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CAPE TOWN



ANNALS OF THE
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VOLUME 64

ANNALS OF THE SOUTH AFRICAN MUSEUM
ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

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THE TRUSTEES OF THE
SOUTH AFRICAN MUSEUM
CAPE TOWN

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STUDIES ON VERTEBRATE PALAEOLOGY

A collection of invited scientific papers

presented to

LIEUWE DIRK BOONSTRA

Palaeontologist at the South African Museum, 1927-72

in recognition of his contributions to

Karoo palaeontology



CONTENTS

	<i>Page</i>
Lieuwe Dirk Boonstra	1
Scientific papers of L. D. Boonstra	3
In reminiscent vein, by S. H. HAUGHTON	7
The braincase and associated structures of the cotylosaur reptile <i>Procolophon triconiceps</i> Owen, by T. S. KEMP	11
On the source of therapsids, by E. C. OLSON	27
A new genus of gorgonopsid from East Africa, by F. R. PARRINGTON	47
The inner ear of Gorgonops (Reptilia, Therapsida, Gorgonopsia), by D. SIGOGNEAU ..	53
Étude du crâne d'un jeune specimen de <i>Moschorhinus kitchingi</i> Broom, 1920 (? <i>Tigrisuchus</i> <i>simus</i> Owen, 1876), Therocephalia, Pristerosauria, Moschorhinidae d'Afrique australe. (Remarques sur les Moschorhinidae et les Whaitsiidae), par C. H. MENDREZ	71
A new dicynodont ancestor from the Upper Ecca (lower Middle Permian) of South Africa, by T. H. BARRY	117
The skull and mandible of a new cistecephalid dicynodont, by M. A. CLUVER	137
A new dicynodont (Reptilia, Therapsida) from <i>Cynognathus</i> zone deposits of South Africa, by N. HOTTON III	157
The alleged synonymy of <i>Lycorhinus</i> and <i>Heterodontosaurus</i> , by A. CHARIG & A. W. CROMPTON	167
The tarsus of theropod dinosaurs, by S. P. WELLES & R. A. LONG	191
Alfred Sherwood Romer	219
Aquatic adaptation in reptiles—primary or secondary, by A. S. ROMER	221
Migrations of the Multituberculata and the late Cretaceous connections between Asia and North America, by Z. KIELAN-JAWOROWSKA	231
Dérive des continents et paléontologie: quelques réflexions, par J.-P. LEHMAN	245



NEW GENERIC NAMES PROPOSED IN THIS VOLUME

	<i>Page</i>
<i>Cephalicustriodus</i> Parrington, 1974	51
<i>Cistecephaloides</i> Cluver, 1974	139
<i>Eodicynodon</i> Barry, 1974	121
<i>Kombuisia</i> Hotton, 1974	158
<i>Watongia</i> Olson, 1974	28



LIEUWE DIRK BOONSTRA

LIEUWE DIRK BOONSTRA

The contributions to this volume of the *Annals of the South African Museum* are dedicated to Dr Lieuwe Dirk Boonstra, who in January 1972 retired as Head of the Department of Palaeontology at the South African Museum.

Born in Volksrust, Transvaal, in 1905, Dr Boonstra completed his school education in Durban in 1923, and commenced his studies at the University of Stellenbosch, where he qualified with the degrees B.Sc. (1926) and M.Sc. (*cum laude*) (1928). In 1927 he was appointed as Assistant in Palaeontology at the South African Museum for a period of three years but in 1930, having completed a D.Sc. thesis on the osteology and myology of the pareiasaurian hind-limb, he accepted the post of Palaeontologist at the South African Museum, a position he held until his retirement. During his distinguished career, Dr Boonstra published numerous scientific papers and books, as well as many popular articles. His awards include the Queen Victoria Scholarship of Stellenbosch University (1933) and the Havenga Prize in Natural Science and Technology (Biology Section) of the South African Academy of Science and Art in 1959.

For the greater part of 45 years Dr Boonstra was in sole charge of the South African Museum's collection of Karroo vertebrates, and it was through his personal efforts in the field that this collection has grown, from the nucleus established by R. Broom and S. H. Haughton to the extensive and representative record that it is to-day.

Boonstra's collecting trips in the early years of his career were a far cry from the four-wheel drive vehicle and caravan luxury of to-day. With only very limited funds, and carrying his equipment and supplies in a rucksack, he started on his survey of the vast Karroo on foot, relying on friendly farmers for assistance in crating and dispatching any specimens he found. A donkey-drawn cart was later a decided improvement, but many years were to pass before the comparative luxury of even a second-hand truck could be afforded.

In spite of these difficulties, Boonstra's flair for collecting laid the basis for some extremely significant faunistic and palaeoecological research, and his collections are a record of thoroughness and an ability to see value in every identifiable specimen. Happily, the area on which Dr Boonstra concentrated most of his research was the *Tapinocephalus* zone, lowermost part of the Karroo succession. Although notorious for the difficulties it imposes on collector and preparator alike, this zone is central to the problems surrounding the origins and early radiation of the mammal-like reptiles. Using the wealth of morphological and faunistic information available to him through his own collections, and supplementing this with the results of personal examination of related material in the United States, Britain and Russia, Dr Boonstra was able to prepare a series of major contributions dealing with therapsid origins and early interrelationships.

But the study of fossil vertebrates encompasses more than the establishment of phylogenetic 'family trees', and in the early 1950s Dr Boonstra began incorporating his knowledge of the skeleton and inferred musculature of several important *Tapinocephalus* zone reptiles into a series of striking, life-size reconstructions. These groups, popular as they are, serve a wider purpose than public appeal—as recent trends in research show, more and more attention is being given to a hitherto neglected aspect of palaeontology, namely, the interaction between the animal and its environment, with particular emphasis on probable behavioural and physiological activities. Taken together, Dr Boonstra's morphological, functional and faunal analyses of the early Karroo reptiles have set the scene for an important new approach to our understanding of the extinct vertebrate assemblages of the Karroo, and it is perhaps fitting that his work in this field is now forming a framework for several wide-ranging research projects. It can fairly be said that Boonstra set the pace, and that it is now up to a succeeding generation to continue the course.

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1929

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3. Pareiasaurian studies. Part IV. On the pareiasaurian pes. *Ann. S. Afr. Mus.* **28**: 113-122.

1930

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1932

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1933

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20. Pareiasaurian studies. Part X. The dermal armour. *Ann. S. Afr. Mus.* **31**: 39-48.
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1935

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IN REMINISCENT VEIN

By

S. H. HAUGHTON

The first fossil reptilian remains from the Karroo system in southern Africa to be studied scientifically were collected by Andrew Geddes Bain, the 'father of South African geology', during the course of his labours as a road-maker and engineer. The story of his enthusiasm for geological observations, fired by a perusal of Lyell's classic *Principles*, of his abortive attempts to house a fossil collection in Grahamstown, and of his association with Professor (later Sir) Richard Owen has been told more than once and needs no repetition here.

Early studies of fossil material collected by Bain and others in the latter half of the nineteenth century were concentrated mainly on osteological description with a view to assessment of the taxonomic position of the bones in the animal kingdom. To each specimen was assigned a generic and specific name and a place in a recognized family and order. The total amount of material available for study was, by modern standards, small and some of it was decidedly of a scrappy nature, scarcely warranting selection as the types of new genera and species, at least in the eyes of modern students. Nevertheless, study of the relevant literature shows that, by the end of the year 1911, descriptions had been published of about 100 new genera containing some 168 new species of Karroo Reptilia by authorities such as Owen, Cope, Lydekker, Seeley, Weithofer, and Broom. Most of the types of these forms were housed outside South Africa.

When the present writer first arrived at the South African Museum from England in September 1911, to take up the post of geologist-palaeontologist, he was instructed by the then Director, Dr L. A. Péringuey, to pay attention to vertebrates from the Karroo strata, the somewhat small collection of bones in the Museum being at that time under the honorary curatorship of Dr R. Broom, who was not resident in the city but had arranged for any new acquisitions acquired by the Museum to be sent to his home for study and description.

At that time, the Museum's most enthusiastic amateur collector was the Rev. (later Archdeacon) J. H. Whaits, the Anglican rector of Beaufort West, who was recompensed financially by the Museum for out-of-pocket expenses incurred by him on his collecting expeditions. A number of the specimens collected by Whaits and sent to Broom for study never reached the Museum, but were acquired from Broom by the American Museum of Natural History in New York where they now lie. Broom prepared for that Museum a descriptive catalogue of the specimens there housed.

Quite early in his service with the South African Museum, the writer was given the opportunity of spending some time under the hospitable roof of Mr W. Musto, owner of the farm Dunedin, Beaufort West, lying north of the Nieuweveld escarpment, and of searching for fossil reptiles there. 'Searching'

meant solitary walks from and to the house, looking for likely outcrops and, if finds of bone were made, the personal transport of the unearthed material to the house for packing and preparation for dispatch to Cape Town. Among the finds on this expedition was a fairly complete skeleton, with skull, of a pareiasaurian in a mudstone below a slightly overhanging sandstone whose excavation took most of the working hours of three days and whose transport to the house, in sacks, proved somewhat tiring to the writer. This find, after preparation at the Museum with the primitive tools then available, was described in 1913 as the type of *Pareiasuchus peringueyi* Broom & Haughton.

From then until his appointment to the post of Senior Geologist on the Geological Survey of the Union, with an office in the Museum grounds, the writer was given a number of opportunities of field-collecting, mainly of Karroo reptiles. Much hospitality was tendered to him by interested farmers, whether he arrived by cart, drawn by one horse, or by a donkey-drawn fitted covered wagon kindly placed at his disposal by the Geological Survey office in Cape Town. Attention was paid particularly to outcrops of the *Tapinocephalus* zone in the Prince Albert and Beaufort West districts, of the *Cistecephalus* zone in the Graaff-Reinet-Murraysburg area, and of the Red Beds in the Herschel district. Among the kindly hosts whose names have been perpetuated in the specific designations given to some of the numerous reptilian types collected may be mentioned the late Mr W. van der Byl of Abrahams Kraal, Prince Albert district (who employed a very keen-eyed shepherd, Ou Jan, who located many of the specimens coming from that farm in his daily care of the flocks and who remembered the positions of most of his finds), the late Rev. J. H. Whaits, then of Beaufort West, the late Mr B. Read, then Head of the Teachers' Training College at Bensonvale in the Herschel district, and the late Mr B. Cullingworth of Kromme Spruit store in Herschel. These, and many others, turned the otherwise arduous task of 'tramping the veld', digging and transporting fossils back to base into enjoyable experiences.

Broom's transactions with the American Museum of Natural History led to a decision by the South African Museum authorities to divorce him from his titular position on the Museum staff, and thereafter the writer was left alone to develop and, if thought desirable, to name and describe the finds that he had added to the collection. In those days, release of the bones from their enclosing matrix was accomplished with the primitive equipment of manual hammer and chisels of varying sizes and carried out in a galvanized iron shed, which also acted as an office. Under these circumstances, little more could be achieved but the removal of bones from their enclosing, and often very hard, matrix and to display their external features. Modern methods of preparation, especially of the internal structure of skulls, were not available and, for much of the time, the research workers had to do the preparatory cleaning single-handed.

At the end of 1920, the writer was appointed to the staff of the Union Geological Survey with an office in the cottage in the Museum grounds, but was

authorized to maintain an association with the palaeontological section of the Museum. Not long afterwards, the Museum Trustees appointed Mr (now Dr) L. D. Boonstra, a graduate of Stellenbosch University, as a palaeontologist to the Museum with the special task of working on Karroo fossil vertebrates. From the time of his appointment until the writer's transfer to Pretoria at the end of 1933, we worked in close collaboration, particularly on the fairly large collection of pareiasaurian material that had accumulated, in an attempt to systematize the nomenclature of this herbivorous group. What we devised in this regard, primarily basing ourselves on the external characters of skulls and teeth, has not proved wholly acceptable to later investigators; but that is not an unusual fact in the whole field of fossil reptilian nomenclature.

In the course of more than forty years of service with the Museum Dr Boonstra has devoted himself to collecting fossil reptilian remains especially from the Lower Beaufort beds, to the recovery of the bones from the matrix surrounding them, to their study as osteological specimens, and to the conditions of life and the forms of the animals of which the bones were the framework. In each of these areas of work and study his contributions are of outstanding value. The opportunities that he made of studying South African (and other) materials in museums in the United States and various European countries were used to the full in enabling him to become an expert in his chosen field, while the restorations which were made under his supervision and placed in the exhibition halls of the Museum have aroused a public interest far greater than that which were ever accorded to collections of bone specimens set out in glass cases.

To the knowledge that is being acquired of the kinds of continental animals and of the environment in which they lived and died during the Karroo period, Dr Boonstra's decades of study and of papers that enshrine many of his findings have contributed in great measure. For this, all students in the subject, both present and future, owe and will owe him a debt of gratitude.



THE BRAINCASE AND ASSOCIATED STRUCTURES OF THE
COTYLOSAUR REPTILE *PROCOLOPHON TRIGONICEPS* OWEN

By

T. S. KEMP

University Museum and Department of Zoology, Oxford

(With 1 plate and 5 figures)

CONTENTS

	PAGE
Introduction	11
Description of the braincase and associated bones	12
Discussion	19
Summary	24
Acknowledgements	25
References	25
Abbreviations	25

INTRODUCTION

It is an extraordinary and unexplained fact that while the skull of the cotylosaurian reptile *Procolophon* is quite common in Lower Triassic Karroo deposits of South Africa, the braincase is almost always missing. Thus the description by Watson in 1914 of most of the skeleton, including the braincase, has remained practically the sole source of information about this part of the skull, although a figure and a very brief description of the ventral aspect has been published by Broili & Schröder (1936). Watson's description showed great insight for its time and remains, indeed, surprisingly modern. However, it lacks adequate illustration and certain aspects of the braincase were not visible in his material.

This present study is based upon a single, particularly large specimen of *Procolophon trigoniceps*, consisting of the skull, lower jaws and anterior part of the postcranial skeleton. It was collected by Dr F. R. Parrington in 1964 from Klipfontein, Bethulie, South Africa and forms part of his collection. Dr Parrington's collection has since been donated to the Museum of Zoology, Cambridge University where this particular specimen is housed, under the catalogue number **T** 1026.

Only the skull has been prepared so far. The matrix is a hard, red, fine sandstone which is barely affected by acetic acid. Thus preparation has been entirely mechanical, using a Burgess 'Engraver'. The dorsal roof of the skull has been weathered away with almost surgical precision, making it possible to prepare the braincase and the palate from the dorsal aspect as well as from the more conventional views. The postero-lateral part of the right side of the skull is also missing although the braincase of that side is complete. Distortion has

been slight and consists mainly of a degree of dorso-ventral crushing of the occipital region.

DESCRIPTION OF THE BRAINCASE AND ASSOCIATED BONES

Supraoccipital

The supraoccipital has suffered slightly from the dorso-ventral crushing but its form is clear. A narrow dorsal process runs postero-dorsally to make contact with the posterior edge of the skull table. It is triangular in section with a sharp median posterior edge and a flat antero-dorsal face. Ventrally the supraoccipital roofs over the posterior part of the brain cavity by means of a pair of wing-like lateral processes. Each of these processes is fairly thin (about 3 mm)

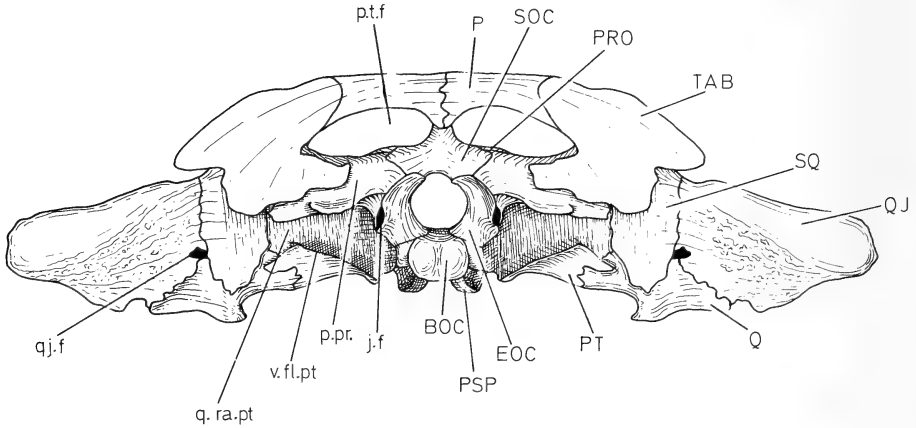


Fig. 1. *Procolophon trigoniceps* CUMZ T 1026.
Occipital view of skull, restored. $\times 1$. For abbreviations see page 25.

but wide and lies in an approximately horizontal plane. The distal end contacts the prootic bone in front, the opisthotic extensively and the exoccipital posteriorly, and each of these respective sutures is in the form of a flush abutment. A laterally directed ridge crosses the upper surface of each lateral process, in continuation of the sharp postero-dorsal edge of the paroccipital process. The anterior edge of the supraoccipital is slightly upturned and sharp.

Exoccipital

As a result of the slight downward displacement of the supraoccipital bone, the exoccipital of each side has been pushed a small degree backwards. On the right side the contacting faces of the supraoccipital and exoccipital have been exposed and are seen to be flat, buttressing surfaces of small extent. Below this suture the exoccipital is a narrow pillar, triangular in section, with a flattened lateral-facing surface. It is in contact with a posterior-facing facet

of the opisthotic until, about half-way down the bone, they separate to form the large jugular foramen. Below the foramen contact between the exoccipital and the opisthotic is regained briefly so that the jugular foramen is entirely surrounded by those two bones.

The ventral region of the exoccipital expands, particularly laterally, so that it forms a broad base resting upon the postero-lateral corner of the basioccipital. As described by Watson (1914), two hypoglossal foramina lie near the ventral edge of the internal (intracranial) surface of the bone, but no external opening can be discerned and thus this specimen must be assumed to differ from Watson's in that the hypoglossal foramina open directly into the jugular canal.

Basioccipital

The occipital condyle is formed exclusively from the basioccipital and it is incipiently double, consisting of two low convexities separated by a medial cleft which together form a kidney-shape. Three ridges surround the ventral surface of the condyle, a pair of lateral ones and an anterior, transverse one. From the two points where these ridges meet, a pair of arm-like processes, separated from one another by a deep cleft, run forwards and slightly downwards to meet the parasphenoidal tubera and indeed to participate in the construction of these tubera.

The side of the basioccipital is vertical and high and makes flush contacts with the exoccipital and the para-basisphenoid. A process of the opisthotic overlies it postero-dorsally. A sharp longitudinal ridge runs backwards across the lateral basioccipital surface from the level of the tubera and turns slightly dorsally just in front of the exoccipital, finally to be continued across the base of the latter bone right to the anterior margin of the jugular foramen.

The dorsal surface of the basioccipital is constricted posteriorly by the exoccipitals but further forwards it forms a broad floor to the braincase, slightly concave from side to side. A low median ridge is present.

Para-basisphenoid

Although the basisphenoid cannot be distinguished from the parasphenoid by suture, the surface texture seems to indicate which part is dermal bone and which endochondral.

The paired tubera formed by the parasphenoid together with the basioccipital are massive, narrow and are separated by a very deep cleft. From the tip of each tuber there runs forwards a rounded ridge which rapidly loses height until it merges with the swelling of the basipterygoid process. The basipterygoid process itself faces antero-laterally and fits into the deep socket in the pterygoid (as described by Parrington 1962) as an apparently kinetic joint. A very slender processus cultriformis arises medially between the basipterygoid processes and runs steeply upwards. Its ventral surface is convex from side to side and it narrows evenly to a sharp point.

The huge size of the tubera may be appreciated in lateral view. The posterior surface of each tuber is deeply hollowed out and, since the tuber expands laterally a little compared to the basioccipital, there are a pair of high, narrow concavities facing freely posteriorly and presumably being the sites of attachment of a pair of muscles. Above the level of the tubera, the parasphenoid runs postero-laterally as an otic process which reaches to the level of the fenestra ovalis, although it does not appear to have participated in the true margin of the fenestra as the rest of the margin is formed by unfinished bony lips which must have been covered by a cartilage layer in life. The parasphenoid has no such lip, and it is most probable that an unossified part of the basisphenoid lay immediately internal to the parasphenoid and formed the actual margin of the fenestra ovalis. The otic process of the parasphenoid is continued anteriorly as a broad, rounded ridge all the way to the basipterygoid process. The endochondral, basisphenoidal part of the complex rises as a delicate, less well-ossified vertical sheet of bone above this ridge. It forms the actual sidewall of the braincase and is in sutural contact with the anterior end of the prootic. However, between the prootic, the basisphenoid and the otic process of the

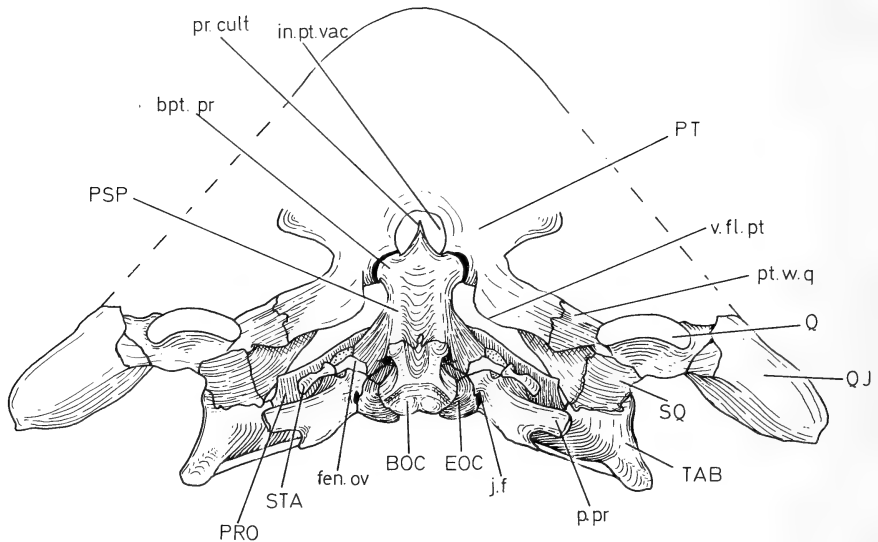


Fig. 2. *Procolophon trigoniceps* CUMZ T 1026.
Ventral view of the posterior part of the skull. $\times 1$.

parasphenoid, the sidewall of the braincase is unossified, leaving a fairly large aperture anterior to the fenestra ovalis. The side of the basisphenoid gradually merges anteriorly with more compact, well-ossified bone until by the level of the basipterygoid process the parasphenoid part of the complex has apparently completely taken over.

The dorsal surface of the basisphenoid has been exposed completely on the left side of the skull. The posterior part continues the braincase floor forwards from the basioccipital although these two bones are separated by a narrow unossified zone. The sides of the braincase too are formed from the basisphenoid, in continuity with the prootic. However, the sides converge and after a very short distance they turn medially to form the vertical dorsum sellae. This structure is thus composed exclusively of the basisphenoid bone. The sella turcica is a very large, deep pit, divided by a thin median septum in its

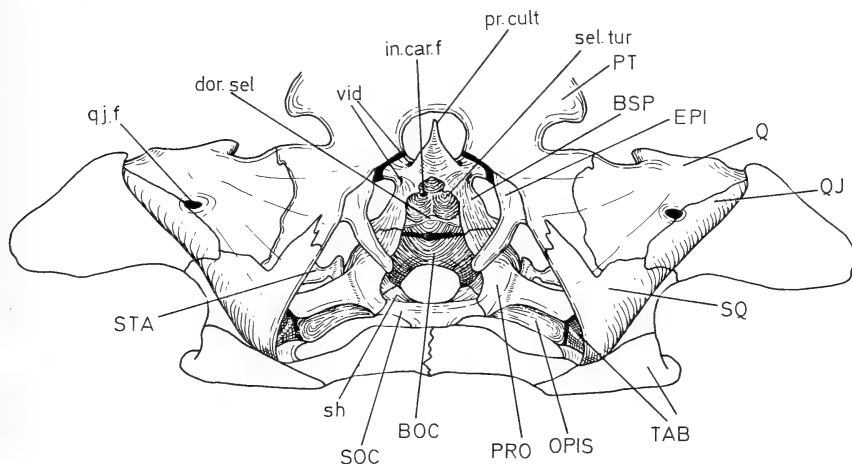


Fig. 3. *Procolophon trigoniceps* CUMZ T 1026.
Anterodorsal view of the posterior part of the skull. $\times 1$.

posterior part. The more anterior part of the sella lacks the septum and its floor slopes quite steeply upwards to end abruptly at the base of the processus cultriformis. A medially directed spur of the basisphenoid slightly constricts the anterior part of the sella on either side.

As Watson (1914) suspected, a vidian canal pierces the basiptyergoid process. The posterior foramen opens immediately behind and above the basiptyergoid process and the anterior foramen is to be found above the anterior part of the process. That these two foramina do indeed connect with one another is shown by a break on the right side through the canal itself. An internal carotid foramen emerges on the left side of the sella turcica in the region referred to as the anterior part. Whether or not there is a corresponding foramen on the right side is unknown since this side has not been prepared (for the sake of the strength of the specimen).

The dorsal surface of the basiptyergoid process is divided by a ridge into antero-dorsal and postero-dorsal faces. The ridge continues medially and antero-dorsally to form the lateral edge of the processus cultriformis. The upper surface of the processus itself is broadly concave from side to side.

Opisthotic

The sutures between the opisthotic and the other bones of the braincase are all clearly distinguishable. The medial end forms a long suture with the supraoccipital, behind which the opisthotic turns to form a posterior facing facet which is in contact with the exoccipital, as described. The massive paroccipital process is formed from both the opisthotic and the prootic. The opisthotic part runs horizontally and somewhat posteriorly and slightly ventrally, as a very well-developed process. The dorsal surface is deeply concave and it gradually widens laterally. It is marked off from the posterior surface by a high, narrow ridge which continues the line of a much less marked ridge on the supraoccipital. The posterior surface of the paroccipital process is smooth and bears a horizontal shelf along most of its ventral edge. The upper part of the distal end of the posterior surface is overlapped by a process of the tabular bone. The ventral surface of the paroccipital process is smoothly rounded and is continuous with the ventral surface of the shelf referred to above. The distal end of the process ends freely as an unfinished bone surface that presumably remained cartilage-covered in life. The only direct contact of the opisthotic in the region of the distal end of the paroccipital process is with the tabular bone, so far as can be ascertained in the slightly damaged case of this specimen, by means of the overlap of its posterior surface noted above.

The anterior surface of the paroccipital process is smoothly concave from top to bottom, forming as it does the posterior wall of the middle ear cavity. The upper part is in contact with the prootic over much of its length as described below. Ventral to the prootic, the opisthotic sends a process antero-medially which contacts the basal region of the exoccipital and the side of the basioccipital. The upper part of this process bears a lip of unfinished bone which makes the postero-ventral rim of the fenestra ovalis. The lower part contributes the posterior margin of the jugular foramen. Between the fenestra ovalis and the jugular foramen, the opisthotic process is strongly concave and carries a small foramen.

Prootic

The prootic meets the supraoccipital along a short suture at its postero-medial extreme. A second contact between these two bones occurs at a slightly more ventral level, because a horizontal shelf extends medially from the prootic into the brain cavity, about 1 mm below the dorsal edge of that bone. The shelf meets a similarly developed shelf arising from the antero-lateral face of the supraoccipital. It seems likely that the shelf marks the area of contact of the persistently cartilaginous taenia marginalis of the chondrocranium, as implied by Price (1935) for a similar structure in *Captorhinus*.

A slight ridge marks the medial part of the prootic, which forms the braincase wall, from the paroccipital process of the prootic, which extends laterally in contact with the opisthotic. The inner part of the prootic is in the same plane as the adjacent opisthotic, but laterally it twists to form a horizontal shelf in

contact with the dorsal edge of the more or less vertical opisthotic. Thus the prootic constitutes a definite roof over the middle ear cavity, extending as far laterally as does the opisthotic which forms the hind wall of the cavity. The distal part of the prootic actually contacts the quadrate ramus of the pterygoid although no suture seems to form.

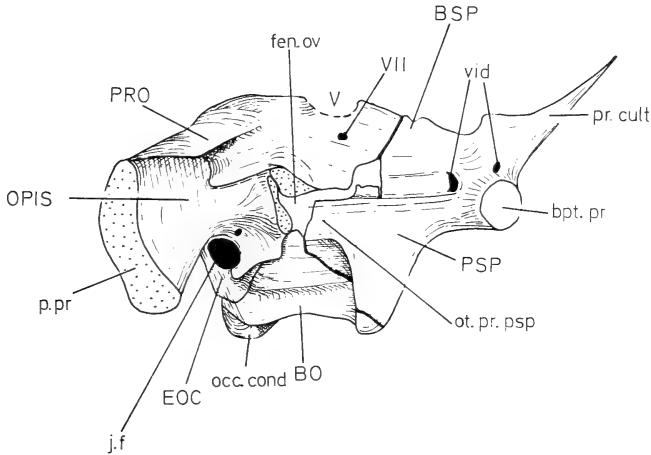


Fig. 4. *Procolophon trigoniceps* CUMZ T 1026.

Right lateral view of the braincase, with certain details added from the left side. $\times 2$.

In front of the paroccipital process, the prootic expands to form a broad, thin sheet making the sidewall of the braincase. A lip of unfinished bone on the ventral edge constitutes the dorsal margin of the fenestra ovalis, while half-way up the bone is a foramen which presumably transmitted the facial nerve (VII). The dorsal edge of the prootic of both sides has been slightly damaged and obscured by the epipterygoid collapsing across it. It appears to bear a notch of some sort exactly where the epipterygoid lies, and if this is true, then it would be reasonable to suppose that such a notch marks the region of exit from the cranial cavity of the trigeminal nerve (V).

The internal surface of the prootic could not be widely exposed in this specimen. The anterior part is certainly well ossified but posteriorly, at the level of the paroccipital process, ossification seems to have been absent, in relation to the formation of the inner ear structures.

Stapes

The left stapes is perfectly preserved and is at least approximately in its correct position with the proximal end adjacent to the fenestra ovalis. It is surprisingly small, about 6 mm in length. The proximal end is swollen and roughly triangular in end-on view, and it narrows rapidly but smoothly into the very slender shaft. The distal end is expanded asymmetrically into a broad

but very thin plate. The ventral surface (as oriented in the specimen) is slightly convex from anterior to posterior edges and the posterior edge continues the line of the shaft of the bone. Apart from the proximal surface, the whole bone is formed from well-ossified, finished bone and does not appear to have suffered any damage. Neither stapedial foramen nor dorsal process is present.

Quadrate

The narrow, kidney-shaped articulating surface of the quadrate condyle is oriented transversely with the convex edge at the front. It faces very slightly forwards and is gently concave from side to side. Above the condyle the medial part of the quadrate expands to form a very extensive but thin pterygoid wing, which is plastered on to the anterior surface of the quadrate ramus of the pterygoid and also contacts both the squamosal and the quadratojugal bones. In posterior aspect the pterygoid wing of the quadrate is hidden by the underlying pterygoid meeting a large ventral extension of the squamosal, the latter itself also a thin sheet of bone in contact with the back of the quadrate. Only the ventral part of the quadrate is visible and is seen to form a suture with the lateral end of the ventral flange of the pterygoid (described below). There is no distinct boss on the quadrate in this region of this particular specimen, unlike the case of the specimen described by Parrington (1962).

Lateral to the condyles the quadrate has the form of a thick, stout process which buttresses powerfully against the quadratojugal, the latter bone extending a little way medially behind the quadrate to further strengthen this contact. The quadratojugal foramen lies in the suture between the quadrate and the quadratojugal above the middle of the condyle. In posterior view the foramen is actually bounded medially by the ventral process of the squamosal.

Pterygoid

The deep sockets for reception of the basipterygoid processes appear to face postero-medially and to have the form of more or less hemispherical cups, as described by Parrington (1962). Immediately behind and lateral to them, the quadrate rami of the pterygoids arise as broad, thin sheets of bone. Each one is extensively overlain by the quadrate as described, and also by a long spur of the squamosal lying along the dorsal region. The postero-ventral surface of the pterygoid is, however, more or less completely exposed. It carries a well-developed crest along its antero-lateral margin which is horizontal at its front end but gradually twists until it is approaching a vertical plane by the time it sutures with the quadrate.

Epipterygoid

The epipterygoids of both sides are present but have been distorted so that they apparently lie more horizontally than in life. The base of each one is a thin, broad sheet of bone plastered against the lateral face of the pterygoid. The ascending process is narrow and typically reptilian.

Quadratojugal

The extraordinary postero-lateral extension of the quadratojugal of *Procolophon* is of course well known. The medial connections of the bone are with the quadrate as described and also with the ventral process of the squamosal behind the quadrate. The posterior face is sculptured in a manner suggestive of superficial dermal bone and not at all in keeping with attachment of muscles or other soft parts.

Squamosal

The small component of the squamosal that lay on the skull roof has weathered away but two internal processes remain. An anterior process overlies the dorsal edge of the quadrate ramus of the pterygoid, and a ventral process, in the form of a flat sheet, runs down over the back of the quadrate as described earlier by both Watson (1914) and Parrington (1962). It is in contact with the medial edge of the quadratojugal for most of its height. From the dorso-medial part of the squamosal where the two processes meet, the bone turns medially and runs along the anterior face of the occiput, presumably to the parietal. This part is completely covered behind by the tabular.

Tabular

Again, most of the dorsal part of this bone has been lost by weathering. Anteriorly the tabular forms a strong buttressing suture with the squamosal, a connection which would have been obscured had the skull roof been present. From here the tabular curves ventrally becoming thinner, and medially it covers the dorso-lateral part of the paroccipital process. The lateral part is produced as the triangular tabular 'horn', which bears a distinct groove on its ventral surface. The groove runs from the distalmost tip of the bone along its posterior edge, in an antero-medial direction, to disappear at the level of the ventral occipital process of the tabular.

DISCUSSION

As members of the cotylosaur reptiles, the procolophons are involved in the debate about the interrelationships of early tetrapods, despite their relatively late occurrence, and in this context the most important regions of the skull are the middle ear, the braincase (particularly the otic region) and the pattern of bones in the temporal region (see Panchen 1972 for a recent review). Since the latter part of the skull of procolophons is so specialized while the former two parts have hitherto remained poorly known, it is not surprising that the phylogenetic position of this group is still unclear. Olson (1965) succinctly indicated the general possibilities as twofold. In the first place it is possible that the procolophonids, with or without their putative relations the pareiasaurs, arose directly from the seymouriamorph amphibian complex independently of the captorhinomorphs. This opinion has been held tentatively by Parrington

(1962) on the basis of the temporal bones, and by Daly (1969). In the second place, the procolophons may be a very early divergence from primitive but recognizably captorhinomorph reptiles, a view associated with Romer (1968) and, less confidently, Carroll & Gaskill (1971).

We may now consider what bearing the present study has upon this problem.

Middle ear

The position of the fenestra ovalis is typically reptilian and there is no development of a tube-like extension of the parasphenoid and otic bones carrying the fenestra laterally as in seymouriamorphs (White 1939). The lateral expansion of the parasphenoid at the level of the middle ears is in fact no more extensive than in *Captorhinus* (Price 1935) or *Sphenodon* for example.

The position of the tympanic membrane, always assuming it was present, is problematical. Since the time of Watson (1914) stress has been laid on the otic notch of *Procolophon* and its allies, by which was meant the posterior margin of the quadrate along with the corresponding concavity in the superficial dermal bones. In fact the situation is less simple because in the procolophonids secondary extension of the tabular and the quadratojugal has resulted in a large semicircular notch in the posterior margin of the skull roof, which has a marked but superficial similarity to the otic notch of the labyrinthodonts. This secondary, dermal notch does not reflect at all closely the form of the underlying primary otic notch. While Romer (1956, 1968) uses the term 'otic notch' for the primary notch, Colbert (1946) and Parrington (1962), among others, use the term for the secondary notch, and the implication is that these two usages of 'otic notch' refer to two different possible positions for the tympanic membrane.

There are good reasons for doubting that the tympanum lay within the secondary, dermal notch. Particularly, the stapes of the present specimen lies approximately in its natural position with its swollen footplate more or less in contact with the fenestra ovalis, yet its undamaged distal end lies a relatively huge distance from the dermal notch (Figure 2; Plate 1). In order to reach the notch, a cartilaginous extrastapes some 15 mm in length would have been necessary. This represents 250% of the length of the stapes and seems most unlikely on mechanical grounds, and there is no modern reptile known which has such an arrangement (Baird 1970).

The actual edges of the dermal notch give no indication that they supported any part of a tympanic membrane. The edges of the tabular and the squamosal are smoothly rounded, while that of the quadratojugal is sculptured in the manner of the rest of the superficial dermal bones, which does not suggest the presence of soft tissues. It would seem therefore that the tympanum did not lie within this dermal notch, although it remains possible that the notch marks the outer opening of an external auditory meatus which led internally to the ear drum.

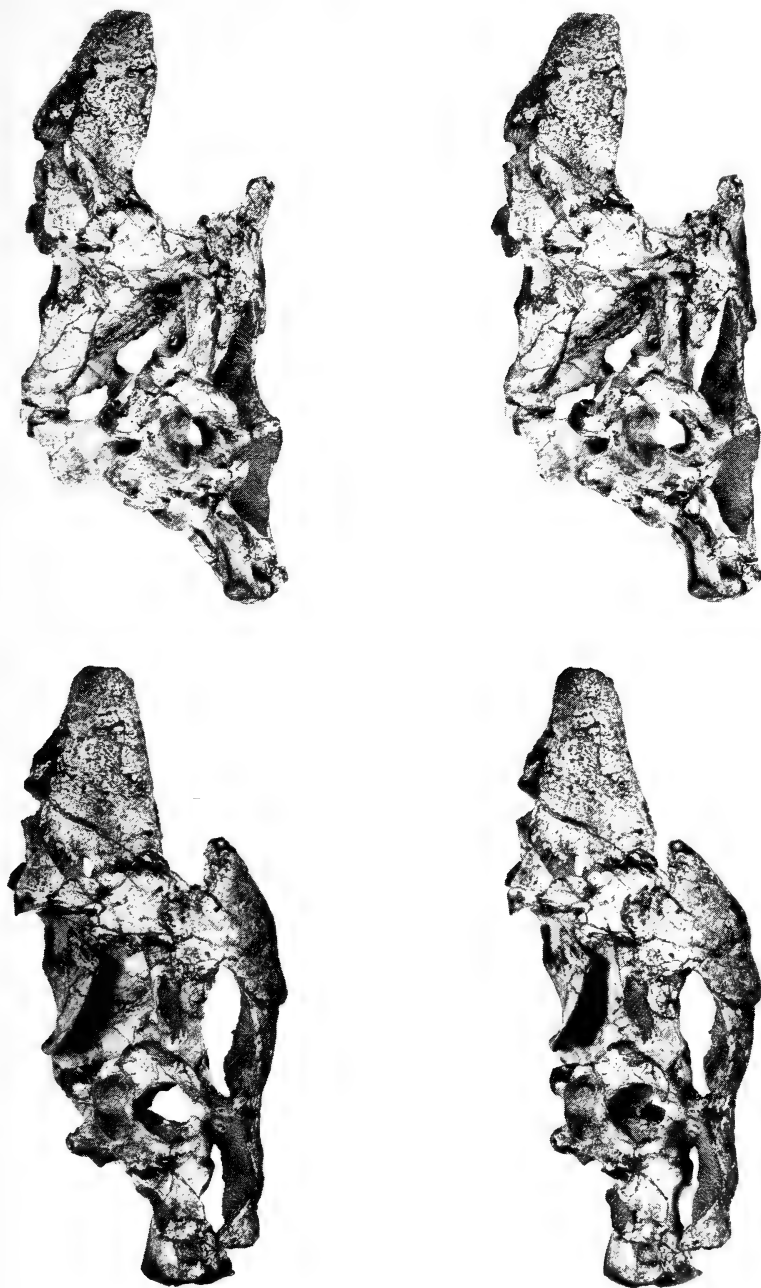


PLATE 1. *Procolophon trigoniceps* CUMZ T 1026.

Stereophotographs of the skull, natural size. Above, ventral and slightly posterior view; below, occipital view. (Photographs by Mr William Lee.)

If the stapes is to be taken as a guide, the tympanum must have been somewhere around the distal end of the paroccipital process, which in turn is posterior to the medial part of the quadrate. There are no markings on the bones of this region so the precise position can only be guessed, but in any case this represents a generally reptilian, post-quadrate position.

The stapes itself is specialized from the presumed primitive condition by the absence of both stapedia foramen and dorsal process. Regarding the latter, it is possible that the expanded distal end of the bone represents a broad dorsal process, although there are no serious indications of this. It is difficult to see how such a process could have contacted the paroccipital process, for example. The generally small size, delicacy and abrupt expansion of its footplate all give the stapes a rather 'sauropsid' appearance (Olson 1966; Baird 1970).

The tympanic cavity too, as far as can be judged from its osteological features, has the arrangement of a 'sauropsid' reptile like *Sphenodon* or the lizards. The manner in which the prootic contributes to the roofing of the cavity at the level of the top edge of the paroccipital process, and the extensive anterior limit formed by the quadrate ramus of the pterygoid, support such a comparison, which can be extended, too, to *Captorhinus*.

Thus the evidence of the middle ear structure points towards a true reptilian affinity of *Procolophon*, rather than to a particular relationship with the seymouriamorphs, despite certain difficulties in the form of the stapes and the absence of a clear-cut indication of the position of the tympanum. In fact, it would not be surprising for loss of the tympanum to have occurred, a common phenomenon amongst modern squamates (Baird 1970).

Braincase

The form and relations of the paroccipital process are often used to distinguish between labyrinthodonts (including seymouriamorphs) and reptiles. In the labyrinthodonts the paroccipital process runs dorso-laterally and contacts the tabular bone at its distal end, thus forming a brace between the skull roof and the basis cranii. The supraoccipital is usually unossified. In contrast, the reptilian paroccipital process typically runs laterally to contact the suspensorial (squamosal-quadrate) region of the skull, bracing of the roof to the basis cranii involving a well-ossified supraoccipital bone.

In the case of *Procolophon*, the paroccipital process has a perfectly reptilian form and it extends laterally towards the suspensorial region; and a well-developed supraoccipital bone, closely similar to that of *Sphenodon* for example, is present. The difficulty is that the distal end of the paroccipital process is in contact with the tabular bone, and fails to reach the squamosal or quadrate, and thus the technical reptilian requirement is not met. However, the temporal region of the *Procolophon* skull is extremely modified from the primitive tetrapod condition, and in particular the quadrate bone is much further forwards, the squamosal reduced and the tabular (if indeed this bone is correctly homologized)

greatly enlarged and extended on to the occipital surface. It is not safe therefore to assume that the failure of the paroccipital process to contact the squamosal and/or the quadrate is anything more than a further manifestation of the extensive remodelling of this part of the skull.

The processus cultriformis of the parasphenoid of *Procolophon* is very much reduced compared to that of *Seymouria* (White 1939) or *Kotlassia* (Bystrow 1944), a feature in which it resembles all typical reptiles.

Like the middle ear, the structure of the braincase is essentially reptilian but shows certain peculiarities, in this case the relation of the distal end of the paroccipital process to the rest of the skull.

Primitive procolophons

The strongest arguments for relating procolophons directly to seymouriamorphs are based on certain forms which combine some of the procolophonid

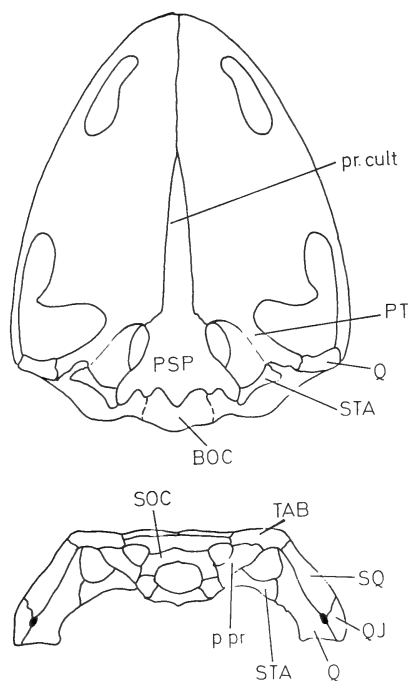


Fig. 5. *Nyctiphruetus acudens*.

Skull in ventral and occipital views to show braincase and stapes. Natural size.

(Redrawn from Efremov 1940.)

specializations with seymouriamorph characters. The most important is *Nyctiphruetus* (Fig. 5) from the Upper Permian of Russia (Efremov 1940) which shows shortening of the jaw length, reduction of the skull table coupled with loss

of the supratemporal, relatively huge orbits and an enlarged pineal foramen. These *Procolophon*-like characters are however associated with a seymouriamorph-like braincase in which the paroccipital processes extend dorso-laterally to make firm contact with the tabulars at the postero-lateral corners of the skull. The tabulars do not extend down the occipital surface. Also like the seymouriamorphs, the processus cultriformis is unreduced. On the other hand, the middle ear is peculiar for there is no otic notch in the rear margin of the skull roof and the stapes runs ventro-laterally from the fenestra ovalis to a firm contact with the quadrate, and thus this part of the skull resembles neither *Procolophon* nor the seymouriamorphs. Clearly convergence has occurred. If *Nyctiphruretus* does link *Procolophon* directly to the seymouriamorphs, then *Procolophon* has achieved a reptile-like braincase and ear independently of captorhinomorphs. If *Nyctiphruretus* and *Procolophon* are related and are descended from true reptiles, then the braincase of *Nyctiphruretus* has converged upon the structure of the seymouriamorph braincase. And if *Procolophon* is a captorhinomorph derivative, while *Nyctiphruretus* is a seymouriamorph, then the similarities between these two genera have arisen independently, presumably in relation to the adoption of a similar mechanical jaw function. As long as it is held that braincase and middle ear structure are the best guides to lower tetrapod phylogeny, the latter hypothesis will remain the most attractive.

None of the other supposed primitive procolophons help in this problem. *Nycteroleter*, also from the Russian Upper Permian (Efremov 1940), is even more seymouriamorph-like with its dorsal otic notch. The Upper Permian form *Owenetta*, from South Africa (Broom 1939), has a skull roof which appears to be ideally primitive procolophonid but unfortunately nothing is yet known about the details of its braincase.

The recent description of a Lower Permian tetrapod *Acleistorhinus* by Daly (1969) as a primitive procolophon has been doubted by Carroll & Gaskill (1971) and receives no support from the present work. The extraordinary structure of the braincase and stapes of *Acleistorhinus* only serve to highlight the unremarkably reptilian-like form of the corresponding structures in *Procolophon*.

SUMMARY

A detailed, bone by bone description of the braincase, stapes, pterygo-quadrate and parts of the quadratojugal, squamosal and tabular of a large specimen of *Procolophon trigoniceps* is given.

The middle ear, paroccipital process and processus cultriformis are all basically reptilian in form, and point towards a captorhinomorph ancestry of procolophons, rather than their direct derivation from seymouriamorphs.

Nyctiphruretus is problematical and may resemble the procolophonids by convergence, being itself a seymouriamorph.

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ABBREVIATIONS

BOC—basioccipital
 bpt.pr—basipterygoid process
 BSP—basisphenoid
 cond—condyle
 dor. sel—dorsum sellae
 EOC—exoccipital
 EPI—epipterygoid
 fen. ov—fenestra ovalis
 in. car. f—internal carotid foramen
 in. pt. vac—interpterygoid vacuity
 j.f—jugular foramen

occ. cond—occipital condyle
 OPIS—opisthotic
 ot. pr. psp—otic process of the parasphenoid
 p. pr—paroccipital process
 pr. cult—processus cultriformis
 P—parietal
 PRO—prootic
 PSP—parasphenoid
 PT—pterygoid
 p.t.f—post-temporal fenestra
 pt. w. q—pterygoid wing of the quadrate

Q—quadrate
QJ—quadratojugal
qj. f—quadratojugal foramen
q. ra. pt—quadrate ramus of the pterygoid
sel. tur—sella turcica
sh—shelf for cartilaginous taenia marginalis
SOC—supraoccipital

SQ—squamosal
STA—stapes
TAB—tabular
V—notch for the trigeminal nerve
vid—opening of the vidian canal
v. fl. pt—ventral flange of the pterygoid
VII—foramen for the facial nerve

ON THE SOURCE OF THERAPSIDS

By

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(With 2 plates, 5 figures and 1 table)

CONTENTS

	PAGE
Introduction	27
A North American gorgonopsian	28
Chronofaunas in the mid-continental United States	37
Significance of North American therapsids	
The Chickasha gorgonopsian	41
The San Angelo therapsids	42
Interpretation and summary	43
References	45

INTRODUCTION

The very fragmentary evidence of therapsids in North America during the Permian has provided interesting but uncertain information concerning the geographic distribution of this order and the times of origin of different evolutionary lines. Many questions were raised in a general report (Olson 1962), but few of them have been touched on more than lightly since that time. They were summarized as far as possible in my recent book (Olson 1971: 641-655). Some aspects of the problems have been treated by Chudinov, in particular in Sigogneau & Chudinov (1972).

Discovery of vertebrates in the Chickasha Formation, Guadalupian of Oklahoma (Olson 1965), has added information. A better understanding of the vertebrates of the Cutler and Abo Formations, Wolfcampian of northern New Mexico and south-western Colorado, through the work of Vaughn (1966, 1969a, b) and Lewis & Vaughn (1965) has given new insights into the significance of this faunal complex. Together these studies have produced substantial evidence of faunal assemblages which evolved largely independently of those of south-western New Mexico, Texas, and Oklahoma. The latter have been grouped into what has been termed the Permo-Carboniferous Chronofauna; the former assemblages have been termed the Caseid Chronofauna (Olson 1971: 839, fig. 145E). Only recently has it been determined that the Caseid Chronofauna has any relationship to the origin of therapsids.

Study of a new specimen found during the summer of 1972 in the Chickasha Formation revealed that it is not, as informally reported at the time of discovery, a somewhat therapsid-like sphenacodontine, but rather that it is a very primitive gorgonopsian. The implications of this find are, of course, manifold and form an important part of the substance of this paper. Following a descrip-

tion of the new animal, they are considered in relationship to the broader problem of the source of therapsids.

The figures in this paper were drawn by Mrs Kathryn Bezy and the photographs were taken by Mr Rick Lassen. The study was supported by a National Science Foundation Grant, GB 31283X.

A NORTH AMERICAN GORGONOPSIDIAN

Class **REPTILIA**
 Subclass **SYNAPSIDA**
 Order **THERAPSIDA**
 Suborder **GORGONOPSIA**
 Family **Gorgonopsidae**
Watongia gen. nov.

Diagnosis: A very primitive, sphenacodont-like gorgonopsian reptile. Estimated body length 1,22 to 1,52 metres. Skull with large preparietal bone. Ten to 12 simple, recurved, conical cheekteeth, diminishing in crown height from anterior to posterior; a large, anterior, canine-like tooth.

Vertebrae with centra relatively short (see measurements, Table 1), deeply amphicoelous and sharply keeled. Neural arch with a deep pit on either side above the diapophysis. Neural spine slender, height about equal to $\frac{1}{2}$

TABLE 1

Measurements of *Watongia meieri* gen. et sp. nov. in millimetres.

VERTEBRAE	1	2	3	4
Length, centrum, basal	21	20	—	—
Total height, anterior	85	—	—	—
Height neural spine, anterior	43	—	—	—
Width posterior zygapophyses	26	27	—	—
Length diapophysis, dorsal	—	12	12	14
LIMB BONES	L	PW	DW	WS
Humerus	125	65	—	16*
Radius	89	18	19	10**
Ulna	116***	33	30	17

Abbreviations: L, maximum length; PW, maximum proximal width;

DW, maximum distal width; WS, minimum shaft width. *—with ventral surface dorsal; **—anterior view;

***—including olecranon process.

of total vertebral height. Diapophysis short, stocky and with heart-shaped articular surface. Posterior cervical and anterior dorsal ribs with tuberculum somewhat reduced and not fully separated from capitulum.

Scapula moderately high and narrow; cleithrum present but very slender. Humerus lightly structured with well-defined shaft and angle between two 'blades' of about 60 degrees. Carpus with very large, pisiform element; distal

5 present and not fused with distal 4. Phalangeal formula 2?453, with distal phalanges rather short and unguals strongly claw-shaped.

The name is after the town of Watonga, Blaine County, Oklahoma.

Watongia meieri sp. nov.

Holotype: UCLA VP 3132. Part of the frontal-parietal region of the skull, including the dorsal part of the orbital margin and fragments of the maxilla with teeth in place. Three anterior dorsal vertebra with fragments of others. Left scapula and part of right; left clavicle; part of left cleithrum; and part of interclavicle. Several ribs and numerous gastralia. Right and left fore limbs with carpus and partial complement of phalanges.

Horizon and locality: Chickasha Formation, level of middle part of Flowerpot Formation, El Reno Group, Guadalupian, Upper Permian. From fossil site BC 7 (Olson 1965), NW. $\frac{1}{4}$, NE. $\frac{1}{4}$, Sec. 33, T. 18 N., R. 11 E., Blaine County, Oklahoma. The species name is given for Mr Meier of Hitchcock, Oklahoma, on whose land the specimen was found.

Description: The specimen was found somewhat scattered in red, sandy shale. It lay near the base of a gently dipping deposit formed in a stream channel. Only the anterior part was found; the skull had weathered out and much of it had disintegrated and disappeared. At about the same level in this site have been found specimens of *Rothianiscus* and *Cotylorhynchus*.

1. *Skull*: Figure 1B, Plate IA, B. Part of the skull roof and fragments of the maxilla are all that have been preserved. The most significant feature is the presence of a large preparietal bone in the skull roof. There were about 12 teeth in the postcanine series. The exact number is uncertain for some of the fragments cannot be certainly placed in the series. The teeth appear to have decreased regularly in crown height from anterior to posterior. A single 'canine' is present. Its height is estimated as 20 to 25 mm, somewhat more than twice the height of the longest postcanine. Skull length is estimated to have been about 24 to 26 cm on the assumption that proportions were more or less those of *Dimetrodon*.

2. *Vertebrae*: Figure 2A, B, Plate IID. Three anterior dorsal vertebrae and fragments of others have been recovered. Many of the features are those found in sphenacodonts. Neural spines, however, are not elongated or heavy as in sphenacodontines. Centra are strongly keeled, deeply amphicoelous and not elongated. Measurements in Table 1 show the major dimensions. Transverse processes are relatively short and thick and terminate in stout, heart-shaped articular surfaces. Above the diapophysis on each side, as in sphenacodontines, the neural arch has a deep pit on its lateral surfaces. A small intercentrum is present on the anterior margin of one of the vertebrae.

3. *Ribs*: Figures 1 EF, 2D; Plate IIE. The ribs are slender and gently curved. Comparisons of the shapes of the heads with those of sphenacodonts and gorgonopsians are shown in Figure 2D. The structure of the head is some-

what more like that in gorgonopsians, with the tuberculum reduced and the bifid character much less well expressed than in sphenacodonts. Tooth-pick shaped gastralria were found scattered throughout the deposit in the vicinity of the specimen, Plate IIA, B.

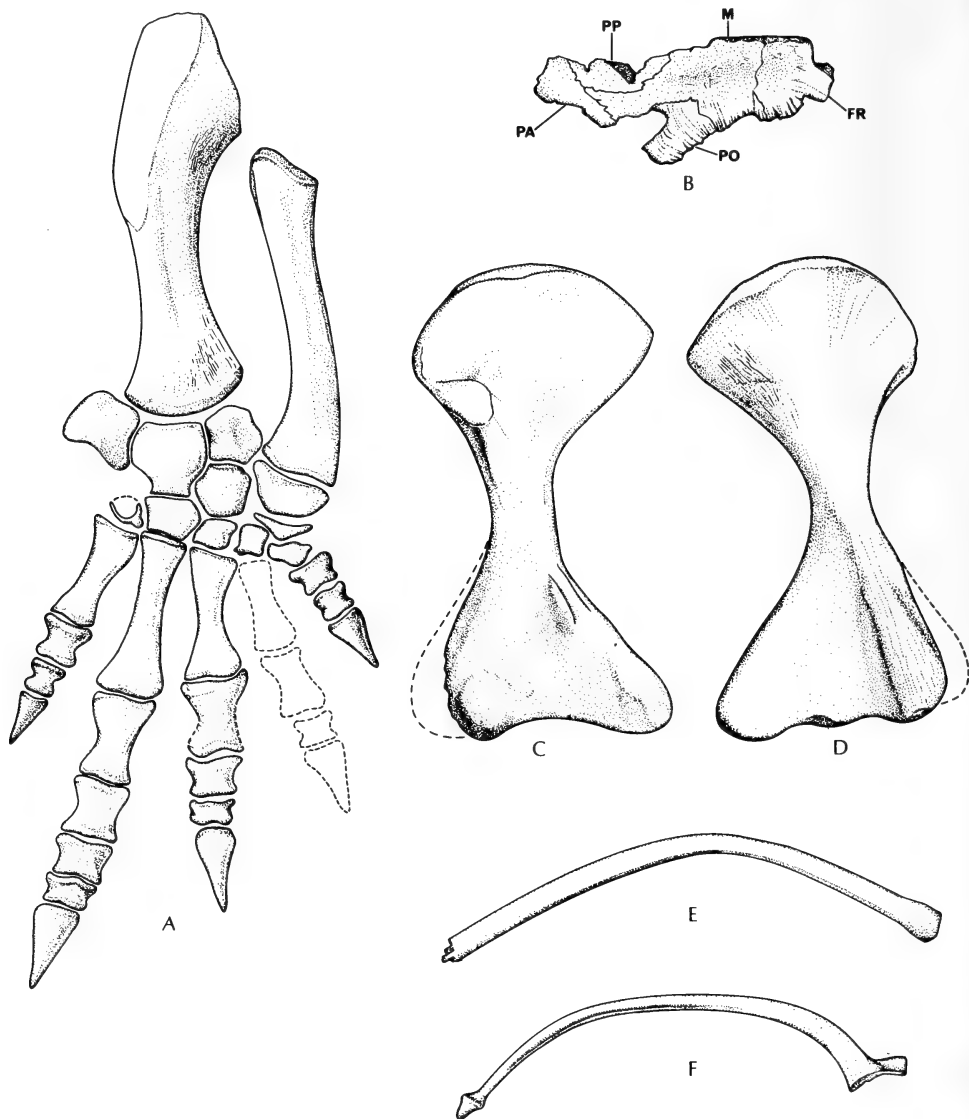
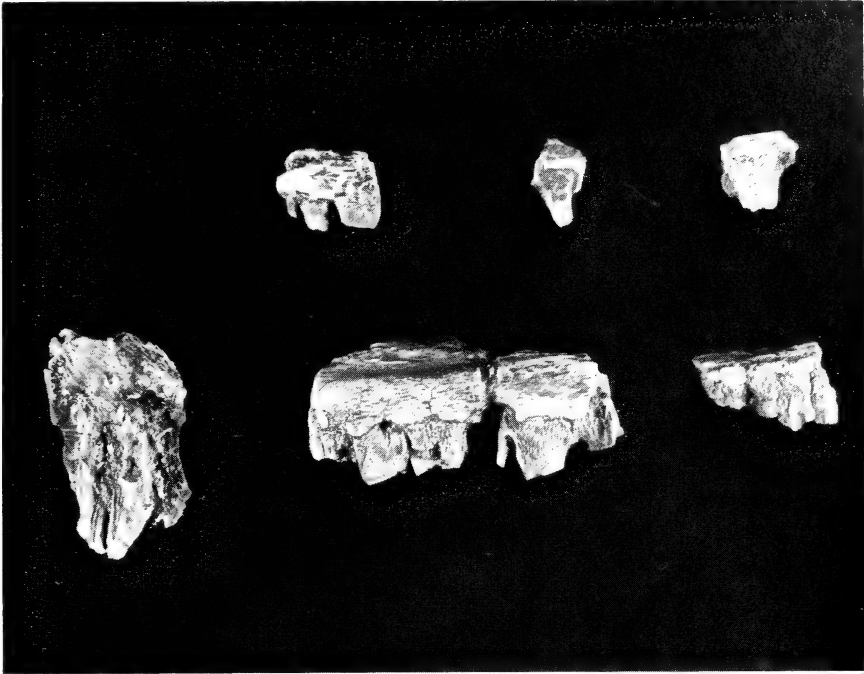


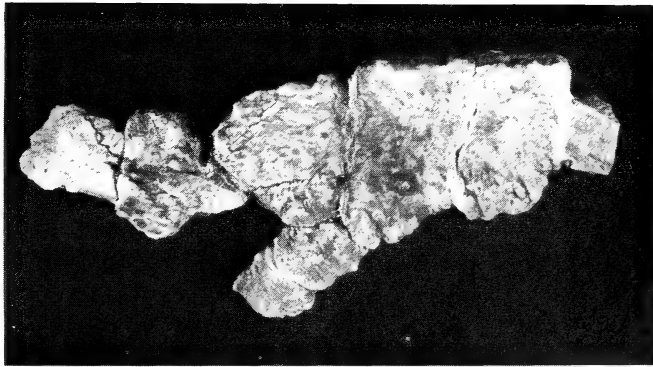
Fig. 1. *Watongia meieri* gen. et sp. nov.

A. Reconstruction of the left lower limb, based on data from both right and left. B. Skull fragment, showing midline, orbital margin and preparietal element. C. Right humerus, dorsal. D. Right humerus, ventral. E. Dorsal rib, head missing. F. Anterior dorsal rib. Abbreviations: FR, frontal; M, midline; PA, parietal; PO, post-orbital; PP preparietal. All $\times \frac{1}{2}$.

4. *Shoulder girdle*: Figure 3A, B. A somewhat broken left scapula, part of the right scapula, a partial left clavicle, a cleithrum and part of the interclavicle provide the information on this part of the skeleton. The scapula is



A



B

PLATE I. *Watongia meieri* gen. et sp. nov.

A. Fragments of jaws and teeth in medial aspect. Lower set roughly in order in jaw. B. A fragment of the dorsal platform of the skull showing the preparietal bone. See Fig 1B for identification of elements. Midline of skull to top of page and anterior to the right. Both $\times 1$.

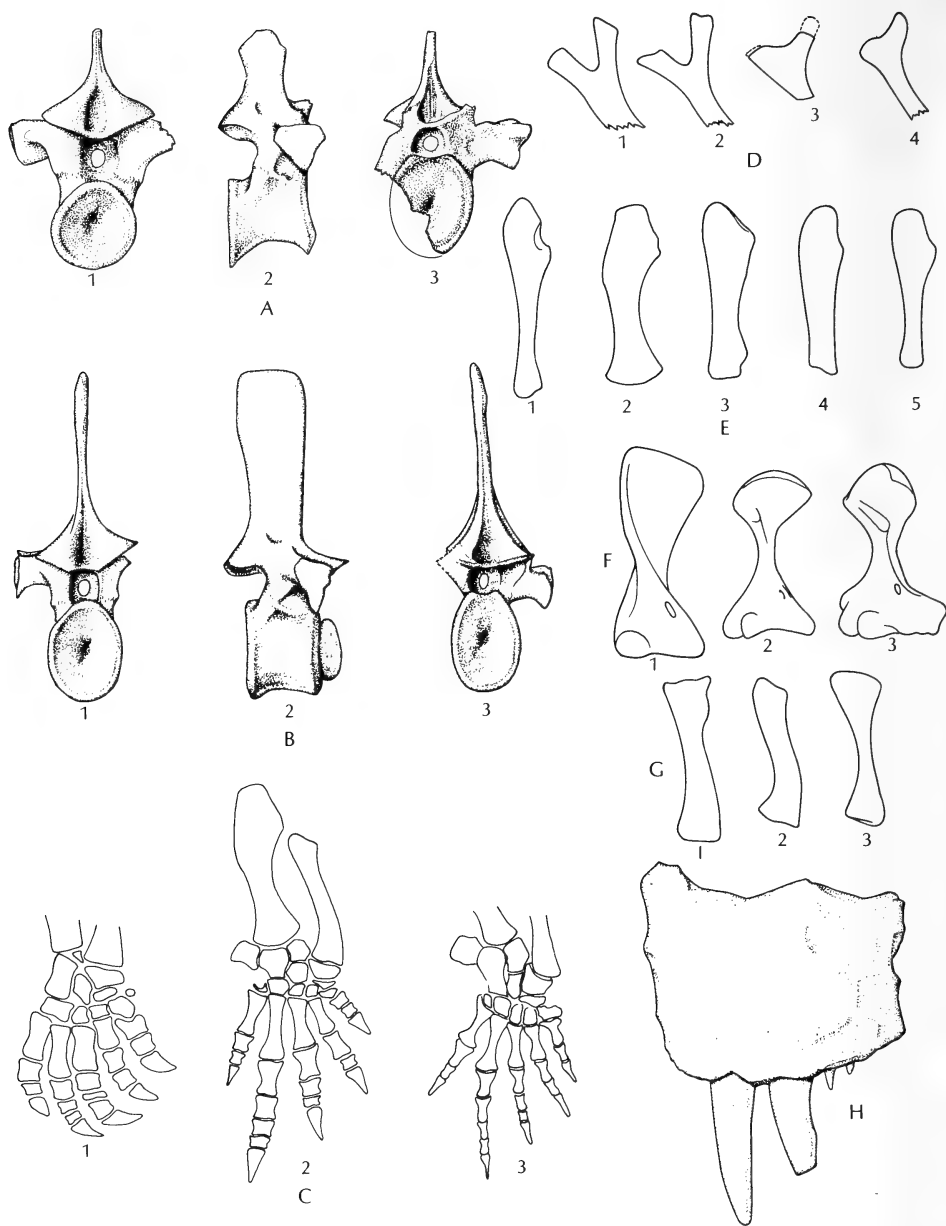


Fig. 2.

A. Anterior dorsal vertebra of *Watongia meieri* gen. et sp. nov.: 1. posterior, 2. lateral, 3. anterior. B. Anterior dorsal vertebra of *Watongia meieri* gen. et sp. nov.: 1. posterior, 2. lateral, 3. anterior. C. Manus: 1. *Aelurognathus* (Boonstra 1934), 2. *Watongia*, 3. *Dimetrodon* (Romer 1956). D. Heads of anterior dorsal ribs: 1. *Ctenospondylus*, 2. *Dimetrodon*, 3. *Watongia*, 4. gorgonopsian. E. Ulna: 1. *Dimetrodon* (Romer 1956), 2. *Watongia*, 3. *Gorgonops* (Broili & Schroeder 1935), 4. *Aelurognathus* (Boonstra 1934), 5. *Lycaenops* (Colbert 1948). F. Humerus: 1. gorgonopsian, 2. *Watongia*, 3. *Dimetrodon* (Romer 1956). G. Radius: 1. *Dimetrodon* (Romer 1956), 2. *Watongia*, 3. *Aelurognathus* (Boonstra 1934). H. *Knoxosaurus* (Olson 1962). A and B $\times \frac{1}{2}$.

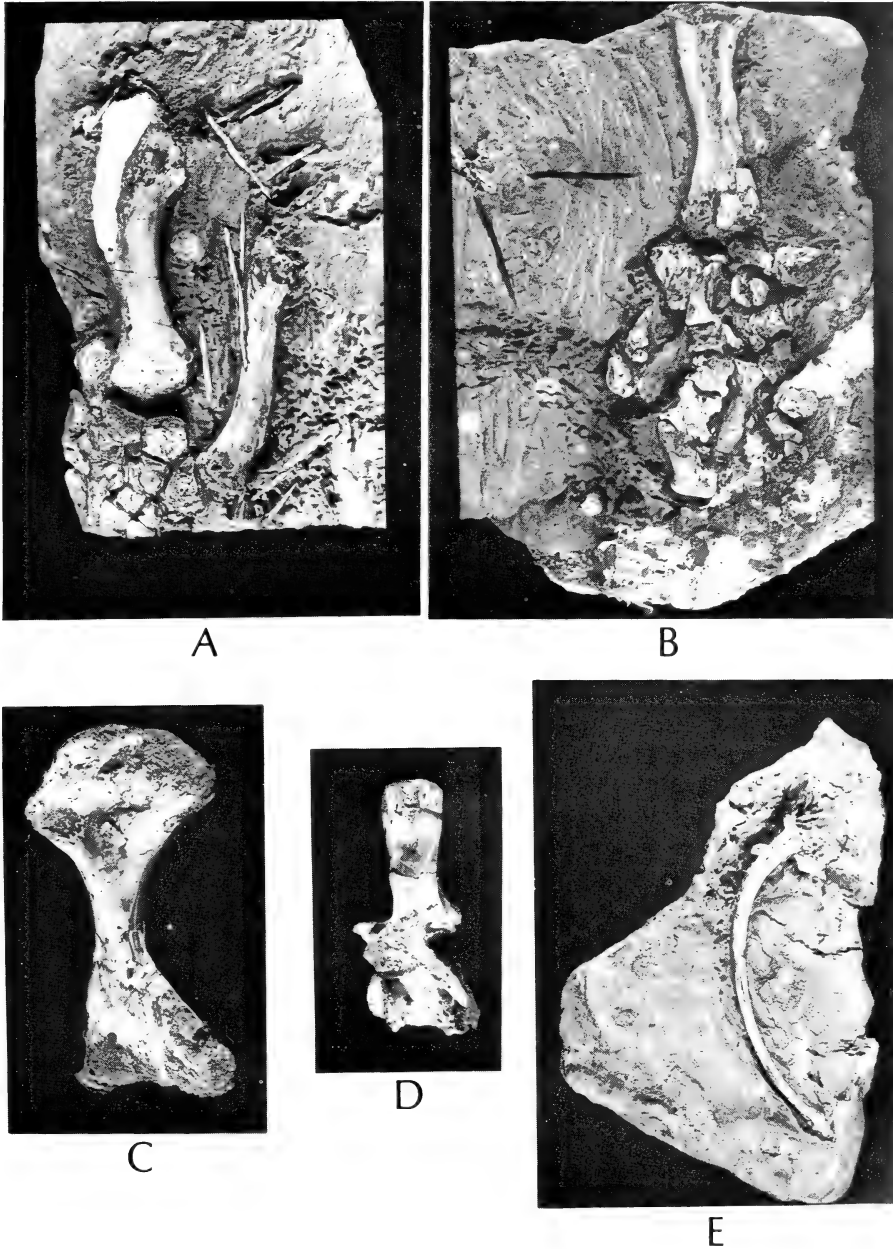


PLATE II. *Watongia meieri* gen. et sp. nov.

A. Right lower limb and carpus. Reconstructed part of ulna in white based on impression in the enclosing matrix. B. Left fore limb including carpus and manus. Under side of limb with digits flexed. Radius absent. C. Right humerus in ventral aspect. D. Anterior dorsal vertebra, from left side. E. Anterior cervical rib. All $\times \frac{3}{8}$.

high, rather narrow, and the cleithrum is small. The most distinctive feature of the scapula is a strong rugosity on the inner surface adjacent to the area of attachment of dorsal part of the clavicle. This extends inward over about $\frac{1}{3}$ of

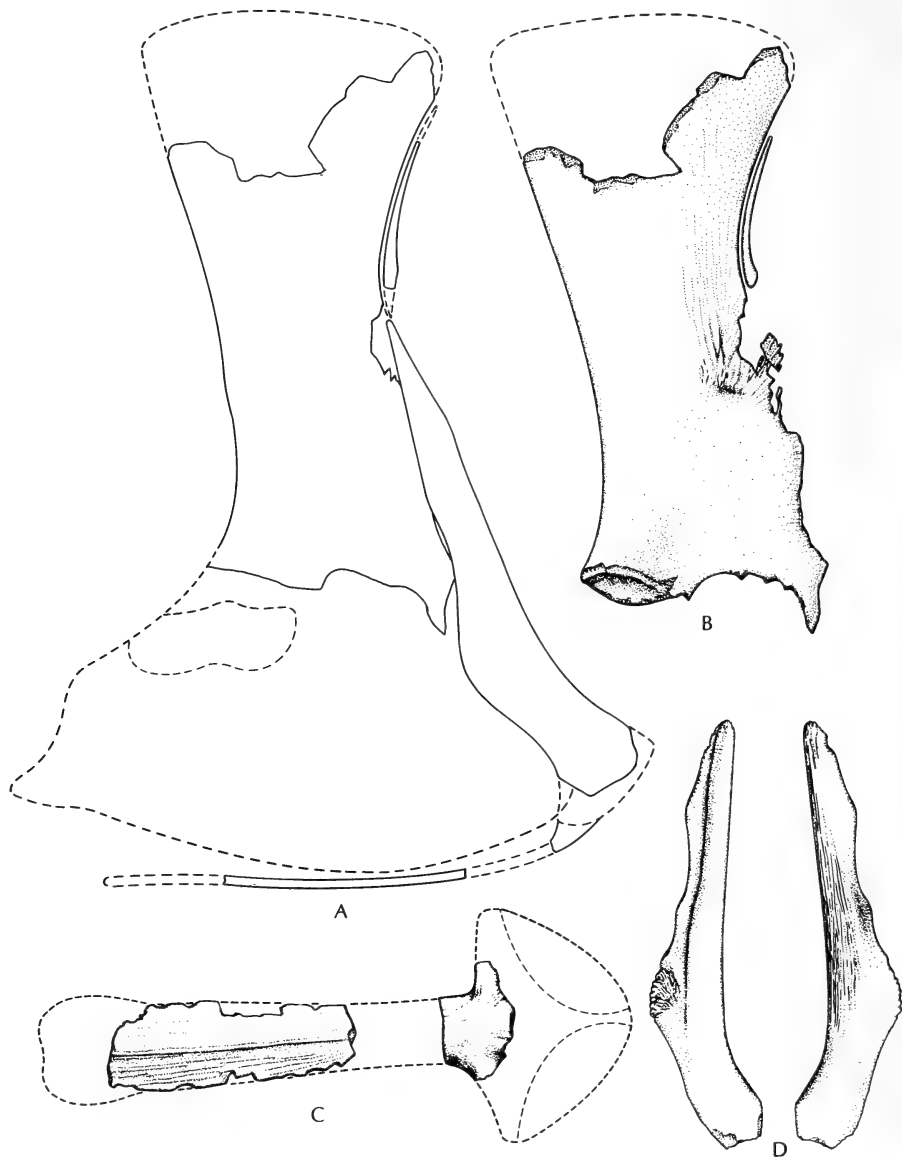


Fig. 3. *Watongia meieri* gen. et sp. nov.

A. Reconstruction of right shoulder girdle. B. Left scapula and part of cleithrum, inner side. C. Interclavicle, preserved parts and suggested relationships in reconstruction. D. Clavicle, left inner and outer aspects. All $\times \frac{1}{2}$.

the scapular blade and carries dorsally in a slightly depressed area marked by vertical striae. Apparently this represents an area of insertion of ligaments from the clavicle, although the area seems excessively extensive for such ligaments. It is possible that it marks the insertion of tendons of a large, levator scapulae which invaded the inner surface of the scapula. Again, the extent is considerably greater than would be expected. Various pelycosaurs and primitive therapsids have a somewhat similar small area of striated markings in this vicinity, but the development is much less. The functional significance in the new animal remains uncertain.

The clavicle and interclavicle, as shown in Figure 3C, D, fall well within the range of structures found among the pelycosaurs and primitive therapsids and have few unusual features. At the level of flexure between the shaft and ventral blade of the clavicle the anterior and inner margin of the bone has a strongly rugose surface, much like that on the inner surface of the scapula. Presumably this also was the site of attachment of ligaments.

5. *Fore limbs*: Figures 1A, 2C, E, F, G; Plate IIA, B, C. Most features are well shown in the figures and plates. Comparisons with sphenacodonts and gorgonopsians are shown in outline in Figure 2C and measurements are given in Table 1. It will be seen from these that in general the limb elements are intermediate between sphenacodonts and gorgonopsians, with the humerus, radius and ulna somewhat more like comparable bones in the latter and the manus closer to that of sphenacodonts.

The humerus is lightly built. The right humerus is well preserved and the left is crushed. The two blades in the right make an angle of about 60 degrees with each other. The deltopectoral crest has a well-developed boss for the insertion of the pectoralis muscle but is rather weak distally. The ectepicondyle is strong but the supinator process, which is not well preserved in either humerus, appears to have been weak. The entepicondyle is strong but is not greatly expanded. An entepicondylar foramen is present, but is not visible in dorsal aspect. No ectepicondylar foramen has been identified. The area in which it would be, were it present, is damaged and its existence is not out of the question.

The radius is slender, curved and slightly twisted along the long axis. It is much more like the radii of primitive therapsids than those found in sphenacodonts. The ulna is thick relative to its length. The olecranon process is moderately developed and the distal end of the ulna is broad. Except for the last feature, the ulna resembles that of various gorgonopsians, Figure 2E. It is not basically sphenacodont in its principal features.

The carpus, metacarpus and phalanges are preserved, mostly intact as shown in Plate IIA, B. The carpus is basically sphenacodontine in character. Distals 4 and 5 are not fused. Fusion is indicated in all figures of the gorgonopsian carpus. Were it not for the presence of a remnant of distal 5 in *Watongia*, this interpretation would undoubtedly have been made, for the shape of distal 4 is essentially that of the supposedly fused element in various primitive therapsids.

The pisiform is extremely large and presumably the tendon of the flexor musculature was unusually strong. This is in marked contrast to the known feet of gorgonopsians and the element is as strong as or stronger than in *Dimetrodon*.

The phalangeal formula apparently was of the primitive 23453 pattern, although the second digit has not been identified. There is only moderate reduction of the more distal phalanges, much as in *Dimetrodon* and the gorgonopsian, *Aelurognathus*, Figure 2C.

6. *Systematic position*: *Watongia* is placed with the Gorgonopsia primarily upon the undeniable presence of the preparietal. This element is present only among gorgonopsians and anomodonts and its form in the latter is quite different from that in the gorgonopsians. It is, of course, possible that it was developed independently in *Watongia* and gorgonopsians but, in view of the many other structures in which *Watongia* tends towards the gorgonopsian condition, it seems unlikely that this is the case.

The specimen shows a mosaic of sphenacodont and gorgonopsian characters. In it we find one of the rare instances of an almost ideal intermediate between two major groups, but one in which a definitive feature makes placement in one or the other plausible. Although solving an otherwise annoying taxonomic dilemma, the presence of the preparietal does not detract from the essentially intermediate nature of the *Watongia*.

The family Gorgonopsidae, as revised by Sigogneau (1970) has 22 genera which, while coherent in fundamental characteristics, have considerable variation in skull form, dentitions, and development of limb structure. The Russian gorgonopsians, *Amalitzkia* and *Inostrancevia* (Pravoslavlev 1927a, b), not treated by Sigogneau, fall within the gorgonopsids. Sigogneau recognized two subfamilies, Gorgonopsinae and Rubidgeinae. Major differences separate the two and it is to the former that *Watongia* bears close resemblance.

Much of the work on gorgonopsian systematics has treated skull structure and dentitions. The postcranium has not been studied for most genera so that the range of variation is not well known. Most of what is available is the result of work by Broom (1930), Broili & Schroeder (1935a, b), Boonstra (1924, 1953, 1963, 1965), Pravoslavlev (1927a, b), Colbert (1948) and the summary by Sigogneau (1970). Little is known of the postcranium of the oldest specimens from South Africa. Most generalized of the better known materials from later times appears to be *Aelurognathus* from the *Endothiodon* and *Cistecephalus* Zones. *Gorgonops* (Broili & Schroeder 1935a, b), from the base of the *Endothiodon* Zone is at much the same level, and *Lycaenops* (Colbert 1948) is much more advanced.

Watongia, although more primitive than any genus heretofore assigned, can be included in the family Gorgonopsidae and the subfamily Gorgonopsinae without seriously modifying the morphological limits given by Sigogneau.

CHRONOFAUNAS IN THE MID-CONTINENTAL UNITED STATES

The persistence and coherence of ecological systems during the late Pennsylvanian and early Permian of the United States is being increasingly documented. The vertebrate portions of these temporally persistent ecological systems have been termed chronofaunas, or more precisely vertebrate chronofaunas (Olson 1952, 1958). A useful way to view and study the evolution of particular phyla is in the chronofaunal context, and that is the approach used in the remainder of this paper.

The excellent record of lowland, deltaic vertebrates in North America is the basis for what has been termed the Permo-Carboniferous Chronofauna (Olson 1971: 645-654). This is characterized by an aquatic base of the food chain, with the large carnivore *Dimetrodon* standing at the peak of the pyramid. It is best known from Texas, Oklahoma and southern New Mexico, Figure 4. It ranges through the Wolfcampian and Leonardian, Figure 5. In the eastern

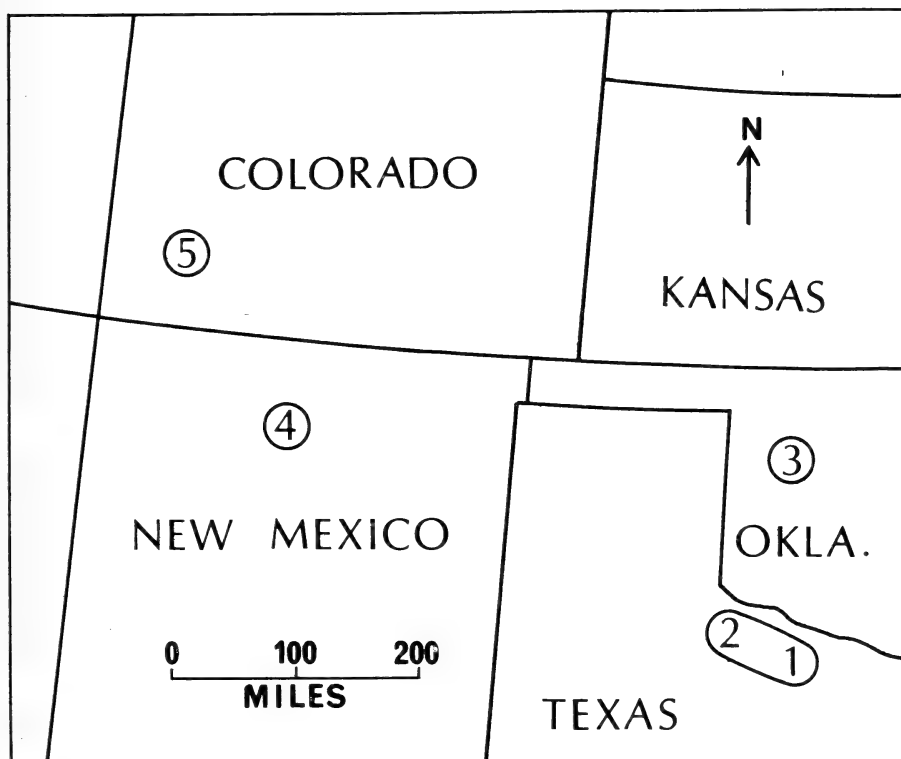


Fig. 4. Sketch map showing areas that have yielded specimens of Caseid Chronofauna as cited in text.

1. Lower Permian (Leonardian) of Texas. 2. Area of San Angelo Formation of Texas from which fossils have come. 3. Area of fossiliferous Chickasha beds of Oklahoma. 4. Northern New Mexico site. 5. The south-western Colorado site.

part of the United States, in Ohio, Pennsylvania, and West Virginia, a somewhat similar chronofauna exists. It is less well known and was partially isolated from the Permo-Carboniferous Chronofauna. European Autunian deposits, although showing little temporal continuity, indicate the existence of a generally similar system in the Old World during the very early Permian and, from what little is known, the early Permian vertebrates in many parts of the world were quite similar.

Less well known, but slowly becoming clearer, is a second chronofauna of the Mid-Continent area of the United States. This is the complex called

S. W. COLORADO
N. NEW MEXICO

TEXAS

OKLAHOMA

U. S. S. R.

	GUADALUPIAN	PEASE RIVER GR.	DOG CREEK FM. BLAINE FM. FLOWER POT FM. SAN ANGELO FM.	DOG CREEK FM. BLAINE FM. FLOWER POT FM. DUNCAN FM.	CHICKASHA FM.	KAZANIAN	ISHEEVO ZII OCHER ZI
	LEONARDIAN	CLEAR FORK GR.	CHOZA FM. VALE FM. ARROYO FM.	HENNESSEY FM. GARBER FM.		KUNGURIAN	
CUTLER - ABO FMS.	WOLFCAMPIAN	WICHITA GROUP	LEUDERS FM. CLYDE FM. BELLE PLAINS FM. ADMIRAL FM. PUTNAM FM. MORAN FM. PUEBLO FM.	WELLINGTON FM. (WICHITA)			

Fig. 5.

A stratigraphic chart of the pertinent geological subdivisions and their temporal relationships.

the Caseid Chronofauna (Olson 1971). It existed in somewhat more upland circumstances (see Olson & Vaughn 1970) and is characterized by varanopsids, caseids, or caseid-like, primitive edaphosaurians, and the absence of *Dimetrodon*. Its basic characteristics relate to a food chain in which terrestrial reptiles, caseids and captorhinids, occupy the role of secondary producers. Predators include varanopsids, and haptodontine-sphenacodontine pelycosaurs, but not *Dimetrodon*.

Its earliest manifestation in the Permian record is in the Cutler and Abo Formations of northern New Mexico and south-western Colorado, Figure 4. Both the known faunas and the sedimentation support the conclusion that this is not a truly deltaic fauna, but one that lived somewhat more in uplands, and in the case of the Colorado fauna, near to highlands (Vaughn 1969b). This earliest phase has not produced caseids, although possible relatives, such as *Oedaleops* (Langston 1965) are known. *Sphenacodon* is present, *Aerosaurus*, very close to *Varanops*, is present in New Mexico, and in Colorado a haptodontine, *Cutleria*, has been found (Lewis & Vaughn 1965).

The youngest representation of this chronofauna is in the Chickasha Formation of Blaine County, Oklahoma. It is from this assemblage that the new gorgonopsian, *Watongia*, has come. In the same beds occur the caseids, *Cotylorhynchus* and *Angelosaurus*, the varanopsid, *Varanodon*, a captorhinid, *Rothianiscus*, and *Fayella*, a highly terrestrial dissorophid amphibian (Olson 1965, 1972). Both the Cutler-Abo and the Chickasha assemblages include other genera. The number of truly aquatic forms is low in both instances, although some are present.

It has long been apparent that the therapsids arose from among the pelycosaurs and largely if not entirely from the Sphenacodontidae. It is also evident that they did not arise from the principal sphenacodontid of the Permian-Carboniferous Chronofauna, *Dimetrodon*, or any of its less well-known associates. *Dimetrodon* is an excellent morphological forerunner in many respects, but it is too highly specialized, especially in the vertebral spines, to be close to the actual ancestry. The same applies to *Sphenacodon* of the New Mexico assemblage.

Earlier (Olson 1962) I suggested that it might be necessary to seek the ancestry of the therapsids among the Lower Permian haptodontines. At the time these were known only from Europe. This interpretation was based primarily upon the basically primitive nature of this group, which is an assemblage of unspecialized sphenacodontids, grouped for convenience by Romer & Price (1940). Sigogneau & Chudinov (1972) show this group as basal to various primitive therapsid lines, with Old World therapsid evolution being the source of the later therapsid stocks.

Increasing evidence of close association of the Old World and New World Permian, both on physical and biological grounds, brings into serious question the idea of an exclusively Old World origin of therapsids. Likewise, similar chronofaunal structures in different regions suggest the possibility that similar evolution may have produced therapsid lines in more than one area and from

more than one haptodontine-sphenacodontine line. Lewis & Vaughn (1965) describing a haptodontine, *Culleria*, from south-western Colorado, noted its significance in this respect. Also haptodontines are now being identified in the rocks of the Upper Pennsylvanian of North America.

Evolution leading to therapsids presumably passed through the haptodontine to the sphenacodontine level and thence to the therapsid level. *Dimetrodon* and *Sphenacodon*, as well as other less well-known sphenacodontines, are examples of the intermediate level, but are somewhat specialized offshoots. The presumed sphenacodontines from which therapsids arose are not known. It appears likely that they evolved under the general conditions shown by the Caseid Chronofauna. Only where faunas have been sampled in the areas in which they lived, in the Cutler-Abo Formations and the Chickasha Formation, have representatives of a haptodontine-generalized sphenacodontine lineage been found. What we see for the most part are offshoots living under different conditions to which they are specifically adapted, the adaptations being the specializations that exclude them from therapsid ancestry.

The limitations of sampling, both faunal and geographic, are severe. Within these it is reasonable to suppose that the Caseid Chronofauna, and probably others like it, represent a somewhat upland complex in which haptodontines evolved into sphenacodontines and thence to primitive therapsids. The gorgonopsid line represented by *Watongia* is the result of this process. No remains of one of the principal groups of carnivores, the haptodontine-sphenacodontine lineage, have been found in the 'erratic' remnants of the Caseid Chronofauna. This term 'erratic' is used to refer to occurrences of remains of genera and species that are foreign to the normal assemblages of animals and not associated with normal constituents of the *in situ* chronofauna. That these carnivores were a part of the chronofauna in spite of their absence in the erratics is reasonable under the concept that, within the complex, herbivores outnumbered the predators many times over. Where the chronofauna is well known, representatives of the lineage have been found. Still, of course, existence of such a line between the Wolfcampian and the Guadalupian is conjectural.

Beyond the fairly large assemblage from northern New Mexico and south-western Colorado, in the Cutler and Abo Formations, and the Chickasha Formation of Oklahoma, the evidence of the Caseid Chronofauna comes entirely from erratics. In the present instance such genera and species occur within the geographic range and sediments of the Permo-Carboniferous Chronofauna, but are not a part of it. Such interpretations, of course, require extensive information about the primary faunas and are reliable only after thorough and repeated samplings have been made.

The principal evidence for the Caseid Chronofauna may be summarized as follows:

1. Cutler-Abo Formations (Wolfcampian)
 - a. Northern New Mexico. Large faunal assemblage, including *Aerosaurus* (varanopsid), *Sphenacodon*, *Oedaleops* (possible caseid relative), various aquatic, semi-aquatic and terrestrial amphibians and reptiles.

- b. South-western Colorado. Somewhat similar, less extensive assemblage with a more 'upland' fauna. *Cutleria* present, varanopsids not reported.
2. Lower part of Vale Formation (Clear Fork, Leonardian, Texas)

Small pocket, about 1,52 by 3,04 and 0,91 metres thick. With *Varanops*, *Casea*, and *Cacops* (unique dissorophid). Association with other types of vertebrates reported, intimacy uncertain. Some Permo-Carboniferous Chronofaunal elements present. None of 3 genera listed above occurs in 'normal' assemblages of the Arroyo or Vale Formations of Texas or Oklahoma.
3. Upper part of Vale Formation (Clear Fork, Leonardian, Texas)
 - a. Two specimens of *Casea* in single nodule, no other genera closely associated (Olson 1954, 1958).
 - b. Palate of large captorhinomorph with 8 rows of teeth (Olson 1956).
4. Middle part of Choza Formation (Clear Fork, Leonardian, Texas)

Partial skeleton of *Casea*, probably complete at deposition (Olson 1954). Not associated with other vertebrates. Not in usual Choza assemblage.
5. Hennessey Formation (Clear Fork, Leonardian, Oklahoma)

Many skeletons of *Cotylorhynchus* (caseid). Apparently floated in (Stovall, Price & Romer 1966; Olson 1968). One tooth of varanopsid character, associated with washed-in scrap of *Captorhinikos* (Olson 1970).
6. San Angelo Formation (Guadalupean, North Central Texas)

A mixed assemblage with elements from Caseid Chronofauna, and also Permo-Carboniferous Chronofauna (association uncertain). In addition, 'advanced elements' of unknown origin.
7. Chickasha Formation (Guadalupean, North Central Oklahoma)

An assemblage with *Varanodon* (varanopsid), *Watongia*, *Rothianiscus* and caseids, *Cotylorhynchus* and *Angelosaurus*. Some 'erratic' elements, as *Diplocaulus*, a member of the Permo-Carboniferous Chronofauna.

SIGNIFICANCE OF THE NORTH AMERICAN THERAPSID

I. THE CHICKASHA GORGONOPSID

The new genus, *Watongia*, sheds some light upon the problem of therapsid origins, but it also adds confusion to an already complex situation. It goes without saying, of course, that the data are insufficient for firm conclusions and that new information, which comes bit by bit, can merely point towards a better understanding. Currently new discoveries continue to suggest a complex rather than simple transition from pelycosaur to therapsid.

It is assumed in the following discussion that *Watongia* arose from a haptodontine-sphenacodontine lineage in the context of the Caseid Chronofauna. Temporally it is slightly younger than the San Angelo therapsids (Olson 1962) and probably slightly older than the Ocher (Yezhova) therapsids from the early Kazanian of the U.S.S.R., Figure 5 (see Chudinov 1960, 1965; Efremov 1956; Olson 1962).

Watongia is such an excellent intermediate between the sphenacodontines and gorgonopsids that it could in fact represent the actual transitional stage. In this role it represents the only known instance of such an intermediate. The suggestion of Kemp (1969, 1972) that the gorgonopsians represent a distinct line, separate from therapsids, is supported, at least as far as the Gorgonopsidae are concerned. Parallelism, of course, cannot be ruled out, but with current evidence it seems an unnecessary complication.

Watongia may be more or less at the developmental level of *Phthinosuchus* and *Eotitanosuchus* of the Russian early Kazanian. Because of the absence of comparable parts, except as the fragments of the skull of *Watongia* can be matched with the skulls of the other two, little direct comparison can be made.

The relationships of the Russian genera to each other and to *Biarmosuchus* have been the subject of much speculation and are not yet resolved. Most recently Sigogneau & Chudinov (1972) have related eotitanosuchids to gorgonopsids and biarmosuchids to ictidorhinids. So interpreted, these two families of the Gorgonopsia (following Sigogneau 1970) diverged very early, probably at what can be considered a sphenacodontine level. Boonstra (1963) considered *Eotitanosuchus* and *Phthinosuchus* as relict representatives of an earlier stock, but not themselves on the line to other therapsids. Kemp (1969) showed the phthinosuchids as a side branch of the gorgonopsian line.

Biarmosuchids show many structural resemblances to ictidorhinids and the association seems reasonable. If *Watongia* is, as argued in this paper, a very primitive gorgonopsid, then it follows that *Phthinosuchus* and *Eotitanosuchus* grouped here as Phthinosuchidae, cannot be on the line to this family. Rather, the family originated directly from a sphenacodontine ancestry, without such intermediates.

Watongia most closely resembles the less specialized members of the subfamily Gorgonopsinae, forms such as *Galesuchus* from the *Tapinocephalus* Zone and *Aelurognathus* from the *Endothiodon* and *Cistecephalus* Zones. It is, however, decidedly more primitive than any of these. It differs in many ways from members of the subfamily Rubidgeinae (Sigogneau 1970). The rubidgeines are characterized by the absence or near absence of the preparietal bone and by the exclusion or near exclusion of the frontal from the orbital margin. Although many of their features are gorgonopsian, their relationship to the gorgonopsines is not clear. *Watongia* has little direct bearing upon this problem, other than that it is a very primitive gorgonopsine, the subfamily within which the origin of the rubidgeines may lie, and that it has a preparietal and a frontal which makes broad contact with the orbit.

2. THE SAN ANGELO THERAPSID

In 1953 (Olson & Beerbower) and in 1962 (Olson) several therapsid-like reptiles were described from the San Angelo Formation of Texas. Intermittent searches in these beds, both in old sites and in new areas, have not added materially to what was known by 1962. The remains which have been recovered are tantalizing but in many ways unsatisfactory because of their incompleteness. It is, however, possible to say with confidence that in North America at the time of deposition of the San Angelo Formation there existed a wide array of non-pelycosaurian synapsids which show affinities to members of several groups of therapsid reptiles from the Ocher region and Copper Sandstones of the U.S.S.R. In 1962 these were associated as follows:

Phthinosuchids: *Gorgodon*, *Knoxosaurus*, *Steppesaurus*

Deinocephalians (Eodinocephalians): *Driveria*, *Mastersonia*, *Tappenosaurus*

Brithopodidae: *Eosyodon*

Venjukovoidea: *Dimacrodon*

These assignments still appear to be the most reasonable possible for these genera. Both the San Angelo and the Ocher assemblages indicate that extensive radiations had taken place by very early Guadalupian-Kazanian times. Neither in Europe nor in North America is there a trace of the direct source of these forms, except the probable ultimate pelycosaurian origin from very early Permian haptodontines. The only possibility, now that the association of *Watongia* and caseids is known, is that some of the genera assigned to the phthinosuchids are actually gorgonopsids, close to *Watongia* and with a source in the Caseid Chronofauna. The most likely candidate is *Knoxosaurus*, Figure 3H, which has two large canine teeth and small postcanines, somewhat a gorgonopsian pattern but one also not greatly different from that of phthinosuchids.

Except for this rather remote and indeterminable possibility, the San Angelo and Ocher forms have no known sources. We may speculate that there existed one or more unknown chronofaunal types from which they arose and that these existed outside of areas where deposition and preservation are currently known. The San Angelo complex appears to include a variety of ecological types and probably a considerable mixing of animals from different adaptive zones. Elements of the Caseid Chronofauna are present. The only sphenacodont is *Dimetrodon*, from the Permo-Carboniferous Chronofauna. It is known from specimens from two widely separated sites.

Close resemblances between some of the San Angelo genera and those from the upper Permian of the Soviet Union indicate similar sources. The postcrania of *Driveria* and *Mastersonia* are of the same general type found in *Estemnosuchus* from Ocher. They seem somewhat more primitive. The various parts of the skull, jaw and postcranium of *Eosyodon* show close resemblances to these elements in *Syodon*, from Ishevo, but are clearly more primitive. The supposed phthinosuchids seem to be at about the level of the Ocher *Eotitanosuchus*, but resemblances are at best vague. *Dimacrodon* is clearly trending in the general direction of venjukovoids, but the differences are marked. In addition to the therapsids, *Kahneria* of the San Angelo is very similar to *Hecatagomphius* of the U.S.S.R. as far as the lower jaw and dentition are concerned. Likewise, *Cotylorhynchus* and *Ennatosaurus*, caseids, have many features in common, although there are differences in cheek teeth and in skeletal proportions.

INTERPRETATION AND SUMMARY

Therapsids from the San Angelo Formation of Texas and now from the Chickasha Formation of Oklahoma have added a new geographic dimension to the analysis of the very early, primitive therapsids. The strong resemblances between some of the North American and Russian genera, therapsids, caseids

and captorhinids, indicate the existence of close geographic ties between the areas. The general circumstances may be interpreted somewhat as follows. We may suppose that the areas that have yielded fossil remains of terrestrial vertebrates lay in a continuous continental belt. This area as a whole probably was tropical to subtropical, lying more or less along the equator (see Olson & Vaughn 1970). Over the area existed a series of different adaptive zones, or habitat types. These differed from each other in general faunal and environmental characteristics. Similarities of environments within each of the several zones, as well as the differences between the zones, depended primarily upon topographic elevation and the amount and distribution of rainfall. Each of the adaptive zones was occupied by faunas which were fairly similar throughout but which had distinct local differences. In general, it appears, the topographically lowest adaptive zone lay near the seas or large bodies of water in evaporite basins and deposition was very broadly deltaic in nature.

It is probable that there were intermittent interconnections between the various local faunal units of each adaptive zone and, on occasion, between local units in different adaptive zones. This probably was accomplished primarily by particular species that developed capabilities of extending beyond the ecological system in which they originated. Patterns of crossing between systems probably were complex and it is likely that interchanges were accompanied by speciation as migrants adapted to the new circumstances which they encountered. The integrity of the local faunal units through time, as far as their basic ecological structure is concerned, appears to have been strong. Marked changes in an area were the result of replacement, not of local faunal evolution.

The vertebrates of the local ecological units form the chronofaunas. We may envisage many of these existing over the broad continental area, with suites of chronofaunas with similar characteristics occupying similar environments in different places. The ecological structure, although much the same within a single adaptive zone, appear to have been different in the several adaptive zones. In addition, the evolutionary levels were different between at least some of the zones.

This interpretation produces a model within which it is possible to view therapsid origins in ways which seem to give excellent fit to the rather meagre data now available.

From this model it follows that the development of haptodontine-sphenacodontine lines toward the therapsid level may have taken place in many areas. Relatively few of the evolving phyla would have passed the therapsid threshold and most of those that did probably would have been only temporarily successful. From the successful few came the major groups of therapsids for which we have an excellent fossil record.

Each of these major groups, to the extent that it is monophyletic, may be supposed to have originated in some local area—that is, within a particular chronofauna. Origins of the different groups probably took place at various places over the continental area and these may have been more extensive

than present records show. Species transfer between chronofaunas both within and between adaptive zones, and replacements of one type of chronofauna by another, from a different adaptive zone, undoubtedly had a part in producing the complex situations which we find in the record. Taphonomic mixing certainly tends to make more obscure an otherwise complicated record.

From the information available it seems safe to say that no therapsids arose in the Permo-Carboniferous Chronofauna and probably not in any chronofauna similar to it. We appear to have one instance in which a therapsid arose in the Caseid Chronofauna, this, of course, involving *Watongia*. During the times that these two chronofaunas existed there were others, those in which the types of therapsids recorded in the San Angelo Formation and the Ocher site originated. We have no first-hand knowledge of where or under what circumstances these origins were taking place. What indirect evidence there is, from the San Angelo and from at least some of the Russian sites, shows that materials were transported into lowland depositional sites. Presumably the chronofaunas tapped by these samplings were more upland than any for which we have first-hand knowledge of areas of habitation. Whether such areas will be found preserved, of course, is an open question; but on the basis of present information, the prognosis is negative.

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A NEW GENUS OF GORGONOPSID FROM EAST AFRICA

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(With 2 figures)

CONTENTS

	PAGE
Introduction	47
Description	47
References	51

INTRODUCTION

In his account of the theriodonts from the Ruhuhu Valley in south-west Tanzania Huene (1950) described a somewhat poorly preserved skull of a gorgonopsid as a new species of the genus *Lycaenops*, *L. kingoriensis*. The illustrations of this form immediately recalled a much better specimen collected by the writer in 1933 (no. 42) from Stockley's (1932) site B.4 at Katumbi vawili. This site is in Stockley's so-called 'Lower bone bed' which has produced both *Endothiodon* and *Cistecephalus*, and which Charig (1963) has recommended should be called the Kawinga Formation. The site B.4 has yielded, among other things, the amphibian *Peltobatrachus pustulatus* Panchen (Panchen 1953) and the gorgonopsid *Leontocephalus intactus* Kemp (Kemp 1969).

The identification of gorgonopsid skulls is made difficult by reason of the fact that many names have been given to very poorly preserved and incomplete specimens but the fact that the specimen called *Lycaenops kingoriensis* was immediately recognizable among the writer's collection seems to establish it as a valid form. However the shape of the skull, which may be said to be triangular, is in marked contrast to the material referred to the genus *Lycaenops* where, by contrast, the skulls are comparatively narrow (e.g. *L. ornatus* Broom; *L. kingwilli*, see Sigogneau 1970). Sigogneau (1970) defines the genus *Lycaenops* as having 'Crâne étroit, museau long, plus haut que large'. Neither this author nor Watson & Romer (1956) accepted Huene's reference to the genus, the former suggesting a possible reference to the genus *Sycosaurus*, the latter to the family Gorgonopsidae but without any reference to a genus.

DESCRIPTION

The specimen described here is most unusual in that it does not appear to have undergone any distortion. The teeth are missing, as are the quadrate complexes, and small parts have been lost by breakage but, on the whole, the

skull is exceptionally well preserved. It was prepared by means of automatic mallets before the acid techniques had been perfected.

The skull measures about 300 mm in length and about 235 mm at its broadest point and is, therefore, a moderately large form. Seen from above the

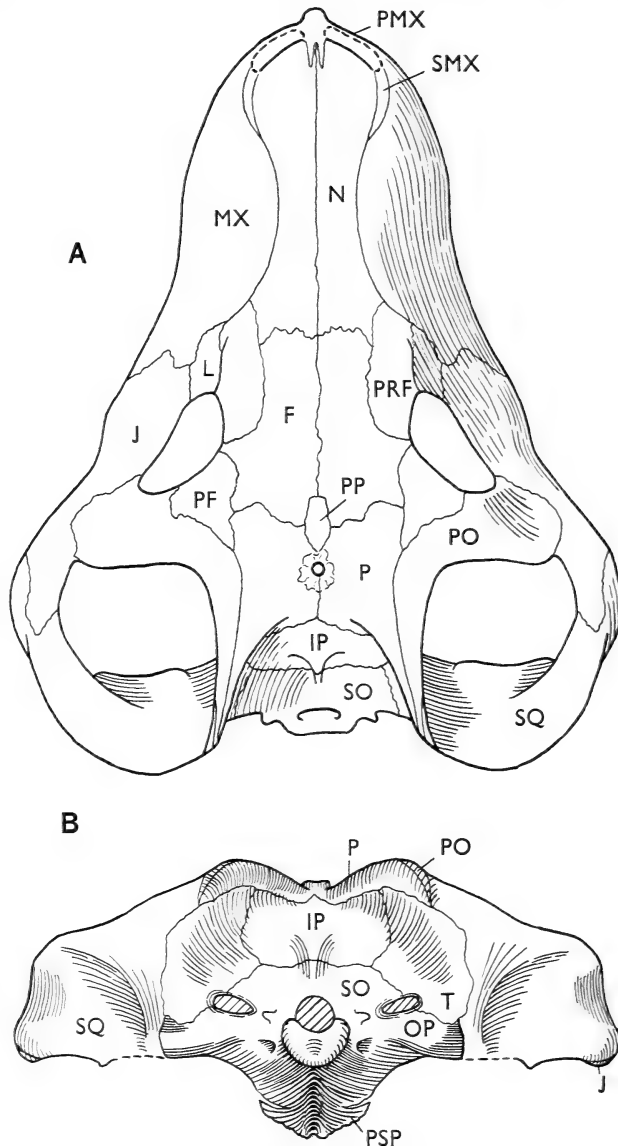


Fig. 1. A dorsal and B occipital views of *Cephalicustriodus kingoriensis* (Huene), gen. nov. $\times \frac{1}{3}$. F, frontal; IP, interparietal; J, jugal; L, lacrimal; MX, maxilla; N, nasal; OP, opisthotic; P, parietal; PF, postfrontal; PMX, premaxilla; PO, postorbital; PP, preparietal; PRF, prefrontal; PSP, parasphenoid; SMX, Septomaxilla; SO, supraoccital; SQ, squamosal; T, tabular.

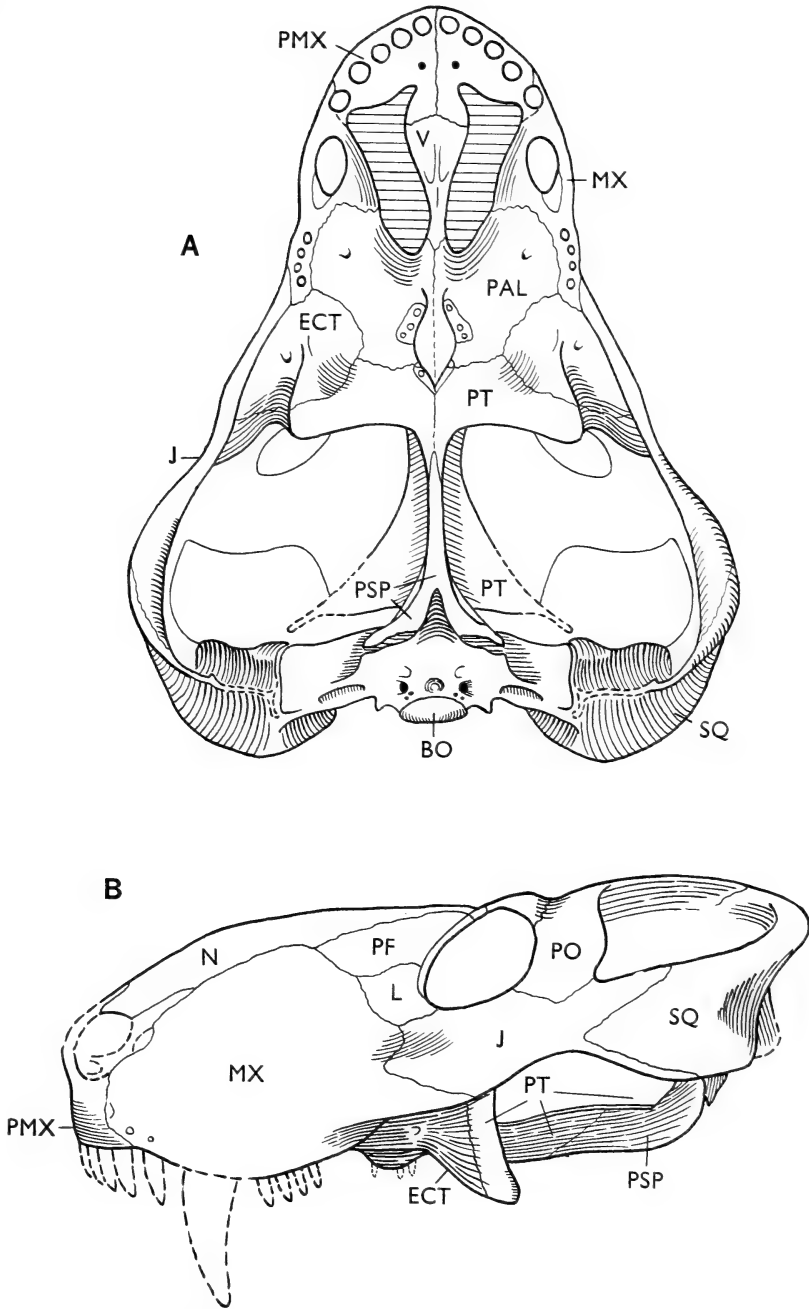


Fig. 2. A palatal and B side views of *Cephalicustriodus kingoriensis* (Huene), gen. nov. $\times \frac{1}{3}$. BO, basioccipital; ECT, ectopterygoid; PAL, palatine; PT, pterygoid; V, vomer; other letters as in Figure 1.

skull is markedly triangular in outline, the snout being broad, the jugals are flared out at their junction with the maxillae, and the parietal region and temporal vacuities are wide. In general the arrangement of the bones is straightforward with a moderate preparietal and the pineal surrounded by a well-developed boss. Apart from the proportions the outstanding feature lies in the nasals, coarsely sculptured bones which meet along the midline at an angle of about 90° for most of their length. In gorgonopsids in general (as far as is known) the snout is either rounded or flattened.

In occipital view the appearance is straightforward but the skull is very wide for its depth. The relationships of the bones are normal but it is noteworthy that the spike on the bottom of the squamosal, behind the recess for the quadrate complex, is clearly developed. This spike almost certainly fitted into a pit in the quadratojugal and helped to prevent the quadrate complex from moving too much in its recess in the squamosal (Parrington 1955).

The palate is well shown (Fig. 2A). The dentition must have been of normal gorgonopsid type there being sockets for five powerful incisors, a large canine (followed by a bony plug), and four diminutive postcanines. There are at least three small teeth on the ridge of the palatine but only one can be seen for certain on the pterygoid, this on the right side.

The fused vomers are clear and of characteristic form being expanded anteriorly but tapering posteriorly where they disappear above the palatines at about the level of the posterior borders of the internal nares. The importance of this feature, which is in contrast to the condition in *Terocephalia*, *Bauriamorpha* and *Cynodontia*, in all of which the vomers grow backwards below the palatines and pterygoids, was first recognized by Boonstra (1934) who questioned the then widely accepted view that the cynodonts were descendants of the gorgonopsids, and was the first person to do so. Subsequent work on both the early cynodonts (e.g. Broom 1938a) and gorgonopsids (Kemp 1969) have established the fact that the gorgonopsids and cynodonts are not closely related, the latter being descendants of the *Terocephalia*.

Posteriorly no interpterygoid vacuity can be detected though one might be exposed if the specimen were subjected to acid treatment. Very marked incisures are present between the wings of the parasphenoid-basisphenoid complex and the basioccipital. Taken in conjunction with the unossified zone (Olson 1944) and the frequency with which the occipital component of the brain case is found separate in synapsid reptiles, the possibility of kinesis in these forms appears to be real. Movement of the anterior region of the skull about the lateral expansions of the supraoccipitals is a possibility, but only a closely sectioned skull, when reconstructed, would establish the matter.

The form of the zygomatic arch strongly suggests that there must have been ample room for an external component of the adductor muscle mass (Fig. 2A, B). This is shown also in *Arctognathus breviceps* and the forms *Dinogorgon quinquemolaris*, where the lower jaw is present, and *Rubidgea atrox*, also with the lower jaw in place (Sigogneau 1970). The writer has suggested that a masseter muscle ran

from the anterior region of the jugal (which is deep and thickened in gorgonopsids) and the reflected lamina of the angular, thereby accounting for that peculiar structure (Parrington 1955) but Barghusen (1968) claims that only in cynodont theriodonts was this muscle evolved and Kemp (1969) has postulated in the gorgonopsids the presence of a zygomatico-mandibularis muscle between the posterior region of the arch and the reflected lamina, this in view of the special strengthening of the bone of the lamina.

Examination of Dr Sigogneau's invaluable monograph on the gorgonopsids (Sigogneau 1970), and other sources, has failed to disclose at all a close match in form with the skull from Katumbi vawili though similar broadening of the posterior region of the skull is present in a number of forms, notably *Sycosaurus*, *Prorubidgea* and *Rubidgea*, and it may well be allied to these forms. Also the meeting of the nasals at about a right angle along much of their length does not appear to have been reported elsewhere, the snout of gorgonopsids as a whole being either flattened or rounded in section.

There is some resemblance to *Gorgonops torvus* but this latter form has a proportionately much longer antorbital region and in occipital view the East African animal is much flatter.

In the new form the width across the paroccipital processes is approximately half the posterior total width, whereas in *Sycosaurus* it is distinctly more than half, in *Dinogorgon quinquemolaris* it is about three-fifths, and in *Rubidgea atrox* it is slightly less than half. Again in posterior view the depth of the occiput, taken to the bottom of the condyle, is about one-third of the total width, a character it shares only with *Rubidgea atrox*, the depth in *Dinogorgon quinquemolaris* being a little less than half and other forms being much deeper in proportion. The shape in *Rubidgea atrox* is quite different from that of the Ruhuhu specimen (Broom 1938b).

In accordance with the foregoing discussion it is proposed to erect a new genus *Cephalicustriodus*, defined principally on the triangular shape of the skull, for Huene's *Lycaenops kingoriensis* which now becomes *Cephalicustriodus kingoriensis* (Huene). It can probably best be placed in Sigogneau's (1970) subfamily Rubidgeinae. The specimen described here is catalogued number T.891 in the University Museum of Zoology, Cambridge.

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THE INNER EAR OF *GORGONOPS* (REPTILIA, THERAPSIDA,
GORGONOPSIA)

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(With 6 figures)

I welcome the opportunity to express my admiration and thankfulness to Dr Boonstra, to whom the mammal-like reptiles and myself are greatly indebted.

It is to Watson that we owe the first tentatives toward elucidating the structure of the inner ear in mammal-like reptiles (cynodonts), but it was Olson (1944) who undertook a systematic study of this region of the skull in the main therapsid infra-orders. Olson's work included two gorgonopsians: the type of *Cyonosaurus longiceps*, and a form not generically identified, but which he considered as 'more primitive than *Cynariops robustus*,' the genus to which he had originally (1938a) assigned it. Thus it is only a modest supplement to his comparative study that is presented here. The genus *Gorgonops* would be situated, according to the conclusion I reached in 1970, at a higher evolutionary level than the two forms studied by Olson.

The method employed here to study the specimen of *Gorgonops* (B.P.I. 277) was that of serial sectioning, such as was used by Olson (1944) and previously by Romer & Price (1940) for the study of the inner ear of *Dimetrodon*. Details of the process I used (in reality not sectioning, but a grinding of the specimen) will be given later in a publication on the ensemble of the skull; it should be mentioned here that the latter measured about 237 mm long, and that grinding proceeded at $\frac{1}{4}$ mm intervals.

The preservation of the specimen turned out to be less satisfactory than was initially expected, and flattening of the posterior part of the skull is rather marked. The ear region is in reasonably good condition, but the defective ossification of this region renders its interpretation delicate and numerous uncertainties remain.

The inner ear is lodged, in *Gorgonops*, in the prootic, the opisthotic, the supraoccipital and the basioccipital. It is situated between sections 230 A—300 A.¹

An immediately noteworthy fact concerns the inclination, dorsally and anteriorly, of the ear, this being in correlation with the same slope of the basi-cranial axis (Fig. 1). The mesial wall of the ear is only ossified at the back; there does not exist, therefore, on the endocranial face a proper internal auditive foramen, but a vast opening which leads into the cavity of the bony ear in which was contained the membranous ear. Obviously, the eighth cranial nerve

¹ The section numbers cited in this work refer to the left side, but in fact there is very little offsetting from one side to the other.

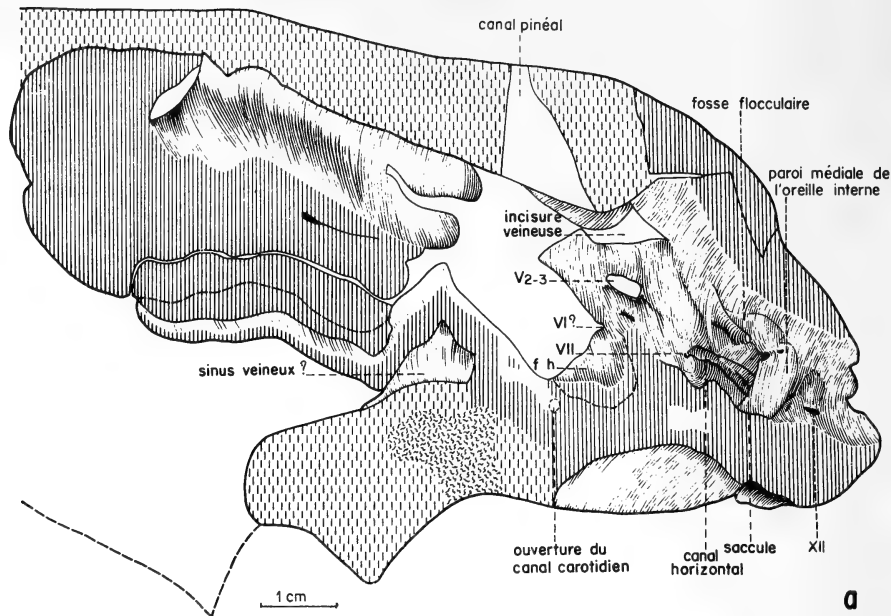


Fig. 1. Longitudinal section of the posterior part of the skull of *Gorgonops torvus* (B.P.I. 277), reconstructed from serial sections (from Sigogneau 1970). $\times 1$.
f h: hypophyseal fossa.

also traversed this opening. The latter, in conjunction with the cavity of the bony ear, correspond to the vestibule of some authors, but it would be preferable, as noted by Romer (1955), to avoid this term originally applied to the upper part of the internal bony ear. The absence of ossification is such that the interior of the horizontal semicircular canal, contained in the lateral wall of the ear, is visible mesially; the canal, nearly totally lacking an internal wall, seems to open into the utriculo-saccular cavity. The same absence of ossification is responsible for the opening of the vertical anterior semicircular canal into the bony floccular fossa.

Indeed, intruding between the elements of the inner ear was an enormous flocculus (o),² directed postero-laterally after having passed anteriorly under the anterior semicircular canal. This flocculus must have been remarkably developed, and even partially covered the crus communis canalium. Opening anteriorly into the cerebral cavity, the floccular fossa penetrates first the prootic, which surrounds it on three sides; at the same time its floor, oblique ventrally and toward the median line, progressively rises until it becomes horizontal. But soon the supraoccipital invades both the roof and the floor, and when the fossa closes mesially (section 278 A), it is nearly completely included in the supraoccipital; it narrows progressively within this bone and terminates 1,5 mm behind its mesial closure.

² This and following numbers refer to features in the figures.

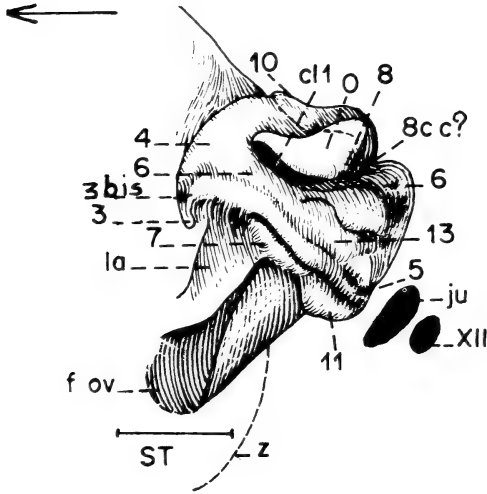
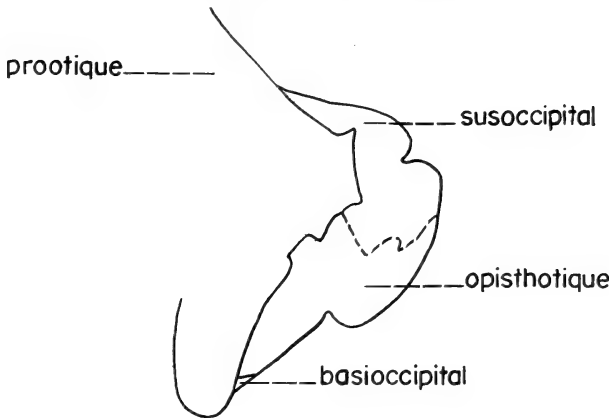


Fig. 2. Lateral view of the internal ear of *Gorgonops torvus* (B.P.I. 277), reconstructed from serial sections. $\times 2$.

cl₁: emplacement of the partition between the floccular fossa and the ear proper; f ov: fenestra ovalis; ju: jugular foramen; la: lagenar recess; z: perilymphatic cistern? o: floccular fossa; 3: anterior ampulla; 3 bis: external ampulla; 4 and 10: anterior vertical canal; 5: horizontal canal; 6: utriculus; 7: ventral part of the sacculus; 8: 8 cc: crus communis? 11: posterior ampulla; 13: dorsal part of the sacculus.
ST: antero-posterior extension of the stapes.



Oreille gauche . Vue latérale

Fig. 2 bis. The same as Figure 2, showing the emplacement of the sutures.

In the ear itself the three semicircular canals, the utriculus, the sacculus and the lagenae were sought. The perilymphatic system certainly left traces, but they are difficult to identify.

The vertical anterior canal (4) is distinctly longer than the posterior canal; also, because of the inclination of the ear, the dorso-posterior slope of the canal is slight; it bends mesially to meet the vertical posterior canal. This anterior canal originates in a very short ampulla (probably the external ampulla) (3 *bis*), the latter being preceded by a small but deeper cavity inclined ventro-laterally (anterior ampulla) (3). Soon the ventral edges of the anterior canal approach each other (section 258 A), and it becomes enclosed within the thickness of the prootic, lateral to the floccular fossa. It rises progressively inside this bone, passes above the prootic partition which separates the floccular fossa from the internal ear, and attains thereby the roof of this fossa. When the supraoccipital invades this roof (*c.* 270 A), a curious phenomenon is observed: the orifice becomes double, with the lateral part (enclosed in the prootic) closing rapidly, and the mesial part (10) (situated first at the prootic-supraoccipital limit (Fig. 4, section 268 A), then in the supraoccipital alone) increasing in size and relaying the first canal; it then encircles the floccular fossa and mesially joins the posterior part of the ear. I originally saw, here, the replacement of the anterior canal by the posterior canal, especially since the situation is identical on both sides of the skull. But the utriculus is not visible at this level: we are above the floccular fossa in which the two canals open ventrally. An interpretation of this mesio-lateral doubling remains to be found; I have seen no example of it in the literature. For the present, I will consider that it is all the same anterior canal which continues until opening into the utriculus at section 285 A; this canal terminates 2 mm farther.

The posterior canal was much more difficult to identify. It is regarded here as being formed by the mesial half of the posterior otic cavity (Fig. 4, section 295 A), and is, in consequence, masked in lateral view by the other constituents of the latter; there would be no bony separation between the two. But Olson shows the posterior canal in the sections of '*Cynarioops robustus*' (1938a, fig. 7, sections A and D) as being more lateral than the vertical anterior canal. I have found nothing equivalent; in any case, this canal must constitute the most posterior part of the ear; as a final argument, I will add that the structure here identified as the posterior canal terminates, as it should, in what is considered to be the posterior ampulla (11). This canal would be very short.

The horizontal canal (5), on the other hand, is easy to follow: it begins in the prootic in the same ampulla as the vertical anterior canal, and closely behind it (section 247 A). At first they are separated only by a fine crest, then after the definitive individualization of the latter, the horizontal canal penetrates laterally, slightly sloping downwards; its floor becomes formed by the opisthotic (section 272 A) and, one millimetre farther, the roof becomes formed by the supraoccipital. It continues, totally enclosed in the latter bone, as far as section 285 A, still sloping downward but bending mesially, and terminates in

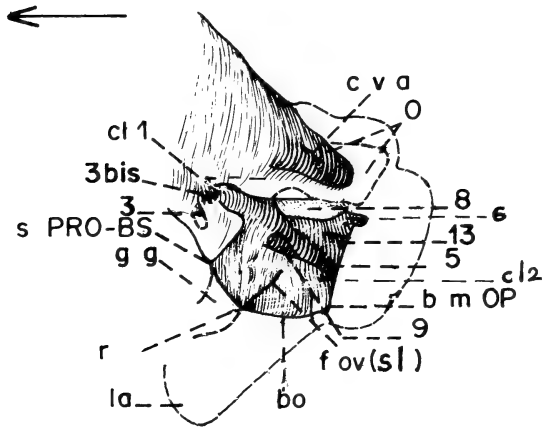
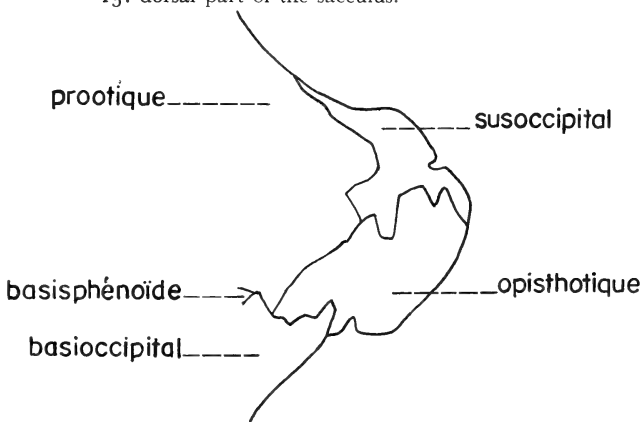


Fig. 3. Cavity of the internal ear of *Gorgonops torvus* (B.P.I. 277) seen in mesial view; reconstructed from serial sections. $\times 2$.

b m OP: mesial border of the opisthotic closing the ear mesially; bo: mesial ossified border of the lagenar recess; cl₁: partition between the floccular fossa and the ear proper; cl₂: prootic then opisthotic partition closing cavity g mesially, and constituting the lateral wall of the lagenar recess; c v a: opening of the vertical anterior canal in the floccular fossa; g g: fossa situated under the cranial floor and corresponding perhaps to the geniculate ganglion; la: lagenar recess; r: level where the basioccipital replaces the basisphenoid as the dorso-mesial border of the lagenar recess; s PRO-BS: separation of the basisphenoid and the prootic allowing the passage of the lagena above the cranial floor; sl: slit prolonging the fenestra ovalis. o: floccular fossa; 3: anterior ampulla; 3 bis: external ampulla; 5: horizontal canal; 6: utriculus; 8: see text p. 58; 9: ventral part of the sacculus? 13: dorsal part of the sacculus.



Oreille droite. Vue mésiale

Fig. 3 bis. The same as Figure 3, showing the emplacement of the sutures.

the posterior ampulla just behind the opening of the sacculus. Taken in its entirety, the horizontal canal is, therefore, inclined postero-ventrally and scarcely rises again at the rear; it is rather convex laterally. Its mesial wall is more or less ossified according to the location, but never completely.

The ampullae are not as clearly recognizable as one would expect; this is particularly true for the anterior and external ampullae. The ear begins with a minute recess (1 mm by 2,5 mm) directed laterally and ventrally (Fig. 4a, section 240 A, 3); this should represent the anterior ampulla since it precedes the depression (1 mm by 1 mm) in which the anterior and horizontal canals originate and which should therefore be the external ampulla. The recess here interpreted as the posterior ampulla is, on the contrary, very well developed. In fact, its great antero-posterior extension created some doubt about this interpretation, and I at first thought it to be an element of the perilymphatic system. But its mesial situation, and especially its posterior connection with the horizontal canal, seemed to constitute convincing arguments in favour of the ampullar hypothesis; the vertical posterior canal then, would communicate with this ampulla dorsally and mesially with respect to the horizontal canal.

The crus communis canalium (8 cc), very mesially situated, starts also, in my interpretation, very posteriorly (section 282 A); it should open into the utriculus.

The central part of the ear presents a series of concavities which overlap each other latero-mesially. One of them (6) begins at the front of the ear and communicates there with the anterior and horizontal canals; it continues all the way to the posterior part of the ear where it receives, on its mesial side, the posterior canal; it should therefore represent at least the dorsal part of the utriculus. Ventrally this utriculus communicates first (Fig. 4a) with the lagena (1a), then (Fig. 4b) with that which is interpreted here as the sacculus (9), and finally with the posterior ampulla, from which it is isolated farther on by the posterior canal. The utriculus terminates very posteriorly (at about section 295 A). It is doubled mesially by a cavity (8), of which we also have only the roof (the latter being at first constituted by the prootic, then by the supraoccipital) and from which it is separated by a crest. This cavity, the most mesial element of the ear, begins about section 260 A and also continues all the way to the rear. I could not identify it with certainty; it probably could not be the endolymphatic sac, which would thus be intraotic.

Between the utriculus and the horizontal canal is a cavity still better delimited dorsally (13) as well as ventrally (7) and more prominent than the preceding ones, but of smaller dimensions (approx. sections 260 A-290 A), and that I have regarded as corresponding to the sacculus. Its floor is in fact divided (7 and 9) for a great part of its length, but it is difficult to know if the two cavities are parts of the same element. The horizontal canal opens directly into this cavity, which, as noted above, communicates dorsally and mesially with the utriculus. Antero-ventrally the pocket opens into the lagena (Fig. 4a,

section 260 A); when the latter closes, a crest rises from the opisthotic isolating the sacculus from the posterior ampulla (Fig. 4b, sections 268 A and 278 A). This so-called sacculus goes farther dorsally than ventrally. The interpretation given here for the sacculus is in opposition to that of Olson (1938a), where the saccular recess, indistinctly separable from the lagena, does not extend above the level of the horizontal canal, and to that of Romer & Price (1940), where the sacculus in *Dimetrodon* is situated below the level of the cranial floor. In this feature in *Gorgonops*, I had thought to recognize an element of the perilymphatic system, but it would be surprising that such an element would be so dorsal, that it would intergrade with the parts of the ear properly speaking,³ and that it would be so distant from the fenestra ovalis.

Finally, the lagenar recess (la) constitutes an elongate tube sloping slightly antero-ventrally. Its anterior limit is difficult to determine (perhaps section 232 A), being situated in a very poorly ossified zone. The anterior part of the recess is lodged between the basisphenoid dorsally, the prootic dorso-laterally, and the basioccipital ventrally; then farther posteriorly (section 244 A), the opisthotic starts to form its lateral wall. Anteriorly, the lagenar recess is entirely below the level of the cranial floor. It opens laterally in a deep depression (Fig. 4a, z), the edge of which receives the stapes, and mesially in a small rounded recess interpreted as the receptacle for the geniculate ganglion (gg). When the prootic and basisphenoid separate, the dorsal part of the lagena passes above the level of the cranial floor, and soon (section 250 A) opens directly into the cerebral cavity. Only after the anterior third of the ear (section 260 A), and by the junction of the lateral and mesial parts of the opisthotic, is the lagenar recess completely closed laterally. It then narrows and terminates by a small circular fossa excavated in the opisthotic alone, in the floor of that which I have interpreted above as the posterior ampulla (Fig. 4b, section 268 A). In its middle part this recess communicates dorsally with the utriculus and mesially with the sacculus.

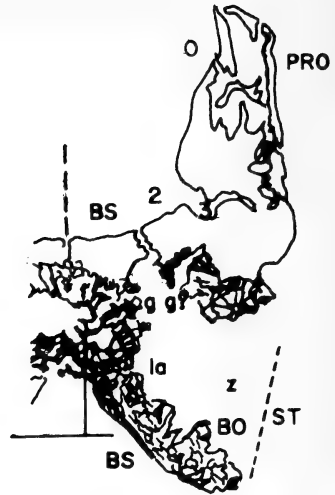
Concerning the perilymphatic system, three elements have been sought: the cistern, or reservoir of liquid at the level of the upper, or vestibular, part of the ear; the duct which prolongs the cistern and parallels the lagena particularly at the level of the basilar papilla (scala tympani); and finally the perilymphatic sac, the termination, in part at least extraotic, of the duct, lodged in what is improperly called the recessus scalae tympani.

On this subject a parenthetical explanation is perhaps not superfluous. In tetrapods, and with the appearance of the fenestra ovalis, the perilymphatic space which isolated, in fishes, the membranous ear from the bony ear becomes organized into a specialized system for the conduction of vibrations from the outside environment to the properly sensorial zone of the membranous ear, the basilar papilla of the lagena. This system is composed of, first of all, a

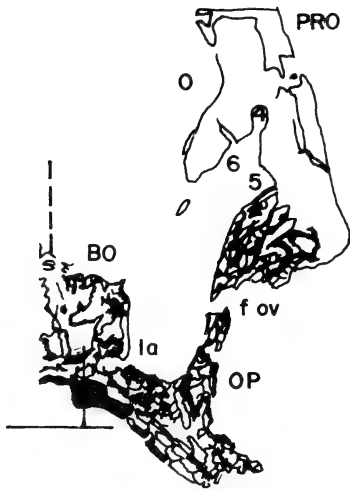
³ However Romer & Price write (1940) with respect to *Dimetrodon*: 'Cavities which are apparently associated with the perilymph system push outwards within the loops of the two vertical canals. . . .'



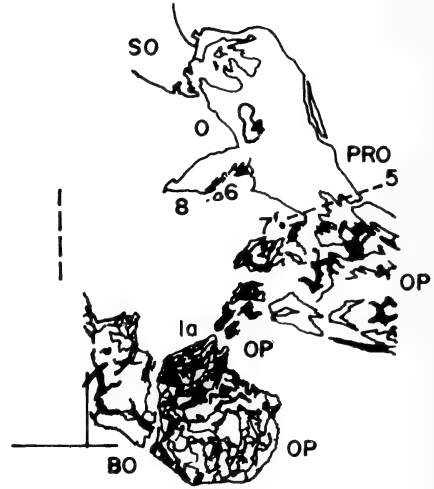
230 A



240 A



250 A



260 A

Fig. 4a

Fig. 4a. See legend opposite page.

roughly circular cavity, the perilymphatic cistern, applied to the lateral opening that is the fenestra ovalis,⁴ and therefore against the stapes. From this cistern

⁴ Or foramen vestibuli, called thus because it is situated at the level of the vestibule of the ear. This is not true, however, in certain living reptiles, nor in the mammal-like reptiles, where it opens at the level of the lagena.

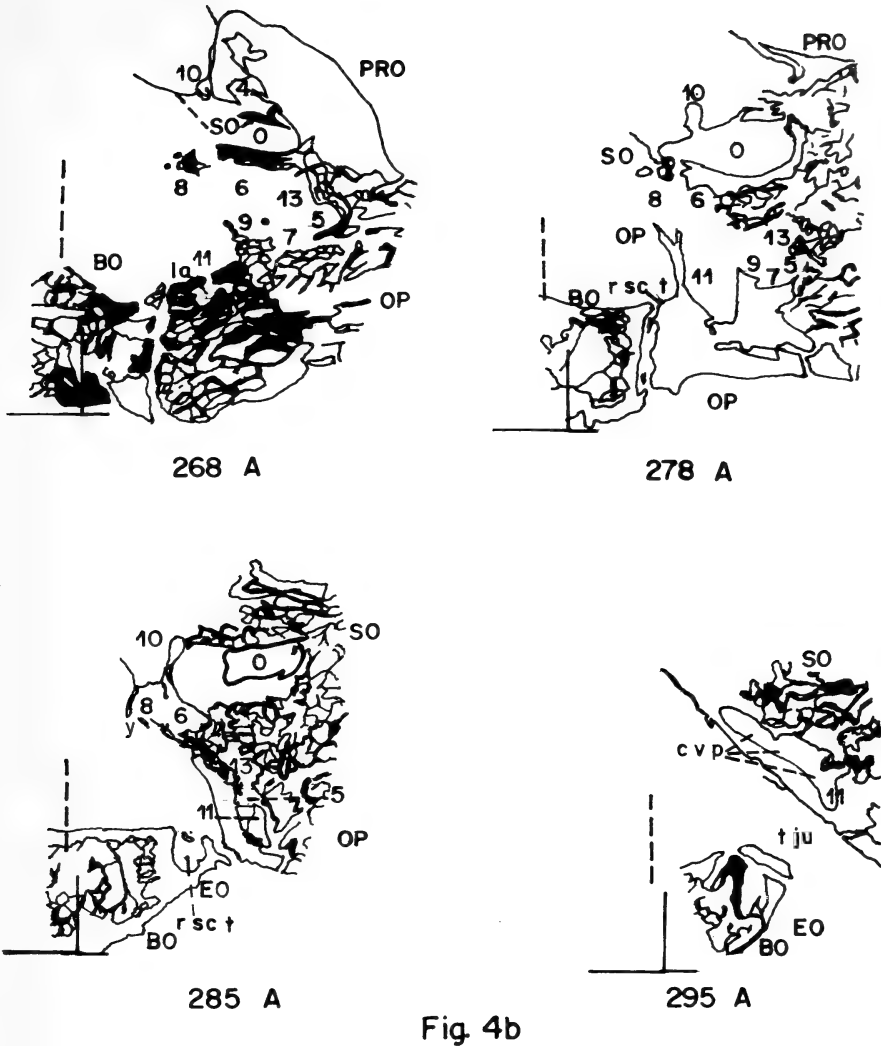


Fig. 4b

Fig. 4. Some of the serial sections of the ear region of *Gorgonops torvus* (B.P.I. 277).
 × 2. a) anterior part of the ear; b) posterior part.

c v p: posterior vertical canal; f ov: fenestra ovalis; g g: fossa corresponding perhaps to the geniculate ganglion; la: lagenar recess; r sc t: recessus scalae tympani? t ju: jugular canal; y: foramen corresponding perhaps to the endolymphatic duct; z: perilymphatic cistern?

o: floccular fossa; 2: fossa from which the ampullae will develop; 4 and 10: anterior vertical canal; 5: horizontal canal; 6: utriculus; 7 and 9: ventral part of the sacculus; 11: posterior ampulla; 13: dorsal part of the sacculus.

BO: basioccipital; BS: basisphenoid; PRO: prootic; OP: opisthotic; SO: supra-occipital; ST: emplacement of the stapes.

The sutures have been omitted in the interest of clarity, although they are discernible in the sections.

The dotted line corresponds to the median axis of the cerebral cavity.

a tube leaves, the perilymphatic duct; in lower tetrapods the latter is applied against the basilar papilla for part of its length by the intermediary of the basilar membrane. Beyond this papilla it attains the lower posterior bony wall of the otic capsule, a wall that it traverses by the perilymphatic foramen (called in error by some authors the fenestra cochleae). From there it spreads out into another evagination, the perilymphatic sac. The latter, apart from its dorsal opening into the duct, opens mesially into the cerebral cavity (by an internal jugular foramen, so-called because it is utilized at the same time by the jugular or posterior cerebral vein) and extends into the subarachnoid lacunae. Laterally, it comes in contact with the tympanic cavity, where an opening

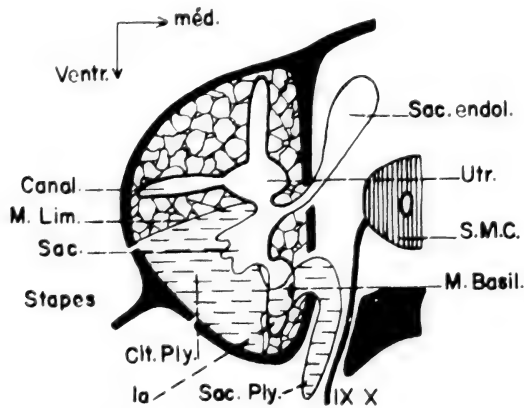


Fig. 5. Interrelationship of the peri- and endolymphatic systems in *Sphenodon* (from De Burlet).

pierces the wall of the otic capsule, the fenestra rotunda sensu lato, or pseudo-fenestra rotunda. Thus, not only are the vibrations transmitted by the stapes received by the perilymphatic liquid, which fills all of the system described, and conducted to the level of the basilar papilla where the sensorial cells receive the excitation, but the lower part of the system has, in addition, a compensating role necessitated by the incompressibility of liquids; thus a mesiad depressing of the tympanum results in a laterad depressing of the secondary tympanic membrane, which obstructs this pseudo-fenestra rotunda.

On this scheme a certain number of variations are realized. It is necessary, if not logical, to begin with mammals, because it is with them that the terms were first defined. In this class, then, the lagena has acquired such a length that it coiled up in a cochlea. The perilymphatic sac has become intraotic, and it is this structure (not the perilymphatic duct) that is applied against the basilar membrane. This perilymphatic sac has followed the coiling of the cochlea (or scala media) along each side, forming thereby a double tube: one part, the vestibular ramp, or scala vestibuli, is directly connected to the fenestra

ovalis; the other part, terminating at the secondary tympanic membrane (closing the fenestra rotunda sensu stricto), is the tympanic ramp or scala tympani. It follows, therefore, that, according to this definition, it is the scala tympani which is applied against the basilar papilla (in mammals called the organ of Corti).⁵

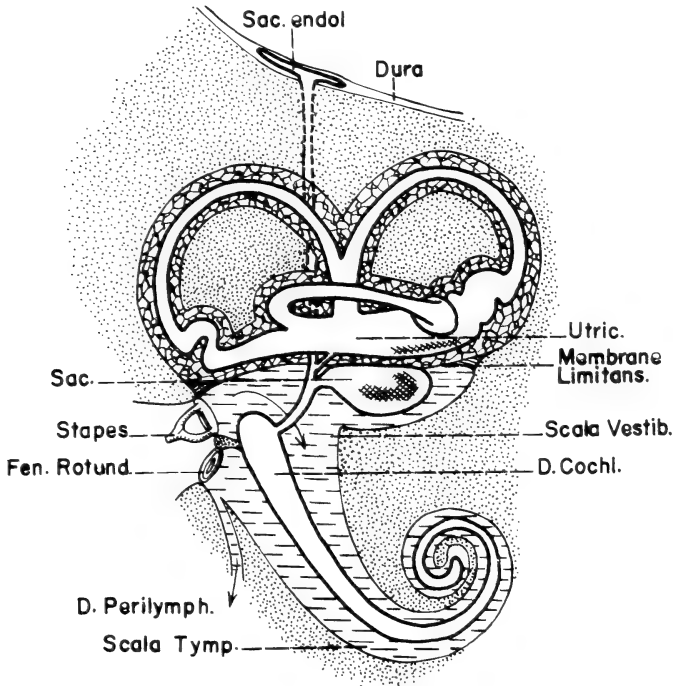


Fig. 6. Interrelationships of the peri- and endolymphatic systems in mammals (from De Burlet).

By homology, the part of the perilymphatic system which in reptiles forms the same support for the basilar papilla is also called the scala tympani,⁶ even though it concerns the perilymphatic duct, and not, as in mammals, the perilymphatic sac. This difference leads to a dislocation of the terms: the bony cavity which in mammals encloses the scala tympani (that is, the whole perilymphatic sac) constitutes the recessus scalae tympani. By homology, but a somewhat perverse homology, the (incomplete) bony cavity which houses the

⁵ It should be noted that, despite this development, the internal ear is entirely included in the periotic; this is also the case in living reptiles, but in mammal-like reptiles, as was seen above, not only the periotic but also the basioccipital participates in the bony internal ear. In cynodonts, however, this bone is reduced to a minimal participation.

⁶ This term is all the more improper in that the lagena is here short and straight, and that the duct is not parallel, but perpendicular to it; there are not, therefore, two ramps. In crocodiles the lagena is elongate and the ramps are discernible, but they remain straight.

perilymphatic sac in reptiles has received the name of recessus scalae tympani, even though, let it be repeated, the scala tympani is here constituted by the duct and not by the perilymphatic sac, and is not, in consequence, contained in the 'recessus scalae tympani'. Moreover, this recessus is in reptiles an extraotic and extracerebral space (enclosed either between the periotic and the supraoccipital, or within the exoccipital). Its embryological origin goes back to the metotic fissure, that is, the space left between the embryonic otic capsule and the base of the skull. This fissure, in the embryo, serves not only as an opening for the perilymphatic sac, but it forms also a passage for the cranial nerves IX, X, XI, and the jugular vein.⁷ In mammals (as well as in crocodiles and in birds, although by a different process) the recessus has become entirely closed and intraotic by the secondary formation of a bony floor. In the course of this process the openings have been preserved, but at the same time submitted to modifications which result in, for example, the lateral opening (or fenestra rotunda) not being entirely homologous to the opening of the same name in reptiles.

Many other homologies have been proposed. I have lightly touched upon the problem here, only wanting to explain the terms utilized.

To come back to *Gorgonops*, this cistern is probably indiscernible at the level of the fenestra ovalis, unless, ventrally and laterally to the lagenar recess, a non-ossified region between the basioccipital and the prootic (sections 230 A-246 A) represents a trace of this cistern (Fig. 4a, z). The perilymphatic duct also remains indistinct, although a part of the cavity interpreted as the posterior ampulla may correspond to it. On the contrary, it has been thought possible to detect a trace of the perilymphatic sac in the form of a 'recessus scalae tympani': there exists (Fig. 4b, section 278 A), on the mesial side of the opisthotic partition closing the ear posteriorly, a depression which opens farther to the rear (section 284 A) into the jugular passage; the latter must therefore represent the whole of the metotic fissure (the jugular foramen plus the pseudo-fenestra rotunda).

Finally, concerning the endolymphatic sac, I have evoked the possibility that the depression (discernible in the prootic, then supraoccipital, partition) which separates the floccular fossa from the ear proper (8) could represent the trace of this sac. Another possibility is that the orifice which persists posteriorly (Fig. 4b, section 285 A, y), in the mesial wall of the bony ear, corresponds to the passage of the endolymphatic duct towards this sac, which would be, in that case, more mesial.

The fenestra ovalis is situated very anteriorly; moreover, it does not open at the base of the lagenar recess, but ventro-laterally with respect to it (Fig. 2). One can, therefore, consider that it has started to rise towards the vestibular part of the ear, where it lies in living reptiles and mammals, and where it is properly a 'fenestra vestibuli'. Furthermore, whereas in these two cases it pierces the otic capsule, it is here included between the otic capsule and the

⁷ In the adult, different cases are possible: the recessus scalae tympani can fuse with the jugular canal; it can also contain only the perilymphatic sac and the nerve IX.

base of the skull. Olson had already noted this last point in 1938, but the fenestra ovalis and the metotic fissure are, in *Gorgonops*, independent of each other. The anterior edge of the fenestra ovalis is no more distinct than that of the lagenar recess. Anteriorly it is bounded dorsally by the prootic, ventrally by the basioccipital. It almost closes (section 248 A) by the intervention of the mesial part of the opisthotic, but it is prolonged by a slit (2.5 mm long) as far as the complete junction of this mesial part with the lateral part of the bone, which results in the disappearance of the prootic from its roof (section 261 A). Behind its closure persists, in the opisthotic, a conical depression one millimetre long. The stapes covers all of the fenestra ovalis, and half of the slit. One might suppose that the two millimetres remaining behind the stapes (half of the slit plus the posterior fossa) were occupied by a cartilaginous expansion.

That which has been very tentatively interpreted here as the mesial orifice of the nerve VII is situated slightly in front of the level of the horizontal canal; the nerve would then cross the bone, somewhat obliquely towards the front and laterally, and would exit just in front of the ear (Fig. 1). The position of the geniculate ganglion would be visible ventrally and behind nerve VII, between the prootic and the basisphenoid (Fig. 4a, section 240 A, g g).

The nerves IX, X and XI must have exited by the jugular canal, which passes first between the opisthotic and the exoccipital then, farther toward the rear, inside the exoccipital (Fig. 4b, section 295 A); this canal is completely separated from the posterior part of the ear by a bony wall.

COMPARISON WITH OTHER GORGONOPSIANS

As has been noted above, the internal ear has already been studied in *Cyonosaurus longiceps* (*Cistecephalus* zone⁸) by Olson in 1937, and the same author in the following year sectioned a skull of '*Cynariops*' (*Endothiodon* zone⁸) and reconstructed the membranous labyrinth. In 1944 he made several modifications in his reconstructions. The comparison of these with that proposed here for *Gorgonops torvus* (*Endothiodon* zone⁸) may indicate a certain evolution of this region within the gorgonopsians.⁹

In all three cases a feeble degree of mesial ossification can be observed. The separation of the floccular fossa from the internal ear proper intervenes in the three cases also, but the partition is here parallel to the horizontal canal, whereas it forms with the latter an angle of about 65° in *Cyonosaurus* and 45° in '*Cynariops*'. One would witness here, if the proposed morphologic sequence is accepted, a dorsal migration of the floccular fossa, which, from an anterior position, would become dorsal.

The floccular fossa seems to have approximately the same depth in the three forms. Also it is partially enclosed in the supraoccipital.

⁸ *Sensu* Broom.

⁹ In a previous study (1970), I considered that *Cyonosaurus* was the most primitive gorgonopsid, that *Gorgonops* would be a rather evolved form, and that '*Cynariops*' would be situated morphologically between the two.

The anterior semicircular canal is always longer than the posterior, but the difference in length is greater in *Gorgonops* and in '*Cynariops*' than in *Cyonosaurus*. As for the individualization of the posterior canal from the crus communis, it is the least marked in *Gorgonops*. The horizontal canal would be more convex here than in the genera studied by Olson, a fact which, according to him, would constitute a primitive character.

The anterior and external ampullae seem to have been well individualized, in *Cyonosaurus* at least; the external ampulla is not figured in '*Cynariops*', and the difficulty met with in distinguishing both of them in *Gorgonops* has already been commented on; they seem to have been, in any case, smaller here.

The comparison becomes more difficult for the utriculo-sacculus region, due to the fact that my interpretation differs from that of Olson. The latter considered that the sacculus was entirely situated in the lower part of the ear, indistinct from the lagena, with the ensemble forming what he calls the sacculo-cochlear recess. I have, on the contrary, suggested that the cavity, above and below the horizontal canal and mesial to it, could hardly represent anything but the sacculus, whereas the crus communis and the utriculus would be less well individualized. A side by side comparison of the material is needed to resolve this matter.

The lagenar recess is even longer here than in *Cyonosaurus*; it was very short in '*Cynariops*'. It is very mesially situated in *Gorgonops* and oriented ventro-anteriorly, whereas it is directed towards the rear in *Cyonosaurus* and becomes vertical in '*Cynariops*' and a little more anterior than in the preceding genus. One can therefore confirm the tendency noted by Olson, wherein the lagena would migrate anteriorly and mesially in an evolutionary sequence. *Gorgonops* would then be situated above the two others in this regard.

The fenestra ovalis, instead of being, as it is here, antero-lateral with respect to the lagena, is definitely ventral in the two genera studied by Olson, and even oriented a little posteriorly in *Cyonosaurus*. This situation, like that of the lagena, makes of the ear of *Gorgonops* an evolved structure with respect to that of the two preceding genera.

But, on the contrary, the supposed position of the orifice for nerve VII, slightly in front of the horizontal canal, does not prolong the sequence sketched according to Olson by the two other gorgonopsians; in his view this orifice should migrate toward the rear in an evolved form. This point will be taken up further on.

As in *Cyonosaurus* and '*Cynariops*', the jugular foramen is isolated from the internal ear by a bony wall, although this foramen is less posteriorly situated here.

In 1938 Olson indicated the trace in '*Cynariops*' of an endolymphatic duct, leading to an endolymphatic sac situated against the suture separating the prootic and the supraoccipital, behind the floccular fossa. But in 1944 he interpreted this opening as the 'dorsal entrance of the sinus utricularis into the periotic' and as indicating 'the level of the junction of the utriculus with the crus communis canalium'. Whatever may be the interpretation of this structure,

it seems that it agrees with that cited above in the mesial wall of the ear of *Gorgonops*.¹⁰

From this short comparison it can be seen, first of all, that the region of the internal ear shows a definite homogeneity in the three gorgonopsians discussed. But one can also discern indications of variability, even though it is difficult to decide in which direction the evolution occurred. To determine this, it would be necessary to methodically explore the infra-order. Neither does one know if this evolution was harbingering that was undergone by the more evolved theriodonts in their tentatives toward mammalness, or if, like the prootic bone, the ear of Gorgonopsidae evolved more or less against the trends seen in the other theriodonts.

On this topic, and in conclusion, some of the evolutionary tendencies presented by the therapsid internal ear can be envisaged. These were essentially brought out by Olson (1944).

According to this author, the relationship of the ear length to the length of the skull diminishes when the latter increases in absolute value. The specimen of *Gorgonops*, larger than all the theriodonts described by Olson, fully confirms this point of view, with a proportion of 0,06, which is lower than all the indices obtained by him. The relationship of ear width over length is very 'gorgonopsian' with 0,06, but it does not appear possible to follow a progression throughout the therapsid series. On the other hand, the height of the ear would make this specimen the most evolved of all, with 0,1 (the cynodonts, however, could not be evaluated in this respect).

The feeble degree of mesial ossification seems general, from the pelycosaurs to the cynodonts, with no sign of progress even in the latter. In most of the forms also, the anterior vertical canal apparently opens, by the same lack of ossification, into the floccular fossa. Finally, and paradoxically, it is only in *Dimetrodon* and the gorgonopsians that the jugular canal is separated by a bony wall from the labyrinthine cavity.

If the floccular fossa was shallow in pelycosaurs and the first anomodonts, it is, however, difficult to discern a precise evolutionary direction of this structure in the therapsid series, and still less to recognize a relationship between the fossa and the flocculus. One can say that it is in the three gorgonopsians, the therocephalian B of Olson, and in the cynodonts (Olson and Simpson), that the fossa is the deepest. On another point it seems to me that one can follow the migration of the flocculus from in front of the internal auditive foramen (anomodonts, gorgonopsians A and B of Olson), toward the dorsal side (*Pristerodon*, *Gorgonops*, therocephalians and cynodonts), and then toward the rear (mammals). But *Dimetrodon* adds a disturbing element to this sequence with a flocculus placed above the internal ear.¹¹

According to Olson, the inequality between the anterior and the posterior

¹⁰ And with that noted by Simpson (1933) above and behind the floccular fossa in a cynodont.

¹¹ This constant reference to the specialized form that is *Dimetrodon* is hardly justified, except that it constitutes the only source of information we have for the pelycosaurian ear.

vertical canals increases as one rises stratigraphically through the anomodontid series. This is not valid in the gorgonopsids, since, by this trait also, *Gorgonops* differs from the other forms and attains the degree reached by the more advanced and later theriodonts. On the other hand, the canals are generally more distinct from the *crus communis* than they are here.

The lagena is contained in the prootic dorsally and in the basioccipital ventrally, an arrangement that began with *Captorhinus*. But the participation of the basioccipital diminishes progressively (cynodonts) as the ear rises in the periotic to attain a mammalian position. In this regard, *Gorgonops* occupies a primitive position; on the contrary, the migration of this structure anteriorly is as advanced in this genus as it is in the known cynodonts, and the mesial migration is even more marked. The fenestra ovalis would have followed the migration of the lagena.

As expressed by Olson, one could expect that the orifice of nerve VII would migrate toward the rear progressively with the increase in the general degree of mammalness. Unhappily, the available facts hardly confirm this supposition, since Olson's gorgonopsians A and B are in this respect 'evolved', and *Gorgonops* and the cynodonts lag behind.

It is supposed that the nerves IX, X and XI exited through the jugular canal in all forms. Let us keep in mind that this canal is isolated from the ear only in pelycosaurs, gorgonopsians and the cynodont studied by Simpson. The dicynodont ear described by Cox (1962) agrees, on the contrary, with the more general condition.

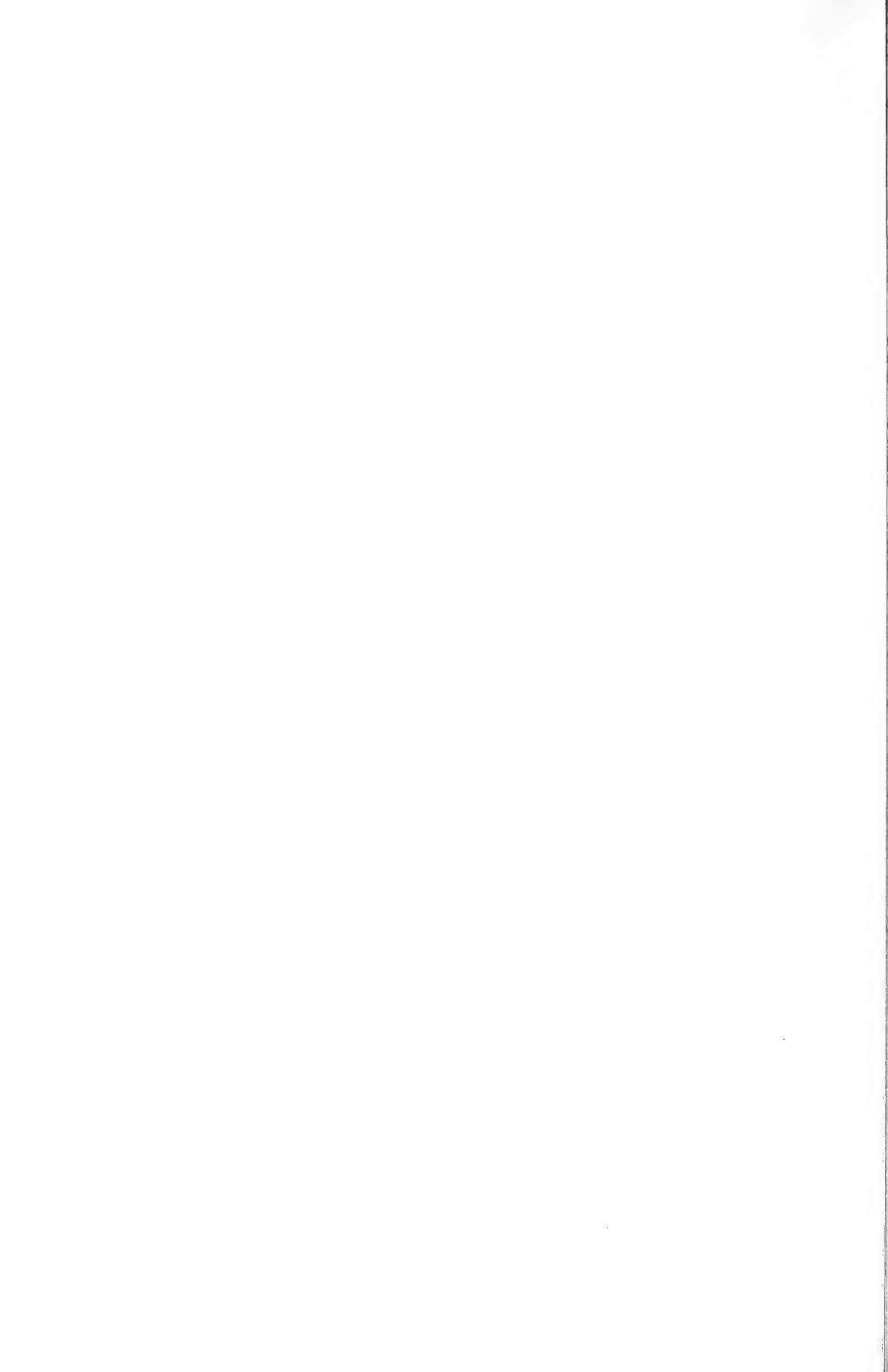
The nerve XII leaves by a single orifice in pelycosaurs, anomodonts, and gorgonopsians, and by two orifices in cotylosaurs, certain thercephalians and cynodonts.

In summary, defining a primitive stage for the therapsid ear as well as a general evolutionary direction is hardly easier than it is for the gorgonopsians alone. It is probable that each infra-order tried the ascension independently, by beginning at nearly the same low level. But there exists an obvious necessity to considerably extend our knowledge of each of these infra-orders before we can validly appreciate their positions with respect to each other, even as concerns only the internal ear region. This is all the more desirable since the latter is a very stable region, unaffected by secondary adaptations, and which, in consequence, should contribute to our understanding of the acquisition of the mammalian stage.

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ETUDE DU CRANE D'UN JEUNE SPECIMEN DE *MOSCHORHINUS KITCHINGI* BROOM, 1920 (? *TIGRISUCHUS SIMUS* OWEN, 1876),
THEROCEPHALIA PRISTEROSAURIA MOSCHORHINIDAE
D'AFRIQUE AUSTRALE

(Remarques sur les Moschorhinidae et les Whaitsiidae¹)

Par

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(Avec 7 planches, 12 figures et 1 tableau)

PLAN

Introduction	72
Description	72
I. Crâne	73
A—Crâne dermique	73
1. Face dorsale	73
2. Occiput	79
3. Joue	79
4. Palais	80
B—Endocrâne	83
C—Principales fosses et ouvertures de la région postérieure du crâne	86
II. Mandibule	88
III. Splanchnocrâne	90
IV. Dentition	94
Discussion	94
I. Comparaison entre les Moschorhinidae et les deux autres familles	100
A—Moschorhinidae et Whaitsiidae	100
B—Moschorhinidae et Annatherapsididae	102
II. Composition des Whaitsiidae et des Moschorhinidae	103
A—Les Whaitsiidae	103
1. Moschowhaitsiinae	104
2. Whaitsiinae	104
B—Les Moschorhinidae	105
1. Annatherapsidinae	105
2. Moschorhininae	106
3. Euchambersiinae	109
C—Genres exclus des Whaitsiidae et Moschorhinidae	109
Conclusion	110
Liste des abréviations des noms de collections	111
Résumé	112
Abstract	112
Zusammenfassung	112
Resumen	113
Remerciements	113
Littérature citée	114

¹ Bien que le nom de genre *Waitsia* tombe en synonymie avec *Theriognathus* qui lui est antérieur, il ne nous a pas paru nécessaire de remplacer le nom de famille Whaitsiidae, consacré par l'usage, par celui de Theriognathidae.

INTRODUCTION

Le crâne étudié ici appartient au plus petit spécimen connu actuellement du genre *Moschorhinus* (la possible synonymie avec *Tigrisuchus* est discutée plus loin). L'espèce-type de *Moschorhinus* est *M. kitchingi*; Kitching (1968: 67) a regroupé dans cette espèce les spécimens jusqu'alors considérés comme *M. esterhuyseni* et *M. natalensis* et laissé à part *M. warreni*. Celui-ci, tout comme *M. minor*, est également à intégrer dans *M. kitchingi* (?*Tigrisuchus simus*).

Matériel: crâne, fragments de mandibule et d'éléments post-craniens, recueillis par l'équipe Crompton (A. W.), Ewer (R.F.), Griffin (B. S.) et Malan (M. E.), en janvier 1958.

Collection: South African Museum (Cape Town, Afrique du Sud), n°K.118.

Horizon: non indiqué.

Localité: Skerpioenkraal, Middelburg, Province du Cap, Afrique du Sud.

Seul le crâne est étudié ici.

DESCRIPTION

Le crâne du genre *Moschorhinus* (?*Tigrisuchus*) est remarquable par la brièveté et la massivité de son museau. Le spécimen S.A.M. n°K.118 ne fait pas exception à la règle. Il présente également une constriction postcanine très peu marquée. Les orbites sont relativement petites et les fosses temporales vastes. La crête sagittale est apparemment peu élevée.

Les principales mesures du crâne (reconstruit) de S.A.M. n°K.118 sont les suivantes:

Longueur du crâne	160 mm environ
Largeur maximale	122 mm environ
Largeur intertemporale minimale	14 mm
Largeur interorbitaire minimale	36 mm environ
Distance entre le bord antérieur des prémaxillaires et le bord antérieur de l'orbite	66 mm environ
Distance entre le bord antérieur des prémaxillaires et le bord antérieur de la fenêtre temporale	95 mm environ
Largeur du museau au niveau de la constriction postcanine	62 mm environ
Hauteur du museau au même niveau	45 mm environ
Hauteur maximale de l'occiput	58 mm environ
Largeur maximale de l'occiput	122 mm environ
Longueur totale de la denture maxillaire	{ à gauche	24 mm environ
	{ à droite	27 mm environ
Longueur totale de la rangée postcanine	{ à gauche	11 mm environ
	{ à droite	14 mm environ

Figures: Les figures sont des reconstitutions. Le léger aplatissement dorso-ventral a été corrigé et les régions manquantes d'un côté (région postérieure droite, côté gauche de la surface dorsale du museau, processus transverse du ptérygoïde gauche, . . .) ont été reconstituées par symétrie. Tandis que l'arrière-crâne est bien conservé à gauche, les dessins de détail représentent cette région

retournée comme s'il s'agissait d'un côté droit pour faciliter une comparaison ultérieure avec les autres Thérocéphales.

I—CRANE

A—Crâne dermique

Le crâne de ce spécimen est assez bien conservé malgré l'érosion du côté gauche de la face dorsale du museau, des arcades zygomatiques (dont subsiste une empreinte du côté gauche), des barres sousorbitaires et d'une partie des arcades postorbitaires.

1. Face dorsale (Fig. 1; Pl. I)

Les deux prémaxillaires (*Pmx*, Figs 1, 3; Pls I, III A, B, VII B), soudés sur la ligne médiane, sont presque complets, hormis le processus nasal dont il ne subsiste que la base. Près de celle-ci, on observe dorsalement le foramen prémaxillaire postérieur (*f.pmx.p*, Figs 1, 3; Pl. I) et antérieurement les foramens prémaxillaires dorsaux (*f.pmx.d*, Figs 2, 3; Pl. VII B), au nombre de trois du côté droit, le mieux conservé. Selon Brink (1958: 46-47), chaque prémaxillaire de B.P.I. n°F.1713/M.295 ne présenterait qu'un foramen prémaxillaire dorsal. Le nombre d'orifices de sortie des ramifications du rameau frontal de la branche ophthalmique du nerf trijumeau semble donc assez variable: le maximum connu serait trois. Le degré de recouvrement par le maxillaire est ici incertain du fait de l'érosion de ces régions.

Chaque prémaxillaire porte cinq incisives.

Le septomaxillaire (*Smx*, Figs 1, 3; Pls I, III A, B, VII A) est large et bien développé sur la face. La région de la fosse maxillo-septomaxillaire est abîmée ici, mais chez un autre spécimen (B.P.I. n°F.2205/M.193) est représentée une configuration comparable à celle d'*Akidnognathus* décrite par Brink (1960: 156, fig. B, C, D; 164), de *Regisaurus* décrite par Mendrez (1972a: 192-196, fig. 6) et d'un *Whaitsiidae*, Tü.n°K.65 (observation personnelle). Il est à noter que chez les différents Thérocéphales où cette fosse a pu être observée en détail, sa structure est comparable à celle que Sigogneau (1970b: 26, fig. 1) a étudiée chez un Gorgonopsien Ictidorhinidé: *Rubidgina* sp., B.P.I. n°F.3924. Si l'érosion de la partie antérieure du museau a détérioré la région de la fosse maxillo-septomaxillaire, elle a mis en évidence le canal septomaxillaire (*c.smx*, Pls III, VII B).

Le maxillaire (*Mx*, Figs 1, 3; Pls I, III) est élevé et participe largement à la barre sousorbitaire; ce que Brink (1958: 47) remarquait chez le spécimen B.P.I. n°F.1713/M.295. La limite postérieure du maxillaire n'est ici pas connue en raison de l'érosion partielle des barres sousorbitaires. La région de contact entre maxillaire et préfrontal (*Pfr*) est également endommagée, mais, à droite, l'empreinte du préfrontal montre que ce contact, classique chez les Thérocéphales, était loin d'être aussi réduit que chez le spécimen B.P.I. n°F.2205/M.192, tel que Brink l'a représenté (1958: 41, fig. 16-A; 42, fig. 16-B). Ce

dernier spécimen est en réalité très dissymétrique et si sur le côté droit endommagé le contact entre le maxillaire et le préfrontal est bref, il est par contre important sur le côté gauche (observation personnelle). La surface du maxillaire

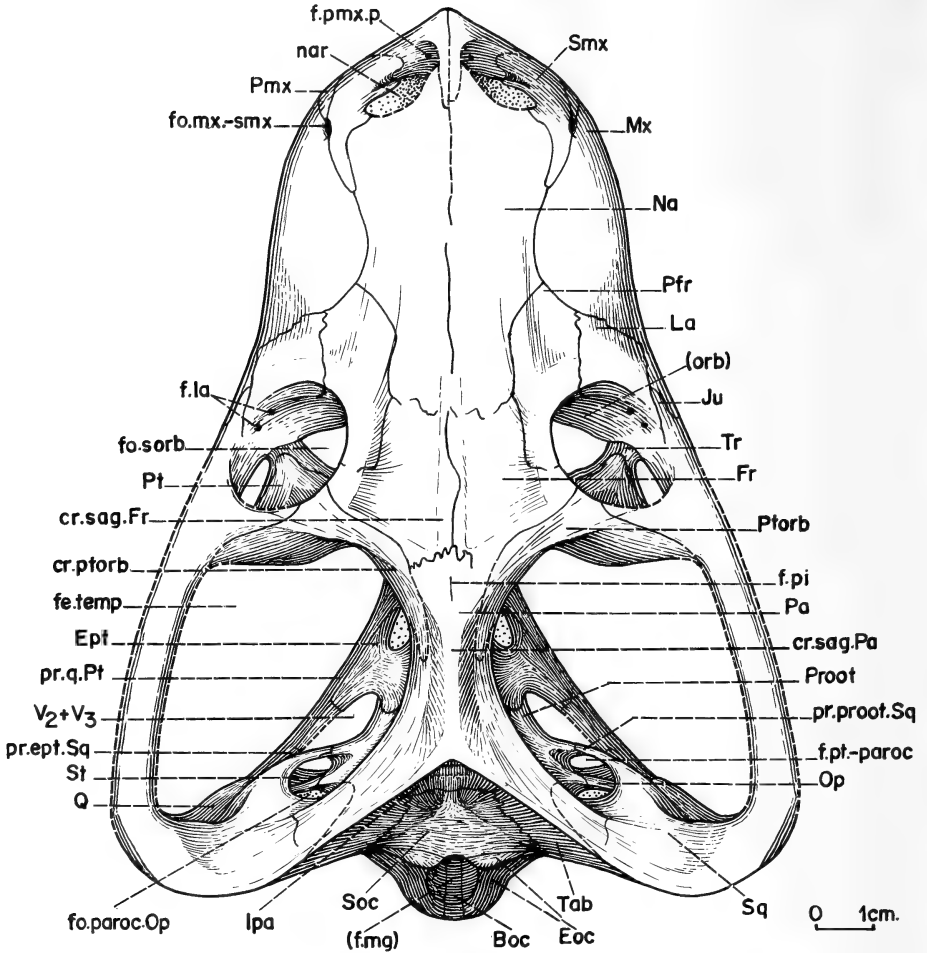


Fig. 1. *Moschorhinus kitchingi*, Moschorhinidae, S.A.M. n°K.118. Vue dorsale du crâne ($\times \frac{3}{4}$).

Boc, basioccipital; *cr.ptorb*, crête postorbitaire; *cr.sag.Fr*, crête sagittale du frontal; *cr.sag.Pa*, crête sagittale du pariétal; *Eoc*, exoccipital; *Ept*, épiptérygoïde; *f.la*, foramens lacrymaux; (*f.mg*), foramen magnum; *f.pi*, foramen pinéal; *f.pmx.p*, foramen prémaxillaire postérieur; *f.pt.-paroc*, foramen ptérygo-paroccipital; *fe.temp*, fenestra temporalis; *fo.mx.-smx*, fosse maxillo-septomaxillaire; *fo.paroc.Op*, fosse paroccipitale de l'opisthotique; *fo.sorb*, fosse sousorbitaire; *Fr*, frontal; *lpa*, interpariétal; *Ju*, jugal; *La*, lacrymal; *Mx*, maxillaire; *Na*, nasal; *nar*, narine; *Op*, opisthotique; (*orb*), orbite; *Pa*, pariétal; *Pfr*, préfrontal; *Pmx*, prémaxillaire; *pr.ept.Sq*, processus épiptérygoïde du squamosal; *pr.proot.Sq*, processus prootique du squamosal; *pr.q.Pt*, processus carré du ptérygoïde; *Proot*, prootique; *Pt*, ptérygoïde; *Ptorb*, postorbitaire; *Q*, carré; *Smx*, septomaxillaire; *Soc*, supraoccipital; *Sq*, squamosal; *St*, stapes; *Tab*, tabulaire; *Tr*, transverse; *V2 + V3*, lieu de sortie des branches maxillaire et mandibulaire du nerf trijumeau.

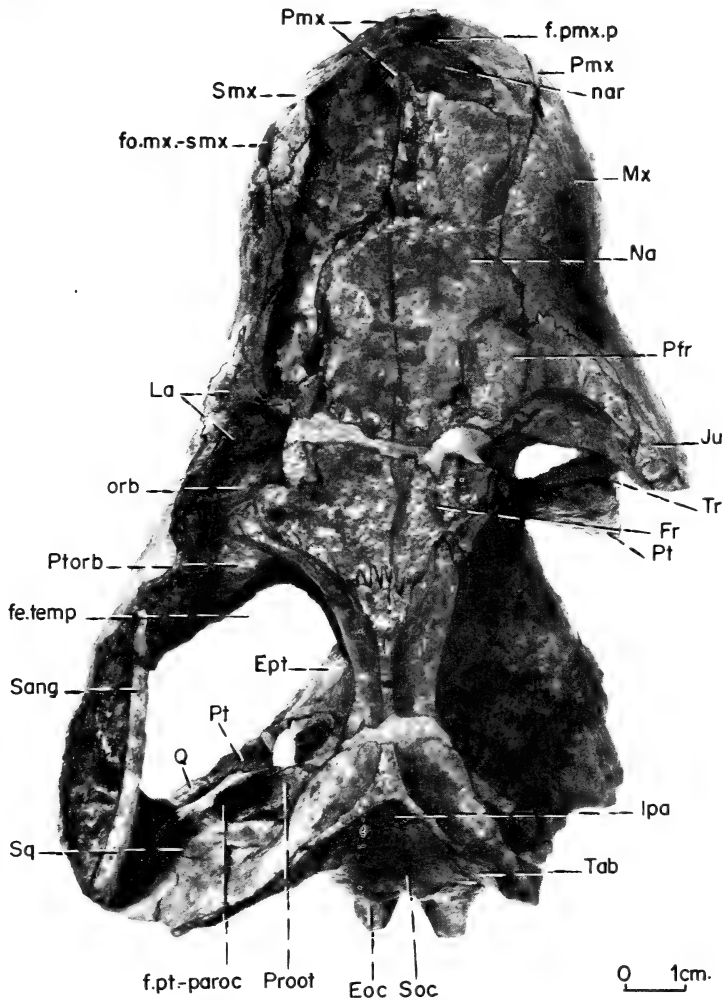


PLANCHE I. *Moschorhinus kitchingi*, Moschorhinidae, S.A.M. n°K.1118, vue dorsale du crâne ($\times \frac{1}{2}$).

Ept, épiptérygoïde; *Eoc*, exoccipital; *f.pmx.p*, foramen prémaxillaire postérieur; *f.pt.-paroc*, foramen ptérygo-paroccipital; *fe.temp*, fenestra temporalis; *fo.mx-smx*, fosse maxillo-septomaxillaire; *Fr*, frontal; *lpa*, interpariétal; *Ju*, jugal; *La*, lacrymal; *Mx*, maxillaire; *Na*, nasal; *nar*, narine; *orb*, orbite; *Pfr*, préfrontal; *Pmx*, prémaxillaire; *Proot*, prootique; *Pt*, ptérygoïde; *Ptorb*, post-orbitaire; *Q*, carré; *Sang*, susangulaire; *Smx*, septomaxillaire; *Soc*, supraoccipital; *Sq*, squamosal; *Tab*, tabulaire; *Tr*, transverse.

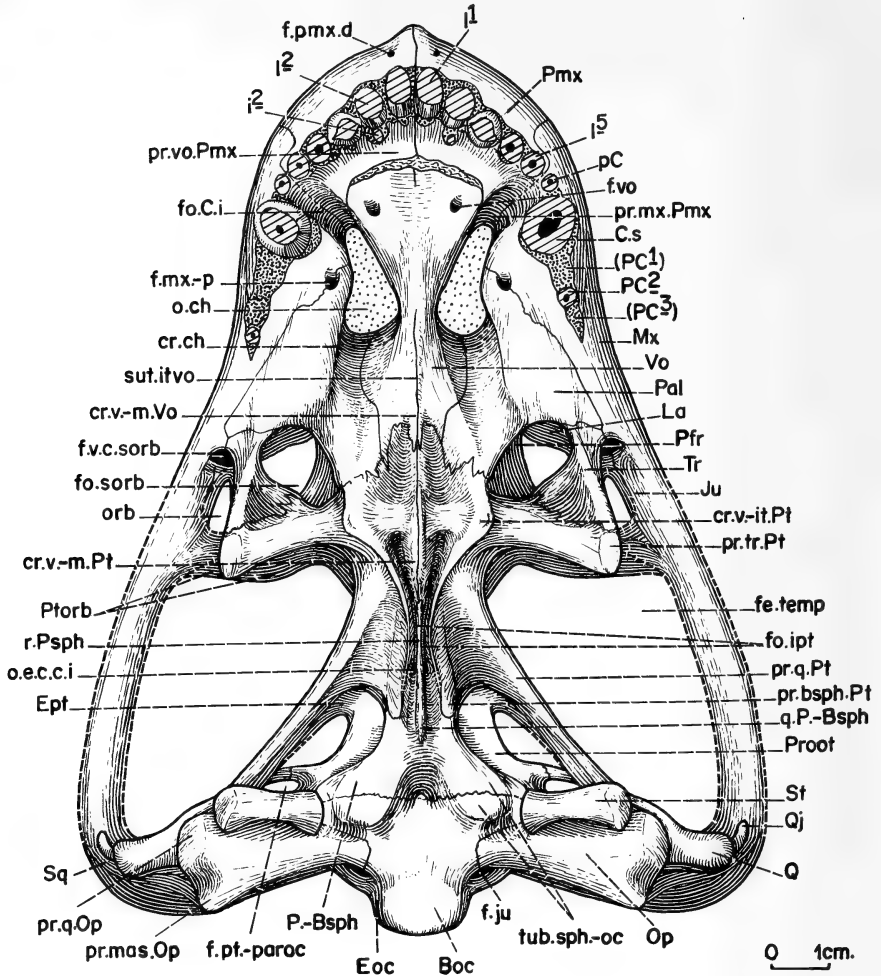


Fig. 2. *Moschorhinus kitchingi*, Moschorhinidae, S.A.M. n°K.118. Vue ventrale du crâne ($\times \frac{3}{4}$).

Boc, basioccipital; *C.s.*, canine supérieure; *cr.ch.*, crista choanalis; *cr.v-it.Pt.*, crête ventro-intermédiaire du ptérygoïde; *cr.v-m.Pt.*, crête ventro-médiane du ptérygoïde; *cr.v-m.Vo.*, crête ventro-médiane du vomer; *Eoc*, exoccipital; *Ept*, épiptérygoïde; *f.ju.*, foramen jugulaire; *f.mx-p.*, foramen maxillo-palatin; *f.pmx.d.*, foramen prémaxillaire dorsal; *f.pt-paroc.*, foramen ptérygo-paroccipital; *f.v.c.sorb.*, foramen pour les vaisseaux du canal sousorbitaire; *f.vo.*, foramen voméro-nasal; *fe.temp.*, fenestra temporalis; *fo.C.i.*, fosse pour la canine inférieure; *fo.ipt.*, fosse interptérygoïdienne; *fo.sorb.*, fosse sousorbitaire; *I1*, première incisive supérieure; *I2*, deuxième incisive supérieure; *I3*, cinquième incisive supérieure; *I5*, deuxième incisive supérieure de remplacement; *Ju*, jugal; *La*, lacrymal; *Mx*, maxillaire; *o.ch.*, ouverture choanale; *o.e.c.i.*, orifice externe du canal de la carotide interne; *Op*, opisthotique; *orb*, orbite; *P.-Bsph.*, complexe para-basisphénoïde; *Pal*, palatin; *(PC1)*, alvéole de la première postcanine supérieure; *PC2*, deuxième postcanine supérieure; *(PC3)*, alvéole de la troisième postcanine supérieure; *pC*, précanine; *Pfr*, préfrontal; *Pmx*, prémaxillaire; *pr.bsph.Pt.*, processus basisphénoïde du ptérygoïde; *pr.mas.Op.*, processus mastoïde de l'opisthotique; *pr.mx.Pmx.*, processus maxillaire du prémaxillaire; *pr.q.Op.*, processus carré de l'opisthotique; *pr.q.Pt.*, processus carré du ptérygoïde; *pr.tr.Pt.*, processus transverse du ptérygoïde; *pr.vo.Pmx.*, processus vomérin du prémaxillaire; *Proot*, prootique; *Ptorb*, postorbitaire; *Q*, carré; *q.P.-Bsph.*, quille du complexe para-basisphénoïde; *Qj*, quadratojugal; *r.Psph.*, rostre du parasphénoïde; *Sq*, squamosal; *St*, stapes; *sut.itvo.*, suture intervomérine; *Tr*, transverse; *tub.sph-oc.*, tuberculum spheno-occipitale; *Vo*, vomer.

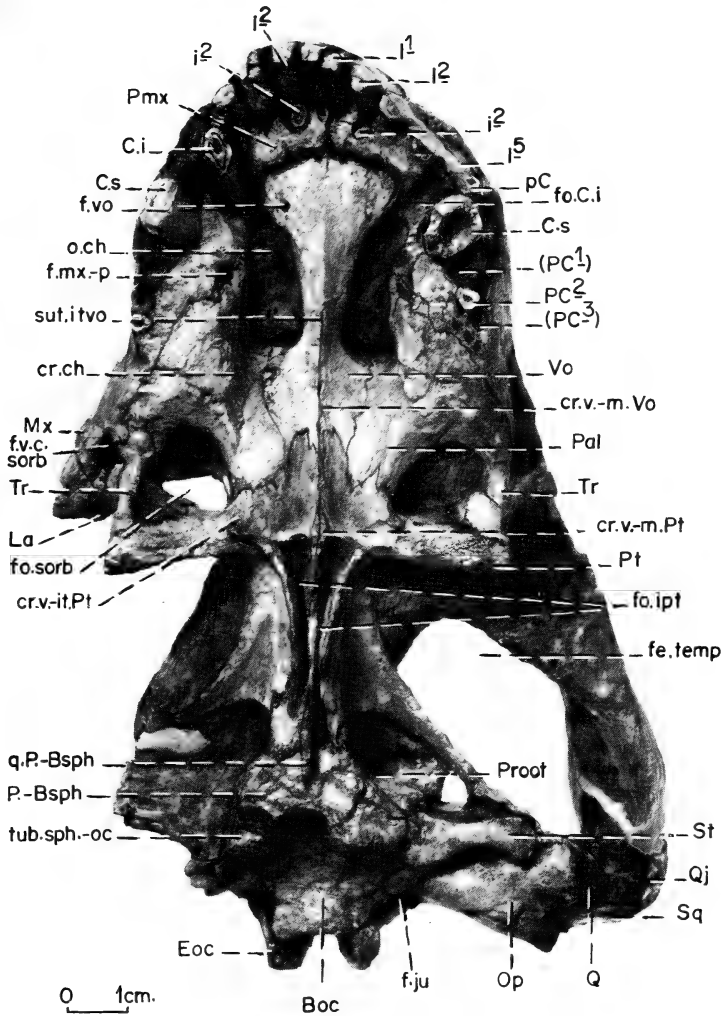


PLANCHE II. *Moschorhinus kitchingi*, Moschorhinidae, S.A.M. n°K. 118, vue ventrale du crâne
($\times \frac{5}{8}$).

Boc, basioccipital; *C.i*, canine inférieure; *C.s*, canine supérieure; *cr.ch*, crista choanalis; *cr.v.-it.Pt*, crête ventro-intermédiaire du ptérygoïde; *cr.v.-m.Pt*, crête ventro-médiane du ptérygoïde; *cr.v.-m.Vo*, crête ventro-médiane du vomer; *Eoc*, exoccipital; *f.ju*, foramen jugulaire; *f.mx.-p*, foramen maxillo-palatin; *f.v.c.sorb*, foramen pour les vaisseaux du canal sousorbitaire; *f.vo*, foramen voméro-nasal; *fe.temp*, fenestra temporalis; *fo.C.i*, fosse pour la canine inférieure; *fo.ipt*, fosse interptérygoïdienne; *fo.sorb*, fosse sousorbitaire; *I¹*, première incisive supérieure; *I²*, deuxième incisive supérieure; *I⁵*, cinquième incisive supérieure; *i²*, deuxième incisive supérieure de remplacement; *La*, lacrymal; *Mx*, maxillaire; *o.ch*, ouverture choanale; *Op*, opisthotique; *P.-Bsph*, complexe para-basisphénoïde; *Pal*, palatin; *(PC¹)*, alvéole de la première postcanine supérieure; *PC²*, deuxième postcanine supérieure; *(PC³)*, alvéole de la troisième postcanine supérieure; *pC*, précanine; *Pmx*, prémaxillaire; *Proot*, prootique; *Pt*, ptérygoïde; *Q*, carré; *q.P.-Bsph*, quille du complexe para-basisphénoïde; *Qj*, quadratojugal; *Sq*, squamosal; *sut.itvo*, suture inter-vomérine; *St*, stapes; *Tr*, transverse; *tub.sph-oc*, tuberculum spheno-occipitale; *Vo*, vomer.

est 'grêlée' et marquée de très petits foramens pour les diverses branches cutanées du nerf alvéolaire supérieur.

La brièveté des nasaux (*Na*, Figs 1, 3; Pls I, III) est en relation avec celle du museau. Il est à noter cependant que la suture fronto-nasale est située en arrière du niveau du bord antérieur des orbites.

Le lacrymal (*La*, Figs 1, 3; Pls I, III) est haut et bien étendu sur la face, en avant des orbites. Par contre, il participe peu à la face externe de la barre sousorbitaire.

Le préfrontal (*Pfr*, Figs 1, 3; Pls I, III) est très développé, tant vers l'avant que vers l'arrière. Son bord antérieur présente un important contact avec le maxillaire (contact comparable à celui indiqué par Brink (1958: 44, fig. 18; 46, fig. 20) chez le spécimen B.P.I. n°F.1718/M.295). L'extension postérieure du préfrontal est telle qu'il forme plus de la moitié du bord supérieur de l'orbite, ce qui s'observe également chez les autres spécimens de *Moschorhinus* (? *Tigrisuchus*).

Les frontaux (*Fr*, Fig. 1; Pl. I) sont relativement brefs mais larges. Leur participation au bord supérieur de l'orbite est assez faible en raison de l'extension des préfrontaux.

La partie antérieure du postorbitaire (*Ptorb*) est courte, tandis que son expansion postérieure est importante. Son processus latéral, long et massif, participe de façon importante à l'épaisse arcade postorbitaire.

On n'observe ni postfrontal ni prépariétal.

Les pariétaux (*Pa*, Figs 1, 3; Pls I, III) sont assez épais. Du fait de la relative brièveté de la crête sagittale (*cr.sag.Pa*, Fig. 1) et de sa division précoce en crêtes postorbitaires (*cr.ptorb*, Fig. 1) mousses, la partie antérieure des pariétaux forme chez les divers spécimens de *Moschorhinus* (? *Tigrisuchus*), une plateforme triangulaire à sommet postérieur. La crête sagittale du frontal (*cr.sag.Fr*, Fig. 1) est ainsi séparée de façon marquée de celle du pariétal. Chez les *Annatherapsididae* de l'U.R.S.S., *Annatherapsidus* Kuhn, 1961 (= *Anna* Amalitzky, 1922 préoccupé) (P.IN. Mw. n°2005/1993) selon Vjushkov 1955 (fig. 1) et *Chthonosaurus* Vjushkov, 1955 (P.IN. Mw. n°521/1-1) également selon cet auteur (p. 147 et fig. 5) la situation est voisine de celle existant chez *Moschorhinus* (? *Tigrisuchus*): 'Du côté dorsal, dans leur partie antérieure, ils (les pariétaux) ont la forme d'un triangle équilatéral dont la pointe dirigée vers l'arrière se transforme en une crête sagittale étroite et longue . . . '.

Chez le *Whaitsiidae* d'U.R.S.S., *Moschowhaisia* (P.IN. Mw. n°1100/20) un très petit creux existe à la place de cette plateforme. Chez les *Whaitsiidae* africains du genre *Theriognathus* Owen, 1876 (*syn.*: *Alopecopsis* Broom, 1920, *Aneugomphius* Broom & Robinson, 1948—celui-ci étant un sujet très jeune à crêtes peu marquées présente un aspect différent de celui des adultes—, *Hyenosaurus* Broom, 1935, *Moschorhynchus* Broom, 1936, *Notaelurops* Broom, 1936, *Notosollasia* Broom, 1925, *Whaitsia* Haughton, 1918), la crête sagittale pariétale ne se divise qu'au niveau de la suture fronto-pariétale en deux crêtes postorbitaires aiguës soulignées par les concavités du frontal de part et d'autre de la

crête sagittale du frontal qui ici, est en continuité avec celle du pariétal.

La région intertemporale est assez étroite, comme il est de règle chez les Thérocéphales Pristerosauria.

Le foramen pinéal (*f.pi*) est ici une fente extrêmement étroite située antérieurement. Chez le spécimen B.P.I. n°F.1713/M.295, Brink (1958: 43) fait la même remarque. Chez *Annatherapsidus* (cf. Vjushkov 1955: 135) et *Chthonosaurus* (Vjushkov 1955: 147) ce foramen serait même pratiquement fermé. Chez *Chthonosaurus*, un léger 'ourlet' des pariétaux indiquerait son emplacement. Chez *Moschowhaisia*, ce foramen manque complètement selon Tatarinov (1963: 78), tandis que chez les Whaitsiidae africains, ce foramen pinéal subsiste.

2. Occiput (Figs 4, 9; Pls IV A, B)

Comme chez de nombreux Thérocéphales et en particulier chez les Whaitsiidae, le pariétal contribue de façon assez importante à la face occipitale, au-dessus de l'interpariétal (*Ipa*) et d'une partie des tabulaires (*Tab*).

L'occiput est large et moyennement élevé, et la crête occipitale aiguë.

Sur la face occipitale, l'interpariétal est ovulaire, assez élevé par rapport à sa largeur. Il participe en outre, entre le pariétal, le supraoccipital et le squamosal, à l'angle postéro-médial de la fenêtre temporale (Fig. 3).

Le tabulaire, plus large que long, est totalement exclu du bord supérieur de l'ouverture postérieure de la fosse posttemporale (*fo.pttemp*) par une barre épaisse formée de l'association du processus postéro-dorsal de l'opisthotique (*pr.p.-d.Op*) et du processus intermédiaire du squamosal (*pr.it.Sq*). Il est également exclu du bord latéral de cette fosse par le processus mastoïde du squamosal (*pr.mas.Sq*, Fig. 9).

3. Joue (Fig. 3; Pl. III)

Du jugal (*Ju*) ne subsiste qu'une empreinte du côté gauche et un fragment mince sous la partie antérieure de l'orbite droite. Il s'étend vers l'avant à peine plus loin que le bord antérieur de l'orbite.

Le squamosal (*Sq*, Figs 1, 3, 4, 6, 7, 8, 9; Pls I, III, IV, V) est bien conservé à gauche; il ne manque que le processus jugal. Antérieurement (Fig. 6), le squamosal participe largement à la paroi postérieure de la fenêtre temporale (*fe.temp*):

— Le processus dorsal (*pr.d.Sq*, Figs 3, 6, 7, 8; Pl. V) recouvre le pariétal latéralement; son extrémité est brisée, mais son empreinte montre qu'il n'atteignait pas l'angle postéro-interne de la fenêtre temporale. Entre la base de ce processus et le bord supérieur du processus intermédiaire (*pr.it.Sq*) est pincée l'extrémité externe de l'interpariétal.

— Le processus intermédiaire est donc ici en contact non seulement avec le prootique et le supraoccipital mais encore d'une part, dorsalement, avec l'interpariétal et d'autre part, ventralement, avec le processus postéro-dorsal de l'opisthotique qui l'isole du bord supérieur de l'ouverture antérieure de la fosse posttemporale.

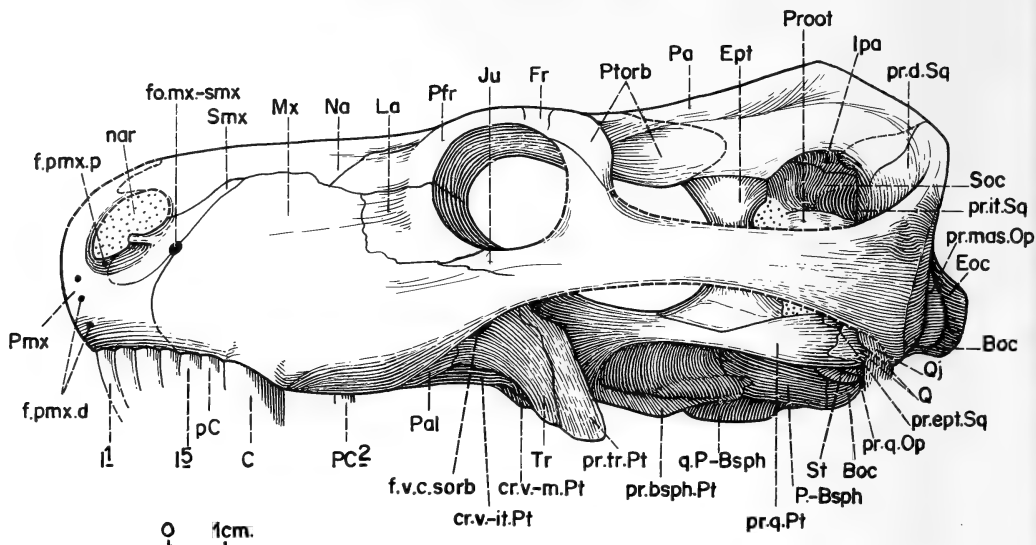


Fig. 3. *Moschorhinus kitchingi*, Moschorhinidae, S.A.M. n°K.118. Vue latérale gauche du crâne ($\times \frac{3}{4}$).

Boc, basioccipital; *C*, canine; *cr.v-it.Pt*, crête ventro-intermédiaire du ptérygoïde; *cr.v-m.Pt*, crête ventro-médiane du ptérygoïde; *Eoc*, exoccipital; *Ept*, épiptérygoïde; *f.pmx.d*, foramen prémaxillaire dorsal; *f.pmx.p*, foramen prémaxillaire postérieur; *f.v.c.sorb*, foramen pour les vaisseaux du canal sousorbitaire; *fo.mx-smx*, fosse maxillo-septomaxillaire; *Fr*, frontal; *I¹*, première incisive supérieure; *I²*, cinquième incisive supérieure; *Ipa*, interpariétal; *Ju*, jugal; *La*, lacrymal; *Mx*, maxillaire; *Na*, nasal; *nar*, narine; *P-Bsph*, complexe para-basisphénoïde; *Pa*, pariétal; *Pal*, palatin; *pC*, précanine; *PC²*, deuxième postcanine supérieure; *Pfr*, préfrontal; *Pmx*, prémaxillaire; *pr.bsph.Pt*, processus basisphénoïde du ptérygoïde; *pr.d.Sq*, processus dorsal du squamosal; *pr.ept.Sq*, processus épiptérygoïde du squamosal; *pr.it.Sq*, processus intermédiaire du squamosal; *pr.mas.Op*, processus mastoïde de l'opisthotique; *pr.q.Op*, processus carré de l'opisthotique; *pr.q.Pt*, processus carré du ptérygoïde; *pr.tr.Pt*, processus transverse du ptérygoïde; *Proot*, prootique; *Ptorb*, postorbitaire; *Q*, carré; *q.P-Bsph*, quille du complexe para-basisphénoïde; *Qj*, quadratojugal; *Smx*, septomaxillaire; *Soc*, supraoccipital; *St*, stapes; *Tr*, transverse.

— Le processus antéro-ventral (*pr.a-v.Sq*) est caractérisé par sa situation nettement en-dessous du bord supérieur du processus paroccipital de l'opisthotique et par sa subdivision en deux processus: l'un, le processus prootique (*pr.proot.Sq*), fusionné avec le processus central du prootique (*pr.c.Proot*), l'autre, le processus épiptérygoïde (*pr.ept.Sq*) dont il ne subsiste ici que la racine. Cette subdivision du processus antéro-ventral existe également chez les *Whaitsiidae*.

Le quadratojugal (*Qj*) n'est représenté que par un petit fragment (Figs 2, 3; Pls III, V, VII A).

4. Palais (Figs 2, 5; Pls II, VII A)

La structure du palais est une des différences essentielles entre *Moschorhinidae* et *Whaitsiidae*, les premiers ayant un palais nettement plus primitif

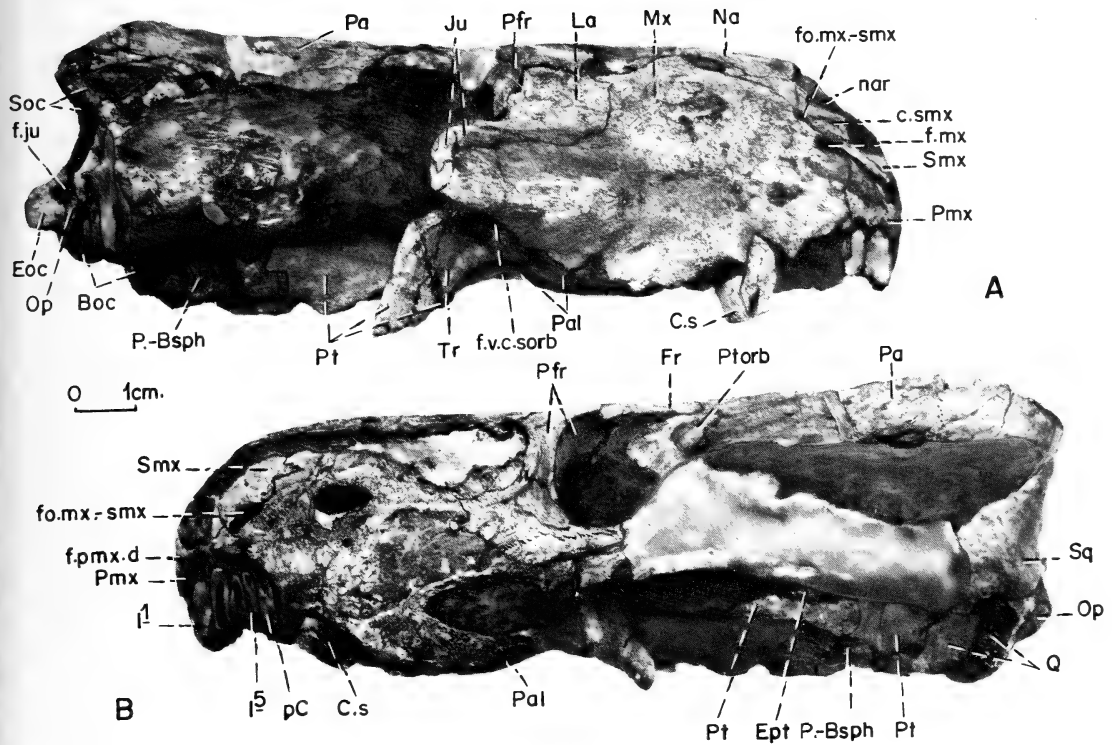


PLANCHE III. *Moschorhinus kitchingi*, Moschorhinidae. S.A.M. n°K.118; A, vue latérale droite du crâne ($\times \frac{1}{2}$); B, vue latérale gauche du crâne ($\times \frac{1}{2}$).

Boc, basioccipital; *C.s*, Canine supérieure; *c.smx*, canal septomaxillaire; *Eoc*, exoccipital; *Ept*, épiptérygoïde; *f.ju*, foramen jugulaire; *f.mx*, foramen maxillaire; *f.pmx.d*, foramen prémaxillaire dorsal; *f.v.c.sorb*, foramen pour les vaisseaux du canal sousorbitaire; *fo.mx-smx*, fosse maxillo-septomaxillaire; *Fr*, frontal; *I¹*, première incisive supérieure; *I⁵*, cinquième incisive supérieure; *ju*, jugal; *La*, lacrymal; *Mx*, maxillaire; *Na*, nasal; *nar*, narine; *Op*, opisthotique; *P.-Bsph*, complexe para-basisphénoïde; *Pa*, pariétal; *Pal*, palatin; *pC*, précanine; *Pfr*, préfrontal; *Pmx*, prémaxillaire; *Pt*, ptérygoïde; *Ptorb*, postorbitaire; *Q*, carré; *Smx*, septomaxillaire; *Soc*, supraoccipital; *Sq*, squamosal; *Tr*, transverse.

que les seconds, tant dans sa région antérieure que dans sa région postérieure.

Les prémaxillaires (*Pmx*) sont brefs médialement mais très étendus latéralement. Le processus maxillaire (*pr.mx.Pmx*, Fig. 2) est, ainsi que la partie antérieure du maxillaire, creusé d'une fosse en grande partie aveugle pour la canine inférieure (*fo.C.i*, Fig. 2; Pl. II) en continuité avec l'ouverture choanale (*o.ch*, Fig. 2; Pl. II). Cette dernière est réniforme, son bord latéral étant concave du fait du renflement de la paroi médiale du maxillaire et du palatin au niveau de la canine et des premières prémolaires. Ce renflement peut: soit être dû au grand diamètre de la canine, soit correspondre à un début de palais secondaire osseux. Dans la dernière hypothèse, il est à noter que cette région est plus primitive chez *Moschorhinus* (? *Tigrisuchus*) que chez les Pristerognathidae *Pristerognathus* et *Ptomalestes*, telle qu'elle fut décrite par Mendrez (1972b: 2960-1961, figs A, B). En effet, chez le premier, la *crista choanalis* (*cr.ch*, Fig. 2; Pl. II) est moins marquée à l'avant de ce renflement.

Les vomers (*Vo*, Fig. 2; Pls II, VII) ne sont fusionnés que de façon très incomplète: un reste de suture subsiste à l'avant de la plaque antérieure, interchoanale et une suture bien visible (*sut.itvo*, Fig. 2; Pl. II) sépare sur toute leur longueur les deux éléments qui forment la plaque postérieure qui s'étale sur les palatins et les ptérygoïdes. Comme chez les Thérocéphales primitifs, et en particulier les Annatherapsididae, la plaque antérieure et la plaque postérieure du vomer sont situées à peu près sur le même plan, tandis que chez les Whaitsiidae, l'inclinaison de la plaque postérieure est plus marquée et la plaque antérieure apparaît comme plus ventrale. Une autre caractéristique qui fait rapprocher *Moschorhinidae* et *Annatherapsididae* est l'étalement de la plaque antérieure 'en éventail' notait Brink (1958: 48) chez *Moschorhinus* (? *Tigrisuchus*) B.P.I. n°F.1713/M.295, 'en rame' observait Vjushkov (1955: 138) chez *Annatherapsidus* P.IN. Mw. n°2005/1933. Chez les Whaitsiidae de l'U.R.S.S., de Tanzanie et de l'Afrique du Sud, par contre, cette plaque est un élément cruciforme dont la partie antérieure est convexe ventralement, les branches latérales plates et recouvertes par des processus émis par les maxillaires et la région basale postérieure réduite à une étroite crête.

Chaque vomer est percé à l'avant d'un foramen voméro-nasal (*f.vo*, Fig. 2; Pl. II) bien développé.

La suture avec les ptérygoïdes est large, à fortes indentations.

Les ptérygoïdes (*Pt*, Figs 2, 3, 5; Pls I, II) bordent l'angle postéro-médial de la fosse sousorbitaire (*fo.sorb*, *id.*). Leurs crêtes ventro-intermédiaires (*cr.v.-it.Pt*, *id.*), à l'inverse de ce qui est connu chez les *Annatherapsididae* (cf. Vjushkov 1955) et les *Whaitsiidae* (cf. Mendrez 1965) ne semblent pas porteuses de dents (Kemp 1972: 32, considère que la perte des dents du palais est une des caractéristiques des *Whaitsiidae*, ceci est contraire aux observations de Mendrez 1965), mais ces régions étant altérées, on ne peut être absolument certain de ce fait. Comme chez certains *Scaloposauridae* et les *Annatherapsididae* *Annatherapsidus* (cf. Vjushkov 1955; fig. 3) et *Chthonosaurus* (Vjushkov 1955: 153, fig. 6), le processus carré (*pr.q.Pt*, Figs 2, 3, 4, 5, 8, 9, 10, 11; Pls II, V) et le pro-

cessus transverse (*pr.tr.Pt, id.*) sont reliés par 'une fine lame osseuse', comme le notait Vjushkov (1955). Chez les *Whaitsiidae*, cette lame n'existe pas. La relation entre les processus basisphénoïdes (*pr.bsph.Pt, id.*), dont les bords sont ourlés, est comparable à celle décrite par Vjushkov (1955) chez *Chthonosaurus*: ces deux processus ne sont pas jointifs sur la ligne médiane et sont séparés par le rostre du parasphénoïde (*r.Psph*, Figs 2, 5; Pl. V). Chez *Moschorhinus* (?*Tigrisuchus*) S.A.M. n°K.118, cette région a pu être dégagée assez profondément et on peut ainsi observer deux petits processus (*pr.psph.Pt*, Fig. 5; Pl. V) qui pincet ce rostre, dans la partie antérieure de la fosse interptérygoïdienne (*fo.ipt*, Figs 2, 5; Pls II, V). De ce fait, cette dernière forme deux fentes étroites de chaque côté de la poutre constituée par le rostre du parasphénoïde et les processus parasphénoïdes des ptérygoïdes (*pr.psph.Pt*). Chez *Annatherapsidus* par contre, les processus basisphénoïdes des ptérygoïdes sont jointifs sur presque toute leur longueur et ne laissent à l'avant qu'une petite fosse (Vjushkov 1955). Chez les *Whaitsiidae*, hormis *Moschowhaisia* chez qui subsiste une étroite fente antérieure séparant partiellement les processus basisphénoïdes, les processus basisphénoïdes sont jointifs sur toute leur longueur, ventralement par rapport au rostre du parasphénoïde.

Les palatins (*Pal*, Figs 2, 3, 5; Pls II, III, V, VII), bien développés, recouvrent les processus antérieurs des ptérygoïdes jusqu'à la moitié de la longueur des fosses sousorbitaires. Ces dernières sont vastes comme chez la presque totalité des Thérocéphales, hormis les *Whaitsiidae* de Tanzanie et d'Afrique du Sud et le *Moschorhinidae* *Euchambersia*.

Les transverses (*Tr*, Figs 2, 3, 5; Pls I, II, III, V) ou ectoptérygoïdes ont leur partie postérieure érodée: aussi est-il impossible de préciser le degré exact de recouvrement des apophyses transverses des ptérygoïdes. Le foramen des vaisseaux du canal sousorbitaire (*f.v.c.sorb*, Fig. 2; Pl. II) est très grand.

B—Endocrâne

La base de l'endocrâne est particulièrement bien exposée en vue ventrale (Figs 2, 5; Pls II, V).

Seuls les processus basiptérygoïdes du complexe para-basisphénoïde (*pr.bspt.P.-Bsph*) sont recouverts par les ptérygoïdes. La quille de ce complexe (*q.P.-Bsph*) apparaît beaucoup moins importante que chez les *Whaitsiidae* africains. Elle est endommagée chez les *Whaitsiidae* et *Annatherapsididae* russes. Le rostre du parasphénoïde est très robuste et son extrémité antérieure est recouverte par les petits processus parasphénoïdes du ptérygoïde (*pr.psph.Pt*). Pratiquement à la limite quille-rostre, à la base de la quille, s'ouvrent de chaque côté de celle-ci les orifices externes du canal de la carotide interne (*o.e.c.c.i.*). Le complexe para-basisphénoïde participe, pour une faible part, semble-t-il, et de façon très superficielle, au bord de la fenêtre ovale, en partie endommagée. Chez les *Whaitsiidae* sud-africains, il en paraît exclu (observation personnelle). Les *tubercula spheno-occipitalia* (*tub.sph.-oc*), formés moitié par le

basioccipital (*Boc*) recouvert par le complexe para-basisphénoïde, moitié par le basioccipital seul, sont volumineux. A l'avant de ces tubérosités, le complexe para-basisphénoïde est beaucoup moins étroit que chez les *Whaitsiidae* africains.

L'épiptérygoïde (*Ept*, Figs 1, 2, 3, 6, 11; Pls I, III B, VI, VII A) est une plaque aplatie moyennement élargie, à petite apophyse postérieure (*a.p.Ept*), et qui ressemble assez à l'épiptérygoïde du générotipe d'*Annatherapsidus* (observation personnelle). Cet os est dans les deux cas bien moins élargi que chez les *Whaitsiidae* africains. Le bord postérieur de l'épiptérygoïde de ceux-ci présente en outre un processus supplémentaire (le processus prootique de l'épiptérygoïde) qui recouvre le prootique et est lui-même recouvert par l'apophyse postérieure. Celle-ci en outre s'étend assez pour entrer également en contact avec le prootique (observation personnelle). Il est possible que les branches maxillaire (*V2*) et mandibulaire (*V3*) du trijumeau soient séparées. Il faudrait que des spécimens de *Moschorhinus* (? *Tigrisuchus*) présentent cette région en meilleur état pour que l'on soit sûr de l'homologie de ces processus. Le processus postéro-ventral (*pr.p.-v.Ept*), élevé, devait être relié au squamosal, car le processus ventral de celui-ci est, comme nous l'avons vu plus haut, divisé en deux processus, l'un soudé au processus central du prootique (*pr.c.Proot*), l'autre se dirigeant vers l'épiptérygoïde. Une situation analogue a pu être observée chez des *Whaitsiidae* africains. Le *cavum epipticum* (*ca.ept*, Fig. 6) est important.

Les os otiques

Comme l'auteur l'a observé chez un *Scaloposauria*, *Regisaurus* Mendrez, 1972 (F.R.P. n° 1964/27 in Mendrez 1972a: 201) et chez des *Pristerosauria*

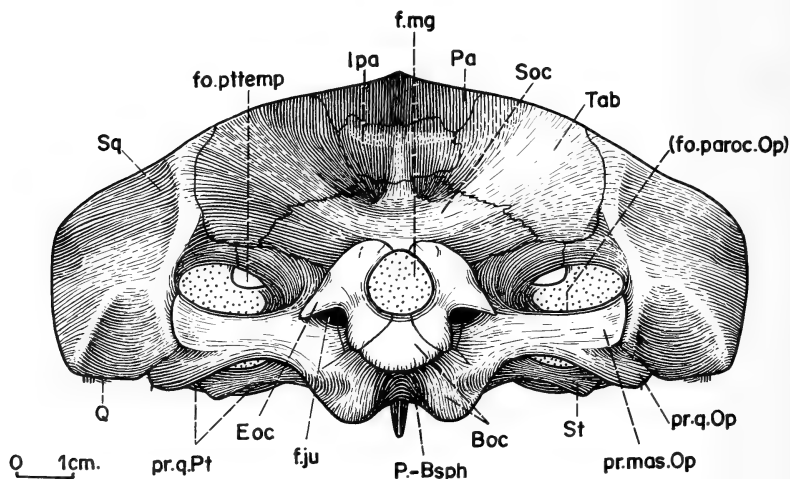
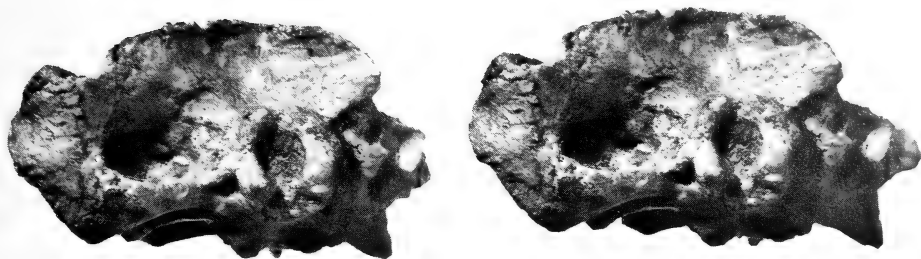
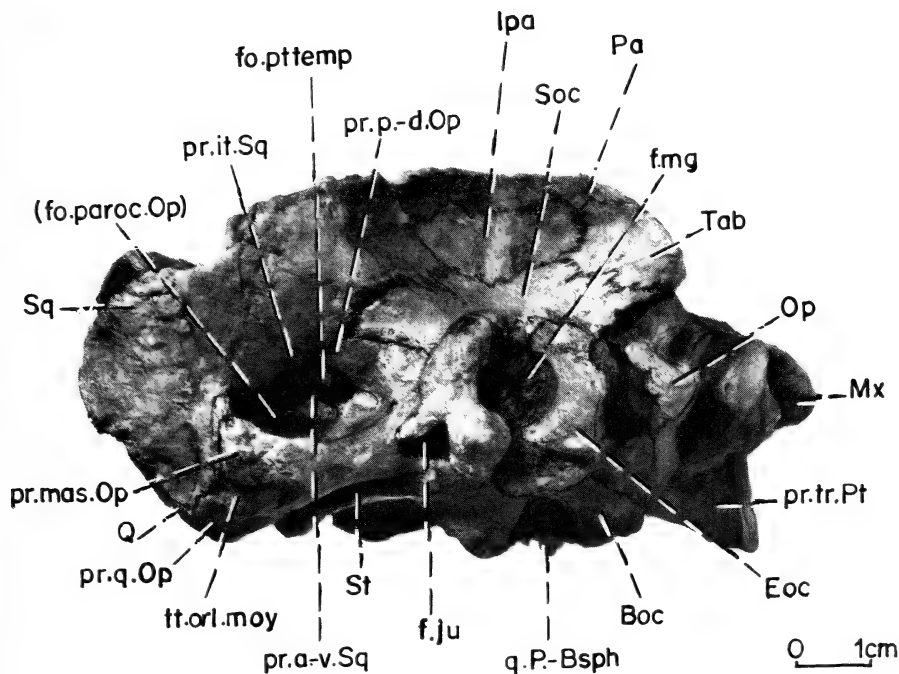


Fig. 4. *Moschorhinus kitchingi*, Moschorhinidae, S.A.M. n°K.118. Vue occipitale du crâne ($\times \frac{3}{4}$). *Boc*, basioccipital; *Eoc*, exoccipital; *f.ju*, foramen jugulaire; *f.mg*, foramen magnum; *fo.paroc.Op*, fosse paroccipitale de l'opisthotique; *fo.pttemp*, fosse posttemporale; *Ipa*, interpariétal; *P.-Bsph*, complexe para-basisphénoïde; *Pa*, pariétal; *pr.mas.Op*, processus mastoïde de l'opisthotique; *pr.q.Op*, processus carré de l'opisthotique; *pr.q.Pt*, processus carré du ptérygoïde; *Q*, carré; *Soc*, supraoccipital; *Sq*, squamosal; *St*, stapes; *Tab*, tabulaire.



A 0 1cm.



B

PLANCHE IV. *Moschorhinus kitchingi*, Moschorhinidae, S.A.M. n°K.118; vue occipitale du crâne; A, ($\times 0,6$ env.); B, ($\times 1$).

Boc, basioccipital; *Eoc*, exoccipital; *f.ju*, foramen jugulaire; *f.mg*, foramen magnum; (*fo.paroc.Op*), fosse paroccipitale de l'opisthotique; *fo.pttemp*, fosse posttemporale; *lpa*, interpariétal; *Mx*, maxillaire; *Op*, opisthotique; *Pa*, pariétal; *pr.a-v.Sq*, processus antéro-ventral du squamosal; *pr.it.Sq*, processus intermédiaire du squamosal; *pr.mas.Op*, processus mastoïde de l'opisthotique; *pr.p.-d.Op*, processus postéro-dorsal de l'opisthotique; *pr.q.Op*, processus carré de l'opisthotique; *pr.tr.Pt*, processus transverse du ptérygoïde; *Q*, carré; *q.P.-Bsph*, quille du complexe parabasiphénoïde; *Soc*, supraoccipital; *Sq*, squamosal; *St*, stapes; *tt.ori.moy*, toit de l'oreille moyenne.

Whaitsiidae, *Theriognathus* (B.P.I. n°F.100/M.141) et Pristerognathidae, *Ptomalestes* Boonstra, 1954 (S.A.M. n°11942)², le prootique (*Proot*) et l'opisthotique (*Op*) sont bien individualisés (Figs 6, 7, 12); ce qui est visible de la suture qui les sépare correspond à ce qui a été déjà décrit chez *Regisaurus* (Mendrez 1972).

Le prootique est en partie endommagé et, de ce fait, le processus antéro-ventral n'a pu être observé. Cet os apparaît massif, à région dorsale nettement plus ossifiée que chez *Regisaurus*. Le prootique de *Moschorhinus* (?*Tigrisuchus*) comme celui de *Theriognathus* présente le même nombre de processus que celui de *Regisaurus* tandis que, chez *Ptomalestes*, un processus centro-ventral supplémentaire est situé juste sous le processus central (observation personnelle).

L'aspect général de l'opisthotique ne diffère pas essentiellement de celui de *Regisaurus*: le processus postéro-dorsal (*pr.p.-d.Op*) est moins allongé, il est également moins recouvert par le processus intermédiaire du squamosal (*pr.it.Sq*) et par conséquent est apparent en vue antérieure au-dessus de l'ouverture de la fosse posttemporale (*fo.pttemp*). Le processus paroccipital (*pr.paroc.Op*) est particulièrement massif et est creusé d'une vaste fosse paroccipitale (*fo.paroc.Op*). Sur la face ventrale, entre le processus carré (*pr.q.Op*) et le processus mastoïde (*pr.mas.Op*), la fosse qui correspondrait à l'extrémité latérale du toit de l'oreille moyenne (*tt.orl.moy*) est peu profonde.

Le supraoccipital (*Soc*), trapu, apparaît largement dans la fenêtre temporale (*fe.temp*, Figs 3, 6 7; Pls III A, VII A). En vue occipitale (Fig. 4; Pl. IV), ses processus latéraux sont brefs et leur limite correspond à peu près au niveau du bord médial de la fosse posttemporale. Chez *Theriognathus* également, ces processus sont courts tandis que chez *Annatherapsidus*, ils sont plus allongés.

L'exoccipital (*Eoc*) est aussi important et participe pour une bonne part au bord supérieur du *foramen magnum* (*f.mg*, Fig. 4; Pls I, IV) tout comme au condyle occipital (*cdy.oc*). Avec l'opisthotique, il élimine le basioccipital du plancher du foramen jugulaire (*f.ju*, Figs 4, 9; Pl. IV).

Le basioccipital (*Boc*) participe au plancher du *foramen magnum* et forme avec les exoccipitaux un condyle tripartite (Fig. 4; Pl. IV). Sa participation au bord de la fenêtre ovale est assez réduite (Figs 2, 10; Pls II, V).

Du carré (*Q*, Figs 1, 2, 3, 6, 10; Pls II, IV, V) ne subsiste qu'un fragment comportant le processus ptérygoïde (*pr.pt.Q*).

C—Principales fosses et ouvertures de la région postérieure du crâne

La fenêtre ovale (*fe.ov*, Figs 2, 10; Pls II, V) est ici masquée par le stapes. Il est cependant possible de remarquer que ce sont essentiellement le prootique et l'opisthotique qui forment la majeure partie de son bord. Le basioccipital et le complexe parabasisphénoïde y participent pour une bien plus faible part, et le

² Cette dernière observation est à l'inverse de celle faite par Olson (1944: 11-15, fig. 6C) sur le 'Thérocéphale' qui semble être un Pristerognathidae également. Il faut donc admettre soit que les Pristerognathidae présentent une région otique diversement consolidée, soit que la technique des sections sériées transversales fait disparaître la suture entre prootique et opisthotique (celle-ci se trouve effectivement dans un plan pratiquement transversal). La même remarque serait à faire chez les Scaloposauria à propos de la différence existant entre *Ictidosuchops* (*in*: Crompton 1955: 165-167, figs 6 A, B, C) et *Regisaurus*.

complexe parabasisphénoïde seulement très superficiellement. Il est à noter que chez *Theriognathus* (B.P.I. F.100/M.141), ce dernier os est complètement exclu du bord de la fenêtre ovale qui, dans ce cas, est bordée, de façon égale, par seulement les trois autres os (observation personnelle).

La fosse posttemporale (*fo. pttemp.* Figs 2, 6, 7, 9; Pls IV, VI), qui s'ouvre postérieurement et vers le haut, est vaste. Il s'agit ici comme chez la plupart des Thérocéphales d'une 'fenêtre' plutôt que d'une 'fosse', car l'ouverture postérieure et l'ouverture antérieure coïncident en partie. Chez le Pristerognathidae *Ptomalestes* au contraire, l'ouverture antérieure, minuscule, est décalée médialement par rapport à l'ouverture postérieure et, en vue occipitale, on ne voit à travers cette dernière que le processus intermédiaire du squamosal.

L'ouverture antérieure (Fig. 7; Pl. VI) est bordée essentiellement par l'opisthotique avec une faible participation du squamosal dans l'angle latéral et une encore plus faible participation du prootique dans l'angle médial. Ces os sont bien visibles en vue antérieure étant donné la faible hauteur de la paroi antérieure du foramen ptérygo-paroccipital (Fig. 6). Chez *Theriognathus* au contraire, cette paroi, plus élevée, masque le bord inférieur de l'ouverture antérieure de la fosse posttemporale. En outre, la participation du prootique au bord supérieur est moindre (observation personnelle).

L'ouverture postérieure (Figs 2, 9; Pl. IV) est uniquement bordée par l'opisthotique et le squamosal. Les processus intermédiaire et mastoïde de ce dernier sont très réduits par rapport à ceux de *Theriognathus*; d'autre part, tandis que, chez ce dernier, le squamosal forme la majeure partie du bord dorsal, l'angle latéral et près de la moitié du bord ventral de l'ouverture postérieure de la fosse posttemporale, chez *Moschorhinus* (?*Tigrisuchus*) il n'en forme que la moitié du bord supérieur et la plus grande part de l'angle latéral.

La fosse paroccipitale (Figs 2, 9; Pl. IV) est vaste. Cette fosse existe également chez *Regisaurus* et *Theriognathus* mais est totalement absente chez *Ptomalestes* (observation personnelle). Elle existe également chez *Annatherapsidus* (cf. Vjushkov 1955: 137) et *Chthonosaurus*. Il serait intéressant de savoir si cette fosse est homologue de celle observée par Olson (1968: 243) chez les Pelycosauria Caseidae et décrite comme suit: '... Sur la face dorso-latérale de l'opisthotique, se trouve une fosse profonde qui aboutit par un sillon à la fenêtre posttemporale...?'

Le foramen ptérygo-paroccipital (*f.pt.paroc.* Figs 1, 2, 6, 10; Pls I, VI) diffère de celui de *Regisaurus* et de *Theriognathus* par la moindre hauteur de sa paroi antérieure formée par le processus antéro-ventral du squamosal et le processus central du prootique.

Le foramen magnum (Figs 4, 9; Pl. IV) est bordé essentiellement par les exoccipitaux. Le supraoccipital ne forme qu'une partie du bord dorsal tandis que la participation au bord ventral est limitée à une bande étroite.

Le foramen jugulaire (Figs 4, 9; Pl. IV) est bordé exclusivement par l'exoccipital et l'opisthotique, comme chez *Theriognathus*.

II—MANDIBULE

Des fragments de mandibule sont inclus dans un bloc contenant également des restes du squelette postcranien.

Le dentaire est surtout remarquable par son très fort angle mentonnier tandis que chez *Theriognathus*, cette région forme une pente douce. Paradoxalement l'aspect de la région mentonnière est ainsi plus proche de celle de *Moscho-whaitsia* que de celle d'*Annatherapsidus*.

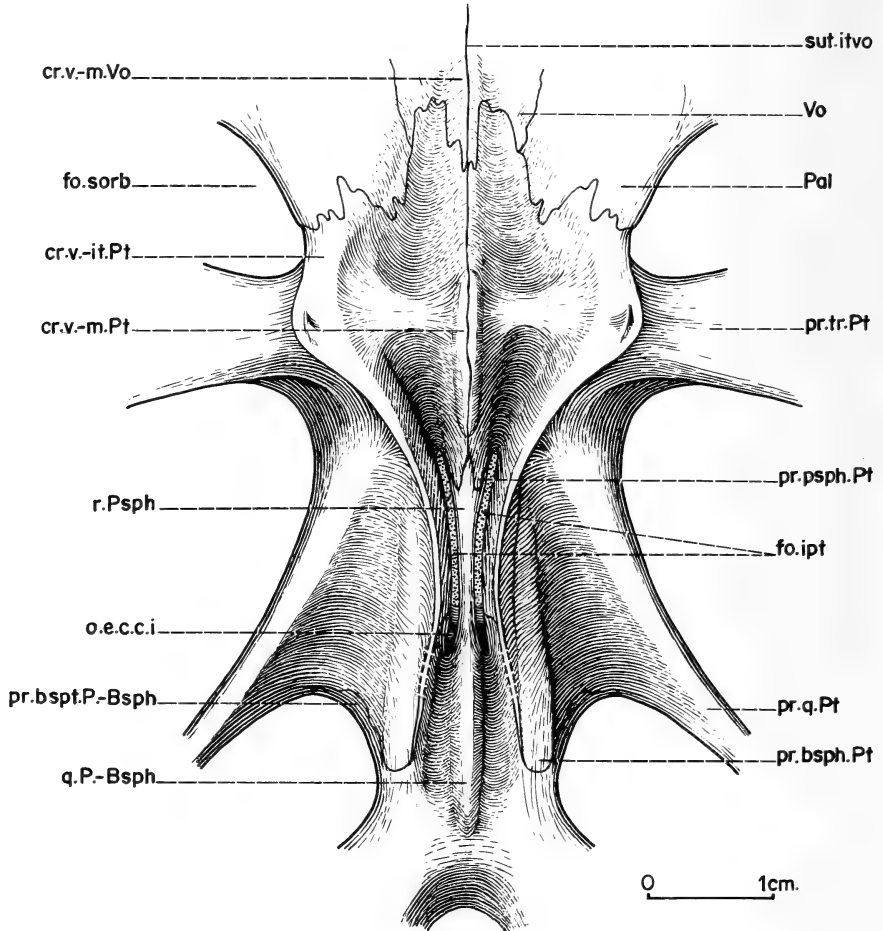


Fig. 5. *Moschorhinus kitchingi*, Moschorhinidae, S.A.M. n°K.118. Détail de la fosse interptérygoïdienne en vue ventrale ($\times 5/3$).

cr.v.-it.Pt, crête ventro-intermédiaire du ptérygoïde; *cr.v.-m.Pt*, crête ventro-médiane du ptérygoïde; *cr.v.-m.Vo*, crête ventro-médiane du vomer; *fo.ipt*, fosse interptérygoïdienne; *fo.sorb*, fosse sousorbitaire; *o.e.c.c.i*, orifice externe du canal de la carotide interne; *Pal*, palatin; *pr.bsph.Pt*, processus basisphénoïde du ptérygoïde; *pr.bspt.P.-Bsph*, processus basiptérygoïde du complexe para-basisphénoïde; *pr.psph.Pt*, processus parasphénoïde du ptérygoïde; *pr.q.Pt*, processus carré du ptérygoïde; *pr.tr.Pt*, processus transverse du ptérygoïde; *q.P.-Bsph*, quille du complexe para-basisphénoïde; *r.Psph*, rostre du parasphénoïde; *sut.itvo*, suture intervomérine; *Vo*, vomer.

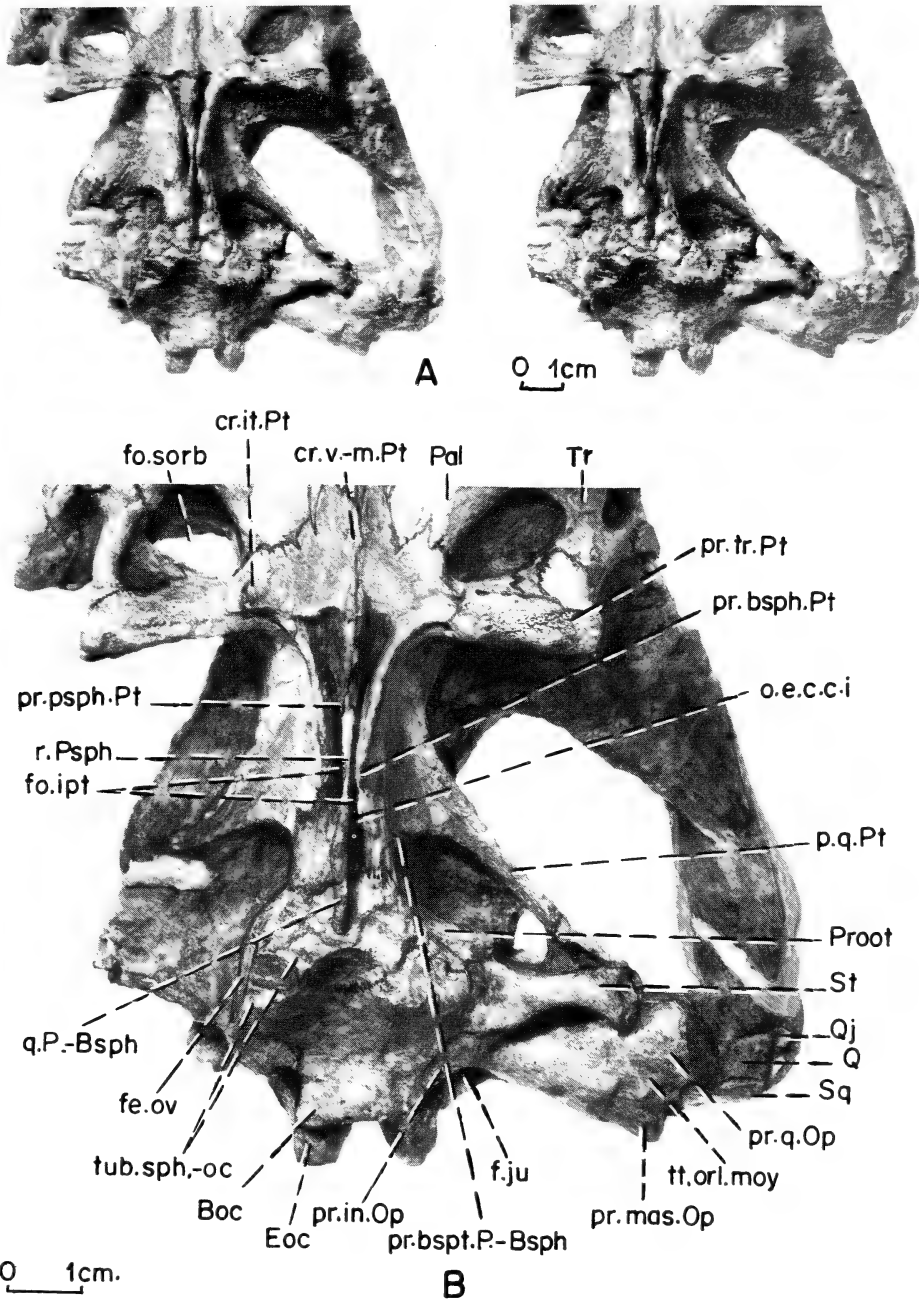


PLANCHE V. *Moschorhinus kitchingi*, Moschorhinidae, S.A.M. n°K.118; vue ventrale de la partie postérieure du crâne. A, ($\times 055$, env.); B, ($\times 1$).

Boc, basioccipital; *cr.it.Pt*, crête intermédiaire du ptérygoïde; *cr.v.-m.Pt*, crête ventro-médiane du ptérygoïde; *Eoc*, exoccipital; *f.ju*, foramen jugulaire; *fe.ov*, fenêtre ovale; *fo.ipt*, fosse inter-ptérygoïdienne; *fo.sorb*, fosse sousorbitaire; *o.e.c.c.i*, orifice externe du canal de la carotide interne; *Pal*, palatin; *pr.bsph.Pt*, processus basisphénoïde du ptérygoïde; *pr.bspt.P.-Bsph*, processus basiptérygoïde du complexe para-basisphénoïde; *pr.in.Op*, processus interne de l'opisthotique; *pr.mas.Op*, processus mastoïde de l'opisthotique; *pr.bsph.Pt*, processus parasphénoïde du ptérygoïde; *pr.q.Op*, processus carré de l'opisthotique; *pr.q.Pt*, processus carré du ptérygoïde; *pr.tr.Pt*, processus transverse du ptérygoïde; *Proot*, prootique; *Q*, carré; *q.P.-Bsph*, quille du complexe para-basisphénoïde; *Qj*, quadrato-jugal; *r.Psph*, rostre du parasphénoïde; *Sq*, squamosal; *St*, stapes; *Tr*, transverse; *tt.ori.moy*, toit de l'oreille moyenne; *tub.sph.-oc*, *tuberculum spheno-occipitale*.

III—SPLANCHNOCRANE

Le stapes (*St*, Figs 2, 4, 7, 9, 10; Pls II, IV, V), en forme d'haltère, n'a pu être dégagé complètement. Il n'y a pas de foramen stapédial visible en vue ventrale ou en vue occipitale. Ce foramen est pourtant vaste chez le Théro-

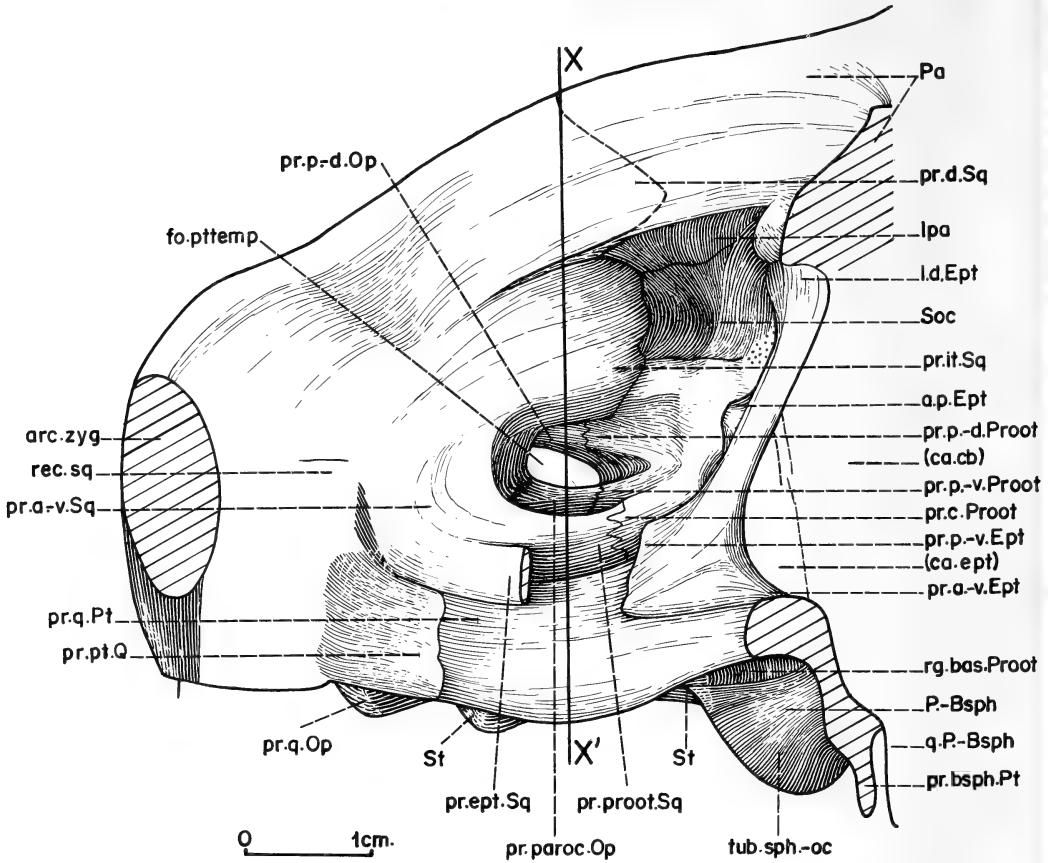


Fig. 6. *Moschorhinus kitchingi*, Moschorhinidae, S.A.M. n°K.118. Vue antérieure du mur postérieur de la fosse temporale droite, reconstruite par symétrie ($\times 5/3$).

a.p.Ept, apophyse postérieure de l'épiptérygoïde; *arc.zyg*, arcade zygomatique; (*ca.cb*), cavité cérébrale; (*ca.ept*), *cavum epiptericum*; *fo.ptemp*, fosse posttemporale; *lpa*, interpariétal; *l.d.Ept*, lame dorsale de l'épiptérygoïde; *P-Bsph*, complexe para-basisphénoïde; *Pa*, pariétal; *par.a-v.Ept*, processus antéro-ventral de l'épiptérygoïde; *pr.a-v.Sq*, processus antéro-ventral du squamosal; *pr.bsph.Pt*, processus basisphénoïde du ptérygoïde; *pr.c.Proot*, processus central du prootique; *pr.d.Sq*, processus dorsal du squamosal; *pr.ept.Sq*, processus épiptérygoïde du squamosal; *pr.it.Sq*, processus intermédiaire du squamosal; *pr.p-d.Op*, processus postéro-dorsal de l'opisthotique; *pr.p-d.Proot*, processus postéro-dorsal du prootique; *pr.p-v.Ept*, processus postéro-ventral de l'épiptérygoïde; *pr.p-v.Proot*, processus postéroventral du prootique; *pr.paroc.Op*, processus paroccipital de l'opisthotique; *pr.proot.Sq*, processus prootique du squamosal; *pr.pt.Q*, processus ptérygoïde du carré; *pr.q.Op*, processus carré de l'opisthotique; *pr.q.Pt*, processus carré du ptérygoïde; *q.P-Bsph*, quille du complexe para-basisphénoïde; *rec.sq*, recessus squamosal; *rg.bas.Proot*, région basale du prootique; *Soc*, supraoccipital; *St*, stapes; *tub.sph-oc* *tuberculum spheno-occipitale*; *XX'*, plan de la section parasagittale en Fig. 8.

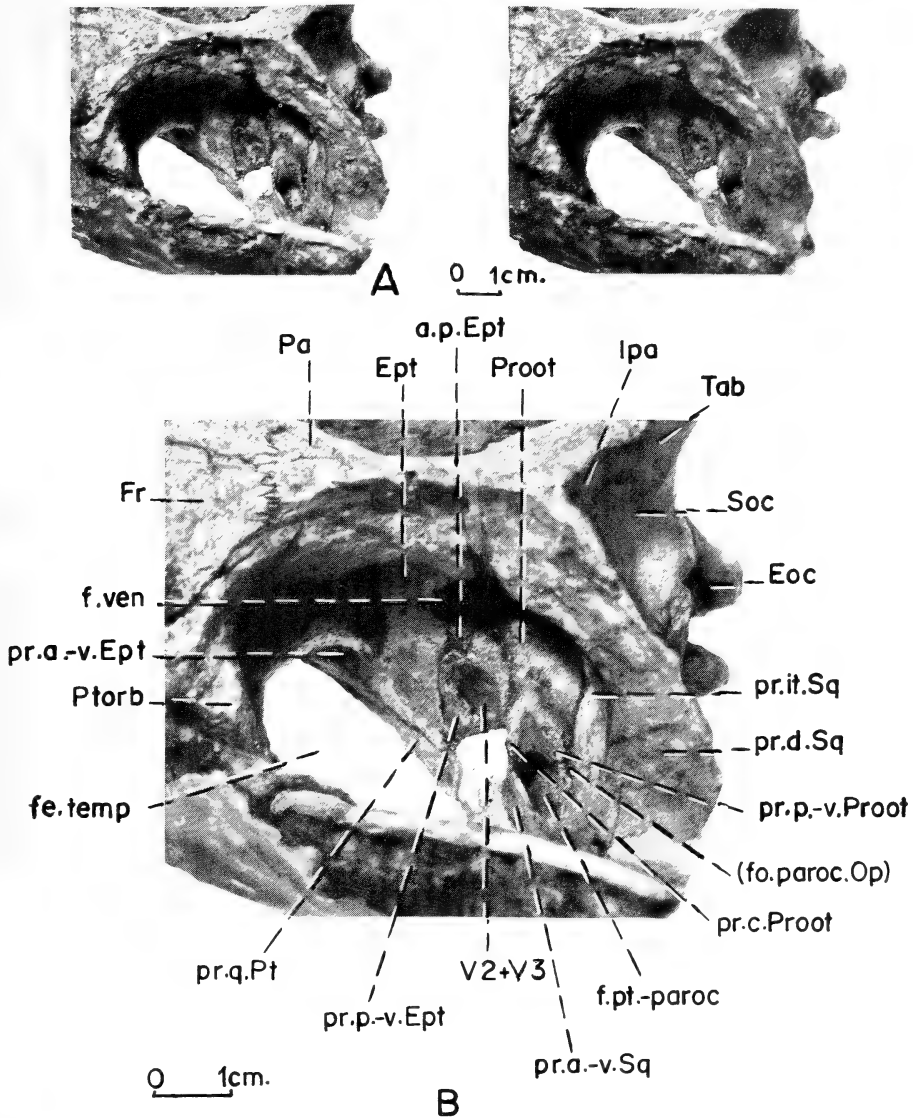


PLANCHE VI. *Moschorhinus kitchingi*, Moschorhinidae, S.A.M. n°K.1118; vue dorso-latérale de la fosse temporale gauche. A ($\times 0,55$ env.); B, ($\times 1$).

a.p.Ept, apophyse postérieure de l'épiptérygoïde; *Eoc*, exoccipital; *Ept*, épiptérygoïde; *f.pt.-paroc*, foramen ptérygo-paroccipital; *f.ven*, foramen veineux; *fe.temp*, fenestra temporalis; (*fo.paroc.Op*), fosse paroccipitale de l'opisthotique; *Fr*, frontal; *Ipa*, interpariétal; *Pa*, pariétal; *pr.a.-v.Ept*, processus antéro-ventral de l'épiptérygoïde; *pr.a.-v.Sq*, processus antéro-ventral du squamosal; *pr.c.Proot*, processus central du prootique; *pr.d.Sq*, processus dorsal du squamosal; *pr.it.Sq*, processus intermédiaire du squamosal; *pr.q.-v.Ept*, processus postéro-ventral de l'épiptérygoïde; *pr.p.-v.Proot*, processus postéro-ventral du prootique; *pr.q.Pt*, processus carré du ptérygoïde; *Proot*, prootique; *Ptorb*, postorbitaire; *Soc*, supraoccipital; *Tab*, tabulaire; *V2 + V3*, lieu de sortie des branches maxillaire et mandibulaire du nerf trijumeau.

céphale B décrit par Olson (1944: 41; fig. 12 A, E). A ce propos, Cys (1971: 124) a fait la remarque suivante: 'A part le Thérocéphale B (Olson 1944: 39-41), tous les Thérocéphales et Bauriamorphes chez lesquels le stapes est connu n'ont pas de foramen stapédial. Les Cynodontes et les Gorgonopsiens cependant, possèdent un foramen stapédial'. Les relations exactes du stapes et carré sont impossibles à connaître ici.

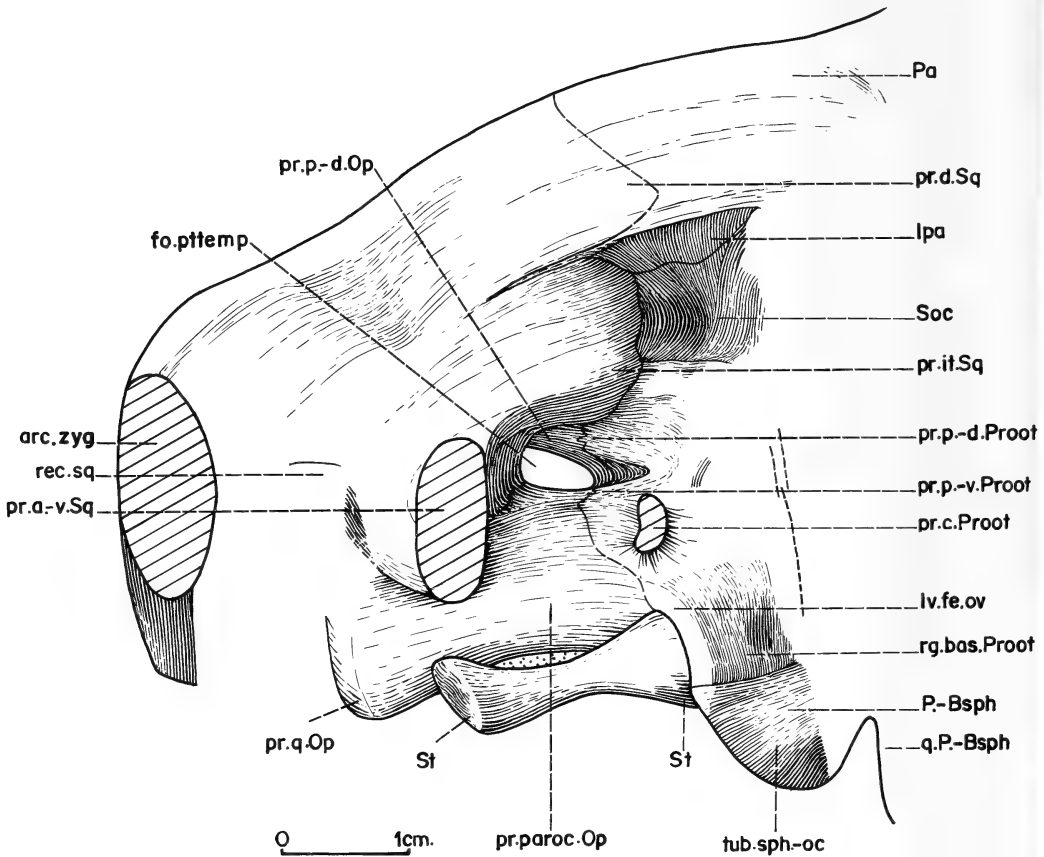


Fig. 7. *Moschorhinus kitchingi*, Moschorhinidae, S.A.M. n°K.118, Vue antérieure du côté droit de l'occiput, reconstruit par symétrie ($\times 5/3$).

arc.zyg, arcade zygomatique; *fo.ptemp*, fosse posttemporale; *Ipa*, interpariétal; *lv.fe.ov*, lèvres de la fenêtre ovale; *P.-Bsph*, complexe para-basisphénoïde; *Pa*, pariétal; *pr.a.-v.Sq*, processus antéro-ventral du squamosal; *pr.c.Proot*, processus central du prootique; *pr.d.Sq*, processus dorsal du squamosal; *pr.it.Sq*, processus intermédiaire du squamosal; *pr.p.-d.Op*, processus postéro-dorsal de l'opisthotique; *pr.p.-d.Proot*, processus postéro-dorsal du prootique; *pr.p.-v.Proot*, processus postéro-ventral du prootique; *pr.paroc.Op*, processus paroccipital de l'opisthotique; *pr.q.Op*, processus carré de l'opisthotique; *q.P.-Bsph*, quille du complexe para-basisphénoïde; *rec.sq*, recessus squamosal; *rg.bas.Proot*, région basale du prootique; *Soc*, supraoccipital; *St*, stapes; *tub.sph-oc*, tuberculum sphenoccipitale.

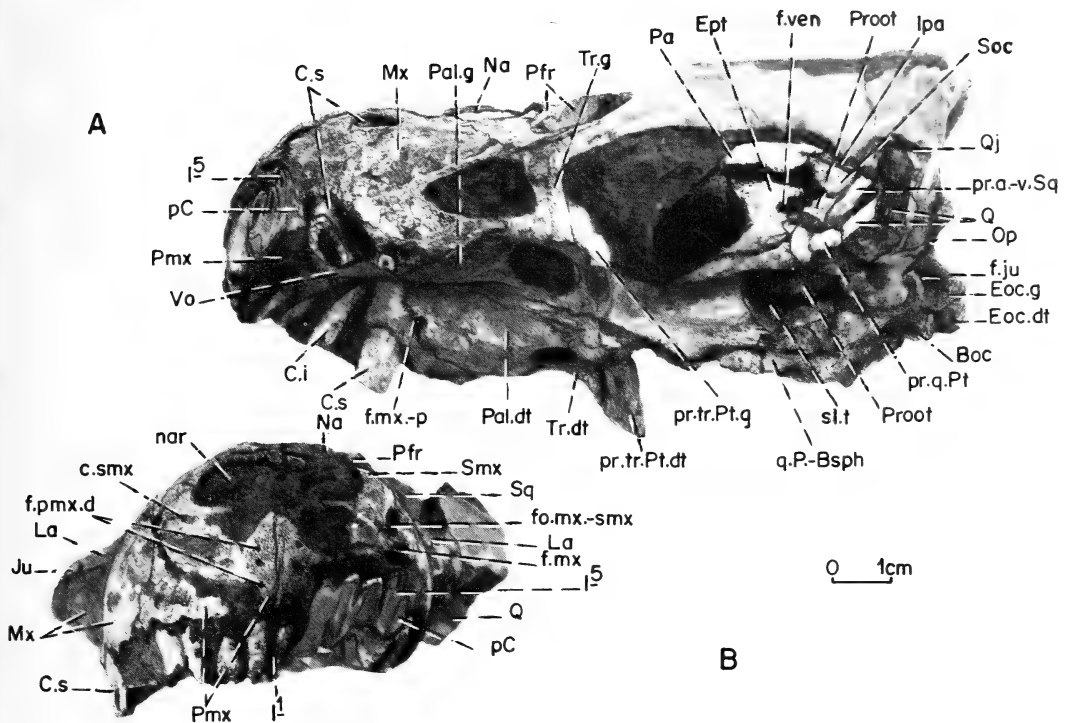


PLANCHE VII. *Moschorhinus kitchingi*, Moschorhinidae, S.A.M. n°K.118; A, vue latéro-ventrale gauche du crâne ($\times \frac{5}{8}$); B, vue antérieure du museau ($\times \frac{5}{8}$).

Boc, basioccipital; *C.i*, canine inférieure; *C.s*, canine supérieure; *c.smx*, canal septomaxillaire; *Eoc.dt*, exoccipital droit; *Eoc.g*, exoccipital gauche; *Ept*, épiptérygoïde; *f.ju*, foramen jugulaire; *f.mx*, foramen maxillaire; *f.mx.-p*, foramen maxillo-palatin; *f.pmx.d*, foramen prémaxillaire droit; *f.ve*, foramen veineux; *fo.mx.-smx*, fosse maxillo-septomaxillaire; *I¹*, première incisive supérieure; *I⁵*, cinquième incisive supérieure; *Ipa*, interpariétal; *Ju*, jugal; *La*, lacrymal; *Mx*, maxillaire; *Na*, nasal; *nar*, narine; *Op*, opisthotique; *Pa*, pariétal; *Pal.dt*, palatin droit; *Pal.g*, palatin gauche; *pC*, précanine; *Pfr*, préfrontal; *Pmx*, prémaxillaire; *pr.a.-v.Sq*, processus antéro-ventral du squamosal; *pr.q.Pt*, processus carré du ptérygoïde; *pr.tr.Pt.dt*, processus transverse du ptérygoïde droit; *pr.tr.Pt.g*, processus transverse du ptérygoïde gauche; *Proot*, prootique; *Q*, carré; *q.P.-Bsph*, quille du complexe para-basisphénoïde; *Qj*, quadrato-jugal; *sl.t*, selle turcique; *Smx*, septomaxillaire; *Soc*, supraoccipital; *Sq*, squamosal; *Tr.dt*, transverse droit; *Tr.g.*, transverse gauche; *Vo*, vomer.

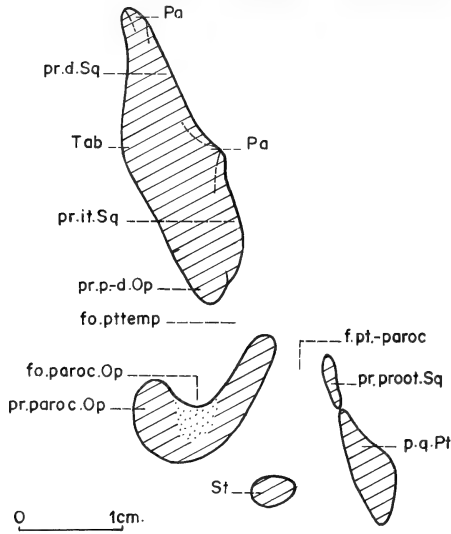


Fig. 8. *Moschorhinus kitchingi*, Moschorhinidae, S.A.M. n°K.118. Coupe parasagittale, selon l'axe XX' de la Fig. 6 ($\times 5/3$).

f.pt-paroc, foramen ptérygo-paroccipital; *fo.paroc.Op*, fosse paroccipitale de l'opisthotique; *fo.pttemp*, fosse posttemporale; *Pa*, pariétal; *pr.d.Sq*, processus dorsal du squamosal; *pr.it.Sq*, processus intermédiaire du squamosal; *pr.p-d.Op*, processus postéro-dorsal de l'opisthotique; *pr.paroc.Op*, processus paroccipital de l'opisthotique; *pr.proot.Sq*, processus prootique du squamosal; *pr.q.Pt*, processus carré du ptérygoïde; *St*, stapes; *Tab*, tabulaire.

IV—DENTITION

La formule dentaire est 5 I, 1 pC, 1 C, 3 PC. Les Moschorhinidae présentent la réduction de la série postcanine si courante chez les Pristerosauria et qui atteindra son maximum chez les Whaitsiidae et chez *Euchambersia*. La formule antécanine est intéressante par le fait qu'elle est encore relativement primitive avec 5 I et 1 pC. Cette formule se retrouve chez *Moschowahitsia* (cf. Tatarinov 1963: fig. 2) et chez *Annatherapsidus* (observation personnelle). Vjushkov (1955) considère par contre que ce genre ne présente que 4 I et 1 pC, mais reconstruit le museau de *Chthonosaurus* avec 5 I et 1 pC. Chez les Whaitsiidae africains la précanine a disparu, mais deux canines en croc à fonctionnement alternatif subsistent (cf. Brink 1948: 31-34).

DISCUSSION

Par son palais, et ses régions pariétale et épiptérygoïdienne, *Moschorhinus* semble se rapprocher plus des Annatherapsididae d'U.R.S.S. que des Whaitsiidae, mais il s'en éloigne par l'aspect de son dentaire essentiellement. Les caractères qui nous ont paru intéressants à retenir sont les suivants:

TABLEAU I

		ANNIDAE = Annatherapsididae		MOSCHORHINI- DAE	WHATSIIDAE	
		U.R.S.S.		Afrique australe	Afrique	U.R.S.S.
		<i>Anna</i> = <i>Annatherapsidus</i>	<i>Chthonosaurus</i>	<i>Moschorhinus</i> (? <i>Tigrisuchus</i>)	<i>Therionathus</i>	<i>Moschochaitsia</i>
		Permien supérieur: zone IV, Tatarien	Permien supérieur: zone IV, Tatarien	Permien supérieur: zones à <i>Daplocephalus</i> et à <i>Lystrosaurus</i>	Permien supérieur: — Tanzanie: Kawinga Formation — Afrique australe: zone à <i>Cistecephalus</i> <i>s.l.</i>	Permien supérieur: zone IV, Tatarien supérieur peut-être équivalent à la zone à <i>Cistecephalus</i> <i>s.l.</i> (cf. Tatarinov 1963: 78)
Museau		— de longueur moyenne — pas de constriction postcanine	— probablement assez allongé — ?	— court — à constriction post- canine peu marquée	— de longueur moyenne — à constriction post- canine marquée	— de longueur moyenne — à constriction post- canine marquée
Arcades zygomatiques et postorbitaires		d'épaisseur moyenne	très faibles	épaisses	en voie d'affinement	moyennement épaisses
Barres sousorbitaires		presque totalement formées par le jugal	presque totalement formées par le jugal	à très forte participa- tion du maxillaire	essentiellement formées par le jugal	essentiellement formées par le jugal
Frontaux		brefs	longs	brefs	brefs	brefs
	Longueur	— plus courte que le pariétal	— plus courte que le pariétal	— plus courte que le pariétal	— atteignant à l'avant la suture fronto-pariétale	— à aspect très voisin de celui de <i>Therionathus</i> mais précédée d'une minuscule fossette — ?
	hauteur	— moyennement haute probablement	— ?	— moyennement haute	— haute	
Pariétal	crête sagittale pariétale					

		ANNIDAE = Annatherapsididae		MOSCHORHINI- DAE		WHATSIIDAE	
		U.R.S.S.		Afrique australe		Afrique	
		<i>Anna</i> = <i>Annatherapsidus</i>	<i>Chithonosaurus</i>	<i>Moschorhinus</i> (? <i>Tigrisuchus</i>)	<i>Therionathus</i>	<i>Moschowaitzia</i>	
		Permien supérieur: zone IV, Tatarien	Permien supérieur: zone IV, Tatarien	Permien supérieur: zones à <i>Daptocephalus</i> et à <i>Lystrosaurus</i>	Permien supérieur: —Tanzanie: Kawinga Formation —Afrique australe: zone à <i>Cisticephalus</i> <i>s.l.</i>	Permien supérieur: zone IV, Tatarien supérieur peut-être équivalent à la zone à <i>Cisticephalus</i> <i>s.l.</i> (cf. Tatarinov 1963: 78)	
	région antérieure	plateforme triangulaire à l'avant de la crête sagittale	plateforme triangulaire à l'avant de la crête sagittale		absence de cette plateforme	absence de cette plateforme	
	foramen pinéal	absent	fermé	correspondant à une fente étroite	fente de taille variable	absent	
	Interpariétal	participation à la fenêtré temporale mal définie, car cette région est en partie abimée		largement exposé dans la fenêtré temporale	moeynement exposé dans la fenêtré temporale	?	
	contact voméro-maxillaire	absent	?	absent	présent; début de palais secondaire osseux	?	
	<i>crista choanalis</i>	mousse	moeynement marquée	mousse, n'atteignant pas à l'avant le niveau des canines	bien marquée	bien marquée	
	fosses canines et orifice choanal	en continuité	?	en continuité	séparées par le pont voméro-maxillaire	séparées par le pont voméro-maxillaire	
	Palais						

Prémaxillaires	à région médiane moyennement longue, large	?	à région médiane brève et large	à région médiane longue et étroite	à région médiane longue et étroite
Vomers	— à plaque antérieure et plaque postérieure à peu près sur le même plan — à plaque antérieure étalée en éventail, sans contact avec le maxillaire	— ? — ?	— à plaque antérieure et plaque postérieure à peu près sur le même plan — à plaque antérieure étalée en éventail, sans contact avec le maxillaire	— inclinaison de la plaque postérieure marquée, ce qui la fait paraître plus dorsale — à plaque antérieure cruciforme	— inclinaison de la plaque postérieure marquée, ce qui la fait paraître plus dorsale — à plaque antérieure cruciforme
Fosses sousorbitaires	grandes	grandes	grandes	de réduites à nulles	grandes
Ptérygoïdes	— présence d'une fine lame osseuse reliant le processus carré et le processus transverse — processus basisphénoïdes partiellement jointifs — présentes	— présence d'une fine lame osseuse reliant le processus carré et le processus transverse — processus basisphénoïdes très écartés — présentes	— présence d'une fine lame osseuse reliant le processus carré et le processus transverse — processus basisphénoïdes écartés — apparemment absentes	— processus carré et processus transverse non reliés par une lame osseuse — processus basisphénoïdes jointifs — présentes	— processus carré et processus transverse non reliés par une lame osseuse — processus basisphénoïdes presque totalement jointifs — absentes
Fosses interptérygoïdiennes	ouvertes seulement à l'avant	très ouvertes	ouvertes	fermées ventralement par rapport au reste du parasphénoïde	ouvertes à l'avant en une fente très étroite
Complexe para-basisphénoïde	— moyennement étroit à l'avant des <i>tubercula spheno-occipitalia</i> qui sont ici très volumineux — participe au bord de la fenêtre ovale	— moyennement étroit à l'avant des <i>tubercula spheno-occipitalia</i> — participe au bord de la fenêtre ovale	— moyennement étroit à l'avant des <i>tubercula spheno-occipitalia</i> — participe faiblement au bord de la fenêtre ovale	— très étroit à l'avant des <i>tubercula spheno-occipitalia</i> — exclu du bord de la fenêtre ovale	— ? — ?

ANNIDAE = Annatherapsididae		MOSCHORHINI- DAE	WHAITSIIDAE
U.R.S.S.		Afrique australe	Afrique
<i>Anna</i> = <i>Annatherapsidus</i>	<i>Chthonosaurus</i>	<i>Moschorhinus</i> (? <i>Tigrisuchus</i>)	<i>Theriognathus</i>
Permien supérieur: zone IV, Tatarien	Permien supérieur: zone IV, Tatarien	Permien supérieur: zones à <i>Daptocephalus</i> et à <i>Lystrosaurus</i>	Permien supérieur: zone IV, Tatarien supérieur peut-être équivalent à la zone à <i>Cistecephalus</i> s.l. (cf. Tatarinov 1963: 78)
— en plaque aplatie, moyennement élargie	— ?	— en plaque aplatie, moyennement élargie	— ?
— il semble qu'il y ait une apophyse posté- rieure mais cette région est endom- magée	— ?	— a une apophyse postérieure	— ?
— à processus latéraux assez allongés	— à processus latéraux brefs	— à processus latéraux brefs	— à processus latéraux brefs
bordée par quatre os: prootique, opistho- thique, basioccipital, et complexe para- basiphénoïde	il semble qu'elle soit bordée par quatre os: prootique, opis- thotique, basioccipital et complexe para- basiphénoïde cependant le basioccipital est très endommagé dans cette région et ses relations exactes avec les autres os sont incertaines	bordée par quatre os: le prootique et l'opisthotique, chacun pour un tiers; l'autre tiers étant formé par l'ensemble basi- occipital et complexe para-basiphénoïde	? bordée par trois os: prootique, opisthotique et basioccipital, chacun pour un tiers
Epitérygoïde			
Supraoccipital			
Fenêtre ovale			

	ANNIDAE = Amnatherapsididae		MOSCHORHINI- DAE	WHATSIIDAE	
	U.R.S.S.	Afrique australe	Afrique	U.R.S.S.	
	<i>Anna</i> = <i>Amnatherapsidus</i>	<i>Chthonosaurus</i>	<i>Moschorhinus</i> (? <i>Tyriscuchus</i>)	<i>Therionathus</i>	<i>Moschouhaisia</i>
	Permien supérieur: zone IV, Tatarien	Permien supérieur: zone IV, Tatarien	Permien supérieur: zones à <i>Daplocephalus</i> et à <i>Lystrosaurus</i>	Permien supérieur: — Tanzanie: Kawinga Formation — Afrique australe: zone à <i>Cistecephalus</i> <i>s.l.</i>	Permien supérieur: zone IV, Tatarien supérieur peut-être équivalent à la zone à <i>Cistecephalus</i> <i>s.l.</i> (cf. Tatarinov 1963: 78)
Mandibule	à région mentonnière en pente douce, mais à rupture de pente à la base de la symphyse	?	à angle mentonnier très marqué	à région mentonnière en pente douce et régulière	à angle mentonnier marqué
Précanine	1	1	1	0	1
Canines	1	1	1	2	2
Postcanines	6	6	3	0	7

I. COMPARAISON ENTRE LES MOSCHORHINIDAE ET LES DEUX AUTRES FAMILLES

A—Moschorhinidae et Whaitsiidae

D'après le tableau précédent on remarque que les Moschorhinidae diffèrent des Whaitsiidae d'Afrique d'une part, par la rétention de caractères structuraux primitifs et d'autre part, par des éléments correspondant à des insertions musculaires. La rétention de caractères structuraux primitifs touche surtout la région du palais (absence de contact voméro-maxillaire correspondant à un début de palais secondaire, et donc fosses canines et orifice choanal en continuité, *crista choanalis* brève et mousse, présence de grandes fosses sous-orbitaires), l'endocrâne (épiptérygoïde plus étroit, incomplète séparation des sorties des branches maxillaire et mandibulaire du nerf trijumeau, fosse interptérygoïdienne ouverte, fenêtre ovale bordée par quatre os) et la denture maxillaire (rétention d'une précanine et de quelques postcanines, bien que réduites). Les différences d'attaches musculaires s'observent au niveau des ptérygoïdes, des pariétaux et du complexe para-basisphénoïde. Cependant, les

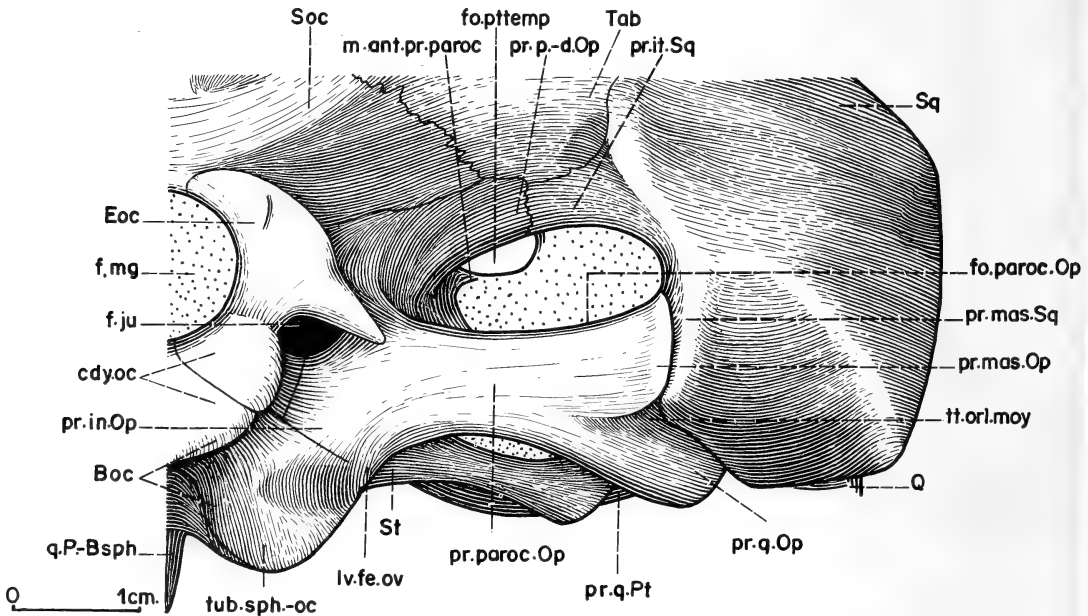


Fig. 9. *Moschorhinus kitchingi*, Moschorhinidae, S.A.M. n°K.118. Détail de la partie inférieure du côté droit de l'occiput, reconstruit par symétrie ($\times 5/3$).

Boc, basioccipital; *cdy.oc*, condyle occipital; *Eoc*, exoccipital; *f.ju*, foramen jugulaire; *f.mg*, foramen magnum; *fo.paroc.Op*, fosse paroccipitale de l'opisthotique; *fo.pttemp*, fosse posttemporale; *lv.fe.ov*, lèvre de la fenêtre ovale; *m.ant.pr.paroc*, mur antérieur du processus paroccipital; *pr.in.Op*, processus interne de l'opisthotique; *pr.it.Sq*, processus intermédiaire du squamosal; *pr.mas.Op*, processus mastoïde de l'opisthotique; *pr.mas.Sq*, processus mastoïde du squamosal; *pr.p-d.Op*, processus postéro-dorsal de l'opisthotique; *pr.paroc.Op*, processus paroccipital de l'opisthotique; *pr.q.Op*, processus carré de l'opisthotique; *pr.q.Pt*, processus carré du ptérygoïde; *Q*, carré; *q.P.-Bsph*, quille du complexe para-basisphénoïde; *Soc*, supraoccipital; *Sq*, squamosal; *St*, stapes; *Tab*, tabulaire; *tt.ori.moy*, toit de l'oreille moyenne; *tub.sph-oc*, tuberculum spheno-occipitale.

Whaitsiidae ont conservé deux canines tandis que les Moschorhinidae n'en présentent plus qu'une. Par ailleurs, la mandibule des Moschorhinidae présente une région mentonnière très anguleuse tandis que celle des Whaitsiidae africains est en pente douce. *Moschorhinus* (? *Tigrisuchus*) diffère également de *Theriognathus* par un museau court à constriction postcanine peu marquée, à arcades zygomaticques et postorbitaires et à barres sousorbitaires épaisses. Il s'en rapproche par contre par l'aspect du bord de la fenêtre ovale. Les Moschorhinidae diffèrent moins du Whaitsiidae d'U.R.S.S. dans la mesure où celui-ci a conservé certains caractères primitifs tels qu'une grande fosse sous-orbitaire, la présence d'une précanine et de postcanines. Ils s'en rapprochent également par l'épaisseur des arcades et la forme du menton.

Il faut noter que les palais des Moschorhinidae et des Whaitsiidae ne diffèrent pas seulement par la rétention ou la disparition de caractères primitifs

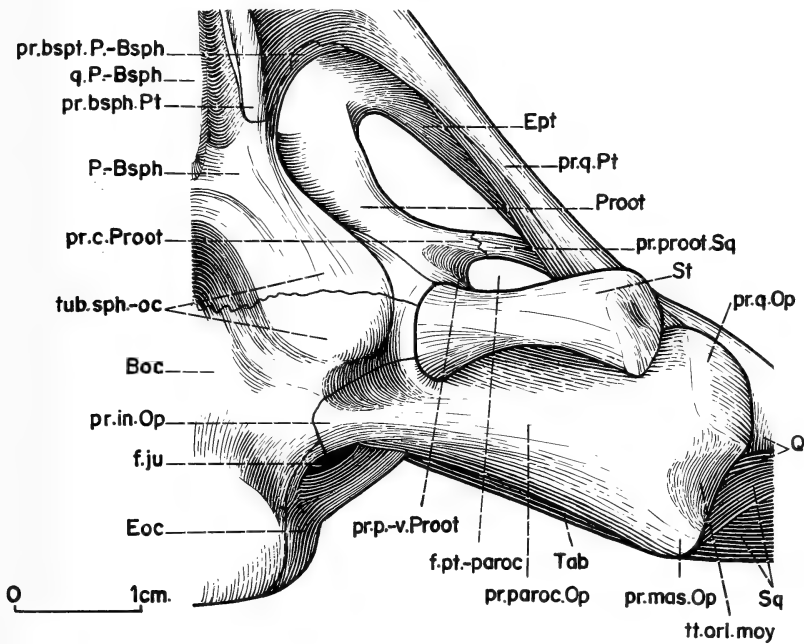


Fig. 10. *Moschorhinus kitchingi*, Moschorhinidae, S.A.M. n°K.118. Détail de la vue ventrale de la partie postérieure du côté droit du crâne, reconstruit par symétrie ($\times 5/3$).

Boc, basioccipital; *Eoc*, exoccipital; *Ept*, épiptérygoïde, *f.ju*, foramen jugulaire; *f.pt.-paroc*, foramen ptérygo-paroccipital; *P.Bsph*, complexe para-basisphénoïde; *pr.bsph.Pt*, processus basisphénoïde du ptérygoïde; *pr.bspt.P.-Bsph*, processus basiptérygoïde du complexe parabasisphénoïde; *pr.c.Proot*, processus central du prootique; *pr.in.Op*, processus interne de l'opisthotique; *pr.mas.Op*, processus mastoïde de l'opisthotique; *pr.p.-v.Proot*, processus postéro-ventral du prootique; *pr.paroc.Op*, processus paroccipital de l'opisthotique; *pr.proot.Sq*, processus prootique du squamosal; *pr.q.Op*, processus carré de l'opisthotique; *pr.q.Pt*, processus carré du ptérygoïde; *Proot*, prootique; *Q*, carré; *q.P.-Bsph*, quille du complexe para-basisphénoïde; *Sq*, squamosal; *St*, stapes; *Tab*, tabulaire; *tt.ori.moy*, toit de l'oreille moyenne; *tub.sph-oc*, *tuberculum sphenoccipitale*.

mais encore par une spécialisation différente: il en est ainsi de l'aspect en éventail du vomer des Moschorhinidae.

B—Moschorhinidae et Annatherapsididae

On voit que la plupart des caractères qui éloignent les Moschorhinidae des Whaitsiidae les rapprochent au contraire des Annatherapsididae. Par certains caractères, ils se rapprochent plutôt de *Chthonosaurus*: par l'aspect de la fosse interptérygoïenne et du supraoccipital; mais les caractères qui les rapprochent de *Annatherapsidus* sont plus nombreux: brièveté des frontaux, aspect de la *crista choanalis*, dimensions de la quille du complexe para-basisphénoïde. Il faut noter toutefois que la région antérieure du palais de *Chthonosaurus* n'est pas connue.

Les Moschorhinidae diffèrent des deux genres d'Annatherapsididae par la brièveté du museau, la présence d'un foramen pinéal, peut-être l'absence de dents ptérygoïennes et la faible participation du complexe para-basisphénoïde au bord de la fenêtre ovale.

Moschorhinus (?*Tigrisuchus*) diffère également d'*Annatherapsidus* par des caractères qui ne sont pas connus chez *Chthonosaurus* tels que la brièveté de la région médiane des prémaxillaires sur la face ventrale et l'aspect anguleux

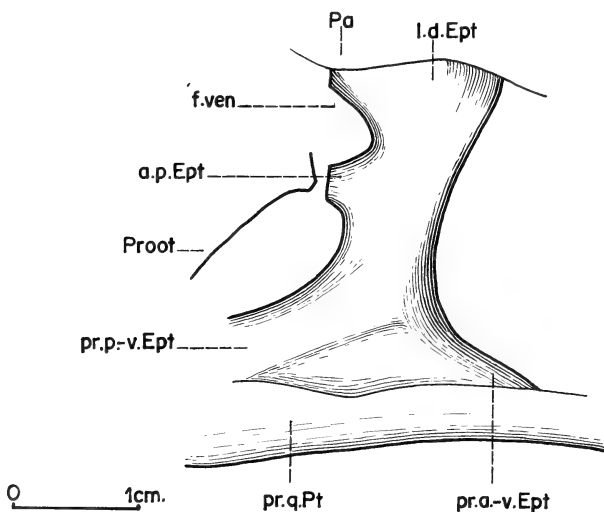


Fig. 11. *Moschorhinus kitchingi*, Moschorhinidae, S.A.M. n°K.118. Vue latérale de l'épiptérygoïde droit, reconstruit par symétrie ($\times 5/3$).

a.p.Ept, apophyse postérieure de l'épiptérygoïde; *f.ven*, foramen veineux; *l.d.Ept*, lame dorsale de l'épiptérygoïde; *Pa*, pariétal; *pr.a.-v.Ept*, processus antéro-ventral de l'épiptérygoïde; *pr.p.-v.Ept*, processus postéro-ventral de l'épiptérygoïde; *pr.q.Pt*, processus carré du ptérygoïde; *proot*, prootique.

de la région mentonnière. La différence d'aspect de cette dernière région est moins grande entre *Annatherapsidus* et *Theriognathus*.

II—COMPOSITION DES WHAITSIIDAE ET DES MOSCHORHINIDAE

Une discussion détaillée concernant chacune de ces familles devant paraître ultérieurement, nous ne présenterons ici qu'un bref résumé.

A—Les Whaitsiidae

Parmi les Thérocéphales, les Whaitsiidae ont l'exclusivité d'un palais secondaire osseux rudimentaire, à vomers cruciformes en contact avec les maxillaires dont les processus vomérins sont suivis d'une *crista choanalis* marquée. Ils ne partagent qu'avec les Euchambersiidae la tendance à la disparition des fosses sousorbitaires et des postcanines. Il faut noter cependant que la tendance à la réduction de la série dentaire maxillaire postcanine est une caractéristique commune aux Thérocephalia Pristerosauria dont ces deux familles font partie. D'autres caractères ont été cités dans la diagnose établie par Tatarinov (1963: 76-77); soit 'un crâne bas et large, un museau à forte constriction postcanine, l'absence de postpariétal'. Chez les Whaitsiidae la fosse interptérygoïdienne tend à se fermer et la canine à disparaître. En outre, cette famille conserve

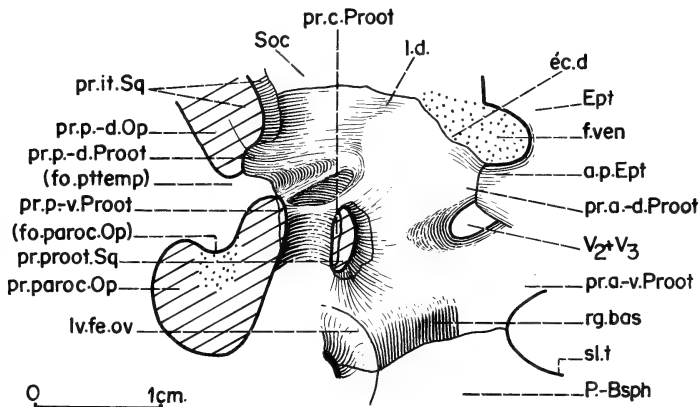


Fig. 12. *Moschorhinus kitchingi*, Moschorhinidae, S.A.M. n°K.118. Vue latérale du prootique droit, reconstruit par symétrie ($\times 5/3$).

a.p.Ept, apophyse postérieure de l'épiptérygoïde; *éc.d*, échancrure dorsale; *Ept*, épiptérygoïde; *f.ven*, foramen veineux; (*fo.paroc.Op*), fosse paroccipitale de l'opisthotique; (*fo.pttemp*), fosse posttemporale; *l.d.*, lame dorsale; *lv.fe.ov*, lèvre de la fenêtre ovale; *P.-Bsph*, complexe para-basisphénoïde; *pr.a.-d.Proot*, processus antéro-dorsal du prootique; *pr.a.-v.Proot*, processus antéro-ventral du prootique; *pr.c.Proot*, processus central du prootique; *pr.it.Sq*, processus intermédiaire du squamosal; *pr.p.-d.Op*, processus postéro-dorsal de l'opisthotique; *pr.p.-d.Proot*, processus postéro-dorsal du prootique; *pr.p.-v.Proot*, processus postéro-ventral du prootique; *pr.paroc.Op*, processus paroccipital de l'opisthotique; *pr.proot.Sq*, processus prootique du squamosal; *rg.bas*, région basale; *sl.t*, selle turcique; *Soc*, supraoccipital; *V2 + V3*, lieu de sortie des branches maxillaire et mandibulaire du nerf trijumeau.

deux canines à fonctionnement alternatif. Malheureusement la région postérieure du crâne des *Whaitsiidae* *Moschowhaiitsiinae* n'est pas connue, ce qui limite la définition de la famille.

En l'état actuel de nos connaissances, les *Whaitsiidae* se réduisent à deux genres correspondant aux deux sous-familles créées par Tatarinov.

1. *Moschowhaiitsiinae*

Cette sous-famille se distingue des *Whaitsiinae* par la présence d'une 'précanine' et de 'nombreuses postcanines' (7 chez le seul genre connu), l'épaisseur moyenne des arcades zygomatiques et postorbitaires, la 'grande taille des fosses sousorbitaires', la persistance d'une étroite ouverture dans la partie antérieure de la 'fosse interptérygoïdienne', l'absence de foramen pinéal et de dents ptérygoïdiennes; un seul spécimen est connu, il serait nécessaire d'en avoir plusieurs pour être certain de la validité de ce dernier caractère. D'autre part, la mandibule est caractérisée par un angle mentonnier fortement marqué. (Les caractères indiqués entre guillemets faisaient partie de la diagnose et de la liste comparative établies par Tatarinov (1963: 78).)

Moschowhaiitsia vjuschkovi Tatarinov: Permien supérieur d'U.R.S.S., partie supérieure de la zone IV (ou Tatarien); 'équivalent possible de la zone à *Cistecephalus* d'Afrique du Sud' selon Tatarinov (1963: 78).

2. *Whaitsiinae*

Cette sous-famille est caractérisée par l'absence totale de pré et postcanine (il n'y a aucune raison de penser que le spécimen considéré jusqu'à présent comme le type de *Alopecopsis* ait possédé, à un plus jeune stade, des postcanines à chaque mâchoire), l'affinement des arcades postorbitaires et zygomatiques, la réduction ou la disparition des fosses sousorbitaires (il peut y avoir chez le même spécimen une fosse réduite d'un côté et pas de fosse de l'autre), la fermeture de la fosse interptérygoïdienne chez l'adulte, la présence de foramen pinéal et de dents ptérygoïdiennes. La mandibule présente une région mentonnière en pente douce.

D'autres caractéristiques ont pu être observées dans cette sous-famille dans une région qui n'est pas connue chez les *Moschowhaiitsiinae*. Ainsi, les *Whaitsiinae* ont l'exclusivité, parmi les Thérocéphales connus, d'un épIPTérygoïde extrêmement élargi dont le bord postérieur présente à la fois une apophyse postérieure et un processus prootique. D'autre part, la fenêtre ovale des *Whaitsiinae* n'est bordée que par trois os: le prootique, l'opisthotique et le basioccipital, à parts égales.

Theriognathus microps Owen: Permien supérieur d'Afrique.

Theriognathus Owen, 1876 est connu en Afrique orientale et australe:

— Tanzanie: zone à *Cistecephalus s.l.* (cf. Huene 1950: 105, 124), Kawinga Formation (cf. Charig 1963: 52).

— Afrique australe: zone à *Cistecephalus s.l.* (existe dans la zone à *Cistecephalus s.s.*, mais est particulièrement abondant dans la zone à *Daptocephalus* selon

Kitching (information orale, septembre 1970).

Broom (1932: 90) fut le premier à reconnaître l'appartenance du type aux Whaitsiidae.

B—Les Moschorhinidae

Jusqu'ici nous avons traité des 'Moschorhinidae' et des 'Annatherapsididae' comme de deux familles indépendantes; cependant, étant donné le nombre de leurs caractères communs, il nous semble préférable de les considérer comme deux des trois sous-familles (la troisième étant les Euchambersiinae) de Moschorhinidae au sens large. A ce sujet, il est intéressant de noter que Watson & Romer (1956: 72) considéraient les Annatherapsididae comme des 'Therocephalia *incertae sedis* (cf. Whaitsiidae primitifs)' à une époque où ce dernier terme recouvrait à la fois les Whaitsiidae et les Moschorhinidae d'Afrique.

Les Moschorhinidae sont essentiellement caractérisés par l'élargissement en éventail de la plaque antérieure du vomer. Ils présentent en outre une plateforme triangulaire sur la face dorsale du pariétal, à l'avant de la crête sagittale, un épitérygoïde moyennement élargi, une fenêtre ovale entourée de quatre os: le prootique, l'opisthotique, le basioccipital et le complexe para-basisphénoïde, ces deux derniers de façon moindre. La constriction du museau à l'arrière des canines est très peu ou pas marquée. La fosse interptérygoïdienne est ouverte. Le processus carré et le processus transverse du ptérygoïde sont reliés par une fine lame osseuse. Il n'y a pas de postfrontal. Cette famille conserve la précanine, tandis qu'elle ne possède qu'une canine fonctionnelle.

1. *Annatherapsidinae*

Les Annatherapsidinae se distinguent des deux autres sous-familles de Moschorhinidae par la longueur du museau, l'absence de constriction post-canine, la formule dentaire maxillaire la plus complète (1 pC, 1 C, 6 PC). C'est dans cette sous-famille que la forme en éventail de la plaque antérieure des vomers est la moins marquée et la lame entre le processus carré et le processus transverse des ptérygoïdes la plus large. Ils diffèrent des Moschorhininae par la présence de dents ptérygoïdiennes, l'absence de foramen pinéal, la participation à égalité des prootique, opisthotique, basioccipital, complexe para-basisphénoïde au bord de la fenêtre ovale, des barres sousorbitaires presque totalement formées par le jugal. De plus, ils se distinguent, des Euchambersiinae (outre les caractères de spécialisation de ceux-ci) par la grande taille des fosses sousorbitaires.

La comparaison entre les deux genres d'Annatherapsidinae est incomplète du fait de l'érosion de la partie antérieure du museau de *Chthonosaurus*.

Annatherapsidus petri Kuhn: Permien supérieur d'U.R.S.S., zone IV (Tatarien).

Annatherapsidus Kuhn, 1961 diffère de *Chthonosaurus* par un museau de longueur moyenne, des arcades zygomatiques et postorbitaires d'épaisseur

moyenne, des frontaux courts, l'absence de trace du foramen pinéal, une *crista choanalis* mousse, des processus basisphénoïdes des ptérygoïdes jointifs dans leur partie postérieure, ne laissant la fosse interptérygoïdienne ouverte qu'à l'avant. La quille du complexe para-basisphénoïde est relativement peu importante. Les processus latéraux du supraoccipital sont assez allongés.

En outre, la région médiane des prémaxillaires est moyennement longue, large et la région mentonnière de la mandibule est en pente douce bien qu'à rupture de pente à la base de la symphyse.

Chthonosaurus velocidens Vjushkov: Permien supérieur d'U.R.S.S., zone IV (Tatarien).

D'après l'aspect de ce qui reste du museau de *Chthonosaurus* Vjushkov, 1955, celui-ci devait posséder un museau assez long. Les arcades zygomatiques et postorbitaires de faible épaisseur, des frontaux longs, une trace de foramen pinéal sous l'aspect d'un rebord ourlé des pariétaux, une *crista choanalis* moyennement marquée, des processus basisphénoïdes écartés sur toute leur longueur laissant une fosse interptérygoïdienne complètement ouverte. La quille du complexe para-basisphénoïde est relativement élevée. Les processus latéraux du supraoccipital sont courts.

2. *Moschorhininae*

Les Moschorhininae sont caractérisés par la robustesse du museau, une très faible constriction postcanine, une formule dentaire maxillaire en régression (1 pC, 1 C, 3-5 PC). L'élargissement de la plaque antérieure des vomers en éventail est accentuée; la lame entre le processus carré et le processus transverse des ptérygoïdes est de taille moyenne ou réduite. Les dents ptérygoïdiennes paraissent absentes. La quille du complexe para-basisphénoïde est moyenne ou peu importante. Le frontal est court et le foramen pinéal est présent chez les spécimens autres que *Promoschorhynchus* chez lequel cette région n'est pas connue. Chez *Moschorhinus* (?*Tigrisuchus*) et *Promoschorhynchus* le prootique et l'opisthotique forment chacun un tiers du bord de la fenêtre ovale (cette région n'est pas connue chez *Cerdops*). Les fosses sousorbitaires sont grandes.

Promoschorhynchus platyrhinus Brink: Permien supérieur d'Afrique australe, zone à *Cistecephalus* s.l. (plus précisément zone à *Daptocephalus* selon Kitching, information orale, septembre 1970).

Promoschorhynchus Brink, 1954 est le genre de Moschorhininae dont le nombre de postcanines est le plus grand (5). Son museau est moyennement long et ses arcades zygomatiques et postorbitaires peu importantes. Le maxillaire participe fortement à la barre sousorbitaire. La *crista choanalis* est bien marquée, tandis que la plaque antérieure des vomers, moyennement élargie, s'unit à des processus vomérins des prémaxillaires assez longs et larges; cette situation est très voisine de celle que l'on observe chez *Annatherapsidus* (ceci a pu être observé sur le type du genre B.P.I.n°F.484/M.192, après nouvelle préparation et sur un autre spécimen plus complet R.C.n°116). La fosse interptérygoïdienne est ouverte sur toute sa longueur. Les processus carré et transverse

des ptérygoïdes forment un angle très aigu; la lame unissant ces deux processus est réduite. L'angle mentonnier est bien marqué, beaucoup moins toutefois que chez *Moschorhinus* (?*Tigrisuchus*).

Moschorhinus (?*Tigrisuchus*) *kitchingi* Broom: Permien supérieur d'Afrique australe. Zone à *Cistecephalus* *s.l.* en général, plus précisément zone à *Daptocephalus* selon Kitching (information orale, septembre 1970); se perpétue dans la zone à *Lystrosaurus* (cf. Brink 1958: 42). Cette dernière zone est classiquement considérée comme étant la base du Trias inférieur, mais certains auteurs (Cosgriff 1965: 89; Anderson 1970: carte n°5) considèrent qu'elle forme la partie terminale du Permien; ceci d'après la faune.

Moschorhinus Broom, 1920 est caractérisé par un nombre réduit de post-canines (3), un museau court, des arcades zygomatiques et postorbitaires très épaisses. Le maxillaire participe fortement à la barre sousorbitaire. La *crista choanalis* est mousse; la plaque antérieure des vomers est fortement élargie et unie à l'avant au bref processus vomérin des maxillaires. La fosse interptérygoïdienne est ouverte sur toute sa longueur. Les processus carré et transverse des ptérygoïdes forment un angle aigu peu accentué et sont unis par une lame osseuse de dimension moyenne.

L'angle mentonnier est fortement marqué.

Problèmes de synonymie avec *Moschorhinus*

Tigrisuchus simus Owen. Permien supérieur d'Afrique australe. Horizon incertain. Zone à *Cistecephalus* *s.l.* selon Watson & Romer (1956: 61).

Tigrisuchus fut placé suivant les auteurs tantôt parmi les Gorgonopsiens, tantôt parmi les Thérocéphales et tout récemment (cf. Sigogneau, 1970a: 375-376) parmi les Theriodontia *incertae sedis*. Boonstra fut le premier (1934: 260-261) à le considérer comme un *Whaitsiidae* *s.l.* Malheureusement le spécimen type de *Tigrisuchus* Owen, 1876 (B.M.N.H. n°R. 1721) n'est qu'un fragment antérieur de museau, brisé postérieurement au niveau des canines, et ventralement, suivant un plan frontal, un peu plus bas que le bord inférieur des septomaxillaires, au ras de deux foramens prémaxillaires dorsaux. Ce fragment est cependant suffisant pour que l'on puisse noter son aspect globuleux, le degré d'étalement du septomaxillaire et la disposition de ses foramens ainsi que l'aspect de la région antérieure du palais. Celle-ci est identique à celle des divers spécimens de *Moschorhinus*: les prémaxillaires sont brefs sur la ligne médiane et unis à la plaque antérieure des vomers fortement élargie en éventail. Un léger doute quant à la synonymie persiste en raison du nombre des dents antérieures à la canine: dans le maxillaire on observe quatre sections d'incisives et du côté gauche l'extrême pointe d'une alvéole; par contre, il n'y a pas trace de précanine et la suture entre prémaxillaire et maxillaire est très proche de la canine. Seules, des sections frontales de museaux de '*Moschorhinus*' pourront donner des renseignements sur la profondeur de l'alvéole de la précanine (probablement moindre que celle des incisives et canine). Si c'est le cas, il faudra considérer *Tigrisuchus* et *Moschorhinus* comme synonymes.

Cerdops burgheri Broom. Permien supérieur d'Afrique australe. Zone à

Cistecephalus s.l. (plus précisément, zone à *Daptocephalus* selon Kitching, information orale, septembre 1970).

Ce genre a déjà été placé (bien qu'avec doute) parmi les *Whaitsiidae s.l.* Romer (1966: 373 L).

Cerdops Broom, 1948 se rapproche beaucoup par la brièveté de son museau et la réduction du nombre de ses postcanines (3) de *Moschorhinus* (?*Tigrisuchus*). Cependant, il semble que le nombre des dents antérieures à la canine soit différent: 5 dents correspondant à 4 I et 1 pC ou à 5 I et 0 pC, selon les avis. Les arcades zygomatiques et postorbitaires sont moyennes. La barre sousorbitaire est presque exclusivement formée par le jugal qui en exclut pratiquement le maxillaire (le spécimen de *Moschorhinus* (?*Tigrisuchus*), B.P.I. n°F. 1713/M.295 montre dans cette région un épaississement du jugal qui n'est pas sans rappeler celui de *Cerdops*, mais toutefois le maxillaire participe largement à cette barre). La partie postérieure de la plaque antérieure des vomers montre qu'elle s'étale en éventail. La *crista choanalis* est moyennement marquée. Les processus basi-phénoïdes des ptérygoïdes jointifs dans leur partie postérieure, ne laissent, comme chez *Annatherapsidus*, que la partie antérieure de la fosse interptérygoïdienne ouverte. Les processus carré et transverse des ptérygoïdes semblent former un angle moyennement aigu (ceci compte tenu de l'écrasement latéral du spécimen) et sont reliés par une petite lame osseuse. L'angle mentonnier n'est pas très marqué en raison de la courbure de la partie antérieure de la symphyse.

Kitching (information orale, avril 1966) pense que ce spécimen devrait être considéré comme une forme jeune de *Moschorhinus* (?*Tigrisuchus*). En raison des quelques caractères cités plus haut et surtout de l'ignorance dans laquelle nous sommes quant à l'aspect de la partie antérieure du palais et par conséquent des rapports entre prémaxillaires et vomers (ceux-ci constituant dans ce groupe un critère essentiel), il nous semble prudent de laisser ce genre subsister pour le moment.

Hewittia albanensis Brink. Permien supérieur d'Afrique australe. Zone à *Cistecephalus s.l.* (plus précisément zone à *Daptocephalus* selon Kitching information orale, septembre 1970).

Hewittia Brink, 1958 est également représenté par un seul spécimen fragmentaire: partie antérieure du crâne brisée à l'arrière des orbites. Kitching (information orale, juillet 1972) considère que *Hewittia* est un synonyme de *Moschorhinus*. En faveur de cette hypothèse on peut noter (seulement d'après les figures 14 A-B et 15 et la description de Brink 1958: 37-40, le spécimen A.M.G. n°4206 étant introuvable): la réduction des postcanines en nombre et en taille et la forte angulation mentonnière. Cependant le museau de *Hewittia* est sensiblement plus allongé et étroit que chez *Moschorhinus* (?*Tigrisuchus*), quatre postcanines sont présentes, la barre sousorbitaire est peu épaisse, les nasaux très fortement resserrés en leur milieu, les fosses sousorbitaires sont relativement petites et l'aspect de la plaque antérieure des vomers incertain. De plus, selon la figure 14-A, les lacrymaux auraient un assez large contact

avec les nasaux; ceci est complètement opposé à ce qui est représenté figure 15. Dans ces conditions, il est préférable de ne tirer aucune conclusion tant que le spécimen n'a pas été retrouvé.

3. *Euchambersiinae*

Les *Euchambersiinae* sont les seuls Thérocéphales présentant une canine à cannelure et, à avant de l'orbite, une profonde fosse sur la face externe du maxillaire et du lacrymal; la face externe du maxillaire est en outre marquée de fines rigoles dans la région de la canine. Ils partagent avec *Moschorhinus* (?*Tigrisuchus*) la massivité du crâne, en particulier l'aspect très lourd du museau, et la faible longueur des processus vomérins des prémaxillaires. La formule dentaire est encore plus réduite que chez ces derniers puisqu'il n'y a pas de postcanine. A l'emplacement de celles-ci se trouve une subdivision de la fosse citée plus haut. L'élargissement de la plaque antérieure des vomers est extrême. Cette plaque est marquée de légères ondulations au niveau de son contact avec les prémaxillaires. La lame entre le processus carré et le processus transverse des ptérygoïdes est très étroite; par contre une lame extroversée, très développée unit le processus basisphénoïde et le même processus transverse. Les processus basisphénoïdes sont unis de sorte que la fosse interptérygoïdienne n'est visible que dans sa partie antérieure. Il ne semble pas qu'il y ait de dents ptérygoïdiennes. Les fosses sousorbitaires sont extrêmement réduites. Les arcades zygomatiques et postorbitaires sont grêles mais complètes (observation personnelle sur un second spécimen, B.P.I. n°F.4009/M.384). L'extension des préfrontaux vers l'arrière est encore plus poussée que chez *Moschorhinus* (?*Tigrisuchus*) et le frontal est presque totalement éliminé du bord supérieur de l'orbite. Ce frontal est bref. La région intertemporale est élargie. Il n'y a pas de foramen pinéal visible. La crête sagittale pariétale est basse. La région dorsale de l'épiptérygoïde est plus étalée que chez les autres *Moschorhinidae* connus. La fenêtre ovale semble bien entourée par quatre os mais son bord étant fortement érodé, il est impossible d'apprécier dans quelles proportions le prootique, l'opisthotique, le basioccipital et le complexe para-basisphénoïde y participent.

La mandibule n'est pas connue.

Cette sous-famille n'est représentée que par un seul genre:

Euchambersia mirabilis Broom. Permien supérieur d'Afrique australe. Zone à *Cistecephalus s.l.* (plus précisément zone à *Cistecephalus s.s.*—c'est-à-dire partie inférieure de la zone à *Cistecephalus s.l.*—selon Kitching, information orale, septembre 1970).

Le genre *Euchambersia* Broom, 1931 n'est actuellement représenté que par deux spécimens.

C—Genres exclus des *Whaitsiidae* et des *Moschorhinidae*

Hofmeyria atavus Broom. Permien supérieur d'Afrique australe. Zone à *Cistecephalus s.l.* (zone à *Cistecephalus s.s.*, selon Kitching, information orale, septembre 1970).

Hofmeyria Broom, 1935 possède un museau lourd, une région intertemporale élargie et une crête sagittale pariétale basse, caractère que l'on retrouve chez *Euchambersia* mais aussi chez certains 'Ictidosuchidae' (terme employé ici selon la définition de Brink 1965: 35). *Hofmeyria* a également en commun avec les 'Ictidosuchidae' les caractères suivants: des crêtes ventro-intermédiaires des ptérygoïdes dentigères et très allongées, un foramen pinéal de grande taille et surtout une plaque antérieure des vomers étroite. D'autre part, *Hofmeyria* présente deux canines sur chaque maxillaire. Ce genre serait à rapprocher de *Ictidostoma hamburgi* Broom tel que l'a décrit Brink (1960: 169-171, fig. 38 A, B, C).

Mirotenthes digitipes Attridge. Permien supérieur d'Afrique australe. Zone à *Cistecephalus s.l.*

Mirotenthes Attridge, 1956, après la récente révision de Cys (1971: 124), est assigné par cet auteur aux 'Nanictidopsidae, famille primitive des Bauriamorphes telle qu'elle est définie par Watson & Romer (1956: 74) ou aux Ictidosuchidae, famille primitive des Scaloposaures telle qu'elle est définie par Brink (1965)'. Ce spécimen présente un caractère qui n'a encore jamais été observé chez un Thérocéphale qu'il soit de la lignée des Pristerosauria ou de la lignée des Scaloposauria, à savoir la présence de dents ptérygoïdiennes sur la crête ventro-médiane des ptérygoïdes (p. 122, fig. 1), en plus de la présence assez courante de dents sur les crêtes ventro-intermédiaires des mêmes os.

Proalopecepsis haughtoni Brink & Kitching. Permien supérieur d'Afrique australe. Zone à *Cistecephalus s.l.* (zone à *Cistecephalus s.s.*, selon Kitching, information orale, septembre 1970).

Proalopecepsis Brink & Kitching, 1951, serait à placer, selon Kitching (information orale, juillet 1972), parmi les Ictidosuchidae tels que ceux-ci ont été définis par Brink en 1965.

La révision des 'Ictidosuchidae' n'étant pas terminée, ces diverses attributions à cette famille sont à considérer comme provisoires.

CONCLUSION

Il semble maintenant qu'il faille admettre que les ressemblances notées chez le *Whaitsiidae* d'U.R.S.S. et les *Moschorhinidae* sud-africains correspondent à la conservation de caractères ancestraux (présence de pré et postcanines, fosses sousorbitaires grandes) ou à une caractéristique générale à la lignée *Pristerosauria* (tendance à la réduction des dents postcanines).

Les différences dans la structure du palais nous paraissent plus importantes et éloignent ces deux familles l'une de l'autre et nous fait abandonner la subdivision des *Whaitsiidae*, adoptée par Tatarinov (1963: 77), en trois sous-familles: *Whaitsiinae*, *Moschowaitsiinae* et *Moschorhininae*. Il semble préférable de conserver (bien qu'en en modifiant la composition) les familles des *Whaitsiidae* et des *Moschorhinidae* redéfinie pour la première et créée pour la seconde par Brink (1958: 40). Les *Whaitsiidae* seraient subdivisés en Mos-

chowhaitsiinae d'U.R.S.S. (*Moschowhaitsia*) et Whaitsiinae d'Afrique (*Theriongnathus*); les Moschorhinidae seraient subdivisés en Annatherapsidinae d'U.R.S.S. (*Annatherapsidus* et *Chthonosaurus*), en Moschorhininae d'Afrique australe (*Promoschorhynchus*, *Moschorhinus* (?*Tigrisuchus*), *Cerdops*, ?*Hewittia*) et Euchambersiinae également d'Afrique (*Euchambersia*). Il est curieux de noter que dans les deux familles, c'est chez les formes d'U.R.S.S. que le foramen pinéal disparaît tandis qu'il persiste chez les formes africaines (*Euchambersia* mis à part). Par contre, c'est dans des sous-familles sud-africaines que, à l'intérieur des deux familles, on observe la disparition des postcanines et la fermeture de la fosse sousorbitaire.

Dans l'ensemble, les formes russes (mise à part la fermeture du foramen pinéal) paraissent plus primitives que les formes africaines. Elles pourraient être plus proches de la souche commune. A ce sujet il est intéressant de noter que *Annatherapsidus* fait partie du 'complexe à Pareiasaure' de la zone IV d'U.R.S.S., à propos duquel Chudinov (1965: 128) n'exclut pas 'la possibilité qu'il ait été placé quelque peu trop haut dans la section du Permien supérieur d'U.R.S.S. et qu'en réalité il corresponde à un horizon plus ancien que la zone à *Cistecephalus*'. Cette opinion est en faveur d'une migration à une époque soit antérieure à la zone à *Cistecephalus s.l.*, soit équivalente à sa base pour les Moschorhinidae. Rappelons qu'il a dû en être de même pour les Whaitsiidae que l'on trouve déjà dans la partie inférieure de la zone à *Cistecephalus* (zone à *Cistecephalus s.s.* de Kitching) et qui s'épanouirait dans le sommet de cette zone (ou zone à *Daptocephalus* de Kitching) à tel point que cet auteur hésitera entre la dénomination de 'zone à *Daptocephalus*' et 'zone à *Waitsia*' (voir synonymie ci-dessus). Les Whaitsiinae semblent être parvenus en Afrique australe plus tôt (zone à *Cistecephalus s.s.*) que les Moschorhininae (zone à *Daptocephalus*). A propos de la faune de la zone à *Tapinocephalus*, qu'il compare à celle de la zone II du Permien supérieur d'U.R.S.S., Boonstra (1968: 203) admet que la 'faune sud-africaine serait une faune immigrante originaire de Russie'. Il en est de même, en partie tout au moins, de la faune de la zone à *Cistecephalus s.l.* (puis de celle de la zone à *Lystrosaurus* du moins en ce qui concerne les Moschorhininae). Ces mouvements de faune témoignent d'au moins deux périodes de contact entre Laurasia et Gondwanaland au Permien supérieur. Mais, comme le notait Houghton (1953: 30), aucun document paléontologique ne permet de connaître, à l'heure actuelle, quelles voies ont emprunté ces immigrants entre les différentes régions d'U.R.S.S. dont ils sont originaires et la région Tanzanie-Nyasa.

LISTES DES ABRÉVIATIONS DES NOMS DE COLLECTIONS

A.M.G. Albany Museum, Grahamstown, Afrique du Sud.

B.P.I. n°F. . . /M. Bernard Price Institute for Palaeontological Research, Johannesburg, Afrique du Sud.

F = numéro du catalogue de fouille.

M = numéro du catalogue de musée.

F.R.P.	Collection du Dr F. R. Parrington, Museum of Zoology, Cambridge.
P. IN.Mw	Paleontologitcheskij Muzei, Moscou, U.R.S.S.
R.C.	Rubidge collection, Wellwood, Graaff-Reinet, Afrique du Sud.
S.A.M.	South African Museum, Cape Town, Afrique du Sud.
Tü	Institut und Museum für Geologie und Paläontologie der Universität, Tübingen, République Fédérale Allemande.

RÉSUMÉ

L'anatomie du crâne d'un jeune *Moschorhinus* (?*Tigrisuchus*) est étudiée ici, tout particulièrement les régions du palais et de l'arrière-crâne. La relation existant entre les Whaitsiidae russes (*Moschowaitsiinae*) et les Whaitsiidae africains (*Whaitsiinae*) est notée brièvement. Les ressemblances entre les Annatherapsididae russes et les Moschorhinidae sudafricains conduit à les inclure dans une même famille, les Moschorhinidae, qui sont redéfinis. Cette famille comprend une sous-famille russe (*Annatherapsidinae*) et deux sous-familles sudafricaines (*Moschorhininae* et *Euchambersiinae*). Il est suggéré que les faunes ancestrales des Whaitsiinae d'une part et les faunes ancestrales des Moschorhininae d'autre part aient migré de la Laurasia vers le continent de Gondwana avant ou au début de la zone à *Cistecephalus s.l.*

ABSTRACT

The skull anatomy of a young *Moschorhinus* (?*Tigrisuchus*) is discussed with special reference to the palate and posterior part of the skull. The relationship between the Russian Whaitsiidae *Moschowaitsiinae* and the African Whaitsiidae *Whaitsiinae* is briefly discussed. The similarities between the Russian Annatherapsididae and the South African Moschorhinidae lead to their inclusion in the family Moschorhinidae, subdivided into Russian Annatherapsidinae and South African Moschorhininae and Euchambersiinae. It is suggested that the forms leading to the Whaitsiinae on one hand and those leading to the Moschorhininae on the other hand migrated from Laurasia towards Gondwanaland before or at the beginning of the *Cistecephalus* zone *s.l.*

ZUSAMMENFASSUNG

Die Anatomie des Schädels eines jungen *Moschorhinus* (?*Tigrisuchus*) wird hier untersucht, speziell die des Gaumens und des Hinterschädels. Die Beziehungen zwischen den russischen Whaitsiidae (*Moschowaitsiinae*) u. den afrikanischen (*Whaitsiinae*) werden kurz erwähnt. Die Ähnlichkeit zwischen den russischen Annatherapsididae und den südafrikanischen Moschorhinidae

führt dazu, sie in eine Familie der Moschorhinidae zusammen zu fassen; der eine neue Definition gegeben wird.

Zu diesser Familie gehören eine russische Unterfamilie (Annatherapsidinae) und zwei südafrikanische (Moschorhininae und Euchambersiinae).

Es ist angedeutet, dass die Urstämme der Whaitsiinae, einerseits und der Moschorhininae andererseits vor oder am Beginn der *Cistecephalus*-Zone *s.l.* von Laurasia in den Gondwana Kontinent eingewandert sind.

RESUMEN

La anatomía del cráneo de un joven *Moschorhinus* (?*Tigrisuchus*) está estudiada aquí, muy particularmente en las regiones del paladar y del cráneo posterior. La relación existente entre los Whaitsiidae rusos (Moschowhaitsiinae) y los Whaitsiidae africanos (Whaitsiinae) está indicada brevemente. Las semejanzas entre los Annatherapsididae rusos y los Moschorhinidae sud-africanos conducen a incluirlos en una misma familia, los Moschorhinidae, que están definidos de nuevo. Esta familia comprende una subfamilia rusa (Annatherapsidinae) y dos subfamilia sudafricanas (Moschorhininae y Euchambersiinae). Está sugerido que las formas ancestrales de los Whaitsiinae por una parte, y las formas ancestrales de los Moschorhininae por otra parte, han migrado desde Laurasia hasta el continente de Gondwana antes o al principio de la zona de *Cistecephalus s.l.*

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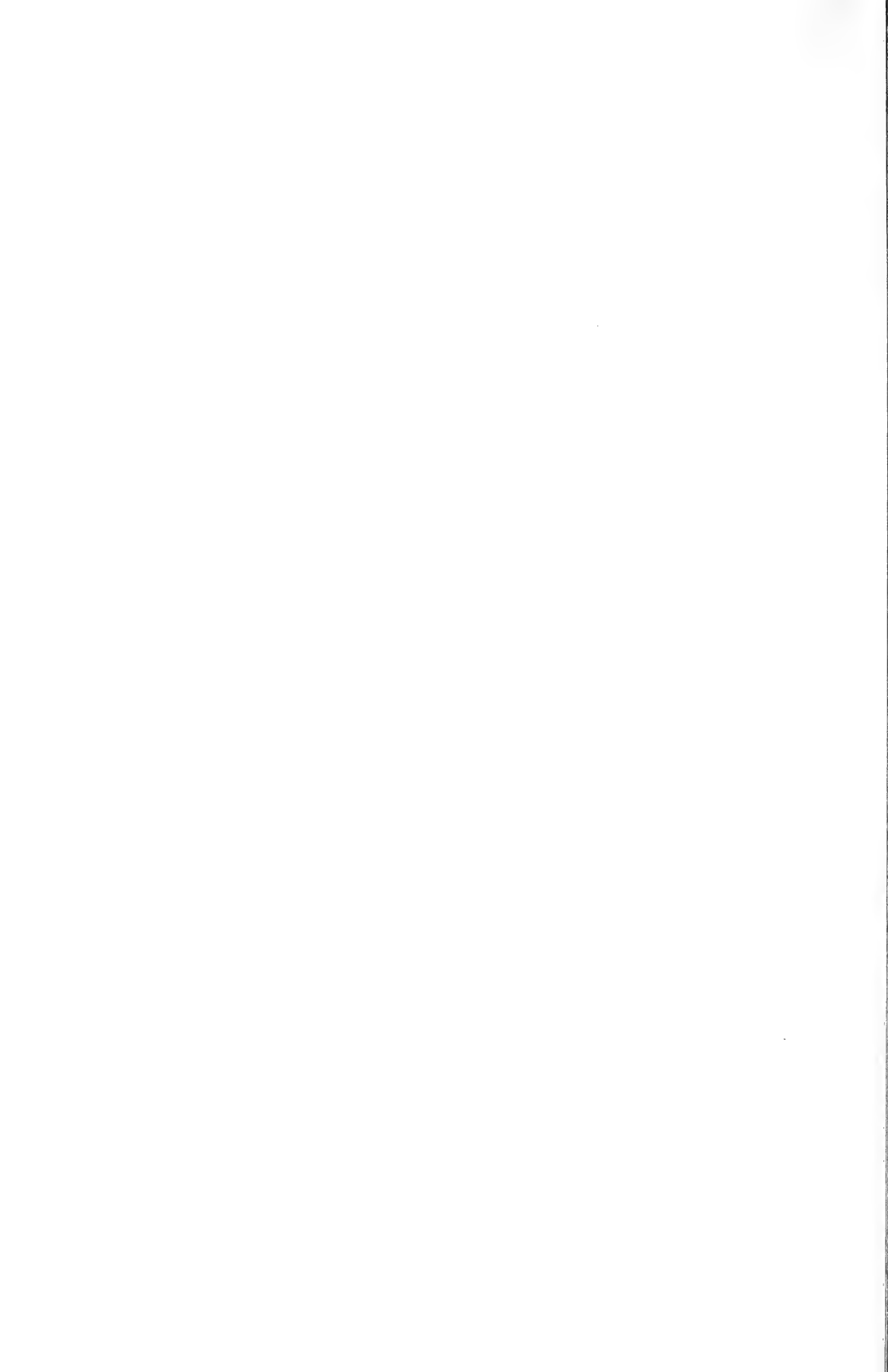
Que tous veuillent bien trouver ici l'expression de ma reconnaissance.

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A NEW DICYNODONT ANCESTOR FROM THE UPPER ECCA
(LOWER MIDDLE PERMIAN) OF SOUTH AFRICA

By

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(With 13 figures in the text)

CONTENTS

	PAGE
Introduction	117
Stratigraphic and locality data	121
Systematics	121
Cranial osteology	121
Summary	134
Acknowledgements	134
References	135
Abbreviations	136

INTRODUCTION

The South African Karroo (Fig. 1) is well known for the abundance and variety of reptilian forms found in its bedded shales. Of the four major constituent series, viz. the Dwyka, the Eccla, the Beaufort and the Stormberg, the Beaufort Series has yielded the majority of fossils. The relative abundance and variety of forms found in the lowest layers of the Beaufort Series and the virtual total absence of fossil discoveries in the underlying Eccla Series led to the generally accepted view that the Eccla was barren.

This view was supported on tectonic evidence by many geologists, amongst them the noted South African geologist Alex du Toit (1948), who states that the absence of Lower Permian vertebrates, save fishes, from the deep and presumably cold-water geosynclinal deposits, such as the 'Green' or 'Blue Eccla' facies of the South African Cape Province or the 'Coal Measure' deltas and swamps to the north east, was understandable, for whereas tropical to subtropical climatic conditions would seem to have ruled in the Northern Hemisphere during Permo-Carboniferous times, the land in the Southern Hemisphere was still recovering from a great Ice Age. He maintained further that it was only during the later Permian that silting, coupled with the initiation of the Cape Fold Ranges within the geosyncline, produced shallowing. By intercepting moisture from the ocean to the south, the Fold Ranges would have reduced precipitation over the interior basin, the drier climate producing sediments of a more terrestrial nature which would have enabled tetrapods to enter the southern section of the hollow. This, according to Du Toit, was the reason for the abundance of new life during the Lower Beaufort in the southern and central Karroo region, in contrast to its scarcity, in equivalent horizons, further north.

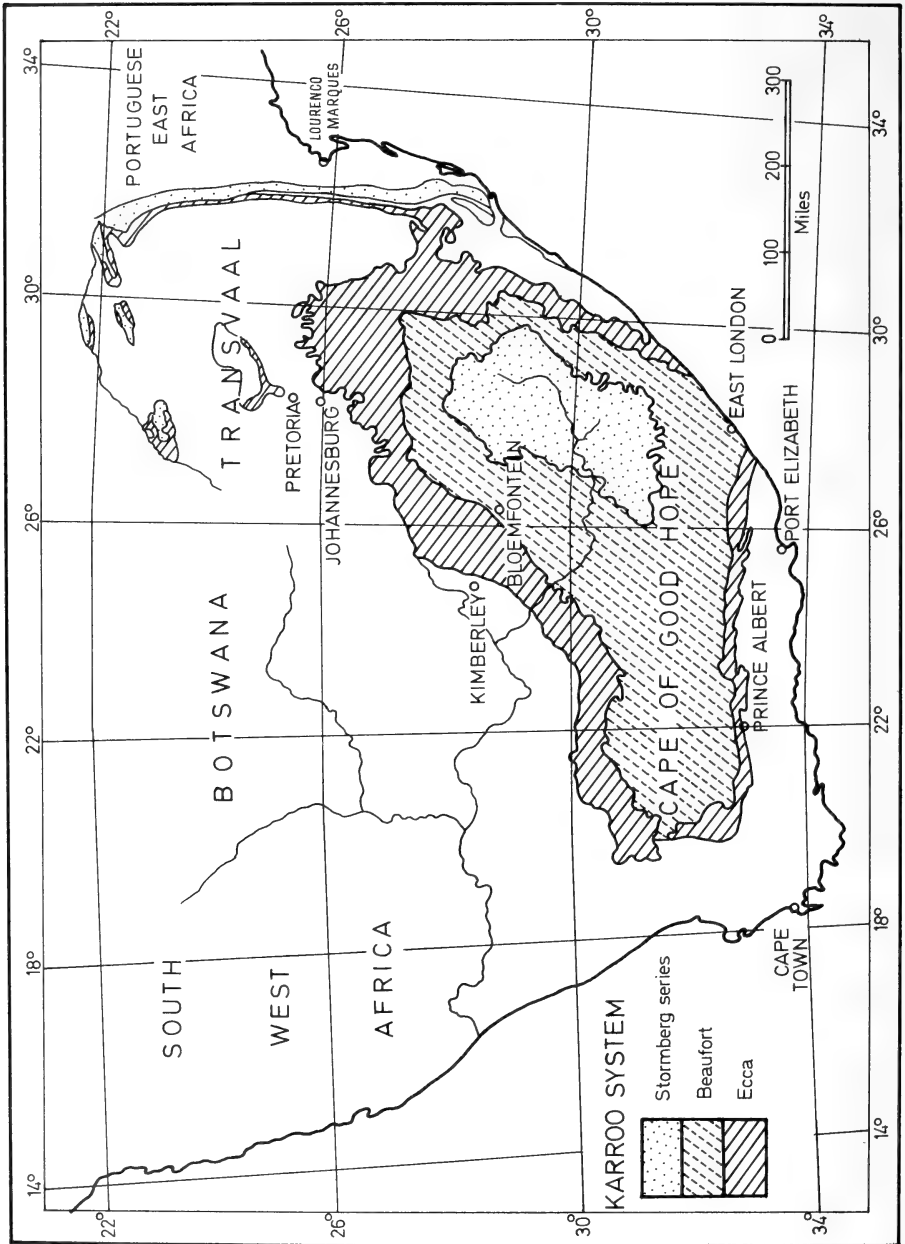


Fig. 1. Sketch map of the Karroo System.

The fact that Du Toit's views regarding the climatic conditions which prevailed during Ecca and Beaufort times were generally accepted by geologists and palaeontologists alike was probably a contributing factor why such scant attention was paid to Broom's claims that the terrestrial forms *Eccasaurus priscus* (Broom 1905a, 1912) and *Archaeosuchus cairncrossi* (Broom 1905b, 1909) came from Ecca beds. The announcement (Barry 1972) of the discovery by Mr Roy Oosthuizen of the farm Zwartskraal, Prince Albert district, of some 50 nodules containing fossil remains in beds which are Ecca (Lower Middle Permian) according to present stratigraphical definition, seemed to warrant the reopening of the 'barren Ecca' theory.

The southern or 'Green' facies in which the latest fossils were found was deposited within the Karroo Geosyncline. The strata occur south of a line drawn from Calvinia (latitude $31^{\circ}30'S$) in the west to East London (latitude $33^{\circ}S$) in the east, and range in thickness from 2 000 metres near Prince Albert to over 3 000 metres north of Grahamstown. The beds are involved in the Cape foldings and consist of green, bluish, olive and variegated mudstones and argillaceous sandstones and of a blue-green and yellow fine- to medium-grained hard and sometimes quartzitic spheroidally-weathering sandstones, but without any coarse or conglomeratic kinds.

Because of the Cape folding the strata are in places tilted up vertically and even overturned towards the north as between Prince Albert and Klipplaat (Du Toit 1954). Duplication of exposures of the same beds are commonly found, thus complicating the determination of fossil horizons, but on site investigations of the layers and folding patterns at Zwartskraal show the fossil sites to lie within the Upper Ecca (Figs 2 and 3). Lower Beaufort exposure is limited to a narrow projection eastwards along the Sandriver valley with the fossils occurring to the north, south and east of this exposure.

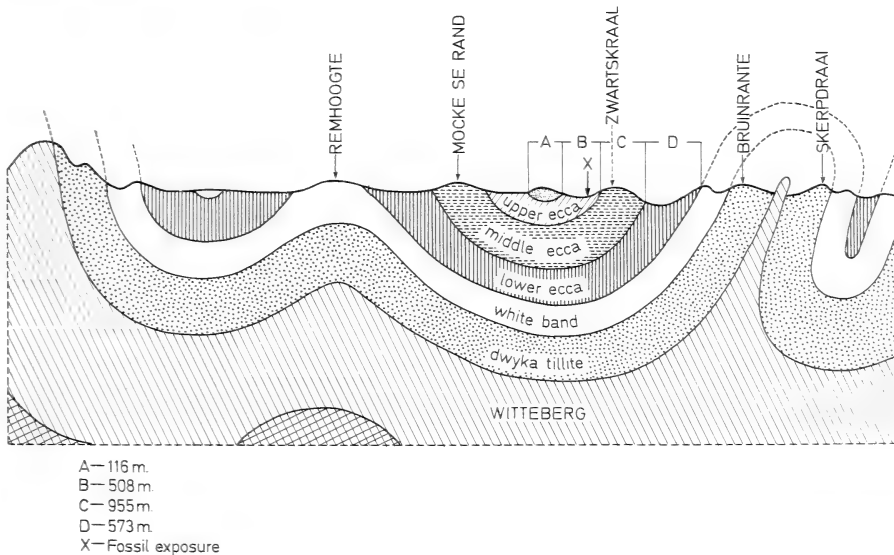


Fig. 2. Cross-section of the strata at Zwartskraal, Prince Albert.

As mentioned earlier, the first major deposits of reptilian fossils in the South African Karroo system occur in the *Tapinocephalus* zone of the Beaufort Series. This fauna is rich in numbers and established genera and already displays a diversified and balanced ecological composition (Boonstra 1969). Considering this, and the fact that the lithology does not show a sudden transition between the underlying Eccca and the Lower Beaufort, Barry (1972) contended that these factors were not consistent with the generally held view that climatic conditions during Upper Eccca times were such that they mitigated against the existence of land vertebrates during this period.

This view would seem to be borne out by comparative osteological studies carried out on the fossil material which forms the subject of this paper.

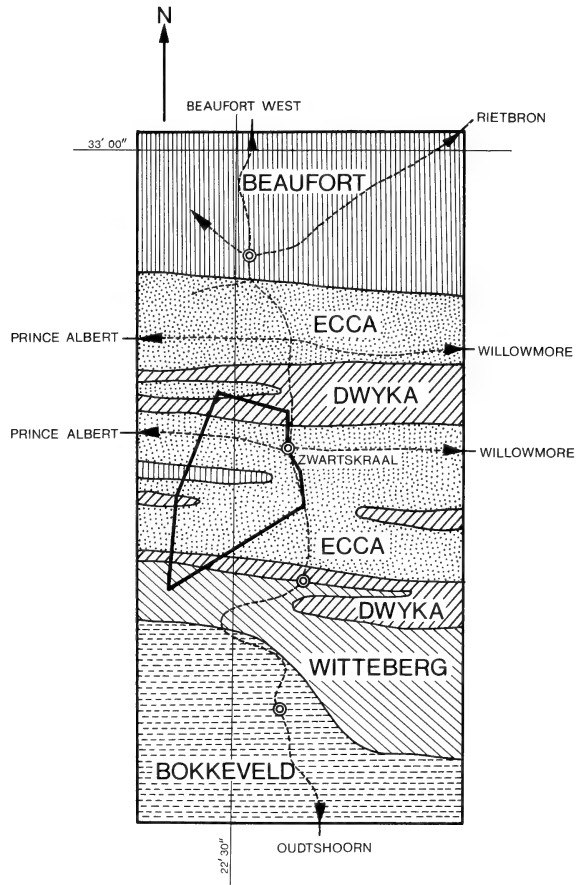


Fig. 3. Geological map of the Zwartskraal area.

STRATIGRAPHIC AND LOCALITY DATA

Eodicynodon oosthuizeni and other specimens still to be described came from Mr Roy Oosthuizen's farm Zwartzkraal in the Prince Albert District of the Cape Province, Republic of South Africa, and were collected by him between 1964 and 1970. A schematic cross-section of the area in which the fossil was found is shown in Figure 2.

The Zwartzkraal material found to date includes the following:

- (1) the skull of a new species, designated *Eodicynodon oosthuizeni*
- (2) portion of a basicranial axis
- (3) the skull of a small dicynodontid
- (4) the palate, quadrate and articular of a small endothiodontid
- (5) eroded skull of a small dicynodontid
- (6) postcranial skeleton of small therapsid
- (7) snout of small dicynodontid
- (8) many small unidentifiable pieces

With the exception of specimen no. 3, which was sectioned using the Croft Parallel Grinding method, all specimens were acid prepared using weak formic acid to remove the matrix.

SYSTEMATICS

Class **REPTILIA**

Order THERAPSIDA

Suborder **ANOMODONTIA**

Infra-Order DICYNODONTIA

Family **Dicynodontidae**

Sub-Family Dicynodontinae

Eodicynodon gen. nov.

Diagnosis: Skull small, *Dicynodon*-like in skull form and possession of a pair of canine tusks, but showing ancestral features. Vomers paired, lateral pterygoid processes strongly developed, premaxillaries partly paired.

Eodicynodon oosthuizeni sp. nov.

Holotype: Skull lacking anterior portion of snout and mandible. R.O.Z. No. 1 (collection of Mr Roy Oosthuizen).

Horizon and locality: Upper Ecca (Lower Middle Permian), Zwartzkraal, Prince Albert District, Cape Province, Republic of South Africa.

Diagnosis: Same as for the genus.

CRANIAL OSTEOLOGY

The skull lacks the mandible, the right temporal arch and the anterior portion of the snout (Figs 4 and 5). For an unknown reason the latter is a

feature common to all of the skulls found to date. Because of this, few longitudinal measurements could be taken but of these the ratio 'anterior limit of the squamosal to pineal'/'pineal to anterior limit of orbit' would seem to be of some significance. In *Eodicynodon* this is 1 : 3,6, compared with 1 : 1 or an outside limit of 1 : 2 ratio in all *Dicynodon* species measured. It is of interest to note that nearest ratio in the Dicynodontia would seem to be the 1 : 4 ratio of *Lystrosaurus*.

The interorbital width is less than the intertemporal width, giving a ratio of 3 : 4. The postorbital is broad, sloping ventro-laterally at an angle of 35° to the top of the skull roof. The parietal becomes slightly narrower posteriorly, a postero-laterally directed flange extending posteriorly well beyond the medial termination of the bone.



Fig. 4. *Eodicynodon oosthuizeni*, dorsal view.



Fig. 5. *Eodicynodon oosthuizeni*, ventral view.

The pineal foramen is oval-shaped and situated on a slightly raised triangular platform (Fig. 6). The surface of the platform, and especially the V-shaped portion extending posteriorly from the rim of the pineal, is rugose. The rim itself projects above the platform.

A posteriorly directed process of the frontal reaches a point in line with the front of the pineal foramen. The postfrontal lies lateral to this process. The parietal is well developed, an anteriorly extending process reaching the level of the postorbital arch. The medianly situated preparietal is wedged in between the frontals and parietals, the frontals meeting its anterior and anterolateral borders.

Although the configuration of most of the dermal bones of the skull roof would seem to resemble that of the genus *Dicynodon*, the preparietal does not participate in the formation of the rim of the pineal foramen, as is generally found in *Dicynodon* species. In *Eodicynodon* it lies 3 mm in front of the foramen, a distinct suture indicating the line along which the parietals meet anterior to the pineal foramen to separate the preparietal from the pineal foramen.

Although both Broom (1935) and Toerien (1953) have considered the relationship between the pineal foramen and the preparietal, it would seem advisable to re-analyse the position in the light of conditions found in *Eodicynodon*. Broom (1935: 7) found that in *Dicynodon grimbeeki* 'The pineal foramen is rather small and rounded and behind it a little median boss of bone. The preparietal lies in front of the pineal, but on the surface at least it is covered by the parietal, so that the posterior end of the preparietal is 3.5 mm in front of the foramen. A second skull has a similar condition. In one of the male skulls the preparietal nearly reaches the pineal. In others the preparietal forms the anterior wall of the foramen. In some of these the bone is a little weathered, and possibly a bridge of the parietal in front of the foramen has been weathered off. In the type skull the parietal forms the surface bone in front of the foramen, but it sends forward a process on each side of the preparietal.' Toerien (1953: 54) re-examined Broom's material and states that he found this deviation from the

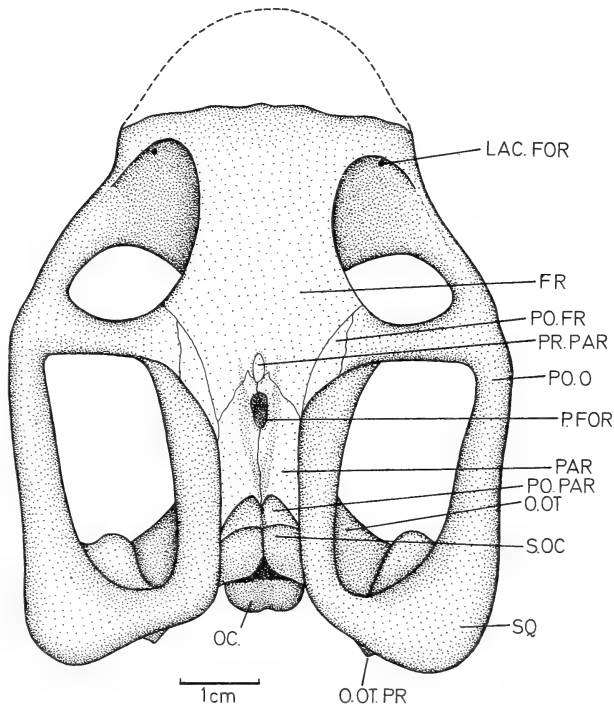


Fig. 6. *Eodicynodon oosthuizeni*, dorsal view.

general dicynodont condition to be the case in only 4 specimens of *D. grimbeeki*, including the type, and concluded that the non-participation of the preparietal in the formation of the pineal foramen 'is a rare feature in Dicynodonts, but is not uncommon in some of the small Endothiodonts'.

Phylogenetically the preparietal makes its first appearance in the therapsids. Even amongst them it is not universally present but confined to the Gorgonopsia and Dicynodontia. Huxley (1865: 10) was the first to describe this '... undivided bone wedged in anteriorly between the two parietals' in a skull fragment from the Panchet Rocks in Bengal. He identified the fragment as belonging to the genus *Dicynodon* on the strength that in a specimen of *Dicynodon murrayi* and in *D. lacerticeps*, '... while the two parietal bones are separated by a median suture a single intercalary, or wormian, bone is interposed between them and the frontals, and bounds the parietal foramen, in just the same way as the single median bone limits it in the Indian fossil' (p. 11). Seeley (1895) appears to be the first worker to have referred to this bone as the preparietal.

The preparietal retains a fairly constant position at the median intersection of the frontals and parietals which would seem to be commensurate with its identification as a 'Wormian bone'. Its relationship with the pineal foramen, which in both the ancestral Pelycosauria and Cotylosauria retains a fairly constant position well inside the borders of the parietals, is variable within the Gorgonopsia and the Dicynodontia.

In the majority of the Gorgonopsia the preparietal occupies a position anterior to the pineal foramen. The exceptions to the rule include *Aloposaurus ?tenuis* from the *Cistecephalus* zone in which 'le grand preparietal touche l'orifice pineal' (Sigogneau 1970: 111) and forms such as *Sycosaurus laticeps* (Houghton 1924), *Sycosaurus brodiei* (Broom 1941) and *Leontocephalus cadlei* (Broom 1940) similarly from the *Cistecephalus* zone, in which the preparietal is entirely absent. Sigogneau (1970) has interpreted this latter condition as secondary.

In the majority of Dicynodontia again, the preparietal is closely associated with the pineal foramen, participating to a lesser or larger degree in the formation of the rim of the foramen. The exceptions here include the Ecca form *Eodicynodon*, the *Endothiodon* zone forms *Emydops arctatus* (Owen 1876), *Emydops longus* (Broom 1921), *Emyduranus platyops* (Broom 1921), *Emyduranus granilis* (Broom 1936), *Emydorhynchus formosus* (Broom 1936), and the *Cistecephalus* zone form *Emydorhinus sciuroides* (Broom 1921), in all of which the preparietal lies anterior to the pineal foramen. In what is considered to be a secondary condition the preparietal increases its participation in the formation of the borders of the pineal foramen. This trend is illustrated in *Diictodon galeops* (Broom 1913), *Aulacephalodon peavoti* (Broom 1921) and *Aulacephalodon tigriceps* (Broom 1932), all from the *Cistecephalus* zone in which the hind portion of the preparietal very nearly or completely surrounds the foramen. In others such as the genera *Cistecephalus* and *Myosauroides minnaari* (Broom 1941) from the *Cistecephalus* zone the preparietal is entirely absent.

Thus, in the Dicynodontia as in the Gorgonopsia, the primary position of

the preparietal would seem to be the one in which the preparietal is situated anterior to the pineal foramen. The increased participation of the bone in the formation of the borders of the pineal foramen in some forms and its absence in others can be considered to be stages in the later development of the skull roof.

Judging by its relationships with surrounding elements it would seem certain that the pineal foramen retains a fairly constant position in the skull roof and that it is the preparietal which is subject to backward displacement. In forms such as *Dicynodon woodwardi* (Broom 1921), *Aulacephalodon peavoti* (Broom 1921) and *Aulacephalodon haughtoni* (Broom 1921), all from the *Cistecephalus* zone, this backward movement would seem to be accompanied by an increase in the relative size of the preparietal.

The postparietal(s?) occupies the dorsomedial area of the slanting occipital plate (Fig. 13). The name postparietal is here preferred to that of interparietal, usually used, as the bone is not situated between the parietals in this form. It also differs significantly from the usual dicynodont condition in that a medial postero-ventrally directed longitudinal ridge divides the bone into bilateral concave elements. The longitudinal ridge shows a pronounced midline groove or cleft extending the length of the bone. It is not possible to see whether this represents an entire or partial separation of the postparietal into two elements, but it would seem to reflect the ancestral paired condition of this element as found in *Captorhinus* and other cotylosaurs.

It is interesting to note that the postparietal is single in most pelycosaurs (Romer & Price 1940: 50). Although a well-developed ridge is absent, a longitudinal mound in the midline separates the concave areas on its sides. In most known Gorgonopsia the bone is also single but the median ridge is prominent, extending even on to the supraoccipital, the concavities following the general outward sweep of the tabulars and squamosals.

As mentioned earlier, the front portion of the snout has been eroded away.

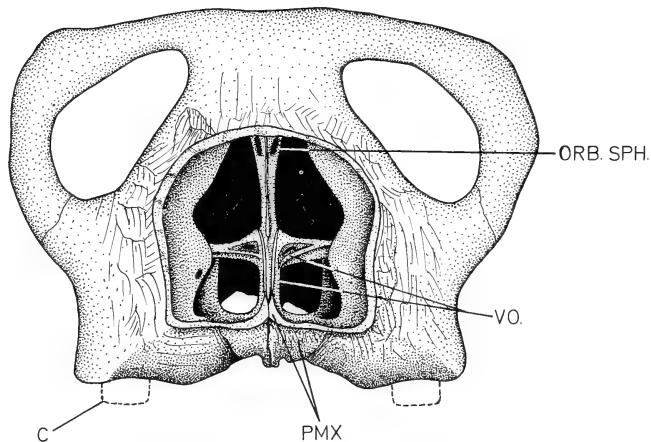


Fig. 7. *Eodicynodon oosthuizeni*, anterior view.

However, part of the premaxillary is still present and shows signs of being paired. A hairline suture extends the length of the palatal face of the bone and is seen to continue dorsally into the short dorsally directed median process of the premaxillary (Figs 7 and 8). The two relatively thin plates thus formed represent the single dorsal premaxillary process commonly found in *Dicynodon*.

Paired premaxillaries are not known in any other member of the Dicynodontia. Its presence in the presumably related, but primitive, Russian forms *Venyukovia* and *Otsheria* and in the sphenacodont Pelycosauria would seem to point to the fact that the paired condition in *Eodicynodon* represents the ancestral condition. The fusion of the premaxillaries in all Beaufort Series Dicynodontia is a secondary evolutionary trend which has not been followed by the other synapsid groups.

The premaxillary ends postero-medially in a short palatal process which makes contact with the vomer (Fig. 8). A postero-laterally directed tapering extension continues some distance backward so that the premaxillary forms the anterior and antero-lateral borders of the choana. The presence in Pelycosauria of a similar relationship would seem to point to a primitive condition, for in later dicynodonts the palatal face of the premaxillary increases in size thereby pushing the choanae further back. *Robertia broomiana*, a small endothiodont from the lowest division of the *Tapinocephalus*, which Toerien (1953) suggests is the most likely ancestor of *Oudenodon*, shows close resemblance to the *Eodicynodon* condition with the difference that, although the secondary palate is still short and the internal nares reach the level of the tusks, the anterior parts of the choanae are reduced to slits and therefore open functionally more posteriorly. In *Eodicynodon* the functional anterior limit of the choana lies in line with the canine tusk. Within the nasal cavity there is a longitudinal groove on either side of the median premaxillary septum which leads to the anterior notch of the choana. Camp & Wells (1956) suggested that a similar groove found in *Placerias* served to transmit the duct of Jacobson's organ. A similar groove is found in *Lystrosaurus* (Cluver 1971).

Due to a pronounced overlap of the ventro-lateral portion of the palatal surface of the premaxillary by the maxillary the palatal surface of the former shows as relatively narrow (Fig. 8). In later dicynodonts such as *D. grimbeeki*, *Pristerodon buffaloensis*, etc., this relationship is reversed, the lateral border of the premaxillary lying ventral to the maxillary. The condition in *Eodicynodon* seems to be a retention of the pelycosaurian condition as in the latter the premaxillary is 'deeply overlapped by the maxilla' (Romer & Price 1940: 54). The increased contribution of the premaxillary to the composition of the secondary palate as seen in later dicynodonts would thus necessitate the development of a new premaxillary process covering the maxillary from below.

In all known dicynodonts the vomer is a median unpaired sheet of bone, bifurcated anteriorly and posteriorly. One of the most important features distinguishing *E. oosthuizeni* from other dicynodonts is that the vomer is distinctly paired in this species (Fig. 8). Anteriorly the vomers form the inter-

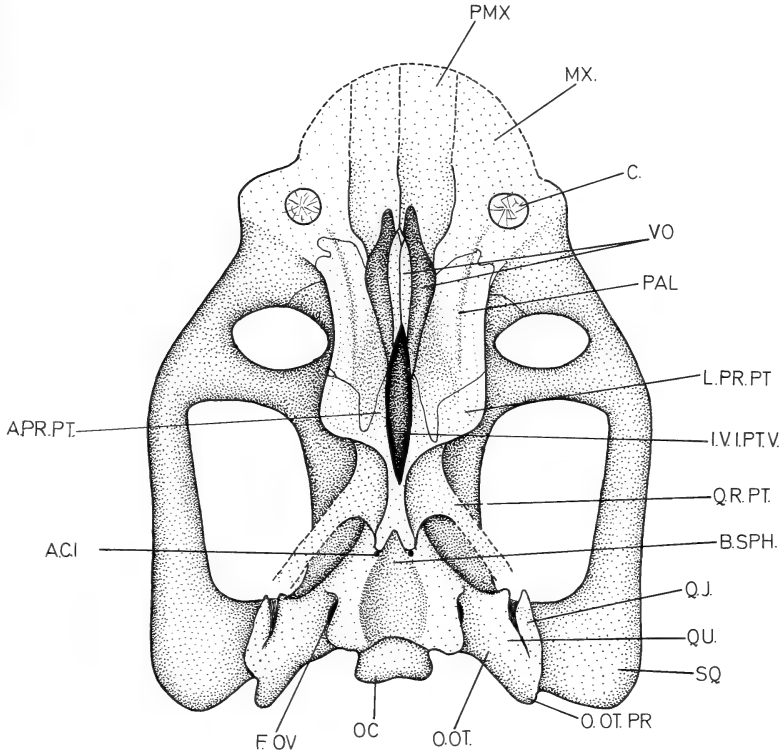


Fig. 8. *Eodicynodon oosthuizeni*, ventral view.

digitating contact with the premaxillaries as seen in *Pristerodon* (Barry 1967) but behind this area the palatal surface of the anterior third of the vomers is a pair of relatively broad, rounded ridges. Immediately behind this region the vomers curve upwards above the general palatal level of the palate, and the ridges now become thin and blade-like with a V-shaped groove developing between them. In this way the vomers form the anterior and antero-lateral borders of the interpterygoid vacuity. As vomeral elements participate in the formation of the boundaries of this vacuity, the interpterygoid vacuity in *Eodicynodon* technically becomes an intervomero-interpterygoid vacuity (Fig. 8). This is also the case in most dicynodonts. In many *Tapinocephalus* zone dicynodonts the vomers form more than one half of the borders of the intervomero-interpterygoid vacuity. The evolutionary development leading up to this condition has been dealt with in a separate paper (Barry, in press).

The vomers are continued dorsally to form a paired median septal sheet. Dorsally each half of this paired sheet flares out laterally in a horizontal plane, thus forming the median and dorsal walls of the internal nares. It is in contact laterally with the palatine and posteriorly with the pterygoid.



Fig. 9. *Eodicynodon oosthuizeni*, stereoview.

Paired vomers reflect the primitive tetrapod condition, being present not only in sphenacodont pelycosaurs but also in the captorhinomorph cotylosaurs. The paired condition has also been recorded for the Russian Zone II form *Venyukovia* (Efremov 1940) which according to Watson (1948) occupies a position between the Dinocephalia, which similarly retain paired vomers, and Dicynodontia, in which the vomers have become fused. It is of interest to note that the vomers have become secondarily fused in only two of the main groups of the Therapsida, viz. the Dicynodontia and Gorgonopsia.

The palatine is developed along two planes; a rugose ventral, comparatively broad kidney-shaped section extending along the general palatal line from just behind the canine tusk to a tapering point in line with the anterior limit of the inter-ptyergoidal vacuity, and a dorso-medially curving section which meets the dorso-lateral flange of the vomer to form the lateral and dorsal walls of the internal nares (Fig. 8). Postero-medially the palatine meets the pterygoid in a long suture.

The ectopterygoid forms part of the outer edge of the palate and is wedged between the pterygoid, palatine and maxillary. Its ventral surface is as rugose as that of the palatine, from which it is separated by a deep longitudinal groove.

The rugosity of the ventral surfaces of the ectopterygoid and palatine could possibly be related to the clusters of small teeth on corresponding areas on the palatine, pterygoid and ectopterygoid in pelycosaurs such as *Dimetrodon* and *Edaphosaurus*. In *Eodicynodon*, the antero-ventral portion of the vomer is similarly covered with small ring-like protuberances resembling the small vomerine teeth in *Edaphosaurus*. In most gorgonopsians sparse clusters of small teeth occur on the palatine and pterygoid.

The pterygoid has 3 main processes extending from the median plate, viz. the anteriorly directed palatal ramus, the laterally directed lateral process and the postero-laterally directed quadrate ramus of the pterygoid. Postero-medially

the pterygoid meets the parabasisphenoid. As in other dicynodonts the pterygoid bears no teeth.

In Pelycosauria, the pterygoid possesses a long anterior process running horizontally in the palate to meet the vomer. The process meets its mate along their entire length. The anterior process has undergone a drastic reduction in length in *Otsheria* and *Venyukovia* but the processes still meet in the midline anterior to the interpterygoidal vacuity and before making contact with the vomer. In *Eodicynodon* as in all other dicynodonts the anterior processes do not meet in the midline but are separated to form the postero-lateral walls of the intervomero-interpterygoidal vacuity (Fig. 8). As shown elsewhere (Barry, in press) this development is not restricted to the dicynodont line but is also evident in the Dinocephalia.

In the region of the intervomero-interpterygoidal vacuity the pterygoid sends out a broad ventro-lateral projection, the lateral process (Figs 8 and 10). As the lateral process is strongly developed in the pelycosaur and is absent in dicynodonts, it would seem to indicate the retention in *Eodicynodon* of a primitive character. *Otsheria* still shows a prominent lateral process but it is less well developed in *Venyukovia*.

The basicranial axis of *Eodicynodon* consists of the basioccipital, the basisphenoid and the dermal parasphenoid which is fused with the latter (Figs 10 and 11). The median sphenethmoid complex is situated anterodorsally to the parabasisphenoid. The paired carotid arteries enter the basisphenoid ventrally and emerge dorsally through a single canal posterior to the base of the parabasisphenoid rostrum (Fig. 12). Unfortunately the proximal portion of the parabasisphenoid rostrum is missing so that it is not possible to determine

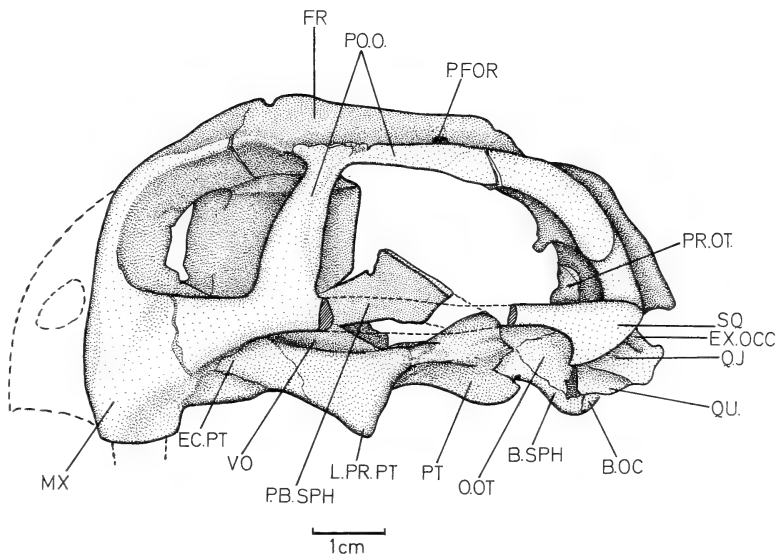


Fig. 10. *Eodicynodon oosthuizeni*, lateral view, left side.

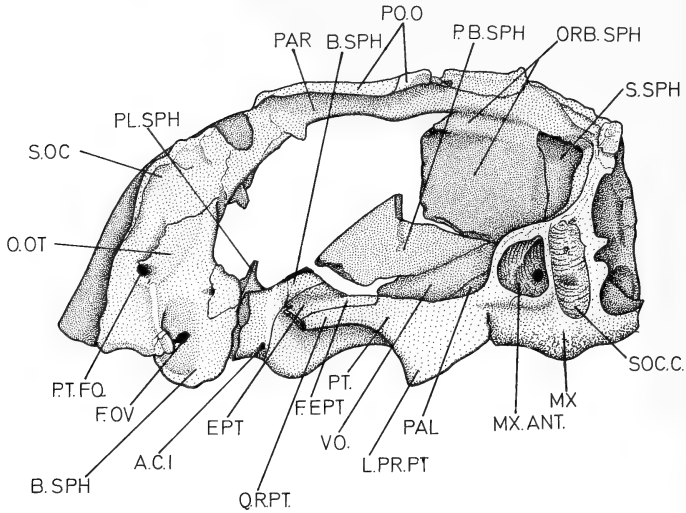


Fig. 11. *Eodicynodon oosthuizeni*, lateral view, right side.

whether the basisphenoid and parasphenoid are indistinguishably fused throughout its length as would seem to be the case in dicynodonts and also in the pelycosaurs (Romer & Price 1940).

The parabasisphenoid arches upwards and forwards at an angle of 45° before levelling off to run parallel to the main axis of the skull. A short distance behind the interorbital plate the dorsal portion of the bone ends abruptly as if it butted against an unossified posterior portion of the interorbital plate (Fig. 11). It is not clear from the specimen whether the dorsal portion of the parabasisphenoid must be regarded as a dorsal process of the parabasisphenoid rostrum, whether it represents a separate septal ossification (the so-called presphenoid claimed for most dicynodonts), or whether it is an anterior extension of the basisphenoid within the parabasisphenoid rostrum. Although there is no sutural evidence of dorsal and ventral elements in the parabasisphenoid in *Eodicynodon* this possibly cannot be ruled out. Near similar conditions are found in pelycosaurs where according to Romer & Price (1940: 76) '... in some cases the basisphenoid terminates abruptly within the parasphenoid trough...' just behind the posterior end of the orbitosphenoid. Barry (1967) found questionable indications in *Pristerodon* of a suture dividing the rostrum horizontally and states that the shape of the posterior part of the rostrum lends support to the conclusion that it consists of two fused elements, the rostrum parasphenoidale ventrally and either a rostrum basisphenoidale or rostrum praesphenoidale dorsally. The latter alternative depends upon whether the ossification in the trabecula communis represents an extension anteriorly into the trabeculae of the ossification of the basisphenoid or whether it is a separate ossification in the trabecula communis. It can also be pointed out that amongst recent reptiles, lizards have a rostrum parasphenoidale while *Chelone* has a rostrum basi-

sphenoidale. Judging by the flatness and slightly roughened condition of the dorsal surface of this process it would seem possible that the braincase wall was continued by cartilage above this point (Fig. 10).

Anterior to this process, the dorsal surface of the parabasisphenoid rostrum, which probably now represents parasphenoidal elements only, is deeply grooved to accommodate the lower end of the interorbital plate. Approximately half-way along the ventral border of the plate, the upwardly expanded median sides of the vomer take over the function of providing a groove for the plate (Fig. 11). It is not certain how far anteriorly the parasphenoid rostrum continues within the trough formed by the vomers.

The interorbital plate is roughly rectangular in shape and extends anteriorly from a point in line with the postorbital bar to the anterior rim of the orbit (Fig. 11). There are definite indications that the plate consists of two median ossifications separated by a vertical division. The homology of the elements comprising the sphenethnoid complex and the terminology used by different authors varies considerably and has been dealt with by Barry (1967) and Cluver (1971). For reasons set out previously (Barry 1967), the posterior of these two ossifications will be referred to as the orbitosphenoid and the anterior ossification as the septosphenoid.

The median keel of the orbitosphenoid is roughly square in outline. Dorsally it bears two concave lateral wings which dorsally make contact with the longitudinal ridges on the inner surfaces of the frontals. The median longitudinal trough thus formed is not subdivided by bone. The trough ends anteriorly at the front margin of the orbitosphenoid. From this point forward, at least, the brain must have been subdivided to form the olfactory lobes as the median septosphenoid extends upwards beyond the level of the trough before expanding laterally to form two narrow, slightly convex wings. The latter projections probably covered the olfactory lobes from above.

The palato-quadrate complex in dicynodonts comprises two separated bones, viz. the quadrate, with its two ventrally directed limbs which form the medial and lateral condyles, and the epipterygoid. The latter is usually L-shaped, a thin, dorsally projecting columella, rising from a footplate which rests upon and partly covers the dorsal surface of the quadrate ramus of the pterygoid.

In *Eodicynodon*, the lateral condyle of the quadrate and part of the medial one have been eroded away, but in spite of this the quadrate does not appear to have marked differences from the general dicynodont condition. It is not clear whether the quadratojugal participates in the formation of the lateral condyle.

The epipterygoid is unusual in that its base or footplate is more expanded than in dicynodonts in general. As can be seen in Figure 11 the footplate extends from a point in line with the posterior surface of the dorsal wing of the vomer to the root of the quadrate ramus of the pterygoid where it covers more than half the dorsal surface of the quadrate ramus of the pterygoid. Unfortunately the latter is broken off so that it is impossible to determine the length of the quadrate ramus of the epipterygoid but judging by its breadth at the break it could have

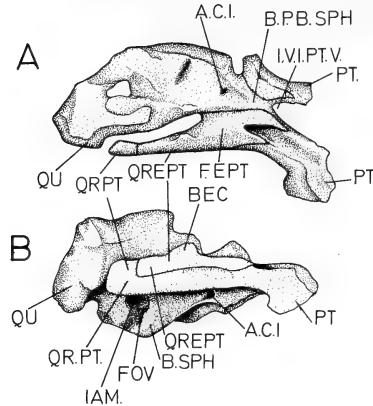


Fig. 12. *Eodicynodon oosthuizeni*, A. Dorsal view. B. Lateral view of palatoquadrate complex.

continued some distance posteriorly. At the break, the quadrate ramus of the epipterygoid has a distinct dorsally directed ridge, which probably represents the basal portion of the dorsally directed columella of the epipterygoid. A separate skull fragment featuring the basicranial axis confirms this view (Fig. 12).

Anterior to the base of the columella the footplate shows a broad medial expansion which stretches across the dorsal surface of the pterygoid and ends medially against the base of the parabasisphenoid (Fig. 12). The exceptional development of this part of the footplate of the epipterygoid is most unusual for dicynodonts. In the latter the footplate is only weakly developed, or not at all, and the columella is anterior to the base of the columella. In *Kannemeyeria* (Case 1934) and *Daptocephalus* (Ewer 1961) the footplate is continued anteriorly but as a much less extensive and narrower bone. Ewer (1961) suggested that this extension was possibly developed to compensate for the weakening of the middle region of the skull resulting from the narrowing of the parietal region. This interpretation does not hold true for *Eodicynodon* as the parietal region is relatively broad in this form. Being a dicynodont ancestor it is more likely that *Eodicynodon* would display the more primitive condition. The remarkable similarity of the *Eodicynodon* and *Dimetrodon* (Romer & Price 1940) footplates would seem to justify this conclusion. The anterior process found in *Daptocephalus* represents the retention in this form of a primitive feature rather than a later development. In all known Gorgonopsia too the epipterygoid still retains a long tapering anterior extension.

As in *Pristerodon* (Barry 1967) a well-demarcated groove is formed between the quadrate and quadratojugal, the latter being attached only at its ventral and dorsal extremities.

The occiput (Fig. 13) resembles a trapezoid with the oblique sides bowed gently outward. The cartilage bones of the region do not show many differences

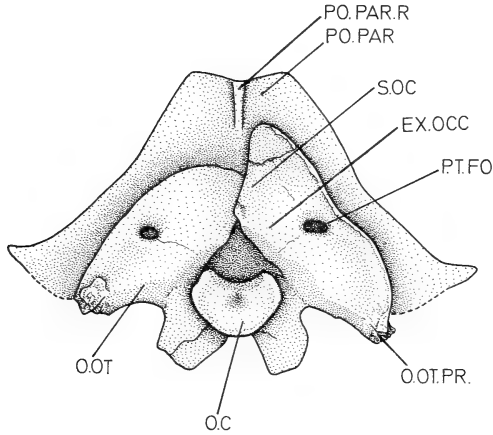


Fig. 13. *Eodicynodon oosthuizeni*. Occipital view.

from the general *Dicynodon* condition. The borders of the supraoccipital are only faintly recognizable but it would seem that its ventro-medial border forms the dorsal rim of the foramen magnum in the usual way. From here it fans out dorsally and laterally to meet the postparietal and tabulars.

The line of fusion between the supraoccipital and exoccipital cannot be traced. The exoccipital forms the lateral rim of the foramen magnum and extends outward to the post-temporal fossa. From its base a flat roughly triangular flange extends to cover the ventro-medial portion of the opisthotic. Although the sutures are indistinct it seems that the exoccipitals also form the lateral borders of the foramen magnum. The basioccipital forms the ventro-medial portion of the occipital condyle, it is continued anteriorly in the midline from where two ventro-laterally directed triangular extensions develop to cover the posterior surface of the prominent tubera, which form the bony casing of the fenestra ovalis and for the cochlear recess of the internal ear. In most dicynodonts the tubera are described as being formed by the basioccipitals, but in *Eodicynodon* each structure is quite clearly formed by the basioccipital and the basisphenoid, with the opisthotic forming the postero-lateral rim.

The opisthotic, similarly, is a roughly triangular plate. Its dorsal boundary extends from the ventro-lateral corner of the foramen magnum to the ventral rim of the post-temporal fossa. A ventro-medially directed flange forms the postero-dorso-lateral rim of the prominent tuber. As in *Pristerodon* (Barry 1967) the opisthotic carries a strongly developed ridge-like opisthotic process which laterally tapers into a posteriorly directed point (Fig. 13). As stated in the aforementioned paper it is believed that this process is associated with the origin of the m. obliquus capitis below it, and the m. rectus capitis posterior lateralis et medialis dorso-medially to it, as still found in some of the recent turtles in which an analogous process occurs.

The post-temporal fossa is small, as in *Tapinocephalus* zone dicynodonts.

The reduction in its size, in comparison with ancestral tetrapods, appears to be due to an increase in the size of the opisthotic. The reduction in size of the post-temporal fenestra would give support to the views of Watson (1911, 1913), Cox (1959) and Cluver (1971) that the fenestra probably served as a passage for the *v. capitis dorsalis*, which in modern reptiles such as *Sphenodon* drains the occipital musculature and passes forward to enter the braincase in front of the auditory capsule. In *Eodicynodon* a shallow, antero-dorsally directed groove on the pro-otic could indicate the passage of the vein within the braincase. However, a second shallow groove-like depression on the pro-otic, similarly emanating from the post-temporal fenestra, runs antero-medially along the surface of the pro-otic. The latter groove and the general smoothness of the bone anteriorly and antero-laterally to the inside edge of the fenestra suggest that in the ancestral forms, with its wide fenestra, and possibly still in *Eodicynodon*, other elements apart from the *v. capitis dorsalis* passed through the fenestra.

SUMMARY

Unlike the *Tapinocephalus* zone (Lower Beaufort) beds of South Africa, which have yielded an abundance of diversified terrestrial forms, the *Ecce* beds which underlie them were considered to be devoid of such remains. This assumption was based on the view that these layers were deposited during a time when deep water conditions prevailed in the Karroo. It was strengthened by the fact that apart from two claims made by Broom, which were refuted, no terrestrial remains had been definitely reported from these beds.

The discovery, from 1964 to 1970, of a number of skulls and vertebrae of dicynodont-like animals in *Ecce* defined beds, reported during the 2nd International Gondwana Symposium (Barry 1972) resulted in the reappraisal of this view. Comparative osteological studies of the skulls show that they predate the *Tapinocephalus* zone forms in the retention of primitive features such as paired vomers, paired premaxillaries and the retention of the lateral processes of the pterygoid. These features are reminiscent of the Pelycosauria but have disappeared in the Lower Beaufort forms.

Eodicynodon has proved to be more primitive than any known dicynodont from the *Tapinocephalus* zone. On the other hand it shows so many typically dicynodont features that it cannot be excluded from the direct ancestry of at least some branches of the *Tapinocephalus* zone dicynodonts.

The affinities and systematic position of *Eodicynodon* formed the subject of a paper presented to the 3rd International Gondwana Symposium. It is scheduled to appear in 1974.

ACKNOWLEDGEMENTS

I wish to record my sincere thanks to Mr Roy Oosthuizen for bringing his finds to my attention and for allowing me to have them prepared for description. My thanks are also due to Mrs I. Rudner for the meticulous acid preparation of the skulls. Mr V. Branco is thanked for the illustrations and Mr A. Byron for photographing the fossils.

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ABBREVIATIONS

A.C.I.	Arteria carotis interna	ORB.SPH.	Orbitosphenoid
A.PR.PT.	Anterior process of the pterygoid	PAL.	Palatine
B.E.C.	Base of the epipterygoid columnella	PAR.	Parietal
B.O.C.	Basioccipital	P.B.SPH.	Parabasisphenoid
B.P.B.SPH.	Base of the parabasisphenoid	P.FOR.	Pineal foramen
B.SPH.	Basisphenoid	PL.SPH.	Pleurosfenoid
C.	Canine tusk	P.MX.	Premaxillary
EC.PT.	Ectopterygoid	PO.FR.	Postfrontal
EPT.	Epipterygoid	PO.O.	Postorbital
EX.OCC.	Exoccipital	PO.PAR.	Postparietal
F.EPT.	Footplate of the epipterygoid	PO.PAR.R.	Post parietal ridge
F.OV.	Fenestra ovalis	PR.OT.	Prootic
FR.	Frontal	PR.PAR.	Preparietal
I.A.M.	Internal auditory meatus	PT.	Pterygoid
I.V.I.PT.B	Intervomero-interpterygoidal vacuity	P.T.FO.	Posttemporal fossa
LAC.FOR.	Lacrymal foramen	Q.J.	Quadratojugal
L.PR.PT.	Lateral process of the pterygoid	Q.R.EPT.	Quadrate ramus of the epipterygoid
MX.	Maxillary	Q.R.PT.	Quadrate ramus of the pterygoid
MX.ANT.	Maxillary antrum	QU.	Quadrate
O.C.	Occipital condyle	S.OC.	Supra-occipital
O.OT.	Opisthotic	SOC.C.T.	Socket of the canine tusk
O.OT.PR.	Opisthotic process	S.Q.	Squamosal
		VO.	Vomer

THE SKULL AND MANDIBLE OF A NEW
CISTECEPHALID DICYNODONT

By

MICHAEL A. CLUVER

South African Museum, Cape Town

(With 4 figures)

CONTENTS

	PAGE
Introduction	137
Classification	138
Cranial morphology of <i>Cistecephaloides boonstrai</i>	
Skull	139
Snout and skull roof	140
Occipital region	141
Basicranial axis and palate	143
Temporal region	146
Lower jaw	147
Comparison with <i>Cistecephalus</i> and <i>Kawingasaurus</i>	147
Functional considerations	150
Summary	153
Acknowledgements	154
References	154
Abbreviations	155

INTRODUCTION

The dicynodont genus *Cistecephalus* is one of the more well-known groups of South African therapsids, and its unusual, readily identifiable skull form and stratigraphically limited occurrence (Keyser 1965; Kitching 1970) make it a valuable marker genus in the Beaufort Series zoning system. Several species (11) have to date been described but reviews of the genus have shown that only 9 of these are in fact based on specimens of *Cistecephalus*. These are *C. microrhinus*, *chelydroides*, *planiceps* and *bathygnathus* (Owen 1876); *angusticeps* (Broom 1932); *major*, *rubidgei* and *platyfrons* (Broom 1948) and *laticeps* (Brink 1950). Several synonymies have at various times been declared among these species (see Brink 1950; Keyser 1965); in the most recent review, Keyser (1965) recognizes only *C. microrhinus* Owen but at the same time has found evidence for a new species.

Cox (1972) has recently described a new East African dicynodont, *Kawingasaurus fossilis*, which he states is fairly closely related to *Cistecephalus* but has important differences in the skull and especially the postcranial skeleton.

The specimen at present under discussion (SAM 6243) could at first glance be regarded as a species of *Cistecephalus* with somewhat unusual skull proportions, but removal of the lower jaw and exposure of the palate and basicranium revealed a basic skull structure which differs widely from the *Cistecephalus* and, indeed, the standard dicynodont condition. These differences

appear to warrant generic distinction, and are summarized in the following section.

CLASSIFICATION

The creation of a new genus, closely allied to *Cistecephalus*, raises the question of the status of *Cistecephalus* itself. Although the recent classification of Romer (1966) places the genus in the family Dicynodontidae, earlier workers tended to emphasize the unusual skull structure of the genus by setting it apart from other dicynodonts. Thus Seeley (1894) was led by the unusual skull roof (the palate was at that stage unknown) to regard the genus as being sufficiently far removed from his suborder Dicynodontia to warrant a separate suborder, Kistecephalia. Most subsequent authors have, however, been content to leave the genus in a separate family. Broom in 1903 proposed a family Cistecephalidae for the genus, distinct from the Endothiodontidae, Dicynodontidae and Lystrosauridae, and distinguished from these by the structure of the quadrate and occipital regions. Broili & Schröder (1935: 17) found additional grounds for maintaining this family, which they diagnosed as:

'Skull short-snouted, relatively high, intertemporal width greater than interorbital width, no preparietal, no independent postfrontal and probably no tabulars, and also no interpterygoidal opening. Toothless.'

Haughton & Brink (1954: 69) have retained the family Cistecephalidae, which they define as having:

'Small broad skull. Molarless. Very wide and flat intertemporal region.'

Investigations into the anatomy of *Cistecephalus* undertaken for the purposes of the present work make it clear that the genus's strikingly unusual cranial structure demands familial distinction, on the lines proposed by Broili & Schröder (1935) and Haughton & Brink (1954). The pertinent cranial characters of the family and genus, and the relationships of Cox's *Kawingasaurus* and the proposed new genus and species, may be formalized as follows:

Class **REPTILIA**

Order THERAPSIDA

Suborder ANOMODONTIA (*sensu* Romer, 1966)

Infraorder DICYNODONTIA (*sensu* Romer, 1966)

Family **Cistecephalidae** Broom, 1903

Diagnosis: Small, toothless dicynodonts with very broad intertemporal region, lacking a preparietal and postfrontal. Squamosal not extended posteriorly beyond level of the supraoccipital; stapes perforated or deeply incised; interpterygoidal vacuity vestigial or absent.

Genus *Cistecephalus* Owen, 1876

Diagnosis: Cistecephalids with broad or narrow interorbital region. Lacrimal foramen absent or low down within orbit; pterygoids meeting below parabasisphenoid complex; interpterygoidal vacuity absent.

Genus *Kawingasaurus* Cox, 1972

Diagnosis: Cistecephalids with moderately broad interorbital region and relatively small orbits. Postorbital and prefrontal separated by frontal. Lacrimal foramen in normal dicynodont position, pineal foramen absent. Zygomatic arch slender. Stapedial foramen present and interpterygoidal vacuity absent.

Genus *Cistecephaloides* gen. nov.

Diagnosis: Cistecephalids with broad intertemporal and interorbital regions, reduced orbits and robust postorbital bars. Prefrontal meeting postorbital, lacrimal foramen in usual dicynodont position; stapes deeply incised and reduced to slender bar; pterygoids extending far backwards onto basioccipital tubera, separated in midline by parasphenoidal rostrum which runs forward in palatal view to meet vomer. Interpterygoidal vacuity represented by small fossae (possibly foramina) alongside parasphenoid. Dorsal dentary surface of jaw ramus drawn up laterally as a sharp, longitudinal blade.

Cistecephaloides boonstrai sp. nov.

Diagnosis: as for genus.

Holotype: SAM 6243. Partially weathered skull and mandible.

Locality: Ely Cottage, near Alice, Cape Province, South Africa.

Horizon: *Cistecephalus* zone (*Daptocephalus* zone of Kitching, 1972) of Upper Permian Middle Beaufort Series.

I have pleasure in naming the new species after Dr L. D. Boonstra, who introduced me to vertebrate palaeontology.

Haughton & Brink (1954) include the genus *Emydorhinus* Broom under their Cistecephalidae, but, with the exception of the loss of the postfrontal, there do not appear to be any significant resemblances between this genus and *Cistecephalus*, *Kawingasaurus* and *Cistecephaloides*.

CRANIAL MORPHOLOGY OF *CISTECEPHALOIDES BOONSTRAI*

SKULL

The skull lacks the left zygomatic arch, the right quadrate and otic region, and a portion of the skull roof above the left temporal fossa. In addition, the left cheek region and the adjoining palatal surface is incomplete, while in ventral view the anterior portion of the palate and basicranium is displaced dorsally at a shear just anterior to the level of the internal carotid artery canals. These imperfections are relatively easily compensated for, and the illustrations of the reconstructed skull may be regarded as being reasonably accurate.

The skull shows the usual cistecephalid proportions and is triangular in dorsal view, being widest over the rear of the squamosals. In the actual specimen, before allowance is made for distortion, the width of the skull over this region is 58 mm, as compared with the basioccipital-premaxilla skull length of

61 mm. In the reconstructed skull, these measurements become respectively 63 and 62 mm.

Snout and skull roof

The edges of the palatal rim are lacking, and the ventral limits of the snout are thus difficult to determine. On the more complete right-hand side the maxilla is flared out laterally in front of the orbit to form a prominent and robust ledge, which lies as a forward prolongation of the zygomatic arch. The septomaxilla is exposed on the surface of the snout behind the external naris, and forms a small part of the floor of the anterior nasal chamber. Behind the septomaxilla the maxilla rises up high in the side of the snout to meet the nasal.

The nasal covers a relatively large area on the snout and skull roof, and forms a small boss over the external naris. Anteriorly, in the region of the external naris, the nasal is perforated by numerous nutritive foramina and channels.

The small size of the orbit is one of the striking features of the skull. The postorbital bar is a robust pillar, and the bone extends forward above the orbit to make contact with the prefrontal, thereby excluding the frontal from the orbital border. The lacrimal and prefrontal have little exposure on the lateral snout surface, but the lacrimal forms a large part of the inner wall of the orbit, and is pierced by a foramen for the duct of the lacrimal gland in the anteroventral corner of the orbit, in the normal dicynodont position. The prefrontal forms only the anterior half of the inner orbital border, and behind it the lacrimal makes contact with a forward extension of the frontal.

The maxilla does not reach far back on the zygomatic arch, and the jugal, extending out from below the lacrimal inside the orbit, forms the major part of the infraorbital bar.

The intertemporal part of the skull roof is weathered and discoloured, and sutures are consequently difficult to trace. The frontonasal suture is clear, and extends back to the level of the rear of the orbits. This level is well within the rear half of the skull, and accordingly the frontals and parietals are short, wide elements. A frontoparietal suture can be distinguished near the midline of the skull, while traces of a parietal-interparietal contact can be seen on the rear edge of the skull table. From these it appears that the frontals are considerably shorter than the nasals, while the parietals, shortest of all, are confined to the extreme rear of the skull roof. Laterally each parietal passes forward for a short distance, between the postorbital and frontal of its side. An inner flange of the frontal passes forward and down medially to the postorbital to form part of the inner wall of the orbit, where it meets the prefrontal and lacrimal. A similar but more vertical flange of the parietal forms the median wall of the temporal chamber and meets the dorsal tip of the epipterygoid.

No clear parietal foramen can be made out, but a circular, damaged area in the midline of the skull in the parietal region has within it portions of smooth,

vertically standing bone, which may represent part of the pineal canal. In any event, the parietal foramen, if present, could not have been more than a small, relatively insignificant opening.

Occipital region

As in *Cistecephalus*, the squamosals in *Cistecephaloides* do not extend back beyond supraoccipital level, and the occiput (Fig. 4) is thus an open and slightly rounded surface, the occipital condyle being the most posterior structure. From the condyle the occiput slopes forward fairly steeply, so that the plane of the occiput meets that of the skull roof at an angle slightly in excess of 90°.

Considerable damage to the occipital region has been caused through weathering, and some doubt exists as to the exact relationships held between supraoccipital, interparietal and squamosal, especially in the dorsal part of the occiput. In addition, the presence or absence of a tabular is open to question. The interparietal forms a low nuchal crest immediately behind its meeting with the parietal and extends down and laterally on the occiput to meet the supraoccipital and squamosal. Both supraoccipital and interparietal slope back towards the exoccipital, the condyle of which lies in the most posterior plane of the skull. Medially the exoccipital carries a short, blunt process for the proatlas on the margin of the foramen magnum, and laterally it terminates in the inner corner of the posttemporal fossa. Above the condyle it forms the posterior wall of the jugular foramen.

Because of the considerable lateral extent of the exoccipital, the opisthotic does not make any contact with the supraoccipital on the occipital surface. From the posttemporal fenestra the opisthotic-squamosal suture is deeply interdigitated and runs ventrolaterally, but the meeting lower down between the squamosal and the lateral paroccipital process is, in contrast, a fairly loose one. Ventrolaterally (Figs 1, 3, 4) the opisthotic bears a sharp crest which is drawn out posteriorly as a fairly prominent 'opisthotic' process, the equivalent of the tympanic process of Cox (1959). Below this is the channel for the lateral head vein, narrower than in other dicynodonts, and deeply incised into the opisthotic's ventral border.

The dorsal extent of the squamosal is uncertain, but below its meeting with the postorbital it forms an extensive sheet-like border to the occiput; in common with species of *Cistecephalus*, this occipital part of the squamosal is flat and lacks the posterior flanges found in other dicynodont groups.

The occipital condyle is the most posterior part of the skull. The lower half is formed by the basioccipital, while the two exoccipitals complete the structure dorsally. The exoccipital part of the condyle does not project back farther than the basioccipital part, as is the case in some dicynodonts, and, since the basioccipital and exoccipitals are depressed to form a notochordal pit in the centre of the condyle, the actual articular surface is a flat, ring-shaped area.

The quadrate and quadratojugal hold the normal dicynodont relation-

ships with each other. Ventrally the quadratojugal is indistinguishably fused with the dorsal surface of the lateral quadrate condyle, but dorsally its suture with the squamosal is clearly visible above the quadrate foramen, where the quadratojugal and quadrate are separated by a ventral process of the squamosal.

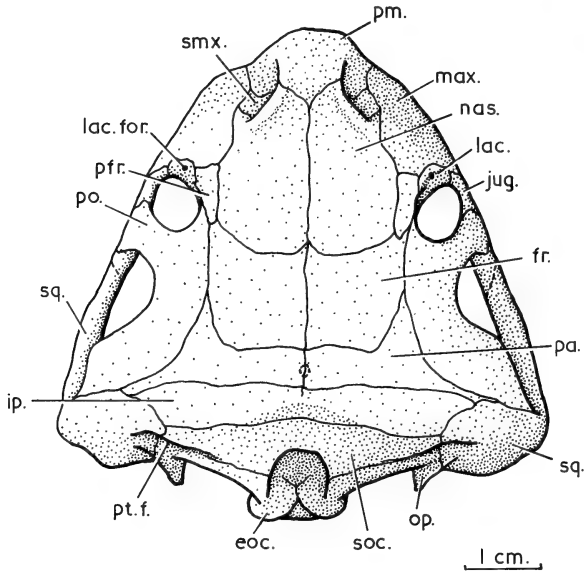


Fig. 1. *Cistecephaloides boonstrai* gen. et sp. nov.
Skull in dorsal view. Natural size.

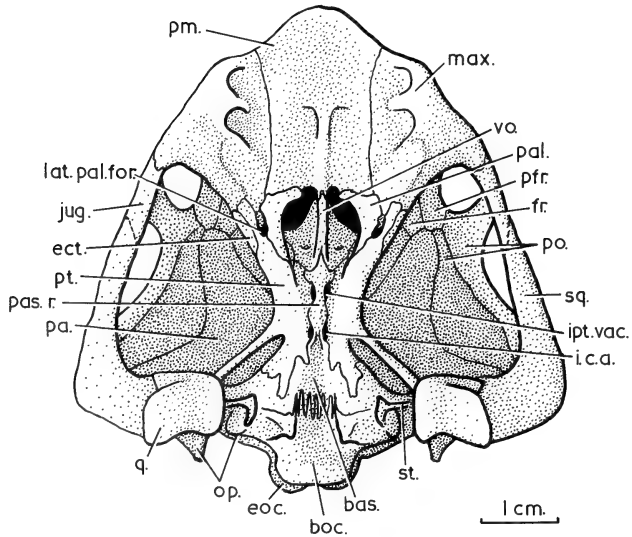


Fig. 2. *Cistecephaloides boonstrai* gen. et sp. nov.
Skull in ventral view. Natural size.

The articular surface of the quadrate has the form of a wide trough, dorsally curved anteriorly and posteriorly, and is not easily divided into distinct lateral and medial condyles. The major part of the articular area faces forwards and down, but at the rear this surface curves sharply upwards to meet the ventral edge of the squamosal.

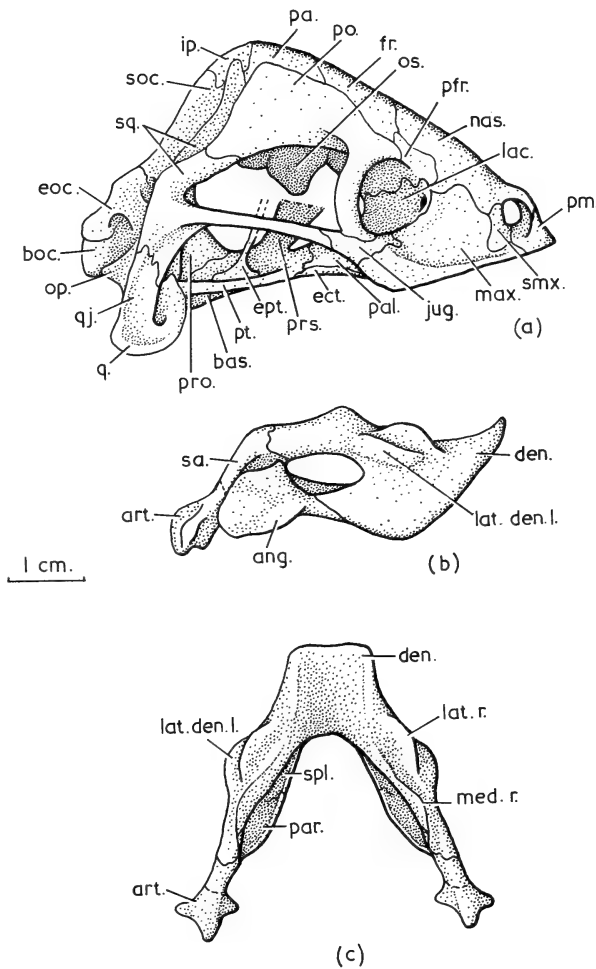


Fig. 3. *Cistecephaloides boonstrai* gen. et sp. nov.
 (a) Skull in lateral view. (b) Mandible in lateral view. (c) Mandible in dorsal view. Natural size.

Basicranial axis and palate

The basioccipital-basisphenoidal tubera are prominent features in the ventral part of the braincase, and their structure can be fairly accurately determined in the more complete left-hand side. The rear of the tuber is widely

excavated over the basioccipital-basisphenoid suture, and it is possible that this part, which is unfinished in periosteum, was completed in cartilage during life. Above this area, the opisthotic is flared backwards as a slightly concave, horizontal ledge, below and lateral to the opening of the jugular foramen.

In the ventral midline the highly interdigitating basioccipital-basisphenoid suture is clearly visible. The suture straightens out on the inner side of each tuber, but weathering on these ventralmost points in the skull obscures the meeting between basioccipital and basisphenoid in the region of the fenestra ovalis. Interpretation of this area is further complicated by the unfinished, porous nature of the bone surface, suggesting that the rim of the fenestra ovalis was at least partly formed in cartilage.

The stapes itself appears to have been partly cartilaginous. A fairly substantial footplate is present, but the body of the element is represented only by a very thin bony splint, arising from the anterior end of the footplate and not quite reaching the quadrate. As such, the stapes is an extremely light and delicate structure, and the considerable posterior extent of the footplate, finished in periosteum, suggests that the bone was deeply notched, possibly to allow passage for the stapedia artery and chorda tympani nerve. The distal end of the stapes, which normally abuts against the inner side of the quadrate condyle, is not preserved, and during life was probably present as cartilage.

On the anterior slope of the basioccipital tuber the basisphenoid is overlain by a long, irregular posterior extension of the pterygoid, which reaches back almost to the level of the fenestra ovalis. In front of the meeting between the body of the pterygoid with the quadrate ramus, the basicranial girder is sheared through, and the anterior portion displaced dorsally, but in spite of this complication it is possible to make out the relations which the various bones hold with each other. Most striking is the lack of contact between the pterygoids in the ventral midline. In front of the internal carotid artery foramina

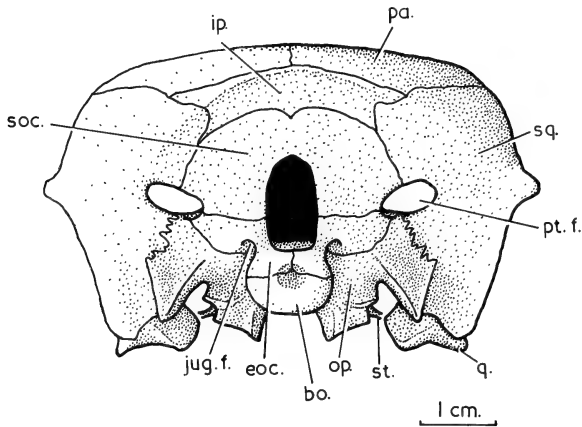


Fig. 4. *Cistecephaloides boonstrai* gen. et sp. nov.
Skull in posterior view. Natural size.

the pterygoids approach each other, but are clearly separated by an anterior extension of the parabasisphenoid complex. Anterior to this, the pterygoids diverge to form the lateral borders of the internal choanae, and a pair of deep recesses are formed between the pterygoid and the median, parabasisphenoid bar. These recesses are apparently vestiges of the interpterygoidal vacuity which is found in other dicynodonts (except *Cistecephalus*). The lateral borders of the choana, formed by pterygoids, palatines and ectopterygoids, are criss-crossed by a network of small cracks, and sutures are thus difficult to determine with complete certainty. It seems, though, that each pterygoid extends forward to make a short contact with the maxilla and, together with the palatine and a posterior process of the premaxilla, closes off a large lateral palatal foramen at the level of the anterior part of the choana. In this region the pterygoid is wedged between the palatine medially and the ectopterygoid laterally.

The palatine has a limited palatal portion and the major part of the bone lies as a low outer wall of the choanal passage. Posteriorly this palatine wall makes contact with an anterior extension of the parabasisphenoid complex laterally, and with the vomer medially, where this latter bone curves outwards to form the posterior wall of the choanal passage. Anteriorly the palatine passes forward to the ventral part of the orbital wall, where an anterior lappet meets the lacrimal and jugal.

The ectopterygoid is a thin splint of bone lying entirely lateral to the anterior part of the pterygoid. It makes contact with the maxilla but does not border onto the lateral palatal foramen. The vomer, on the other hand, is an important bone in the palate and lies as a deep and stout median septum which descends to the level of the lateral, pterygoidal borders of the choana, effectively separating the two internal nares from each other. Dorsally the septum widens as the vomer curves out on each side to form a partial median roof for the choanal passage, the roof becoming complete at the meeting of the vomer with the palatine at the rear of the choana. Anteriorly the vomer is clasped by a pair of diverging processes of the premaxilla, while posteriorly it, in turn, contains the anterior parasphenoidal prolongation of the parabasisphenoid.

The bony secondary palate, formed by premaxilla and maxilla, is wide and bounded by a low palatal rim. On either side of its median palatal ridge (a functional continuation of the parasphenoid-vomer bar), the premaxilla slopes away to form a pair of shallow recesses, which merge in front of the median ridge to create a vaulted area behind the anterior palatal rim. Medial to the lateral palatal rim, along the maxilla-premaxilla suture, the palate is raised as a narrow ledge, which terminates anteriorly as a weak lateral palatal ridge on the premaxillary palatal rim. The palatal rim itself is damaged on both sides of the snout, but it is nevertheless apparent that the rim was thin and sharp-edged anteriorly, while posteriorly it probably became more robust near the short, blunt caniniform process. The posterior, maxillary portion of the palatal rim is medially scalloped, and two embayments lead onto the lateral palatal ledge. The posterior of these is the more pronounced, and lies

anterior to a smooth, concave portion of the maxilla which slopes postero-medially from the caniniform process to merge with the palatal surface level with the anterior margin of the choana.

Temporal region

The left side of the skull has been completely cleared of matrix and portions of the braincase and basicranial axis have been exposed. The prootic-basisphenoid suture is clear, and a small depression, half-way along its length, leads to the foramen for the exit of the facial nerve. There is no deep sulcus in the prootic in front of the posttemporal fenestra, such as is found in many other dicynodonts and which appears to have stood in connection with the venous system of the head (Cox 1959; Cluver 1971), and no notch (venous notch of Agnew 1959) is found between the prootic and parietal in the sidewall of the braincase.

The braincase lies deep within the greatly enlarged temporal vault. Frontal, postorbital and parietal combine to make an extensive roof behind the orbit, and the temporal fenestra opens almost entirely laterally, the roofed-over area being best developed posteriorly, where the skull roof joins the occipital plate. The bone forming the temporal roof is uniformly thin, but above the temporal fenestra the ventral border of the postorbital is inflated to a powerful, bar-like rim, which extends from behind and medial to the postorbital bar to the posterolateral corner of the temporal fenestra (Fig. 2).

In front of the hypophyseal region the basisphenoid lies as a horizontal sheet, meeting the pterygoids laterally and the palatine anteriorly, and carrying the presphenoid dorsally. A notch visible in lateral view between the basisphenoid and the anteroventral edge of the presphenoid lies above the pair of deep fossae in the palate which represent the vestigial interpterygoidal vacuity. In typical dicynodonts a similar notch serves as the dorsal opening of the interpterygoidal vacuity, and although it is reduced in *Cistecephaloides*, its presence suggests that the interpterygoidal openings might in fact pass upwards to open out above the pterygoids, a condition which has been lost in *Cistecephalus*. Verification of this possibility by further preparation was, however, prevented by the delicate nature of the bones in this region of the skull.

As stated earlier, the rear of the palate in the type specimen has been displaced upwards at the level of the internal carotid artery canals, and the presphenoid is consequently partly concealed behind a sheet of bone descending from the skull roof. This bone (os, Fig. 3), wedged between the descending laminae of the parietal and frontal, appears to be part of a damaged orbitosphenoid complex. Few details can be made out, but it is clear that it forms a considerable part of the upper sidewall of the braincase, and is slightly curved. There is no clear division of the element into a dorsal trough-like portion and a ventral keel.

A small portion of the epipterygoid footplate, in front of the ascending shaft, is present on the dorsolateral edge of the pterygoid, but the major part

of the bone was apparently damaged by the displacement of the palate, and is only partially preserved. Dorsally a lappet of the parietal, descending to meet the upper extremity of the epipterygoid, can be distinguished.

LOWER JAW

The mandible is short and deep in its overall dimensions. The powerful dentaries are completely fused in the symphyseal region and carry a sharp, transverse cutting edge anteriorly. Behind this blade the dentaries are scooped out as a wide trough, and no dentary tables, as found in dicynodonts such as *Lystrosaurus* (Crompton & Hotton 1967; Cluver 1971), are present. Behind the symphyseal region, however, the dorsal edge of the dentary widens, and a wide, shallow dentary groove is formed. The medial wall of this groove rises posteriorly as a sharp blade (med.r., Fig. 3c) forming the medial edge of the dorsal dentary surface. Below this sharp edge the inner surface of the dentary is slightly concave, so that the Meckelian sulcus in the prearticular is exposed in dorsal view. The lateral wall of the dorsal dentary groove, on the other hand, is highest anteriorly, where it rises as a sharp, delicate cutting edge (lat.r., Fig. 3c). Below and lateral to this the dentary is expanded above the mandibular fenestra to form a robust lateral dentary ledge. Below the large mandibular fenestra the dentary passes back to meet the angular.

The dorsal, surangular margin of the jaw curves down steeply, and the articular is consequently carried relatively low in the mandible; this feature may, however, be partly the result of distortion which the mandible appears to have undergone. The main articular condyle is a wide, slightly concave facet, while a smaller median facet is carried on a delicate inner ledge. The two surfaces are separated by a rounded and ventrally curved longitudinal ridge. The ventral extremity of the articular, together with any evidence of a retroarticular process, has been lost through weathering.

The medial border of the Meckelian sulcus is formed by the prearticular posteriorly and the splenial anteriorly. As stated earlier, the inner surface of the dentary above the sulcus is hollowed out, and a wide, smooth depression leads down anteroventrally into the trough.

COMPARISON WITH *CISTECEPHALUS* AND *KAWINGASAURUS*

A number of skull features, notably in the skull roof, occiput and palate, indicate that the affinities of *Cistecephaloides* lie more with *Cistecephalus* and *Kawingasaurus* than any other dicynodont genera. The broad intertemporal region in *Cistecephaloides* is (as in *Cistecephalus*) composed of the very wide frontals and parietals, which on each side meet the sheet-like postorbitals. In *Cistecephaloides*, however, an additional feature is the enlargement of the nasals, which extend farther laterally and posteriorly than in any *Cistecephalus* species. Their lateral extent is reflected in the small size of the orbits, while their posterior borders are well within the rear half of the skull. The frontals and parietals are consequently confined to a relatively short and wide area of the skull roof.

The parietals in *Cistecephaloides* do not pass forward between the frontals in the midline, as they do in *Cistecephalus*, but laterally each parietal curves forward between the frontal and postorbital of its side. In dorsal view, therefore, the parietals together cover an open, horseshoe-shaped area on the skull roof, in contrast to the triangular area common in *Cistecephalus*. The fronto-parietal suture is not shown in Cox's (1972) illustrations of *Kawingasaurus*.

The enlargement of the nasal in *Cistecephaloides* and the accompanying increase in the interorbital width and reduction in orbit size have resulted in crowding together of the circumorbital bones and an unusual meeting of the prefrontal with the postorbital above the orbit. The frontal is thereby excluded from the orbital border, but, passing down medially to the prefrontal and postorbital, still forms part of the inner wall of the orbit. Although a prefrontal-postorbital contact does not occur in *Cistecephalus*, these bones do approach each other in some species (*C. planiceps* of Broili & Schröder 1935; *C. laticeps* of Brink 1950), and an anterior extension of the postorbital seems to be characteristic of the genus.

The roofing-over of the intertemporal region in *Cistecephaloides* has been accompanied, as in *Cistecephalus* and *Kawingasaurus*, by the loss of the posterior flange of the squamosal, so that the occiput is an open, slightly convex surface and totally unlike that of other dicynodonts. Apparently related to this modification of the squamosal is the relatively low position of the zygomatic arch in the skull of both *Cistecephalus* and *Cistecephaloides*.

In the basicranium and palate similarities between *Cistecephalus* and *Cistecephaloides* are fewer, although some features appear to parallel each other functionally. Thus an apparent tendency in both genera to strengthen the basicranial girder (connecting the palate with the floor of the braincase) by the reduction or loss of the interpterygoidal vacuity has been accomplished in two different ways. In *Cistecephalus* the pterygoids meet in the midline in front of the internal carotid artery foramina in normal dicynodont fashion, but this contact is strengthened anteriorly by medial pterygoidal extensions which meet the rear end of the vomer, completely obliterating the interpterygoidal vacuity. In at least one species of *Cistecephalus* (*C. microrhinus* of Keyser 1965) a small area of parabasisphenoid complex is still visible in ventral view in the midline between the pterygoids and vomer. Cox (1972) has not given a detailed illustration of this region in *Kawingasaurus*, but states that the interpterygoidal vacuity is absent, and from the drawings it appears that the pterygoids meet in the midline as in *Cistecephalus*.

In *Cistecephaloides*, on the other hand, the pterygoids have parted in the ventral midline but have improved their attachment to the basicranium by developing extensive posterior processes which overlap the basisphenoid to the level of the fenestra ovalis. The parabasisphenoid lies exposed in ventral view between the pterygoids, and the parasphenoid rostrum, which in dicynodonts is usually clasped by the vomers above palatal level (cf. *Lystrosaurus*, Cluver 1971) lies low down in the palate and is clasped by posterior diverging wings of the

vomer to form part of the median septum separating the internal nares.

The parting of the pterygoids has caused the basicranial girder of *Cistecephaloides* to become unusually wide, and this may be associated with the very broad and shallow secondary palate, formed by the maxillae and premaxilla. A second result of the pterygoidal separation is the apparently incomplete closure of the interpterygoidal vacuity, since the pair of deep fossae in front of the internal carotid artery foramina, and in the position of the primitive interpterygoidal opening, may possibly lead to foramina which open out in front of the presphenoid above the level of the pterygoids.

In both *Cistecephalus* and *Cistecephaloides* the vomer lies as a low, stout septum within the choana and, meeting either the pterygoid (*Cistecephalus*) or the basi-sphenoid complex (*Cistecephaloides*) posteriorly, acts as a median strut between the palate and basicranium.

Several similarities in the palate of *Cistecephalus* and *Cistecephaloides* also exist. In both, the trough-shaped central portion of the premaxilla, which is divided by the median palatal ridge, is separated from the palatal rim by a lateral maxillary ledge, while the anterior part of the palatal rim lacks the anterior palatal ridges which are found in many dicynodonts. Also in both genera, the palatine meets the premaxilla anteriorly, so that the maxilla is excluded from the choana. However, in *Cistecephaloides* the ectopterygoid is reduced to a thin, lateral splint of bone, unlike the relatively large ectopterygoid of *Cistecephalus* and *Kawingasaurus*. Associated with the small ectopterygoid in *Cistecephaloides* is the unusual forward extension of the pterygoid, which meets the maxilla laterally to the lateral palatal foramen.

Both *Cistecephaloides* and *Kawingasaurus* lack the two curious circular depressions in the caniniform process region of *Cistecephalus*, one medial to and the other lateral to the palatal rim. In *Cistecephaloides*, instead, the palatal rim is notched medially in two places at the caniniform process, the posterior notch being the larger and in the position of the inner circular depression found in *Cistecephalus*. *Kawingasaurus* represents a third type, as Cox (1972) states that the palate is unusually flat, and lacks sharp cutting edges.

The structure of the mandible in *Cistecephalus* and *Cistecephaloides* is basically the same. The dentary is widely excavated in the symphyseal region behind the transverse anterior cutting edge, and the dorsal dentary surface of each jaw ramus bears a pair of ridges (more pronounced and sharp in *Cistecephaloides*). Above the mandibular fenestra a distinct lateral dentary shelf is present. Comparisons with *Kawingasaurus* are difficult, as the symphyseal region is incompletely preserved, but Cox's (1972) drawings suggest a low, blunt symphysis, and it seems unlikely that an upright, anterior cutting blade, such as in *Cistecephaloides*, could have been present. All three genera, however, resemble each other in that the dorsal, dentary part of the jaw ramus is bowed out laterally so that the Meckelian sulcus is exposed in dorsal view.

From these comparisons, it appears that *Cistecephaloides*, *Cistecephalus* and *Kawingasaurus* all fulfilled certain common functional requirements but, by

following slightly different, parallel pathways, arrived at their general adaptational level with considerable differences in their cranial structure.

FUNCTIONAL CONSIDERATIONS

The unusual skull morphology of *Cistecephalus* has prompted a number of workers to speculate on the most likely mode of life common to the various species of the genus. The possibility of an aquatic or semi-aquatic way of life was mentioned by Broom (1948) and Brink (1950), but Brink in 1952 described the left manus of a specimen of *C. microrhinus* which, he suggested, indicated a burrowing existence. Brink was led to this opinion by the fusion of the distal phalanges in the 2nd and 3rd digits, and the degeneration of the 1st, 4th and 5th digits. According to Brink the hand had only two powerful, functional fingers, and was thus well adapted for fossorial or burrowing habits.

Keyser (1965) argued that Brink (1952) had misinterpreted his specimen, stating that the digital formula in additional specimens of *Cistecephalus* was of the standard therapsid type, although the two distal phalanges of the 3rd and 4th digits were fused, strongly developed and elongate, and were probably equipped with strong claws during life. In addition, Keyser maintained that the 4th and 5th digits could probably appose the 1st, 2nd and 3rd digits, so that the hand was of the grasping type. Keyser concluded that these features, taken together with indications of stereoscopic vision (such as the large, anteriorly directed orbits) were strongly suggestive of arboreal activities.

Cox (1972) has interpreted the unusual pectoral girdle, humerus and forelimb of *Kawingasaurus* as being adapted for powerful digging, and suggests that the animal might have rooted in mudflats in search of small invertebrates. As stated by Cox, this view is supported by the absence of sharp 'herbivore' cutting edges which form the palatal rim in other dicynodonts.

The skull of *Cistecephaloides boonstrai* does not in itself offer conclusive evidence in support, or otherwise, of any of these theories, but a consideration of the three obviously related genera does to an extent reveal that several of their specializations are the consequence of broadly similar functional requirements. Thus it could be argued that the reduction and loss in all three genera of the interpterygoidal vacuity, together with the increase in thickness and vertical extent of the vomerine septum, represent strengthening of the basi-cranial axis of the skull to withstand fore-and-aft stress. Again, the broadly roofed-over intertemporal region strengthens the overall skull structure, but this feature of the cistecephalids has an important corollary, and may not have arisen as a purely reinforcing device. Thus, the relatively lateral position of the cistecephalid temporal fenestra, a direct consequence of the broadened intertemporal region, must have brought about considerable changes in the jaw adductor musculature, the deep part of which arose from the bones surrounding the fenestra. Crompton & Hotton (1967) have reconstructed this muscle, the external adductor muscle, in dicynodonts, and suggest the dorsal surface of the postorbital and posterior flange of the squamosal (being respectively the

medial and posterior margins of the fenestra) as the most likely areas of origin. The moulding of these bones in dicynodonts, especially of the postorbital behind the postorbital bar, makes such an arrangement very probable. Crompton & Hotton (1967) have indicated the dorsal surface of the dentary and, possibly, surangular as the main insertion areas of this muscle, and suggest that a portion may have extended a short way down the medial side of the mandible.

Of interest in this connection is the fact that in *Cistecephalus*, *Cistecephaloides* and (judging by Cox's 1972 illustrations) *Kawingasaurus*, the dorsum of the dentary is bowed out laterally and the inner surface, together with that of the surangular, moulded to form a wide, shallow trough leading down to the exposed Meckelian sulcus. The sulcus, bounded by prearticular and splenial medially and angular and dentary laterally, is in a position equivalent to the opening described as the adductor fossa by Romer (1956) in reptiles, and which is primitively the major insertion area of the external jaw adductor muscles. The condition in cistecephalids can, it appears, be best explained in terms of a fairly substantial slip of the medial external adductor muscle inserting on the bones surrounding the Meckelian sulcus in dicynodonts, while in dicynodonts with narrow or medium-width intertemporal regions this adductor fossa would be an easily accessible insertion area for such a muscle, in cistecephalids the inner surfaces of the dentary and surangular above the sulcus and mandibular fenestra would inevitably have been influenced by the lateral migration of the muscle's temporal area of origin, and the course of the fibres is thus more clearly shown in them than in other dicynodonts.

Thus reconstructed, three sets of external adductor muscles appear to have inserted on the mandible in cistecephalids and presumably in other dicynodonts as well. An inner division of the medial external adductor muscle inserted in the adductor fossa, while, as reconstructed in dicynodonts by Crompton & Hotton (1967) and Cluver (1970, 1971), a lateral division of the medial external adductor muscle inserted on the dorsal dentary surface. (In *Cistecephaloides* this surface is slightly excavated to receive the muscle's insertion.) On the outer side of the dentary a lateral dentary shelf is developed in *Cistecephalus* and *Cistecephaloides*, and the lateral external adductor muscle would have inserted here. Cox (1972) does not mention a dentary shelf in *Kawingasaurus*, and the muscle would presumably have inserted on the outer side of the dentary, as suggested for *Dicynodon testudirostris* by Cluver (1970).

The effect of widening of the skull roof in cistecephalids would, it seems, have resulted in an overall lateral shift of the areas of origin of the external adductor muscles relative to their areas of insertion. A result of this would be increased control by these muscles over any lateral movement of the mandible across the palate. Indications that such movement was in fact possible are provided in the structure of the palate and the mandible, which differ in important respects from the condition in other dicynodonts. Among forms in which the jaw musculature and jaw movements have been reconstructed

Emydops (Crompton & Hotton 1967) could have utilized only a straightforward anteroposterior displacement during the masticatory stroke, guided by adjacent rows of upper and lower postcanine teeth, while a step in front of the articulation surface of the articular condyle prevented excessive sliding over the quadrate. In *Lystrosaurus* (Crompton & Hotton 1967; Cluver 1971) the anterior symphyseal region of the lower jaw was guided by the tight-fitting tusks, caniniform processes and palatal rim, and the quadrate and articular surfaces are closely-matched counterparts which appose any tendency for lateral displacement during the jaw movements. In a third group, represented by *Dicynodon testudirostris* (Cluver 1970), strongly developed caniniform flanges act as lower jaw guides, and enlarged crushing areas on the dorsal surface of the dentary meet apposing surfaces on the palate. In effect, in all these forms the dentary is so controlled as to meet specific areas of the palate during each masticatory stroke.

In cistecephalids, on the other hand, no such restrictions on the mandibular movements appear to be developed. The articular surface of the quadrate has two rounded condyles, but they are not separated by a deep cleft as in *Emydops* or *Lystrosaurus*, and there is considerable freedom of movement between it and the articular bone. No bony step, such as is found in *Emydops*, is present in cistecephalids, and, in *Cistecephalus* at least, the articular surface continues from the articular itself on to the surangular (this area is not clearly preserved in *Cistecephaloides* or described in *Kawingasaurus*). Anteriorly, the palatal rim is low in *Cistecephalus* and *Cistecephaloides* and evidently almost absent in *Kawingasaurus*. In none of the genera is a proper caniniform process found. The palate itself is wider than the symphyseal region of the lower jaw, and no crushing dentary tables are developed to appose raised areas of the palate. A sharp, spade-like anterior termination of the lower jaw is found in *Cistecephalus* and *Cistecephaloides*, but in *Kawingasaurus* the mandible appears to have been blunt anteriorly. In *Cistecephalus* and *Cistecephaloides*, and possibly in *Kawingasaurus*, the mandible is too short to meet the anterior part of the palate in 'beak bite' (Crompton & Hotton 1967), while contact between mandible and the lateral palatal rim could not have been achieved without sideways movement of the lower jaw.

In brief, then, the possibility of controlled lateral movements of the lower jaw during the masticatory cycle cannot be ruled out in the three cistecephalid genera, and there is in fact some positive evidence to show that this type of movement did take place, and was associated with the broadening of the intertemporal region.

The broad, open and slightly convex occiput of cistecephalids, which contrasts sharply with the condition in other dicynodonts, might be considered next. The loss of the posterior flange of the squamosal, which served as part of the area of origin of the medial external adductor muscle in other dicynodonts, might have been associated with the roofing-over of the temporal region, whereby the root of the zygomatic part of the squamosal lies virtually within the

temporal vault. Alternatively, the shape of the occiput may well have been determined by changes in the neck musculature. Here comparison with recent mammals yields suggestive results. Among insectivores, inferences may be drawn from the skull of the Cape Golden Mole (*Chrysochloris asiatica*). In this fossorial form the rounded occipital region, lacking pronounced occipital and sagittal crests, is reminiscent of the condition in cistecephalids, and has evidently been strongly influenced by development of the powerful neck and shoulder muscles (Dobson 1882) required for its digging and burrowing way of life. Gregory (1951) discussed the muscular and osteological adaptations in a number of insectivores, including the Oligocene *Apternodus*, where a special squamosal flange in the temporal region served to accommodate forwardly extended neck and forelimb muscles.

Direct and detailed comparisons between dicynodonts and fossorial mammals must inevitably be undertaken with caution, but it is tempting to link the insectivore-like occiput in cistecephalids with the digging adaptations in the forelimb of *Kawingasaurus*, described by Cox (1972). The manus in *Kawingasaurus* is unfortunately not known, but if the fused and elongated distal phalanges of two digits of the hand in *Cistecephalus* are taken into consideration, together with evidence of adaptations for skull strengthening and reinforcement in all three cistecephalid genera, then it seems reasonable to suggest that an at least semi-fossorial mode of life was generally selected for in the family. That this direction of specialization was accompanied by basic changes in mastication is suggested by the unusual palate-mandible relationships and the changed orientation of the medial division of the external jaw adductor muscles. However, differences between the palate and mandible of *Kawingasaurus* on the one hand and *Cistecephalus* and *Cistecephaloides* on the other show that more than one type of feeding activity was developed within this adaptive framework. While the varying degree of commitment to digging and perhaps burrowing activities in the three genera can be determined only when the postcranial skeleton of each group becomes better known, it does seem that the sharp, shovel-shaped jaw symphysis of *Cistecephaloides*, and to an extent *Cistecephalus*, indicates dietary preferences quite different to those of the possibly carnivorous *Kawingasaurus*, which (Cox 1972) may have dug for small, mudflat-dwelling invertebrates.

SUMMARY

The skull and mandible of a new dicynodont genus are described and figured. It is concluded that the new form, for which the name *Cistecephaloides boonstrai* is proposed, is closely allied to *Cistecephalus* and the newly established *Kawingasaurus* (Cox 1972) and that a family, Cistecephalidae, should be retained to include these three genera. *Cistecephaloides* is unusual in the small size of the orbits, the prefrontal-postorbital contact, and the separation of the pterygoids in the ventral midline, with consequent incomplete closure of the interptery-

goidal vacuity. Comparisons between the three cistecephalid genera indicate the possibility of parallel evolution, and it is suggested that digging and perhaps burrowing activities were characteristic of this family, and could account for the specializations encountered in the group.

ACKNOWLEDGEMENTS

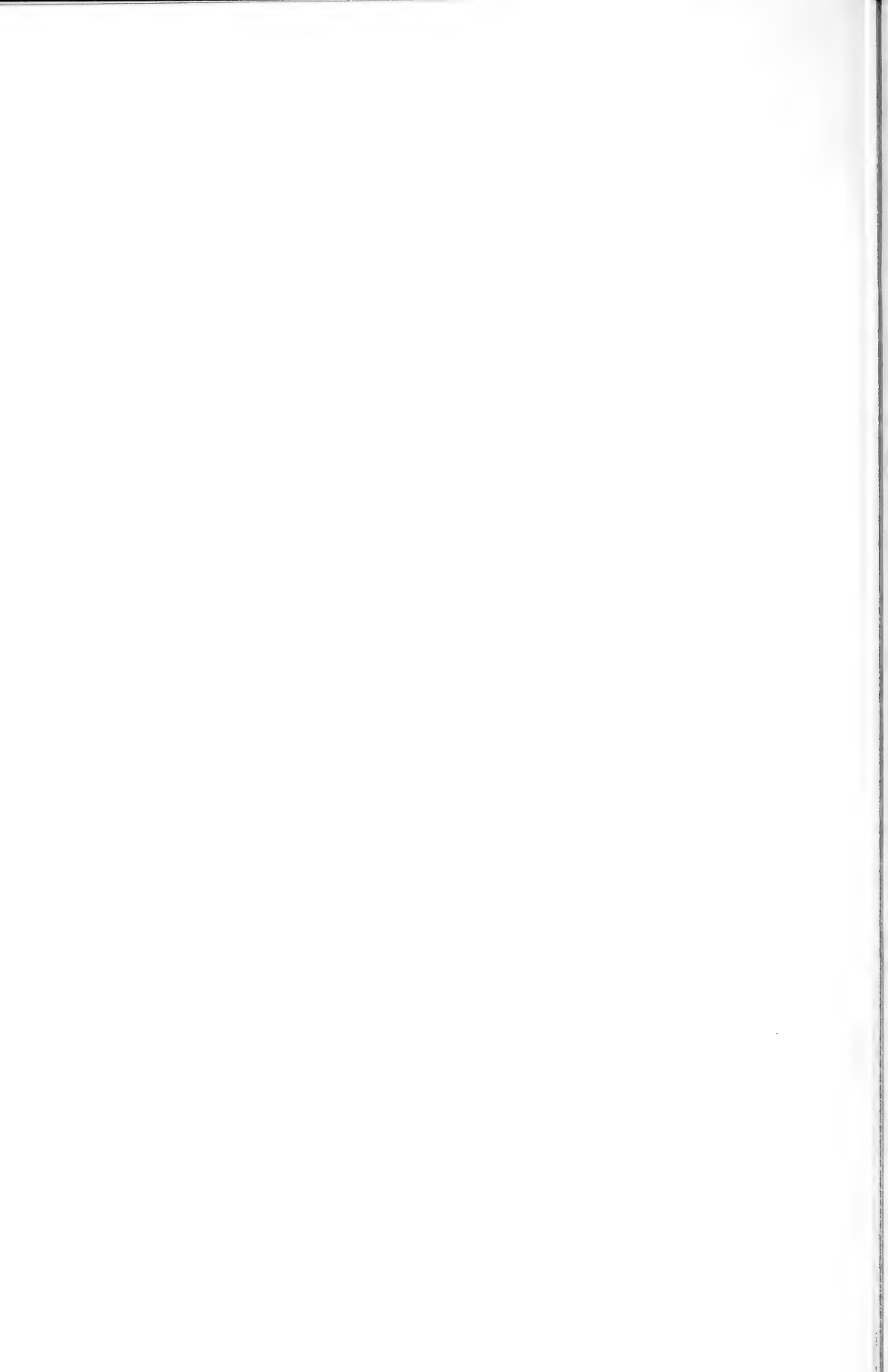
I am grateful to Professor M. E. Malan for her helpful suggestions and critical reading of the manuscript. Mrs I. M. Chesselet of the Department of Palaeontology was responsible for the skilful preparation of much of the cistecephalid material used in this investigation.

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ABBREVIATIONS

ang.	— angular	nas.	— nasal
art.	— articular	op.	— opisthotic
bas.	— basisphenoid	os.	— orbitosphenoid
boc.	— basioccipital	pa.	— parietal
den.	— dentary	pal.	— palatine
ect.	— ectopterygoid	par.	— prearticular
eoc.	— exoccipital	pas. r.	— parasphenoid rostrum
ept.	— epipterygoid	pfr.	— prefrontal
fr.	— frontal	pm.	— premaxilla
i.c.a.	— foramen for internal carotid artery	po.	— postorbital
ip.	— interparietal	pro.	— prootic
ipt.vac.	— interpterygoidal vacuity	prs.	— presphenoid
jug.	— jugal	pt.	— pterygoid
jug. for.	— jugular foramen	pt.f.	— posttemporal fenestra
lac.	— lacrimal	q.	— quadrate
lac.for.	— lacrimal foramen	qj.	— quadratojugal
lat.den.l.	— lateral dentary ledge	soc.	— supraoccipital
lat.pal.for.	— lateral palatal foramen	smx.	— septomaxilla
lat.r.	— lateral ridge on dentary	spl.	— splenial
max.	— maxilla	sq.	— squamosal
med. r.	— medial ridge on dentary	st.	— stapes
		vo.	— vomer



A NEW DICYNODONT (REPTILIA, THERAPSIDA) FROM
CYNOGNATHUS ZONE DEPOSITS OF SOUTH AFRICA¹

By

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(With 2 plates, 1 figure and 1 table)

CONTENTS

	PAGE
Introduction	157
Taxonomy	158
Discussion	161
References	165

INTRODUCTION

A small dicynodont skull, complete with lower jaw and stapes, was collected by J. W. Kitching about 1,6 km south of Lady Frere, Cape Province, on the north side of the Cacadu River in 1961, during the writer's first visit to South Africa. It was originally catalogued as number 22936 in the collections of the National Museum of Natural History, Smithsonian Institution, but as it must be designated the type of a new genus, it has been transferred to the collections of the Bernard Price Institute for Palaeontological Research, Johannesburg, where it is catalogued as Museum Number 430.

The specimen is clearly a member of the *Cynognathus* zone fauna, for it was found in the same shale layer as a good skull of the *Cynognathus* zone gomphodont *Diademodon*, about 275 m west of the latter. No. 430 lay right side up, about 0,3 m below a layer of fine gray sandstone that was about 0,6 m thick. Although the skull is markedly distorted by dorsoventral flattening, preservation of the bone is good and I do not think it possible that the specimen was reworked from older deposits. The area is part of Lady Frere Commonage, which has yielded numerous specimens characteristic of the *Cynognathus* zone but nothing to suggest the presence of any other therapsid faunal element, either by survival or by reworking of older sediments.

The specimen is definitely not a member of the genus *Kannemeyeria*, which until now was the only dicynodont present in the *Cynognathus* zone fauna. It is also distinguishable from other dicynodont genera, and so constitutes a second, very rare, dicynodont member of the *Cynognathus* fauna.

¹ The research upon which this paper is based was supported by a National Science Foundation Grant, G 14705.

TAXONOMY

Class **REPTILIA**

Order THERAPSIDA

Family **Dicynodontidae**Genus *Kombuisia*² gen. nov.*Kombuisia frerensis*³ sp. nov.

Genoholotype. No. 430. Skull with articulated stapes and lower jaw, strongly distorted by dorsoventral flattening, but very little cracked or broken; zygomae lost. Sub-periosteal bone very well preserved; little evidence of surface cracks due to subaerial weathering.

Generic diagnosis. Small dicynodont (see Table I for dimensions) without post-canine teeth, much like *Kingoria* (Cox 1959) in the following features. Inter-

TABLE I

Measurements of *Kombuisia frerensis*, No. 430, TYPE, in millimetres.
Greatest height and height at snout omitted because of crushing.

Overall length, occipital condyle to tip of premaxillary beak (L)	76,8
Width at postorbital bar (W)	52,3
Smallest interorbital distance (Wio)	16,1
Intertemporal width, anterior end of intertemporal bar (Wit)	12,7
Width across paroccipital processes (Wo)	32,2
Bottom of occipital condyle to top of occipital plate, direct (Ho)	18,6
Horizontal distance, anterior margin of orbit to tip of premaxillary beak (Rao)	15,9
Horizontal distance, posterior margin of orbit to tip of premaxillary beak (Rpo)	35,1
Length of temporal fossa, medial side (Rt)	27,5
Length of intertemporal bar, postorbital bar to top of occiput (Rit)	26,0
Posterior width of mouth, measured between posteromedial margins of caniniform processes at level of anterior maxillary margin (P ₁)	20,0
Length of mouth, along midline from P ₁ to tip of premaxillary beak (P ₂)	23,0

orbital bar wider than intertemporal bar, and length of postorbital region nearly equal to distance from postorbital bar to snout (Plate 1 A). Nasal boss expressed only as a low, rugose median swelling on frontals, nasals, and premaxilla; no postfrontal bone; preparietal fusiform, long and narrow; postorbitals cover only about three-quarters of medial sides of temporal fenestrae; parietals exposed dorsally as narrow ridge between postorbitals. Caniniform processes small, rounded. Secondary palate very long, choanae well behind back of caniniform processes (Plate 2 A). Secondary palate consists almost entirely of premaxilla, which is in contact with small palatal process of palatine bone and blocks maxilla from contact with choanal margin (Plate 2 A). Palatine makes very minor contribution to secondary palate; ectopterygoid separates maxilla from pterygoid. Insertion of temporal musculature on lateral face of dentary produced laterally to form prominent shelf or 'wing' (cf. Cox 1959).

² The genus is named for its discoverer, J. W. Kitching, who during his military service bore the nickname 'Kombuis', Afrikaans for kitchen.

³ The specific name refers to the type locality of *Kombuisia*.

Dentary symphysis long. External naris large, distance from front of orbit about twice diameter of external naris, which lies very close indeed to margin of upper jaw.

Differs from *Kingoria*, and from other dicynodonts as well, in configuration of dentary. Symphysis shallow, broad, flat dorsally; ventral profile slopes upward and forward very gently from splenial margin to tip of beak, so that general appearance of front of beak is spatulate (Plate 2 C). Front and side margins of beak sharp. In dorsal aspect (Plate 2 B) the symphysis is not parallel-

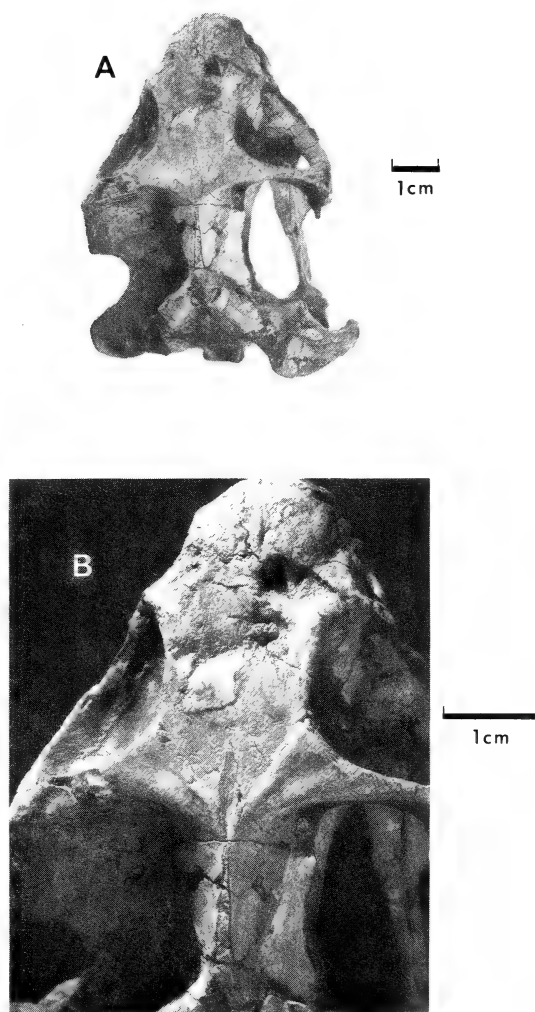


PLATE 1. *Kombuisia frerensis*. No. 430.

A. Skull, dorsal aspect. B. Parietal region, enlarged to show condition of bone surface and absence of pineal opening.

sided as in most dicynodonts, but tapers forward to a squared-off anterior margin. Median groove between dentary tables, which is deep and distinct in nearly all dicynodonts (Crompton & Hotton 1967), is very shallow in *Kombuisia*; in fact, dentary tables are separated from median groove only by a pair of low, sharp ridges that run straight back from the corners of the squared-off anterior margin of the beak. Lateral and parallel to each of these ridges is a low, rounded ridge

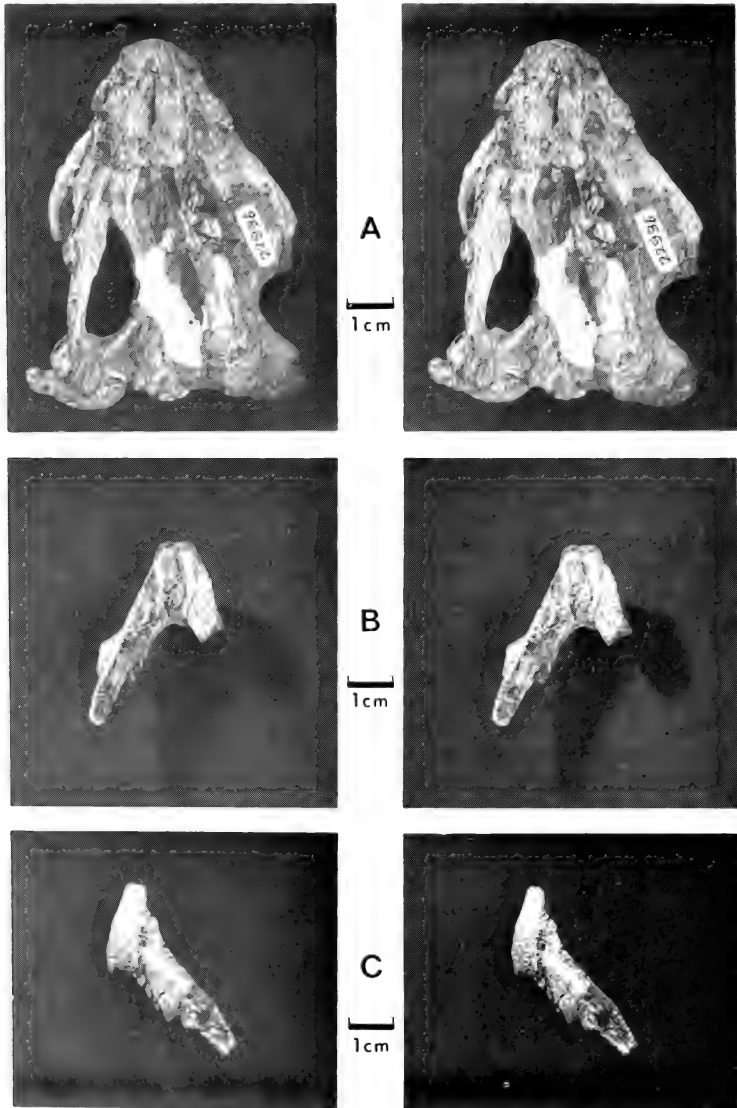


PLATE 2. *Kombuisia frerensis*. No. 430. Stereo pairs.

A. Skull, palatal aspect. B. Dentary, dorsal aspect. C. Dentary, left lateral aspect.

that rises at the symphyseal margin about half-way between the tip of the beak and the splenial margin, and runs back to disappear a little behind the splenial margin.

DISCUSSION

The most distinctive single feature of the type of *Kombuisia* is that it has no pineal opening. In the type specimen, the pineal region of the skull roof is virtually undistorted and the surface of the bone is undamaged (Plate 1 B); there is thus no evidence of pathology and the lack of a pineal opening appears to be the normal condition. A second specimen (National Museum, Bloemfontein, C. 3006, excellent stereophotographs of which were provided by A. R. I. Cruickshank) comes from a *Cynognathus* zone locality and is clearly referable to *Kombuisia* on the basis of palate and dentary symphysis. Unfortunately the Bloemfontein specimen consists of snout and dentaries only, and the presence or absence of a pineal opening cannot be confirmed. Because the lack of a pineal opening is so unexpected in dicynodonts, and because at present it is indicated in *Kombuisia* by only the one specimen, I prefer to delay incorporating this character into the formal diagnosis of the genus until more evidence comes to light.

The two identified specimens of *Kombuisia* are very nearly the same size, and are slightly less than half as large as the genotype of *Kingoria*, University of Tübingen, catalogue number K. 12. This specimen, as well as those described by Cox, appear to have been adult at the time of death, as does the type of *K. galecephalus* (Broom & Robinson 1948), Rubidge Collection, catalogue number 97.⁴ The type of *Kombuisia*, though smaller, does not appear to have been appreciably younger at time of death than the various specimens of *Kingoria*, and it is therefore probably close to the adult size of the genus.

Kombuisia and *Kingoria* are most usefully compared with the more common Beaufort dicynodonts, animals of small to moderate size that lack postcanine teeth, including *Dicynodon* as it is generally accepted at the present time, and *Lystrosaurus*. The genus *Dicynodon* is under study by the writer and M. A. Cluver, and there is every indication that the name as currently used includes two distinct genera. However, differences between these groups are not critical to comparison with *Kombuisia* and *Kingoria*, and for present purposes the name *Dicynodon* is employed in its current usage. The informal term 'common dicynodonts' as used in the remainder of this discussion includes both *Dicynodon*, in this inclusive sense, and *Lystrosaurus*.

Neither the type nor the Bloemfontein specimen of *Kombuisia* has any trace of tusks. The caniniform processes are small and the snout is short and delicate. These facts alone are not sufficient to indicate that tusks were absent in all

⁴ Listed by Houghton & Brink (1954) as catalogue number 77 (*in errore*). Number 77 is the type of *Dicynodon clarencei* Broom, which Houghton & Brink list incorrectly as number 97. The two specimens are quite distinctive, and the error seems to be simply a matter of catalogue numbers having been switched inadvertently.

individuals of the genus for, as Broom notes (1935), tuskless specimens of *Dicynodon grimbeeki* have more lightly-built snouts than tusked specimens. Cox reports that only two of ten specimens of *Kingoria* at his disposal had tusks, but describes no differences between the snouts of tusked and tuskless individuals. However, in *Kombuisia* the snout is more delicate and the caniniform processes are proportionately smaller than in most other dicynodonts, including tuskless specimens of *Kingoria* and *D. grimbeeki*, and it seems unlikely that any individuals of *Kombuisia* had tusks.

The palates of *Kombuisia* and *Kingoria* are distinctive in their lack of relief. In most dicynodonts (cf. Ewer 1961; Crompton & Hotton 1967; Cluver 1970, 1971) there is a pair of strong ridges on the back of the premaxillary beak, one on either side of the midline, and the contact between the vomer and the premaxilla is produced into a prominent midline ridge. In *Kombuisia* and *Kingoria* the premaxillary ridges are lacking and the midline vomerine ridge is much subdued; there is, however, a low, longitudinal ridge just medial to each maxillo-premaxillary suture (Fig. 1: LR) which is not present in other dicynodonts.

The punctate and rugose sculpture on the beaks of dicynodonts is generally agreed to indicate the presence, in life, of a horny covering, because of its resemblance to comparable areas in birds and chelonians. On the rostral

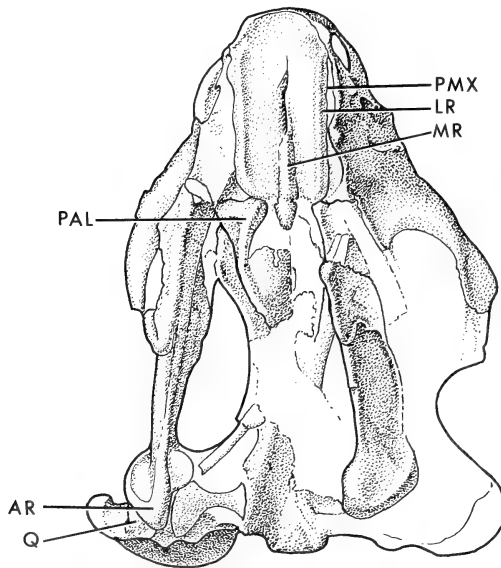


Fig. 1. *Kombuisia frerensis*. No. 430.

Skull, palatal aspect: AR, articular; LR, longitudinal ridge at lateral edge of premaxilla; MR, median ridge at junction of premaxilla and vomer; PAL, palatine; PMX, maxillo-premaxillary suture; Q, quadrate.

surface of the snout and on the dentary symphysis the distribution of this covering must have been relatively uniform throughout the Dicynodontia; it is much the same in *Kombuisia* and *Kingoria* as in other dicynodonts. On the buccal surfaces of the palate, however, it shows much greater variation; *Kombuisia* and *Kingoria* represent one extreme and common dicynodonts the other, and these extremes parallel the differences in relief of the palate. In common dicynodonts the entire buccal surface of the palate is punctate, even to the hollows between the ridges, and was presumably entirely covered by horn. In *Kombuisia* and *Kingoria*, punctate sculpture, and hence a putative horn covering, is restricted to the buccal surfaces of premaxilla and maxillae, to the latero-posterior corners of the premaxilla, and to the small palatal processes of the palatines adjacent to the latter. This leaves most of the premaxillary secondary palate smooth and presumably covered by mucous membrane, much like the mesial surface of the palate in chelonians. Because punctate sculpture is not developed medial to the low, longitudinal ridges at the lateral margins of the premaxilla in *Kingoria*, Cox (1959) suggests that these ridges merely reflect the medial margins of horn covering. The structure of *Kombuisia* should probably be interpreted in the same way.

In the common dicynodonts, the horn-covered secondary palate, with its elaborate system of ridges and rugosities, is associated with a mouth of trenchant appearance: maxillary and premaxillary margins are blade-like, the dorso-lateral margins of the dentary symphysis are squared off, and the tip of the dentary beak supports a transversely oriented blade. This arrangement forms a system of blades and surfaces on the upper and lower jaws (Crompton & Hotton 1967) that comminuted food by a shearing action, the force being provided by retraction of the jaw; it probably arose co-ordinately with the retractive sliding action of the jaw that defines the Dicynodontia as a group. In various pristerodonts and *Lystrosaurus* (Crompton & Hotton, 1967), and in most other dicynodonts as well, the jaw joint is characteristically very unstable in full protraction, because the bearing surfaces of the joint that are in contact during full protraction, i.e. the posterior surface of the articular and the front of the quadrate, are both convex. Because of this instability, the vertical force that could be exerted on the jaw at this time was limited to the small vertical component of the very obliquely directed anterior fibres of the temporalis musculature, which served primarily to initiate elevation of the jaw. Elevation and retraction were concurrent, but the bulk of force exerted on the lower jaw in early stages was horizontal, and the motion that was most effective in shearing was retraction. The more vertically oriented posterior temporalis fibres must have been relaxed at protraction, and came fully into play only as the jaw approached full retraction.

In *Kombuisia* and *Kingoria*, in which the secondary palate lacks horn covering and marked relief, the appearance of the mouth is less trenchant than in most other dicynodonts. Although maxillary and premaxillary margins are sharp in *Kombuisia*, the shallow palate is occluded by a flattened, spatulate

dentary. The lateral premaxillary ridges are not comparable in either position or prominence to the ridges of common dicynodonts. In *Kingoria*, both upper and lower jaw margins appear to be rounded and smooth, and the tip of the beak tapers to a blunt point. The palate is deeper than that of *Kombuisia* but is equally featureless.

Reduction of trenchancy of mouth and palate suggests marked modification of the shearing function in *Kombuisia* and *Kingoria*. In *Kingoria* this modification does not seem to have affected the jaw mechanism, which is much the same as in other dicynodonts, but in *Kombuisia* it apparently extends to the jaw joint. The lower jaw of the type specimen of *Kombuisia* is articulated in full protraction, and the right articuloquadrate joint is quite well preserved and exposed. The retroarticular portion of the articular bone is produced backward so that the lower (and posterior) part of the bearing surface lies beneath the quadrate in full protraction (Fig. 1: AR), rather than in front of it as in most dicynodonts. The posterior bearing surface is therefore somewhat concave, so that the surfaces of quadrate and articular are more nearly congruent and the joint is correspondingly more stable when the jaw is fully protracted. Thus it is possible that in *Kombuisia* greater vertical force could be applied at the beak much earlier in the cycle, perhaps even during full protraction.

The mouth of *Kombuisia* more than that of any other dicynodont is like the mouth of many chelonians, in the characteristic flatness of the dorsum of the dentary symphysis and the restriction of horn to the margins of the palate. Furthermore, the ridges at the lateral margins of the premaxilla (Fig. 1: LR) appear to meet the dentary tables, i.e. the grooves between each of the pairs of lateral ridges on the dorsum of the dentary (Plate 2 B), when the jaw is at or close to full protraction. The dorsum of the symphysis thus appears to be more nearly congruent to the buccal surface of the shallow palate than in most dicynodonts, another characteristic reminiscent of chelonians. There is no doubt that *Kombuisia* retained the retractive sliding mechanisms of the dicynodont jaw, but the stability of the joint during protraction, coupled with morphological features of the mouth, suggest that it had superimposed a more turtle-like anterior bite upon the basic dicynodont jaw mechanism.

Conclusions about the habits of *Kombuisia* must await the appearance of new material, for verification of the patterns described here and for information as to the postcranial structure of the animal. The possibly superficial resemblance of the feeding mechanism to that of chelonians is not very useful in this context, for chelonians exhibit the widest range of habitats and habits of living reptiles. However, the fact that the clearest distinctions among *Kombuisia*, *Kingoria* and most other dicynodonts are associated with the feeding mechanism indicates that dicynodont radiation, like dicynodont origin, was primarily a matter of exploiting the possibilities of different modes of feeding.

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THE ALLEGED SYNONYMY OF *LYCORHINUS* AND
HETERODONTOSAURUS

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(With 11 figures.)

For more than half a century the only pre-Jurassic ornithischian known was *Geranosaurus atavus* Broom, 1911, an incomplete lower jaw (with some doubtfully associated postcranial bones) from the Upper Triassic Cave Sandstone of South Africa. In 1962, however, Crompton & Charig gave a preliminary description of an almost complete and extremely well-preserved skull, also from the Cave Sandstone, which they named *Heterodontosaurus tucki*. One of the most remarkable features of *Heterodontosaurus* is its dentition, shown in Figures 10 and 11. There are (a) simple pointed premaxillary teeth working against a toothless predentary, (b) one enlarged pointed caniniform tooth in each jaw, this being the last premaxillary tooth in the upper jaw and the first dentary tooth in the lower, and (c) more complex, closely packed maxillary and dentary teeth, with ridged lateral and medial surfaces and with enamel on one side only, abrading and sharpening each other like opposing chisels to produce oblique, flat, continuous occlusal surfaces. These cheek teeth are set in from the side of the face. Most curious of all, there seems to be no tooth replacement whatever in the type skull of *H. tucki* or in another nearly complete skull of the same species collected subsequently (S.A.M. No. K1332). In their original description Crompton & Charig noted also the verbal observation of their colleague, J. Attridge, that an incomplete dentary from the underlying Red Beds (Figs 8, 9), described by Haughton in 1924 as *Lycorhinus angustidens* gen. et sp. nov. and believed to belong to a cynodont, possessed a dentition very like that of *Heterodontosaurus* and probably represented an ornithischian dinosaur rather than a therapsid. Romer (1966) classified *Lycorhinus* as an ornithischian, placing it tentatively in the family Hysilophodontidae of the suborder Ornithopoda. A very detailed description of the holotype skull of *Heterodontosaurus tucki* has now been prepared by Charig & Crompton (in press) and it is intended that a similar description of S.A.M. No. K1332 shall follow.

Since 1962 Upper Triassic ornithischians have been turning up more often, mostly in the Stormberg Series of southern Africa (Republic of South Africa and Lesotho) but elsewhere too. Until now, however, only one other Stormberg ornithischian has been named—*Fabrosaurus australis* Ginsburg, 1964—and once again the holotype consists of nothing more than a fragment of a dentary from

the Red Beds. This has virtually no distinguishing features other than the highly characteristic features of its teeth, which are clearly very different from those of *Heterodontosaurus*. In *Fabrosaurus*—if we assume its complete dentition to have been like that of similar specimens discovered later (Fig. 1)—the heterodonty is less marked, without development of caniniforms; the more posterior teeth are of a leaf-like shape, probably not very different from the unworn teeth of *Heterodontosaurus* but more widely spaced and never worn down to a flat continuous occlusal surface; the cheek teeth are not set in from the side of the face, and normal alternating reptilian replacement appears to occur. We think it very likely that such teeth will prove to be common to several early ornithischian genera as well as to persistently primitive forms of later date, e.g. *Echinodon* Owen, 1861 from the Purbeck Beds of England (on the Jurassic–Cretaceous boundary). Indeed, this ‘fabrosaur’ type of tooth is accepted by all workers as primitive for the Ornithischia; Bakker & Galton (1974) are even claiming that the basic pattern of the dentition in primitive ornithischians (such as *Fabrosaurus*) was similar to that of small prosauropods. But if this characteristic tooth structure is diagnostic of a whole family (or of an even higher taxon) rather than of a single genus, then the nominal genus *Fabrosaurus* must be indeterminate. The names *Fabrosaurus* and *F. australis* must therefore be regarded as *nomina dubia*; no other material should be referred to the species, and no other species to the genus.

Thulborn has nevertheless described more ornithischian material from the Stormberg Series, including both skull (1970b, 1971a) and postcranial elements (1972), and he refers it all to *Fabrosaurus australis*; he does so because of the ‘highly distinctive’ nature of the teeth (Fig. 1). But for the reasons given above, and because it is evident from our own collections that the Stormbergs of southern Africa contain other, hitherto undescribed ornithischians, we cannot accept that Thulborn’s reference of this material to *F. australis* is justified—even though the reptile he described is again very different from *Heterodontosaurus*. We should prefer to call it ‘fabrosaurid gen. et sp. indet.’.

It is therefore apparent that all the Triassic ornithischians that have been found in southern Africa up till now (even the little-known *Geranosaurus*) may be classified as either ‘*Heterodontosaurus*-like’ or ‘*Fabrosaurus*-like’, according to the nature of their teeth. The rest of this paper is mainly concerned with those resembling *Heterodontosaurus* in this respect.

Our greatest concern is with Thulborn’s contention (1970a) that *Lycorhinus angustidens* and *Heterodontosaurus tucki* are congeneric, i.e. that the nominal genus *Heterodontosaurus* Crompton & Charig, 1962 is a subjective junior synonym of *Lycorhinus* Houghton, 1924, is therefore invalid and should be discarded. (At the same time he agrees that the skull from the Cave Sandstone merits specific separation as *L. tucki*.) In consequence he now uses the name *Lycorhinus* instead of *Heterodontosaurus* in his published discussions on ornithischian phylogeny (1970a, 1971a, b, 1972), sometimes adding the name ‘*Heterodontosaurus*’ in parentheses or square brackets with or without inverted commas. He also con-

tends (1970a, 1971b) that both valid genera of ornithischians from the Upper Trias of southern Africa (i.e. *Lycorhinus* and *Fabrosaurus*, according to him) should be placed in the family Hypsilophodontidae, the type-genus of which is Wealden in age; and (1971b) that these Upper Triassic forms should be classified further into two subordinate 'groups' of that family, to be called 'lycorhinids' and 'fabrosaurs' respectively.

In this connection it should be mentioned that in Britain and the U.S.A. there are—apart from Thulborn himself—four established palaeontologists who have worked on primitive ornithischians within the last few years: Charig, Crompton, Galton and Ostrom. None of the four accepts Thulborn's synonymy. Nor does Cluver, Curator of Fossil Vertebrates in the South African Museum, the museum where all the material of both genera is housed. Why, then, should we bother to discuss the synonymy further? We do so partly to determine our position in relation to such a declared synonymy, whether we are free to accept it or reject it as we think fit, and partly to consider, if we *are* free to reject it, whether we should be justified in so doing. But we are less concerned with resolving this particular case than with using it as an illustration of certain general points, especially the inadvisability of publishing a synonymy without logical consideration of all the available evidence and without due regard for its taxonomic and nomenclatural consequences.

What, then, are our opinions of the generic synonymy proposed by Thulborn? First, we believe that such a synonymy can serve no useful purpose whatever; indeed, from a practical point of view it is highly undesirable. We shall explain this further below. Secondly, it seems to us that the synonymy is based upon alleged similarities for which the evidence, in many instances, is either incorrect or not pertinent or both; that, because of the fragmentary nature of the *Lycorhinus* material, the only useful evidence concerns the lower teeth; that there is as much evidence of differences between the teeth of the two genera as of similarities; and that this severe limitation of the comparison, coupled with our lack of knowledge of the variability of the tooth structure of Triassic ornithischians, would probably make it difficult, if not impossible, to estimate the closeness of the relationship between the two holotypes. Did they belong to the same genus, as claimed by Thulborn, or only to the same sub-family? Perhaps only to the same family? Obviously this problem requires detailed consideration.

Before embarking on this, however, we shall deal briefly with Thulborn's other contention, concerning his two special 'groups' within the family Hypsilophodontidae. These, being suprageneric, are manifestly of subfamilial rank and should be recognized as such; yet one of the names he gives to those sub-families is incorrect in its stem, irrespective of whether or not his synonymy be accepted, and both names are incorrect in their terminations (even in their vernacular forms). Our first objection to Thulborn's subfamily names is based on the provisions of Article 40 in the International Code of Zoological Nomenclature, which states: 'Synonymy of the type-genus. When, after 1960, a

nominal type-genus is rejected as a junior synonym (objective or subjective), a family-group name based on it is not to be changed, but continues to be the valid name of the family-group taxon that contains both the senior and junior synonyms.' In other words, a family or subfamily name must be retained even though the type-genus on which it is based has been rejected as a junior synonym. Applying this to our particular case, the family name Heterodontosauridae Kuhn or Romer (which?), 1966 could not be replaced by a new family name Lycorhinidae, even if *Heterodontosaurus* were accepted as a junior synonym of *Lycorhinus*; and the same is true of the corresponding subfamily names. As for our second objection, Article 29 of the Code lays down that 'A family-group name is formed by the addition, to the stem of the name of the type-genus, of . . . -INAE in the case of a subfamily'. Thulborn's two 'groups', therefore, should be called Heterodontosaurinae and Fabrosaurinae respectively. In any case, Galton (1972) has already pointed out the undesirability of placing these Triassic forms within the Hysilophodontidae; although we do not agree with every aspect of Galton's phylogeny and classification, we do agree with him that Thulborn's two 'groups' merit independent familial status, as Heterodontosauridae and Fabrosauridae. (Authorship of the latter family is attributable to Galton 1972.)

Let us return to our central theme—the matter of the alleged generic synonymy. It sometimes happens that the Law of Priority (Article 23 of the Code) obliges one to place a well-established, familiar name in the junior synonymy of one much less familiar or altogether unknown; or, even more unfortunate, to place a taxon based on excellent type-material in the subjective junior synonymy of another based on poor type-material. The placing of *Heterodontosaurus* in the junior synonymy of *Lycorhinus* would have both these unhappy consequences without any possible advantage accruing therefrom. *Heterodontosaurus* is already a well-established name appearing in many articles and recent textbooks, for, as the first fairly complete skull of a Triassic (or indeed pre-Upper Jurassic) ornithischian, it attracted a great deal of attention; *Lycorhinus* is a name familiar to no one and, where it does appear in lists of genera (e.g. in Romer 1956), it has usually been classified as a therapsid. The *Heterodontosaurus* holotype has now been completely developed and the detailed description of its skull (Charig & Crompton, in press) is likely to make it the most completely described dinosaur skull in existence; moreover (as mentioned above) there is now another skull (S.A.M. No. K1332), equally good if not better, in association with good postcranial material. The *Lycorhinus* holotype, on the other hand, was an incomplete left dentary, with eight teeth and the impressions of four others, and is today (see p. 174) represented only by the most anterior, caniniform tooth, and the impression of the dentary with its row of posterior teeth (S.A.M. No. 3606). If the two holotype specimens were congeneric, beyond all reasonable doubt, and if we were given the choice of which to use as our standard of reference for the combined genus, the choice would obviously fall upon *Heterodontosaurus*; the use of the now very fragmentary

Lycorhinus type would impose great practical difficulties.

But we should have no such choice. *L. angustidens* is the type-species of *Lycorhinus*, and must remain so. The true systematist is like a judge in a civil case; he must apply the law impartially, interpreting it rigidly where the wording is unequivocal even though he may think it to be unjust. To disregard the law (even in some small particular) or to permit others to do so can only bring about a general disregard for the law as a whole. If the systematist feels that a certain Rule should not be applied in a certain case, he can request the International Commission on Zoological Nomenclature to exercise its plenary powers; if he thinks that a particular Rule or part thereof is a bad rule, his remedy is to seek to change it through the next Congress. The wisest course, however, for anyone suspecting that a possible synonymy might prove inconvenient or embarrassing could well be to ignore it altogether; on the other hand, once it has been dragged into the open it must be judged on only one aspect—not on its consequences or its practicability but simply on whether or not it is possible to show, to the reasonable satisfaction of other workers in the field, that the specimens or taxa concerned are sufficiently alike to be given the same name. Charig & Reig (1970) state that: 'In deciding synonymy or otherwise the onus of proof lies with him who wishes to establish it.' Kermack, Mussett & Rigney (1973) are even more positive: 'Once a genus has been described and named, the onus is entirely on those who wish to make the name a synonym to show that the two genera concerned are identical *beyond any possible doubt* [their italics]: the onus is in no way on those who wish to maintain the *status quo* to prove that the names are not synonyms.'

This is the case with *Lycorhinus* and *Heterodontosaurus*. It should have been obvious to Thulborn that, even if he could have proved the synonymy, here was a case for letting sleeping dogs lie; but once he had chosen to stir them up we found ourselves compelled to examine his arguments very carefully in order to determine the degree of acceptability of his conclusions. We have done this as objectively as possible, well aware of the fact that, as co-authors of the name *Heterodontosaurus*, we might be accused of some emotional attachment thereto!

Essentially Thulborn's arguments for synonymizing *Heterodontosaurus* with *Lycorhinus* rely upon a new specimen, U.C.L. No. A.100 (Figs 4-7); he claims that this specimen, a block of sandstone with dissociated pieces of skull, is a topotype of *L. angustidens*. (While he admits that the holotype of *L. angustidens* did not provide enough evidence even to investigate the possibility that *Lycorhinus* was an ornithischian, apparently a latex impression of that holotype now affords sufficient proof of its specific identity with A.100!) A.100, in turn, is regarded as congeneric with *Heterodontosaurus tucki*.

The first question is, is such use of intermediate specimens legitimate? If the holotype of one species cannot be synonymized generically with the holotype of another, is it proper to synonymize one with an assumed topotype—or even a mere referred specimen—of the other? The answer to this question,

in general, is indubitably yes. It may well be that two well-preserved but incomplete holotypes in the same deposit consist of different parts of conspecific individuals but cannot be shown to belong to the same species until a new, more complete specimen including both parts associated proves to be identical to both. For example, most species of chelonian in the London Clay are based either on skulls or on shells; it is likely that many 'skull species' could be paired up with 'shell species', but this can be done only by the finding of well-preserved specimens with skull and shell in association. Such specimens are rare.

The case of *Lycorhinus* and *Heterodontosaurus*, however, is not like that at all. All that we have of *Lycorhinus angustidens* is an impression of the dentary, an element of which the greater part is present also in the holotype of *Heterodontosaurus tucki*; the use of another dentary as an intermediate cannot help matters at all because, without any additional elements in common to the two specimens concerned, we are no better equipped to prove the identity of that dentary with the *Lycorhinus* holotype either. Indeed, even if we were provided with an absolutely perfect skull as our intermediate we should not be able to prove that its dentary and lower teeth were identical with those of *Lycorhinus angustidens*, although we might be able to prove the identity of that perfect skull with the type skull of *Heterodontosaurus tucki*. The simple fact is that the holotype of *Lycorhinus angustidens* seems to be too incomplete and too poorly preserved to allow anything to be certainly identified with it.

Thulborn fails to comment on the fact that specimen No. A.100 has heavily worn maxillary teeth and unworn dentary teeth; it is interesting to speculate as to how he imagines the animal wore down the former while preserving the latter in their newly erupted condition. This apparent anomaly did lead us to suspect, albeit fleetingly, that the lower jaw of A.100 might not have belonged to the same animal as did the upper jaws; we now regard that possibility, however, as no more than extremely remote because the various elements present on the A.100 block (premaxilla, maxillae, jugals, frontal, postorbital, dentary) show no duplication and are all of commensurate size. In any case, the premaxilla, maxillae and upper teeth all give clear indications of heterodontosaurid affinities, and the lower jaw—except for its unworn teeth—does the same. Even so, we remain puzzled by the unworn condition of those lower teeth. Thulborn, on the other hand, appears to ignore the fact that those unworn lower teeth do not bear much resemblance to any *Heterodontosaurus* teeth described by Crompton & Charig in the holotype of *H. tucki* but are in some respects more reminiscent of the teeth of *Fabrosaurus australis*. The details which he gives of the 'second specimen of *Heterodontosaurus*', which he refers to as being in the care of one of us (A.J.C.) in the British Museum (Natural History), are inaccurate; and, while it seems very likely that the fragment of maxilla in question belonged to a member of the family Heterodontosauridae, it differs in several particulars from the holotype of *Heterodontosaurus tucki*. (Had we known that he intended to mention our research material in his article we should gladly have supplied him with the necessary information.)

Thulborn takes sufficient cognisance of the differences between the lower caniniform teeth of *Lycorhinus* and those of *Heterodontosaurus*—the former crenellated on the anterior¹ margin only, the latter on both margins—to admit that this signifies a specific difference between the two forms. We agree that this difference exists; for we maintain that the type of *Lycorhinus angustidens*, while too incomplete and too poorly preserved to permit anything to be certainly identified with it, was well enough preserved to show that it was different from both A.100 and *Heterodontosaurus tucki*.

Despite this minor difference there is no doubt that all three specimens concerned possess four common characters of the dentition which are typical of the '*Heterodontosaurus*-like' forms and which are lacking altogether in *Fabrosaurus* and its allies, the only other ornithischians from the Upper Trias of southern Africa of which we have any real knowledge. These are (a) the prominent caniniform tooth at the front of the dentary, (b) a trend towards the possession of closely packed postcaniniform teeth which are worn down to a continuous occlusal surface, (c) the apparent complete absence of any tooth replacement (see Charig & Crompton, in press), and (d) the mediad recession of the tooth row into the side of the face, suggesting the presence of muscular cheeks (see Galton 1973). Thulborn, oddly enough, draws attention only to the first of these. Characters (a) and (c) are unique to this particular group within the Ornithischia, but (b) is found also in some Cretaceous members of the order and (d) in all post-Triassic members.

Let us now analyse Thulborn's comparison of *Lycorhinus* with *Heterodontosaurus*, detail by detail. It relies entirely on the unquestioned acceptance of two points: his unproven, tacit but very evident assumption that all the material on the A.100 block represents a single individual, and his allegedly proven belief that 'specimen A.100 does represent *Lycorhinus angustidens*' (p. 242). We shall—with some hesitation—accept the former point, supposing that all the elements visible on the A.100 block (Fig. 1) belonged to the same animal and ignoring the surprising and seemingly inexplicable fact that the maxillary teeth are heavily worn while the dentary teeth are scarcely worn at all. But we feel that his reference of A.100 to *Lycorhinus angustidens* should be submitted to a critical examination.

The lower jaw of A.100 is exposed only on its lateral side (Fig. 4). Thulborn (p. 241) refers it to *L. angustidens* because, according to him, it shares the following common features with Haughton's holotype:

1. The mandible is exceptionally deep.
2. There is a large, caniniform first dentary tooth, with only its anterior edge crenellated.

¹ Thulborn uses terms employed in dentistry and human odontology when describing the teeth of reptiles; thus anterior becomes 'mesial', posterior 'distal' and so on. We disagree with Edmund (1969) that the use of these terms is convenient and that 'The terms distal and mesial are to be preferred to anterior and posterior because of the curved shape of the dental arcade.' 'Distal', in particular, is generally used by comparative anatomists to mean something entirely different (namely, opposite to proximal) and it is therefore ambiguous or misleading to apply it to reptile teeth.

3. There is a small gap between the first (caniniform) and second dentary teeth.

Haughton, however, described and figured (1924: 343-344, fig. 8; our Fig. 8) only the *medial* aspect of his holotype. Later the specimen itself became separated from the piece of matrix to which it had been attached by its lateral surface and was lost; the *lateral* aspect of the dentary, as evidenced by its natural mould on the matrix, was described and figured by Broom (1932: 307, fig. 104, I; our Fig. 9). It is of this lateral aspect that Thulborn possesses a latex impression (p. 236) and we ourselves have another. But Thulborn does not mention Broom's account of *Lycorhinus* (although it is evident from personal communication that he is aware of its existence, indeed we must acknowledge our gratitude to him for reminding us of it) and he tacitly implies that his latex impression is of the surface described by Haughton, without indicating at this point whether Haughton described the medial or the lateral surface. Later, however (p. 242), Thulborn states that further comparisons are difficult because only the medial side of the *Lycorhinus angustidens* holotype was exposed and described by Haughton, whereas, of course, the mandible and lower teeth of specimen A.100 are visible only in lateral aspect; had Thulborn used his latex impression of the lateral side of the holotype the comparison would have been easier and more meaningful.

Whichever surface of the *Lycorhinus* mandible be compared with the lateral surface of the A.100 mandible, it is immediately obvious to us that the two specimens are different in many respects. With regard to the three similarities cited by Thulborn (see above), the second—concerning the presence of a caniniform with only its anterior edge crenellated—is certainly correct. But the illustrations by Haughton, Broom and Thulborn, taken in conjunction with the latex mould, suggest that the base of the caniniform tooth is relatively more slender in A.100 than in *Lycorhinus*. Further, the tip of the *Lycorhinus* caniniform is bevelled off anteromedially, as shown in Haughton's figure and described in his text; the lower caniniform of A.100 is not exposed on its medial side, but Thulborn's illustration of it in lateral view suggests that the tooth is unworn right up to its remarkably acute tip. (Haughton commented that in *Lycorhinus* it was 'bevelled off by rubbing against the canine of the upper jaw', but, with no upper jaw preserved, this was pure speculation; in *Heterodontosaurus* the upper and lower caniniforms, seemingly in their natural relative positions, are nowhere near each other.) The same illustrations by Haughton, Broom and Thulborn suggest also that Thulborn's other two similarities are not especially close: the mandible beneath the caniniform is much shallower in A.100 than in *Lycorhinus*, and the gap between the first (caniniform) and second dentary teeth is much wider.

There are other differences too, outweighing the similarities in number and importance. The postcaniniform teeth of *Lycorhinus* are inclined slightly forwards, they are so close together that the distal ends of their crowns are in contact with each other, and they are heavily worn down to a continuous,

though rather irregular, occlusal surface. On the other hand, the teeth of A.100 show no forward inclination whatever, they do not touch each other (Thulborn's fig. 5, our Fig. 4, suggests that the third and fourth teeth might have touched before the third was broken) and, as illustrated, they show no signs of wear; this last point is confirmed by Thulborn's description (p. 240). In both specimens a cingulum separates the more or less parallel-sided root from the upwardly widening crown, the anterior and posterior edges of the latter diverging towards the occlusal margin; in *Lycorhinus* this cingulum is absent on the lateral surface and present (*fide* Haughton) on the medial surface, but in A.100 (where the medial surface of the lower teeth is unknown) it is well developed on the lateral surface. The teeth of *Lycorhinus* are not each symmetrical in lateral or medial view, for on each tooth from the fifth onwards ('4th molar' of Haughton) there is 'a large anterior cusp occupying two-thirds of the grinding surface, and a much smaller, somewhat lower posterior cusp' (Haughton 1924: 344); the groove on the medial surface, running between the ridges which descend from the cusps to the cingulum, is therefore markedly posterior in position. But in A.100, where we can see only the lateral surface of the tooth row, each crown has the form of a symmetrical arrowhead; there are three or four small cuspules on either side (anterior and posterior) of the tip, and the well-pronounced ridges which run down from each cuspule are roughly symmetrical on either side of a stronger central ridge. (It must be admitted that the lateral surfaces of the teeth of the *Lycorhinus angustidens* holotype, as figured by Broom and as shown in the latex mould, *do* look a little more symmetrical than the medial surfaces, but they are still quite unlike the lateral surfaces of the teeth of A.100.)

Because of the difficulties alleged by Thulborn of comparing the lower teeth of *Lycorhinus* with those of A.100 (difficulties which, as we have seen, are actually unnecessary if use be made of Broom's description and figure and of the latex mould), Thulborn also compares the medial aspect of the dentary teeth of the former—as described and figured by Haughton—with the medial aspect of the *maxillary* teeth of A.100 (Fig. 7); this comparison, of extremely dubious validity, enables him to claim (p. 242) of the teeth in the latter specimen that their 'worn crowns (Fig. 4) are virtually identical with those described and figured by Haughton (1924). In each case the lingual crown surface bears a broad median rib and the distal [posterior] margin is produced as a thin and erect ridge, the mesial [anterior] edge showing only a faint tendency towards elaboration into a similar ridge.' In fact none of these features is apparent in Haughton's figure of the *Lycorhinus* holotype or mentioned in his description, unless we include 'the ridges which descend from the cusps to the cingulum'. According to Thulborn, these alleged but actually non-existent similarities between the upper teeth of one specimen and the lower teeth of another 'leave little doubt that specimen A.100 does represent *Lycorhinus angustidens*'. We repeat that the medial surfaces of the dentary teeth of A.100 remain unknown and may well differ from those of the *maxillary* teeth; but they could not have

resembled the corresponding surfaces in *Lycorhinus*, for, as indicated above, the dentary teeth of A.100 are unworn and their whole shape is quite different from that found in *Lycorhinus*.

Thulborn goes even further and states (p. 236) that: 'Since both of these specimens are from the same locality there is a slight possibility that they might represent different parts of a single individual, though this seems unlikely in view of the great hiatus between their two dates of collection.' He ignores the several differences that we have pointed out between *Lycorhinus* and A.100, evidently preferring to believe that it is possible for the teeth on the left dentary to undergo extensive wear while those on the right dentary of the same animal remain virtually unworn! He also ignores the fact that the exposure of the Red Beds at Paballong (neither Haughton nor Thulborn localized their specimens more precisely than that) is so large as to render negligible the chances of two bones found on different occasions being parts of the same individual—especially when those two occasions are separated by more than 40 years. In any case, the rate of erosion at Paballong during the rainy season is so high that the time required for the destruction of a piece of bone weathered out of the rock is more likely to be, on average, a matter of days or even hours rather than of decades.

In conclusion, we are much less impressed by Thulborn's similarities between *Lycorhinus angustidens* and A.100 than by the differences between them; and we feel that we have established a *prima facie* case for their generic separation.

Because of his determination of A.100 as *Lycorhinus angustidens* Thulborn next claims that 'Specimen A.100, imperfect though it is, considerably amplifies our knowledge of *Lycorhinus*', and then proceeds, in the light of that 'amplified' knowledge, to compare *Lycorhinus* with the holotype of *Heterodontosaurus tucki*; in that comparison he draws his *Lycorhinus* characters partly from the holotype, partly from the A.100 lower jaw, but mostly from the upper jaw and skull of A.100. He concludes that: 'Whilst there are definite differences between *Lycorhinus angustidens* and *L. (Heterodontosaurus) tucki* these serve only to distinguish the animals at species level and do not warrant their separation into distinct genera.' But we have rejected his determination of A.100 as *Lycorhinus angustidens*. In that circumstance *Lycorhinus* and A.100 should be compared separately with *Heterodontosaurus*: first the holotype dentary of *Lycorhinus* with the dentary of the holotype of *Heterodontosaurus*, then the dentary of A.100 with the dentary of the holotype of *Heterodontosaurus*, and finally the various elements of the upper jaw and skull of A.100 with the corresponding elements of the *Heterodontosaurus* upper jaw and skull. Further, since we believe that *Lycorhinus* and A.100 are *not* identical, it follows that—in our view—*Heterodontosaurus* cannot be the same as both of them; it may be *either* the same as *Lycorhinus*, or the same as A.100. (If it is not the same as A.100, then the latter must represent yet another ornithischian in the Upper Trias of southern Africa.) It is even possible that *Heterodontosaurus* is not the same as either *Lycorhinus* or A.100, in

which case we must be dealing with *three* separate forms.

First let us compare the *Lycorhinus* holotype (Fig. 8) directly with the dentary and lower teeth of *Heterodontosaurus* (Fig. 10). Thulborn, drawing his *Lycorhinus* characters from the holotype and not from A.100, can claim only three points of similarity: the presence of a prominent caniniform first dentary tooth, the planing-off of the lateral sides of the mandibular crowns to produce sharp chisel-like ends, and the size gradation of those mandibular crowns so that the largest are in the middle of the tooth row. (It is not clear from his paper (p. 243) whether the size gradation is supposed to pertain to the upper cheek teeth only or to the lower teeth as well, but it does in fact pertain to both.) We indeed agree that all three features appear to be present in both genera. On the other hand, Thulborn admits to one difference: the lower caniniform is crenellated only on its anterior edge in *Lycorhinus*, on both edges in *Heterodontosaurus*. There are also other important differences, unrecognized by Thulborn. Haughton (1924) mentioned that the 'molars' of *Lycorhinus* had a pronounced cingulum, which, as pointed out by Crompton & Charig (1962), is absent in the postcaniniforms of *Heterodontosaurus*. The crowns of *Lycorhinus* taper down towards that cingulum so that, although they touch their neighbours occlusally, large triangular gaps are left between their more basal portions; the latex impression shows that their lateral surfaces are convex in both directions, vertical and horizontal. In *Heterodontosaurus*, by contrast, the lateral surface of each lower postcaniniform crown has sub-parallel edges which touch (or almost touch) its neighbours throughout its length and is more or less flat. There is a further difference in the vertical ridging-and-grooving on the medial surface of the teeth: in *Lycorhinus* a narrow groove lies behind a wide anterior ridge, in *Heterodontosaurus* a wide shallow trough lies behind a narrow anterior ridge. Because the similarities between *Lycorhinus* and *Heterodontosaurus* are so few and so general (indeed, they could well be family characters rather than generic) we regard the generic identity of *Lycorhinus* and *Heterodontosaurus* as unproven; because there are also certain differences between them, we consider it unlikely. As we wrote in 1962: 'This [the possession by *Lycorhinus* of a distinct cingulum] and the nature of the wear of the teeth appear to indicate that *Heterodontosaurus* and *Lycorhinus* are generically distinct.' We see no reason to change our minds; rather has our detailed analysis confirmed our opinion. The fragmentary nature and poor preservation of the *Lycorhinus angustidens* holotype, taken together with the fact that it is now represented only by an impression, make it improbable that the matter could ever be settled really conclusively one way or the other, and for that reason we prefer to regard the names *Lycorhinus* and *L. angustidens* as *nomina dubia*, names which have been founded on inadequate material and which ought not to be used except in connection with the holotype itself.

Adoption of this point of view is not only *sufficient* in itself to justify rejection of any synonymy involving the name *Lycorhinus* but logically *requires* such rejection. Charig (in press) states that '... no worker can be compelled to accept

the validity of a specific or generic name based on type-material which he considers unsatisfactory; if he rejects such a name it becomes—to him—a *nomen dubium*, and on those grounds he is not only entitled to reject other authors' synonymies involving the name in question but is logically *obliged* to do so'.

The alleged identity of the lower jaw of A.100 (Fig. 4) with that of *Heterodontosaurus tucki* (Fig. 10) is another matter. Comparison of the postcaniniform teeth is difficult because specimen A.100 includes only anterior dentary teeth (numbers 1-7) and the *H. tucki* holotype includes only the caniniform and the more posterior teeth (numbers 1 and probably 7-14); further, the lower jaw of A.100 and its teeth are exposed only on the lateral side, while the lower teeth of *H. tucki*, though visible in both aspects, are *well* exposed only on the medial side. Even so, the alleged identity is easy to disprove, for though the similarities are few the differences are many. In fact, a list of those differences is essentially the list of differences between A.100 and the *Lycorhinus angustidens* holotype given earlier in this article together with another couple of differences between *Lycorhinus* and *Heterodontosaurus* as given immediately above. We shall put these down in tabular form. Let us include also a column for the corresponding condition in the *Lycorhinus* holotype—where known—and insert it between the A.100 and *Heterodontosaurus* columns (the reason for this arrangement will soon become apparent). Let us include also two additional characters in which A.100 differs from *Lycorhinus* but which are not visible in the holotype of *Heterodontosaurus tucki*.

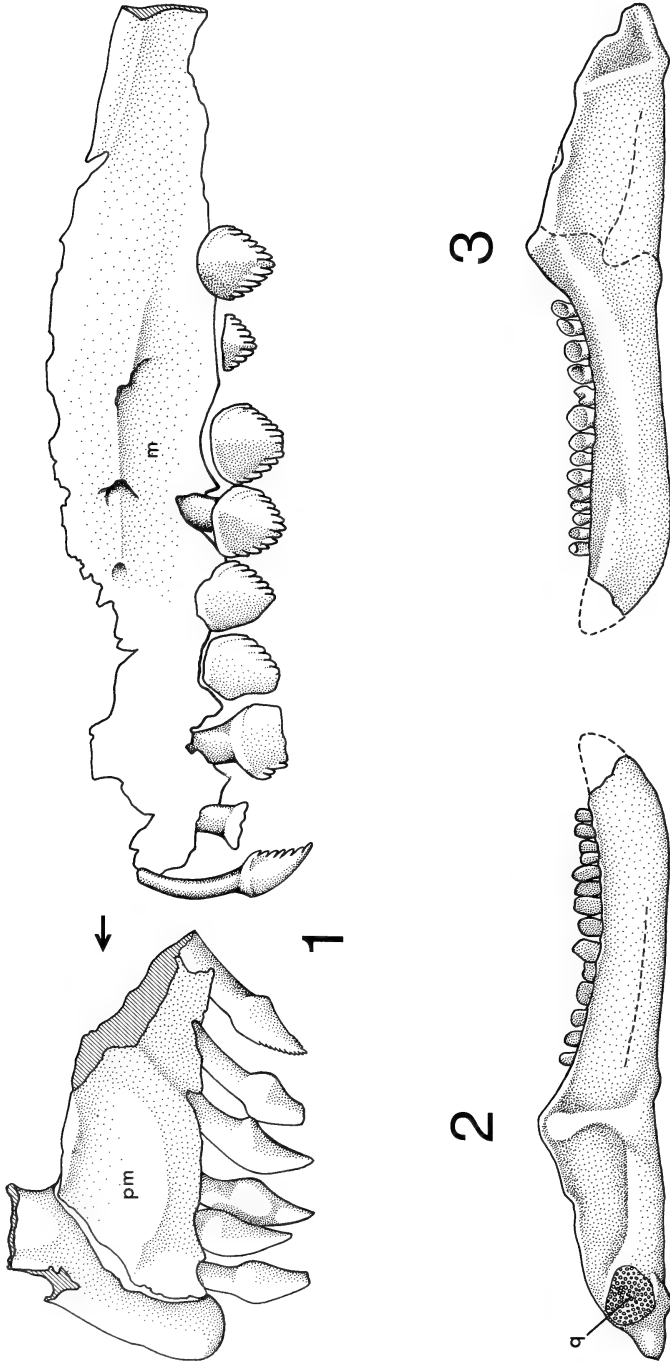
Thulborn also writes (p. 243): 'The teeth of *Lycorhinus* [viz., A.100] bear on their labial surfaces median ribs which are neither as thin nor as sharp as those in *Heterodontosaurus*.' From the context he could be referring to vertical ridges on either the lateral surface or the medial surface of either the upper or the lower teeth of *Heterodontosaurus*, all of which are different. On the next page (p. 244), where he is presumably referring to the same feature, he partly clarifies the situation by writing: 'Fluting on the labial surfaces of the cheek teeth is more pronounced in the species *tucki*.' In *Heterodontosaurus*, however, there are no thin sharp median ridges on the lateral surfaces of the *lower* teeth, indeed all that is known of the ornamentation of the lower teeth in the type of *H. tucki* (where they were badly damaged during development) is that a broad vertical ridge appears to have been present; yet a comparison of the lateral surface of the lower teeth of A.100 with the lateral surface of the *upper* teeth of *Heterodontosaurus* would mean nothing.

It is obvious from the comparative table that A.100 is the least specialized and *Heterodontosaurus* the most specialized of the three forms, with *Lycorhinus angustidens* fitting in as an intermediate. This accords with their stratigraphical positions: A.100 and *Lycorhinus* are from the same locality and therefore from approximately the same horizon within the Red Beds, *Heterodontosaurus* is from the overlying Cave Sandstone and is likely to be a little younger.

Heterodontosaurus tucki (Figs 10, 11) and A.100 (Figs 5-7) may also be com-

COMPARISON OF LOWER JAWS AND TEETH		A.100	Holotype of <i>Lycorhinus angustidens</i>	Holotype of <i>Heterodontosaurus tucki</i>	
depth of mandible beneath caniniform		much shallower	exceptionally deep		
caniniform tooth	width of base at alveolar margin	more slender	broader		
	crenellate edges	anterior edge only		both edges	
width of gap between caniniform and second dentary tooth		wider	narrower	? (not seen)	
postcaniniform teeth	distance apart	well apart, no contact	close together crowns in contact distally crowns in contact throughout length		
	inclination of anterior teeth	not inclined	crowns inclined slightly forwards ? (not seen)		
	wear	virtually unworn	heavily abraded to form continuous occlusal surface occlusal surface irregular occlusal surface smooth		
	appearance of each crown in lateral or medial view	symmetrical (shown by cusps & ridging-&-grooving on lateral surface)	asymmetrical (shown by ridging-and-grooving on medial surface)		
	distinct neck between root and crown	present	?	absent, teeth essentially columnar	
	cingulum	present on lateral surface (medial not seen) on medial surface only		absent	

pared on the upper jaw and the rest of the skull, parts which are lacking entirely in *Lycorhinus angustidens*. Both specimens have (a) a large, triangular and widely open antorbital fossa, (b) a premaxilla which is remarkably deep below the external naris, (c) a wide, deep diastema between the premaxilla and the maxilla, and (d) a distinct recess, forming a 'step', in the lateral surface of the maxilla above the tooth row (possibly more pronounced in *Heterodontosaurus* than in A.100). In both specimens a wide edentulous zone at the front of the premaxilla is followed by three teeth, the first two being simple conical pegs and the third a prominent caniniform (large, but not as large as the lower caniniform) with its posterior border crenellate (in *Heterodontosaurus* the anterior



border is not visible). The maxillary teeth number about a dozen (12 in *Heterodontosaurus*, 13 in A.100) with the largest crowns in the middle of the series; their medial sides are planed off to produce sharp, chisel-like ends. This planing-off is oblique in *Heterodontosaurus*; in A.100, however, although Thulborn does mention in his text (p. 243) that the medial sides of the maxillary teeth are planed off, his Figure 4 gives no indication whatever of this character.

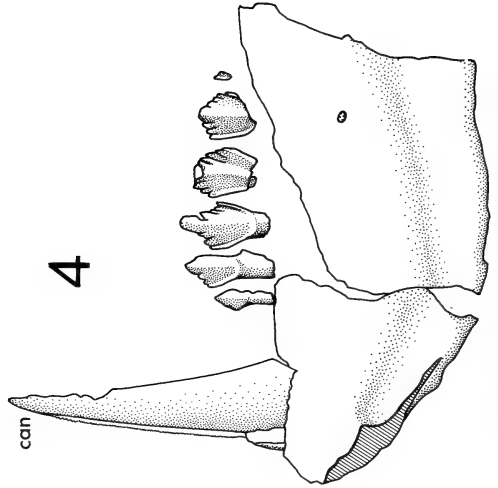
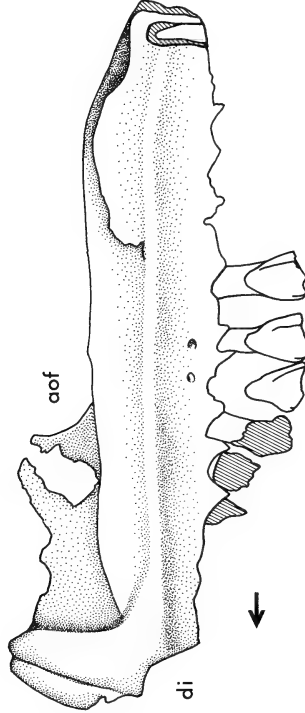
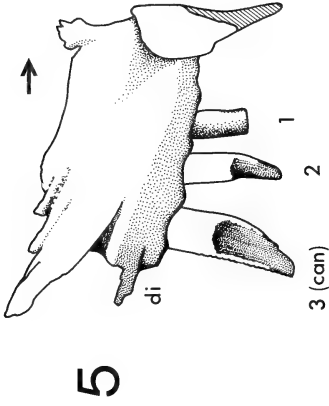
On the other hand, there are also a number of differences. Specimen A.100 seems to lack the suborbital boss and the jugal process which are so characteristic of the jugal of *Heterodontosaurus*, indeed the whole form of the jugal seems to be very different. The disparity between the lengths of the upper caniniform and of the other premaxillary teeth is less marked in A.100 than in *Heterodontosaurus*. In *Heterodontosaurus* the most anterior tooth in the maxilla lies immediately beneath the anterior end of the antorbital fossa; in A.100, however, the maxilla itself and its tooth row extended forwards far beyond the limits of that fossa. The maxillary teeth of *Heterodontosaurus* are close together, with only small gaps between them at the alveolar margin and touching each other occlusally, even overlapping a little in most instances; but those of A.100 are separated by wide gaps at the alveolar margin, sometimes wider than the teeth themselves. The maxillary teeth of *Heterodontosaurus* possess no neck and are essentially columnar in form, while those of A.100 have a pronounced neck and cingulum demarcating the root from the crown. In *Heterodontosaurus* the lateral surface of each maxillary tooth bears three prominent ridges— anterior, central and posterior— separated by sharply defined excavated regions, the central ridge in particular being thin and sharp; the medial surface, however, is quite different in that it has only a poorly developed central ridge. In A.100, by contrast, the lateral and medial surfaces of the maxillary teeth are essentially alike, the central ridges being weaker, thicker and blunter than on the lateral surfaces of the maxillary teeth of *Heterodontosaurus*.

Fig. 1. Fabrosaurid gen. et sp. indet. Described and figured Thulborn 1970b, 1971a as *Fabrosaurus australis*. Department of Zoology, University College London, field no. B.17. Likhoele Mountain, near Mafeteng, Lesotho; Red Beds. Left premaxilla and maxilla. Lateral view, $\times 3\frac{3}{4}$. (After Thulborn 1971a; maxilla reversed from right side.)

Fig. 2. *Pisanosaurus mertii* Casamiquela, 1967. Holotype. Laboratorio de Paleontología de Vertebrados, Instituto Miguel Lillo, Tucumán, Argentina, no. 2577. 'Agua de las Catas', opposite Km 461 on Ruta Nacional no. 40, La Rioja Province, Argentina; middle section of Ischigualasto Formation. Left mandible. Medial view, $\times \frac{3}{4}$. (After Bonaparte, in press; reversed from right side.)

Fig. 3. Same individual. Left mandible. Lateral view, $\times \frac{3}{4}$. (After Bonaparte, in press; reversed from right side.)

Abbreviations: m—maxilla; pm—premaxilla; q—fragment of the quadrate.



All the premaxillary teeth of *Heterodontosaurus* (including the caniniform) appear to have more or less rounded tips; but they are seen only in lateral view, and it is not possible to be sure that they do not have wear facets on the medial side like those of A.100 which, Thulborn suggests, 'resulted from their working against a horn-sheathed prementary at the mandibular symphysis'.

There are also certain very characteristic features of the cheek teeth of *Heterodontosaurus*, both upper and lower, which cannot be used in this comparison because Thulborn does not mention the corresponding condition in the latter specimen. In *Heterodontosaurus* the cheek teeth are curved in the transverse plane so that, in anterior or posterior view, the lateral profile of each upper crown is convex with a distinct 'knee', the medial profile is more or less straight, and the planar occlusal surface faces medioventrally; the opposite holds true for the lower crowns, though their convexity (on the medial side) is weaker. There is an extremely thin layer of enamel on the occlusal half of each convex surface only, i.e. on the lateral surface of each upper tooth and the medial surface of each lower tooth. Thulborn does state, however, that the *unworn* cheek teeth of *Lycorhinus* (by which he presumably means the lower postcaniniform teeth of A.100) are completely enamelled.

In this connection it may be noted that Galton (1973) reproduces (fig. 2 K) Thulborn's figure 3 of the right maxilla of A.100; his new caption reads: '*Heterodontosaurus* sp., right maxilla in lateral view, figured as *Lycorhinus angustidens* by Thulborn (1970a) who does not and cannot demonstrate that this specimen is identical to the lost holotype of *Lycorhinus angustidens* Haughton (1924).' While we agree with Galton that A.100 cannot be referred to *Lycorhinus angustidens*, we would certainly not place it in the genus *Heterodontosaurus* (see our conclusions below); the differences between A.100 and the type of *H. tucki* are too many and too substantial.

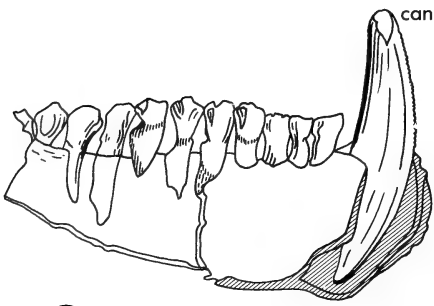
Fig. 4. *Heterodontosaurid* gen. et sp. indet., described and figured Thulborn 1970a as *Lycorhinus angustidens*. Department of Zoology, University College London, no. A.100. Paballong, near Mount Fletcher, Herschel District, Cape Province, South Africa; Red Beds. Left dentary, with teeth. Lateral view, $\times 2$. (After Thulborn 1970a; reversed from right side.)

Fig. 5. Same specimen. Left premaxilla, with teeth. Medial view, $\times 2$. (After Thulborn 1970a; reversed from right side.)

Fig. 6. Same specimen. Left maxilla, with teeth. Lateral view, $\times 2$. (After Thulborn 1970a; reversed from right side.)

Fig. 7. Same specimen. Left maxillary teeth. Medial view, $\times 2$. (After Thulborn 1970a.)

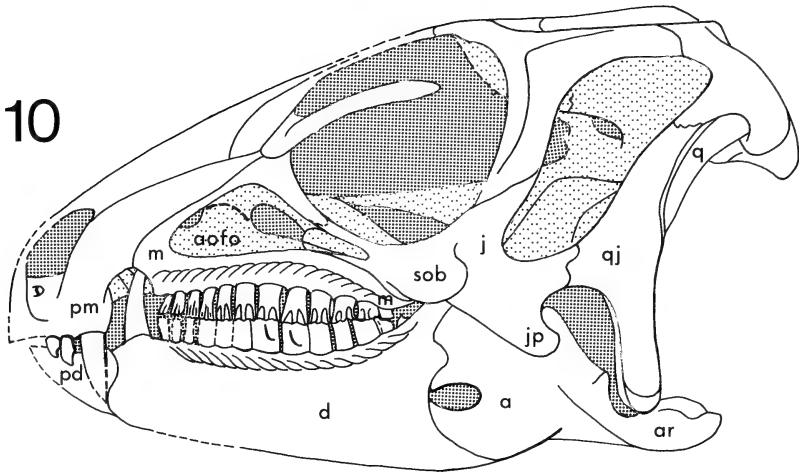
Abbreviations: aof—antorbital fenestra; can—caniniform tooth; di—diastema.



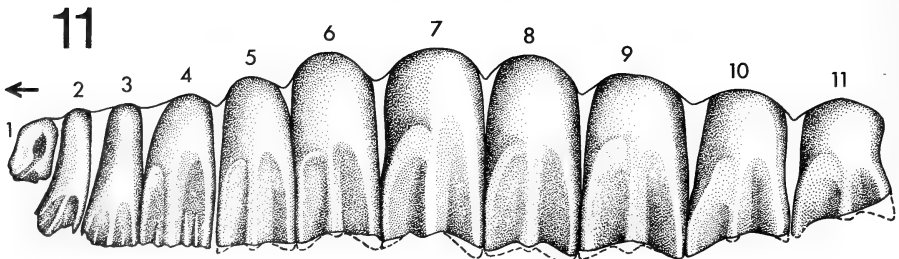
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11

If it be accepted that the whole of specimen A.100 represents a single individual, then certain characters of the upper jaw and its teeth also accord with the view that A.100 is less specialized than *Heterodontosaurus*. They include the simpler form of the jugal (without suborbital boss or jugal process), the slightly weaker development of the upper caniniform, the wider spacing of the maxillary teeth in the tooth row, the simpler form of those teeth with lateral and medial surfaces more or less alike, and possibly a lesser development of the recess and 'step' in the lateral surface of the maxilla above the tooth row.

The graded differences between A.100, *Lycorhinus* and *Heterodontosaurus* are indeed significant; but, as mentioned above, they do not obscure the essential similarities of the three forms—some of them unique to the group. There are three characters which are diagnostic of the group, no matter what rank the latter may be accorded in the classification: the prominent caniniform at the front of the dentary, a trend towards the possession of closely packed post-caniniform teeth with antero-posteriorly expanded crowns worn down to a continuous occlusal surface (not evident in the lower jaw of A.100), and the concavity extending along the outer sides of the maxilla and dentary above and beneath the postcaniniform tooth row (suggesting a mediad recession of the tooth row into the side of the face). We believe that this suite of common characters justifies the association of the forms in question into a taxon of suprageneric rank—the family Heterodontosauridae.

The three specimens considered here also share a unique peculiarity in that their teeth show no signs of replacement. It seems, however, that this character is not invariably associated with the rest of the suite; we have the incomplete maxilla of what appears to be another heterodontosaurid from

Fig. 8. *Lycorhinus angustidens* Haughton, 1924. Holotype. South African Museum, no. 3606. Paballong, near Mount Fletcher, Herschel District, Cape Province, South Africa; Red Beds. Left dentary, with teeth. Medial view, $\times 1\frac{1}{2}$. (After Haughton 1924.)

Fig. 9. Same individual, same bone. Lateral view, $\times 1\frac{1}{2}$. (After Broom 1932.)

Fig. 10. *Heterodontosaurus tucki* Crompton & Charig, 1962. Holotype. South African Museum, no. K337. Mountain behind Tyindini trading store, Herschel District, Cape Province, South Africa; Cave Sandstone. Reconstruction of skull. Left lateral view, natural size. (After Charig & Crompton, in press; reversed from right side.)

Fig. 11. Same individual. Left maxillary teeth. Lateral view, $\times 4$. (After Charig & Crompton, in press; reversed from right side.)

Abbreviations: a—angular; afo—antorbital fossa; ar—articular; can—caniniform tooth; d—dentary; j—jugal; jp—jugal process; m—maxilla; pd—pre-dentary; pm—premaxilla; q—quadrate; qj—quadratojugal; sob—suborbital boss. On all the illustrations the arrow indicates the anterior direction.

the Stormberg Series with functional teeth possessing the typical characters of the family but also with two unerupted replacing teeth and other evidence of replacement. This is the fragment referred to by Thulborn (1970a: 243) as 'A second specimen of *Heterodontosaurus*'.

The relative sizes of specimen A.100, *Lycorhinus* and *Heterodontosaurus* may be of interest. Comparisons are difficult, but the average interval at which the teeth are inserted in the middle of the dentary seems to be about the same (3.6 mm) in all three. The depth of the dentary beneath those teeth, however, is a little greater in specimen A.100 than in either *Heterodontosaurus* or *Lycorhinus*, and the maxilla is approximately one-third longer in A.100 than in *Heterodontosaurus*.

Also relevant to our discussion is the genus *Pisanosaurus* Casamiquela, 1967 (only species *P. mertii* Casamiquela, 1967 from the Ischigualasto Formation of Argentina), which is of Carnian or perhaps even of Ladinian age; it is therefore older than the African forms with which this paper is mainly concerned and which are generally considered to be Norian or Rhaetian. Indeed, *Pisanosaurus* is the earliest ornithischian known. The unique holotype comprises a fragment of maxilla and an almost complete mandible (Figs 2, 3), both with teeth; cervical, dorsal and (as natural moulds) sacral vertebrae; a little rib material; an incomplete scapula and an impression of part of the pelvis; the impressions of three metacarpals; and a good part of the hind limb. *Pisanosaurus* has been variously placed in the families Pisanosauridae (Casamiquela 1967), Hypsilophodontidae (Thulborn 1971b², 1972; Galton 1972, 1973) and Heterodontosauridae (Bonaparte, in press). The last work cited, a redescription and reassessment of *Pisanosaurus*, shows that it possesses all the heterodontosaurid tooth characters mentioned above and several others too, with the notable exception of the caniniform teeth; and even the absence of those teeth is by no means certain because *Pisanosaurus* lacks both the premaxilla and the front end of the mandible—a sufficient length thereof to have borne a caniniform. Galton (1972, fig. 1) indicates his belief that *Pisanosaurus* occupies a position in ornithischian phylogeny at the base of the ornithopod line of ancestry, just after the diverging of the heterodontosaurid, ankylosaur and stegosaur lines; indeed, he places it on or close to the line of ancestry of all other ornithischians except *Fabrosaurus* and *Echinodon*. He therefore regards it as the earliest and most primitive hypsilophodontid, for he writes (p. 466): 'All hypsilophodonts were probably derived from a form similar to *Pisanosaurus*.'

It seems to us, however, that Bonaparte's revelation of the specialized, truly heterodontosaurid character of the *Pisanosaurus* dentition makes Galton's beliefs completely untenable; we therefore support Bonaparte's reference of the genus to the Heterodontosauridae, a family known otherwise only from southern Africa. But the higher tooth count (maxillary teeth estimated at 16–18 by Bonaparte, 15 dentary teeth actually preserved) suggests that *Pisanosaurus* is

² Thulborn (1971b) includes *Pisanosaurus* among the 'fabrosaur group' of the family Hypsilophodontidae. The separate family Fabrosauridae was formally proposed by Galton in 1972.

more primitive than its African relatives; this suggestion, which will probably be confirmed by other characters of the genus when they become known, accords with its lower stratigraphical position.

Our conclusions may be summarized as follows:

1. All three specimens considered here—holotype of *Lycorhinus angustidens*, holotype of *Heterodontosaurus tucki* and specimen A.100—are sufficiently alike to be placed in the same family, for which the correct name is Heterodontosauridae. The diagnostic characters of that family are the prominent caniniform tooth at the front of the dentary (and in the premaxilla too where known), a trend towards the possession of closely packed postcaniniform teeth which are worn down to a continuous occlusal surface, and the mediad recession of the postcaniniform tooth row into the outer side of the jaws. The three specimens concerned are also remarkable in their apparent total lack of tooth replacement, but this cannot be regarded as an absolutely diagnostic character because another heterodontosaurid jaw fragment from the Stormbergs shows unequivocal evidence of replacement.
2. Whether the lower jaw of A.100 did in fact belong to the same individual as the other skull elements, or even to the same species, might be considered a little doubtful because of the unworn nature of the lower teeth and the heavily worn nature of the uppers. On the other hand, the various skull elements of A.100 show no duplication, they are all of commensurate size, and both upper and lower jaws give clear indications of heterodontosaurid affinities.
3. The lower jaw of A.100, however, is sufficiently distinct from *Lycorhinus* and *Heterodontosaurus*, and the upper jaw (unknown in the former genus) is sufficiently distinct from *Heterodontosaurus*, to rule out any possibility that A.100 might be congeneric with either. It must represent a new genus of heterodontosaurid from the Upper Trias of southern Africa.
4. *Lycorhinus angustidens*, as far as can be seen in so imperfect a specimen, bears a strong resemblance to *Heterodontosaurus tucki* but differs sufficiently in certain details of tooth structure to rule out any possibility of conspecificity. The fragmentary nature, poor preservation and subsequent loss of most of the *Lycorhinus angustidens* holotype make it impossible to determine whether or not the two forms were congeneric, but without positive evidence of congenericity we are obliged to regard them as separate genera. In any case, we consider the names *Lycorhinus* and *L. angustidens* to be *nomina dubia*.
5. If all three lower jaws be compared together, *Heterodontosaurus* and A.100 seem to be very different; *Lycorhinus* is intermediate between them, resembling *Heterodontosaurus* rather than A.100 in most of the contrasting characters but more like A.100 in a few. A.100 is the most primitive of the three and *Heterodontosaurus* the most specialized. This is borne out by a comparison of the upper jaws and teeth (also the jugal) of A.100 with the corresponding elements of *Heterodontosaurus*.

6. The slightly earlier genus from Argentina, *Pisanosaurus*, is also a heterodontosaurid, probably more primitive than the forms from southern Africa but certainly too specialized to be ancestral to any post-Triassic ornithischians known.
7. As will be shown elsewhere, the heterodontosaurids possessed highly specialized masticatory and locomotor adaptations which indicated that they had moved into ecological niches quite distinct from those occupied by other contemporary dinosaurs, both ornithischian and saurischian. Diversity at the generic level might therefore be expected.

ACKNOWLEDGMENTS

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THE TARSUS OF THEROPOD DINOSAURS

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(With 13 figures)

CONTENTS

	PAGE
Introduction	191
General evolution of the reptilian tarsus	191
The pivot tarsus of the crocodylids	195
The hinge tarsus of the dinosaurs	196
The ceratosauroid tarsus	197
The allosauroid tarsus	203
The albertosauroid tarsus	207
The ornithomimid tarsus	211
The tyrannosauroid tarsus	213
Summary	215
Acknowledgements	215
Postscript	216
References	217

INTRODUCTION

The theropod tarsus is a very highly evolved structure, and the investigation of its origin and development is a most intriguing subject. As with most such studies, each new discovery reveals new unsolved problems, most of which cannot be pursued because they diverge too far from the main topic of research. Our interest in this rather specialized subject was aroused by the tarsi of two individuals of *Dilophosaurus*, both in a fine state of preservation. We have long searched for theropods that might show relationship to *Dilophosaurus*. This led us to a comparative study of theropod tarsi and an inquiry into the origin of this peculiar mechanism. We have tried to limit our thoughts to the tarsus, but we must caution the reader that, consciously or unconsciously, our conclusions have probably been influenced by our knowledge of other parts of the skeleton.

GENERAL EVOLUTION OF THE REPTILIAN TARSUS

The theropod hind limb was derived from that of a quadrupedal archosaur or protoarchosaur, probably by or in the early Triassic. In the ancestral forms the femur is essentially horizontal, projecting laterally and swinging forward and backward about the knee. It has been customary to think of the leg as rotating in the acetabulum, and this is indeed the condition in the recovery stroke. However, once the foot becomes planted in its forward position the whole action is reversed and the foot becomes the pivot about which the epipodials and propodial revolve. We therefore think of a fixed pes with the limb lever

Relationships of theropod tarsi

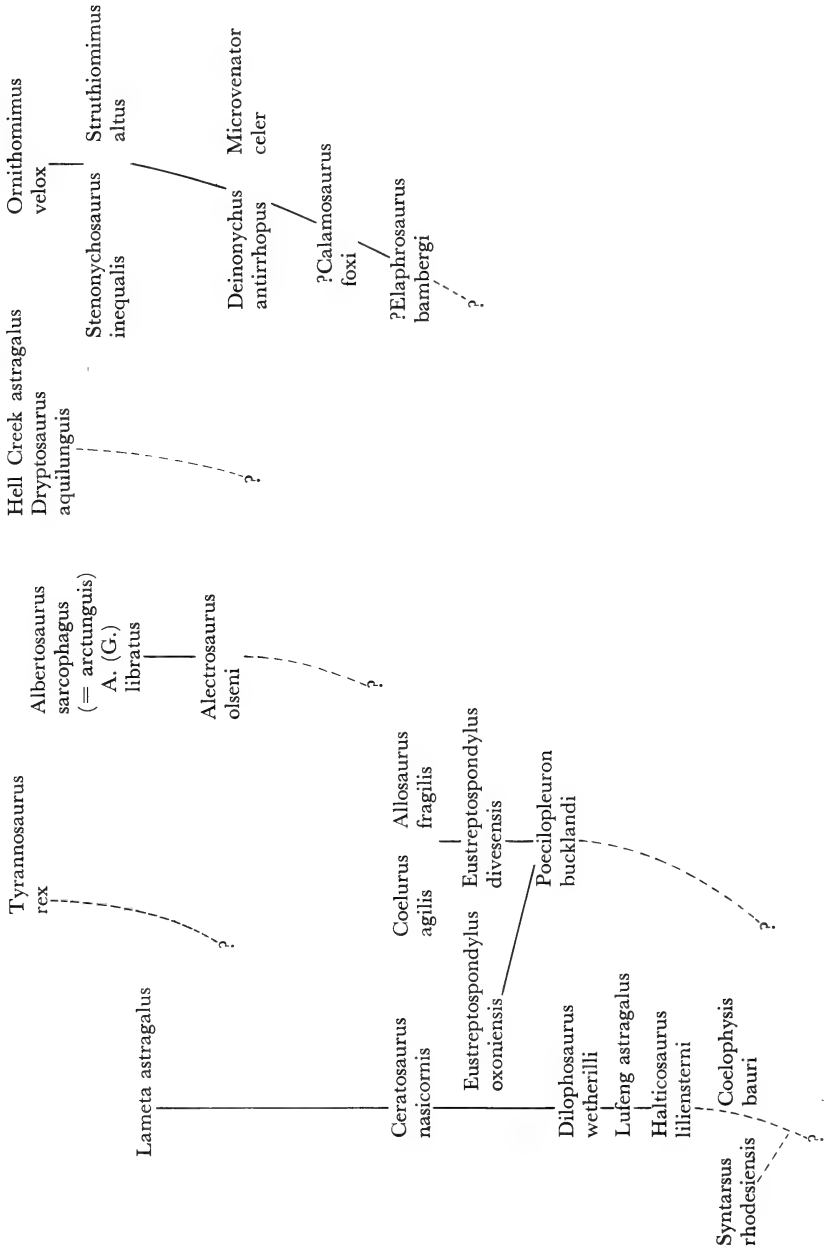


Table of indices and measurements of theropod tarsi

	H:B index from straight line across bottom of astragalus	H:B index including calcaneum	Dip of medial edge of dorsal process	Breadth of astragalus in mm.	Breadth of astragalus plus calcaneum in mm.
Tyrannosaurus rex	86	—	10	372	—
Hell Creek LACM	—	—	—	196	—
Ornithomimus velox	154	123	60	52	65
Albertosaurus sarcophagus (Dryptosaurus incrassatus, cfd.)	97	—	52	248	—
Albertosaurus sarcophagus, cfd. (A. arctunguis)	123	—	—	216	265
Struthiomimus altus Lamb 1902	174	154	—	129	146
Albertosaurus libratus (Gorgosaurus 1.)	148	128	67	212	246
Alectrosaurus olseni	150	129	55	120	141
Deinonychus antirrhopus	142	129	72	59	65
Microvenator celer	190	—	75	22,3	—
Calamosaurus foxi estimated	132	—	—	25	—
Coelurus agilis	78	—	—	74	—
Allosaurus fragilis cast	87	77	50	185	208
A. f. juv. cast	104	93	—	98	110
Ceratosaurus nasicornis, type	—	46	35	—	130
C. n., type, left, YPM	—	45	—	—	118
C. ?n. UUVP 5682	—	49	—	—	147
C. ?n. UUVP 5681	—	42	—	—	175
Elaphrosaurus bambergi	—	100	—	88	—
?Eustreptospondylus Dives. Cuvier's	86	—	38	120	—
Eustreptospondylus oxoniensis	71	—	32	87	—
Poecilopleuron bucklandi	75	—	60	148	—
Dilophosaurus wetherilli UCMP 37302	77	61	27	91	—
D. w., cfd. UCMP 37303 estimated	58	48	20	—	114
Lufeng astragalus	—	53	18	—	157
Halticosaurus liliensterni	65	53	11	65	79
Syntarsus rhodesiensis	—	49	12	—	20
'Coelurosaur' Bonaparte est.	60	60	—	15	15
Coelophysis bauri	—	65	20	—	23

acting from this base. It functions by lifting the lower leg and foot, swinging them forward in a nearly horizontal arc centred at the acetabulum, or even farther inward if there is a concomitant sigmoid flexion of the vertebrae. This plants the foot in a forward position. Next there is a transfer of part of the

body weight to this new base and its epipodial pillar. Then follows a horizontal rotation of the femur about the knee, atop the more or less fixed epipodials, which moves the acetabulum forward. At the same time the body weight is held above the ground, or at least lifted enough to be slid forward. The mechanics are first to lift and swing the epipodium and foot forward, then to reverse the forces and lift the body on this new fulcrum and propel the body forward.

As described by Schaeffer (1941: 412) in the salamanders, the propulsion phase begins immediately on the contact of the plantar surface of the foot with the ground. The recovery phase starts with the dorsal surface of the foot turning laterally into a vertical position. The crus is carried forward as an extension of the femur until just in front of a position at right angles to the body. The last movements involve a flexion of the knee, the extension of the foot and its rotation into a horizontal plane. This kind of limb movement, Schaeffer noted, was probably used by the smaller primitive amphibians. He went on to point out that Gregory & Camp (1918) had described the Permian reptile knee as permanently bent, and he thought that the heavier labyrinthodonts must have had similarly permanently flexed knees.

Broom (1921) presented the first general review of the reptilian tarsus, tracing it from the early Permian labyrinthodont *Trematops milleri* up into the therapsid reptiles. While he did include some other reptiles, he did not discuss the thecodonts or the dinosaurs. He noted Gegenbaur's pioneer work and used his terminology.

Schaeffer (1941) also began with the tarsus of *Trematops*. From this he derived that represented by the early Permian cotylosaur *Labidosaurus*, and this became the ancestral pattern for later tetrapods. He found these later forms to have three divergent kinds of tarsi. His type I is a retention of the primitive pattern or its modification into an aquatic paddle as seen in the marine reptiles. The movement is originally infratarsal. Type II developed a mesotarsal joint with various specializations. Here the astragalus and calcaneum are functionally part of the epipodium, except in the crocodiles and most thecodonts. This joint developed in the Chelonia and, independently, in the lines leading from the Eosuchia, although not present in the Eosuchia themselves. In this type the distal tarsals become reduced. Type III is that leading to the epitarsal joint of the pelycosaur, therapsids, and mammals.

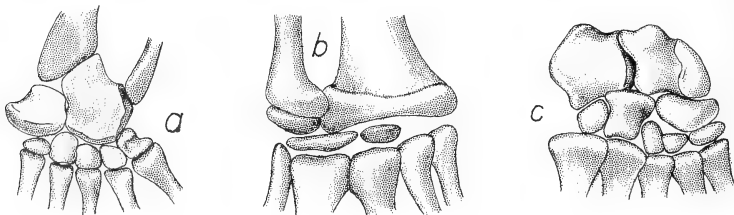


Fig. 1. Reptilian tarsi.

a, type I, *Mesosaurus*; b, type II, *Plateosaurus*; c, type III, *Youngina*. Modified from Schaeffer 1941, fig. 11, not to scale.

Schaeffer's type II is, of course, the one that interests us. He wrote (p. 446), 'the final stage in the perfection of the mesotarsal joint is found in the Saurischia, Ornithischia, Aves, and Pterosauria'. Here the astragalus and calcaneum have become depressed and the distal tarsalia are reduced to two or three. The astragalus and calcaneum may become fused, and are attached to the tibia and fibula. The distal surfaces of the astragalus and calcaneum become rounded into a transverse hemicylinder. At the same time the femur develops a medial head and the tibia becomes the prominent weight-bearer, with the fibula much reduced. In the theropods the tibia develops a distal lateral flange that extends behind the fibula. It also develops a sulcus on the anterolateral distal face, into which fits the ascending process of the astragalus.

Since the publication of Schaeffer's work evidence has accumulated to indicate that there are at least two basic kinds of tarsi in the archosaurs. The first is the crocodyloid tarsus with its intertarsal movement, having the astragalus locked to the tibia and the calcaneum locked to the pes. Movement between the astragalus and calcaneum is rotation about a horizontal axis. The second kind has both astragalus and calcaneum locked to the epipodials, or at least moving with them, and the movement is a hinge below these proximal tarsals. We can therefore expand Schaeffer's classification to include II A, the crocodyloid tarsus, and II B, the dinosauroid tarsus.

THE PIVOT TARSUS OF THE CROCODYLOIDS

The crocodyloid tarsus probably had as its ancestral stages those of the amphibians, cotylosaurs, and eosuchians. The movement was originally one of flexion, but later, in the thecodonts developed into a pivot, a rotation of the crus on or through the tarsus as the body moved forward. Some of this rotation was absorbed in the knee but much or most of it involved the crurotarsal joint. This pivot joint is found in such crawling forms as aetosaurs and crocodylians where the tibia can rotate upon the astragalus. Especially in the aetosaurs, this resulted in spiral articular surfaces between the two bones. This prohibited any hinge motion between tibia and astragalus and caused them to act as a unit so that the hinge developed between the astragalus and the distal tarsals on the inside, and the fibula and the calcaneum on the outside.

The astragalus in this foot was so named as early as Cuvier (1836, 9:207). Gegenbaur (1864: 88) first demonstrated that the bone was a composite of tibiale, intermedium and centrale, based on his embryological studies. Rabl (1910: 242) also found it to originate in three embryonic centres and so called it the 'tritibiale'. This was later beautifully demonstrated in the cotylosaur *Captorhinus* by Peabody (1951: 340). Steiner, however, (1934, *vide* Krebs, 1963: 92) derived the astragalus from four embryonic centres representing the intermedium, proximal centrale, distal tibial centrale, and tibiale. Gegenbaur (1864: 92) noted the unique character of the crocodile foot and wrote 'Der Calcaneus bewegt sich mit dem Unterschenkel fester verbundene Astragalo-

Scaphoideum nur mit dem Unterschenkel sich bewegt'. He named this kind of joint, with the movement between the astragalus and calcaneum 'intertarsal' (p. 93). Schaeffer (1941: 442) considered the crocodyloid tarsus unique, yet noted the similarity between that of *Protosuchus* and *Aetosaurus*. He analysed the motion as a 45° rotation of calcaneum on astragalus, the latter immobile and functionally united with the crus, while the calcaneum moved as a part of the foot.

This crocodyloid intertarsal joint is widespread among the thecodonts. Ewer (1965: 426) described an ideal pre-crocodyloid ankle in the Olenekian *Euparkeria* and demonstrated that its astragalus functions as a unit with the tibia, while the calcaneum is attached to and works with the foot. This is the same crocodyloid structure that was described by Gegenbaur (1864: 92) in the crocodile but is more primitive in lacking the peg-and-socket joint between astragalus and calcaneum that is found in the crocodiles. Although Ewer considered *Euparkeria* to be the earliest example of such a tarsus, a calcaneum was referred to *Wangisuchus tzeyii* Young (1964: 179, fig. 60 A) which has a well-defined astragalar sulcus, head, and tuber. This is from the Ehrmayng Series (Olenekian), the same age as *Euparkeria*, but has a more advanced, truly crocodyloid structure.

A possible mechanical explanation for the retention of this peculiar tarsus in the living crocodiles is that these reptiles have two distinct gaits. In the slow gait the animal crawls with the body close to the ground. The femur is horizontal and a certain amount of rotation of tibia on astragalus is required. Also, the fibula must be free to rotate on the calcaneum, which explains the ball-on-ball articulation between the two bones. In the fast gait the body is held high off the ground, the femur moves in a plane that dips about 60° laterally, and the astragalus is locked to the tibia. The movement then becomes entirely hinge, or dorsoflexion, between the metatarsals and the unit composed of tarsalia, astragalus and tibia on the inside, and the calcaneum and fibula on the outside.

THE HINGE TARSUS OF THE DINOSAURS

The dinosaur tarsus with its mesotarsal hinge is very different from the tarsus discussed above. Krebs (1963: 91), Ewer (1965: 426), and Bonaparte (1969: 474) each maintained, and we agree, that the mesotarsal joint cannot be derived from the intertarsal joint. Furthermore, as noted by Bonaparte, the twisted tibia of the Triassic dinosaurs is very different from the straight tibia of the pseudosuchians. Attridge (in Bonaparte) pointed out the association of the twisted tibia with this mesotarsal dinosaur articulation. Present evidence indicates an entirely separate origin for the dinosaur mesotarsal hinge.

The mesotarsal joint is also correlated with an inturned head of the femur and with the femur moving in a nearly vertical plane. The mesotarsal joint limits the movement to a parasagittal plane and is an adaptation to bipedal locomotion. However, bipedal locomotion may also develop in the crocodyloid

tarsus, as in *Saltopus*. Furthermore, Dr Alan Leviton of the California Academy of Sciences informs us that several of the desert lizards, including *Callisaurus* and *Crotaphytus* can run bipedally with the femur in a vertical plane and the feet under the body. This is to say that although the mesotarsal joint is a bipedal adaptation, bipedalism may also develop in reptiles with other kinds of tarsi.

The earliest of the mesotarsal ankles are in the two ?Anisic genera *Lagerpeton* and *Lagosuchus* described by Romer (1971, 1972). *Lagerpeton* has a short astragalus, fused to the calcaneum, and with a dorsal process up the posterior side of the tibia. This is a unique arrangement among dinosaurs, for in all other known forms the dorsal process develops up the anterior face of the tibia. The question naturally arises as to whether *Lagerpeton* can truly be included in the dinosaurs. *Lagosuchus* has a quite different tarsus in that the astragalocalcaneum is much longer, there is no dorsal process, and there is a small posterior spur on the calcaneum. These two reptiles are quite different from each other and neither shows any direct relationship to later archosaurs.

Our studies indicate that the theropod tarsi can be grouped into five rather distinct kinds:

1. Ceratosauroid—the astragalus with a low dorsal process that is sunk into the tibia, and a large calcaneum that is closely applied to or fused with the astragalus. Late Triassic to late Cretaceous. *Ceratosauros*, *Coelophysis*, *Dilophosaurus*, *Halticosaurus*, Lameta astragalus, Lufeng astragalus, *Syntarsus*.
2. Allosauroid—the astragalus with a moderately high dorsal process that is set into the anterior face of the tibia and yet has a free horizontal medial component. The medial condyle is large and the medial end rounded. A deep upper horizontal groove develops at the anterior base of the dorsal process and a deep lower horizontal groove across the face of the condyles. The calcaneum is free and large, and in *Allosaurus* develops a medial tongue and two pits to fit the astragalus. Middle Jurassic to late Jurassic. *Allosaurus*, *Coelurus*, *Eustreptospondylus*, '*Megalosaurus bucklandi*', Phillips, *Poecilopleuron*.
3. Albertosauroid—the astragalus with a high dorsal process that is applied to the entire anterior and anterolateral faces of the tibia. A deep upper horizontal groove develops above the condyles. This is interrupted laterally by a ventrolateral buttress to the lateral condyle. The condylar surface does not develop the lower horizontal groove. The calcaneum is reduced and free from the astragalus. Late Cretaceous. *Albertosaurus*, *Alectrosaurus*, *Dryptosaurus*, Hell Creek astragalus.
4. Ornithomimid—the astragalus with an extremely high dorsal process that is applied to the entire anterior face of the tibia. The calcaneum is reduced or absent. Late Jurassic to late Cretaceous. ?*Calamosaurus*, *Elaphrosaurus*, *Microvenator*, *Ornithomimus*, *Stenonychosaurus*, *Struthiomimus*.
5. Tyrannosauroid—the astragalus with a high, wide dorsal process. The upper horizontal groove shallow and restricted to the medial half. No lower horizontal groove, but a large oval foramen in the centre of the anteroventral condylar face. The medial condyle high, its dorsal border sloping steeply ventromedially; the lateral condyle weakly developed.

These five kinds of tarsi will be described in the following paragraphs.

THE CERATOSAUROID TARSUS

Coelophysis bauri from the upper Chinle Formation of New Mexico, was previously thought to have an astragalocalcaneum without a dorsal process, but preparation of the tarsus at the American Museum of Natural History (block 5) has revealed a well-developed dorsal process on the astragalus. This

was not known to Dr E. H. Colbert and so was not indicated in the figure published by Raath (1969, fig. 6d) on information from Colbert. Dr Colbert is preparing a monograph on *Coelophysis* but he has kindly consented to our advance publication of this information. This astragalocalcaneum is skewed anterointernally, has a maximum breadth of 23 mm anteriorly and 22 mm posteriorly. It is 11 mm long internally and 12 mm externally. The dorsal process is 15 mm high above the plane of the distal condyles, yielding an H:B

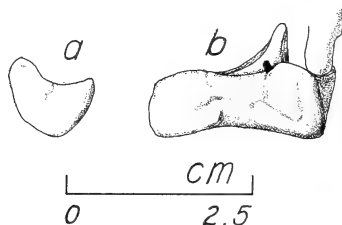


Fig. 2. *Coelophysis bauri*. a, internal view, dorsal process not shown; b, anterior view, of left astragalocalcaneum and distal end of fibula. AMNH block 5. $\times 1$.

index of 65. The dorsal process has a bearing surface 3 mm wide that underlies a flange of the tibia, and dips 20° medially. There is a shallow upper horizontal groove across the anterior face separating the condyles from the dorsal process. This groove ends laterally in a notch in the calcaneum. Just above this groove, and 5 mm medial to the fibular edge, a 2 mm foramen marks the opening of a canal which penetrates laterodistally into the bone. The body of the astragalus

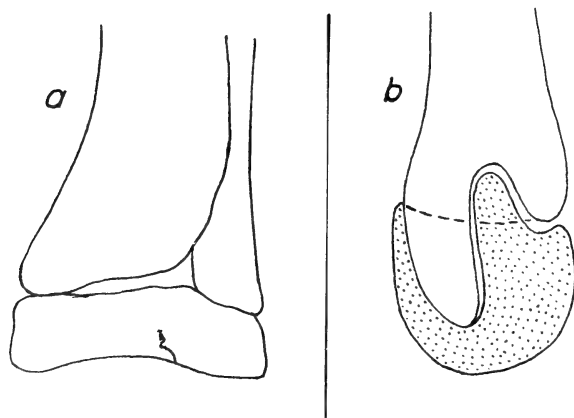


Fig. 3.

Syntarsus rhodesiensis, left tarsus in a, anterior; b, section through centre, anterior to right. From Raath 1969, fig. 6, approximately $\times 1,75$.

is but 4 mm thick laterally below the tibia. Its medial edge slopes 45° posterolaterally. The posterior edge is sharp and rounds upward about 4 mm so that the astragalocalcaneum forms the entire bearing condyle. The calcaneum is fused, is 8 mm deep below the fibula and forms the lateral part of the condyle.

Syntarsus rhodesiensis Raath, 1969, from near the top of the Forest Sandstone of Rhodesia (equivalent to the upper Red Beds of the Stormberg Series, of Norian age), is a small theropod with an astragalocalcaneum but 20 mm wide and 9.7 mm high, an H:B index of 49. This is a very low, almost incipient dorsal process, the slope of its medial surface but 12° . However, the cross section of the right tarsus given by Raath shows that the ascending process continues up into the tibia and is covered anteriorly by an overlap of the tibia. The true H:B index is therefore somewhat greater than 49. The general structure of this tarsus, with its low, deeply set dorsal process seems to us to be ceratosauroid, although it should be noted that Galton (1971: 788) considers the ankle to be 'typically sauropodomorph'.

Young (1951: 75, fig. 15) describes a theropod astragalocalcaneum (no. V 73) from the Dark Red Beds of Haungchiatien, the uppermost beds of the Lower Lufeng Series, generally considered to be upper Norian to Rhaetic. This is a gigantic bone, 157 mm broad, with a total height of 84 mm, an H:B index of 53. The slope of the dorsal process is 18° and it begins at the lateral

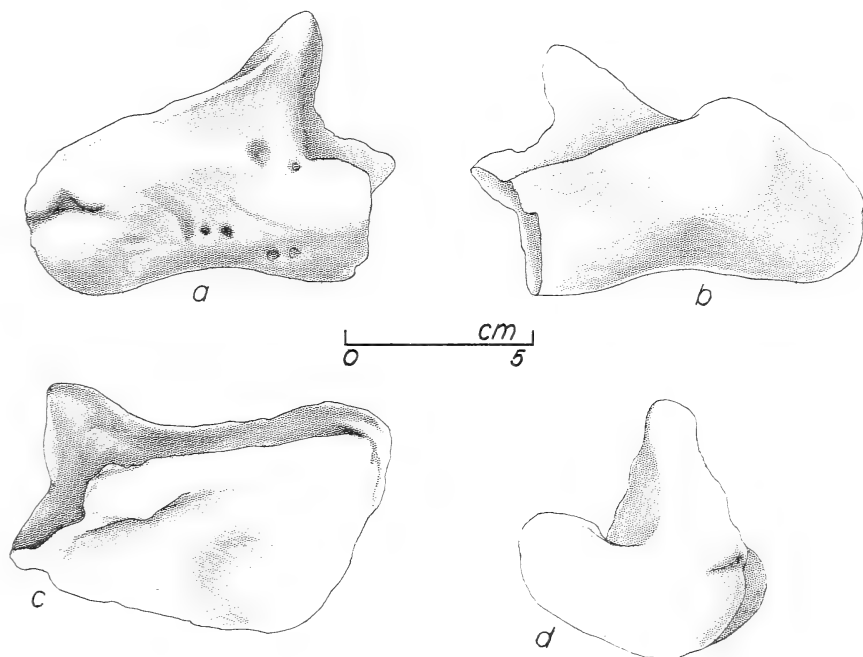


Fig. 4. Ceratosauroid from Lufeng Beds.

Left astragalocalcaneum in a, anterior; b, posterior; c, dorsal; d, medial views. From Young 1951, fig. 15. $\times \frac{1}{4}$.

border and is almost straight. The fusion of the two bones and the medial extent of the dorsal process are not allosauroid but are similar to *Dilophosaurus* and *Ceratosaurus*.

Halticosaurus liliensteri (Knollenmergel, Norian, of Thuringia) has a primitive astragalus, with the calcaneum solidly fused into an astragalocalcaneum. The two bones are 79 mm wide anteriorly, the astragalus 65 mm. The dorsal process is 42 mm high and dips medially 11° , the H:B index is 65. The dorsal

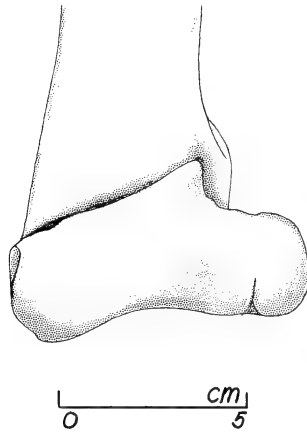


Fig. 5. *Halticosaurus liliensteri*, type.
Anterior view of left astragalus and distal end of tibia.
 $\times \frac{1}{2}$.

process is thick (16 mm) and in lateral view the entire element, including the dorsal process, is almost circular, measuring 46 mm anteroposteriorly.

The type of *Dilophosaurus wetherilli* (UCMP 37302) has an astragalus 91 mm broad anteriorly and but 76 mm broad posteriorly. In anterior view the dorsal process is 70 mm high above a straight line across the base (H:B index 76), 14 mm thick at mid-height, and shows little if any bearing surface. It begins at the median border and rises in a uniform slope of 16° to about 20 mm from the summit where the slope increases to give a total slope of 27° . The anterior condylar surface is concave transversely, and rounds below into a medial condyle and a lateral condyle that continues onto the calcaneum. There is a slight transverse groove in the centre of the rounded medial edge. The anterodorsal border of this surface projects forward and is separated from the dorsal process by a broad upper horizontal groove that deepens laterally and terminates at the fibular socket. The rounded anterolateral projection of the astragalus forms the anterior border of the fibular socket. About half of this socket is in the astragalus. A rounded buttress runs down the anterolateral corner of the dorsal process and extends onto the anterolateral projection of the lateral condyle. In dorsal view the sulcus for the tibia runs posterolaterally,

and a small boss in the posterior border, towards the medial edge, fits into a socket in the tibia. The tibial sulcus does not extend behind that for the fibula, as it does in *Allosaurus*, indicating that the distal end of the tibia lacks the great

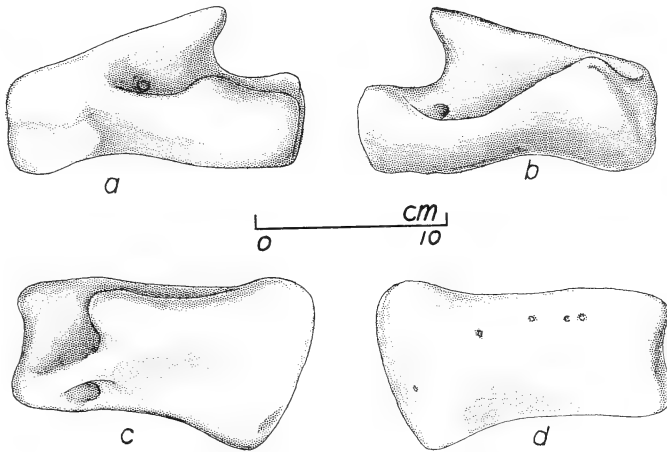


Fig. 6. *Dilophosaurus wetherilli*, type.

Left astragalus in a, anterior; b, posterior; c, dorsal; d, ventral views. UCMP 37302. $\times \frac{1}{2}$.

lateral expansion of the latter, as is shown by the tibia itself. The socket for the fibula is 17 mm broad in front and wedges out posteriorly, its bearing surface increasingly taken over by the calcaneum. In medial view the bone is very thick beneath the tibia, contrasting strongly with the thin bone of *Allosaurus*. In posterior view the lateral edge is sharp, but it thickens medially to form a posteromedial knob. A sharp ridge runs down posterolaterally from the dorsal process to project above and behind the calcaneum, and to divide the tibial sulcus from that for the fibula. There is a pit near the base of the dorsal process, probably for ligaments binding the astragalus to the tibia. The medial surface of the dorsal tip of the dorsal process is a flattened surface 14 mm wide that faces toward the anteromedial corner. The ventral surface of the astragalus is saddle-shaped, convex anteroposteriorly and concave laterally. It forms a lateral and a medial condyle, constricted between. Its lateral and medial edges converge posteriorly, the former sharp and forming a straight suture with the calcaneum. The medial edge is rounded. In lateral view the socket for the fibula is 30 mm above the distal end, 10 mm higher than that for the tibia. The surface for the calcaneum is subcrescentic, slightly concave, with a triangular projection overhanging the calcaneum near the posterior edge.

The isolated right tarsus of another specimen (UCMP 37303) also from the base of Kayenta Formation of Arizona (late Triassic or early Jurassic) has the calcaneum solidly in place and the total breadth is estimated to be 114 mm. The dorsal process has been crushed down somewhat by the anterolateral shoulder of the tibia and it is but 55 mm high, an H:B index of 48.

In the right tarsus of the type of *Ceratosaurus nasicornis*, from the late Jurassic

Morrison Formation of Colorado USNM 4735 *vide* Gilmore (1920: 111, fig. 65) the two proximal tarsalia are fused into an astragalocalcaneum and the dorsal process of the astragalus is quite restricted. In anterior view the dorsomedial border slopes upward rather regularly from the inner base instead of beginning part way laterally as in *Allosaurus*—a difference noted by Gilmore. There is a triangular area above the lateral border of the astragalus and below the tibia and fibula which does not seem to have been filled by the dorsal process. This triangle is evident on the right and left type tarsi and also on two others at the University of Utah. This area seems to be ossified differently from the rest of the bone and could possibly have been occupied by calcified cartilage. The lateral end of the tightly fused calcaneum is deeply concave. The left tibia and astragalocalcaneum of this same individual, YPM 4681, has a breadth of 118 mm and an H:B index of 45, and is similar to

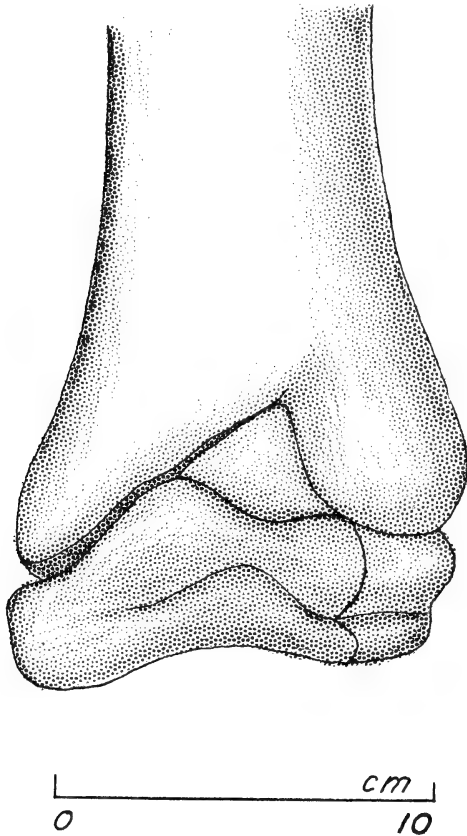


Fig. 7. *Ceratosaurus nasicornis*, type.
Anterior view of left astragalocalcaneum and distal end of tibia, YPM 4681. The rest of this skeleton is at the United States National Museum. $\times \frac{1}{2}$.

that of the left side. On both right and left the suture between astragalus and calcaneum is visible on the anterior face.

A fine right tibia and tarsus at the University of Utah (UUVP 5682), referable to the genus *Ceratosaurus*, if not the type species, has a breadth of 147 mm and an H:B index of 49. A second associated specimen (UUVP 5681), the largest known, has a breadth of 175 mm and an H:B index of 42.

Huene (1933: 56, pl. 19, fig. 1) describes an astragalus that he identifies as allosaurid, from the Lameta beds (Turonian) of Jubbulpore. This astragalus (K27/684) is incomplete medially and is described as thick laterally and very thin, almost platelike in all other parts. It is 50 mm anteroposteriorly, with the dorsal process 20 mm high and 30 mm broad. It is 'twisted in the direction of the transverse axis'. Huene gives no reasons for identifying this as allosaurid and his illustrations do not support his view. His 'dorsal view', fig. 1a, is, with the tibia vertical, evidently posterodorsal with the dorsal process down. The ligamentary pit is near the base of the dorsal process. Figure 1b, an anterior view, shows a low dorsal process with an external vertical ridge curving ventromedially from the summit. The lateral face of the tibial sulcus rises into a high wall behind the sulcus. The lateral view shows a smooth calcaneal face. All of these features contrast with those of the allosauroids and are much more ceratosauroid. An isolated calcaneum is also ceratosauroid in being broad and parallel-sided.

THE ALLOSAUROID TARSUS

Phillips (1871: 214) describes an astragalus as that of *Megalosaurus bucklandi*. It rises upward in a broad flat plate which fits in a well-defined hollow in the flattened anterior face of the tibia. Its lateral extension toward the fibula is cut off by a nearly vertical surface for the calcaneum. Phillips makes no mention of an interdigitation of calcaneus and astragalus, but the dorsal process and bulbous medial condyle are of the general allosauroid pattern. We therefore consider this a possible early allosauroid pending further investigation. It is presumably from the Oxford Clay.

Deslongchamps (1838, pl. 6, fig. 12) described and illustrated the astragalus of his *Poecilopleuron bucklandi*. This specimen was formerly at Caen but Dr Donald Russell informs us that it was destroyed during the war. It came from Vesulian or Lower Bathonian rocks, approximately equivalent to the Stonesfield deposits. The astragalus is large, its breadth 148 mm and the H:B index is 75. The medial edge of the dorsal process begins rather far laterally, and slopes upward at about 60°. The medial half is low, the condyle gently convex transversely. The lateral face for the calcaneum is concave dorsoventrally and is much the thickest part of the body. The astragalus is advanced in the height of the dorsal process and its lateral restriction. The shape and position of the dorsal process, and the free medial condyle, are allosauroid but there does not seem to have been any interdigitation of astragalus and calcaneum. It could be a primitive representative of this group.

Eustreptospondylus oxoniensis Walker, 1964 (UMOJ 13558), is from the Middle Oxford Clay (Upper Callovian) of Wolverton, southern England. The astragalus is separate from the calcaneum and measures 87 mm broad and 62 mm high, an H:B index of 7.1. The right astragalus

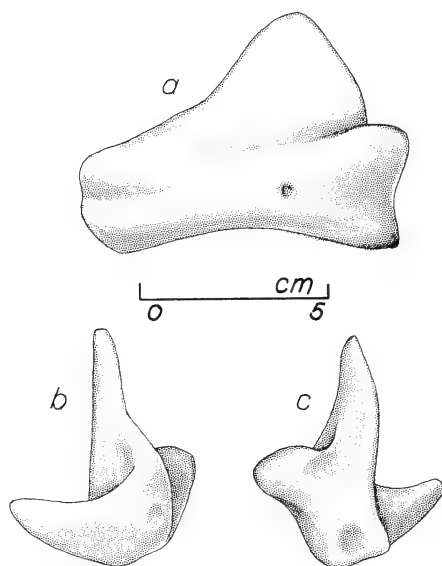


Fig. 8. *Eustreptospondylus oxoniensis*, type.
Right astragalus (reversed to left) in a, anterior;
b, medial; c, lateral views. $\times \frac{1}{2}$.

was sketched by Huene (1926, fig. 36) and he also illustrated the separate calcaneum, since lost. A detailed drawing sent us by Mr H. P. Powell allows us to make a more complete description. It has a breadth of 87 mm and a height of 62 mm, an H:B index of 7.1. The anterior view shows a 33° slope of the medial edge of the dorsal process. This edge is concave and slopes but 26° at the base. It has a long, low, rounded medial condyle and a fairly sharp ventrolateral border of the lateral condyle. The dorsal edge of the calcaneal border is set forward of the dorsal process and has a rounded dorsolateral projection. The dorsal process is separated from the anterior surface by an upper horizontal groove that fades out medially. There is no deep pit for a process of the calcaneum as in *Allosaurus*, but there is a concave edge for the calcaneum. A slight lower horizontal groove runs about a quarter of the way inward from the centre of the medial condyle. The lateral view shows a high calcaneal facet with the upper horizontal groove at the base of the dorsal process separating the rounded anterodorsal projection. The posterior foot below the tibia is bluntly rounded behind and becomes longer anteroposteriorly on the inner side. The striking features of this view are the strong posterodorsal projection above the lateral condyle and the upper horizontal groove above and behind it.

The medial view shows a rather thick (high) medial condyle that is 43 mm anteroposteriorly on the right astragalus and 48 mm on the left. The foot is rounded posteriorly. The general shape of the dorsal process and its upper horizontal groove, and the bulbous medial condyle are allosauroid, but the deep interdigitation of the astragalus and calcaneum found in *Allosaurus* has not developed.

The famous Honfleur specimen described by Cuvier (1836, 10:204, pl. 249, figs 34–36) in his 4th edition, and probably earlier, was stated to have come from one of the two blue marls above the Caen stone. Huene (1926: 38) places the horizon as Upper Callovian. It consists of the right astragalus and the distal end of the tibia. The taxonomic problems arising out of this and the other Honfleur material are very difficult and need not concern us here, but Walker (1964: 122) reviewed them and referred this specimen to his *Eustreptospondylus divesensis*. Cuvier's original description was inadequate for our comparisons, and he used a different orientation. The specimen was well illustrated by Piveteau (1923: 9, pl. 4, figs 4, 5). One of us (Welles) was privileged to examine this specimen at Paris and noted that the tibia had a sharp bend in the supra-astragal shelf and no real bearing surface. The astragalus had a breadth of 115 mm and a height of 94 mm, a H:B index of 82. In anterior view the dorsal process is evidently nearly entire, its tip of 2 mm finished in plaster, and is broad and rounded above. Its inner edge is concave, the slope 30°. The upper horizontal groove is very weak, present laterally but fading out medially, and there is a strong dorsolateral process above the lateral condyle, widely separate from the dorsal process. The lower horizontal groove is very poorly developed. In dorsal view the sulcus for the tibia is very narrow laterally and there is no development of a projection to insert in the tibia. In lateral view the calcaneal facet is a vertical oval with a fibular sulcus 41 mm above the base. In posterior view the posterior edge is sharp laterally but thickens medially. In general features this astragalus is allosauroid, but much more primitive than *Allosaurus*. In addition to the astragalus, Cuvier (pl. 249, fig. 38) illustrates a bone that he identifies as a tarsal bone. This is evidently an allosauroid calcaneum in that it has a central projection below the fibular facet. There is no proof that the two bones are from the same individual, but if they are, this is the earliest known occurrence of the pattern found in *Allosaurus*, consisting of separate though interlocked astragalus and calcaneum.

An astragalus at Yale (YPM 1252) from the Morrison Formation at Como Bluff is possibly referable to *Coelurus agilis*. In anterior view it is 74 mm broad and 58 mm high, an H:B index of 78. It has a vertical lateral base to the dorsal process and an inner border that slopes about 68°. The dorsal process is confined to the lateral half and there is a broad upper horizontal groove at the lateral base of the dorsal process. This groove separates a posterodorsal projection of the lateral condyle from the dorsal process. The posterior face shows a ligamentary pit at the centre of the base of the dorsal process. The body is deepest medially, about the same depth below the ligamentary pit, and thinnest

laterally. The sulcus for the distal end of the tibia is divided into halves, the inner half sloping slightly medially (3°) and the lateral half rather steeply (10°) laterally. All of these features are of a general allosauroid nature.

A cast of a large specimen of *Allosaurus fragilis* from the Upper Morrison Formation of central Utah sent us by Professor James H. Madsen, Jr., of the University of Utah, has a maximum breadth of 185 mm along the anteroventral border, a posterior breadth of 160 mm, and a height of 160 mm. The H:B index is 87. (The specimen illustrated by Gilmore (1920, fig. 50, USNM 7336) has a breadth of 200 mm and a height of 170 mm, an H:B index of 85.) In anterior view the dorsal process begins 67 mm lateral to the inner edge and rises at a steep slope (53°) to the summit. This slope is interrupted by a dorsal bulge near the top. A strip along the lateral border, its widest part

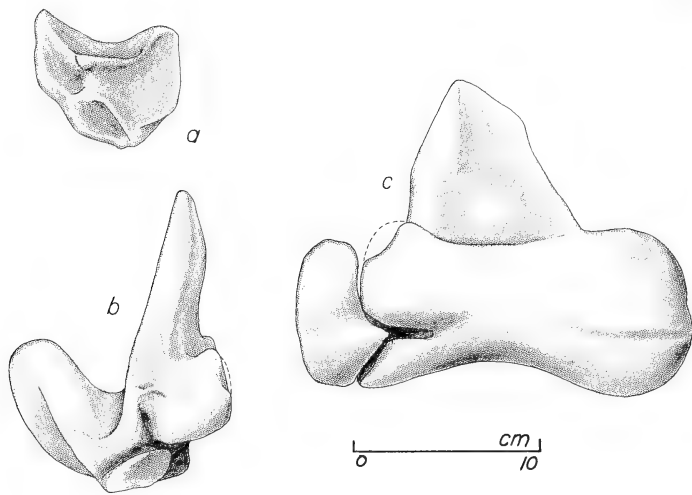


Fig. 9. *Allosaurus fragilis*, cast of right astragalus and calcaneum from University of Utah.
a, internal view of calcaneum; b, lateral view of astragalus; c, anterior view of both. $\times \frac{1}{4}$.

30 mm, is set at an angle of 35° to the anterior face, and forms a plane surface for the fibula. The upper horizontal groove, along the base of the dorsal process, is deep and rounds posterolaterally into the sulcus for the fibula. This groove is deepest laterally and ends medially at the base of the dorsal process. The dorsal process is broad, flat, and thin, extending laterally and not excavated by the fibular socket. The lower horizontal groove is pronounced and extends laterally for half the width of the astragalus. The lateral edge, against the calcaneum, has a deep notch that received a point of the calcaneum. In posterior view the ligament pit at the base of the dorsal process is large and deep. The lateral half forms a fairly thin (20 mm) floor below the tibial sulcus and has a sharp posterior edge. The medial half thickens, both upward and downward, to form a bulbous medial condyle rising 70 mm above the base. Behind this

condyle the floor of the tibial sulcus is 42 mm thick. This floor is obscured by the upturned posterior edge, but the medial 70 mm makes an angle of 17° with the outer 110 mm. In dorsal view the sulcus for the distal end of the tibia is 83 mm broad medially and but 32 mm broad laterally. In lateral view the socket for the distal end of the fibula is set into the astragalus between the dorsal process and the anterodorsal knob above the lateral condyle. This inset is a continuation of the upper horizontal groove. Below and behind the fibular sulcus is a complex notch for the calcaneum, and although not fused, the two bones are deeply interlocked. In addition to the deep notch in the centre of the astragalus below the fibular socket there are two rounded processes which project into sockets in the calcaneum. One of these processes is anterodorsal, the other ventral, and this complex interdigitation of the notch and two processes prevents any movement between astragalus and calcaneum. The socket for the fibula is high above that for the tibia. (A specimen illustrated by Gilmore (1920, fig. 48, USNM 4734) is pathologic in having a crushed, and evidently healed, distal end of the fibula that lowered the calcaneum about half its height. This same specimen was illustrated by Marsh (1896, pl. 11) with the distortion corrected.) In ventral view the astragalus is distinctive in that it narrows laterally to about half of its medial anteroposterior dimension. The medial border is at nearly right angles to the posterior border but makes only a 55° angle with the anterior border. The lateral border is rounded, but the notch for the process of the calcaneum is evident.

The calcaneum of *Allosaurus* has its medial face modified to match the astragalus. There is a central projection that carries the floor of the fibular socket into the astragalus. Anteroventral to this is a socket that receives the anterodorsal projection of the astragalus, and posteroventral to this is another socket facing ventromedially, below and anteromedial to the tibial sulcus. This socket receives the ventral projection of the astragalus. The posteromedial face of the calcaneum is a concave semilunar sulcus for the lateral edge of the tibia. The lateral face is also semilunar with its upper concavity forming the outer rim of the fibular socket. The calcaneum is larger than in ornithomimoids or albertosauroids, but smaller than in ceratosauroids.

Another *Allosaurus* astragalus cast, representing a small, immature individual, was also sent to us by Professor James J. Madsen, Jr. This specimen is particularly interesting in that it has an H:B index of 104, much greater than the 87 of the large cast. The dorsal process also differs from the adult in that the inner edge begins to slope up gently at 22° from the inner border, then, about half-way out the dip increases gradually to about 72° .

THE ALBERTOSAUROID TARSUS

Gilmore (1933: 38, fig. 10) describes the astragalus and calcaneum of *Alectrosaurus olseni* from the Iren Dabasu Formation (Cenomanian) of Mongolia. This is his second specimen, AMNH 6554. Gilmore designated this and the fore limb from 30.5 m away (AMNH 6368) cotypes yet treated them as repre-

senting two individuals. To avoid confusion we here designate this specimen, AMNH 6554, the type of the species. The fore limb therefore becomes a referred specimen. The tibia and tarsus were seen by Gilmore to be closest to *Albertosaurus libratus* (which he called *Gorgosaurus sternbergi*). He also noted the difference in the proportion of the dorsal process of the astragalus in the two species, rising $\frac{1}{3}$ of the height of the tibia plus astragalus in *A. libratus* while it is $\frac{1}{4}$ in *Alectrosaurus olseni*. The height of the astragalus is given as 180 mm and measurements taken from the illustration give an estimated breadth of 120 mm, an H:B index of 150. The medial edge of this specimen is missing but enough is present to show the deep upper horizontal groove. The lateral part shows a slight ventrolateral buttress against the lateral condyle, weaker than in *Albertosaurus arctunguis*, but stronger than in *A. sarcophagus*. The calcaneum is more strongly developed and has a higher anteromedial process than in *A. arctunguis*.

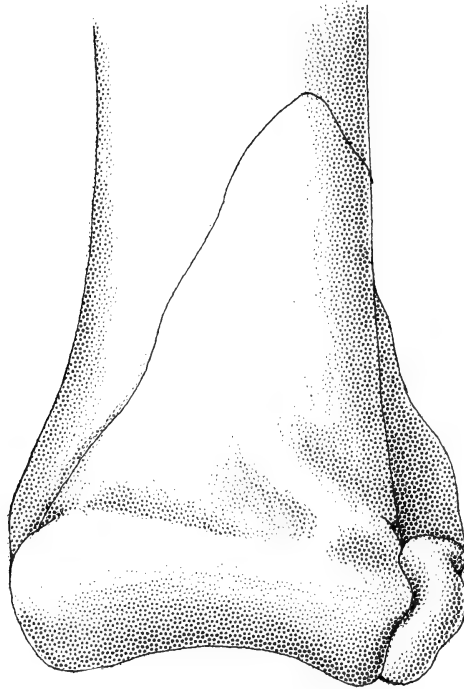


Fig. 10. *Albertosaurus libratus*, type.

Anterior view of left tarsus and distal end of tibia, from Lambe 1917, fig. 42.

$\times \frac{1}{4}$.

Lambe (1917: 69, fig. 42) described and figured the tibia and tarsus of *Gorgosaurus libratus* from the Belly River Formation (Judith River, Campanian) of Alberta. This was placed in the genus *Albertosaurus* by Russell (1970: 4). The dorsal process of the astragalus is nearly as broad as the base and the inner face of the base is 'flat or only slightly concave'. The dorsal process is set back from the body and separated by a deep upper horizontal groove which is very deep at the centre. The height of the astragalus, taken from the figure, is 314 mm, the breadth 212 mm, an H:B index of 1.48. The laterodistal buttress against the top of the lateral condyle is rather strongly developed, not so pronounced as in *A. sarcophagus*, referred (= *A. arctunguis*), but more so than in either *A. sarcophagus*, referred (= *Dryptosaurus incrassatus*, referred, Lambe 1904) or *Alectrosaurus olseni*. The calcaneum is also intermediate in its stage of reduction between *A. olseni* and *Albertosaurus 'arctunguis'*.

Parks (1928: 29, fig. 12) described the astragalus of *Albertosaurus arctunguis* from the Horseshoe Canyon Formation (Campanian-Maastrichtian) of Alberta. This was placed in synonymy with *A. sarcophagus* by Russell (1970: 4). It has the calcaneum in place, although probably not fused because it is free in the specimen described as *Dryptosaurus incrassatus* (Cope) by Lambe (1904: 20, pl. 6, fig. 6), later referred to *A. sarcophagus* by Osborn (1905: 263). The breadth of the combined astragalus and calcaneum is 265 mm, that of the astragalus 216 mm (from the illustration). Parks notes 'no significant difference between' this astragalus and that ascribed by Lambe to *A. sarcophagus*, except that the dorsal process is a little wider and the body a little thicker. However, a comparison of the two illustrations shows a considerable difference in the shallowness of the body, the deep narrow anterior concavity, and especially the development of the large rounded ventrolateral buttress onto the lateral condyle in *A. arctunguis*. Although the two species have astragali developed on the same basic principles, that of *A. arctunguis* is more specialized.

Lambe (1904: 20, pl. 6, figs 6-8) illustrated and described an astragalus and the distal end of a tibia as *Dryptosaurus incrassatus* (Cope). This was referred to *Albertosaurus sarcophagus* by Osborn (1905: 265), and is from the Horseshoe Canyon Formation (Campanian-Maastrichtian) of Alberta. Russell (1970: 10) identified this as NMC 5601. The breadth is given as 248 mm and an estimate of the height is 241 mm, an H:B index of 0.97. The dorsal process is set laterally about 30 mm, its lateral edge rising steeply at first, then sloping more gently at about 52°. In anterior view this astragalus has a large medial condyle that is 86 mm high. The central constriction is roughened by vertical grooves and ridges. The condylar body is separated from the dorsal process by a deep upper horizontal groove that is deepest in the centre. The surface for the calcaneum is notched anteroventrally and this surface is described as a concave area. The medial and lateral ends of the bone are oblique, a common feature that makes the posterior border narrower than the anterior. The calcaneum is said to have contributed only to the support of the fibula.

Cope (1866: 316; 1870: 105, pl. 9, fig. 3) described the astragalus of his

Laelaps aquilunguis from the Barnsboro marl pits of Gloucester Co., New Jersey. The generic name was preoccupied and Marsh (1877: 88) proposed *Dryptosaurus* to replace it. The horizon is the Greensand Navesink Formation, of Maastrichtian age (Miller 1962: 195). Cope's figures show an astragalus that underlies only the anterior half of the tibia and has a very peculiar dorsal process. This is probably a badly eroded specimen and should be restored along the lines of *Albertosaurus*. This would make the dorsal process at least 50% higher than the breadth of the astragalus. It would make the peculiar opening near the lateral base into the lateral, eroded edge of the upper horizontal groove. The ventral posterior projection below the tibia should be somewhat increased. So restored, the astragalus has a breadth of 184 mm. The ventrolateral buttress does not reach the calcaneal surface and its development is between that of *Albertosaurus libratus* and *A. arctunguis*. The facet for the calcaneum indicates that the calcaneum was nearly as reduced as in the latter species. This, therefore, seems to be an albertosauroid astragalus.

An astragalus from an incomplete skeleton collected in the Hell Creek Formation (Maastrichtian) of Garfield Co., Montana in the Los Angeles County Museum collections (LACM 23849) kindly lent us by Dr Ralph Molnar is badly broken, but the lateral and medial ends are preserved along with the base of the dorsal process. It can be restored with confidence, except for the dorsal process, with a breadth of 196 mm. In anterior view the dorsal process arises 17 mm late-

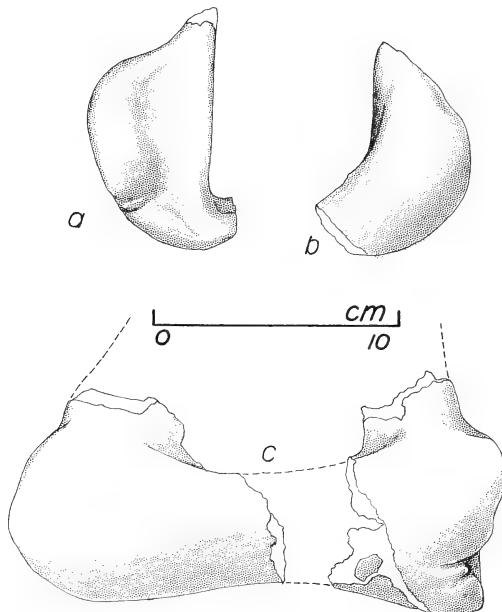


Fig. 11. Albertosauroid astragalus (right, reversed) from the Hell Creek Beds.
a, lateral; b, medial; c, anterior views. LACM 23849. $\times \frac{1}{3}$.

rally from the bulbous medial condyle. The upper horizontal groove at the base of the process is shallow medially and laterally, so was probably not very deep centrally. A 5 mm perforation enters the body of the bone at the lateral end of the groove. The tunnel from this perforation leads ventromedially. The ventrolateral buttress is weak and rounds gently into the lateral condyle. In ventral view the condyles are smoothly rounded and not marked by the lower horizontal groove that in *Allosaurus* separates a distal face from an anterior face. The medial condyle is very large, bulbous, and smoothly rounded, somewhat like that of *Dryptosaurus*, except that the lower posterior edge slants more steeply anterolaterally. The lateral condyle is also round, yet has a flattening of the anteroventral face. The lateral condyle has a narrow cleft near the base, in the same position as that of *Allosaurus*, but very much smaller. No such cleft is evident in *Dryptosaurus*.

THE ORNITHOMIMOID TARSUS

The astragalus of the partial skeleton from the late Jurassic Tendaguru beds referred to *Elaphrosaurus bambergi* by Janensch (1925: 41, pl. 6, fig. 1) is 88 mm broad and 56 mm anteroposteriorly. The condyles are nearly equal and are separated by a gentle constriction. The condylar surface ends posteriorly in a sharp, straight edge. In anterior view the bone is pinched in between the condyles. There is a dorsolateral projection that is separated from the dorsal process by the upper horizontal groove, which runs across the front of the bone. Janensch describes a dorsomedial projection in front of this groove which is a triangular process about 13 mm high. The dorsal process is described as weakly developed and near the medial edge, yet its height is indicated by an 85 mm high sulcus on the anterior face of the tibia. From this we estimate an H:B index of 100. In dorsal view the tibial sulcus is divided by a central rise. Its lateral half narrows and also has a concavity for the fibula. We have not examined this specimen but Janensch's description indicates that it is the only theropod astragalus with a dorsomedial process in front of the upper horizontal groove. Janensch considers the entire bone to be astragalus, yet he describes a suture near the lateral edge which sets off a small dorsally-narrowed surface that he thought must be the calcaneum. If the astragalocalcaneum is shifted to its proper position on the ventral face of the tibia, we find that the lateral part is in the proper position for a calcaneum, and that the resulting calcaneum is rather large. This is considerably advanced over the coelophysoid type and the height of the dorsal process excludes it from the ceratosauroids. It lacks the ventrolateral buttress of the albertosauroids and seems to represent a primitive ornithomimid.

Ostrom (1970: 75, pl. 13, figs D, E) described his *Microvenator celer* from the Cloverly Formation of Montana (Aptian-Albian) as having the astragalus extending the full breadth of the tibia with a small recess for a tiny, chiplike calcaneum. The breadth is 22.3 mm, the height 42.3 mm so the H:B index is 190, the highest known. The dip of the inner margin of the high dorsal process is

75°. This is certainly an advanced tarsus of the ornithomimid pattern, to be expected in a form of Aptian-Albian age.

Stenonychosaurus inequalis Sternberg, from the Judith River Formation was figured by Russell (1969 fig. 11). The tibia and astragalus of the type specimen is broken some 65 mm up the shaft so the dorsal extent of the astragalus is not known. It shows an astragalus very much like that of *Microvenator* but the inner condyle slants more medially and the lateral condyle is more nearly vertical.

Lydekker (1891, pl. 5, fig. 2) described the tibia of a small theropod from the Wealden of the Isle of Wight, BMNH R186. This he referred to *Calamosaurus foxi*. There are no tarsal bones associated with this tibia but the area for articulation of the dorsal process of the astragalus is an acute triangle, indicating a high dorsal process with an estimated H:B index of 132.

Ostrom (1969: 120, fig. 68) described the astragalus and calcaneum of his *Deinonychus antirrhopus* from the Cloverly Formation of south-central Montana. The two bones were not fused, nor were they fused to the tibia. The astragalus is described as similar to that of *Ornithomimus* (YPM 542) but larger and more perfectly rounded distally. This distal rounding is extreme, given by Ostrom as 155° to 180° of arc, and evidently continued by the tibia to approximately 200°, providing an 'unusual extension of the foot'. The breadth is 59 mm and the H:B index at least 142. The dorsal process is very thin and at least 84 mm high. It rises about 5 mm from the medial edge at a steep angle of 72° and is very broad (52 mm) at the base, extending laterally behind the calcaneum. The tibial sulcus is carried laterally onto the posterior face of the calcaneum behind the high, small fibular sulcus. This tarsus is ornithomimid in its extremely high dorsal process, but is aberrant in retaining so large a calcaneum.

Gilmore (1920: 138) describes the astragalus that he considers to be a cotype of *Ornithomimus affinis*, from the Arundel Formation, Lower Cretaceous of Maryland. This is 78 mm broad, the dorsal process much eroded to a height of 56 mm, and is narrow anteroposteriorly. Russell (1972: 379) transfers this species to the genus *Archaeornithomimus*.

Lambe (1902: 50, fig. 11) described the right hind limb of *Ornithomimus altus* from the Judith River Formation, (Russell 1972: 383), Red Deer River, Alberta. This was referred to the genus *Struthiomimus* by Osborn (1917: 744). From the illustration the astragalus is 129 mm wide and 224 mm high, an H:B index of 174. The dorsal process lies along the fibular side of the tibia, the lower border of each concave, with the tibia expanding rapidly distally. Lambe does not describe this bone in detail, but later (1904: 20) notes that the medial and lateral ends are less oblique than in *Dryptosaurus incrassatus* (referred specimen). He also states that the astragalus does not coalesce with the tibia. The calcaneum has an upper sulcus for the fibula and 'one behind to aid the astragalus in supporting the tibia'.

Ornithomimus velox was figured by Marsh (1890, pl. 1, fig. 1), as from the *Ceratops* beds of Colorado, the Denver Formation, Maastrichtian (Russell 1972: 379). The astragalus is 52 mm broad and 80 mm high, an H:B index of

154. The calcaneum is very thin and Marsh did not state whether it was fused or not. If fused, the astragalocalcaneum had a breadth of 65 mm. This is an

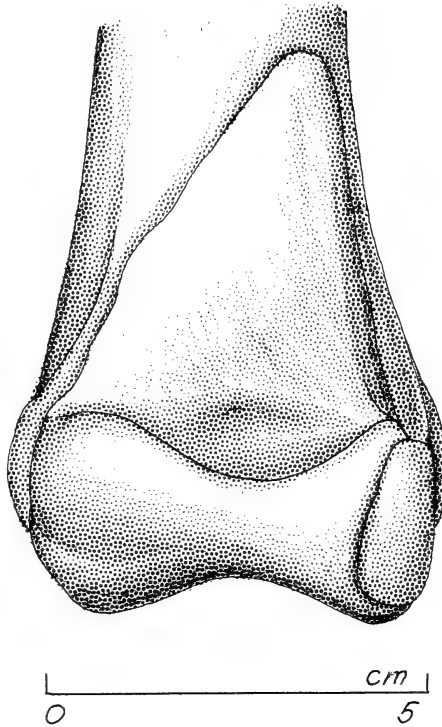


Fig. 12. *Ornithomimus velox*, type.

Anterior view of distal end of left tibia and tarsus, from Marsh 1890, pl. 1, fig. 1. $\times 1$.

extremely specialized tarsus in that the calcaneum is so reduced that there was little or no support for the fibula, and this, in turn, must have been greatly reduced. These features were noted by Marsh, who likened it to the ostrich tarsus. The dorsal process is extremely high, its lateral edge nearly vertical and its medial edge dipping 67° near the base, the total angle of dip being 60° . Another specialization of this tarsus is seen in ventral view where the astragalus does not completely cover the lower end of the tibia, but the tibia forms a narrow rim of bearing surface along the posterior edge and wraps around the medial edge of the astragalus. This narrow tibial rim also extends laterally behind the calcaneum.

THE TYRANNOSAUROID TARSUS

The astragalus of *Tyrannosaurus rex*, from the Hell Creek beds of Montana, was illustrated by Osborn (1917, pl. 25) as about 425 mm broad and 530 mm

high, an H:B index of 125. However, in the archives of the American Museum of Natural History we found a detailed unpublished illustration by Erwin S. Christman, which was probably done under the supervision of Osborn or Barnum Brown. This differs drastically from Osborn's illustration and it evidently represents an entirely different kind of astragalus. It therefore seems likely to us that Osborn's illustration was based on *Allosaurus*. We made a thorough search for the specimen, and although we failed to locate it we feel that Christman's drawing is authentic. It bears the same number (AMNH 5027) as the beautiful skull from the Hell Creek Formation of Montana collected by Brown in 1907. The locality is the east side of Big Dry, 13 km from Willis Ranch, 40 km south of Lisman, Mont., top of basal ss., 24 m above the Fox

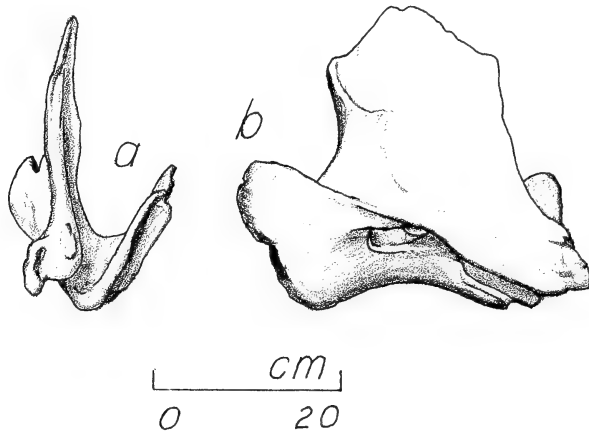


Fig. 13. *Tyrannosaurus rex*. Left astragalus in a, lateral view; b, anterior view. Redrawn from unpublished illustration by Erwin S. Christman. AMNH 5027. $\times \frac{1}{4}$.

Hills. From Christman's illustration the anterior view shows a breadth of 372 mm and a height of 320 mm, yielding an H:B index of 86. The dorsal process is broad and is distinctive in that the medial edge slants dorsomedially and is concave. The lateral edge slopes ventrolaterally and ends above the pit for the calcaneum. The upper horizontal groove is but weakly developed medially and is entirely absent laterally where the dorsal process rounds gently into the lateral condyle. The medial condyle is 160 mm high, protrudes dorsomedially, and its upper edge slopes ventrolaterally to form a shelf above a groove (? the lower horizontal groove) which ends by rounding back and down into the lateral condyle 60 mm internal to the calcaneal border. At about the centre of the astragalus, just below the shelf is a large (68 \times 28) horizontal foramen that opens into the tibial sulcus. In lateral view the edge of the dorsal process is rounded and does not seem to have formed the usual flat surface for the fibula. The lateral condyle is low, rounding gently into the dorsal process without the separation of an upper horizontal groove. An open vertical groove

could be for either the fibula or the calcaneum, probably the latter. The posterior process is very thin, with its edge high (172 mm) above the condyle. The trough for the tibia is very narrow laterally where it descends to within 20 mm of the base. It broadens medially, as with most theropod astragali.

SUMMARY

In reviewing this study of the theropod astragali, the ceratosauroids develop a low, thick dorsal process which is sunk into the tibia. The calcaneum is large and may be free or fused. This tarsus undergoes little change from late Triassic to late Cretaceous and does not seem to have given rise to any other line. The allosauroids have a moderately high dorsal process which is confined to the lateral half of the tibial surface. The medial condyle is large and rounded. The calcaneum is large and free, and in *Allosaurus* is deeply interdigitated with the astragalus. The time range is Middle Jurassic through late Jurassic. The albertosauroid astragalus has a high, broad dorsal process with a deep upper horizontal groove at its anterior base. This groove is interrupted laterally by a ventrolateral buttress to the lateral condyle. There is no lower horizontal groove and the calcaneum becomes very small and is loosely attached to the astragalus. This kind of tarsus is found throughout the late Cretaceous. The ornithomimoid astragalus develops an extremely high and very thin dorsal process that overlies the face of the tibia without being deeply inset. Distally it is equal to the tibia in breadth. The upper horizontal groove at the anterior base of the dorsal process is strongly arched ventrally and there is no lower horizontal groove. The calcaneum becomes extremely reduced and may be lost. The time range is late Jurassic to late Cretaceous. The tyrannosauroid tarsus only appears in the latest Cretaceous in a single known form. The astragalus bears a high, wide dorsal process as in other late Cretaceous theropods, but it differs in numerous other characters and appears to indicate a separate origin from known Cretaceous forms.

It is obvious that there has been a general tendency among theropods to increase the height of the dorsal process of the astragalus. The ceratosauroids seem to have minimized this tendency, the ornithomimoids to have maximized it. Whether or not this tendency can be used as an indicator of geologic age, as was attempted by Welles (1954: 597), can only be determined by additional specimens and further study.

This survey suggests some tentative relationships based on a very few specimens. Many undescribed astragali are known, and when they are studied we will have a much more solid basis for our conclusions.

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POSTSCRIPT

Upon the receipt of page proof we note the subsequent papers that include descriptions of theropod tarsi which have not been included in our survey:

BIDER, A., DEMAY, L. & THOMEL, G. 1972. *Compsognathus corallestris*, nouvelle espèce de dinosaurien théropode du Portlandien de Canjuers (Sud-Est de la France). *Annls Mus. Hist. nat. Nice* 1 (1): 9-40.

OSMÓLSKA, H., RONIEWICZ, E. & BARSBOLD, R. 1972. A new dinosaur, *Gallimimus bullatus* n. gen., n. sp. (*Ornithomimidae*) from the Upper Cretaceous of Mongolia. In: KIELAN-JAWOROWSKA, Z., ed. Results of the Polish-Mongolian Palaeontological Expeditions. IV. *Palaeont. pol.* 27: 103-143.

The tarsi of *Compsognathus corallestris* and *Gallimimus bullatus* display numerous characters which undoubtedly place them in our ornithomimid group.

It should also be noted that Cruickshank has recently described the tarsus of the *Lystrosaurus* zone thecodont *Proterosuchus* which is 'almost identical to that of an eosuchian'. The calcaneum has a well-developed tuber.

(CRUICKSHANK, A. R. I. 1972. The proterosuchian thecodonts. In: JOYSEY, K.A. & KEMP, T. S., eds. *Studies in vertebrate evolution*: 89-119. Edinburgh: Oliver & Boyd.)

Also Bonaparte has described the astragalus of an indeterminate saurischian from the upper Los Colorados Formation (Norian), of La Rioja, Argentina. This is a very primitive astragalus with only an incipient dorsal process and its relationship to theropod tarsi is uncertain.

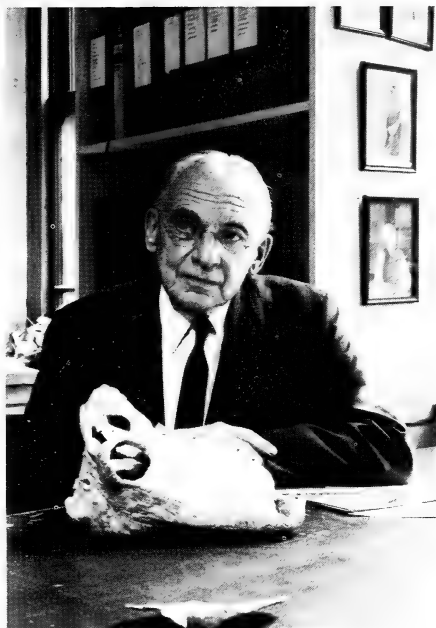
(BONAPARTE, J. 1971. Los tetrápodos del sector superior de la Formacion Lós Colorados, La Rioja, Argentina. (Triásico Superior.) I Parte. *Op. lilloana* 22: 1-185.

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ALFRED SHERWOOD ROMER

Professor Alfred S. Romer was fond of comparing vertebrate palaeontologists with the conies (Hyracoidea) of Scripture: 'a feeble folk, which dwelleth among the rocks.' Through the sudden death of Professor Romer in November 1973, this 'feeble folk' has lost an able and courageous leader, and one of its best-known and loved members.

Born in 1894, Alfred Sherwood Romer completed a doctoral thesis at Columbia University in 1921 before joining the faculty of the University of Chicago in 1923 as Assistant Professor, becoming Professor of Vertebrate Paleontology in 1931. In 1934 he moved to Harvard as Professor of Zoology and Curator of Vertebrate Paleontology. In 1947 he received the Alexander Agassiz Professorship in Zoology, and was director of the Museum of Comparative Zoology from 1946 to 1961. He retired from the Harvard staff in 1965, becoming Professor Emeritus, but was actively involved in research up to the time of his death.

Among the medals and awards received by Professor Romer during his long career were the Thompson Medal of the National Academy of Sciences for 1956, the Academy's Elliot Medal for 1960, the Hayden Memorial Geological Award of the Philadelphia Academy of Natural Sciences for 1962, the Penrose Medal of the Geological Society of America in 1962, the Medal of the Linnean Society of London 1972, and the Wollaston Medal of the Geological Society of London in 1973. He held honorary doctorates from the universities of Harvard, Amherst, Dartmouth, Buffalo and Lehigh.

Besides regular collecting in the Permian red-beds of Texas, and (most recently) pioneering field work in two rich Triassic deposits in western Argentina, Romer became the first American to make an important collection of South African Karroo reptiles when in 1929, accompanied by the veteran collector Paul C. Miller of Chicago's Walker Museum, he spent seven months collecting in most of the classic Karroo localities.

The wideness of the field that Professor Romer covered during his career makes a full appreciation of his contribution to science difficult. Always the biologist, he applied biological principles to the extinct organisms which he studied. To him a fossil vertebrate was a once-living animal, to be recreated in its body form, its functional activities, and its way of life within its contemporary environment, and to him this may have represented the ultimate achievement of palaeontology. His standard textbooks *The vertebrate body* (4th ed. 1970), *Vertebrate paleontology* (3rd ed. 1966) and *Osteology of the reptiles* (1956) need no introduction, nor do his more general works *Man and the vertebrates* (1933) (retitled *The vertebrate story* in 1959) and *The procession of life* (1968). His monographs include 'Review of the Pelycosauria' (1940), 'Review of the Labyrinthodontia' (1947) and the series (up to 1973) 'The Chañares (Argentina) Triassic reptile fauna'. These works, and his numerous other publications, all bear a very typical Romerian stamp: a combination of clear, logical reasoning, a total morphological insight, and a presentation couched in the clear, uncluttered literary style that set Romer apart from nearly all his contemporaries.

Romer the scientist, Romer the writer, and Romer the man will be sorely missed in the forums of comparative anatomy and vertebrate palaeontology, where he was for so long a dominant figure.

AQUATIC ADAPTATION IN REPTILES—PRIMARY OR SECONDARY?

By

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A fair number of modern reptiles, such as the crocodylians, most chelonians and a number of ophidians, are amphibious to aquatic in habits and, in the Mesozoic, aquatic reptiles were abundant—ichthyosaurs, plesiosaurs and mosasaurs being the most prominent forms. Are such forms secondarily aquatic, descended from purely terrestrial ancestors, or may certain of them have been derived from primitive reptiles which had never completely abandoned the aquatic habitat of their lower vertebrate ancestors? Since the most positive definitive characteristic of the Reptilia is their amniote mode of development that freed them from the water, and since, farther back, limbs capable of terrestrial locomotion were developed in even the oldest known amphibians of the late Devonian, it seems reasonable, at first sight, to believe that early tetrapods rapidly emerged from the water onto land, and that water-dwelling was a secondary condition.

This is not necessarily the case. Despite the development of limbs in early amphibians, few members of this class ever achieved a truly terrestrial mode of life. And although the evidence is none too clear, it seems far from certain that all aquatic reptiles have reverted from land to water.

THE AMPHIBIAN STAGE

Let us broadly review the early history of tetrapods. The oldest known amphibians—the late Devonian ichthyostegids (Jarvik 1955)—were crossopterygian descendants which, despite the retention of certain primitive features, had developed their paired fins into short but sturdy tetrapod limbs, enabling them to leave the water and travel overland. Offhand, one would assume that with the development of paired limbs the ancestral amphibians immediately took up a terrestrial existence. But further reflection brings one to conclude that nothing could be further from the truth. For what purpose would these early amphibians come forth on to the land? It has been suggested that they were taking refuge from enemies in the water; but that can hardly be the case, for the amphibians are an offshoot of the rhipidistian crossopterygians who were the most predaceous of fishes in Devonian fresh waters. More reasonable, at first sight, is the belief that these fish descendants were setting forth to explore the terrestrial environment where new opportunities might await them. Here, however, the fatal objection is that there was precious little on land for them to eat. The rhipidistians were predaceous, eaters of smaller fishes and, presumably, freshwater invertebrates. It seems certain that all early amphibians

were likewise eaters of animal food; universally, the teeth, like those of crossopterygians, were sharp-pointed conical structures quite incapable of dealing with vegetable materials. It is possible that there were already present on land in the Devonian some soft-bodied invertebrates which have escaped detection as fossils, but the only land animals known in the Devonian upon which a hopefully terrestrial amphibian could feed were tiny Collembola (known from the Rhynie chert of Scotland) and a few myriapods. Most notably, not a single true insect is known from the Devonian.¹

Amphibians attempting to live on land in the Devonian might admire the scenery; but they would surely starve to death. And in the early Carboniferous the terrestrial food supply was little better. One might expect primitive insects to appear, but none have as yet been found. It appears possible that in the Carboniferous scorpions were in process of migrating from water to land. But even the possible addition of scorpions to a diet of centipedes and microscopic soil-dwelling springtails does not appear to make life on land too attractive for eaters of animal food. It was not until the later Carboniferous that land life really became possible with the appearance of a wealth of insects of primitive types. It is only toward the end of the Carboniferous that we find among early reptiles (and perhaps in one family of amphibians) forms which at long last were adapted to feed upon the readily available vegetation.

Why, then, the development of land limbs in amphibians? The answer, apparently, is a paradoxical one—that these limbs, which enabled them to walk on land, were an adaptation for water-dwelling under the conditions in which early amphibian evolution took place. Barrell (1916) long ago pointed out that the late Paleozoic, when tetrapod evolution was taking place, is characterized by an abundance of 'redbeds' formations. Beds of this sort are frequently indicative of their having been laid down under climatic conditions of seasonal drought such as are found in limited regions of the tropics today. For part of the year, rainfall is abundant, and life for water-dwellers is easy. When a drought comes, streams dry up, waters become stagnant, and oxygen is at a premium. However, a good fraction of Paleozoic freshwater fishes appear to have had lungs (which very few fish have today), and atmospheric oxygen was available to them if they came to the surface. But if the stream or pond dried up completely in the drought, what then? An ordinary fish would be, literally, stuck in the mud, and if the water did not return quickly would soon perish. But if rudimentary limbs of tetrapod type were present, the animal might be able to leave his dried-up pool, crawl up or down the streambed or even travel some distance overland, find a pool with water still in it, plunge in, and resume his normal aquatic life. Under seasonal drought conditions, tetrapod limbs, even if little developed, would be of immediate selective advantage to a freshwater dweller.

Watson years ago (1926) suggested this use of legs in the Carboniferous

¹ Originally described as insects were two specimens from the Devonian of the USSR; these, however, were subsequently recognized as crustacean.

and I have since pointed out (Romer 1957, 1958, etc.) that this situation may have been true of early amphibians generally. Had early limb development been for the 'purpose' of exploring land life, one would expect that the post-Devonian history of early amphibians would have exhibited the retention and even improvement of the limb development seen in the Devonian ichthyostegids. But the opposite is almost always the case. In the Carboniferous, with the frequent development of coal-swamp conditions, the importance of limbs as a means of survival under drought conditions would decrease; and if, in any standard text (such as Romer 1966: 87-98), we follow through the history of amphibians in the post-Devonian periods, we see, in accordance, a strong trend for limb reduction, rather than limb improvement, in most amphibian groups.

Pre-Jurassic amphibians are currently customarily divided into two major groups: the Lepospondyli (very probably an artificial assemblage) and the Labyrinthodontia. The Lepospondyli include a considerable variety of small Carboniferous and early Permian forms, apparently mainly coal-swamp dwellers, in nearly all of which the paired limbs are greatly reduced and may be lost completely. Exceptional are a number of late Carboniferous and early Permian members of the Microsauria in which rather well-developed limbs are present.

The much more important ancient group is that of the Labyrinthodontia. Here, as in the lepospondyls, there is in general a strong trend toward limb reduction, although not as marked or as rapid as was the case in most lepospondyls. We are not sure that the primitive ichthyostegids were directly ancestral to any later labyrinthodonts; however, one restricted series of Carboniferous forms, the Colosteidae (which I hope to discuss in the near future) may be ichthyostegid descendants; however, they have limbs more feebly developed than in the Devonian forms.

Ichthyostegids apart, however, nearly all labyrinthodonts may be arrayed in two main series, the Temnospondyli, in which a key character is the dominance in the vertebral column of the intercentrum, and the Anthracosauria, in which the pleurocentrum develops (to become eventually the true centrum of reptiles). The temnospondyls are by far the more abundant of the two, and are the only amphibians (apart from a 'pre-frog') present in the later Permian and Triassic. In some Carboniferous and early Permian forms the legs are reasonably well developed, as in the familiar *Eryops* of the early Permian which could quite surely waddle comfortably about its native swamps, and in one group, the dissorophoids, there was apparently, in the Permian, a considerable trend toward true terrestrial existence.²

But while limbs were maintained in proper fashion in certain temnospondyls, the trend toward reduction was strong within the group. Even among

² See, for example, the dissorophids *Cacops* and *Broiliellus* (Williston 1914, etc.), in which there were not only well-developed limbs but also dorsal armor, suggesting a terrestrial life where there was danger from reptile predators. These forms lived at a time in the Permian when terrestrial food was becoming more abundant.

primitive temnospondyls, such as the trimerorhachids, the limbs were much reduced, and from the later Permian on through the Triassic there was continued reduction, so that in typical Triassic members of the group, such as *Capitosaurus* and *Metoposaurus*, we find amphibians with a broad flat head and body with tiny limbs quite incompetent to support them out of the water. In the later Paleozoic and Triassic the dangers of seasonal drought were much less than in earlier days, and in correlation with this, there was a strong trend to reduction of the limbs. But if drought did occur, these late temnospondyls were helpless. I have described a locality in the Triassic of New Mexico (Romer 1939) in which a mass death of a myriad of metoposaurs ('*Buettneria*') occurred, obviously because of the drying up of the swamps and pools in which they lived.

The other main division of the labyrinthodonts is that of the Anthracosauria,³ much less abundant but of interest as the group from which the Reptilia arose. Here, as in the temnospondyls, we see considerable variation in limb development. Most prominent of anthracosaurs in the Carboniferous (and persisting into the early Permian) were the Embolomeri, good-sized amphibians, essentially water-dwellers, quite surely with paired limbs of relatively small size which, nevertheless, could enable them to walk on land to some degree. Quite rare, known only from a few genera, were Carboniferous forms in which sturdy limbs persisted. One is *Gephyrostegus*, known only from two specimens from the European Upper Carboniferous; long confused with other genera, its nature and structure has been recently clarified by Carroll (1970b: 268-286). An apparently similar form, *Mauchchunkia*, has now been discovered in the Lower Carboniferous of Greer, West Virginia. So far there has been published (Hotton 1970) only an account of a fragmentary skull and incomplete skeletal materials. Now available to me, however, are two excellent postcranial skeletons, which I hope to describe shortly. The structure is quite similar to that of *Gephyrostegus*; we appear to have here a fortunate persistence of anthracosaurs with well-developed limbs through the 'hard times' (for potential terrestrial life) of the early Carboniferous. From forms of this sort the earliest reptiles presumably arose in the latter half of the Carboniferous. But also there may have come from this stock the Seymouriamorpha of the Permian, best known from *Seymouria* of the early Permian of Texas, but also represented by a number of European genera. Derived from the same general stock as the ancestral reptiles, the seymouriamorphs show many reptile-like characteristics, but although taking advantage of the relatively favourable conditions of Permian

³ O. Kuhn, in his *Handbuch der Palaeoherpetologie* (Panchen 1970), has, regrettably, tended to bring about confusion in amphibian terminology by substituting for Anthracosauria the Efremov term Batrachosauria (Efremov 1946) and reducing Anthracosauria to cover merely the embolomerids. But Efremov intended Batrachosauria (as the name implies) to apply only to reptile-like amphibians, notably the Seymouriamorpha, and not to such unreptile-like forms as the embolomerids. And for the latter Cope nearly a century ago coined the term Embolomeri, of which Anthracosauria, as used by Kuhn, becomes merely a junior synonym. I trust that Kuhn's nomenclatorial aberration here will be generally neglected and presently forgotten.

times to become essentially terrestrial in habits, they remained, it appears, in an amphibious stage as regards reproduction.

Above, we have reviewed the history of the older amphibious groups as regards their locomotor potentialities and general mode of life. Tetrapod limbs were early developed and in a few cases, such as Permian dissorophoids and seymouriamorphs, were not merely retained but used for terrestrial locomotion. But in general there appears to have been a strong trend for limb reduction. The story agrees well with the assumption that the Amphibia were, and generally remained, aquatic or at the most amphibious in habits; that limb development at the beginning was not related to any trend toward terrestrial life but as a useful aid to successful aquatic life under seasonal drought conditions; and that when such climatic conditions were lessened, limb reduction very generally took place.

EARLY REPTILES

What was the mode of life of the earliest reptiles, descended from water-dwelling amphibian ancestors? How rapidly did they take on the terrestrial mode of life, facilitated by the 'invention' of the amniote type of development? In recent years it has become increasingly clear that the basic stock of the Reptilia lies in the cotylosaur group termed the Captorhinomorpha. Members of this group have long been known from the early Permian, but in recent years it has become clear, mainly through an excellent series of papers by Carroll (1969, 1970*b*, etc.), that they were already flourishing in the late Carboniferous (the Pennsylvanian of American usage). We are here at a stage when, in contrast to earlier times, true land life had at long last become possible; with a known wealth of primitive insects present, there was now available a basic source of food upon which a terrestrial fauna might feed. Central in this picture are members of the family Romeriidae. These were small reptiles whose appearance in life might have been rather like that of modern lizards, but which were very different from any modern reptiles in that their structure was of a very generalized and primitive type, of a sort from which, one may believe, later reptiles of almost any group might have been derived. Still more primitive are members of the family Limnoscelidae. The type form, *Limnoscelis palustris* (Williston 1912; Romer 1946), is of early Permian age, but representatives are now known from the Carboniferous, and one form, *Romeriscus* (Baird & Carroll 1967) from the Westphalian A of Cape Breton, is the oldest known reptile. It seems certain (as the scientific name suggests) that the limnoscelids were persistently primitive in retaining amphibious habits. But it is generally agreed that the limnoscelids were already technically reptiles, strongly suggesting that the amniote type of development had already been invented before the reptiles had abandoned the amphibious mode of life of the older tetrapods.

Carroll believes, however, that the limnoscelids were too archaic in structure to have been a group from which the radiation of later reptilian groups

could have taken place, and that the basic stock from which higher reptiles evolved was that of the more advanced family Romeriidae. What was the mode of life pursued by the romeriids—was it, at this level, completely terrestrial, or were these forms still somewhat aquatic in habits? Carroll gives a good argument for the terrestrial side of the question—namely, that the skeleton in romeriids is well ossified, whereas in amphibious reptiles, generally, ossification is less complete. Had we good continental beds in the Upper Carboniferous, with a true land fauna, the case for the purely terrestrial nature of the romeriids would be greatly strengthened. Unfortunately, our knowledge of Upper Carboniferous vertebrate faunas is almost entirely confined to those of coal swamps. In these, as at Linton and Mazon Creek, romeriids are relatively rare, but are present. Only in the fossil tree stumps of the Nova Scotia Joggins does Carroll (1969: 36) believe that he has a truly 'terrestrial' fauna in which romeriids are abundant.

I have a very high regard for Carroll's work on Carboniferous tetrapods, but I think that here he has (like the contained fauna) fallen into a trap. The Joggins region, well known since the days of Dawson (and recently redescribed briefly by Carroll and others in 1972) consists of a series of Carboniferous exposures along the bluffs at the head of the Bay of Fundy in western Nova Scotia. Here there are present thousands of feet of Upper Carboniferous deposits which include some dozens of coal seams separated by intervening shales. We are dealing with a long-persisting coal basin in which, time after time, a coal swamp developed. Between successive swamp deposits the area was invaded by mud flows which hardened into shales. The lycopod trees of the coal swamps tended to die, leaving hollow stumps that (as well shown by Carroll 1970a, fig. 3) acted as traps for unwary amphibians and reptiles which wandered about the mud flats of the region in the periods between times of coal seam formation. The contents of the traps consist mainly of romeriids, microsaur with well-developed limbs, and a rhachitome (*Dendrerpeton*) with rather good legs; absent are nectrideans, aïstopods and other coal-swamp dwellers in which limbs were lost or poorly developed. Is this a 'terrestrial' fauna? Hardly. We are still present in a coal-swamp basin, and there is no guarantee that we are not within a short distance of the water. It simply means that we have a selective screening of a coal-swamp fauna. As Rayner (1971) notes: 'The pure water-dwellers, such as the aïstopod and nectridean lepospondyls, are absent. Those found are more 'terrestrial' than in other Carboniferous faunas; they walked, ambled or waddled across the muddy or sandy flats among the rotting tree trunks. The sediments they traversed, however, and which finally buried animals and trees, were purely aqueous—the normal type laid down in the open stretches of the coal forests and swamps.'

It is highly probable that some Carboniferous romeriids were completely terrestrial; but those which we do know were persistent coal-swamp dwellers. It would appear, as far as present knowledge goes, that despite the advantage given them by their amniote mode of life, and despite the fact that the abundant

insect fauna of the later Carboniferous afforded a terrestrial food supply for eaters of animal food, early reptiles were slow to abandon the amphibious mode of life of their ancestors.

By the close of the Carboniferous and the beginning of the Permian, many reptiles were already fully 'ashore' and even (as shown for example by the presence of *Edaphosaurus* in the late Carboniferous) some were shifting from animal to vegetable food supplies. As noted later, in the case of many aquatic and amphibious reptiles of the Mesozoic and Cenozoic, evidence is lacking as to whether or not the forms leading to them had become fully terrestrial and only later returned to the water. Is there, however, any evidence in early reptile history suggesting a primitive retention of an amphibious to aquatic habit? Apart from the primitive limnoscelids, there are two positive examples of water-dwelling reptiles which are of such an early age that it seems unlikely that their pedigree included forms which had become completely terrestrial in habits.

One example is *Mesosaurus* of South Africa and southern Brazil (Rayner 1971: 472-476). The phylogenetic position of this small amphibious reptile is uncertain (it has been variously referred to the diapsids and synapsids, and some recent evidence suggests that it may be anapsid—an early cotylosaur offshoot). Highly specialized for feeding on minute crustaceans, *Mesosaurus* occurs at a horizon close to the Carboniferous-Permian boundary in the 'white band' of the South African Dwyka and comparable beds in Brazil. Occurring at this early stage in reptilian history, it is difficult to believe that its ancestors could have become completely terrestrial and then rapidly shifted back to an amphibious mode of life, with the speedy acquisition of its unique type of cranial and dental structures.

More striking is the story of the ophiacodont pelycosaurs. The subclass Synapsida, of which the pelycosaurs are the primitive members, is in its more advanced stages an almost purely terrestrial group. But while among the pelycosaurs the sphenacodontoid and edaphosauroid suborders are terrestrial in nature, *Ophiacodon* and its relatives, most primitive of pelycosaurs, are quite surely still amphibious in habits (Romer & Price 1940). The two other pelycosaur groups flourished greatly in the early Permian, but only appear in the fossil record at the very close of the Carboniferous. Quite different is the story of the ophiacodonts. One ophiacodont, *Clepsydrops*, has long been known from the Upper Carboniferous of Danville, Illinois, and it has been demonstrated that ophiacodonts were present nearly as far down in the sequence of Carboniferous coal-swamp deposits (Romer 1961; Carroll 1964; Reisz 1972) as reptiles of any sort.

The ophiacodonts differ little from primitive captorhinomorphs, apart from the development of the synapsid temporal opening, and it seems completely reasonable to believe that this basal group of synapsids branched off from the basal reptile stock while this was still persistently amphibious in habitat.

LATER AMPHIBIOUS AND AQUATIC REPTILES

Notable in the known paleontological history of reptiles is our almost complete lack of knowledge of groups other than cotylosaurs and synapsids until late Permian and Triassic days, and the early stages in the evolutionary story of most reptile groups is purely guesswork. For example, the Chelonia is an order which includes among the tortoises a few purely terrestrial forms, and on the other hand gave rise to a number of high seas types, but in general they are typically amphibious in habits.

The first chelonians appear in the late Triassic, and while a bit more primitive in some regards, already show the basic structural pattern of the order and, it would seem, lived the typical amphibious life characteristic of most of their descendants. It is quite possible that in the long stretch of time between the Carboniferous and the late Triassic the chelonians had become purely terrestrial and then reverted to an aquatic mode of life. But it is equally possible that we have in the typical members of this order a retention of a truly primitive mode of amphibious life.

Unknown, too, is the pedigree of the great group of aquatic reptiles currently grouped in the subclass Euryapsida—the placodonts, nothosaurs and plesiosaurs. The mollusc-eating placodonts and the nothosaurs appear in the Middle Triassic oceans; in the Jurassic these forms disappear, to be replaced by the purely aquatic plesiosaurs, which had a spectacularly successful career in the middle and later parts of the Mesozoic. Where did these euryapsids come from? We have no clues as to their history. *Araeoscelis* of the early Permian has an euryapsid type of temporal opening, but Vaughn (1955) has pointed out that this genus shows no resemblance to later euryapsids in other regards.

Similarly blank is the history of the ichthyosaurs, most completely adapted of all reptiles to a marine existence. The ichthyosaurs first appear in the Middle Triassic, and although the members of the order were at that time somewhat less advanced than their abundant Jurassic (and less abundant Cretaceous) descendants, they were already definitely ichthyosaurs, quite distinct from members of any other reptilian group. I have recently (Romer 1968) demonstrated that, in contrast to earlier beliefs, their temporal structure was similar to that of the typical euryapsids; but this only adds further puzzlement to the problem of their ancestry. I have pointed out (Romer 1948) that except for the temporal opening, their skull structure is basically similar to that of ophiacodont pelycososaurs, and like these pelycososaurs, could reasonably have originated from captorhinomorph cotylosaurs. But there is absolutely no trace of transitional forms. The ichthyosaurs could, like the ophiacodonts, have come directly from early reptiles still in an amphibious ecological condition. But the gap in time between the Carboniferous and Middle Triassic is great enough so that it is possible to argue here, as in the case of euryapsids and chelonians, that their ancestors might have become purely terrestrial and secondarily reverted to aquatic life.

The archosaurs, which include, as well as ancestral thecodonts and croco-

dilians, the great dinosaurian orders, the flying pterosaurs and bird ancestors, appear at first sight to have been *ab initio* a terrestrial group, in which there was a strong tendency toward a bipedal stance and, in pterosaurs and birds, on toward aerial life. But Charig (1966) has recently pointed out that there are suggestions of amphibious habits in early archosaurs. The strong hind legs and tail which were highly useful in the development of bipedal habits, may have been initially developed in relation to an amphibious mode of life (*Mesosaurus* is comparable). Further, many early archosaurs show aquatic tendencies (Charig & Reig 1970). The oldest and most primitive of archosaurs, the Proterosuchidae (such as '*Chasmatosaurus*') were quite certainly amphibious in habits; crocodylians developed early from the thecodont base; the most abundant of later Triassic thecodonts were the amphibious crocodile-like phytosaurs; and the Middle Triassic thecodonts include a further family, Proterochampsidae, which were certainly phytosaur-like in habits (Romer 1971). All in all, it is not impossible that the ancestral archosaurs were derived from primitive reptiles which were still amphibious in habits. But the first known archosaur is late Permian in age, and it can be argued, as in the groups already discussed, that their ancestors had become completely terrestrial in Permian times before amphibious trends developed.

Of all reptile groups it is the Lepidosauria—the lizards, snakes, and rhynchocephalians—for which the best argument for a firm terrestrial ancestry can be made. The ancestors of the subclass, the Eosuchia, appear before the end of the Permian, and there is no positive evidence of any aquatic trend in the group. There are, to be sure, sea snakes and some water-living lizards in the recent fauna, but derivation of them from terrestrial ancestors can be reasonably made. *Champsosaurus* of the late Cretaceous and earliest Tertiary is amphibious, and certain Jurassic forms look suspiciously amphibious in nature but descent from terrestrial ancestors can be reasonably argued. Most prominent of aquatic lepidosaurs were the mosasaurs, which flourished greatly in the late Cretaceous; but these can be derived from amphibious ancestors in the early Cretaceous and, hence, mosasaur descent from Jurassic terrestrial forms can be reasonably argued.

If we attempt to sum up this story of terrestrial versus aquatic trends in reptile history, it seems that the Reptilia were not too speedy in the late Paleozoic in leaving their ancestral home in fresh waters; and that some, at least, of the aquatic and amphibious members of the group may have persistently retained a primitive mode of life rather than having returned to the water from a purely terrestrial ancestry. But the question in many cases must remain an open one until new fossil evidence appears to fill in the major gaps still present in the Permian and early Triassic history of reptiles.

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MIGRATIONS OF THE MULTITUBERCULATA AND THE LATE CRETACEOUS CONNECTIONS BETWEEN ASIA AND NORTH AMERICA

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(With 3 figures)

CONTENTS

	PAGE
Fossil records	231
Discussion	236
Conclusions	239
Summary	241
Acknowledgements	241
Addendum	241
References	242

FOSSIL RECORDS

The Multituberculata are the longest lived order of mammals. If we take into account the records generally accepted as belonging to the Multituberculata, they first made their appearance in the Kimmeridgian and became extinct at the end of the Eocene, which means that they evolved for about 118 million years. It was tentatively claimed by some students of early mammals (Parrington 1967; Hahn 1969; Simpson 1971) that the Rhaetic Haramiyidae are related to the Multituberculata. If we regard the Haramiyidae as the earliest Multituberculata (Fig. 1), the vertical range of this group would be extended to 160 million years.

The time distribution of the multituberculates is usually illustrated in diagrams as a continuous line, extending from Kimmeridgian through Eocene. However, if one combines all known data about the distribution of this group, the line would be broken in several places (Fig. 1). The first gap in the fossil records (if we accept the Haramiyidae as belonging to the Multituberculata) embraces the whole early Jurassic through Oxfordian, which is about 42 million years. The oldest known true multituberculates were found in the Kimmeridgian of Portugal (Kuehne 1961; Hahn 1969, 1971); they embrace three genera, two of which, *Paulchoffatia* and *Kuehneodon*, are assigned to the Paulchoffatidae, suborder Plagiaulacoidea, while *Guimarotodon* is attributed to an undefined family, probably within the Plagiaulacoidea. After Kimmeridgian there is a second gap in the multituberculate time records, which embraces the Portlandian (possibly also latest Kimmeridgian and earliest Purbeckian); its duration was at least 7 million years. The next records are from the Purbeckian of

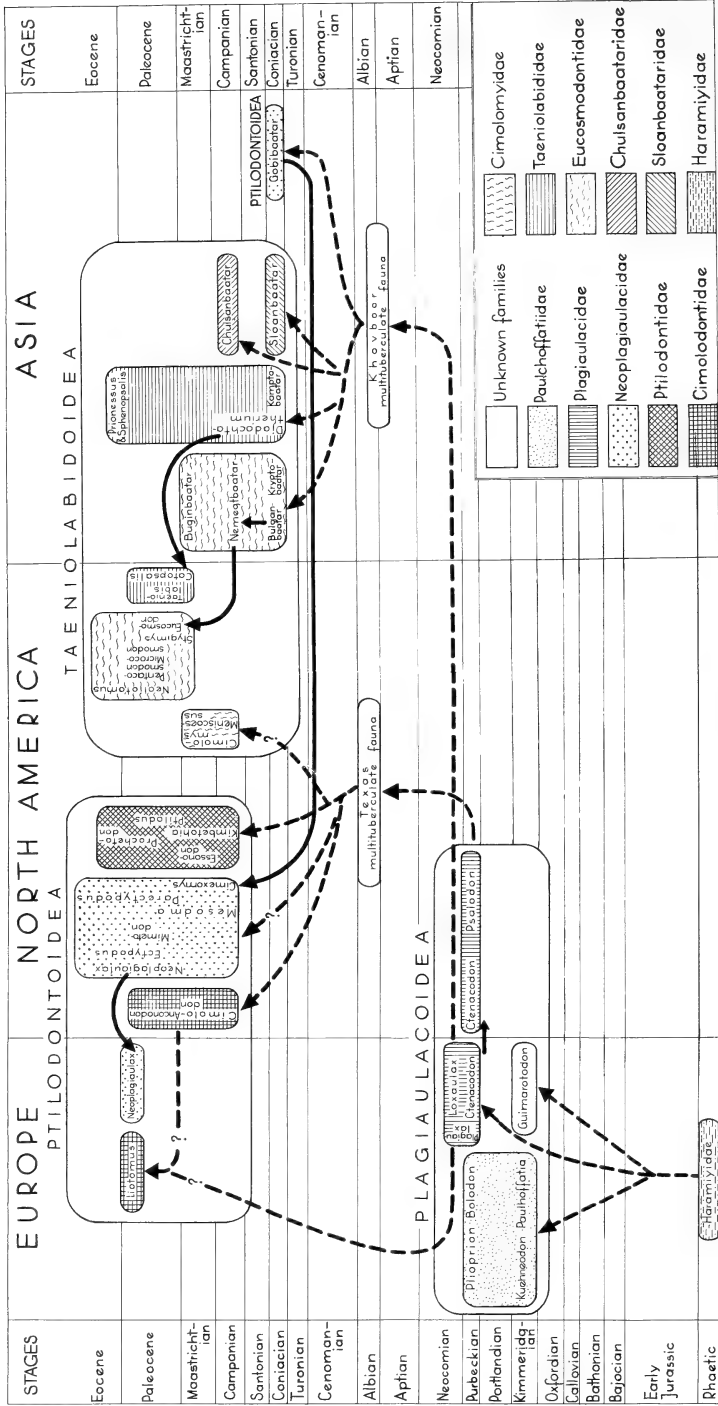


Fig. 1. Geographical and stratigraphical distribution of the multituberculate genera. Each family is marked by a different hatching. The shapes of hatched surfaces are not in proportion to the taxonomic diversity of the families. Discontinuous arrows indicate the probable phylogenetic and migration surfaces are not in proportion to the reasonably well-established migration lines. Stratigraphical ranges of North American genera are based on Sloan & Van Valen (1966).

Poorly known genus *Virtidomys* from Upper Milk River Formation of Canada is omitted.

Erratum: read *Paultschaffatia* for *Paultschaffatia*.

Great Britain and from the Morrison Formation of North America, which are probably of the same age. Five genera are known from these beds—the Paulchoffatidae: *Bolodon* and *Pliopriion* from Purbeck of Great Britain; Plagiaulacidae: *Plagiaulax* from Great Britain, *Ctenacodon* from Great Britain and North America, and *Psalodon* from North America (Simpson 1928, 1929; Hahn 1969). Of the latest Jurassic genera, uncertain remains of *Plagiaulax* are known from the Wealden of Great Britain, where, in addition, one more plagiaulacid genus *Loxaulax* was found (Woodward 1891; Clemens 1963a). In contradistinction to the Jurassic multituberculates, which are represented by lower jaws with dentition, and in one case also a part of the braincase, the Wealden records are extremely scanty, represented only by a few isolated teeth. After the Wealden there is a third gap in multituberculate records, which extends for the second half of the Neocomian, through the Aptian, and embraces about 15 million years.

In 1969 the Soviet-Mongolian Palaeontological Expedition discovered in the Gobi Desert, at the locality of Khovboor, in Guchin Us somon (county), situated at 102°34 eastern longitude and 45°21 northern longitude, a fauna of early Cretaceous mammals. According to Barsbold *et al.* (1971) the assemblage contains the Multituberculata in addition to the Triconodonta, Symmetrodonta and Insectivora, while according to Kalandadze & Reshetov (1971), in addition to the above mentioned orders, there are also representatives of the Trituberculata. The fauna has not been described as yet and the family assignment of the multituberculates is not known. Barsbold *et al.* (1971) claimed Aptian-Albian as the presumed age of this fauna.

Another early Cretaceous fauna, which is known, but has not been adequately described, is that from the Albian of Texas. Patterson (1956: 9) when describing the Albian fauna from the locality of Forestburg stated: 'Multituberculates are the commonest fossils at Forestburg. . . . All specimens found may be referred to the Plagiaulacidae.' He gave a short description of the Albian multituberculate lower and upper molars, but as the specimens have not been figured, it is difficult to get an idea about their affinities. Slaughter (1965) mentioned some isolated multituberculate teeth in samples from Butler Farm in Texas, which are of the same age as those of Forestburg, described by Patterson. These multituberculates were neither figured nor described by Slaughter.

The fourth gap in the multituberculate record is after the Albian and embraces Cenomanian, Turonian and perhaps also Coniacian, or a part of it, depending on whether the Djadokhta Formation of Asia is of Coniacian or Santonian age. In this discussion let us assume that the Djadokhta Formation is of Coniacian age (Fig. 1). This would mean that the fourth gap in the multituberculate records extends until the end of the Turonian and embraces about 19 million years.

Beginning with the Djadokhta Formation, the multituberculate records are more or less continuous through the Eocene. In the Djadokhta Formation

the representatives of modern multituberculate orders made their appearance: the Ptilodontoidea and Taeniolabidoidea.*

The only representative of the order Ptilodontoidea in Asia is the Djadokhta Formation *Gobibaatar*, assigned to the Neoplagiulacidae. Four other multituberculate genera recorded from this formation belong to the Taeniolabidoidea; these are *Sloanbaatar*, assigned to the monotypic family Sloanbaatariidae, *Kryptobaatar* and *Bulganbaatar*, assigned to the Eucosmodontidae and *Kamptobaatar* and *Djadochtatherium*, assigned to the Taeniolabididae (Simpson 1925; Kielan-Jaworowska 1969, 1971, 1974). In the younger Asiatic Barun Goyot Formation, which is of Campanian age, the multituberculate fauna so far described consists of three genera: *Chulsanbaatar*, assigned to the monotypic family Chulsanbaataridae, the taeniolabidid *Djadochtatherium*, represented by a more advanced species than its ancestor from the Djadokhta Formation, and the eucosmodontid *Nemegtbaatar*, derived from the Djadokhta genus *Bulganbaatar*. In addition there are in the Barun Goyot Formation three or more, as yet not described, multituberculate genera, none of which appears to belong to the Ptilodontoidea (Kielan-Jaworowska 1974). The post-Campanian multituberculate records are very scanty in Asia. A single genus *Buginbaatar* is known from Bugeen Tsav locality in the Gobi Desert. This is from the beds which are of the late Maastrichtian or early Paleocene age (Kielan-Jaworowska & Sochava 1969). *Buginbaatar* has been tentatively assigned to the ?Cimolomyidae, but in the discussion the authors pointed out (p. 363) that: '*Buginbaatar* n. gen. shares the characters of both the Cimolomyidae and the Eucosmodontidae.' Now it seems more probable to me that it is an eucosmodontid.

The Asiatic records of Paleocene multituberculates are extremely small. Only two taeniolabidoid genera *Prionessus* and *Sphenopsalis* are known from Khashaat (Gashato) and Naran Bulak localities, from beds belonging to either the Paleocene or Eocene (Matthew *et al.* 1928; Szalay & McKenna 1971).

The late Cretaceous multituberculate records in North America begin with the early Campanian Upper Milk River Formation (Fox 1971, 1972). Younger than the Upper Milk River Formation is the Middle Campanian Judith River Formation (Sahni 1972). Beginning with the Judith River Formation there is a nearly continuous multituberculate record in North America through the late Eocene (Granger & Simpson 1929; Jepsen 1930, 1940; Clemens 1963*b*; Lillegraven 1969 and others). The multituberculate assemblages in the Upper Milk River and Judith River Formations are very different from that in the Barun Goyot Formation and in the younger Djadokhta Formation in Asia. In the Campanian of North America, in contradistinction to the conditions in Asia, the Ptilodontoidea prevail over the Taeniolabidoidea.

* In the present paper Sloan & Van Valen's (1965) division of Cretaceous and Tertiary Multituberculata into the Ptilodontoidea and Taeniolabidoidea is tentatively accepted, although I believe that these suborders do not form natural units. The North American taeniolabidoid family Cimolodontidae probably arose independently from the Taeniolabididae and Eucosmodontidae which are of Asian origin. Formal modification of this classification requires, however, a detailed comparative study of North American and Asian multituberculates.

The only taeniolabidoid family represented in these formations are the Cimolomyidae (unknown outside of North America), represented by two genera: *Meniscoessus* and *Cimolomys*. The familial and ordinal assignment of the genus *Viridomys* Fox from the Upper Milk River Formation is uncertain, and that is why *Viridomys* is not shown in Figure 1. In addition to these three genera, in the Campanian of North America three ptilodontoid families are present: the Cimolodontidae, represented by *Cimolodon*, the Ptilodontidae, represented by *Kimbetohia* and the Neoplagiaulacidae (former Ectypodontidae), represented by *Cimexomys* and *Mesodma*. All the multituberculate genera recorded in the Judith River Formation continue through the Upper Edmonton and Lance Formations (Lillegraven 1969; Clemens 1963b) to the latest Cretaceous Hell Creek Formation (Sloan & Van Valen 1965; Van Valen & Sloan 1966). In addition, in Lance Formation the ?ptilodontoid *Essonodon*, which continues through Hell Creek Formation, made its appearance and in Hell Creek the eucosmodontid *Stygimys* and taeniolabidid *Catopsalis* appear.

The above data show that there are no pre-Campanian late Cretaceous multituberculate records in North America. In the Campanian only one taeniolabidoid family, Cimolomyidae, endemic for North America, is present on this continent, accompanied by the representatives of three ptilodontoid families: the Neoplagiaulacidae, Cimolodontidae and Ptilodontidae. By the time of the latest Cretaceous two other taeniolabidoid families, known from older beds of Asia, reach North America: the Taeniolabididae and Eucosmodontidae; while two taeniolabidoid families, the Sloanbaataridae and Chulsanbaataridae, remain so far monotypic and endemic for Central Asia.

The Paleocene and Eocene multituberculate records of North America bring the continuation of the Cretaceous genera and in addition the appearance of new genera in each of the families known in latest Cretaceous on this continent. Within the Neoplagiaulacidae, in addition to *Cimexomys*, which continues in early Puercan, and *Mesodma*, which continues through Clarkforkian (Krishtalka 1973), the four new genera made their appearance: *Mimetodon*, *Ectypodus*, *Neoplagiaulax* and *Parectypodus*, the three latter continuing in the Eocene. One new representative of the Cimolodontidae is recorded: *Anconodon*, while within the Ptilodontidae, in addition to *Kimbetohia*, which continues through Puercan time, two new genera, *Ptilodus* and *Prochetodon*, made their appearance, the latter continuing into the Eocene (Graybullian).

Within the Eucosmodontidae, in addition to *Stygimys*, which continues through the Torrejonian, *Eucosmodon* appears in the Puercan and continues through Torrejonian time, while *Microcosmodon*, *Pentacosmodon* and *Neoliotomus* appear in the Tiffanian, the *Neoliotomus* continuing through the Graybullian.

In the Paleocene the multituberculates appear again in Europe, in France (Russell 1964) and are represented there by the North American genus *Neoplagiaulax* (representative of the Neoplagiaulacidae) and the endemic genus *Liotomus*, assigned by Van Valen & Sloan (1966) to the Cimolodontidae.

DISCUSSION

The data presented above show that during the 160 million years of presumable multituberculate evolution, there are gaps in time records that embrace at least 73 million years. This shows that our information on the development of this group, especially in the first half of its evolution, is extremely scanty.

The oldest Kimmeridgian multituberculates (Hahn 1969, 1971) already show all the essential features of this group. The subsequent evolution concerned only the changes of the dentition, the reduction of the first incisors, the gradual reduction of the premolars and the change of the premolars from chewing into the cutting type. But the essential features of the multituberculate skull and lower jaw structure are already developed by the Kimmeridgian. In the dentary structure there are no great changes between the Kimmeridgian and Tertiary forms. It should be also added that the multituberculate dentary as early as in Kimmeridgian has an entirely mammalian appearance, which is not the case with other groups of mammals from the same beds (Krebs 1971). This shows that the multituberculates are a group which very early branched off from the main evolutionary line of mammals.

All records of multituberculates are confined only to the three continents of the Northern hemisphere: Europe, Asia and North America. The Harniyidae are known from the Rhaetic of Europe—Switzerland and Great Britain (Peyer 1956; Simpson 1928). The Kimmeridgian multituberculates are known also from Europe only, from the single locality in Portugal (Hahn 1969, 1971). In Purbeck time the multituberculate record has been spread from Europe (Great Britain) to North America (Morrison Formation). One genus (*Ctenacodon*) is common for latest Jurassic of North America and Europe, the others are fairly closely related. The earliest Cretaceous fauna (Wealden) is very poorly known and again only from Europe. The above data may lead to the conclusion that the multituberculates originated in Europe.

More detailed data on the evolution of this group have been gathered from the Cretaceous period, particularly so from the late Cretaceous. In the second half of the late Cretaceous the multituberculates were found in two continents: in North America (Albian of Texas) and in Asia (Khovboor locality), the age of which it is either Aptian or Albian. Unfortunately, there are no data about the evolutionary level of the multituberculates at that time, except for the statement of Patterson (1956) that the multituberculates from the Albian of Texas belong to the Plagiaulacidae. It appears from the studies of Hahn (1969, 1971) and others, that of the two plagiaulacoid families, the Plagiaulacidae rather than the Paulchoffatidae are the group which gave rise to the Ptilodontoidea.

The question arises whether in the early part of the late Cretaceous the earliest Ptilodontoidea developed in one part of the globe from the Plagiaulacidae and then migrated to other continents, or whether the different families of the Ptilodontoidea developed independently in various areas. The hitherto recorded data speak rather for the second hypothesis. The oldest known

ptilodontoid is the Djadokhta Formation *Gobibaatar*, belonging to the Neoplagiaulacidae. Unfortunately, the mammals of the same age as those from the Djadokhta Formation are not known from Europe or North America. In the Campanian Upper Milk River Formation, which is the youngest late Cretaceous formation yielding the multituberculates in North America, the Ptilodontoidea are already represented by three families, among the representatives of which only one genus, *Cimexomys*, may be regarded as related to the Asian *Gobibaatar*. All other representatives of the Campanian Ptilodontoidea are much more advanced in structure than the possible Campanian descendants of *Gobibaatar* could be at that time. This indicates that most probably the main stock of ptilodontoid families originated in the first half of the late Cretaceous in North America. Whether *Cimexomys* is a descendant of Asian *Gobibaatar* cannot be asserted with certainty, as the skull of *Cimexomys* is not known and it is difficult to base conclusions on the evolution of multituberculate genera on teeth only. Such possibility is, however, very probable. It is thus an open question whether the Neoplagiaulacidae are a group of monophyletic (Asiatic) or diphyletic (Asiatic and North American) origin.

Nothing can be said about the origin of the North American taeniolabidoid family, the Cimolomyidae. This family embraces two genera: *Cimolomys* and *Moeniscoessus*, which in my opinion are not very closely related to each other. Both are poorly known, we do not know their skull structure and the development of the palate. Therefore it is extremely difficult to discuss their origin, and this question must remain open until more material from this family is collected. As far as the origin of the Taeniolabididae and Eucosmodontidae is concerned, the oldest representatives of both families were found in the Djadokhta Formation of the Gobi Desert. It is very interesting that the Djadokhta eucosmodontid *Kryptobaatar* is extremely similar in the general shape of the skull and in the structure of the cheek teeth to the neoplagiaulacid *Gobibaatar*, which occurs in the same formation (Kielan-Jaworowska 1970, 1974). The differences between the two genera in question concern only the shape of the lower jaw and the structure of the incisors, which in *Gobibaatar* are entirely covered by the enamel, while in *Kryptobaatar* the enamel is restricted to the antero-ventral band. It seems that restriction of the enamel to a band must be considered as the specialized character. It follows that the derivation of Taeniolabidoidea from Ptilodontoidea is theoretically the most probable hypothesis, especially considering the similarity of *Gobibaatar* and *Kryptobaatar*. Even though these two are contemporaries, the ptilodontoid *Gobibaatar* appears to have remained very similar to the forms that gave rise to the eucosmodontid *Kryptobaatar*. In the Djadokhta Formation another eucosmodontid, *Bulganbaatar* also occurs, as well as the oldest representatives of the Taeniolabididae: *Djadochatherium* and *Kamptobaatar* (the latter genus is very different from *Djadochatherium*).

The recent findings of a rich multituberculate fauna in the Campanian of the Gobi Desert cast new light on the origin of North American representatives

of the Taeniolabididae and Eucosmodontidae (Kielan-Jaworowska 1974). The eucosmodontid *Bulganbaatar nemegtbaataroides* from the Djadokhta Formation is now regarded as an ancestor of the Campanian (Barun Goyot Formation) *Nemegtbaatar gobiensis*, which seems to be close to the ancestors of the earliest Paleocene North American eucosmodontid *Eucosmodon* (Fig. 2). The

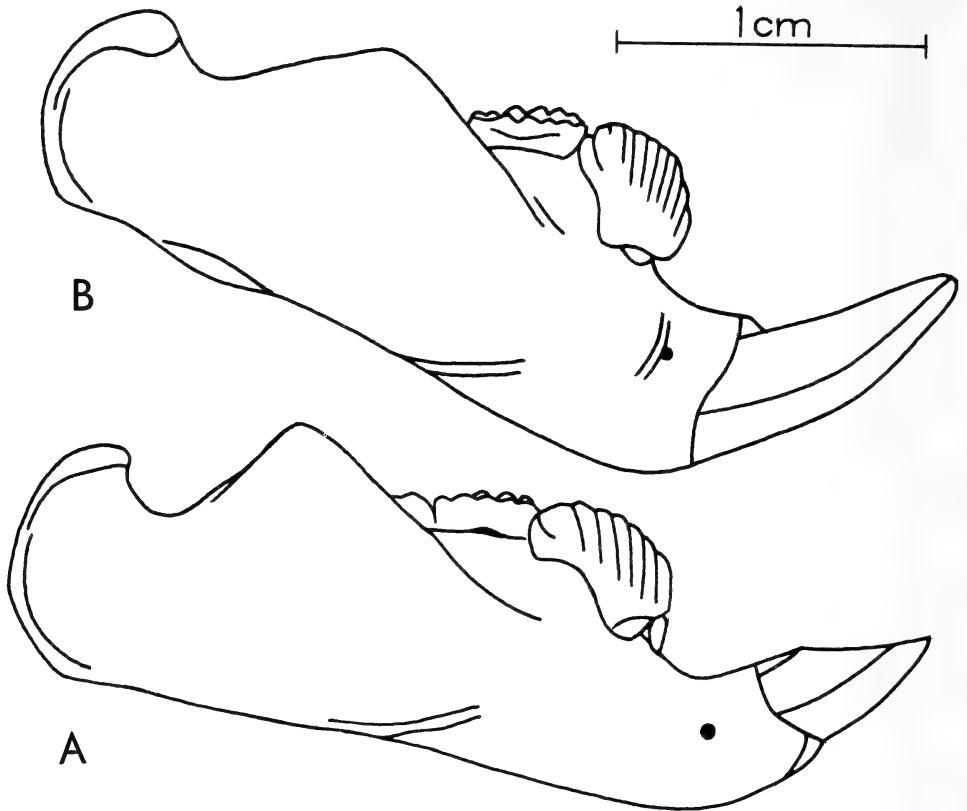


Fig. 2. Comparison of lower jaws in outer view of:
 A. *Nemegtbaatar gobiensis* Kielan-Jaworowska, from the Campanian of Asia. B. *Eucosmodon gratus* Jepsen from the early Paleocene of North America. (A.—After Kielan-Jaworowska 1974. B.—After Jepsen 1940.)

Djadokhta Formation taeniolabidid *Djadochtatherium matthewi* is regarded as an ancestor of the Campanian (Barun Goyot Formation) *Djadochtatherium catopsaloides*, which again is an ancestor of the North American species *Catopsalis joyneri*, known from the latest Cretaceous Hell Creek Formation (Fig. 3).

This indicates that two taeniolabidoid families, the Eucosmodontidae and Taeniolabididae, first developed in the early part of the late Cretaceous in Asia and reached North America in the latest Cretaceous.

Nothing is known on the development of the multituberculates in the

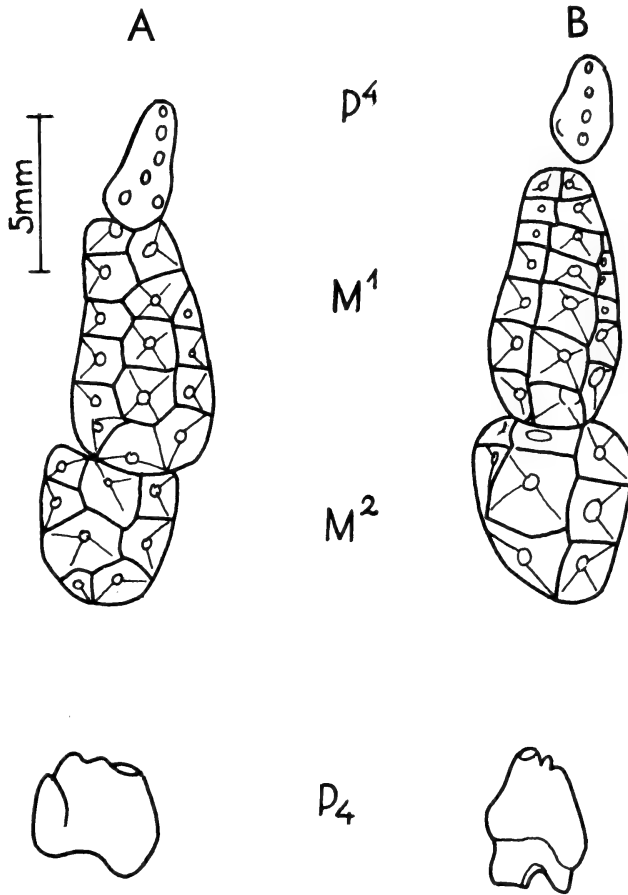


Fig. 3. Comparison of P^4 - M^1 in occlusal view and P_4 in labial view of: A.—*Djadochtatherium catopsaloides* Kielan-Jaworowska from the Campanian of Asia, B.—*Catopsalis joyneri* Sloan & Van Valen, from the latest Maastrichtian of North America. (A.—After Kielan-Jaworowska 1974; B.—After Sloan & Van Valen 1965.)

late Cretaceous of Europe. It is probable that the descendants of European Jurassic multituberculata will be found in Cretaceous and Tertiary strata of this continent. The only known so far early Tertiary representatives of the multituberculata found there, appear to be closely related to the North American forms.

CONCLUSIONS

It appears from the data presented above that in the late Cretaceous three multituberculata lines invaded North America from Asia. One of them (not very certain), the *Gobibaatar* → *Cimexomys* line, belongs to the pre-Campanian

migration, while two others, the *Djadochtatherium* → *Catopsalis* line and the *Nemegtbaatar* → *Eucosmodon* line, belong to the post-Campanian migration. There are no data which indicate that any of the multituberculate groups that flourished in the Cretaceous of North America reached Asia in the late Cretaceous. It follows that in the late Cretaceous the connections between these continents allowed the migration from Asia to North America, but not vice versa.

This conclusion, based on the evolution and distribution of the multituberculates, is partly supported by the data on the distribution of the marsupial and eutherian mammals.

A major component of the North American late Cretaceous mammalian fauna consists of marsupials. As far as the occurrence of marsupials in Asia is concerned, it has been generally accepted until recently that this group never reached Asia. Butler & Kielan-Jaworowska (1973) have shown that two late Cretaceous Asian genera, *Deltatheroides* and *Deltatheridium*, assigned to the Deltatheridiidae, have a marsupial dental formula; however, they classified the Deltatheridiidae as Theria of metatherian-eutherian grade. There is no evidence that any of the late Cretaceous North American marsupials migrated to Asia.

With regard to Cretaceous Theria from North America, Slaughter (1971) believes that among the therians from the Albian of Texas true eutherians occur.

Present knowledge on the early evolution of both eutherian and marsupial mammals is too limited to draw a conclusion concerning the place of origin of both groups. However, even now it can be stated that some of the North American latest Cretaceous eutherian mammals are of Asiatic origin, which has been suggested earlier by Lillegraven (1969).

Simpson (1962) recognized three main paths of faunal interchange for land animals: corridors, filters, and sweepstakes routes. The faunistic differences between Asia and North America in the late Cretaceous are so great that one can reasonably conclude the absence of a corridor. If there was a land connection between these continents one should assume the existence of a filter which prevented the marsupials and certain North American dinosaurs from invading Asia. Such a filter could be the cold climatic zone in north-eastern Siberia, which would be in agreement with the position of the north pole in this region in the late Cretaceous. However, the filter (in Simpson's sense) acts in both directions while the evidence presented in the present paper shows that with respect to mammals this filter acted in one direction only. While the Asiatic multituberculates and eutherians invaded North America, neither the marsupials nor the North American multituberculates reached Asia in the late Cretaceous. The sweepstakes route, in contradistinction to the filter, usually permits rare migrations in one direction only.

An analysis of the late Cretaceous mammalian fauna of Asia and North America leads to the conclusion that these continents were probably separated by a barrier, possibly by marine straits, and the faunal interchange was of the

sweepstakes route type. The existing currents allowed occasional drifts of some invaders from Asia to North America but not vice versa.

The limitation of the present hypothesis is that it is based on the study of the mammals only. Detailed comparisons of other land vertebrates that occur in the Cretaceous of both continents are needed to support or contradict the above hypothesis.

SUMMARY

The stratigraphical and geographical distribution of all described multituberculate genera is discussed. It is shown that the Multituberculata originated in the early Mesozoic in Europe and then migrated to North America and Asia. In the Cretaceous of Asia the Taeniolabidoidea prevail, while in North America it is the Ptilodontoidea. The two taeniolabidoid families: Eucosmodontidae and Taeniolabididae originated in Asia and reached North America in the latest Cretaceous. In addition to the multituberculates, the eutherian mammals migrated from Asia to North America during the late Cretaceous, while the groups of North American origin (e.g. late Cretaceous marsupials and certain multituberculates) never reached Asia. The possibility of a land connection between Asia and North America with a cold zone filter preventing the migration of certain vertebrates is discussed. But inasmuch as the existing barrier, with respect to mammals, allowed one-way migrations only, it is concluded that the faunal interchange between Asia and North America in the late Cretaceous was not of the filter type, but rather of the sweepstakes route type. These continents were probably separated by marine straits and the currents allowed occasional drifts from Asia to North America, but not vice versa.

ACKNOWLEDGEMENTS

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ADDENDUM

After this paper was submitted for publication, two papers relevant to the problems discussed herein appeared.

(1) Lillegraven (1972) gives a preliminary description of mammals from the El Gallo Formation (late Campanian) of Mexico. In this paper he described M^1 of ?*Stygimys* sp. This tooth is very similar to that of the Asian *Nemegtbaatar* and probably belongs to the Eucosmodontidae. Be this the case, the Eucosmodontidae should have migrated from Asia to North America at the middle-late Campanian boundary, and not in Maastrichtian as may appear from the data discussed herein and from Figure 1.

(2) Hahn (1973) erects for the Haramiyidae the new suborder Haramiyoidea, within the Multituberculata. This suborder could not be introduced into Figure 1.

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DÉRIVE DES CONTINENTS ET PALÉONTOLOGIE: QUELQUES RÉFLEXIONS

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(Avec 3 figures)

La théorie de la dérive des continents a été proposée avec netteté pour la première fois par A. Wegener en 1915. On insiste souvent sur le fait que Wegener avait eu des précurseurs mais ceux-ci tels que Bacon ou le père Placet étaient des philosophes et leur intuition n'avait pas de fondement vraiment scientifique. Il est indéniable au contraire que les idées de Suess concernant l'existence d'un continent de Gondwana regroupant l'Amérique du Sud, l'Afrique du Sud, l'Inde et Madagascar en une seule unité, impliquaient une séparation d'une masse continentale unique en blocs distincts et que l'existence du Gondwana devrait être un important argument en faveur de la théorie de Wegener. La théorie de Wegener toutefois ne permettait pas d'expliquer pourquoi les masses continentales s'étaient séparées. Les travaux récents ont abouti à élaborer la théorie dite de la tectonique des plaques qui complète, mais sans l'infirmer en général, la théorie de Wegener.

Les critiques formulées à l'encontre de la théorie de Wegener avant guerre étaient surtout d'ordre géophysique: on n'avait pas observé de façon incontestable de variations de latitudes, d'écartements manifestes de continents (depuis lors le paléomagnétisme a permis de calculer des paléolatitudes). Les paléontologistes dans l'ensemble n'étaient pas hostiles à la théorie de Wegener, mais ils pensaient que les connexions continentales, auxquelles ils devaient faire manifestement appel, devaient être expliquées par les géologues et les géophysiciens, ces problèmes ne pouvant être résolus par la Paléontologie; l'hypothèse évidemment curieuse des ponts continentaux ne faisait que traduire l'affirmation de l'existence de connexions intercontinentales. Elle ne semble plus avoir été prise bien au sérieux dans les années 1940 'Chose curieuse, cette théorie commode, voire nécessaire, ne peut être prouvée par aucun argument d'ordre géologique' (R. Furon).

Actuellement le faisceau de preuves géophysiques assemblées en faveur de la théorie de la dérive continentale est réellement impressionnant (voir par exemple Tarling 1971, Coulomb 1969, etc.) et il est probablement temps d'essayer de voir comment cette théorie s'accorde avec les résultats de la Paléontologie. Il y a eu d'ailleurs à ce propos de nombreux colloques ou congrès où ce problème a été débattu (Congrès du Gondwana de Buenos Aires 1967 et du Cap 1970; Congrès du Nato Advanced Study Institute à Newcastle 1972; Congrès géologique international de Montréal 1972; Congrès zoologique international de Monaco 1972, etc). On doit constater qu'en particulier au

Congrès de Montréal les discussions entre 'mobilistes', partisans de la dérive, et 'fixistes' adversaires de celle-ci, ont été souvent très vives, voire passionnées. Notons brièvement que si le terme de mobiliste peut-être maintenu, celui de fixiste doit être résolument proscrit, puisque ce terme est déjà employé en Géologie dans le sens d'adversaire de l'Evolution ('Cuvier était fixiste') et que son introduction en tectonique ne peut être que source de confusion. Je ne chercherai pas ci-dessous à trouver des preuves paléontologiques en faveur de la théorie de Wegener ou contraires à celle-ci; je chercherai simplement à voir comment on peut utiliser les fossiles en tant que témoins de la paléogéographie continentale.

L'idée même du continent de Gondwana a été fondée sur des ressemblances de composition floristique. Ainsi cette flore se caractérise depuis le Stéphanien jusqu'au début du Trias par la présence des genres *Glossopteris* et *Gangamopteris*, sans Sigillaires ni Lépidodendrons, ni Calamites mais à Lycophytes et Conifères distincts de ceux de l'hémisphère nord. Les travaux de Zalesky (1932) affirmant la présence d'une flore à éléments gondwaniens dans le bassin du Kouznetzk semblent reposer sur des erreurs de déterminations (Emberger). L'individualité de la flore gondwanienne paraît donc bien certaine; s'en suit-il que la répartition des Plantes est un bon critère pour affirmer l'existence d'un continent disparu? Nous ne le pensons pas: en effet les spores des plantes terrestres (ou les 'graines' des Ptéridospermées et celles des Conifères) sont facilement transportables soit par le vent, soit par les animaux volants, soit par les courants. D'ailleurs la carte des empires floraux actuels (voir Emberger 1968: 640, fig. 740) ne correspond nullement aux continents: par exemple (Fig. 1), l'Afrique du Nord a une flore holarctique et l'Afrique est traversée par

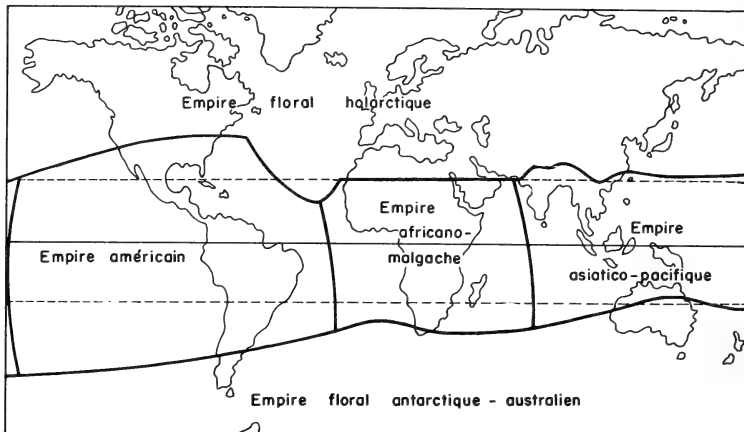


Fig. 1. Les empires floristiques du monde actuel (d'après Emberger).

la limite entre l'empire holarctique et l'empire africano-malgache; de même l'Amérique du Nord est séparée en deux par la frontière de l'empire holarctique et de l'empire américain, etc. De sorte que, s'il existe bien une flore à *Ganga-*

mopteris, celle-ci ne *prouve* pas pour autant l'existence d'un continent de Gondwana; cependant le fait que cette flore se retrouve en Amérique du Sud, en Afrique du Sud, à Madagascar, aux Indes et en Australie et pas ailleurs est évidemment une forte *présomption* en faveur du continent de Gondwana.

L'étude des Invertébrés fossiles peut évidemment permettre des comparaisons intéressantes s'il s'agit d'Invertébrés exclusivement continentaux. Qu'en est-il au contraire des Invertébrés marins? Les Invertébrés marins à larves planctoniques—et ils sont très nombreux—ont évidemment des possibilités d'expansion d'autant plus grandes que la durée de vie larvaire est plus longue, comme l'a montré Mortensen (voir Ekman 1953); ces Invertébrés doivent logiquement avoir une répartition soumise à des conditions de température, mais elle doit être très vaste. Il en est probablement de même des Algues marines. Il faut aussi se souvenir que dans une telle discussion les arguments négatifs ont moins de valeur que les arguments positifs: ainsi Meyerhoff & Teichert notent la présence en Australie occidentale de séquences permianes très épaisses à fossiles à affinités téthysiennes; ces auteurs en déduisent que les reconstitutions paléogéographiques (Ahmad, Veevers) qui raccordent l'Australie à l'Inde sont fausses; mais ces schémas pourraient être partiellement incorrects sans que l'existence d'un continent de Gondwana soit mise en question. L'argument positif favorable est la ressemblance des formes de Stégocéphales entre l'Inde, l'Australie, l'Afrique du Sud (présence de Brachyopidés en Australie [*Blinasaurus*] et aux Indes) et la présence de Procolophonidés en Australie (Bartholomai & Howie 1970; voir Romer 1972: 8) et en Afrique du Sud. Du point de vue paléobiogéographique, les arguments admettant le rattachement de l'Australie à l'Inde nous paraissent donc pour l'instant assez peu nombreux. Se fondant d'autre part sur la répartition des Invertébrés fossiles dans la nature actuelle, beaucoup d'auteurs font appel à la notion de gradient de

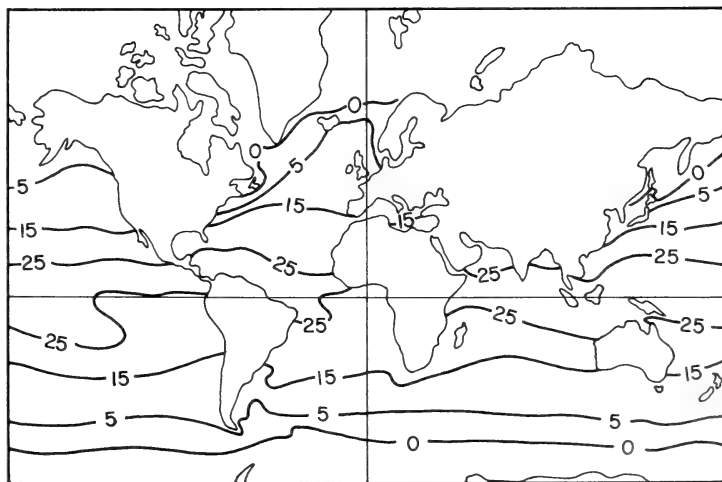


Fig. 2. Isothermes d'hiver (dans les deux hémisphères) (d'après Stehli).

diversité pour déterminer des paléolatitudes. Le principe de cette méthode est simple: on constate que sur la terre actuelle, dans l'ensemble, le nombre des différentes espèces décroît régulièrement de l'équateur au pôle. Or les températures de la mer sont représentées par des isothermes qui, pour des raisons particulières non liées au rayonnement solaire (courants, vents locaux, etc.), ne sont pas parallèles à l'équateur (Fig. 2). On peut alors par des méthodes mathématiques éliminer en quelque sorte ces phénomènes 'de bruit' et construire des isothermes (Fig. 3) qui apparaissent être essentiellement fonction de

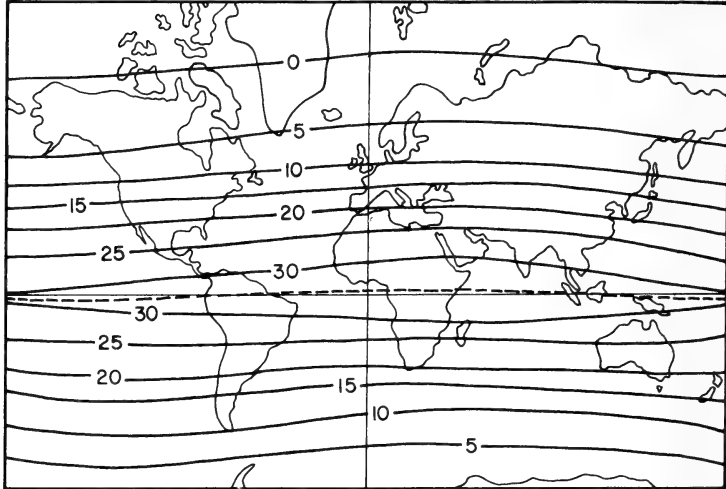


Fig. 3. Diagramme obtenu à partir du précédent (Fig. 2) en corrigeant les effets de bruit (d'après Stehli).

la latitude (Stehli 1968); on constate alors que, dans la nature actuelle, les gradients de diversité de tous les groupes majeurs d'organismes à vaste distribution sont fonction de la latitude et en général (il y a évidemment des exceptions telles que les Pingouins) atteignent leur maximum à l'équateur. Appliquée aux fossiles, cette méthode devrait permettre de localiser pôles et équateur à une époque géologique donnée et donc de savoir par rapport à l'actuel s'il y a eu ou non dérive.

Il n'est pas sûr que, même si on pouvait connaître de façon précise et complète l'ensemble des fossiles ayant vécu pendant un étage donné, une telle méthode serait logiquement fondée. Il est évident comme l'a déjà noté Mamet (1972) que le gradient de diversité est d'abord fonction de nos connaissances et que celui-ci sera plus élevé dans les régions de la Terre les mieux connues. De plus, il faut être sûr que les fossiles d'un même étage sont bien contemporains; or un étage, surtout au Primaire, peut être très long; il faudrait restreindre la méthode à une seule assise mais la stratigraphie n'est pas en mesure actuellement de préciser à distance les synchronismes à cette échelle (c'est la restriction temporelle de Mamet [1972]). De plus il est bien clair que le témoignage des

fossiles n'est que partiel et que rien ne permet de supposer que les gradients de diversité des fossiles d'une même assise sont bien proportionnels à ceux des organismes qui vivaient effectivement lors de la formation de l'assise. Mais surtout la méthode suppose qu'il y ait toujours eu sur la terre une zonation climatique du type actuel, c'est-à-dire liée à des calottes glaciaires sur les pôles: or les glaciations ne sont pas connues pendant le Secondaire et le Tertiaire par exemple et la distribution des êtres vivants en fonction de la latitude n'est peut-être caractéristique que du Quaternaire; il n'est pas sûr que le principe des causes actuelles s'applique effectivement ici (Olson 1972, Schwarzbach 1963). Enfin comme le souligne justement Mamet: 'Les variations de température de l'eau de mer en un point donné étant bien plus influencées par la bathymétrie que par la latitude, nous devons nous borner à comparer des biota de même bathymétrie.'

Dans une communication intéressante au Congrès de Montréal, M. Mamet a montré que les microflores algales du Viséen (couches de passage du Viséen moyen au Viséen supérieur) se groupaient d'une façon similaire à la distribution actuelle des températures des eaux de l'hémisphère nord; cette distribution semble donc en désaccord avec la plupart des reconstitutions paléogéographiques admettant des mouvements importants des continents par rapport à leur latitude actuelle. Cette conclusion (d'ailleurs beaucoup plus nuancée dans la conclusion de cet article que dans le résumé) est une interprétation d'une distribution microfloristique remarquable mais cependant trop partielle pour permettre d'en tirer des déductions sûres; ce n'est que si on avait affaire à des répartitions variables suivant les latitudes sur toute la terre et pour des groupes différents qu'une conclusion 'fixiste' pourrait être considérée comme valable. Rappelons à ce propos que le Carbonifère inférieur est considéré classiquement par les géologues comme une période de climat chaud et uniforme (Schwarzbach 1963), ce qui n'est pas conforme à l'observation de B. Mamet et semblerait plutôt indiquer que cette distribution de la microflore n'est pas la conséquence des latitudes, mais d'autres causes telles que par exemple l'existence d'un courant froid local, de variations de salinité (?), etc. De plus, il est évident que, dans un tel exemple, l'objection du pourcentage de fossilisation joue et que cette raréfaction peut n'être due qu'à une insuffisance de témoins fossiles. Il nous paraît, dans ces conditions, nettement abusif de conclure avec Teichert que les gradients de diversité spécifique sont symétriques par rapport à l'Equateur actuel; nous ne croyons pas d'ailleurs l'espèce suffisamment bien définie en Paléontologie (ce n'est souvent guère plus qu'un numéro de catalogue de collection) pour qu'une telle assertion soit admissible. On doit noter aussi que des fossiles identiques surtout sensibles aux variations de température peuvent vivre à l'Equateur, en profondeur, et, en surface, dans les zones actuellement tempérées, et ainsi que certains genres se retrouvent dans les eaux superficielles au Nord et au Sud de l'Equateur: c'est le phénomène de la bipolarité; la comparaison des fossiles ne peut donc avoir de sens que dans des conditions de faciès comparables, mais celles-ci doivent être souvent difficiles

à rétablir. Pour cette raison, comme par suite, des autres arguments cités ci-dessus, la méthode des gradients de diversité nous paraît inapplicable aux organismes fossiles.

Les Vertébrés terrestres nous paraissent seuls des fossiles de choix pour juger de la valeur de l'hypothèse de la dérive des continents; les Vertébrés marins, au contraire, sont en général peu caractéristiques d'une région: certains genres de Poissons sont pratiquement répartis dans toutes les mers à une même époque: les genres *Boreosomus*, *Perleidus*, *Australosomus* sont au Trias inférieur connus au Groenland, au Spitsberg, en Angola, à Madagascar etc. Toutefois les Vertébrés marins des mers épicontinentales peuvent être très localisés: c'est le cas des Placodontes. De même il est probable que la répartition géographique des Reptiles volants, des Oiseaux et des Cheïroptères ne peut guère fournir, au sujet du problème de la dérive, des renseignements faciles à interpréter. Mais en raison de l'évolution qui est beaucoup plus rapide en général chez les Vertébrés que chez les Invertébrés, les Vertébrés terrestres nous permettent d'affirmer l'existence de phénomènes de dérive. Ainsi, si nous observons dans deux continents aujourd'hui séparés deux faunes de Vertébrés ayant même composition globale dans deux formations correspondantes, puis si, dans les formations plus élevées, nous trouvons des faunes de Vertébrés de plus en plus distinctes dans les assises plus jeunes, on doit en conclure que les deux masses continentales ont été continues et se sont ultérieurement séparées, probablement par dérive des continents puisque c'est le seul processus de séparation en faveur duquel nous avons des arguments géologiques et géophysiques. Un des exemples les plus classiques est la parenté des faunes entre l'Afrique du Sud et l'Amérique du Sud. Rappelons par exemple, et sans entrer dans les détails, que le Mésosaure n'est connu qu'en Afrique du Sud (formation de Dwyka) et au Brésil. De même, les fouilles récentes de Bonaparte et de Romer ont montré que l'on retrouvait au Trias inférieur non seulement les mêmes familles de Reptiles mais les mêmes genres. Les genres sud-africains *Cynognathus* et *Kannemeyeria* sont connus à la fois en Argentine et dans le Karroo; un Cynodonte en Argentine (*Colbertosaurus*) est, comme le genre *Diademodon* d'Afrique méridionale, un Gomphodonte. Au Trias moyen, les ressemblances sont encore très marquées (présence de Gomphodontes évolués et de Rhynchocéphales des deux côtés de l'Atlantique).

Les travaux récents de Colbert concernant l'Antarctide ont aussi mis en évidence l'existence de relations fauniques entre l'Afrique du Sud et l'Antarctide: on sait que ce savant a montré la présence dans ce continent d'un Lystrosaur (qui appartiendrait même, selon Colbert, à l'espèce *L. murrayi*, comme en Afrique du Sud), d'autres Thérapsidés, de petits Thériodontes et d'un Labyrinthodonte; c'est une faune qui rappelle celle du Karroo et le fait est d'autant plus remarquable qu'aujourd'hui l'Antarctide est très isolée de tous les autres continents.

De toute façon, Piveteau a montré depuis longtemps déjà, quand il a fait connaître la présence d'un Dicynodonte en Indochine, que le continent de

Gondwana ne devait pas en tout cas être considéré comme isolé; des migrations ont du être possibles à partir de Gondwana et c'est la même explication que l'on peut donner de la présence de *Lystrosaurus* accompagné de restes de grands Thériodontes au Turkestan chinois (Sinkiang; formation de Tunghungshan). Il est certain que, comme groupes, les Thériodontes et les Dicynodontes ont eu une répartition quasi-mondiale; on en connaît classiquement en Europe et un Dicynodonte, proche de *Kannemeyeria*, vient d'être découvert en Afrique du Nord. Les Thérapsidés sont surtout abondants en Russie, en dehors de l'Afrique du Sud. Ce n'est donc que la présence de genres ou d'espèces, identiques ou voisins, qui peut être interprétée comme conséquence de la dérive et encore peut-il y avoir des exceptions.

De même en ce qui concerne l'hémisphère nord, la présence des Pélycosaures exclusivement aux Etats-Unis, en Europe occidentale et en URSS, est un argument fort en faveur de l'existence de la Laurasia au Permien inférieur. L'identité spécifique de deux Vertébrés fossiles d'un même genre dans des continents différents mais autrefois réunis doit cependant être très rare; les Vertébrés terrestres semblent en effet plus dépendants morphologiquement du milieu que les Vertébrés marins; ainsi il est rare de trouver des Stégocéphales de mêmes genres dans des régions différentes du monde, comme si ces animaux étaient particulièrement sensibles aux conditions locales et subissaient facilement la ségrégation géographique. Enfin il serait absurde d'essayer d'utiliser des gradients de diversité pour les Vertébrés terrestres, car les gisements sont si rares et si localisés que de tels gradients n'ont certainement aucun sens. Certains Vertébrés terrestres de petite taille comme les Rongeurs, certains Singes etc. . . . peuvent avoir été transportés sur des radeaux naturels par des courants ('islands hoppers'); ces Vertébrés sont évidemment sans intérêt pour mettre en évidence des phénomènes de dérive.

L'étude du Karroo malgache n'apparaît pas favorable à l'existence d'un continent Afrique-Madagascar-Indes; en effet il n'y a pas d'espèces communes de Stégocéphales à Madagascar et en Afrique du Sud (du moins pas d'espèces certaines) et pour l'instant aucun Reptile mammalien n'est connu à Madagascar; les faunes de Poissons d'eau douce sont aussi différentes; le rapprochement avec l'Angola est plus net (Lehman *et al.* 1959). D'après les schémas paléogéographiques des mobilistes, Madagascar était au Permo-Trias plus au N qu'aujourd'hui, étant coincée entre l'Afrique et l'Inde environ au niveau de la Somalie ex-italienne; mais ces différences de faune avec l'Afrique du Sud peuvent, dans le cas de Madagascar, être la conséquence de circonstances fortuites: les formations sédimentaires d'origine continentale sont relativement peu développées à Madagascar; les Stégocéphales continentaux (Benthosuchides, Rhinésuchides) y sont connus dans des formations marines (Lehman 1961, 1966). Quant aux Thérapsidés il est possible que l'on ne les ait pas encore découverts. Cet exemple illustre le fait que seules les *présences* de Vertébrés fossiles peuvent servir d'argument valable, mais que les *absences* sont d'interprétation dangereuse. Les découvertes toute récentes d'un Paréiasaure et d'un

Cotylosaure au Niger, d'un Dicynodonte au Maroc montrent que l'inventaire paléontologique mondial est loin d'être achevé.

Enfin il est clair que la distribution des Vertébrés terrestres, si elle dépend de conditions géographiques, est aussi fonction de nombreux autres facteurs; la mer n'est pas la seule barrière écologique possible. Il ne faut donc pas s'attendre à ce que les données concernant les paléofaunes terrestres de Vertébrés traduisent de façon fidèle la disposition et les rapports des anciens continents.

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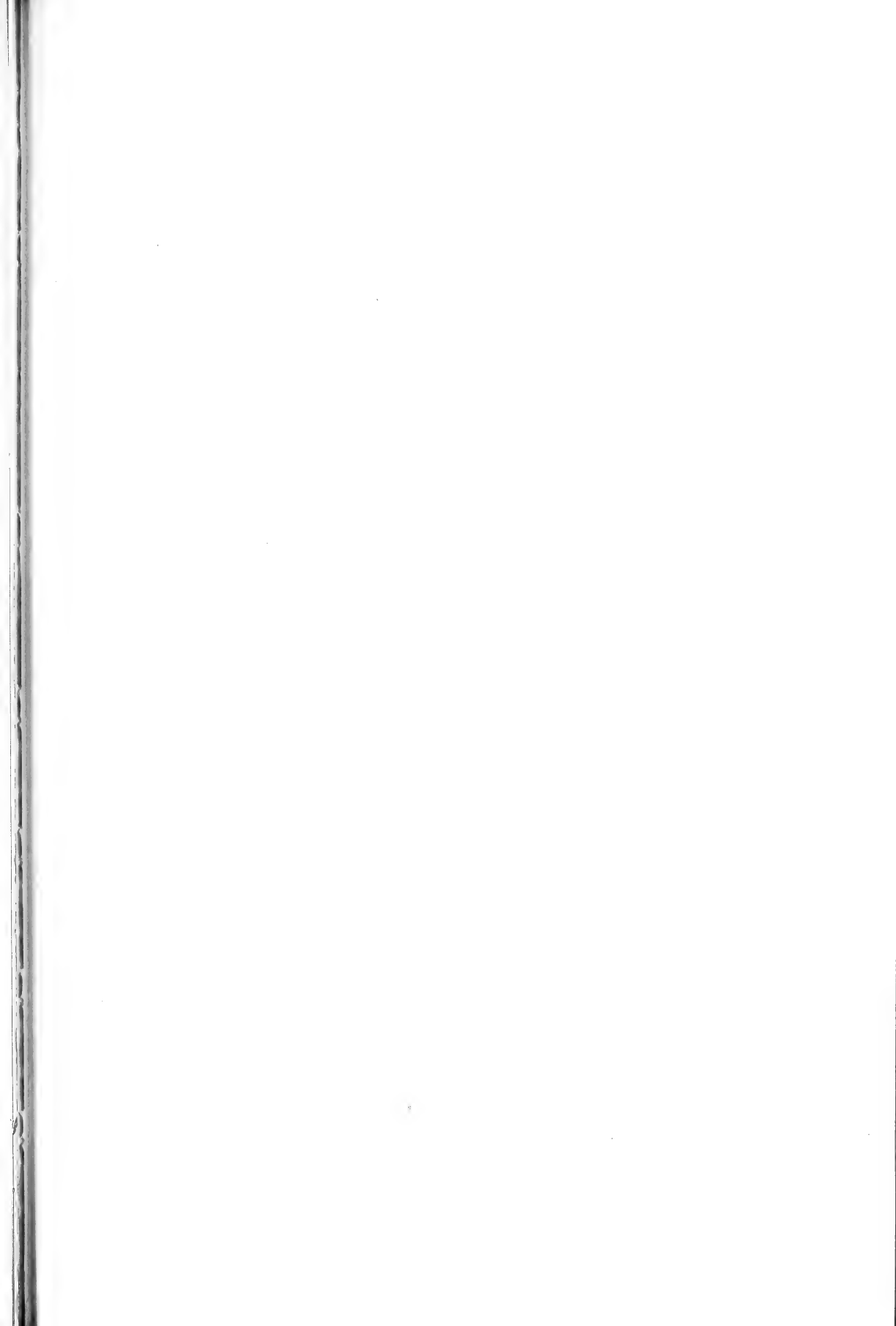
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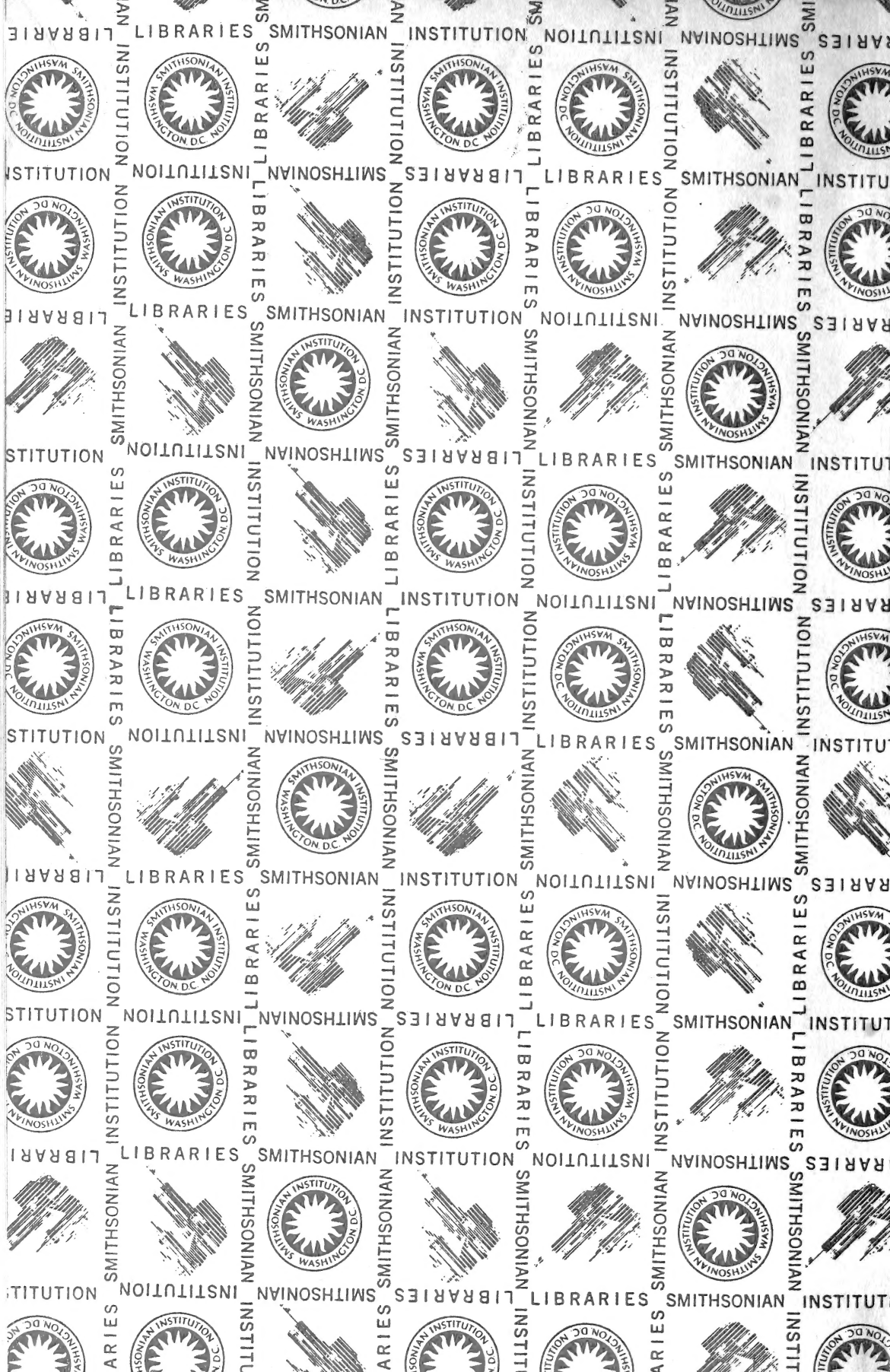
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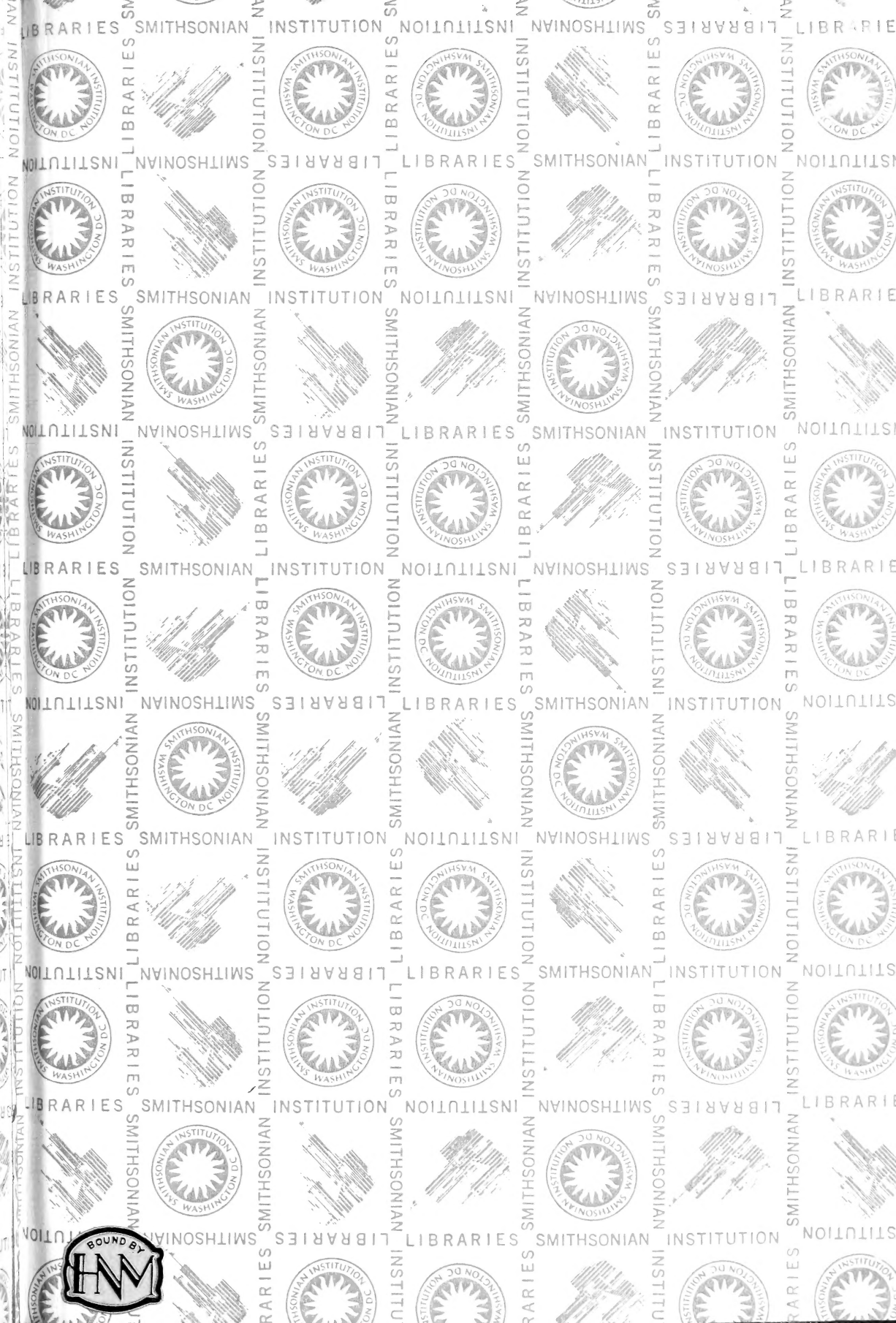
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