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

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(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.

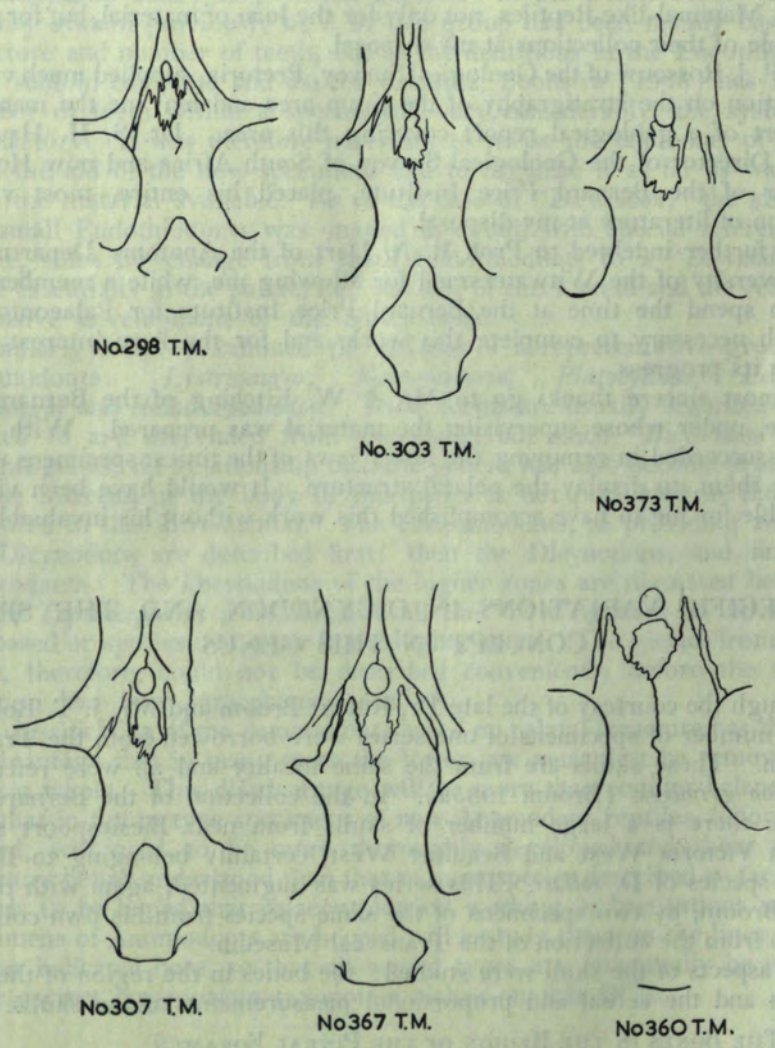


Fig. 43.—*Dicynodon grimbeeki* Broom. Parietal region of the skull showing sutural variations. T.M.: Specimens belonging to the Transvaal Museum.

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

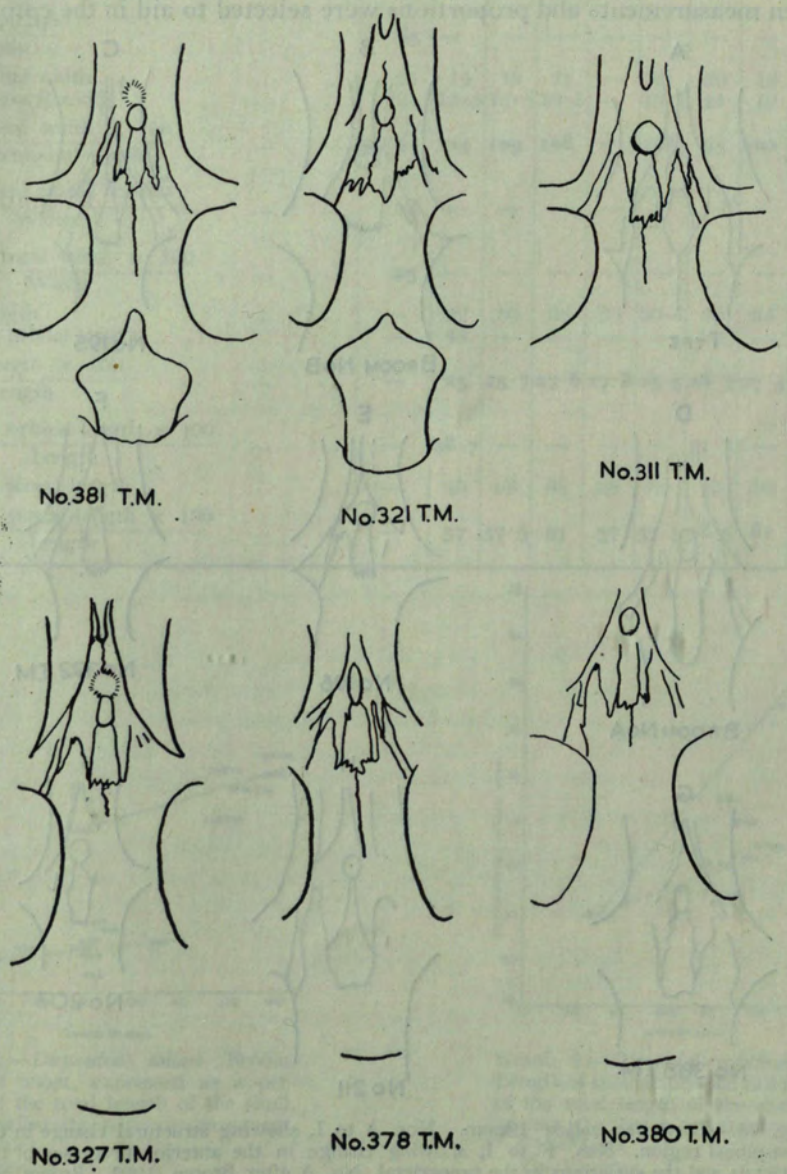


Fig. 44.—*Dicynodon grimbeeki* Broom. Parietal region of the skull showing sutural variations. T.M.: Specimens belonging to the Transvaal Museum.

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

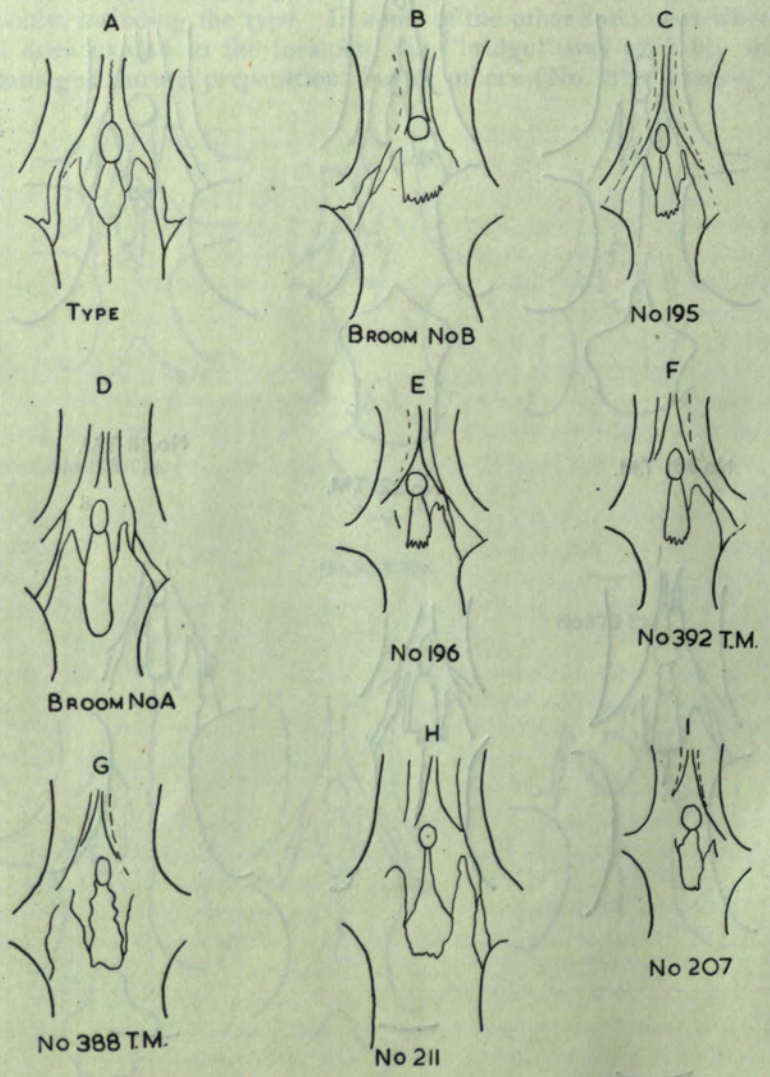
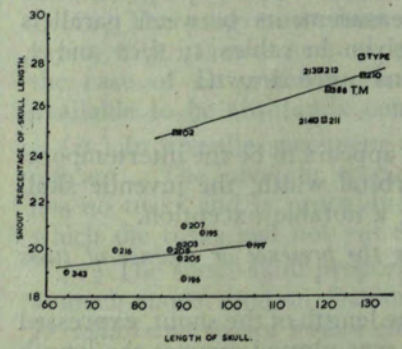


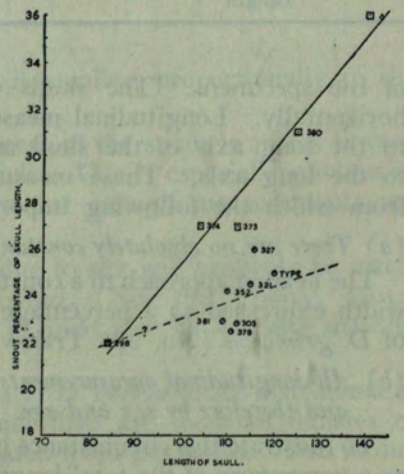
Fig. 45.—*Dicynodon sollasi* Broom. Nos. A to I, showing structural change in the post-pineal region. Nos. F to I, showing change in the anterior processes of the parietals and the variations in the preparietal. No. A after Broom, 1921. Broom No. A and No. B, specimens that belonged to the late Dr. Broom.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

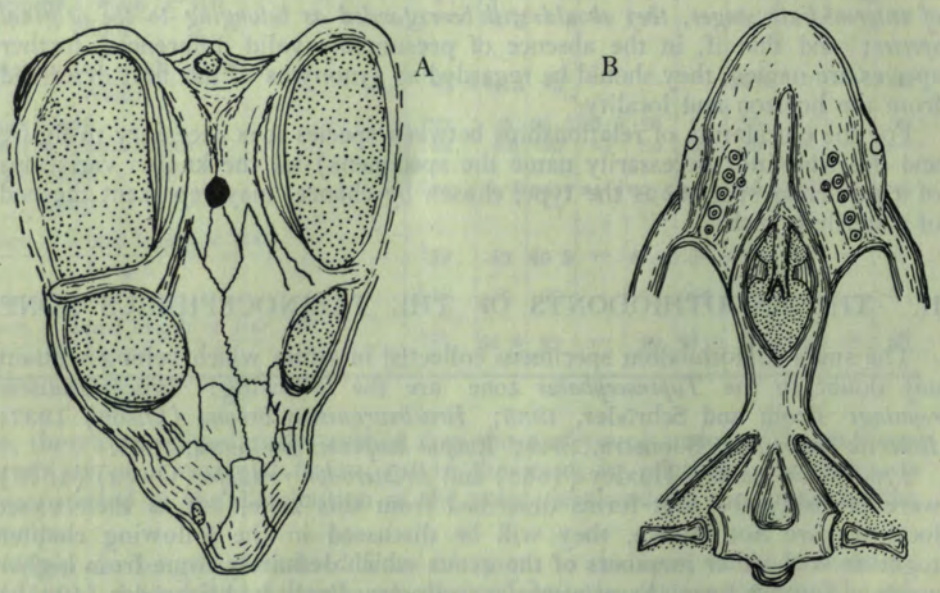


Fig. 46.—*Brachyuraniscus merwevillensis* sp. nov. (A) Dorsal view, distortion not corrected but partially reconstructed. (B) Palatal view, distortion corrected. (x1)

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

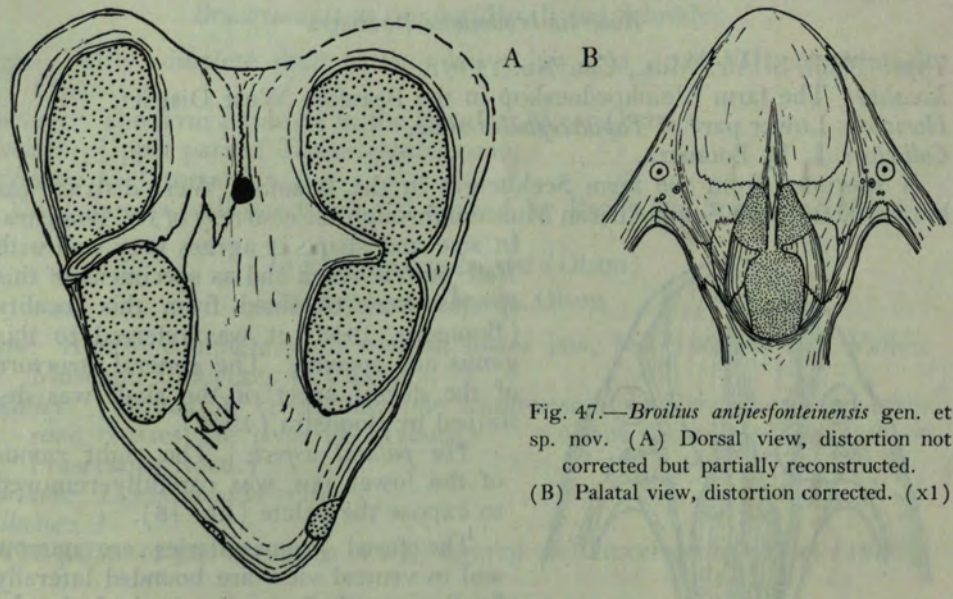


Fig. 47.—*Broilius antjiesfonteinensis* gen. et sp. nov. (A) Dorsal view, distortion not corrected but partially reconstructed. (B) Palatal view, distortion corrected. (x1)

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

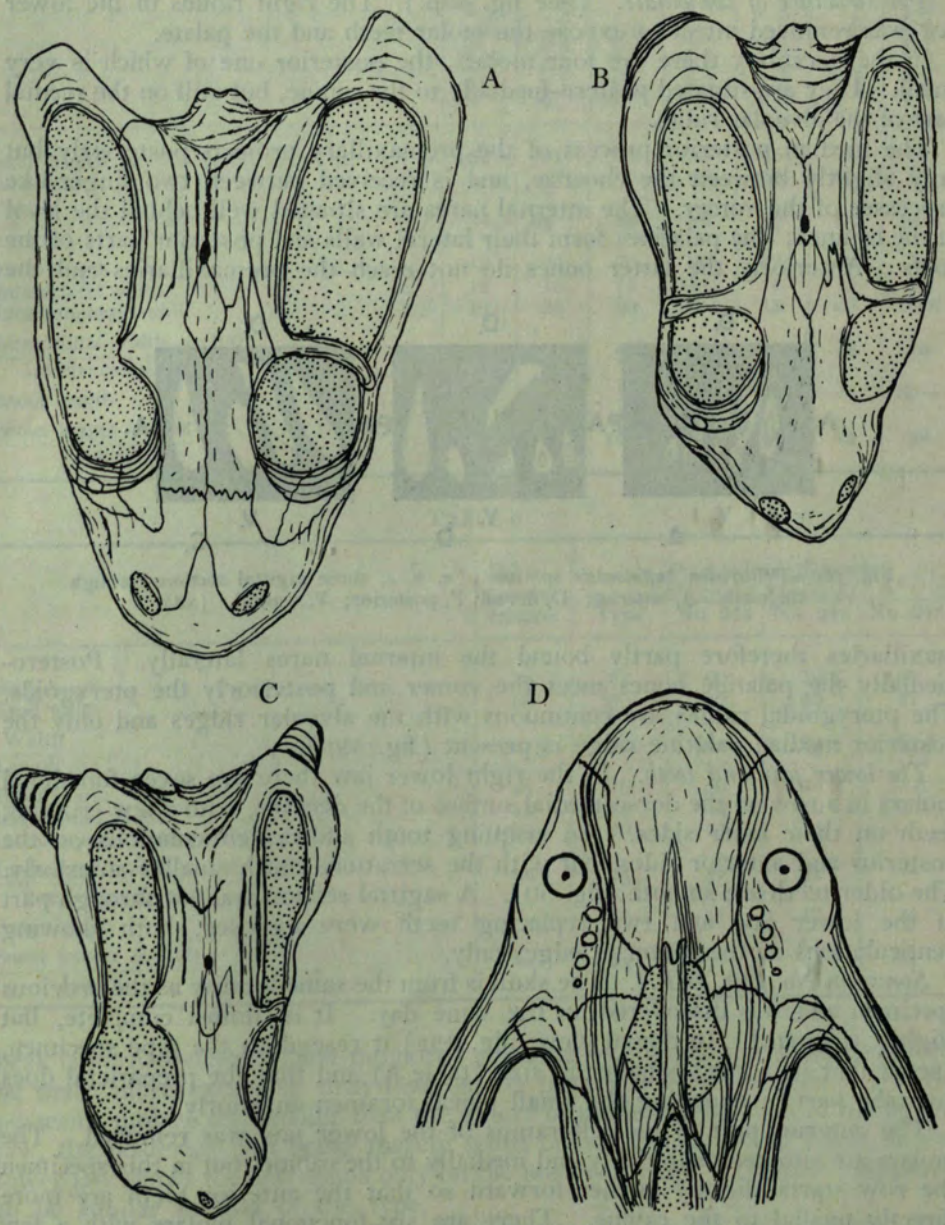


Fig. 49.—*Pristerodon buffaloensis* sp. nov.; A, B, C, dorsal views of three different skulls, distortion not corrected; A, type; D, palatal view of type, left side reconstructed according to right side. (x1). (Drawing of palatal view x1½).

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

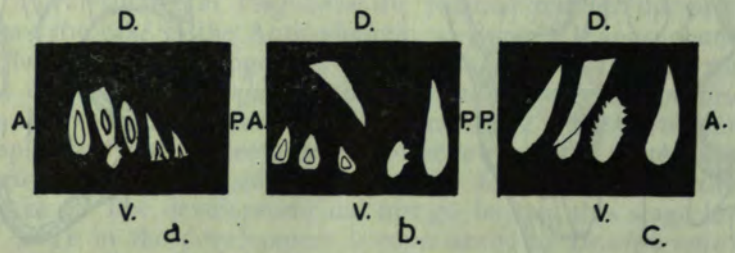


Fig. 50.—*Pristerodon buffaloensis* sp. nov.; *a*, *b*, *c*, three sagittal sections through the teeth. A, anterior; D, dorsal; P, posterior; V, ventral. (x3).

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

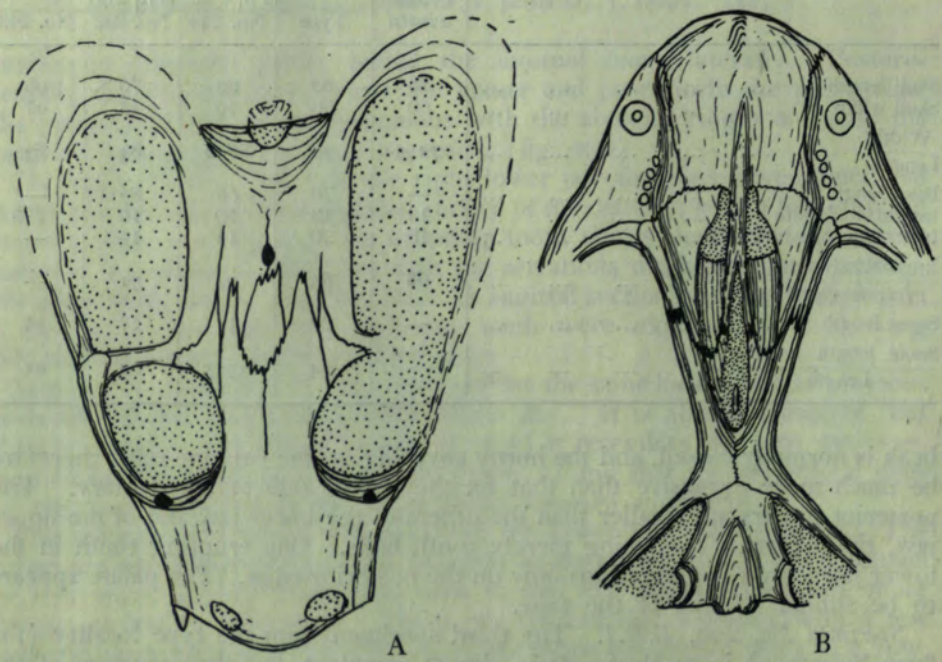


Fig. 51.—*Emydops murraysburgensis* sp. nov. (A) Dorsal view, distortion not corrected but partially reconstructed. (B) Palatal view. (x1.)

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.

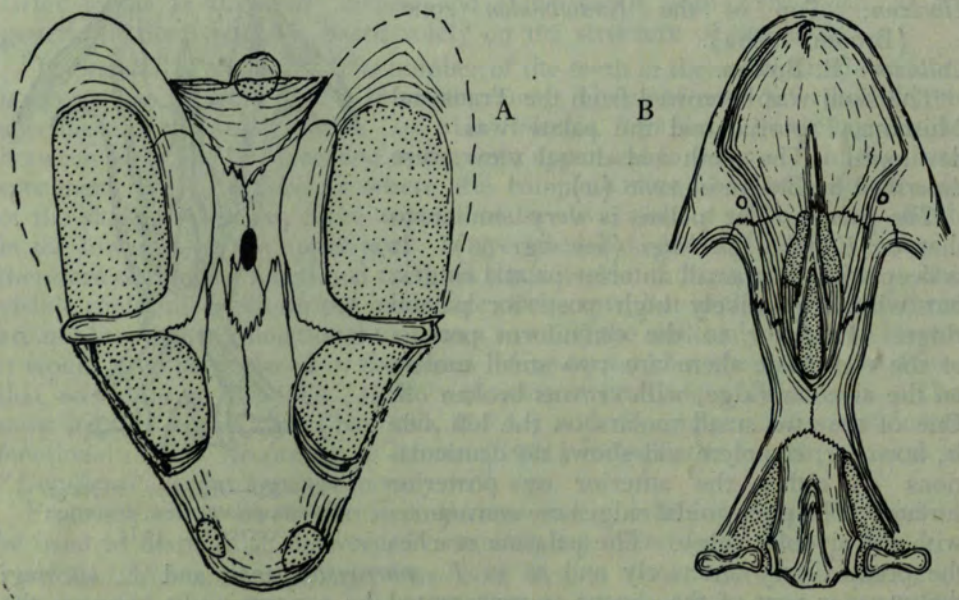


Fig. 52.—*Emydops kitchingi* sp. nov. (A) Dorsal view, partially reconstructed. (B) Palatal view. (x1).

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

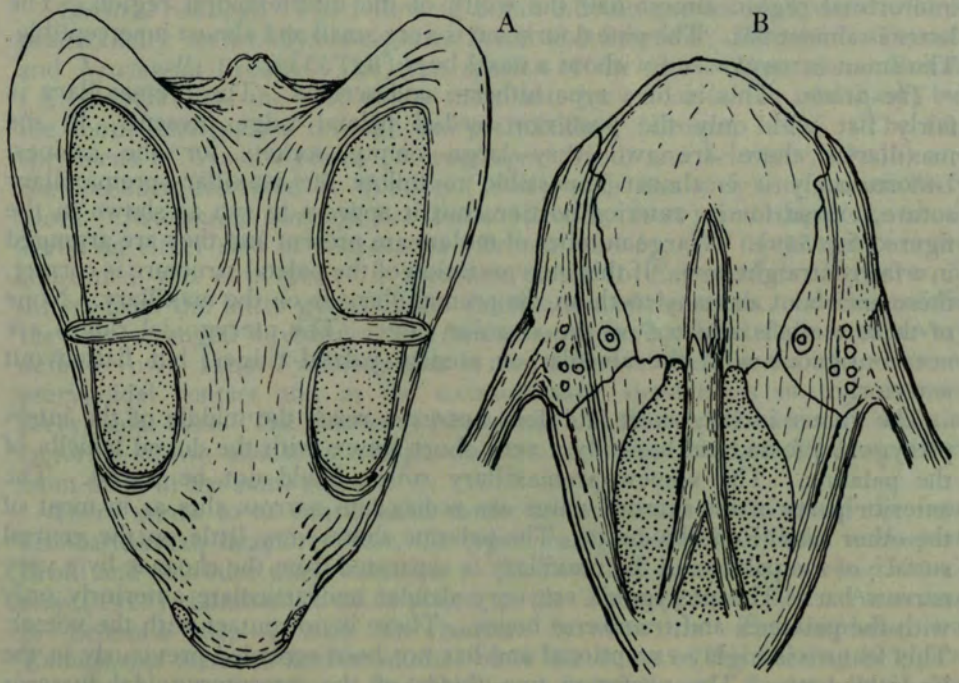


Fig. 54.—*Parringtoniella broomi* gen. et sp. nov. (A) Dorsal view, reconstructed. (x1). (B) Palatal view, distortion corrected. (x1½.)

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.

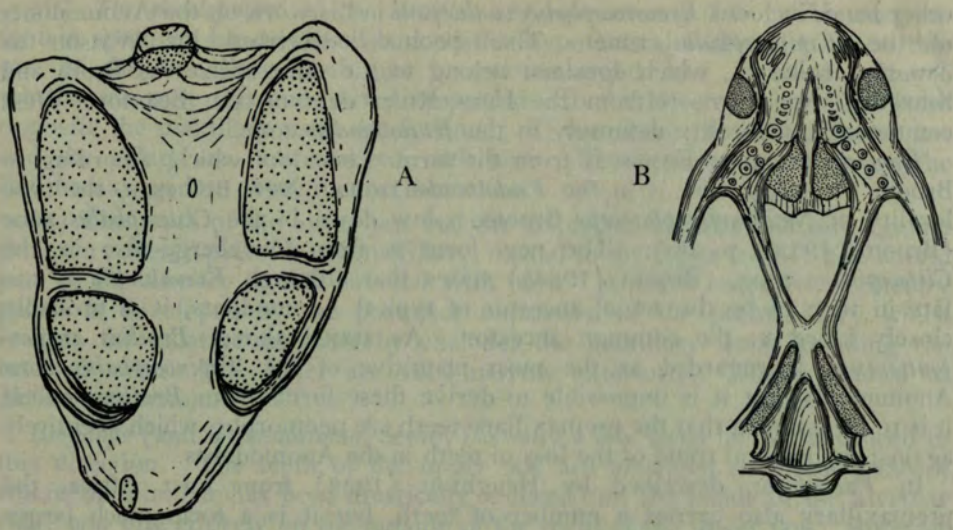


Fig. 55.—*Hueneus oudebergensis* gen. et sp. nov. (A) Dorsal view, distortion not corrected. (B) Palatal view distortion corrected. (x1.)

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).

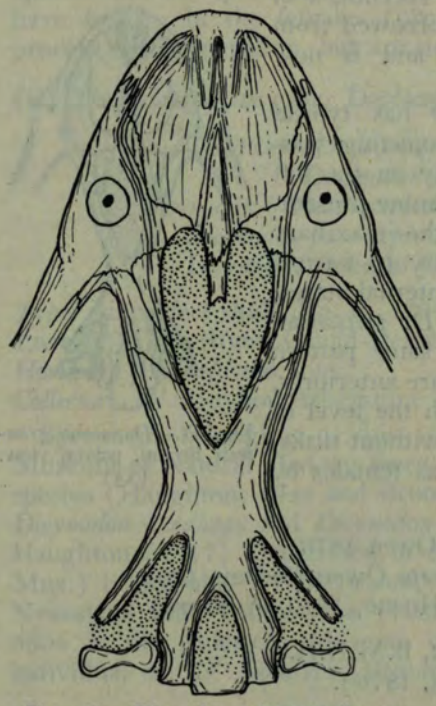


Fig. 56.—*Dicynodon psittacops* Broom, palatal view. (x1.)

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*).

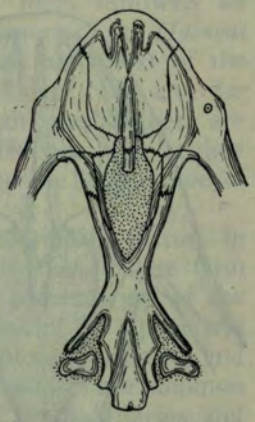


Fig. 57.—*Dicynodon grimbeeki* Broom, palatal view. (x½)

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).

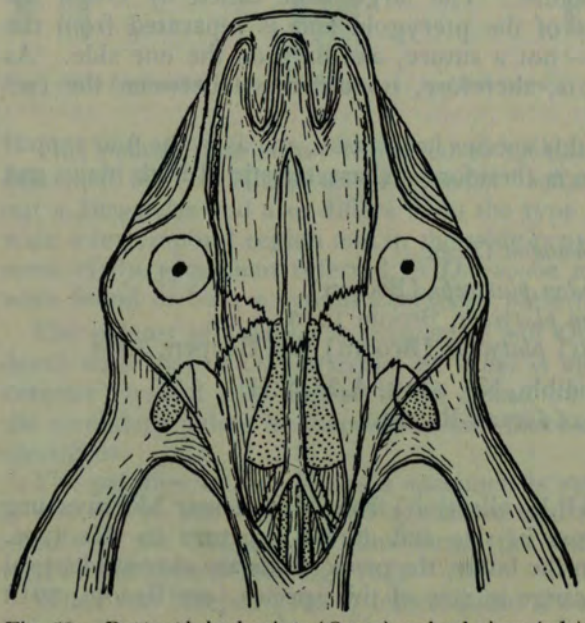


Fig. 58.—*Daptocephalus leoniceps* (Owen), palatal view. (x⅓.)

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).

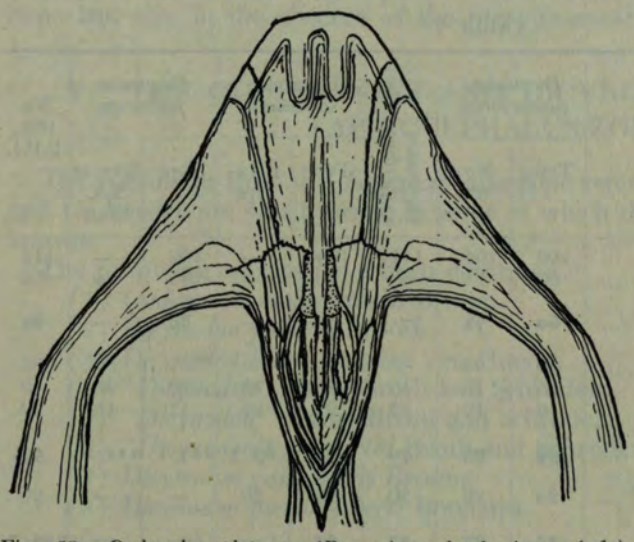


Fig. 59.—*Oudenodon platyceps* (Broom), palatal view. (x⅓.)

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.

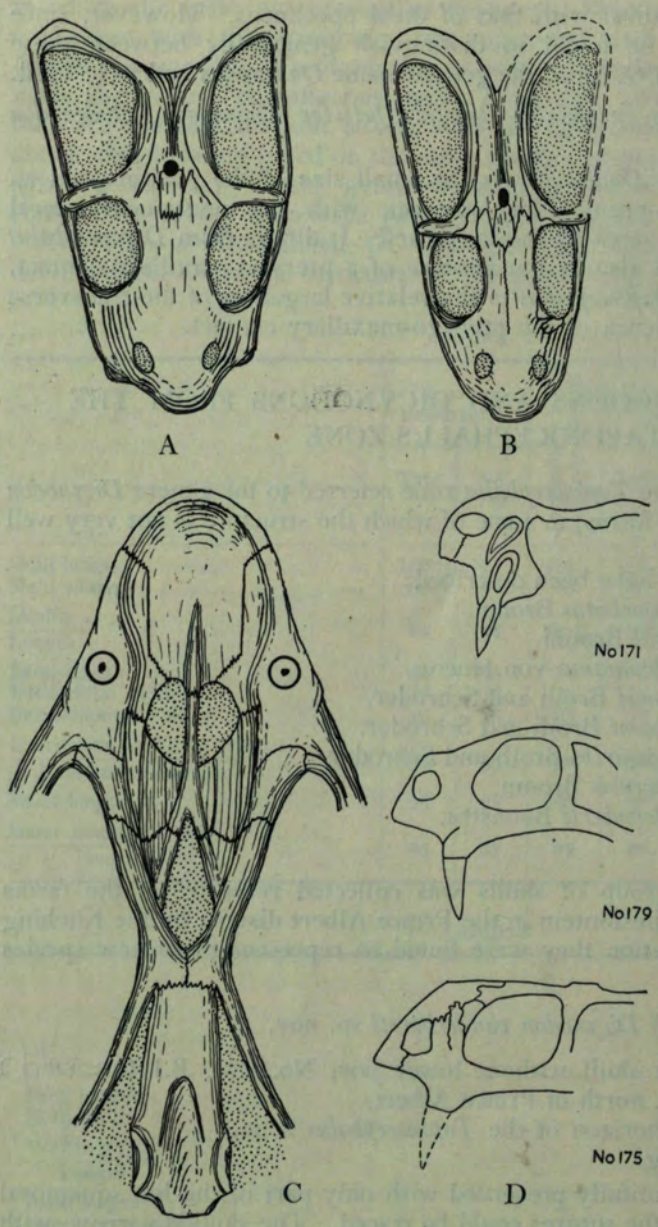


Fig. 60.—*Dicynodon vanderhorsti*, sp. nov. (A) and (B) Dorsal views of two skulls, distortion not corrected but partially reconstructed. (x½.) (C) Palatal view. (x1.) (D) Lateral views of three skulls to show variation in contour and the replacement of a canine.

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).

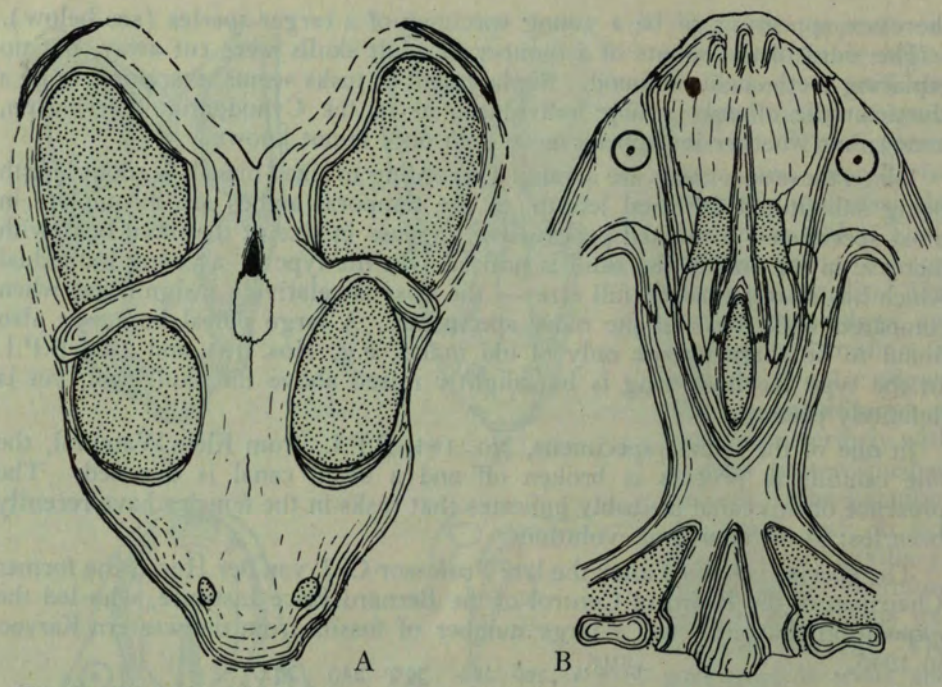


Fig. 61.—*Dicynodon antjiesfonteinensis* sp. nov. (A) Dorsal view, distortion not corrected but partially reconstructed. (x1.) (B) Palatal view. (x1.)

(*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.

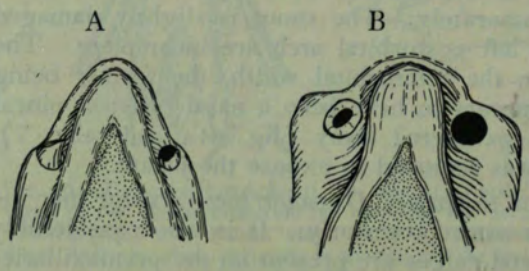


Fig. 62.—(A) *Dicynodon antjiesfonteinensis* sp. nov. ventral view of snout with lower jaw in position. (x½.) (B) *Dicynocon schroederi* sp. nov., ventral view of snout with lower jaw in position. (x½.)

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).

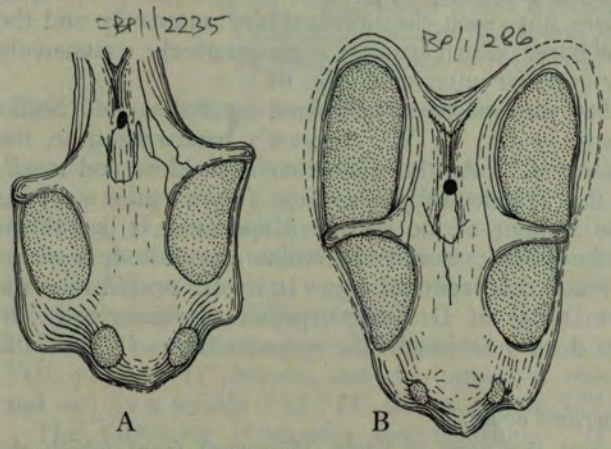


Fig. 63.—*Dicynodon schroederi* sp. nov., dorsal views of the type (A) and paratype (B). (x½.)

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.

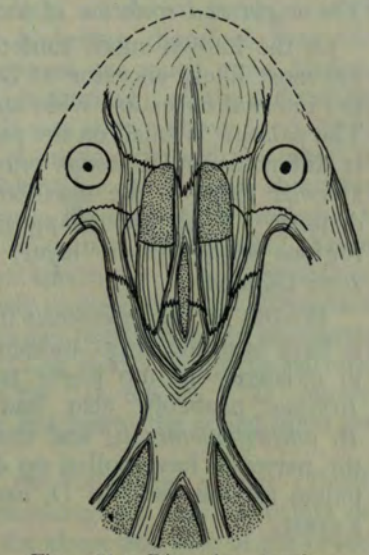


Fig. 64.—*Dicynodon pseudojouberti* Boonstra, palatal view, partially reconstructed. (x1.)

(*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).

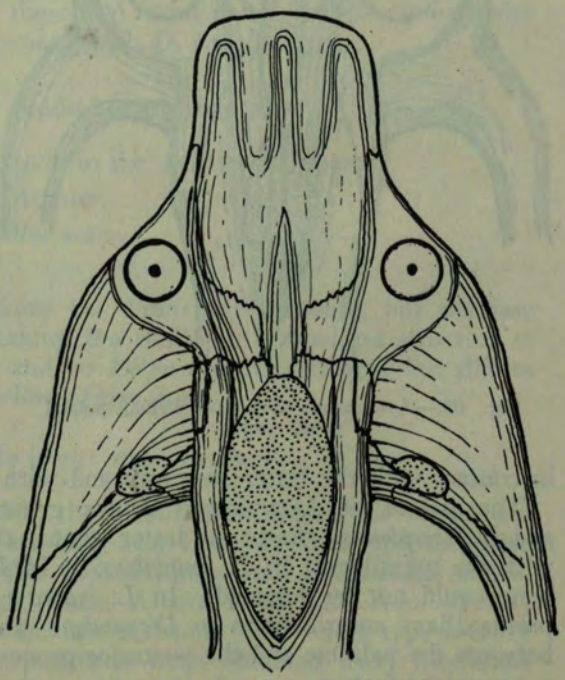


Fig. 66.—*Kannemeyeria latifrons* Broom, palatal view. (x½.)

(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).

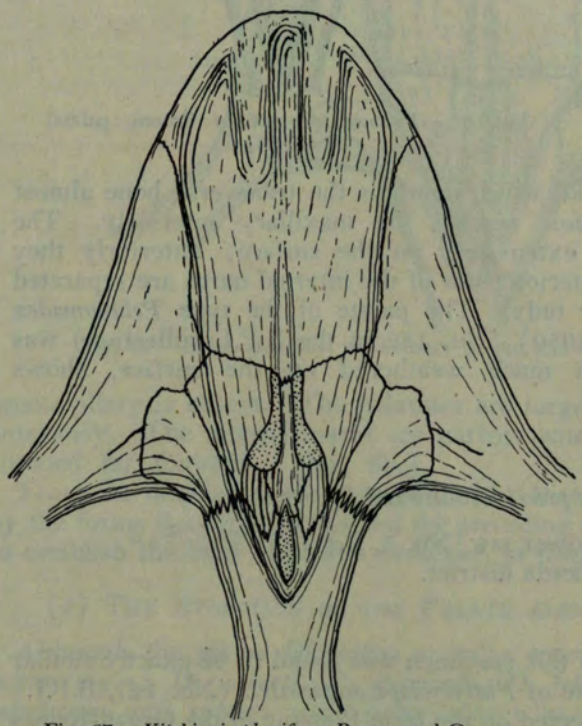


Fig. 67.—*Kitchingia planifrons* Broom and George, palatal view. (x ½.)

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.

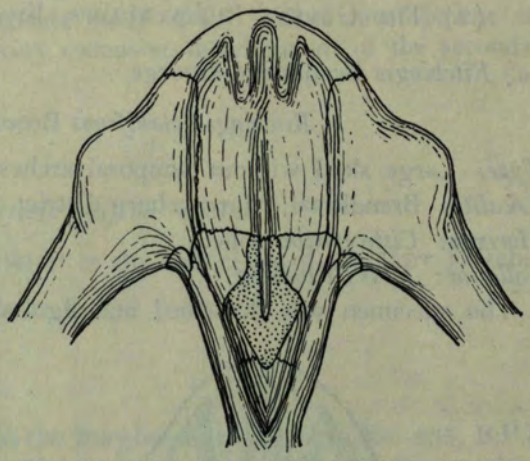


Fig. 68.—*Pelanomodon rubidgei* Broom, palatal view. (x¼.)

(*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

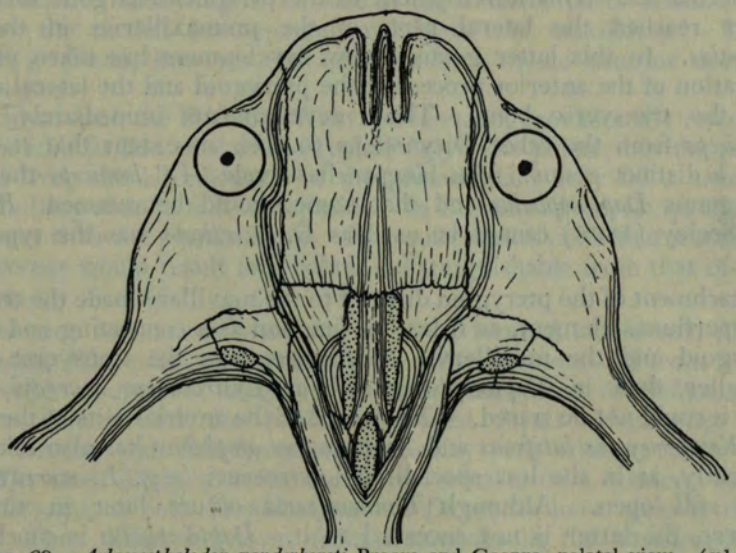


Fig. 69.—*Aulacocephalodon vanderhorsti* Broom and George, palatal view. (x¼.)

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

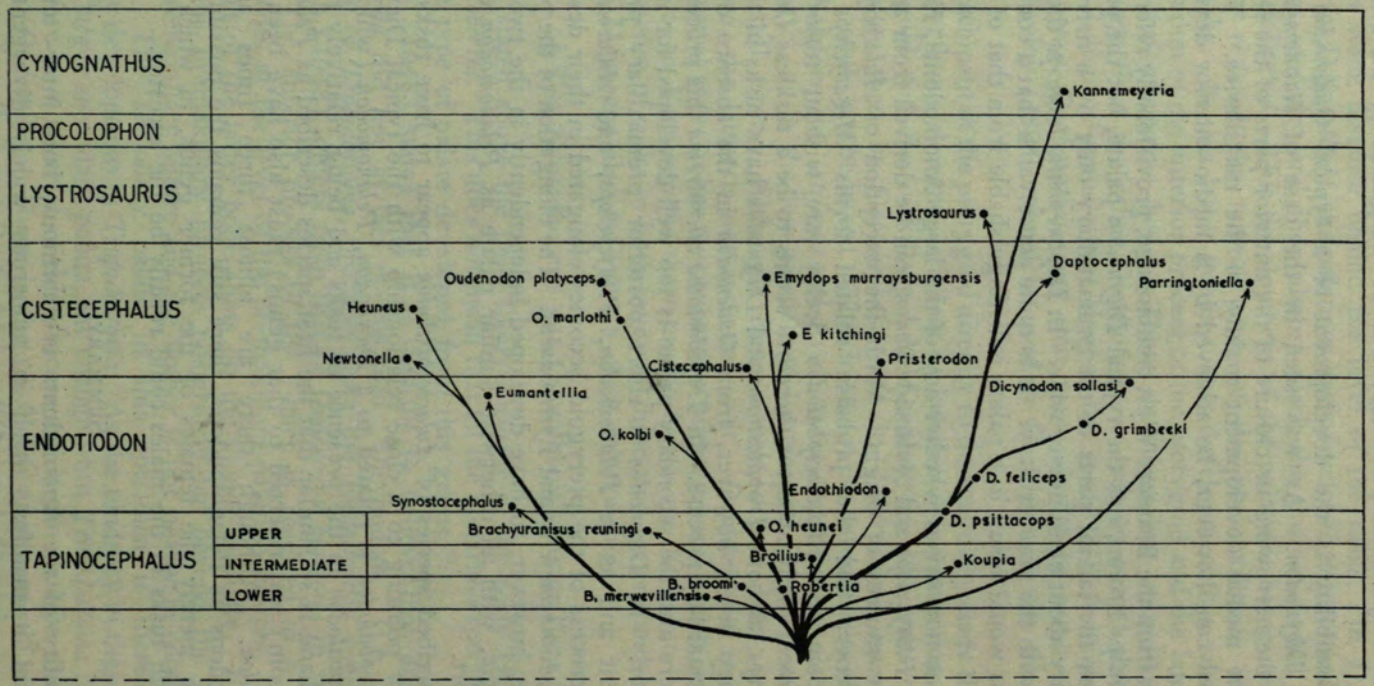


Fig. 70.—Genealogical tree to show the relationship of the main South African Anomodonts.

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.

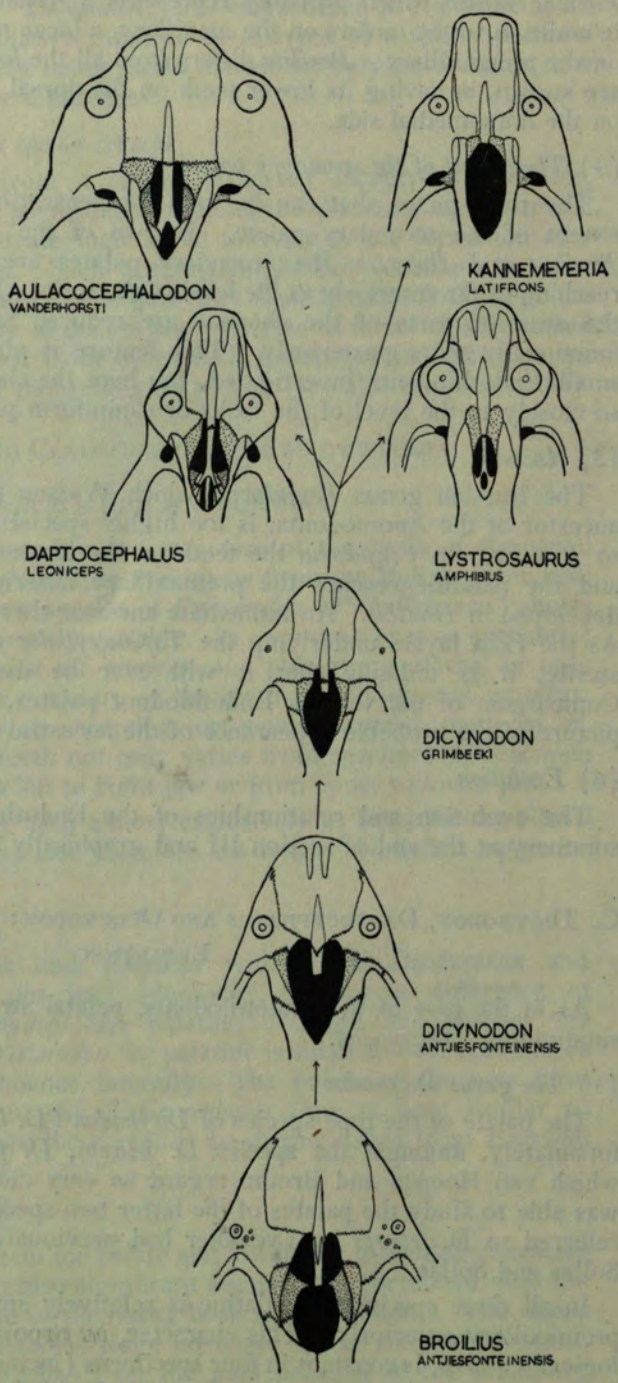


Fig. 71. — Morphological stages in the Evolution of a more extensive secondary palate in *Dicynodon* and related forms from the Endothiodont condition.

(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*,

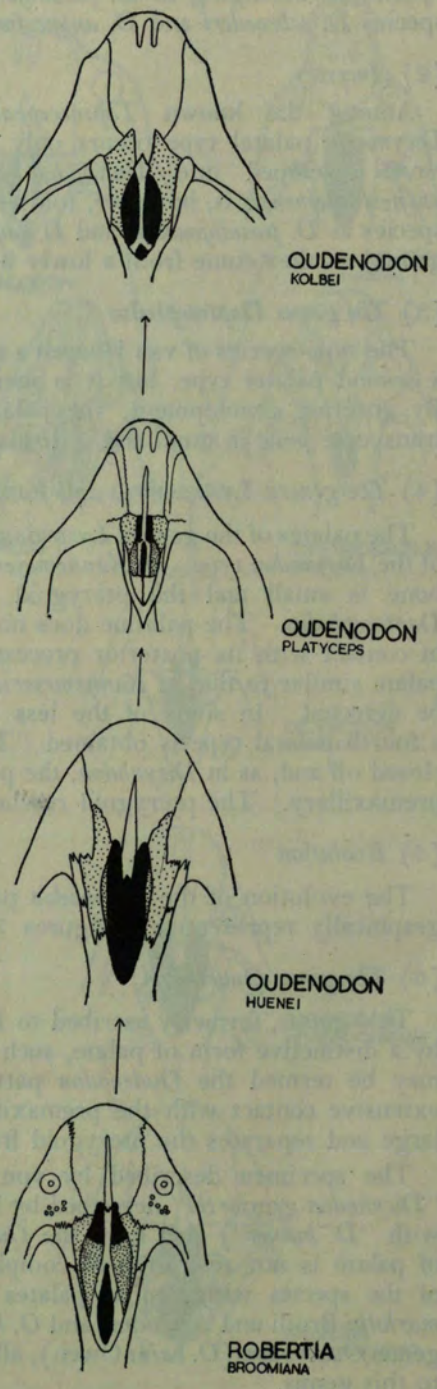


Fig. 72.—Morphological stages in the Evolution of a more extensive secondary palate in *Oudenodon* from the Endothiodont condition.

(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*.

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