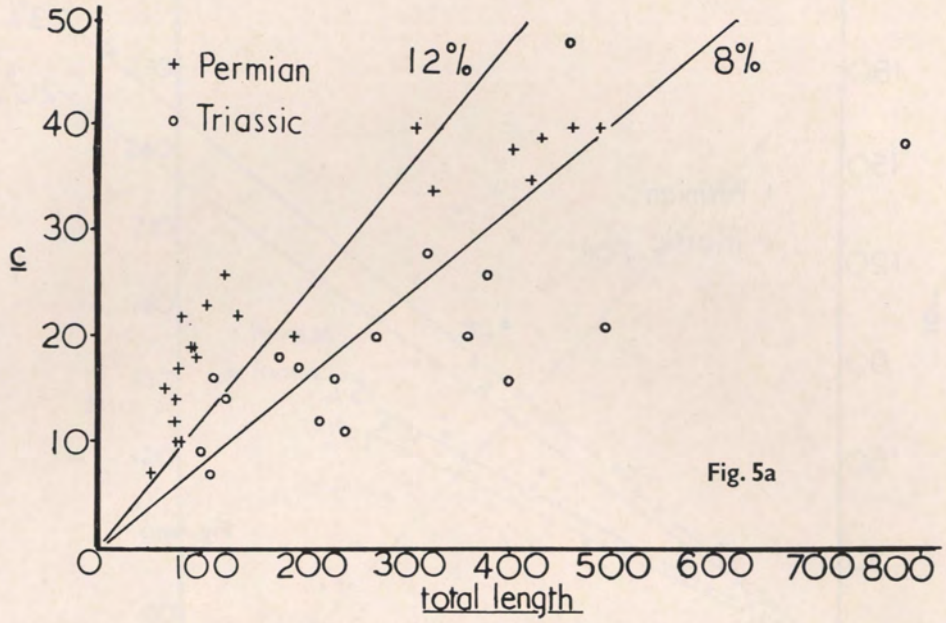
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Fig. 5a

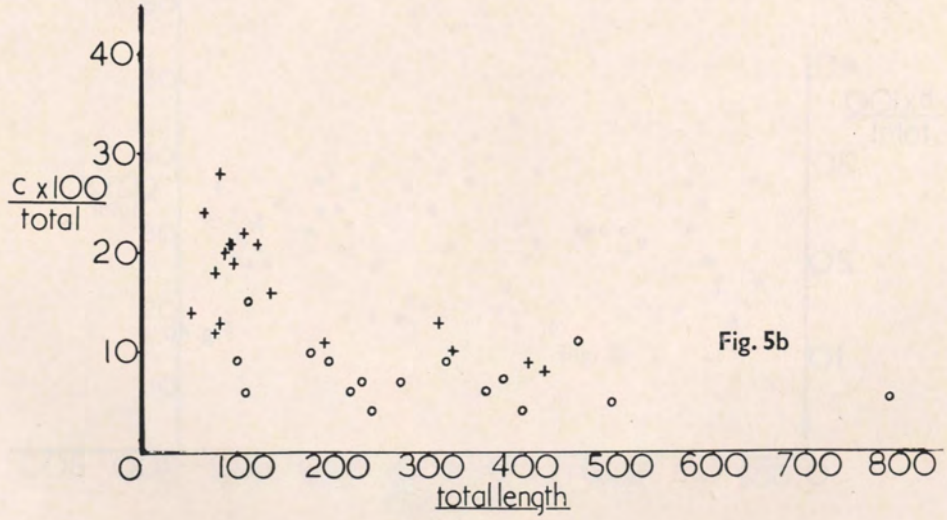
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Fig. 5b

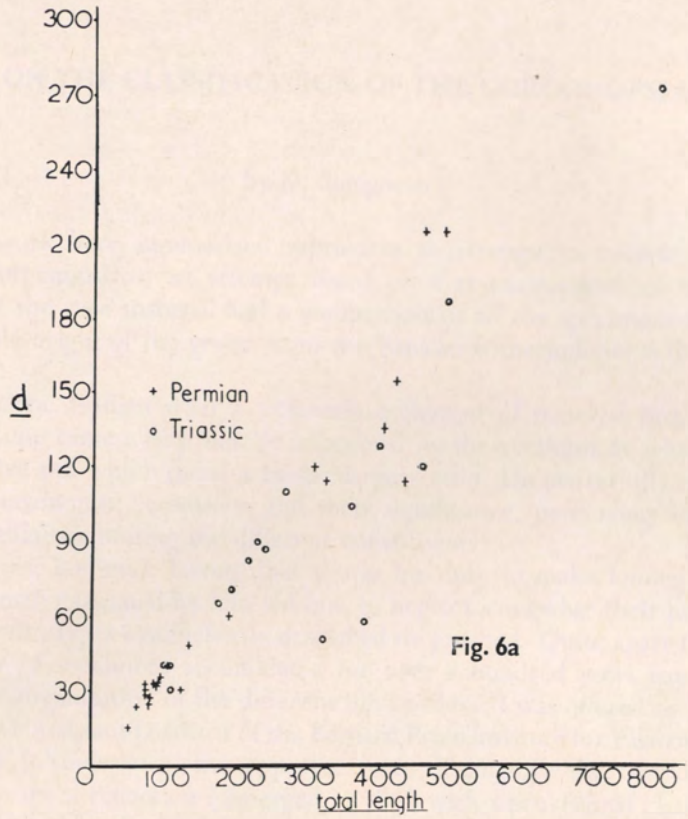
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Fig. 6a

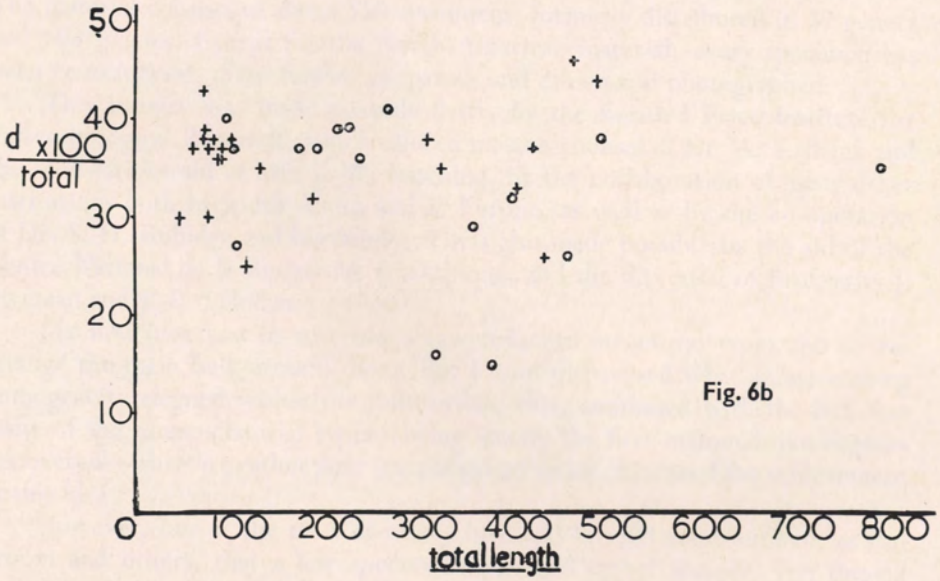
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Fig. 6b

ON THE CLASSIFICATION OF THE GORGONOPSIA

by D. Sigogneau[1]

The work here summarized represents an attempt to review the South African Gorgonopsians, an attempt based on a re-examination of the cranial anatomy of the type material and a comparison of all the specimens available[2]. The possible origin of the group from the Russian eotheriodonts is discussed in conclusion.

When one realizes what a tremendous amount of material Broom had to deal with, one cannot help but be impressed by the synthesis at which he was able to arrive and which remains to-day largely valid. He masterfully recognized the major taxonomic boundaries and their significance, perceiving within each group the affinities uniting the different constituents.

However, his inner feeling that it was his duty to make known each and every specimen examined by him led him to neglect somewhat their preparation and to establish types insufficiently described or justified. Quite apart from that, the number of specimens accumulated for over a hundred years naturally demanded a re-organization of the different infra-orders; I was offered by Dr. A. S. Brink, former Assistant Director of the Bernard Price Institute for Palaeontological Research of Johannesburg, the opportunity to disentangle the Gorgonopsians. After four years of reflection I emerged in 1967 with a provisional classification, the sole pretention of which being to present some new morphological data. The material consists of about 150 specimens, formerly distributed in 67 genera and 108 species. Except for the North American material, every specimen has been re-examined, often further prepared, and drawn and photographed.

This activity was made possible firstly by the Bernard Price Institute for Palaeontological Research, which offered me the counsel of Dr. A. S. Brink and the multifarious aid of Mr. J. W. Kitching, by the collaboration of many other institutions both in South Africa and in Europe, as well as by the co-operation of Dr. S. H. Rubidge and his family. It was also made possible by the aid of the Centre National de la Recherche Scientifique, and the direction of Professors J. Piveteau and J.-P. Lehman.

My first idea was to sort out a few principal structural types and to rearrange the main bulk around them. But I soon discovered what an astonishing homogeneity reigned within the infra-order; this, combined with the fact that many of the nomenclatorial types—being among the first mammal-like reptiles discovered—were in a rather poor state of preservation, hindered the achievement of this idea.

However, out of the mass of nearly identical forms I soon noticed, as had Broom and others, that a few specimens emerged rather sharply. For these I

maintained the family Ictidorhinidae created by Broom, even though I have lately come to doubt the familial status of the group; this will be discussed later.

In this view, the rest of the Gorgonopsians had to be united in a single family, the Gorgonopsidae, and any subdivision within them had to be infra-familial since the anatomic divergences that could be picked out among them were always less in degree than those between them and the Ictidorhinidae. I have therefore been led to distinguish two subfamilies, the Gorgonopsinae and the Rubidgeinae.

Haughton and Brink were the first authors to give generic diagnoses which took into account, in the Gorgonopsidae, the shape of the skull, the particularities of the frontal and the prearietal, the morphology of the palate and the number of post-canines. In a previous article I have already stated the necessity for more criteria, but a few complementary remarks are needed here. It is obvious that, as far as shape is concerned, post-mortem deformation has to be considered, but it is possible that the present shape is more indicative than previously thought; indeed, one may presume that a skull will not generally be deformed in just any manner, but that a narrow skull will be compressed laterally while a wider one will see its width accentuated. Still on the subject of shape, we do not know for sure what modifications are to be expected between juveniles and adults; no more do we know the amplitude of individual variation in this and other characters.

I eventually accorded a generic value to the following ensemble of characters; the general shape of the skull, the size and shape of the temporal fossae, the ratios of the inter-orbital and inter-temporal widths, the shape of the post-orbital, sub-orbital and zygomatic arches, the relation of the frontal to the supra-orbital rim, the presence of the prearietal, the dimensions of the post-frontal and lacrymal, details of the occiput, the degree of ossification of the braincase wall, and the relative position of the pterygoid transverse apophyses. In spite of the number of criteria utilized, it was often difficult to decide to which genus a specimen should be referred, and some of them even did not fit at all into this scheme. One of the reasons for this difficulty is, of course, the fact that as yet very rarely are post-cranial elements known, and this accentuates the artificial character of this classification.

Nevertheless, I arrived, for the family Gorgonopsidae, at a total of 22 genera; these shall be quickly reviewed.

Three of them—*Broomisaurus* Joleaud, *Galesuchus* Haughton and *Eoarctops* Haughton, all monotypic and represented by a single specimen—are among the oldest South African gorgonopsids known, since they come from the bottom of the *Tapinocephalus* zone of the Beaufort series[3]. Unfortunately, they all are in a rather bad state of preservation (one of them is even reduced to a weathered snout), but they show rather clearly that the gorgonopsid structural type was already fully established at this time. Moreover, they do not appear as the most primitive members of the family, if one takes as a point of reference their sphenacodont ancestors. From the same zone, Dr. L. D. Boonstra has collected,

and generously lent to me, other specimens which possess with the above genera a number of common characters, thus making the "*Tapinocephalus* assemblage" a rather homogeneous one. It was therefore tempting to group these specimens in a subfamily, the Galesuchinae. But, for one thing, its definition would not have been really in opposition to that of the two other subfamilies; furthermore there remains the question of what to do with the genera which begin in this zone as "Galesuchinae" (*Aelurosaurus felinus*[4], for example) and continue into the following zone as Gorgonopsinae (*Aelurosaurus wilmanae* (Broom), for example). From these considerations came my decision to maintain this assemblage within the Gorgonopsinae.

Indeed, the genus *Aelurosaurus* Owen, in the form of its type-species, *A. felinus*, would fit perfectly well in the "*Tapinocephalus* assemblage". There is even a good similarity between this species (known only by snouts) and the only species of *Galesuchus*, both in proportions and in details of the bones, and it is not impossible that the two species belong to the same genus; but there remain uncertainties in the palate of *G. gracilis* and in the posterior part of the skull of *Aelurosaurus felinus*; moreover I have now extended the genus *Aelurosaurus* to a number of later species. Thus conceived, it appears as a rather primitive form of small size, as the first representatives of the infra-order might be expected to be; the skull is lightly built, the skull roof relatively narrow, but the snout is already short. The preparietal, anteriorly situated in the type-species, underwent some backward displacement in the two latest species; the facial part of the lacrymal is short and the cheek dentition has begun a reduction, but the transverse apophyses are still found rather posteriorly. Besides the species individualized by Broom, and which I have for the most part maintained, the genus comprises now two other species: *Aelurosaurus* ("*Aelurosauropsis*") *wilmanae* (Broom) and *A.* ("*Galerhinus*") *polyodon* (Broom), as well as an uncertain third, *A.*? ("*Scylacocephalus*") *watermeyeri* (Broom), whose affinities tend also toward *Cyonosaurus*.

Morphologically very close to the preceding comes the genus *Arctognathus* Broom. The differences noted between the two genera are often due to a simple progression: the small forms of the beginning would have increased in size, their snout shortened even more; the frontals would have reduced their participation in the supra-orbital rim, and the preparietal would have become smaller; at the same time the transverse apophyses would have become edentulous. However, one would not have expected, of forms so late, a braincase so little ossified, no more than one would expect, in the course of evolution, the accentuation of the sinuosity in the maxillary alveolar border and the retreat of the pterygoid transverse apophyses. The existence of a specimen attributed to *Arctognathus* in the *Tapinocephalus* zone would seem to confirm my hypothesis that a separation of the two genera has taken place early. "*Lycaenodontoides bathyrhinus*" Haughton is definitely a synonym of the type-species, *Arctognathus curvimola*. It is less sure that "*Arctognathoides*" *breviceps* (Boonstra) finds its place here. As for the inclusion in the genus *Arctognathus* of "*Dixeya*" *nasuta* (von Huene), this remains somewhat

open to discussion, all the more since the details of the cranial roof of this species are not known.

It is not impossible that the small "*Galerhinus*" *rubidgei* of Broom should be, like the type-species "*Galerhinus*" *polyodon*, incorporated in the genus *Aelurosaurus*. But in order to decide it would be necessary to know the modalities of differential growth, for it is perhaps a juvenile form. This uncertainty obliged me—since I had suppressed the type-species—to create for this small skull a new generic name, according to a rule of nomenclature which does not always appear defensible.

The affinity which unites *Aelurosaurus* to *Scylacognathus* Broom (another genus beginning in the *Tapinocephalus* zone) is not less probable, but it occurs on another plane than for *Arctognathus*: it is a question here of two contemporaneous forms not long detached from a common stock. One finds again the short snout and the preparietal anteriorly situated, but a beginning of specialization would appear in the frontal tending to become isolated from the supra-orbital rim, in the inter-orbital roof enlarging, and the post-canines reducing even more in number. Beside synonymizing the two species of Broom, *Sc. parvus* and *Sc.* "*major*", I introduced into the genus the stocky "*Cynariops*" *robustus* (Broom) and the three species "*Cynarioides*" *gracilis* (Broom), *grimbeeki* (Broom) and *laticeps* (Broom).

It seems that *Scylacops* Broom is to *Scylacognathus* what *Arctognathus* was to *Aelurosaurus*. In the course of evolution there would have been an increase in size, an attenuation of the ventral sinuosity of the skull, complete elimination of the frontal from the supra-orbital rim, and forward displacement of the transverse apophyses. These modifications make of *Scylacops* a somewhat evolved genus, even though its prootic remains apparently little ossified. The incorporation of "*Sycocephalus*" *bigendens* (Brink and Kitching) into *Scylacops* has the merit of underlining the resemblance that exists between this genus and *Gorgonops*, a resemblance which does not however, in my opinion, correspond to a close relationship.

Gorgonops torvus, the first Gorgonopsian species to be described, by Owen in 1876, was based on a rather poorly preserved skull. At present the species is represented by four specimens (a fifth one has been serially sectioned), of which only one comes from the *Cistecephalus* zone. Like *Scylacops*, it is a middle-sized form (the type was thought to be juvenile, but further studies and comparisons do not confirm this hypothesis) and, contrary to what was supposed until now, does not appear very primitive. It is true that the snout is still long, the preparietal and the lacrymal well developed, the frontal largely open on to the orbit, the palate provided with an abundance of teeth, and the transverse apophyses remain posterior. But the shape of the skull, the inter-orbital width, the number of post-canines and above all the degree of ossification of the prootic (of which the dorsal and ventral processes close in front of the fifth nerve) testify already to a certain degree of evolution. Furthermore, the most recent specimen of the species is distinguished by a reinforcement of the divers arches, an inter-temporal enlargement, and a reduction of the preparietal and the supra-orbital frontal,

all of which are advances tending to fill in the space between *Gorgonops torvus* and *G. whaitsi*.

The latter constituted previously the type of the genus "*Scymnognathus*" Broom. This form was represented by five specimens, unhappily very fragmentary and poorly preserved, of which three are at present in the collections of the American Museum of Natural History, New York, and were, in consequence, not examined. When Broom created the species, he said that he hesitated to distinguish it generically from *Gorgonops torvus*, and he did not in fact justify his ultimate distinction. However, according to Boonstra, it is a form clearly more evolved than *G. torvus*. A detailed analysis led me back to the first opinion of Broom. For example, going back to the arguments given by Boonstra, one sees that the snout is in fact equally rounded in both cases, the temporal fossae are scarcely more developed in *G. whaitsi*, while the orbits are relatively a little smaller; the tooth row was probably convex in both species, and the ossification of the prootic has progressed equally in the two forms; lastly, the supra-orbital frontal appears a little narrower in *G. whaitsi*, but, as noted above, it is tending toward reduction in the last specimen of *G. torvus*. It is true that there are real differences, such as a great disparity in size and perhaps in the position of the transverse apophyses, but these differences do not, in my view, exceed a generic level. As a matter of fact, the two species appear to be very close to each other, with *G. torvus* remaining slightly retarded. I have considered it possible to include as well in this genus the large "*Gorgonognathus*" *longifrons* (Haughton), whose differences with respect to *G. whaitsi* are only of degree and which, according to its author himself, would only be an advanced form of the latter. I have also adopted Boonstra's opinion according to which "*Leptotrachelus*" Watson would be close to "*Scymnognathus*". The inclusion of "*Chiwetasaurus*" *dixeyi* Haughton in this genus is perhaps more disputable. On the other hand, "*Pachyrhinos*" *kaiseri* (Broili and Schroeder), from the top of the *Tapinocephalus* zone, seems rather clearly related to *G. whaitsi*, even though its type and only specimen is too incomplete for certainty, and though a resemblance between it and *Aloposaurus*? ("*Aloposauroides*") *tenuis* (Brink and Kitching) has been noted: they both show the same particularities of the snout, of the orbits and of the post-orbital arches. But the amplitude of the posterior widening and the position of the transverse apophyses are not known in *G. kaiseri* where, moreover, the post-canines are much larger.

The genus *Aloposaurus* Broom itself remains rather poorly defined, the type-specimen, which I have not seen, being apparently very badly preserved. Its affinities appear to be divided between *Gorgonops* and *Scylacops*.

It is not impossible that there exists also a relationship between the same genus *Gorgonops* and *Leontocephalus* Broom, at least as regards the type-species, *L. cadlei* Broom. But for the time being the affinities of this snout, and the reference of the two other species to this genus, *L.* ? (*Aelurognathus*) *haughtoni* (von Huene), remain doubtful.

Situated more or less at the heart of the Gorgonopsians is the genus *Cyonosaurus* Olson[5]. This essentially replaces the genus *Cyniscops*, established three months later by Broom on a different number of incisors; this number having since been shown to be identical[6] in the two cases there is no longer any reason to separate *Cyonosaurus longiceps* and *Cyniscops longiceps*. We are dealing here with one of the best represented species of all the Gorgonopsians, as well as one of the most primitive. This middle-sized animal has retained, cranially, a long snout; the temporal fossae are also elongated, but not extended posteriorly by ample squamosal wings; the gracility of the arches, like the proportions of the cranial roof, are certainly original, confirmation of which can be seen in the large size of the frontal, preparietal and lacrymal; the same thing applies to the posterior position of the toothed transverse apophyses and the feeble degree of ossification in the prootic; lastly, it is the species which, after "*Galerhinus*" *rubidgei*, has retained the greatest number of small post-canines. Only the downward extension of the lateral postorbital appears evolved in this species, along with the elongated temporal fossae. Two of the other species formerly included in this genus, *Cyonosaurus rubidgei* (Broom) and *C. kitchingi* (Broom) (with which "*Alopecorhynchus rubidgei*" Brink and Kitching has been synonymized), are somewhat more specialised. Of the two others, "*Cyniscops*" *cookei* (Broom) and "*Cyniscops*" *broomianus* (von Huene), the first is now referred to *Arctognathus*, the second synonymized with "*Scylacocephalus*" *watermeyeri* and therefore included with it in *Aelurosaurus*. As has been noted above, the distinction between this genus and *Cyonosaurus* remains, with respect to the latter species, a little vague.

Lycaenops ornatus Broom is almost as primitive as *Cyonosaurus*; in fact, the general shape of the skull appears more sphenacodont-like than that of *Cyonosaurus longiceps*, but the palate is undoubtedly more evolved and the cheek dentition already somewhat reduced. The two other species, *Lycaenops* ("*Lycaenoides*") *angusticeps* (Broom) and *L.* ("*Tigricephalus*") *kingwilli* (Broom), form with the type-species something of a morphological succession by a progressive increase in size, in general massiveness, and a reduction of the preparietal. On the contrary, the three other species remain as primitive as the type. But all three are questioned, *L.?* ("*Tangagorgon*") *tenuirostris* (Boonstra) because of its affinities with *Cyonosaurus*, *L.?* (*Aelurognathus*) *minor* (Brink and Kitching) and *L.?* (*Aelurognathus*) *microdon* (Boonstra) because of their affinities with *Aelurognathus* (Broom and Haughton).

This last genus retains, like *Lycaenops*, a convex dorsal profile and temporal fossae lacking a posterior extension; the prootic is scarcely more evolved and the details of the bones differ little in the two cases. Only a greater massiveness, both general and local, can be noted in *Aelurognathus*, but the basic affinity is indisputable. Besides the synonymization of *A. nyassaensis* Haughton with *A. tigriceps* Broom and Haughton and the suggested exclusion of *A. microdon* and *A. minor*, the principal innovation concerning this genus resides in the incorporation of "*Dixeya*" *quadrata* (Haughton). This species is now well represented and responds in a satisfactory manner to the definition of the genus *Aelurognathus*.

One finds in *Arctops* Watson the general massiveness of *Aelurognathus*, together with the primitive characters of *Lycaenops*. In addition, the cranial roof proportions of *Arctops* seem to me directly inherited from the sphenacodonts, the prootic remains very short anteriorly, and the palate itself has evolved but little: one of the most primitive genera of the Gorgonopsidae is the result. I have thought it possible to include in the type-species, based on the posterior part of the skull, *A.* "*watsoni*" Brink and Kitching, as well as another skull, undescribed. "*Gorgonorhinus*" *minor* (Broom) follows most of the definition of *Arctops*. This genus contains the only new species here proposed of the Gorgonopsidae; the specimen upon which it is based was previously classed in *Aelurognathus minor*, but it seems more comfortably situated in the genus *Arctops*, mostly because of the morphology of the ventral surface of the skull. The above discussion stresses the affinity which unites *Arctops* and *Aelurognathus*.

The species *Arctops?* ("*Smilesaurus*") *ferox* (Broom) (="*Pardocephalus*" Broom) offers another testimony to this affinity; indeed it allies not only *Arctops* to *Aelurognathus* but both of them to *Lycaenops*, morphologically extending just beyond *L. kingwilli* in the sequence already mentioned (*L. ornatus*, *L. angusticeps*, *L. kingwilli*). At the same time *Arctops? ferox* considerably evokes *A. willistoni*, by its form, its massiveness (increased here), its posterior width, the proportions of the cranial roof, and the large size of the post-canines (fewer in number); the palate, on the contrary, is like that of *Aelurognathus*. The choice of *Arctops* for this species derives from the fact that the only difference between this genus and "*Smilesaurus*" is one of an order of evolution (advancement of the pterygoid transverse apophyses), whereas in order to go from *Aelurognathus* or *Lycaenops* to "*Smilesaurus*", one must imagine a "regression" (inter-orbital shrinking for the first, inter-temporal widening for both). But it would perhaps have been preferable to simply retain the genus "*Smilesaurus*", all the more since the Russian *Inostrancevia* Amalitzki seems to have affinities with this form.

Within this ensemble, restricted to a narrow evolutionary framework, was however born another survival attempt in the form of the Rubidgeinae. This attempt consisted essentially in an increase of the power of aggressivity, manifested by larger size, the reinforcement of the snout and the development of the anterior dentition at the expense of the post-canines. The widening of the cranial roof and of the diverse arches must have corresponded to more extensive muscle insertions, as did, presumably, the hollowing of the occiput. Perhaps the tendency toward closure of the cerebral wall by the coming together of the prootic and the orbitosphenoid could be interpreted in the same sense (it should be noted that the epipterygoid not only remains always exterior to the wall, but that it never manifests any tendency to widen). At the same time and as in all the large forms, one is confronted with a reduction of the preparietal and a retreat of the frontal from the supra-orbital rim.

This attempt appears timidly in *Sycosaurus* Haughton, is expressed more or less clearly in *Prorubidgea* Broom and *Clelandina* Broom, and attains its full

development in *Dinogorgon* Broom and *Rubidgea* Broom; the succession thus evoked remains for the most part purely morphological.

Sycosaurus somewhat brings to mind *Scylacops*, with its snout scarcely as high as wide and narrowed anteriorly, and with the posterior broadening of the skull. But the large size of the post-canines and the posterior situation of the transverse apophyses also remind one of *Arctops*. Be that as it may, the specialization of the cranial roof has already advanced and one can note an incipient zygomatic widening in *Sycosaurus laticeps* and *S.* ("*Leontosaurus*") *vanderhorsti* (Broom), but less clearly in *S.*? (*Lycaenops*) *kingoriensis* (von Huene). As for the species "*Sycosaurus*" *brodiei* Broom, it seems to me to participate more directly in the following genus.

Prorubidgea Broom appears derived more or less directly from a form close to *Aelurognathus*: one finds again the elevated shape of the skull with its rounded snout, the small orbits and the transverse apophyses anteriorly situated (with one exception). The zygomatic arches and the cranial roof, while more evolved than in *Aelurognathus*, are less so than in *Sycosaurus*, which might explain the exclusion of *Prorubidgea* from the Rubidgeidae by Haughton and Brink (but not Watson and Romer). The various species of this genus have diversely developed the generic plan, but their affinities with each other seem to me difficult to question.

From a strictly morphological point of view, *Dinogorgon* Broom prolongs in a very satisfactory fashion *Prorubidgea*. Not only is the shape the same and the orbits of similar proportions, but the only differences that one can find constitute evolutionary advances with respect to *Prorubidgea*: the cranial roof is barely enlarged and there are still five post-canines, but neither a preparietal nor a supra-orbital frontal exist any longer; the ventral zygomatic apophyses are strongly developed, and the pterygoid transverse apophyses are placed even more anteriorly. Lastly, an elongate swelling is formed, increasing the thickness of the supra-orbital rim, which extends onto the post-orbital arch in the form of an oblique ridge.

It seems to me that there is an identity between the three species previously attributed to this genus. I would go even further and consider this single species as referable to the genus *Rubidgea* Broom. But *Dinogorgon* was created first and on a snout in rather poor condition; the synonymy of the two genera would lead me to base all this assemblage on an incomplete specimen, a deed that would always be open to suspicion. Consequently, *Rubidgea* is maintained.

This genus *Rubidgea* prolongs in turn (especially in the form of *R. atrox*) the *Dinogorgon* "stage"; the maximum of force developed in the Gorgonopsians is attained here. The development of the cranial roof is such that the small orbits are practically invisible dorsally, and the zygomatic projection is so developed that it constitutes the most ventral point of the skull; the post-canines are reduced to one or two and the palatine teeth tend to disappear. The divergences that are visible between the three principal specimens do not seem easily attributable to individual variation. As for the skull of "*Tigrisaurus*" *pricei* Broom, this appears to me too incomplete to permit its attribution to any of the three recognized species.

It remains to discuss, in this subfamily, two forms which are rather exceptional by the width of their skull: this width is only extreme in the small *Clelandina rubidgei* Broom and *C.* (''*Dracocephalus*'') *scheepersi* (Brink and Kitching); it becomes extraordinary in *Broomicephalus laticeps* Brink and Kitching (= *Rubidgea laticeps* Broom) since here it exceeds the skull length. The last-named species has attained a level of specialization identical to that of the other *Rubidgea* and was previously classified in the same genus. However, I have tried to maintain a consistency with the rest of this classification by following Brink's suggestion and by placing it in a parallel genus.

It does appear that this specialization of the Rubidgeinae was fatal; there, where suppleness and invention were needed in order to adapt to ecologic change, they reacted with a deploying of force and an increase in power and aggressiveness. It is perhaps not just due to chance that the only Gorgonopsian found in the *Lystrosaurus* zone belongs to the genus considered as the most primitive, *Cyonosaurus*.

The Ictidorhinidae still remain very poorly known; at present only nine specimens are available[7]. They contrast with the Gorgonopsidae in the shape of the skull (very convex in dorsal profile), in the small size of the temporal fossae and the large size of the orbits, in the constitution of the basicranium, in the stage of evolution of the mandible (lack of a coronoid apophysis, reflected lamina of the angular reaching posteriorly to the articular region), and in the persistence of numerous and small post-canines. One notes, however, that a certain number of characters as significant as the position of the vomer and its shape, the position of the nostrils, and the nature of the teeth are not constant within the group. And even characters common to all the specimens (like the inter-temporal width, the proportions of the orbits and the temporal fossae) may in fact have a different significance according to the case. It thus appears probable that in an early form like *Hipposaurus* (from the base of the *Tapinocephalus* zone) these particularities, exemplified in moderation, only testify to an especially primitive state. On the contrary, in forms like *Lemurosaurus* Broom or *Ictidorhinus* Broom (which are as late as *Rubidgea*) these traits, which are here particularly evident, could indicate a specialized state. Under these conditions one can wonder if the status of this group is really taxonomically equivalent to that of the Gorgonopsidae (the generic criteria are not only different in the two cases but of inequal value), or if we are dealing with an infra-ordinal unit; the presence of a preparietal and the absence of a parietal crest do not require *ipso facto* a gorgonopsian identification.

But for the time being, this ''family'' comprises the four genera previously recognized, to which must be added the type of the infra-order Rubidginoidea, *Rubidgina* Broom. Of these five forms, as we have already noted, *Hipposaurus* appears as the least specialized; it seems also that the genus tended toward the gorgonopsid structural type: its vomer appears to have been already deeply situated (but its shape remains incompletely known) and the septomaxillary presents a transversal blade dividing the nostril into two compartments. What is more, an undescribed specimen (generously put at my disposal by Boonstra) that

I have referred to this genus differs from the type-species by the greater size of the temporal fossae and the beginning of a flattening of the cranial profile, accompanied by a correlative displacement of the nostrils; there is also a retreat of the mandibular and occipital articulations. These are all advances which make of it an intermediary between *Hipposaurus boonstrai* and the Gorgonopsidae. One may, however, object to this reasoning, based mostly on the generic identification of S.A.M. 122252 (object all the more since the anterior position of the occipital condyle is probably not an eo-gorgonopsid character). Recent information from Boonstra indicating that the stapes of *H. boonstrai* lacks a stapedial foramen contributes to this ambiguity.

Lycaenodon longiceps Broom (''*Hipposauroides rubidgei*'' Broom), known only by two anterior skull portions, approaches *Hipposaurus* by the proportions of the orbits and the temporal fossae. But the skull must have been wider and lower, evoking somewhat the Russian brithopodid *Syodon*. In fact, a certain parallelism with this family is found here in the length of the dorsal premaxillary processes, the constitution of the septomaxillary, the superficial position of the vomer and its concave form, in the reduction of the palatal tuberosities and in the position and form of the canines. However, it does not seem that one has here even an incipient indication of the inter-temporal constriction and the post-orbital twisting characteristic of this family.

The present position of the nostrils in the single specimen of *Ictidorhinus martinsi* Broom seems extremely suspicious, all the more since the septomaxillary appears to be of the same type as in *Lycaenodon* and that the vomer retains the same position and form. But the inter-orbital roof is here so wide posteriorly that the enormous orbits are masked in dorsal view, and the length of the temporal fossae is reduced to one third of the orbits. The opisthotic-quadrate contact is wide in posterior view (from which one may deduce that there was no coronoid process in the lower jaw). Nothing is known of the cheek dentition of the genus.

In *Lemurosaurus pricei* Broom one observes the same development of the orbits and the cranial roof, but, as in *Hipposaurus*, the vomer would occupy a dorsal position while the occipital condyle and the quadrate would be slightly displaced anteriorly. The great particularity of this skull (if one does not dwell upon the strange formation which covers the bone) resides in its dentition: its first anterior elements intermesh with corresponding teeth of the lower jaw and develop an incipient lingual talon. The post-canines themselves are more symmetrical and more coarsely denticulated than is usual in Gorgonopsians. The dental particularities bring to mind the condition in the Brithopodidae and the Dinocephalia.

If there is no doubt that *Rubidgina* can be integrated within this assemblage, it is less certain that it would not belong to the genus *Lemurosaurus*. The proportions of the orbits and the temporal fossae are similar, the upper and lower anterior incisors must have intermeshed, and the post-canines present a comparable morphology. But the details of the dentition in the other genera are not

known; moreover, the palatal dentigerous tuberosities are here much longer than in *Lemurosaurus*, and the proportions of the snout and of the inter-orbital roof are different. This could be only an effect of its small size or it could indicate a juvenile state (contradicted, though, by the size of the foramen magnum). However that may be, there do not seem to have been sub-orbital vacuities on the palate, as Broom suggested.

There remains a very small, hitherto undescribed, snout that I have referred to this family. The intermeshing of the first incisors and their incipient talon induced me to refer it at first to *Lemurosaurus*. However, the shape of the snout, for one thing, and of the palate (vomer and palatal tuberosities) for another, are very similar to those of *Lycaenodon*, but it should be kept in mind that the dental morphology is unknown in this genus.

The multiplicity of combinations of primitive and specialized characters would not be surprising did they not concern points as important as those cited above. But perhaps, morphologically, we are here at the heart of the great theriodont-anomodont subdivision; the resemblances of the Ictidorhinidae to the Russian eotheriodonts (*sensu lato*) would tend to confirm this interpretation. These resemblances left us also with the hope of finding there the origin of the Gorgonopsians.

Biarmosuchus Chudinov, one of the genera from the base of the Russian late Permian, strangely resembles the genus *Hipposaurus*. They both display the same cranial shape, the same proportions of the orbits and the temporal fossae, the same relation between the inter-orbital and the inter-temporal widths, the same position of the nostrils, the same orientation of the occiput, the same length of the prefrontals and lacrymals, the same position of the suspensorium, the same degree of evolution of the palate and the common persistence of numerous post-canines. The mandible in both cases is also very similar (absence of a coronoid process, posterior position of the reflected lamina of the angular). Lastly, the elements of the skeleton present the same gracility in the two genera. However, not only does *Biarmosuchus* lack those specializations of the Gorgonopsians already developed in *Hipposaurus*, but it has developed others, which orient it more in the direction of the brithopodids. We cite in particular the beginning of twisting in the post-orbital arch, with, correlatively, an incipient opening of the inter-temporal roof. The fact that the vomer is already deep and the stapes perforated is not in opposition to this interpretation; it only indicates that, on the brithopodid stem, a parallel, if not ancestral, line to ictidorhinids[8] would have rapidly developed.

The two other principal Russian eotheriodont genera, *Eotitanosuchus* Chudinov and *Phtinosuchus* Efremov, do not seem to provide us with more fruitful results. I have seen on these two skulls the same beginning of torsion of the post-orbital arch which, it seems to me, immediately isolates them from the gorgonopsian path. But, for *Eotitanosuchus* at least, evolution would have paralleled the gorgonopsids rather than the ictidorhinids.

The conclusion of this research on gorgonopsian origins remains therefore still rather negative. There is, however, no doubt that it is in detailing and enriching our knowledge of these intermediary forms—the ictidorhinids and the eotheriodonts—that the untangling of the threads of this evolution will be accomplished. All that can be said at present, in agreement with Boonstra, is that this theriodont branch became individualized early and quite probably rather rapidly. It thus arrived at a structure which was later but little modified and which found in this very precociousness the cause of its evolutionary sterility.

I

GENERA RETAINED*

Aelurognathus	Aelurosaurus
Aloposaurus	Arctognathus
Arctops	Broomicephalus
Broomisaurus	Cerdorhinus
Clelandina	Cyonosaurus
Dinogorgon	Eoarctops
Galesuchus	Gorgonops
Leontocephalus	Lycaenops
Prorubidgea	Rubidgea
Scylacops	Sycosaurus
Hipposaurus	Ictidorhinus
Lemurosaurus	Lycaenodon

Rubidgina

* Only type-species are considered here.

II

GENERA SYNONYMIZED*	WITH

1—*Gorgonopsidae*

Aelurosauroides	Aelurosaurus
Aelurosauropsis	Aelurosaurus
Alopecorhynchus	Cyonosaurus
Aloposauroides	Aloposaurus?
Arctognathoides	Arctognathus
Chiwetasaurus	Gorgonops
Cynarioides	Aloposaurus?
Cynariops	Scylacognathus
Cyniscops	Cyonosaurus
Cyniscopoides	Cyonosaurus
Dixeya	Aelurognathus
Dracocephalus	Clelandina
Galerhinus	Aelurosaurus
Galerhynchus	Cerdorhinus?
Gorgonognathus	Gorgonops
Leontosaurus	Sycosaurus
Leptotrachelus	Gorgonops
Lycaenodontoides	Arctognathus
Lycaenoides	Lycaenops
Nanogorgon	Aelurosaurus?
Pachyrhinos	Gorgonops
Pardocephalus	Arctops?
Scylacocephalus	Aelurosaurus?
Scymnognathus	Gorgonops
Smilesaurus	Arctops?
Sycocephalus	Scylacops
Tangagorgon	Lycaenops?
Tigricephalus	Lycaenops
Tigrisaurus	Rubidgea

* Only type-species are considered here.

2— *Ictidorhinidae*

Hipposauroides	Lycaenodon

III

UNCERTAIN GENERA

Arctosuchus
Cyniscodon
Delphaciognathus
Genovum
Lycosaurus
Cerdognathus
Cynodraco
Eriphostoma
Gorgonorhinus
Tetraodon

Tigrisuchus

1 Institut de Paléontologie, Muséum National d'Histoire Naturelle, Paris.

2 Exception made of those in the collections of North America.

3 In fact six genera are known from this zone, but the three others, continuing into the upper zones, will be discussed further on.

4 In the form of "*Aelurosauroides watsoni*" Boonstra.

5 Which I consider as homologous to *Cerdorhinus* Broom; but the law of priority would have demanded the abandonment of *Cyonosaurus* and the acceptance of *Cerdorhinus*, which I could not compel myself to do.

6 It still seems doubtful that any Gorgonopsian has less than five incisors.

7 Not counting the type of *Pseudohipposaurus kitchingi* Broom, which I was not able to locate.

8 It is not impossible that there was in *Biarmosuchus* some intermeshing of the incisors.

ON THE SCALOPOSAURID SKULL OF *OLIVIERIA PARRINGTONI*, BRINK WITH A NOTE ON THE ORIGIN OF HAIR

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Olivieria parringtoni was described by Brink in 1965 as a new genus and species. It stands closest, among the scaloposaurids, to *Ictidosuchops intermedius* (Broom). In general shape and size, their skulls are virtually indistinguishable from one another, but *Olivieria* comes from the top of the *Lystrosaurus*-zone (early Triassic) while the type-locality of *I. intermedius* is the *Cistecephalus*-zone (Upper Permian). Differences in dentition and differences in detailed skull moulding had argued for the creation of the new genus.

The writer undertook an examination of the type specimen of *Olivieria* because it seemed well suited to a study of the sensory nerve supply of the muzzle. Ever since Watson (1931) suggested that one might gauge the sensitivity, suppleness and therefore the possible hairiness of the muzzle by studying the size, numbers and position of the sensory nerve foramina in the fossil skull, it has seemed likely to point, albeit indirectly, to the origin of hair in the pre-mammalian stem. Such an abundance of nerves supplying the muzzle in scaloposaurid and bauriamorph reptiles would hardly be needed for scaly and inelastic cheeks. More probably, as Brink (1956) has emphasized, a mammalian type of tactile hair with soft cheeks had already come into being in these animals.

Proof for the existence of hair in these fossil animals is lacking entirely, yet there are several points favouring this idea. Firstly, the scaloposaurid-bauriamorph line is thought to be close to the mammalian stem where hair growth could be expected. Secondly, evidence from the structure and function of the eye in living mammals makes it likely that mammals are descended from a nocturnal reptilian stem with dark-adapted eyes (Walls, 1942). In such animals, sensitive tactile hairs would make up for poor vision at night. Thirdly, if the animal was adapted to life at night, the need to remain active and warm in the cold would be favoured by an insulating hairy coat. Such a dependence on touch, warmth in cold surroundings and a dominance of sound over sight would represent the preliminary ecological niche required for ground-living reptiles to emerge in due course as mammals.

The original description of *Olivieria* was based on an external preparation of the skull, principally of the left side. It seemed desirable to clean the right side and extend the preparation into areas hitherto conjectural or unknown. Camera lucida drawings of these new views are presented here (Figs. 1–5),

comprising the snout, orbit, temporal fossa, occiput and the ventral surface as far as preparation was possible without disarticulating the lower jaw. The two maxillae were also investigated for their foraminal patterns, and these have been illustrated (Figs. 6–7). To facilitate comparison and avoid duplication, the writer would advise reference to Crompton's (1955) text on *I. intermedius* as a guide to these illustrations. Crompton's lettering has also been adopted. The probable course of the trigeminal branches from the base of the epipterygoid, through the lacrymal and out through the sidewall of the snout can be deduced by conjecture from the foramina.

Comment

As no full description is necessary, only certain points of opinion will be noted.

(i) Brink's text and drawings (Figs. 49 and 50) are at variance. Five upper incisors are described and four are illustrated. The correct number is four according to my examination (Fig. 1).

(ii) The snout is shaped like the prow of a boat (Fig. 6) and is not rounded as restorations might suggest. The shape of the front ends of the nasals is not therefore a significant or dependable character because of ready damage to this region.

(iii) With one "incisor" less, there is one more canine in the maxilla—four on the left and possibly even five on the right (Figs. 6–7). There are three postcanines in both maxillae, as Brink described.

(iv) In *Olivieria* the incisors are bigger and fewer and occupy twice the space as compared with *I. intermedius*. The main canine is also a little longer and situated farther back along the alveolar margin. This produces a broader and bolder front half of the mouth, associated with an insignificant post-canine portion. In *I. intermedius* the teeth are smaller, more numerous, more evenly functional and are arranged on an alveolar margin with more nearly parallel sides along the palate.

(v) With this separation of the mouth in *Olivieria* into a more stumpy, butt-like front portion and a virtually non-biting back portion behind the main canine, one finds the internal nares flaring widely and coming level with the buccal cavity near the main canine. In *I. intermedius* this levelling takes place behind the last postcanine.

(vi) The alveolar arcade of the maxilla and premaxilla forms a U-shaped curve about 87 mm. long, measured from the posterior end of the alveolar fold on either side round the outer borders of the teeth. On Crompton's figures the same distance in *I. intermedius* is a little more—say 90 mm. The available tooth space is therefore about the same, the final dental formula being determined by tooth size, and by the maxillary tooth which becomes the main canine.

(vii) Along with this heavier front part of the mouth, the temporal and occipital muscles were clearly much stronger than in *I. intermedius*. Thus, the

parietals, squamosals, as well as their occipital counterparts, are sharply crested (Fig. 4). This difference leads to some re-shaping of the details in the upper half of the skull without altering either gross external measurements or the ventral surface of the skull as compared with *I. intermedius*. In the lower jaw, the dentary also becomes straighter, but not longer (80 mm.).

(viii) To interpret the bony structure in terms of biting function, one may investigate the way in which the tooth rows are stabilised across the skull in relation to the jaw joint. On the ventral surface, the bony support of the upper jaws from the jaw joint is arranged across the skull in a simple X-shaped pattern. If one draws a line from the jaw joint on one side to the posterior end of the alveolar margin of the maxilla of the opposite side, this line lies neatly along the quadrate ramus of the pterygoid, crosses the midline at the interpterygoid vacuity where, in this specimen, the pterygoid is heavily keeled anteriorly, and passes up the palatine to the hind end of the maxilla in the mouth. Except for the presence of a pterygoid keel, these relationships are the same in *Olivieria* and *I. intermedius*. Fig. 5 shows these points in part.

(ix) On the dorsum of the skull, the two limbs of the X-pattern are not the simple intersecting straight lines as described above. With the cresting of the parietals, this bone appears pinched together just above the epipterygoids and behind the pineal, at a point where the epipterygoid summits are only 10 mm. across (Fig. 4). From this area, where the limbs of the X appear to be fastened together as with a short tie-rod, the posterior limbs of the X curve out to the quadrates along the bony parietal and squamosal plates. The front limbs of the X, and the associated bony ridges on the skull roof, are clearly directed towards the root of the main canine.

(x) It would appear as if all other differences in skull form are subservient to this strengthening of the jaws as compared with *I. intermedius*. The top of the epipterygoid and the pineal foramen would be squeezed or pulled farther forward and the upper orbital margins would be outwardly displaced by increasing participation of the strengthened frontals. The prootic would have its anterior end turned more sharply medially by the posterior buttressing of the skull. These rotations, strengthenings and adjustments would lead to a relative constriction behind the canines, a virtual enlargement of the cavum epiptericum, a shift of the internal nares and a broadening in the form of the commencing secondary palate, a ready forward shift of the postorbital bar and a possible exclusion of the supraoccipital from the temporal fossa.

(xi) From Crompton's account of *I. intermedius*, it is clear that the connection between the X-shaped central skull structure and the back and base of the skull may not be united by closed sutures. The significance of this kinetism or looseness in structure, even in the components of the X itself, has been related to three things: ability to take bigger bites, ability to absorb shock during biting, ability for the bones to give way to an expanding brain. As will be noted below in the case of the hair, an evolutionary trend may well be established because of a group of minor advantages accruing simultaneously. A study of *Olivieria* shows

a combination of more powerful biting, a cramped brain space, a reduction in kinetism and a more reptilian palate. *I. intermedius* shows a less powerful bite, a more mammalian palate, a less cramped brain and more kinetism. It seems therefore as if kinetism, or failure of certain sutures to unite, may be a combined feature related more to a weaker dentition and greater brain growth—an evolutionary compromise resembling paedomorphism, and not the result of more violent eating habits alone. Violent eating would lead, *per se*, to loss of kinetism.

(xii) If the above interpretation of the skull structure in *Olivieria* is accepted, then this specimen must be regarded as a late form of *Ictidosuchops intermedius* in which a carnivorous habit was accentuated, associated with stabilization of the skull and loss of kinetism, and constriction of the cranial cavity.

Significance Of The Foramina For The Origin Of Hair

In *Olivieria parringtoni* there are to be found on each maxilla a large number of foramina which diverge and branch out over the outer surface of the bone. They appear to radiate from an imaginary central point which can be placed quite readily in the region of the main canine root. In the bone below the incisors of the dentary, the outer surface is likewise perforated by a number of foramina.

The only structures likely to have lain in the grooves on the maxilla are branches of the maxillary division of the trigeminal nerve. Among the alternative possibilities, arteries and veins to this area come from the external carotid and jugular systems, and would not enter or leave the cheek through the bone. Compound glands supplying the mouth or nose would, if they were the cause of the grooving, show a converging pattern of ducts from the acini and not a divergence from their acinar ends, as would have to be the case here if glands lay in the grooves. As causes of the grooving, none of these alternatives seems likely.

In mammals, the greatest part of the infra-orbital branch of the maxillary division of the trigeminal nerve usually reaches the cheek from the interior of the maxilla through the infra-orbital foramen. This foramen is situated not far from the canine root, and thereafter the nerves break up into a plexus in the tissues of the cheek. In the same way the mental branch of the inferior dental nerve reaches the chin by a single foramen. In the mammal-like reptile under discussion, one cannot help supposing that an earlier arrangement is present, wherein the nerve branches break up *inside* the bone to start with, and they reach the outside through a host of separate openings. A later mammalian development would comprise a transfer of the nerve plexus to the external surface of the bone, thus consolidating and confining the foramina to a few strategic points of more constant position.

Since the cheeks and chin are the sites in mammals of tactile vibrissae belonging to the infra-orbital, jugal, labial, angular and sub-mental groups supplied by the second and third divisions of the trigeminal nerve, one is justified in thinking that these mammal-like reptiles possessed sensory organs of similar importance in this area. It seems to matter little in principle whether these

sensory organs were activated by hairs or by some amplifying receptor which was converted eventually into a true hair. The difference depends on one important consideration only—how far did the amplifying receptor project? Tactile spots which exist in modern reptiles, and lie between the scales, require a touch stimulus which is applied directly on to the body surface. For an animal moving at night such a system would be highly unsatisfactory, since manoeuvrability and speed depend on having evidence of a safe span on all sides.

Although mammalian hair, once present, has been put in different species to numerous new uses, principally defensive or communicative in one way or another, the question as to whether hair was initially tactile or thermoregulatory in origin seems somewhat artificial. With the growth of hairs from the body surface the sensory enhancement and thermal resistance would both develop at the same time. Subsequent differentiation in texture and length would favour the one or the other function by further selection.

Palaeontology offers little help on the origin of body hair, although Broili (1941) has brought forward some evidence for its presence in extinct flying reptiles. The facts reviewed here, however, make it seem possible that hair arose in reptiles perhaps as far back as the Upper Permian, and that tactile vibrissae may have been one of the earliest types of hair to become differentiated. Their very early appearance in the skin of mammalian embryos may not merely be a sign of their greater complexity of development, but could point to their establishment far back in phylogeny.

Summary

In a study of the scaloposaurid skull of *Olivieria parringtoni*, it was concluded that it was a late relative of *Ictidosuchops intermedius* with a stronger carnivorous habit, but with little to separate them in other respects. Indirect evidence for the presence of hair in these mammal-like reptiles is discussed in the light of palaeontological and other evidence.

Acknowledgments

The writer wishes to thank the Bernard Price Institute of Palaeontology for loan of the specimen of *Olivieria*, and the Photobiology Research Group, C.S.I.R., whose facilities were used in part during the present study.

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EXPLANATIONS OF TEXT FIGURES

Fig. 1 —*Olivieria parringtoni*. View of snout showing foramina in the dentary.

Fig. 2 —View of right half of occiput. Skull tilted to show part of ventral surface. Intervening stapes and hyoid apparatus removed.

Fig. 3 —View of right orbital region seen from above.

Fig. 4 —View of right temporal fossa, seen obliquely from tle dorsolateral aspect with the jugal arch removed.

Fig. 5 —Ventral view of skull. The jugal arch is removed, and the anterior point of the preparation goes forward to a point where the vomer and maxilla are 1-2 mm. apart.

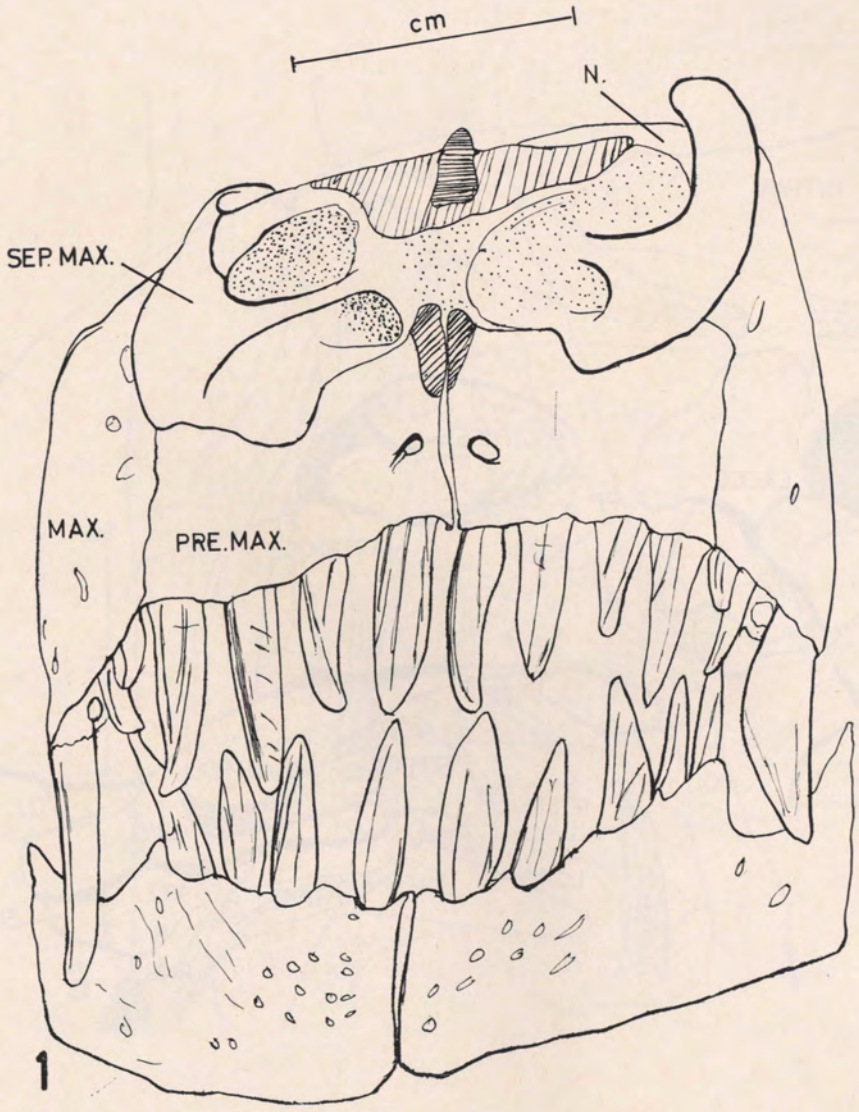
Figs. 6-7 —Lateral views of the right and left maxillae respectively. The alveolar portion of the maxilla extends about 8 mm. behind the last post canine.

KEY TO LETTERING OF FIGURES

A.D.P.	Anterior dorsal process of the periotic.
ANG.	Angular.
ART.	Articular.
A.V.P.	Anterior ventral process of the periotic.
BO.	Basioccipital.
BP. PROC.	Basipterygoid process.
BS.	Basisphenoid.
CAV. EPI.	Cavum epiptericum.
COR. PROC.	Coronoid process.
EPI.	Epipterygoid.
EX. OCC.	Exoccipital.
F.	Frontal.
I.C.	Internal carotid foramina.
INT. VAC.	Interpterygoid vacuity.
INT. PAR.	Interparietal.
J.	Jugal.
JC.	Jugular canal.
LAC.	Lacrymal.
LAC. FOR.	Lacrymal foramen.
LO. RG.	Longitudinal ridge.
MAST. PROC.	Mastoid process (paroccipital).
MAX.	Maxilla.
M.P. SQ.	Mastoid process (squamosal).
N.	Nasal.
P.	Parietal.
PAL.	Palatine.
PF.	Prefrontal.
PIN.	Pineal foramen.
PIT. FOS.	Pituitary fossa.
PO.	Postorbital.

Key to Lettering of Figures continued

POST. FOSS.	Post-temporal fossa.
P.P.	Paroccipital process.
P.P.E.	Pterygoid process of epipterygoid.
PRE. ART.	Prearticular.
PRE. MAX.	Premaxilla.
PRO.	Prootic.
PS.	Parasphenoid.
PTER.	Pterygoid.
PT. PROC.	Pterygoid process of the quadrate.
QJ.	Quadratojugal.
Q.R.P.	Quadrate ramus of the pterygoid.
QUAD.	Quadrate.
QUAD. PROC.	Quadrate process of the paroccipital.
SCL. PL.	Sclerotic plates.
SEP. MAX.	Septomaxillary.
SPL.	Splenial.
SQ.	Squamosal.
SQ. PROC. 1, 2 and 3	First, second and third processes of the squamosal.
ST.	Stapes.
ST. PROC.	Stapedial process.
SUP. OCC.	Supraoccipital.
SUR. ANG.	Surangular.
S.V.	Suborbital vacuity.
TAB.	Tabular.
TRAV.	Transversum.
V.	Vomer.
V 2 and 3	Notch in epipterygoid for 2nd and 3rd divisions of the trigeminal nerve.
VII	Foramen for facial nerve.
XII	Hypoglossal nerve foramen.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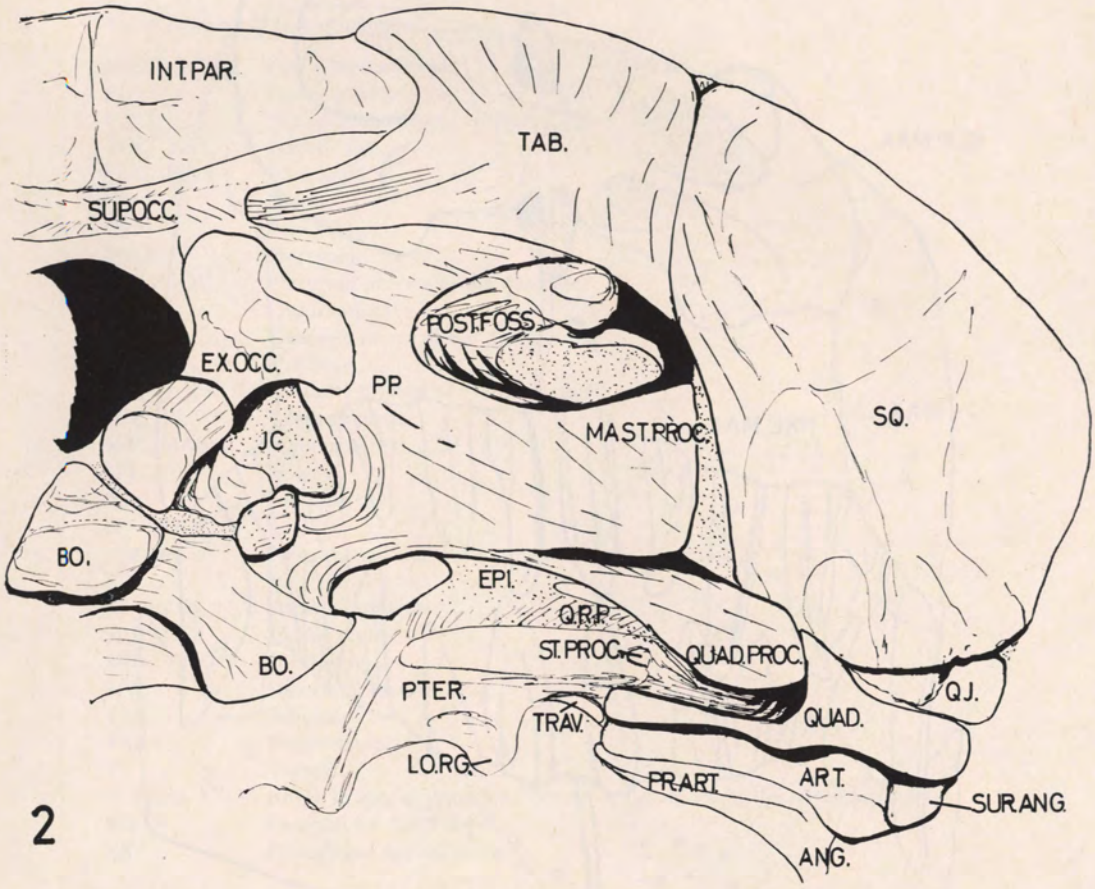
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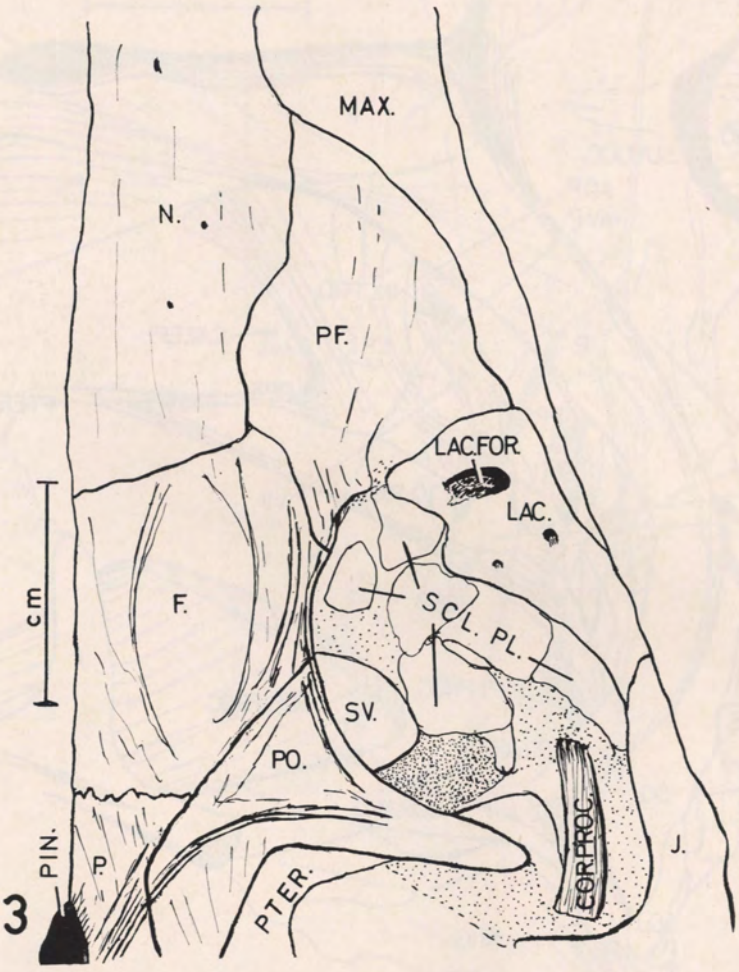
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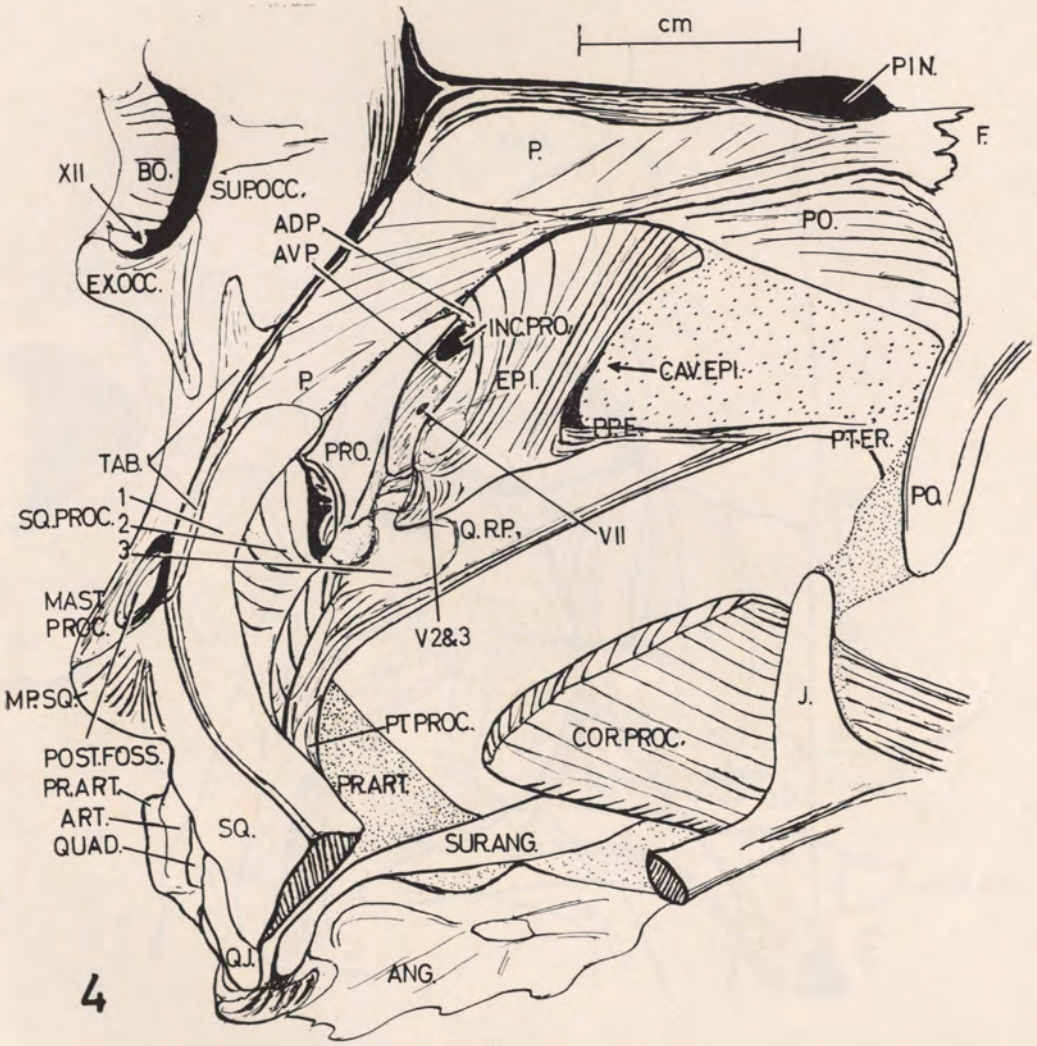
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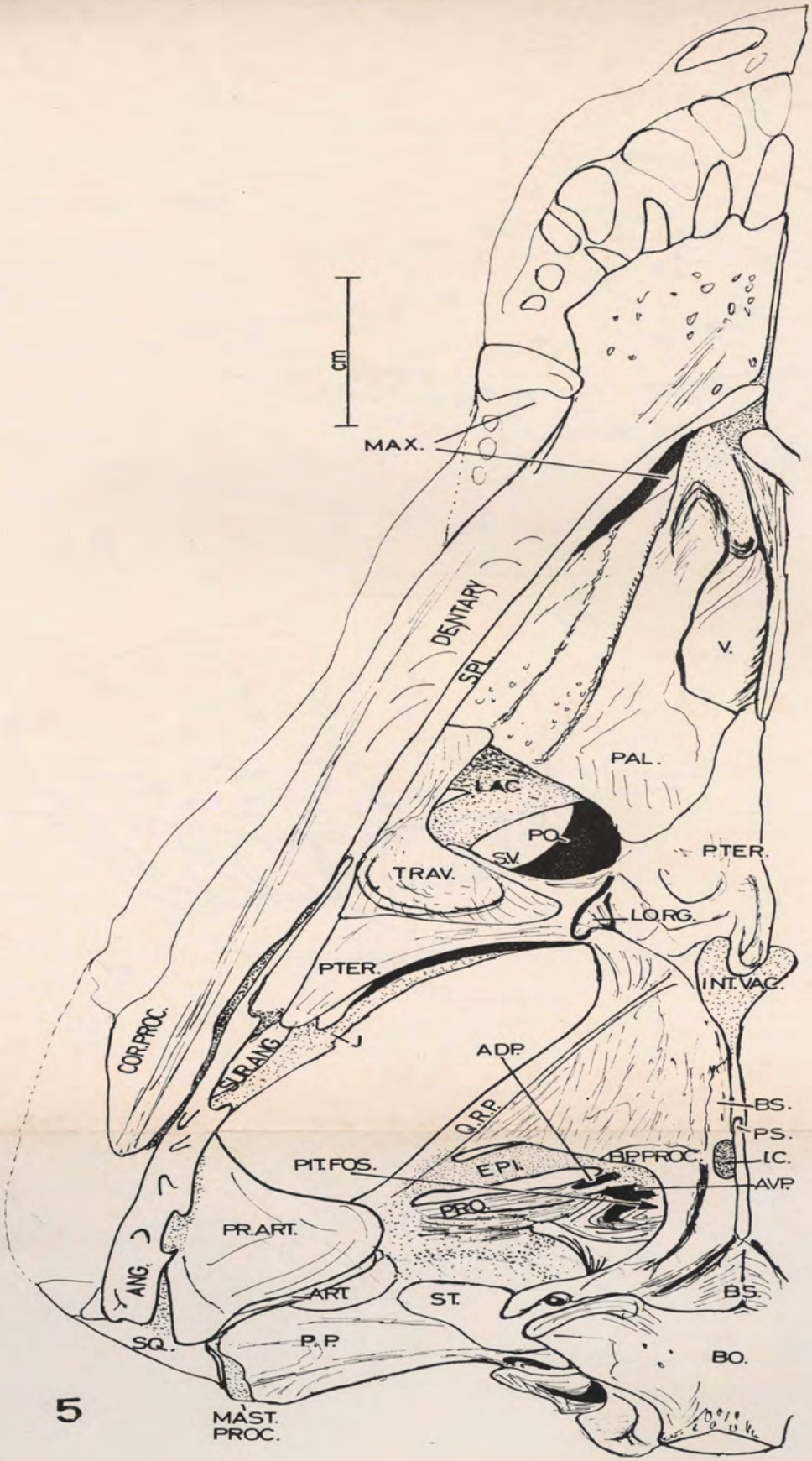
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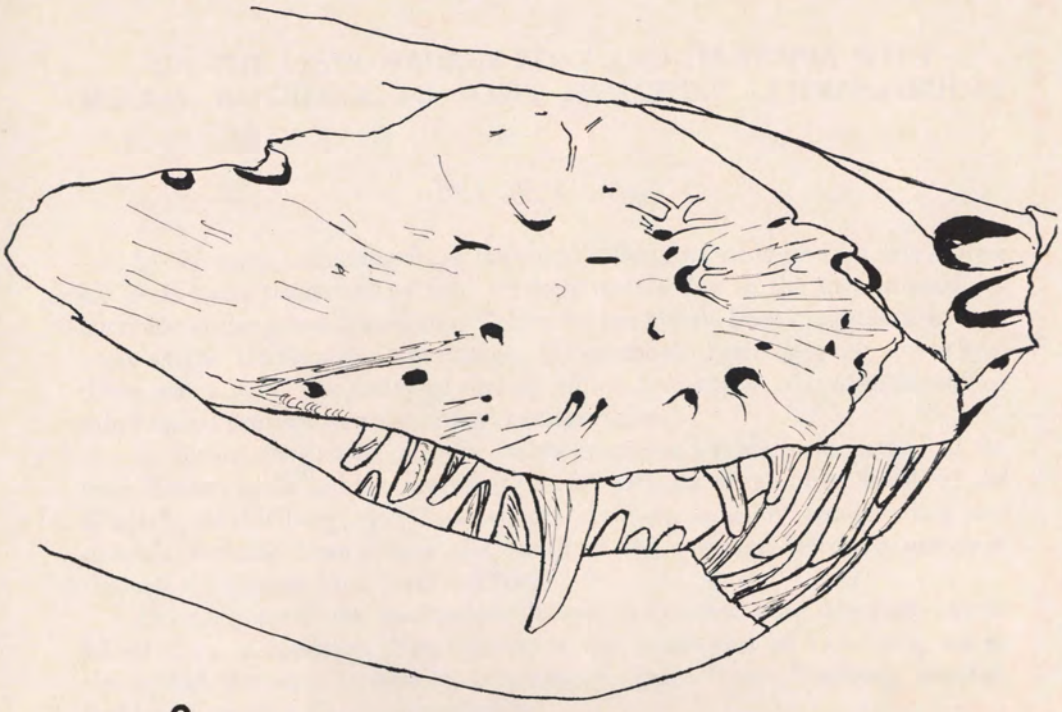

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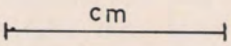



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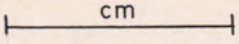


ON THE LYSTROSAURUS ZONE AND ITS FAUNA WITH SPECIAL REFERENCE TO SOME IMMATURE LYSTROSAURIDAE

By J. W. Kitching

In the past, collecting from the middle Beaufort Beds or *Lystrosaurus* zone has been badly neglected by field workers mainly due to the monotonous occurrence of the genus *Lystrosaurus*. Collecting has mostly been undertaken in such areas as the Harrismith Commonage, Oliviershoek Pass, Bergville or where there was a good possibility of finding either *Thrinaxodon*, *Glochinodontoides* or other faunal remains more exciting than *Lystrosaurus*.

In outline the *Lystrosaurus* zone follows more or less the same pattern as the main Karroo Basin and the Stormberg series with the shape of a "heel" in the Cradock, Middelburg, and Naauwpoort districts, roughly straightening out towards Bethulie from where the width of the outcrops becomes narrower through the Orange Free State and Natal.

From a point in the Sneeuwberg Range, at Compass Berg, the zone can be followed to Middelburg, Naauwpoort, to the south east of Colesberg, on to Venterstad, Bethulie, Smithfield, Dewetsdorp, Thaba N'chu, Winburg, Senekal, Bethlehem and the Harrismith districts.

In the Harrismith-Bezuidenhouts Pass area the *Lystrosaurus* zone is overlain by an outlier of the Stormberg series, but it appears again on the Natal side in the Oliviershoek Pass, Bergville and Estcourt districts; it can thence be followed to the west of Nottingham Road to Impendle, Bulwer, Cedarville, Umtata, Cathcart, Tarkastad and Cradock districts and back to Compass Berg.

In the Rhenosterberg Range to the west of Middelburg, Cape, the *Lystrosaurus* zone reaches a thickness of 1,000 feet, while in the Naauwpoort-Carlton Siding area a thickness of 1,200 feet was measured. From Naauwpoort the zone thins out considerably towards Venterstad and Bethulie where it is reduced to an overall thickness of about 500 feet. It persists at this thickness through the Orange Free State and Natal, but increases again to about 800 feet in the Tarkastad and Cradock districts.

There is no definite marker such as a consistent band or layer of sandstone anywhere between the top of the preceding *Cistecephalus* zone and the base of the *Lystrosaurus* zone, but there is a marked change in colour of the shales, mudstones and sandstones.

At the base of the *Lystrosaurus* zone the shales and mudstones are normally greenish-grey in colour, above which they alternate with bright coloured reddish-maroon and purple shales and mudstones, with a light bluish-grey medium grained to almost coarse grained felspathic sandstone. In comparison the dark bluish-green shales of the *Cistecephalus* zone occasionally alternate with red and

purple shales and mudstones, with yellowish, fine to medium-grained felspathic sandstone. In general the *Lystrosaurus* shales and mudstones are more variegated than those of the other zones.

The grey-green, reddish-maroon and purple shales of the *Lystrosaurus* zone are very soft and weather very rapidly. During rainy seasons when they are soaked, they become more like a sticky clay and completely lose their shaly nature. (Shales are defined here according to the "Principles of Physical Geology" by Arthur Holmes, 1944, p. 54.)

Lenticular masses of sandstones are very abundant measuring from eighteen inches to over five feet in thickness, indicating that the *Lystrosaurus* strata were in all probability laid down more rapidly and under wetter conditions than those of the preceding zones. In many areas, the top of the zone is indicated by a thick stratum of sandstone interbedded with thin bands of shale and mudstone.

Other factors that might also indicate a more rapid deposition of the *Lystrosaurus* beds include the presence of a mud pebble conglomerate at the base of almost every sandstone layer. A large proportion of these pebbles or nodules very frequently contain skull and skeletal fragments, most commonly those of the genus *Lystrosaurus*. Also, complete skeletons of *Lystrosaurus*, *Thrinaxodon* and *Lydekkerina* are frequently found completely embedded in hard grey-green calcareous nodules weathering out of the surrounding shales, as if these animals had been completely engulfed in mud.

To determine the top of the *Cistecephalus* and the base of the *Lystrosaurus* zones on the colours of the shales and mudstones only may not be an easy task for the untrained field worker, but through observations in the field the author has found that the genus *Daptocephalus* of the *Cistecephalus* zone is always more abundant where the *Lystrosaurus* zone is in close proximity. In many instances the first *Lystrosaurus* skull has been found *in situ* within 10 feet above the strata from which *Daptocephalus* has been removed.

In areas where there is a certain amount of relief the above can be a very misleading feature because the genus *Daptocephalus* has often been recorded as coming from the *Lystrosaurus* zone when in actual fact it has *not* been observed that the accompanying *Lystrosaurus* zone fauna has either been washed or has rolled down from the slope or gradient above, the higher strata belonging to *Lystrosaurus* zone.

At the following localities it is known that both the *Cistecephalus* and *Lystrosaurus* zones are exposed:

Afdeel Native Trust, Polela, Bulwer, Natal.
Beskuitfontein, Venterstad, Cape.
Bethulie Commonage.
Bluegum House, Graaff-Reinet.
Diepkloof, New Bethesda, Graaff-Reinet.
Droogefontein, Bethulie.
Eerstestap (Part of Elswald), Burghersdorp.
Ennersdale, Estcourt, Natal.

Grassridge, Cradock.
Karreelaagte, New Bethesda, Graaff-Reinet.
Klippoort, Cradock.
Leeufontein, New Bethesda, Graaff-Reinet.
Little Tugela River, Bergville, Natal.
Lootsberg, Graaff-Reinet.
Melsetter, Middelburg, Cape.
Middelwater, Bethulie.
Modderfontein, Middelburg, Cape.
Nooitgedacht, Bethulie.
Rhenosterberg, Middelburg, Cape.
Ripplemead, New Bethesda, Graaff-Reinet.
Schalkwykskraal, Venterstad, Cape.
Sneeuwberg, Cape (unreliable locality).
Springfield, Middelburg, Cape.
Springfontein, Middelburg, Cape.
Spitzkopvlei, Middelburg, Cape.
Staatsdrift, Bethulie.
Stoffelton, Bulwer, Natal.
Thaba N'chu Commonage, O.F.S.
The Rest, New Bethesda, Graaff-Reinet.
The Willows, Middelburg, Cape.
Tweefontein, Bethesda Road area, Graaff-Reinet.
Uitsicht, Cradock.
Wapadsberg, Graaff-Reinet.
Waterval (Part of Zeekoeigat) Venterstad, Cape.
Wilgerbosch, New Bethesda, Graaff-Reinet.
Zeekoeigat, Venterstad, Cape.

Not only does a lithological change take place at the incoming of the *Lystrosaurus* zone strata, but also in the fauna. The large variety of forms from the preceding *Cistecephalus* zone almost disappears completely except for a few genera such as *Moschorhinus*, *Ictidosuchops*, *Tetracynodon*, *Nanictosaurus*, *Galeophrys* and the amphibian *Lydekkerina*. The abundant and common Dicynodont fauna of the *Cistecephalus* zone is replaced by only two anomodonts—the comparatively large and very abundantly represented genus *Lystrosaurus* and the small *Myosaurus*. The latter is represented by eight well preserved skulls and to date all have come from the old Brickfield Dongas on the Harrismith Commonage.

The diapsid *Chasmatosaurus*, now better known from eight skulls and skeletal elements, eight genera of specialised cynodonts, the two large amphibians *Uranocentrodon* and *Laccocephalus*, and the small comparatively abundant *Lydekkerina huxleyi* constitute the bulk of the known *Lystrosaurus* zone fauna.

To the following brief summary of the *Lystrosaurus* zone fauna are added the genera *Procolophon* cf. *trigoniceps* and *Cyonosaurus* cf. *longiceps*, for the first time.

Summary of the Lystrosaurus Zone Fauna

Sub-class *ANAPSIDA*

Order — Cotylosauria.
Infra-order — Procolophonia.
Family — Procolophonidae.

(1) *Procolophon* cf. *trigoniceps*.
(2) *Procolophon* sp. — Represented by skull and skeletal remains from Lystrosaurus zone sandstones.
(3) (*Spondylolestes*) — Parrington (1948) included this small Procolophonid in his summary of the *Lystrosaurus* zone fauna, but the type of this genus came from Bethesda Road in the *Cistecephalus* zone.

Sub-class *LEPIDOSAURIA*

Order — Eosuchia.
Family — Prolacertidae.

(1) *Pricea longiceps*.
(2) *Prolacerta broomi*.

Sub-class *ARCHOSAURIA*

Order — Thecodontia.
Sub-order — Pseudosuchia.
Family — Erythrosuchidae.

(1) *Chasmatosaurus vanhoepeni* — Represented by eight good skull and skeletal elements.
(2) (*Elaphrosuchus rubidgei*) = *Chasmatosaurus vanhoepeni*, a juvenile specimen.
(3) *Proterosuchus fergusi*. (Type lost.)

Sub-class *SYNAPSIDA*

Brink (1963) considers that the Synapsids be raised to the level of a class.
Sub-order — Anomodontia.
Sub-family — Pristerodontinae (Myosaurinae).

Myosaurus gracilis—Represented by eight well preserved skulls—all from the Harrismith Commonage. This seems to be an environmental factor. It is generally felt that *Myosaurus* should be transferred to a new sub-family Myosaurinae, as this species is out of place among the Pristerodontinae, most of which have molar teeth on the alveolar ridges of the maxillae and broad strong maxillae and palatal regions.

Sub-order — Anomodontia.
Family — Lystrosauridae.

(1) *Lystrosaurus amphibius.*

(2) *Lystrosaurus andersoni.*

(3) *Lystrosaurus bothai*= Adult *L. murrayi.*

(4) *Lystrosaurus curvatus.*

(5) *Lystrosaurus declivis.*

Brink (1951) includes the following described forms in *Lystrosaurus declivis* (5)—*L. alfredi*, *L. boopis* and *L. depressus*. All of these are imperfectly preserved, being badly crushed and distorted.

(6) *Lystrosaurus maccaigi.*

(7) *Lystrosaurus murrayi.*

Broom (1932) includes the following described forms in *Lystrosaurus murrayi* (7)—*L. alfredi*, *L. boopis*, *L. breyeri*, *L. declivis*, *L. depressus*, *L. frontosus*, *L. jorisseni*, *L. latirostris*, *L. oviceps*, *L. putterilli*, *L. theileri*, *L. verticalis*, *L. wageri*, *L. wagneri*, *Prolystrosaurus natalensis*, and *Prolystrosaurus* (Dicynodon) *strigops*. Brink (1951) includes the following described forms in *Lystrosaurus murrayi* (7)—*L. frontosus*, *L. jeppei*, *L. jorisseni*, *L. latirostris*, *L. theileri*, *L. wageri* and *L. wagneri*.

(8) *Lystrosaurus oviceps.*

Brink (1951) includes *Lystrosaurus breyeri* in *L. oviceps.*

(9) *Lystrosaurus platyceps.*

(10) *Lystrosaurus primitivus.* This skull came from the same horizon as *Lystrosaurus amphibius*, approximately eight feet apart.

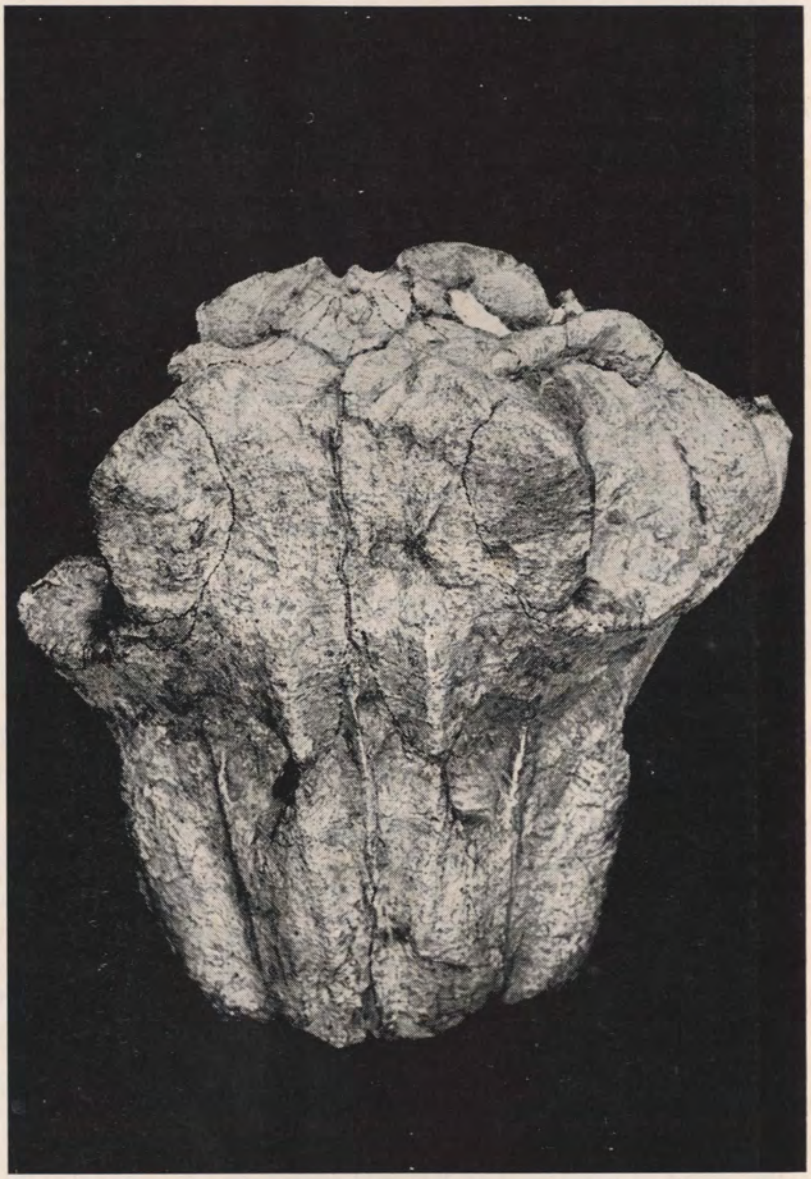
(11) *Lystrosaurus putterilli.* Broom (1932) includes *Lystrosaurus putterilli* in *L. murrayi*, giving no reason for doing so. Kitching (1960) re-examined the type and considered it to be an adult male of *L. murrayi.*

(12) *Lystrosaurus rubidgei*—The type consists of the anterior two-thirds of a skull; very badly crushed antero-posteriorly and can be either a young *L. amphibius* or an adult male of *L. murrayi.* Broom (1940) when describing *L. rubidgei* suggests that it should be looked upon as coming from the *Cistecephalus* zone, but the specimen came from lower *Lystrosaurus* zone strata in the old Lootsberg Pass, six miles north of Bethesda Road. This Pass used to be the main road to Middelburg via Blaauwater (Blouwater) Siding.

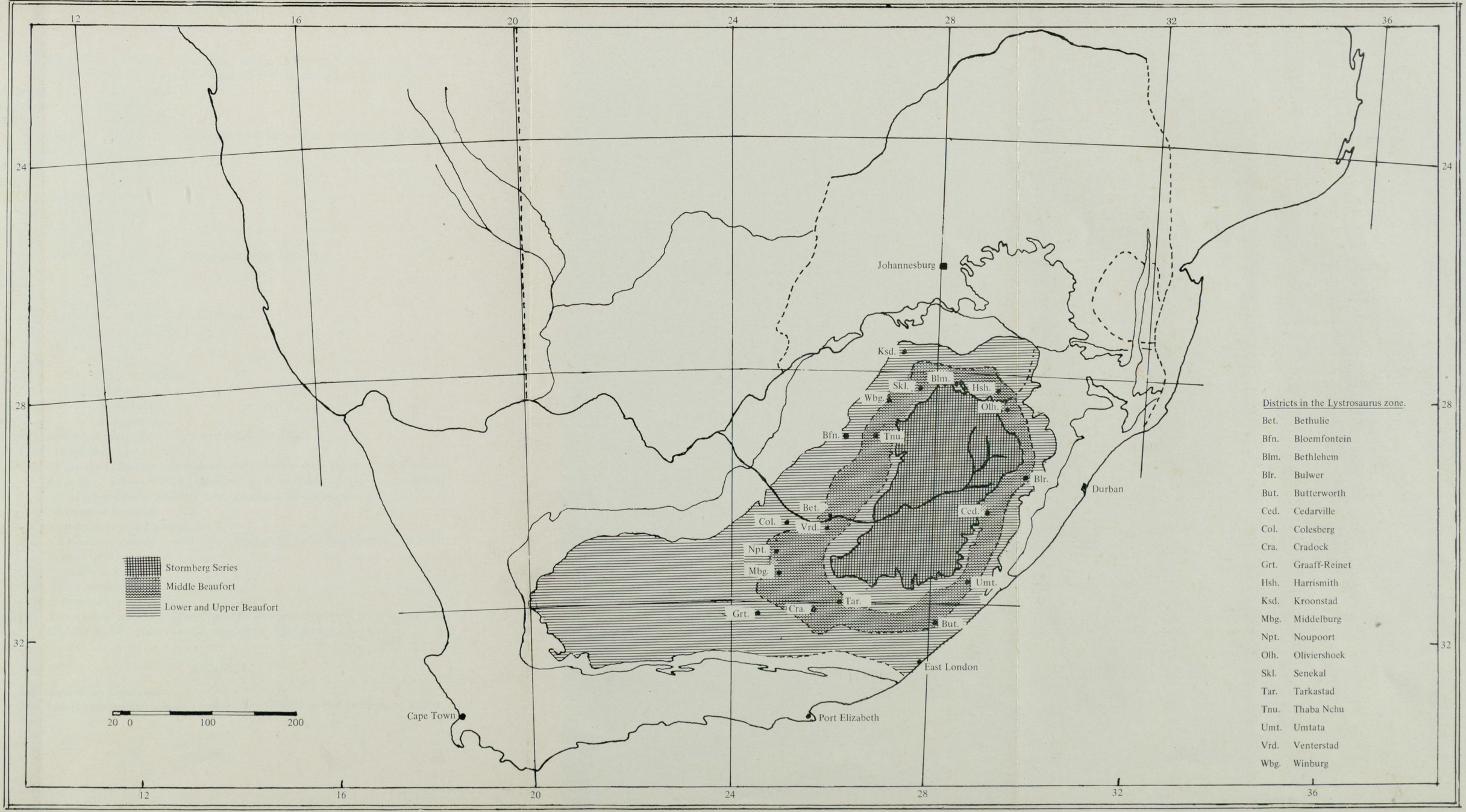
(13) *Lystrosaurus verticalis*—This species was founded on a very imperfect skull and all its characteristics are close to those of *L. murrayi.*

(14) *Prolystrosaurus natalensis*—Broom (1932) refers this genus to *Lystrosaurus murrayi.* Brink (1951) refers *Prolystrosaurus* to the genus *Lystrosaurus* as it is *not* a natural ancestor to the latter. Cruickshank has recently examined the type in the South African Museum and reported it to be a dorso-ventrally distorted *L. murrayi.*

Fig. 2



Large, badly distorted *Lystrosaurus murrayi* (Lystrosaurus rubidgei)


12
16
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Johannesburg
Durban
Cape Town
Port Elizabeth
East London
Ksd.
Blm.
Skl.
Hsh.
Wbg.
Olh.
Bfn.
Tnu.
Blr.
Bet.
Ced.
Col.
Vrd.
Npt.
Mbg.
Umt.
Tar.
Cra.
Grt.
But.
Stormberg Series
Middle Beaufort
Lower and Upper Beaufort
20 0 100 200
Districts in the Lystrosaurus zone.
Bet. Bethulie
Bfn. Bloemfontein
Blm. Bethlehem
Blr. Bulwer
But. Butterworth
Ced. Cedarville
Col. Colesberg
Cra. Cradock
Grt. Graaff-Reinet
Hsh. Harrismith
Ksd. Kroonstad
Mbg. Middelburg
Npt. Noupoort
Olh. Oliviershoek
Skl. Senekal
Tar. Tarkastad
Tnu. Thaba Nchu
Umt. Umtata
Vrd. Venterstad
Wbg. Winburg

Fig. 1

(15) *Prolystrosaurus strigops* (*Dicynodon strigops*). Broom (1932) refers this form to *Lystrosaurus murrayi*. Brink (1951) to the genus *Lystrosaurus*.

Sub-order — Theriodontia.
Infra-order — Gorgonopsia.
Family — Gorgonopsidae.

Cyonosaurus c.f. longiceps. (Found in the same horizon as *Lystrosaurus*, *Thrinaxodon* and *Tetracynodon*.)

Infra-order — Therocephalia.
Family — Scaloposauridae.

(1) *Ericiolacerta parva*.
(2) *Olivieria parringtoni*.
(3) *Tetracynodon darti*.
(4) *Scaloposaurus hoffmani*.
(5) *Scaloposaurus constrictus*. (From unreliable locality.)

Infra-order — Therocephalia.
Family — Whaitsidae.

(1) *Moschorhinus kitchingi*.
(2) *Moschorhinus* (esterhuizeni) *kitchingi*.
(3) *Moschorhinus* (natalensis) *kitchingi*.
(4) *Moschorhinus warreni*.

Infra-order — Cynodontia.
Family — Procynosuchidae.

Galeophrys kitchingi.

Infra-order — Cynodontia.
Family — Galesauridae.

(1) *Galesaurus planiceps*. (From unreliable locality.)
(2) *Glochinodontoides gracilis*.
(3) *Glochinodon detinens*—Broom (1932) refers this genus to *Galesaurus planiceps*: Brink (1954) describes a second specimen referring *Glochinodon detinens* and the new specimen to *Galesaurus*.
(4) *Micrictodon marionae*.
(5) *Nanictosaurus c.f. kitchingi*.
(6) *Notictosaurus gracilis* and *N. trigonocephalus* = *Notictosaurus luckhoffi* Brink (1965).
(7) *Nythosaurus larvatus*.
(8) *Platycraniellus elegans*.
(9) *Thrinaxodon luirhinus*.
(10) *Thrinaxodon putterilli*. (The type of this species is held by a son of the late Mr A. W. Putterill still resident in Harrismith.)

AMPHIBIA

(1) *Limnoiketes paludinatus*.
(2) *Lydekkerina huxleyi*. (Most common amphibian in the *Lystrosaurus* zone).

(3) *Lydekkerina putterilli*.

(4) *Uranocentrodon* (Rhinesuchus) *senekalensis*.

Over the past twenty years it has been observed that *Procolophon* skull and skeletal remains occur in conglomerates at the base of three upper *Lystrosaurus* zone sandstones, on the Harrismith Commonage as well as at Oliviershoek Pass, Excelsior, Wheatlands-Tarkastad, Klipfontein-Bethulie and Joubertsberg-Middelburg, Cape.

In 1964, B. J. Kitching, while examining *Lystrosaurus* zone strata in the Lootsberg Pass, Graaff-Reinet district, found a well preserved *Procolophon* cf. *trigoniceps* in a horizon which also yielded *Lystrosaurus murrayi* and *L. declivis*.

It may also be relevant to record at this stage that the genus *Procolophon* has been found in the *Cistecephalus* zone at locality 14, in the Upper Luangwa Valley, Zambia.

On a re-examination of the strata on the farms Hales Owen-Cradock and Colton-Dewetsdorp, it was found that in both localities *Procolophon* skulls occur in nodules at the base of the sandstones well within the *Lystrosaurus* zone. Some of these nodules also yielded fragmentary *Lystrosaurus* skull and skeletal remains.

The occurrence of a *Cistecephalus* zone Gorgonopsid—*Cyonosaurus*—in the *Lystrosaurus* zone was an unexpected discovery more especially since it was found high in the *Lystrosaurus* zone strata, which also yielded a number of *Lystrosaurus*, *Thrinaxodon*, *Tetracynodon* and *Lydekkerina* skulls. The skull came from Oliviershoek Pass-Bergville district and was found by Albert Hotton, son of Nicholas Hotton III of the Smithsonian Institution, Washington, D.C., during 1964. The specimen was subsequently described by D. Sigogneau in her D.Sc. thesis (1967).

The nearest *Cistecephalus* zone strata to the above locality are to be found approximately 30 miles away in the Little Tugela River, Bergville district, or some 45 miles south-east of the Pass on the farm Ennersdale in the Estcourt district. The water-worn texture of *Cyonosaurus* and the fragmentation of the maxillary and squamosal regions suggests that the skull had in all probability been washed from the *Cistecephalus* zone strata and had subsequently been re-deposited where it was found in *Lystrosaurus* zone times.

Seeley, Broom and Watson believe that *Lystrosaurus* was aquatic, which may account for the wide distribution of this genus. Being able to swim, these creatures could have been carried by streams or floods over large distances with many surviving whole, but some being dismembered and giving rise to the skull and skeletal fragments in the pebble conglomerates.

The sudden appearance of this new form of Anomodont, *Lystrosaurus*, and its abundance throughout the zone is more indicative of an immigrant form, than of one evolved from a branch of the Lower Beaufort Anomodonts.

From observations in the field and from the records it is obvious that the first forms to appear in the lower *Lystrosaurus* zone strata are *Lystrosaurus murrayi* and *L. declivis* together with such large species as *Lystrosaurus amphibius*, *L. andersoni*, *L. platyceps* and *L. maccaigi*. These latter species feature less prominently in the upper strata of the zone.

Had the genus *Lystrosaurus* been evolved from a Lower Beaufort Dicynodont then corroborative evidence should have been found among the very large variety of *Cistecephalus* zone Dicynodonts.

Broom (1932) suggested that a species such as *Dicynodon gilli* from the *Cistecephalus* zone could be near to the ancestral type from which the genus *Lystrosaurus* could have evolved. However, although *Dicynodon gilli* is stratigraphically old enough to be ancestral, the frontals in this species meet the premaxillae, a feature not found in *Lystrosaurus*.

Yuan and Young (1934) remarked that some of the Russian Dicynodonts are very *Lystrosaurus*-like. Toerien (1954) described *Lystrosaurus primitivus* from low in the *Lystrosaurus* zone, stating that the specimen shows characters intermediate between *Dicynodon* and *Lystrosaurus* and that it appears to be a late survivor of the earliest Lystrosaurs which were very similar to some of the Russian Dicynodonts.

Broom (1932) considered the Lystrosauridae by far the most difficult genus of South African fossil reptiles with which to deal, and that this group was in great confusion. He then went on to revise the genus *Lystrosaurus*, referring some of the described species to *Lystrosaurus murrayi*. (See summary of *Lystrosaurus* zone fauna.)

In the same paper he also states "that where many specimens of the same genus are found at *one* locality and in one horizon the presumption should be that most will belong to *one* species, and that many distinct characters must be evident before a distinct species can be created". Unfortunately very little notice was taken of this advice, either by himself or by other workers on the genus *Lystrosaurus* or for that matter on various other genera of the mammal-like reptiles.

Brink (1951) again revised the twenty-two already described South African species of *Lystrosaurus*, reducing them to eleven and suggested that the generic name *Prolystrosaurus* should be altered to *Lystrosaurus* as the former is not a natural ancestor of the latter. The strata on the farm Loskop in the Estcourt district lie well within the *Lystrosaurus* zone. He also introduced a new species *Lystrosaurus amphibius* based on a large skull from the lower strata of the zone, with characteristics pointing more clearly to the aquatic features of this genus than any of the previously described species.

Neither of the above authors gave very definite reasons for reducing the number of the described species, but from a recent survey it became evident that the majority of specimens were either badly preserved or distorted and some of them possessed no characteristics sufficiently distinctive to justify their separation into different species.

In recent years, it has become increasingly obvious that more attention should be given to depositional distortion, variations within species and growth stages within the various groups of mammal-like reptiles. Lack of information concerning these features, let alone the badly weathered state or incomplete nature of the material, has been the underlying reason for the creation of a fair number of new genera and species.

In the genus *Lystrosaurus* many skulls are badly distorted, some almost beyond recognition. This distortion can in all probability be attributed to the fragility of the thin bony structure of the skulls, the skull bones being much thinner than is characteristic of Dicynodonts of the same size from the *Cistecephalus* zone. However, the bone could also have been distorted by long periods of submergence in water or in mud, which caused the skulls to become almost plastic or flexible. Yet another, but lesser, cause could have been the contraction of skin, muscle and tendons in cases where the skulls have been exposed to air and sun.

Variations within species, and growth stages, should be very carefully studied. Consideration of these phenomena has been given by work on various lower and upper Beaufort forms, and over the past ten years a number of very immature and intermediate growth stages in *Lystrosaurus* skulls have been collected from different horizons together with adult and already described *Lystrosaurus* species.

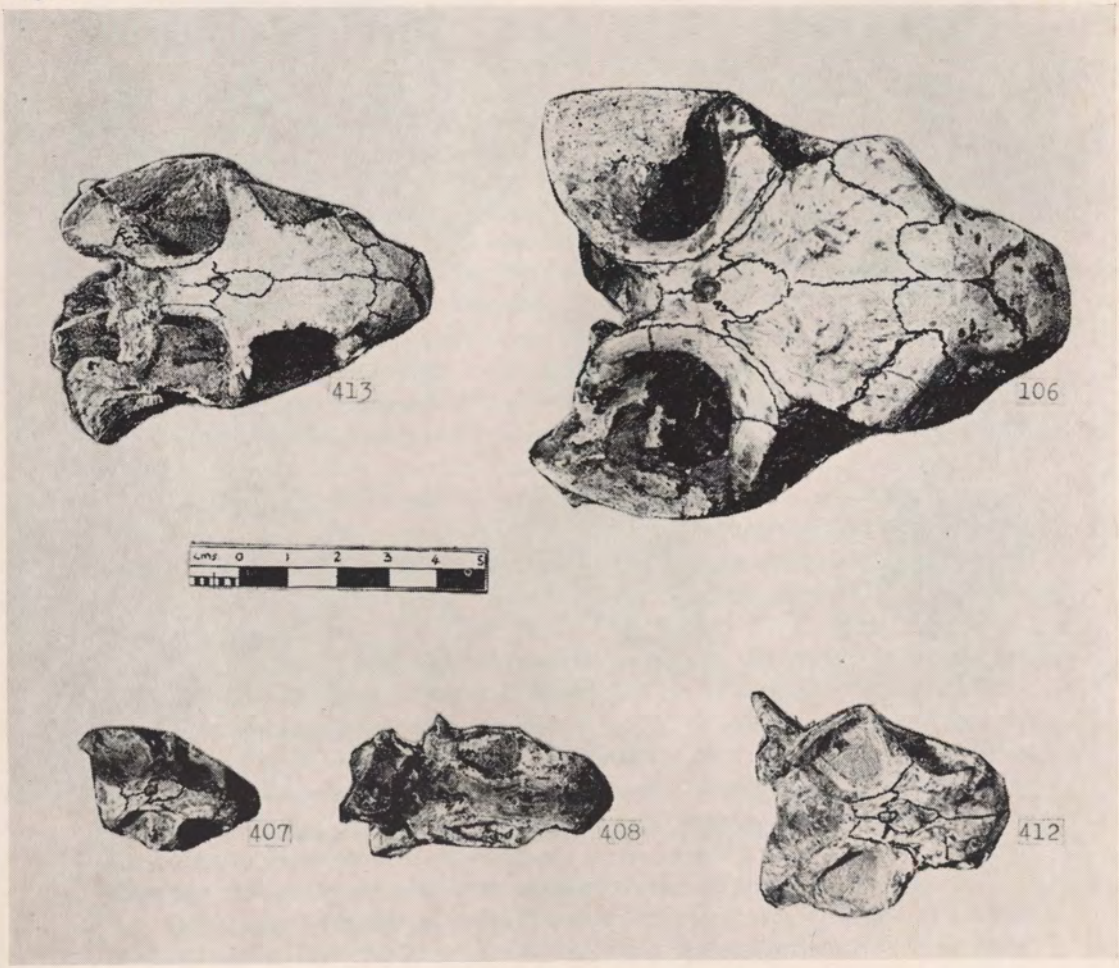
For this preliminary description, six of the smallest *Lystrosaurus* skulls yet recorded as well as two intermediate stages have been selected. These can all be referred to *Lystrosaurus murrayi*. In the curvature of the snouts, parietals, preparietals and in all other aspects the eight skulls agree completely with *Lystrosaurus murrayi* except that six of the specimens are very immature. All the selected specimens have their lower jaws in place making it difficult to study the palates.

The following tables give the museum numbers, locality, and state of preservation of the eight specimens as well as the principal measurements of the skulls in millimetres.

B.P.I. Mus. No.	*Locality*	*State of preservation*
407	Oranje, Bethulie.	Skull with lower jaw. Skull distorted laterally. Tusks not yet erupted.
408	Old Brickfield Donga. Harrismith Commonage.	Skull with lower jaw, cervical vertebrae and shoulder girdle. Skull slightly distorted laterally. Tusks not yet erupted.
409	Nooitgedacht, Bethulie.	Skull with lower jaw. Partial skeleton. Skull slightly distorted laterally. Tusks not yet erupted.
410	Nooitgedacht, Bethulie.	Skull with lower jaw, snout weathered, almost complete skeleton. Skull distorted laterally. Tusks not yet erupted.
411	Nooitgedacht, Bethulie.	Skull with lower jaw. Partial skeleton. Skull flattened dorso-ventrally. Tusks not yet erupted.
412	Donovan, Bethulie.	Skull with lower jaw, slightly distorted dorso-ventrally. Tusks just erupting.

413	Nooitgedacht, Bethulie.	Skull with lower jaw. Skull distorted ventrally. Tusks not fully erupted.
106	Edenvale, Naauwpoort.	Undistorted—skull with lower jaw. Tusks fully erupted.

Fig. 3



Dorsal view of a growth series of *Lystrosaurus murrayi* skulls.

Fig. 4



Side view of a growth series of *Lystrosaurus murrayi* skulls.

	Museum No. 407	Museum No. 408	Museum No. 409	Museum No. 410	Museum No. 411	Museum No. 412	Museum No. 413	Museum No. 106
Maximum skull length ..	49	50	51	51	61	65	97	143
Maximum basal length ..	42	46	±44	—	50	58	83	111
Maximum skull width across interorbital bars	29	28	±30	±26	41	50	60	97
Interorbital width Max.	—	16	16	—	18	22	28	65
Min.	±16	14	15	—	15	20	26	52
Intertemporal width Max.	10	13	15	—	15	17	19	29
Min.	8	11	13	12	12	15	15	25
Snout+orbital length	±29	31	31	—	34	42	73	88
Tip of snout to pineal ..	30	±29	29	—	40	41	50	103
Minimum outside width between caniniform processes	16	14	14	13	17	23	35	54
Maximum length of orbit ..	±15	15	15	—	17	21	±28	36
Maximum height of orbit ..	13	12	12	—	14	15	26	31

All measurements in millimetres.

Three of the skulls with partial skeletons, B.P.I. museum numbers 409–411, are embedded in a block of grey-green matrix measuring approximately 100 square inches. The skull of specimen 411 is flattened dorso-ventrally with the result that it resembles that of *Lystrosaurus declivis*, but the skeletal parts attached to the three skulls have exactly the same measurements and it is therefore probable that all were born at the same time.

It is at present still difficult to determine whether a specimen is a juvenile or an adult. On re-examining some of the known *Lystrosaurus murrayi* skulls it was found that the intermediate and what was at first thought to be the adult stages of this species have all the characteristics of the large *Lystrosaurus putterilli* which in all probability is an adult male of the former.

It is also difficult to establish when the tusks in *Lystrosaurus* erupt. In five of the specimens, museum numbers 407–411, the tusks have not yet erupted, and there is no swelling of the caniniform processes. In specimen museum number 412 the tusks are just erupting while in the intermediate stage 413 the tusks are not fully erupted.

Although six of the eight specimens mentioned above are immature the skulls and skeletal elements are well developed, the bone well ossified, and there is no marked expansion of the sutures.

In the past it was thought that when sutures tend to part or are expanded that this was an indication that the skull was that of a juvenile. This may be so in some cases, but it now seems likely that the opening of sutures can also be attributed to distortion by submergence in water and mud, or to the length of time that the specimens have been exposed to the air and sun.

On dealing with the mammal-like reptiles, palaeontologists are well aware of their mammalian characteristics in skull and skeletal structures, these being more advanced than those of reptiles. However, for many years there has been

Fig. 5



Block of matrix containing three small skulls with skeletal remains of *Lystrosaurus murrayi*. B.P.I. Museum Numbers 409, 410 and 411.

speculation as to whether the mammal-like reptiles were oviparous or viviparous, since no eggs or traces of eggs have yet been found, even where depositional conditions appear to have been favourable. In many instances extremely fragile skull and skeletal elements as well as plant remains have been preserved and for this reason eggs or embryo-like forms ready to be hatched should have also been preserved.

Even when living reptiles lay soft-shelled eggs, these tend to harden or toughen considerably when exposed to the air and sun thus protecting the embryo during incubation which in some instances may last from six to nine months.

Since many well developed immature specimens of various mammal-like reptiles have been recovered from the Beaufort Beds, but as yet no traces of eggs, it could well be possible that live birth had taken place. The type of birth here visualised may have been similar to that found in certain of the living reptiles such as *Mabuya*, *Cordylus* and *Platysaurus* to mention only a few, and where from two to eight young are born alive.

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THE CONFUSED STATE OF CLASSIFICATION WITHIN THE FAMILY PROCYNOSUCHIDAE

By J. M. Anderson

Introduction

To date, fourteen Procynosuchid specimens have been discovered, thirteen from the *Cistecephalus* beds in the New Bethesda and Murraysburg districts in the Southern Karroo and one very poor specimen from the Ruhuhu Beds to the N.E. of Lake Malawi. Five genera, including eight species, have been created. This paper briefly describes the history of the classification within the family and notes some of the difficulties encountered.

History of the Classification

Broom (1937) gave a preliminary description of a skull with primitive Cynodont characteristics and named it *Procynosuchus delaharpeae* (Fig. 1a). In 1938 he gave fairly detailed descriptions of this form together with a second specimen which he found sufficiently different to warrant the creation of a new species—*Procynosuchus rubidgei* (Fig. 1b).

The following differences were noted:

Procynosuchus rubidgei has relatively much larger nasals, much broader frontals having a broad articulation with the parietals, smaller parietals, larger pineal foramen, less elevated intertemporal crest and jugular foramina situated a little farther back.

Broom (1940) gave a very brief description of a fairly complete small skull which he named *Paracynosuchus rubidgei* (Fig. 1c). Although there are clear affinities with *Procynosuchus*, the skull is far more slenderly built and there are only 7 "molars" as against 8 in the two species of *Procynosuchus*.

Broom (1948) created three new genera and species, *Leavachia duvenhagei* (Fig. 1d), *Galeophrys kitchingi* (Fig. 1g) and *Galecranium liorhyncus* (Fig. 1h) and Broom and Robinson (1948) created a new genus and species *Aelurodraco microps*. They were all recognised to be related to one another and to *Procynosuchus* and *Paracynosuchus*.

Broom attached very great importance to the upper dental formula in his classification.

i.e. *Paracynosuchus* $i^5c^2m^7$
Procynosuchus $i^6c^2m^{10}$

Aelurodraco	$i^6c^2m^8$
Leavachia	$i^6c^3m^8$
Galeophrys	$i^6c^3m^9$
Galecranium	$i^6c^3m^{11}$

Von Huene (1950) gave a very brief description of a poor anterior fragment of a skull found in the Ruhuhu Beds to the N.E. of Lake Malawi. He correlated it with *Procynosuchus delaharpeae*.

Brink and Kitching (1951) after further preparation of the type of *Aelurodraco microps* stated that it had a dental formula of $i^6c^3m^8$ and that in general proportion it was remarkably similar to *Leavachia*. They announced the existence of a second specimen in the collection of the Bernard Price Institute identical to the type in size and proportions and noted that it also had a dental formula of $i^6c^3m^8$. They therefore sank the generic name *Aelurodraco* and created a new combination for the two specimens of *Leavachia microps*. At the same time a third specimen which agreed perfectly in general proportions with *Leavachia duvenhagei and Leavachia microps* (Fig. 1e) and was of the same size as the latter was described. They found sufficient differences however to create a third species, *Leavachia gracilis* (Fig. 1f) (Table 1).

TABLE 1

	L. duvenhagei	*L. microps*	*L. gracilis*
Backward extension of post orbitals	to level of posterior border of pineal foramen	to level well in front of pineal foramen	to anterior margin of pineal foramen
Position of postorbitals just anterior to pineal foramen	postorbitals well separated	postorbitals nearly meet each other	postorbitals well separated
Shape of nasals	posterior breadth only slightly greater than anterior breadth	condition intermediate between *L. d.* and *L. g.*	large difference between anterior and posterior breadths of nasals
Overlap of squamosal on parietals	appears to be no overlap	condition intermediate between *L. d.* and *L. g.*	considerable overlap

In the same paper they set out a table of characteristics showing the differences between the four genera, *Procynosuchus*, *Leavachia*, *Galeophrys* and *Galecranium*. They excluded dental formulae since they felt that the number of "molars" changes with maturity (Table 2).

TABLE 2

	Procynosuchus	*Leavachia*	*Galeophrys*	*Galecranium*
Breadth/length ratio of skull	59%	71%	64%	60%
Parietal region	Short	intermediate	intermediate	long
Posterior extension of post-orbitals	terminate well in front of pineal foramen	extend past pineal foramen	extend to middle of pineal foramen	extend to anterior margin of pineal foramen
Length of Snout	Long	Short	Short	Long

Brink and Kitching (1953) re-described the type specimen of *L. duvenhagei* after further preparation and gave a brief account of a second specimen which was slightly smaller than the type but in all other respects exactly similar.

They found the following important factors relating to dental formulae within the genus *Leavachia*:

Leavachia duvenhagei (type) $i^5c^3m^8$

Leavachia duvenhagei (2nd spec.) $i^5c^3m^{7+1}$ apparently not yet erupted

Leavachia gracilis (type) $i^5c^3m^7$

Leavachia microps (type) $i^5c^3m^8$

Leavachia microps (2nd. spec.) $i^5c^3m^8$

They also described a second more complete specimen of *Galecranium liorhyncus* and a second specimen of *Procynosuchus rubidgei*. The *Galecranium* specimen agreed in every detail with the type. They gave a dental formula of $i^5c^3m^{11}$ and (not having seen the type) believed that Broom probably counted one too many incisors, just as he had in the type of *Leavachia duvenhagei*.

The second specimen of *Procynosuchus rubidgei* was slightly smaller than the type. They expressed the opinion that the only real difference between *Procynosuchus delaharpeae* and *Procynosuchus rubidgei* was in the shape of the frontals and that the two species were possibly synonymous. Since the shape of the frontals in the new specimen agreed better with the latter species they referred to it as *Procynosuchus rubidgei*. This specimen they found to have a dental formula of $i^5c^3m^{10}$ and not $i^6c^2m^{10}$ as Broom gave for both types. They stated that the

new specimen showed very distinctly the suture between the maxillary and premaxillary passing in front of the second small tooth anterior to the large canine and expressed doubt (again without having investigated the type) as to Broom's interpretation.

Brink (1963) gave a detailed description of an excellently preserved third specimen of *Leavachia duvenhagei*. It was exactly the same size as the type. He gave a dental formula of $i^5c^3m^{10}$ which differed in the number of "molars" from the type and the second specimen. In the new specimen the postorbital extended backwards only to the level of the anterior end of the pineal foramen.

He suggested that the upper dental formula for all the Procynosuchidae might well be $i^5c^3m\pm^{10}$ and concluded that it was difficult apart from general proportions to distinguish between the different genera.

Discussion

Broom differentiated his genera on upper dental formulae and general proportions and size. It has since been shown that many faulty counts have been made regarding dental formulae. Also, when it is considered how much the general proportions and size can vary according to maturity, sex, environmental conditions and postmortem distortion, it would seem that many more specimens must be found before a reasonably decisive sub-division of the family Procynosuchidae can be reached.

Specific diagnoses have rested more on the sizes, shapes and relationships between the various bones of the skull, none of which would appear very reliable, considering the paucity of comparative material.

Acknowledgments

I would like to thank Dr A. S. Brink and Mr J. W. Kitching for supervising this project, and for their helpful and stimulating discussions.

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KEY TO FIGURES

All diagrams half natural size.

FIG. 1

a) *Procynosuchus delaharpeae* (Type. After Broom 1938).
b) *Procynosuchus rubidgei* (Type. After Broom 1938).
c) *Paracynosuchus rubidgei* (Type. After Broom 1940).
d) *Leavachia duvenhagei* (3rd specimen. Drawn from specimen).
e) *Leavachia microps* (Type. After Broom and Robinson 1948).
f) *Leavachia gracilis* (Type. After Brink and Kitching 1951).
g) *Galeophrys kitchingi* (Type. After Broom 1948).
h) *Galecranium liorhyncus* (Type. After Broom 1948).

KEY TO ABBREVIATIONS

ASPH.	Alisphenoid.
F.	Frontal.
IP.	Interparietal.
J.	Jugal.
L.	Lachrymal.
MX.	Maxillary.
N.	Nasal.
P.	Parietal.
PMX.	Premaxillary.
PO.	Postorbital.
PRF.	Prefontal.
PRO.	Prootic.
PT.	Pterygoid.
SQ.	Squamosal.
pin f.	Pineal foramen.

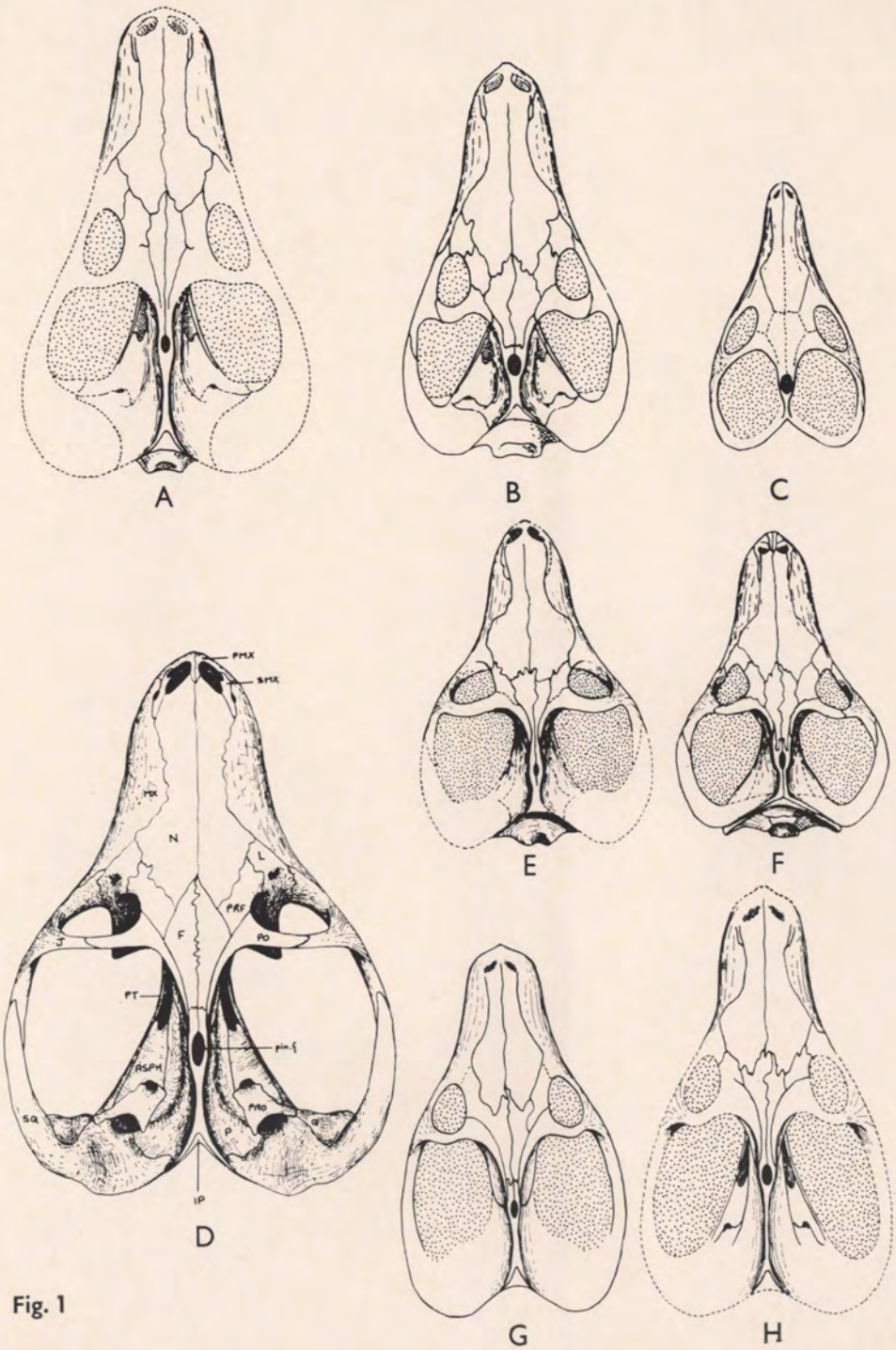

Fig. 1

TABLE 3

		FARM LOCALITY	NUMBER AND COLLECTION	REMAINS AND CONDITION OF SPECIMEN	DESCRIPTIONS AVAILABLE					
					Author	Dorsal skull	Ventral skull	Occiput	Lower jaw	Posterior skeleton
Leavachia duvenhagei	Type	Doornkloof	Number 92 Rubidge Collection	good skull with lower jaw nearly complete skeleton	*a*) Broom 1948	fairly good	—	fairly good	fairly good	fairly good
					b) Brink & Kitching 1953	notes on dentition	brief	—	—	—
	2nd spec.	Doornbosch	Number 304 Rubidge Collection	skull with posterior portion weathered away	Brink & Kitching 1953	notes on similarity with type	—	—	—	—
	3rd spec.	Town Commonage New Bethesda	Number 357 B.P.I.	complete skull and lower jaw	Brink 1963	very detailed	very detailed	very detailed	very detailed	brief
Leavachia microps	Type	Ringfontein	Number 8 B.P.I.	good skull lacking the arches lower jaw in place	*a*) Broom & Robinson 1948	good	—	brief	brief	—
					b) Brink & Kitching 1951	notes on dentition	—	—	—	—
	2nd spec.	Hoeksplaas	Number 226 B.P.I.	skull	Brink & Kitching 1951	notes on dentition	—	—	—	—
Leavachia gracilis	Type	Leeufontein	Number 234 B.P.I.	good skull with lower jaw partial skeleton	Brink & Kitching 1951	good	—	brief	good	brief
Procynosuchus delaharpeae	Type	The Glen	Number 5 Rubidge Collection	good skull lacking the arches	*a*) Broom 1937	brief	brief	—	—	—
					b) Broom 1938	good	good	brief	—	—
	2nd spec.	(East Africa) Ruhuhu Beds	K. 92 Tübingen Collection	poor anterior section of snout	Von Huene 1950	very brief	very brief	—	—	—
Procynosuchus rubidgei	Type	Afrikanerskloof (Garnora)	Number 12 Rubidge Collection	well preserved skull. Arches of right side missing	Broom 1938	good	good	brief	—	—
	2nd spec.	Seekoegat	Number 306 Rubidge Collection	somewhat crushed skull	Brink & Kitching 1953	brief	—	—	—	—
Galecranium liorhyncus	Type	Afrikanerskloof (Garnora)	Number 87 Rubidge Collection	good skull lacking the arches	Broom 1948	brief	—	—	—	—
	2nd spec.	Karreelaagte	Number 305 Rubidge Collection	skull with right arch missing	Brink & Kitching 1953	brief	—	—	—	—
Galeophrys kitchingi	Type	Town Commonage New Bethesda	Number 72 Rubidge Collection	nearly complete skull somewhat crushed. Much of neck present	Broom 1948	brief	—	—	—	—
Paracynosuchus rubidgei	Type	Grootdriefontein	Number 17 Rubidge Collection	fairly complete skull weathered on one side. Lower jaw present	Broom 1940	very brief	—	—	—	—

THE CULTURAL IMPLICATIONS OF THE RHINOCEROS TEETH FROM LIMEWORKS, MAKAPANSGAT

By J. M. Anderson

Introduction

The evidence concerning the behaviour and Osteodontokeratic culture of the australopithecines that can be assessed from a study of the rhinoceros teeth found in the grey breccia at the Limeworks cavern, Makapansgat is discussed.

The material examined consists of ninety-nine identifiable teeth or portions of teeth, only a few of which are still attached to jaw fragments, and eighty-two tooth fragments too small to be identified.

Identification of the Material (tables 1, 2 and 3)

Hooijer (1958) recognised the Limeworks rhinoceros material as belonging to the two extant African species, *Ceratotherium simum* (White or Broad-Lipped rhinoceros) and *Diceros bicornis* (Black rhinoceros). Only the upper molars of the two species differ sufficiently in morphological characters to enable them to be classified.

Of the 99 identifiable teeth 94 are deciduous molars and of these the great majority have either unworn or only very slightly worn occlusal surfaces indicating the very young age of the animals represented. 68 of the deciduous molars are upper and of these 52 derive from *Ceratotherium* and 16 from *Diceros*. These molars can be identified further according to their position in the jaw (fig. 1 and 2).

Signs of Preparation and Use of the Teeth as Tools

Of the 99 identifiable teeth 70 are detached and only 29 remain attached to fragments of jaw (either singly, six specimens; in pairs, two specimens; in threes, five specimens or as in one particular specimen, a complete deciduous tooth row of four teeth) (tables 1, 2 and 3).

27 of the 70 detached teeth display fine markings, possibly indicating where they have been chipped away from the jaws. The unnatural nature of this damage was first observed and commented upon by J. W. Kitching (1957) (pers. comm.) In the case of the upper molars of *Diceros*, this chipping occurs mostly along the cingulum and is continued at approximately the same level across the buccal face. In the upper molars of *Ceratotherium*, in which the cingulum is neither as continuous nor as well developed, the majority of the teeth have been broken off along the enamel line (i.e. the junction between the roots and the crown). This is also the case in the lower molars.

The chipping best displayed in specimen M2096 (Plate I fig. 1b) must have been accomplished by some hard sharply pointed object. The markings show clearly that the teeth were struck with oblique blows directed towards the roots. It is possible to deduce these facts from the fine shallow asymmetrical punctate marks deepening in towards the freed edge and from the triangular shaped flaking adjacent to this edge.

Well worn notches, ranging in width from 5mm to 20mm, have been developed along the chipped edges of ten upper molar specimens (table 4). The best defined and preserved of these are to be found in specimens M2096, M169, M171 and M2364 (plate I).

A very interesting comparison can be made between these notched teeth from the grey breccia and the abundant notched stone tools found by Maguire in the succeeding pink breccias and overlying surface soil, and which are described elsewhere in this journal.

Thus not only were skeletal parts used for making notched tools during australopithecine times, but also a variety of lithic materials, and preponderantly those native to the dolomitic cavern site viz. dolomite, chert and vein quartz. These materials were furthermore supplemented by waterworn quartzite pebbles that were seemingly first introduced into the cavern at a fairly late stage in the accumulation of pink breccia. Although hard, relatively intractable and primarily used for pounding (Maguire 1965) many of the resultant accidental (sometimes apparently deliberate) flakes and fragments were utilised as notched scrapers.

Discussion

The following discussion will be carried out under the assumption that research to date (Dart 1956, 1957, 1958, 1964a, 1964b, 1965a, 1965b) has proved that the abundant bone, tooth and horn-core material found in the Limeworks cavern was accumulated by australopithecines and that they fashioned a large variety of tool forms from them.

The first point to note is the very great discrepancy between the numbers of deciduous and permanent teeth that have been found in the deposit. The australopithecines apparently concentrated their efforts on the very young calves. The fully-grown white rhinoceros weighs 3½ tons (the black rhinoceros 2½ tons) and has a hide an inch thick. It is, therefore, not surprising that the adults were left unscathed.

The second interesting point is that, considering only the upper milk molars (tables 1 and 2), a minimum of 28 *Ceratotherium* calves is represented as compared with a minimum figure of 6 for the *Diceros* calves. This uneven distribution is most likely due to environmental factors. *Ceratotherium* keeps to open grassy plains, whilst *Diceros* prefers bushy acacia country. Both conditions probably prevailed in and around the Makapansgat valley, but with a bias towards the grassy plain type. The lethargic docile nature of *Ceratotherium* as opposed to the irritable inquisitive ways of *Diceros* could also have had a bearing on the problem.

Unlike the great apes, the australopithecines appear to have had permanent (or possibly seasonal) abodes, in this case the Limeworks cavern. Co-operation between members of a tribe must have been essential to their existence. The females probably stayed at the cave with the young children, whilst the males went out to hunt. In the case of rhinoceros calves one group of hunters probably diverted the mothers' attention, whilst the others moved in for the kill. Under this set of circumstances it is most likely that the whole animal would have been carried back to camp.

Dart (1965b) described a number of skin working tools from Limeworks and wrote that these "would be meaningless if the australopithecine phase of human existence had not brought with it the discovery of dorsal load-carrying with the aid of cordage and thongs". The preparation and use of thongs is strongly supported by the presence of the worn notches in the freed edges of the rhinoceros teeth. If this theory is correct then the hunters had a quick and efficient means of transporting the rhinoceros calf back to the cave.

At the cave the meat was shared out and the potential tool-making parts of the skeleton retained. Numbers of skeletal remains, other than teeth, have been found in the deposit.

It is obvious that the teeth were found most useful when detached from the jaws. As scrapers the attached teeth and jaw are not as efficient as the maxillae and mandibles of medium and small bovidae. The few attached specimens that there are must almost certainly have been used as scrapers, but there are not sufficient signs of wear, distinct from that caused by chewing in the living animal, to demonstrate this conclusively.

Specimens M2107 (left jaw with $\frac{1}{2}$ DM^2 + DM^3 + DM^4) and M2108 (right jaw with DM^2 + DM^3 + $\frac{1}{2}$ DM^4) from the same *Diceros* individual provide the best evidence as scrapers. Both specimens, unfortunately, have been partially damaged by the blasting of the limeworkers. The teeth are fairly deeply worn due to chewing, but in each set the highest points on the occlusal surfaces (the exposed enamel rim of the paracone style (fig. 3) of DM^3 + DM^4 in M2107 and of DM^3 in M2108) are slightly rounded, possibly due to post-mortem abrasion.

When considering the detached teeth the selection of conveniently sized material becomes apparent (fig. 2). *Ceratotherium* teeth are larger than their counterparts in *Diceros*, DM^2 in the former being roughly the same size as DM^3 in the latter. The fact that these two teeth are the most common, in the respective animals, indicates that this size of tooth must have been the most convenient to handle.

Conclusions

The peculiarly damaged rhinoceros teeth from the Limeworks cavern provide concrete evidence of the relatively advanced mental capacity of the australopithecines. The ability to fashion a sharp pointed object in order to chip a tooth from a jaw and then to use the chipped edge of that tooth as a scraper,

requires foresight and imagination superior to that found in any of the great apes. The notches in the chipped edges of the teeth are suggested to have been worn during the softening of thongs, which were very possibly used in dorsal load-carrying.

Acknowledgments

I would like to thank Professor R. A. Dart for suggesting this project to me, and for his help and stimulation. I also received much assistance from Mr J. W. Kitching and Mr B. Maguire, who both read the manuscript in addition to discussing various aspects of the problem.

The photographs were taken by Mr Alun Hughes.

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EXPLANATION OF PLATE 1

Fig. 1: Rhinoceros upper milk molars. Occlusal edge downwards.
a: M169, *Diceros bicornis*, DM^3 left, buccal view.
b: M2096, *Diceros bicornis*, DM^3 right, buccal view.

Demonstrating the irregular markings resulting from deliberate chipping of the tooth away from the maxillae. The chipping occurs across the buccal face just within the enamel line.

Fig. 2: Rhinoceros upper milk molar. Occlusal edge downwards.

An enlargement of M2096 (see Fig. 1b) tipped slightly to improve the view of the two obviously chipped notches worn smooth by abrasive use.

Fig. 3: Rhinoceros upper milk molars. Occlusal edge downwards.
a: M2364, *Ceratotherium simum*, broken DM^2 left, buccal view.
b: M171, *Ceratotherium simum*, DM^3 right, buccal view.
Demonstrating notches of a size larger than those seen in Fig. 2. In M171 damage along the remaining edge can clearly be seen as partly deliberate and partly accidental (part which might have occurred prior to fossilisation and part during preparation of the specimen).

EXPLANATION OF TEXT FIGURES

Fig. 1: Diagram to show frequency of occurrence of the different Makapansgat Limeworks rhino teeth.

Fig. 2: Diagrammatic representation of the upper milk molars of the two species of rhinoceros to indicate the frequency of occurrence of the respective teeth.

Fig. 3: Occlusal view of a slightly worn left DM^3 of *Ceratotherium simum* showing the parts of the tooth.
Natural size.

a. parastyle.
b. paracone style.
c. mesostyle.
d. metacone style.
e. metastyle.
f. enamel.
g. dentine.
h. postsinus.
i. metaloph.
j. medisinus.
k. crochet.
l. cingulum.
m. protoloph.
n. medifossette.
o. crista.
p. ectoloph.

TABLE 1

Upper Molars of CERATOTHERIUM SIMUM

DM^1	DM^2	DM^3	DM^4
M 8219 rt.	M 8219 rt.	M 8219 rt.	M 8219 rt.
	M 164 rt.	M 164 rt.	M 164 rt. (probably not of same set)
	M 2105 left	M 2105 left	
	M 2102 rt.		
	M 168 left		
	M 166 (+ jaw) left		
	M 2094 left		
	M 2089 rt.		
	M 172 (+ jaw) rt.		
	{ M 174 left M 2091 rt.		
	M 2095 left		
	M 178 rt.		
	M 2090 rt.		
	M 2092 left		
	M 2102 rt.		
	M 2099 left		
	M 641 rt.		
	M 2093 rt.		
	M 2088 left		
	M 2097 left		
	M 2359 rt.		
	M 170 rt.		
	M 2364 left		
	M 176 rt.		
	M 2125 left		
	M 2129 rt.		
	M 2123 rt.		
	M 2130 rt.		
		{ M 2104 rt. M 2098 left	
		M 2112 rt.	
		M 640 (+ jaw) left	
		M 171 rt.	
		M 167 rt.	
		M 2358 left	

TABLE 1 (*Continued*)

DM [1]	DM [2]	DM [3]	DM [4]
M 179 left M 2103 left		M 2362 left M 2363 rt. M 2360 left	M 2110 left M 639 (+ jaw) left { M 2357 rt. { M 2111 left M 2356 rt.
L. R. 2 1	L. R. 12 17	L. R. 6 7	L. R. 3 4
Total No. of teeth 3	Total No. of teeth 29	Total No. of teeth 13	Total No. of teeth 7
Total No. of animals 3	Total No. of animals 28	Total No. of animals 12	Total No. of animals 6

Where two teeth are bracketed pairing is indicated (i.e. the teeth are from the corresponding positions of the right and left jaws of the same animal.)

TABLE 2

Upper Molars of DICEROS BICORNIS

DM 1	DM 2	DM 3	DM 4
M 180 left	M 2108 rt. M 2107 left M 2106 (642) rt. M 165 left	M 2108 rt. M 2107 left M 2106 (642) rt. M 165 left M 169 left M 2100 rt. M 2096 rt. M 2368 left	M 2108 rt. M 2107 left M 2106 (642) rt.
L. R. 1 0	L. R. 2 2	L. R. 4 4	L. R. 1 2
Total No. of teeth 1	Total No. of teeth 4	Total No. of teeth 8	Total No. of teeth 3
Total No. of animals 1	Total No. of animals 3	Total No. of animals 6	Total No. of animals 2
M 1 M 2109 left			

TABLE 3

Lower Molars of CERATOTHERIUM plus DICEROS

Left	Right	Left	Right
Deciduous		Permanent	
M 2114	M 175	M 2164 (3 teeth and jaw)	
M 2115	M 2113	M 2120	
M 2116	M 2353		
M 2118	M 2354		
M 2127	M 8252		
M 2355	M 8259		
M 2117 (+ jaw)	M 8258		
M 8253 (+ jaw)	M 177		
M 8254			
M 8261			
M 8264			
M 173			
M 8253			
M 8257			
M 8256			
M 8262			
M 8260			
M 8263			
Total No. of teeth 18	Total No. of teeth 8	Total No. of teeth 4	Total No. of teeth 0

TABLE 4

Upper Milk Molars Displaying Chip Marks

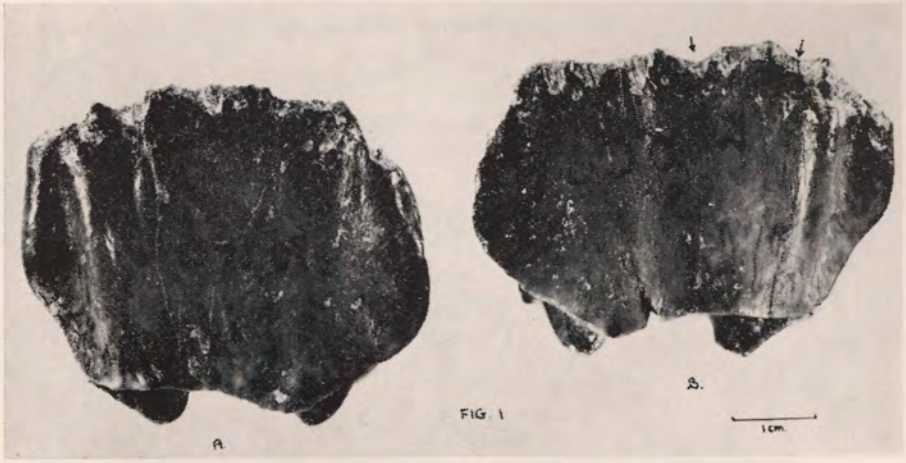
Chip marks and small notch or notches	Chip marks and relatively large notch	Chip marks only
M 170 6 mms	M 2359 12 mms	M 2363
M 2096 6 mms and $5\frac{1}{2}$ mms	M 171 15 mms	M 174
	M 2102 (20) mms	M 2358
	*M 2100 (12) mms	*M 169
	M 2364 15 mms	M 2362
	M 2095 (?) mms	M 2110
	†M 2104 (13) mms	†M 2098
	M 2097 (10) mms	M 2103
		M 179

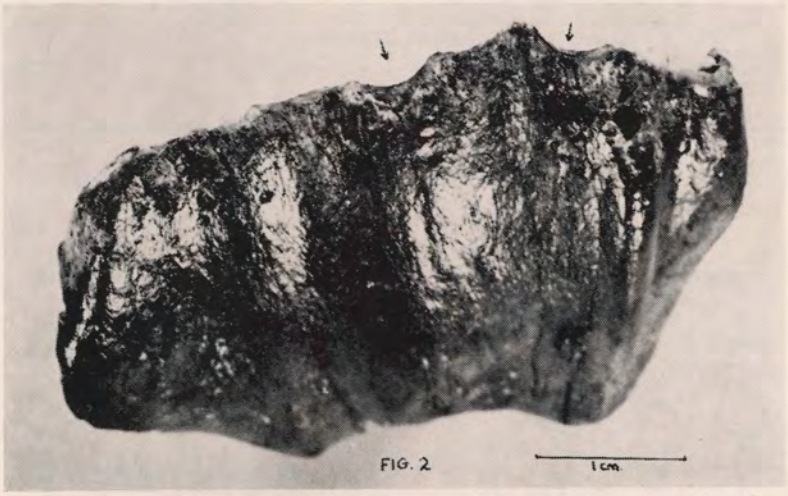
* and † indicate pairs.

The millimetre measurements refer to the breadth of the notches. Where the figure is put in brackets the notch has been partially broken and its original size has been estimated. On M 2095 only a very small portion of the notch remains and no estimation was possible. On M 2096 two notches occur.

Lower Milk Molars Displaying Chip Marks

	Chip marks only
	M 2120
	M 2116
	M 8262
	M 175
	M 8255
	M 8288
	M 2115
	M 8259





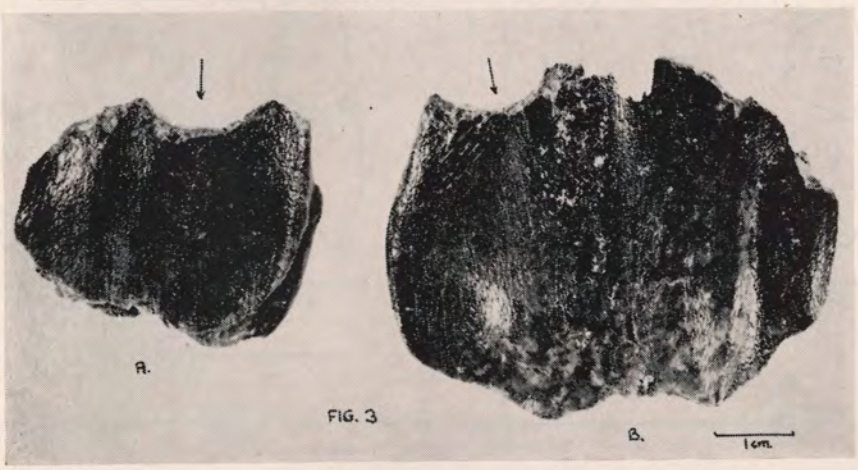


Plate 1.

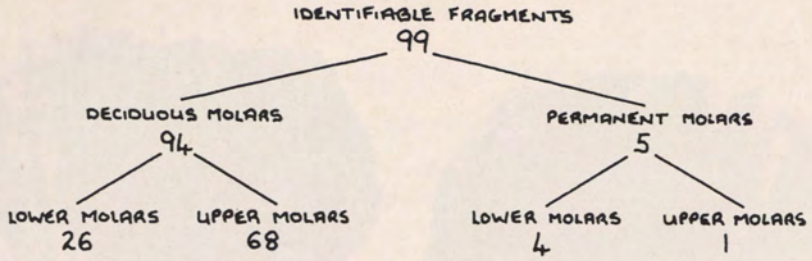

IDENTIFIABLE FRAGMENTS
99
DECIDUOUS MOLARS
94
PERMANENT MOLARS
5
LOWER MOLARS
26
UPPER MOLARS
68
LOWER MOLARS
4
UPPER MOLARS
1

Fig. 1

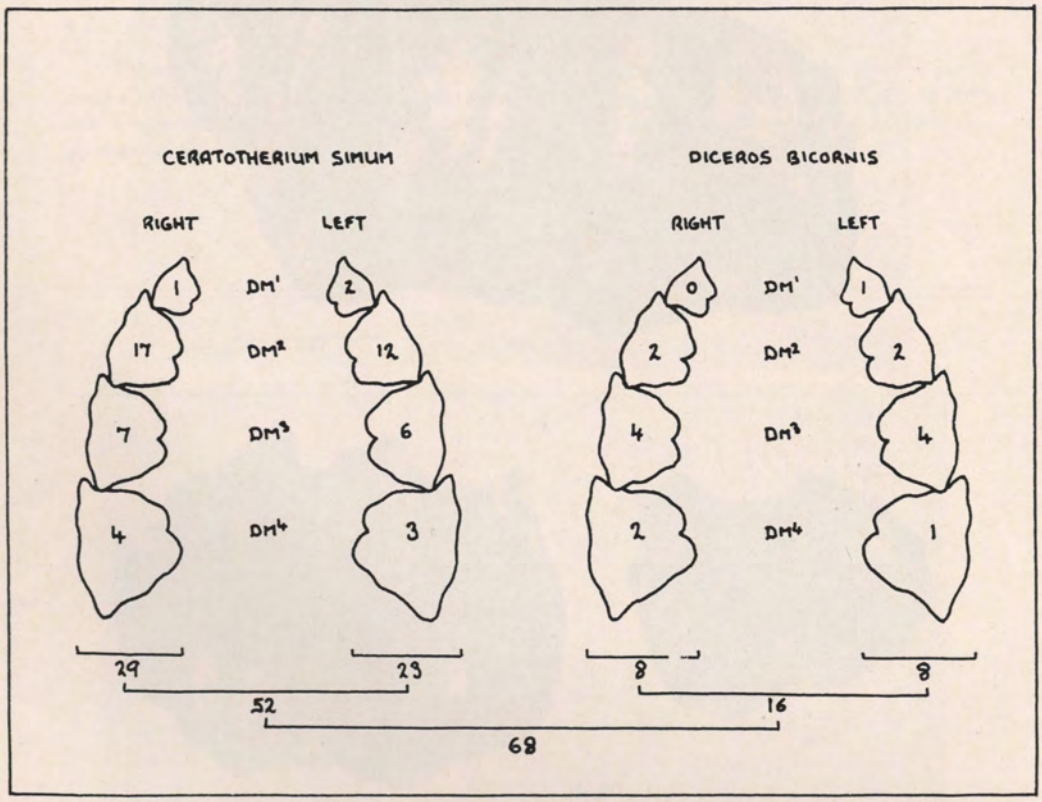

CERATOTHERIUM SIMUM
RIGHT
LEFT
DM¹
DM²
DM³
DM⁴
1
17
7
4
2
12
6
3
29
23
52
DICEROS BICORNIS
RIGHT
LEFT
DM¹
DM²
DM³
DM⁴
0
2
4
2
1
2
4
1
8
8
16
68

Fig. 2

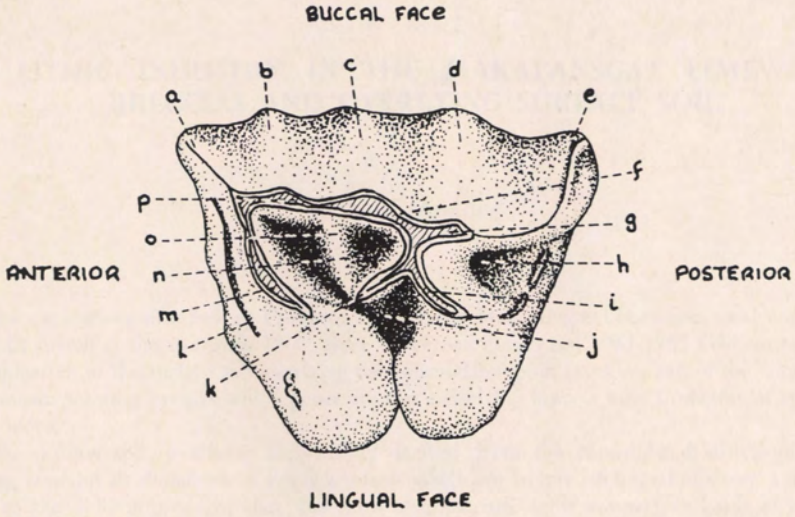

BUCCAL FACE
a
b
c
d
e
f
g
h
i
j
k
l
m
n
o
p
ANTERIOR
POSTERIOR
LINGUAL FACE

Fig. 3

THE LITHIC INDUSTRY IN THE MAKAPANSGAT LIMEWORKS BRECCIAS AND OVERLYING SURFACE SOIL

By Brian Maguire

ABSTRACT

The excavations directed by Professor Dart at the Makapansgat Limeworks, and conducted mainly by myself at the site since 1960, were concerned during the 1963-1965 field seasons with an examination of the surface soil overlying the consolidated pink breccias, and of the contents of the abundant solution cavities which penetrate the underlying breccia mass to depths of up to 15 feet or more.

The shallow soil, overlying and mainly derived from the consolidated australopithecine breccias, contains an abundance of crude artefacts which are largely composed of chert, a material native to the dolomitic cavern site. The most characteristic tools are various kinds of notched scrapers which are more particularly described. The undoubted relationship of these artefacts to those occurring in the underlying breccias is also discussed.

INTRODUCTION

The Site

Covered rather uniformly by a thin dark layer of very rubbly surface soil which only ranges up to 12 or 18 inches in depth, the calcified infill of the vast ancient Limeworks cavern extends as an uninterrupted and highly consolidated huge mass over an area of more than three acres on the north-west facing Limeworks hillside (Brain 1958). Surface erosion has removed the roof of the ancient cavern and worn down the consolidated infill to general conformity with the moderately sloping dolomite hillside, the remaining infill extending to a depth of 50 or 60 feet below the present surface. This consolidated infill accumulated upon a limestone floor sometimes of great thickness and frequently of great purity. The extensive limeworkers quarries and underground excavations (fig. 1) which almost completely encircle the whole deposit, and have exposed so much of the breccial infill, were designed to exploit the underlying limestone (travertine) forming the ancient cavern floor, and which ranged up to 40 or 50 feet in thickness. Until the removal of most of the vegetation in 1961 and 1962, the Limeworks site was covered by a fairly close growth of trees and shrubs resembling that covering the neighbouring slopes (Dart 1965b; Maguire 1965).

By far the largest volume of the calcified deposit is composed of pink breccia. Occasionally shallowly outcropping through the thin layer of surface soil, this breccia covers the entire area of the deposit, and extends downwards to depths of 30–50 feet or more.

The older and more extensive of the two rather ill-differentiated pink breccias is the pale pink and very highly calcified *upper phase* 1 *breccia* of Brain

(1958) which contains abundant blocks and smaller fragments of dolomite and chert, and scattered, mainly primate, fossil remains. Sometimes resting directly upon the ancient cavern floor, it may represent at such points the full depth of the breccial deposit. This breccia occupies the entire area between the main and east quarries and the back wall of the ancient cavern (fig. 1), but at the site of the cone mouth, and thinning considerably at the same time, it dipped fairly steeply beneath a 35 ft. depth of the later-formed, darker and generally less heavily calcified *phase* 2 *breccia* (Brain 1958).

The area defined by the cone mouth was extensively undermined by miners in search of the underlying cavern travertine some 30 years ago, resulting in the collapse of most of the relatively small deposit of phase 2 breccia, together with a 15-ft. thick underlying layer of upper phase 1 breccia, on to the floor of the underground workings some 70 feet below the present surface. The cone mouth is the 80-ft. wide circular opening to the surface formed at the site of the

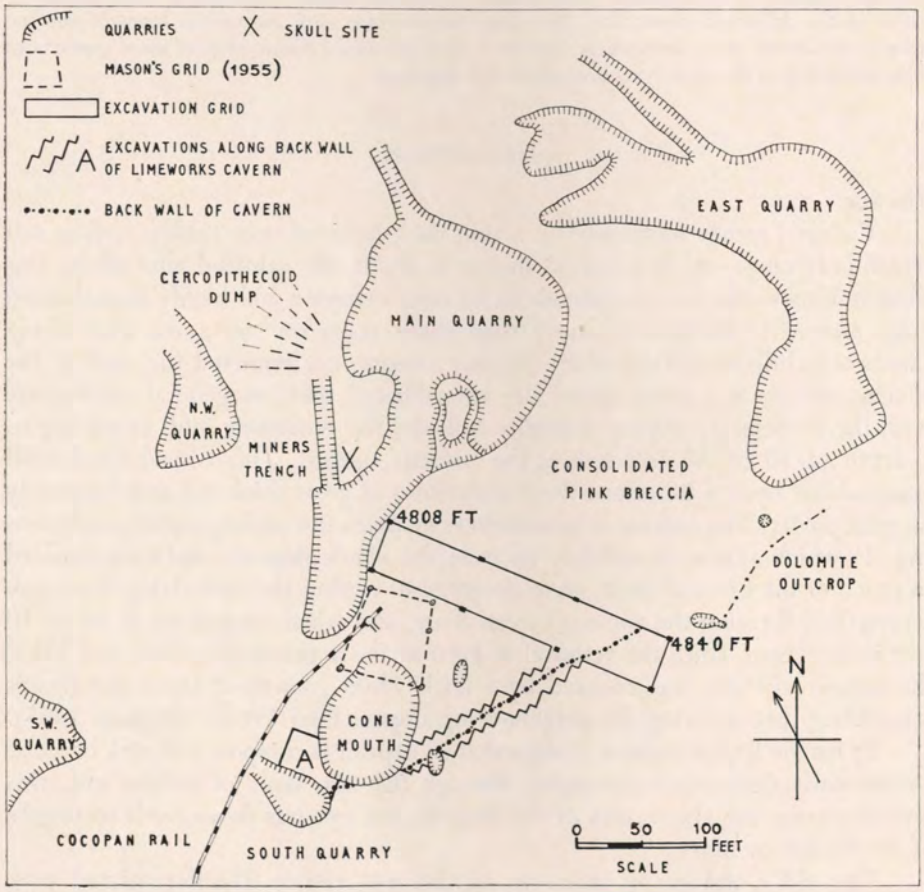


Fig. 1

collapse, the cone being the 15,000-ton conical hillock of collapsed pink breccia now resting on the floor of the limeworkers underground excavations.

The large numbers of dolomite and chert artefacts extracted in 1960 from the collapsed phase 2 breccia of the cone (Maguire 1965) are mainly referable to the two broad pebble ('gravel') bands represented in this breccia, and will be later discussed.

The most basal and oldest of the Limeworks breccias completely underlie the pink breccias. These two strongly calcified layers, comprising the *lower phase 1 breccias* of Brain, are the sparsely bone-bearing calcified red muds ranging up to 20 feet or more that accumulated on the lowest-lying parts of the ancient cavern floor, and the 1–3 ft. thick, exceedingly richly bone-bearing layer of grey breccia that formed in places upon these muds.

The faunal content of the grey breccia, while widely varied, is mainly (92% bovid, and the many thousands of utilised bones, teeth and horn cores extracte from it have been described at various times by Professor Dart (Dart 1957) The most extensive exposure of grey breccia is that preserved some 30 fee below the present surface, beneath the overhanging dolomitic west wall of th main quarry, and generally opposite the more northerly end of the grid (fig. 1). This dolomitic overhang, incidentally, formed part of the western wall and roof of the ancient cavern. The point at the edge of the main quarry marked with a cross is where J. W. Kitching found a loose block of pink breccia containing the larger part of an australopithecine skull in 1955 (Dart 1959). This block of upper phase 1 breccia must have been blasted by miners from the adjacent main quarry, the weathering on one of its faces indicating that it had formed part of the present breccial surface.

The unconsolidated surface materials and the recent excavations

The thin dark layer of surface soil overlying the breccias averages only about 12 inches in depth, and is extremely rubbly. The rocky fraction, which in volume about equals or even considerably exceeds the earthy fraction, is composed almost exclusively of weathered chert fragments ranging up to about 8 or 10 inches in length. Due to surface weathering, smaller dolomite fragments of any kind are rare.

The preliminary work during the 1963–1965 excavations involved the stripping and examination of the surface soil from the entire excavation grid (fig. 1) and from an area approximately one half as great extending along the back wall of the ancient cavern (a total area of 1500 square yards or 1250 square metres). The subsequent excavation, at 6-inch intervals, of the unconsolidated filling of 120 of the solution cavities on the grid clearly revealed the underlying very highly consolidated upper phase 1 pink breccia throughout the length of the grid.

The irregular-shaped mouths of the abundant vertically-descending solution cavities closely reticulate the strongly eroded but exceedingly compact, breccial

surface. Generally only 2–4 feet across, and tapering downwards, these solution cavities penetrate the breccia to depths of 15 feet or more.

The unconsolidated filling of the solution cavities comprises a red earth with a variable fraction of small rock fragments and is regarded primarily as a decalcified breccial residue. Apart from its reddish colour, and the slightly poorer state of preservation of its lithic components (almost exclusively chert) the uppermost foot or more of this filling closely resembles the very rubbly surface soil. The stony fraction diminishes fairly rapidly with increasing depth, at the same time becoming progressively more poorly preserved. Upwards, the red filling is fairly abruptly succeeded by the overlying dark surface soil.

Apart from the recovery of cultural or fossil material in the surface soil, the main purpose of the excavation work along the back wall of the ancient cavern was to define the exact extent of the cavern infill in the area lying between the excavation grid and the cone mouth.

More than 16,000 suspected chert artefacts were extracted from the surface soil of the grid and from the excavations along the back wall of the cavern, together with some 16,000 fragments of vein quartz; and, representing materials geologically foreign to the dolomitic cavern site, 1,977 pebbles and fragments of quartzite. Lesser, but quite comparable numbers of suspected fragments composed of the same materials, were retrieved from the red earthy contents of the 120 solution cavities of the grid.

After a stringently objective analysis of the 16,139 suspected chert fragments extracted from the surface soil, nearly 7,000 were considered to be definite artefacts, and of these a special group of 2,328 was selected as being the best preserved and most demonstrative of artificial fabrication and utilisation. A total of 1,881 of these selected specimens was recovered from the excavation grid (see Table 1), their description forming the main object of this paper.

These chert tools are relatively crude, and ranging in length from ½–7 inches are very variable in size. Both technologically and morphologically, however, they exhibit considerable uniformity, and are characterised by the following features:

1. The major preparatory fracturing has involved splitting (often along natural fracture surfaces) and crude, occasionally more precise, flaking quite opposed to natural surfaces of fracture.
2. The abundant minor damage attributable to trimming rather than utilisation is almost entirely unifacial. This often strictly uni-directional damage is usually displayed with striking clarity.
3. Many of these artefacts (perhaps one half, or more) are clearly multiple-purpose tools.
4. Notched scrapers alone comprise almost half of the entire assemblage, and outnumber the three next most important groups combined. In order of importance these smaller groups are planes, convex scrapers and straight-edged scrapers (figs. 2–4).

Earlier excavations and the artefact content of the breccias

The completely basal red breccia is virtually devoid of rocky inclusions, and no suggestive lithic fragments have yet been recovered from it.

In the extremely ancient and bone-rich grey breccia, however, stalactites and very occasionally fragments of other lithic materials displaying signs of deliberate use (Dart, 1965a; Partridge 1965) occur intermixed with the enormous numbers of utilised and unutilised bones (Dart 1957). The native lithic fragments comprise stalactites, shale, chert and dolomite; materials geologically foreign to the cavern site are represented by several small fragments of grey quartzite, one of these being wedged in the interarticular cleft of an antelope metatarsal that was removed from a block of this grey breccia.

The upper phase 1 breccia (the first and major stage in the accumulation of the huge mass of pink breccia) is extremely compact, and due to the problem of extracting a sufficient number of artefacts undamaged from the rocky matrix, a picture of tool-making in upper phase 1 times is incomplete.

Sufficient material is however available to show that the deliberate splitting as well as crude flaking and trimming of the native chert and dolomite was certainly practised. Quartzite riverbed pebbles were introduced into the cavern mainly for percussional activities, but seemingly only at a late stage in the accumulation of the upper phase 1 breccia, and only in small numbers.

Brain's profile 10 was sited on the vertical to overhanging northern wall of the cone mouth, where a 15-ft. layer of upper phase 1 breccia rests directly upon the travertine of the ancient cavern floor. Above this layer, and traversed by two broad pebble bands, 35 feet of the darker phase 2 breccia extends to the present surface (Brain 1958). The pebbles forming these two bands average about 1–5 inches in diameter, but range up to 10–14 inches in diameter, most of them being composed of dolomite. The proportion of chert pebbles is small, while pebbles and fragments of quartzite are comparatively rare.

In 1954 Brain extracted 129 suspected artefacts from the base of the phase 2 breccia in profile 10. Professor C. van Riet Lowe considered 17 of these specimens to be Kafuan-type artefacts, 15 of them being deeply leached dolomite, one of vein quartz and one of dark grey quartzite (Brain *et al*, 1955). In 1960 A. R. Hughes and I extracted 22,000 pebbles, almost all of them composed of dolomite or chert, from 1,600 tons of the collapsed phase 2 breccia forming a part of the cone adjacent to profile 10. I estimated that between 15% and 30% of these pebbles exhibited signs of artificial damage although only 346 specimens were then selected for further examination (Maguire 1965).

It is readily evident that these crude, sometimes massive, cleaver and hand-axe-like tools, and the usually lighter planes and great variety of convex, straight and concave scrapers, have their counterparts in the surface collections. Despite their crudity and the indifferent state of preservation of many of the more dolomitic of these tools, I was then struck by, and noted (unpublished MS. 1960),

exactly the same features that distinguish the presently described surface collections, viz.

1. The splitting and crude flaking of the native raw materials had very frequently been practised. Most, or at least many of the slabs or fragments providing these raw materials had suffered some degree of weathering *prior to their use for tool-making.*

2. The abundant fine damage attributable to trimming and/or utilisation is characteristically unifacial.

3. Many of the smaller tools are multiple or compound, and had evidently subserved more than one function.

4. Concave scrapers and planes constitute important elements in the assemblage.

The chert artefacts are usually well-preserved, but most of the dolomitic specimens, which constitute by far the greater percentage of the assemblage, are heavily weathered, their surfaces sometimes being white and chalky. However, in all but the most excessively weathered of these artefacts from the phase 2 breccia, *there should generally be no difficulty whatsoever in recognising the nature of the grosser fracturing damage they have suffered, or of appreciating the characteristically unifacial and repetitive nature of the damage done to working edges, even where much of the finer detail has been lost* (Maguire 1965, figs. 1 and 2).

A very much smaller number of quartzite pebbles and fragments has been recovered from the phase 2 breccia, almost half of them (60) being either very crude flakes, or demonstrating crude flaking damage. Many of them are waterworn pebbles that have been scarred and quite frequently fractured by deliberate pounding, the fragments generally appearing to have resulted from the deliberate or accidental fragmentation of the waterworn pebble pounders. The fresh-looking, 4½ inch long, coarsely and unifacially trimmed triangular quartzite artefact illustrated by Partridge (1965) from the phase 2 breccia, and described by him as an 'irregular artefact', has lately been partially reconstituted by the addition of a missing fragment. This irregular artefact is now recognisable as the one half of a very broadly ovato-triangular deliberately struck flake with a prominent bulb. The small added fragment was intentionally pointed at one end, and trimmed at the other end into a scraping edge, subsequent to its seemingly accidental detachment.

The artefact content and derivation of the surface soil

In 1965 I described the recovery during 1961 and 1962 of more than 1,300 deliberately and repetitively percussed quartzite river-bed pebbles and pebble fragments from the thin layer of vegetation soil covering the consolidated breccias (Maguire 1965). I referred also to similar quartzite artefacts embedded within, and protruding from, the weathering surface of the strongly calcified pink breccias (mainly phase 2) about the cone mouth (fig. 1), as well as to the very definite concentration in this vicinity of both the surface specimens and those *in situ* in the breccias.

These surface-soil quartzite artefacts were found to be *locally confined to the cavern site* and to be *between twenty and forty times more abundant at, and about the cone mouth, than over the entire more northerly half of the deposit.* This marked concentration, in the vicinity of the cone mouth, has been confirmed by the recent excavations.

Almost half of these very crude quartzite artefacts were simply referred to as regular and irregular pounders, while the remainder, on the basis of shape and presumed function, were described as scrapers and planes. Those possessing one or more marginal notches and frequently a utilisable point as well, were by far the most abundant and characteristic of the scraping tools, and were termed "notch and point scrapers".

The abundance of repetitive percussional damage evidenced throughout the assemblage led me to conclude that the artificial fragmentation of many of these pebbles was entirely incidental or accidental. It seems probable, however, that a small percentage of such fragments represent deliberately struck, albeit very crude, flakes *and are therefore not altogether fortuitous fragments.* The close examination and reconstruction of the long-separated parts of some 40 quartzite pebbles and artefacts (or their fragments) that have been excavated to date from the surface soil overlying the breccias, and the varied and invaluable evidence furnished by them, is briefly referred to in the discussion. *These parts, for example, prove conclusively that the pounding and fragmentation of waterworn quartzite pebbles was carried out on the site.*

Of the 1,977 quartzite pebbles and fragments recovered during the recent stripping of the surface soil from the grid and back wall of the ancient cavern, only 8% appear to be deliberately struck flakes or flaked artefacts, or their fragments. These often very crude and indeterminate, but generally Acheulean-type artefacts, include two handaxes and two cleavers (?). The last mentioned four tools are bifacial and show considerable though mainly poor preparation.

The 94 fragments of other foreign materials (mainly irregular utilised mudstone fragments, and very much weathered diabase spheroids) include four felsite fragments of Middle Stone Age facies.

Vein quartz is a material native to the site, although very much less abundant than the chert. In view of the particular difficulty of immediately recognising the unnatural damage suffered by fragments of this material, all available fragments (some 16,000) were extracted from the excavated soil for later examination. While probably one third of this number have been utilised and variously fractured, the raw material is extremely rough and intractable, and either by intention or lack of skill on the part of the users, very few of them appear to have been specially shaped.

The most definitely shaped artefact in vein quartz so far recovered is, however, an unusually good example of the notch-and-point scraper. (An equally noteworthy specimen was later excavated from a solution cavity.)

These utilised rough vein quartz fragments were frequently used percussionally, probably as fabricating tools. While a quite undoubted polyhedral-

spheroidal pounder, some 3 inches in diameter and with adherent phase 2 breccia matrix, has lately been recovered from a dump of mining waste, rounded vein quartz pounders of this size are rare in the surface soil. The many fragments that have not been used primarily for percussional activities have been crudely pointed, notched, or used as straight-edged or convex scrapers.

It should be remembered that there has been a virtually total recovery of every fragment of quartzite and other foreign materials upwards of $\frac{3}{8}$ inch in length (or diameter) from the 1,500 square yards of excavated surface soils. The inherent difficulty of extracting the frequently crude chert artefacts from this rubbly soil is obvious, since more than one half (by volume) of this soil solely comprises variously weathered chert fragments ranging up to about eight or ten inches in length.

Some idea, therefore, of the almost negligible role played by quartzite as compared with the overwhelming dominance of chert as a toolmaking material in the deposit can be gained from the following figures:

The careful working of the single grid square A13 (78 x 78 inches), resulted in the recovery of 879 chert artefacts (212 *of which were worthy of special selection for the present analysis*) and 673 probable artefacts. Only 18 quartzite pebbles and fragments (mostly pounders or their percussed fragments, but all of them unflaked and conventionally indeterminate) were recovered.

The number of chert artefacts recovered from this grid square, even excluding probable tools, therefore outnumbers the total number of quartzite fragments of every description by nearly fifty times. Furthermore, the total of 1,552 definite and probable chert artefacts retrieved from this single grid square outnumbers the total number of quartzite fragments of every description (1,414) recovered from the surface soil of the entire excavation grid, *an area* 216 *times as great!*

The occurrence throughout the surface soil overlying the breccia of large numbers of chert tools unmistakably resembling the artefacts of chert and dolomite extracted from the phase 2 breccia, strongly suggests that the surface soil (and certainly its heavier fractions), primarily represents a decalcified breccial residue. This conclusion is quite independently confirmed by the distribution both in the pink breccia and in the overlying surface soil of the repetitively percussed artefacts that have been derived from waterworn quartzite pebbles. This conclusive evidence may be briefly summarised:

1. The more than 1,300 repetitively percussed quartzite artefacts that were recovered from the surface of the deposit were locally confined to the cavern site. Incontrovertible evidence demonstrates that a number (at least!) of these percussed artefacts were artificially fragmented on the site.

2. These artefacts have been derived from waterworn quartzite pebbles which are geologically completely foreign to the dolomitic cavern site and must have been carried into the ancient cavern by human or protohuman means.

3. The artefacts occurring *in situ* in the pink breccia, as well as those recovered from the surface soil, have suffered the same kind of artificial damage by repetitive percussion.

4. Both the breccial and the surface artefacts were very strongly concentrated at, and near, the cone and cone mouth (Fig. 1).

That these artefacts displaying the same unusual kind of unnatural damage, and made from the same kind of foreign stone, are locally confined to the cavern site, and furthermore, that both the breccial and the surface specimens are concentrated in the same area on the cavern site, are facts of crucial importance. It can only be concluded that the repetitively percussed quartzite artefacts in the surface soil were inclusions of an integral part of the ancient cavern infill that overlay the present deposit of pink breccia, i.e. they have been derived from the upper part of an originally thicker deposit of breccia that has been completely decalcified by weathering.

The upper phase 1 breccia is represented uninterrupted over more than 90% of the breccial surface of the deposit, being overlain by the phase 2 breccia only at, and about the cone and cone mouth.

Therefore, the original deposit probably comprised a greater depth of both these breccias. However, the phase 2 breccia, besides being thicker, was probably also much more extensive and was not confined as at present to the cone and cone mouth vicinity, but overlay the original deposit of upper phase 1 breccia over a considerably larger area.

It is not impossible that the extra depth of original cavern infill included breccia(s) of a different type. However, it is evident from the numbers of quartzite artefacts recovered from the surface soil that, whatever the nature of the overlying infill, percussed quartzite artefacts must have been inclusions of at least part of it.

A comparison of the cone and grid areas, based in each case on the ratio of the number of quartzite pebbles and artefacts recovered from the surface soil to the number of such objects visible on the surface of the underlying breccia, indicates that a disproportionately large number of pebbles and artefacts was recovered from the surface soil of the grid. This suggests that the more richly (quartzite) artefact-bearing phase 2 breccia originally extended over the upper phase 1 at the site of the grid. Therefore, part of an originally much more extensive deposit of phase 2 breccia, that was subsequently completely decalcified by weathering, seems to have been the main source of the unexpectedly large numbers of percussed quartzite artefacts found in the surface soil overlaying the upper phase 1 breccia on the grid site.

The extremely slow rate of downhill movement (if any) of quartzite pebbles and artefacts on the cavern site subsequent to their release by weathering from the breccia mass and incorporation in the surface soil is demonstrated not only by the above evidence, but also by the disposition of such elements in the surface soil along the back wall of the ancient cavern. Numbers of quartzite artefacts, both with and without adherent breccia matrix and evidently very long separated from the parent breccia mass, were recovered within a foot or two of the well-defined and up-slope back wall of the cavern.

For these many reasons, the surface soil overlying the consolidated breccias, and at least its heavier (non-earthy) fraction, has been regarded primarily as a decalcified breccial residue.

The Recovery of the Chert Artefacts from the Surface Soil Overlying the Pink Breccias, and the Method of Analysis

Altogether 16,139 suspected chert artefacts and fragments were extracted rom the surface soil excavated from the grid and an area approximately half as reat along the back wall of the ancient Limeworks cavern, during the 1963–1965 eld seasons of excavation at Makapansgat.

All of the excavated surface material was put through a $\frac{3}{8}$-inch sieve and, to facilitate the extraction of artefacts, the sieved materials were first sluiced through water. The procedure was rendered somewhat laborious by virtue of the fact that an attempt was made to recover not only all of the foreign stones present, but also all suspected artefacts composed of the local materials viz. chert, dolomite and vein quartz.

The first stage of the critical examination of the excavated chert material was conducted during September and October 1966 at Makapansgat.

The procedure adopted was more objective than that normally employed in examining an artefact assemblage. While the deliberate flaking of some of the chert artefacts has proved acceptable to many competent observers, and a small number of outstandingly clear examples were extracted for final analysis, I employed neither this feature, nor that of tool-shape, as the main criteria in my examination. The overwhelming majority of suspected objects was selected almost solely on the basis of the minor damage present i.e. the perceptible (and usually abundant) fine chipping and wear that could be attributed to trimming or utilisation or both. The nature and distribution of this damage on every fragment was meticulously examined with a view to assessing its probable artificiality or not.

The following combination of features relating to the fine chipping and perceptible wear exhibited by the individual objects was regarded as particularly suggestive of artificial damage:

1. An abundance of such chipping or fine damage.
2. The contemporaneity of all such damage as assessed by the patination characteristics of the individual specimen.
3. The definite concentration (and especially complete confluence) of chipping and other scarring.
4. The noticeable restriction of such repetitive damage to well defined working features, such as entire edges, notches, or points.
5. The blows or pressures responsible for the fine chipping have been of equal intensity, or otherwise suggestively regulated, and also definitely controlled or patterned in their spacing and direction.

By such methods, the 16,139 chert specimens proved separable into three groups:

Definite artefacts (6,787).

Probable artefacts (5,991).

Doubtful, much weathered and other reject material (3,361).

Finally 2,328 of the best-preserved and most illustrative specimens from the group termed "Definite artefacts" were extracted for the purpose of the final analysis which was carried out at the Bernard Price Institute for Palaeontological Research in Johannesburg.

I felt that attempting the systematic arrangement into categories of tools of a large group of this size, *all of whose members displayed definitely unnatural kinds of contemporary and differential damage* (over and above whatever deliberate flaking had occurred) would clearly demonstrate whatever recognisable types of tools, if any, were present in the assemblage. Most of the selected specimens, many of them individually recognisable as artefacts, fell fairly readily into one of the limited number of groups listed in Table 1; a smaller number, having clearly subserved two or more separate uses and being of compound or multiple nature, were obviously classifiable only with some difficulty.

Table 1 refers to those 1,881 of the 2,328 finally selected specimens that were recovered from the vegetation soil of the excavation grid.

TABLE I

		Numbers of Tools		Percentages	
I	*SCRAPERS*				
	1 NOTCHED	842		44·8	
	2 POINTED	75		4·0	
	3 CONVEX	224		11·9	
	4 STRAIGHT EDGED	173		9·2	
	5 BLUNT-NOSED	29	1343	1·5	71·4
II	*PLANES*				
	1 STRAIGHT EDGED	39		2·1	
	2 CONVEX	64		3·4	
	3 POINTED	77		4·1	
	4 NOTCHED	100		5·3	
	5 COMPOUND	73		3·9	
	6 MISCELLANEOUS	49	402	2·6	21·4
III	*POUNDERS*		13		0·7
IV	*ANVILS*		1		0·1
V	*CORES*		39		2·1
VI	*UNUTILISED AND LITTLE-USED FLAKES AND FRACTURED FRAGMENTS*		83		4·4
			1881		100·1

TOOL SIZES IN INCHES	$\frac{1}{2}$–1	1–2	2–4	4–8
NUMBERS	81	875	808	117

It was apparent, on investigating the fracturing properties of the local chert, that *most of the major, usually multiple fractures suffered by these chert tools were opposed to the natural surfaces of fracture.* Prior, however, to describing the fracturing characteristics of the local chert, brief reference will be made to but two of the many features independently corroborating the artefactual nature of these tools.

1. The best-defined and most evident of the elementary cores present, and all of the many tools that are very densely and evenly manganese-stained, have clearly suffered no perceptible further damage whatsoever in the deposit subsequent to their manufacture (or staining). Beyond perhaps the almost imperceptible faint blunting or smoothing due to natural weathering in the deposit, there is not the faintest trace of palpable suggestive damage to the edges of the cores, or of damage of any kind to the edges of the evenly black-stained tools.

2. Some 90% of these chert tools have been trimmed in a very consistently unifacial (unidirectional) manner. This damage is almost invariably displayed with unusual clarity and sharpness of definition, due mainly to its unnaturally strict confinement to a working edge, and its abrupt and total absence on an adjacent face. Many of the notched scrapers (which comprise almost half the total assemblage), evidence this feature so remarkably that it seems attributable not only to a very specific type of preparation, but also to a very specific kind of use.

I could only conclude after my analysis of the whole assemblage that *the incidence of readily perceptible natural damage resembling in any way that attributed to deliberate trimming and utilisation is so low as to be completely negligible.*

The Fracturing Characteristics of the Native Raw Materials

The native rock in the immediate vicinity of the Limeworks cavern, and within which the ancient cavern was formed, is Transvaal System Dolomite. This minutely granular or crypto-crystalline blue-grey dolomite (impure dolomitic limestone) yields a conchoidal to uneven or flat fracture. It is unfortunately extremely susceptible to weathering processes, hence while artefacts of dolomite and cherty dolomite have sometimes been well preserved in the phase 2 breccia, and almost invariably so in the upper phase 1 breccia, no well preserved or sufficiently conclusive specimens have so far been retrieved from the relatively small number of dolomite fragments occurring in the overlying vegetation soil.

Chert bands ranging up to four or six inches, or perhaps even a foot in thickness, are abundantly interbedded in the local dolomite. This chert is usually crypto-crystalline and whitish to greyish or very pale blue and, being essentially siliceous, resists weathering to a far greater degree than the dolomite. It weathers free from the dolomite generally in the form of slabs, those surfaces that were in contact with the dolomite being characteristically rough and dark coloured. Such rough natural cortex has frequently been retained on some part(s) of the tools derived from these *weathered slabs*. Both sides of the planes pictured in figs. 2 and 4 are of natural cortex, and in fig. 3, the viewed face of the single-notched scraper seen in the top row (extreme left).



Fig. 2

The natural break-up of weathering chert slabs occurs along well-defined fracture surfaces which are generally flat or flattish. These surfaces, although typically smooth-textured and flat, will be referred to as *fracture surfaces* rather than fracture planes. The fracture surfaces comprise not only the very abundant parallel bedding planes (fig. 3, the second specimen from the left, in the top row), but also numerous planes inclined at various angles to the bedding planes and running in a variety of directions.

A weathering slab of chert that was excavated together with the artefacts from the rubbly surface soil of the grid, is illustrated in fig. 2 (the middle specimen in the top row). Natural disintegration has resulted in the loss of nearly all of the rough natural cortex and produced the sharply angular and straight-edged appearance of this slab. The fine dark lines seen on the pictured face (and also similar lines lying parallel with the upper and lower surfaces that are present along the sides of the slab) indicate incipient and potential natural surfaces of fracture.

The stout notched plane, pictured rather obliquely and from above (fig. 2, top on left), was excluded from the listed tools, since it did not clearly demonstrate repetitive artificial damage, although both the notch and the two shoulders on either side of it have been artificially abraded.

The specimen is of comparatively coarse-grained chert, rough natural cortex being seen on the obliquely exposed side (right). The smooth flat upper face represents a natural fracture surface; this may have been a pre-existing feature, but it appears to have been derived by deliberately fracturing (splitting) along a natural fracture plane. The roughish-textured and irregularly conchoidal flake scar forming the notch contrasts strongly with the other two viewed surfaces. This flake scar resulted from the deliberate detachment of a small stout flake by a sharp and forceful localised blow delivered on the lower surface of the tool, and is opposed to any natural fracture surfaces.

A fairly stout cortical flake of fine-grained chert is also illustrated in fig. 2 (top row on the right). Considerable force was required to detach this flake whose rather conchoidal fracturing is clearly contrary to the natural surfaces of fracture.

The very predominantly unifacial and uniform nature of the damage suffered by the artificially prepared concave and convex margins of chert tools throughout the assemblage, is also shown in fig. 2 (the three specimens in the bottom row.)

The small stout plane of fine-grained chert, on the left, is viewed obliquely from below, to show the comparatively flat planing base; the steeply-prepared, regularly convex and finely damaged planing edge is seen towards the top. While the two sides (one of which is seen on the right) are of dark natural cortex, all the other surfaces of this tool, including the flattish base, have been produced by bold fracturing contrary to natural fracture surfaces.

Two notched scrapers are seen on the right (fig. 2). Note the abundance of consistently very fine chipping along the concave working edge of the larger, dorsally flaked specimen. (This tool has also been utilised at both extremities.) The notch of the smaller slab-like specimen (on the right), displays very similar damage and wear, evidenced by the multiple almost imperceptibly fine "stepping" extending from within the notch and on to the upper surface.

General Description and Statistical Analysis of the Tools

The types of tools, their numbers and their relative proportions are reflected in Table 1.

For the present purpose this table has been considerably simplified, the number of tools occurring in the different size groups not being given here. Also, the relatively small numbers of larger tools (4 inches or more in length) have been classified in the same manner as the smaller. Some of the large convex and straight-edged scrapers might more properly be classified as cleaving or chopping tools.

1. *Scrapers*

These tools, provided with scraping or cutting edges, comprise the bulk of the artefact assemblage (70.8%), and have been separated from the planes usually by their lesser stoutness and relatively greater breadth. Five categories have been described, *viz.* notched, simple-pointed, convex-edged, straight-edged and

blunt-nosed; the first, third and fourth of these groups, respectively, being the most important.

(i) Notched

These scrapers are distinguished by the presence of one or more marginal notches or concavities, and are extremely varied both in shape and size, as well as in the position, shape and size of the prepared marginal indentation(s).

The preparatory fracturing by splitting, crude flaking and chipping is frequently opposed to the natural surfaces of fracture, in which respect they differ from the plane-like tools where naturally flat surfaces have often been incorporated into the tool.

While the one or more notches are very variable in their position and size, and range from very narrow (and more strictly notch-like) to widely concave, they display, almost without exception, *definite signs of preparation and (or) considerable wear by use*. It is the almost total confinement to the notches of this fine damage by utilisation, or preparation, or both, that so clearly characterises these scrapers as deliberately made tools.

I am discussing these notched scrapers in some detail, not only because of their great dominance in numbers, but also to illustrate generally the nature of

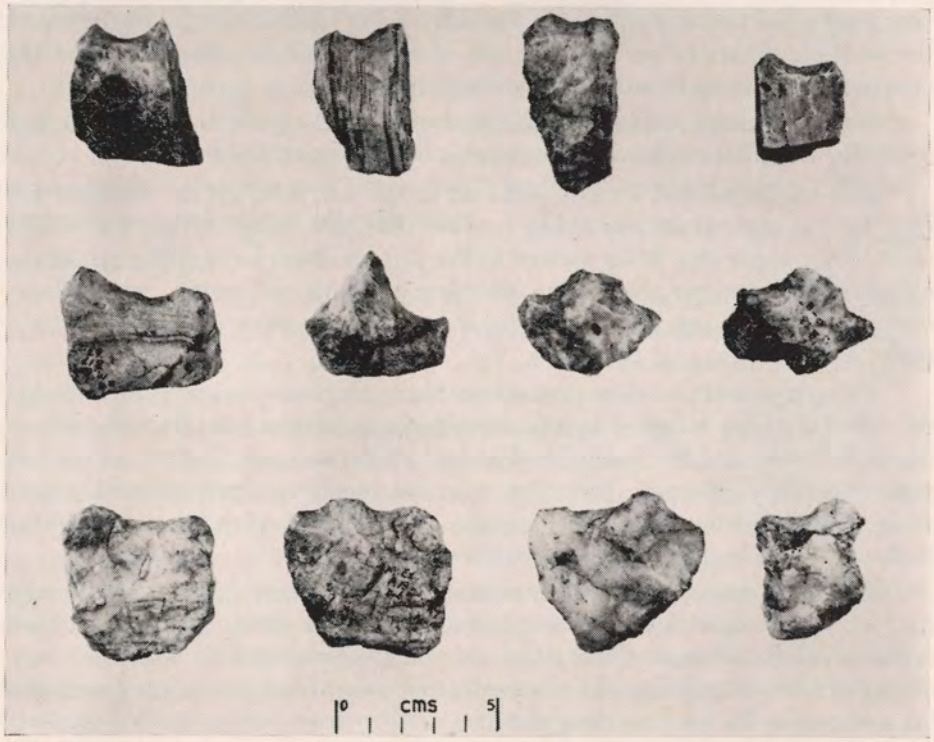


Fig. 3

the artificial damage suffered by chert tools throughout the assemblage. The accompanying plates have therefore been almost entirely devoted to illustrating scrapers of this type. The two specimens pictured in figure 2 (in the bottom row on the right), the twelve specimens pictured in figure 3, and the three top specimens in figure 4, demonstrate the wide range in form of these notched scrapers.

The 842 specimens comprise 332 single-notched scrapers, 414 double-notched scrapers and 96 specimens of rather point-like form, and constitute 44.8% or nearly one half of the total assemblage. Outnumbering the planes, the next most important group, by more than twice, they are by far the most abundant of the chert tools.

Six single-notched and six double-notched scrapers are illustrated in the third figure. The four single-notched specimens are those occupying the top row, and the extreme left specimens in the middle and bottom rows respectively; the remainder are double-notched. Each has been pictured with the assumed dorsal (upper) face uppermost, the notched working edge(s) being seen in profile at the top.

The small stout specimen in the bottom row, on the extreme right, is actually a thrice-notched strangulated scraper, the most heavily worn notch being seen at the top end, the other two on the adjacent sides. This completely prepared scraper which is provided in addition with a sharp-edged broad point (top right), and two acutely convergent sharp edges (bottom left), well illustrates the multiple nature of perhaps one half or more of all the chert tools and the consequent difficulty in satisfactorily classifying them.

Notched scrapers sometimes show rough natural cortex on both faces, but generally it has been removed from one or both of these surfaces.

The single notched scraper pictured in the top row, on the extreme left (fig. 3), was made from a spall-like cortical flake, the rough cortex that covers most of the upper face being viewed in the picture. Both faces of the remaining eleven tools, however, have been denuded of all natural cortex by splitting, coarse and fine flaking, and chipping that has generally been opposed to natural surfaces of fracture.

This preparatory work has sometimes been completely overall, and included the removal of the marginal cortex as well (the third specimen from the left in the middle row, and the strangulated scraper on the extreme right in the bottom row). Generally, however, the rough marginal cortex has been retained, either along the back of the tool, or sometimes (as in the case of the three specimens in the top row, on the right) along one or both sides.

A striking exception is that illustrated on the extreme right in the top row (fig. 3), where the fullest possible advantage has been taken of natural fracture surfaces. All the surfaces of this thin once-notched slab, with the exception only of part of the working edge, have been derived either from pre-existing naturally flat surfaces, or by fracture along them.

The preparation of all of the individual notches of the scrapers seen in fig. 3 has been in the unifacial (or uni-directional) manner characteristic of the working edges of some 90% of all the cutting, scraping and planing chert tools. This work has been directed towards the upper face (towards the observer), in all but three of the figured specimens. One of the exceptions is the small triple-notched strangulated scraper already referred to (in the bottom row on the extreme right); the other two are the third specimens from the left, in the middle and bottom rows respectively, where the right hand notch of each has been worked in the reverse direction (i.e. towards the lower surface, or in a direction away from the observer).

The three rather larger notched scrapers illustrated in fig. 4 (the top row) are well-preserved, despite their staining by manganese and their somewhat crude appearance. The bold fracturing involved in their manufacture has been extensive, but mainly confined to their upper faces which are viewed in the picture. While rough natural cortex may be seen on the back of the somewhat compound specimen on the right, the remainder of its perimeter provides a continuous series of concave to convex scraping edges.

The presence of one or more useful points in addition to the notch(es) is evident in the accompanying illustrations and a common feature of these tools. This compound or multiple feature occurred so frequently in the originally described quartzite specimens retrieved from the surface soil, that they were referred to as *notch-and-point scrapers* rather than merely notched scrapers.

(ii) Simple-pointed

This small group of scrapers resembling sharp- or blunt-tipped points is represented by only 75 specimens or 3.4% of the artefact total. They are frequently rather stout and irregular, and may have been used for boring or piercing purposes, but in the presence of their well-developed scraping edge(s) they have primarily been regarded as scraping tools.

(iii) Convex-edged

This group of 224 scraping tools (11.9% of the total number of artefacts) is exceeded in size only by two other groups, the notched scrapers and planes. While it includes scrapers of rounded, oval and even fan-shaped or sectorial plan form, the great majority are plain-backed side-scrapers.

The fairly large backed side scraper illustrated in fig. 4 (bottom row, on the right) is a broad specimen, and is viewed from above. The dorsal and ventral surfaces are equally fresh, though very slightly weatherworn. The unifacially and fairly steeply prepared long cutting or scraping edge is seen on the left side, and the completely plain or unworked back, which is of rough natural cortex, on the right. Most of them retain the rough natural cortex along the back which is often straight and usually shows no signs of special preparation or use.

These backed scrapers range from narrowly crescentic or lunate, to broadly semi-circular or D-shaped in plan form, many of them being slightly to quite definitely pointed at one, or even both extremities.

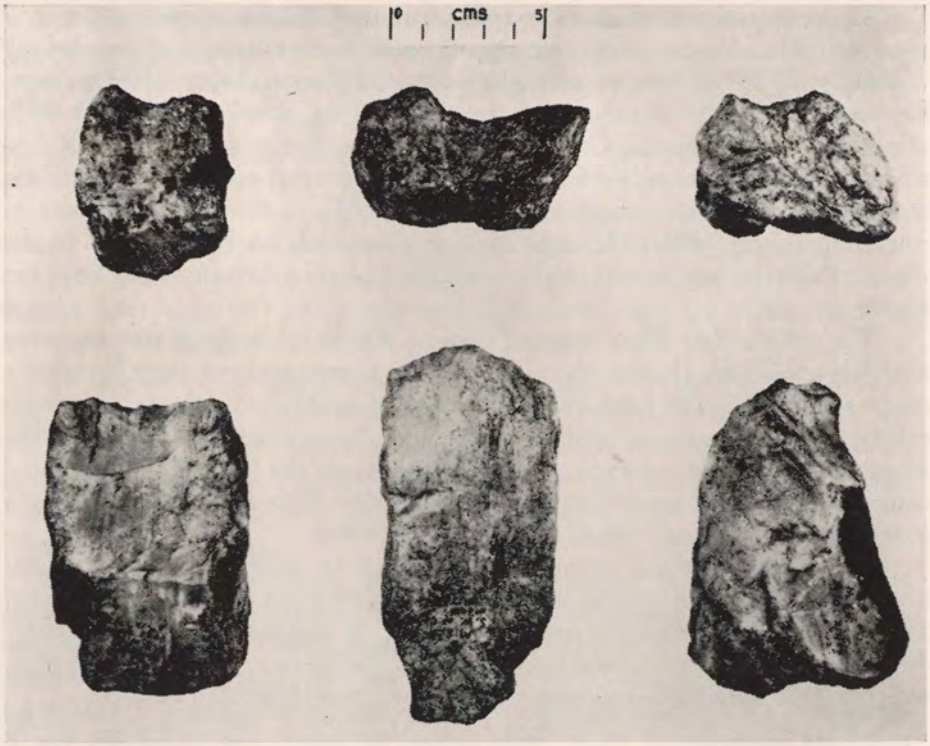


Fig. 4

(iv) Straight-edged

The 173 straight-edged scrapers constitute 9.2% of the artefact total. Mainly comprising crudely quadrilateral or nearly quadrilateral forms showing preparation and scraping use along one, two, three, or all of their four sides, they form a group almost as large as that of the convex scrapers. Some show extensive though elementary preparation, but quite frequently the ventral or dorsal surface, or sometimes even both, may be of natural cortex. They have often been distinguished from the planes only by their lesser stoutness, their relatively greater breadth, or by means of the working edge(s), which is generally less robust and less steeply prepared.

(v) Blunt-nosed

This ill-defined small group of 29 scraping tools constitutes only 1.5% of the total assemblage. Of varied shape and usually moderately stout, they are chiefly characterised by a rather projecting or distinctly terminal scraping edge which is sometimes straight, but more frequently convex.

2. *Planes*

Those tools described as planes, by analogy with a carpenter's plane, are second only in importance to the notched scrapers. The planes are relatively

stouter tools than the scrapers, often of cuboidal or wedge-like form, and range from squat and compact to narrow and chisel-like.

The first four of the six categories described include the simpler forms, which are distinguished by the nature of the terminal working edge *viz.* straight-edged, convex, pointed and notched. The two remaining categories, the compound and the miscellaneous (together comprising some 25% of the total number of planes) are frequently provided with additional working features such as lateral or transverse planing or scraping edges, or prepared points, or they may be merely somewhat irregular in form.

Either by its direct incorporation into the tool, or by fracture along it, advantage has usually been taken of a natural fracture plane in the raw material to provide the relatively smooth flat base characteristic of most of these tools. The working edge may be provided simply by the convergence of a second such fracture plane with the flat base, and (or) by unifacial, usually steep, crude marginal flaking or trimming.

The sides are usually of rough natural cortex, as in the case of the two fairly large specimens pictured in fig. 4 (the first two specimens in the bottom row), and the two planes which have already been described i.e. *the breadth of this tool is usually dependent on the thickness of the weathered chert slab from which it was fabricated.*

The working edges of the two specimens pictured in fig. 4 are seen at their top end, that of the first being very slightly concave, and that of the second distinctly convex. The working edge of the pointed planes may be merely more exaggeratedly convex or pointed than that of the last-mentioned specimen, or it may run obliquely (and not at right angles) to the length of the tool.

The comparatively large group of notched planes (100) comprises rather inconspicuously and terminally, once or twice notched forms, and some of them, despite their relative stoutness, are virtually indistinguishable from the very prolific notched scrapers.

3. *Pounders*

The thirteen pounders included in the present analysis range from nearly spheroidal to completely irregular. This small number, only 0.1% of the total number of chert tools, is no true reflection of the actual number present in the surface soil overlying the breccias. The subjection of these tools to repetitive and vigorous percussion has rendered the working faces very susceptible to weathering processes, and because of their frequent lack of clearly diagnostic repetitive damage, large numbers of such suspected fragments were excluded from the present analysis despite the obviously, sometimes grossly, damaged condition of their percussed surfaces. The very characteristic damage by repetitive percussion suffered by the more weather-resistant quartzite pounders has usually been well preserved (Maguire 1965).

4. *Anvils*

These stout tools, like the pounders, have suffered very repetitive percussion, and for the same reason all but a single slab-like specimen were excluded from the present list of tools.

A second stout narrow slab, similar in shape and size (and weighing approximately three pounds), was retained from the materials excavated from the back wall of the cavern. Each displays gross damage at the end of one long face, the damage extending over about half the length of the tool.

5. *Cores*

The 39 cores listed in Table 1 represent but a small fraction of those actually present in the surface soil overlying the breccias, since only the most evident specimens were retained for analysis. A few are rather globular or polyhedral, but most are quite irregular. Up to five or seven larger flakes or fragments have been struck from many of them, and in most cases in a manner contrary to the natural surfaces of fracture.

In marked contrast to the 1,670 scrapers and planes, the edges of these cores are generally strikingly free of palpable damage, whether it be artificial or natural.

6. *Utilised and little-used flakes and fractured fragments*

As in the case of the pounders, anvils and cores, only the most demonstrable and indisputable flakes and deliberately fractured fragments were retained for analysis. Some of these fragments probably represent elementary cores. While the fracture scars very rarely show the characteristic features usually attributed to deliberate flaking, they are readily diagnosable, in the manner earlier described, as the scars resulting from the deliberate fracturing of the native chert.

The edges of nearly all of the 83 selected specimens (4.4% of the artefact total) are fresh or comparatively fresh looking, and display no damage whatsoever that is suggestive of human interference.

Discussion and Conclusions

The very great age of the Limeworks cavern deposit, possibly one or more million years, implies that whatever stone tool-making occurred there during the accumulation of the infill, and particularly as evidenced at the lower levels, was of a low order, and perhaps not easily recognised. This is not altogether so, and my main reason for exhaustively examining the well-preserved and large collections of crude chert artefacts from the surface soil overlying the consolidated breccias was firstly to establish clearly their artefactual nature, and secondly to compare them with the often less well-preserved but abundant phase 2 artefacts, and the well-preserved but small collection of artefacts extracted from the extremely compact upper phase 1 breccia.

The chert tools comprising the assemblage extracted from the surface soil overlying the breccias display such uniformity throughout, that they can be

collectively described as representing a single industry. Furthermore their undoubted similarity to the abundant artefacts of chert and dolomite occurring in the pink breccias suggests that both the superficial and the breccial specimens may be regarded as facies of the same lithic industry.

The pink breccia that has been exposed over the entire area of the grid by the recent excavations is Brain's upper phase 1, and it would therefore appear that all of the chert tools recovered from the overlying surface soil should be referred to a late stage in the accumulation of this breccia. It is quite possible, however, that the phase 2 breccia, which at the present day overlies the upper phase 1 breccia only in the vicinity of the cone, may originally have extended over part, or even the whole, of the grid area. (An opinion confirmed by Brain—1965—after a re-assessment in 1962 of his original geological interpretation of the Limeworks deposit.) The possibility exists, therefore, that the artefacts have been derived by weathering from both the upper phase 1 breccia and part of an originally more extensive deposit of overlying phase 2 breccia.

The phase 2 pink breccia is generally regarded as having been a relatively rapid accumulation, and there is no evidence of any major temporal unconformity between it and the often rather poorly differentiated upper phase 1 pink breccia (Brain *et al* 1955). Therefore, whether derived from only one, or from both phases of the pink breccia, there should be no very significant variation in the ages of the chert tools extracted from the surface soil of the excavation grid.

The absence of identifiable dolomite artefacts in the rubbly soil overlying the breccia may be attributed to the great solubility of the local dolomite. Being only slightly less soluble than the breccia matrix itself, the usually abundant dolomite inclusions in the upper phase 1 pink breccia become heavily eroded, or even completely dissolved, while still partly embedded in the decalcifying breccia mass. Therefore, while large numbers of chert artefacts, which are relatively insoluble, have been preserved in the shallow layer of soil derived from the underlying breccia, smaller dolomite fragments of any kind are rare.

The utilised bones and bone flakes preserved in the grey breccia enormously outnumber the utilised stalactite and other lithic fragments associated with them, hence the Limeworks cavern deposit, in its entirety, demonstrates a transition from the prolific and virtually exclusive use of bone as a tool-making material to the abundant use of stone, and perhaps ultimately the almost complete replacement of bone tools by those of stone. Moreover, it is significant that the raw materials used for toolmaking, as they successively appear to have been used in the cavern breccias, provide a sequence very closely expressing both their availability and their tractability. Thus:

The prolific *bone* tools in the grey breccia occur together with, but perhaps generally precede, the occasional utilised fragments of cavern *stalactite* (and possibly *shale*). Artefacts of the harder and more durable native lithic materials, *dolomite* and *chert*, then make their appearance in the upper phase 1 pink breccia. Relatively intractable *quartzite*, in the form of waterworn river-bed pebbles, is introduced into the cavern at a late stage of the accumulation of upper phase 1

breccia. *Vein quartz*, although a native material, is not only relatively scarce, but also extremely intractable. It seems to have been first used for tool-making about contemporaneously with the introduction of the quartzite pebbles into the cavern, although it appears to have been used abundantly only at a very late stage in the cavern's history.

It should be strongly emphasised that *there has been an overwhelmingly preponderant usage of the native chert and dolomite as stone tool-making materials throughout the Limeworks deposit*, while the part played by quartzite (at least in terms of numbers) is by comparison virtually negligible.

Nevertheless the introduction of quartzite river-bed pebbles into the cavern at a more terminal stage of the accumulation of the pink breccia (in later upper phase 1 times) is for several reasons of particular importance.

1. The foreign, readily identifiable nature of these artificially damaged stones was the most important single feature ensuring their practically total recovery from the excavated areas, and enabling their distribution throughout the deposit to be determined. In demonstrating that their very markedly unequal distribution in the breccia was directly reflected in the overlying surface soil, they were thus directly responsible (to a greater extent than the chert artefacts), for conclusively demonstrating the crucially important feature that the surface soil (at least its heavier fractions) primarily represents a decalcified breccial residue.

2. Very few chert fragments have been reconstituted from their isolated and separately-discovered parts during the excavation of the surface soil overlying the breccia. However, quite invaluable information has been obtained by the examination and reconstitution of some 40 quartzite pebbles and artefacts (or their fragments) from their separately-discovered parts.

Such information relates not only to technological features and damage by utilisation, but to the manner and rate of natural weathering of quartzite artefacts in the surface soil overlying the breccias.

In the course of their long separation from each other, none of the edges of the matched (last-separated) surfaces has suffered natural damage resembling in any way that attributed to deliberate trimming or utilisation, thus independently corroborating, yet again, the observations made during the analysis of the chert artefacts. Excepting those few instances where the raw material used was a weakly-compacted grit or sandstone, rather than a quartzite, there has usually been no palpable weathering of the matched surfaces.

Finally, these lithic parts furnish conclusive proof of the deliberate pounding and artificial fragmentation of the quartzite pebbles on the cavern site.

3. The transport to the cavern of these quartzite pebbles displays an awareness on the part of the users of possibly more desirable extraneous raw materials for tool-making or tool-using (at least for certain purposes), as well as the expenditure of effort in obtaining them.

4. This less tractable material was handled in a manner obviously commensurate with the limited abilities of tool makers accustomed only to the more

tractable materials calcite, chert and dolomite which are native to the cavern site.

While the dolomite and chert tools frequently display deliberate splitting and crude flaking, the solely percussional damage sustained by many of the quartzite pebbles suggests that they were generally employed in cultural activities of a consistently low order.

Most of these fragments that have obviously been employed more specifically, despite their crudity, closely resemble the notched scrapers and planes fabricated from the more tractable native materials dolomite and chert that predominate throughout the deposit above the grey breccia. These demonstrate yet further the repetitiveness of these tool forms and their successful reproduction in a material both less tractable, and with different fracturing properties.

5. Because of their extremely durable and weather-resistant nature, and the very characteristic type of damage they exhibit when repetitively percussed, these quartzite pebbles and fragments have provided a virtually permanent record of early percussional activity on the site, extending from later upper phase 1 times onward (Maguire 1965).

6. The fragments resultant from pounding activities, sufficiently shapely to describe as more specific types of tools, were previously regarded as quite fortuitous. Some of them at least were probably deliberately struck, though very crude flakes, and it is likely that these may represent, at the Limeworks site, the beginnings of definitely flaked tools made of materials more durable and efficient than the native dolomite and chert.

The differences between the types of deliberate damage generally evidenced by tools of quartzite, and those of dolomite or chert on this site, are fairly readily recognisable, and quite diagnostic, and acquaintance with these differences is considered to be essential to any understanding of the lithicultural history of the Limeworks deposit (and most probably of other dolomitic australopithecine sites as well).

Both types of damage have been simulated experimentally (that by pounding to quartzite being also plentifully illustrated in the Bernard Price Institute for Palaeontological Research by comparative material ranging in age from Middle Stone Age times onward to the present).

Lately conducted experiments, using a stone anvil, and a quartzite river-bed pebble as a fabricator, demonstrated the difficulty of detaching flakes possessing a clearly defined or conventional bulb of percussion from the local chert. Furthermore, the brittle splintery nature of the local chert and the presence of abundant, variously orientated natural fracture surfaces making control of the core difficult, may be the reason for the often irregular and very elementary nature of the Limeworks cores.

However, these experiments reproduced exactly the type of fracture referred to throughout this paper as 'crude flaking' or 'deliberate fracturing contrary to

the natural fracture surfaces', and also the fine and very clearly defined unifacial trimming characteristic of the Limeworks chert artefacts.

The fine unifacial trimming was simulated with comparative ease, but since it demanded the employment of deliberately controlled manual activities, its artificial nature would be readily assessed by the criteria used in my analysis of the Limeworks artefacts.

A further (hitherto unmentioned) deliberate feature of the Limeworks chert artefacts became evident in the course of experimental work, when it was found that the margins of the experimentally produced tools could be trimmed with approximately equal facility either towards the assumed upper face, or towards the flatter and more regular lower face. The Limeworks artefacts have almost invariably been trimmed in the direction of the upper face, while tools consistently trimmed towards the flatter lower face are very rare, constituting less than 1% of the total assemblage.

The elementary nature of the Limeworks cores, rather than suggesting some specific lack of ability on the part of the makers, is more suggestive of ignorance of any special core technique. In contrast to the relatively crude cores, many of the tools exhibit relatively delicate trimming, and on occasion natural chert slabs barely $\frac{1}{8}$ inch in thickness were selected for tool making. The makers of these tools were, therefore, manifestly capable of precisional work demanding a relatively high degree of manual dexterity. However, although the major fracturing involved in producing the Limeworks artefacts often demonstrates considerable ability, it often does not closely resemble, nor has it been regarded as, accomplished or precisional flaking. This preparatory major fracturing has therefore been referred to as deliberate splitting or crude flaking.

The repeated appearance of certain tool types, and especially of those tools termed notched scrapers and planes, is regarded as a consistent and traditional feature of stone tool making throughout the deposit. The distinctive notched scrapers are particularly abundant, both within the breccias and in the overlying soil, and have been fabricated from all the available lithic materials *despite their widely varying fracturing properties*.

No conclusion has certainly been reached concerning the use of these notched scrapers, although many were probably used as decorticating tools during the preparation of wooden tools. They range from extremely small-notched specimens less than one inch long and showing fine wear, to very coarsely used large-notched tools four to five or more inches in length or breadth, which suggests that they may have been used for a variety of purposes.

Australopithecine remains (some forty or more fragments) have been recovered from all of the Limeworks breccias, above, and including the rich basal bone bed of grey breccia. The fact that no remains of other hominids have yet been found indicates that australopithecines may have been the only hominid occupants of the ancient Limeworks cavern, and the makers of all of the Limeworks artefacts. This is especially probable in view of the consistently crude nature of the lithic artefacts, and the seemingly total absence of even Earlier

Acheulean artefacts throughout the consolidated breccias, and, with the below-mentioned exceptions, throughout the overlying surface soil as well.

The small number of crudely (usually) but definitely flaked quartzite artefacts retrieved from the soil overlying the breccias at the Limeworks appears to represent an accumulation over a very long period extending up to Middle Stone Age times. While all evidence strongly indicates that the later of these represent contaminating elements in post-breccial times, the earlier may have been derived by weathering from an extremely late stage of the original accumulation of the phase 2 breccia.

Mason refers to the "immense segment" of the Stone Age record that is missing from the Transvaal sequence. This period spans the time between the Limeworks bone industry and the Earlier Acheulean (Earlier Chelles-Acheul) artefacts extracted from the Sterkfontein middle (or red-brown) breccia and also represented at Klipplaatdrif (Mason and Robinson 1962).

This segment, or a facies of that segment, would appear to be that represented by the wealth of crudely (not precisionally) flaked chert, dolomite and vein quartz artefacts (and more occasional quartzite percussion tools), occurring both within the pink breccias and in the soil overlying and derived from these breccias at the Makapansgat Limeworks. I feel it is extremely likely (and in much the same manner as at Makapansgat) that parts of this segment will also be represented at the other dolomitic australopithecine sites in the Transvaal. I would again stress, however, the overwhelming dominance of the native chert and dolomite as stone tool-making materials at the Makapansgat Limeworks site.

Acknowledgments

I record here my great indebtedness to Professor Raymond Dart who made this investigation possible, and my thanks to Professor P. V. Tobias and Mr A. R. Hughes for arranging additional assistance with excavations. I am very grateful to the following: For helpful discussion to Dr C. K. Brain and Messrs H. F. Sentker, P. Beaumont, C. G. Sampson and J. W. Kitching; for geological opinion to Messrs J. S. McKinney, P. J. Ryan and T. Stratten; for various assistances at the site to Mr and Mrs G. R. Peppercorn and Messrs James Mathewson, John Anderson and Jonathan Jennings; for photography to Mr Mark Hudson; and finally, for assistance in typing the manuscript to Miss J. Kallenbach and Mr Richard Cheales.

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EXPLANATION OF TEXT FIGURES

Fig. 1 Diagram of the Makapansgat Limeworks quarries. The more easterly part of the back wall of the ancient cavern is approximately defined by the dolomite outcrop.

Fig. 2 A series of six specimens illustrating the natural fragmentation and crude flaking and trimming of chert.

Top row (left to right)

A stout plane deliberately notched by the removal of a terminal flake. Note the coarse texture of the somewhat conchoidal flake scar. The main viewed face is a smooth flat natural fracture surface.

A naturally disintegrating slab of chert. Note its angular appearance, the undamaged edges and also the fine dark lines traversing the viewed face indicating potential natural lines of fracture.

A deliberately struck stout cortical flake of fine-grained chert showing the conchoidal cleavage face.

Bottom row (left to right)

A small, stout, steeply trimmed convex plane, seen obliquely and from below; and respectively, a larger and a smaller notched scraper. The single-notch scrapers show the assumed dorsal face; note the fine artificial damage by preparation and/or wear within the notches.

Fig. 3 A series of twelve smaller notched scrapers in chert, showing their assumed dorsal faces and the notching of the top edges. The six single-notched scrapers are those occupying the top row, and the extreme left specimen in the middle and bottom rows respectively. The remainder are double-notched, the extreme right specimen in the bottom row actually being a triple-notched strangulated scraper. The first specimen in the top row was made from a spall-like flake and is the only tool shown here that retains most of the natural cortex on the dorsal face.

Fig. 4 A series of six medium- and large-sized chert tools. The three notched scrapers occupying the top row all show their dorsal face, the notch(es) being seen on their top edge. In the bottom row are seen from left to right: a shallowly notched plane, a convex plane and a convex (backed) side scraper. Note the unworked back of rough natural cortex (right side) of the convex side scraper.

SOME MAIN CONCLUSIONS DRAWN FROM A BASINAL ANALYSIS OF THE DWYKA SERIES IN THE KARROO BASIN

By T. Stratten

I. Introduction

The investigation of the Dwyka glaciation and its relationship to the pre-Karroo surface was undertaken as a research project at the University of the Witwatersrand under the sponsorship of Union Corporation, Limited. A thesis on this study has been submitted for the degree of Doctor of Philosophy under the supervision of Professor T. W. Gevers.

The research fell mainly into two separate but related fields of study.

The first field was to investigate the pre-Karroo surface with special reference to the geology beneath the Karroo System.

The second field was to investigate the paleo-ice flow directions of the Dwyka Tillite and relate this to the position and lithology of the source areas.

II. Sub-Karroo Geology

The Sub-Karroo geology illustrates the geology as it would appear at present if the rocks of the Karroo System were removed. Only a very brief summary of the main results will be given here.

The sub-Karroo geology of the central part of the Karroo Basin consists of granite, while in the more northern parts, rocks of the Swaziland System become widespread. Towards the periphery of the Karroo Basin rocks more recent than the Swaziland System and Basement Granite make their appearance.

III. Paleo-ice flow Analysis and Conditions of Deposition

The more important measurements used in this study were till fabric and glacial striae. This research has disclosed two new source areas giving rise to ice sheets which were previously unknown. These are:

1. The newly discovered granitic source area off the present Western Cape coast produced an ice sheet for which the name *Atlantic Ice Sheet* has been proposed (Stratten, 1967). This ice sheet flowed towards the east and deposited material in the western and southern parts of the Karroo Basin (Plate **1**).

2. The newly discovered granitic source area off the present southern Cape coast produced an ice sheet for which the name *Southern Cape Ice Sheet* has been proposed (Stratten, 1967). This ice sheet flowed towards the north and deposited a little material in the southern Cape (Plate **1**).

Du Toit (1921, p. 193) named the four previously known ice sheets. The present work has confirmed their source areas and enlarged the known extent of their ice radiation. These are:

1. The Windhoek Highlands in South West Africa produced the *Namaland Ice Sheet* which flowed towards the south. It deposited some material in the western part of the Karroo Basin but its main depositional area was in South West Africa outside the Karroo Basin (Plate **1**).
2. The Kaap Plateau produced the *Griqualand Ice Sheet* which radiated a short distance towards the south-east, south and south-west and deposited a little material in the vicinity of the Kaap Plateau (Plate **1**).
3. The central and eastern Transvaal source area produced the *Transvaal Ice Sheet* which radiated towards the south-east, south, south-west and west to deposit material throughout the Karroo Basin but mainly in its eastern and northern parts (Plate **1**).
4. The granitic source area off the present Natal coast produced the *Natal Ice Sheet* which flowed towards the west and south-west and deposited material on the eastern side of the Karroo Basin (Plate **1**).

The periods of maximum ice production from the source areas moved from west to east across the country.

The Dwyka Tillite reaches a thickness of almost 3,000 feet in the southern Cape. For such a vast thickness to be deposited, it seems probable that there were a number of advances and retreats of the ice. These are indicated by intercalated sandstones and varve shales, striations on the tillite and boulders of the older Dwyka Tillite held as clasts in younger Dwyka Tillite.

There was an opening to the Karroo Basin towards the north-west between Loeriesfontein and Lüderitz, in the general region of the Orange River mouth. This was the main opening to the sea during the deposition of the Upper Dwyka Shales. There was probably a second opening to the basin in the vicinity of East London. That this area provided an opening for a marine incursion is indicated by the presence of *Eurydesma*, *Conularia*, *Peruvispira* and echinoids in the Upper Dwyka sediments (Martin, 1961, p. 32). The main area covered by this sea during the Dwyka Period is shown by the occurrence of Upper Dwyka Shales, which are present in the southern and western parts of the Karroo Basin. The Upper Dwyka Shales occur south-west of a line drawn very approximately from Vryburg through Kimberley and central Lesotho to Port St Johns, and reach their greatest thickness of over 900 feet north-west of Beaufort West.

The Upper Dwyka Shales were deposited in a nearly isolated sea in which the muds are rich in organic matter. The deeper water is toxic, through the presence of hydrogen sulphide, to scavengers and stagnation prevents oxidation.

IV. Implications Relative to Continental Drift

The present research is in some ways complementary and in other ways contradictory to recent suggestions regarding the Theory of Continental Drift. A possible reconstruction of Gondwanaland during the Dwyka Period is appended (Plate II). The main difference between this reconstruction and that more normally presented for Gondwanaland is that South America is placed a little farther away from South Africa to accommodate the source area off the present western Cape coast between the two continents; and that Antarctica is placed a little farther south relative to South Africa in which position the high land area of Queen Maud Land would be very suitably situated as the source area off the present Natal coast.

V. References

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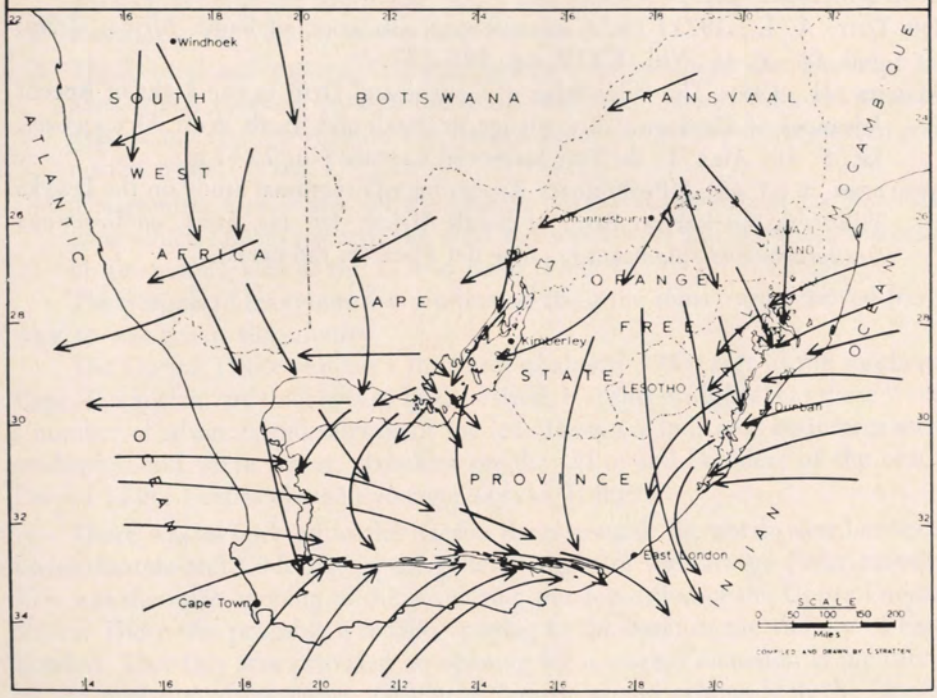
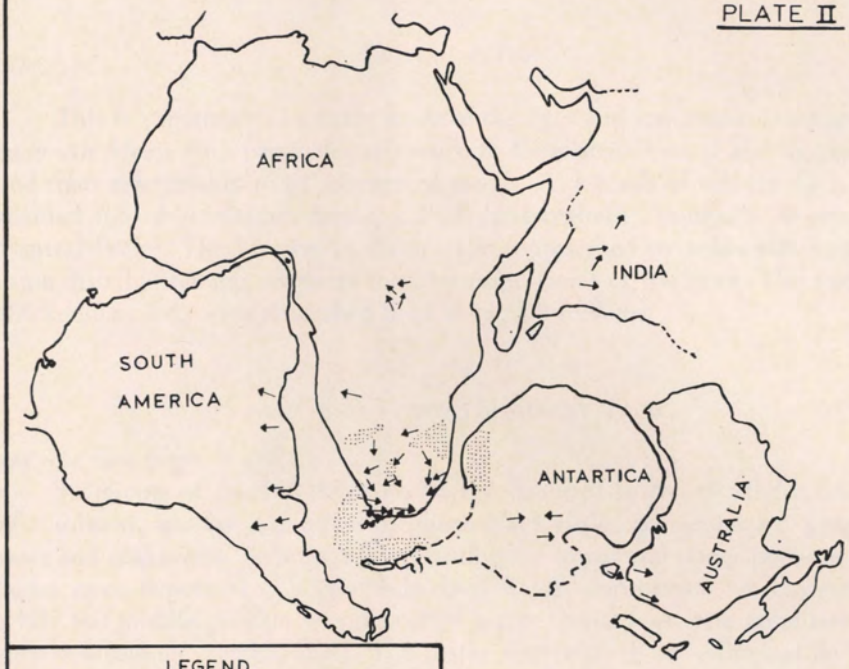
PLATE I

SPECULATIVE PALEO-ICE FLOW MAP



REASSEMBLY OF GONDWANALAND DURING THE DWYKA PERIOD

PLATE II



LEGEND

DIRECTION OF ICE FLOW DURING THE DWYKA PERIOD

APPROXIMATE POSITION OF HIGHLANDS PRODUCING THE DWYKA ICE SHEETS IN SOUTH AFRICA

MODIFIED AFTER DU TOIT, 1937

DRAWN BY T. STRATTEN

SOME CONCLUSIONS DRAWN FROM A BASINAL ANALYSIS OF THE ECCA SERIES IN THE KARROO BASIN

By P. J. Ryan

Introduction

This is a summary of a study made of the Ecca and lowermost Beaufort rocks in South Africa with particular reference to the distribution of the various facies and their relationship to palaeocurrent trends. As a result of this the Ecca can be divided into four distinct facies, called the Northern, Southern, Western and Central Facies. The lowermost Beaufort is represented by sediments having the same distribution and origin as the first three facies of the Ecca. The maximum thickness of sediments described here is 11,000 feet.

Ecca and lower Beaufort Facies

(a) *The Ecca* (Figs. 1 and 2)

Sediments of the Northern Facies are confined to the Northern one-third of the basin, and are composed of bluish-black shale, coarse arkose, conglomerates and coal seams. Sediments constituting the lower and upper portions of this facies were deposited in a relatively deep water, continental sea environment, while the middle portion was deposited under fluviatile-deltaic conditions on a slowly subsiding cratonic shelf. The major source of these sediments lay to the East and Northeast of the present Natal Coast. These source rocks were predominantly granitic in composition as revealed by the heavy minerals and abundance of microcline felspars.

The Southern Ecca Facies is confined to the Karroo Trough and outcrops along the Southern structural margins of the basin as well as along the Transkei coast. It is composed of a thick sequence of greenish-grey and bluish-black shale, greywacke and sub-greywacke sandstone. Sedimentary structures indicate that the lower portion of the succession was deposited under deep-water conditions and that turbidity currents were active. Progressively shallower water conditions prevailed during deposition of the upper portion of the succession and the facies as a whole was deposited in a rapidly subsiding trough which formed part of the Cape-Karroo Geosyncline. Although the majority of the sediments were derived from a source lying South of the Southern Cape Folded Belt, transport also took place in an Easterly direction along the axial portion of the Karroo Trough. Heavy mineral studies and thin-section examination of these rocks indicate that their

source was not only predominantly granitic, but that sedimentary, metamorphic and basic igneous rocks also contributed to their formation.

The Western Ecca Facies occurs in the South-western portion of the Basin and is composed of bluish-black shale, sub-greywacke and greywacke sandstones. These sediments were deposited partly in the Western portion of the Karroo Trough and partly on the unstable shelf to the west of the Trough. The lower one-third of this facies was deposited under relatively deep water conditions while the upper two-thirds was deposited under fluvio-deltaic conditions. The source of these sediments lay to the West and South-west and was composed mainly of granitic rocks.

The Central Ecca Facies sediments were deposited in an extensive, moderately deep inland sea. These rocks actually are a mixture of the fine-grained facies equivalents of the other three facies, and derived from three different source areas.

(b) *The Beaufort*

The lowermost Beaufort Beds are composed of fine to coarse-grained sandstones interbedded with blue, green and occasionally maroon and purple shales and mudstones. Three distinct facies, derived from separate sources, composed mainly of granitic rocks, are recognised within these beds. They have essentially the same distribution as the Southern, Western and Northern Facies in the Ecca Series, except that they do not grade into a facies composed entirely of shale. Instead the lithological units constituting the various facies interfinger with each other towards the central portion of the basin. The rocks of the lowermost Beaufort were deposited in an aqueous continental environment.

Palaeogeographical reconstructions indicate that the present South African sub-continent was more extensive during deposition of the Ecca and lowermost Beaufort Beds. In Lower Ecca times the Karroo Basin was probably connected to the oceans by means of two narrow openings, one situated in the South Eastern portion of the Basin and the other in the vicinity of the present Orange River Mouth (Fig. 3).

Acknowledgments

This work was undertaken in the University of the Witwatersrand with a grant from the Anglo American Corporation of South Africa. I would like to thank Dr J. Truswell for his help and guidance in supervising the work.

Explanation of Text Figures

Fig. 1: Facies distribution Map of the Ecca Series in the Karroo Basin.

Fig. 2: Interpretive palaeocurrent Map of the Ecca Series in the Karroo Basin.

Fig. 3: Tectonic framework of Southern Africa during the Ecca period.

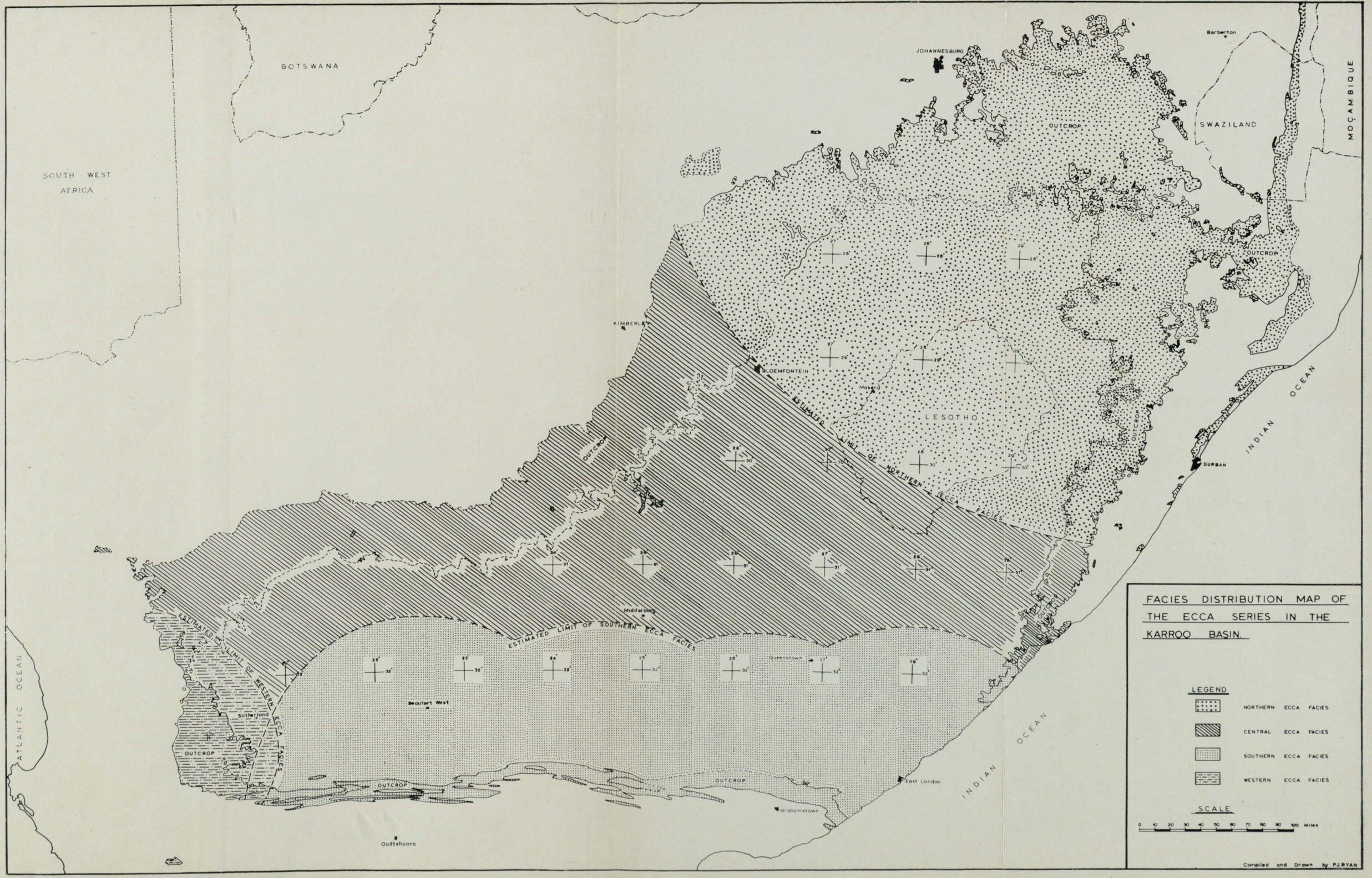

BOTSWANA
SOUTH WEST AFRICA
JOHANNESBURG
Barberton
SWAZILAND
MOÇAMBIQUE
OUTCROP
KIMBERLEY
BLOEMFONTEIN
Masaru
LESOTHO
ESTIMATED LIMIT OF NORTHERN ECCA FACIES
ESTIMATED LIMIT OF SOUTHERN ECCA FACIES
ESTIMATED LIMIT OF WESTERN ECCA FACIES
Middelburg
Queenstown
Beaufort West
Sutherland
East London
Grahamstown
DURBAN
Oudtshoorn
ATLANTIC OCEAN
INDIAN OCEAN
FACIES DISTRIBUTION MAP OF THE ECCA SERIES IN THE KARROO BASIN.
LEGEND
NORTHERN ECCA FACIES
CENTRAL ECCA FACIES
SOUTHERN ECCA FACIES
WESTERN ECCA FACIES
SCALE
0 10 20 30 40 50 60 70 80 90 100 Miles
Compiled and Drawn by P.J.RYAN

Fig. 1

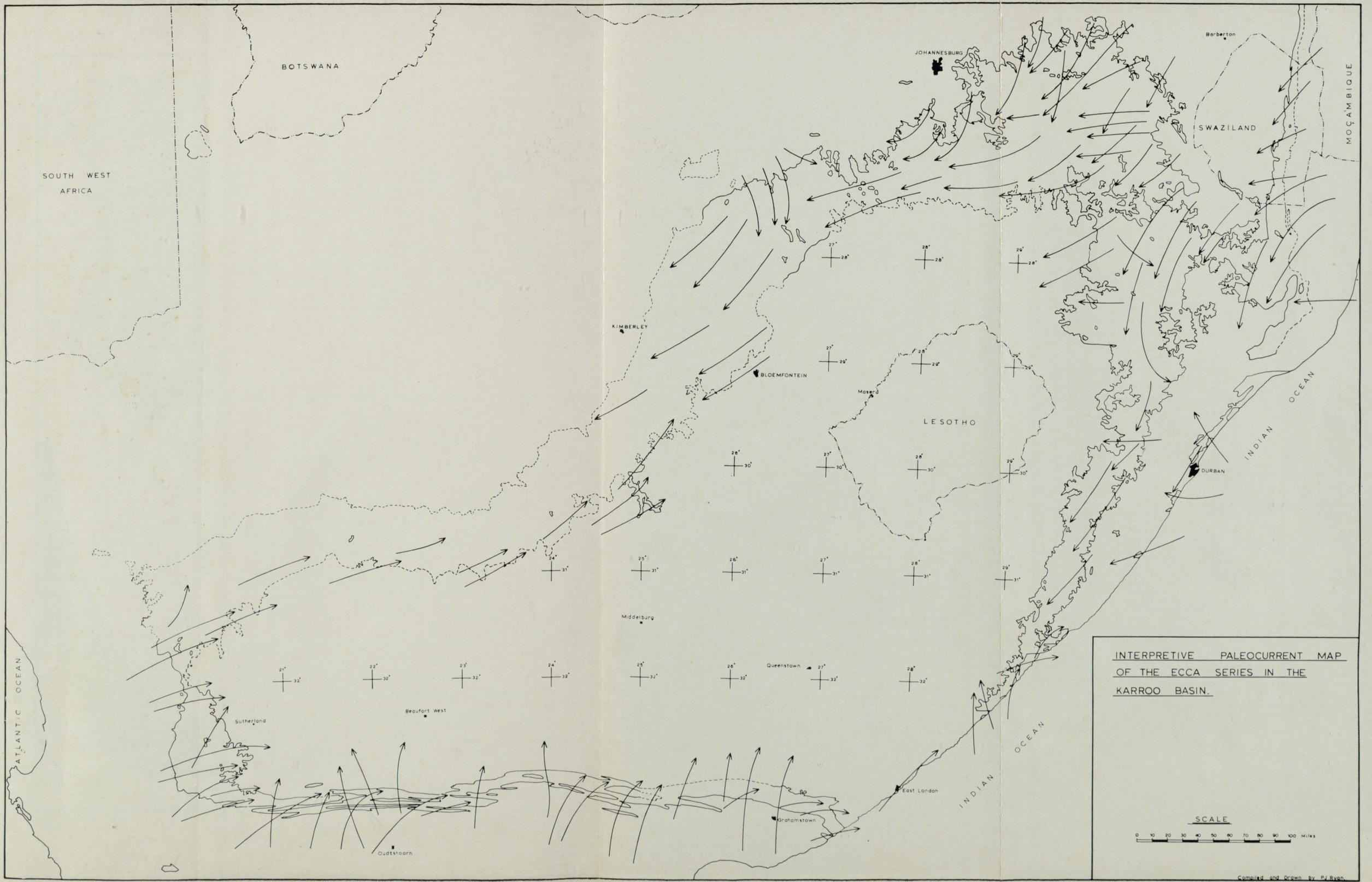

BOTSWANA
SOUTH WEST AFRICA
JOHANNESBURG
Barberton
SWAZILAND
MOÇAMBIQUE
KIMBERLEY
BLOEMFONTEIN
Maseru
LESOTHO
DURBAN
INDIAN OCEAN
Middelburg
Queenstown
Beaufort West
Sutherland
Oudtshoorn
Grahamstown
East London
ATLANTIC OCEAN
INTERPRETIVE PALEOCURRENT MAP OF THE ECCA SERIES IN THE KARROO BASIN.
SCALE
0 10 20 30 40 50 60 70 80 90 100 Miles
Compiled and Drawn by P.J. Ryan.

Fig. 2

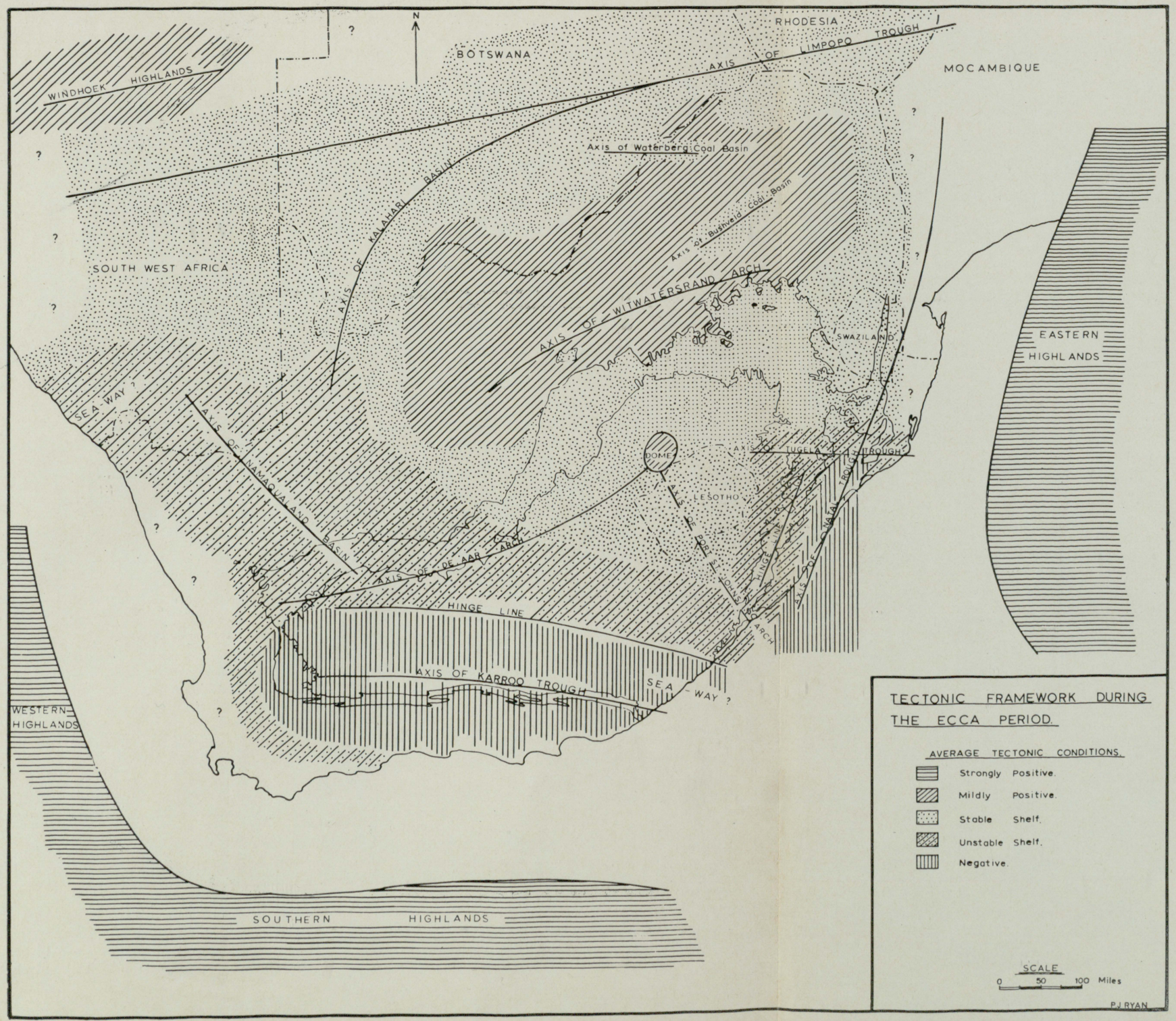

N
RHODESIA
BOTSWANA
MOCAMBIQUE
WINDHOEK HIGHLANDS
AXIS OF LIMPOPO TROUGH
Axis of Waterberg Coal Basin
AXIS OF KALAHARI BASIN
Axis of Bushveld Coal Basin
SOUTH WEST AFRICA
AXIS OF WITWATERSRAND ARCH
SWAZILAND
EASTERN HIGHLANDS
SEA WAY ?
AXIS OF NAMAQUALAND BASIN
DOME
AXIS OF TUGELA TROUGH
LESOTHO
AXIS OF DE AAR ARCH
AXIS OF PORT ST JOHNS ARCH
HINGE LINE
AXIS OF KARROO TROUGH
SEA WAY ?
WESTERN HIGHLANDS
SOUTHERN HIGHLANDS
TECTONIC FRAMEWORK DURING THE ECCA PERIOD.
AVERAGE TECTONIC CONDITIONS.
Strongly Positive.
Mildly Positive.
Stable Shelf.
Unstable Shelf.
Negative.
SCALE
0 50 100 Miles
P.J RYAN.

Fig. 3