PALAEONTOLOGIA AFRICANA

Annals of the

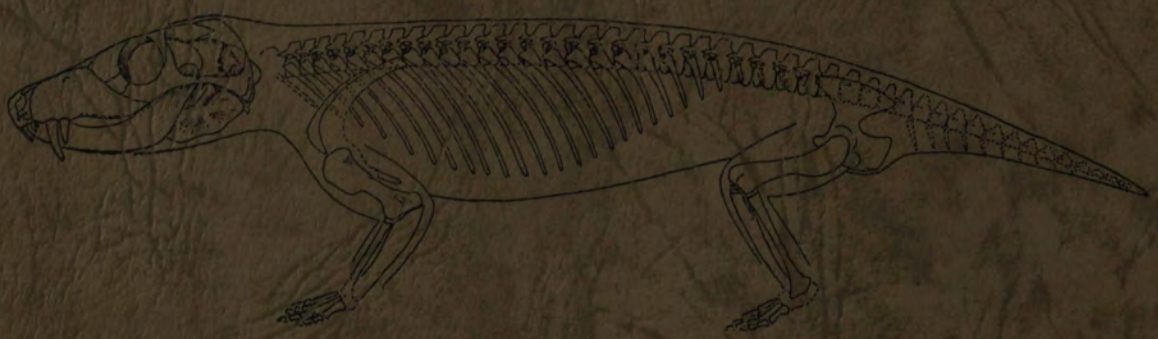
BERNARD PRICE INSTITUTE

for

PALAEONTOLOGICAL RESEARCH

UNIVERSITY OF THE WITWATERSRAND

JOHANNESBURG



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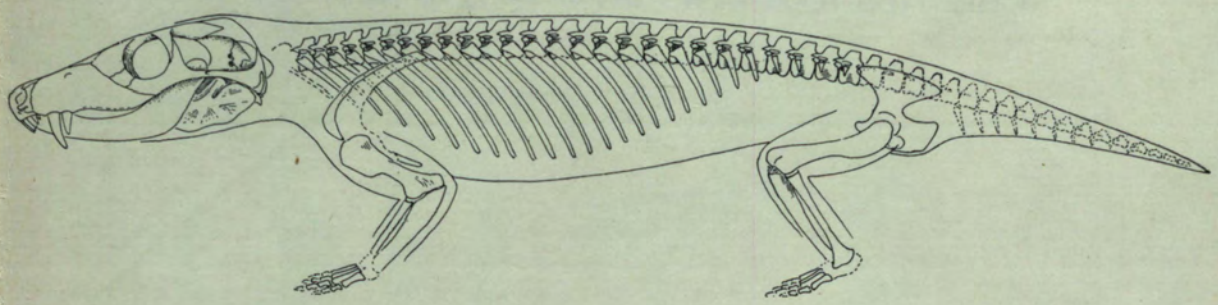

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REPORT OF THE HONORARY SCIENTIFIC DIRECTOR FOR THE YEAR 1st APRIL, 1957 TO 31st MARCH, 1958

The year has been noteworthy for a considerable variety of activities on the part of the permanent staff and of scientific workers who have devoted part of their time to association with the Institute and to the examination and study of its rapidly growing collections of material and of information. The problem of accommodation becomes ever more pressing; so also does that of the calls upon the time and duties of the two full-time members of the staff. The former problem will, we hope, be solved by the erection of the planned new Institute; but the completion of this new home will add still more to the burdens laid on the staff, since it will be necessary to arrange, display and maintain the exhibits which will be set up in the museum which is designed to promote public interest in palaeontology and, in all probability, will increase the amount of teaching and demonstration on behalf of the University. The Board will have to consider the question of additional full-time staff at the Institute. Two possibilities may be suggested as alternatives — the appointment of an administrative officer to undertake the work connected with correspondence, the library, card indexing, cataloguing, and the arrangements for producing "Palaeontologia Africana", or the appointment of a junior research officer who can share these responsibilities with Dr. Brink and undertake some research studies.

Publications:

Volume IV of "Palaeontologia Africana" was issued in the early part of the year under review. It contained 7 original papers with 39 text figures, in the same format as previous volumes. It bears the date of publication 3rd April, 1957. Unfortunately, a number of corrigenda slips had to be inserted. Although, as Editor-in-Chief, I had corrected the page-proofs submitted to me, the printers did not utilise these corrected proofs but relied on a preliminary set submitted by Dr. Brink on which pagination and the distribution of figures in the text only had been indicated. Unfortunately, too, Dr. Brink did not personally check the machine proof with my corrected master page proofs, as he had done for the earlier volumes, thinking that the printers' page-proof readers would have satisfied themselves in that respect.

Every effort will be made to ensure that Volume V will be issued without corrigenda slips. Papers for this volume have been assembled, and corrections have been made to the typescripts which I have critically read. The volume will go to press shortly.

Collecting:

Several visits to the Makapansgat Limeworks deposit were made by Mr. Kitching for the purpose of selecting material of bone-bearing breccia and transferring it to the Institute.

On a visit to the Cave of Hearths with Professor Flint of Yale University, it was noticed that the travertine floor on which the hearth rests was in a state of collapse. Methods of preventing further damage were discussed by Mr. Kitching with Professor Dart and Mr. B. D. Malan, and eventually Dr. Gevers authorised Mr. Kitching to undertake the work necessary to support the travertine floor and the sides of the excavation closest to the hearth. The work was completed on September 11th after three weeks spent at the site.

Together with Mr. A. R. Hughes of the University Medical School, Mr. Kitching paid a visit to the Zaka district of Southern Rhodesia, with the approval of the local authorities, in order to collect skeletons of animals that were being killed under Government authority. These skeletons (of crocodile, waterbuck, kudu, buffalo and elephant) together with a growth series of elephant teeth and three elephant skulls will be available as comparative material after cleaning at the Medical School.

A short visit was paid by Dr. Brink, Mr. Kitching and Mr. De Graaff to the Karroo exposures on Harrismith Commonage, Oliviershoek Pass, and Golden Gate. A number of interesting small amphibian and reptilian skulls and skeletal remains were collected.

Preparation:

A fair amount of preparatory work on Karroo material has been completed, in some cases with the assistance of the acetic acid technique. Among the outstanding material prepared are a complete large skull of *Struthiocephalus* which was in nine pieces in an extremely hard matrix; specimens of *Ictidodraco* and a Moschorhinid; a skull and skeleton of a small *Thrinaxodon;* a small, fairly complete amphibian from the Engcobo district from the collection of the Albany Museum, Grahamstown; and two skulls of *Myosaurus*.

Considerable progress has been made in the preparation of mammalian fossils. From breccia collected at an open site at Kalkbank, near Pietersburg, by the Archaeological Survey and deposited in the Institute, some 3200 bone specimens have been extracted. These are to be studied by Professor Dart.

A very large number of specimens have been extracted from Limeworks breccia, bringing the total at present cleaned from this deposit to about 35,000.

A small collection of mammals from Chelmer Spruit, S. Rhodesia, belonging to the Rhodes-Livingstone Museum, was brought to the Institute by Dr. H. B. S. Cooke. The material was very fragile; but after treatment with dilute glyptal it was possible to clean the specimens by means of the acetic acid technique.

Sorting of cleaned material:

Working conjointly, Mr. De Graaff and Mr. Kitching sorted and analysed the specimens extracted from the Kalkbank breccia, preparatory to their study by Professor Dart.

Mr. Kitching undertook the detailed sorting of some seven thousand bones from the Cave of Hearths deposit. In doing so, he discovered two pieces of human radii (from the Middle Stone-age layers). He also separated those fragments which owe their fragmentation to the action of carnivores from those which appear to have

been broken by human agency. He considers that the basis on which this separation has been made can also be used in the study of broken bones in the Limeworks deposit.

Mr. De Graaff has taken official control of the Institute's mammalian material and is responsible for its proper registration after preparation and sorting.

Research work:

Increasing administrative duties have prevented Dr. Brink from devoting as much time as desirable to research on the Karroo fossils. He has, however, completed a description of the large *Struthiocephalus* referred to above and has decided to consider it as representative of a new species of that genus. He has completed a description of the nearly complete skeleton belonging to a skull that was described by Broom as *Aneugomphius ictidoceps,* a skeleton which had been ignored by the founder of the species. The specimen required very careful preparation, which Dr. Brink effected manually under binocular enlargement.

Dr. Brink gave considerable assistance in the study of the amphibian specimen belonging to the Albany Museum and prepared the illustrations to accompany a descriptive paper on it which will appear under Mr. Kitching's name. He also began studies of several other important specimens.

Reference has already been made to conclusions drawn by Mr. Kitching which have resulted from his careful sorting of mammalian remains.

Studies of *Emydops* and related small endothiodonts in the collection have been pursued by Mr. Agnew of Pretoria University under the guidance of Dr. Barry. Dr. Barry himself has submitted for publication a paper on the supposed relationships between tusks and sex in the *Dicynodont* skull.

Dr. A. W. Crompton, Director of the South African Museum, is investigating the Institute's cynodonts from the *Cistecephalus* zone and a specimen of *Youngina.*

Mr. De Graaff is making a statistical and systematic study of the microfauna of the Transvaal cave deposits. Dr. R. F. Ewer of Grahamstown has continued her studies on our fossil pigs.

Among material developed from the Limeworks breccia is a well-preserved fossil chrysalis of a dipterid insect. With expert advice from Drs. Zumpt and De Meillon of the S.A. Institute of Medical Research and Dr. Bolwig of the University's Department of Zoology, Mr. Kitching has prepared a short note on this interesting specimen.

Library:

The library continues to expand. We have to express again our gratitude to Mrs. Sutherland for gratuitously giving us her efficient services in this important department of the Institute's activities. Cataloguing and card-indexing are essential in the proper functioning of a specialised library. Without Mrs. Sutherland's help, the time available for research would be considerably restricted.

Donation:

Thanks are due to Professor Dart for generously donating a collection of about

160 complete skeletons of contemporary South African animals for purposes of comparison.

Visitors:

In addition to members of the public and of the staffs of this and other South African universities, as well as some groups of students, the Institute has been visited by Dr. Chalmers of N. Rhodesia, M. Adrey of Switzerland, Professor von Bonin of Chicago, Dr. A. Wetmore of the United States National Museum, Professor Flint of Yale University, Dr. Scott of Belfast, and Dr. A. Hooijer of Leiden University.

During the first Congress in Johannesburg of the Geological Society of South Africa, the Institute was open during one afternoon to members of the Congress who desired to visit it.

Programme:

It is hoped to carry out further collecting in the Upper Beaufort and Stormberg sediments of the N.E. Free State and Natal during the coming year. Mr. Kitching will be on leave during July, and intends to follow up rumours of the occurrence of fossils in red shales in the Bulwer and Impendhle districts of Natal.

For the rest, routine and research work will continue. Assistance will be given to Professor Stebbins of the University of California who is to visit the Union to pursue studies on the pineal eye in fossil reptiles.

A COLLECTION OF PHACOCHOERUS AETHIOPICUS TEETH FROM THE KALKBANK MIDDLE STONE AGE SITE, CENTRAL TRANSVAAL

By R. F. Ewer*

I. Introduction

A Middle Stone Age site at Kalkbank, near Pietersburg in the northern Transvaal, has recently been excavated for the Archaeological Survey[1] by R. Mason: a description of the site and the archaeological findings is shortly to be published (Mason, in press). In addition to the cultural material, animal remains are abundant; the present paper deals with the Suid material which has been found at Kalkbank. This consists of a large collection of teeth, almost all isolated, comprising (apart from much damaged fragments) 53 reasonably complete third, 29 second and 10 first molars, together with 29 upper and 25 lower canines and a single last milk molar.

As will be shown later, this material is all referable to the extinct *Phacochoerus aethiopicus* (Pallas). It constitutes the best collection of material of this species from a single locality that is at present available for study, and therefore adds something to our knowledge of the characteristics of the dentition of this species.

II. Description

The specimens all belong to an advanced species of *Phacochoerus,* clearly either the extant *P. africanus* (Gmelin) or the extinct *P. aethiopicus* (Pallas). Since the main difference between these two species lies in the later rooting of the third molars in the latter, it will be convenient to consider these teeth first.

(i) *Third molars*

The 53 reasonably complete specimens may be grouped, according to their state of wear, into 6 categories as follows:—

Stage 1: not yet fully erupted.

„ 2: just fully erupted, with wear on posterior columns very slight.

„ 3: posterior columns fully in wear, but no fusion of columns at the anterior end of the tooth has yet occurred.

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* From the Department of Zoology, Rhodes University.

1 The Kalkbank excavation was made possible by the generous financial assistance of the Wenner Gren Foundation for Anthropological Research.

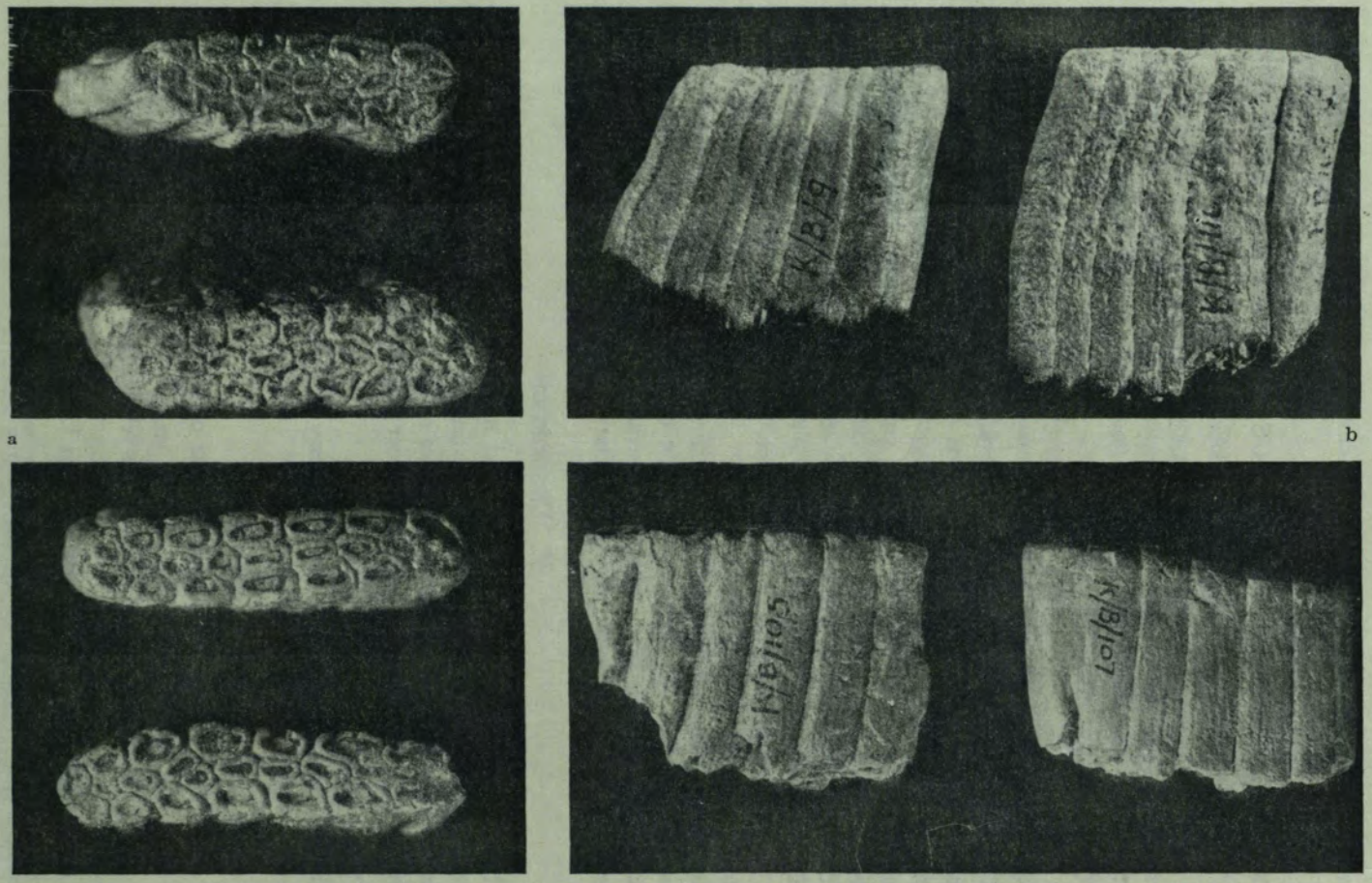

Figure 1—(a) & (b) occlusal and side views of third molar teeth in wear stage 3. The crowns are fully in wear, but root formation has not yet started.
(c) & (d) occlusal and side views of third molar teeth in wear stage 5. Fusion of cusps at the anterior end involves lateral columns of both sides: root formation is taking place.

Stage 4: wear sufficient for traces of fusion of cusps to be evident at the anterior end of the tooth, but the process of fusion as yet involves lateral columns of one side only.

„ 5: wear sufficient for the anterior columns of both sides of the tooth to be involved in fusion.

„ 6: heavily worn.

The teeth were first sorted into these categories, and then the state of root formation in each specimen was noted, with the following results:—

Stage no.	*No. of specimens*	*No. with roots*
1	13	0
2	3	0
3	11	0
4	18	3 distinct, 3 incipient.
5	6	6
6	2	2

Root formation starts during stage 4, well after the whole tooth is erupted and by stage 5 roots are clear in all specimens (Figure 1). There is no evidence of any heterogeneity in the material, and no reason to do otherwise than refer all the specimens to the late-rooting *P. aethiopicus*.

There is considerable variation in the number of cusps composing the marginal and median rows. Shaw (1939) notes that the same is true of *P. africanus* and gives the following values for that species.

	$M^{\frac{3}{2}}$		$M_{\overline{3}}$	
	marginal	median	marginal	median
Mode	7	7	7	8
Range	6-10	7-13	6-9	7-13

For the Kalkbank material the corresponding figures are:—

	$M^{\frac{3}{2}}$		$M_{\overline{3}}$	
	marginal	median	marginal	median
Mode	7	7	7	10
Range	5-8	5-12	6-8	8-13

The figures are very similar, and such differences as there are can hardly be taken as sufficient evidence of a specific difference in cusp numbers. There may, however, be some difference in the frequency with which extra cusps occur in the median row. In the Kalkbank specimens 8 out of 32 complete and fully erupted specimens show extra medians, whereas Shaw (1939) reports only 6 cases out of what appears to have been a larger collection of teeth of the extant species. The extra cusps are of the same type as those described by Shaw — the majority confined to the posterior part of the tooth, and lacking the regularity of arrangement characteristic of *P. compactus* (van Hoepen & van Hoepen).

Table 1

Dimensions of third molar teeth — fully erupted but not heavily worn. All measurements in this and the succeeding tables are given in millimeters.

$M\frac{3}{3}$

Specimen no.	Stage of wear (see text)	Occlusal length	Maximum length	Occlusal breadth (at 2nd cols.)	Maximum breadth	Maximum height preserved
K/B/108	3	47·9	52·2	11·3	11·7	42·5
K/B/101	„	ca. 47	ca. 49	11·5	12·2	46·8
K/B/104	„	56·0	63·8	12·8	13·1	45·2
K/B/87	4	57·3	57·3	13·7	15·3	47·8
K/B/55	„	47·3	48·4	12·2	12·3	49·6
K/B/102	„	ca. 48	ca. 48	ca. 11	13·7	45·9
K/B/92	„	56·5	56·9	11·0	13·7	43·2
K/B/98	„	54·1	56·2	11·1	14·3	43·1
K/B/72	„	53·0	54·0	12·0	12·2	44·3
Mean & standard error		51.90±1·44	53·98±1·88	11·84±0·31	13·17±0·39	
Standard deviation		4·32	5·65	0·93	1·18	
Coefficient of variation		8·3	10·5	7·8	9·0	
Range		ca. 47—57·3	ca. 48—63·8	ca. 11—13·7	11·7—15·3	
Range for *P. africanus* (given by Cooke 1949)		45—50	50—60	11—14		

$M\frac{3}{3}$

Specimen no.	Stage of wear (see text)	Occlusal length	Maximum length	Occlusal breadth (at 2nd cols.)	Maximum breadth	Maximum height preserved
K/B/16*	3	44·4	51·7	13·4	14·4	51.8
K/B/74*	„	42·3	50·0	13·5	14·6	50·5
K/B/116	„	47·7	54·0	15·9	16·5	59·5
K/B/69	„	46·8	50·5	12·6	13·8	42·4
K/B/5	„	52·4	62·1	15·6	16·4	68·4
K/B/2	„	58·5	58·5	14·2	15·6	46·0
K/B/9	„	44·5	53·7	14·6	15·3	45·9
K/B/110	„	44·8	49·7	14·7	15·0	57·0
K/B/6	4	52·1	54·6	14·6	16·2	50·5
K/B/53	„	54·0	56·3	14·8	16·0	51·0
K/B/17	„	ca. 53	53·3	16·2	17·0	52·6
K/B/8	„	48·2	50·5	13·9	15·0	42·1
K/B/54	„	50·2	55·2	14·9	15·5	59·7
K/B/18	„	50·2	56·8	15·5	16·1	50·3
K/B/48	„	53·6	54·9	16·2	16·5	51·0
K/B/1	„	ca. 58	59·5	16·0	16·8	51·2
K/B/125	„	ca. 51·5	53·9	13·3	14·0	42·8
K/B/11	„	47·8	48·7	14·2	15·4	48·7
K/B/7	„	62·1	62·1	15·5	16·0	49·7
K/B/12	„	62·1	64·8	15·6	16·1	53·1
Mean & standard error		51·08±1·25	55·04±0·98	14·76±0·23	15·61±0·20	
Standard deviation		5·57	4·39	1·03	0·89	
Coefficient of variation		10·9	8·0	7.0	5·7	
Range		42·3—62·1	48·7—64·8	12·6—16·2	13·8—17·0	
Range for *P. africanus* (given by Cooke 1949)		45—55	55—65	12—15		

* Probably left and right teeth of a single individual.

Measurements of the third molars are given in table 1. Since the tooth dimensions change considerably during growth and attrition, the measurements have been restricted to teeth in stages 3 and 4, i.e. they refer to fully erupted teeth which are not yet heavily worn and they are thus comparable with the estimates given by Cooke (1949) for teeth of *P. africanus* which are "fully erupted but at an early stage of root formation". Cooke's figures for what he describes as a reasonable range of variation for certain dimensions of the third molars in the living species are given for comparison in table 1. Specimens as much as 5 mm. in excess of the limits given, Cooke considers to be "extremely rare", but Leakey (1942) is of the opinion that the range is greater than this and gives 33-75 mm. as the range for the length of 10 specimens of M_3 in his collection. He does not, however, specify the stages of wear represented, and, of course, younger and older teeth will be expected to cover a greater size range than Cooke's selected material.

In the Kalkbank material three specimens of M^3 (numbers K/B/ 5, 7 & 12) are rather larger than the others, but do not exceed Cooke's limits, while one M_3 (K/B/ 104) exceeds his limits, but by less than 5 mm. In other respects these three teeth resemble the rest of the material and there seems to be no justification for concluding that they do not belong to the same species. It is, of course, quite possible that large individuals may have been commoner in *P. aethiopicus* than they are in extant *P. africanus*.

(ii) *Anterior cheek teeth.*

The second and third molars do not show any characters which differentiate them from those of *P. africanus*. Unfortunately, no complete jaws are known, so that it is not possible to see whether the anterior cheek teeth are shed any earlier than in the extant species. Measurements of the second and first molars and the single dm_4 are given in tables 2 and 3.

(iii) *Lower canines.*

Nineteen lower canine specimens from Kalkbank are available. They appear to differ from those of the extant species in three respects (see figures 2 and 3). Firstly, the curvature appears to be rather less. To make certain that this difference is real would require for comparison a much larger collection of tusks of *P. africanus* at different ages than is at my disposal, so that at present this remains purely as a subjective "impression".

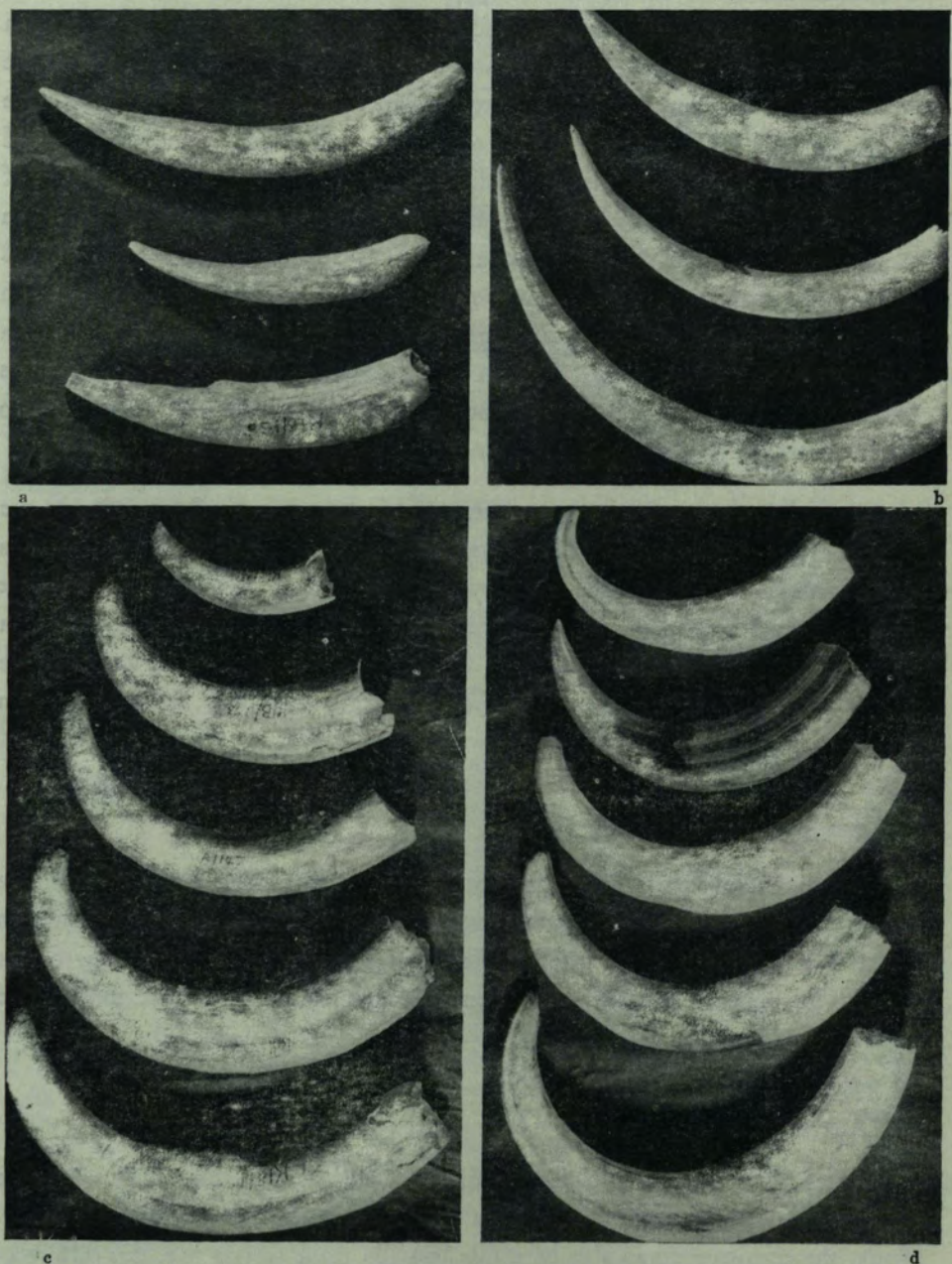

Figure 2—(a) & (c) lower and upper canines of *P. aethiopicus* from Kalkbank.
(b) & (d) lower and upper canines of extant *P. africanus*.

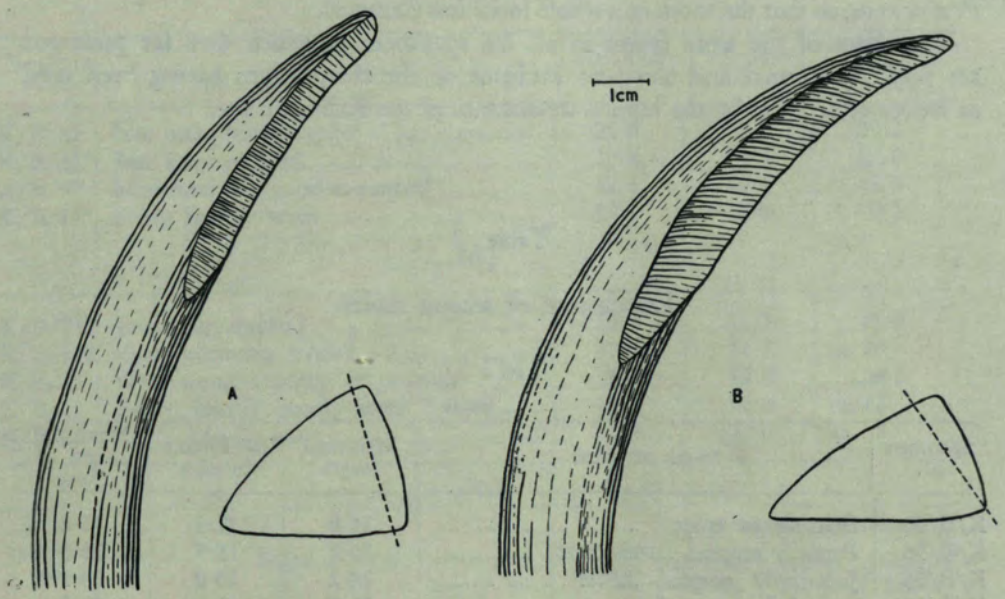

Figure 3—Lower canines of (A) *P. aethiopicus* (specimen K/B/157) and (B) extant *P. africanus* in side view and transverse section. The broken lines through the sections represent the direction of the plane of the wear facets. The scale refers to the side views; in the transverse sections the magnification has been doubled.

Secondly, the angle of the wear facet is slightly different. In *P. africanus* the wear facet usually makes an angle with the posterior face of the tooth, so that the dorsal corner (i.e. the junction of posterior and antero-dorsal faces) is sliced off and considerably more of the antero-dorsal than of the antero-ventral face is removed by wear. In most of the fossil teeth the wear is more nearly parallel to the posterior face and consequently antero-dorsal and antero-ventral faces are almost equally reduced by wear. There is considerable individual variation both in the fossil and in the extant species and not every tusk could be assigned to its correct species on this character, but parallel wear does seem to be distinctly commoner in the former than in the latter — presumably reflecting a slight difference in the orientation of the teeth in the jaw.

Thirdly, the teeth are less flattened in the fossil than in the extant species. This can be expressed numerically in terms of the ratios of the widths of the antero-dorsal and antero-ventral faces to the width of the posterior face. In the extant species these ratios remain reasonably constant over a wide size range and there is no evidence of any consistent change with increasing size. The lengths of the

three faces and the ratios are given in table 4. Although the ranges overlap slightly, the differences between the means for *P. africanus* and *P. aethiopicus* are statistically significant: for both ratios $P < 0.01$. We may therefore conclude that in *P. aethiopicus* the posterior face of the lower canine is relatively wider than in *P. africanus*, so that the tooth as a whole looks less flattened.

The edges of the wear facets in all the specimens in which they are preserved are perfectly normal and show no evidence of the sharp edges having been used as knives or scrapers by the human inhabitants of the Kalkbank site.

Table 2

Dimensions of second molars

$M\frac{2}{2}$

Specimen no.	Stage of wear	Maximum length	Maximum breadth	Maximum height of crown
K/B/68	Starting to erupt	24·8	11·1	25·8
K/B/56	Partially erupted	26·1	11·3	33·5
K/B/66	Just fully erupted	24·2	10·0	30·2
K/B/112	Just fully erupted	25·5	12·6	42·2
K/B/61	Fully erupted, not yet rooted	24·1	10·7	37·0
K/B/75	Moderately worn, not yet rooted	21·0	10·7	35·8
K/B/89	Moderately worn, root formation starting	22·2	11·7	ca. 35
K/B/109	(Incomplete) Moderately worn	—	11·3	30·6
K/B/32	Roots formed	20·0	12·3	23·0
K/B/88	Roots formed	21·9	12·3	ca. 24
K/B/121	Well worn	20·0	10·9	20·0
K/B/57	Heavily worn	ca. 19	12·5	ca. 12
K/B/31	Very heavily worn	18·8	13·2	ca. 7
K/B/36	Very heavily worn	—	12·4	—

$M\frac{2}{2}$

K/B/81	Partially erupted	26·5	13·5	—
K/B/118	Partially erupted	24·2	13·1	—
K/B/24	Just fully erupted, not yet rooted	22·9	13·5	39·0
K/B/27	(Incomplete) Fully erupted	20·5	13·5	—
K/B/29	Root formation started	20·8	16·6	36·9
K/B/28	Well worn — roots present	19·1	15·5	24·8
K/B/34	Well worn — roots present	18·8	14·9	23·3
K/B/30	Very heavily worn	19·4	15·9	ca. 8

Table 3

Dimensions of first molars and milk molar.

M^1

Specimen no.	Stage of wear	Maximum length	Maximum breadth	Maximum height of crown
K/B/82	Not quite fully erupted	21·6	9·7	29·2
K/B/85	Just fully erupted	22·8	9·8	27·8
K/B/97	Moderately worn, roots formed	19·6	10·4	12·5
K/B/117	Fairly heavily worn	17·3	10·0	9·5

M_1

K/B/73	Just fully erupted	22·9	11·5	31·9
K/B/124	Root formation started	17·4	11·7	ca. 20
K/B/33	Well worn; rooting in progress	18·7	12·8	20·3
K/B/63	Fairly heavily worn; roots formed	18·0	12·0	ca. 12
K/B/26	Fairly heavily worn	15·4	12·0	ca. 7

dm_4

Specimen no.	Stage of wear	Maximum length	Maximum breadth		
			anterior pillars	middle pillars	posterior pillars
K/B/65	Crown just fully in wear	18·7	6·1	7·8	9·1

(iv) *Upper canines*

The 29 upper canine specimens include tusks belonging to animals of all ages. They range from small immature specimens, with a maximum diameter near the base of ca. 25 mm. to tusks of mature animals with a maximum diameter of ca. 45 mm. which would be regarded as large, but by no means abnormal, for the extant species.

As in the case of the lower tusks, the uppers give the impression of being slightly less curved than those of *P. africanus* (see Figure 2). It would, however, be even more difficult than in the case of the lower tusks to establish the reality of this difference, for the range of variation shown in the living species is very great, including marked sexual dimorphism (Ewer, in press). Moreover, since the curvature is greatest near the tip, a slightly incomplete tooth may give a misleading impression.

A number of the upper tusks have been gnawed by rodents. In most cases the tooth marks are so large that the only reasonable suggestion as to their authorship is that they have been made by porcupines. This suggests that the K'lkbank tool-makers did not attach particular value to the tusks, but left them lying about where they were easily accessible to porcupines.

Table 4

Dimensions of lower canines

Specimen no.	Widths measured between wear facet & gum line			Ratios	
	(1) Posterior face	(2) Antero-ventral face	(3) Antero-dorsal face	(2): (1)	(3): (1)
K/B/158	8·7	12·1	12·0	1·39	1·38
K/B/162	9·0	14·0	13·4	1·55	1·49
K/B/167	9·1	11·5	12·4	1·27	1·36
K/B/168	9·4	12·5	13·1	1·33	1·40
K/B/166	9·5	13·2	13·5	1·39	1·42
K/B/176	9·7	13·3	13·2	1·37	1·36
K/B/177	9·7	12·3	12·0	1·27	1·24
K/B/180	9·7	12·4	13·2	1·28	1·32
K/B/164	9·8	12·9	11·0	1·32	1·12
K/B/178	9·8	13·5	13·7	1·38	1·40
K/B/172	9·9	15·7	14·4	1·59	1·46
K/B/161	10·0	13·4	13·4	1·34	1·34
K/B/173	10·3	13·4	13·6	1·30	1·32
K/B/165	10·5	14·9	14·7	1·42	1·40
K/B/160	10·6	15·6	15·5	1·47	1·46
K/B/159	11·0	14·4	13·4	1·31	1·22
K/B/171	11·0	17·0	16·2	1·55	1·47
K/B/181	11·1	16·8	16·1	1·51	1·45
K/B/156	11·4	14·6	15·3	1·28	1·34
K/B/174	11·8	18·9	16·3	1·60	1·38
K/B/182	11·8	15·4	15·4	1·31	1·31
K/B/157	12·5	17·5	17·0	1·40	1·36
K/B/163	13·1	16·8	16·6	1·28	1·27
K/B/175	14·8	20·6	18·7	1·39	1·27
K/B/155	15·1	24·3	19·8	1·61	1·31
Mean & standard error				1·396±0.0220	1·354±0·0171
Standard deviation				0·1099	0·0854
Coefficient of variation				7·9	6·3
Range				1·27—1·61	1·12—1·49

Table 4 (continued)

Dimensions of lower canines of extant *Phacochoerus africanus*

Specimen no.	Widths measured between wear facet & gum line			Ratios	
	(1) Posterior face	(2) Antero-ventral face	(3) Antero-dorsal face	(2): (1)	(3): (1)
A.M. 1644	7·6	12·2	12·0	1·61	1·58
R.U. 2	9·5	16·5	16·1	1·74	1·70
R.F.E. 2	9·5	16·2	15·5	1·71	1·63
A.M. N875	10·2	15·5	14·4	1·52	1·41
R.U. 1	10·5	19·2	18·8	1·83	1·79
R.F.E. 3	10·8	19·1	18·2	1·77	1·69
A.M. Ohl.	10·8	15·2	14·6	1·41	1·35
R.F.E. 4	11·0	20·2	19·7	1·84	1·79
R.F.E. 1	12·0	20·0	19·1	1·67	1·59
A.M./G.C.	12·3	20·7	19·8	1·68	1·62
A.M.5829	12·8	19·2	20·0	1·50	1·56
		Mean and standard error		1·662±0·0418	1·610±0·0417
		Standard deviation		0·1389	0·1383
		Coefficient of variation		8·4	8·6
		Range		1·41—1·84	1·35—1·79

Dimensions of lower canines of Cape Warthog

N.M. A 1411 right	ca. 14·0	19·6	17·5	ca. 1·40	ca. 1·25
N.M. A 1411 left	ca. 14·0	ca. 19·5	17·5	ca. 1·39	ca. 1·25
S.A.M. 21370	12·0	16·6	14·9	1·38	1·24
S.A.M. 21371	13·1	17·8	16·4	1·36	1·25

III. Discussion

The name *Phacochoerus aethiopicus* is normally used by palaeontologists to denote an advanced phacochoere which differs from the extant *P. africanus* in the later rooting of the third molar teeth. In practice this means that third molars which root early are identified as *P. africanus,* while later rooting specimens are referred to *P. aethiopicus.* A neontologist might be inclined to question the legitimacy of this procedure and feel tempted to suggest that a difference of this type may have a very simple genetic basis and be no more indicative of specific distinction than are blood group differences in man. It is therefore necessary to consider whether there is indeed sufficient evidence to warrant the specific distinction.

A second question concerns the relationship of the fossil *P. aethiopicus* to the recently extinct Cape Warthog, to which the same name is normally applied: they agree in the single character of late-rooting molars, but is it certain that the two are in fact the same species?

Lönnberg (1908), on the basis of differences in skull proportions attempted to characterise what he called "races" of Warthog — but since he referred to them by the normal binomial nomenclature used to designate species, it is not clear exactly what he meant by the term. His "races" include *P. aethiopicus,* of which vestigial incisors shed earlier than in other "races" is given as one diagnostic character. Lönnberg's differences in skull proportion have subsequently been shown by Shaw (1939) to be useless as taxonomic characters, but the van Hoepens (1932), in a study based largely on a single skull thought to belong to the Cape Warthog, pointed out the delayed rooting of the molar teeth and confirmed the great reduction of the incisors. This skull, number 1411 in the National Museum collection, is the only known Cape Warthog skull to be found in any South African museum collection, and even its origin is not certain. It is therefore necessary firstly to consider all the characteristics now known for fossil *P. aethiopicus* and decide whether these warrant separation from *P. africanus;* secondly, to see whether all of the characters are also shown by the van Hoepen's Cape Warthog skull.

The characters of fossil *P. aethiopicus* distinguishing it from *P. africanus* are as follows:—

1. Rooting of the third molars does not start until well after the tooth is fully erupted and the whole length of the crown in wear.

2. The lower incisors are vestigial. This character is not visible in the Kalkbank material, but is shown by a mandible from Florisbad described in a previous paper (Ewer 1957).

3. The anterior cheek teeth are probably shed a trifle earlier. This character is also shown in the Florisbad material.

4. The lower canines are less flattened, the wear facet tends to be less sloping and the curvature of both upper and lower tusks appears to be a trifle less.

Thus, although the single character of early or late rooting of the third molars is alone normally used to distinguish *P. africanus* and *P. aethiopicus* the two do in

fact differ not in one but in a number of characters affecting the whole of the dentition. It seems difficult to believe that such a constellation of characters could exist unless it did reflect a specific difference, and it therefore seems justifiable to regard *P. aethiopicus* as a valid species, distinct from *P. africanus*.

The van Hoepen's Cape Warthog skull is described as showing two of the *aethiopicus* characters listed above — late rooting molars and vestigial incisors. Examination of the specimen shows that in fact the others are also present (see figure 4). Although the third molars are not much worn the other cheek teeth have been lost, the second molars not long before the death of the animal, for partially filled alveoli are still present. At a comparable stage of third molar wear, *P. africanus* normally possesses at least last premolars and second molars, while the first molars may either be present but much worn or have been recently shed. The characters of the lower canines of specimen N.M. 1411 agree perfectly with those of fossil *P. aethiopicus*: they are not much curved, have a wear facet which is very little slanted and are less flattened than is usual in *P. africanus*. Measurements of the lower canines are included in table 4. This specimen therefore agrees in all particulars with the fossil *P. aethiopicus,* and there thus seems to be no doubt of the specific identity of the latter with the Cape Warthog.

On a recent visit to the South African Museum two of the Warthog skulls in the collection were found to agree in all particulars with *P. aethiopicus*. Unfortunately no details as to their dates and localities are known, but there is no doubt of their being Cape Warthog and they are easily distinguishable from specimens of the extant *P. africanus,* as shown by the following particulars:—

Specimen no. S.A.M. 21370

Third molars at wear stage 5, but only the merest indications of root formation starting at the anterior end of the teeth: lower incisors worn off level with the bone: no cheek teeth other than third molars present, but small alveoli of a recently used upper premolar are present: lower canines broad, rather forwardly directed and worn off abruptly.

Specimen no. S.A.M. 21371

Third molars at wear stage 3, with no sign of root formation: lower incisors only represented by minute vestiges: anterior cheek teeth comprise much worn M^2 and small premolar alveolus in the maxilla and in the mandible alveoli for two teeth anterior to M_3: of the lower canines only a small stump remains on one side, but this suffices to give the relative lengths of the three faces. Measurements of the lower canines of these two specimens are given in table 4, and it can be seen that both agree with those of fossil *P. aethiopicus*.

Another characteristic of these skulls is that the sinuses in the zygoma below the orbit are extensive, so that the bone has a more inflated appearance than is usual in the extant species. This character is highly variable and is affected by the age and sex of the individual and its importance could therefore be assessed only by a comparison of extensive series of skulls. It is, however, of some interest to note that Lydekker (1894) distinguishes two types of Warthog — one "distributed

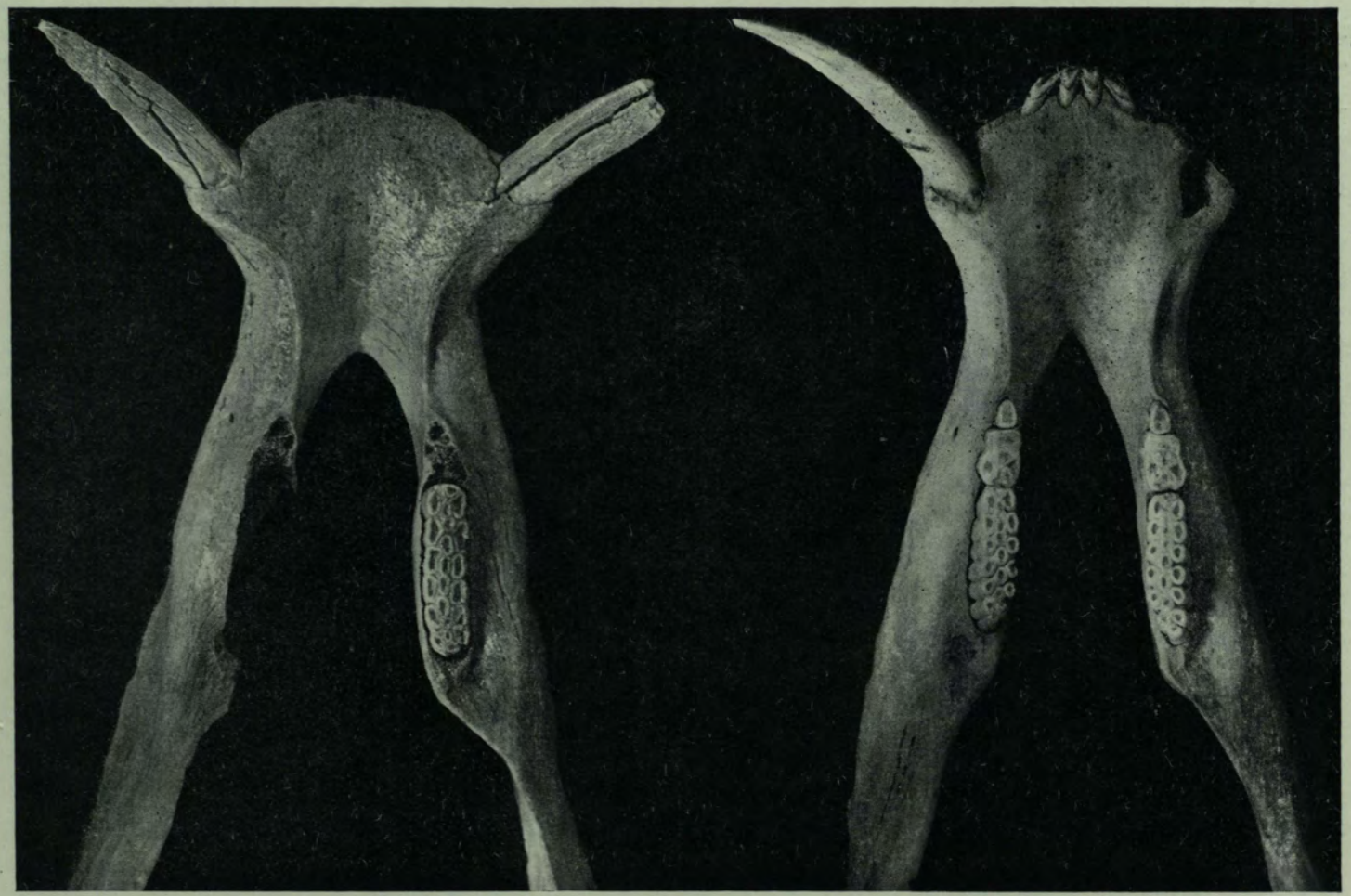

Figure 4—**Mandibles of, on left, Cape Warthog, N.M. 1411 and, on** right, extant *P. africanus* with third molars at similar stages of wear.

over a large part of the eastern side of Africa, ranging as far north as Abyssinia", the other "confined to south eastern Africa". In the latter the sub-orbital warts are described and figured as long and pendulous. My own observations on living Warthog have been confined to Zululand, but I have not seen an animal with warts resembling those figured by Lydekker. It seems possible that Lydekker's southern type was the now extinct *P. aethiopicus* and that in this species the sub-orbital warts differed from those of *P. africanus* — a difference which might well be accompanied by a difference in the structure of the bone underlying and supporting the wart.

I have not been able to find any accurate records of the distribution of the Cape Warthog within historic times but, from the writings of the early naturalists, it is clear that the animal was found as far south as the Cape Province, although it was not abundant. At some time towards the end of the nineteenth century the Cape Warthog was shot out. This suggests that northward from the Cape its range cannot have been very extensive — possibly it did not occur north of the Vaal river — for Warthog were not eliminated from Zululand and the Transvaal, but the survivors in these areas are *P. africanus*. In the past the range of *P. aethiopicus* must have been wider, since at Kalkbank it was clearly abundant in Middle Stone Age times. What caused the restriction in range between the Middle Stone Age and historic times remains unclear. Competition with *P. africanus* appears to have been involved, with climatic and associated vegetational change possibly playing a part. It seems clear that *P. aethiopicus,* once abundant and widespread, as shown by its fossil remains, had become rare and restricted in range by the time European colonisation of the Cape took place, and that fire arms only accounted for the remnants of a species already well on the way to extinction. It is therefore very important that careful specific identification should be made of all fossil and sub-fossil Warthog remains from South Africa, so that more detailed information about the southward spread of *P. africanus* and disappearance of *P. aethiopicus* may be obtained. Such information may be of value in determining the relative ages of archaeological sites in southern Africa.

IV. Summary

Fossil suid remains from Kalkbank are identified as belonging to *Phacochoerus aethiopicus* (Pallas). Measurements of the teeth are given and a new specific character, namely that the lower canines are less flattened than in *P. africanus,* is noted.

The validity of the specific distinction between *P. aethiopicus* and *P. africanus* is considered and it is concluded that the two are distinct species.

The Cape Warthog skull described by van Hoepen & van Hoepen (1932) is found to show all the diagnostic characteristics of fossil *P. aethiopicus* and it is concluded that the identification of the recently extinct Cape Warthog with the fossil *P. aethiopicus* is correct. Two skulls in the South African Museum collection are identified as belonging to *P. aethiopicus.*

Acknowledgements

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A NEW CHRYSOCHLORID FROM MAKAPANSGAT

By G. DE GRAAFF

ABSTRACT

In this paper a new species of golden mole *Chrysotricha hamiltoni* sp. nov. from Limeworks, Makapansgat, is described. This is the first occurrence of a fossil golden mole at this site; two fossil forms (*Proamblysomus antiquus* Broom and *Chlorotalpa spelea* Broom) have previously been recorded from Sterkfontein.

INTRODUCTION

During a visit to the fossil-yielding dumps at Limeworks in the Makapansgat valley near Potgietersrus in the Central Transvaal in April 1957, Mr. J. W. Kitching of the Bernard Price Institute for Palaeontological Research discovered a small skull embedded in a piece of yellowish grey breccia. The exposed portion was the dorsal part of a cranium from which the parietals had been flaked off leaving a well preserved endocranial cast in position within the remainder of the skull.

On development the specimen proved to be the virtually complete skull of a new species of golden mole. Hitherto only two genera have been found as fossils in the dolomite caves of the Transvaal. These were both discovered in the Sterkfontein valley near Krugersdorp. These two fossil types, *Proamblysomus antiquus* Broom, from the locality known as Bolts Farm, and *Chlorotalpa spelea* Broom from the *Plesianthropus* cave at the Sterkfontein site were identified and described by Broom (1941). A third golden mole fossil skull has been found at Kromdraai: it possibly belongs to the species *Proamblysomus antiquus* but its identity is uncertain owing to the damaged condition of the palate and the teeth. (Broom 1948).

The specimen to be described here ranks in size with *Proamblysomus antiquus* but diverges in its morphology. It is the first fossil golden mole to be recorded from Makapansgat and in consequence of that fact it is proposed to name it after the original owner of the farm, who first permitted the Historical Monuments Commission to declare the Cave of Hearths site a national monument and thus inadvertently set in train the series of discoveries made upon this farm since 1936.

The exact horizon from which the specimen originally hailed cannot be determined accurately because the breccia was found amongst the sorted material from the dumps. Judging from its appearance the breccia was probably from the top *Australopithecus*-bearing layer near the dolomitic roof.

No other skeletal remains were closely associated with the specimen so that it had not formed part of an owl pellet. These fossilized owl pellets display a characteristic conglomeration of small partially digested bones, jaws and teeth chiefly of rodents. It may therefore be looked upon as an article of australopithecine

diet concerning which the late Dr. Robert Broom (1946) said: "To have obtained the giant rodent moles (*Gypsorhychus*) he (*Australopithecus*) must have been able to dig with either sticks or stones: and it is unlikely that he could have captured a spring hare (*Pedetes*) except by digging." Alternatively, one may say in the case of the capture of the golden mole that this specimen could have been dug up by *Australopithecus* with either horns or bones.

Preparation

Despite its fragility and small size the specimen was developed manually with a small hammer and chisel. After the main bulk of breccia had been removed the specimen was subjected to the acetic acid technique.

The individual bones in the skull cannot be demarcated with certainty. This is partially due to the fact that it appears to be an adult specimen in which the cranial bones are anchylosed and during the processing the skull acquired a number of layers of glyptal cement to protect the specimen against the corrosive action of the acid. When removing the excess cement with a suitable thinner the glyptal was dissolved but tended simultaneously to remove the thin and fragile bones. As the glyptal holds together the fragile material it was decided rather to preserve the specimen with the protective layers of glyptal surrounding the bones than to risk further damage.

Chrysotricha hamiltoni sp. nov.

The original owner of the Makapansgat farm was the late Mr. J. M. Hamilton and the estate on which the remarkable palaeontological discoveries were made that have made this site known internationally is today the property of his daughter Mrs. M. J. Bonamour of Durban. As amongst the various numerous fossils from this site none have hitherto commemorated the ancestral owner's name it has been decided to name this particular specimen *Chrysotricha hamiltoni* sp. nov. It is housed in the fossil mammal collection of the Bernard Price Institute, Catalogue Number MF. 1.

The skull is virtually complete except for some slight damage to the anterior part of the snout and the region inside the orbit. The principal dimensions upon which the identification is based are given in table I.

A brief description of the dorsal, ventral, occipital and lateral aspects of the skull will indicate the amount of damage suffered by it during the process of fossilization.

a. *Norma dorsalis*. The anterior portions of the nasals and premaxillaries with their characteristic projections for the attachment of nose pads in the living animal are not present. The posterior parts of the nasals are complete and the junction of the nasals with the frontals is clear in the form of a small but distinctly raised ridge. The nasal-maxilla suture is not clear. The right frontal is undamaged while the left frontal has been flaked off latero-posteriorly. The large parietals have, as stated, been flaked off entirely, exposing the well preserved endocranial cast.

The delicate zygoma have nevertheless survived the rigours of fossilization and it has been possible to keep the arches intact while removing the breccia surrounding them. The posterior zygoma forms a slightly broader plate at the point of fusion with the undamaged squamosal elements. There is no trace of a jugal bone in the arch and the arches are formed by a backward process of the maxilla.

b. *Norma ventralis*. The maxillaries are well preserved. The premaxillaries are intact on the palatal aspect, containing the large incisor sockets of the first large incisors. The anterior palatine foramina are visible as two small breccia-filled cavities. The maxillaries furthermore form the greater part of the palate. The posterior portion of the right maxilla has been damaged slightly but that of the left side has been preserved. The intact sockets thus afford information about the number of teeth. There were nine in each tooth row.

5 6

Figures 5 and 6—Dorsal and ventral views of the skull of *Chrysotricha hamiltoni* sp. nov.

The boundary between the palatines and the maxillaries is not distinct. The palatine bones are preserved, being strengthened above by the breccia filling the internal choanae. Consequently the vomer cannot be seen clearly. The pterygoidal elements are present, though without their characteristic pterygoidal processes.

The base of the cranium (the basisphenoid and the basioccipital) is undamaged.

The area covered by these bones is relatively small. The tympanic bullae are well preserved and rather large, the right bulla being slightly damaged in the petrosal area.

The passage leading to the external auditory meatus is visible from the outside in the shape of a small raised ridge.

The norma dorsalis and norma ventralis are shown in figures 5 and 6 respectively.

c. *Norma occipitalis.* The dorsal part of the supra-occipital has flaked off with the parietals. On the lateral side of the supraoccipitals there is a rounded area of bone of moderate size which Broom regards as the tabular. (Broom 1916). This area is somewhat flaked on the right side. The occipital condyles are well formed and strong while the associated exoccipitals are undamaged. The foramen magnum is a well-defined aperture rather arched dorsally.

d. *Norma lateralis.* The condition of the zygomatic arches has already been described. The lachrymal is small and cannot be made out in this skull. The infraorbital foramen, damaged on the left side, is large, while the deep parts of the orbits are somewhat damaged and distorted so that the alisphenoid and orbitosphenoid bones and the associated foramina cannot be distinguished with certainty. The bullae do not extend farther down ventrally than the occipital condyles.

Discussion

Simpson (1945) has placed the Chrysochloroidea together with the Tenrecoidea as a fairly well defined group among the recent Insectivora. In addition, he remarks: " . . . Broom especially has shown that the Chrysochloroids are basically different from the other 'zalambdodonts'. (i.e. Tenrecoidea). He removed them from the Insectivora and made a new Order for them. This seems too radical, but the structural difference is so great that it cannot be affirmed that the Chrysochloroids are phyletically closer to the tenrecoids than to the other insectivores, although the two share the common anatomical feature of being zalambdodont, that is, having a single outer V on the upper molars instead of two."

Roberts (1951) has followed Broom's concept and has placed the golden moles of South Africa in a separate Order. This paper is not intended to discuss the intricate taxonomic position of these animals and the classification presented by Roberts in "The Mammals of South Africa" has been followed for this fossil specimen.

Roberts has subdivided the Chrysochloridae into nine genera. The specimen under review here does not belong to the genera *Chrysospalax* (Gill) and *Bematiscus* (Cope) because it has a far smaller type of skull and the zygomatic arches are not produced upwards posteriorly to form a broad plate covering the temporal region, meeting dorsally on the cranium to form a raised ridge.

The fossil cannot be placed in the genera *Cryptochloris* (Shortridge & Carter), *Chrysochloris* (Lacépède) and *Eremitalpa* (Roberts) because the former two possess

characteristic temporal bullae which are absent in the fossil while the latter has a skull very broad in relation to its length, the index being 85-90 (Roberts).

Of the remaining four genera, *Chrysotricha* (Broom) *Neamblysomus* (Roberts), *Chlorotalpa* (Roberts) and *Amblysomus* (Pomel) this specimen is most closely related to the genus *Chrysotricha* as is evidenced by the following characteristics:

1. The width to length index of the fossil skull is high: 75. The highest index found in the Chrysochlorid genera to which this specimen might possibly be referred is 69-73 (Roberts). This genus is *Chrysotricha*. The remaining genera all vary between 58 and 66 (Roberts).

   Seven *Chrysotricha* skulls were measured and the average breadth to length index value was found to be 71.33, while the variation in the seven specimens was between 69.7 — 72.9 with $\sigma = 0.38$. The fossil differs by $9.5 \times \sigma$ from the mean value of the seven examples. In comparisons of a series with a single specimen a difference of $9.5 \times \sigma$ may be regarded as being of specific value.

2. The number of upper teeth in the fossil has been taken as nine judging from the sockets on the left maxilla. Assuming that the number of teeth in the lower jaw is the same, the fossil had a dental complement of 36 teeth: a feature characteristic of the recent genus *Chrysotricha* but exhibited also by the genus *Amblysomus*.

3. The overall shape of the fossil skull resembles that of *Chrysotricha* the closest of all the living genera: both have a rather stout muzzle compared with the more slender and elongated muzzles of the other genera.

4. In shape, the dental arch of the fossil approximates that of *Chrysotricha* more nearly than that of all the other living genera.

5. The first upper premolar has been compared with the equivalent tooth in recent comparative material. It resembles that of *Chrysotricha* in shape although it is very much larger and more robust as is to be expected from teeth developed in such a relatively big skull.

The fossil golden moles found and described by Broom clearly belong to different genera. *Proamblysomus antiquus* and *Chlorotalpa spelea* are not as robust as the Makapansgat form, the muzzle of the Makapansgat example being shorter and heavier than the lighter and more slender muzzles of both Sterkfontein examples. The dental arch in *Chrysotricha hamiltoni* is also much more curved than the former two.

The Makapansgat specimen thus differs from all hitherto found fossil golden moles and it may represent a new genus. However, until more material of this animal is found, it is preferable to refer the fossil to a recent genus and of these *Chrysotricha* appears to be the most suitable. The establishment of a new species

Table

	Greatest length	Greatest width	Greatest height	Interorbital constriction.	Upper tooth row	Palate length	'Width across frontals'
*Chrysotricha o. obtusirostris	24.0	17.0	—	—	—	—	—
*C.o. limpopoensis							
Min.	23.2	15.7	10.7	7.0	9.2	8.5	—
Max.	24.2	16.8	11.3	8.7	10.0	9.2	
*C. chrysilla							
Min.	21.5	15.8	10.5	6.8	8.5	8.5	—
Max.	22.6	16.7	11.5	7.5	9.2	9.2	
**Proamblysomus antiquus	?29.0	20.2	—	—	—	—	8.4
**Chlorotalpa spelea	23.4	14.9	—	—	—	—	7.2
Chrysotricha hamiltoni	26.4	19.8	12.8	7.7	—	11.7	—

* Measurements after Roberts (1951).
**Measurements after Broom (1941).
All measurements in millimetres.
Method of measurements taken, as defined by Roberts (1951).

is based primarily on the substantially greater size of the fossil compared with the living members of this genus. (See Table)

The present distribution of the living species of *Chrysotricha* is important. According to Roberts (1951) the genus is confined to the eastern littoral from Zululand, north of Natal, to Inhambane, about 200 miles north-east of Lourenco Marques, in Portuguese East Africa. It is also interesting to note that the northern limit of this species is approximately on the same latitude as the Potgietersrus area i.e. 24° S. This littoral coastal area is rather moist and hot in contrast to the arid, semi-subtropical climate that the Makapansgat valley experiences today. Assuming that the Pleistocene fossil moles prospered under ecological conditions favourable to the recent members of their several genera, the occurrence of a fossil *Chrysotricha* in the Makapansgat valley would indicate a considerably more humid climate in the Central Transvaal during deposition of the grey breccia deposits than prevails today.

It has been noted in some animal groups (e.g. in some genera of the Bovidae) that in occasional instances the ancestral forms tend to approach the upper size limit of the existing species. If the diagnosis made is correct, then this fossil *Chrysotricha,* which has dimensions far beyond the upper means of any of the existing species, exhibits the same principle.

Acknowledgements

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ON THE SKELETON OF ANEUGOMPHIUS ICTIDOCEPS BROOM AND ROBINSON

By A. S. Brink

Abstract

The skeleton of *Aneugomphius ictidoceps* was not taken into consideration with the original description and became separated from the type skull. After the present author had submitted a more detailed description of the type skull for publication, the skeleton was discovered where it had been kept in store. Subsequently the skeleton was cleaned and is described and figured in this paper. A dorsal and a side view of the reconstructed skeleton are also given.

Introduction

In April, 1946, Mr. J. W. Kitching collected a small specimen low in the upper part of the *Cistecephalus* zone of the Karroo, on the farm Hoeksplaas in the Murraysburg district. In our field catalogue he made an entry at field number 182, reading: "small Therocephalian skull and portion of skeleton". The specimen was collected in two pieces, one containing only the skull and the other the skeleton, both bearing the same field number. Shortly afterwards he proceeded to clean the skull, but before he had made reasonable progress, Dr. Broom, on a visit to the Bernard Price Institute, recognised it as a remarkable new form and took it with him for investigation and description. The skull was eventually described as *Aneugomphius ictidoceps* by Broom and Robinson (1948), but the fact that the specimen includes the greater part of the skeleton was not mentioned. When the skull was returned it was placed with other cleaned, identified and described specimens and it received the official museum number 11. When it was recorded in the museum catalogue, the skeleton again passed unnoticed.

Subsequently the present author subjected the skull to the acetic acid preparation technique and submitted a more detailed description for publication (1956). The author obtained his field information from the museum catalogue and he did not notice that there is a skeleton on record. Shortly after this paper was submitted for publication, Mr. Kitching checked certain specimens in store against the field catalogue and discovered the skeleton bearing the same field number as the type skull of *Aneugomphius ictidoceps*. This portion of the type specimen was immediately subjected to preparation.

As the acetic acid technique proved so remarkably successful in the case of the skull this method was employed at first but, on account of an intricate system of cracks and the porous nature of some weathered areas in the matrix, it was considered too dangerous. It has also been mentioned in the description of the skull that the bone is a great deal more vulnerable to the acid than the matrix, and in the case of this skeleton greater difficulty was encountered to protect the more delicate bones. Especially the ribs were very prone to attack by the acid. The alternative method then resorted to was the dental automatic mallet.

The specimen is very flat and before preparation commenced, many bones were partially exposed equally on both upper and lower surfaces. It was decided to expose these bones on both sides as clearly as possible, in spite of the danger of complete disintegration. The method employed to avoid this danger is as follows. The specimen was given a substantial border around its edge of Calistone, leaving both dorsal and ventral aspects open. The ventral aspect was then secured in a thick bed of plasticine which adhered well to the table surface. Under the binocular microscope as many bones as possible were exposed with the aid of the automatic mallet. Thereafter the cleaned upper surface was properly treated with glyptal for strength and then in its turn secured in a thick bed of plasticine. With the lower plasticine bed removed, preparation was carried to a similar extent on the ventral surface. In places the thickness of the matrix between the bones was reduced to an extent where the mallet inclined to strike through the specimen, but the Calistone border kept it as a whole intact while the plasticine below cushioned much of the shock and prevented local damage. Eventually some additional details had to be exposed by gently employing the otherwise objectionable dental emery disc.

Nearly all the vertebrae included in the specimen were exposed on both surfaces, the centra below and the neural arches above, and the humeri also show equally in the two aspects.

The two surfaces were then photographed accurately to the same scale. The photographs were traced separately and the one trace was transferred to the reverse side of the paper containing the other in a manner allowing as true an apposition as in the specimen itself. On a tracing table the information contained on the one side was traced through on to the other, both ways. Information not actually exposed in the specimen could then readily and quite accurately be sketched in. Thus figures 7 and 8 were obtained.

In producing the dorsal and lateral views of the reconstructed skeleton (figure 9), the following factors were taken into consideration:

(1) The body was evidently not carried high on the legs and when not in motion it was probably lowered to the ground in typical reptilian fashion. This assumption is based on the reptilian nature of the limb articulations, the relatively

small feet, the weak shoulder girdle, the broad, flat trunk (see 2 below) and the nature of the vertebral column (see 3 below).

(2) The trunk is interpreted as broader than high, that is, reptile-like, judging from the long slender ribs as seen in relationship to the short and outwardly inclined legs. The mammalian trunk is normally higher than broad, usually corresponding to a somewhat similar ratio in the skull, while in reptiles in general these ratios are also somewhat similar, but breadth normally exceeds height. Although it is by no means a common characteristic, one could with some degree of confidence attribute to the trunk a height-breadth ratio approximating that of the skull, because it appears that when an animal passes through obstructions or goes into hiding in secluded spaces, if the head finds that there is room available, the body would follow without it being necessary for the animal to turn it to a different angle. Another characteristic supporting the view that the trunk was flat and reptile-like is the insignificant height of the dorsal processes of the vertebrae and their uniform inclination (see 3 below).

(3) In side view the vertebral column is interpreted as fairly straight or evenly curved. Only in mammals and certain larger extinct reptiles (considering only these two classes of vertebrates) does the vertebral column develop particular curves, where the trunk is carried well above the ground and suspended across the front and hind limbs. Then the vertebrae develop dorsal processes of varying lengths and inclined at various angles. These angles are such that the dorsal processes incline away from the girdles, that is, forward in the cervical region, backward in the thorax, forward in the lumbar region and backward in the caudal vertebrae, while they attain their greatest lengths in the girdle regions. This arrangement, very well displayed in the dog, is obviously an adaptation advantageous to the general muscular strength of the vertebral column. In mammals these lengths and inclinations of the dorsal processes are more exaggerated anteriorly, because the weight of the head as balanced across the shoulder girdle is more significant than that of the tail as balanced across the pelvic girdle. Where the arrangement is as in the present specimen or any average reptile, that is, no differentiation in the size and inclination of the dorsal processes, the conclusion is arrived at that the vertebral column did not carry much strain and that the trunk was lifted off the ground only when the animal was in motion.

The Vertebral Column

The pro-atlas, atlas and axis are included in the specimen, but they are very indistinct. They suffered some weathering and with every attempt at exposing them properly more damage was done to them than the probable successful preparation warranted.

The atlas is large with wide transverse processes but the detailed shape can not clearly be ascertained. Only the dorsal process of the axis could be exposed. It is covered to some extent by the transverse processes of the atlas. The axis appears

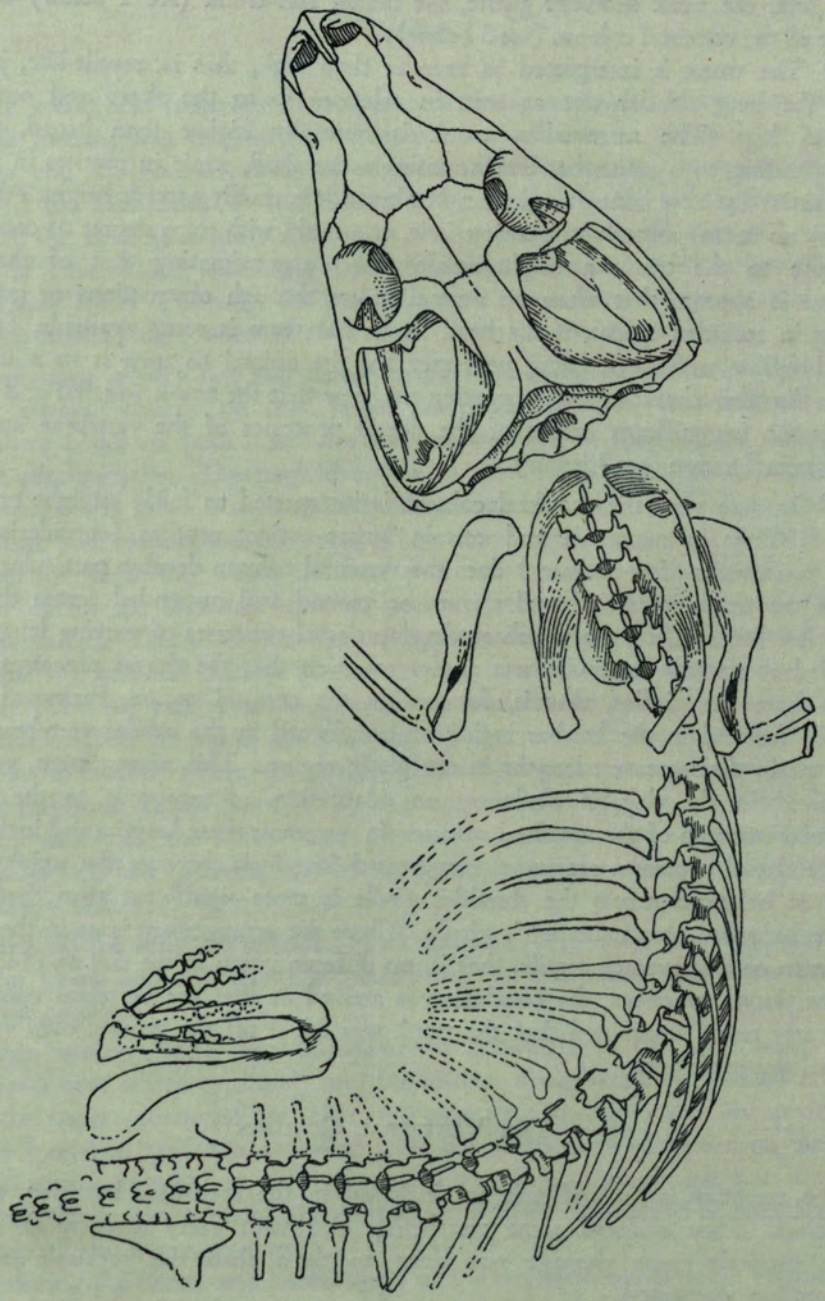

Figure 7—Dorsal view of the skeleton of *Aneugomphius ictidoceps*, as preserved, with information shown in ventral view traced in. Natural size.

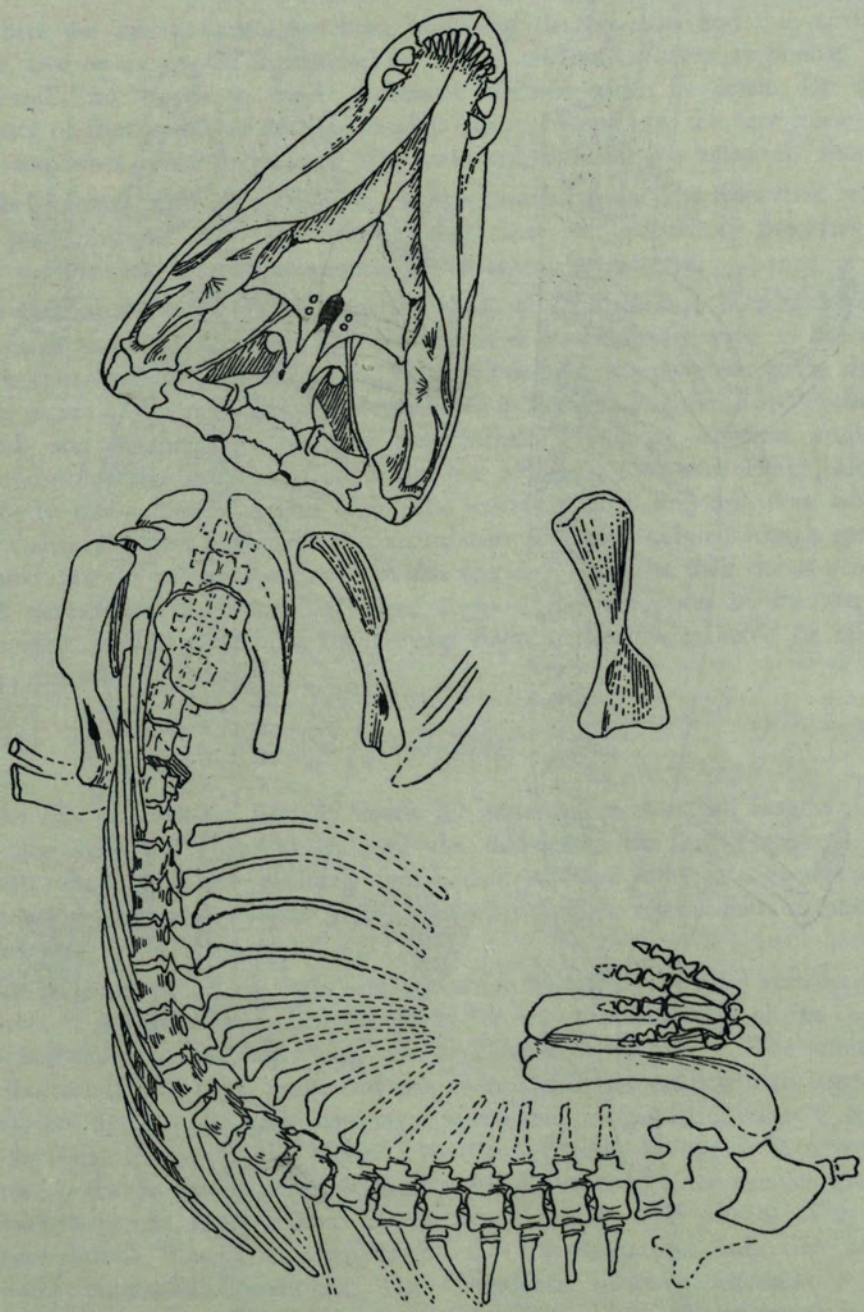

Figure 8— Ventral view of the skeleton of *Aneugomphius ictidoceps*, as preserved, with information shown in dorsal view traced in. Natural size.

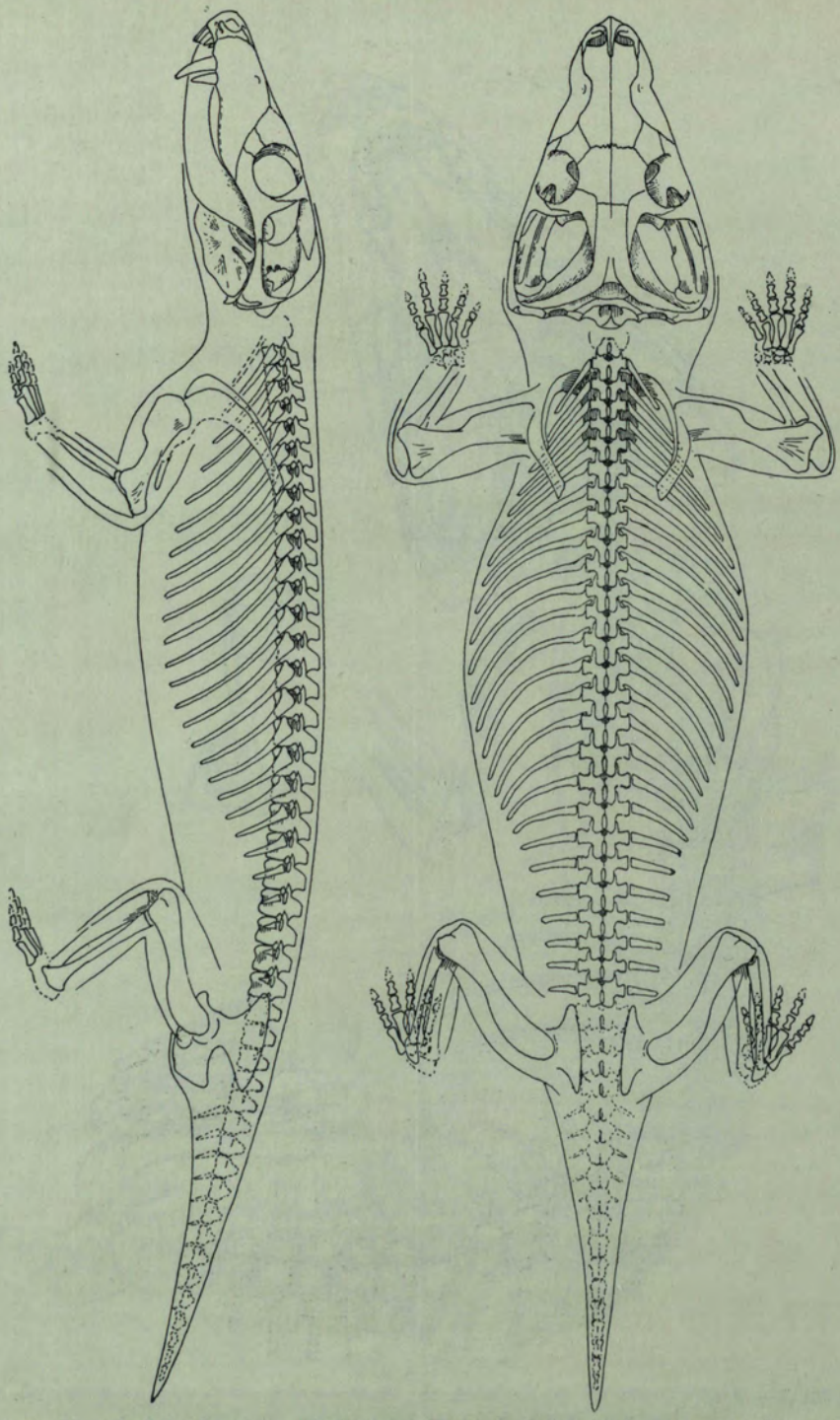

Figure 9—Dorsal and side views of the reconstructed skeleton of *Aneugomphius ictidoceps*. Approx. x$\frac{2}{3}$

to be rather small and not very different in shape from the following cervical vertebra.

There are twenty seven vertebrae, excluding the pro-atlas and the sacrals. Of these, five or six can be interpreted as cervical and six or seven as lumbar. There is actually no feature on which a definite subdivision can be based. The sacrum consists of four vertebrae and the caudals are represented by the first three. There is a somewhat rapid decrease in size backward, indicating a relatively short tail.

The post-zygapophyses are broadest in the lumbar region. The transverse processes are fairly uniform. It is not clear whether there are articulatory processes other than the pre- and post-zygapophyses. There are no intercentra.

In general the vertebrae are very like those of *Ictidosuchops* but, in the several specimens at hand, it is not clear whether there is a differentiation in the nature of the dorsal processes in this genus. In the Cynodonts the vertebrae in the shoulder girdle region have longer dorsal processes, even in *Leavachia* of the *Cistecephalus* zone (Brink and Kitching, 1951), and they incline at slightly different angles. In *Scaloposuchus* this differentiation is not yet apparant (Watson, 1931), although the body was evidently carried high. The vertebrae of *Bauria* are more advanced in the shape of their transverse and articulatory processes, judging from a specimen at hand, but the vertebrae included in this specimen have lost their dorsal processes. It is nevertheless apparent that there is some differentiation in the angles of inclination in this genus and the varying sizes at their bases could be taken as indicating varying lengths.

The Ribs

The ribs of the right side are nearly all preserved in their full lengths. On the left side only the proximal ends of the mid-dorsal ribs are preserved. These indicate clear, but not distinctly subdivided, separate tubercular and capitular articulations, better developed in the posterior thoracic region than anteriorly or posteriorly.

The foremost rib on the right side appears to belong to the third vertebra behind the axis. It has quite appreciable length and it is not unlikely that all the cervicals, including the axis, had fairly long ribs, as illustrated in figure 9. The lumbar ribs are shortened, with blunt ends, and this reduction is just sufficient to suggest the probability that a developing diaphragm is revealing its presence, but it is certainly not as suggestive as in the higher Cynodonts (Brink, 1956). It is nevertheless interesting that in this specimen, with its reduced lumbar ribs, the peculiar glandular depressions in the upper regions of the maxillaries are also present. The author has interpreted these characteristics in the Cynodonts as indicative of very advanced mammalian conditions. The Cynodonts, however, represent a branch which did not give rise to mammals. The more likely "Bauriamorph" branch apparently did arise in the Therocephalia not far from the Whaitsiid origin, with

the Cynodont origin in the "Bauriamorph" branch also not far removed. It is therefore not strange that this primitive Whaitsiid should reflect some advances which were actually achieved in a more substantial way in later descendants in either of these branches.

The Girdles

The girdles are not very satisfactorily displayed in this specimen. Only the dorsal portions of the scapulae are exposed. These portions are very slender and they are interpreted as inclining sharply backward in their natural positions, because, as preserved, they are strongly curved backward. The glenoid regions and the coracoids and precoracoids are not exposed, except for a small piece of bone on the right side, which could be part of the precoracoid. The clavicles are well exposed. These bones are long and slender and articulated substantially with the scapulae. Ventrally they form flat portions which evidently completely overlapped the interclavicle. The latter bone is also well exposed and shows clearly two areas where the clavicles articulated. These areas are bordered on the anterior margin by distinct, delicate ridges.

The pectoral girdle shows very close affinities with the "Bauriamorph" branch. (The Bauriamorpha is interpreted here as including all the families listed by Watson and Romer 1956). From *Ictidosuchops* it differs only in the scapulae being more delicate and more curved (compared with actual specimens), while this difference is more pronounced when compared with *Scaloposuchus*. In the Cynodonts the scapula is broader, straighter, with its outer surface distinctly concave, while the clavicles are shorter.

The pelvic girdle is less satisfactorily exposed. The ilia have intimate articulations with broad transverse processes of the sacral vertebrae. They appear to be delicate, not high, but the alae are long antero-posteriorly. The ischia are more substantial. Only the left ischium is exposed, its ventral surface being completely displayed. It has a broad, flat wing, a narrow neck and a significant portion contributing to the acetabulum. The obturator foramen is large. The margin articulating with the right ischium is slightly shorter than the free edge forming the ventral margin, posteriorly, of the pelvic canal. The extent and shape of the pubis cannot be ascertained. It appears to be the weakest of the three bones.

The Limbs

Both humeri are fairly well exposed. The proximal ends of the radii and ulnae of both sides are preserved and partially exposed. The radius is a slender, round bone, while the ulna is flat. There is no distinct olecranon projection. The proximal and distal articulations of the humeri are primitive, reptile-like, unlike the more advanced condition in *Ictidosuchops* and *Scaloposaurus* where the limb bones are longer.

The left femur, tibia and fibula are preserved, but not well exposed. The left pes is well preserved and displayed in its ventral aspect. Only the terminal phalanx of the first toe is present, but it is quite clear that there are no reduced phalanges and that the digital formula is 23333 according to the Whaitsiid pattern.

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STRUTHIOCEPHALUS KITCHINGI sp. nov.

By A. S. Brink

Abstract

In this paper a new species of the Tapinocephalid Dinocephalian *Struthiocephalus* (*S. kitchingi*) is described, based on a good skull without lower jaw, adding not only to our knowledge of the structure of the skull of this genus, but also exhibiting more pronounced features on the strength of which some idea may be formed regarding the mode of living of the animal. This specimen differs appreciably from the known species, *S. whaitsi, S. rheederi, S. milleri,* and *S. akraalensis,* but where some of the differences appear even to transgress the generic boundary, it is considered that previous descriptions are not based on absolutely perfect material. Even the present specimen does not exhibit its structural detail so clearly that a wrong interpretation should be considered as excluded.

Introduction

The generic name *Struthiocephalus* (genotype *S. whaitsi*) was introduced by Haughton in 1915 for a fair skull in the collection of the South African Museum. In 1916 the same author reported on a badly crushed but nevertheless mountable skeleton which belongs to this genus and which Broom in 1932 thought could actually belong to the type skull, but at present this skeleton still bears a catalogue number different from that of the type. Broom (op. cit.) also offered a restoration of the skeleton of this animal in the form of a free hand sketch.

In 1937 two new species were assigned to this genus, *S. rheederi* introduced by Broom, and *S. milleri* introduced by Olson and Broom. A fourth species, *S. akraalensis,* was introduced by Boonstra in 1952, while elsewhere, in the same year, he redescribed the type *S. whaitsi.* In the following year (1953) the same author published a comprehensive paper on this genus, in which he described in detail the genotype, based on two good specimens in addition to the type, after he succeeded in exposing more clearly sutural patterns with the aid of hydrochloric acid. He also listed very useful generic and specific distinguishing characteristics.

Material and Technique

The present description is based on a complete skull without lower jaw, discovered by Mr. J. W. Kitching in *Tapinocephalus* zone beds on the farm De Bad, near Fraserburg Road, south of Beaufort West in the Karroo. It is numbered 284 in the collection of the Bernard Price Institute.

The skull is appreciably larger than any of the previously described specimens and could not be excavated in one piece. In its fairly badly disarticulated condition Mr. Kitching was able to remove virtually all the matrix manually (excluding the matrix within the brain case and nasal cavities) and after thorough treatment with hydrochloric acid he assembled all the pieces, reinforcing the skull internally with metal dowels. Thus, although the skull is particularly large and of great weight due to the pronounced pachyostosis, while it appears fragile on account of the amount of matrix removed it can nevertheless be handled with little fear of damage.

While in its disarticulated condition little structural information could be gathered from fracture surfaces. These fractures were all initiated by weathering, which tended to obscure sutural detail more badly than on outer surfaces, and the tendency was to avoid development of such surfaces for fear of effecting imperfect fits on assembling the pieces.

The skull is virtually complete and not badly distorted. The snout is bent to the right and the roof of the skull inclines somewhat over to the left. In the accompanying figures this distortion is corrected. The quadrates could have been pressed closer to the skull, but apparently not much.

The dorsal surface of the skull suffered some weathering in particular areas where sutures are not easily traceable. In other areas the sutures are beautifully displayed. The ventral surface is very good but some sutures are obscured by fractures.

Small portions of the postorbital bars and the occipital margin are damaged to an extent where reconstructions were necessary, but these areas are so local that they do not affect the structural interpretation and the genuine contours can be followed accurately.

Other damage affects the alveolar margin, but again the actual margin can easily be traced. The proximal halves of both stapes are missing, but their shape and extent can be judged from margins around the fenestrae ovales where they had apparently rather intimate contact.

Most of the teeth are missing, only some sockets containing fragmentary roots.

Build and Posture of the Skull

The general build of the skull is that of a typical *Struthiocephalus*. The posterior portion appears to be less high than in *S. whaitsi* and *S. akraalensis,* while the snout seems also flatter and more pointed, both in side and dorsal views. The occipital plate is almost in the same plane as the general ventral surface of the skull, so that the occipital condyle is situated relatively farther forward than in previously described specimens.

There is a very large frontonasal boss, larger than in *S. rheederi* which, according to published information, has the largest boss in the known species. This boss towers high above the general dorsal surface of the skull and is virtually confined to the nasals. It has steeply sloping side walls and a generally flattened dorsal

surface, the plane of which slopes forward. There can be little doubt that this boss is actually the core of a horn structure, ideally situated for the purpose of defence.

For several reasons the author is convinced that the head was posed with the snout directed sharply downward, at least as much as indicated in figure 11. These reasons are:

(1) With the skull at this inclination the plane of the occipital plate is vertical. With the snout pointing forward, the occiput extends so nearly horizontally that it is difficult to visualise how the muscles of the neck could keep the skull thus orientated.

(2) The occipital condyle points nearly ventrally when the snout is horizontal.

(3) The floor of the cerebellum also extends horizontally only when the skull is inclined as illustrated.

(4) With the skull horizontal, the quadrates are so far forward that it is difficult to visualise how the lower jaw could operate effectively. With an inclination as illustrated, the quadrates are situated ventrally, in perfectly normal relationship relative to other occipital structures.

(5) At this inclination the jaw muscles extend vertically and they have the effect of swinging the lower jaw to and fro. With the head horizontal, the muscles would also extend horizontally and, judging from the space available to them, they could not have been strong enough to keep the relatively long lower jaw in a closed position, let alone lift it in an effective bite.

(6) The horn structure points forward at this inclination and is thus a more effective weapon in an animal which certainly could not have had the agility of a mammal. Horned mammals rely to a large extent on agility to outmanoeuvre their foes, while in all horned reptiles (Ceratopsia especially) these weapons are normally directed forward to offer resistance to an adversary directly in the line of its approach, without demanding much manoeuvrability on the part of the head and neck, relative to the body.

This inclination of the head, the nature of the jaw articulation, and the peculiar dental arrangement, appear to indicate a specialised diet not uncommon in a great variety of animals. A near parallel may be found in the not too distantly related and reasonably near contemporary form, *Lystrosaurus*. Although the dentition is elaborate, the lower jaw could not have been very effective in a horizontal attitude, judging from the size of the jaw muscles and the direction in which they exerted their force. Nevertheless, in spite of this weak articulation arrangement, the very foremost teeth are the strongest, their size decreasing backward till they disappear at the level of the middle of the length of the snout and well forward of the posterior ends of the maxillaries. With the teeth in addition inclined forward, there can be little doubt that the anterior ones fulfilled the more important function.

Taking all these pecularities into consideration it would appear that this animal

fed under water, like a duck, the platypus, or *Lystrosaurus,* which may also account for the general shape of the snout. The animal then either drove its snout downward into the mud, nibbling around for embedded food, or it would feed directly on subaquatic weeds. The downward inclined upper teeth would then rather have been used for digging, gathering and grasping than for biting purposes. With a mouthful of weeds it then apparently lifted its head and strained the material in a higher level of cleaner water to wash out the excess mud. This habit of feeding does not demand strong jaw musculature and the general shape of the skull and mechanism of the lower jaw are thus quite effectively adapted.

The following are some useful measurements for comparison with the previously described species:

Greatest length	700 mm
Greatest width	442 mm
Interorbital width	144 mm
Intertemporal width	203 mm
Pineal foramen to occipital edge	82 mm
Anterior margin of external nares to premaxillary edge	122 mm
Posterior margin of occipital condyle to occipital edge, in the plane of the axis of the skull	112 mm

The Structure of the Skull

The author would like to emphasise that the structural detail of the present skull is not as distinctly displayed in the specimen as the figures would tend to suggest. In the subsequent descriptions it will be stipulated where interpretations are based on what appear to be "likely", but by no means "clear", arrangements. Where the structure of the present specimen differs in places rather appreciably from that of the previously described species, the tendency should not be to regard it as generically distinct. While the chances are not excluded that the present author has misinterpreted this specimen, it is perhaps as likely that previous authors have also encountered similar difficulties in view of the problematic nature of this *Tapinocephalus* zone material. It is therefore considered more advisable to state what this specimen appears to convey than to be influenced by previous descriptions.

The *basioccipital* (bo, fig. 12) forms a single rounded condyle directed more ventrally than posteriorly*. The upper surface is cleaned for some distance into the brain case and this surface (the floor of the cerebellum) extends sharply upward in a direction opposite to that assumed by the condyle (see fig. 11). The basioccipital does not contribute to the lateral margins of the foramen magnum. It articulates with the exoccipitals at the level of the ventral margin, where the latter expand into small bosses (see *exoccipitals*). In front of these contacts are

* Relative directions here and subsequently are to be interpreted with the long axis of the skull horizontal.

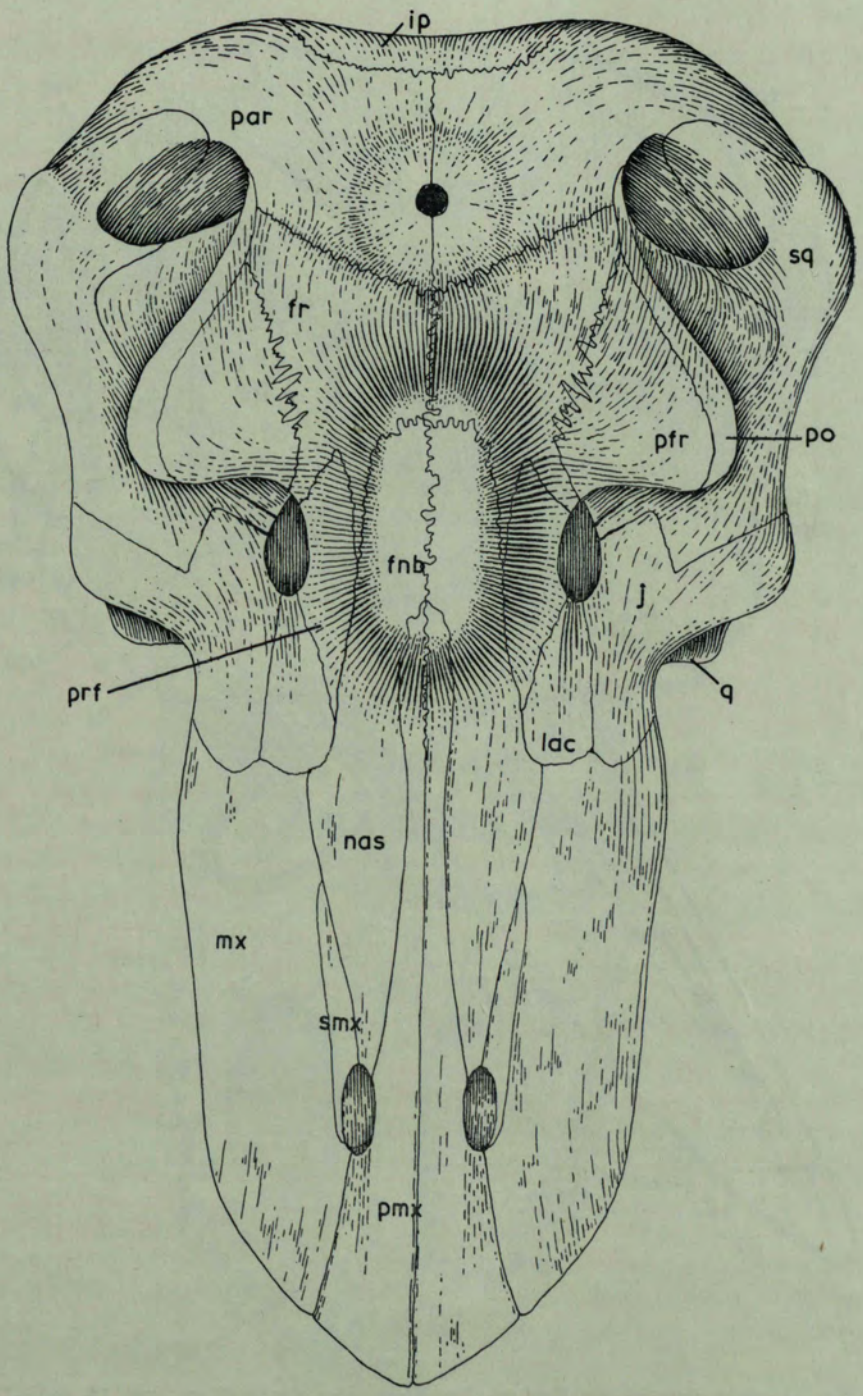

Fig. 10—Dorsal view of the skull of *Struthiocephalus kitchingi* sp. nov. (¼ natural size).

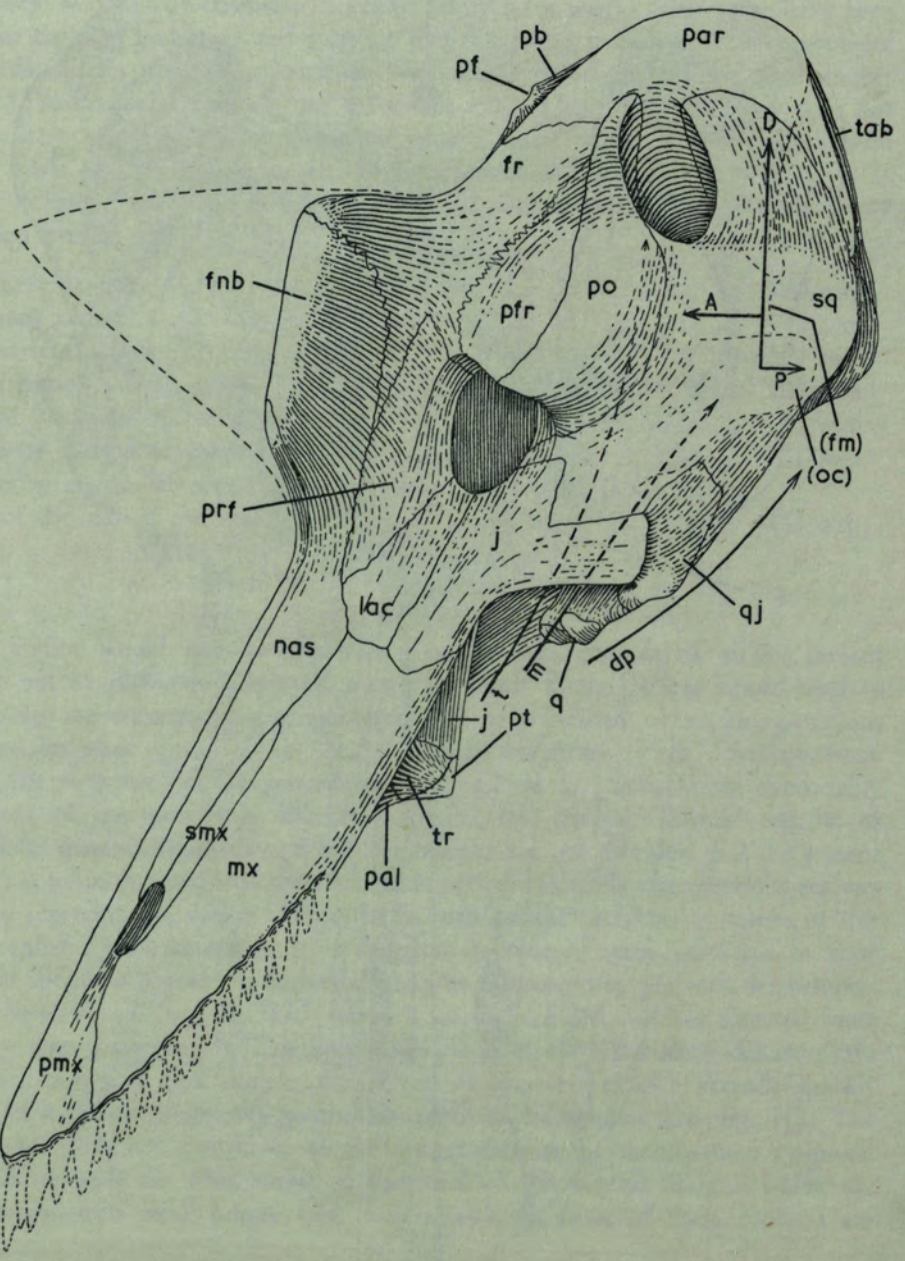

Fig. 11—Side view of the skull of *Struthiocephalus kitchingi* sp. nov. ($\frac{1}{4}$ natural size).

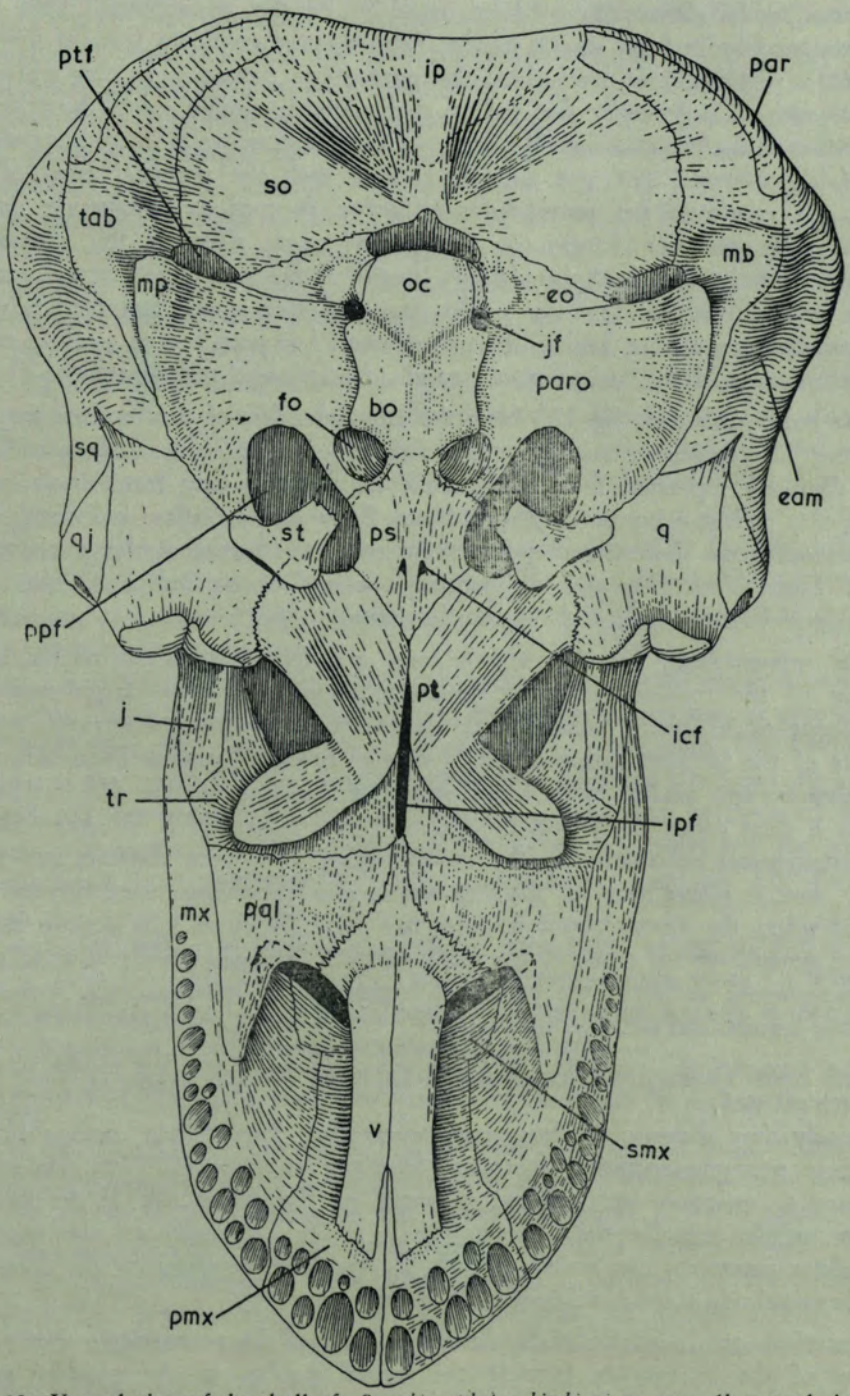

Fig. 12—Ventral view of the skull of *Struthiocephalus kitchingi* sp. nov. (¼ natural size).

the two jugular foramina, bordered medially by the basioccipital. This bone expands laterally in front of the jugular foramina and continues forward between, and at a slightly lower level than, the paroccipital processes. In this region its ventral surface is generally flat with a slight, broad, median ridge. Anteriorly it contributes to the posterior-medial margins of the fenestrae ovales where it apparently had fairly intimate, but not sutural, contact with the proximal ends of the stapes. It continues for some distance farther forward as a tapering process between the posterior flanges of the parasphenoid, although this portion is almost certainly the basisphenoid. A vague indication of a suture extends across between the two fenestrae ovales, but this effect could have been achieved if a portion of a median keel to the parasphenoid had been broken away to expose a small triangle of the basisphenoid (see also *basisphenoid* and *parasphenoid*).

The *exoccipitals* (eo, fig 12) form the lateral borders of the foramen magnum and they also contribute slightly to the occipital condyle. Immediately laterally to, and distinctly separated from, these condylar portions they form small bosses. Posteriorly to these bosses they spread out flatly and articulate indistinctly with the supraoccipital. Laterally they appear to reach the border of the post-temporal fossa. Their relationship with the paroccipitals is also very indistinct. The bosses form the posterior margins of the jugular foramina.

The *supraoccipital* (so, fig. 12) is large and forms the whole of the dorsal border of the foramen magnum. From the middle of this margin two very prominent ridges extend outward and backward. They start so abruptly on the border of the foramen magnum that a median notch is formed. From this notch a rather massive median ridge arises, extending backward to the occipital border, across a deep concavity behind the postero-lateral ridges. It is not clear whether the interparietal contributes to this median ridge. It is even possible, and rather likely, that it covers most of the area within this depression. Anteriorly to these lateral ridges the supraoccipital occupies two large flat areas very slightly inclined to the general ventral plane of the skull, where it articulates with the exoccipitals. Antero-laterally it forms the posterior borders of the post-temporal fossae and laterally it articulates with the tabulars.

The *paroccipitals* (paro, fig. 12) are extremely wide and flat in the plane of the ventral surface of the skull. Posteriorly they have some vertical thickness, but anteriorly they decrease to thin plates where they form deeply concave margins to large pterygo-paroccipital foramina. Medially to these foramina they extend forward to articulate with the parasphenoid, on the dorsal side of the fenestrae ovales, while laterally they swing widely around, medially to the quadrates (quadrate processes), to articulate with the quadrate processes of the pterygoids on the dorsal side of the distal ends of the stapes.

Posteriorly to the quadrates the lateral margins of the paroccipitals abut against ridges of the squamosals forming the medial borders to the auditory meatus grooves. Still farther back, these ridges expand into prominent mastoid bosses,

formed largely by the tabulars, on the inside of which the paroccipitals form distinct but not very significant mastoid processes, bending ventrally, not posteriorly. Medially to these processes, the post-temporal fossae are enclosed between the paroccipitals anteriorly, the supraoccipital posteriorly, with the tabulars contributing, apparently not insignificantly, to the lateral margins. These fossae, although they face ventrally, penetrate the skull in a sharply anterior direction above the paroccipitals.

The paroccipitals form the lateral borders of the jugular foramina.

The general arrangement is not unlike that described by Boonstra for *S. whaitsi*. The detailed differences are: (a) in the present specimen the quadrate processes are stronger and extend farther forward; (b) the mastoid processes are weaker and not inclined backward; (c) the contact between the paroccipital and pterygoid is at the level of the distal end of the stapes; (d) due to the shorter quadrates, the paroccipitals articulate with the squamosals farther forward, so that they have more significant contact with the tabulars. These differences, although rather pronounced, could pass as specific variations, with the exception of the paroccipital-pterygoid-stapes relationship, which could be regarded as a generic distinction, but distortion or insufficiently clear preservation could account for this difference. If this is the case, *S. whaitsi* is more likely to be at fault, because the structure and relationship of the paroccipitals are rather well displayed in the present specimen.

The *prootics* are not exposed.

The *tabulars* (tab, fig. 12) are peculiarly wedged between the squamosals and the mastoid processes of the paroccipitals, where they appear to penetrate to some appreciable depth, while they are little exposed on the surface. In this region they extend some 30 mm. farther ventrally than the mastoid processes. Behind the latter the tabulars expand and are exposed over greater areas where they form pronounced mastoid bosses. Still farther back they taper between the supraoccipital and the parietals, curving inward to articulate with the interparietal. They are not visible in dorsal view.

The major difference between the tabular relationship in the present specimen and *S. whaitsi* is that in the latter it is situated farther back so that it is wedged to a lesser extent between the mastoid process and the squamosal and its contribution to the mastoid boss therefore appears to be less significant.

In the present specimen the tabular sutures are, in general, very distinctly displayed.

The *interparietal* (ip, figs 10, 12) is very indistinct and its position and extent is judged by the relationship of the surrounding bones. Ventrally it could contribute to the median ridge extending to the foramen magnum, or even cover most of the depression that this ridge traverses, but this region is badly damaged. Dorsally there are vague indications of a suture with the parietals in the position as figured (fig. 10), so that the interparietal builds the middle portion of the vertically thickened, well rounded, and horizontally slightly concave occipital border. It is visible in dorsal view.

The *parietals* (par, fig. 10) are well fused along the midline so that the median suture is extremely difficult to trace. Between them they enclose a large, perfectly round, pineal foramen, situated on a low, but nevertheless distinct circular boss. Their sutures with the frontals extend through slight depressions extending transversely, but slightly forward from the dorsal borders of the temporal fossae to a point on the midline of the skull between the pineal boss and the fronto-nasal boss. Laterally they form the dorsal borders of the temporal fossae, where they are overlapped for some distance from front to back by the posteriorly extending processes of the postorbitals. Behind the temporal fossae they articulate with the squamosals, where they penetrate deeply down between the long tapering processes of the latter anteriorly and the tabulars posteriorly.

The parietals in the present specimen differ from those of *S. whaitsi* as described and figured by Boonstra (op. cit.) in that they have no contact with the post-frontals. In this respect they agree with *S. akraalensis*. The overlaps between the parietal flanges and the squamosal processes are also more extensive. They differ from *S. akraalensis* in being more extensively flanked by the postorbitals along the antero-dorsal borders of the temporal fossae. The latter species is also figured as though there is little, if any, articulation between the parietals and squamosals, the tabulars apparently reaching the borders of the temporal fossae. The general build of this region in the present specimen is inclined to create a similar impression but, fortunately, on the right side enough of a tabular-parietal suture is discernable to show that the actual structure is more like that of *S. whaitsi*. On account of the difficulty in tracing sutures in *Tapinocephalus*-zone material, this difference in *S. akraalensis* should not be regarded as a "specific" variation; it could be a wrong impression created by the specimen.

The *frontals* (fr, fig. 10) are not unlike those of *S. whaitsi* and *S. akraalensis*. They build the posterior slopes of the fronto-nasal boss and contribute only slightly to the dorsal flattened surface. They differ from *S. whaitsi* in that they articulate with the postorbitals, as in *S. akraalensis*. Their delicate extensions to the dorsal borders of the orbits appear to reach the latter farther posteriorly than in the described specimens. The processes flanking the nasals are also longer. The main difference, however, is that they build much steeper posterior slopes to the fronto-nasal boss.

The *postfrontals* (pfr, fig. 10) have a similar structural relationship to those of *S. akraalensis*, but they agree more with those of *S. whaitsi* in general shape, that is in their greater breadth and in being more laterally situated. As the postorbital bosses form more pronounced protrusions on the orbital borders, their orbital margins extend more perpendicularly to the axis of the skull.

The *postorbitals* (po, fig. 11) form pronounced bosses (jointly with the post-frontals) which appear to extend more forward than in the described species. The resultant protrusions on the orbital borders can be considered as a distinguishing characteristic of this species.

These bones extend backward dorsally to the temporal fossae, where they flank

the parietals. They contribute to the ventral borders of the orbits. They are separated from the anterior margins of the temporal fossae by short extensions of the squamosals.

The postorbitals are almost thrice as long (antero-posteriorly) as they are high (vertically). In *S. whaitsi* the length is apparently equal to the height, while in *S. akraalensis* the height appears to be twice the length. Extremely broad and short postorbital bars, added to the forward protruding postorbital bosses, furnish a rather prominent distinguishing characteristic for this species.

The *prefrontals* (prf, figs. 10, 11) are situated more directly above the orbits than in the previously described species. They contribute substantially to the dorsal borders of the orbits and extend from there backward as well as forward as they rise, almost vertically, to add to the lateral sloping walls of the fronto-nasal boss. Their greater size and these backward extensions, penetrating the frontals more deeply than in the existing species, provide a further distinguishing characteristic.

The *lachrymals* (lac, fig. 11) are not different from those of the previously described species.

The *nasals* (nas, figs. 10, 11) form the bulk of the fronto-nasal boss. They form a great deal of the lateral sloping walls and their median suture is restricted to the dorsal flattened surface. The size and shape of this fronto-nasal boss could be the most conspicuous characteristic of this new species, but it could also be subject to sex and age.

The nasals taper gradually forward from a level shortly in front of the orbits, where their combined breadth is greatest, to the posterior borders of the external nares.

The *septomaxillaries* (smx, figs. 10, 12) form "floors" to the external nares, which enter the snout sharply inward and backward. The external nares are small and narrow transversely. The greater portions of the septomaxillaries extend backward between the nasals and maxillaries. These extensions appear to be superficial posteriorly, where the maxillaries and nasals meet below them.

Ventrally, in the palate, the portions of the septomaxillaries forming the "floors" to the external nares articulate with the premaxillaries anteriorly and with the maxillaries laterally. Actually, these portions lying within the external nares and visible in dorsal view lie intimately above the posterior ends of the premaxillaries, seen in the palatal view on either side of the vomer. The portions of the septomaxillaries seen in ventral view are posterior extensions of the "floor" portions, not visible in dorsal view. The areas in front of the internal nares slope evenly inward and backward, while they grow narrower between the palatines and the vomer. The choanae are broadly oblong in the vertical plane, and face forward and outward over the fan-like excavation. They are bordered dorsally by the septomaxillaries, medially by the vomer, laterally by the palatines and maxillaries, and ventrally by the vomer and palatines. The dorsal septomaxillary border is a free edge over which the cavity passes forward to the external nares.

This arrangement, where both external and internal nares open forward, gives support to the view that these animals fed under water and that their teeth were largely used for straining muddy vegetation. Water caught in the nasal cavity would, on lifting the head above the water, run down and forwards through the internal nares and through the teeth, thus additionally washing the food.

The *premaxillaries* (pmx, figs. 10, 12) form the inter-narial bridge and send extremely long tapering processes backward between the nasals. At about the level where the nasals are broadest, in front of the orbits, these processes are narrowest, but from here they expand again slightly, where they extend up the anterior slope of the fronto-nasal boss. They terminate somewhat abruptly after extending some short distance on to the upper flattened surface of the boss.

From the level of the anterior margins of the external nares the premaxillaries fan out forward to the alveolar margin, the dorsal outer surfaces not bending down. Ventrally they taper backward, not as evenly, and a short distance from the choanae they articulate with the septomaxillaries along transverse sutures. From shortly behind the front teeth, up to this level, they articulate medially with the vomer, which forms a prominent median beam situated at a level appreciably lower than the areas on either side.

Boonstra (1953) illustrates the premaxillaries as being confined to the area in front of the vomer in the palatal aspect in *S. whaitsi,* but this impression could be created by imperfect preservation. However, with the additional specimens at his disposal, his interpretation of narrower premaxillaries in this species is accepted as genuine, and the fact that each covers in breadth only three teeth is considered here as a rather serious difference. In the present specimen each premaxillary covers in breadth the equivalent of approximately five teeth, as is also the case in *S. rheederi.* This difference could nevertheless pass as a specific and not generic distinction, because the dentition as a whole in this genus appears to be inconstant (see maxillaries). In the present specimen there are five large teeth in a row on the right side, with three occasional teeth, smaller in size, behind in a second row, while on the left there are four teeth in the front row, one exceptionally large, with five in a very distorted second row.

The *maxillaries* (max, fig. 12) articulate with the premaxillaries medially, in the palatal aspect, in the surfaces sloping backward to the choanae. Behind these sutures they articulate with the septomaxillaries to where they contribute themselves to the dorso-lateral margins of the choanae. The ventro-lateral and ventral margins are formed by the palatines, which send tapering processes forward on the inside of the teeth, to continue the ventral margins of the choanae as fairly prominent ridges across the maxillaries. Laterally to the palatines the maxillaries extend backward as a plate, exposed more on the lateral surface of the snout, but sufficiently represented in the palatal aspect to be of significance to a more elaborate dentition, but these extensions behind the level of the choanae are free of teeth. The posterior ends are intimately clasped by the jugals.

The right maxillary contains sockets of about 16 teeth (some damage in one area makes it difficult to be sure of the exact number). These teeth are arranged very roughly in two rows, in fact, so indistinctly that had it not been for the more recognisable two rows of the premaxillaries, they could not be interpreted in terms of rows. All the teeth on the right side occupy a distance of 150 mm. which could as well be covered by about 10 teeth of similar size.

The left maxillary has 17 sockets, also roughly distributed in two rows, and occupy a distance of 190 mm, which could be covered by 13 similarly sized teeth. On both sides these sockets decrease in size backward, although some sockets are appreciably larger than others farther forward. Posteriorly the "two rows" of each side merge into one.

This arrangement is not due to tooth replacement. All the sockets are distinctly separate. Boonstra (1953) mentions the presence of additional teeth behind the main row in *S. whaitsi* and interprets them as replacing teeth, but in the light of the new specimen, they may also prove to be regular teeth.

Judging from the difference in the distribution of the sockets between the left and right sides, the difference in number and the different distances they cover, it is to be expected that there could be even greater variations from individual to individual, so that it is not advisable to select any feature in this dentition as a distinguishing characteristic for the new species.

The *transverse* bones (tr, fig. 12) appear to be longer and narrower in the new species than in *S. whaitsi*. They are more clearly locked between the pterygoids ventrally and the maxillaries dorsally. It appears as if the pterygoids extend farther laterally in forming their processes for guiding the lower jaw, so that they cover more of the transverse bones in ventral view. Laterally the jugals cover them for some distance and posteriorly they extend for a longer distance backward, intimately on the inside of the jugals, than in *S. whaitsi*. In ventral view their extreme posterior ends are obscured from view by the quadrates which, in this specimen, are also situated farther forward.

The *jugals* (j, figs. 11, 12) are rather small and mainly build the suborbital bars, where they are fairly flat. Anteriorly they form two distinct flat and blunt processes, one articulating with the maxillaries on the outer face of the snout, the other articulating mainly with the transverse bones, but also supporting the posterior ends of the maxillaries below with considerable overlaps. Dorsally and medially they have substantial contact with the lachrymals. Posteriorly, still generally within the suborbital bars, they articulate with the squamosals, allowing the latter to penetrate forward into them with broad wedges. Postero-laterally they overlap the quadrato-jugals, but the articulation appears to be somewhat feeble.

Both jugals display their sutures very clearly.

The *squamosals* (sq, fig. 11) contribute with very small, slender processes to the ventral borders of the orbits, over which extend forward projections of the postorbitals. They have long massive contacts with the postorbitals all the way back to the temporal fossae, to which they contribute the ventral, posterior, and the

lower halves of the anterior borders. Posteriorly they overlap extensively the lateral occipital flanges of the parietals. Ventrally the squamosal-tabular sutures extend across the prominent mastoid bosses, laterally to the mastoid processes of paroccipitals. Immediately laterally to these bosses the broad, shallow external auditory meatus grooves extend forward and slightly inward across the ventral surfaces of the squamosals, from levels where the latter bones form prominent bosses directed outward. These bosses merge upward, on the outer face of the skull, into the anterior borders of the temporal fossae. On the ventral surface the external auditory meatus grooves extend forward, widening, and disappearing as distinct concavities at the level where the squamosals have their contacts with the paroccipitals medially and the quadrates and quadratojugals anteriorly. The squamosals clasp the blunt posterior ends of the quadratojugals (laterally) within broad notches.

The external auditory meatus grooves start distinctly farther forward than in *S. whaitsi* and the general arrangement of the sutures between the squamosals, quadrates and quadratojugals is also different. Once again this may be due to incorrect interpretation of either specimen. The squamosal-parietal relationship in *S. akraalensis* is completely different but, as stated above (under *parietals*), this difference is most likely due to a misinterpretation.

The *quadrates* (q, fig. 12) are broad, long and very flat in the horizontal plane, and their articulation surfaces are rather small compared with the size of the skull, although not when compared with the size of the lower jaw. The cavities between the quadrates below and the jugals above are very flat (between 30 and 40 millimeters high in a skull with a total length of 700 millimeters) and with the articulars in position the space on either side for the masseter and temporal muscles is extremely restricted. These muscles could obviously not have been very strong. Even their apparent restricted lengths are out of proportion to the size and shape of the skull. The general structure and build of the surrounding areas show no indication of distortion. Had the quadrates been pressed closer to the jugals, the amount could not have been much and it would make little difference to the size of the jaw muscles, while their lengths and the directions in which they extended would not have been altered.

The pterygoid processes to the quadrates articulate firmly with the latter along fairly broad and blunt contacts. Behind these contacts the distal ends of the stapes are lodged in very intimate contact with both bones, more with the quadrates than with the pterygoids, and more posteriorly also with the quadrate processes of the paroccipitals. On the right side the stapes-paroccipital contact appears to be a firm suture. On the whole both stapes appear to have been virtually immovable. The general arrangement is again completely different in *S. whaitsi,* but allowance should be made for an incorrect interpretation.

Posteriorly, the quadrates have blunt articulations with the squamosals, that is, they do not taper into sharp points as in *S. whaitsi.* Laterally the quadratojugals extend far back, also unlike the condition displayed in *S. whaitsi.*

The quadrates are separated from the posterior ends of the jugals by only a few millimeters.

The *quadratojugals* (qj, figs. 11, 12) separate the posterior ends of the jugals from the quadrates. Posteriorly they are wedged bluntly into the squamosals, as seen in the lateral face of the skull. A process of the squamosal extends forward laterally to the quadratojugal of the left side. Both quadratojugals are damaged so that their surface topography is not clear. On the left side sutures are nevertheless well displayed.

The *stapes* (st, fig. 12) are each represented only by the distal end. These ends are well locked in fixed positions behind the pterygo-quadrate suture. Proximally they also appear to have been well held in position by prominent margins around the fenestrae ovales. It is not clear at all how and where a tympanum could have been located and how it could have functioned.

The *vomer* (v, fig. 12) is very distinctly paired. The premaxillaries send processes backward medially between the left and right portions. It forms a solid median beam in the palate, extending backward well below the level of the choanal excavations on either side. Its flat ventral surface is even at a lower level than the plane of the alveolar borders. As it extends backward it increases in vertical thickness, apparently solidly. Deep notches in the lateral vertical faces form the medial borders of the choanae. Behind this level the palatal surface rises to join the general plane of the palatines, while the vomer fans out to build the medial halves of the postero-ventral borders of the choanae. Posteriorly it tapers to a point and terminates on the anterior border of the interpterygoid fossa.

The *palatines* (pal, fig. 12) build the postero-ventral free margins of the choanae. These margins are directed forward with the choanae entering the nasal cavity backward and inward above them. More medially these margins are formed by the vomer, but the palatines still extend intimately above, inward to within the vomerine notches forming the medial borders of the choanae. Laterally the palatines swing forward as ridges forming lateral borders to the general choanal excavations and also supporting the maxillaries below.

The pterygo-palatine sutures are indistinct, but traceable. The left and right palatines do not meet in the midline, the vomer intervening. *S. whaitsi* displays in this area two short and sharp longitudinal ridges, but in the present specimen the two equivalent ridges are so slight that they would not have been recognised as such if they had not been demonstrated in a previous description. More laterally than in *S. whaitsi* there are also slight bulges, but definite miniature teeth can not be recognised.

The *pterygoids* (pt, fig. 12) enclose between them a long and very narrow interpterygoid fossa. In front of this fossa, without meeting medially, they articulate with the palatines and laterally they swing outward to build buttresses for guiding the lower jaw. These processes do not project strongly in a ventral direction. The ventral surfaces of these portions of the pterygoids are concave. Behind the palatine sutures they build strong transverse ridges increasing gradually in size laterally

to where they overlap the transverse bones. Medially these ridges swing backward and join the lateral margins of the inter-pterygoid fossa at about the middle of its length. The posterior margins of these depressed areas are free and swing sharply back and outward again at the level where the anterior ridges join the inter-pterygoid fossa, to form the anterior free edges of the quadrate processes. These edges incline sharply downward, with deep troughs medially, extending from the pterygo-paroccipital fossae to the inter-pterygoid fossa. For a short distance behind the latter fossa the pterygoids form a median suture, where they cover the parasphenoid.

The quadrate processes of the pterygoids appear to meet the quadrate processes of the paroccipitals above the distal ends of the stapes.

The *alisphenoids* are not exposed.

The *parasphenoid* (ps, fig. 12) forms a broad, flat bridge extending between the pterygoids and basioccipital. Its lateral edges form the medial borders of the pterygo-paroccipital foramina, where it has contact with the paroccipitals above the fenestrae ovales. Anteriorly it extends flatly over the pterygoids, disappearing between them, in ventral view, in a tapering point. A low median ridge extends over the parasphenoid, the areas on either side being broadly and slightly concave. Just forward of the middle of the length of this ridge the internal carotid foramina enter the skull in a backward direction. The ridge appears to have been more prominent posteriorly between the fenestrae ovales and, being damaged, a small portion of the basisphenoid is exposed. The parasphenoid forms the anterior borders of the fenestrae ovales, where the basisphenoid is also apparently slightly exposed.

The *basisphenoid* is interpreted here as lying above the basioccipital and parasphenoid and is only slightly exposed between them as a result of damage. The bone described by Boonstra (op. cit.) as the basisphenoid for *S. whaitsi* is here interpreted as a parasphenoid, because posteriorly this bone has a suture with the basioccipital (and portions of the basisphenoid) in typically dermal bone fashion. Normally the basioccipital-basisphenoid suture is indistinguishable in Therapsids, especially in old specimens, and in this *Tapinocephalus*-zone material one would expect this to be more definitely the case, but in the present specimen the suture in this region is exceptionally well displayed.

Distinguishing Characteristics

The present specimen is recognised as a distinct species (*Struthiocephalus kitchingi*) on the strength of the following characteristics.

From *S. whaitsi* it differs in the following respects:

(1) The snout is narrower and more pointed, both horizontally and vertically, and is narrower posteriorly across the jugals than across the pterygoid processes.

(2) The posterior portion of the skull is broader and flatter, with the occipital condyle situated farther forward. The occipital plate is broader and lower, and its dorsal border extends farther backward so that the greatest breadth of the skull is at a level farther forward, although this level is still across the squamosals and

occipital condyle. The articular surfaces of the quadrates are virtually at the level of the middle of the length of the skull.

(3) The fronto-nasal boss is considerably more prominent. This may, however, be subject to sex and age.

(4) Although the present skull is reasonably larger, the interorbital width is smaller, while the intertemporal width is, out of proportion, twice that of *S. whaitsi.*

(5) The external nares are smaller and narrower.

(6) The premaxillaries are broader.

(7) The pterygoid processes swing farther outward.

(8) The postorbital bosses incline more forward so that the posterior borders of the orbits extend more transversely. The postorbital bars are shorter and stouter.

(9) The prefrontals extend farther backward, contributing more to the dorsal borders of the orbits.

(10) The post-temporal fossae are more laterally situated.

(11) The quadrate processes of the pterygoids are shorter and articulate differently with the quadrates, especially relative to the stapes.

(12) The quadrate processes of the paroccipitals are longer.

(13) The tabulars and squamosals partake more significantly in forming the mastoid bosses.

(14) The tabulars are not visible in dorsal view.

Other structural differences mentioned above are regarded as being possibly due to incorrect interpretations as a result of the problematic nature of this *Tapinocephalus*-zone material. In this respect, although the present author has described what appears to be most likely the correct structural arrangement, the present specimen is not so perfectly preserved and its structure so clearly displayed that *S. whaitsi* should invariably carry the blame.

From *S. akraalensis* it differs in the following respects:

(1) The snout is shorter, narrower and more pointed, but it agrees in being slightly constricted across the jugals.

(2) The posterior portion of the skull is less high and apparently also inclines more backward over the occipital region.

(3) Although the skull is some 45 mm. larger, the interorbital width is less.

(4) The external nares are smaller and more posteriorly situated.

(5) The prefrontals are situated more posteriorly, more directly above the orbits and contribute more significantly to their dorsal borders.

(6) The postfrontals are broader and more laterally situated, contributing to the postorbital bosses.

(7) These bosses incline more forward so that the posterior margins of the orbits extend more transversely.

(8) The occipital margin across the interparietal is concave.

(9) The tabulars do not show in dorsal view.

Again some structural differences, especially the tabular-squamosal-parietal relationship, are considered to be due to incorrect interpretation.

From *S. rheederi* it differs as follows:

(1) There is a sharper demarcation between snout and skull.
(2) The snout is shorter, smaller and more pointed.
(3) The temporal openings and pineal foramen are situated farther forward.
(4) The postorbital bosses incline more forward.
(5) The intertemporal width is greater.

On account of the unsatisfactory description of *S. rheederi* it is not possible to give a more detailed list of differences. The above list is nevertheless sufficient to show that *S. kitchingi* is distinct from *S. rheederi.*

From *S. milleri* it differs as follows:

(1) The external nares are situated farther back.
(2) The postorbital bars are more stout.
(3) The pineal foramen is smaller.
(4) The snout is smaller.

Otherwise the new specimen agrees with *S. milleri* in the shape of the fronto-nasal boss and the general flatness of the skull.

Because *S. whaitsi* is the only other species sufficiently well known for detailed comparison, and while it is not safe at present to accept certain structural interpretations in the described forms as perfectly reliable, it is preferable not to be too definite on the matter of finer relationship, either between the species, or to add to what is already indicated as the likely relationship of this genus with other near forms.

Acknowledgements

I wish to record my sincere thanks to Mr. J. W. Kitching for not only procuring this specimen under difficult circumstances, but especially for the magnificent preparation work he has done to expose sutural detail.

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ON THE SIGNIFICANCE OF TUSKLESS SPECIMENS OF DICYNODON GRIMBEEKI BROOM

By T. H. Barry*

Abstract

It has hitherto been accepted that *Dicynodon grimbeeki,* a species of the extinct Karroo mammal-like reptiles, possesses canine tusks in the males only. This theory is discussed in detail. An investigation is also made of the extent of the influence of sexual dimorphism on the dentition of extant forms. It is concluded that the evidence against the theory that the males only are tusked is such that it cannot be accepted.

Dicynodon grimbeeki is one of the relatively abundant species of fossil mammal-like reptiles. To date some 98 specimens have been found, mainly on the farm Leeukloof, in the district of Beaufort West, South Africa. This collection, housed in the Transvaal Museum, consists mainly of skulls. The majority are relatively big, have large canine tusks in the upper jaw, and have a relatively strong pre-orbital region, while the others are either tuskless, possess small canines or have buds only of these teeth. Those skulls without tusks and those with rudimentary tusks are usually smaller and the pre-orbital region is relatively more weakly developed (See figure 13.)

Investigations show that all the specimens possess a peripheral bony ridge in both the upper and lower jaws. This ridge is reminiscent of the condition found in the Chelonia and was probably similarly covered by a horn-like beak in the living animal.

The first specimens of *D. grimbeeki* were described by Broom (1935) who stated that of the nineteen good skulls he had received from Mr. Grimbeek, the collector, " . . . fourteen have tusks and are doubtless males and five have either no tusks or quite rudimentary tusks and are doubtless females" (p. 7). In making this deduction Broom was probably influenced by the fact that in some mammals the expression of some characteristics are more pronounced in the male than in the female. For instance, in some primates the canine teeth in the male attain a length far in excess of that of the female. The skull of an old baboon, for instance, can be sexed on this feature alone. These differences are usually ascribed to sexual dimorphism, a term which denotes the differences in phenotypic effect in the two sexes and which, as far as we know, are due to the influence of the sex hormones on the expression of certain characters. These hormones exert their influence from the pubertal stage of life onward.

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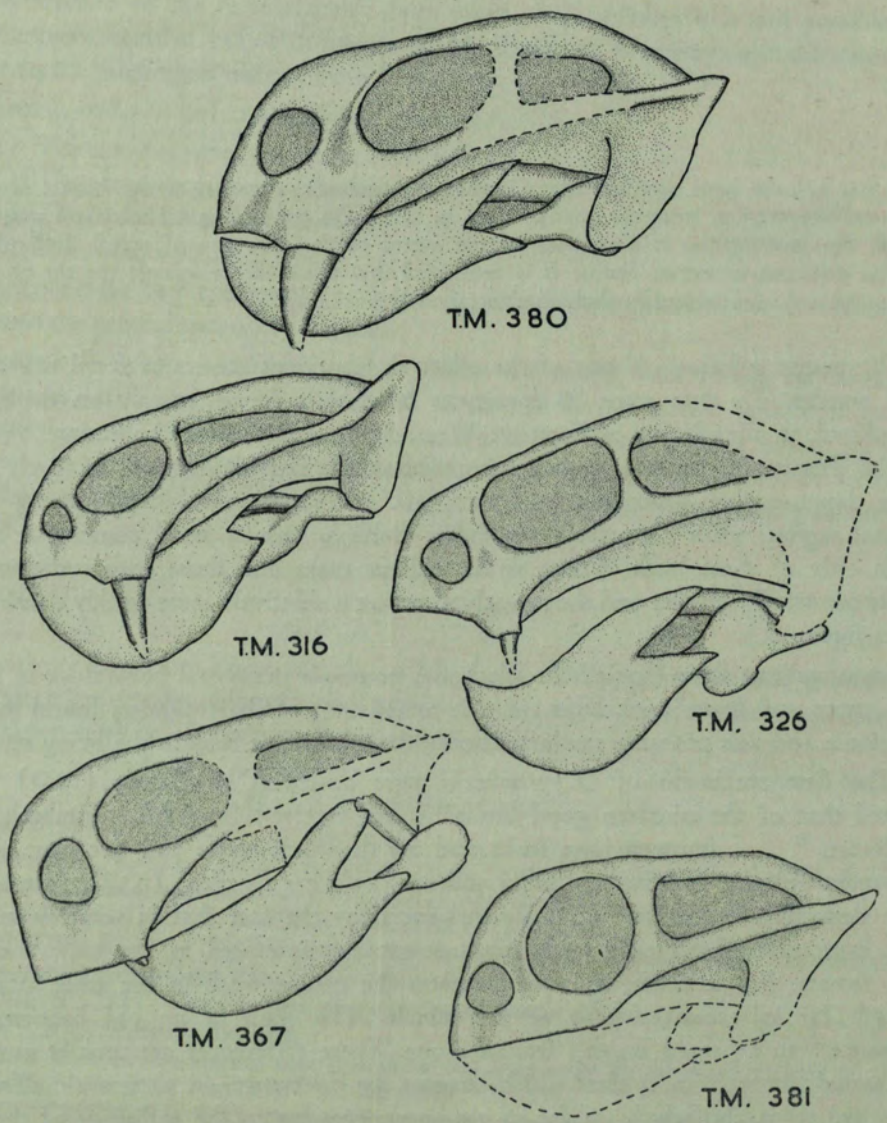

Fig. 13—Lateral views of *Dicynodon grimbeeki* specimens to illustrate the size and form of the canine tusks. Transvaal Museum (T.M.) specimen number 381 is tuskless. (x ½)

The questions that arose in studying *D. grimbeeki* were the following: are the differences that can be seen in these skulls linked to the sex of the animal, are they due to the action of the sex hormones, or are they due to an entirely different cause.

The history of the problem dates back almost to the first *Dicynodon* specimens that were found. The latter, all tusked forms, were sent to Owen at the British Museum of Natural History. When Owen later received similar but tuskless specimens he referred them, in 1860, to a new genus *Oudenodon*. He was, however, doubtful about the validity of this new genus and expressed the view that " . . . the composition and general form of the skull of *Oudenodon* so clearly resembles *Dicynodon* and *Ptychognathus* as to indicate a general family relationship. Viewing, indeed, the ridged indication of the sockets of the pair of upper canines in *Oudenodon,* the surmise is suggested whether the species of this genus may not originally have possessed tusks, which after having been shed had not been replaced, leaving the cavity of the sockets to absorption and obliteration. Or it might be asked whether the Oudenodons may not be the females of Dicynodons, in which as in the Narwhal rudimental tusks may have been originally hidden in the substance of the ridged tracts of the upper jaw, and afterwards absorbed." (p. 57).

In 1912, therefore, when Broom and Watson discovered tusked and tuskless specimens of *Dicynodon bolorhinus* in the same locality, Broom believed that he had produced all the evidence needed to prove that some species, through their possession of tusks in the males only, could be sexed by this feature. Toerien (1953), in reviewing the Dicynodontidae, advanced a similar theory. He stated that: "In the two species of *Dicynodon, D. grimbeeki* and *D. sollasi,* sex determines the presence of well developed tusks in the male and their absence (or vestigial appearance) in females . . ." (p. 109). Boonstra (1948), similarly announced that *D. jouberti,* from the *Tapinocephalus* zone, has tusks in the male only.

Once this method of sexing fossils gained ground it was not only accepted almost universally but sexing was sometimes done on very slender evidence. We find that the ratio of tusked to tuskless specimens was used as criterion to determine whether two sexes were being dealt with or not. For instance, *Aulacocephalodon* is a tusked form found in the *Cisticephalus* zone. When *Pelanomodon moschops,* the first species of that genus, was found in the same zone, it was seen to differ superficially from *Aulacocephalodon* only in having no tusks. Toerien (1955), however, states: "The possibility of *Pelanomodon* being the female of *Aulacocephalodon* can, however, be ruled out since specimens of the latter genus are far more plentiful than those of *Pelanomodon*" (p. 154). This refers to the number of specimens that had been *discovered* up to that date and of which *Aulacocephalodon* outnumbered *Pelanomodon* by three times. Although this ratio suggested to Toerien that he was not dealing with two sexes here, the same ratio of tusked and tuskless specimens of *D. grimbeeki* was accepted by Broom as constituting two sexes of the same species. Toerien suggested that the similarity between *Aulacocephalodon* and *Pelanomodon* might be explained by presuming that *Pelanomodon* descended from *Aulacocephalodon* through the loss of tusks.

In dealing with the genus *Dicynodon,* where tusked "male" and tuskless "female" specimens are found, Toerien (1955) concludes that " . . . some *Dicynodon* species have lost their tusks in the female" (p. 153). Although the latter theory can not be rejected without further knowledge of the inheritance of possible sex-linked characters in extant and extinct animals, it can, on the other hand, hardly be accepted on the meagre evidence of fossils, with and without tusks, being found in the same locality.

If we take into consideration the extreme size of the canine in the "male" *D. grimbeeki,* its entire absence in some "females", the fact that some fossils are found with small buds while others have short slender canines, it seems advisable to take into consideration that more than one conclusion can be arrived at from the available evidence. The first possibility to be considered is that we might have here a population in which the canine has become lost in some individuals as a result of alterations in the hereditary materials of an ancestor or ancestors. It is probable that a similar mutation in the ancestors of *Dicynodon* was responsible for the loss of the post-canine teeth, and that in these animals the loss of the teeth was not limited to one sex. The available evidence would seem to support the theory that the loss of the canines was similarly effected in both sexes. In this case specimens showing short, slender canines could be interpreted as being adult descendants of crosses between tusked and tuskless forms showing an intermediate size for the hybrids. It can, however, be accepted that it would be extremely difficult to distinguish between such a hybrid and an immature tusked parental type. This also applies to those specimens having bud-like canines.

A second possibility, seemingly the more logical and one the author is inclined to consider seriously, is that the tusked and tuskless specimens represent different age groups in a species in which both sexes are tusked in the adult. Tuskless specimens may therefore be either males or females in which the canines have not yet erupted while a specimen with rudimentary tusks has an equal chance of being a young male or female, and not only the latter as Broom suggested. It is significant that no specimen of *D. grimbeeki,* tuskless or having rudimentary tusks, was classified as a young male by Broom. Toerien classified one specimen only, a tuskless one, as a juvenile, and stated that it was probably a female although it might be a male with unerupted canines.

An investigation of 37 skulls of *D. grimbeeki,* in which the size and form of the canine could be determined, revealed the following types: (1) 4 skulls possess no externally visible tusks. These skulls are smaller on the average than the others, and it is suggested that they are juvenile forms in which the canines have not yet erupted. Through the courtesy of the Transvaal Museum the author was allowed to section one of these tuskless skulls to ascertain whether this was indeed the case. It was found that this specimen *does possess canines.* The latter, however, are small and are situated deep in the bone sockets (see fig. 15). It is therefore quite understandable that such a specimen would be classified as tuskless when viewed externally only. The dimensions of the canine of the right side are approximately

1.5 x 1.75 x 1.6 mm. and that of the left canine approximately 1.0 x 2.25 x 1.25 mm. The large size of the bone socket of the tooth indicates that the canine is that of a young animal, and that the tooth would probably have expanded to fill the cavity had the animal lived to maturity. (2) In 3 skulls only the buds of the canines are present. In one of these skulls a bud is present on the one side only. In order to find out whether these buds were in fact vestigial, a portion of the side wall of the maxillary of one specimen was carefully cut away. It revealed the root of the canine as well developed as would be expected in a newly erupted tooth (see fig. 14). A comparison with newly erupted canine teeth in the skulls of *Papio porcarius* revealed as remarkable a similarity in size and form as was found between the fully developed canine tusks of *Dicynodon* and *Papio*. (3). In 4 skulls the canine has a length that might be described as ranging from short to medium. Two of these

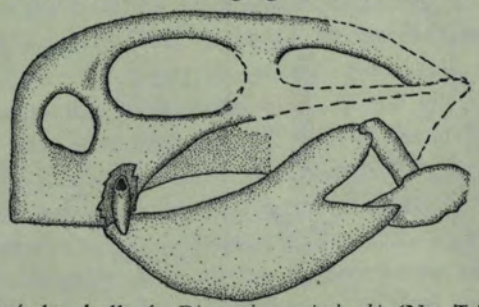

Fig. 14—Lateral view of the skull of *Dicynodon grimbeeki* (No. T.M.367). A portion of the maxillary has been cut away to show the root of the canine. (x ½)

specimens have tusks that are approximately half the length of that of the more robust fully developed types. (4) In the remaining 26 skulls, the canines are typically well developed and strong and probably represent the fully developed tusks of the adult.

It is possible, although it cannot be accepted without additional evidence, that the tusk could be accentuated in the male after puberty. It should, however, be borne in mind that if we are to postulate, as has been done by various authors, that the differences between two sexes of extinct animals are due to sexual dimorphism, then these differences and characters in the extinct forms should be subject to the same rules, modifications, etc., that apply to living animals. After all, this principle is applied to fossil material on the evidence in living forms.

An investigation of the dentition in living mammals has shown the following:— (1) Differences in the size or form of the canine in the two sexes, ascribed to sexual dimorphism, usually appear after puberty. The gorilla seems to be an exception to this rule. (2) The canine, when present in the male, is invariably represented in the female as well. In forms in which the canine is accentuated in the male, the canine of the female might, as in some cases, be much more weakly developed. *Monodon,* the Narwhal, has been cited as an exception to this rule, some authors postulating that females are found which have no canines. This case will be discussed later.

In the primates, Ashton (1956) has shown that the manifestations of sexual

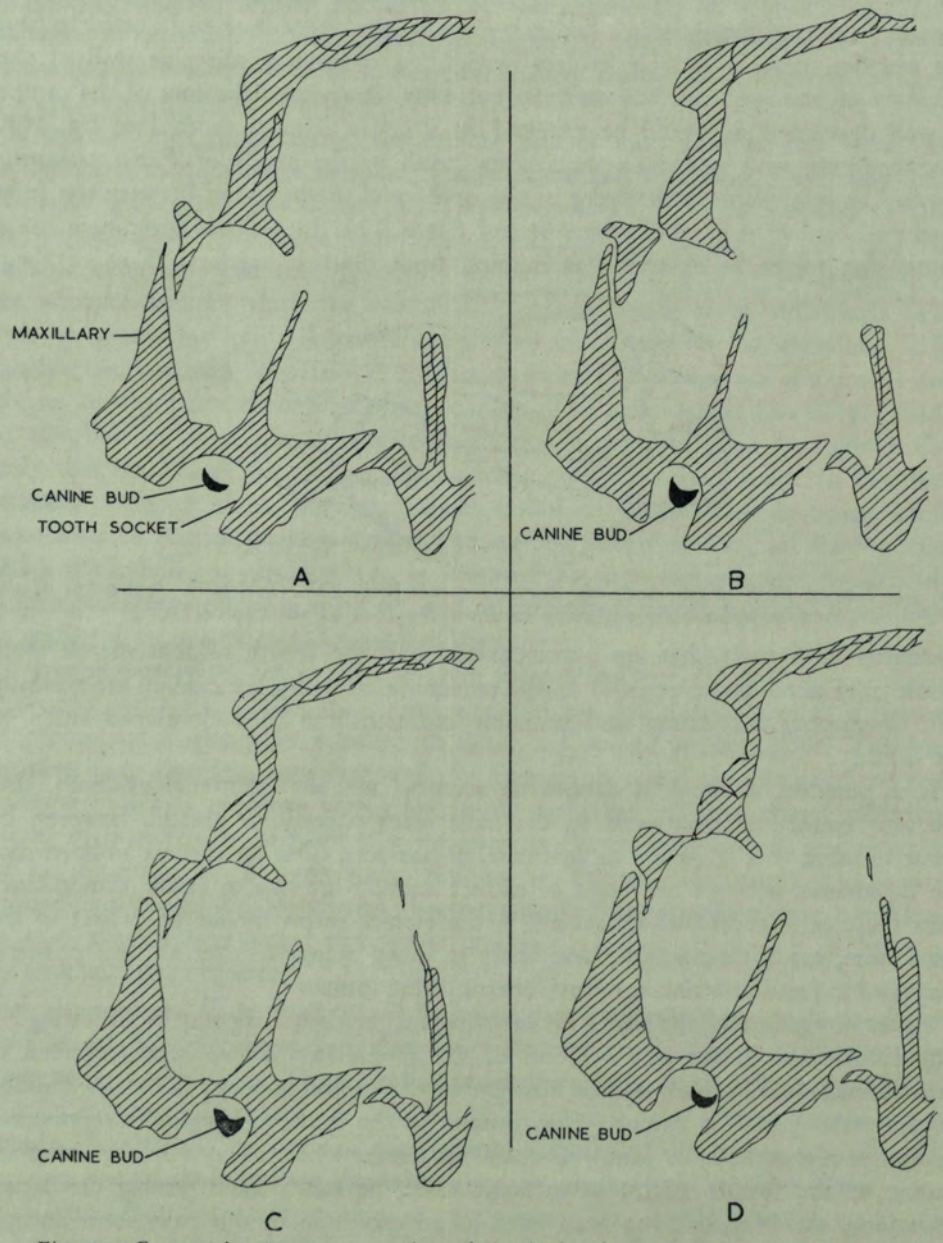

Fig. 15—Consecutive transverse sections through the skull of *Dicynodon grimbeeki* (No. T.M.381) to show the anlage of the canine tusk. (x2)

dimorphism vary considerably. In the gorilla and orang-outang, for instance, the supposed influence of sex hormones is more pronounced than in the chimpanzee, while with the exception of the siamang the cranial differences between the male and female gibbon can only be demonstrated biometrically (Hooijer, 1952). According to Ashton and Zuckerman (1950) the size and dimensions of the canines and lower first premolars are different in the two sexes of the great apes but, as far as can be ascertained from their work, not a single case was found in which either the canine or premolar is absent in any one sex.

Ashton (1956) undertook a further quantitative study to ascertain whether a comparable dimorphism characterizes the milk teeth of the apes. Sexual dimorphism, he found, mainly manifested itself during the phase of growth following puberty, when the canines and third premolars erupt and the temporal and nuchal muscles grow rapidly, especially in the male. As an exception, he found . . . "that sexual dimorphism does in fact characterize the milk teeth of the gorilla long before the hormonal factors responsible for the pubertal growth spurt in males become operative" (p. 124). He believes that this phenomenon in the gorilla might have a genetic basis. No evidence was found that the milk teeth of the male and female chimpanzee differ in size. Dimorphic differences in the chimpanzee only become noticeable after the canine teeth have erupted at about the age of seven years.

The great apes are primarily herbivorous. The tusk-like canines would, therefore, probably be used principally as a weapon in defence or attack, and as the role of defender is normally taken by the male the accentuated canine would be a distinct advantage. In contrast to this, the canines of the carnivores are essential in feeding, with the result that we find only a slight difference, if any, in the size of the canine of the male and the female.

A similar case is found in the baboon. These animals are similarly primarily herbivorous and the tusk-like canine of the male would, therefore, not be directly advantageous in feeding. Instances have, however, often been reported of male baboons killing and devouring small buck and sheep. The massive canines of the male here play a leading part in the killing and in tearing the meat from the carcass.

An investigation of a collection of *Papio porcarius* skulls housed in the Transvaal Museum has shown that it is quite possible to sex the old males on the size of the canine alone. The latter is usually more than twice the size of that of the female. If the extent to which the other teeth have been worn down is taken into consideration, the older females could also be sexed. The younger males and females, in which the length of the canine and the wear on the other teeth are not as marked as in the older forms could, however, not be sexed with accuracy. Two skulls in which the permanent canines had just erupted illustrate this point as, although their dentitions seemed identical, they proved to be a male and a female.

In 1951 Roberts stated that the canines in the Equidae are usually present in the male only, but an investigation of 36 sexed *Equus* skulls has shown that this is by no means the case. Of these, 13 males proved to have large canines while 16 females

had small but distinct canines. In only 4 skulls was the canine absent but these proved to include a male. Doubtless these animals were still young, for according to Sisson and Grossman (1940) the permanent canines only erupt at an age of 4 to 5 years. The canines in *Equus* are not nearly as well developed as in the other examples that have been quoted, but the difference in size in the old male and old female is just as distinct.

The best known example of an animal carrying tusks is probably that of the elephant. Here again the tusks, which in this case are the incisors, are present in the female although they are usually only about a quarter of the length of that of the male (Roberts, 1951).

The only animal in which the development and expression of the canines do not seem to conform to the accepted principles is the Narwhal. The latter, a highly specialized cetacean, " . . . in the adult differs from all other mammals in the complete absence of hairs, and from other Odontoceti in that instead of numerous similar teeth in both jaws, it has one very large straight tusk in the upper jaw in the male, and a pair of short tusks or none in the female, neither sex having teeth in the lower jaw" (Eales, 1950, p. 1). This tusk, usually the left one, may attain a length of more than half that of the body, and is spirally coiled sinistrally. The canine on the right side may remain rudimentary and concealed, or it may sometimes form a sinistrally coiled tusk. It is, however, difficult to assess the true position in regard to the tusks in the two sexes as the authors mostly do not deal with, or know, the ages of the specimens they describe.

Fraser (1938), in a paper on the vestigial teeth of the Narwhal, described the tusks of 12 skulls, 8 of which were females. Investigating the latter he found the following: In a juvenile and in an adolescent the left and right tusks were still imbedded in the bone of the rostrum. In two other skulls, with lengths of 21¼in. and 22⅛in. respectively, the tusks were still imbedded but had grown more forward than in the preceding cases. Three specimens were described as "Bidental", the tusks protruding beyond the anterior tip of the rostrum. In one such case the tusks measure 6 ft. 2½in. for the left, and 5 ft. 7½in. for the right tusk respectively. Curiously enough one skull, 23½in., in length, has no tusks, the sockets being filled with bone. To explain the latter phenomenon some authors have suggested that the tusks of the females are discarded or reabsorbed at a certain age. If this is the case, it would probably be unique in the mammals. In the males a steady increase, in accordance with the probable age, is evident in the size of the left tusk, but the right one is rudimentary. In the biggest skull investigated by Fraser, the left tusk, for instance, measured 6 ft. 3in. while the right one was so small that the point of the tusk was still 7¼in. behind the tip of the rostrum.

This phenomenon of asymmetrical growth is, however, not confined to the male but is also evident in the female where it is recorded that in the "Bidental" skulls, the left tusk is always rather longer than the right one.

The evidence of the position in the Narwhal has, the author believes, confirmed the view that even in this exceptional case the canine tusks are inherited and formed

in both the male and the female. The mechanism responsible for their later asymmetrical development, especially in the male, has, however, not been fully investigated. The Narwhal, therefore, supplies no evidence on which a hypothesis can be formed in regard to the absence of tusks in the females.

Taking into consideration the probability that *Dicynodon* possessed a horny beak in life, and that it would therefore probably have been herbivorous, as well as the fact that the tusks are situated in the upper jaw only, it would seem that these tusks were of no value in feeding and would either have been used in defense or might have been purely ornamental.

The following conclusions have been arrived at:

1. That the available evidence does not support the theory that *Dicynodon* skulls (in particular *D. grimbeeki*) can be sexed on the presence or absence of canine tusks.

2. No evidence was found of living mammals in which the canine is present in the male only. This had been claimed in support of the above-mentioned theory.

3. That sexual dimorphism might play a part in determining the size and form of the tusk in the male. This does not, however, imply that the canine is absent in the female.

4. That if sexual dimorphism does not play a part the females might conceivably have tusks of similar dimensions to those of the males.

5. That the differences in the size of the canine of the 37 specimens investigated suggest that *D. grimbeeki* might be tusked in both sexes. It has hitherto been accepted that the males only possessed tusks.

6. Tuskless specimens of *D. grimbeeki*, hitherto regarded as females, could be juvenile males or juvenile females in which the canines have not yet erupted. Specimens with "rudimentary" canines or with canine "buds" probably represent young males or females with newly erupted canines.

7. That the possibility should also be considered whether certain definitely tuskless species of *Dicynodon* could not have lost their tusks through a mutation (or mutations) such as caused the loss of the cheek teeth in the ancestors of *Dicynodon*. The phylogenetic history of the genus suggests that such mutations occurred at more than one time level. It is improbable though that a reduction of the dentition such as this would be limited to one sex, the female, as Broom suggested.

Acknowledgements

The author wishes to express his indebtedness to Dr. J. T. Robinson of the Transvaal Museum for placing the fossil material at his disposal, and to Mr. J. Meester for the facilities to study the collection of mammal skulls in his care. The author's thanks are also due to Dr. A. S. Brink of the Bernard Price Institute for Palaeontological Research for his helpful suggestions after studying the manuscript.

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A NEW SMALL STEREOSPONDYLOUS LABYRINTHODONT FROM THE TRIASSIC BEDS OF SOUTH AFRICA

By J. W. KITCHING

ABSTRACT

This paper describes an interesting new Amphibian, *Laidleria gracilis* gen. et sp. nov., from the Lower Triassic of South Africa (*Cynognathus-zone*). It is a Stereospondylid Labyrinthodont, belonging to the family Trematosauridae, but it differs in being exceptionally small. Most of the skeleton is preserved and with it are associated masses of small dermal scutes reflecting the nature of the skin. A combination of some peculiar characteristics encourages the recognition of this specimen as representing a new family.

INTRODUCTION

In July 1954, Dr. F. E. Peabody of the University of California at Los Angeles wrote to Dr. A. S. Brink of this Institute, drawing his attention to a small, uncleaned specimen in the Albany Museum, Grahamstown, which he had casually seen in 1948 and which he describes as a "turtle-like Labyrinthodont". He requested this Institute to investigate the specimen, as he considered it of exceptional interest.

In February 1955, while the present author was in the Karroo area on a field expedition, he visited the Albany Museum to see this specimen. It was still unprepared and Dr. Hewitt kindly agreed that the specimen could be taken to the Bernard Price Institute for preparation and description.

This remarkable specimen consists of a complete skull and the greater part of the skeleton, with dermal ossicles associated. It was presented to the Albany Museum by Dr. P. W. Laidler, who collected it at Elucwecwe in the Engcobo district, Eastern Cape Province. When discovered the specimen was in situ, embedded upside down in a slab of hard grey sandstone, the grain of which agrees very favourably with the sandstones of the *Cynognathus*-zone in the Burghersdorp and Lady Frere districts. With this evidence and the close proximity of the Stormberg series to Engcobo, it is almost certain that the specimen comes from the *Cynognathus*-zone and thus from the lower Triassic.

Most of the skeleton and dermal ossicles were exposed by weathering, but the skull was almost completely embedded in the hard sandstone, except the angulars, which were slightly damaged.

The preparation of the skull was very difficult, due to the hardness of the sandstone, but the palate and occipital region could be exposed beautifully. An attempt

was made to clear the matrix from the dorsal surface of the skull, but this endeavour was abandoned due to the bulk and hardness of the sandstone and the extreme flatness of the skull. A small portion of the dorsal surface of the snout was uncovered and it appears that the general preservation of the rest of this surface is most unsatisfactory. The specimen was evidently embedded within a cleavage plane in the sandstone, this plane passing along the dorsal surface of the skull, so that a certain degree of weathering occurred on this surface, while the ventral surface remained beautifully preserved.

Classification

In 1947 Romer recognised the Trematosauria and Stereospondyli as two separate suborders, the latter including the superfamilies Rhinesuchoidea, Capitosauroidea and Brachyopoidea. As the present specimen is stereospondylous, but at the same time showing closer affinities with the Trematosauria than with the other above-mentioned groups, it adds support to the revised classification which Romer used in 1950. Here he excluded the Rhinesuchidae from the Stereospondyli and placed it (with the Lydekkerinidae and Benthosuchidae) under the suborder Neorhachitomi, while the Stereospondyli included the families Capitosauridae, Trematosauridae, Metoposauridae and Brachyopidae.

The present specimen shows a remarkable mixture of Trematosaurid and Capitosaurid characteristics, as well as some Neorhachitomous features, with the scale balancing slightly in favour of the former. It is not unlikely that it may eventually be taken as the type genus of a new family, but provisionally its classification is given as follows:

Superorder Labyrinthodontia.
Order Stereospondyli.
Family Trematosauridae.
Genus *Laidleria* nov.
Species *gracilis* nov.

Laidleria gracilis gen. et sp. nov.
(Figures 16—19)

Diagnosis: Small Labyrinthodont with typically stereospondylous vertebrae. Skull flat, slightly elongated, with pointed snout. External nares large, close together, but still on the lateral margins of the snout. Orbits large, approximately at the middle of the length of the skull, and oval longitudinally. Palatal fossae very large and pterygo-jugal openings very small. Large ectopterygoids separating pterygoids from palatines. Pterygoid-parasphenoid contacts moderate in length, situated far back. Delicate pterygoid-exoccipital contacts not visible in ventral view. Apparently very reduced cartilaginous basioccipital and basisphenoid. Otic notches closed. Basicranial region broad and cultriform process narrow and very flat.

Type: A complete skull with lower jaw and the nearly complete skeleton with dermal ossicles associated, in the collection of the Albany Museum, Grahamstown (Cat. No. 4313), from *Cynognathus*-zone beds (Lower Triassic) at Elucwecwe in the Engcobo district, Eastern Cape Province.

I name this specimen *Laidleria gracilis* gen. et sp. nov., generically after the collector, Dr. P. W. Laidler, and specifically to emphasise its delicate size as compared with other Trematosaurids.

Description

There is no visible distortion of the skull. The skull is small, but adult, rather flat and triangular in outline, with the snout tapering Trematosaurid-like to a narrow point with a breadth of approximately 10 mm. in front of the external nares. The orbits are oval longitudinally and large, placed slightly posteriorly of the middle of the length of the skull as in the Capitosaurids, but on the lateral margins of the skull as in the Trematosaurids, facing dorsally. The external nares are fairly large and round, and placed 12 mm. behind the tip of the snout.

Besides the extreme difference in overall size, this specimen is also rather unlike its Capitosaurid allies in the shapes and positions of the external nares and the orbits. In these respects it agrees fairly well with its Rhinesuchid allies, especially with *Lydekkerina*.

The following is a list of useful measurements, given in millimeters:

Greatest length, from tip of snout to condyles	86
Greatest width, across quadrates	75
From tip of snout straight to quadrate	93
Length of snout in front of external nares	12
Diameter of external naris	6
Inter-narial width	6
Inter-orbital width	16
Distance from back of external naris to front of orbit	23
Length of orbit	16
Width of orbit	9
Distance from posterior border of orbit to occipital border	29
Narrowest width of cultriform process	4
Maximum width of palatal vacuity	16
Maximum length of palatal vacuity	39
Length of internal naris	10
Width of internal naris	3
Shortest distance between internal nares	7
Occipital height (total, constant from left to right)	11

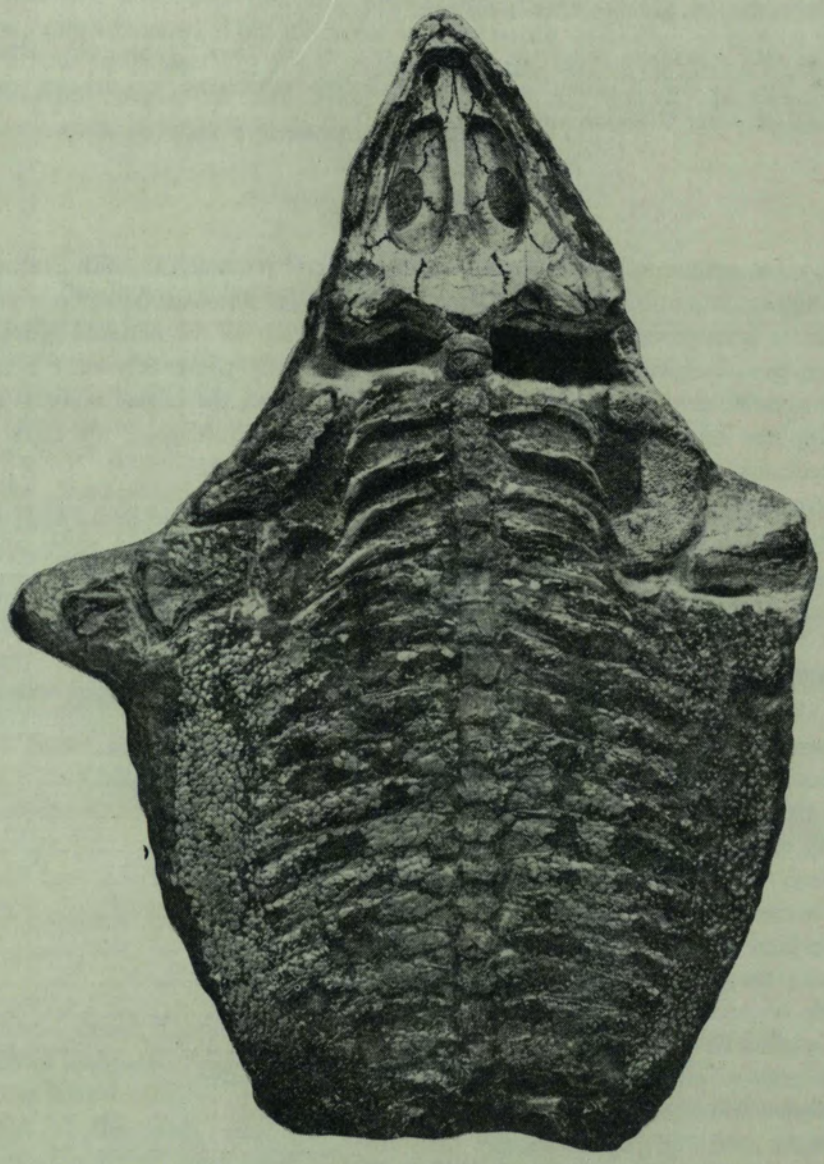

Fig. 16—Photograph of the type specimen of *Laidleria gracilis* gen. et sp. nov. (x½).

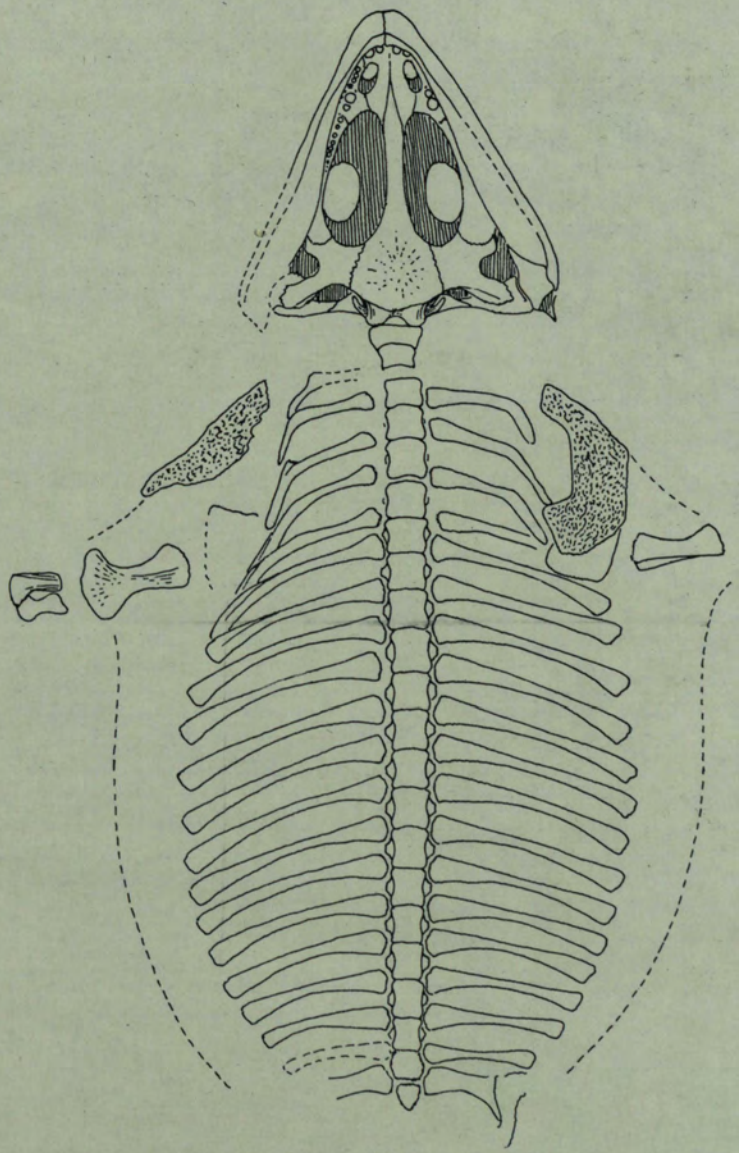

Fig. 17—Trace of figure 16. ($x\frac{1}{4}$)

Fig. 18—Portion of the type specimen of *Laidleria gracilis* gen. et sp. nov. showing details of the dermal ossicles (x 2).

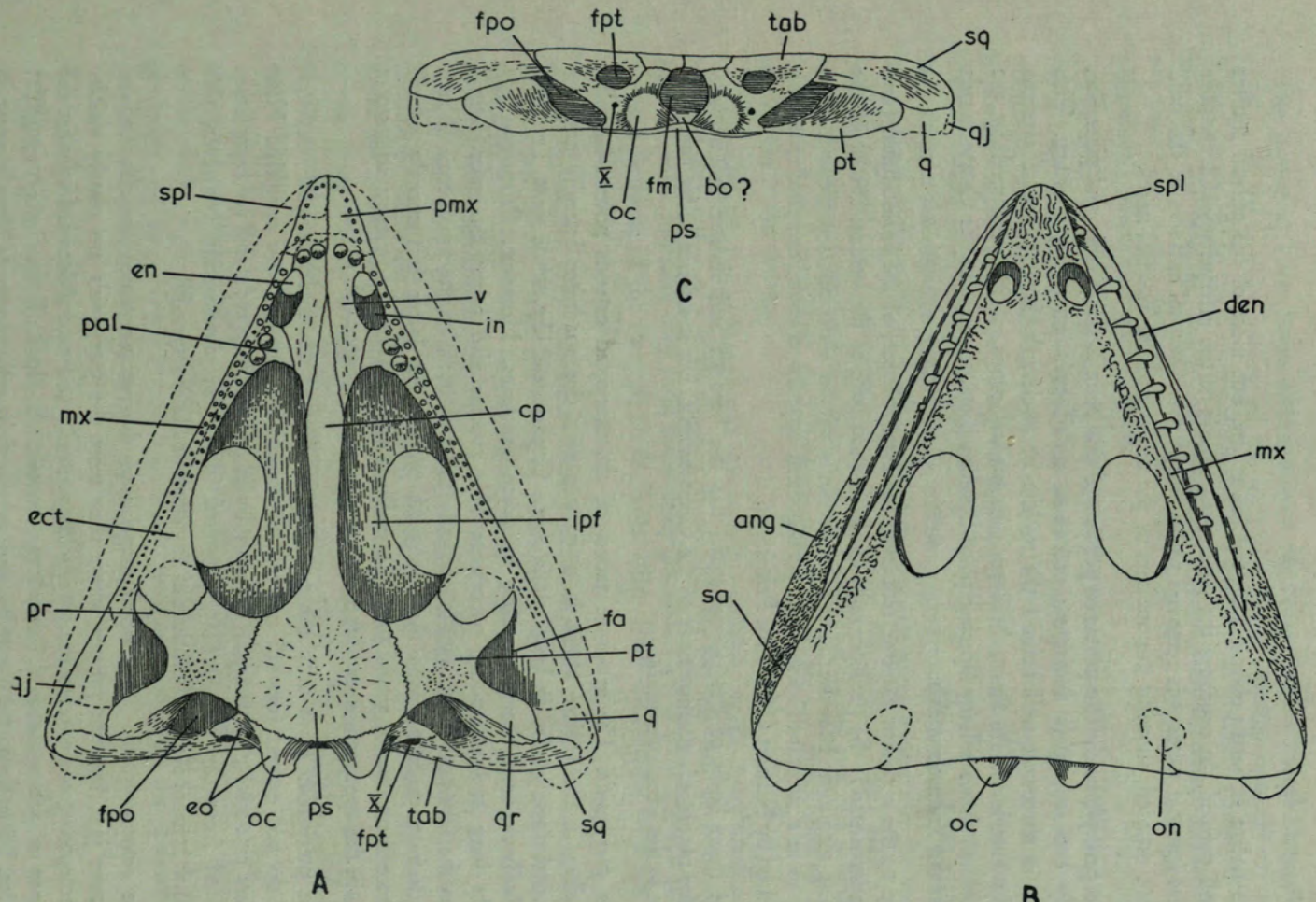

Fig. 19—A — ventral, B — dorsal and C — posterior view of the skull of *Laidleria gracilis* gen. et sp. nov. (Posterior view restored, outline of lower jaw added in ventral view). (x1).

The Palatal Aspect.

The palate is partly obscured by the lower jaw, but most of the palatal sutures are well defined. In exposing the palate, the matrix in the interpterygoidal vacuities and the internal nares was removed to an extent where ventral surfaces of the skull roof are exposed, showing the outlines of the orbits and the external nares.

The *parasphenoid*. The posterior portion of this bone is fairly large and plate-like, slightly concave, with a narrow processus cultriformis extending forward. This process is narrowest well behind the middle of its length, from where it expands slightly anteriorly. In front, between the internal nares, it is overlapped by the vomers and shows a long tapering point between them, more as in the Capitosaurids than in the Trematosaurids.

Due to the apparent extreme reduction, or even absence, of the basioccipital (and the basisphenoid), the parasphenoid tends to contribute to the ventral border of the foramen magnum. However, inward extensions of the exoccipitals prevent it from doing so in a substantial way. The arrangement appears to have been similar to that illustrated by Nilsson (1946) for *Peltostega*.

The main body of the parasphenoid has the breadth and shorter articulations with the pterygoids characteristic of the Capitosaurids, but it extends as far back as is typical in the Trematosaurids.

The *pterygoids*. The quadrate ramus of the pterygoid extends postero-laterally, expanding in the region where it articulates with the quadrates laterally and the squamosal dorsally. In its length it is again Capitosaurid-like, while most Trematosaurids have very short, tapering quadrate processes. However, *Peltostega* has equally long and expanding processes. This process also forms an antero-lateral wall to the fenestra pteroccipitalis, medially to its suture with the squamosal. Where the quadrate process leaves the pterygoid proper, the latter is distinctly pitted, but there is no sign of actual teeth. Laterally to this area lies the fenestra adductoria which, in this specimen, is smaller than in any other Stereospondyl.

The pterygoids form only the posterior borders of the interpterygoid vacuities. They do not extend forward around the lateral borders of these vacuities. Here they are extensively overlapped ventrally by large ectopterygoids and are completely separated from the palatines as is typical in the Trematosaurids. However, this condition is more exaggerated than in any described Stereospondyl.

The *ectopterygoids*. The lateral margins of the ectopterygoids are obscured by the lower jaw, but the sutures where they meet the pterygoids are clearly visible. The ectopterygoids overlap the pterygoids ventrally and extend forward to meet the palatines a short distance behind the anterior borders of the inter-pterygoidal vacuities. Nine sharp teeth can be seen on the right ectopterygoid. They increase in size forward.

The *palatines*. These bones articulate with the vomers medially and form greater portions of the anterior borders of the inter-pterygoidal vacuities than in any other related forms, while their contribution to the antero-lateral borders is smaller. They also form the posterior borders of the closely adjacent, large internal nares. There are two large tusks, situated close together, with a very small tooth in front, immediately behind each internal naris.

The *vomers*. The vomers are Capitosaurid-like in receiving the cultriform process for a long distance between them, the latter being exposed up to the level of the middle of the lengths of the internal nares. Their posterior tapering ends project backward for some distance along the antero-medial borders of the inter-pterygoid vacuities. They are, however, Trematosaurid-like in being very narrow, in contributing very little to the anterior borders of the inter-pterygoid vacuities, but they contribute more substantially to the medial borders of the internal nares. Anteriorly the vomers expand to meet the premaxillaries and in front of the internal nares each carries two tusks, situated transversally, almost as in *Lyrocephalus*, and not one behind the other as is more typical of the Trematosaurids. There are no indications of other small teeth on the vomers.

The *premaxillaries*. These bones are largely obscured by the symphysial region of the lower jaw, but a short suture can be seen on the left side in front of the internal naris. Dorsally they form the sharply pointed snout extending some 12 mm. forward in front of the external nares. They carry teeth conforming with those of the maxillaries.

The *maxillaries*. The maxillaries show four small teeth on the lateral borders of the internal nares. These fall more or less in line with the tusks posteriorly and anteriorly (although they belong to the outer row), an arrangement unlike that found in other stereospondyls.

Only the outer edges of the internal nares, bearing these teeth, represent the maxillaries in palatal view. The lateral views of both maxillaries are exposed. The lower jaw bends sharply outward so that figure 16 does not indicate the actual width of the skull and its acutely tapering outline. For this reason an outline diagram of the dorsal view of the skull is given in figure 19(B). The lateral margin of the snout is virtually concave.

The relationship of the maxillaries to their neighbouring bones is not clear. They are visible on both sides as slender bones, not contributing much to the lateral face of the skull. They show on both sides a very even row of small teeth, increasing gradually in size forward, but anteriorly, in the region of the palatal and premaxillary tusks, these tend to be somewhat irregular in size.

The Occipital Aspect.

The occipital region of the skull is well preserved. It was possible to excavate the matrix between the skull and the first cervical ribs to a depth beyond the level of the dorsal surface of the skull so that the dorsal occipital margin is clearly displayed.

The occiput is rather peculiar in having its dorsal margin virtually straight. The squamosals extend horizontally at the same level as the tabulars, with the quadrates situated not lower than the condyles. The total height of the occiput (11 mm.) is, therefore, the same across the whole width. It is also straight transversely and in the vertical plane.

The *exoccipitals*. These bones are fairly large. Posteriorly they form the double condyles and anteriorly they have a strong sutural union with the parasphenoids. They do not quite meet on the midline, so that the parasphenoid tends to contribute very slightly to the ventral margin of the foramen magnum. However, this interval between the exoccipitals probably housed a small cartilaginous basioccipital, as illustrated by Nilsson (1946) for *Peltostega*.

The exoccipitals have delicate contacts with the pterygoids, not visible in ventral view. Laterally they send out wing-like processes (evidently the paroccipitals). A small foramen for the Xth nerve can be clearly seen on the left side, slightly removed from the margin of the condyle and more on the wing-like process. This process extends a short distance over the fenestra pteroccipitalis and terminates abruptly, but it is evident that at this level it articulated with an extension of the tabular, this bridge being artificially lost on both sides. However, there are on both sides small bones in the position of the stapes. These could actually be the stapes, but they could equally well be interpreted as the dislocated tabular bridges.

Dorsally the exoccipital articulates with the dermo-supraoccipital and here there appears to be a contact with the tabular medially to the fenestra post-temporalis, in addition to the ordinary contact on the bridge between this fenestra and the fenestra pteroccipitalis, which is damaged in this specimen.

The *tabulars*. The relationship of these bones to the exoccipitals is described above (see *exoccipitals*). The fenestra post-temporalis appears to be small. Laterally they articulate intimately with the squamosals, thus closing the otic notches. It is not clear whether these notches are preserved as foramina on the dorsal face of the skull as in *Cyclotosaurus* and *Tertrema,* or whether they have merely been straightened out as in the Brachyopids.

The *squamosals*. The squamosals extend horizontally in posterior view. In the Trematosaurids the closest parallel is found in *Peltostega*. Other Labyrinthodonts in which this condition is vaguely similar are the Neorhachitome *Uranocentrodon* and the Brachyopid *Plagiosaurus*. The squamosals overlap the quadrates laterally and the pterygoids ventrally, and are themselves overlapped by the tabulars medially.

The *quadrates*. Ventrally the quadrate articulates with the quadrate ramus of the pterygoid, showing a triangle between this bone and the prearticular. Only a small, almost circular portion of the bone is visible in posterior view, it being largely covered by the pterygoid and squamosal medially, the quadrato-jugal laterally and the articular ventrally.

The *quadratojugal*. Only the left quadratojugal is preserved and it is a very small bone, situated more on the outer surface of the skull. Most of the bone is obscured by the articular of the lower jaw.

The Lower Jaw.

The lower jaw is virtually complete, but the ventral margins of both rami suffered some weathering posteriorly, damaging the angulars and the right prearticular. The rami are distorted, with the ventral margins displaced farther outward than the dorsal margins. Anteriorly the rami are very slender.

The dentaries are very long and slender, but they bulge substantially on the symphysis, unlike the condition in the average Stereospondyli. Posteriorly their ventral margins have long articulations with the angulars and extend to make delicate contact with the surangulars. Anteriorly the ventral margins of the dentaries articulate with the postsplenials and splenials. These sutures along the ventral margins of the dentaries fall within distinct very straight grooves.

The dentition in the lower jaw is singularly different from its counterpart in the upper jaw. Where the latter shows on each side a double row of small teeth, interrupted anteriorly by short blunt tusks (two each on palatine and vomer), the lower jaw has only one row of teeth. These teeth are all very large, of about the size of the tusks in the upper jaw, but sharper, longer and more slender. They are almost perfectly spaced at intervals of 5 mm. (4 mm. diastemes). There are no small teeth within the diastemes; these were excavated — in one place completely through on to the palatal side — and so sign of teeth, or even pitmarks, could be discovered. A close parallel to this condition is found in the Rhachitome genus *"Loxomma"* (Watson, 1912 — *Orthosaurus* fide Watson, 1926), where the teeth of the lower jaw are larger than the outer maxillary teeth and inclined to be more spaced. It was thought that the condition was somewhat like that of the Crossopterygian Osteolepid fish *Megalichthys* (Watson, 1926), but if smaller teeth had been present between these large evenly spaced teeth in some ancestral form, they are definitely completely lost in *Laidleria*.

The angulars form the great parts of the outer faces of the rami posteriorly and are well pitted. The surangulars are small, situated in the articulation region and their outer faces tone in well with those of the angulars.

On the left, the prearticular covers the articular ventrally so that little information about the latter is available. It extends forward on the inner face of the ramus to meet the dentary. This region on the right side is too badly preserved to yield more detailed information.

The contacts between the angulars and postsplenials, and between the latter and the splenials, are clearly visible. There is no clear fossa marking the entrance to the Meckelian canal and the regions on both sides are not well enough preserved to ascertain the presence and nature of the coronoids. The splenials also bulge on the symphysis and they protrude farther forward than the dentaries.

The Skeleton.

The skeleton is completely flattened within the cleavage plane in the sandstone in which it is preserved. However, individual bones show no indication of distortion as a result of pressure. The upper layer of sandstone was weathered away so that the skeleton was almost completely displayed when discovered. It is fairly complete, except for the caudal vertebrae, portions of the clavicles, right radius and ulna, left and right manus, and most of the hind limbs. The cervical and anterior thoracic ribs are in good condition, but the rest have disappeared, leaving only their impressions and articulation heads.

The vertebrae are stereospondylous, that is the intercentra alone form the whole of the central bodies, completely surrounding the notochord. An excavation was slowly and systematically ground between two thoracic vertebrae with the aid of a dental emery disc, studying the details exposed at short intervals, but no sign of pleurocentra was discovered. No space is allowed between the intercentra for pleurocentra, even had they been very flat, cartilaginous wedges.

The ventral surfaces of 22 well ossified central bodies are exposed. The first two vertebrae immediately behind the occipital condyles are rather short discs. The thoracic vertebrae are slender, but the vertebrae become more robust in the lumbar region, and tend to shorten again in the sacral region. All vertebrae carry ribs. An excavation was made on the side of two thoracic vertebrae, penetrating to the dorsal side, and it was found that the transverse processes and the neural spines are not well developed.

The cervical and anterior thoracic ribs are rather slender, triangular in cross section near the vertebrae, and they bend backward as flat (dorso-ventrally) extensions, evidently supporting the pectoral girdle. The ribs in the lumbar region are more robust and straight. They are all holocephalous, with slender shafts and expanded ends.

Only a portion of the blade of the left scapula is exposed, the rest being obscured by the clavicle. The blade is very thin and concave on what appears to be its outer surface. The clavicles are expanded and heavily pitted on their outer surfaces.

Both humeri are present, well ossified and in size and proportions they are not much different from those of *Lydekkerina*. There is a well developed pectoral crest preserved on the left humerus, decreasing gradually in size distally.

Only the right radius and ulna are preserved. They are both very short, about half the length of the humerus. The proximal end of the radius is small and almost flat. The distal end is well expanded with a process supporting the ulna. Both the proximal and distal ends of the latter are somewhat expanded and round, with the shaft constricted.

The ilium and ischium are present on both sides, but only those on the left are in fair condition of preservation. The ilium is round and slender, expanding distally to form articulation facets for the ischium and pubis. Proximally it articulates apparently directly with two sacral vertebrae, the transverse processes being very highly reduced. The ischium is a small quadrangular bone, not well ossified,

articulating with the ilium and pubis. Very little of the latter is exposed. There is a definite but incomplete acetabular face on the ischium.

The skeleton is elaborately covered with small dermal scutes. Dorsally the scutes are larger, irregular and oblong transversely. They decrease in size laterally to become smaller on the ventral side of the body. The dorsal scutes are seen in ventral view between the ribs and their inner surfaces are smooth. The ventral scutes cover the dorsal ones laterally to the ends of the ribs and their outer surfaces are convex. All the scutes articulate intimately with their neighbours (see fig. 18).

Such dermal scutes are rarely found preserved in fossil Amphibian specimens. Romer and Witter (1941) describe similar scales for *Eryops*, but these appear to be less ossified and to articulate more loosely. The type specimens of *Uranocentrodon senekalensis* (Van Hoepen, 1915) exhibit elaborate skin impressions, but these scales are of a totally different nature. They are very elongated rods, closely and regularly packed to form a distinct pattern.

Relationship

As stated above, the present specimen shows an interesting mixture of Trematosaurid and Capitosaurid characteristics, together with some Neorhachitomous features. However, there can be no doubt that it belongs to the Stereospondyli, for the following reasons:

(1) Pleurocentra are absent.
(2) The intercentra form complete discs surrounding the notochord.
(3) The skull is very flat.
(4) The two distinct occipital condyles formed by the exoccipitals are well separated.
(5) The basioccipital was apparently highly reduced and cartilaginous.
(6) The palatal vacuities are large.
(7) The pterygoids do not reach the vomers.
(8) The cultriform process of the parasphenoid is narrow and flattened.
(9) The quadrates are level with the occipital condyles.
(10) The limbs are very small.

In size and general proportions it has no comparable relative in the Trematosaurids, Capitosaurids and Metoposaurids. As far as size is concerned, the Brachyopids can be taken into consideration, but their proportions and structure are completely different. In these respects the specimen is rather comparable with the local small Neorhachitomous genera *Lydekkerina* (Watson 1920, Broili and Schröder 1937, Broom 1950), *Putterillia* (Broom 1930), *Limnoiketes* (Parrington 1948), and *Broomulus* (Broom 1930, Romer 1947), especially in the size and position of the orbits, but other proportions as well create a general Neorhachitomous impression. However, it differs significantly from these Neorhachitomous forms in that the snout is not broadly rounded; the external nares are not widely separated; the

otic notches are not normal; the skull is greatly depressed; the pterygoids do not reach the palatines; and above all, the vertebrae are not Neorhachitomous.

Laidleria is certainly not closely related to the Brachyopids, although it agrees in having no distinct otic notches; the skull being greatly flattened; the pterygoids not reaching the palatines; and especially the vertebrae being fully stereospondylous. It differs significantly in that the skull is pointed and elongated; the orbits are situated farther back; the basicranial region is not as broad and flat; the pterygoid-exoccipital contact is not as elaborate; and the occipital face is not slanting.

The Metoposaurids are completely different in being very large forms with large external nares and the orbits placed well forward. The cultriform process is broad and the pterygoid-exoccipital contact elaborate. The occiput slopes; the otic notches are normal; and the occipital condyles project behind the level of the quadrates. Only in one respect is there a reasonable point of comparison, that is the intervention of the ectopterygoids between the pterygoids and the palatines. Geographically and to some extent chronologically, they are too secluded a group to have had a significant relationship with *Laidleria.*

Laidleria differs from the Capitosaurids in having a more depressed skull, no pterygoid-palatine contact, and in the vertebrae not being neorhachitomous. The orbits in this group are also situated too far back. However, it agrees in having the snout moderately elongated. In the Trematosaurids the skull is also not depressed, but they have the ectopterygoids intervening between the palatines and the pterygoids as in *Laidleria,* and the vertebrae are more inclined to be stereospondylous. The snout of *Laidleria* is more Trematosaurid-like, that is sharply pointed, although not as elongated as in *Tertrema* and others where this conditon is highly specialised. The shape of the snout is more like that of *Platystega* (fide Romer 1947), *Lyrocephalus* (Efremov 1940) and *Rhytidosteus* (*R. capensis* Owen 1884, *"Microposaurus"* Haughton 1925). The latter, however, has smaller orbits, situated far anteriorly, while the former two genera have normal otic notches. Closed otic notches as in *Laidleria* are found in the Trematosaurid genus *Tertrema* and in *Cyclotosaurus* of the Capitosauridae, both genera differing very greatly in most other respects.

The parasphenoid of *Laidleria* is Trematosaurid-like, extending far back to level with the quadrates, but Capitosaurid-like in having moderate articulations with the pterygoids. The palatal rami of the latter bones agree with the Trematosaurids in not reaching the palatines, but the quadrate processes differ in being elongated as in the Capitosaurids. The vomers are small, with the internal nares close together in typical Trematosaurid fashion, but the anterior vomerine tusks align more transversely as in the Capitosaurids. In the general flatness of the skull it is Capitosaurid, and it agrees rather well with *Peltostega* (Nilsson 1946) of this family. *Peltostega* also agrees with *Laidleria* in the relationship of the pterygoids, that is their contacts with the parasphenoid are moderate, the palatal rami short and the quadrate rami elongated.

It appears, therefore, that in the Trematosauridae, *Laidleria* has a more readily comparable ally in *Peltostaga*, and perhaps *Lyrocephalus* (and *Thoösuchus* Efremov 1940) than in its local contemporary *Rhytidosteus*. The other local contemporaries, *Trematosaurus kannemeyeri* (Broom 1909 = *Rhytidosteus?*) and *Trematosaurus sobeyi* (Haughton 1915) are very large forms, while *Tertrema*, *Gonioglyptus* and *Aphaneramma* are too highly specialised to be taken into consideration.

The closed otic notches, the peculiar dentition, the exceptional shortness of the palatal rami of the pterygoids and the peculiar low, straight occiput in *Laidleria*, separate this specimen again from all the described genera of this family to such an extent that it is likely to represent the type of a new family, the Laidleriidae.

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Abbreviations

ang, angular; bo, basioccipital; cp, cultriform process; den, dentary; ect, ectopterygoid; en, external naris; eo, exoccipital; fa, fenestra adductoria; fm, foramen magnum; fpo, fenestra pteroccipitalis; fpt, fenestra post-temporalis; in, internal naris; ipf, inter-pterygoid fossa; mx, maxillary; oc, occipital condyle; on, otic notch; pal, palatine; pmx, premaxillary; pr, palatal ramus of the pterygoid; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadrato-jugal; qr, quadrate ramus of pterygoid; sa, surangular; spl, splenial; sq, squamosal; tab, tabular; v, vomer; x, foramen for the vagus nerve.

THE SPECIES RELATIONSHIPS AND STRATIGRAPHIC DISTRIBUTION OF SOUTHERN AFRICAN UPPER CRETACEOUS EPISTOMINA

By Yvor H. Smitter

Abstract

Briefly set forth are the phylogenetic inter-relationship of the various species of the foraminiferal genus *Epistomina* occurring in the upper Cretaceous of Southern Africa. The known stratigraphic ranges of the forms as they occur in Southern Africa are presented.

One of the most striking features in Southern Africa of many upper Cretaceous microfossil assemblages is the profusion of Foraminifera belonging to the genus *Epistomina*. With this abundance of individuals of *Epistomina*, there is associated an interesting diversity of speciation within the genus and excellent opportunity is afforded, consequently, for the study of species interrelationships. In addition to the purely phylogenetic considerations of such a study, however, an appreciation of the development of the various forms of *Epistomina* with regard to their stratigraphic distribution is of further value in providing supplemental means for the indexing or dating of Southern African upper Cretaceous sediments.

Of the upper Cretaceous group under consideration, the unornamented form of *E. caracolla* (Fig. 20(a)) is the first of the Epistomina to appear in the column. The form occurs in what are probably Santonian beds at Umkwelane Hill and Umsinene and is found thereafter in Campanian, Maestrichtian and Montian material. Somewhat higher in the section, *E. caracolla* evidences, in many specimens, a tendency to develop irregular wall thickenings of both dorsal and ventral surfaces (b). This expression of the species has a known stratigraphic range extending from the Campanian again through to Montian. Both the unornamented and ornamented *E. caracolla* have been recorded from Europe and North America, although the vertical occurrences of the two forms have not been differentiated in these areas.

In the uppermost Campanian or possibly lower Maestrichtian horizons of the Umzamba and Zululand strata, *E. zuluensis* (c) and *E. pondensis* (d, e) appear. *E. zuluensis* it seems is restricted in range to upper Campanian and Maestrichtian whereas *E. pondensis* ranges through to Montian. *E. pondensis* manifests a considerable variation in degree of wall ornamentation and, as might be expected, expressions of the species showing a lesser amount of wall development occur in the Campanian and lower portion of the Maestrichtian. Highly reticulated forms, on

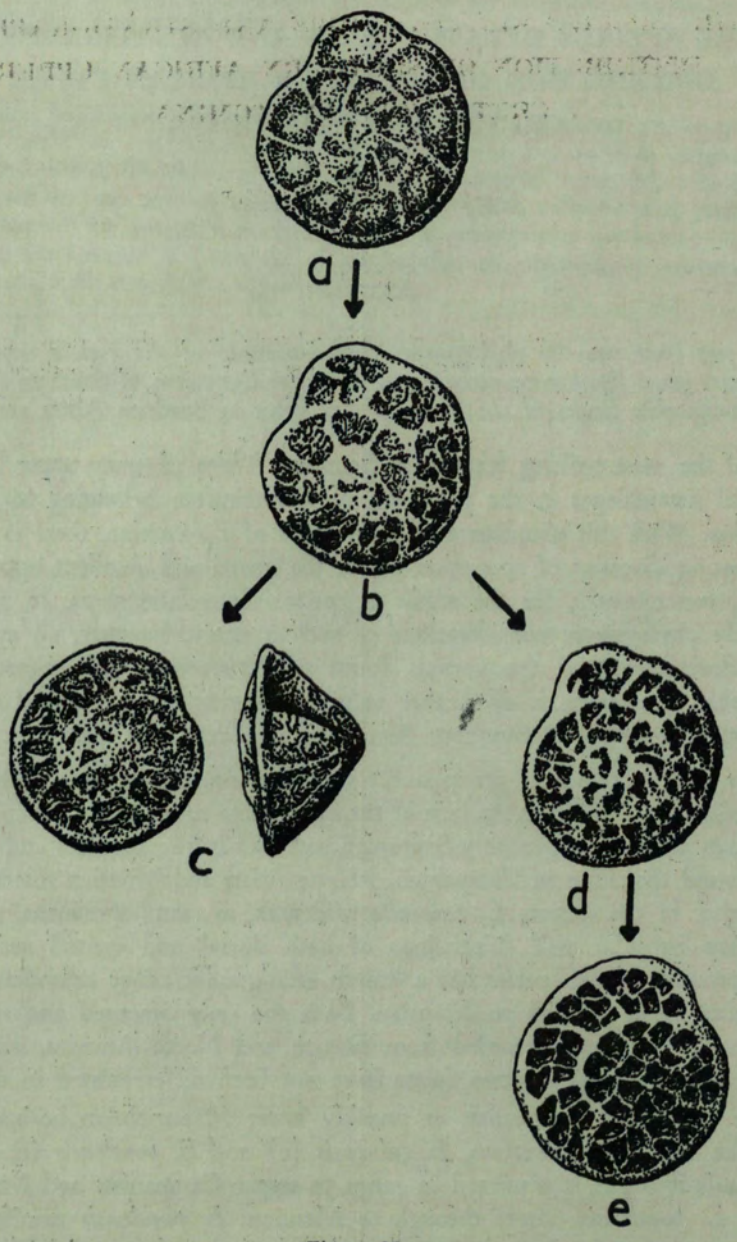

Figure 20

the other hand, seem to be characteristic of the later upper Maestrichtian and Montian.

It is interesting to note that the three species discussed are all very closely interrelated and, although the accompanying figures indicate more or less arbitrarily the various stages in the development of these *Epistomina,* the many intergradations in the group can only be appreciated on inspecting a complete range of study material. It is quite evident that in the group the principal direction of development involves the growth and specialization of the wall structure of the test. Commencing with *E. caracolla,* a progressive development of the ornamentation of the test wall leads to a heightening and increased reticulation of these surface structures, presumably terminating in development with the rather bizarre *E. pondensis. E. zuluensis* also evidences the irregular thickenings of the wall and is unquestionably an outgrowth of *E. caracolla,* but the species is set apart from the others in having a flattened dorsal surface and highly convex ventral surface.

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