

https://dspace.org/

Palaeontologia africana Volume 1

1953
Bernard Price Institute for Palaeontological Research
http://hdl.handle.net/10539/17099

Downloaded from a DSpace repository. https://dspace.org/

PALAEONTOLOGIA AFRICANA

Annals of the

BERNARD PRICE INSTITUTE

for

PALAEONTOLOGICAL RESEARCH

UNIVERSITY OF THE WITWATERSRAND

JOHANNESBURG



VOLUME I 1953

Published with financial assistance from the Council for Scientific and Industrial Research and the University Publications Committee.

BERNARD PRICE INSTITUTE FOR PALAEONTOLOGICAL RESEARCH

BOARD OF CONTROL

T. W. GEVERS (Chairman), R. A. DART, S. H. HAUGHTON, F. G. HILL, B. W. PRICE, H. R. RAIKES, J. C. M. SHAW, C. VAN RIET LOWE.

STAFF

Honorary Director & Editor:

S. H. HAUGHTON, B.A. (Cantab.), D.Sc., Hon. L.L.D. (Cape Town).

Scientific Officer & Assistant Editor:

A. S. BRINK, M.Sc. (Stell.), Ph.D. (Lond.).

Field Officer and Laboratory Technician:

J. W. KITCHING

PALAEONTOLOGIA AFRICANA

Annals of the

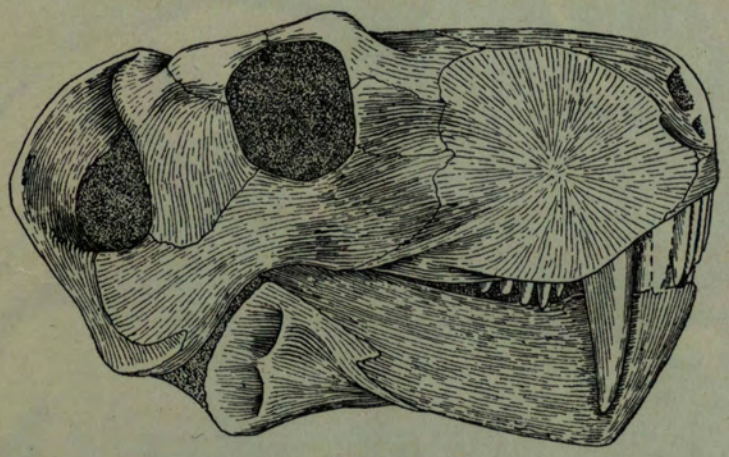
BERNARD PRICE INSTITUTE

for

PALAEONTOLOGICAL RESEARCH

UNIVERSITY OF THE WITWATERSRAND

JOHANNESBURG

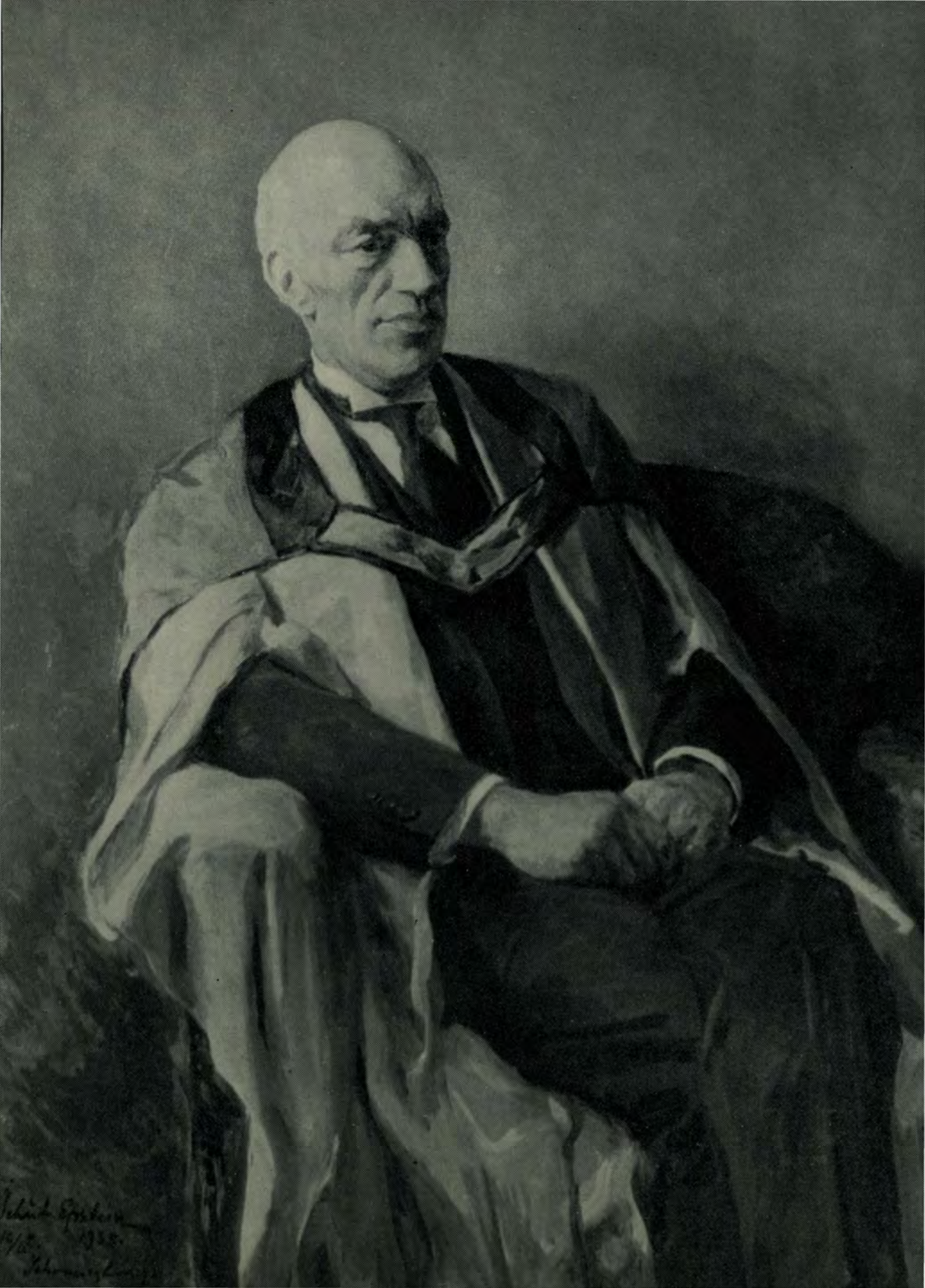


VOLUME I 1953

Published with financial assistance from the Council for Scientific and Industrial Research and the University Publications Committee.

DR. BERNARD PRICE,
FOUNDER OF THE INSTITUTE.

PHOTO: *Leon Levson, from a life size painting by J. Epstein*



CONTENTS

EDITORIAL i

PUBLICATIONS ON SPECIMENS IN THE COLLECTION OF THE BERNARD PRICE INSTITUTE iv

STUDIES ON NEW SPECIMENS OF THE GORGONOPSIA by A. S. BRINK and J. W. KITCHING 1

ON SOME NEW CYNOGNATHUS ZONE SPECIMENS by A. S. BRINK and J. W. KITCHING 29

THE EVOLUTION OF THE PALATE IN SOUTH AFRICAN ANOMODONTIA AND ITS CLASSIFICATORY SIGNIFICANCE by M. J. TOERIEN 49

INDEX TO GENERA AND SPECIES DESCRIBED IN THIS ISSUE 118

EDITORIAL

This is the first number of a new publication devoted to palaeontological work which, with the approval of the Council of the University of the Witwatersrand, will be produced by the Bernard Price Institute for Palaeontological Research. It is appropriate to place on record some of the salient points in the history of this Institute and to pay tribute to the generosity and sympathy for scientific research displayed by its founder, the late Dr. Bernard Price.

After attending a lecture by the late Dr. R. Broom in June, 1944, Dr. Price had discussions with Broom and the late Dr. Van der Horst — then Professor of Zoology in the University — regarding ways and means of "putting the collection of fossils on a proper organised basis." Professors R. A. Dart, T. W. Gevers, and C. van Riet Lowe collaborated with Broom and Van der Horst in preparing a memorandum on the subject, and proposed the employment of a collector "to salvage and store valuable material that would otherwise be lost" as a first step, with ultimate adequate provision for the study of such material by competent scientists and the adequate exhibition of the specimens publicly "in a proper museum."

This memorandum was submitted to Dr. Price, and officially endorsed by the Principal of the University in April 1945. The Principal pointed out that, although the proposal was initially a modest one, he felt confident that the endeavour might ultimately grow into an Institute of Palaeontological Research that would be of great benefit to the University and would lead to important results in the advancement of knowledge.

On receipt of the Principal's letter, Dr. Price agreed to donate to the University a sum of £2,000 as a separate fund for the purpose envisaged in the memorandum, which sum he estimated would be sufficient to cover expenses for the first two years of operation, and stated that his further support would be dependent on his estimation of the results shown during the trial period of two years. He stipulated that the work should be controlled by a Committee consisting of the signatories of the 1944 Memorandum, who would submit periodic reports in order to keep him in touch with the work and its results. Professor van der Horst became the first Chairman of the Committee of Control.

Late in 1945, on his discharge from the South African Armed Forces, Mr. James Kitching was appointed to a post of Technical Assistant and immediately began to collect fossil reptiles for the Institute from the Karroo beds, a task for which he, and his two brothers, had already displayed a remarkable aptitude and enthusiasm. At the same time, the Committee subvented collecting work at Makapan by a student at the University (now Dr. P. V. Tobias) and a colleague on condition that the material obtained was added to the Committee's collection.

To house the collections and to enable them to be properly prepared, a

large ex-military hutment was made available to the Committee by the University at the end of 1945. A year later (towards the end of 1946) Dr. Price, who had visited the Makapan Caves, announced to the Committee that he would finance the continuation of the work and would double his donation, making it £2,000 per annum, in order to provide for systematic exploration of the Cave of Hearths at Makapan. The University Senate recommended, and the University Council approved, that the project be given a more permanent character by naming it "The Bernard Price Foundation for Palaeontological Research" and that its administration be placed in the hands of a joint committee of Council and Senate, including Dr. Price. The Committee was therefore constituted of Professors van der Horst (Chairman), Dart, Gevers, Shaw, and van Riet Lowe, Dr. Broom (all nominated by Senate), Dr. Bernard Price, Dr. Raikes (ex officio) and Mr. F. G. Hill (all nominated by Council). In October, 1947, Dr. S. H. Haughton was added to the Committee by the University Council.

From the time of his appointment to the death of Dr. Price in July, 1948, Mr. Kitching spent in all 28 months collecting in the field, half of them in the Karroo and half in the Makapan Valley area. For a year or more, his brothers B. J. and S. C. Kitching were also employed as collectors. A very considerable amount of material was thereby accumulated, some of which would otherwise have been lost. Preparation of the material was carried on as fast as circumstances permitted, and a number of descriptive papers were published in various scientific periodicals.

The death of Dr. Price revealed that he had willed a share of his estate as a bequest to the Foundation, a share which amounted to £49,200. In accordance with a request contained in his will, the University Council resolved to reconstitute the Foundation as "The Bernard Price Institute for Palaeontological Research" and to place the control of this Institute in the hands of a Board which should function as a Committee of the University Council. The Board was formed of the members of the previous Committee, with Mr. B. W. Price (Dr. Price's son) added in place of his late father. The Board was formally constituted on February 25th, 1949.

In the latter half of 1949, the Board appointed Dr. A. S. Brink to an approved permanent post of Research Officer in Palaeontology and Mr. J. W. Kitching to an approved permanent post of Grade I Laboratory Technician. Mr. M. J. Toerien occupied temporarily a post of Research Assistant. In order that the scientific work of the Institute should be properly supervised the Board appointed Professor van der Horst as Honorary Director in February, 1951, in addition to his position as the Board's Chairman.

Professor van der Horst, however, died on October 10th of that year. His advice and counsel had been largely responsible for the beginning of Dr. Price's donations to palaeontological studies, and his wise guidance of the operations of the early collecting expeditions subsidised by Dr. Price was undoubtedly one of the major factors which led to the generous bequest on which the Institute was founded.

The University Council requested Professor Gevers to assume temporarily the posts rendered vacant by Professor van der Horst's untimely death; but, at his request, Council subsequently appointed him as Chairman of the Board

and made Dr. S. H. Haughton Honorary Scientific Director of the Institute.

The acquisition of palaeontological material, both by institutional collecting and by exchange, proceeded so rapidly that the accommodation originally allotted became far too small. Towards the end of 1952, therefore, the University made available two large hutments which had formed part of the School of Dentistry. One of these has become primarily an exhibition hall, with subsidiary office accommodation; the other is a store and preparation building.

In another section of this volume will be found a list of papers that have been published on material belonging to the Institute. It will be seen that these have been distributed among a number of scientific periodicals, whose producers have, by the very fact of publication, subvented in part the work of the Institute. Deeming that publication of research work carried out on its material is an essential part of the contribution that the Institute has to make to the advancement of palaeontological knowledge, the Board decided to combine papers concerning Institute material into a periodic publication of its own, to be known as "Palaeontologia Africana." The present is the first issue of this periodical.

PUBLICATIONS ON SPECIMENS IN THE COLLECTION OF THE BERNARD PRICE INSTITUTE

1946, *Broom, R. and Jenson, J. S.*,
A new fossil baboon from the caves at Potgietersrust.
Ann. Transv. Mus., vol. xx, pt. 4, p. 337.

1946, *Mollet, O. D. v.d. S.*
Fossil mammals from the Makapan Valley: 1. Primates.
S. Afr. Journ. Sci., vol. xliii, p. 295.

1948, *Kitching, J. W., Wells, L. H. and Westphall, E.*,
Fossil Cercopithecid Primates from the Limeworks quarry, Makapansgat, Potgietersrust.
S. Afr. Sci., vol. i, No. 9, p. 171.

1948, *Dale, M. M.*,
New fossil Suidae from the Limeworks quarry, Makapansgat, Potgietersrust.
S. Afr. Sci., vol. ii, No. 5, p. 114.

1948, *Broom, R. and Robinson, J. T.*,
On some new types of small carnivorous Mammal-like reptiles.
Broom Commemorative Volume Roy. Soc. S. Afr., p. 29.

1948, *Broom, R. and Robinson, J. T.*,
Two new Cotylosaurian reptiles.
Ann. Transv. Mus., vol. xxi, pt. 1, p. 51.

1948, *Broom, R. and Robinson, J. T.*
Some new fossil reptiles from the Karroo beds of South Africa.
Proc. Zool. Soc., vol. 118, pt. II, p. 392.

1948, *Dart, R. A.*,
An Australopithecus from the central Transvaal.
S. Afr. Sci., vol. i, No. 11, p. 200.

1948, *Dart, R. A.*,
The first human mandible from the Cave of Hearths.
S. Afr. Archaeol. Bull., vol. iii, No. 12, p. 96.

1948, *Dart, R. A.*,
The Makapansgat proto-human *Australopithecus prometheus*.
Am. Journ. Phys. Anthrop., n.s., vol. 6, No. 3, p. 259.

1948, *Dart, R. A.*,
An Adolescent Promethean Australopithecine Mandible from Makapansgat.
S. Afr. Sci., vol. ii, No. 3, p. 73.

1948, *Dart, R. A.*,
The adolescent mandible of *Australopithecus prometheus*.
Am. J. Phys. Anthrop., n.s., vol. 6, No. 4, p. 391.

1949, *Broom, R. and Hughes, A. R.*,
Notes on the fossil baboons of the Makapan Caves.
S. Afr. Sci., vol. ii, No. 9, p. 194.

1949, *Dart, R. A.*,
The cranio-facial fragment of *Australopithecus prometheus*.
Am. J. Phys. Anthrop., n.s., vol. 7, no. 2, p. 187.

1949, *Dart, R. A.*,
The first pelvic bones of *Australopithecus prometheus*.
Am. J. Phys. Anthrop., n.s., vol. 7, No. 2, p. 255.

1949, *Dart, R. A.*,
Inominate fragments of *Australopithecus prometheus*.
Am. J. Phys. Antrhop., n.s., vol. 7, No. 3, p. 301.

1949, *Dart, R. A.*,
A second adult palate of *Australopithecus prometheus*.
Am. J. Phys. Anthrop., n.s., vol. 7, No. 3, p. 335.

1949, *Broom, R.*,
New fossil reptile genera from the Bernard Price Institute.
Ann. Transv. Mus., vol. xxi, pt. 2, p. 187.

1950, *Broom, R. and George, M.*,
Two new Gorgonopsian genera from the Bernard Price Collection.
S. Afr. Journ. Sci., vol. 46, No. 6, p. 188

1950, *George, M.*,
A Chalicothere from the Limeworks quarry of the Makapan Valley, Potgietersrust district.
S. Afr. Journ. Sci., vol. 48, No. 6, P. 241.
1950, *Broom, R. and George, M.*,
Some new Anomodont reptiles in the Bernard Price Collection.
S. Afr. Journ. Sci., vol. 46, No. 10, p. 275.
1950, *Broom, R.*,
A new small Labyrinthodont from the Karroo beds of South Africa.
Ann. Transv. Mus., vol. xxi, pt. III, p. 251.
1950, *Brink, A. S.*,
Notes on a second specimen of *Homodontosaurus kitchingi*.
S. Afr. Journ. Sci., vol. 47, No. 4, p. 118.
1950, *Brink, A. S.*,
On the genus Cistecephalus Owen.
Ann. Mag. Nat. Hist., Ser. 12, vol. iii, p. 985.
1951, *Brink, A. S.*
On the compound eye of an unusually large Trilobite etc.
S. Afr. Journ. Sci., vol. 47, No. 6, p. 162.
1951, *Wells, L. H.*,
A large fossil klipspringer from Potgietersrust.
S. Afr. Journ. Sci., vol. 47, No. 6, p. 167.
1951, *Kitching, J. W.*,
A new species of Hippopotamus from Potgietersrust.
S. Afr. Journ. Sci., vol. 47, No. 7, p. 209.
1951, *Toerien, M. J.*,
Notes on the genus Kannemeyeria.
S. Afr. Journ. Sci., vol. 47, No. 10, p. 279.
1951, *Brink, A. S.*,
Some small Cynodonts.
S. Afr. Journ. Sci., vol. 47, No. 12, p. 338.
1951, *Brink, A. S. and Kitching, J. W.*,
On Leavachia, a Procynosuchid Cynodont from the middle Cistecephalus zone.
S. Afr. Journ. Sci., vol. 47, No. 12, p. 342.
1951, *Brink, A. S.*,
On the genus Lystrosaurus Cope.
Trans. Roy. Soc. S. Afr., vol. xxxiii, pt. I, p. 107.
1951, *Brink, A. S. and Kitching, J. W.*,
Some Theriodonts in the collection of the Bernard Price Institute.
Ann. Mag. Nat. Hist., Ser. 12, vol. iv, p. 1218.
1952, *Toerien, M. J.*,
The fossil Hyaenas of the Makapan Valley.
S. Afr. Journ. Sci., vol. 48, No. 9, p. 293.
1952, *Brink, A. S.*
The manus of Cistecephalus.
S. Afr. Journ. Sci., vol. 49, No. 1, p. 13.
1952, *Kitching, J. W.*,
A new type of fossil baboon, *Brachygnathopithecus peppercorni*.
S. Afr. Journ. Sci., vol. 49, No. L, p. 15.
1952, *Brink, A. S.*,
Fossil Hunters.
Convocation Commentary, University of the Witwatersrand, No. 4, (October).
1953, *Brink, A. S. and Kitching, J. W.*,
On *Leavachia duvenhagei* and some Procynosuchids in the Rubidge Collection.
S. Afr. Journ. Sci., vol. 49, No. 10, p. 313.
1953, *Kitching, J. W.*,
A new species of fossil baboon from Potgietersrust.
S. Afr. Journ. Sci., vol. 50, No. 3, p. 66.
1953, *Brink, A. S.*,
On the Whaitsiidae,
Trans. Roy. Soc. S. Afr. (in the press).

STUDIES ON NEW SPECIMENS OF THE GORGONOPSIA

By A. S. Brink and J. W. Kitching

Abstract

In this paper a list is given of all the described Gorgonopsian genera and species of Africa. The types are listed in a particular order according to dental formulae and age, but attention is drawn to the fact that the number of molars is unreliable for use as a basis for classification. The list also brings out that age or horizons can be very misleading unless localities are registered with greater accuracy.

The paper continues with the description of four specimens in the Rubidge Collection. *Broomicephalus laticeps* and *Dracocephalus scheepersi* are described as new genera and species, *Dinogorgon oudebergensis* as a new species, and the fourth is described as *Alopecorhinus rubidgei* Broom M.S.S., a name suggested by Broom but never used in publication.

Further descriptions are based on specimens in the Bernard Price Institute's collection. *Cyniscopoides broomi*, *Aloposauroides tenuis* and *Sycocephalus bigendens* are described as new genera and species; *Rubidgea majora*, *R. platyrhina*, *Prorubidgea robusta*, *Lycaenops alticeps*, *Aelurognathus minor* and *Arctops watsoni* are described as new species. In addition further information is given on the known genera and species *Rubidgea laticeps*, *Cyniscops longiceps*, *Cynarioides gracilis*, *Scylacocephalus watermeyeri*, *Lycaenoides angusticeps* and *Lycaenops ornatus*.

Dr. S. H. Rubidge of Wellwood, Graaff-Reinet, very kindly placed his entire collection of Gorgonopsids at the disposal of the Bernard Price Institute for comparison with the forms in its collection. After a recent visit to Graaff-Reinet, Kitching brought the specimens to the Institute, where they have been additionally cleaned at the request of Dr. Rubidge. The collection includes 20 type specimens and 7 recently collected undescribed specimens. We were asked to describe and establish the relationships of the latter specimens and we proceed to do so in this paper.

We would like to make use of this opportunity to express once again sincere thanks to Dr. Rubidge for so generously placing this valuable collection of specimens at our disposal.

In the collection of the Bernard Price Institute there are 32 specimens of Gorgonopsids, the majority of which are complete skulls, perfectly preserved and prepared. Six of these specimens have already been described (*Cyniscops cookei*, No. 12, Broom, R., 1948, Trans. Roy. Soc. Edinb., vol. lxi, pt. 2, p. 597, fig. 15 B; *Lycaenops pricei*, No. 4, Broom, R. and Robinson, J. T., Proc. Zool. Soc., 118, pt. 2, p. 400, figs. 5, 6; *Nanogorgon gracilis*, No. 3, idem, p. 398, figs. 3, 4; *Lemurosaurus pricei*, No. 13, Broom, R., 1949, Ann. Transv. Mus., xxi, p. 189, figs. 3, 4, 7c; *Tigrisaurus pricei*, No. 125, and *Leontosaurus vanderhorsti*, No. 126, Broom, R. and George, M., S. Afr. Journ. Sci., 46, 6, p. 188, 1950.)

In the past, authors have been inclined to rely to some extent on dental formulae in their descriptions of Gorgonopsids, but we consider that much weight cannot under all circumstances be attached to the number of post-canine teeth. The number of incisors may well form a sound basis for

distinguishing between different forms, but the molars are so degenerated that their number could easily differ even in specimens of the same species. However, we do not imply that within a species, or even within a genus, the number of molars can differ by more than one and a specimen with a certain number of large molars certainly belongs to a different form from a similar specimen with the same number of small insignificant molars. We do not intend relying on the number of molars as a basis for distinguishing between different forms, but we do find dental formulae in general very useful as a guide. We distinguish between Gorgonopsids with four and five incisors. In each category we distinguish between Gorgonopsids from different horizons, and lastly we use the number of molars, as well as their degree of degeneration, as a guide for additional distinction.

The following is a list of the described Gorgonopsian genera from this continent, roughly arranged according to their dental formulae and age. (In this list, the names of the zones in which the genera occur are indicated by the following abbreviations: Tap. for *Tapinocephalus* zone; End. for *Endothiodon* zone; Cist. for *Cistecephalus* zone.)

Gorgonopsids with 4 incisors

i4 — c1 — m9	Cist. —	*Galerhynchus.*
i4 — c1 — m7	Cist. —	*Cyonosaurus.*
i4 — c1 — m6	Cist. —	*Arctognathoides, Arctognathus, Cyniscopoides.*
i4 — c1 — m5	End. —	*Arctosuchus.*
i4 — c1 — m4	Cist. —	*Alopecorhynchus, Arctognathus, Ictidorhinus.*
	End. —	*Tetraodon.*
i4 — c1 — m3	Tap. —	*Eoarctops.*
i4 — c1 — m2	Tap. —	*Eriphostoma.*

Gorgonopsids with 5 incisors

i5 — c1 — m8	Cist. —	*Cyniscops, Galerhinus, Lemurosaurus.*
i5 — c1 — m7	Cist. —	*Aloposauroides, Cyniscops, Nanogorgon.*
i5 — c1 — m6	Cist. —	*Cyniscops, Cynarioides, Lycaenodon, Lycaenodontoides, Scylacocephalus.*
	End. —	*Cynarioides, Lycaenodontoides.*
i5 — c1 — m5	Cist. —	*Aelurognathus, Aelurosauropsis, Dinogorgon, Gorgonorhinus, Prorubidgea, Scylacognathus, Scylacops?, Sycosaurus.*
	End. —	*Aelurognathus, Aelurosaurus, Aloposaurus, Cerdorhinus, Cynarioides, Leptotrachelus?, Scymnognathus.*
	Tap. —	*Aelurosauroides, Cerdorhinus(?), Scylacognathus.*
i5 — c1 — m4	Cist. —	*Aelurognathus, Arctops, Broomicephalus, Dinogorgon, Dixeya, Genovum, Gorgonognathus, Leontocephalus, Lycaenoides, Lycaenops, Lycosaurus?, Prorubidgea, Scymnognathus.*
	End. —	*Aelurognathus, Arctops, Cynarioides. Cynariops, Gorgonops, Leptotrachelus?, Lycaenops, Lycosaurus, Scymnognathus, Tangagorgon.*
	Tap. —	*Galesuchus?, Lycosaurus(?), Pachyrhinos.*

i5 — c1 — m3 Cist. — *Aelurognathus, Broomisaurus, Leontosaurus, Prorubidgea, Scylacops, Scymnognathus, Tigricephalus.*
End. — *Scymnognathus.*
Tap. — *Broomisaurus.*
i5 — c1 — m2 Cist. — *Chiwetasaurus, Rubidgea, Sycocephalus, Smilesaurus.*
End. — *Smilesaurus.*
i5 — c1 — m1 Cist. — *Pardocephalus, Rubidgea.*
i5 — c1 — m0 Cist. — *Dracocephalus, Tigrisaurus.*
End. — *Clelandina.*

Gorgonopsids with uncertain dental formulae

Cerdognathus: Only the dental formula of the lower jaw is known: i4 — c1 — m5.

Cyniscodon: Only the lower jaw is known: i4 — c1 — m4.

Cynodraco: Five upper and four lower incisors.

Delphaciognathus: The dental formula of the lower jaw alone is known, which is given as i5 — c1 — m2. We doubt the presence of five incisors.

Hipposaurus:

While this paper was in preparation the genus *Hipposaurus* was very badly known. Specimens were described under this genus with three to seven molars and species were reported from *Tapinocephalus* to *Cistecephalus* zones. In the mean time, however, Boonstra prepared a paper on this genus which appeared after the present paper was ready for publication, so that his diagnosis could not effectively be incorporated in the above list. He distinguishes the following forms in the family Ictidorhinidae: *Hipposaurus boonstrai, H. major, Ictidorhinus martinsi, Lemurosaurus pricei, Hipposauroides rubidgei* and *Pseudohipposaurus kitchingi.* With this paper of Boonstra the genus *Hipposaurus* has now become one of the better known genera of the Gorgonopsia. (Boonstra, 1952, Tydskrif vir Wetenskap en Kuns. Deel XII, Nr. 1, April 1952.)

In the above list the genera *Burnetia, Megalesaurus, Megalesuchus* and *Rubidgina* are not mentioned, because they are quite distinct from the rest of the Gorgonopsians. A separate infra-order, the Rubidginoidea, was created for the latter three, while *Burnetia* used to be the single genus of another infra-order.

Broomicephalus laticeps gen. et sp. nov.

Perhaps the most interesting of the new specimens described in this paper is a complete skull with lower jaw, differing from any of the known Gorgonopsids to such a degree that it is difficult to ascertain its relationship within this family.

The skull is proportionately peculiarly short and broad. Apart from *Rubidgea laticeps*, this is the only Gorgonopsid in which the skull is broader than it is long. It is possible that the breadth of the skull is slightly exaggerated by the posterior portion being compressed antero-posteriorly; but if the posterior portion of the skull is distorted, it is only to a very slight extent. Certainly the posterior portion of the skull of *Rubidgea laticeps* is considerably more distorted and its breadth is definitely exaggerated to a great

extent. Although superficially it resembles the *Rubidgea* type of skull, it is less than half the size of *Rubidgea atrox*, but it appears as though it could have been, more reasonably than *Prorubidgea*, an ancestor to *Rubidgea*.

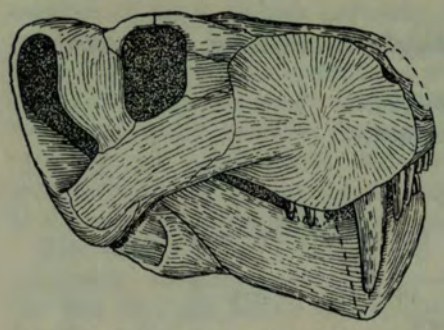


Fig. 1.—Side view of the skull of *Broomicephalus laticeps*, gen. et sp. nov. (x¼).

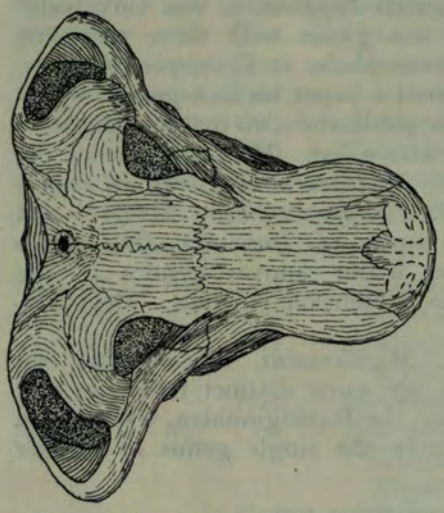


Fig. 2.—Dorsal view of the skull of *Broomicephalus laticeps*, gen. et sp. nov. (x¼).

The posterior portion of the skull is extraordinarily short, notwithstanding the possibility that it may be compressed anteroposteriorly. The temporal fossae are about three times as high as they are long. The snout is very broad, short and high. The anterior portion is considerably broader than in the region of the molars, and it is, contrary to the condition in almost all other Gorgonopsids, well rounded in all directions.

The symphysial region of the lower jaw is as broad as it is high (65 mm.). The incisors of the upper jaw form a crescent of much less than a quarter of a circle, in contrast with most other Gorgonopsids where the incisors form an arc of more than half of a circle.

There is a low longitudinal ridge medially between the orbits. Otherwise the dorsal surface of the skull is flat. The pineal foramen is situated on a very slight elevation which cannot be called a boss.

There are five incisors on each side in the upper jaw, and four in the lower jaw. The incisors of the upper and lower jaws are of the same size. The canine of the right side has fallen out and anteromedially in its socket a new canine is situated. This new canine has nearly reached its full length. On the left side there is a large canine situated postero-laterally in its socket, with room antero-medially for a new canine. The latter was apparently in the act of starting to replace the former, but was lost before fossilization. There are four molars on each side of which the second and fourth are preserved on the right, and the second and third on the left. We could not establish the number of molars in the lower jaw.

There is definitely no preparietal. The frontals are excluded from the margins of the orbits. The postfrontals are large and broad.

The skull is 210 mm. long, measured from the interparietal to the premaxillaries, and across the squamosals it is 260 mm. broad. The snout is 95 mm. broad anteriorly and in the middle of its length it is 85 mm. broad.

The interorbital and intertemporal breadths measure 72 mm. and 125 mm. respectively.

This specimen was discovered by Mr. Charles Rubidge on the farm Soetvlei in the Richmond district in upper *Cistecephalus* zone beds. We propose the name *Broomicephalus laticeps* gen. et sp. nov. and suggest that it be numbered 101 R.C., which follows on the list of numbered type specimens in the Rubidge Collection.

Dracocephalus scheepersi gen. et sp. nov.

The type of this new genus and species is also a skull and lower jaw differing from any of the known Gorgonopsids. In proportions it may be possible to compare with the other Gorgonopsids, but its dental characteristics, combined with some other general characteristics, separate this specimen so markedly from the other members of the family that it is difficult to establish its relationship. The skull is furthermore so distorted that it may be misleading to base conclusions on the skull proportions.

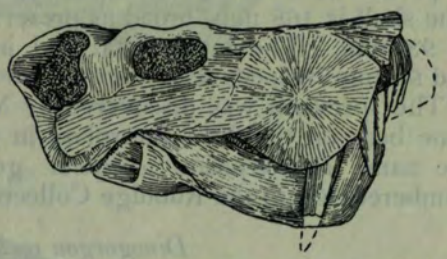


Fig. 3.—Side view of the skull of *Dracocephalus scheepersi*, gen. et sp. nov. (x¼).

There can, however, be little doubt that this new specimen had a snout not unlike that of *Broomicephalus*. It is much broader in front than in the middle of its length and was apparently as well rounded as in the previous specimen.

The roof of the skull appears to have been flat. The pineal foramen is situated on an elevation of slightly more prominence than in the previous specimen and there is a small depression in front. There is no longitudinal ridge or groove medially between the orbits.

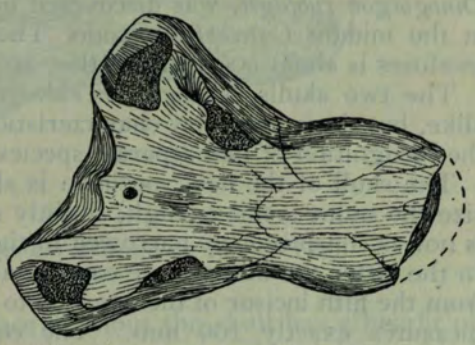


Fig. 4.—Dorsal view of the skull of *Dracocephalus scheepersi*, gen. et sp. nov. (x¼).

The skull is as long as that of *Broomicephalus*, but is much narrower posteriorly. The snout does not appear to have been narrower. The temporal region is half as high and the intertemporal region much narrower.

The symphysial region is very like that of *Broomicephalus*. It is 60 mm. broad and high. In both forms the splenials are large and form the ventral margin of the chin.

There is no Gorgonopsid other than *Broomicephalus* to which this new specimen shows even the slightest resemblance.

The dental characteristics are peculiar. There are five incisors on each side in the upper jaw and apparently four in the lower jaw. Of the five incisors in the upper jaw the first is the smallest and the fifth is by far the largest.

In most Gorgonopsids the distal incisors tend to be larger, but in this new specimen they are quite conspicuously so. On the left the canine is in the act of being replaced. On the right side the old canine has already fallen out and the new canine is practically fully grown. Most important is the fact that there are no molars in both the upper and lower jaws. In this characteristic this new skull can only be compared with *Clelandina* and *Tigrisaurus*, two forms which differ absolutely from the new form as well as from each other. While there may be some doubt as to whether the molarless Therocephalia belong to a natural monophyletic family, it is quite certain that the molarless Gorgonopsia do not belong to a monophyletic sub-family of the family Gorgonopsidae.

The skull is 194 mm. long, from the occipital condyle to the premaxillaries, as preserved. When reconstructed, it may have an actual length of 215 mm. The skull is 168 mm. broad as preserved. The snout has a maximum breadth of 93 mm. The interorbital and intertemporal breadths measure 57 mm. and 90 mm. respectively.

The specimen was discovered by Mr. S. C. Kitching in middle *Cistecephalus* zone beds on the farm Zuurplaas in the Graaff-Reinet district. We propose the name *Dracocephalus scheepersi* gen. et sp. nov. and suggest that it be numbered 102 in the Rubidge Collection.

Dinogorgon oudebergensis sp. nov.

The type of this new species of *Dinogorgon* was discovered on the Oudeberg plateau, fairly high in the middle *Cistecephalus* zone. The type species *Dinogorgon rubidgei*, was discovered on the farm Wellwood in beds very low in the middle *Cistecephalus* zone. The difference in height between the two localities is about 500 feet and they are 15 miles apart.

The two skulls, *Dinogorgon rubidgei* and the new species, are very much alike, but there are a few characteristics in which they differ, enough to justify the recognition of two separate species, disregarding their difference in age.

The skull of the new specimen is slightly smaller, but in proportion to its size the snout is not as high, slightly shorter and much narrower. The snout is not as conspicuously narrowed in the region of the molars as in *D. rubidgei*. In the latter the incisors are considerably larger; the distance straight across, from the fifth incisor of the one side to its fellow of the opposite side, inclusive, measures exactly 100 mm. The corresponding measurement in the new specimen is 75 mm.

The symphysial region, in anterior view, differs markedly in the two species. In *D. rubidgei* it is nearly as broad as it is high (82 mm. broad and 95 mm. high). In the new specimen it is 62 mm. broad and 100 mm. high.

The suborbital bar is 80 mm. high in *D. rubidgei* and 45 mm. in the new species.

There are five molars, somewhat smaller than the four of *D. rubidgei*.

The new specimen is a perfect skull, complete and undistorted. Only the left postorbital bar required restoration and the extreme anterior faces of the premaxillaries are damaged. The skull has a total length of 367 mm., measured from the premaxillaries to the posterior margins of the squamosals. Across the squamosals the skull has a breadth of 223 mm. From the ventral

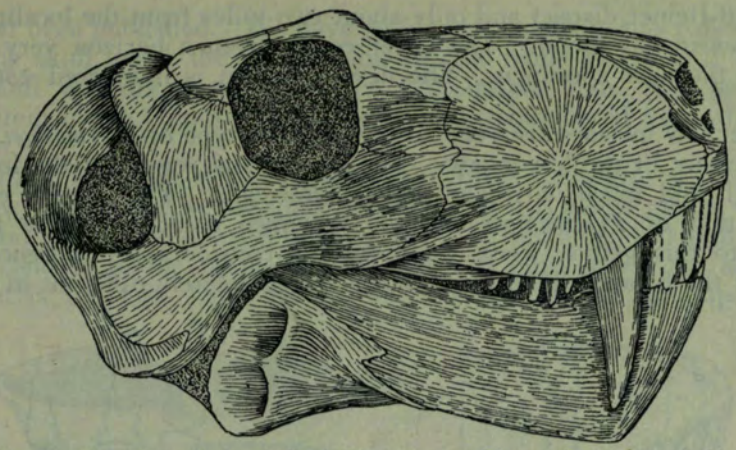


Fig 5.—Side view of the skull of *Dinogorgon oudebergensis*, sp. nov. (x¼).

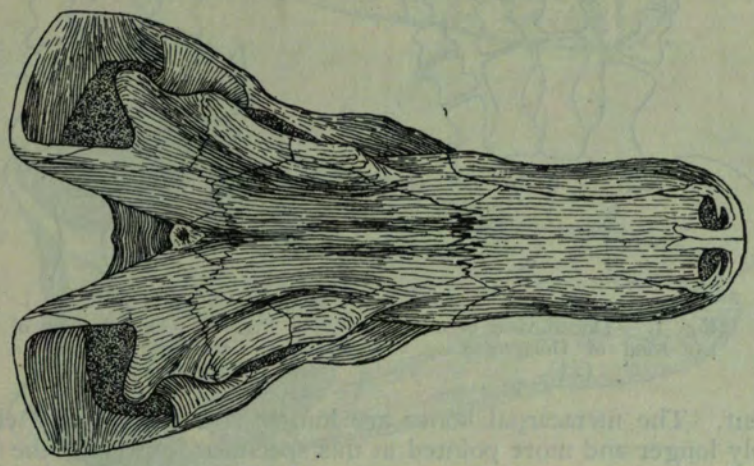


Fig. 6.—Dorsal view of the skull of *Dinogorgon oudebergensis*, sp. nov. (x¼).

margin of the dentary to the dorsal surface of snout the skull has a height of 206 mm. The snout is 89 mm. broad; the intertemporal and interorbital breadths measure 90 mm. and 100 mm. respectively.

For this specimen we propose the name *Dinogorgon oudebergensis* sp. nov., and suggest that it be numbered 103 in the Rubidge Collection.

Dinogorgon sp.

This specimen consists of the anterior portion of the snout, the symphysial portion with part of the left ramus of a mandible, a perfect left hand and a nearly perfect right foot. The specimen is slightly larger than *Prorubidgea*, slightly smaller than the lower *Cistecephalus* zone *Dinogorgon rubidgei* and of the same size as *Dinogorgon oudebergensis* described above. The new specimen was found by Kitching in middle *Cistecephalus* zone beds on the farm Ferndale

in the Graaff-Reinet district and only about two miles from the locality where *D. oudebergensis* was found. The latter comes from a horizon very slightly lower than the new specimen. The new specimen is numbered 250 in our collection.

The upper jaw incisors are very large, as in the type of *D. rubidgei*. There are four incisors in the lower jaw. The symphysial region of the lower jaw is very high and much narrower than in *Rubidgea*. This region compares well with that of *Prorubidgea* and the specimen could easily be taken as belonging to this genus, were it not for the considerable difference in the structure of the hands. The carpal bones are completely different in size and

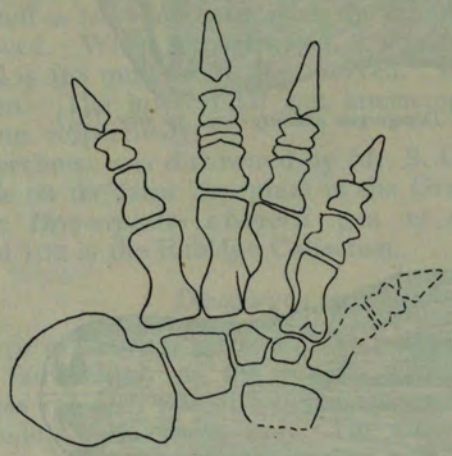


Fig. 7. — Dorsal view of the left hand of *Dinogorgon* sp. (x¼).

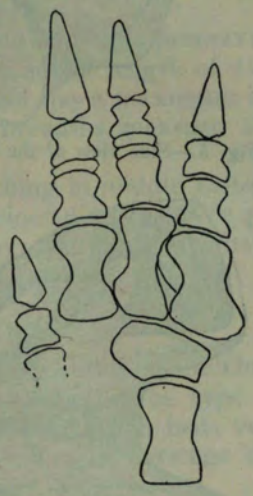


Fig. 8. — Dorsal view of the right foot of *Dinogorgon* sp. (x¼).

arrangement. The metacarpal bones are longer and the terminal claws are considerably longer and more pointed in this specimen, especially the terminal claws of the foot (compare figures 7, 8 and 18). The hands show the difference between *Dinogorgon* and *Prorubidgea*, although these forms are contemporaries, of about the same size and fairly similar in skull structure. Even in dental formulae the two forms agree. In skull proportions, however, they differ quite considerably. *Dinogorgon* has a long, high and narrow skull, whereas the skull of *Prorubidgea* is shorter, broader and not very high. The anterior portion of the snout of *Dinogorgon* is also larger, much higher and better defined than in *Prorubidgea*. In the former, too, the incisors are much larger.

The type specimen of *D. rubidgei* has only four molars, but *D. oudebergensis* has five molars. It is possible that the larger type specimen could have lost a molar on each side.

Alopecorhynchus rubidgei Broom MSS.

The name *Alopecorhynchus rubidgei* was given by Broom to a specimen in the Rubidge Collection, but as far as we can establish a description of the specimen

has not yet been published. We have decided to include in this paper a description of the skull under the generic and specific name given to it by Broom.

The skull was discovered in upper *Cistecephalus* zone beds on the farm Patrysfontein in the Graaff-Reinet district and is numbered 51 in the Rubidge Collection.

We do not know on what characteristics Broom recognised this specimen as a distinct genus, but we are quite satisfied that it is a new genus. The skull is long and slender, and exceptionally flat. It measures 187 mm. from the occipital condyle to the premaxillaries and 110 mm. across the squamosals. The snout is 102 mm. long and 40 mm. broad. It does not taper forward

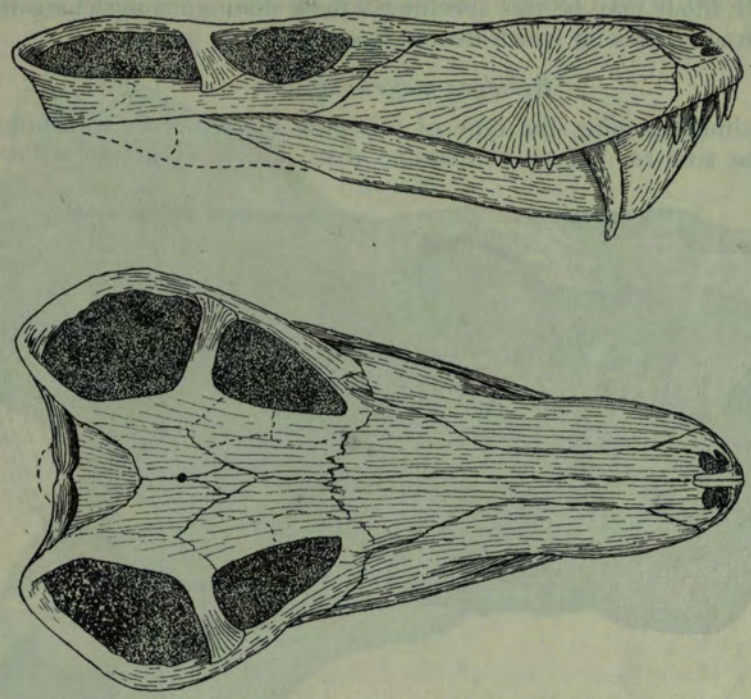


Fig. 9.—Side view of the skull of *Alopecorhynchus rubidgei* Broom MSS (x½).
Fig. 10.—Dorsal view of the skull of *Alopecorhynchus rubidgei* Broom MSS (x½).

and is not narrower in the region of the molars. The interorbital breadth is 35 mm. and the intertemporal breadth 40 mm. The orbits are larger 37 mm. in length, and the postorbital bars and zygomatic arches are slendel. The pineal foramen is large and is situated well forward, at the level of the posterior margins of the postorbital bars. It is difficult to trace sutures over the roof of the skull, as it is much cracked and weathered. The preparieta, can, however, be recognised as a small bone lying well forward, almost between the orbits, and it has a long slender backward extension reaching to the pineal foramen. The interparietal is largely situated on the dorsal surface, but not quite at the same level as the parietals. Posteriorly it curves down and inward into a deep depression where it meets the supraoccipital.

The external nares are small and the whole premaxillary region is delicate. There are four incisors on each side. The fourth on the left is being replaced by another tooth, only the tip of which shows antero-medially in the socket. On the right side the fourth incisor is also being replaced, but the replacing tooth is situated posteriorly in the socket. The incisors are well spaced.

The canine is large and extends below the level of the ventral side of the dentaries. It points slightly forward. The anterior margin of the canine is 36 mm. behind the tip of the snout, and is placed unusually far back in the maxilla. There are four small molars on each side, also well spaced.

The presence of only four incisors, the distance between the teeth, and the long slender snout may be this specimen's most distinguishing characteristics, and the characteristics on which Broom based this new genus.

Rubidgea majora sp. nov.

The specimen forming the type of this new species is an enormous skull, of the same size as, but more massive than, the skull in the collection of

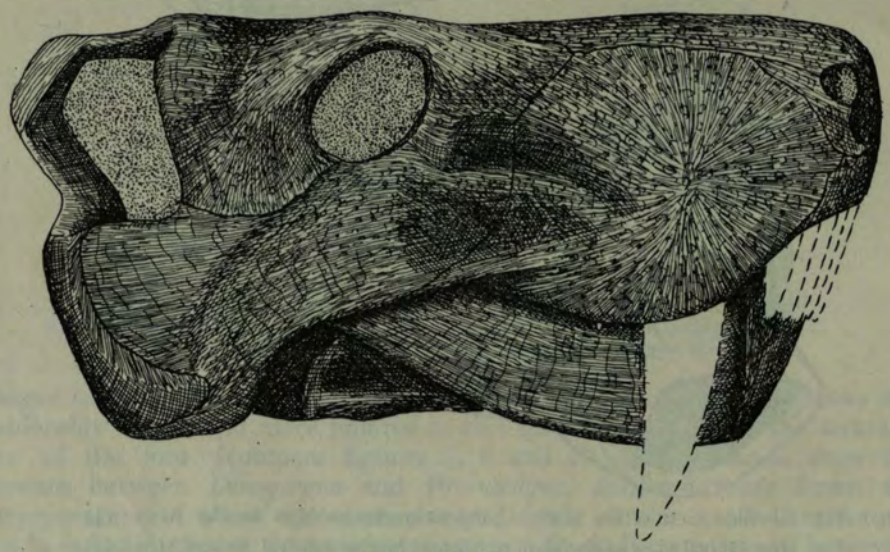


Fig. 11.—Side view of skull of *Rubidgea majora* sp. nov. (x¼).

Dr. S. H. Rubidge described by Broom in 1939 as *Rubidgea atrox* (Proc. Zool. Soc., 108 B, p. 527, figs. 1, 2.) This skull was collected by Mr. B. J. Kitching on the farm Coetzeeskraal in the Murraysburg district in upper *Cistecephalus* zone beds. It is numbered 246 in the collection of the Bernard Price Institute.

If the distance from the locality where *Rubidgea atrox* was found and the difference in horizon of the two localities (*Rubidgea atrox* was found in middle *Cistecephalus* zone beds) could be disregarded this new specimen could possibly be mistaken for a male of the latter species, but there are some structural differences.

The most striking differences are the heavier, more massive posterior

portion of the skull and the shorter snout in the new specimen. The snout of *Rubidgea atrox* is very distinctly longer and more slender. The breadth of the skull is 430 mm. in both specimens. The total length of the skull of *R. atrox* is 490 mm.; in the new specimen it is 470 mm. The breadth of the snout is 145 mm. in the new specimen and 135 mm. in *R. atrox*.

The postorbital arches of the new specimen are heavier and broader and the temporal vacuities somewhat differently shaped. The interorbital and intertemporal breadths of the new skull are appreciably greater.

The roof of the skull in both species is depressed to the same extent, but the dorsal margins of the orbits of the new specimen are more massive. The pineal foramen is situated on a fairly prominent boss, which is entirely absent in *R. atrox*. It is impossible to trace sutures on the roof of the skull.

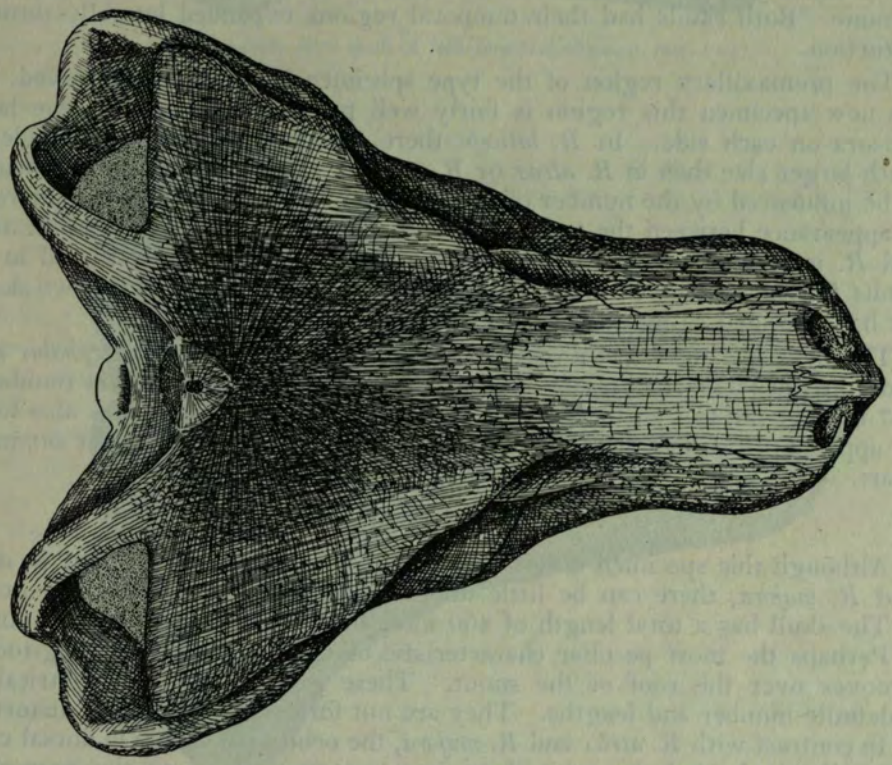


Fig. 12.—Dorsal view of skull of *Rubidgea majora* sp. nov. (x¼).

There are five incisors on each side, one large canine and, as in *R. atrox*, only a slight trace of a tiny molar on the right side. Both canines are broken off but, judging from their diameters, it is certain that they extended to well below the level of the ventral sides of the dentaries, another characteristic in which the new specimen agrees with *R. atrox*.

We consider that this new specimen represents a new species of *Rubidgea* and we propose the name *Rubidgea majora* sp. nov.

Rubidgea laticeps Broom

Included in the collection of the Bernard Price Institute is a specimen of exactly the same size and proportions, with even the same condition of preservation and degree of distortion, as the specimen in the Rubidge Collection described by Broom as *Rubidgea laticeps* (1940, Ann. Transv. Mus., xx, p. 173, fig 15). In the length and breadth of the skull, the breadth of the snout, the interorbital and intertemporal breadths, and the size of the orbits, the two skulls agree. In both specimens the pineal foramen is situated on a fairly prominent boss.

Both skulls have their posterior portions distorted to the same degree, as if pushed in from behind. It is more obvious from the new specimen that the breadth of the skull as reconstructed by Broom (op. cit.) is not quite genuine. Both skulls had their temporal regions expanded laterally through distortion.

The premaxillary region of the type specimen is perfectly preserved. In the new specimen this region is fairly well preserved and shows five large incisors on each side. In *R. laticeps* there are two molars on each side, of much larger size than in *R. atrox* or *R. majora*. Although we are not inclined to be influenced by the number of molars, their size and the general difference in appearance between the two skulls of *R. laticeps* and the skulls of *R. atrox* and *R. majora* induce us to regard the former two as wrongly placed in the genus *Rubidgea*. However, on account of the bad preservation of the two skulls, we have decided to leave them provisionally in this genus.

The new specimen was discovered by Kitching in upper *Cistecephalus* zone beds on the farm Hoeksplaas in the Murraysburg district and is numbered 247 in the collection of the Bernard Price Institute. The type was also found in upper *Cistecephalus* zone beds, but the two localities are about 50 miles apart.

Rubidgea platyrhina sp. nov.

Although this specimen differs to a very considerable extent from *R. atrox* and *R. majora*, there can be little doubt that it belongs to the same genus.

The skull has a total length of 400 mm. and a total breadth of 350 mm.

Perhaps the most peculiar characteristic of this species is the longitudinal grooves over the roof of the snout. These grooves are asymmetrical, of indefinite number and lengths. They are not formed as a result of distortion.

In contrast with *R. atrox* and *R. majora*, the orbits are visible in dorsal view. Immediately behind the orbit there is a prominent boss on the postorbital bar. This boss is also found in *R. atrox* and *R. majora*, but it is not so conspicuous in *R. laticeps*.

The pineal foramen is situated on a boss of slightly less prominence than that of *R. laticeps* and *R. majora*.

The snout is longer and more slender than in the other species and, in contrast, tapers forward. The external nares are dorso-ventrally flattened and extend far laterally. The septomaxillaries form prominent bridges dividing the external nares nearly completely in two. The external nares spread ventrally and laterally below these bridges to cover large areas of the

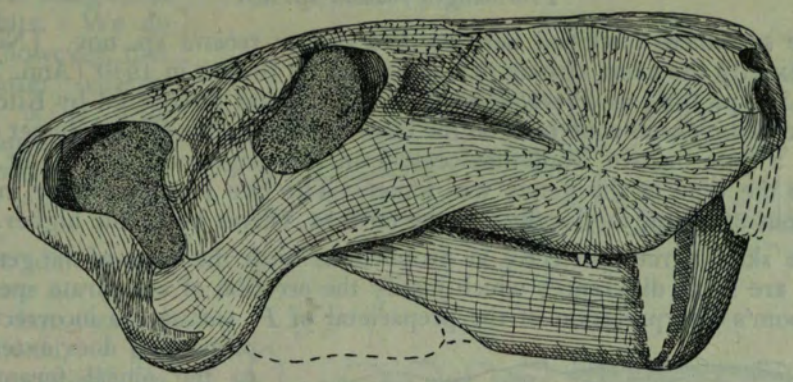


Fig. 13.—Side view skull of *Rubidgea platyrhina* sp. nov. (x¼).

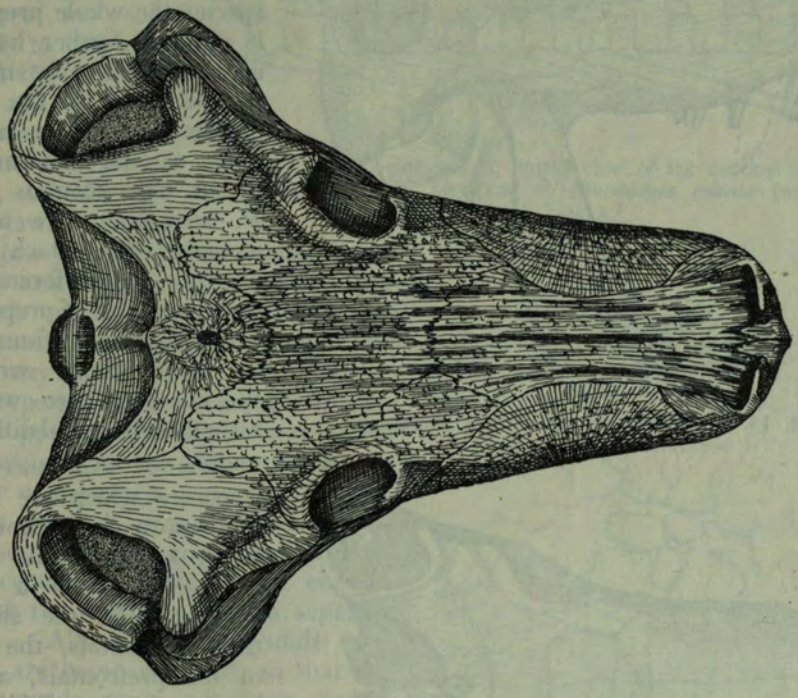


Fig. 14.—Dorsal view of the skull of *Rubidgea platyrhina* sp. nov. (x¼).

premaxillaries. The dorso-ventrally flattened characteristic of the external nares is so markedly different from the more upright type of nares of the other species that we have decided to name this specimen *Rubidgea platyrhina* sp. nov. It was discovered by Kitching in upper *Cistecephalus* zone beds on the farm Doornberg in the New Bethesda district and is numbered 248 in the collection of the Bernard Price Institute.

Prorubidgea robusta sp. nov.

The specimen described here as *Prorubidgea robusta* sp. nov. (No. 249) is of exactly the same size as that described by Broom in 1940 (Ann. Transv. Mus. xx, p. 169) as *Prorubidgea maccabei*. It was discovered by Kitching in middle *Cistecephalus* zone beds on the farm Poortjie in the Graaff-Reinet district, about a mile or two from the locality on the neighbouring farm St. Olives where the type of the genus was found. The two localities differ in height by about 300 feet, the locality on the farm St. Olives being the higher.

The skull agrees perfectly in proportions with the type of the genus, but there are some differences which justify the erection of a separate species.

Broom's interpretation of the preparietal of *P. maccabei* is incorrect. The preparietal does extend back to the pineal foramen and forms part of the latter's margin, but in the new species the whole preparietal is situated farther back and forms considerably more of the margin of the pineal foramen. It does not extend as far forward between the frontals as in *P. maccabei*. We are not inclined to attach much weight to differences in shape and size of preparietals as we have often found them to differ much within a species, but here we have rather a substantial difference.

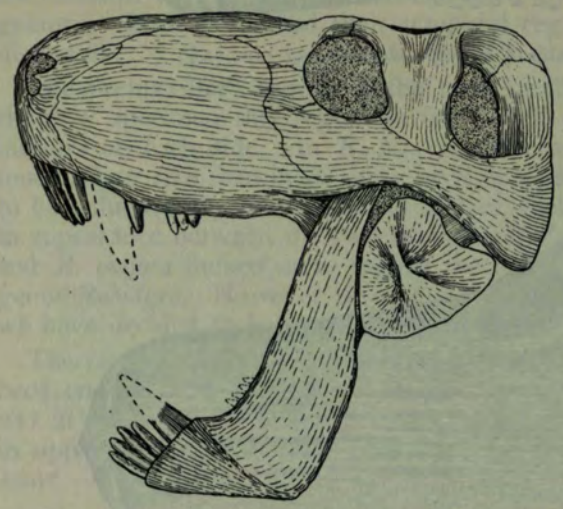


Fig. 15.—Side view of the skull of *Prorubidgea robusta* sp nov. (x¼).

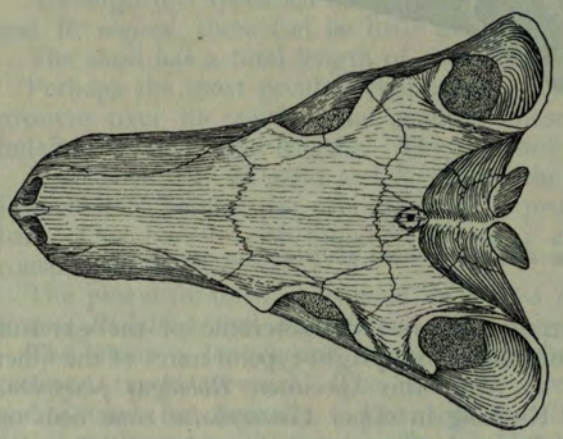


Fig. 16.—Dorsal view of the skull of *Prorubidgea robusta* sp. nov. (x¼).

Other differences in structure which are reasonably more conspicuous than those we have thus far encountered within a species are found in the shape of the postfrontals, the length of the prefrontals, and the level of the fronto-nasal suture relative to the anterior margins of the orbits. In addition the frontals are excluded from the margins of the orbits in the new specimen, whereas in the type of the genus narrow extensions of the frontals still

reach the margins of the orbits. We do admit, however, that the latter characteristic is of little importance and that both conditions may occur within one species.

Other differences, which are not structural, but rather proportional, are found especially in the orbital and temporal regions and they are too substantial to be considered the result of sex or age.

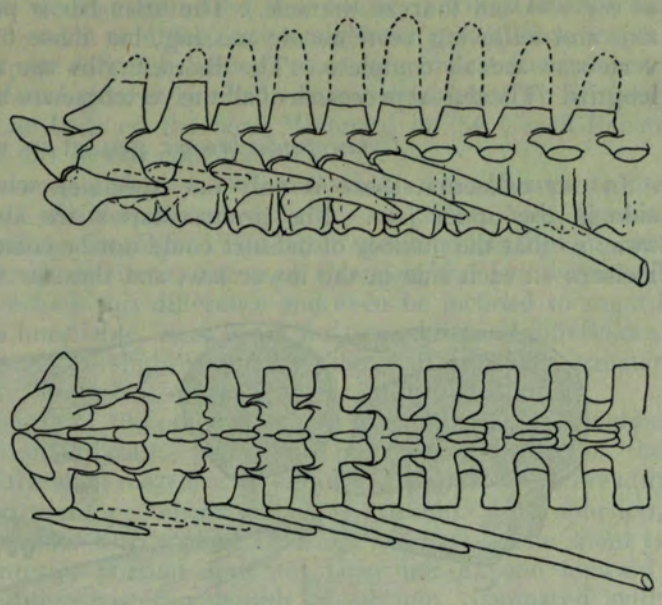


Fig. 17.—A, side and B, dorsal view of the cervical and anterior thoracic vertebrae of *Prorubidgea robusta* (x¼).

The dental formula of the new species is i5, c1, m3 for the upper jaw. In the lower jaw there are four incisors, one canine and apparently four molars of which one is preserved on the left and two on the right. In the upper jaw there may have been four molars. In the type species there are five molars in the upper jaw. We do not attach much weight to the difference in the number of molars as a generic feature, but the number of molars considered with their size and degree of degeneration certainly are significant enough to allow the dinstinction of a separate species. Although fully adult, the canines are being replaced, so that the Gorgonopsids could not have had a single dental succession like the higher Cynodonts.

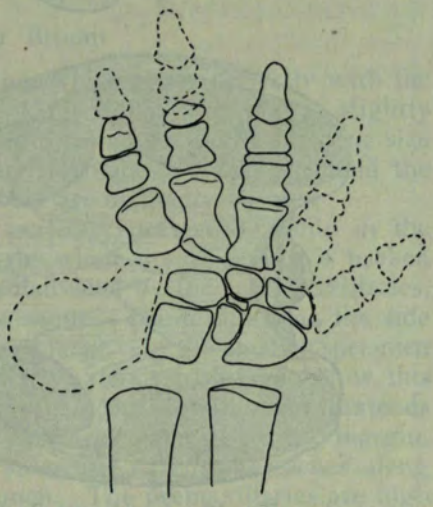


Fig. 18.—Dorsal view of the left hand of *Prorubidgea robusta* (x¼).

In addition to the perfectly complete, undistorted and marvellously prepared skull, the specimen includes a nearly perfect left hand with the distal ends of the radius and ulna, a complete humerus, clavicle, precoracoid and coracoid and the lower portion of the scapula. Furthermore, the specimen includes the proatlas, atlas and axis, and eight vertebrae of which four are regarded

as cervical and four as thoracic. The atlas rib is perfect. The ribs of the axis and following vertebra are missing, but those of the rest of the cervical vertebrae are all complete. The thoracic ribs are not present in their full lengths. The dorsal processes of all the vertebrae are broken off. (See fig. 17.)

Cyniscopoides broomi gen. et sp. nov.

In our collection there is only one specimen with four incisors on each side in the upper jaw. The premaxillaries are almost completely broken away so that the number of incisors could not be counted; but there are three incisors on each side in the lower jaw, and thus far we have not encountered

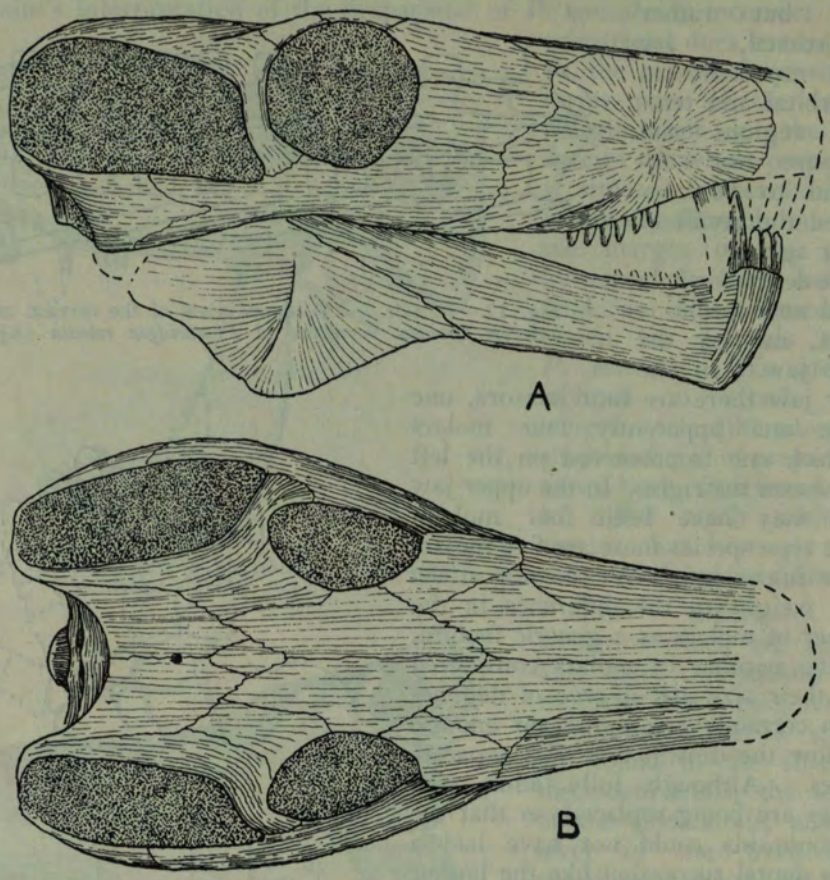


Fig. 19.—A, side and B, dorsal view of the skull of *Cyniscopoides broomi* gen. et sp. nov., with lower jaw placed in position (x½).

a Gorgonopsid in which the number of incisors in the upper jaw does not count one more than in the lower jaw.

There is one canine on each side with six small molars. From the list given above it will be seen that this new specimen can only be compared with *Arctognathoides* and *Arctognathus*, but keeping in mind that the number of

molars may be deceptive we also compared this specimen with *Galerhynchus* and *Arctosuchus*, but we found it to differ completely from any of these forms. This specimen therefore quite definitely belongs to a new genus and we propose the name *Cyniscopoides broomi* gen. et sp. nov. It was discovered by Kitching in upper *Cistecephalus* zone beds on the farm Waterval in the Graaff-Reinet district and is numbered 251 in our collection.

Both the skull and lower jaw show a very remarkable resemblance to the specimen in the Rubidge Collection described by Broom (1941, Ann. Transv. Mus., xx, p. 197) as *Cyniscops longiceps*. The latter specimen has five incisors and seven molars, of the same size as those of *Cyniscopoides*, but we would have been inclined to overlook this difference and even be inclined to regard the number of incisors as unreliable, were it not for two additional differences. Although *Cyniscops longiceps* is slightly smaller, the dentary has a greater vertical height. Secondly, the orbits of the latter are much smaller.

The skull has a total length of 200 mm., measured from the occipital condyle to the reconstructed premaxillaries. From the posterior margins of the squamosals the length of the skull measures an additional 10 mm. The breadth of the skull, measured across the zygomatic arches, is 110 mm. In proportion, this skull is somewhat broader than that of *Cyniscops longiceps*. The snout is 43 mm. broad. The anterior portion does not taper nor expand forward. The orbit has a total antero-posterior length of 42 mm., compared with 34 mm. in *Cyniscops longiceps*, while the latter skull is only 10 mm. shorter. The interorbital and intertemporal breadths are also, proportionally, less in *Cyniscops longiceps*.

Cyniscops longiceps Broom

There are three specimens in our collection which agree perfectly with the type of *Cyniscops longiceps* in the Rubidge Collection. The one is slightly smaller, the second is slightly larger, and the third is of exactly the same size as the type. The former two have a dental formula of i5, c1, m7 and the latter may also have seven molars, but only six are distinctly visible.

All three specimens have their snouts perfectly preserved, while in the type the snout is considerably crushed and the whole dorsal surface is broken away. The external nares are high, well subdivided by the septomaxillaries, which cover large areas on the sides of the snout. The foramen on the side of the snout, below the septomaxillary, is very large. In the smaller specimen only a very tiny portion of the septomaxillary extends backward below this foramen. In the intermediate specimen a portion of the septomaxillary extends backward for about half of the length of the foramen, along its ventral margin, and in the larger specimen, on the right side, this extension reaches along the whole of the ventral margin of the foramen. The premaxillaries are high anteriorly and form a narrow bridge between the nares.

The roof and sides of the skull, the orbital and temporal regions, and the posterior face of the skull, of all three specimens, agree perfectly with the type. The ventral surface of the type skull is unknown, due to the lower jaw being in position, but in each of the new specimens the ventral surface of the skull is perfectly preserved and cleaned. The intermediate specimen has the right half of the lower jaw preserved in position, but the palate could

nevertheless be cleaned perfectly. Figures 20A, B and C show the build of the skull of *Cyniscops longiceps*, as illustrated by the three skulls.

We do not know the exact horizon of the locality whence the type came; the three specimens in our collection come from middle *Cistecephalus* zone beds in the Murraysburg district. The smaller specimen (No. 252) was found on the farm Ringsfontein; the intermediate specimen (No. 253) was found on the farm Hoeksplaas immediately north of Ringsfontein, and the larger specimen (No. 254) was found on the farm Milton, about 15 miles north of Hoeksplaas.

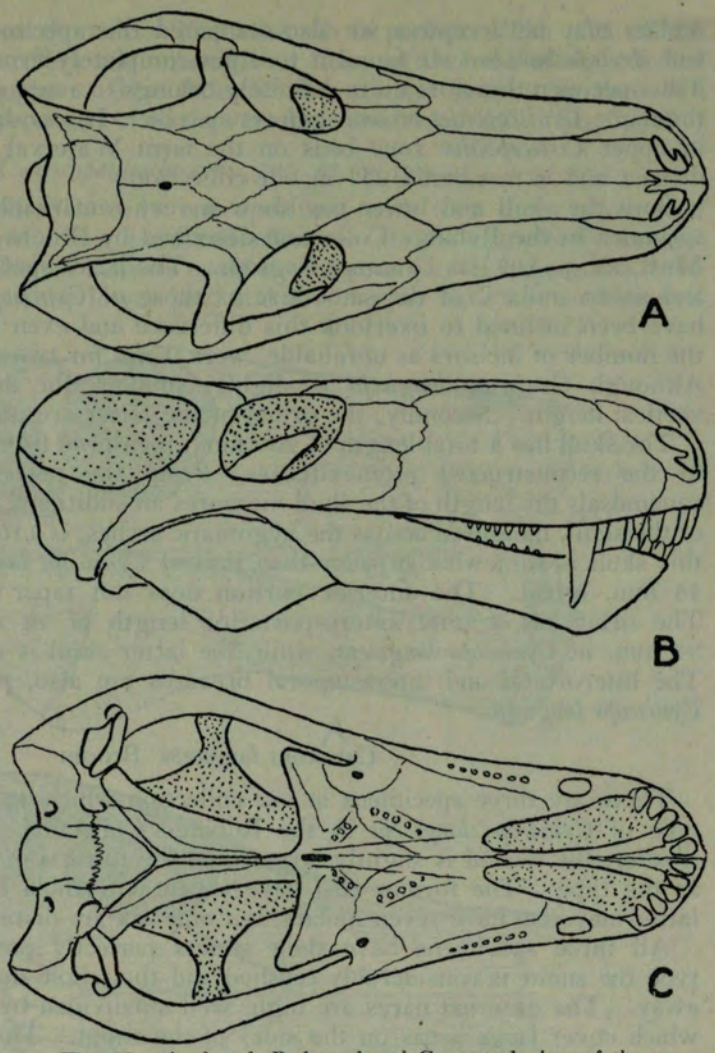


Fig. 20.—A, dorsal, B. lateral and C, ventral view of the skull of *Cyniscops longiceps*, restored (x½).

The following are some measurements of the three skulls:

	252	253	254
	mm.	*mm.*	*mm.*
Length of skull to occipital condyle	170	175?	203
Length to posterior margin of squamosals ...	173	180	210
Breadth across zygomatic arches	75?	90	103
Intertemporal breadth	35	40	46
Interorbital breadth	29	31	34
Diameter of orbit	34	36?	28?
Breadth of snout	35?	40	46
Length of snout from anterior margin of orbit...	91	96	111

Cynarioides gracilis Broom

In 1930 Broom (Phil. Trans. Roy. Soc., Ser. B, vol. 218) described a specimen as *Cynarioides gracilis*, but the type was cut into sections. Now we have in our collection a complete specimen of exactly the same size as this type, which we are positive belongs to the same genus and species. It was discovered by Mr. S. C. Kitching in middle *Cistecephalus* zone beds on the farm Vleiplaas in the Murraysburg district. The type was found in upper *Endothiodon* beds. The difference in age may justify the recognition of the new specimen as a distinct species, but it agrees so well with the type that we consider it unnecessary to do so. It is numbered 255 in our collection.

According to Broom (op. cit.) the type has five molars, but he stated that an older specimen could have had six molars. Our specimen has five molars on the right side and six on the left side.

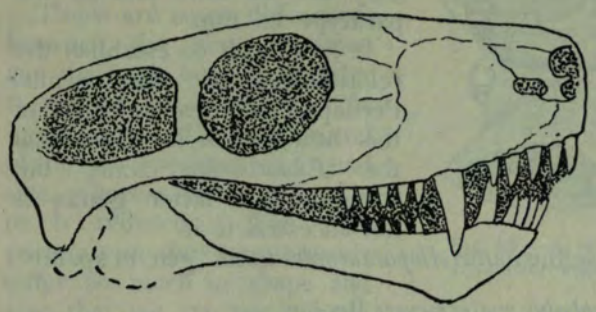


Fig. 21.—Side view of the skull of *Cynarioides gracilis* Broom, distortion corrected (natural size).

The posterior portion of the skull is distorted and the roof of the skull is not very well preserved. In side view the premaxillary bridge between the external nares extends more forward than shown in Broom's figure 46 (Mammal-like Reptiles of South Africa, 1932, p. 131) and appears more angular where it meets the nasals. The lower jaw also has an angular chin, which apparently Broom's specimen did not have. Otherwise the new specimen agrees very well with the type and could serve as an example of this genus and species in the absence of the complete type.

Aloposauroides tenuis gen. et sp. nov.

There are two specimens in our collection belonging to this new genus and species. The one has a total skull length of 133 mm. and is the better preserved of the two. We make this specimen the type. It was discovered by Mr. S. C. Kitching in middle *Cistecephalus* zone beds on the farm St. Olives in the Graaff-Reinet district and is No. 256 in our collection. The second skull is 122 mm. long and although it is less distorted it is more cracked and the structure more difficult to establish. We have no record of the locality of this specimen. It is No. 257 in our collection.

There is a large diamond shaped preparietal, the posterior angle of which does not reach the parietal foramen. The frontals form much of the dorsal margins of the orbits. The postorbital is slender and overlaps the equally slender jugal laterally, where it is in contact with the squamosal. The postfrontal extends down in front of the postorbital so that the latter forms very little of the orbital margin.

The skull is very slender and delicate. There are five incisors, one canine

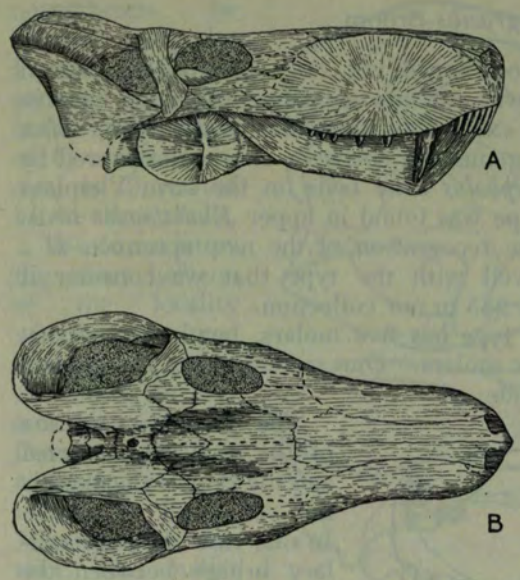


Fig. 22.—A, side and B, dorsal view of the skull of *Aloposauroides tenuis* gen. et sp. nov., distortion corrected (x½).

and apparently seven molars. It is very difficult to ascertain whether the second specimen also has seven molars. The two specimens agree perfectly in all their skull characteristics.

Both skulls are much distorted and it is advisable not to rely on any measurements other than their lengths, the interorbital and intertemporal breadths. In both specimens the latter two measurements are the same. In the type they are 26 mm. and in the paratype 25 mm.

It is difficult to establish the relationship of this genus. Perhaps the nearest ally of this new genus is *Aloposaurus* the *Endothiodon* zone, but certainly the latter genus is not ancestral to it.

For this new genus we propose the name *Aloposauroides tenuis* gen. et sp. nov.

Scylacocephalus watermeyeri Broom

There is in our collection a small skull 100 mm. long, which agrees with a skull in the Rubidge Collection, described by Broom as *Scylacocephalus watermeyeri* (1940, Ann. Transv. Mus., xx, p. 79). The latter skull is larger, approximately 135 mm. long. The anterior portion of the snout of the type is missing but, judging from the four incisors in the lower jaw, there must have been five in the upper jaw. In the new specimen there are five incisors and five molars. It appears as though there was a sixth tooth posteriorly on the right side. In the type there are also five on the left and apparently six on the right side.

The frontals contribute to the margins of the orbits in the new specimen, but in the type they are excluded. This is the only difference between the two skulls.

The snout does not taper nor expand forwards, and anteriorly it is fairly blunt.

The new specimen was discovered by Mr. B. J. Kitching in middle *Cistecephalus* zone beds on the farm Ringsfontein in the Murraysburg district. The type comes from the same horizon, but the two localities are eight miles apart. The new specimen is No. 258 in our collection.

Lycaenoides angusticeps Broom (figs. 23 A and B)

We have in our collection a very fine specimen of *Lycaenoides angusticeps*. It was discovered by Kitching in upper *Cistecephalus* zone beds on the slopes

of a koppie about two miles west of Richmond. It is No. 259 in our collection.

The skull is slightly smaller than the type. From the occipital condyle to the premaxillaries the skull measures 265 mm. and the preorbital portion measures 152 mm. The snout is 59 mm. broad as preserved and the interorbital and intertemporal breadths both measure 64 mm. The orbit measures 46 mm. antero-posteriorly.

There are some differences between the new specimen and the type, but we consider them not to be of specific importance. The preparietal of the new specimen is of usual size, whereas in the type it is much reduced. The preparietals in the Gorgonopsids differ so much in shape and size that we are not inclined to take the difference in characteristics between the preparietals of the new specimen and the type as being important.

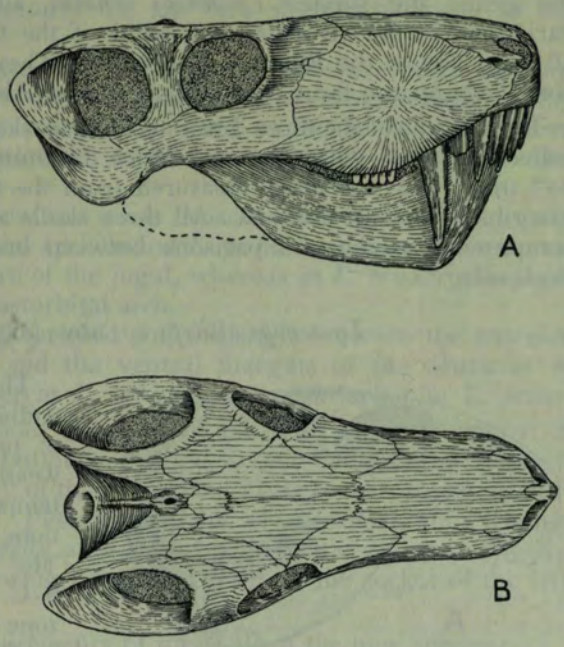


Fig. 23.—A, side and B, dorsal view of the skull of *Lycaenoides angusticeps* Broom, distortion corrected (x¼).

The parietal foramen is large and situated on a small boss. A fairly prominent ridge, in places quite 5 mm. high, extends from this boss down to the foramen magnum.

Due to the large preparietal, the parietals do not extend as far forward between the frontals as in the type. The frontals appear to be excluded from the margins of the orbits, but they reach to within a millimeter of the latter.

The zygomatic arch of the new specimen is somewhat more slender than in the type. Otherwise, in structure, the two skulls agree perfectly.

There are five molars in the new specimen, whereas in the type there are only four. As the type is a larger and older specimen, the latter could have lost a molar on each side.

Lycaenops ornatus Broom

We have in our collection a specimen of *Lycaenops ornatus* but, as the type is so well known and the new specimen reveals no additional information on this species, it is not worth describing. The new specimen comes from high in the middle, or rather low in the upper, *Cistecephalus* zone. It was discovered by Kitching on the farm Waterkrans on the border between the Graaff-Reinet and Richmond districts, and is No. 260 in our collection.

There are two specimens borrowed from Mr. Rubidge, which we refer to

the genus and species *Lycaenops ornatus*, although there are some minor variations in the structure and build of the two skulls. We number them 301 and 302 in the Rubidge Collection. They come from lower *Cistecephalus* zone beds on the farm Matjiesfontein near Aberdeen.

The lengths of the three *Lycaenops ornatus* skulls, Nos. 301 and 302 (Rubidge collection) and 260 (Bernard Price Institute) are respectively 210 mm., 247 mm., and 226 mm., measured from the premaxillaries to the posterior margins of the squamosals. All three skulls are to different extents laterally compressed so that comparisons between breadth measurements would be misleading.

Lycaenops alticeps sp. nov. (figs. 24 A and B)

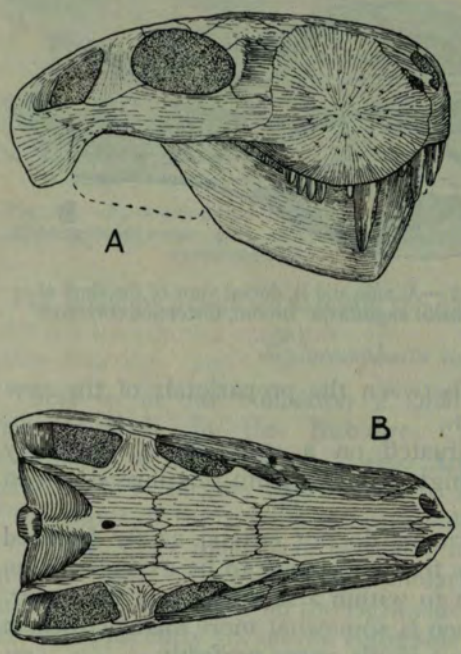


Fig. 24.—A, side and B, dorsal view of the skull of *Lycaenops alticeps* sp. nov. (x¼).

The type of this new species is an undistorted skull in fair condition of preservation. It suffered some weathering along the margins of the temporal vacuities, but reconstructions can be carried out accurately. The skull was discovered by Mr. S. C. Kitching in middle *Cistecephalus* zone beds on the farm Hoeksplaas in the Murraysburg district and is numbered 261 in our collection.

Superficially, in structure and general build, the skull of the new species agrees very well with *L. pricei* and *L. ornatus*, but in proportions it differs so remarkably that it cannot be confused with either of those two species. The snout has a considerable height and, in side view, the anterior portion is well rounded.

The differences between the three species are the following: The skull of *L. pricei* is low and broad. In *L. ornatus* the skull is somewhat higher, but much narrower. In *L. alticeps* the skull is as narrow, but much higher. The squamosals extend well back on each side of the occipital region in *L. ornatus*, while this region is more shallow in *L. pricei* and *L. alticeps*. In *L. ornatus* the nasals extend back on each side of the anterior ends of the frontals. In the other two species the fronto-nasal suture runs straight transversely. The preparietal is large in *L. ornatus* and small in the other two species. In all three species the preparietal lies well in front of the parietal foramen.

The nasals of *L. ornatus* are much broader posteriorly than anteriorly. In *L. pricei* they are very slightly broader posteriorly, and in *L. alticeps* they

are as broad anteriorly as posteriorly but are very slightly narrower in the middle.

There are four molars in *Lycaenops* and as the molars are large and not much degenerated, this number may be considered as characteristic of the genus. In *L. pricei* the molars are quite as long as the incisors, but more slender. In the other two species the molars are slightly shorter than the incisors, as well as more slender.

The postorbital arch of the new species is broader than in the two already described species. In both the new species and *L. pricei* the postorbital extends down to well over the lateral face of the jugal, whereas in *L. ornatus* the jugal tends to form a portion of the postorbital arch.

The chin of *L. alticeps* is well forward and the angle between the anterior face of the symphysial region and the ventral margins of the dentaries is nearly 90°. This angle is larger in *L. ornatus* and much larger in *L. pricei.*

A very interesting feature about the skull of the new specimen is that it demonstrates most clearly a continuous dental succession for the canines. On the right side, anteromedially of the canine and in its socket, there are still traces of the previous canine. Postero-medially of the functioning canine the tip of another canine is already appearing, in the same socket. The tip of a replacing canine is also showing postero-laterally in the socket of the left canine.

The following are some measurements of the skull of the new species:

Length of skull, squamosals inclusive	240 mm.
Length of skull to occipital condyle	231 mm.
Distance from premaxillaries to pineal foramen	186 mm.
Distance from premaxillaries to anterior margin of orbit	127 mm.
Distance between preparietal and pineal foramen ...	12 mm.
Interorbital and intertemporal breadths	53 mm.
Breadth across squamosals	130 mm.
Breadth of snout	70 mm.
Maximum height of snout	92 mm.

Aelurognathus minor sp. nov. (figs. 25 A and B)

The type of this new species of *Aelurognathus* is a nearly complete skull and lower jaw, discovered by Kitching in upper *Cistecephalus* zone beds near Bethesda Road Station. It is No. 262 in our collection.

The posterior portion of the skull is dorso-ventrally compressed and bent down. The margins of the temporal fossae have weathered away, but their impressions on the matrix made accurate reconstruction possible. The posterior half of the skull is restored in the figures.

Specimen No. 303 in the Rubidge Collection is a skull and lower jaw of nearly the same size, but it has suffered considerable lateral compression so that hardly any transverse proportional measurements of the skull can be compared. The only measurements that can be compared with safety are the lengths of the skulls and the lengths of the snouts. The skull is 180 mm. long in our specimen, and 170 mm. in Dr. Rubidge's specimen. In both the measurements are taken from the premaxillaries to the dorsal margin of the foramen

magnum. In the former the snout is 102 mm. long, measured from the anterior margins of the orbits, and in the latter the snout is 98 mm. long.

The occipital region is very open; the squamosals do not extend much backward on each side. Due to lateral compression, the occipital region of Dr. Rubidge's specimen appears more depressed.

In structure, the two skulls agree very well with that of *Lycaenops* and these two genera may be fairly closely related. The main differences between *Lycaenops* and *Aelurognathus* appear to be the following: In the former the preparietal is well separated from the pineal foramen. In the latter the preparietal is only a few millimeters in front of the parietal foramen. In *Aelurognathus* the four molars are much smaller than in *Lycaenops*, apparently more degenerated, so that the occurrence, occasionally, of three molars, as in *Aelurognathus sollasi*, should not be considered abnormal. *Aelurognathus* further differs from *Lycaenops* in that the "chin" projects ventrally well below the level of the ventral margins of the dentaries.

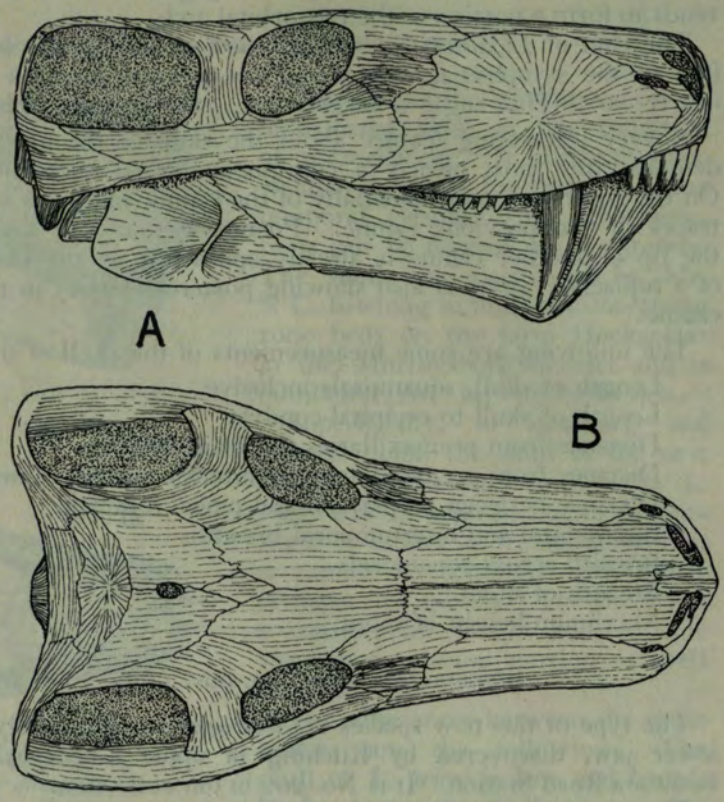


Fig. 25.—A, side and B, dorsal view of the skull of *Aelurognathus minor* sp. nov., with distortion of posterior portion corrected (x½).

Aelurognathus occurs in upper *Endothiodon* and lower *Cistecephalus* beds. This new specimen is therefore peculiar in being an upper *Cistecephalus* form. It differs reasonably from *A. microdon*, *A. serratidens*, and *A. tigriceps*, and compares rather well with *A. sollasi*, but it is a much later form than the latter and is smaller than the already described species.

As our specimen (No. 262) is the better preserved of the two and the structure more easily determinable on this skull, we make it the type, and Dr. Rubidge's specimen the paratype.

We have two additional specimens, Nos. 264 and 265, which agree perfectly in structure with the above two skulls. It is difficult to compare their proportions as these two additional skulls are also distorted to different extents. The skull is 169 mm. long in No. 264 and 164 mm. in No. 265; in both the measurement is taken from the premaxillaries to the dorsal margin of the foramen magnum. From the premaxillaries to the anterior border of the orbit the snout measures 95 mm. in the former and 93 mm. in the latter. The two specimens were found by Kitching in middle *Cistecephalus* zone beds on the neighbouring farms Mishoek (No. 264) and Leeufontein (No. 265) in the Murraysburg district. Specimen No. 265 appears to have had four molars, but specimen No. 264 definitely has only three molars on each side.

Arctops watsoni sp. nov. (figs. 26A and B)

Specimen No. 263 in our collection is a skull, without lower jaw, considered as belonging to the genus *Arctops*. It was discovered by Mr. B. J. Kitching in middle *Cistecephalus* zone beds on the farm Aasvogelkrans in the Murraysburg district.

Unfortunately the dental characteristics of the type of *Arctops willistoni* are not known, and although the posterior two-thirds of the skull compares perfectly with our specimen, it is nevertheless unsafe to refer the latter with absolute certainty to this genus, especially as we have not yet had the privilege of investigating the type.

In proportions the skulls agree perfectly, and in structure very reasonably. The only differences between the skulls are the following: The postorbitals are longer and narrower in the new species. The parietals of *A. willistoni* extend forward on each side of the preparietal to nearly level with the anterior margin of the latter, whereas in our specimen the parietals extend not nearly half way on each side of the preparietal. The interparietal of the new species is not as broad, so that consequently the tabulars are broader. Furthermore in our specimen the posterior molars reach to well behind the level of the posterior margins of the choanae. In *A. willistoni* these margins are included in the specimen, but molars are not included in the portions of the maxillaries as preserved.

These differences, in addition to the considerable difference in age (*A. willistoni* being of *Tapinocephalus* zone age) make us confident in distinguishing the new specimen as a distinct species. Otherwise, in structure and proportions, even in size, the skulls agree so well, that we are bound to consider it as belonging to the genus *Arctops*. Especially in the palatine and pterygoid region of the palate there is a most remarkable resemblance. In most Gorgonopsids the teeth-bearing ridges extend postero-laterally over the palatines and postero-medially over the pterygoids, with definite intervals where they cross the palatino-pterygoid sutures. In the new species the condition is perfectly similar to that in *A. willistoni*. The ridges in this genus do not rise near the midline anteriorly, but are well separated from each other. They reach their greatest height on the palatino-pterygoid sutures, where they come very close to the midline. Posteriorly over the pterygoids they separate again, and gradually smooth out, but before doing so they curve

inward again slightly, towards a long, narrow, interpterygoid fossa. This fossa was not demonstrated for *A. willistoni*, but perhaps it has been overlooked.

The transverse bones of the new specimen taper forward and extend well between the palatine and maxillary of each side. The condition in *A. willistoni* is somewhat different.

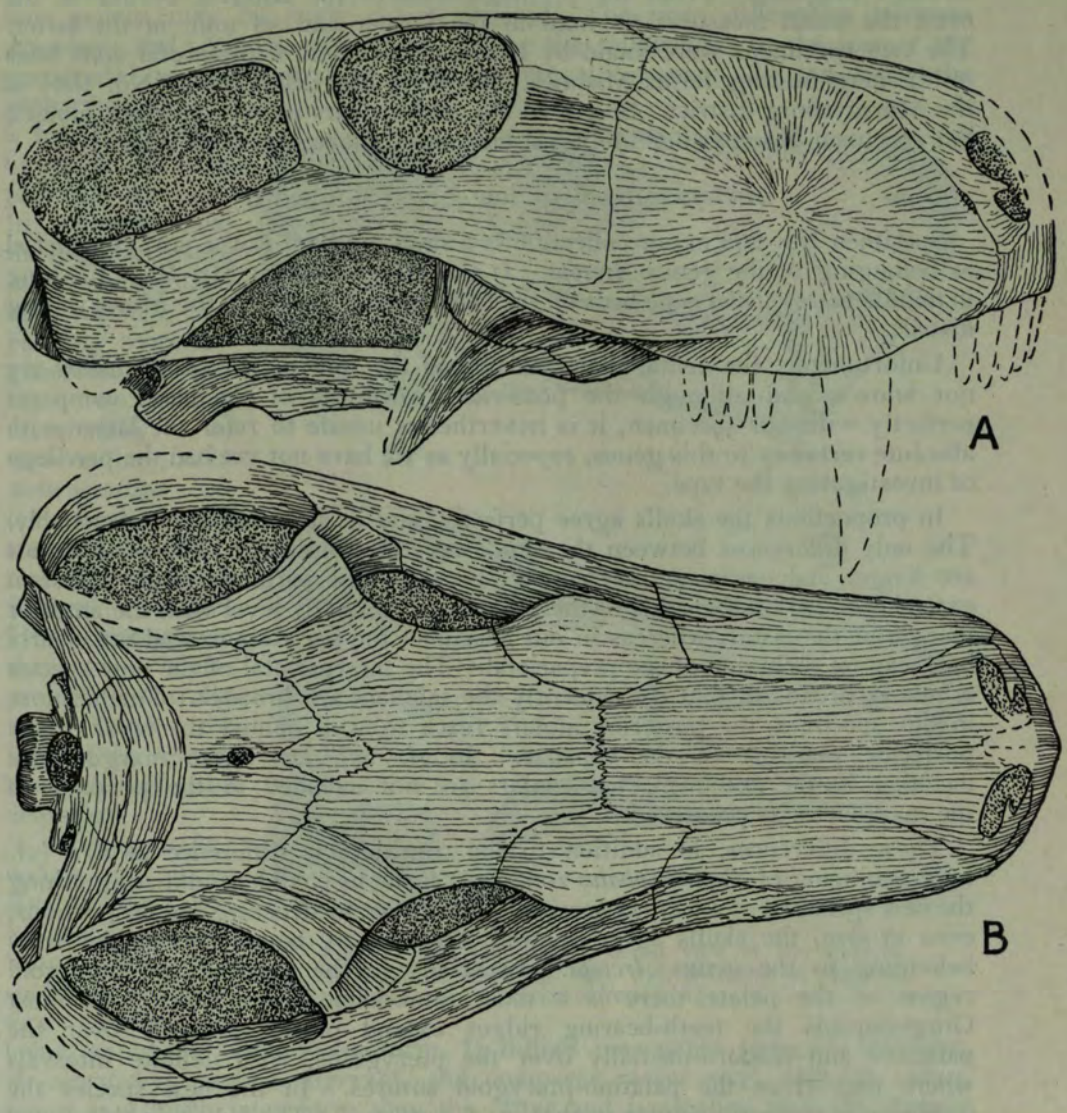


Fig. 26.—A, side and B, dorsal view of the skull of *Arctops watsoni* sp. nov. (x½).

If the new specimen is actually an *Arctops*, we now know the dental characteristics of this genus. There are five incisors and four molars. In

the specimen only the sockets of all the teeth are preserved. The sockets of all the molars are as large as those of the incisors, so that the molars could have been as large, proportionally, as in *Lycaenops*, but the incisor sockets show that the incisors were rather small for a Gorgonopsid.

The following are some measurements of the new skull:

Total length from premaxillaries to squamosals	278 mm.
Length from premaxillaries to occipital condyle	272 mm.
Length from premaxillaries to parietal foramen	210 mm.
Length of snout to anterior border of orbit	142 mm.
Length of orbit	47 mm.
Breadth of snout	77 mm.
Interorbital breadth	67 mm.
Intertemporal breadth	79 mm.
Height of snout	90 mm.

Sycocephalus bigendens gen. et sp. nov. (figs. 27A and B)

The type of this new genus is a skull comparable in proportions and structure

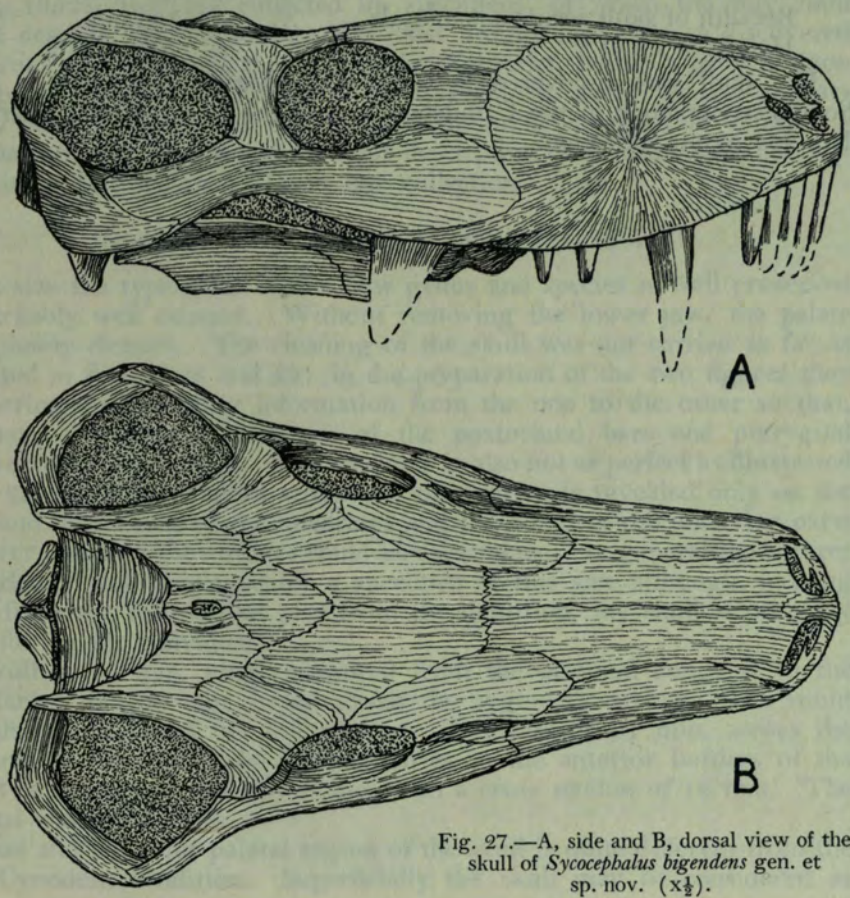


Fig. 27.—A, side and B, dorsal view of the skull of *Sycocephalus bigendens* gen. et sp. nov. (x$\frac{1}{4}$).

with *Cyniscops longiceps* or *Cyniscopoides broomi*. The new skull is, however, very slightly larger and proportionally somewhat broader over the squamosals. The preparietal and parietal foramen are very large and the frontals contribute very little to the margins of the orbits. Otherwise the three skulls agree perfectly and if their dental characteristics were not known they could easily be mistaken as belonging to the same species. However, *Cyniscops* has five incisors and *Cyniscopoides* only four. The former has seven tiny molars and the latter six, equally small. The new specimen is well separated from these two genera on account of having only two large molars, half the size of the incisors, and the incisors are fairly large. There are five incisors on each side.

The following are some measurements of the new skull:

Length of skull, squamosals inclusive	219 mm.
Length to occipital condyle	217 mm.
Length to parietal foramen	169 mm.
Length of snout to anterior margin of orbit ...	112 mm.
Breadth of snout across canines	54 mm.
Breadth of skull across orbits	98 mm.
Breadth of skull across squamosals	136 mm.
Height of snout	60 mm.

The skull was discovered in lower *Cistecephalus* zone beds on the farm Sondagsriviershoek in the Camdeboo area of the Graaff-Reinet district and is No. 266 in our collection.

ON SOME NEW CYNOGNATHUS ZONE SPECIMENS

By A. S. Brink and J. W. Kitching

Abstract

This paper describes a number of new specimens recently collected in *Cynognathus* zone beds, now in the collection of the Bernard Price Institute for Palaeontological Research. These specimens include two new genera and species, *Cistecynodon parvus* and *Inusitatodon smithi*. The former is related to the Galesauridae, but it may perhaps represent a new family of Cynodonts. The latter is a Gomphodont Cynodont. In addition a very perfect specimen of *Bauria cynops* is described and descriptions based on two other specimens affirm the validity of Broom's genus *Cyclogomphodon*. The paper also includes a short description of a specimen of *Diademodon broomi*.

On a fossil-collecting expedition to localities in the *Cynognathus* zone (October, 1952), Kitching collected 98 specimens, of which the tiny skull which we describe first is perhaps the most interesting. It was discovered on the farm Luiperdskop in the Aliwal North district, within a grey horizon which appears to be in the middle of the *Cynognathus* zone. It also appears as though this grey horizon is continuous with similar horizons on Winnaarsbaken, Vaalbank and Matyantya (see our description of *Bauria cynops* below). The specimen is numbered 318 in our collection.

Cistecynodon parvus gen. et sp. nov. (figs. 28-31)

For its size the type skull of this new genus and species is well preserved and remarkably well cleaned. Without removing the lower jaw, the palate was completely cleaned. The cleaning of the skull was not carried as far as is suggested in figures 28 and 29; in the preparation of the two figures they were superimposed to bring information from the one to the other so that, for instance, the relative positions of the postorbital bars and pterygoid processes could be illustrated. The specimen is also not as perfect as illustrated in figure 29. Certain detailed structural information is revealed only on the one side and in the case of the quadrates and the bones in the posterior parts of the lower jaw only the outlines could be ascertained. In general the sutures are remarkably well displayed for a specimen of this size although, judging not only from the sutures but also from the dentition, the skull is certainly that of a fully adult individual.

The skull is 55 mm. long, measured from the occipital condyles to the premaxillaries, and 50 mm. broad across the zygomatic arches. The snout is very short and broad for a Cynodont. It measures 21 mm. across the canines and 23 mm. from the premaxillaries to the anterior borders of the orbits. The orbits are perfectly round, with a cross section of 12 mm. The interorbital width is 15 mm.

The base and posterior palatal region of the skull is quite different from the average Cynodont condition. Superficially the skull may be considered as

belonging to the family Galesauridae, especially as far as the dentition is concerned, but there are some peculiarities about the skull which induce us to consider this specimen as perhaps representing a new family of Cynodonts. These peculiarities are the absence of a pineal foramen, a fully developed secondary palate to which the palatines do not contribute, the short, broad and blunt snout, the two perfect and well separated occipital condyles, the peculiar pterygoids, and the alisphenoid prolongations to the quadrates.

The *basioccipital* does not take part in the occipital condyles. It contributes

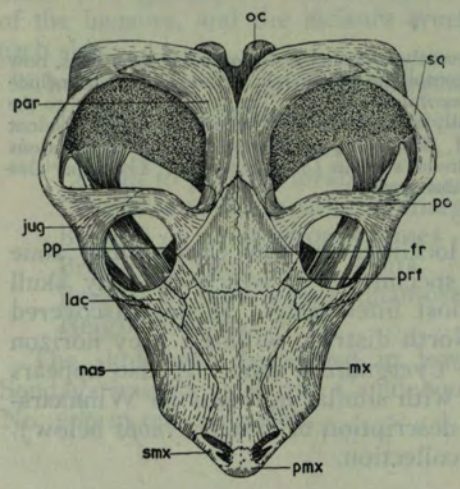


Fig. 28.—Dorsal view of the skull of *Cistecynodon parvus* gen. et sp. nov. natural size.

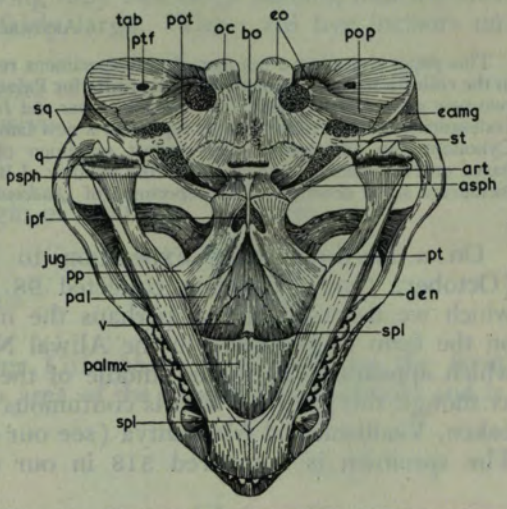


Fig. 29.—Ventral view of the skull of *Cistecynodon parvus* gen. et sp. nov. natural size. For abbreviations see page 31.

to the ventral margin of the foramen magnum. The bridge between the two occipital condyles is much reduced so that the condyles are well defined. The basioccipital does not contribute to the margins of the jugular foramina. It articulates with the parasphenoid relatively far forward. There are two longitudinal depressions immediately behind this suture.

The *exoccipitals* form the two large and well defined occipital condyles and the postero-medial halves of the margins of the large jugular foramina. They also form for short distances part of the margin of the foramen magnum, dorsally to the occipital condyles. Each exoccipital articulates with the prootic on the medial margin of the jugular foramen, laterally to the basioccipital, and with the opisthotic on the posterior margin of the jugular foramen.

The *supraoccipital* is relatively large and reaches fairly high. It articulates with the exoccipitals on the lateral margins of the foramen magnum and extends sidewards almost as far as these bones.

The *opisthotic* forms the paroccipital process, which is inclined forward. The paroccipital process appears to be a rather flat bone. Along the whole of its dorsal margin the opisthotic articulates with the tabular, and antero-medially it articulates with the prootic. Laterally it merely rests against the

squamosal. It is not clear to what extent the opisthotic contributes to the fenestra ovalis.

The *prootics* are not well preserved on either side, but their ventral surfaces could not have been much different from our interpretation as figured in fig. 29. They articulate medially with the basioccipital, anteriorly with the parasphenoid, while their lateral margins are free. The base of the skull is very broad across the prootics. The fenestrae ovales are evidently situated immediately above the lateral margins of the prootics.

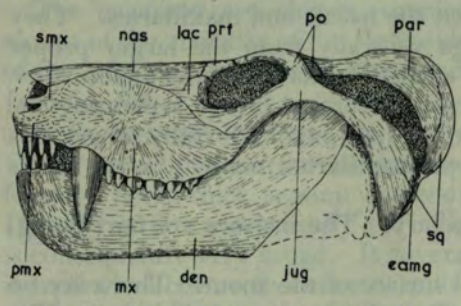


Fig. 30.—Lateral view of the skull of *Cistecynodon parvus* gen. et sp. nov. natural size.

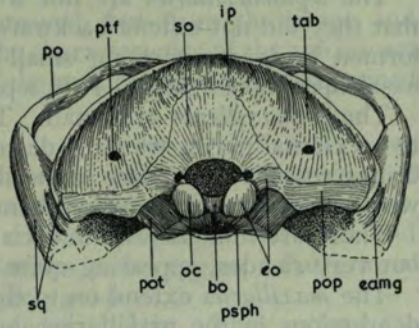


Fig. 31.—Posterior view of the skull of *Cistecynodon parvus* gen. et sp. nov. natural size.

Abbreviations: art, articular; asph, alisphenoid; bo, basioccipital; den, dentary; eamg, external auditory meatus groove; eo, exoccipital; fr. frontal; ip, interparietal; ipf, inter pterygoid fossa; jug, jugular; lac, lachrymal; mx, maxillary; nas, nasal; oc, occipital condyle; pal, palatine; palmx, palatal plate of the maxillary; par, parietal; pmx, premaxillary; po, postorbital; pop, paroccipital process; pot, prootic; pp, pterygoid process; prf, prefrontal; psph, parasphenoid; pt, pterygoid; ptf, post temporal fossa; q, quadrate; smx, septomaxillary; so, supraoccipital; spl, splenial; sq, squamosal; st, stapes; tab, tabular; v, vomer.

The *tabulars* are relatively large and cover the posterior faces of the squamosals completely. They do not overlap the paroccipital processes. The posttemporal fossae are situated well within the tabulars.

The *interparietal* is relatively small.

The *parietals* form the parietal crest, but contribute very little to the occipital crests. They diverge posteriorly in front of the margins of the occipital crests and extend far laterally, articulating throughout with the squamosals. Anteriorly they diverge and extend forward on each side of the frontals as tapering processes. These anterior processes are overlapped laterally by the postorbitals. There is no parietal foramen and the preparietal is missing. The parietal region is fairly broad.

The *postorbitals* are typical. Their posterior prolongations are very short and do not extend farther back than the frontals. It is not clear where exactly they meet the jugals on the postorbital bars. They form half of the dorsal margins of the orbits.

The *frontals* are large and broad. They extend up to the margins of the orbits without actually forming part of the latter. At the level of the anterior borders of the orbits they articulate with the nasals, forming a very broad suture.

The *prefrontals* are very small.

The *lachrymals* are relatively large and form the whole of the anterior borders of the orbits.

The *nasals* are very broad posteriorly, where they are flanked laterally by the lachrymals. Forward of the middle of their lengths they grow extremely narrow, but broaden out again very sharply farther forward. Even where they form the dorsal margins of the external nares, they are still very narrow compared with the breadth of the snout.

The *septomaxillaries* are not well preserved. It is however quite definite that they did not extend backward between the nasals and maxillaries. They formed bridges separating small openings ventrally from the larger proper nasal opening dorsally. This separation appears to have been complete.

The *premaxillaries* are small. They formed a vertical bridge separating the two external nares, which is destroyed in the specimen. Dorsally where this bridge reaches the surface of the skull the premaxillaries merely join the nasals without penetrating between them.

There are four incisors in each premaxillary. The incisors are fairly long, but very slender, appearing quite delicate.

The *maxillaries* extend on to the dorsal surface of the snout. There are no depressions in the maxillaries dorsally. Posteriorly the maxillaries overlap the jugals and extend to the level of the middle of the orbits. There are two tiny foramina on each side, relatively far forward.

Ventrally the maxillaries slope very little inward to the alveolar borders, with the result that the maxillary teeth of the two sides are well separated. There is a broad, fully developed secondary palate.

The canines are large and very long. The postcanine teeth are well cusped. There are six postcanine teeth, measuring 14 mm. in length. The first follows immediately on the canine. It has a simple cone-shaped crown. The second has a trace of an additional cusp posteriorly. These two teeth could possibly be premolars. The following four teeth are much larger, each with a main cusp with a smaller cusp in front and a similar cusp behind, and may be considered as molars.

The last tooth is almost level with the anterior border of the orbit and the posterior border of the palate is level with the penultimate tooth. Immediately behind the ultimate tooth the dentary passes so close to the alveolar border and the maxillary passes so sharply outward that there is no room for an additional tooth, even to develop at a more advanced age. The dentition can therefore be considered as complete.

The dentition is typically Cynodont. The upper jaw molars bite outside of the lower jaw molars.

The *transverse* bone could not be displayed.

The *jugals* are much damaged on both sides, but their outlines could be determined from their impressions on the matrix. They form the suborbital bars which extend sharply upward posteriorly. After evidently contributing to a portion of each postorbital bar each extends downward again farther posteriorly. There is no trace of a jugal process. The zygomatic arch is indeed most peculiarly shaped.

The *squamosals* form the posterior portions of the zygomatic arches, which

now descend practically vertically down to almost level with the ventral margins of the dentaries. At this level the quadrates articulate with the squamosals and immediately behind this articulation the external auditory meatus groove extends medially and anteriorly to level with the medial end of each quadrate. Here the squamosal perhaps articulates with the posterior prolongation of the alisphenoid. From the meatus grooves the squamosals rise directly in a postero-dorsal and later medial direction, posteriorly to the occipital wings of the parietals to form the anterior faces of the occipital crests.

The *quadrates* are almost completely destroyed, but from the shape and extent of the articular of the right side, and the characteristics of the squamosal of the left side, the general shape and size of the quadrate could be ascertained (see fig. 29).

Both *stapes* are missing.

The *vomer* divides the internal nares from each other. In this region it forms a fairly thick septum descending from the roof of the internal nares. Dorsally it forms practically the whole of the roof of each internal naris and is consequently very broad. It covers the palatines in this region. Posteriorly it tapers and covers the anterior ends of the pterygoids.

The *palatines* do not contribute to the secondary palate. They extend for short distances backward along ridges running across the pterygoids to the lateral walls of the internal nares.

The *pterygoids* form delicate pterygoid processes descending medially to the dentaries to a level 3 mm. short of the ventral margins of the latter. They are situated very far forward. It appears as though ridges extended from these processes to the posterior border of the secondary palate. Each pterygoid forms a descending process near the midline, at a level well behind the pterygoid processes, curving over towards its fellow of the opposite side. Both these processes then curve backward to clasp a plate-like extension of the parasphenoid between their ends. Immediately behind this structure, on each side of the parasphenoid plate, there are two cavities filled with matrix. Together they represent the interpterygoid fossa, but we could not establish how far they pass upward or whether they join above the parasphenoid plate.

The pterygoids articulate with the main parasphenoid bone immediately behind the interpterygoid fossa and at this level, but laterally, with the alisphenoids.

There is no suborbital fossa.

The *alisphenoids* could not be exposed, but the extensions of these bones to the quadrates, from the points where they articulate with the pterygoids, could be laid bare. These extensions are very delicate and were somewhat damaged, but enough is preserved to establish that they definitely belong to the alisphenoids.

The *parasphenoid* is most peculiar. It grows fairly narrow posteriorly to its articulation with the pterygoids and from this region it sends a plate-like process ventrally and anteriorly, dividing the interpterygoid fossa in two. The internal carotid foramina evidently passed into the brain cavity immediately above the anterior end of the parasphenoid, where the bone is narrowest. Farther back the bone grows extremely broad very suddenly,

from above the internal carotid foramina backward and downward to the prootics. Medially, behind the plate-like process, the parasphenoid descends into a transverse crest with an almost vertical posterior face rising towards the basioccipital suture.

The *dentary* has a very distinct angular process and a well developed coronoid process, the posterior margin of which extends very close to the squamosal. The symphysial region is broad and low, with a well rounded "chin." There are three incisors on each side, smaller and more delicate than those of the upper jaw. The lower jaw canines are not exposed. The post-canine teeth of the lower jaw could barely be reached from the palatal side. There are four large molars exactly opposite the four of the upper jaw, and slight indications of two small pointed teeth in front, also opposing the upper jaw premolars. Unless there are more premolars farther forward in the lower jaw, which we strongly doubt, there should be a diasteme behind the canine.

The dental formula for this specimen is therefore:

$i\frac{4}{3}$, $c\frac{1}{1}$, $pm\frac{3}{2}$, $m\frac{4}{4}$.

The rest of the lower jaw bones are very badly preserved. The splenials can only be traced anteriorly and the articular on the right posteriorly. In figure 29 merely a general outline is given of the bones posteriorly in the lower jaw.

Bauria cynops Broom (figs. 32-35)

The following description is based on a complete skull and lower jaw,

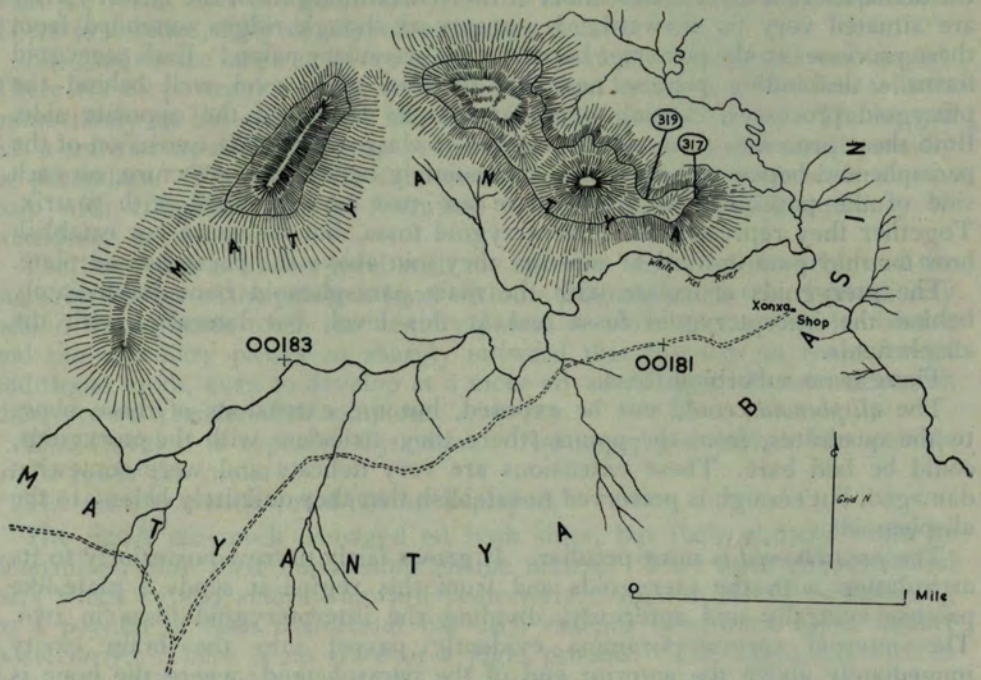


Fig. 32.—Trace of aerial photographs 00181 and 00183, Strip No. 9, Job 236, to show the exact locality where the new specimen of *Bauria cynops* was found.

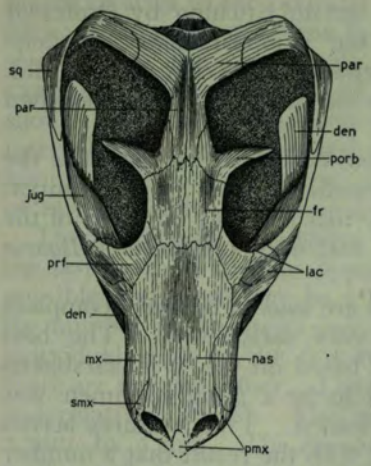


Fig. 33.—Dorsal view of the skull of *Bauria cynops* (½ natural size).

Abbreviations; ang, angular; art, articular; bo, basioccipital; den, dentary; eo, exoccipital; fr, frontal; ipf, inter pterygoid fossa; jug, jugular; lac, lachrymal; mx, maxilla; nas, nasal; pal, palatine; palmx, palatal plate of the maxilla; par, parietal; pmx, premaxilla; poc, paroccipital process; porb, post-orbital; pp, process of parasphenoid; prf, prefrontal; psph, parasphenoid; pt, pterygoid; q, quadrate; smx, septomaxilla; sof, suborbital fossa; sq, squamosum; st, stapes; tr, transverse bone; v, vomer.

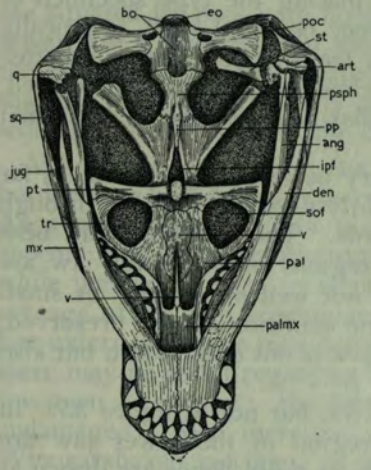


Fig. 34.—Ventral view of the skull of *Bauria cynops* (½ natural size). For abbreviations see fig. 33.

discovered by Kitching in *Cynognathus* zone beds in the Matyantya basin south-west of Lady Frere. The specimen also includes a portion of the skeleton; an isolated left dentary of another individual, with fairly well preserved teeth, was found about four feet away. These specimens come from a horizon consisting of coarse grained grey shale, about four feet in thickness. This horizon is exposed on the slopes of the Matyantya feature itself, in the middle of the basin, about half way up. The latter feature is 1,678 ft. high, measured from the level of the river south of it. All the strata above and below this horizon, excluding the sandstone horizons at regular intervals, consist of reddish brown shale and the fossils occurring in these layers are characterized by the typical dark red brown oxidation coating, which is not found over fossils of the grey horizon.

Figure 32 is a trace of the aerial photographs on which the exact locality of the specimen is registered (Air Force: job 235/6, Sept. 1949 16035-7; Trigonometrical Survey: Job 236, Strip 9, No. 00181-3).

The new specimen is slightly smaller than the type in the South African Museum and the second specimen in the American Museum of Natural History. The latter comes from Winnaarsbaken, where the grey horizon forms the topmost layer, with the reddish shales below it well exposed. The farm Vaalbank, where the type was found, derives its name from this grey horizon, which is the only layer exposed. The exact

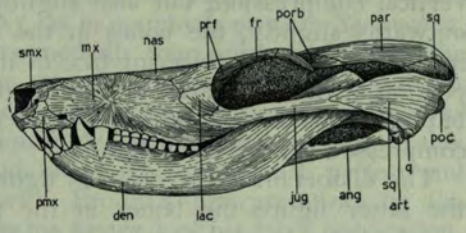


Fig. 35.—Side view of the skull of *Bauria cynops* (½ natural size). For abbreviations see fig. 33.

locality where the type was found was pointed out to Kitching by Professor Watson in 1948. We do not know whether the Winnaarsbaken specimen comes from the grey horizon, but we are prepared to accept that it did. Although the type was not in situ, there can be no doubt that this specimen is from the grey horizon.

The grey horizon is one of the lowest layers on Vaalbank, whereas it is the topmost layer on Winnaarsbaken and an intermediate layer in Matyantya. If there may have been doubt over the possibility that the grey horizons of the three different localities are identical, the fact that each produced a *Bauria cynops* now settles the question.

Although the two already described specimens are said to be fairly complete and well preserved, the descriptions are not very satisfactory. The best description was published by Boonstra in 1938, based on the Winnaarsbaken specimen, but he acknowledged that what used to be a good specimen was ruined by Broom in a very hurried attempt to clean it. Two fractures across the skull were ground down to produce sections, with the result that a number of points of evidence were destroyed. Even then the specimen was apparently not even half cleaned, and after Boonstra prepared it properly for a description, Broom intervened and published a hurried description which appeared before Boonstra's (1937).

Broom's description of the type (1909) is so unsatisfactory that we can hardly compare our new specimen with it. Our comparisons are largely based on Boonstra's descriptions of the Winnaarsbaken specimen. There are some points of difference, at first sight of enough importance to warrant the recognition of our specimen as a separate genus, but we consider these differences to be artificial, perhaps as a result of distortion or bad preservation, but more likely bad preparation, and in this respect we do not blame Boonstra for any misinterpretations.

We would like to thank Dr. Barnard, the Director of the South African Museum, and Dr. Boonstra very sincerely for placing the type specimen of *Bauria cynops* at our disposal. The type is a very beautiful skull, practically complete and not distorted at all. We certainly feel that it warrants a better description than Broom's of 1909, but the specimen is so poorly developed, largely with the aid of grinding instruments, that any attempt at additional development appears to be futile.

Our specimen is a very perfect one. It is very beautifully prepared, as far as the hard matrix would allow. It is only slightly distorted, largely through vertical compression, but also slightly rightwards. The mandibles are bent outwards slightly, the bones in the posterior regions of the lower jaw are imperfect, and the posterior face of the skull is not well preserved. A small portion of the internarial bridge is missing. The dentition is well preserved, but could not be cleaned properly, as the lower jaw is not only in situ but also compressed against the palate.

The distortion is corrected in figures 33 and 34, but not in figure 35. In the latter figure the bones in the posterior region of the lower jaw are reconstructed from the right side, while in figure 34 these bones are drawn as they appear on the specimen.

The new specimen is 117 mm. long, measured from the reconstructed

premaxillaries to the occipital condyle. The squamosals do not extend farther back; they reach the same level as the occipital condyle. The breadth of the skull across the squamosals is 76 mm., but this breadth may have been exaggerated a millimeter or two as a result of vertical compression. The snout is 27 mm. broad and does not expand anteriorly. The parietal and interorbital widths are 8 and 18 mm. respectively. The zygomatic arch has a minimum vertical thickness of 3 mm. and the dentary has a vertical thickness of 11 mm. in the middle of the row of post-canine teeth.

There are nine postcanine teeth on the left side in the lower jaw, but as the last tooth in the row opposes the penultimate tooth in the upper jaw, it is possible that there may be a tenth tooth in the lower jaw. We cannot count the number in the upper jaw, but taking the total distance (30 mm.) and the individual sizes of the few teeth that are exposed, we could establish that there are ten altogether. The teeth are short (vertically and antero-posteriorly) and relatively broad. The largest tooth in the isolated lower jaw measures 3 mm. by 5 mm. The crowns have flat tops, showing wear, but there is no evidence that cusps were present. The ten post-canine teeth in the isolated lower jaw measure 32 mm.

We disagree with Broom's interpretation of the molars in the type (1909) as well as with Boonstra's interpretation (1938) as figured in their side views. According to Broom's figure the molars are not flat crowned and they are well spaced. According to Boonstra the molars are flat crowned, but we disagree with his spacing. His interpretation of the size and spacing in his palatal view (figure 4) agrees perfectly with our interpretation. The molars are spaced to some extent at the level of their necks, but the crowns expand so that they come in contact with each other. If the crowns are considerably worn with old age, it is possible that the impression may be created that they are well spaced.

The canines are not very powerful; they are only slightly larger than the incisors, but the latter are indeed relatively very large. The upper jaw canines are situated far back with no diastemes between them and the molars. In the lower jaw it appears from the specimen as though there is a diasteme behind the canines, but in the isolated lower jaw this is not the case. The reason is that the lower jaw canine is inclined forward so that although the crowns are well spaced, the necks of the canine and first molar are close together.

Where the maxillary joins the premaxillary on the alveolar border, this border is so reduced that the canine is visible in side view for its whole length. As a result of the slight distortion rightwards, the left lower jaw canine appears to close externally to the maxillary, as in mammals or as in *Sesamodon*, while the right lower jaw canine lies more medially than normal. Taking the average of the two conditions, it is clear that the lower jaw canines did not bite externally to the maxillaries, but exactly on the alveolar border. Whereas there may be doubt regarding the condition in *Sesamodon*, the condition in this specimen is genuine; the maxillaries and lower jaw canines are perfect and undamaged. We therefore disagree with Broom's interpretation of the Winnaarsbaken specimen, as illustrated in his figure 1 of his 1937 publication, where he demonstrates two excavations in the palate medially to the alveolar border. Boonstra (1938) described the condition as though there is still a

thin maxillary edge laterally to the lower jaw canines, but he states that it is clear that this condition is developing into that found in *Sesamodon*. We are not prepared to doubt Boonstra's interpretation; there is actually no reason why both conditions cannot occur within the same species. If the canines of our specimen were placed slightly more laterally in life than in the Winnaarsbaken specimen, they could have worn the maxillary edges away.

There are four incisors in the upper jaw, and only three in the lower jaw, on each side. The number of incisors in the lower jaw is confirmed by the isolated dentary. We are not prepared to accept this as a difference between the new specimen and the two already described specimens; we consider that the latter two specimens were misinterpreted.

The most important difference between our specimen and the two already described lies in the region of the pterygoids. The pterygoids do not extend as far forward as both Broom and Boonstra illustrated, and the vomer extends much farther back. In our specimen the vomer extends to a level well behind the middle of the suborbital fossae and the sutures between the pterygoids and palatines, on each side of the vomer, extend even farther back. According to Boonstra, Broom destroyed this region in the Winnaarsbaken specimen.

Immediately behind the vomer the pterygoids form a bulge on the midline. The vomer extends into two small depressions on each side of the midline. These depressions pass practically underneath the median bulge, which towers 7 mm. above their level (considering the ventral aspect of the skull upside down). Immediately behind the bulge the interpterygoid fossa forms a narrow slit, tapering posteriorly. Anteriorly this fossa passes upward over the bulge. The interpterygoid fossa is exactly like Boonstra's interpretation (1938), but unlike Broom's interpretation (1937) of the same specimen.

The ventrally directed plate of the parasphenoid is broken off in our specimen.

According to both Broom and Boonstra (1937 and 1938), the pterygoid processes incline posteriorly much more than in our specimen. The difference can largely be due to distortion.

The pterygoid prolongations to the quadrates are also different. According to Broom and Boonstra they taper posteriorly. In our specimen they are not quite so delicate, and according to the condition on the left side they expand posteriorly. The lateral margins of these prolongations are stronger and more outstanding than the delicate dorso-medially projecting inner plates, and it is possible that these inner plates were destroyed, or perhaps not properly uncovered, in the Winnaarsbaken specimen. This plate was destroyed on the right side in our specimen.

We could not trace the posterior limits of these pterygoid prolongations, the posterior bones of the lower jaw being in the way.

In the new specimen the parietals penetrate the frontals and small posteriorly projecting processes of the frontals pass back on each side of the anterior ends of the parietals. The postorbitals flank the parietals laterally for a longer distance than illustrated by Boonstra. The laterally extending portions of the postorbitals, forming the posterior borders of the orbits, are at a level some 10 mm. behind the pterygoid processes; Boonstra illustrates them at the same level.

The nasals are well expanded behind, contrary to Broom's definition (1932) of the Bauriidae ("Bauriamorpha").

The lower jaw is 21 mm. broad in the region of the symphysis. The rami diverge suddenly behind the symphysis and progressively less posteriorly. The coronoid process of the dentary is well developed and passes through the temporal opening to the dorsal surface of the skull. The dentary measures 11 mm. across the coronoid process, the same as in the region of the molars, but it has a slight angle postero-ventrally.

The medial surface of the dentary, in the region of the molars, forms a prominent bulge. The maximum thickness of the dentary is 10 mm. in this region. This feature makes the lower jaw of *Bauria* quite unlike that of any Therocephalian or Cynodont. The ventral margin of the dentary folds medially over this bulge, leaving a very restricted crevice into which the splenial fits. Over this portion of its length the splenial is a thin plate-like bone, but anteriorly it could have had more vertical thickness, judging from its impression on the dentary.

All the thin plate-like portions of the angular have been destroyed, leaving only the solid axis. The nature of the rest of the lower jaw bones is somewhat confusing. The articular is recognisable as a bone extending down from the coronoid process and forming the condyle articulating with the quadrate. The lateral surface of this bone was evidently covered by a plate of the angular. What appears to be the retroarticular extends intimately along the inner face of the angular and at its posterior end, antero-medially of the articular condyle, it forms a structure extending medially. The stapes evidently slipped forward so that it appears now as if it extended from this structure to the fenestra ovalis.

The rest of the skull conforms perfectly with Boonstra's description (1938). We are inclined to consider Boonstra's interpretation of the interparietal as correct, and Broom's interpretation as incorrect.

The skeleton is rather good. The first vertebra preserved is well within the thoracic region. There are thirteen vertebrae of which the thirteenth is the first sacral with a transverse process extending 25 mm. from the midline. The vertebra in front has a rib 33 mm. long and a millimeter broader than the thoracic ribs. The next vertebra in front is missing. The two vertebrae farther forward have lost their ribs. The longest thoracic rib measures 96 mm. along the shaft. The capitula and tubercula of all the thoracic ribs form one articulation unit some 15 mm. in length.

All the vertebrae appear to be very similar. The centra are 15 mm. long and 12 mm. broad. Across the transverse processes the vertebrae measure 20 mm. in breadth. These transverse processes are at the level of the middle of the centra of all the vertebrae of the thoracic region, but in the lumbar region they are placed more forward. The distance between the lateral margins of the postzygapophyses is 6 mm. throughout. There was apparently no sudden change in characteristics between the lumbar and thoracic ribs.

The specimen further includes the left half of the pelvic girdle, so badly preserved that little can be deduced from it. The shafts of the femur, tibia and fibula are also included. The radius and ulna of one side are complete, but dislocated.

The Genus *Cyclogomphodon* Broom (figs. 36-38)

In 1913 Broom described a specimen in the Albany Museum as *Diademodon platyrhinus*, the specimen consisting of "most of the skull and lower jaws of a small species." He figured only the lower jaw and paid much attention to dental succession, but he gave no reason why he considered the specimen as belonging to a new species. He also analysed the dental formula in detail, but he did not emphasise its significance or the possible difference between this specimen and other specimens belonging to the genus *Diademodon*. The dental formula is given as i4, c1, pm4, m8 for both the upper and lower jaws. We disagree with the number of incisors in the lower jaw and although we do not doubt that there may actually have been eight molars in both upper and lower jaws, we would have liked to know how Broom arrived at this number. Nevertheless, the presence of only eight molars should make no difference, as the number increased even after full maturity.

In 1919 Broom referred the specimen to a new genus *Cyclogomphodon*, on the strength of the following differences between it and the genus *Diademodon* (*Gomphognathus*): (1) The molars are said to be much narrower than in "*Gomphognathus*." (2) The dental formula (i4, c1, pm4, m8 for the upper jaw) differs from that of "*Gomphognathus*" (i4, c1, pm5, m9 for the upper jaw). Three incisors in the lower jaws of both genera are acknowledged. (3) The posterior molars are more "molariform."

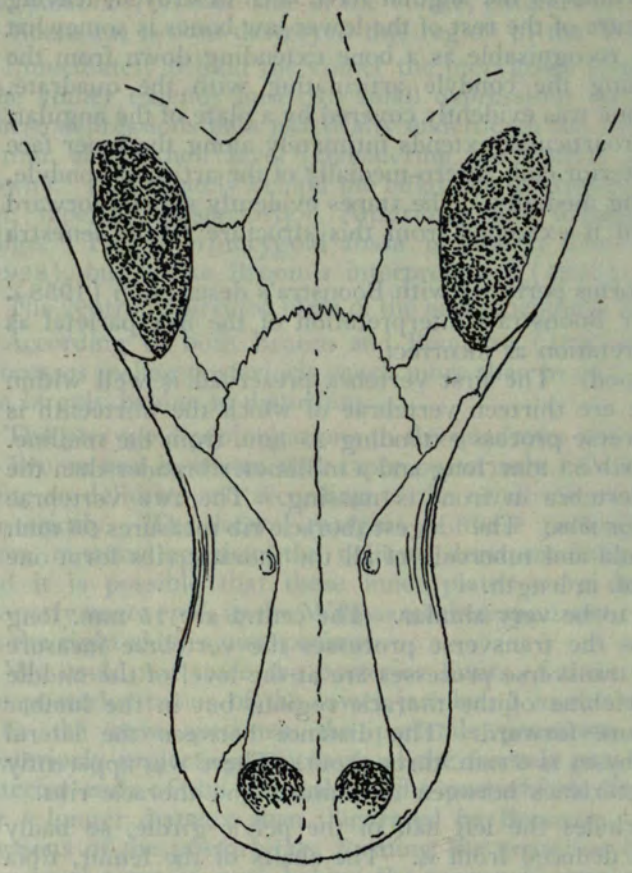


Fig. 36.—Dorsal view of the skull of *Cyclogomphodon platyrhinus* from Matyantya. Natural size.

Broom arrived at this dental formula for "*Gomphognathus*" by guessing that the first premolar on the left side in the type specimen of "*Gomphognathus*" *kannemeyeri* corresponds with the second on the right. The four premolars on the left side were then counted as the second, third, fourth and fifth. To make the right side cor-

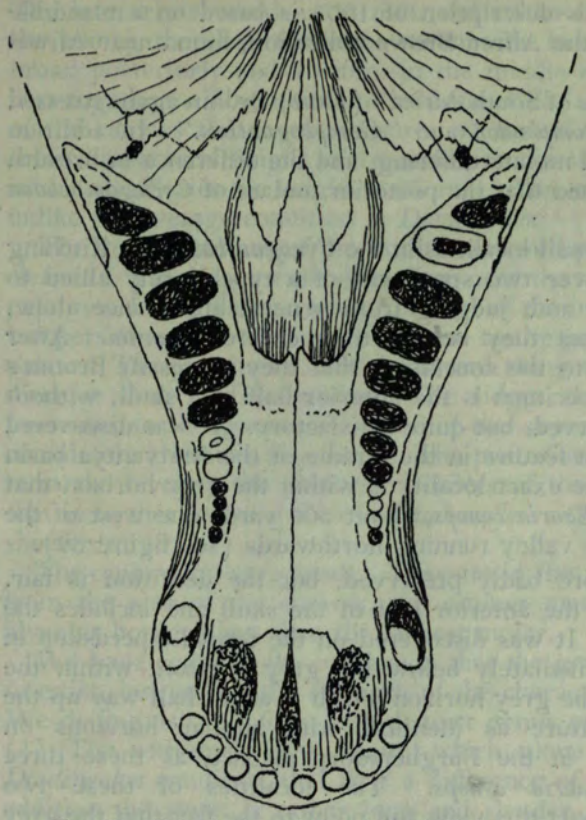


Fig. 37.—Palatal view of the skull of *Cyclogomphodon platyrhinus* from Matyantya. Natural size.

respond, he counted the first molar as the fifth premolar, leaving only eight molars, so he assumed the presence of a ninth molar on the right side. Many times we have been surprised by the remarkable correctness of Broom's assumptions but in this case we are inclined to doubt his interpretation, not of the particular specimen, but of the dental formula in general. If his illustration of the dentition of the type specimen of *"Gomphognathus" kannemeyeri* is absolutely correct, as far as the shapes and sizes of the individual teeth are concerned, it is quite feasible that the ultimate molar of the left side does not correspond with the last molar of the right side, and the first premolar of the right side is actually situated at a level farther forward than the first of the left side. Nevertheless, all the specimens of *Diademodon* which we have investigated show very clearly only 4 premolars, so that if the first tooth on the right side in *"G" kannemeyeri* is not a "milk" molar being replaced by the one behind, it may still be a freak.

In the same publication of 1919 Broom also transferred a specimen which he had described as *Diademodon mastacus* in 1905 to the new genus and species

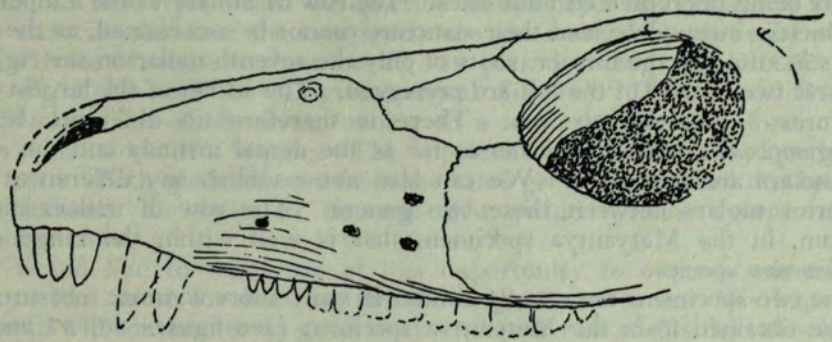


Fig. 38.—Side view of the skull of *Cyclogomphodon platyrhinus* from Matyantya. Natural size.

Cyclogomphodon platyrhinus. His description of 1905 is based on a mandible and some postcranial bones in the Alfred Brown collection, found near Aliwal North.

In his "Mammal-like Reptiles of South Africa" (1932) Broom again stressed the differences between *Cyclogomphodon* and "*Gomphognathus*." In addition to the number of premolars and molars differing, and the difference in breadth of the molars, Broom again stated that the posterior molars of *Cyclogomphodon* are more "molariform."

On his recent expedition to fossil localities in the *Cynognathus* zone, Kitching was fortunate enough to discover two specimens of a type closely allied to *Diademodon*, but much smaller and, judging from general appearance alone, we immediately established that they belong to a different genus. After careful consideration we came to the conclusion that they represent Broom's genus *Cyclogomphodon*. One specimen is the anterior half of a skull, without lower jaw, not very well preserved, but quite satisfactory. It was discovered on the slopes of the Matyantya feature in the middle of the Matyantya basin south west of Lady Frere. The exact locality is within the grey horizon that yielded our new specimen of *Bauria cynops*, about 300 yards due west of the latter's locality, and within the valley running northwards (see figure 32).

The second specimen is more badly preserved, but the dentition is fair. The specimen also consists of the anterior half of the skull and includes the anterior half of the mandible. It was discovered on the farm Luiperdskop in the Burghersdorp district, immediately below the grey horizon, within the reddish shales. We consider the grey horizon which is about half way up the slopes of the Matyantya feature as identical with similar horizons on Winnaarsbaken and Vaalbank in the Burghersdorp district, as these three localities each yielded a *Bauria cynops*. The localities of these two *Cyclogomphodon* specimens support this view and point to the fact that the grey horizon also extends over the farm Luiperdskop. The three farms Luiperdskop, Winnaarsbaken and Vaalbank are situated in a triangle with equilateral sides approximately 15 miles long, Luiperdskop pointing north, Winnaarsbaken south-west, and Vaalbank south-east.

The Matyantya specimen is numbered 319 in our collection, and the Luiperdskop specimen 320.

The dental formula of the Matyantya specimen is i4, c1, pm4, m9, the ninth molars being unerupted on both sides. The row of molars in the Luiperdskop specimen is incomplete, and their structure cannot be ascertained, as the lower jaw is in situ. In the former, roots of only the seventh molar on the right and the first two molars of the left are preserved. The socket of the largest molar measures 5 mm. by 10 mm. There is therefore no difference between *Cyclogomphodon* and *Diademodon* as far as the dental formula and the size of the molars are concerned. We can also not establish any difference in the posterior molars between these two genera. The row of molars measure 43 mm. in the Matyantya specimen, that is well within the range of the *Diademodon* species.

The two specimens are exactly similar in size; more accurate measurements can be obtained from the Matyantya specimen (see figures 36, 37 and 38). The snout is 65 mm. long, measured from the anterior border of the orbit.

The interorbital width is 33 mm. and at the same level, across the middle of the orbits, the skull measures 68 mm. in breadth. The nasals are 28 mm. broad posteriorly and 10 mm. in the middle of their lengths, measuring the two together. The minimum breadth of the snout is 30 mm.; in the region of the canines the snout measures 37 mm. At the level of the canines the snout has a total height of 16 mm.; at the level of the depressions dorsally in the maxillaries the height is 25 mm. The latter depressions are very small, unlike the average condition in *Diademodon*.

The ventral surface of the skull is not well preserved, but nevertheless well cleaned. The ridges extending from near the midline over the pterygoids and palatines do not flatten out on the roof of the internal nares, as in *Diademodon*, but persist around the lateral margins to the posterior border of the secondary palate. The palatines extend backward along these ridges for rather a longer distance than in *Diademodon*. The ridges that extend from the pterygoid processes to the posterior border of the secondary palate in *Diademodon* are completely absent in this form. The posterior border of the secondary palate is at the level of the posterior borders of the fourth molars from the front, that is farther forward than in *Diademodon*. On the whole the palate appears shorter.

The canines are very small. They are in the act of being replaced. Judging from the size of the sockets, the canines measure in cross section (on the alveolar border) less than the largest molar.

We have come to the conclusion that the genus *Cyclogomphodon* has a right to exist, but not on the strength of the characteristics pointed out by Broom. We distinguish this form as a distinct genus on the following characteristics: (1) The extremely low snout, which alone contrasts so to the general *Diademodon* condition that it is a difference of more than specific nature. In addition the snout is rather long and slender. (2) The size of the canines. (3) The short secondary palate. (4) The absence of ridges joining the pterygoid processes with the posterior border of the secondary palate.

Inusitatodon smithi gen. et sp. nov. (Fig. 40)

Mr. M. D. S. Smith, Principal of the Lady Frere school, recently donated two specimens to our Institute, a fragmentary skull of *Diademodon broomi* (*Gomphognathus broomi*, Broili and Schröder) and the anterior two-thirds of the skull of a new type, which we describe in this paper as *Inusitatodon smithi*.

The exact localities of the two specimens are marked on an aerial photograph, a trace of which is shown in fig. 39 (aerial photograph Job 236 Strip No. 6 Print No. 399 — Trigonometrical Survey). These localities are immediately north of the river running in a westerly direction north of the town, on the slope of a koppie. The koppie itself is immediately north-east of the town. Both specimens are from the same grey horizon, and this horizon is not unlikely the same as the one that yielded *Bauria cynops* in the Matyantya basin.

We would like to make use of this opportunity to express our sincere thanks to Mr. Smith for donating these two specimens to us. We hope that Mr. Smith will continue to do good work in the interest of this field of science.

The new genus and species is based on the anterior two-thirds of a small

skull of a gomphodont Cynodont, undoubtedly a member of the family Diademodontidae. . The skull has suffered considerable lateral compression, but otherwise it is beautifully preserved and prepared. Under the circumstances, the dentition is perfect. It is numbered 312 in our collection.

The dentary of the left side is complete; only the posterior edge of the bone is slightly damaged. On the right side this posterior edge is broken away for about half the antero-posterior breadth of the coronoid process. The two dentaries are pressed towards each other so that the palate could not be cleaned without damaging the perfectly preserved teeth.

The parietal crest is preserved for perhaps the greater part of its length, so that it includes the parietal foramen. The whole occipital region and both temporal arches are missing. The orbital region on the left side is as shown in the figure, but on the right side badly preserved fragments of bone and impressions on the matrix made it possible to reconstruct the postorbital arch and the jugal bar below the orbit.

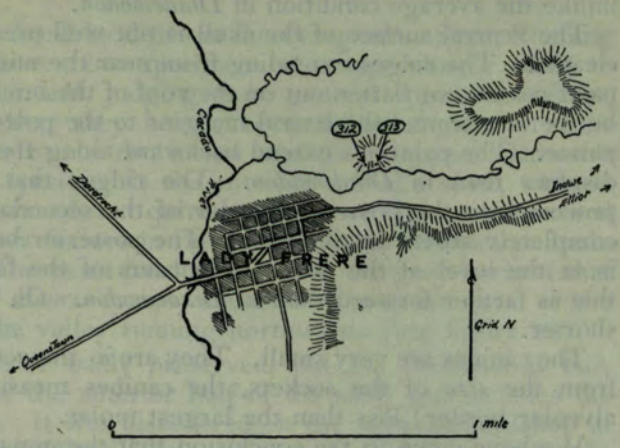


Fig. 39.—Trace of aerial photograph: Trigonometrical Survey, Job 236, Strip No. 6, Print No. 399, showing the exact localities of *Inusitatodon smithi* and *Diademodon broomi* (Nos. 312 and 313 respectively).

The region of the external nares is poorly preserved, largely on account of the lateral compression, and for the same reason very little can be deduced from the dorsal surface of the skull, least of all any transverse measurements.

A striking feature of the lower jaw is its powerful coronoid process and the distinct angular process. It is not clear from the specimen, but it appears as though the rest of the lower jaw bones extended back not far above the general line of the ventral margin of the dentary, so that the articular region could not have been much above this level. If this was the case the posterior region of the skull must have been comparatively high, as the height of the coronoid processes also suggests. It also appears as though the zygomatic arches extended upward initially immediately behind the orbits, so that their descent to the articular region farther back must have been quite conspicuous. The height of the arches cannot be ascertained and it is not clear whether the jugal developed a process as in all the other members of the family Diademodontidae.

The postorbital, frontal, prefrontal and lachrymal are much the same as in *Diademodon*. The maxilla differs only in one feature, the apparent absence of the peculiar depression dorsally.

There is a longitudinal ridge in the region of the frontals which became exaggerated through lateral compression into a prominent crest. Each frontal

occupied a depressed area. The portion of the parietal crest included in the specimen suggests that this region, including the characteristics of the parietal foramen, was similar to that of *Diademodon*.

The skull is that of a mature individual. There is no trace of tooth replacement. The sutures suggest full maturity. Although the anterior face of the symphysial region of the lower jaw has been ground, no trace of a suture could be displayed.

The snout measures 36 mm. from the premaxillaries to the anterior border of the orbit. The orbit has an antero-posterior diameter of 19 mm. The dentary is 12 mm. high in the region of the molars; it has a total height of 41 mm. over the coronoid process, and a total length of 72 mm. The distance from the premaxillaries to the parietal foramen measures 55 mm. The total length of the skull may have been perhaps not more than 90 mm.

Judging from the characteristics of the coronoid process, the temporal region of the skull must have been relatively short. The anterior margin of the coronoid process extends into the orbital cavity. In the higher Cynodonts the posterior end of the dentary usually reaches very close to the squamosal and since this new specimen is evidently a higher Cynodont, with a well developed posterior extension of the dentary, it may be deduced that the latter also reached very close to the squamosal. The squamosal and quadrate region of the skull could therefore not have extended much farther back than as suggested in fig. 40.

The dentition of this specimen is peculiar. There are three fairly small and slender incisors on each side in the upper jaw, and two on each side in the lower jaw. The three of the upper jaw cover a distance of 8 mm. and the two of the lower jaw a distance of 4 mm. There is a diasteme of 4 mm. on each side between the incisors and canines of the upper jaw, and no diasteme in the lower jaw. There is, however, a diasteme of at least 5 mm. on each side behind the canine in the lower jaw, while in the upper jaw this diasteme is only 2 mm.

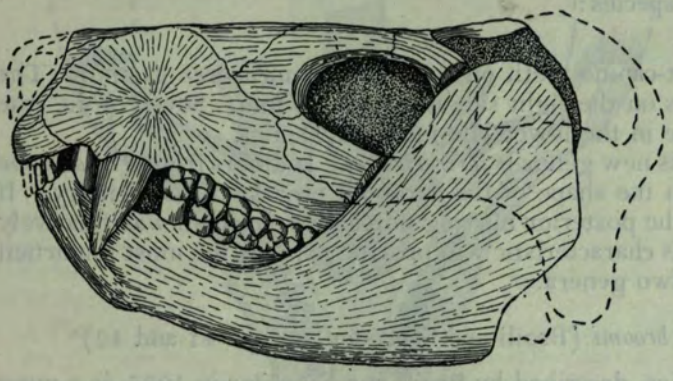


Fig. 40.—Side view of the skull of *Inusitatodon smithi* (natural size).

The canines are powerful. That of the upper jaw measures 8.5 mm. antero-posteriorly at the alveolar border and has a length of 13 mm.

The post-canine teeth are beautifully preserved, but unfortunately we cannot establish their full number, as they are covered posteriorly by the dentary. It is also impossible to establish the structure of the crowns and their breadths.

In the upper jaw the anterior two teeth are much smaller than those following and it is almost certain that they have simple conical crowns. They may be premolars. These two premolars are missing on the right side.

The next tooth has a flat crown and is apparently not very broad. This is apparently the first molar tooth. On the right side we count eight molars, but on the left only seven. The eighth molar on the right is so small that we assume it is the ultimate tooth. It is quite evident that the molars of the upper jaw, as well as of the lower jaw, have one major cusp in the middle of their outer margins.

The two upper jaw premolars are opposed by a large flat crowned tooth in the lower jaw, which is evidently the first true molar of the lower jaw. There may have been two premolars in the lower jaw, but they have been lost and we could not uncover their sockets. There are six molars exposed on the left side and seven on the right. The second has fallen out before fossilization. The seventh tooth opposes the sixth of the upper jaw, leaving the penultimate and ultimate teeth of the upper jaw unopposed. It is almost certain that there must be another tooth in the lower jaw opposing the posterior two of the upper jaw, bringing the total of the lower jaw also to eight. It is unlikely that there could have been a ninth molar in the lower jaw, judging from the size of the available space.

The lower jaw molars are larger than the upper jaw molars. Anteriorly they bite between the molars of the upper jaw, but posteriorly they gain on the upper jaw molars until they oppose them individually. This condition is illustrated on the right side; on the left side it appears as though the posterior molars also bite between the molars of the upper jaw.

We are quite confident in suggesting the following as the dental formula for this new genus and species:

$i\frac{3}{2}$, $c\frac{1}{1}$, $pm\frac{3}{2}$, $m\frac{8}{8}$.

The row of nine post-canine teeth on the left side measures 21 mm. The row of eight true molars on the right side measures 19 mm. Seven of the true molars on the right side in the lower jaw measure 21 mm.

The nearest ally of this new genus is *Trirachodon*. It differs from *Trirachodon* in dental formula and in the shape of the coronoid process of the dentary. If our interpretation that the posterior missing portion of our skull was relatively short is correct, then this characteristic will provide perhaps the most important difference between the two genera.

Diademodon broomi (Broili and Schröder) (Figs. 41 and 42)

The type of this species, described by Broili and Schröder in 1935, is a more complete skull than the specimen which Mr. Smith donated to us, but the latter shows some additional details.

In 1935 Broili and Schröder described specimens of two known species of *Diademodon* (*D. browni*, *D. mastacus*) and introduced three additional species (*D. grossarthi*, *D. broomi* and *D. haughtoni*). These species they described under the generic name *Gomphognathus*, but Brink pointed out in his thesis (unpublished) on the *Diademodon* material in the Watson Collection in the University College of the University of London that the generic name

Gomphognathus has no right to exist. The *Diademodon* material in the Watson Collection includes a specimen each of *D. grossarthi* and *D. haughtoni* and with the specimen described here as *D. broomi* we have now not only a second specimen of each of the three new species introduced by Broili and Schröder, but we also know that their species are genuine. As far as general proportions are concerned, including size, our specimen agrees perfectly with the type.

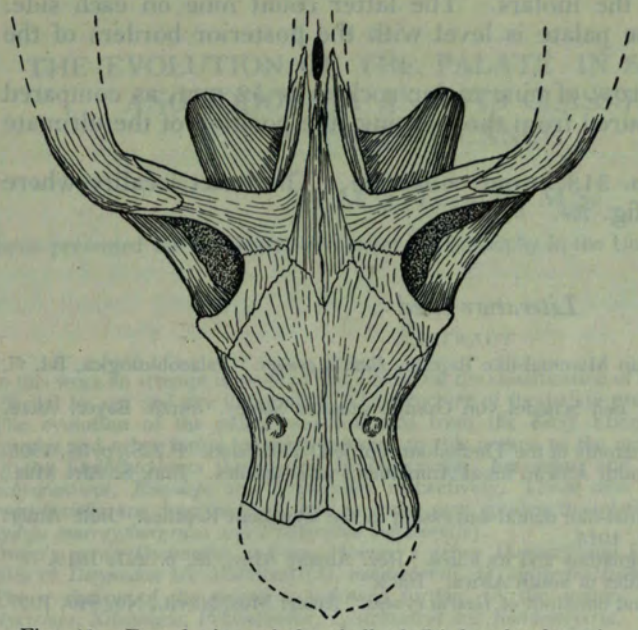


Fig. 41.—Dorsal view of the skull of *Diademodon broomi* (½ natural size).

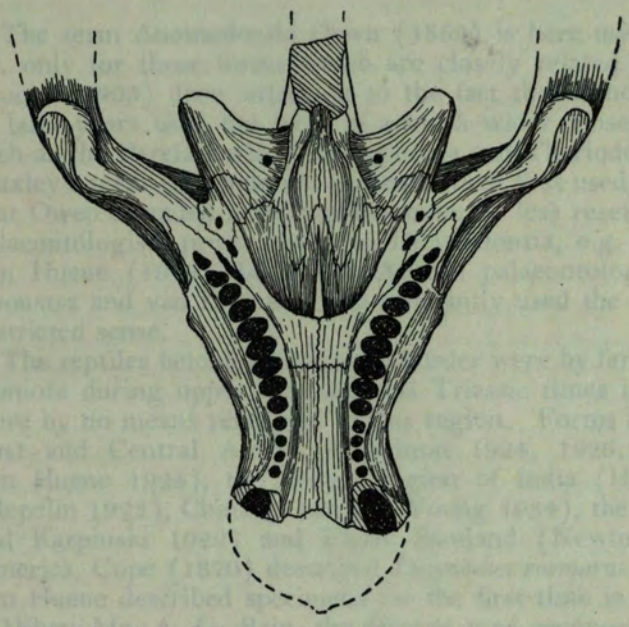


Fig. 42.—Ventral view of the skull of *Diademodon broomi* (½ natural size).

In figs. 41 and 42 we illustrate the sutures on the skull, which are easily traceable, in contrast with the type where, according to Broili and Schröder, few sutures are distinguishable. As in the type the postorbitals extend far back before the two ridges join to form the parietal crest. The parietal foramen is situated level with the posterior ends of the postorbitals.

The orbits face more anteriorly than laterally and very little upward.

The transverse bones extend medially over the ridges running from the pterygoid processes to the posterior margin of the secondary palate. The suborbital foramen lies between the transverse bone, palatine and jugal, but there is an additional foramen within the transverse bone.

There are sockets for four premolars on each side, much smaller and more round than the sockets of the molars. The latter count nine on each side. The posterior border of the palate is level with the posterior borders of the fifth molars from the front.

The total length of the row of nine molar sockets is 52 mm. as compared with 47.5 in the type, measured from the drawing, the position of the ultimate molars being estimated.

The new specimen is No. 313 in our collection. The exact locality where it was found is marked in fig. 39.

Literature cited

Boonstra, L. D., On a South African Mammal-like Reptile, *Bauria cynops*. Palaeobiologica, Bd. vi, 1938.

Broili, F. and Schröder, J., Ueber den Schädel von Gomphognathus Seeley. Sitzb. Bayer. Akad. Wiss., IX, 1935.

Broom, R., On some points in the anatomy of the Theriodont reptile Diademodon. P.Z.S., p. 95, 1905.

Broom, R., Notice of some new South African fossil Amphibians and Reptiles. Ann. S. Afr. Mus., vol. vii, pt. iii, p. 270, 1909.

Broom, R., On evidence of a mammal-like dental succession in the Cynodont Reptiles. Bull. Amer. Mus. Nat. Hist., xxxii, p. 467, 1913.

Broom, R., On the genus Gomphognathus and its allies. Rec. Albany Mus., iii, p. 227, 1919.

Broom, R., The Mammal-like Reptiles of South Africa. 1932.

Broom, R., On the palate, occiput and hind foot of *Bauria cynops*. Amer. Mus. Novit., No. 946, 1937.

THE EVOLUTION OF THE PALATE IN SOUTH AFRICAN ANOMODONTIA AND ITS CLASSIFICATORY SIGNIFICANCE

By M. J. Toerien, M.Sc.

(Thesis presented for the degree of Doctor of Philosophy in the University of the Witwatersrand)

Abstract

In this work an attempt is made to find a basis for the classification of the South African Anomodontia, unaffected by sex and age variations. The structure of the palate provided such a basis.

The evolution of the palate was followed from the early Endothiodonts, through the genus *Dicynodon* and other forms formerly referred to this genus, to the more advanced Anomodonts.

Of the Endothiodonts the genera *Brachyprosopus*, *Emydopsis* and *Diaelurodon* are transferred to *Brachyuraniscus*, *Emydops* and *Pristerodon* respectively. Three new genera, *Broilius*, *Hueneus* and *Parringtoniella* are described, as well as three new species to existing genera (*Emydops kitchingi*, *Emydops murraysburgensis* and *Pristerodon buffaloensis*).

Owen's genus *Oudenodon* and van Hoepen's genus *Daptocephalus* are reintroduced and three new species of *Dicynodon* are described (*D. vanderhorsti*, *D. antjiesfonteinensis* and *D. schroderi*).

The evolution of the palate is followed further to the genera *Cistecephalus*, *Aulacocephalodon*, *Platycyclops*, *Kitchingia*, *Pelanomodon*, *Lystrosaurus* and *Kannemeyeria*.

Introduction

The term Anomodontia Owen (1859) is here used in its restricted sense, i.e. only for those forms which are closely related to the genus *Dicynodon*. Broom (1905) drew attention to the fact that although Owen (and others) in later years used the term in a much wider sense, even to include groups such as the Pareiasauria, Procolophonia and Theriodontia, it has priority over Huxley's term Dicynodontia because, when first used, there can be little doubt that Owen intended it for reptiles more or less resembling *Dicynodon*. Some palaeontologists prefer the term Dicynodontia, e.g. Romer (1931, etc.) and von Huene (1948), but South African palaeontologists, Broom, Haughton, Boonstra and van Hoepen, have constantly used the term Anomodontia in its restricted sense.

The reptiles belonging to this suborder were by far the most numerous of all amniota during upper Permian and Triassic times in South Africa, but they were by no means restricted to this region. Forms have been described from East and Central Africa (Haughton 1924, 1926, 1932; Boonstra 1938; von Huene 1924), the Bengal region of India (Huxley 1885), Indo-china (Repelin 1923), China (Yuan and Young 1934), the Soviet Union (Amalitski and Karpinski 1922) and Elgin, Scotland (Newton 1893). From North America, Cope (1870) described *Dicynodon rosmarus* and from South America von Huene described specimens for the first time in 1927.

When Mr. A. G. Bain, the famous road engineer, geologist and amateur palaeontologist, discovered the first Anomodont reptile in South Africa, he

noticed the two very well developed canines and referred it to a new genus "Bidental." Specimens of the same type were sent to Sir Richard Owen at the British Museum of Natural History, London, who described a specimen as *Dicynodon lacerticeps* (1845) "referable to different species of an extinct genus of reptilia and indicative of a new tribe or suborder of Sauria." During the following years a few more specimens of *Dicynodon* were sent to Owen and described by him; when similar but tuskless specimens arrived at the British Museum of Natural History, Owen (1860) referred them to a new genus, *Oudenodon*.

Although Owen (1860) himself expressed doubt about the validity of the new genus and thought the difference between *Oudenodon* and *Dicynodon* might be due to sexual dimorphism, it was not until 1912 that Broom finally produced the proof. At Kuilspoort in the Beaufort West district he and Watson discovered a number of specimens, some tusked and others tuskless, but otherwise identical, which were eventually all ascribed to the same species, *Dicynodon bolorhinus* (Broom 1912).

In the meantime the number of amateur fossil collectors increased considerably and scores of Dicynodons and Oudenodons were collected by Cairncross, Joubert, Atherstone, Thomas Bain, etc. (see Boonstra 1935) and described by Owen and Seeley. With Broom's arrival in this country at the end of the previous century, the number of species referred to the genera *Dicynodon* and *Oudenodon* started to grow rapidly and over a hundred species ascribed to *"Dicynodon"* are now known to science.

As a result of the intensive collecting of fossils in the Karroo for the Bernard Price Institute by the Kitching brothers, it became increasingly obvious that species identifications of Dicynodons based mainly on variations in the structure of the dorsal aspects of the skull had outlived their usefulness. Nearly every new individual collected could, by the application of generally accepted criteria, be described as a new species.

When I joined the staff of the Bernard Price Institute at the beginning of 1950, therefore, I was given the task of investigating almost 2,000 *"Dicynodon"* specimens in the Institute's collection, with the object of reorganising the genus, a process which Broom (1932) had already recognised to be necessary. This reorganisation was tackled in two different ways:

(1) By studying individual variations in species of *Dicynodon* and especially the effects of sex and age on the structure and relative proportions of the skull parts; then, having eliminated these variations, establishing what might be regarded as genuine evolutionary series, the members of which could reasonably be referred to the same "species."

(2) By examining the morphology of all the available species of *"Dicynodon"* in greater detail, with the objective of finding, in some part or other of the skull, consistent differences which could serve as criteria for splitting the genus into a number of genera or subgenera.

With respect to the first of these two methods, the only previous steps in the direction of determining the effects of sex and age (i.e. absence or presence of tusks) on the proportions of the skull were occasional references to the fact that the absence of teeth is related to the weakness of the snout (e.g. van Hoepen 1934 and Boonstra 1948). The full implication of this

simple observation, however, has been frequently overlooked and usually new species, when tuskless, were described without any recognition of the fact that tusklessness would necessarily imply having a relatively short snout. The technique of establishing a natural evolutionary series to constitute a "species" has been employed by palaeontologists working in other fields, e.g. Mollusca and other Invertebrates, where many specimens have been available, but it has never been applied hitherto to Karroo reptiles, through the lack of sufficient prepared material.

As to the second of these two methods, van Hoepen (1934) attempted to split this cumbersome genus by reintroducing Owen's genus *Oudenodon*; he also created a large number of other genera and subgenera and divided them amongst four families. Unfortunately van Hoepen had to depend mostly on other workers' descriptions and his whole system was necessarily based mainly on relative skull proportions. His classification was criticized by Broom (1935a and 1936b) chiefly because it was diametrically opposed to his own idea about the synonymy of *Dicynodon* and *Oudenodon*. Broom suggested, however, that the following adaptation of van Hoepen's system should be used (1935a and 1936b):

(1) Genus *Dicynodon* Owen; tusked in the males only.
(2) Genus *Daptocephalus* van Hoepen; tusked in both sexes.
(3) Genus *Mastocephalus* van Hoepen; tuskless in both sexes.

The impracticability of a system depending upon the presence or absence of tusks should be obvious and is illustrated by the fact that since 1936 only one specimen, described by Broili and Schröder (1936), has been referred to an *Oudenodon* species (of which *Mastocephalus* is a subgenus, van Hoepen 1934), *Oudenodon marlothi*. A number of new species, clearly related to Broom's typical species of *Mastocephalus*, *M. platyceps*, were described as *"Dicynodon"* by Broom himself. Watson (1948) ultimately stated that "until a far larger number of skulls are fully prepared and adequately figured, such subdivisions cannot be usefully carried further."

Dicynodont species described by Seeley (1890), Lydekker (1889), and Sollas and Sollas (1914) differ from *Oudenodon kolbei* (Broom 1912), *Oudenodon margaritae* (van Hoepen 1934), *Oudenodon marlothi* (Broili and Schröder 1936), *"Dicynodon grossarthi"* (Broili and Schröder 1935) and *"Dicynodon sollasi"* (von Huene 1922), in having a very small palatine bone which does not reach the premaxillary anteriorly.

At an early stage in this investigation I was fortunate in having one series of prepared specimens (ultimately named after the late Professor C. J. van der Horst) which showed that the small palatine bone is a constant feature in a particular species and that this fundamental morphological feature can therefore be used to separate *"Dicynodon"* into at least two groups.

It seems in retrospect now quite remarkable that differences in palatal structure of fully described specimens of *"Dicynodon"* and *"Oudenodon"* were not followed up by previous workers to see whether they were or were not consistent and so possibly capable of serving as a basis for subdividing the group. The omission to investigate whether palatal structure was consistent in these forms is even more remarkable when a relatively unimportant morphological feature, such as the preparietal completely surrounding the

pineal foramen, had been employed by Broom to create a new genus to accommodate a species showing this anomaly (*Diictodon galeops*).

In his recent paper on *Dicynodon* and its allies, Watson (1948) advanced the theory that *Dicynodon* is a form which has arisen more than once at different times and that the small Endothiodonts, characterized only by cheek teeth in the maxillaries and dentaries, form a heterogenous mass, some of which were actually *"Dicynodon"* ancestors, but others have probably not gone further.

As a fair number of small Endothiodonts are present in the collection of the Bernard Price Institute, they were studied (especially those from the *Tapinocephalus* zone) as potential ancestors of the Dicynodons. The classificatory system previously used in this group had been mainly based on the structure and number of teeth, but as the dentitions in the Endothiodonts are very seldom complete and as, for example, Boonstra (1948) has shown the number of teeth within a species can vary considerably, the system is not satisfactory. It was therefore necessary to revise the taxonomy of the group with the aid of the new specimens and to organise it as far as was possible with the material available. As in the case of *"Dicynodon,"* the structure of the small Endothiodonts was studied in detail, with special reference to the palate, since the change from small Endothiodonts to a *"Dicynodon"* takes place essentially in the palate, i.e. the loss of cheek teeth and the related more extensive development of the horny beak.

Similarly I have examined the palates of a representative group of late Anomodonts: *Lystrosaurus*, *Kannemeyeria*, *Platycylcops*, *Pelanomodon*, *Kitchingia* and *Aulacocephalodon*. These forms are usually regarded as closely related to and descended from *Dicynodon*, but since *"Dicynodon"* is not a natural genus, the relationship of these genera had also become problematical.

The material in the body of this paper is not presented in the sequence indicated in this introduction. The Endothiodonts, as providing ancestors of the Dicynodons are described first; then the Dicynodons, and finally their descendants. The Dicynodons of the higher zones are discussed before those of the *Tapinocephalus* zone, because all the "new" genera to be introduced are based or species that occur in the higher zones. The species from the lower zone, therefore, could not be described conveniently before the taxonomic position had been straightened out.

A classification of the Anomodonts based on palatal structure has the obvious disadvantage that in many cases the lower jaw must first be removed in part or as a whole. This disadvantage will be more than counter-balanced by the fact that in future type specimens of new Anomodont reptiles, before they are named, will need to be more thoroughly developed and their anatomical structure better understood than that of most species described so far.

It is to be hoped that palaeontologists working in Institutions where type specimens of Anomodonts are housed will restudy them on the lines of investigation indicated here, so that all named types may eventually be referred to their correct, appropriate taxonomic niches on this basis.

ACKNOWLEDGEMENTS

I wish to extend my sincere thanks to the following persons who either supplied me with information or arranged the loan of material: Dr. J. Hewitt of the Albany Museum, Grahamstown; Mr. J. S. Pringle of the Port Elizabeth Museum and Snake Park; Dr. L. D. Boonstra of the South African Museum, Cape Town; Miss P. L. Robinson of University College, London; Dr. G. G. Simpson of the American Museum of Natural History and Dr. A. S. Brink of the Bernard Price Institute. Particularly I wish to thank Mr. J. T. Robinson of the Transvaal Museum (my indebtedness also goes to the late Dr. Robert Broom) and Dr. S. H. S. Rubidge, owner of the famous Rubidge Collection of fossil Mammal-like Reptiles, not only for the loan of material, but for placing the whole of their collections at my disposal.

Mr. P. J. Rossouw of the Geological Survey, Pretoria, supplied much valuable information on the stratigraphy of the Koup area and lent me the manuscript of a part of a geological report covering this area. Dr. S. H. Haughton, former Director of the Geological Survey of South Africa and now Honorary Director of the Bernard Price Institute, placed his entire, most valuable collection of literature at my disposal.

I am further indebted to Prof. R. A. Dart of the Anatomy Department of the University of the Witwatersrand for allowing me, while a member of his staff, to spend the time at the Bernard Price Institute for Palaeontological Research necessary to complete this work, and for the keen interest he has taken in its progress.

My most sincere thanks go to Mr. J. W. Kitching of the Bernard Price Institute, under whose supervision the material was prepared. With superb skill he succeeded in removing the lower jaws of the tiniest specimens without injuring them, to display the palatal structure. It would have been virtually impossible for me to have accomplished this work without his invaluable help.

I. SPECIFIC VARIATIONS IN DICYNODON AND THE SPECIES CONCEPT IN THIS GENUS

Through the courtesy of the late Dr. Robert Broom and Mr. J. T. Robinson, a large number of specimens of one series were borrowed from the Transvaal Museum. These skulls are from the same locality and all were referred to *Dicynodon grimbeeki* (Broom 1935a). In the collection of the Bernard Price Institute there is a large number of skulls from near Biesiespoort station, between Victoria West and Beaufort West, certainly belonging to Broom's (1921) species of *D. sollasi*. This series was augmented, again with the help of Dr. Broom, by two specimens of the same species from his own collection, and two from the collection of the Transvaal Museum.

Two aspects of the skull were studied; the bones in the region of the pineal foramen and the actual and proportional measurements of the skulls.

(1) THE BONES IN THE REGION OF THE PINEAL FORAMEN

One of the most conspicuous characteristics of the skull of *D. grimbeeki*

is the fact that the preparietal does not always form part of the margin of the pineal foramen (fig. 43). This is a rare feature in Dicynodons, but is not uncommon in some of the small Endothiodonts. That this type of preparietal does not hold true for all specimens of *D. grimbeeki* was observed by Broom (1935a), but he suggested that a bridge of the parietals in front of the foramen was possibly washed away. As illustrated by the line drawings (figs. 43 and 44) the preparietal does not form part of the margin of the pineal foramen in four specimens only, including the type. In some of the other specimens where the preparietal does extend to the foramen, the "bridge" was probably washed away or damaged during preparation, but in others (No. 373 Transv. Mus.

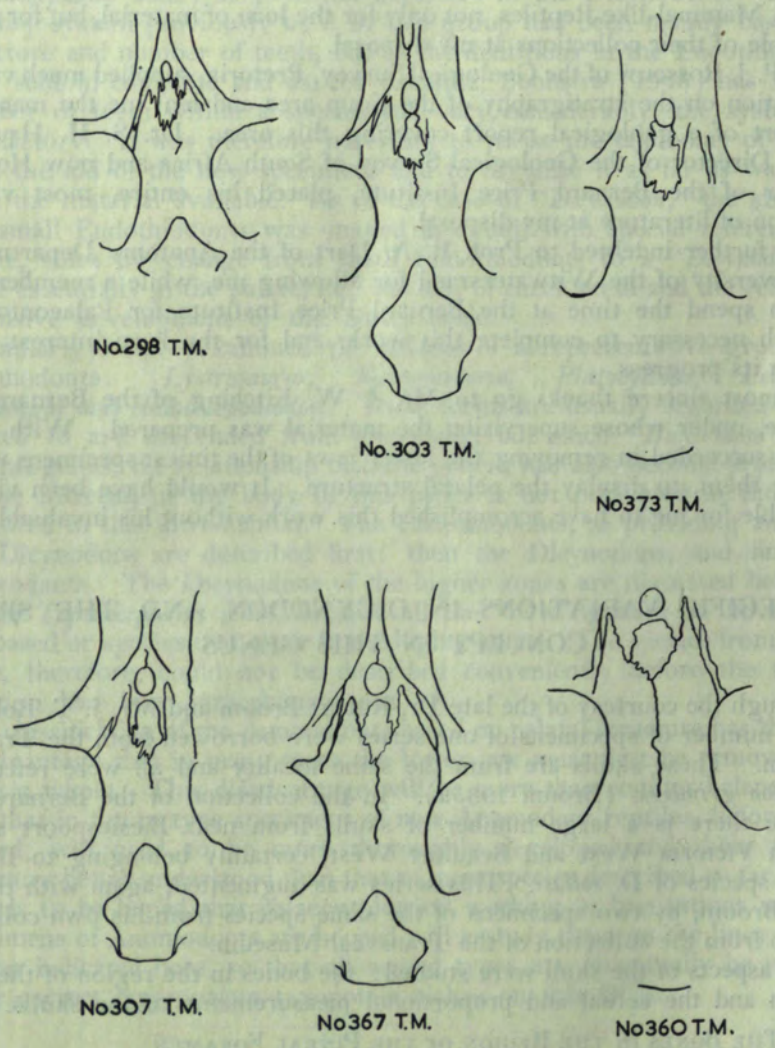


Fig. 43.—*Dicynodon grimbeeki* Broom. Parietal region of the skull showing sutural variations. T.M.: Specimens belonging to the Transvaal Museum.

and No. 298 Transv. Mus.) the surface of the bone is smooth and genuine. All the variations in the sutural patterns are linked by intermediate conditions (figs. 43 and 44) and cannot be attributed to sex or age.

The same phenomenon is encountered in the case of *D. sollasi*. Here too the shapes of the parietals, prepariet al and postfrontals differ greatly, but the patterns are also linked by intermediate conditions (fig. 45). A more important

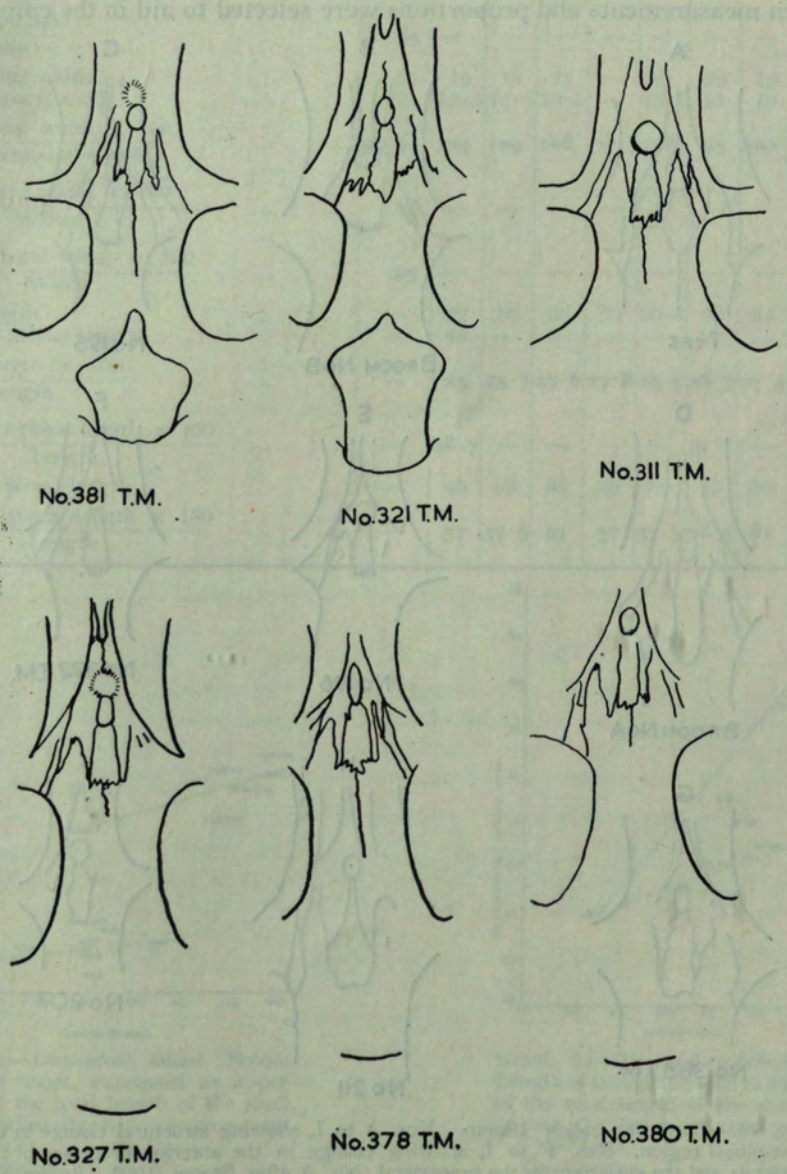


Fig. 44.—*Dicynodon grimbeeki* Broom. Parietal region of the skull showing sutural variations. T.M.: Specimens belonging to the Transvaal Museum.

feature, however, is encountered here in the form of actual structural variation. In some specimens the post-pineal region is grooved, in some the postorbitals approach each other, and in others they actually meet to form a crest (fig. 45).

If only two specimens representing the extremes were known, they would certainly have been regarded as separate species.

(2) The Actual and Proportional Measurements of the Skull

Fifteen measurements and proportions were selected to aid in the comparison

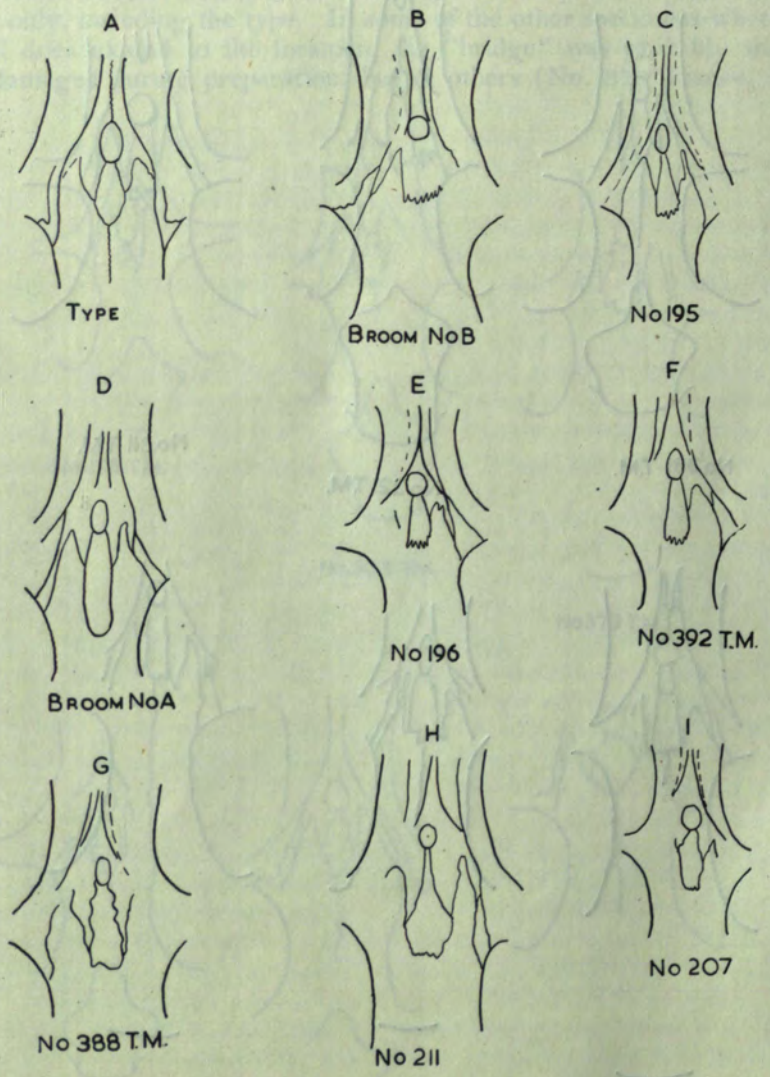
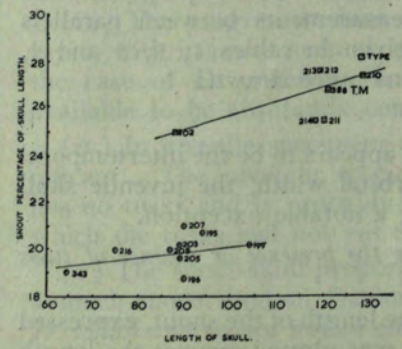


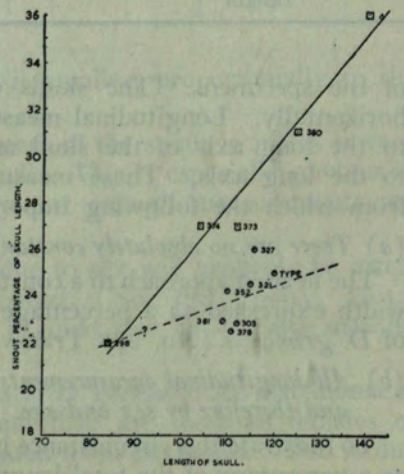
Fig. 45.—*Dicynodon sollasi* Broom. Nos. A to I, showing structural change in the post-pineal region. Nos. F to I, showing change in the anterior processes of the parietals and the variations in the preparietal. No. A after Broom, 1921. Broom No. A and No. B, specimens that belonged to the late Dr. Broom. T.M.: Specimens belonging to the Transvaal Museum.

TABLE 1.—DICYNODON SOLLASI — MALES

Skull Nos.	Type	202	214	212	213	211	388 (TM)	210	Broom A.	Broom B.
Skull length	128	88	118	119	119	120	120	126	—	—
Basal length	—	—	—	—	—	—	—	—	—	—
Skull width	88	—	—	—	—	—	—	—	—	—
Width × 100 / Length	**69**	—	—	—	—	—	—	—	—	—
Interorbital width	21	14	18	21	—	21	20	19	18	21
Intertemporal width	22	13·5	16·5	19·5	—	19·5	21	19	18	22
Interorbital width × 100 / Intertemporal width	**95·5**	**104**	**109**	**108**	—	**108**	**95**	**100**	**100**	**95**
Interorbital width × 100 / Width	**24**	—	—	—	—	—	—	—	—	—
Intertemporal width × 100 / Width	**25**	—	—	—	—	—	—	—	—	—
Snout length	—	22	30	33	33	30·5	32	35	—	—
Snout + orbital length	—	43	—	—	—	—	62	—	—	—
Snout length × 100 / Length	—	**25**	**25·7**	**27·6**	**27·6**	**25·5**	**26·7**	**27·4**	—	—
Snout + orbital length × 100 / Length	—	**48·7**	—	—	—	—	**51·5**	—	—	—
Snout — pineal length	—	49	68	68	68	69	70	76	—	—
Snout — pineal length × 100 / Length	—	**57**	**57·5**	**57**	**57**	**57·5**	**58·5**	**61**	—	—



Graph 1.—*Dicynodon sollasi* Broom. Length of snout, expressed as a percentage of the total length of the skull, plotted against the latter measurement.
□—Males.
O—Females.
Measurements of the type taken from drawings by Broom 1921 and 1932.
T.M.: Transvaal Museum.



Graph 2.—*Dicynodon grimbeeki* Broom. Length of snout expressed as a percentage of the total length of the skull, plotted against the latter measurement.
□—Males.
O—Females.
a—Specimen mentioned by Broom, 1935, not personally investigated.

TABLE 2.—DICYNODON SOLLASI — FEMALES

Skull Nos.	199	195	196	207	203	205	208	216	204	197	343
Skull length	104	94	90	90	89	89	87	75	—	—	64
Basal length	91	83	84	77	82	82	—	66	—	—	60
Skull width	—	—	70	—	—	—	—	—	—	—	46
Width × 100 / Length	—	—	**77**	—	—	—	—	—	—	—	**72**
Interorbital width	17·5	13	14	13	17	13	10	14	13	—	13
Intertemporal width	17	—	13	12	15·5	13	11	—	—	—	12
Interorbital width × 100 / Intertemporal width	**103**	—	**108**	**108**	**110**	**100**	**96**	—	—	—	**108**
Interorbital width × 100 / Width	—	—	**20**	—	—	—	—	—	—	—	**28**
Intertemporal width × 100 / Width	—	—	**18**	—	—	—	—	—	—	—	**26**
Snout length	21	19·5	17	19	18	17·5	18	15	18	19	12
Snout ± orbital length	±47	42	±35	45	41	41	—	30	—	—	32
Snout length × 100 / Length	**20·2**	**20·8**	**16·2**	**21**	**20·2**	**19·4**	**20**	**20**	—	—	**19**
Snout + orbital length × 100 / Length	±45	44·7	38·5	50·1	**46**	**46**	—	40·5	—	—	**50**
Snout — pineal length	56	50	44	51	49	47	49	47	47	48	—
Snout — pineal length × 100 / Length	**45**	**55**	**49**	56·5	**55**	**53**	**56**	**55**	—	—	—

of the specimens. The skulls were all oriented with their dorsal surface horizontally. Longitudinal measurements were taken between perpendiculars to the long axis of the skull and breadth measurements between parallels to the long axis. These measurements are given in tables 1, 2, 3 and 4, from which the following important conclusions were drawn:

(*a*) *There are no absolutely constant proportions*

The nearest approach to a constant proportion appears to be the intertemporal width expressed as a percentage of the interorbital width, the juvenile skull of *D. grimbeeki* (No. 298 Transv. Mus.) being a notable exception.

(*b*) *All longitudinal measurements are affected by the presence or absence of tusks and therefore by sex and age.*

To illustrate this circumstance more clearly, the length of the snout, expressed as a percentage of the total length of the skull, was plotted against the length of the skull for each specimen, on two graphs (Graphs 1 and 2). The following points became evident:

(i) In females the length of the snout remains almost constant, proportionally to the total length of the skull. A very slight progressive increase is observed with increase in size. This is not so clearly illustrated in the case of *D. grimbeeki*, but the reason for this is explained below.

TABLE 3.—DICYNODON GRIMBEEKI — MALES

Skull Nos. ...	298	37	373	380	311	350	360
Skull length	84	104	112	125	—	—	—
Basal length	—	—	—	—	—	—	—
Skull width	±60	—	—	—	—	—	—
Width × 100 / Length	**71**	—	—	—	—	—	—
Interorbital width	14	—	20	15	20	20	22
Intertemporal width	11	—	—	—	19·5	19	24
Interorbital width × 100 / Intertemporal width	**128**	—	—	—	**102·3**	**105·6**	**92**
Interorbital width × 100 / Width	**23·3**	—	—	—	—	—	—
Intertemporal width × 100 / Width	**18·3**	—	—	—	—	—	—
Snout length	18·5	28	30	39	—	31	55
Snout + orbital length	41	±40	55	72	—	67	73
Snout length × 100 / Length	**22**	**27**	**27**	**31**	—	—	—
Snout — orbital length × 100 / Length	**48·7**	?**38·6**	**49**	**52·5**	—	—	—
Snout — pineal length	49	57	69	85	—	71	90
Snout — pineal length × 100 / Length	**58**	**55**	**62**	**68**	—	—	—

(ii) The length of the snout of females is smaller, proportionally to the total length of the skull, than in males.

(iii) The progressive increase in massiveness of the snout in males is very rapid, with increase in total length of the skull. This is especially obvious in the case of *D. grimbeeki*, but unfortunately not enough measurements are available to be absolutely conclusive.

(iv) In juvenile specimens the difference due to sex will probably be insignificant. The juvenile specimen of *D. grimbeeki* (No. 298 Transv. Mus.) has no tusks and is probably a female, but it could also be a young male in which the tusks had not yet erupted.

(v) The snout-skull proportions of females of *D. grimbeeki* are distributed in a much more random fashion on the graph than are those of females of *D. sollasi* and so are not as clearly differentiated from the males. This is due to the fact that, as shown above, the massiveness of the snout is directly affected by the presence and size of tusks; as is also the case in, for example, the gorilla. Broom (1935a) showed that in some of the females of *D. grimbeeki* there occur vestigial tusks, in some on both sides of the jaw, in others only on one side.

It is clear that in this species the tusks are in the process of degeneration, but they still affect the size of the snout. The snouts of some adult females

TABLE 4.—DICYNODON GRIMBEEKI — FEMALES

Skull Nos.	307	381	303	352	378	321	327	367	348	Type 245
Skull length	?108	109	112	110	111	115	115	—	—	120
Basal length	?103	—	99	—	—	—	—	—	—	—
Skull width	82	70	80	70	—	—	80	—	—	100
Width × 100 / Length	**76**	**64**	**71·5**	**64**	—	—	**69·5**	—	—	**83**
Interorbital width	18	17	18	—	17	15	19	21	18	22
intertemporal width	19	17	20	—	17	16	21	22	20	22
Interorbital width × 100 / Intertemporal width	**95**	**100**	**90**	—	**100**	**94**	**90·7**	**95**	**90**	**100**
Interorbital width × 100 / Width	**22**	**24·3**	**22·5**	—	—	—	**23·7**	—	—	**22**
Intertemporal width × 100 / Width	**23·2**	**24·3**	**25**	—	—	—	**26·2**	—	—	**22**
Snout length	?22	25	25·5	26·5	23	23	28	—	—	30
Snout + orbital length	?42	47	50	—	55	59	58	—	—	—
Snout length × 100 / Length	**?20·4**	**22·8**	**22·7**	**24·2**	**22·5**	**24·5**	**26**	—	—	**25**
Snout — orbital length × 100 / Length	**?39**	**43**	**45·5**	—	**49·5**	**51**	**50·5**	—	—	—
Snout — pineal length	?55	58	62	—	66	65	70	—	—	—
Snout — pineal length × 100 / Length	**?51**	**53·2**	**55**	—	**59**	**56·5**	**61**	—	—	**56**

are, therefore, only slightly smaller than those of young males. The extreme variability of a vestigial organ, or, in this case, its effect on the snout, is demonstrated in the distribution of the points assumed on the graph by the females.

When the lengths measured from the snout to the level of the postorbital bars or to the parietal foramen are plotted similarly against the total length of the skull, similar but less instructive graphs can be drawn.

A factor which was not taken into particular consideration in this comparison is the relative geological age of the specimens. In the case of *D. sollasi* it is known that the specimens are not all from exactly the same horizon; specimens may have been separated stratigraphically several feet vertically. This divergence in geological age will certainly influence the structure, but unfortunately this was not realised when the specimens were collected.

From the above account it will be observed that in these two groups of specimens (*D. grimbeeki* and *D. sollasi*) there are two types of variations, one in relative cranial proportions, largely due to sex and age, and the other in cranial structure and not due to sex or age. Therefore when new specimens are to be described, the relative cranial proportions should be cautiously assessed if they are used as distinguishing characters. The same caution should

be applied to the sutural variations on the dorsal aspect of the skull. By including in one species (*D. sollasi*) some specimens with a grooved post-pineal region and others in which it is crested, the species concept is stretched considerably.

It is desirable to follow some practical and workable "definition" of a species to embrace these near forms, as it is undesirable to refer each variation to a separate species. The following rule, based on Romer and Smith's (1934) "working rule," and used later by Romer and Price (1940) in their review of the Pelycosauria, can therefore be used. (The words in italics are added to Romer and Smith's rule):

"If, from a given horizon, and region, one species of a genus has been described, no further species of that genus should be named unless the specimens found exhibit one or more characters which might reasonably be expected to distinguish them from the first, *but if they can be linked to the first by a series of intermediate stages, they should still be regarded as belonging to the original species*; and that if, in the absence of presumably valid differences, further species are named, they should be regarded as synonyms of the first described from the horizon and locality."

For the elucidation of relationships between species it is necessary to figure and describe (not necessarily name the specimens) all the known variations of a particular species, as the type, chosen by chance, may represent the end of a sterile branch.

II. THE ENDOTHIODONTS OF THE TAPINOCEPHALUS ZONE

The small Endothiodont specimens collected in strata which belong without any doubt to the *Tapinocephalus* zone are the following: *Brachyuraniscus reuningi* Broili and Schröder, 1935; *Brachyuraniscus broomi* (Olson) 1937; *Robertia broomiana* Boonstra, 1948; *Koupia koupensis* Boonstra, 1948.

Pristerodon mackayi Huxley (1868) and *Pristerodon raniceps* (Owen) (1876) were probably the first forms described from this zone, but as their exact localities are not known, they will be discussed in the following chapter together with other members of the genus which definitely come from higher zones. Another form, *Synostocephalus vanhoepeni* Broili and Schröder (1935b) is probably also from the *Tapinocephalus* zone, but since there is some doubt (see below) and as it is certainly from a horizon very near the top of this zone, or the bottom of the following, it will not be considered at present.

Two additional species, collected in the *Tapinocephalus* zone recently, are described.

Brachyuraniscus merwevillensis sp. nov.

Type: Almost complete skull with lower jaw, No. 218, B.P.I.*) = BP/1/346
Locality: The farm Buffelsvlei, near Merweville, about 75 miles south-west of Beaufort West.
Horizon: Lower part of *Tapinocephalus* zone.
Collector: (C. J. van der Horst Expedition, July 1945).

*) Bernard Price Institute for Palaeontological Research.

This small, beautifully preserved skull (see fig. 46A) is at first sight not unlike *Dicynodon megalorbinus*. It is distinguished as follows:

Dorsal aspect. The interorbital width is considerably less than the intertemporal, with the latter region slightly concave laterally. The pineal foramen is large and not surrounded by a boss. A well developed boss is present on each nostril.

The structure of the dorsal side of the skull can be seen in fig. 46A. The actual and proportional measurements are given in table 5.

The palatal aspect. The lower jaw was carefully removed to expose the palate. Two very small canines are present. They may be erupting teeth, in which case the animal is not fully mature, but the tusks fill the sockets completely. There appear to be six molars on each side. They are all situated in an irregular row on a ridge on the pars palatina of the maxillary that runs

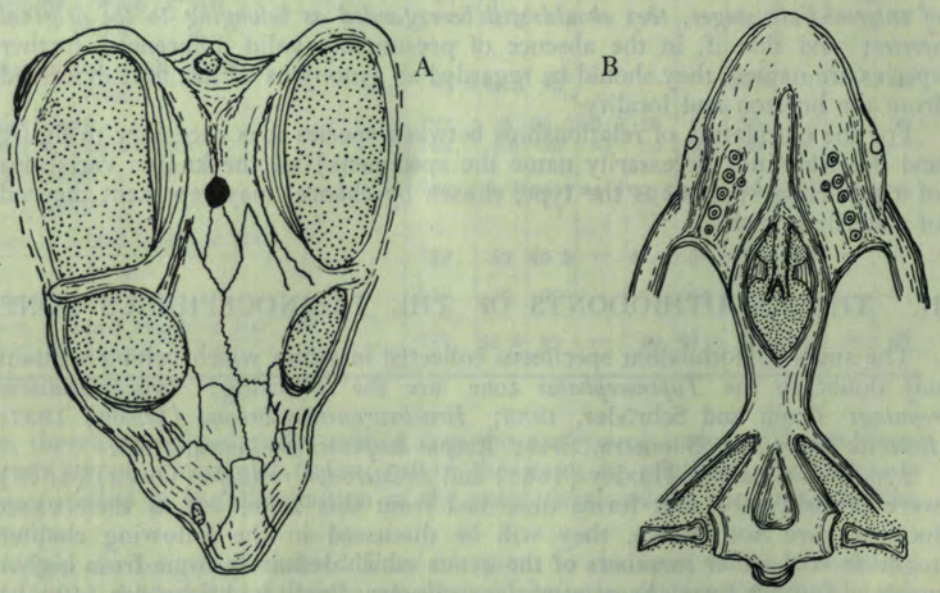


Fig. 46.—*Brachyuraniscus merwevillensis* sp. nov. (A) Dorsal view, distortion not corrected but partially reconstructed. (B) Palatal view, distortion corrected. (x1)

parallel to the alveolar ridge, which is separated from the latter by a groove. The median palatal ridge is very well developed and has the same height as the alveolar ridge. No anterior palatal ridges or grooves are present. Posteriorly the median palatal ridge is continuous with the anteriorly converging pterygoidal ridges. The internal nares open posteriorly to the level of the tusks.

Unfortunately the sutures on the palatal surface could not be followed except for the maxillary-premaxillary suture which could be traced vaguely.

The lower jaw. There are about seven molars on the dentary of each side, all situated on the lingual side of the jaw. The teeth are serrated posteriorly and probably also anteriorly. One tooth shows serrations posteriorly, in

sagittal section, and interlocking with these, there are spicules apparently belonging to the tooth posterior to it. They are probably directed more medially, as the tooth itself could not be seen in the section.

Broilius antjiesfonteinensis gen. et sp. nov.

Type: Complete but compressed skull with lower jaw, No. 178, B.P.I. = BP/1/289
Locality: The farm Antjiesfontein in the Prince Albert District.
Horizon: Intermediate division of the *Tapinocephalus* zone.
Collector: J. W. Kitching, 1946.

The skull is beautifully preserved but unfortunately slightly crushed antero-posteriorly. Some of the sutures on the dorsal surface are distended as a result of distortion. The skull is a little larger than that of the Merweville specimen.

Morphological features of the dorsal aspect. The skull is relatively wide with

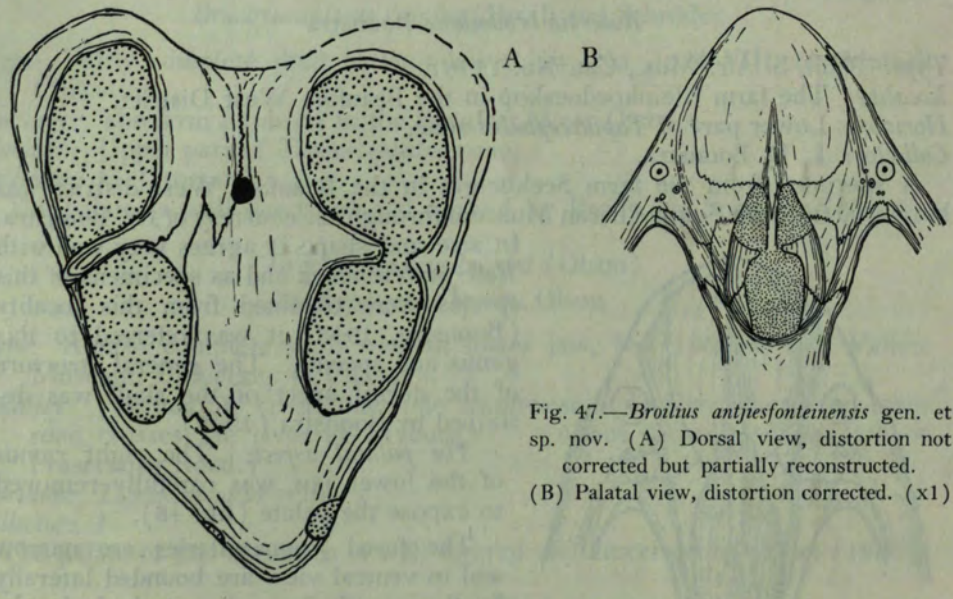


Fig. 47.—*Broilius antjiesfonteinensis* gen. et sp. nov. (A) Dorsal view, distortion not corrected but partially reconstructed. (B) Palatal view, distortion corrected. (x1)

the inter-temporal width much greater than the interorbital width. The pineal foramen is not surrounded by a bony ring, but a flat nasal boss is present. The postfrontal shows large on the surface (fig. 47A). Measurements are given in table 5.

The palatal aspect. One ramus of the lower jaw was carefully removed to expose the palate.

The tusks are erupting; one of them is only a few millimeters above the alveolar ridge. The animal therefore appears to be immature.

The palate is very flat and shallow with only a low median ridge present. A number of small molars (five) are irregularly situated postero-medial to the canines on the alveolar ridge, which is continuous with the pterygoidal ridges. The premaxillary is large and is bounded posteriorly by the maxillary and vomer; its long posterior process is clamped between the fused vomers.

The maxillary articulates with the palatine, transverse bone, jugal and squamosal, the large palatine process of the maxillary reaching the internal nares. The palatines are small and form but little of the roof and lateral walls of the choanae. The transverse bone is relatively large. The anterior portions of the internal nares are at a level anterior to the canines. From the drawing (fig. 47B) it would appear as if the interpterygoidal space is very short, but this is due to antero-posterior compression.

The lower jaw. Very few molars are present; on the right side there is only one and on the left side one is visible, but there may be more hidden underneath the matrix which was not removed. The teeth are situated in a thin-walled groove on the dorsal side of the dentary and not on the inner side. Unfortunately the crowns of the teeth are broken off and their structure could not be determined. There is no marked flaring out of the reflected lamina of the angular.

Robertia broomiana Boonstra

Type: Skull, S. Afr. Mus., Cat. No. 11761.
Locality: The farm Kleinkoedoeskop in the Beaufort West District.
Horizon: Lower part of *Tapinocephalus* zone.
Collector: L. D. Boonstra.

A specimen from the farm Seekoeigat in the Beaufort West district was borrowed from the South African Museum through the courtesy of Dr. Boonstra. In size and shape it agrees very well with *Robertia broomiana* and as specimens of this species were obtained from this locality (Boonstra, 1948) it was referred to this genus and species. The general structure of the dorsal apect of the skull was described by Boonstra (1948).



Fig. 48.—*Robertia broomiana* Boonstra. Palatal view, distortion corrected. (x1.)

The palatal aspect. The right ramus of the lower jaw was carefully removed to expose the palate (fig. 48).

The fused premaxillaries are narrow and in ventral view are bounded laterally by the maxillaries and posteriorly by the palatines and fused vomers. A high median ridge is present, but it flattens out anteriorly. The suture between the vomer and the premaxillary is at the same level as that between the latter and the palatine.

The maxillary is bounded posteriorly by the jugal, squamosal, transverse bone and palatine. According to Boonstra (1948) the teeth in this species vary from 1 to 8 in the upper jaw. In the present specimen there is a group of six teeth on the one side of the jaw. They

are situated posterior and slightly medial to the canine on the alveolar ridge, which is continuous with pterygoidal ridges posteriorly.

The palatine reaches the transverse bone laterally, the pterygoid laterally and posteriorly, and the vomer medially. It forms the dorsal and lateral walls of the internal nares anteriorly.

The vomer is forked posteriorly and articulates on either side of the interpterygoid fossa with the palatines and pterygoids.

The palate in front of the internal nares is short compared with the length of the interpterygoid fossa, but anteriorly the choana is merely represented by two narrow slits between the posterior process of the premaxillary and the anterior parts of the palatines laterally.

The lower jaw. Only a few teeth are present and they are situated on the inside of the dentary.

Brachyuraniscus reuningi Broili and Schröder

Type: Fairly complete skull without lower jaw, No. 1934 VIII 26, Munich Collection.
Locality: The farm La-de-da in the Beaufort West District.
Horizon: Upper part of *Tapinocephalus* zone.
Collector: G. Grossarth.

The palate is well described and figured by Broili and Schröder (1935*b*).

Brachyuraniscus broomi (Olson)
Brachyprosopus broomi Olson

Type: Almost complete skull without lower jaw, No. 1561 in the Walker Museum, University of Chicago.
Locality: "Hottentots river, one mile southwest of locality where the main road crosses the river at Myburg's." (About 30 miles due north of Fraserburg Road.)
Horizon: Tapinocephalus zone.
Collector: ?

The palate of this specimen is well figured and described by Olson (1937).

Koupia koupensis Boonstra

Type: Well preserved skull without lower jaw, No. 11796, S. Afr. Mus.
Locality: Deesweesfontein, a farm in the Laingsburg district.
Horizon: Tapinocephalus zone.
Collector: L. D. Boonstra.

The palate is figured but not described by Boonstra (1948). The sutures on the palate could apparently not be traced and are not shown in the figure.

Horizons in the Tapinocephalus Zone

In a recent (unpublished) geological report, covering unfortunately only part of this zone, Mr. P. J. Rossouw of the Geological Survey of South Africa and his co-workers show that in the part investigated the *Tapinocephalus* zone can be divided into three divisions by two characteristic horizons, i.e.

the Droëfontein chert horizon and the Poortjie sandstone horizon with its accompanying green cherts. In general, except for lateral variation, the tendency is for the Beaufort and Ecca contact to come nearer the surface in a northerly direction, in the area under discussion, i.e. between longitudes 21° 30′ and 22° 30′, and latitudes 32° 30′ and 33°. On the farm Sambokkraal, 13 miles west of Merweville, in the north-western part of the area, a deep borehole shows that there are only 1,480 feet of Beaufort sediments present above the contact, as compared with a thickness of about 6,000 feet immediately north of the southern boundary of this area. In an easterly direction the lower Beaufort layers become thicker and higher horizons crop out on the surface.

All the farms in this area are tabulated in their respective divisions by Rossouw. According to this table the farm Buffelsvlei (*Brachyuraniscus merwevillensis*) is in the division immediately below, and also partly above, the Droëfontein chert horizon, the lowest of the three divisions. The farm Antjiesfontein (*Broilius antjiesfonteinensis*) is in the stratigraphically intermediate division, i.e. between the Droëfontein chert and the Poortjie sandstone horizons. The type specimen of *Robertia broomiana* was collected on the farm Kleinkoedoeskop, presumably in the lowest of the three divisions. However, another specimen (S. Afr. Mus. Cat. No. 11680) referred to this species by Boonstra (1948) comes from Prince Albert Road, a locality which is in the intermediate division, according to Rossouw. The farm La-de-da (*Brachyuraniscus reuningi*) does not fall in the area investigated, but as it is very near the contact between the *Tapinocephalus* zone and the *Endothiodon* zone (see below), it must be very high up in the former zone. The type locality of *Brachyuraniscus broomi* is immediately north of the northern boundary of the investigated area, but if the tendency of the Ecca-Beaufort contact to come nearer to the surface is continued in this direction, the locality must be very low in the *Tapinocephalus* zone. The farm Deesweesfontein (*Koupia koupensis*) also lies west and outside the area covered by the report and falls probably in the intermediate division of the *Tapinocephalus* zone.

Relationship of the Endothiodonts of the Tapinocephalus Zone

The specimen which is made the type of *Brachyuraniscus merwevillensis* agrees very well with *Brachyuraniscus broomi* and *B. reuningi*. In these forms the internal nares are placed behind the level of the canines and, as far as can be judged from the figures, the upper molars are placed in a fairly regular row on a ridge on the palatal part of the maxillary. The ridge is parallel to the alveolar ridge and is separated from it by a groove. The pterygoidal ridges converge anteriorly and become continuous with the median palatal ridge. This similarity in palatal structure in these three forms indicates close affinity and it was therefore decided to refer them all to Broili and Schröder's genus *Brachyuraniscus*. The difference between them is of a specific rather than a generic nature. *B. reuningi* is from a much higher level (upper part of the *Tapinocephalus* zone) than the two other species (lower part of the *Tapinocephalus* zone). *B. merwevillensis* differs from *B. reuningi* in (*a*) its smaller size and different proportions (table 5), (*b*) the more prominent nasal boss and (*c*) the oval-shaped interpterygoidal fossa as compared with its diamond shape in *B. reuningi*.

From *B. broomi* it differs in the following respects: (*a*) it is smaller and of different proportions; (*b*) the preparietal does not bound as much of the parietal foramen; (*c*) a nasal boss is present.

From Olson's figure of *B. broomi* it appears that the palatine reaches the premaxillary anteriorly. This is also the case in *B. reuningi* (Broili and Schröder, 1935*b*), but unfortunately it is not possible to state with certainty whether it reaches the premaxillary in *B. merwevillensis*; most probably it does.

Broilius differs from *Brachyuraniscus* in the following aspects: (1) the internal nares are placed between the canines; (2) the molars are grouped in clusters, posteromedially to the canines on the alveolar ridge; (3) on the lower jaw the teeth are not placed on the medial side of the dentary, but in a groove on its dorsal side.

Broilius and *Robertia* are more closely related. In the latter the internal nares are placed well forward, but the anterior portions are very narrow and functionally they opened at a more posterior level. The most important differences, however, are the facts that the maxillaries participate in forming the margin of the internal nares in *Broilius*, and the molars of the lower jaw are not placed on the lingual side of the dentary.

In *Koupia* the internal nares are placed very far back, their anterior borders not even reaching the level of the posterior molars. In this respect it is nearer to *Brachyuraniscus*, but in the distribution of the teeth it resembles *Robertia* and *Broilius*. The palate is unfortunately not known well enough to decide definitely on its affinities.

The extent of the horny beak in these forms

In *Brachyuraniscus merwevillensis* the teeth of the lower jaw bite on the inside of the maxillary teeth on the palatine and anteriorly apparently also on the maxillary. These parts were therefore evidently covered by horn (see Watson, 1948). The upper molars bite lateral to the mandibular teeth, on the dentary, which was therefore presumably also covered by horn. In the investigated specimen of *Robertia* it was not possible to decide on the exact relationship of the upper and lower dentitions to each other when the jaws are closed, but as the maxillary teeth are spread over a relatively large area, the teeth of the lower jaw probably bit against them and not medially to them. The horny beak was therefore evidently not as well developed as in *Brachyuraniscus* and was probably restricted to the anterior part of the palate, i.e. to the region anterior to the canines. In the lower jaw the teeth are placed on the inner side of the dentary, with the outer part evidently covered with horn for the outer maxillary teeth to bite on. In the Antjiesfontein specimen the horny beak was still less developed. The outer palatal surface of the dentary is very narrow, even narrower than the inner surface, and there could not have been any horny covering on the dentary lateral to the molars. The horny beak must have been restricted to those portions anterior to the canines.

The secondary palate

In two of these forms, *Robertia broomiana* and *Brachyuraniscus reuningi*, the internal nares are very narrow anteriorly. With the exception of the Antjies-

fontein specimen, the maxillary cannot take part in the formation of a more extensive palate, since it is cut off from the internal nares by the palatine. A large secondary palate can therefore only develop by the posterior elongation of the lateral part of the premaxillary and the eventual closing of the gap between the latero-posterior process and the median posterior process, a development that is obviously taking place in the above-mentioned forms.

The Origin of the Tapinocephalus Zone Endothiodonts

Watson (1948) derives the Anomodonts from a form such as the Russian fossil *Venjukovia*. It is, however, almost impossible to see in this form the ancestor of *Broilius*. According to Watson (1948) the most remarkable feature of *Venjukovia* is the presence in the lower jaw of an expansion of the dentary laterally to the cheek teeth, covered with horn, against which the upper teeth bit. In the Antjiesfontein specimen there is no lateral expansion of the dentary. Furthermore, in *Venjukovia* the palatine reaches the premaxillary, which is not the case in the Antjiesfontein specimen. It must therefore have had a different origin altogether. *Brachyuraniscus* and *Robertia* can be reasonably derived from *Venjukovia*, but it is more likely that a form such as *Broilius* is their immediate ancestor. The first stage in the development is the medial displacement of the teeth in the lower jaw and the posterior expansion of the horn on the lateral side of the molars for the outer maxillary teeth to bite against. The development did not go beyond this stage in *Robertia*. A further stage in the development is represented by *Brachyuraniscus*, where the teeth of the upper jaw also become displaced medially and are arranged in a more or less straight line. All the upper cheek teeth bite against the horny shelf on the dentary. A horny pad also developed on the antero-medially expanded palatine for the mandibular teeth to bite against.

III. THE STRUCTURE AND TAXONOMY OF SOME ENDOTHIODONTS FROM THE CISTECEPHALUS AND ENDOTHIODON ZONES

A. The Genera Pristerodon and Emydops

New small species from the Cistecephalus zone

Pristerodon buffaloensis sp. nov.

Type: Well preserved and almost complete skull, No. 241, B.P.I. ~~= BP/1/2134~~
Locality: The farm Swartbos in the Murraysburg district.
Horizon: Lower part of *Cistecephalus* zone.
Collector: J. W. Kitching.

A very interesting group of four small Endothiodonts was collected in the Murraysburg district by Mr. J. W. Kitching in December, 1949. They were all obtained from the bed of the Buffalo river on the two adjacent farms Swartbos and Kraaifontein. From the latter farm a specimen of *Cistecephalus microrhinus* Owen was obtained and another specimen of *Cistecephalus* comes

from a nearby farm Towerfontein. The specimens are therefore from a low horizon in the *Cistecephalus* zone.

The type skull. The intertemporal region is considerably wider than the interorbital region. The parietals form a shallow groove in which the small

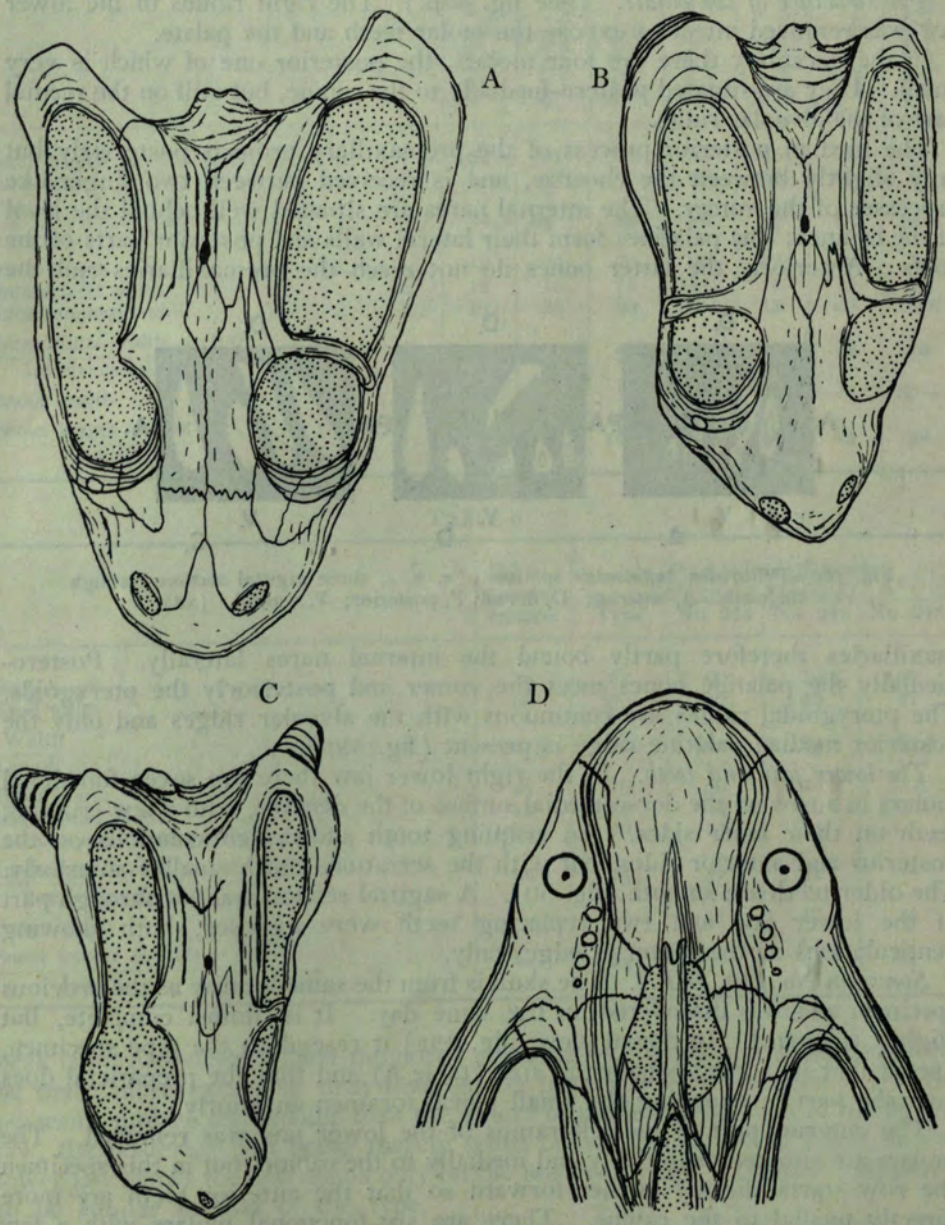


Fig. 49.—*Pristerodon buffaloensis* sp. nov.; A, B, C, dorsal views of three different skulls, distortion not corrected; A, type; D, palatal view of type, left side reconstructed according to right side. (x1). (Drawing of palatal view x1½).

pineal foramen is situated relatively far posteriorly. The preparietal forms but little of the anterior border of the latter foramen. There are no nasal or pineal bosses. The general structure of the dorsal side of the skull can be seen from figs. 49A, B, and C. The measurements are given in table 6.

The structure of the palate. (See fig. 49D.) The right ramus of the lower jaw was removed intact to expose the molar teeth and the palate.

In the maxillary there are four molars, the posterior one of which is very small. They are situated postero-medially to the canine, but still on the medial part of the alveolar ridge.

The median posterior process of the premaxillary projects posteriorly but only slightly between the choanae, and is received between two finger-like processes of the vomer. The internal nares are situated well behind the level of the canines; the palatines form their lateral walls and posterior parts of the roofs. Anteriorly the latter bones do not reach the premaxillaries and the

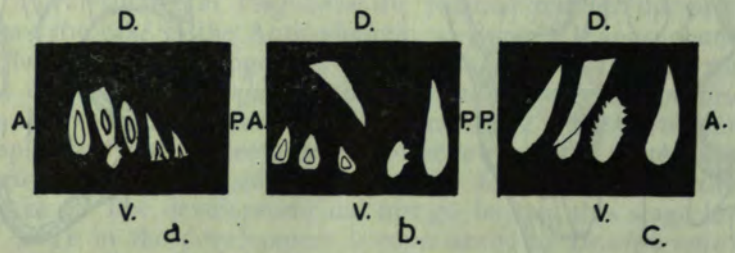


Fig. 50.—*Pristerodon buffaloensis* sp. nov.; *a*, *b*, *c*, three sagittal sections through the teeth. A, anterior; D, dorsal; P, posterior; V, ventral. (x3).

maxillaries therefore partly bound the internal nares laterally. Postero-medially the palatine bones meet the vomer and posteriorly the pterygoids. The pterygoidal ridges are continuous with the alveolar ridges and only the posterior median palatine ridge is present (fig. 49D).

The lower jaw and teeth. In the right lower jaw there are seven functional molars in a row on the dorso-medial surface of the dentary, with a few erupting teeth on their inner sides. An erupting tooth shows denticulations on the posterior and anterior sides, but with the serrations much smaller anteriorly. The older teeth are smooth (fig. 50). A sagittal section was cut through part of the lower jaw and two replacing teeth were exposed, both showing denticulations on the posterior edges only.

Specimen No. 242, B.P.I. The skull is from the same locality as the previous specimen and was discovered on the same day. It is almost complete, but slightly distorted. In dorsal view (fig. 49B) it resembles the type specimen, except that it is much smaller in size (table 5) and that the preparietal does not take part in bounding the small pineal foramen anteriorly.

The anterior part of the left ramus of the lower jaw was removed. The molars are situated posteriorly and medially to the canine, but in this specimen the row starts slightly farther forward so that the anterior teeth are more directly medial to the canine. There are six functional molars with a few replacing teeth medially. In the lower jaw there are twelve teeth in a row, but the posterior half of them have no opposing teeth in the maxillary when the

TABLE 5

	Emydops microdon T.M. 295	*Emydops murrayburgensis*	*Emydops kitchingi*	*Parringtoniella broomi*	*Heuneus oudebergensis*	*Broilius antjiesfonteinensis*	*Brachyuraniscus merwevillensis*
Skull length	62	81	75	85	65	75	72
Skull width	—	67	60	65	50	64	53
Width / Length	—	**83·7**	**80**	**76**	**77**	**85**	**73·6**
Basal length	58	72	70	80	63	68	70
Interorbital width	12	12	11	18·5	8	15	13
Intertemporal width	16	22	20	19·5	13	20	18·6
Interorbital width × 100 / Intertemporal width	**75**	**54·5**	**55**	**94**	**61·5**	**75**	**70**
Snout length	12	19	14	21	13	22	23·5
Snout length × 100 / Length	**18·8**	**23**	**18·6**	**24·6**	**30**	**29**	**32**

TABLE 6

	Pristerodon whaitsi	*Pristerodon buffaloensis* BP/1/2126 Type	BP/1/2127 No. 244	BP/1/2114 No. 242	No. 243
Skull length	83	83	60	70	66
Skull width	60	60	40	45	47
Width / Length	**72·3**	**72**	**66·6**	**64**	**63**
Basal length	—	76	56	65	—
Interorbital width	13	13	10	10	7·5
Intertemporal width	19	20	14	14	—
Interorbital width × 100 / Intertemporal width	**68**	**65**	**71**	**71**	—
Snout length	—	20	11	17	14
Snout length × 100 / Length	—	**24**	**17·5**	**24**	**21**

beak is normally closed, and the horny covering on the palatine must therefore be much more extensive than that on the lateral side of the dentary. The posterior molars are smaller than the others of the lower jaw and of the upper jaw, the posterior two being merely tooth buds. One erupting tooth in the lower jaw shows the serrations only on the posterior edge. The palate appears to be similar to that of the type.

Specimen No. 243, B.P.I. The third specimen from the type locality (the farm Swartbos) is tuskless. It is almost complete, but the structure of the parietal region could unfortunately not be determined due to a fine mosaic

of cracks. It is of about the same size as specimen No. 242, but the interorbital region is relatively narrower. The one ramus of the lower jaw was removed. Three functional molars are present on the alveolar ridge of the maxillary with one visible replacing tooth on the inside. In the lower jaw there is a row of six functional teeth on the dorso-medial aspect of the dentary. One erupting tooth shows serrations on the posterior edge only.

Specimen No. 244, B.P.I. This specimen was collected on the farm Kraaifontein, but from the same horizon as that of the type. It is tuskless and the smallest of the four specimens (table 6). The lower jaw is missing. The snout is narrow, but otherwise very similar to the type (fig. 49c).

On the right maxillary there are three molars, but on the left there are at least four. The crowns are broken off and their structure is unfortunately unknown.

Emydops murraysburgensis sp. nov.

Type: Fairly complete and beautifully preserved skull without lower jaw, No. 300, B. P. I. = BPI 1609

Locality: Blaauwpoort, Murraysburg district.

Horizon: Cistecephalus zone.

Collector: B. J. Kitching.

The skull. The left and most of the right temporal arches are broken off, as well as the very tip of the snout. The intertemporal region is completely flat and considerably wider than the interorbital region. The preparietal

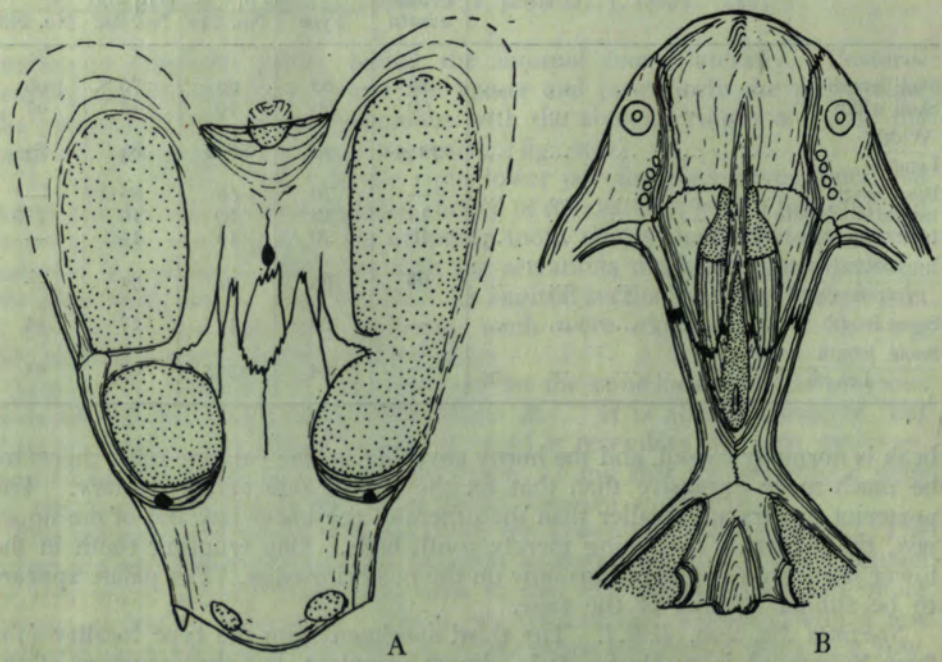


Fig. 51.—*Emydops murraysburgensis* sp. nov. (A) Dorsal view, distortion not corrected but partially reconstructed. (B) Palatal view. (x1.)

is large and does not bound the small pineal foramen. The postfrontals form a considerable part of the postero-medial boundary of the orbits. Nasal and pineal bosses are absent (fig. 51A). The measurements are given in table 5.

The structure of the palate. The maxillary is fairly flat, but the two low anterior ridges and one posterior ridge are present. The molar teeth are situated in a row on the alveolar ridge posterior to the tusks. On the right side there are four and on the left three, but there is an empty socket at the anterior end of the row. The teeth are very well preserved and their lengths can be measured. The longest one is almost four millimeters in length. No serrations are present on any of the teeth. The pterygoidal ridges are not continuous anteriorly with either the alveolar or the median posterior ridges. The internal nares are placed posterior to the level of the canines. The palatine is very well developed antero-medially and it meets the premaxillary. It forms the greater part of the lateral wall and the posterior part of the roof of the internal nares. Medially it has a very long contact with the vomer (fig. 51B).

Emydops kitchingi sp. nov.

Type: Incomplete but well preserved skull without lower jaw, No. 301, B.P.I. = BP/1/625
Locality: Blaauwpoort, Murraysburg district.
Horizon: Cistecephalus zone. From this locality a specimen of *Cistecephalus* was obtained (*C. rubidgei*, see Brink, 1950) and the farm must therefore be low in this zone.
Collector: S. C. Kitching.

The skull. Both temporal arches are broken off, but otherwise the specimen is complete and undistorted.

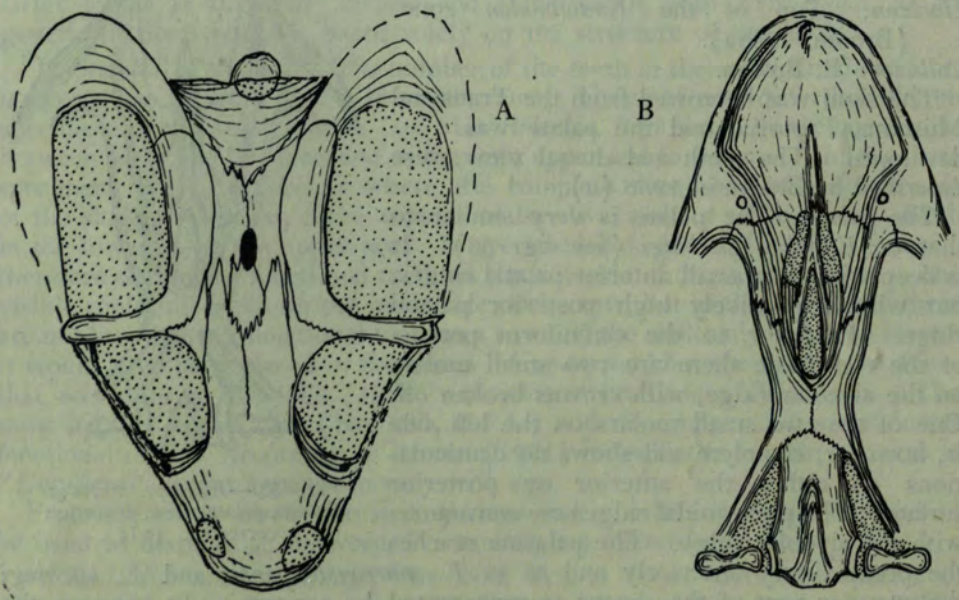


Fig. 52.—*Emydops kitchingi* sp. nov. (A) Dorsal view, partially reconstructed. (B) Palatal view. (x1).

Although it comes from the same farm as specimen No. 300, it is from a different horizon. Superficially the two skulls appear very similar, but they differ as follows: The intertemporal region is fairly flat but the postorbitals are disposed at a low angle towards the parietals in No. 301. Furthermore, the parietal foramen is very large and elongated and its anterior half is bounded by a small preparietal. The postfrontals form an even greater part of the boundary of the orbits than in No. 300 (fig. 52A).

The structure of the palate. The specimen is tuskless. The palate is very deep with the caniniform processes not projecting beyond the level of the alveolar rim. Anteriorly the two palatal ridges are low, but the median posterior palatal ridge is very well developed. On the maxillaries of each side there is only one molar, situated postero-medially to the caniniform process, on the alveolar ridge. The crowns are unfortunately broken off and their structure could not be determined. The pterygoidal ridges are continuous with the alveolar ridges. The palatine has a large flat surface antero-medially; it reaches the premaxillary anteriorly and approximates to the vomer antero-medially, leaving only a narrow slit as the anterior part of the choanae. The minimum interpterygoidal width is relatively much wider than in *E. murraysburgensis* (fig. 52B).

Emydops microdon (Broom)
Emydopsis microdon Broom

Type: Well preserved but distorted skull without lower jaw, No. 269, Transv. Mus.
Locality: Leeuwkloof, in the Nieuwveld, Beaufort West district.
Horizon: Top of the *Endothiodon* zone. (Broom, 1936a).
Collector: R. Broom.

The skull was borrowed from the Transvaal Museum, Pretoria, and the palate was developed. The teeth and dorsal view were described by Broom in 1936 (*a*).

The palate. The palate is very similar to that of *Emydops kitchingi* (see fig. 53). It is deep with very small anterior palatal ridges, but with a relatively high posterior palatal ridge. Posterior to the caniniform process of the right side there are two small molars on the alveolar ridge, with crowns broken off. One of the two small molars on the left side is, however, complete and shows no denticulations on either the anterior or posterior surface. The pterygoidal ridges are continuous with the alveolar ridge. The palatine reaches the premaxillary anteriorly and as in *E. murraysburgensis* and *E. kitchingi* the anterior part of the choana is represented by a narrow slit between the palatine and vomer.



Fig. 53.—*Emydops microdon* Broom, palatal view, distortion corrected. (x1½).

The validity of the Structure and number of Teeth as a basis for Generic Distinction in the Endothiodonts

According to Broom (1932), "*Emydopsis*" is an Anomodont with a few *Pristerodon*-like teeth (posteriorly serrated), apparently four. *Emydops* differs from "*Emydopsis*" in having only a few unserrated molars and the teeth of "*Diaelurodon*" (another small Endothiodont) differ from those of *Pristerodon* in having coarse serrations on the anterior as well as on the posterior border. However, this author (op. cit.) admits that it is not always certain whether a small toothed specimen belongs to "*Emydopsis*," *Pristerodon* or *Emydops*, as it is not always possible to see the condition of the molars without injuring the specimen.

The structure of the teeth. When describing *Cteniosaurus platyceps*, a medium-sized Endothiodont with anteriorly and posteriorly serrated teeth, Broom (1935*b*) noticed that at least one molar in the lower jaw has cusps only on the one side; he suggested that those on the other side of the tooth were worn off. In *Pristerodon buffaloensis* the type shows anterior and posterior serrations on an erupting tooth, with the older teeth completely devoid of denticulations. Two other specimens of *Pristerodon buffaloensis* have the serrations only on the posterior sides of two replacing teeth, the mature teeth also being smooth on both sides. The structure of the teeth is therefore not only affected by wear (see also *Cteniosaurus*), but they also appear to be extremely variable. Although the structure of the teeth may have a phylogenetic significance, it would be irrational to use so variable a morphological feature as a basis for classification. The four specimens belonging to P. *buffaloensis* are far too similar to be separated into two different genera — *Pristerodon* and "*Diaelurodon.*" The latter genus is therefore invalid and synonymous with *Pristerodon*, as its generic distinctiveness is based solely on the structure of the teeth.

The number of the teeth. The number of the teeth in the small Endothiodonts is even more variable than is their structure. They not only differ in different specimens of the same species (see also *Robertia*, Boonstra, 1948), but also as between right and left jaws and as between upper and lower jaws. In the three specimens of *P. buffaloensis* where the complete dentitions of the one side of the skull are known, there appears to be always about twice as many teeth in the lower as in the upper jaw. In specimen No. 243, B.P.I., for example, there are only three functional teeth on the one side of the upper jaw, with one visible replacing tooth on the inner side of the row, but in the lower jaw there are not less than six functional teeth in a row. If the skull only had been known it would have been placed in the genus "*Emydopsis*," but the lower jaw shows that according to Broom's (1932) definition it really is a *Pristerodon*. The same applies to the type (No. 241, B.P.I.) with four upper and seven lower functional teeth. According to Broom (1921) himself, the number of teeth in "*Emydopsis*" *longus* appears to vary with age.

From the above discussion it is obvious that number of teeth alone cannot be used to distinguish between *Pristerodon* and "*Emydopsis*" (see below.)

"*Emydopsis*" *and Emydops.* In 1932 Broom stated that two species of *Emydops* (*E. minor* Broom, 1912*a* and *E. parvus* Broom, 1921) are the smallest known Anomodonts. In 1935*a* he (Broom) described a new species of

"Emydopsis" (*"E" minimus*) in which the number and structure of the teeth are not known. This specimen is no bigger than the two *Emydops* species. The measurements and structure of this specimen agree almost perfectly with *Emydons minor* — much more than with *"Emydopsis" platyceps* (Broom and Haughton, 1921), which Broom regarded as its nearest ally. On the other hand *"Emydopsis" microdon*, known to have only two molars, was not referred to the genus *Emydops* by Broom. However, the structure of the molars was not then determined. *Emydops kitchingi* has only one small probably unserrated molar, but it is larger than many *"Emydopsis"* species. Here again, as the structure and number of teeth (and absolute size) cannot be used to distinguish between the genera *Emydops* and *"Emydopsis,"* the latter genus must be recognised as synonymous with the former, which has priority.

The closer relationship of the new species

The type specimen of *Pristerodon buffaloensis* is in measurements and proportions almost identical with *"Diaelurodon" whaitsi* (table 6). The number of teeth (eight functional) also agrees closely with the number in the latter form. However, it comes from a much higher horizon (*"D" whaitsi* is from the lower part of the *Endothiodon* zone, according to Broom, 1932) and the skull roof is slightly concave antero-posteriorly in the present specimen, whereas it is convex in *"D" whaitsi*, judging from Broom's figures.

Both *Emydops murraysburgensis* and *Emydops kitchingi* resemble *"Emydopsis" longus* Broom, *"Kistecephalus" arctatus* Owen (1876) and *Emydops platyceps* Broom and Haughton. The two new species are, however, larger than these forms. *"Emydopsis" longus* differs from *Emydops murraysburgensis* in having a slightly wider interorbital region (table 5). The preparietal is smaller and bounds the small parietal foramen anteriorly. Posteriorly the postfrontals appear larger on the surface. It differs from *E. kitchingi* in the smaller parietal foramen and the relatively wider snout. In proportions and in dorsal view *"Kistecephalus" arctatus* agrees very closely with *E. kitchingi* as far as can be seen from the incomplete state of the latter skull. The postorbitals also form a large part of the roof of the skull. The latter species differs, however, from *"K" arctatus* in having larger postfrontals and a larger pineal foramen, bounded anteriorly by the parietals. *Emydops platyceps* differs from the two new species in its much narrower snout. *Emydops minor* Broom (1912*a*) and *Emydops parvus* Broom (1921) have the very wide and flat interorbital regions but they are very much smaller than the two new species. Of the species previously mentioned, with the exception of *"Kistecephalus" arctatus* (of which the type locality is not known) only *Emydops parvus* is also from the *Cistecephalus* zone (Broom 1932).

Of the previously described species of *Emydops* (and *"Emydopsis"*) only the palate of *Emydops microdon* is known. The type species of this genus, *Emydops minor* (No. 5525 in the Amer. Mus. Nat. Hist.), was unfortunately not available for this study and until the palate of this specimen is developed and found to differ generically from that of *E. microdon*, the palate of the latter will serve as typical for *Emydops*. The palates of *E. kitchingi* and *E. murraysburgensis* are very similar to that of *E. microdon*.

The specimens from Murraysburg described as *Pristerodon buffaloensis* have an entirely different type of palate. The palatine bone is small and does

not reach the premaxillary anteriorly. The choanae are therefore bounded laterally by the maxillaries. There can therefore be no doubt that these specimens differ generically from *Emydops*. Unfortunately the structure of the palate is not known in any previously described *Pristerodon* (or "*Diaelurodon*"). The type of the genus *Pristerodon* (*P. mackayi* Huxley, 1868, No. R. 1810, B.M.N.H.) is in such a badly preserved state that its palatal structure will probably never be known. I have allocated this new species to the genus *Pristerodon* because the size and structure of the dorsal aspect of the skull are similar to that of "*Diaelurodon*" *whaitsi*, which is a species of *Pristerodon* (see above).

The evidence is somewhat flimsy and indirect but as evidence to the contrary is entirely lacking, the new species will remain in this genus until such contrary evidence is forthcoming.

The relationship of Emydops and Pristerodon to other small Endothiodonts of the Endothiodon zone

The palatal structure is known in a few other small Endothiodonts. In the type species of *Cryptocynodon*, *C. simus* Seeley, 1894, the structure of the roof of the mouth is not clear (see van Hoepen, 1934 and Broili and Schröder, 1935*b*), but a specimen described as *Cryptocynodon* sp. from Noblesfontein, Victoria West, (No. 1934 VIII 25, Munich Collection, Broili and Schröder 1935*b*) shows this region very well. As in *Emydops* the palatine reaches the premaxillaries anteriorly. In this specimen, however, the teeth (5) are situated on the palatal part of the maxillaries, medial to the canines. The palate resembles that of *Brachyuraniscus*, but although the pterygoidal ridges converge anteriorly, they do not meet the median palatal ridge. In *Prodicynodon* Broom (1904*a*) the teeth are also arranged on the pars palatina of the maxillary (see van Hoepen, 1934) and these two forms can therefore easily be distinguished from *Emydops* and *Pristerodon*, in which the teeth are placed on the alveolar ridge.

Eurychororhinus boonstrai Broili and Schröder (1935*b*) from Kuilspoort, Beaufort West (No. 1934 VIII 27, Munich Collection) is very well preserved, but the sutures on the palate apparently could not be followed. The teeth are, however, also placed on the secondary palate and therefore *Eurychororhinus* also appears to be distinct from *Emydops* and *Pristerodon* and more nearly related to *Cryptocynodon* and *Prodicynodon*. *Emyduranus* Broom (1921) probably also belongs to this group, but the palate is not very well known in the two species described as *E. platyops* Broom (1921) and *E. gracilis* Broom (1935*b*) (see also van Hoepen, 1934).

If van Hoepen's interpretation of the palate of *Compsodon* from Maselspoort, Bloemfontein (1934), is correct, it is a form unlike any other small Endothiodont. Although no sutures were visible on the premaxillary, the vomer is figured as lying in the median palatal ridge. The two palatines meet in the middle line anteriorly to the internal nares and posterior to the vomer. This author also states that *Compsodon* is nearly related to *Tropidostoma* Seeley, a large Endothiodont, and he puts the latter in the new family Compsodontidae. The palate of *Tropidostoma* however, according to Watson's figure and description (1948), appears to be much nearer in structure

to that of a form such as *Emydops*, although in dorsal view and in size the skull is entirely different.

The ancestral relationship of Emydops and Pristerodon

Pristerodon agrees with *Broilius antjiesfonteinensis* in the absence of the palato-premaxillary contact. Although this primitive feature was retained, *Pristerodon* diverges from the *Broilius* condition in the following respects; (1) The internal nares are displaced posteriorly through the posterior prolongation of the premaxillaries and to a certain extent also by the enlargement of the palatal parts of the maxillaries. Medially the latter bones and the anterior parts of the palatines approximate the vomer closely, displacing the internal nares functionally even farther posteriorly. (2) The molar teeth of the upper jaw are no longer arranged in an irregular group behind the canine, but are arranged in a single row and bite on the horn-covered lateral shelf of the dentary. (3) The teeth of the lower jaw are placed on the medial side of the dentary and not on its dorsal aspect. In the last two features *Pristerodon* also resembles *Brachyuraniscus*, but in this form the teeth are situated on the pars palatina of the maxillaries.

Emydops seems to have *Robertia* as an ancestor, but it also departed in several respects from that ancestral type: (1) The internal nares are placed more posteriorly and, with the antero-medial expansion of the palatine, their anterior parts are reduced to narrow slits. (2) The molars are stronger and placed in a straight row and not at random as in *Robertia*. (3) Low anterior palatal ridges have developed.

The origin of Cistecephalus Owen 1876

The palatal structure of *Cistecephalus* (*C. planiceps* Owen) is well known through the work of Broili and Schröder (1935*a*). Broom's theory (1932), that a species of *Emydops* or allied genus is the ancestor of *Cistecephalus*, is supported by the similarity in palatal structure. The only feature excluding it as a direct ancestor is the presence of two low anterior palatal ridges in all the investigated *Emydops* specimens. In the specimen of *Cistecephalus* described by Broili and Schröder the tip of the snout is incomplete; the palate of another specimen referred to this species by Brink (1950) was therefore developed, but no anterior ridges were found.

As in *Cistecephalus*, so in at least one species of *Emydops*, *E. longus* (where a large number of specimens are known), both sexes are tuskless. In some species the molars are probably in a process of disappearing as in *E. kitchingi*, where only one small molar on each side is present. Another stage is probably represented by *Emydorhinus fragilis* Broom (1935*b*) from the *Cistecephalus* zone of New Bethesda, in which all the teeth are absent, but the dorsal cranial structure is very similar to that of *Emydops*.

B. Small Endothiodonts with aberrent dentitions

(i) *Parringtoniella broomi* gen. et sp. nov.

Type: Fairly complete but distorted skull without lower jaw, No. 302 in the collection of the Bernard Price Institute. ≈ BP/1/688

Locality: The farm Aasvogelkrans, south of Murraysburg.
Horizon: *Cistecephalus* zone.
Collector: B. J. Kitching.

The specimen is certainly from the *Cistecephalus* zone, as a specimen of that genus but one as yet not specifically identified was collected from the same locality. The specimen has suffered badly from distortion and the measurements given in the table (table 5) are therefore approximations. A drawing of the reconstructed skull is given in fig. 54. Most of the sutures on the dorsal side of the skull unfortunately cannot be traced.

The following are the most important characteristics: The intertemporal and interorbital regions are of about the same width. Both regions are grooved. The pineal foramen is very small. A very large median nasal boss overhangs the nostrils.

The palate: Only the posterior median palatal ridge is present. The palate is relatively wide and shallow. The caniniform process is situated far forward and the maxillary-premaxillary suture passes through the anterior part. The internal nares are situated well behind the caniniform processes with their anterior parts reduced to narrow slits. The palatines articulate anteriorly with the premaxillaries at the level of the vomero-premaxillary suture. The palate is therefore very similar to that of *Emydops*, but differs greatly in the distribution of the teeth (fig. 54B).

A row of very small molars is present on the medial side of the alveolar ridge with one replacing tooth medially. Fully three millimeters farther

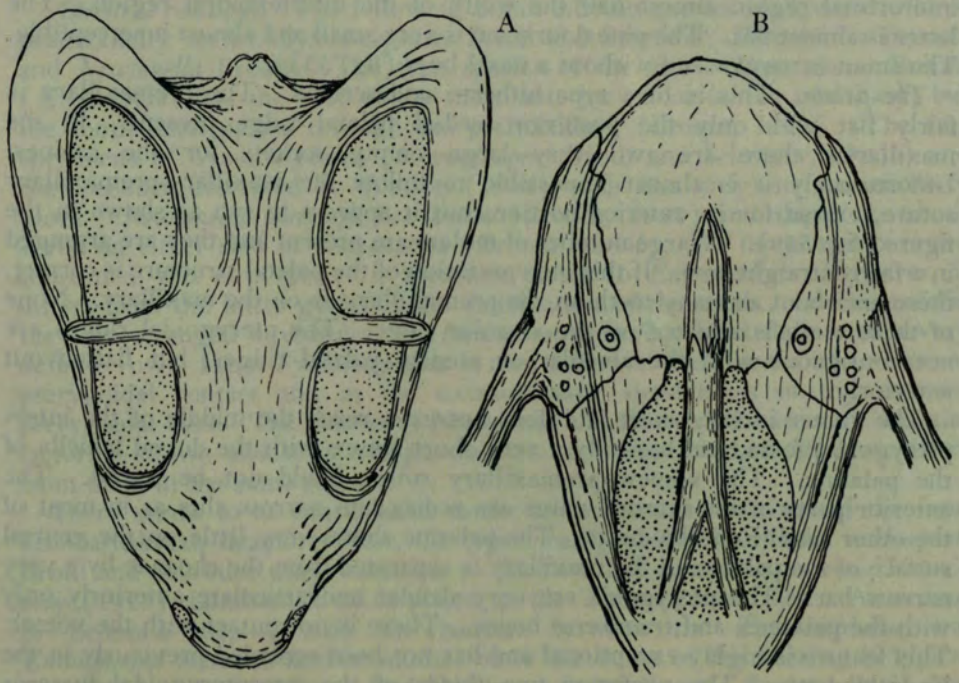


Fig. 54.—*Parringtoniella broomi* gen. et sp. nov. (A) Dorsal view, reconstructed. (x1). (B) Palatal view, distortion corrected. (x1½.)

medially, near the maxillary-premaxillary suture, is a tooth about four to five times as big as the others, situated on the pars palatina of the maxillary. No known Endothiodont has this type of tooth distribution and the creation of a new genus to accommodate the specimen seems justified. The genus is named after Dr. F. R. Parrington, an ardent student of South African palaeontology.

Ancestral relations. As was stated above, the upper teeth of *Robertia* were displaced medially until the condition was reached where all the maxillary teeth lie in a straight row on the pars palatina of the maxillary, e.g. in *Brachyuraniscus*. It is therefore possible that this new form represents a late survivor with a dentition of an intermediate character, i.e. some of the teeth are still on the alveolar ridge, whereas others are on the palatal part of the maxillary.

(ii) *Hueneus oudebergensis* gen. et sp. nov.

Type: Skull lacking lower jaw, No. 303 in the collection of the Bernard Price Institute. = BP/1/866

Locality: The Oudeberg plateau, north of Graaff-Reinet.

Horizon: Upper part of *Cistecephalus* zone.

Collector: J. W. Kitching.

The specimen is slightly distorted and very well preserved. Unfortunately it is almost impossible to trace any sutures on the skull. The principal measurements are given in table 5. The skull is relatively narrow with the interorbital region almost half the width of the intertemporal region. The latter is almost flat. The pineal foramen is very small and almost inperceptible. The snout is narrow and without a nasal boss (fig. 55A).

The palate: This is of a type hitherto undescribed. The premaxillary is fairly flat with only the posterior medial palatal ridge present. In the maxillaries there are two very large empty sockets for the canines. Unfortunately it is almost impossible to follow the maxillary-premaxillary suture, except for its anterior portion, but it appears to run as shown in the figure (fig. 55B). A large number of molars are present and they are arranged in a fairly straight row. If this interpretation of the palatal structure is correct, there are about as many teeth on the premaxillary as on the maxillary. None of these teeth is situated on the alveolar ridge. The pterygoidal ridges are not contiguous with the alveolar or median palatal ridges, but flatten out anteriorly.

The vomer is very short and does not even reach the middle of the interpterygoidal fossa, and has only a very short suture with the dorsal lamella of the palatine. The vomero-premaxillary suture could not be traced. The anterior parts of the internal nares are reduced to narrow slits as in most of the other small Endothiodonts. The palatine shows very little on the ventral surface of the palate and the maxillary is separated from the choanae by a very narrow bar. The pterygoids are very slender and articulate anteriorly only with the palatines and transverse bones. There is no contact with the vomer. This feature is highly exceptional and has not been recorded previously in the Endothiodonts. The posterior two thirds of the interpterygoidal fossa is therefore practically roofless.

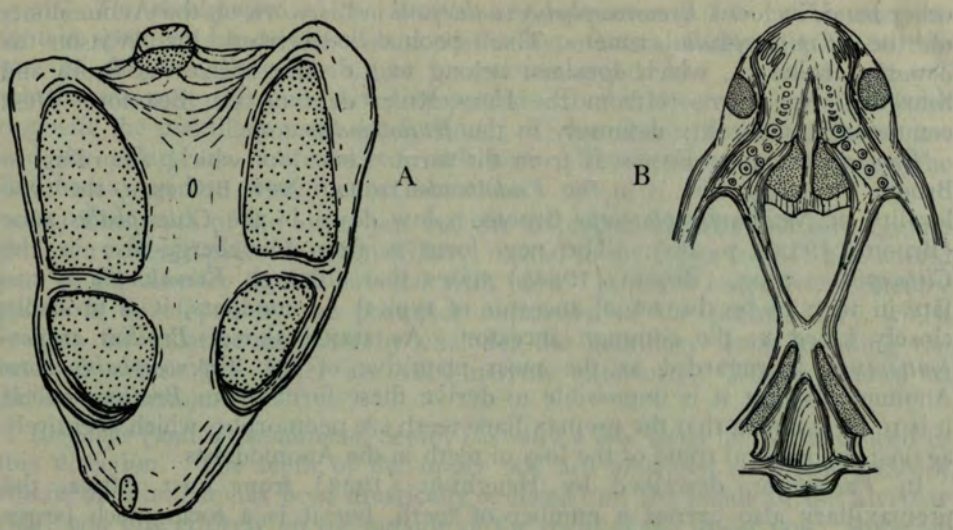


Fig. 55.—*Hueneus oudebergensis* gen. et sp. nov. (A) Dorsal view, distortion not corrected. (B) Palatal view distortion corrected. (x1.)

The genus is named after Prof. F. von Huene of Tubingen, who has made such valuable contributions to South African palaeontology.

Ancestral relations. The following South African genera are known to have premaxillary teeth: *Synostocephalus* Broili and Schröder, *Eumantellia* Broom, and *Newtonella* Broom. The type species of the genus *Emyduranus* Broom (*E. platyops*) has the root of the most anterior molar in the maxillary, but the tooth itself passes through the premaxillary (Broom, 1921). The two specimens of *Synostocephalus* (*S. vanhoepeni* Broili and Schröder, 1935*b*) and the specimen described by Watson (1948) each has only one premaxillary tooth. *Newtonella platyceps* has three (Broom, 1937) and there are about seven on either side in *Eumantellia* (Broom, 1935*b*). As far as numbers are concerned, this new species is therefore closer to *Eumantellia*. However, it differs from the latter genus in the distribution of the teeth. In *Eumantellia* they are arranged in clusters, in *Hueneus* on the other hand they form a very definite row. From *Synostocephalus* it also differs in the absence of a vomero-pterygoidal contact and in the extraordinary slenderness of the anterior pterygoidal bars. The palates of *Newtonella* and *Eumantellia* are very unsatisfactorily known and it is not possible to ascertain whether *Hueneus* differs from them in the same respect.

There seems to be considerable doubt as to the exact horizon of the farm Lombardskraal, Beaufort West, the type locality of *Synostocephalus vanhoepeni*. Broili and Schröder draw attention to the fact that according to von Huene's map (1925) Lombardskraal is placed in the *Tapinocephalus* zone. According to Broom's map (1915) the contact between the *Tapinocephalus* and *Endothiodon* zones is farther south. Since the fauna of this locality is typical Endothiodont, e.g. a large Endothiodont, *Emydochampsa* Broom, Broili and Schröder regard it as lying in the *Endothiodon* zone. Boonstra (1948), on the

other hand, includes *Synostocephalus vanhoepeni* in his work on the Anomodonts of the *Tapinocephalus* zone. The specimen described by Watson as *Synostocephalus* sp., which does not belong to the same species as Broili and Schröder's specimen, is from the Hans River dam on the Beaufort West commonage, a locality definitely in the *Endothiodon* zone.

Eumantellia mirus Broom is from the farm Leeukloof which, according to Broom (1935*b*, p. 60), is in the *Endothiodon* zone. New Bethesda, the type locality of *Newtonella platyceps* Broom, is low down in the *Cistecephalus* zone (Broom, 1935*b*, p. 60). The new form is from Oudeberg, also in the *Cistecephalus* zone. Broom (1935*b*) states that although *Eumantellia* is too late in time to be the actual ancestor of typical Anomodonts, it is probably closely allied to the common ancestor. As stated above, *Broilius antjies-fonteinensis* is regarded as the most primitive of the *Tapinocephalus* zone Anomodonts, but it is impossible to derive these forms from *Broilius*, unless it is to be assumed that the premaxillary teeth are neomorphs, which is entirely against the general trend of the loss of teeth in the Anomodonts.

In *Pachytegos*, described by Haughton (1932) from East Africa, the premaxillary also carries a number of teeth, but it is a form much larger than these South African genera.

The Russian form *Venjukovia*, from which Watson (1948) derives the Anomodonts, and which was shown to be untenable as an immediate ancestor to *Broilius*, fits much better as an ancestral type to *Hueneus*.

Unfortunately the lower jaw in *Eumantellia*, *Newtonella* and *Hueneus* is not known and it is therefore impossible to tell whether a medial displacement has taken place as in *Venjukovia* and all Endothiodonts, except the Antjiesfontein specimen, but it is inconceivable that the upper teeth could have bitten on a horny shelf on the outside of the lower teeth. Although the structure of the teeth in the upper jaws of these three genera is not known, their arrangement, especially that of the large teeth near the midline, suggests that they are crushing teeth and that they bit on the teeth of the lower jaw. The horny covering was therefore restricted to the tips of the snout and lower jaw.

Summary

The main points emphasized in sections II and III can be summarised by creating a generalised hypothetical ancestral type of all Anomodonts exhibiting molars, and then from it follow all the diverging lines of evolution.

(i) *The hypothetical ancestral type.* The palate is fairly flat with only a posterior palatal ridge present. The premaxillary is short and, except for a short median posterior process, does not reach far posteriorly. The large palatal part of the maxillary bounds the internal nares laterally. The palatine is small and does not show extensively on the palatal surface. The internal nares are wide anteriorly and are separated from each other ventrally by the posterior premaxillary process and the posteriorly diverging vomer. The latter bone articulates posteriorly with the pterygoid and postero-laterally with the palatines. The transverse bone connects the lateral flanges of the pterygoid with the maxillary. The teeth are arranged on the alveolar ridge on the premaxillary and maxillary and are crushing teeth, biting on similar teeth in a groove on the dorsal aspect of the lower jaw.

(ii) *The development of the Broilius antjiesfonteinensis line.* The Antjiesfontein specimen has advanced beyond this hypothetical ancestral stage in that one of the maxillary teeth has become enlarged into a canine and the teeth anterior to this one have disappeared. In the lower jaw only the teeth opposite the maxillary teeth are retained. The anterior part of the lower jaw and the palate are now covered with horn. From the ancestral stage the line breaks up into three distinct branches:

(*a*) The teeth of the lower jaw become displaced medially and bite against the horn covered palatine and maxillary, medial to the upper teeth. The lateral part of the dentary is also covered with horn. A more extensive secondary palate is developed by the posterior expansion of the premaxillary which reaches the palatine and thereby excludes the maxillary from bounding the internal nares. The latter are very narrow anteriorly. This is typical of *Robertia broomiana.*

Emydops (and *Tropidostoma*, Seeley) is only a few steps farther advanced in this direction. The teeth of the upper jaw are arranged in a row (except where the number has been drastically reduced) on the inside of the alveolar ridge and bite entirely on the outside of the teeth of the lower jaw. Anterior palatal ridges have developed and the internal nares are posteriorly placed. In *Brachyuraniscus* the condition is essentially similar, except that the upper molars have moved even farther medially and lie entirely on the palatal part of the maxillary.

(*b*) With the medial displacement of the teeth (in the upper jaw they are entirely on the palatal part of the maxillary) and the disappearance of the canines the typical *Endothiodon* (also *Endogomphodon*, *Esoterodon* and *Emydochampsa*) condition is arrived at. Only in one known species of this group, *Esoterodon paucidens* Broom, does the palatine reach the premaxillary anteriorly. This is obviously a secondary feature, since the palatine is in contact with the median posterior process of the premaxilla (according to Broom's figure, 1932) and not with the lateral posterior parts of it, as in all the other Endothiodonts with palato-premaxillary contacts. *Prodicynodon* and *Cryptocynodon* probably also belong to this group but, in the latter at least, the palatine also reaches the premaxillary and tusks are retained.

(*c*) *Pristerodon* shows the same line of development as *Emydops*, except that the primitive feature of the absence of a palato-premaxillary contact has persisted in this group.

(iii) *The line of development of Hueneus.* As in the *Broilius* line, a canine has developed in this group (in one genus at least) only in the males, or is lost again in the females, as in *Synostocephalus* (Watson, 1948). The most anterior premaxillary and dentary teeth have disappeared and this region was probably covered with horn. The teeth, except the canine, have also become displaced medially in the three genera *Hueneus*, *Newtonella* and *Eumantellia.* The anterior teeth are on the palatal parts of the maxillary and premaxillary. In *Synostocephalus* all the small teeth are on the alveolar ridge and, as in the former three genera, the posterior teeth are immediately on the inside of the alveolar ridge. In the three typical genera of this group the teeth apparently retained their crushing character; in *Synostocephalus* they bite on horny pads

(Watson, 1948). The secondary palate has developed more extensively and the premaxillary has made contact with the palatine posteriorly.

(iv) *The line of evolution of Parringtoniella.* This form followed an evolutionary trend similar to that followed by the typical genera of the *Hueneus* line, except that the premaxillary teeth have disappeared and most of the maxillary teeth remained on (or immediately on the inside of) the alveolar ridge. Although the structure of the teeth is not known, the medial teetn are probably also crushing teeth as in the later forms of the *Hueneus* line, as they are too near the midline of the palate to be able to bite on the lateral side of the dentary.

From the above it is clear that parallel evolution is a dominant feature in these groups. The development of a more extensive secondary palate with eventual contact between palatine and premaxillary, and a narrowing of the internal nares anteriorly, as well as the medial displacement of the upper and lower teeth, are features occurring in all three lines. Loss of anterior teeth and covering of the anterior parts of the snout and dentaries with horn are common to all. The phenomenon of the eventual contact of the premaxillaries and palatines is also found in other Anomodonts and will be discussed at a later stage. As will be seen below, the anterior palatal ridges have also developed independently in more than one group.

IV. THE GENERA DICYNODON, OUDENODON, AND DAPTOCEPHALUS

The structure of the palates of a number of specimens referred to the genera *Dicynodon* and *Oudenodon* is well known. Seeley (1889) figured and described the palate of a *Dicynodon* species. In the following year Lydekker (1890) figured the palate of yet another undetermined species of this genus. *Oudenodon kolbei* Broom was described in 1912; the Sollases then described *"Didynodon ? leoniceps"* (1913) and an unknown species of *Dicynodon* (1916). Von Huene (1922) described a specimen which he referred to *"Dicynodon sollasi."* Van Hoepen (1934) and Broili and Schröder (1936) described *Oudenodon margaritae* and *Oudenodon marlothi* respectively.

When the palates of these forms are compared, it is obvious that there are two very distinct types; the palates of the specimens described by Lydekker, Seeley, and Sollas and Sollas (*Dicynodon*) are markedly different from those of the other specimens (*Oudenodon*). An investigation into the palatal structure of a large number of species referred to the genus *"Dicynodon"* proved the existence of a distinct third type (*Daptocephalus*).

(i) *The palate of the genus Dicynodon.*

The palate of the type specimen of this genus, *D. lacerticeps* Owen (No. R. 36233 B.M.N.H.), is not known but two probably closely related species fortunately were available for study. According to van Hoepen (1934), *D. feliceps* and *D. psittacops* are very closely related to *D. lacerticeps.* Broom (1935*a*) regards *D. grimbeeki* as belonging to the same genus as *D. lacerticeps* and *D. feliceps.*

Dicynodon psittacops Broom (1912*a*)
Dicynodon psittacops Seeley (von Huene, 1940, in errore).

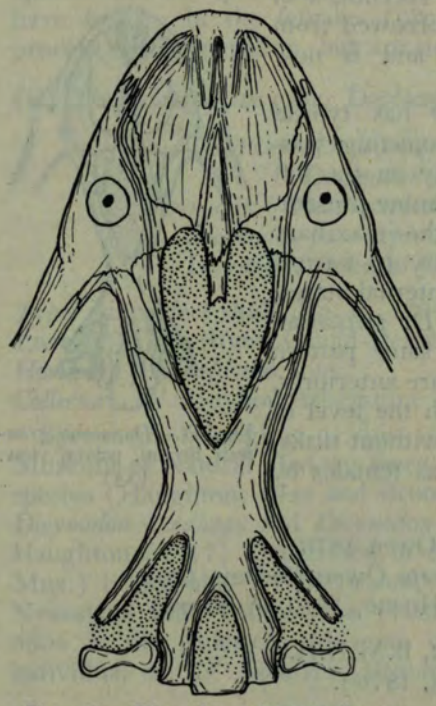


Fig. 56.—*Dicynodon psittacops* Broom, palatal view. (x1.)

Type: No. 5534 A.M.N.H. Nearly complete skull and skeleton.
Locality: Beaufort West.
Horizon: Low in the *Endothiodon* zone.
Collector: The Rev. J. H. Whaits.

A small skull, No. 228 in the collection of the Bernard Price Institute, from the Beaufort West commonage, was collected by the van der Horst expedition and agrees closely with the type of this species. It is almost complete, lacking only the left temporal arch, but has suffered slightly from lateral compression. In length it agrees with Broom's (1912*a*) second specimen (112 mm). Other measurements are given in table 7. It differs from the type as follows: The nostrils are directed more forward than upward; the tusks are directed downward instead of anteroventrally; the snout is relatively shorter. These differences are probably due to the flattening out of the snout of Broom's specimen, as a result of distortion. As far as can be determined from the new skull and the figures of the type and the specimen described by Haughton (1917), there are no other differences. The lateral nasal bosses are present and the post-pineal region is crested. The surfaces of the parietal and preparietal bones are unfortunately too damaged to determine their detailed structure.

The palate. The premaxillaries are relatively large with two anterior and a posterior median palatal ridges. A short process projects posteriorly between the internal nares to meet the vomer. The maxillaries bear two large tusks. The palatines are very small on the palatal surface and are separated from the premaxillaries by the palatal parts of the maxillaries. Laterally they are bounded by the relatively large transverse bones and posteriorly by the pterygoids. The choanae are wide anteriorly and reach the level of the tusks (fig. 56).

Dicynodon grimbeeki Broom 1935

Type: Almost complete skull, No. 245, Transv. Mus.
Locality: "Leeupoort," Beaufort West district (Broom, 1935*a*).*)

*) As it was not possible to find the farm Leeupoort on the Topo-cadastral maps of Beaufort West, a letter was written to the postmaster of this town to enquire after the situation of the farm. In reply Mr. Marais, the postmaster, stated that a farm Leeupoort is unknown there. Enquiries were then made at the Transvaal Museum by post and in reply Mr. J. T. Robinsion states that Dr. Broom is

Horizon: *Endothiodon* zone (probably near the top, Broom, 1935*b*, p. 2).
Collector: S. Grimbeek.

The palate. The palate of one of the specimens of *D. grimbeeki* (No. 307, Transv. Mus.) borrowed from the Transvaal Museum was developed and is now described here for the first time (fig. 57).

As in *D. psittacops*, the premaxillary has typical palatal ridges and a median process projecting posteriorly between the internal nares. Only on the left maxillary there is a root of a very small canine present. A narrow bar of the palatal part of the maxillary separates the palatine and the premaxillary to form a small part of the lateral border of the internal nares. The palatine is relatively small as in *D. psittacops*. The other palatal bones also follow the same pattern as in the latter species. The interal nares are anteriorly, however, much narrower and do not reach the level of the tusks. The specimens of this species, without tusks, or with vestigial tusks, were referred to as females by Broom (1935*a*).

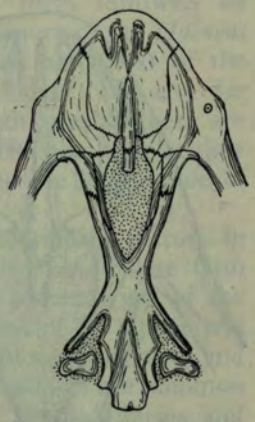


Fig. 57.—*Dicynodon grimbeeki* Broom, palatal view. (x½)

Dicynodon feliceps Owen 1876
Dicynodon (*Rhachiocephalus*) *feliceps* Owen (Seeley, 1898)
Dicynodon felinus Owen (von Huene, 1940, in errore)

Type: Skull with lower jaw, No. R. 47052, B.M.N.H.
Locality: "Basin of Fort Beaufort" (Owen, 1876).
Horizon: *Endothiodon* zone?
Collector: A. G. Bain.

The specimen sectioned and described by the Sollases (1913) as *Dicynodon ? leoniceps* is too small to belong to that species. It is stated (Sollas and Sollas, 1913) that the skull was numbered "R. 857 in the British Museum catalogue and described by Mr. R. Lydekker under the name of *Dicynodon leoniceps* Owen". Lydekker (1890), however, catalogued specimen R.857 under *D. feliceps* and not *D. leoniceps*. Its locality is given (Lydekker, 1890) as "the Gouph district near Beaufort West, south of the Nieuwveld Range." It is therefore a specimen most probably from the *Endothiodon* zone.

The palate. The palate of this specimen is very well figured and described by Sollas and Sollas in 1913. It agrees very closely with that of *D. grimbeeki* and *D. psittacops*. The anterior parts of the internal nares are here also narrow as in *D. grimbeeki*.

The essential similarity in palatal structure of these forms leads to the conclusion that the palate of the closely related *D. lacerticeps* (see above) must also be similar in structure and the generic name *Dicynodon* is retained

definitely certain that the locality is Leeupoort and that "it is about 50 miles north of Beaufort West and quite close to the farm Dunedin. The road branches off at Dunedin and goes a bit north-east from there and the farm is quite close by."

If these directions are followed one arrives at the farm Leeuwkloof, a locality very rich in fossils and from which many new forms have been described by Dr. Broom. However, this farm is 39 miles from Beaufort West.

for these species until it can be proved otherwise. Not only the types (except *D. grimbeeki*) of these four species, but also other specimens referred to these species and the specimens described by Seeley (1889) and Lydekker (1890) have tusks. In the females (presumably) of *D. grimbeeki* they are in the process of degeneration, but are nevertheless still present in some specimens.

(ii) *The palate of the genus Daptocephalus van Hoepen*

Daptocephalus leoniceps Owen (van Hoepen, 1934)
Dicynodon leoniceps Owen 1876
Dicynodon (*Rhachiocephalus*) *leoniceps* Owen (Seeley, 1898)
Dicynodon pardiceps Owen 1876 (Haughton, 1924)
Dicynodon rectidens Owen 1876 (Haughton, 1924)

Type: Imperfect skull, No. R. 47047, B.M.N.H.
Locality: Gats River, Graaff-Reinet.
Horizon: *Cistecephalus* zone.
Collector: W. Guybon Atherstone.

Specimens belonging to this species are very numerous. In the British Museum of Natural History there are two additional skulls belonging to this species (Haughton, 1924 and Broom, 1932) that were originally described as *Dicynodon pardiceps* and *Dicynodon rectidens* by Owen (1876). According to Haughton (1917) a specimen in the Port Elizabeth Museum (No. 68, P.E. Mus.) is probably a *"Dicynodon" leoniceps*, as are the specimens collected in Nyasaland and Tanganyika (Haughton, 1926 and 1932). Specimen No. 5304 in the American Museum of Natural History is apparently a young individual of *"D" leoniceps* (Broom, 1915). In the collection of the Bernard Price Institute there are four good skulls apparently belonging to this species. The specimen described by von Huene (1931) as *D. leoniceps* probably belongs to *Dicynodon leontops* Broom (Broom, 1932).

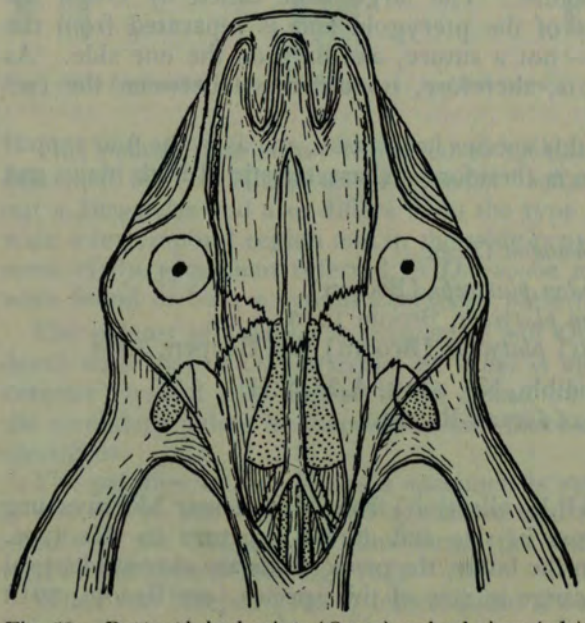


Fig. 58.—*Daptocephalus leoniceps* (Owen), palatal view. (x⅓.)

A specimen from the farm Poortjie near the Gats River, north of Graaff-Reinet (No. 304, B.P.I.), collected by A. S. Brink, was selected for the development of the palate and its description.

The palate. The palate is very deep and narrow. The premaxillary and the maxillary, anterior to the canines, form very sharp cutting edges. The two anterior palatal ridges are on the

anterior wall of the palate and are inclined at an angle of about 45° to the horizontal part of the palate.

The maxillaries are very well developed laterally, to accommodate the roots of the powerful canines. The posterior median palatal ridge is large and continuous posteriorly between the very narrow anterior extensions of the internal nares as a posterior median process of the premaxillary. The pars palatina of the maxillary comes very near to, but does not reach the internal nares. The palatine has a very short contact with the premaxillary; posteriorly it forms most of the lateral and dorsal walls of the choanae. The pterygoid forms the posterior and postero-lateral walls of the choanae; its short antero-medial process meets the vomer and the very long antero-lateral process overlaps the palatine and meets the maxillary anteriorly. The transverse bone is displaced to lie lateral to the pterygoid, instead of anterior to it, as in all the above described specimens.

The interpterygoidal fossa is subdivided into three very definite compartments by the vomer and partly by the pterygoids (fig. 58). The very thin but deep ventral part of the vomer forms the partition between the two anterior compartments. Posteriorly it is forked and the two prongs meet the antero-medial processes of the pterygoids to form the partitions between the anterior and posterior compartments. The dorso-medial walls of the anterior compartment are formed by the lateral flanges of the vomer. The roof of the posterior chamber is formed by the narrow presphenoid.

The palate of the type of *D. leoniceps* was described by Owen and figured by Griesbach (1876). The figure differs considerably from that of the Poortjie specimen. However, Miss P. L. Robinson of University College, London, who kindly re-examined the specimen, informs me that Owen completely misinterpreted the palatal structure. The large bone called by Owen the palatine is the anterior process of the pterygoid and is separated from the body of the latter by a crack — not a suture, and only on the one side. As far as I could ascertain there is, therefore, no difference between the two specimens.

All the specimens referred to this species have tusks, and as in the four typical *Dicynodons* discussed above, this is therefore a characteristic of both males and females.

(iii) *The palate of the genus Oudenodon Owen*

Oudenodon platyceps (Broom)
Dicynodon platyceps, Broom 1913
Oudenodon (*Mastocephalus*) *platyceps* (Broom) van Hoepen, 1934

Type: Complete skull with mandible, No. 5542, A.M.N.H.
Locality: New Bethesda, north of Graaff-Reinet.
Horizon: *Cistecephalus* zone.
Collector: R. Broom.

A specimen (No. 305 in the B.P.I. collection) from Milton near Murraysburg was selected as the skull nearest in size and dorsal structure to this type. Although it is a little larger than the latter, the proportions are almost identical (table 8) and it falls with the range in size of this species (see Broom, 1913 and 1932).

The palate is shallow and the anterior palatal ridges are therefore almost parallel to the plane of the roof of the mouth. As in *Dicynodon* and *Daptocephalus* the posterior palatal ridge is continued posteriorly in the medio-posterior process of the premaxillary between the very narrow anterior parts of the choanae. The lateral walls of the latter are formed by the large palatines which have extensive contacts with the premaxillaries, but they do not reach beyond the level of the internal nares anteriorly. There is almost no indication of a three chambered interpterygoid fossa, its roof being comparatively smooth. The anterior fused part of the vomers is very short, posteriorly it is divided to form the anterior part of the roof of the fossa. The anterior part of the roof and side walls are formed by the pterygoids which do not reach far anteriorly. They are separated from the maxillaries by the large transverse bones and palatines (fig. 59).

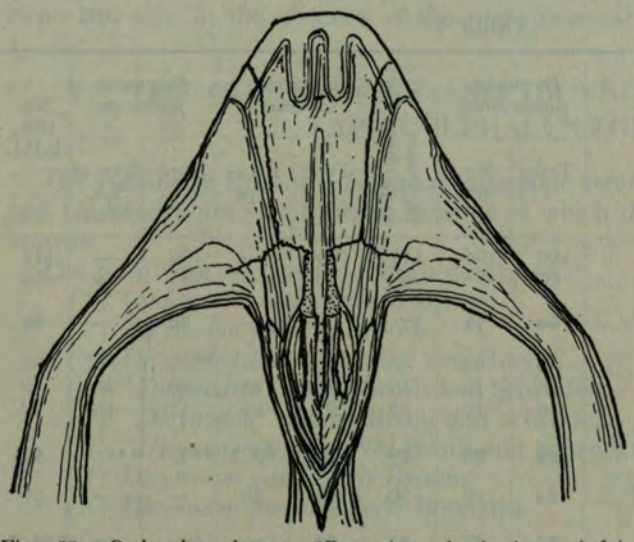


Fig. 59.—*Oudenodon platyceps* (Broom), palatal view. (x⅓.)

Although Broom in 1932 maintained that some of the smaller specimens which he referred to *"Dicynodon" platyceps* have tusks, he stated in 1935(*a*) that "we have quite a large number of specimens of *D. platyceps* all of which are devoid of tusks." Similar statements were made again in 1936(*b*) and 1940.

This palatal type is not restricted to tuskless specimens, e.g. the specimen described by von Huene as *"Dicynodon" sollasi*. This specimen is therefore not a *Dicynodon* and also differs from the type of that species in the relatively wide intertemporal region and in the wide post-pineal groove. The palates of some of the specimens referred to *Dicynodon sollasi* were developed, and they were found to have a typical *Dicynodon* pattern.

The palates of *Oudenodon margaritae* and *Oudenodon marlothi* correspond in detail with that of *O. platyceps*. *O. kolbei* is also closely related, but here the anterior choanal slits appear to be closed off (see Broom's figures, 1932); the secondary palate is, therefore, much more extensive than in the other two specimens.

The palatine in von Huene's specimen is relatively very much larger than in any of the abovementioned specimens and reaches anteriorly as far as the middle of the canines and thus forms the entire anterior part of the lateral wall of the choana (see fig. 78).

When van Hoepen (1934) reintroduced Owen's genus *Oudenodon* it was not intended to include only tuskless specimens in both sexes, but also specimens

in which the tusks are present as vestiges. Broom (1935*a* and 1936*b*) did not agree with this grouping, but suggested that van Hoepen's subgenus (under *Oudenodon*) *Mastocephalus*, of which *O. kolbei* is the type, should be made the genus (or subgenus under *Dicynodon*, 1940) for all the specimens that are tuskless in both sexes, such as *"Dicynodon" platyceps*. As stated above, classification based on the mere absence or presence of tusks in different sexes is useless; so the genus *Oudenodon* was retained for all specimens conforming to the *Oudenodon platyceps* palatal type.

The type of *Oudenodon*, *O. baini* (Owen, 1860) was never sufficiently developed to show the structure of the palate and it is therefore impossible

TABLE 7

	Dicynodon vanderhorsti		*Dicynodon antjiesfonteinensis*	*Dicynodon schroederi*		*Dicynodon psittacops*		No. 288, B.P.I.
	Type	No. 182		Type	Para-type	Type	Spec. in S.A. Mus.	
Skull length	100	104	111	104	—	106	—	112
Skull width	60	74	86	80	—	85	64	75
Width / Length	**60**	**71**	**77·5**	**77**	—	**80**	—	**67**
Basal length	85	95	—	—	—	—	83	95
Interorbital width	15	18	16	19	20	20	20	19
Intertemporal width	16	19	23	27	24	17	18	20
Interorbital width × 100 / Intertemporal width	**94**	**95**	**70**	**70**	**83·3**	**117·1**	**111·1**	**95**
Snout length	25	28	30	23	26	—	—	28
Snout length × 100 / Length	**25**	**27**	**27**	**22**	—	—	—	**25·7**

TABLE 8

	Oudenodon platyceps	
	Type	No. B.P.I. 305
Skull length	270	316
Skull width	217	251
Width × 100 / Length	**80·5**	**79**
Basal length	195	254
Interorbital width	43	43
Intertemporal width	33	35
Interorbital width × 100 / Intertemporal width	**77**	**81**
Snout length	—	70
Snout length × 100 / Length	—	**22**

to tell whether it is identical with that of these specimens. However, since no other feature could be found to distinguish generically between these specimens and the type of *O. baini*, the generic name *Oudenodon* had to be used.

(iv) *The main differences in palatal structure between Dicynodon, Oudenodon and Daptocephalus*

Dicynodon differs from *Oudenodon* in the small size of the palatine and an absence of the palatino-premaxillary contact, with the consequent lateral bounding of the internal nares by the maxillary. It differs from *Daptocephalus* in the same features and also in the absence of a pterygo-maxillary contact. *Oudenodon* differs from *Daptocephalus* in the relative largeness of the transverse bone and also in the absence of the pterygo-maxillary contact.

V. THE OUDENODONS AND DICYNODONS FROM THE TAPINOCEPHALUS ZONE

The specimens from the *Tapinocephalus* zone referred to the genera *Dicynodon* and *Oudenodon* are small forms, in some of which the structure is not very well known.

The following species have been described:

(1) *Oudenodon megalorhinus* Broom.
(2) *Dicynodon jouberti* Broom.
(3) *Dicynodon haughtonianus* von Huene.
(4) *"Dicynodon" huenei* Broili and Schröder.
(5) *"Dicynodon" broomi* Broili and Schröder.
(6) *"Dicynodon" grossarthi* Broili and Schröder.
(7) *Dicynodon gamkaensis* Broom.
(8) *Dicynodon pseudojouberti* Boonstra.

(i) *The genus Dicynodon*

A very interesting group of skulls was collected recently on the farms Klein Waterval and Antjiesfontein in the Prince Albert district by the Kitching brothers. After preparation they were found to represent three new species of *Dicynodon*.

(*a*) *Dicynodon vanderhorsti* sp. nov.

Type: Almost complete skull without lower jaw, No. 175, B.P.I. = BP/1/287
Locality: Antjiesfontein, north of Prince Albert.
Horizon: Intermediate horizon of the *Tapinocephalus* zone.
Collector: J. W. Kitching.

The type skull is beautifully preserved with only part of the left squamosal broken off. Almost all the sutures could be traced. The skull is narrow, with the intertemporal width about the same as the interorbital width. A low boss is present above the nares. Behind the pineal foramen is a deep groove formed by the parietals. A low bony ring surrounds the pineal foramen (fig. 60B). The measurements are given in table 7.

The palate. The palate is very short and shallow. A median groove is present anteriorly, but there are practically no anterior palatal ridges.

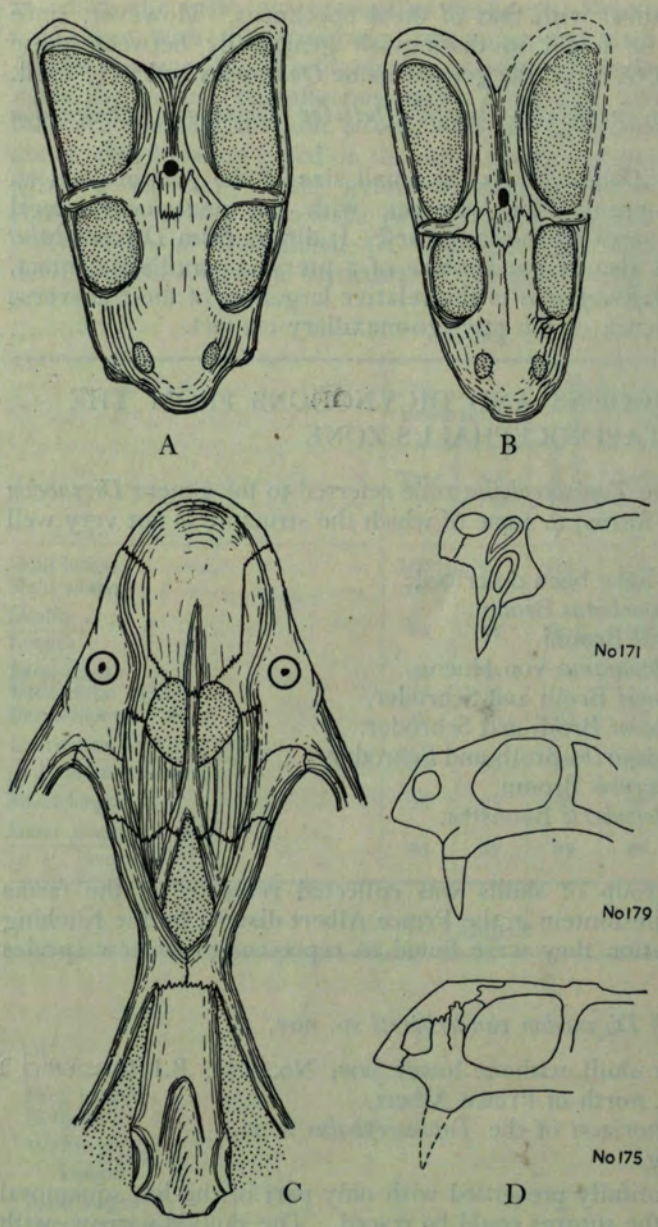


Fig. 60.—*Dicynodon vanderhorsti*, sp. nov. (A) and (B) Dorsal views of two skulls, distortion not corrected but partially reconstructed. (x½.) (C) Palatal view. (x1.) (D) Lateral views of three skulls to show variation in contour and the replacement of a canine.

Fig. 60c appears to show two short ridges. Posteriorly a well developed median ridge is present. The internal nares are placed far anteriorly and reach the level of the tusks. Their anterior parts do not converge into slits. The pterygoidal ridges are high and are continuous with the alveolar ridges. The premaxillary is narrow posteriorly with a short postero-median process. The palatines are small and do not reach the premaxillary; the maxillary therefore bounds the choana extensively laterally. The pterygoid is short and is separated from the maxillary by the large transverse bone. The palate therefore conforms typically to that of *Dicynodon* (fig. 60c).

Of the thirteen skulls referred to this species, four are tuskless and are presumably females. The tusks are very large even in a very small individual. Sections on either side of the snout of the smallest specimen were cut and two replacing tusks were exposed, which are of about the same diameter as the present functioning tusks (fig. 60d). It is therefore possible for a small specimen with large tusks to belong to the same species as a larger specimen showing only the tips of a second pair of teeth erupting, and

therefore appearing to be a young specimen of a larger species (see below).

The sides of the snouts of a number of adult skulls were cut away, but no replacing teeth could be found. Replacement of tusks seems, therefore, to be a characteristic of only young individuals, as in the Cynodontia (Parrington, 1936), but whether it happens more than once is not known.

When these specimens are arranged according to size (pineal — snout length being substituted for total length, as the temporal arches are incomplete in most specimens) a marked progressive increase in size of the nasal boss with increase in the size of the skull is noticed. In the type — a young individual which has nearly reached full size — the boss is relatively insignificant when compared with those of the older specimens. A large pineal boss was also found to be characteristic only of old males, e.g. Nos. 181 and 182, B.P.I. In the type the bony ring is but slightly raised above the skull roof, yet is definitely present.

In one of the female specimens, No. 184, B.P.I., from Klein Waterval, the one caniniform process is broken off and a small canal is exposed. The presence of this canal probably indicates that tusks in the females have recently been lost in the course of evolution.

The species is named after the late Professor C. J. van der Horst, the former Chairman of the Board of Control of the Bernard Price Institute, who led the expedition that collected a large number of fossils from the western Karroo in 1945.

Paratypes: Males; Nos. 162, 168, 171, 176, 179, 181, from Antjiesfontein. No. 182 from Klein Waterval.

Females; Nos. 173 and 180 from Antjiesfontein. Nos. 184 and 189 from Klein Waterval.

Nos. 171 and 180 are immature.

Dicynodon antjiesfonteinensis sp. nov.

Type: Almost complete skull with lower jaw, weathered. No. 219, B.P.I.
Locality: Antjiesfontein, Prince Albert district.
Horizon: Intermediate division of the *Tapinocephalus* zone.
Collector: J. W. Kitching.

The dorsal surface of the skull is considerably weathered and it is almost impossible to trace any sutures accurately. The snout is slightly damaged and the temporal arches and the left postorbital arch are incomplete. The intertemporal width is more than the interorbital width, the former being crested and very short. There appears to have been a nasal boss; a pineal boss, if present, was completely weathered away (fig. 61A and table 7). The left ramus of the lower jaw was removed to expose the palate.

The palate. It is exactly similar to that of *D. vanderhorsti* except that the internal nares are placed slightly more posteriorly. It is also considerably broader and two low anterior palatal ridges are present on the premaxillaries (fig. 61B).

The rami of the lower jaw, when viewed from below, run in front parallel to each other for a short distance before they diverge posteriorly (fig. 62A).

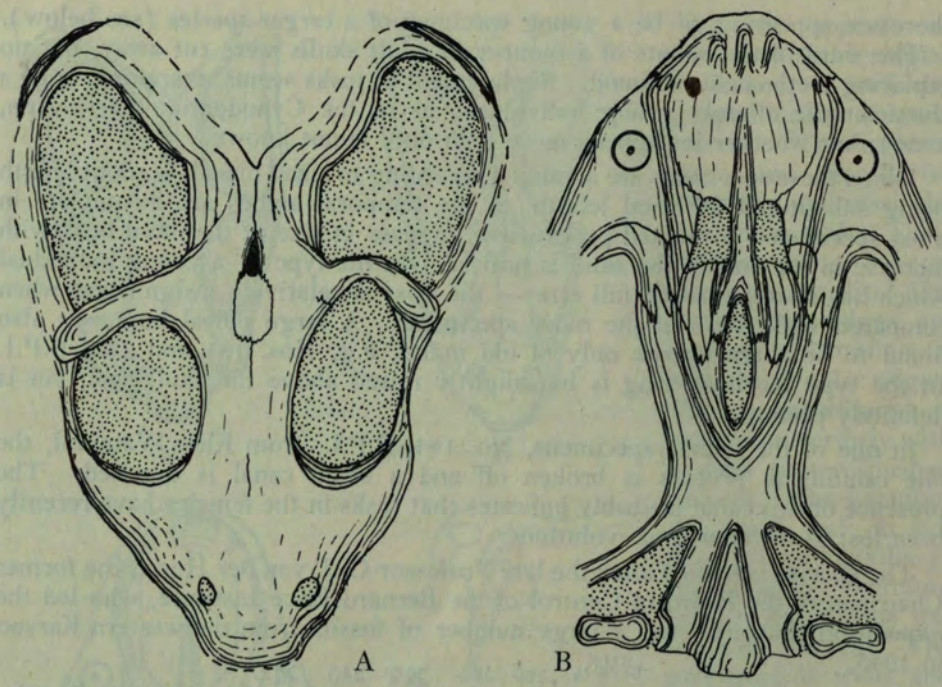


Fig. 61.—*Dicynodon antjiesfonteinensis* sp. nov. (A) Dorsal view, distortion not corrected but partially reconstructed. (x1.) (B) Palatal view. (x1.)

(*c*) *Dicynodon schroederi* sp. nov.

Type: Almost complete skull without lower jaw, No. 190, B.P.I. = B01|1|2235
Locality: Klein Waterval, Prince Albert district.
Horizon: Intermediate division of the *Tapinocephalus* zone.
Collector: J. W. Kitching.

The type skull is very well preserved and undistorted, but both temporal arches are incomplete.

The sutures on the dorsal surface of the skull are very distinct and may indicate a young individual. Another specimen, very much distorted (No. 174), from Antjiesfontein is taken as the paratype.

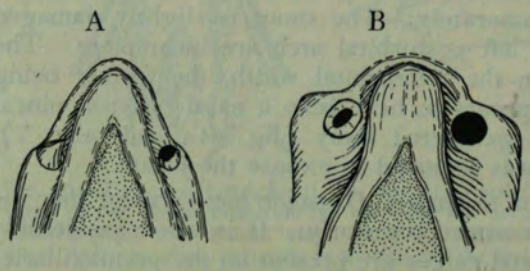


Fig. 62.—(A) *Dicynodon antjiesfonteinensis* sp. nov. ventral view of snout with lower jaw in position. (x½.) (B) *Dicynocon schroederi* sp. nov., ventral view of snout with lower jaw in position. (x½.)

The intertemporal region is very wide, about twice that of the interorbital region. In the paratype this feature is not so conspicuous (fig. 63), but this is due to the distortion of the specimen. A small boss is present above each nostril.

The pineal boss is peculiar, almost the entire preparietal is raised above the surface of the skull roof and forms the anterior part of the low ring surrounding the pineal foramen. In the paratype only the posterior half of the preparietal is raised above the surface (fig. 63A and B).

The most important feature of this species is the extensive lateral development of the maxillaries; the skull therefore has a very broad preorbital region. This development is to house the two exceptionally large tusks (fig. 62B and 63A and B).

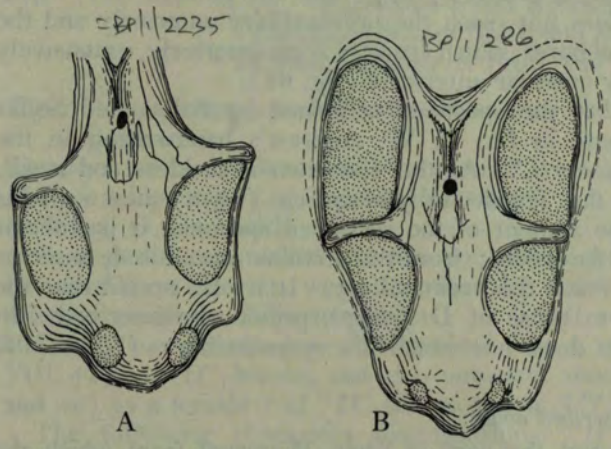


Fig. 63.—*Dicynodon schroederi* sp. nov., dorsal views of the type (A) and paratype (B). (x½.)

The palate. This is similar to that of *D. vanderhorsti* and *D. antjiesfonteinensis* in structure, but much deeper.

The lower jaw of the paratype is interesting. The rami in the anterior part of the jaw are parallel for a longer distance than in *D. antjiesfonteinensis*. When the jaw was closed lateral movement would have been impossible as, with a layer of horn on the palate and lower jaw, there cannot be more than a millimeter of space between the jaw and the tusks (fig. 62B). For mastication of food, therefore, only antero-posterior movement of the jaw could take place. The extent of this movement, however, depended also on the length of the narrow part of the lower jaw, not only on the structure of the articular joint (Watson, 1948).

This species is named after Professor J. Schröder to whom, with the late Professor Broili, we are so greatly indebted for our knowledge of the structure of Karroo reptiles.

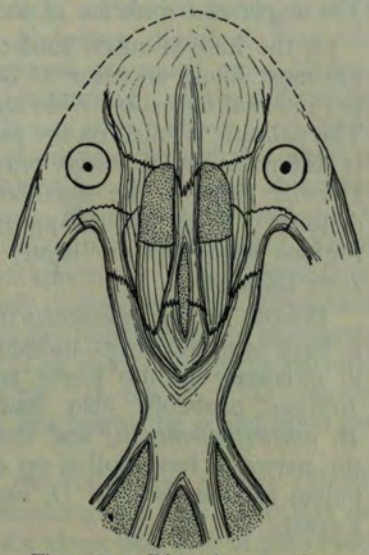


Fig. 64.—*Dicynodon pseudojouberti* Boonstra, palatal view, partially reconstructed. (x1.)

(*d*) *Dicynodon pseudojouberti* Boonstra

Type: No. 774, S. Afr. Mus.
Locality: Prince Albert Road.
Horizon: Intermediate division of the *Tapinocephalus* zone.
Collector: J. Cairncross, 1905.

A specimen was borrowed from the South African Museum, whose dorsal surface is almost completely weathered away, its detailed structure therefore indeterminable, but since the skull is without molar teeth and falls

within the range of size of that of *D. pseudojouberti*, it has been regarded as a plesiotype.

The lower jaw was carefully removed to expose the palate, of which the anterior tip is also weathered away.

The palate. This is very similar to the three species of *Dicynodon* described above. The transverse bone is relatively large and the palatine very small on the ventral surface. It does not reach the premaxillary anteriorly and the maxillaries bound the internal nares, which are very wide anteriorly, extensively on their lateral sides. They open far anteriorly (fig. 64).

Watson (1948) states that the specimen sectioned by Sollas and Sollas (1916) "appears from a note in Dr. C. W. Andrew's handwriting in the museum, to have been *D. jouberti.*" As this specimen is tuskless and small, it is more likely to be the female of Boonstra's (1948) new species *D. pseudojouberti.* From the account of the sectioned specimen it is difficult to discover the structure of the palate; from the sections reproduced, it seems as if the palatine does not reach the premaxillary. It is also stated that the palatines are very similar to those of *D. feliceps*, previously described. In this specimen the palatine does not reach the premaxillary (Sollas and Sollas, 1913).

The horizons of the species described above

The farm Antjiesfontein and the part of Klein Waterval from which the specimens described were collected are in the intermediate division of the *Tapinocephalus* zone, according to Rossouw. Prince Albert Road, the type locality of *D. pseudojouberti* also falls within this division, although some of the specimens referred to this species (Boonstra, 1948) come from the lower division, e.g. those from the farms Buffelsvlei and Kleinkoedoeskop.

The origin and evolution of the Tapinocephalus zone Dicynodons

Of the known small Endothiodonts of the *Tapinocephalus* zone, *Broilius* is the most likely ancestor of *Dicynodon.* The palates are strikingly similar — the internal nares are wide anteriorly and almost reach the level of the tusks. The palatine is small on the palatal surface and does not reach the premaxillary. It differs from *Dicynodon* only in retaining a number of small molars on the alveolar ridge of the maxillary and in a groove on the dorsal surface of the dentary. With the disappearance of the teeth and the investment of these regions with a horny layer, *Broilius* would become a typical *Tapinocephalus* zone *Dicynodon.*

Broilius antjiesfonteinensis from the intermediate horizon is too late in time to have been the direct ancestor of *Dicynodon*, since the latter genus was already in existence in the lower part of the *Tapinocephalus* zone. The ancestral *Broilius* probably also had a broad flat intertemporal region, as in *B. antjiesfonteinensis*, and this was retained by *D. schroederi.* In *D. vanderhorsti* the parietals have rolled up dorsally to form a deep groove posterior to the pineal foramen and in *D. antjiesfonteinensis* the groove is closed off to form a crest.

(ii) *The genus Oudenodon*

Of the remaining molarless Anomodont species of this zone, only the palate

of the specimen described by Broili and Schröder as "*Dicynodon grossarthi*" is known and it can therefore be referred to its proper genus, but it is impossible to place the other species in either *Dicynodon* or *Oudenodon* with certainty.

Oudenodon huenei (Broili and Schröder)
Dicynodon huenei Broili and Schröder, preoccupied
Dicynodon broilii Boonstra
Dicynodon broomi Broili and Schröder
Dicynodon grossarthi Broili and Schröder

Type: Almost complete skull with lower jaw, No. 1934 VIII 46 in the Munich collection.
Locality: La-de-da, Beaufort West district.
Horizon: Upper part of *Tapinocephalus* zone.
Collector: G. Grossarth.

Four skulls, two tusked and two not tusked, from the farm La-de-da in the Beaufort West district, were described by Broili and Schröder in 1937 and referred to three different species. A small tusked specimen (No. 1934 VIII 46) was described as "*Dicynodon*" *huenei*, a larger specimen (No. 1934 VIII 47) as "*D*" *broomi*, and two untusked specimens (Nos. 1934 VIII 47*b* and 48) as a female ? of "*D*" *broomi* and as "*D*" *grossarthi* respectively.

The following characters distinguishing "*D*" *huenei* from "*D*" *broomi* were given: "*D*" *broomi* is larger; the preorbital region is relatively larger; there is a large median boss above the nares; a pineal boss is present, and there is a difference in profile of the anterior parts of the skull and especially the skull roof.

Broili and Schröder (1937) regard "*D*" *huenei* as an adult on account of the large tusks present in the specimen. As in the case of a related genus (*Dicynodon*), they may be the first pair of tusks and, as shown there, another pair could erupt before the animal is adult. Assuming therefore that this individual is immature (the sutures in this specimen are much more distinct than in the others, a feature usually indicative of immaturity), all the differences cited could be attributed to a difference in age. It was shown above (section I) that there is a relatively greater increase in snout length with increase in total skull length; immaturity can therefore account for the relative shortness of the snout in this form. Similarly it was shown in the case of *D. vanderhorsti* that nasal and pineal bosses are characteristic of mature individuals. From the series of profiles (fig. 60c) of *D. vanderhorsti* specimens, it will be noticed that there are great differences in shape, due mostly to distortion and differences in age, within a single species; such differences are therefore very unreliable characters for distinguishing between species. The shape of the preparietal used by Boonstra (1948) as a "key" character for "*D. broilii*" ("*D*" *huenei*, Broili and Schröder) is also extremely variable and cannot be relied upon for species discrimination.

"*D*" *grossarthi* differs from "*D*" *broomi* in the following aspects (Broili and Schröder, 1937): The skull is not so much elongated and the orbits do not fall partly in the posterior half of the skull, the shape and size of the orbits are different, the convexity of the skull roof is different, and the postorbital and sub-orbital arches are more slender.

Unfortunately *"D" grossarthi* was compared only with the male of *"D" broomi* and not with the (supposed) female. When compared with the latter, most of the differences fall away. As will be seen from Broili and Schröder's tables, *"D" grossarthi* differs in proportions much less from the female ? of *"D" broomi* than does the latter from the male. Both tuskless specimens differ from the tusked specimen in the relative shortness of the snout and the fact that the orbits fall within the anterior half of the skull. The reason for this phenomenon (sexual dimorphism) has been discussed above. The relatively great increase in the length of the preorbital region with the increase in total length in the male skull causes the orbits eventually to fall partly within the posterior half of the skull. Slenderness of the post-orbital and sub-orbital bars also appears to be subject to sexual dimorphism. Judging from the figures there is no difference in the size of the arches in *"D" grossarthi* and the female ? of *"D" broomi*. The size and shape of the orbits and the profile of the top of the skull are largely affected by distortion (see above) and cannot be regarded as specific characters. A new species can hardly be based solely on the contours of the skull roof, unless the specimen is a very well preserved one.

From the above discussion it is justifiable to infer that these two tuskless specimens belong to the same species and that they are females of the tusked specimens.

The palate. Of this group the palate of the specimen referred to as *"D" grossarthi* is figured and described by Broili and Schröder. It differs from that of Dicynodons of the *Tapinocephalus* zone in the following aspects: The choanae are very narrow anteriorly, but reach about as far forward as in the latter species. The palatine is very large on the surface and reaches anteriorly between the maxillary and premaxillary. It therefore separates the maxillary completely from bounding the choana laterally. The transverse bone is small. In *"D" grossarthi* the anterior palatal grooves are not shown in the figure and are apparently absent, but in the two specimens referred to as *"D" broomi* they are present.

This palatal type is entirely different from that of *Dicynodon* but is very similar to that described for *Oudenodon*; *"D" huenei* must therefore be transferred to this genus.

As von Huene (1940) and Boonstra (1948) point out, *"D" huenei* (Broili and Schröder) is preoccupied by Haughton's *Dicynodon huenei* from East Africa (1932); Boonstra therefore proposed the name *"D" broilii* for this specimen. It now appears that this specimen belongs to another genus — *Oudenodon*; the name *O. huenei* is therefore in order. *Dicynodon huenei* (Haughton) may, however, eventually also prove to belong to the genus *Oudenodon*, in which case *O. broomi* could have priority as a name for this species.

The origin of the genus Oudenodon

Robertia broomiana from lower down in the *Tapinocephalus* zone is a very good ancestral type for this genus. With the loss of the molar teeth it will become exactly similar in structure to *Oudenodon*. The palatine is, however,

more extensively developed on the ventral surface. The broad and flat intertemporal region of *Robertia* developed as in *Dicynodon* into a narrow and grooved post-pineal region.

(iii) *Notes on the remaining molarless Anomodonts from the Tapinocephalus zone*

(*a*) *Oudenodon megalorhinus* Broom

Dicynodon megalorhinus (Haughton) 1917

Type: Incomplete skull, No. 640, S. Afr. Mus.
Locality: Prince Albert Road.
Horizon: Intermediate division of the *Tapinocephalus* zone.
Collector: R. Broom.

This interesting species is known by only one specimen. It was first described by Broom (1904*b*) and restudied and figured for the first time by Haughton (1917). Von Huene (1931) referred four more specimens to this species, but they definitely do not belong here. Broom (1932) must have been aware of these "additional" specimens (he mentions a new species from the same paper of von Huene), but states that "*D*" *megalorhinus* is only known by a single imperfect skull. Broili and Schröder (1937) also cast doubt on the identification of these specimens. The main difference between the type and these new specimens are the following: Von Huene's (described) specimen is larger. The intertemporal and interorbital ratio is reversed and the pineal-snout length is much less. The wide intertemporal region does not throw much light on its origin as both ancestral types, *Broilius antjiesfonteinensis* and *Robertia broomiana* have this feature in common.

(*b*) *Dicynodon jouberti* Broom

Type: Skull, No. 695, S. Afr. Mus.
Locality: "Koup."
Horizon: *Tapinocephalus* zone.
Collector: J. R. Joubert.

Through the studies of Broom (1905*a*), Haughton (1917) and von Huene (1931), the morphology of the roof of the skull is well known. The species is important as it is the only form in this zone where tusks are known with certainty to be present in both males and females. It was shown that the most probable ancestor of *Oudenodon* is *Robertia broomiana*; in this species, however, the females are tuskless (Boonstra, 1948), which, unless it comes from a very primitive *Robertia* where tusks are still present in the females, exclude it as a likely ancestor of this species. *Broilius antjiesfonteinensis* is known only by one specimen in which small tusks are present. If this latter specimen is a female, it is a very probable ancestor of *D. jouberti*.

(*c*) *Dicynodon haughtonianus* von Huene

Type: Skull in the collection of the University of Tubingen.
Locality: Bloukrans, east of Prince Albert Road.
Horizon: Intermediate division of the *Tapinocephalus* zone.
Collector: F. von Huene.

The type was collected together with specimens referred to *D. jouberti* (von Huene, 1931). One of the skulls referred to *D. pseudojouberti* by Boonstra (1948) — a specimen collected by Haughton (No. 3613, S. Afr. Mus.) — is from the same locality as von Huene's specimen and it will therefore be interesting to compare the two species.

Of the sixteen characteristics of *D. pseudojouberti* given by Boonstra, the majority apply equally well to *D. haughtonianus* as far as can be judged from the drawings and descriptions of the latter. Only on two points do they seem to differ: (1) In *D. pseudojouberti* the external nares are fairly large and extend to near the alveolar margin. This is apparently not the case in *D. haughtonianus*, but this character seems to be subject to a great deal of variation. In the type of *D. schroederi*, for example, which is relatively undistorted, the external naris of the left side is 10 mm. from the alveolar border, but on the right side it is only 3 mm. away. (2) In *D. pseudojouberti* the orbit lies entirely within the anterior half of the skull; in *D. haughtonianus* it partly falls in the posterior half. As was stated above, the length of the snout, and consequently the position on the orbits, depends on age and the presence, or absence, of tusks in these forms. Unfortunately it is not known whether *D. haughtonianus* is tusked or not, but it is dangerous to rely on this feature.

When Boonstra's key (1948) for forms without molar teeth is used for *D. haughtonianus* it falls within the same species as *D. pseudojouberti*.

It therefore seems probable that these two forms belong to the same species and that *D. pseudojouberti* is synonymous with *D. haughtonianus*.

(*d*) *Dicynodon gamkaensis* Broom 1937

Type: Almost complete skull, No. 1570 in the Transvaal Museum.
Locality: Klipbank, Beaufort West district.
Horizon: Upper part of *Tapinocephalus* zone.
Collector: R. Broom.

This specimen was borrowed from the Transvaal Museum, but the jaw could not be removed without breaking the skull. In shape and structure it is very near to *Oudenodon huenei* and to *Dicynodon vanderhorsti*, but differs from both in the more rounded outline of the skull.

Horizons of the species discussed above

The farms La-de-da and Klipbank, the localities of *Oudenodon huenei* and *Dicynodon gamkaensis* respectively, are both near Beaufort West and therefore near the line of contact between the *Tapinocephalus* and *Endothiodon* zones. Bloukrans (*D. haughtonianus*) and Prince Albert Road (*D. megalorhinus*) are placed by Rossouw in the intermediate division. The exact type locality of *D. jouberti* is not known, but specimens were obtained from Bloukrans (von Huene, 1931). According to Broom (1932) the type is from very near the bottom of the *Tapinocephalus* zone.

VI. THE PHYLOGENETIC RELATIONSHIP OF SOME LATE ANOMODONTS AND THE FURTHER EVOLUTION OF THE GENERA DICYNODON, OUDENODON, AND DAPTOCEPHALUS

(1) The Genera Lystrosaurus and Kannemeyeria

(*a*) *Lystrosaurus* Cope

Lystrosaurus amphibius Brink

Type: Almost complete skull without lower jaw, No. 135, B.P.I. = BP/1/2018
Locality: Ripplemead, New Bethesda.
Horizon: *Lystrosaurus* zone.
Collector: J. W. Kitching.

This specimen was described by Brink in 1951, but the palatal structure is here figured for the first time. In structure it is very similar to that of *L. murrayi* (Huxley) as described by van Hoepen (1913, as *L. latirostris* Owen) and by Broom (1932), and to that of the specimen described as *"Ptychosiagum"* sp. by Broom (1902). It differs, however, in the extent of the secondary palate. In *L. murrayi* and *"Ptychosiagum"* (*Lystrosaurus*) the internal nares are fairly wide anteriorly and are bounded in front by the premaxillaries, and laterally by the maxillaries and palatines. In *L. amphibius*, on the other hand, the anterior part of the choana is completely closed off and is bounded anteriorly solely by the palatide. The maxillary is in contact with the median posterior process of the premaxillary; the palatine is also in contact with the latter structure and with the anterior part of the vomer.



Fig. 65.—*Lystrosaurus amphibius* Brink, palatal view. (x½.)

The palate of *Lystrosaurus* shows great similarity to both *Dicynodon* and *Daptocephalus*. As in the latter genus, the anterior process is in contact with the maxillary. In *L. amphibius*, as in *L. murrayi*, a separate transverse bone could not be detected. In *L. murrayi* the palatine does not reach the premaxillary anteriorly as in *Dicynodon*. In L. *amphibius* there is a contact between the palatine and the posterior process of the premaxillary, but this is a secondary feature.

L. amphibius is regarded by Brink (1951) as representing the species farthest

advanced towards a successful aquatic mode of life. This development was therefore also accompanied by very extensive development of the secondary palate (fig. 65).

(*b*) *Kannemeyeria* Broom

Kannemeyeria latifrons Broom

Type: Incomplete skull, No. 1199 P in the collection of the Port Elizabeth Museum.

Locality: Burghersdorp district.

Horizon: *Cynognathus* zone.

Collector: The Rev. Fraser.

A skull from Winnaarsbaken in the Burghersdorp district (No. 235, B.P.I.) was referred to this species (Toerien, 1951). The palate of this species is here figured for the first time. It is essentially similar to the palate of the *Kannemeyeria* described by Pearson (1924), but differs in one important feature. In *K. latifrons* the anterior parts of the internal nares have been closed off as in *Lystrosaurus amphibius* and are now merely represented by the sutures between the palatal parts of the maxillaries and the posterior median processes of the premaxillaries; although the palatines therefore reach the latter structures medially, they are still similar to the *Dicynodon* condition. The figure of the palate of Pearson's *Kannemeyeria, K. simocephalus* (Weithofer), according to Broom (1932), gives the impression of the palatine having reached the premaxillary anteriorly and not medially. However, the specimens on which the description and figure of this region were based are both unsatisfactorily preserved and much weight should not be attached to this difference (Pearson, 1924). The pterygoid reaches the maxillary dorso-medially to the transverse bone and also on the palatal surface. The transverse bone is very small and is displaced laterally as in *Daptocephalus*. In the development of the more extensive palate it is very similar to *L. amphibius* (fig. 66).

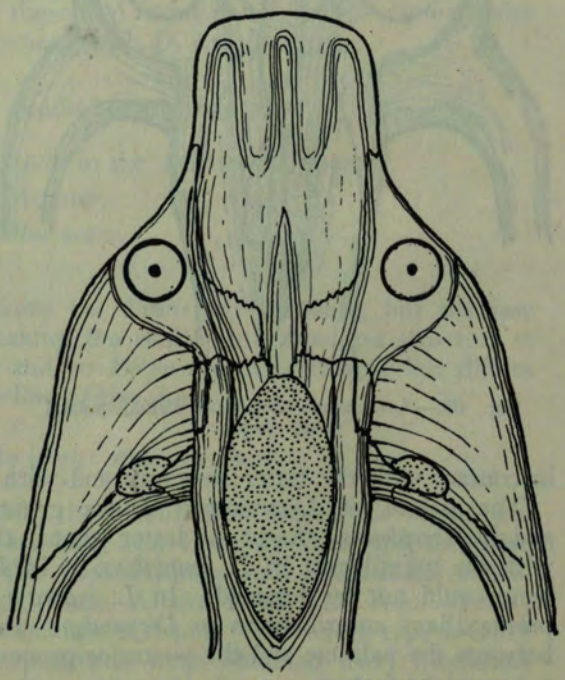


Fig. 66.—*Kannemeyeria latifrons* Broom, palatal view. (x½.)

(2) The Genera Platycyclops, Kitchingia, and Pelanomodon

(*a*) *Kitchingia* Broom and George

Kitchingia planifrons Broom and George

Type: Large skull without temporal arches and lower jaw, No. 124, B.P.I. = BP/1/906
Locality: Brandkraal, Murraysburg district.
Horizon: *Cistecephalus* zone.
Collector: J. W. Kitching.

The specimen was described and figured in dorsal view by Broom and George in 1950. The palate is here figured and described for the first time (fig. 67).

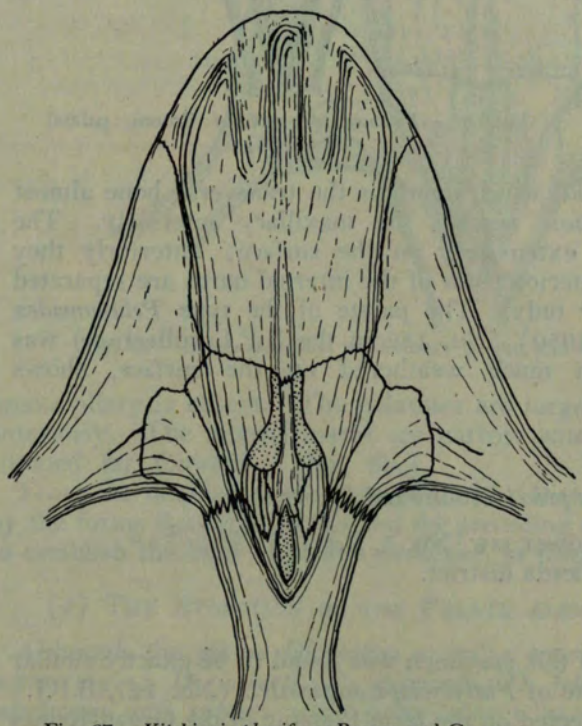


Fig. 67.—*Kitchingia planifrons* Broom and George, palatal view. (x ½.)

The structure of the palate is typically Oudenodont and resembles that of *O. platyceps* closely, but differs from that genus in the shortness of the postero-median process of the premaxillary. In *Oudenodon* the vomero-premaxillary suture is well behind the palatino-premaxillary suture and at the level of the widening of the internal nares. In *Kitchingia* the two sutures are at the same level as the anterior ends of the internal nares. As in *Oudenodon*, the anterior process of the pterygoid is short and is widely separated from the maxillary by the large transverse bone. The palatines are very large on the surface and have long contacts with the premaxillaries. The maxillaries have very small palatal aspects. The narrow anterior slits of the internal nares are bounded medially only by the vomer. Although the palatines suffered somewhat from weathering, traces of the palatal bosses can be seen on their ventral surfaces.

(*b*) *Pelanomodon* Broom

Pelanomodon rubidgei Broom

Type: Complete skull without lower jaw, No. 10 in the Rubidge Collection.
Locality: Karreelaagte, Graaff-Reinet district.

Horizon: *Cistecephalus* zone.
Collector: ?

The type specimen of this species was recently acquired from the Transvaal Museum where it was housed since its description by Broom in 1938. After preparation it was sent back to Mr. Rubidge's museum, where it is now permanently kept. As will be seen in the figure (fig. 68) the palate is very similar to that of *Oudenodon*. In the absence of a postero-medial process of the pre-maxillary, it resembles *Kitchingia*. Extraordinary, however, is the length of the anterior process of the pterygoid, which overlaps the transverse bone almost completely ventrally, and almost reaches the maxillary anteriorly. The palatines are large and show extensively on the surface; anteriorly they meet the premaxillary. The anterior parts of the internal nares are separated from each other by the vomer only. The palate of the type *Pelanomodon kitchingi* Broom and George (1950) (No. 152 in the B.P.I. collection) was also developed and, although much weathered on the surface, shows essentially the same features.

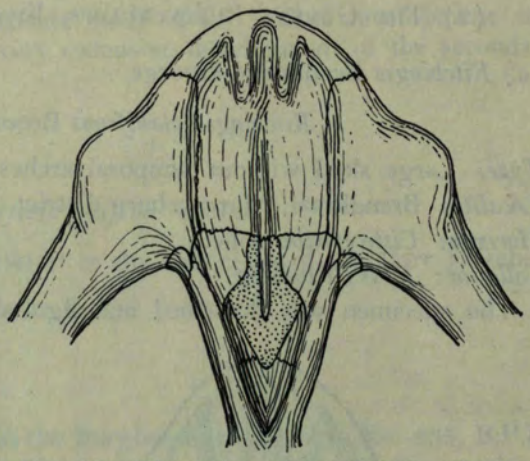


Fig. 68.—*Pelanomodon rubidgei* Broom, palatal view. (x¼.)

(*c*) *Platycyclops* Broom, 1932

Platycyclops pricei Broom and George

Type: Complete skull without lower jaw, No. 1, B.P.I. = BP/1/310
Locality: Doornberg, New Bethesda district.
Horizon: *Cistecephalus* zone.
Collector: B. J. Kitching.

The structure of the palate of this specimen was found to be exactly similar to that of *Kitchingia*. The palate of *Platycyclops acutirostris* (No. 127, B.P.I.) Broom and George (1950), collected on the farm Poortjie in the Graaff-Reinet district, was also developed, but unfortunately no sutures could be traced. In structure, however, it is also similar to that of *Kitchingia*.

(3) The Genus Aulacocephalodon Seeley, 1898

Aulacocephalodon vanderhorsti Broom and George

Type: Complete skull without lower jaw, No. 156, B.P.I. = BP/1/634
Locality: Leeufontein, Murraysburg district.
Horizon: *Cistecephalus* zone.
Collector: J. W. Kitching.

Although many species of *Aulacocephalodon* have been described, the palate

is here figured and described for the first time. *A. vanderhorsti* was described by Broom and George (1950). The palate is very similar to that of *Pelanomodon*, but although the pterygoids also reach far anteriorly, the transverse bone is relatively much bigger. The postero-medial process of the

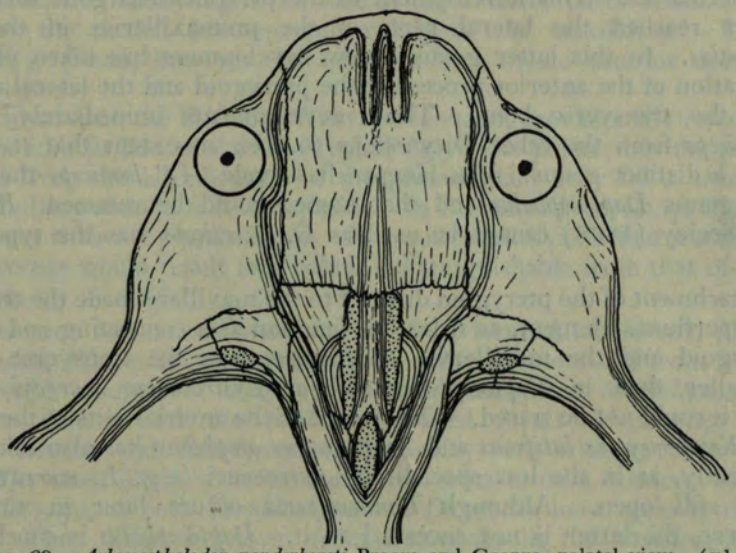


Fig. 69.—*Aulacocephalodon vanderhorsti* Broom and George, palatal view. (x¼.)

premaxillary is absent. The palatines are large and reach the premaxillaries anteriorly. The internal nares are narrow anteriorly. The two canines are situated far forward. (fig. 69.)

From the detailed description of the variations in palatal pattern exhibited by the forms described in this and the preceding two sections, it is now possible to establish the lines of palatal evolution in these forms.

(4) The Evolution of the Palate along the Dicynodon Line

Although the genus *Dicynodon* contains species which are tusked in both sexes, e.g. ? *D. jouberti*, *D. grimbeeki*, *D. feliceps*, *D. psittacops* and ? *D. lacerticeps*, and species with tusks absent in females, e.g. *D. sollasi* and *D. vanderhorsti*, etc., the similarity in palatal structure shows that they are very closely related. The loss of tusks in the females must have occurred independently in different species. *D. grimbeeki* is a perfect transitional form where the tusks are considerably degenerated in some females and are absent in others, but this species lived too late to be ancestral to all species which lost their canines in the females, as almost all *Tapinocephalus* zone Dicynodons already had this character. The latter forms therefore cannot be direct ancestors to the typical Dicynodons, but their palates furnish the morphological stages along which the more extensive secondary palates of the latter forms have developed (fig. 71).

In *D. vanderhorsti* and *D. schroederi* the internal nares are wide anteriorly and reach the level of the tusks. In *D. antjiesfonteinensis* and *D. psittacops*

the premaxillaries and maxillaries have grown posteriorly and the choanae now open some distance behind the level of the tusks. In *D. feliceps* and especially in *D. grimbeeki*, the palatines have developed antero-medially and the maxillaries medially and they almost reach the postero-medial processes of the premaxillaries. This development of the palatines has gone further and they have reached the lateral parts of the premaxillaries in the genus *Daptocephalus*. In this latter genus a new development has taken place, i.e. the elongation of the anterior process of the pterygoid and the lateral displacement of the transverse bone. These developments immediately separate *"D" leoniceps* from the other Dicynodons to such an extent that it must be placed in a distinct genus. Van Hoepen has made *"D" leoniceps* the type of his new genus *Daptocephalus* and that name should be retained. *Rhachiocephalodon* Seeley (1898) cannot be used as *D. lacerticeps* was the type of this subgenus.

The attachment of the pterygoid directly to the maxillary made the transverse bone a superfluous element, as it lost its function as a connecting rod between the pterygoid and the maxillary. In *Kannemeyeria* the transverse bone is even smaller than in *Daptocephalus* and in *Lystrosaurus murrayi* and *L. amphibius* it could not be traced. The closure of the anterior slits of the internal nares in *Kannemeyeria latifrons* and *Lystrosaurus amphibius* has also taken place independently, as in the less specialised Lystrosauri (e.g. *L. murrayi*) these slits are still open. Although *Kannemeyeria* occurs later in time than *Lystrosaurus*, the latter is not ancestral to it. *Daptocephalus* is much nearer to the ancestral type; it has a very narrow intertemporal region, a high narrow skull, and as in *Kannemeyeria* there are no bosses on the snout.

The presence of tusks in both sexes of these two genera and in the typical species of *Dicynodon* also indicates a close relationship.

(5) The Evolution of the Oudenodon type of Palate

As was stated above the most likely ancestor of the early Oudenodons at least is *Robertia*. This does not mean that all the molarless specimens with an *Oudenodon* type of palate developed from this genus.

Watson (1948) states that it is difficult to believe that descendants of *Tropidostoma* did not in fact evolve into "Dicynodons" (i.e. *Oudenodon*). The palate of *Tropidostoma*, probably from the *Endothiodon* zone, as figured by Watson (1948), differs from that of *Oudenodon platyceps* in the following aspects: The anterior process of the vomer is received in a cleft of the premaxillaries at the level of the premaxillary-palatine sutures. The antero-medial part of the latter bone abuts on the vomer medially. In *Oudenodon platyceps* the premaxillary projects posteriorly far beyond the level of the palatino-premaxillary suture and the vomer is not nearly in contact with the palatines. The secondary palate in this specimen is therefore not as extensively developed as in *Tropidostoma*. As the tendency in these forms is to develop a larger secondary palate, the change from *Tropidostoma* to *Oudenodon* will therefore be a reversal of this process and it can thus be excluded as an ancestor to *Oudenodon*. There is the possibility that some of the molarless Anomodonts described as *"Dicynodon"* or *"Oudenodon"* might be found to be

descendants of *Tropidostoma*, but they will be recognised by the structure of their palates.

Another possibility is the development of a typical *Oudenodon* type of palate by a *Dicynodon*. As was seen in the case of *Kannemeyeria* and *Lystrosaurus*, the narrowing or closure of the anterior parts of the choanae is caused by the medial development mainly of the maxillaries. The same functional goal can, however, be achieved by a medio-anterior development of the palatine.

A specimen from the Beaufort West commonage, provisionally referred to as *Dicynodon ictidops* Broom, has the typical *Dicynodon* palate, but the palatine is separated from the lateral parts of the premaxillary only by a narrow strip of the maxillary about a millimeter wide. In *Daptocephalus leoniceps* the palatine is in contact with the premaxillary. It is quite conceivable that a continuation of this process would result in a palate indistinguishable from that of a typical *Oudenodon*.

The question now arises whether any of the large Anomodonts, *Kitchingia*, *Pelanomodon*, *Platycylops* and *Aulacocephalodon*, can be derived from any of the three possible sources of origin. With the exception of *Aulacocephalodon*, the other genera and the probable related forms *Megacyclops* Broom, *Eocyclops* Broom and *Rhachiocephalodon* Seeley are without tusks in both sexes. The most likely ancestor therefore seems to be a tuskless *Oudenodon*, e.g. *O. platyceps*, as both *Tropidostoma* and *Dicynodon* have tusks in the males at least. They differ, however, from *Oudenodon* in the absence of a long posterior premaxillary process. In *Tropidostoma microtrema* this process is also absent, but here also the secondary palate is too well developed for it to be a direct ancestor. In *Dicynodon* a short posterior premaxillary process is usually present and as in *Pelanomodon*, *Platycyclops*, and *Aulacocephalodon* the anterior process of the pterygoid becomes elongated in their descendants *Daptocephalus*, *Kannemeyeria* and *Lystrosaurus*. The elongation of the pterygoid process seems, however, to have developed independently in the two groups, as in *Kitchingia*, with an otherwise similar palate as *Pelanomodon* etc., this process is short.

All the described species of *Aulacocephalodon* appear to have tusks in both sexes, a factor pointing to a close relationship with the typical Dicynodons. But if *Aulacocephalodon* is related to a *Dicynodon*, *Pelanomodon* (which differs from *Aulacocephalodon* in the presence of tusks and being relatively rare, and on the other hand is so similar that the first species described as *Pelanomodon moschops* (Broom) was referred to that genus) must also have been derived from *Dicynodon*. Although there are almost three times as many Aulacocephalodons as Pelanomodons, there still remains the possibility that the latter are merely the females of the former genus, in which case an *Oudenodon* with tusks in the males could readily be the ancestor.

Summary

The variability of the Anomodonts is enormous, both inter- and intra-specifically and it manifests itself in numerous widely divergent forms. However, so many specimens of this sub-order, representing intermediate

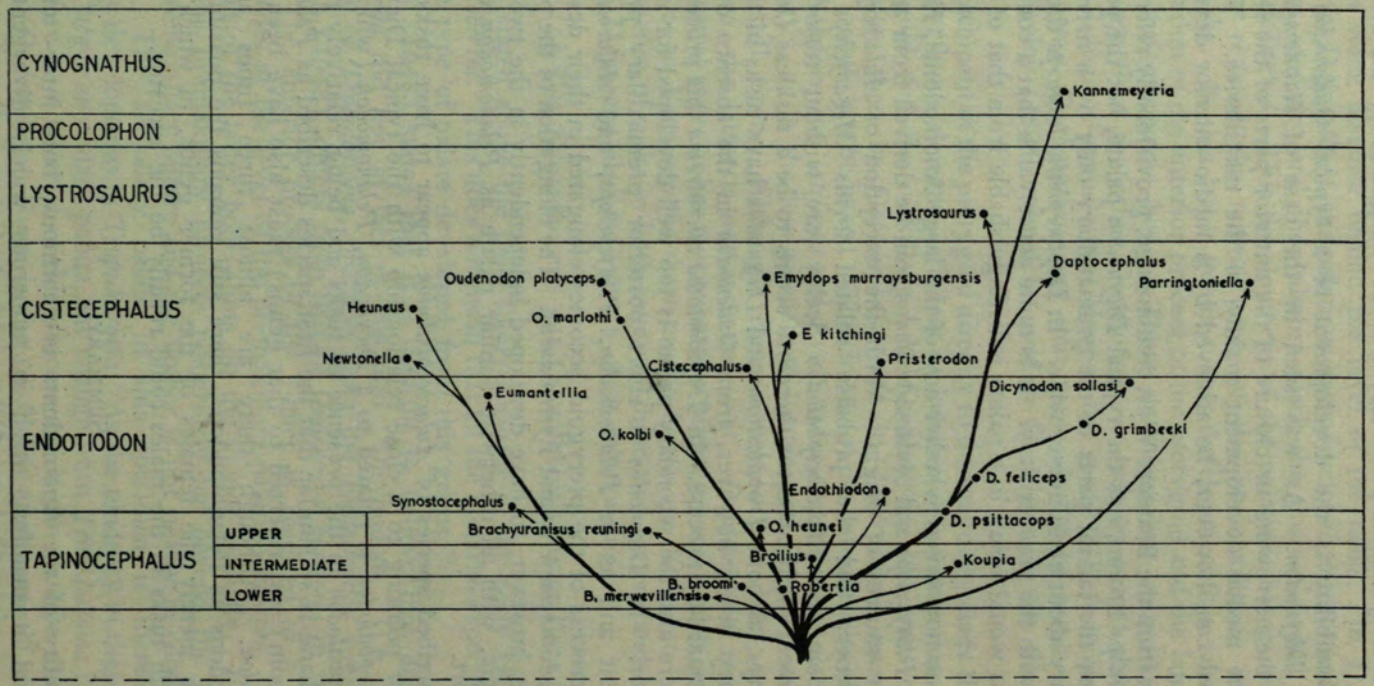


Fig. 70.—Genealogical tree to show the relationship of the main South African Anomodonts.

stages in the development of the different forms, are now known that most of the evolutionary lines can be traced virtually step by step. Although illustrations of two types of "*Dicynodon*" (Sollas and Sollas, and Broili and Schröder, etc.) have been published, the differences previously recognised can now be appreciated as providing an adequate basis for subdividing the genus "*Dicynodon*." The *Oudenodon* and *Dicynodon* palatal types are not merely a secondary development, the one from the other, but have totally different origins. *Dicynodon* can now be traced from a *Broilius* ancestor through the *Tapinocephalus* and *Endothiodon* zones to the *Cistecephalus* zone, where one of them changed into *Daptocephalus*, and others into *Lystrosaurus* and *Kannemeyeria*, forms which persisted into the *Lystrosaurus* zone and *Cynognathus* zone respectively. In these forms the palate remained fairly distinct and the evolution can be followed with ease.

The *Oudenodon* type of palate on the other hand, is most likely at least diphyletic in origin. Although *Tropidostoma microtrema* is excluded as a direct ancestor on account of the well developed secondary palate, there is nothing to bar a slightly more primitive member of this genus from losing its few remaining molars and so becoming an *Oudenodon* with canines in the male.

By the lateral displacement of the palatal part of the maxillary and the antero-medial development of the palatine in *Dicynodon*, another *Oudenodon* type of palate can be arrived at, in which the species can have tusks in both sexes, or in males only.

The most likely ancestor for the early forms of *Oudenodon* is *Robertia broomiana*, which by the loss of its molar teeth could become an almost perfect *Oudenodon*. As in the case of some of the Dicynodons, a reduction of the canines also took place, and in a species such as *O. platyceps* and in related forms only tuskless specimens are known.

A. Variations in Dicynodon

Differences occurring in a group of apparently related *Dicynodon* specimens from the same locality and horizon are generally separable into two main categories, viz. those due to sex and age and those being the result of evolutionary trends in a particular direction.

(1) *Sex and age*

In the two species of *Dicynodon*, *D. grimbeeki* and *D. sollasi*, sex determines the presence of well developed tusks in the males and their absence (or vestigial appearance) in females, and thus comes to affect the size of the snout. Consequently the preorbital region in males is relatively much more massive than that in females. In young males, where the tusks have not yet attained maximum size, the snout is also smaller than that of adult males and a juvenile male with unerupted tusks can easily be mistaken for a female.

In the new species *D. vanderhorsti*, it was also observed that well developed pineal and nasal bosses are restricted to old males. Canine replacement was noticed in this species for the first time in Anomodonts; the replacing tooth has the same diameter as that of the tooth that is being replaced.

When the four specimens described by Broili and Schröder (1935) as

belonging to three species of *"Dicynodon"* are reconsidered in the light of all these observations, these specimens must all be referred to a single species of *Oudenodon*, their distinctiveness being based almost entirely on features now known to be sex and, or, age differences.

(2) *Evolutionary series and the species concept*

Where enough material from a single restricted locality is available, evolutionary changes along a particular morphological direction can be traced in adequate detail to demonstrate their serial unity, e.g. the formation of a post-pineal crest in *D. sollasi*. Such a series might not constitute a strict "species" in the sense that the term is generally used taxonomically, but the term can still be used logically to denote such a series of forms closely linked in their morphology, separated from other such groups or individual forms only by the incompleteness of the geological record (see also Simpson 1945).

B. Structure and Classification of Endothiodonts

(1) *Number and structure of teeth as a basis of classification*

An investigation into the number and structure of the teeth of the small Endothiodonts and particularly the four specimens from the Buffalo river bed, Murraysburg, referred to a new species of *Pristerodon* (*P. buffaloensis*) shows that both these factors are extremely variable. In a species (or even specimen) the teeth can have serrations on the anterior and posterior surfaces, or only on the posterior aspect. The structure of the teeth is also affected by wear, as denticulations only occur on erupting or newly erupted teeth in *P. buffaloensis*. The number of teeth not only varies from specimen to specimen within a species, but also from left to right jaw or from upper to lower jaw.

These two factors, formerly used almost exclusively as basis for the classification of the Endothiodonts, can therefore no longer be relied upon for subdividing the group.

(2) *The structure of the palate*

The palates of *Pristerodon* and *Emydops* with which *Diaelurodon* and *Emydopsis* respectively are put into synonymy, display a difference of classificatory value. In *Emydops* the palatine is large and reaches the premaxillary anteriorly; in *Pristerodon* the palatine is small and the maxillaries participate in bounding the choanae laterally. The palate of the new form *Broilius antjiesfonteinensis* from the *Tapinocephalus* zone is very similar to that of *Pristerodon* and therefore it can readily be distinguished from *Emydops* and forms with similar palates.

(3) *The distribution of the teeth*

The distribution of the teeth on the palate and lower jaw is another character of diagnostic importance and is also significant because it is correlated with the posterior and medial expansion of the horny beak in Anomodonts. The upper teeth can be situated on the alveolar ridge posterior to the canines (*Broilius*, *Robertia*, *Emydops* and *Pristerodon*); on the pars palatina of the maxillary (*Brachyuraniscus*, *Prodicynodon* and *Cryptocynodon*); or on both as in

Parringtoniella which probably represents a transitional stage. In *Hueneus*, in addition to the molars on the maxillary, a large number of teeth are situated on the premaxillary. *Broilius* differs from all the forms, where the lower teeth are known, in having its lower teeth on the dorsal side of the dentary and not on the dorsomedial side.

(4) *The extent of the secondary palate*

The third factor that can be used for separation of Endothiodonts is the extent of the secondary palate. In two of the *Tapinocephalus* zone forms, *Broilius* and *Robertia*, the secondary palates are short, the internal nares reaching as far anteriorly as the level of the tusks. In the latter form, however, the anterior parts of the choanae are reduced to slits and therefore open functionally more posteriorly. This feature is also noticed in all the other small Endothiodonts investigated, but here the choanae do not approximate so closely to the level of the tusks or caniniform processes.

(5) *Ancestry*

The Russian genus *Venjukovia*, which Watson regards as the most likely ancestor of the Anomodonts, is too highly specialised to be directly ancestral to *Broilius*. In *Venjukovia* the teeth on the lower jaw are medially displaced and the palatine reaches the premaxillary anteriorly, two features not yet developed in *Broilius*. An immediate ancestor therefore still awaits discovery. As the Ecca layers underlying the *Tapinocephalus* zone are almost completely sterile, it is unlikely that it will ever be discovered in South Africa. Comparison of the various Endothiodont palates, however, provides a clear picture of the probable appearance of the ancestral palatal form.

(6) *Evolution*

The evolution and relationships of the Endothiodonts are discussed in a summary at the end of section III and graphically represented in fig. 70.

C. Dicynodon, Daptocephalus and Oudenodon: their origin and further Evolution

As in the case of the Endothiodonts, palatal structure provides a basis for subdividing "*Dicynodon*."

(1) *The genus Dicynodon*

The palate of the type species of *Dicynodon* (*D. lacerticeps*) is not known but fortunately, amongst the species *D. feliceps*, *D. psittacops* and *D. grimbeeki*, which van Hoepen and Broom regard as very closely related to the type, I was able to study the palates of the latter two species personally. A specimen referred to *D. feliceps* by Lydekker had previously been studied in detail by Sollas and Sollas.

In all three species the palatine is relatively small and does not reach the premaxillary anteriorly. This character, as opposed to many other morphological features, is constant in four specimens (including a female) investigated, and ascribed to the new species *D. vanderhorsti*, from the *Tapinocephalus* zone.

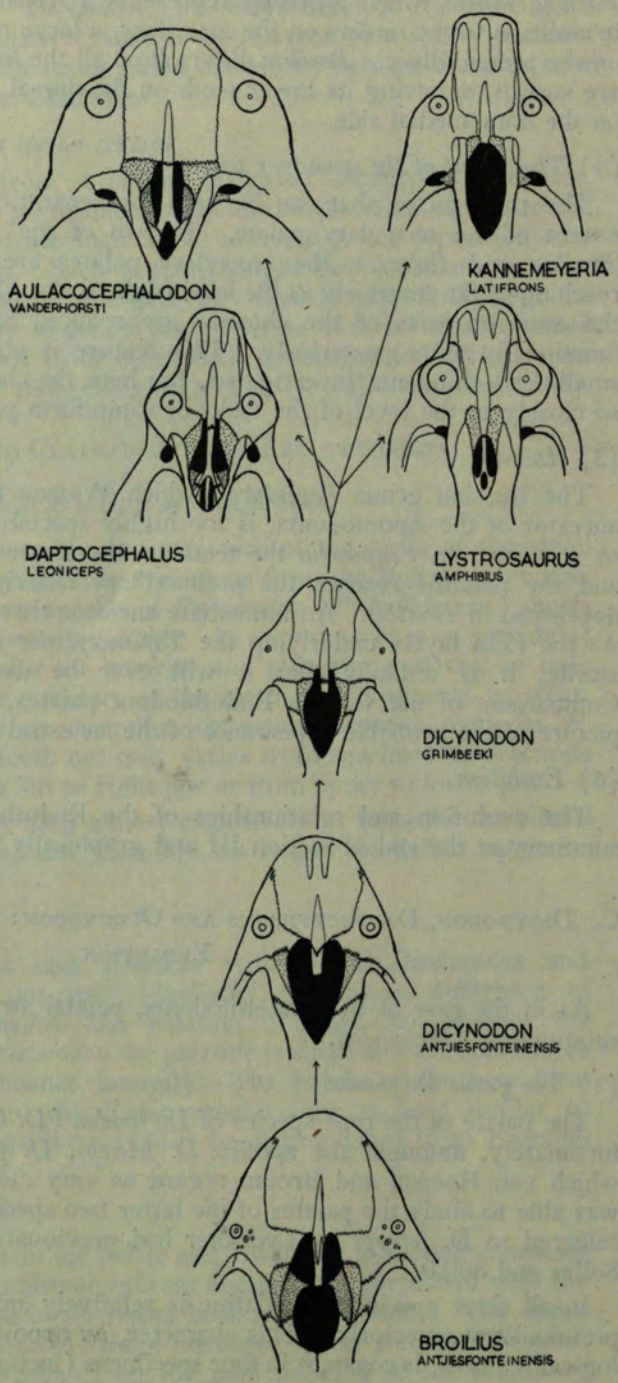


Fig. 71. — Morphological stages in the Evolution of a more extensive secondary palate in *Dicynodon* and related forms from the Endothiodont condition.

(1) The primitive Endothiodont *Broilius antjiesfonteinensis*, by losing its molar teeth and developing anterior palatal ridges, would become:

(2) A primitive *Dicynodon*, represented here by *D. antjiesfonteinensis*, from the same horizon.

(3) In the later forms of *Dicynodon*, e.g. *D. grimbeeki*, the anterior parts of the choanae are reduced to narrow slits; the internal nares are therefore functionally displaced posteriorly. The transverse bone is reduced and the palatine approximates the premaxillary anteriorly.

(4) In *Daptocephalus leoniceps* the palatine reaches the premaxillary anteriorly. The transverse bone is very small and is displaced laterally, the pterygoid being in contact with the maxillary.

(5) In *Kannemeyeria latifrons* the anterior nasal slits are completely closed off and the maxillaries and palatines are in contact medially with the posterior process of the premaxillaries.

(6) The same type of development took place in *Lystrosaurus amphibius*, but here the secondary palate is even more extensive and the internal nares open very far posteriorly. A separate transverse bone is absent in this specimen.

(7) The palatal structure of *Aulacocephalodon vanderhorsti* can also be derived from a form such as *Dicynodon grimbeeki*. The palatine, by anterior development, has made extensive contact with the premaxillary, as is seen to a lesser extent in *Daptocephalus*. The anterior pterygoid process is long, but does not reach as far anteriorly as in *Daptocephalus*, *Kannemeyeria* and *Lystrosaurus*.

Specimens belonging to *D. pseudojouberti*, *D, ictidops*, *D. sollasi* and the new species *D. schroederi* and *D. antjiesfonteinensis* also show this feature.

(2) *Ancestry*

Among the known *Tapinocephalus* zone Endothiodonts, this first or *Dicynodon* palatal type occurs only in *Broilius* and this genus could readily have developed into *Dicynodon* by the loss of its molars. *Broilius antjiesfonteinensis* is, however, too late in time to be the direct ancestor of such species as *D. pseudojouberti* and *D. jouberti* (which most probably belong to this genus) as they come from a lower horizon.

(3) *The genus Daptocephalus*

The type species of van Hoepen's genus *Daptocephalus* (*D. leoniceps*) presents a second palatal type, but it is merely a modification of that of *Dicynodon*. By anterior development, the palatine has reached the premaxillary; the transverse bone is small and is displaced laterally.

(4) *The genera Lystrosaurus and Kannemeyeria*

The palates of the genera *Lystrosaurus* and *Kannemeyeria* are also modifications of the *Dicynodon* type. In *Kannemeyeria*, or the third palatal type, the transverse bone is small and the pterygoid reaches the maxillary anteriorly as in *Daptocephalus*. The palatine does not reach the premaxillary anteriorly but is in contact with its posterior process medially. *Lystrosaurus amphibius* has a palate similar to that of *Kannemeyeria*, except that a transverse bone could not be detected. In some of the less specialised Lystrosauri, e.g. *L. murrayi*, a fourth palatal type is obtained. The anterior parts of the choanae are not closed off and, as in *Dicynodon*, the palatine is therefore not in contact with the premaxillary. The pterygoid reaches the maxillary anteriorly.

(5) *Evolution*

The evolution of the *Dicynodon* palatal type and its further development is graphically represented in figures 70 and 71.

(6) *The genus Oudenodon*

This genus, formerly ascribed to *Dicynodon*, is distinguished from the latter by a distinctive form of palate, such as is found in *Oudenodon platyceps*, which may be termed the *Oudenodon* pattern. The palatine is large and has an extensive contact with the premaxillary anteriorly. The transverse bone is large and separates the pterygoid from the maxillary as in *Dicynodon*.

The specimen described by von Huene as *"Dicynodon sollasi"* and the *"Dicynodon grossarthi"* described by Broili and Schröder (which is synonymous with *"D. huenei"*) also have the *Oudenodon* type of palate. Hence this type of palate is not restricted to completely tuskless specimens. Because some of the species with similar palates (*Oudenodon margaritae* van Hoepen, *O. marlothi* Broili and Schröder, and *O. kolbei* Broom) are similar to the type of the genus *Oudenodon* (*O. baini* Owen), all these specimens are referred provisionally to this genus.

(7) *Ancestry*

Stratigraphically the most ancient known *Oudenodon* is *O. huenei*, from the upper division of the *Tapinocephalus* zone. Of the small Endothiodonts of this zone, *Robertia* from the lowest division is the most likely ancestor of *O. huenei*, as it differs from the latter merely in the retention of a few molars. It is, however, impossible to decide beyond all doubt that all Oudenodons are descended from *Robertia*. Watson suggested that *Tropidostoma* is a very likely ancestor. In the only known species of *Tropidostoma* (T. *microtrema*) the palatines are large and meet the vomer medially; the secondary palate is therefore more extensive than in any known *Oudenodon*. In the latter genus a posterior median process of the premaxillary is always present; in *Tropidostoma* it is absent. Another possible ancestor of *Oudenodon* is a *Dicynodon*. In *Daptocephalus* the palatines reach the premaxillary and if no other features developed parallel to this one, the palatal structure would be indistinguishable from that of *Oudenodon*.

(8) *The origin of the late Anomodonts having Oudenodon palatal types*

The Oudenodon palatal type is also found in the genera *Platycyclops*,

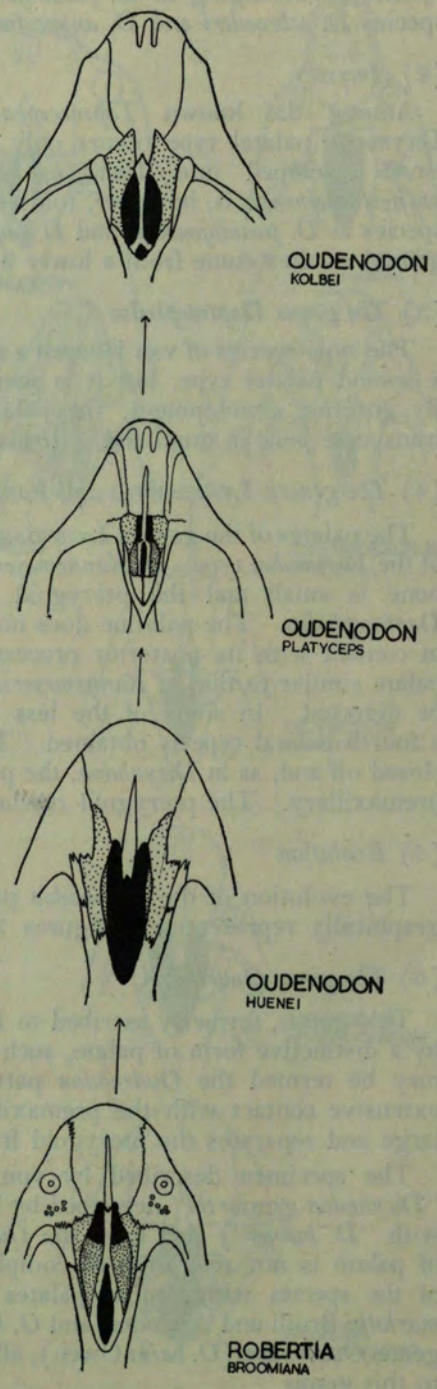


Fig. 72.—Morphological stages in the Evolution of a more extensive secondary palate in *Oudenodon* from the Endothiodont condition.

(1) The small Endothiodont *Robertia broomiana* from the lowest division of the *Tapinocephalus* zone differs from:

(2) *Oudenodon huenei* in possessing a number of molar teeth. With the loss of these teeth it would become very similar to *O. huenei*.

(3) Basically *O. platyceps*, from the *Cistecephalus* zone, is very similar to *O. huenei*, but anterior palatal ridges are present and the anterior parts of the internal nares are narrower.

(4) In *O. kolbei* from the *Endothiodon* zone, these slits are closed off completely and the palatine is in contact medially with the posterior process of the premaxillary and the vomer.

Aulacocephalodon, *Kitchingia* and *Pelanomodon*. With the exception of *Aulacocephalodon*, all these forms are tuskless. The most likely ancestor for them is therefore one of the tuskless Oudenodons. *Aulacocephalodon* is apparently a genus with tusks in both sexes and therefore cannot possibly be derived from *Oudenodon*; it is more likely that it is related to *Dicynodon*, the palate merely secondarily simulating an Oudenodont condition.

(9) *Evolution*

The evolution of *Oudenodon* is graphically represented in figs. 70 and 72.

CLASSIFICATION OF THE GENERA DISCUSSED IN THIS PAPER

Suborder Anomodontia.
- Family Endothiodontidae.
  - Subfamily Endothiodontinae.
    - Genus *Endothiodon*.
  - Subfamily Pristerodontinae.
    - Genus *Pristerodon*, *Emydops*, *Brachyuraniscus*, *Robertia*, *Broilius*, *Koupia*.
  - Subfamily Eumantellinae.
    - Genus *Eumantellia*, *Newtonella*, *Synostocephalus*, *Hueneus*.
  - Subfamily Parringtoniellinae.
    - Genus *Parringtoniella*.
- Family Cistecephalidae.
  - Genus *Cistecephalus*.
- Family Dicynodontidae
  - Subfamily Dicynodontinae
    - Genus *Dicynodon*, *Daptocephalus*, *Kannemeyeria*.
  - Subfamily Aulacocephalodontinae.
    - Genus *Aulacocephalodon*.
- Family Lystrosauridae.
  - Genus *Lystrosaurus*.
- Family Cryptodontia.
  - Genus *Oudenodon*, *Kitchingia*, *Platycyclops*, *? Pelanomodon*.

LIST OF LITERATURE CITED

Amalitski, V. and Karpinski, A., 1922. Diagnoses of the new forms of vertebrates and plants from the upper Dvina. Bull. Acad. Sci. Russ., pp 1-12.

Boonstra, L. D., 1935. Die versamelings van fossiele as basis van die paleontologiese studie. S. Afr. Journ. Sci., xxxii, p. 332-340.

Boonstra, L. D., 1938. A report on some Karoo reptiles from the Luangwa valley, Northern Rhodesia. Q. Journ. Geol. Soc., vol. 94, pp 371-384.

Boonstra, L. D., 1948. On the Anomodont reptiles from the Tapinocephalus zone of the Karoo system. Robert Broom Commemorative Volume, Special Publication Roy. Soc. S. Afr., pp 57-64.

Brink, A. S., 1950. On a new species of *Cistecephalus* Owen. Ann. Mag. Nat. Hist., Ser. 12, vol. 3, pp. 985-997.

Brink, A. S., 1951. On the genus *Lystrosaurus* Cope. Trans. Roy. Soc. S. Afr., vol. 33, part 1, pp. 107-120.

Broili, F. and Schröder, J., 1935*a*. Ueber den Schädel von *Cistecephalus* Owen. Sitzb. Bayer. Akad. Wiss., pp. 1-20.

Broili, F. and Schröder, J., 1935*b*. Ueber einige primitive Anomodontier-Schädel aus den unteren Beaufort-Schichten. Sitzb. Bayer. Akad. Wiss., pp. 223-278.
Broili, F. and Schröder, J., 1936. Ein neuer Anomodontier aus der Cistecephalus-Zone. Sitzb. Bayer. Akad. Wiss., pp. 45-60.
Broili, F. and Schröder, J., 1937. Ueber einige neue Anomodontier aus der Tapinocephalus-Zone. Sitzb. Bayer. Akad. Wiss., pp. 118-168.
Broom, R. 1902. On the structure of the palate of *Dicynodon* and its allies. Trans. S. Afr. Phil. Soc., vol. 11, pt, 3, pp. 169-176.
Broom, R., 1904*a*. On two new Endothiodont genera (*Prodicynodon* and *Opisthoctenodon*). Rec. Albany Mus., vol. 1, pt. 2, pp. 69-73.
Broom, R., 1904*b*. On a new species of *Oudenodon* (*O. megalorbinus*) from the Gouph, South Africa. Rec. Albany Mus., vol. 1, pt. 3, pp. 180-181.
Broom, R., 1905*a*. Notice of some new fossil reptiles from the Karroo beds of South Africa. Rec. Albany Mus., vol. 1, pt. 5, pp. 331-337.
Broom, R., 1905*b*. On the use of the term Anomodontia. Rec. Albany Mus., vol. 1, pt. 4, pp. 266-289.
Broom, R., 1912*a*. On some new fossil reptiles from the Permian and Triassic beds of South Africa. Proc. Zool. Soc., pp. 859-876.
Broom, R., 1912*b*. On some points in the structure of the Dicynodont skull. Ann. S. Afr. Mus., vol. 7, pt. 5, pp. 337-351.
Broom, R., 1913. On some new genera and species of Dicynodont reptiles with notes on a few others. Bull. Amer. Mus. Nat. Hist., vol. 32, pt. 26, pp. 441-457.
Broom, R., 1915. Catalogue of types and figured specimens of fossil vertebrates in the American Museum of Natural History. ii Permian, Triassic and Jurassic reptiles of South Africa. Bull. Amer. Mus. Nat. Hist., vol. 25, pp. 105-164.
Broom, R., 1921. On some new genera and species of Anomodont reptiles from the Karroo beds of South Africa. Proc. Zool. Soc., pp. 647-674.
Broom, R., 1932. The Mammal-like Reptiles of South Africa. Witherby, London.
Broom, R., 1935*a*. A new genus and some new species of Mammal-like reptiles. Ann. Transv. Mus., vol. 18, pt. 1, pp. 1-12.
Broom, R., 1935*b*. On some new genera and species of Karroo fossil reptiles. Ann. Transv. Mus., vol. 18, pt. 1, pp. 55-72.
Broom, R., 1936*a*. On some new genera and species of Karroo fossil reptiles with notes on some others. Ann. Transv. Mus., vol. 18, pt. 4, pp. 349-386.
Broom, R., 1936*b*. Review of some recent work on South African fossil reptiles. Ann. Transv. Mus., vol. 18, pt. 4, pp. 397-413.
Broom, R., 1937. A further contribution to our knowledge of the fossil reptiles of the Karroo. Proc. Zool. Soc., pp. 299-318.
Broom, R., 1938. On two new Anomodont genera. Ann. Transv. Mus., vol. 19, pt. 2, pp. 247-250.
Broom, R., 1940. Some new Karroo reptiles from the Graaff-Reinet district. Ann. Transv. Mus., vol. 20, pt. 2, pp. 71-87.
Broom, R. and George, M., 1950. Some new Anomodont reptiles in the Bernard Price Collection. S. Afr. Journ. Sci., vol. 46, pt. 10, pp. 275-278.
Broom, R. and Haughton, S. H., 1917. Some new species of Anomodontia. Ann. S. Afr. Mus., vol. 12, pt. 5, pp. 119-125.
Cope, E. D., 1870. Observations on the reptilia of the Triassic formations of the Atlantic regions of the United States (*Dicynodon rosmarus*). Proc. Amer. Phil. Soc., vol. 11, pp. 444-446.
Haughton, S. H., 1924*a*. Reptilian remains from the Karroo beds of East Africa. Q. Journ. Geol. Soc., vol. 80, pt. 1, pp. 1-11.
Haughton, S. H., 1924*b*. A bibliographic list of pre-Stormberg Karroo reptilia with a table of Horizons. Trans. Roy. Soc. S. Afr., vol. 12, pt. 2, pp. 51-104.
Haughton, S. H., 1926. On the Karroo vertebrates from Nyassaland. Trans. Geol. Soc. S. Afr., vol. 29, pp. 68-83.
Haughton, S. H., 1932. On a collection of Karroo vertebrates from Tanganyika Territory. Q. Journ. Geol. Soc., vol. 88, pp. 634-671.
Huxley, T. H., 1868. On *Saurosternum baini* and *Pristerodon mackayi*, two new fossil lacertilian reptiles from South Africa. Geol. Mag. London, vol. 5, pp. 201-205.
Huxley, T. H., 1885. On a collection of vertebrate fossils from the Panchet rocks, Ranigunj, Bengal. Palaeont. Indica, Ser. 4, vol. 1, pt. 1, pp. 3-24.
Lydekker, R., 1890. Catalogue of the fossil amphibians and reptiles in the British Museum, London.
Newton, E. T., 1893. On some new reptiles from the Elgin sandstones. Phil. Trans., vol. 184 B, pp. 431-503.
Olson, E. C., 1937. The skull structure of a new Anomodont. Journ. Geol., vol. 14, pt. 8, pp. 851-858.
Owen, R., 1845. Description of certain fossil crania discovered by A. G. Bain Esq. in sandstone rocks at the South Eastern extremity of Africa, referable to different species of an extinct genus of reptilia (*Dicynodon*), and indicative of a new tribe or suborder of Sauria. Proc. Geol. Soc., vol. 4, pp. 500-504.

Owen, R., 1859. On the orders of fossil and recent reptilia and their distribution in time. Rep. Brit. Assoc., pp. 153-166.
Owen, R., 1876. Descriptive and illustrative catalogue of the fossil reptilia of South Africa. Taylor and Francis, London.
Parrington, F. R., 1936. On the tooth replacement in Theriodont reptiles. Phil. Trans. Roy. Soc., Ser. B, vol. 226, pp. 121-142.
Pearson, H. S., 1924. The skull of the Dicynodont reptiles. Proc. Zool. Soc., pp. 793-826.
Repelin, J., 1923. Sur un fragment de crâne de *Dicynodon* des environs de Luang Prabang (Haut Laos). Bull. Serv. Geol. Indochine, vol. 12, pt. 2, pp. 1-7.
Romer, A. S. 1931. Vertebrate Palaeontology.
Romer, A. S. and Price, L., 1940. Review of the Pelycosauria. Geol. Soc. Amer., special papers, No. 28, pp. 1-538 (p. 12).
Romer, A. S. and Smith, H. J., 1934. American carboniferous Dipnoans. Journ. Geol., vol. 42, pt. 7, p. 700.
Seeley, H. G., 1889. Researches etc., (vi) On the Anomodont Reptilia and their allies. Phil. Trans. Roy. Soc., vol. 183 B, pp. 311-370.
Seeley, H. G., 1894. Researches etc., (ix) Section i, On the Therosuchia. Phil. Trans. Roy. Soc., vol. 185 B, pp. 987-1018.
Seeley, H. G., 1898. *Oudenodon* (*Aulacocephalus*) *pithecops* from the Cape Colony. Geol. Mag., vol. 5, pp. 107-110.
Simpson, G. G., 1945. The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist., 85, p. 1-350.
Sollas, I. B. J. and Sollas, W. J., 1913. A study of the skull of a *Dicynodon* by means of serial sections. Phil. Trans., vol. 204 B, pp. 201-226.
Sollas, I. B. J. and Sollas, W. J., 1916. On the structure of the Dicynodont skull. Phil. Trans., vol. 207 B, pp. 531-539.
Toerien, M. J., 1951. Notes on the genus *Kannemeyeria*. S. Afr. Journ. Sci., vol. 47, pt. 10, pp. 279-282.
van Hoepen, E. C. N., 1913. Bydragen tot de kennis der reptielen van de Karooformatie. I De skedel van *Lystrosaurus latirostris* Owen sp. Ann. Transv. Mus., vol. 4, pt. 1, pp. 1-46.
van Hoepen, E. C. N., 1934. Oor die indeling van die Dicynodontidae na aanleiding van nuwe vorme. Palaeont. Navors. Nas. Mus. Bloemfontein. Vol. 11, deel 6, bl. 67-101.
Von Huene, F., 1922. Zur Osteologie des *Dicynodon*-Schädels. Palaeont. Zeitschr., vol. 5, pt. 3, pp. 58-71.
Von Huene, F., 1925. Die südafrikanische Karrooformation als geologisches und faunistisches Lebensbild. Fortschr. der Geol. u. Paläont., Heft 12, pp. 1-124.
Von Huene, F., 1927. Gondwana-Reptilen in Südamerika. Palaeont. Hungarica, vol. 2, pt. 1, pp. 1-108.
Von Huene, F., 1931. Beitrag zur Kenntnis der Fauna der Südafrikanischen Karoo-Formation. Geol. u. Palaeont. Abh., N.F., vol. 18, pt. 3, pp. 1-72.
Von Huene, F., 1940. Die Saurier der Karroo- Gondwana- und verwandten Ablagerungen in faunistischer, biologischer und phylogenetischer Hinsicht. Neues Jahrb. Min. Geol. Paläont., vol. 83, pp. 246-347.
Von Huene, F., 1942. Die Anomodontier des Ruhuhu-Gebietes in der Tubinger Sammlung. Palaeontographica, vol. 94 A, pp. 153-184.
Von Huene, F., 1948. Short review of the lower Tetrapods. Broom Commemorative Volume, special publication Roy. Soc. S. Afr., pp. 65-106.
Watson, D. M. S., 1948. *Dicynodon* and its allies. Proc. Zool. Soc., vol. 118, pt. 3, pp. 823-877.
Yuan, P. L. and Young, C. C., 1934. On the discovery of a new *Dicynodon* in Sinkiang. Bull. Geol. Surv. China, vol. 13, pt. 4, pp. 563-573.

INDEX TO GENERA AND SPECIES DESCRIBED IN THIS ISSUE

Gorgonopsia

Aelurognathus minor sp. nov. 23
Alopecorhynchus rubidgei Broom M.S.S. 8
Aloposauroides tenuis gen. et sp. nov. 19
Arctops watsoni sp. nov. 25
Broomicephalus laticeps gen. et sp. nov. 3
Cynarioides gracilis 19
Cyniscopoides broomi gen. et sp. nov. 16
Cyniscops longiceps 17
Dinogorgon oudebergensis sp. nov. 6
Dracocephalus scheepersi gen. et sp. nov. 5
Lycaenoides angusticeps 20
Lycaenops alticeps sp. nov. 22
Lycaenops ornatus 21
Prorubidgea robusta sp. nov. 14
Rubidgea laticeps 12
Rubidgea majora sp. nov. 10
Rubidgea platyrhina sp. nov. 12
Scylacocephalus watermeyeri 20
Sycocephalus bigendens gen. et sp. nov. 27

Cynodontia

Bauria cynops 34
Cistecynodon parvus gen. et sp. nov. 29
Cyclogomphodon sp. 40
Diademodon broomi 46
Inusitatodon smithi gen. et sp. nov. 43

Anomodontia

Aulacocephalodon vanderhorsti 104
Brachyuraniscus merwevillensis sp. nov. 61
Broilius antjiesfonteinensis gen. et sp. nov. 63
Cistecephalus planiceps 78
Daptocephalus leoniceps 87
Dicynodon antjiesfonteinensis sp. nov. 93
„ *feliceps* 86
„ *gamkaensis* 100
„ *grimbeeki* 85
„ *haughtonianus* 99
„ *jouberti* 99
„ *pseudojouberti* 95
„ *psittacops* 85
„ *schroederi* sp. nov. 94
„ *sollasi* 56
„ *vanderhorsti* sp. nov. 91
Emydops kitchingi sp. nov. 73
„ *microdon* 74
„ *murraysburgensis* sp. nov. 72
Hueneus oudebergensis gen. et sp. nov. 80
Kannemeyeria latifrons 102
Kitchingia planifrons 103
Lystrosaurus amphibius 101
Oudenodon huenei 97
„ *megalorhinus* 99
„ *platyceps* 88
Parringtoniella broomi gen. et sp. nov. 78
Pelanomodon rubidgei 103
Platycyclops pricei 104
Pristerodon buffaloensis sp. nov. 68
Robertia broomiana 64

Printed by Die Afrikaanse Pers, Bpk.,
8, Empire Road Extension,
Auckland Park, Johannesburg.