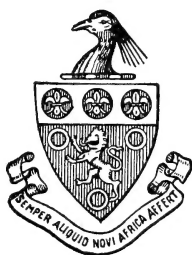


ANNALS
OF THE
SOUTH AFRICAN MUSEUM

VOLUME XXXI

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VOLUME XXXI



PRINTED FOR THE
TRUSTEES OF THE SOUTH AFRICAN MUSEUM
AND THE
GEOLOGICAL SURVEY OF SOUTH AFRICA
BY NEILL AND CO. LTD., 212 CAUSEWAYSIDE, EDINBURGH.
1934-1950.



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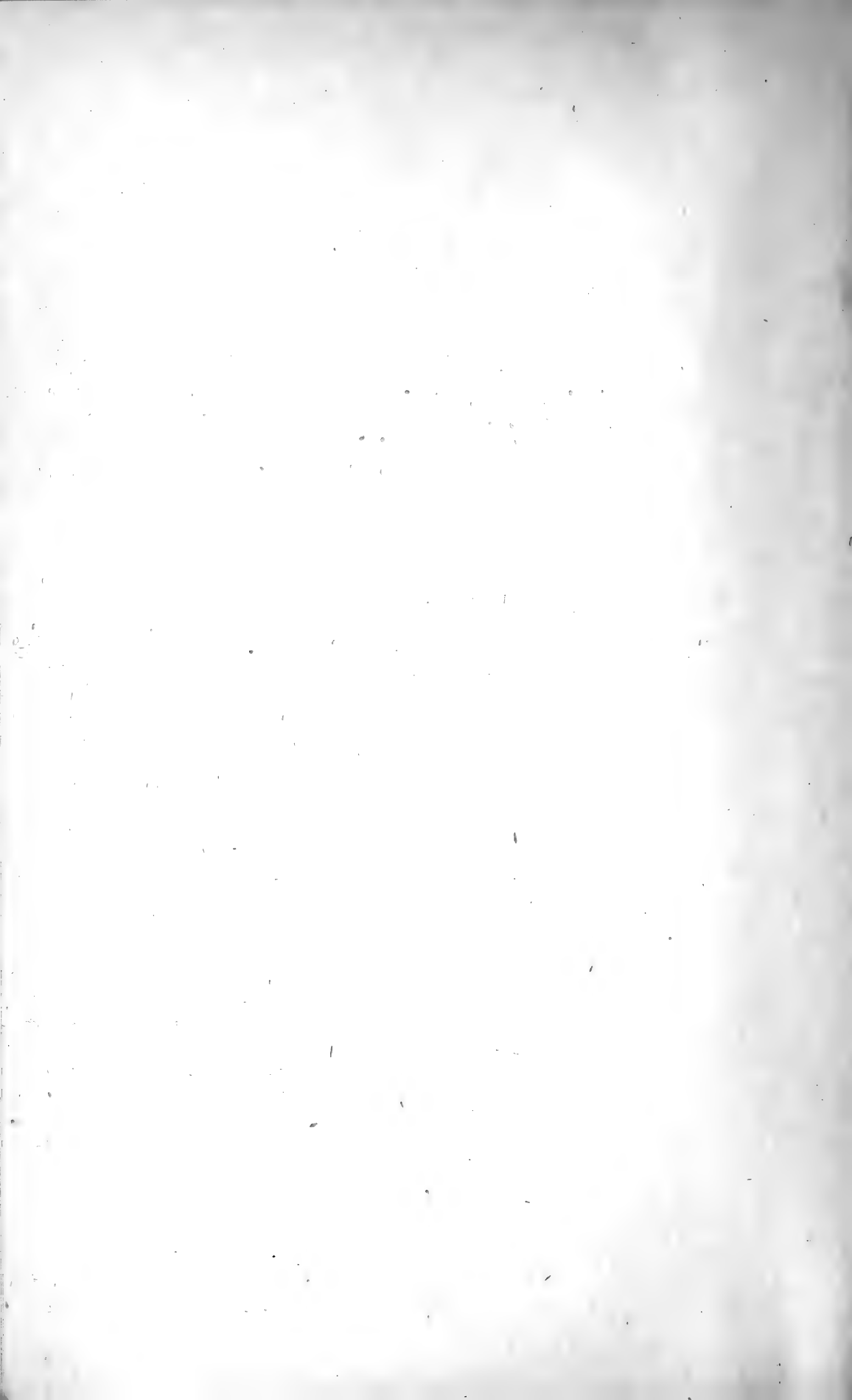
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ANNALS

OF THE

SOUTH AFRICAN MUSEUM

VOLUME XXXI.

DESCRIPTIONS OF THE PALAEONTOLOGICAL MATERIAL
COLLECTED BY THE SOUTH AFRICAN MUSEUM

PART I, containing :—

1. *Pareiasaurian Studies.*

Part IX.—*The Cranial Osteology.*—By LIEUWE D. BOONSTRA, D.Sc., Department of Palaeontology, South African Museum. (With Plates I-XXII and Text-figures 1-5.)

Part X.—*The Dermal Armour.* By LIEUWE D. BOONSTRA, D.Sc., Department of Palaeontology, South African Museum. (With Plates XXIII-XXVII.)

Part XI.—*The Vertebral Column and Ribs.* By LIEUWE D. BOONSTRA, D.Sc., Department of Palaeontology, South African Museum. (With Plate XXVIII and Text-figures 1-7.)

2. *Fossil Plants from Fort Grey near East London.* By Prof. R. S. Adamson, M.A., Botanical Department, University of Cape Town. (With 27 Text-figures.)

3. *On some Karroo Fishes from Central Africa.* By S. H. HAUGHTON, B.A., D.Sc., Hon. Keeper of Palaeontological Collections. (With Plates XXIX-XXXI and 2 Text-figures.)

4. *The Phosphatic Nodules of the Agulhas Bank.* (A Study of Submarine Geology.) By L. CAYEUX, Membre de l'Institut, Professor at the Collège de France, Paris. (Translated into English by Dr. S. H. Haughton.) (With Plates XXXII-XXXV.)

ISSUED APRIL 1934. PRICE 20s.

PRINTED FOR THE
TRUSTEES OF THE SOUTH AFRICAN MUSEUM
BY NEILL AND CO., LTD., 212 CAUSEWAYSIDE, EDINBURGH.

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Department of Palaeontology, South African Museum.

(With Plates I-XXII and Text-figures 1-5.)

INTRODUCTION.

IN this paper the skull features are examined more fully than was possible at the time of the publication of "An Attempt at a Classification of the Pareiasauria based on Skull Features." An examination of the systematic aspect of the cranial features will now better serve to augment the conclusions arrived at in the series of papers which have dealt with the postcranial skeleton, where the tentative preliminary classification has been tested and found to hold good in all but one case, viz. *Platyoropha broomi*. From these papers it has become obvious that the genus *Platyoropha* is invalid. The single specimen referred to it is in reality a member of the genus *Bradysaurus*.

In the preparation of this paper I am greatly indebted to Dr. S. H. Haughton, who has always been ready to offer help by discussion and criticism. I have also had access to his sketches and notes of the material in European institutions. To Mr. J. Hewitt, Director of the Albany Museum, I am grateful for the opportunity of examining the type skull of *Koalemasaurus acutirostris*. Through the kindness of Miss Wilman, Curator of the McGregor Museum, I have been able to study the Pareiasaur material in her charge. To Mr. Barnum Brown and Dr. W. K. Gregory, of the American Museum, I am indebted for the photographs of the Pareiasaurs in that institution.

HISTORICAL.

In his "Descriptive and Illustrated Catalogue of the Fossil Reptilia of South Africa in the Collection of the British Museum," Owen in 1876 described three Pareiasaurs, viz. *Pareiasaurus serridens*, *Pareiasaurus bombidens*, and *Anthodon serrarius*. Notwithstanding the fact that he had three skulls, he did not notice their stegocrotaphic nature, and he classified these three animals as zygodontophic Dinosaurs. The description (pp. 6-8) and two of the illustrations (pls. vi, vii) of *Pareiasaurus serridens* are based on a cast, the original being lost. *Pareiasaurus bombidens*, described (p. 9) and figured (pls. viii, ix), was a species founded on the snout of an animal. Owen confused the mandible with the maxillary portion of the skull, and *vice versa*. The specific differences in his two specimens rested solely on the nature of the teeth. In *P. serridens* there are 15-16 serrate teeth in both upper and lower jaws; but on the next page he says that originally only 14 teeth were counted. In *P. bombidens* there were 19 teeth, which differ in form from those of *P. serridens*, viz. the outer surface of the maxillary teeth are more convex or bulging, the serrations are broader, and some of the linear intervals extend nearer to the base of the crown. *Anthodon serrarius*, described (pp. 14-15) and figured (pl. xiii), differs, according to Owen, from the two species of the genus *Pareiasaurus* "in having the crowns more compressed transversely, and more expanded antero-posteriorly beyond the roots, which are relatively longer and more deeply implanted into the jaw; the crown terminates in a semicircular border, deeply notched, rather crenate than serrate. . . ."

In 1888 Seeley described (pp. 60-77) and figured (pls. xii-xv) a skull of a Pareiasaur from Palmiet Fontein. On plate xvi he also gives the palatal view of the cast of *Pareiasaurus serridens*. Although Owen had based his classification on the teeth, Seeley maintains that this is impossible, and says, "It seems to me that their differentiation must rest upon the form, proportions, and structure of the skulls." But a few lines further on he acknowledges that "As very little is preserved of the skull of *P. bombidens*, and *P. serridens* is only known from the cast of the distorted skull and fragment of the lower jaw, no detailed comparison can be profitably pursued." He then differentiates between *P. serridens* and *P. bombidens*, viz. the former is high and narrow, and the latter depressed and broad. As the specimen from Palmiet Fontein is also depressed and broad it is referred to *P. bombidens*.

In 1892 Seeley obtained another specimen from Tamboer Fontein (skull described, pp. 315–320, figured pl. xx) which he also refers to *P. bombidens* Owen. A third specimen (skull described, pp. 322–329, figured pls. xvii, xviii, xix) from De Bad was described by Seeley as a new species—*P. baini*. The specific differences being “broader and relatively shorter, the rows of palatine teeth are closer together, 16 teeth more slender, smaller, less inflated transversely, overlapping each other less, with the terminal denticles of the crown less prolonged, choana larger, and more elongated.”

Before considering the other Pareiasaurs it will be more profitable to see in what way attempts have been made to settle the taxonomy of these four Pareiasaur specimens. In 1914 Watson defined a number of Pareiasaurian genera. The two of interest here are: *Pareiasaurus*—skull with deep cheek and pointed form, the type skull being the cast made by Owen; *Bradysaurus*—skull depressed and rounded, the type being the De Bad specimen, *Br. baini*. No indication is here given to which genus Owen’s specimen and Seeley’s Palmiet and Tamboer specimens are to be referred; but in a previous paper Watson states that *P. serridens* almost certainly is not congeneric with *P. bombidens*. It would therefore appear that Watson intended the three specimens of *P. bombidens* to be referred to the genus *Bradysaurus*. In their preliminary classification Houghton and Boonstra suggested that Owen’s *P. bombidens* be considered *incertae sedis*, and they proposed to raise Seeley’s two specimens to the rank of a new species—*Bradysaurus seeleyi*. As Owen’s *P. bombidens* certainly cannot be a *Pareiasaurus*, and probably is a *Bradysaurus*, it appears advisable to refer to it as *Bradysaurus? bombidens*.

In 1930 Boonstra described a skull in the collection of the University of Stellenbosch. This was identified as *Pareiasaurus serridens*, and as the type is lost this specimen was proposed as the neo-type. We thus have the following solution:—

Pareiasaurus serridens type skull: Owen’s cast in British Museum.

Neo-type: skull in University of Stellenbosch.

Bradysaurus baini type skull: Seeley’s De Bad specimen in British Museum.

Bradysaurus seeleyi type skull: Seeley’s Tamboer specimen in British Museum.

Bradysaurus? bombidens type skull: Owen’s imperfect specimen in British Museum.

In 1903 Broom (pp. 125–127, pl. xvi) described a nearly complete

specimen as *Pareiasaurus serridens*. Watson subsequently showed that it cannot be referred to this species, and proposed the name *Embrithosaurus schwarzi*. Of this specimen Broom described the teeth, and of the bosses on the skull he gave a detailed account.

In 1910 Broom gave a restored figure of the palate of *Pareiasaurus* (fig. 1) with hypothetical sutures between the various palatal bones and an erroneous suture between the pterygoid and basioccipital. He also mentions (p. 201) a distinct septomaxillary.

In 1912 Versluys gave a good figure of the palate of *Pareiasaurus baini* without attempting to indicate the palatal sutures (fig. R). He also points out Broom's incorrect determination of the pterygoid-basioccipital suture (pp. 364 and 613).

In 1913 Broom and Haughton described (pp. 17-19, pl. v) the skull of a new Pareiasaur, which they named *Pareiasuchus peringueyi*. According to them it differs from the other Pareiasaurs in that the snout is nearly twice as broad as deep, the great size of the temporal roof and the fact that it is turned forwards with a huge rounded boss at the angle, the teeth are relatively larger and flatter than in *Pareiasaurus*, and the cusps are either smaller or more rapidly worn down—there are 13 teeth in the upper jaw with 13-15 cusps. In the same year Broom gave a short account without figures of an imperfect skull, which he called *Pareiasaurus acutirostris*. It differed from the then known Pareiasaurs in being two-thirds their size, and in a few other features.

In 1914 there appeared a photograph, with a short caption, of a skull of a new Pareiasaur, *Pareiasaurus whaitsi*, in the American Museum Journal. In the following year the same illustration is given (fig. 1) accompanied by a short description. It differs from *P. serridens* and *Br. baini* in the much larger size of the orbit and in the lower jaw having two horn-like bosses instead of only one.

In 1914 Watson gave an excellent account of the structure of the Pareiasaurian skull. This was the first account in which an attempt was made to consider the subject morphologically. Previous authors practically confined themselves to vague descriptions of shape and size, with haphazard identification of some of the constituent bones. Watson gives a sketch of the side of the partial skull of *Anthodon serrarius* and the palate of *Bradysaurus seeleyi* with the bones identified, and a good account of the whole skull of a specimen from Hottentots River which he regarded as belonging to *Embrithosaurus schwarzi*. In addition a detailed comparative account is given.

In 1924 Broom described (pp. 499-504, figs. 1-2) the roof bones

of a young skull of a Pareiasaur. In his determinations of some of the bones he rightly differs somewhat from Watson, and, furthermore, reluctantly accepts Watson's classification. The lower jaw and teeth of a new form, *Pareiasaurus strubeni*, is described and figured (pp. 507–508, figs. 5, 6).

Such was the condition when Haughton and Boonstra presented their "Attempt at a Classification of the Pareiasauria based on Skull Features." Here a key was drawn up of 12 genera and 18 species, the basis of the classification being the nature of the teeth, the proportions of the skull, size, and ornamentation. This was followed by an account of the brain-cases of five species wherein attention is drawn to some specific differences.

In the Annals of the University of Stellenbosch, Boonstra described the skull and brain-case of *Pareiasaurus serridens*, and showed that it differed from that of the other Pareiasaurs.

In 1930 Broom published a note, with two figures, on what he considered to be a new species of *Anthodon*.

Outside South Africa other Pareiasaurs had meanwhile also become known. Newton had already, in 1893, described *Elginia mirabilis* from the Elgin Sandstones in Scotland (pls. xxxvii–xl), and shown that this bizarre skull belonged to an animal related to the Pareiasaurs.

Amalitzky, during his work on the North Dwina, had collected numerous remains of Pareiasaurs but never described them, although specimens were mounted and plates prepared. In 1922 Karpinsky published extracts of Amalitzky's memoir. Here four species of *Pareiosaurus* (*sic*) were named, accompanied by very vague short descriptions. There are *P. karpinskii*, *P. horridus*, *P. elegans*, and *P. tuberculatus*. Sushkin in his study "On the Modifications of the Mandibular and Hyoid Arches and their Relations to the Brain-case in Early Tetrapoda" described and figured (figs. 23–26) the features relevant to his subject. The two chief points mentioned being the tubercle on the quadrate for the attachment of the stapes, and the fact that he maintains to have identified a supra-temporal bone in the "cheek."

Hartmann-Weinberg in 1930 gave a fairly full account of the skull of a North Dwina form, and establishes the fact long suspected by other authors that the Russian specimen cannot belong to the genus *Pareiasaurus*. For the specimen newly mounted by herself she proposes the name *Scutosaurus karpinsky* (*karpinskii*?).

In 1931 von Huene, in his "Beitrag zur Kenntnis der Fauna der Südafrikanische Karrooformation," published some notes on the skull of *Bradysaurus baini* (pl. i, figs. 1, 2; pl. ii, fig. 1).

GENERAL OSTEOLOGY.

GENERAL FEATURES.

The Pareiasaur skull is, as is the rule in the Stegocephs, in many cases broad and fairly depressed; but in some forms it is narrow and high. The temporal roof, although stegocrotaphic, is no longer primitive as it has lost one of the three original temporal bones. The quadrate retains the primitive rigid condition in being immovably attached to the ventral surface of the two temporal bones, and was apparently also cartilaginously attached to the brain-case. In addition the pterygoid is also immovably connected to the basi-cranium; this is, however, no primitive condition judging by the condition manifested in *Crossopterygii*, *Stegocephalia*, and primitive and other *Cotylosauria*; the Pareiasaur skull is therefore primarily monimostyle, but secondarily akinetic. Neither is the Pareiasaur skull divisible into two segments—maxillary and occipital—movable relative to each other, the so-called metakinetic condition which still obtains in some *Cotylosauria*, e.g. *Labidosaurus*. The otic notch, well developed in Stegocephs and primitive *Cotylosaurs* (*Seymouria*), is practically obliterated. The primitive long and broad fenestra palatinalis or interpterygoid slit is, in the Pareiasaurs, secondarily partially or totally closed. The choanae retain their primitive condition far forward but are not confluent with each other. All skulls display a certain amount of sculpturing of the superficial dermal bones. In the smoothest skulls each bone has a small low central boss from which indistinct rugae and the fibres of the bone radiate; in addition, the posterior edge and angle of the "cheek" carry large, but low, bosses. In the more highly ornamented skulls the same ground plan is retained, but all the features are remarkably accentuated, so that in some cases actual horns are produced (compare the living forms *Moloch* and *Phrynosoma*); the bosses of the "cheek" are also increased in number and size.

In dorsal view (Pl. II) the Pareiasaur skull appears roughly triangular or in some cases quadrangular. The central part forms a fairly flat or slightly arched table bounded laterally by a ridge running from the orbit to the tabular boss and from the orbit to the lateral margin of the nostril. This ridge is low in some forms but very strong in others. In addition there is in some forms a lateral bulging of the maxilla and lacrymal. It is thus clear that a central table is to be distinguished from the sides which is chiefly formed

by the so-called bony "cheeks." These "cheeks" lie in some cases nearly vertically down from the table; in others they are flattened out and diverge far laterally. The angle of the "cheek" lies far forward—up to the plane of the orbits—or nearly in line with the posterior border of the skull. The central table is generally more or less triangular in shape, the base formed by the posterior border of the skull, the apex by the internasal processes of the nasals; in some cases it is, however, nearly rectangular. This is due to the relative widths between the tabular bosses and orbits, and also to the direction of the ridge running from the orbit to the nostrils. The relation between the length and breadth of the dorsal table produces different types of skull, viz. long and narrow, or short and broad skulls. The posterior edge formed by the tabulars and postparietal is in most forms sharp and abrupt, but in some is bent down to form a flange partly overhanging the occiput. In dorsal view the orbits appear elliptical, and lie either mostly in the anterior half of the skull or mostly in the posterior half. The nostrils can generally be seen in dorsal view, although they must be described as more terminal than dorsal; in some cases they are overhung by nasal bosses; they vary in shape; in some cases the floor of the nostril and even the internal nares can be seen, in others not.

In lateral view (Pl. I) the Pareiasaur skull is roughly triangular in shape, the base being the posterior border of the "cheek" and the apex the snout. In this view the rugosities on the cheek of some forms are well seen. Some skulls are fairly smooth, but even in them the structure and radiations of the bone-fibres show that all skulls are based on the same ground plan and that if bosses are not developed it just means that a potentiality has not been realised. Taking the family as a whole, the orbit can be described as more or less circular, although in some forms it is elliptical with the long axis lying longitudinally or obliquely. The nostril appears more or less kidney-shaped; in some forms it is partially obscured by the bulging of the lacrymal and maxilla. The height of the "cheek" is seen to differ considerably amongst the various forms, and this difference is mainly due to the size of one element—the quadratojugal. It also becomes apparent that amongst the Pareiasaurs there are high and depressed skulls; forms with more or less vertical "cheeks," and forms with "cheeks" diverging laterally. The tabular boss generally forms a prominent dorso-posterior angle, but in forms like *Scutosaurus*, *Pareiasaurus*, *Anthodon*, and *Pareiasuchus* the boss lies more on the lateral surface, and forms a much less prominent feature. From the

figures given in lateral view it is clear that the maxilla is not such a very low bone as Watson has maintained.

In occipital view (Pl. IV) the *Pareiasaur* skull presents either a rounded arch, in the forms where the tabular bosses are not prominent, or a truncated V. The differences in height, the inclination and the rugosity of the "cheek" are very apparent. The shape and size of the post-temporal fenestra also varies considerably, this being largely due to the structure of the paroccipital process. The posterior edge of the tabulars generally forms a slight downhanging shelf, but the postparietal edge is horizontal; in *Pareiasaurus serripedens* both these elements form a large overhanging flange. Morphologically the most important feature is the strength of the supra-occipital pillar and its firm attachment to the postparietal. Both the squamosal and the quadratojugal posteriorly have supporting flanges for the quadrate, which stands either vertically or is inclined slightly in anterior direction.

In ventral view (Pl. III and text-figs. 2 and 3) the primary palate, its dentigerous nature, the premaxillary processes and maxillary flanges, the forward position of the choanae, the immovability of the basisphenoid-ptyergoid junction, the general absence (with a few exceptions) of an interptyergoid slit, the forward position of the inclined quadrates, are prominent features. Differences within the family—the nature of the median ptyergoid suture, the inclination of the quadrate, the shape of the basisphenoid, the overhang of the maxillaries and premaxillaries, the shape of the choanae, etc.—are apparent from the figures.

Nasal.—Together the two nasals form a rough pentagonal. Anteriorly they clasp the lateral edges of the ascending premaxillary processes. They form most of the dorsal and median edges of the nostrils. As a rule each nasal carries a low boss from which the bone-fibres, and sometimes rugae, radiate to the edges of the bone; this boss is sometimes (*Pareiasuchus nasicornis*) forwardly directed and begins to look like a horn. In one form (*Bradysuchus whaitsi*) there is, in addition to these two nasal bosses, one central boss of which half is contributed by each nasal; in another form (*Nochelesaurus alexanderi*) this third boss lies at the junction of the nasal-frontal sutures and all four bones contribute towards it; in still another case (*Nochelesaurus strubeni*) there is only a single median nasal boss—half formed by each nasal.

Frontal.—The two frontals together form a six-sided figure. The

nasal and parietal sutures are parallel, whereas laterally the frontal edge is V-shaped. Roughly at the point of the V the pre-postfrontal suture enters. Each frontal carries a boss from which the bone-fibres or rugae radiate; this boss is often situated in the V and sometimes coalesces with the pre- and postfrontal bosses; in *Elginia* it is hornlike. The anterior part of the sphenethmoid is applied to the ventral surfaces of the two frontals.

Parietal.—The parietals vary in size; sometimes they are larger, sometimes smaller than the frontals. The parietal-postparietal suture does not generally lie parallel to the frontal-parietal suture, but is oblique, with the median end more anterior. On the median line in the anterior half of the parietals lies the parietal foramen—this is generally rounded but is also sometimes oval; it varies somewhat in size but is in general small (except in *Anthodon*), whereas in most other Cotylosaurs it is large. Each parietal carries a boss with radiating fibres, and in some cases rugae; it lies somewhat lateral to the centre of the bone. Ventrally the posterior part of the sphenethmoid and the anterior part of the supraoccipital is applied to the parietal surface. In one case it would appear that the epipterygoid is also applied to the ventral parietal surface.

Postparietal.—The postparietal differs considerably in size and shape, and forms the median portion of the posterior part of the dorsal skull-roof. Watson has figured it as paired; only in one case have I seen anything that may be a median suture; in all other cases there is, to the contrary, a median boss with radiating bone-fibres and sometimes even slight rugae. The posterior edge of this bone is of interest in that it may form either a fairly straight, a slightly curved, or an emarginate edge, or, again, it may be bent downwards to form a flange of bone which in posterior view partly overhangs the occiput. This in no way indicates a tendency of the postparietal of being incorporated into the occiput itself. On its ventral surface it is firmly ankylosed to the ascending strong supraoccipital column.

Tabular.—The tabular bones are prominent elements in the Pareiasaur skull; they form the posterior corners of the dorsal table, are provided on their posterior third with a strong boss which in some cases is very prominent, and in *Elginia* forms the longest horn on the skull. This boss often has a smaller, more median boss partly confluent with it. From the strong tabular bosses well-marked rugae run anteriorly, and weaker rugae medially; near the lateral margin of the tabular a longitudinal ridge forms the edge of the dorsal table; this ridge is sometimes very strong, so that the dorsal and lateral

surfaces of the skull are sharply separated from each other. The posterior edge of the tabular, as in the case of the postparietal, is generally a sharp one, but it sometimes helps to form a posterior overhanging flange. This flange lies in a plane posterior to the occiput; there is therefore no tendency of the dorsal bones entering into the formation of the occiput. On its ventral surface abuts the strong paroccipital process. The otic notch, at the junction of the tabular and squamosal, is practically closed up.

Lacrymal.—This bone retains its primitive position in that it stretches from the orbit to the nostril. It forms an anterior wall to the orbit, where it is perforated by a foramen. It is provided with a boss, from which the fibres radiate, and in some skulls is strongly bulging so that it continues the ridge separating the dorsal from the lateral surface of the skull. It does not stretch very far down on the lateral surface so as to cause a shallow maxilla to be formed. It meets the jugal. In some forms the lacrymal narrows considerably as it approaches the nostril. This is not correlated to the geological sequence, and it cannot be maintained that there is a tendency towards the exclusion of the lacrymal from the nostril. The lacrymal, then, retains its primitive Cotylosaurian character.

Prefrontal.—The prefrontal is a fairly small bone lying on the antero-dorsal border of the orbit. It adjoins the nasal, frontal, postfrontal, and jugal. Its boss is situated on the dorsal orbital border. The prefrontal has a ventrally directed flange, contributing partly to the anterior orbital wall, and reaches the upper surface of the palatine.

Postfrontal.—The postfrontal is a fairly small bone lying on the dorsal orbital border. In all specimens examined both internal and external sutures show that it is a larger element than figured by Watson. In this point Broom is right in his criticism of Watson's figure. It carries a boss on the orbital border, which in some forms is confluent with the frontal boss. The suture between this bone and the prefrontal lies between the two bosses and joins the frontal suture at its middle just where it forms a laterally directed angle.

Postorbital.—The postorbital is larger than the two foregoing bones. It is situated on the dorso-posterior border of the orbit and is provided with a strong boss which continues posteriorly as a ridge running to the tabular ridge. Together they demarcate the dorsal from the lateral surfaces of the skull. This ridge is stronger in some forms than in others. It is thus seen that the three supraorbital bosses lie each on one of the three supraorbital bones. The limiting sutures

are generally visible, but, if they are not, one can obtain a very accurate idea of the lie of the three bones from the three bosses with the concomitant radiation of the bone-fibres.

Jugal.—The jugal is a large bone forming the ventro-posterior border and floor of the orbit. It is provided with a large low boss, or a number of low bosses grouped together, from which rugae radiate. It sometimes (*Bradysaurus vanderbyli*, *Embrithosaurus schwarzi*) stretches far posteriorly, thereby encroaching on the quadratojugal. In some skulls it is intercalated between the quadratojugal and maxilla so that these bones do not meet; in others (*Nochelesaurus strubeni*, *Brachypareia watsoni*) it does not reach the ventral border, so that the maxilla just meets the quadratojugal. In most other Cotylosaurs (*Seymouria*, *Diadectes*, *Limnoscelis*) the jugal forms a large part of the antero-ventral edge of the "cheek," and the maxilla and quadratojugal are thus widely separated. It meets the lacrymal.

Maxilla.—The maxilla is not such a very shallow bone as Watson has maintained. Just back of the nostril it is swollen, and in one skull (*Pareiasaurus serripedens*) even has a prominent conical tubercle. It is high up on this bulge that the lacrymal-maxilla suture runs digitatingly, so that most of the lateral border of the nostril is formed by the maxilla. It also forms about half of the ventral floor to the nostril. As has been pointed out, it either meets or just does not meet the quadratojugal. The outer maxillary surface may be only slightly curved so that the teeth are vertical, or (*Bradysaurus*, *Brachypareia rogersi*) it may be much curved inwards so that the teeth are also directed inwards. In the latter case much of the lateral and anterior portions of the palate are obscured in ventral view. Internally the maxilla sends a thin horizontal plate inwards to form part of the bony palate and the anterior part of the lateral border of the choanae. The maxilla houses a variable number of teeth.

Premaxilla.—The premaxilla houses two teeth; forms half of the floor to the nostril; sends a process dorsally to form part of the internasal bar—this is laterally clasped by a descending nasal process; sends a process inwards on to the palate, where it forms the anterior border of the choanae; dorsally underneath the internasal bar the two premaxillae enclose a foramen—the *foramen incisivum*. In *Dolichopareia*, although this part is well exposed, no foramen is visible. Ventrally, just anterior to the prevomers, three or four small foramina have been located—two lie on the median suture (in *Anthodon* these are fused into one), the other two a little lateral to it; all penetrate the bone and open on to the dorsal surface. In some cases the

internasal bar carried a forwardly directed boss (*Pareiasuchus nasicornis*). The palatal processes of the premaxilla lie on a higher plane than the prevomers, and abut on to the girder formed by the anterior ramus of the pterygoid.

Septomaxilla (fig. 1).—The septomaxilla has been found preserved in only one skull (*Anthodon*). Here it lies wholly within the nostril and cannot be seen in dorsal view. It shows no indication of any sculpturing as is general in the superficial dermal bones of the skull.



FIG. 1.—Septomaxilla in external view. *Anthodon serrarius*. $\times 1$. S.A.M., No. 4020.

Its shape is shown in the accompanying figure. From the available evidence it appears that this bone does not divide the nostril into two compartments.

Squamosal.—There are only two temporal bones. Watson has argued in full that these two bones can only be the squamosal and quadratojugal; Sushkin has claimed to have found another temporal bone in the Russian Pareiasaurs. Hartmann-Weinberg, who has subsequently studied this material, could not locate this “supra-temporal.” In none of the skulls I have examined is there anything that can be considered to form a third bone. I have examined the temporal region internally as well as externally and have also sections through it, and can definitely state that there is no “supra-temporal” bone present.

The squamosal is a fair-sized bone with a not-well-defined central boss, but with clearly visible radiating bone-fibres and a few rugae. The squamosal-tabular suture runs just below the tabular ridge and reaches the posterior surface just below the posterior shelf of the tabular. Here there is a slight notch—a remnant of the large Stegocephalian otic notch. The posterior border of the squamosal is very much thickened and in the majority of forms carries a number of bosses, whereas in *Elginia* a horn is developed. Internally the squamosal sends a flange which posteriorly clasps the quadrate; this is supplemented by a similar flange from the quadratojugal. The squamosal-quadrate, the squamosal-quadratojugal, and the quadratojugal-quadrate suture meet at a small foramen—the *foramen quadrati*.

Quadratojugal.—The quadratojugal forms the angle of the “cheek.” At about the centre of its external surface there lies a centre of radiation of bone-fibres and in some cases of rugae. This centre is in some cases a single boss, but is more often a boss-complex. The relative size of the bone differs considerably, and this is also the case

with reference to its shape. It is of interest to note that in those forms with high "cheeks" this height is due to increased size of the quadratojugal. The angle and posterior border is thickened and is sometimes fairly smooth, but more often houses a series of bosses or, as an extreme, horns. A study of the nature of the thickening and the direction of the bone-fibres seems to indicate that the essential structure is the same in the smooth and the bossed forms, and that the bosses are simply realisations of potentialities innate in the smooth forms. The quadratojugal meets, or just does not meet, the maxilla. The quadrate abuts on its ventral surface which posteriorly sends a flange, which, in conjunction with a similar flange from the squamosal, supports the quadrate from behind. The squamosal-quadratojugal and the quadratojugal-quadrates sutures meet at the small *foramen quadrati*.

Prevomer (figs. 2 and 3).—The prevomer is semicircular in shape, the diameter lying medially and is applied to that of its fellow; at its diameter it is raised to a ridge carrying a row of small sharp and recurved teeth. In some cases (*Pareiasuchus*) the first two pairs of teeth are larger than the rest; along their dorsal surfaces the prevomers are supported by the median pterygoid girder, which meets the palatal processes of the premaxillaries (in some cases the pterygoid girder is very intimately fused to the prevomers, so that, even in section, it has not been possible to determine the limits of the two bones); medially the anterior borders of the prevomers are slightly emarginate. The prevomers differ somewhat in size in the different forms, so that the "comma-shaped" vacuities which housed the choanae vary in size; in some forms the lateral portions of the prevomers do not lie horizontal, so that it appears as if only the anterior part of the "comma-shaped" vacuities could house the choanae.

Pterygoid.—The pterygoids are large elements, together forming the greater part of the bony palate, firmly joined to the basisphenoid and supporting the quadrate. It is a triradiate bone consisting of (a) an anterior flange, (b) a lateral flange, and (c) a posterior flange (quadrate ramus). The basisphenoid-ptyerygoid junction is marked by an oblique ridge. From here the anterior flange stretches anteriorly up to the palatal process of the premaxillaries; along the median line a girder is developed on the dorsal surface of the pterygoids, and this girder continues anteriorly over the dorsal surface of the prevomers to meet the palatal processes of the premaxillaries; posteriorly this girder does not stretch as far back as the parasphenoidal rostrum. (Watson maintained that in his specimen it did.) The

median edges of the two pterygoids are firmly joined to each other along the anterior half of the bone; in the case of two forms (*Scutosaurus*, *Anthodon*) the posterior half of the two pterygoids diverge posteriorly to leave a fairly long interpterygoid slit (typical of primi-

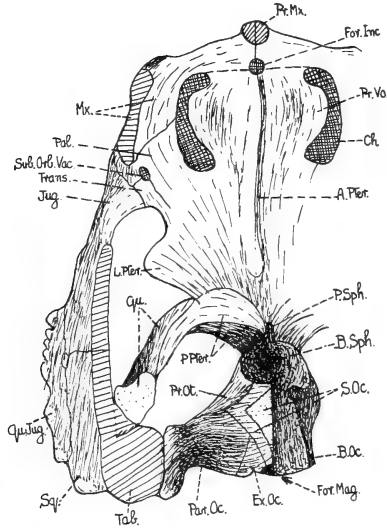


FIG. 2.—Dorsal view of the skull of *Bradysaurus seeleyi*. $\times \frac{1}{6}$. S.A.M., No. 9137, with the roof bones removed. The right half of the brain-cavity is exposed.

A. Pter.	=anterior ramus of the pterygoid.	Pr. Vo.	=prevomer.
B. Oc.	=basioccipital.	Pr. Ot.	=pro-otic.
B. Sph.	=basisphenoid.	P. Pter.	=posterior ramus of the pterygoid.
Ch.	=choanae.	P. Par.	=postparietal.
Ex. Oc.	=exoccipital.	Qu.	=quadrate.
For. Inc.	=foramen incisivum.	Qu. Jug.	=quadratojugal.
For. Mag.	=foramen magnum.	Sub. Orb.	} =suborbital vacuity.
For. Qu.	=foramen quadrati.	Vac.	
Jug.	=jugal.	Sub. Temp.	} =subtemporal vacuity.
L. Pter.	=lateral ramus of the pterygoid.	Vac.	
Mx.	=maxilla.	S. Oc.	=supraoccipital.
Pal.	=palatine.	Sq.	=squamosal.
Par. Oc.	=paroccipital (opisthotic).	Tab.	=tabular.
P. Sph.	=parasphenoidal rostrum.	Trans.	=transversum (ectopterygoid).
Pr. Mx.	=premaxilla.	T. St.	=tubercle for attachment of the stapes.

All illustrations and photographs are, except where otherwise stated, by the author.

tive Stegocephalians and Cotylosaurs) through which the parasphenoidal rostrum is visible; in the other forms the junction of the medial pterygoid edges is carried further back so that the slit is closed and the interpterygoid space has either a shallow concave,

straight, or even convex border through which the parasphenoidal rostrum is in some cases partly visible. In these forms where the slit is closed it is apparent that the closure has not taken place uniformly, viz. in some forms the forward extension of the interpterygoid space is greater than in others; one can thus speak of long and short palates. The anterior pterygoid flange carries a double row of small, sharp,

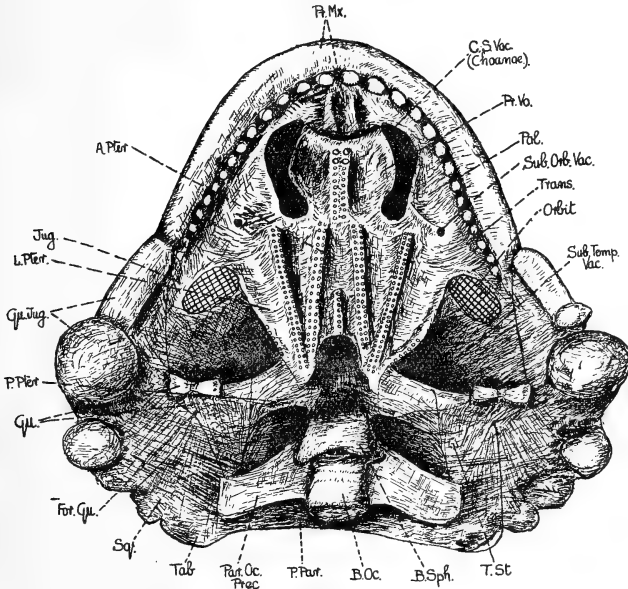


FIG. 3.—Ventral view of the skull of *Pareiasuchus peringueyi*. $\times \frac{1}{2}$. S.A.M., No. 2337. Drawing by Miss M. van der Merwe. For lettering see fig. 2.

recurved teeth; these are implanted on the medial pterygoid edge. In some forms with a closed interpterygoid slit that has continued far posteriorly the teeth do not lie on the medial edge of the part thus closed; here a low vault is formed (*Bradysaurus*, *Embrithosaurus*). In *Pareiasuchus peringueyi* a short median row of teeth is developed on this part of the median line.

From the basiptyergoid junction the lateral flange of the pterygoid stretches anteriorly and laterally to meet the palatine and transversum. Unfortunately these sutures are not often visible. This flange of the pterygoid carries (a) a double row of small, sharp, recurved teeth which begins near the basiptyergoid junction and diverges in antero-lateral direction to where the pterygoid meets the palatine, and (b) separated from the foregoing by a deep groove, the

raised postero-lateral pterygoid edge, which forms the border of the suborbital fenestra, sometimes carries a single row of small, sharp, recurved teeth (I have not been able to determine this in all skulls, and Sushkin also does not figure it in *Scutosaurus*). In between these sets of pterygoid teeth there are deep grooves which carry no teeth; the shagreen mentioned by other authors appears to be loose teeth from these rows lying scattered in the matrix filling these grooves. There is certainly nothing approaching the condition as exemplified by *Pantylus*.

The posterior pterygoid flange commences at the ridge indicating the basiptyergoid junction; from here it extends laterally as a more or less vertical flange directed somewhat posteriorly. This flange is closely applied to the posterior surface of the quadrate; it reaches the temporal roof, and was, together with the quadrate, cartilaginously attached to the brain-case. Medial to the quadrate-ptyergoid suture the posterior surface of the bone is more or less deeply excavated. In the recess so formed the stapes was probably housed. The quadrate sometimes stretches far in median direction along the anterior surface of the pterygoid flange, sometimes (*Anthodon*) even meeting the lateral pterygoid flange; in anterior view the posterior pterygoid flange was thus wholly or only partly covered by the quadrate. It is on the dorsal surface of this ramus of the pterygoid, near its junction with the basisphenoid, that the epiptyergoid stands.

Palatine.—Lateral and anterior to the lateral ramus of the pterygoid lie the palatine and transversum. The palatine, as far as can be determined, meets the lateral ramus of the pterygoid where the middle double row of teeth ends; from here it curves forward along the posterior border of the "comma-shaped" vacuity and, meeting the palatal flanges of the maxilla, forms together with the latter the lateral margin of this vacuity. On its dorsal surface, just posterior to the "comma-shaped" vacuities, it supports the descending process of the prefrontal.

Transversum.—The transversum lies posterior to the palatine, from which it is in part separated by the small lateral palatal foramen (*foramen palatinum*). (A comparison with a similar structure in Therocephalians and Gorgonopsians makes it preferable to call this foramen the suborbital vacuity.) It forms the lateral part of the anterior border of the basitemporal fenestra, the medial part being formed by the lateral ramus of the pterygoid. Although the transversum-ptyergoid suture has not been determined in many skulls,

it can be stated that it does not stretch far medially of the foramen. It is thus quite a small bone and carries no teeth.

Basioccipital.—The basioccipital forms the whole of the unipartite circular articular surface for the vertebral column. Seeley's erroneous account of a tripartite condyle was due to the imperfect nature of the specimen examined by him; what he really described was basioccipital plus basisphenoid. In contrast to the condition in most Cotylosaurs (except *Diadectes* and *Limnoscelis*), the condylar surface is concave and is thus similar to the articular surfaces of the vertebrae. The bone is massive, short, and is firmly ankylosed to the basisphenoid. Through the courtesy of Professor Young of the University of Cape Town I have sections through the basioccipital and basisphenoid but can find no indication of the extent of these two bones. Watson, however, in his figure of the brain-case indicates a suture.

Basisphenoid.—This is a massive bone with prominent tubera on its ventro-posterior angles. Its ventral surface is shallowly or deeply grooved; it continues anteriorly as the parasphenoidal rostrum, which lies in the interpterygoid space on a plane dorsal to that of the palate and meets the sphenethmoid. Laterally the basisphenoid is immovably joined to the pterygoid, the line of junction being indicated by a sharp ridge. The basisphenoid forms the middle portion of the floor of the brain-case; its median upper surface is excavated to form the pituitary fossa; laterally it extends to meet the pro-otic, and thus forms the median part of the side wall of the brain-case; here its outer surface is pierced by the external carotid foramen.

Exoccipital.—The exoccipitals form the lateral borders of the foramen magnum and a small part of the lateral walls of the posterior section of the brain-case. They may or may not, in addition, form the upper border of the foramen magnum, in the former case excluding the supraoccipital. The dorsomedial corner of the paroccipital process is formed by the exoccipital.

Supraoccipital.—The supraoccipital, generally weak in Stegocephalians and Cotylosaurs, is very strong in the Pareiasaurs; it forms a very strong low or high pillar firmly ankylosed to the postparietal; it forms the dorsal border of the foramen magnum, or is excluded from it; anteriorly to the pillar it sends out a thin flange of bone, which forms the side wall of the brain-case right up to the large foramen for the Vth nerve; it forms, together with the pro-otic, the lower part of the side wall of the brain-case.

Paroccipital.—The paroccipital (or ophisthotic) forms the greater

part of the paroccipital process, which is essentially a horizontal bar of bone connecting the brain-case to the dermal roof-bones. It generally abuts on the tabular, but the squamosal may also be included; medially it meets the pro-otic, supraoccipital, and exoccipital. The pro-otic forms the antero-medial corner of the paroccipital bar, the exoccipital the ventro-postero-medial corner, and the supraoccipital the dorso-postero-medial corner. Generally the paroccipital forms a strong bar with a slight dorsal curvature; in *Bradysaurus baini* and *Pareiasaurus serridens* a bulge is developed on its dorso-lateral corner. The extent of its curvature, its length, and the height of the supraoccipital pillar determine the size and shape of the post-temporal fenestra. Its ventral extension also varies so that in occipital view the quadrate-pterygoid bar is obscured to a greater or lesser extent; in some cases it is situated so high up that in occipital view the ptero-occipital fenestra is visible. The paroccipital forms part of the side wall of the brain-case, viz. that part which lies between the *fenestra ovalis* and the *foramen jugulare*; it forms the anterior border of the latter and the posterior border of the former.

Pro-otic.—The pro-otic forms the greater part of the posterior half of the side wall of the brain-case; it forms the posterior border of the irregular opening for the Vth nerve, the anterior border of the *fenestra ovalis*, the posterior border of the pituitary fossa, and is pierced by a small foramen for the VIIth nerve. As already mentioned, it forms the antero-medial corner of the paroccipital bar.

Sphenethmoid (fig. 4).—The whole anterior portion of the brain is enclosed by the sphenethmoid, which really merits its French name—*os en ceinture*. It is, however, only its anterior half that wholly encircles the fore-brain; the posterior half, separated from the anterior by a ridge on the external surface, is merely a thin flange of bone forming the side wall; ventrally it passes into the basisphenoid and dorsally it abuts on the frontal, so that the latter—a dermal bone—forms that part of the dorsal wall; posteriorly this flange does not meet that sent forward by the supraoccipital. Between these two flanges the brain has no bony wall; the ventral part of this—the posterior sphenethmoidal flange—forms the anterior border of the large foramen for the Vth nerve; postero-ventrally the anterior part of the sphenethmoid forms the anterior margin of the pituitary fossa; between these two openings the sphenethmoid meets the ascending process of the pro-otic. A little anterior to and dorsal to the pituitary fossa lies a small fissure through which the IIInd, IIIrd,

and IVth nerves emerged; the 1st nerve emerged through the widely open end of the sphenethmoid. Ventrally the sphenethmoid is supported by the parasphenoidal rostrum.

From the above account of the bones co-operating to form the brain-case, it has become apparent that the Pareiasaur brain-case is long,

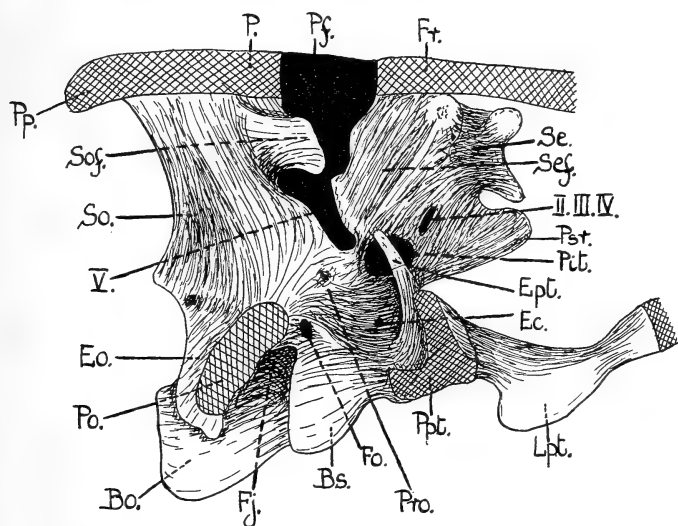


FIG. 4.—External view of right side of brain-case of *Pareiasaurus serridens*. $\times 1$. The paroccipital process and the posterior pterygoid ramus seen in section near their bases.

Bo. = basioccipital.
Bs. = basisphenoid.
Ec. = external carotid foramen.
Eo. = exoccipital.
Ept. = epipterygoid.
Fj. = foramen jugulare.
Fo. = fenestra ovalis.
Fr. = frontal.
Lpt. = lateral ramus of pterygoid.
P. = parietal.
Pf. = pineal foramen.

Pit. = pituitary fossa.
Po. = paroccipital process seen in section.
Pp. = postparietal.
Ppt. = posterior ramus of the pterygoid.
Pro. = pro-otic.
Psr. = parasphenoidal rostrum.
Se. = anterior portion of sphenethmoid.
Sef. = posterior flange of sphenethmoid.
So. = supraoccipital.
Sof. = anterior flange of the supraoccipital.

Roman numerals refer to the cranial nerves.

wide, and, in general, low; in some of the younger forms (*Pareiasaurus*) it is, however, somewhat higher. The internal ear is situated fairly high up on the side wall of the brain-case, and the vestibule has an osseous wall separating it in part from the brain-cavity; the fore-brain is in primitive fashion enclosed by a sphenethmoid; the relative positions of the pituitary fossa and *fenestra ovalis* appear to vary in the different forms.

Epipterygoid.—The epipterygoid is a fairly thick plate of bone standing transversely on the posterior (or quadrate) ramus of the pterygoid, near its articulation with the basipterygoid process of the basisphenoid; it is not attached to the brain-capsule by any bony connections, and dorsally it does not extend further than the plane of the foramen for the Vth nerve. In a specimen of *Pareiasuchus* a remnant of bone attached to the ventral surface of the parietal may indicate that the epipterygoid did in some forms reach the dermal roof-bones.

Quadrate.—The quadrate is a large plate of bone standing transversely in the skull, stretching in dorsal direction from the ventrally directed bipartite condyle to the ventral surface of the temporal bones, and medially to the posterior or quadrate ramus of the pterygoid; it has no osseous connection with the brain-case. It is firmly fixed to the quadratojugal, squamosal, and partly also to the tabular; the two former bones send flanges on to its posterior surface, reaching inwards to the *foramen quadrati*, which appears at the junction of these sutures, and in addition there appear to be very slight flanges on to the anterior surface of the quadrate. The dorso-medial corner of the quadrate just touches the antero-lateral corner of the paroccipital process; from the medial edge of the quadrate there appears to have been, in life, cartilage connecting it to the brain-case. The quadrate is, furthermore, immovably connected with the posterior ramus of the pterygoid; the transverse quadrate plate stretches medially from the condyle, so as to lie anterior to the transverse plate of the posterior pterygoid ramus. The medial extent of the quadrate varies; in some cases (*Anthodon*) it actually reaches the lateral pterygoid ramus, in others it only reaches half-way of the distance between the condyle and the lateral pterygoid flange. In anterior view the quadrate thus covers the posterior pterygoid ramus wholly or partly. In posterior view the reverse is the case, viz. the posterior pterygoid ramus stretches in lateral direction on the posterior surface of the quadrate. The pterygoid ramus, which is more of a bar than a plate, is deeply excavated on its posterior surface to form a recess—the lateral margin of this recess (which probably housed the stapes) is also the limit of the pterygoid; the pterygoid-quadrate suture runs along this margin to the dorso-medial corner of the quadrate plate, where it touches the paroccipital bar; just lateral to the pterygoid recess on the medial edge of the quadrate there is situated a tubercle to which the stapes was apparently ligamentously attached. The articular condyle of the quadrate is bipartite, the inner part being larger than the outer. The quadrate plate, from the

temporal bones to the condyle, stands inclined in anterior direction; the inclination varies from 55° to 85° . In the primitive condition (e.g. *Seymouria*) the inclination is greater. The quadrate is situated further anteriorly in the skull than is the case in most Cotylosaurs (except, for instance, *Diadectes*).

Stapes.—The stapes is not preserved in any skull, but something can be determined from the structure of the surrounding bones. Judging from the nature of the *fenestra ovalis* its medial end must have been slender. If it fitted into the recess in the posterior face of the posterior pterygoid ramus it must have been curved and here have been a fairly massive bone. For the attachment to the tubercle on the quadrate a short process must have been developed, and from here it must have curved to form a posteriorly directed process which lay in the groove between the end of the paroccipital process and the squamosal, and reached the otic notch on the posterior surface between the tabular and the squamosal. The stapes was thus probably a massive curved bone with two lateral processes and a medial process tapering nearly to a point at the *fenestra ovalis*.

Teeth.—The teeth (Pl. V) of the upper jaw are carried by the maxilla and premaxilla. Two teeth are implanted in the premaxilla, whereas a varying number (10–18) is carried by the maxilla. There is no differentiation into incisors, canines, and molars, although there is some variation between anterior and posterior teeth, viz. the former are larger and may have a larger number of cusps.

A tooth consists of a long root and crown separated, to a greater or less degree, by a cingulum. The teeth are thecodont, the roots being very firmly held by the encircling bone-tissue. The crown is flattened extero-internally (labio-lingually) and elongate antero-posteriorly to form, roughly, a semicircular functioning edge. The inner surface is flattened or slightly concave; a cingulum separates the crown from the root; long and deep grooves radiate from the notches between the cusps towards the cingulum. The outer surface is convex, imparting a greater or less degree of inflation; much shorter and shallower grooves radiate from the notches between the cusps. The teeth are more or less crowded, so that in some cases the crowns overlap to a greater or less extent, viz. in that the posterior edges of the crown overlaps the anterior edge of the succeeding tooth. The edge of the crown is developed into a number of cusps whose number varies in the different forms, and in some cases the posterior teeth have fewer cusps than the anterior ones. In the large-bodied forms (*Bradysaurus*, *Nochelesaurus*, *Dolichopareia*, and

? *Bradysuchus*) of the *Tapinocephalus* zone there are 6-8 cusps arranged as follows: 1, 2, or 3 anterior, 3 terminal, and 2 or 3 posterior.

In some of the small-bodied *Tapinocephalus*-zone forms (*Brachypareia*, ? *Koalemasaurus*) there are also few cusps (6-7) arranged as follows: 1 or 2 anterior, 3 terminal, and 2 posterior.

In *Embrithosaurus* there is an intermediate number of cusps (9) arranged as follows: 3 anterior, 3 terminal, and 3 posterior.

In the younger forms the cusps become more numerous and are more evenly arranged around the crown, so that eventually it becomes difficult to maintain the distinction into anterior, terminal, and posterior cusps. In *Propappus* from the *Endothiodon* zone there are 10 cusps—3 anterior, 4 terminal, and 3 posterior. In *Pareiasuchus* (*Cistecephalus* zone) there are 11-13 cusps fairly evenly arranged. In *Pareiasaurus* there are 11 fairly evenly arranged cusps. In ? *Pareiasaurus russowii* there are up to 15 cusps evenly arranged. In *Anthodon* there are up to 15 cusps evenly arranged. In the Russian *Scutosaurus* the number of cusps according to Hartmann-Weinberg vary up to a maximum of 17, and presumably they are evenly arranged. In the Scottish *Elginia* there are, according to Newton, 11 cusps evenly arranged.

MEASUREMENTS.

All but one of these measurements have been taken by Martin's beam-compass and are therefore direct length, *i.e.* projections on to a horizontal or vertical plane. Only the dentigerous length has been taken by means of a tape-measure. Where more than one specimen of a species have been measured, the figures given are the mean.

1. Median length, premaxillary suture to basioccipital condyle.
2. Length from anterior border of pineal foramen to premaxillary suture.
3. Length from posterior border of pineal foramen to posterior margin of postparietal.
4. Width, across angles of "cheeks."
5. Intertabular width, distance between tops of tabular bosses.
6. Interorbital width, minimum distance between dorsal orbital borders.
7. Length from anterior orbital border to premaxillary suture.
8. Length of "cheek," minimum distance from posterior border of orbit to posterior border of cheek.
9. Height of "cheek," top of tabular boss to angle of "cheek."

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.
																	<div> <div>a</div> <div>b</div> </div>
<i>Bradysaurus baini</i> .	445	295	118	500	240	205	210	180	285	83	330	230	380	225	18	70°	105
<i>seeleyi</i> .	420	275	125	445	195	195	185	185	335	75	320	250	345	205	16	80°	83
<i>vanderbyli</i> .	417	310	107	376	194	210	195	190	325	40	300	220	270	258	16	85°	60
<i>Bradysuchus whitai</i> .	410	270	111	405	193	180	196	160	300	70	260	230	270	260	?	?	?
<i>Nocheosaurus alexanderi</i> .	436	310	137	600	220	195	185	165	315	90	380	235	390	254	17	55°	130
<i>strubeni</i> .	380	280	110	355	155	165	177	160	235	95	250	220	250	205	17	85°	75
<i>Dolichopareia angusta</i> .	465	330	125	360	180	180	193	178	313	105	260	305	250	225	18	60°	80
<i>Brachypareia rogersi</i> .	290	270	?	384	180	137	125	135	200	40	230	145	273	160	12-14	80°	?
<i>watsoni</i> .	365	260	103	370	155	193	165	160	243	80	280	200	255	215	16	80°	85
<i>Koalemasaurus acutirostris</i>	315	200	95	300	130	134	135	130	214	60	155	170	170	200	15-16	75°	75
<i>Embrithosaurus schwarzi</i> .	390	280	100	450	190	186	160	150	315	45	260	186	315	220	16	75°	150
<i>Anthodon serrarius</i> .	255	135	?	360	110	110	110	124	175	50	145	80	218	125	14	75°	?
<i>Pareiasuchus peringueyi</i> .	340	255	90	460	170	137	145	130	283	125	245	145	310	210	14	55°	85
<i>nasicornis</i> .	305	200	93	340	110	180	130	145	224	80	235	150	275	140	12	65°	80
<i>Pareiasaurus serridens</i> .	318	260	105	380	200	180	155	150	225	140	195	135	280	180	14	85°	?
<i>Elginia mirabilis</i> .	140	68	67	228	92	60	45	65	109	20	80	63	?	47	12	45°	?
<i>Scutosaurus karpinskii</i> .	480	?	?	600	222	162	182	192	350	124	264	150	378	222	?	?	?
<i>"Pareiasaurus" elegans</i>	410
<i>horridus</i>	410
<i>tuberculatus</i>	410
Cast British Mus. (Russian)	450	590	210	180	220	18

All these measurements are in millimetres.

10. Overhang of "cheek," distance of vertical projection of "cheek" below the horizontal level of dentigerous maxillary border.
11. Palatal width, distance across last teeth.
12. Palatal length, anterior border of prevomer to anterior border of interpterygoid vacuity.
13. Interquadrate width, distance between lateral edges of the condyles.
14. Dentigerous length, from premaxillary suture to last tooth.
15. Number of teeth.
16. Angle of inclination of the quadrate to the plane of the palate.
17. Postparietal: (a) length; (b) width.

Genus *BRADYSAURUS* Watson.

This genus includes forms with large skulls; forms with many (19-20), and forms with an intermediate number (15-16) of teeth; these teeth may have no, slight, or considerable overlap. All the forms have teeth with few cusps (less than 9) arranged as follows: 2 anterior, 3 median, and 1 or 2 posterior; the teeth are moderately, or very much, swollen. The interorbital width is appreciably less than the "tabular width." The posterior border of the "cheek" is very smooth, fairly smooth, or has well-defined bosses. The snout is broad and rounded, and the "cheek" shallow. In general the skull is fairly smooth or is ornamented with pits and deep rugae. The maxilla and lacrymal are only slightly, or very strongly, bulging. Both behind and in front of the orbit the dorsal and lateral surfaces are separated by a strong ridge, or by only a moderate ridge. The postparietal is small to large, square or longitudinally or transversely rectangular. Medially the pterygoids are fused far posteriorly to form a long palate; the border of the interpterygoid vacuity is either concave, straight, or convex; and anterior to the border, in between the median rows of pterygoid teeth, there is a shallow vault. The quadrate is inclined forwards (70° - 85°) and does not stretch far medially, so that in anterior view the quadrate ramus of the pterygoid is partly exposed. The brain-case is fairly low; so is the supraoccipital pillar; the supraoccipital is excluded from the foramen magnum. The tabular boss is either low or very prominent. The maxilla is fairly shallow, and the quadratojugal shallow or fairly deep. The jugal just separates the maxilla from the quadratojugal.

In their preliminary classification Houghton and Boonstra have placed a distorted skull (S.A.M., No. 5002) in a new genus—*Platyoropha*. Subsequent study of the postcranial skeleton has proved that this

specimen does not differ much from the forms referred to the genus *Bradysaurus*. A re-examination of the skull has, moreover, shown that the features considered different are in all probability due to the post-mortem deformation that the skull has suffered. Making allowance for this, and taking into consideration that there are no other characters, either in the skull or in the postcranial skeleton, which could exclude this specimen from the genus *Bradysaurus*, it is best referred to that genus. It most closely approaches the species *baini*. *Platyoropha broomi* thus becomes a synonym of *Bradysaurus baini*.

Bradysaurus bombidens was founded by Owen on a very fragmentary maxilla and mandible. This very unsatisfactory type was founded mainly on the nature of the teeth. The inflation and inward direction of the teeth is, however, also found in other forms. The specimen is therefore specifically indeterminate, but is evidently very close to the large-bodied forms of the *Tapinocephalus* zone.

Bradysaurus baini (Seeley).

(Pls. I–V.)

In this species there are an intermediate number of teeth (15–16), which slightly overlap, have 7 cusps, and are only slightly swollen. The posterior border of the “cheek” is fairly smooth, but the general surface of the skull is strongly rugose and pitted. The maxilla and lacrymal are very strongly bulging. Both behind and in front of the orbit the dorsal and lateral surfaces of the skull are sharply separated by a strong ridge. The postparietal is large and transversely rectangular. The anterior border of the interpterygoid is convex. The tabular boss is low.

The following skulls are assigned to this species:—

Type, Brit. Mus. Nat. Hist.,	No. R1971,	Tapinocephalus zone,	high.
South African Museum, No.	3533	„	high.
„	4347	„	low.
„	4351	„	low.
„	4999	„	high.
„	5000	„	low.
„	5002	„	mid.
„	5127	„	mid.
„	9001	„	mid.
„	9104	„	low.
„	9105	„	low.
Geol. Pal. Inst. Tübingen,		„	low.

Bradysaurus seeleyi (Haughton and Boonstra).

(Pls. I-V and text-fig. 2.)

In this species there are many teeth (19-20), which overlap considerably, have 7 cusps, and are much swollen. The posterior border of the "cheek" has strong, well-defined bosses. In general the skull is rugose and somewhat pitted. The maxilla and lacrymal are bulging. The dorsal and lateral surfaces are separated by a low ridge weaker than in *baini*. The postparietal is of moderate size and is roughly square. The anterior border of the interpterygoid vacuity is nearly straight. The tabular boss is very prominent.

The following skulls are assigned to this species:—

Type, British Museum, No. 49426 (Palmiet Specimen), Tapinocephalus zone, high.

Co-type, British Museum, No. R1970 (Tamboer Specimen), Tapinocephalus zone, mid.

South African Museum, No. 1204, Tapinocephalus zone, mid.

"	"	4346	"	"	low.
"	"	5624	"	"	low.
"	"	8933	"	"	mid.
"	"	9115	"	"	mid.
"	"	9127	"	"	low.
"	"	9121	"	"	mid.
"	"	9137	"	"	mid.
"	"	9168	"	"	mid.
Durban Museum,			"	"	low.

Bradysaurus vanderbyli (Haughton and Boonstra).

(Pls. I-V.)

There are an intermediate number of teeth (15-16), which do not overlap, have 7 cusps, and are moderately swollen. The posterior border of the "cheek" is very smooth, and so is the general surface of the skull. The maxilla and lacrymal are slightly bulging. The dorsal and lateral surfaces are not sharply separated as the ridge is low and rounded. The postparietal is small and is longitudinally rectangular. The anterior border of the interpterygoid vacuity is concave. The tabular boss is prominent.

The following skulls are assigned to this species:—

Type, South African Museum, No. 3718, Tapinocephalus zone, low.

"	"	8941	"	"	mid.
"	"	9169	"	"	mid.

Genus BRADYSUCHUS Haughton and Boonstra.

Bradysuchus whaitsi (Broom).

(Pls. I–II.)

As I have not had the opportunity of seeing the type specimen in the American Museum of Natural History, this diagnosis had to be based on photographs kindly supplied by that institution and also on information received from Dr. R. Broom.

The skull of the single specimen of this form is large; the teeth are badly preserved, but there were probably about 16 teeth with few (less than 9) cusps, probably arranged as in the genus *Bradysaurus*; the interorbital width is appreciably less than the "tabular width." The posterior border of the "cheek" carries well-defined bosses. In general the skull is ornamented with pits and rugae. The maxilla and lacrymal are only slightly bulging. Both behind and in front of the orbit the dorsal and lateral surfaces are separated by a strong ridge. Medially the pterygoids are fused far posteriorly to form a long palate. The quadrate is inclined forwards. The brain-case and the supraoccipital pillar appear to be high. The tabular boss is prominent.

Except for Broom's statement that the lower jaw carries two bosses on the angular, and the fact that the snout appears to be somewhat pointed, this genus is very similar indeed to the forms included in the genus *Bradysaurus*, particularly to *Br. seeleyi*.

Type, Amer. Mus. Nat. Hist., No. 5567, Tapinocephalus zone, low.

Genus NOCHELESAURUS Haughton and Boonstra.

This genus includes forms with fairly large skulls; forms with an intermediate (15–17) number of teeth—these teeth may have a slight or a considerable overlap; all forms have teeth with few cusps (less than 9) arranged as follows: 3 anterior, 3 median, and 2 posterior; they are slightly swollen. The interorbital width is approximately equal to the "tabular width." The posterior border of the "cheek" is smooth, or carries very strong bosses. The snout is rather pointed and the "cheek" deep; the latter is vertical or somewhat diverging. The skull is in general very smooth or strongly ornamented, but with little "crocodilian" pitting. The maxilla and lacrymal are moderately or slightly bulging. The dorsal and lateral surfaces are not separated by a very strong ridge. The postparietal is either transversely or longitudinally rectangular. The pterygoids are fused

far posteriorly so as to form a long palate. The border of the interpterygoid vacuity is concave. There is hardly any vault between the medial rows of pterygoid teeth. The quadrate is much (55°), or slightly (85°), inclined forwards and does not stretch far medially. The brain-case is fairly low; so is the supraoccipital pillar. The tabular boss is low. The maxilla is fairly deep and the quadratojugal moderately deep. The quadratojugal just meets the maxilla or is separated from it by the jugal.

Nochelesaurus strubeni (Broom).

(Pls. I-V.)

The teeth are slightly overlapping; the whole skull is smooth; there is a single nasal boss; the posterior border of the "cheek" has hardly any development of bosses. The snout is higher and more pointed than in *N. alexanderi*, and the "cheeks" are more vertical. The maxilla and lacrymal are slightly bulging. The postparietal is longitudinally rectangular. The quadrate is slightly inclined forwards (85°). The quadratojugal just meets the maxilla. From his description and figures it appears that von Huene is right in assigning the lower jaw in the Tübingen collection to this species.

The following skulls are assigned to this species:—

Type (lower jaw):

Amer. Mus. Nat. Hist., Tapinocephalus zone, low.

South African Museum, No. 1207, Tapinocephalus zone, low.

"	"	4352	"	"	"
"	"	5019	"	"	"
"	"	5590	"	"	"
Geol. Pal. Inst. Tübingen,			"	"	"

Nochelesaurus alexanderi Haughton and Boonstra.

(Pls. I-V.)

The teeth are considerably overlapping; the whole skull is heavily ornamented with bosses and rugae; there are two nasal bosses; there is a great development of bosses on the posterior border of the "cheek" approaching the condition shown in *Pareiasuchus peringueyi*. The snout is lower and broader than in *N. strubeni*, and the "cheek" is more flattened out. The maxilla and lacrymal are moderately bulging. The postparietal is transversely rectangular.

The quadrate is much inclined forwards (55°). The jugal is intercalated between the quadratojugal and the maxilla.

The following skulls are assigned to this species:—

Type, South African Museum, No. 6239, Tapinocephalus zone, mid.			
„ „	6239A	„	„ „
„ „	8944	„	„ „

Genus *EMBRITHOSAURUS* Watson.

Embrithosaurus schwarzi Watson.

(Pls. I–V.)

In this genus the skull is quite large; there are an intermediate number of teeth (15–16), which are considerably overlapping; there are an intermediate number of cusps (9) arranged as follows: 3 anterior, 3 median, and 3 posterior; they are slightly swollen. The interorbital width is approximately equal to the “tabular width.” The posterior border of the “cheek” carries pronounced bosses. The snout is rather pointed and the “cheek” deep. In general the skull is ornamented with pits and rugae. The maxilla and lacrymal are only very slightly bulging. The postparietal is transversely rectangular. Medially the pterygoids fuse far posteriorly to form a long palate; the border of the interpterygoid vacuity is convex. The quadrate has a moderate forward inclination (75°), and it does not stretch far medially. The brain-case and supraoccipital pillar are fairly low. The tabular boss is prominent. The maxilla is fairly deep, but the quadratojugal is shallow and small. The jugal is intercalated between the quadratojugal and the maxilla. The mandible and teeth with 9 cusps described and figured by Broom must be assigned to this species if we are correct in maintaining that the nature of the cusping is a feature of taxonomic importance.

The following skulls are assigned to this species:—

Type, South African Museum, No. 8034, Tapinocephalus zone, mid.		
Brit. Mus. Nat. Hist.,	„	„ high.
(Watson's Hottentots River Specimen.)		

Genus *DOLICHOPAREIA* Haughton and Boonstra.

Dolichopareia angusta Haughton and Boonstra.

(Pls. I–V.)

In this genus the skull is long and fairly narrow; there are many teeth (19–20), which are slightly overlapping; there are few cusps

(less than 9) arranged as follows: 3 anterior, 3 median, and 2 posterior; they are slightly swollen and decrease much in size in antero-posterior direction. The interorbital width is approximately equal to the "tabular width." The posterior border of the "cheek" carries strong bosses. The snout is very pointed and the "cheek" deep. In general the skull is moderately ornamented with pits and slight rugae. The maxilla and lacrymal are only slightly bulging. Posterior to the orbit a strong ridge separates the dorsal from the ventral surface of the skull. The postparietal is irregularly shaped and its posterior border is notched. Medially the pterygoids are fused fairly far posteriorly so as to form a moderately long palate. The border of the interpterygoid vacuity is convex. The quadrate is much inclined (60°) and is not directed medially but anteriorly (see Pl. III, fig. 14). The brain-case and supraoccipital pillar are fairly high, the supraoccipital is not excluded from the foramen magnum. The tabular boss is fairly prominent. The maxilla is fairly deep and so is the quadratojugal. The quadratojugal just fails to meet the maxilla.

The following skulls are assigned to this species:—

Type, South African Museum, No. 6238, Tapinocephalus zone, mid.

„ „ 3717 „ „ „

Genus KOALEMASAURUS Houghton and Boonstra.

Koalemasaurus acutirostris (Broom).

(Pl. III and text-fig. 5.)

Through the kindness of Mr. J. Hewitt, of the Albany Museum, I have been able to study Broom's type, which consists of a little more than the half of the mandible with a very imperfect skull (parts of the cheek, upper jaw, palate, and basis cranii alone are preserved in a bad condition). As is the case in so many of Broom's types, this type is really very bad, and it is with reluctance that an attempt is made to place it in this system of classification. In our preliminary classification we accepted Broom's identification of the specimen in the American Museum of Natural History and based our diagnosis on both specimens. Through the courtesy of the American Museum I have photographs of the specimen in that institution and am able to confirm Broom's identification. Although both skulls are not very well preserved the position of the orbit and the nature of the angular boss justifies such an identification. The skull in this genus is of moderate size; there are an intermediate number (15-16) of

teeth with a fair amount of overlap; the teeth have few cusps (less than 9) arranged as follows: 2 anterior, 3 median, and 1 or 2 posterior. The interorbital width is greater than the "tabular width." The posterior border of the "cheek" carries low but distinct bosses. The snout is high and pointed (but in the American Museum specimen it appears to be truncated). In general the surface of the skull is moderately ornamented. The maxilla and lacrymal are moderately bulging. The dorsal and lateral surfaces are only distinctly demarcated by a ridge behind the orbit. The postparietal is transversely rectangular. The pterygoids are fused far anteriorly so as to form a short palate; the border of the interpterygoid vacuity is convex. The quadrate is inclined forwards (75°) and is situated far forward in the skull. The brain-case and supraoccipital pillar are fairly high. The tabular boss is fairly prominent. The maxilla is fairly shallow

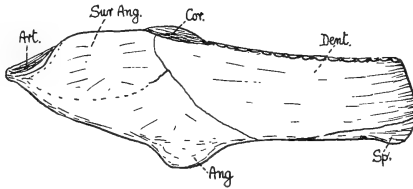


FIG. 5.—External view of lower jaw of *Koalemasaurus acutirostris*. $\times \frac{1}{4}$.
Type in Albany Museum.

Ang. = angular.	Dent. = dentary.
Art. = articular.	Sp. = splenial.
Cor. = coronoid.	Sur Ang. = surangular.

and the quadratojugal deep. The orbit is in the anterior half of the skull. As the angular boss is such a characteristic feature a figure of the lower jaw is included (fig. 5). The following skulls are assigned to this species:—

Type, Albany Museum,	Tapinocephalus zone, high.
American Museum, No. 5568,	„ „ ?
South African Museum, No. 4345,	„ „ high.

Genus BRACHYPAREIA Haughton and Boonstra.

Both species of this genus have medium-sized skulls; an intermediate (15–16) number of teeth, which are slightly overlapping; there are few cusps (less than 9) arranged as follows: 3 anterior, 3 median, and 2 posterior—they are slightly swollen. The interorbital width is appreciably greater than the "tabular width." The snout is either rounded or rather pointed; the "cheek" is broad and

low, and its posterior border is rather smooth or has fairly marked bosses. The orbit does not lie in the anterior half of the skull. In general the skull is fairly smooth, with a slight indication of pitting and rugae. The maxilla and lacrymal are slightly bulging, more so in *rogersi* than in *watsoni*. Medially the pterygoids fuse far anteriorly, thus producing a short palate; in one species the overhang of the maxillaries and premaxillaries increase this appearance of shortness. The quadrate is not inclined much forwards (80°) and it does not stretch far medially. The brain-case and supraoccipital pillar are low. The tabular boss is low. The maxilla and quadratojugal are fairly deep. The jugal is intercalated between the quadratojugal maxilla.

Brachypareia rogersi (Broom).

(Pls. I-III, V.)

The snout is rather rounded and depressed; the posterior border of the "cheek" is rather smooth. The maxillaries and premaxillaries overhang the anterior part of the palate, so that in ventral view the "comma-shaped" vacuities are partly obscured.

The following skulls are referred to this species:—

Neotype, South African Museum, No. 5012, Tapinocephalus zone, low.				
" "	4350	"	"	mid.
" "	9095	"	"	low.
" "	9098	"	"	mid.

Brachypareia watsoni Haughton and Boonstra.

(Pls. I-II, IV-V.)

The snout is rather pointed and high; the surface of the "cheek" is rugose and carries fairly prominent bosses on its posterior border. There is hardly any overhang of the maxillaries and premaxillaries.

Type, South African Museum, No. 6240, Tapinocephalus zone, low.

Genus *PROPAPPUS* Seeley.

Propappus omocratus (Seeley).

Propappus parvus (Haughton).

(Pl. V.)

In *Propappus omocratus* only a fragment of maxilla and premaxilla is known. The lower jaw has two angular bosses; there are an

intermediate number of teeth (14), which do not overlap; there are many cusps (10–11) arranged evenly in a semicircle. Judging from the rest of the skeleton, the skulls must be of medium size in *omocratus* and rather small in *parvus*.

Type, South African Museum, No. 1058, Endothiodon zone.

Genus PAREIASUCHUS Broom and Haughton.

In this genus the skull is of medium size; there are few teeth (14), which do not overlap; there are many cusps (more than 9) arranged evenly around the edge of the crown. The interorbital width is approximately equal to the “tabular width”; the snout is very broad, depressed, and rounded; the “cheek” is deep and carries strong or very strong bosses on its posterior border. In general the skull is rugose and pitted, more so in *peringueyi* than in *nasicornis*. The maxilla and lacrymal are bulging. The postparietal is small and transversely rectangular. The dorsal and lateral skull surfaces are not separated by a ridge. Medially the pterygoids fuse far forward so as to produce a short palate. The quadrate is inclined much forwards (55°–65°) and does not stretch far medially. The brain-case and supraoccipital pillar are low; the opening of the Vth nerve is low. The supraoccipital forms the dorsal border of the foramen magnum. The tabular boss is low. The maxilla is shallow, but the quadratojugal is large and deep; it does not reach the maxilla.

Pareiasuchus peringueyi Broom and Haughton.

(Pls. I–V.)

There are very strong bosses on the posterior border of the “cheek,” whose surface is also rugose. The quadrate is very much inclined forwards (55°). The angle of the “cheek” is situated far forward. The nostrils are visible in dorsal view.

The following skulls are assigned to this species :—

Type,	South African Museum,	No.	2337,	Cistecephalus zone,	low.
„	„		2367	„	low.
„	„		10668	„	mid.

Pareiasuchus nasicornis Haughton and Boonstra.

(Pls. I–III.)

There are strong bosses on the posterior border of the “cheek,” whose surface is fairly rugose. The quadrate is inclined forwards

(65°). The angle of the "cheek" is situated far back. Owing to the forward direction of the nasal bosses the nostrils are not visible in dorsal view.

Type, South African Museum, No. 3016, Endothiodon zone.

Genus *PAREIASAURUS* Owen.

Pareiasaurus serripedens Owen.

(Pls. I-V.)

The skull is medium sized; there are few teeth (14), which overlap considerably; the number of cusps varies—9 on the anterior and up to 11 on the posterior teeth; these cusps are regularly arranged around the crown and are of equal size. The interorbital width is less than the "tabular width." The "cheek" is very deep and carries strong bosses. The snout is high and pointed. In general the skull is fairly rugose and is considerably pitted. The maxilla and lacrymal are only slightly bulging. The dorsal and lateral skull surfaces are not separated by a ridge but pass into each other in rounded curves. The tabular and postparietal have flange-like developments overhanging the occiput. Medially the pterygoids are fused far anteriorly so as to form a short palate. The border of the interpterygoid vacuity is concave, and the parasphenoidal rostrum is partly visible through it. The quadrate is nearly vertical, the forward inclination being 85°; it also stretches far medially so that in anterior view it nearly obscures the posterior pterygoid ramus altogether. The brain-case and the supraoccipital pillar are high, the *fenestra ovalis* is small, and the opening for the Vth nerve is situated high up on the side wall. The supraoccipital forms the dorsal border of the foramen magnum. The maxilla and quadratojugal are deep, and the jugal is intercalated between the maxilla and quadratojugal.

The following skulls are assigned to this species:—

Type (cast), Brit. Mus. Nat. Hist., No. R4063, *Cistecephalus* zone, mid.

Neotype, University of Stellenbosch, *Cistecephalus* zone, high.

As only a part of the lower jaw and some teeth are known of the specimen, which Seeley named *Pareiasaurus russowii* (Brit. Mus., No. R1996), it is not possible to include it in our scheme with certainty. The nature of the teeth is, however, so similar to that of *Pareiasaurus serripedens* that there appears to be little doubt as to the generic

name, but it appears advisable to retain Seeley's specific name—thus *Pareiasaurus russowii*. Recently I collected another mandible (S.A.M., No. 10667) fairly high up in the Cistecephalus zone which I refer to the genus *Pareiasaurus*.

Genus ANTHODON, Owen.

Anthodon serrarius, Owen.

(Pls. I-III, V.)

The skull is small; there are few teeth (11-14), which do not overlap; there are many cusps (8-15) of equal size arranged regularly around the crown. The interorbital width is less than the "tabular width." The posterior border of the "cheek" has small and low bosses. The snout is fairly high and rather pointed; the "cheek" is quite deep. In general the skull is moderately ornamented with pits and rugae. The maxilla and lacrymal are only very slightly bulging, but there is a small prominent tubercle on the maxilla. The dorsal and lateral surfaces are not sharply separated by a ridge. Medially only the anterior half of the pterygoids fuse, so that posteriorly a long interpterygoid slit remains open. The quadrate is moderately inclined forwards (75°), but it extends far medially to meet the lateral pterygoid flange so that in anterior view the posterior pterygoid ramus is altogether covered by the quadrate. The brain-case and supraoccipital pillar are high. The tabular boss is low. The maxilla and quadratojugal are deep. The jugal separates the maxilla from the quadratojugal. The pineal foramen is very large.

The following skulls are assigned to this species:—

Type, Brit. Mus. Nat. Hist., No. 47337, Cistecephalus zone, mid.

Amer. Mus. Nat. Hist., No. 7001 ,, ,, mid.

South African Museum, No. 4020 ,, ,, low.

 ,, ,, 7841 ,, ,, low.

 ,, ,, 10074 ,, ,, low.

Owen's type of *serrarius* is an imperfect skull from which Watson has, however, been able to determine a number of features. I have described a lower jaw of a specimen in the South African Museum (S.A.M., No. 4020) as of this species. This specimen has also a partial skull of which I have been able to determine the whole palatal structure. At the end of 1930 Broom published two photographs and a short description of a specimen in the American Museum, which he maintains is certainly a distinct species—*gregoryi*. In April 1931

I found an impartial skull and some elements of the postcranial skeleton of an *Anthodon* (S.A.M., No. 10074) at Dunedin. The pelvis and part of the hind-limb have been described without a specific determination, as I then doubted the validity of Broom's new species. Measurements of these four specimens show a uniform progression from a small form (Owen's), through two slightly larger forms (Broom's and S.A.M., No. 4020), to another slightly larger form (S.A.M., No. 10074). But they do not differ in any essentials of structure, and in Broom's description of his new species he gives no reasons for believing his specimen to differ from Owen's. He simply states that it certainly is a distinct species. In view of these considerations it is best to refer them all to Owen's *Anthodon serrarius*, and refer the slight variation in size to a variation within the species or, maybe, an age variation. A complete mandibular ramus in the Geological Museum of the University of Stellenbosch is also assigned to this species. *Anthodon minusculus*, from Tanganyika, is only known from the distal ends of two humeri.

Genus SCUTOSAURUS Hartmann-Weinberg.

Scutosaurus karpinskii Amalitzky.

(Pls. I, III-IV.)

The skull is very large; there are a variable number of teeth with many cusps (9-17) arranged regularly around the crown. The interorbital width is much less than the "tabular width." The posterior border of the "cheek" carries well-defined bosses. The snout is fairly broad and deep, and the "cheek" is deep. In general the skull is sculptured with pits and rugae. The maxilla and lacrymal are bulging. The dorsal and lateral surfaces are not abruptly demarcated by a ridge but pass into each other in rounded curves. Medially the pterygoids are only fused along their anterior half, so that posteriorly a long interpterygoid slit remains through which the parasphenoidal rostrum is visible. According to Hartmann-Weinberg the quadrate is nearly vertical, but according to Sushkin inclines at 45°, and it does not stretch far in medial direction. The brain-case and supraoccipital pillar are high. The tabular boss is low.

Type, mounted specimen, Geol. Mus. Acad. Sci., Leningrad.

In Amalitzky's memoir "diagnoses" are given of three further species, but as the figures are so poor, the text so meagre, and other Russian authors do not mention them, it would be foolhardy to

attempt to establish their systematic position. It would, however, appear that one is justified in referring them all to the genus *Scuto-saurus*, for they manifestly cannot be included in the South African genus *Pareiasaurus*.

Genus ELGINIA Newton.

Elginia mirabilis Newton.

(Pls. I–II.)

The skull is small; there are few teeth (12), which do not overlap; there are many cusps (9–10) of equal size arranged regularly around the crown. The interorbital width is less than the “tabular width.” The posterior border carries horns. The snout is high and fairly pointed, and the “cheek” is deep. In general the skull is greatly ornamented, carrying a great development of horns, in some respects of an analogous nature to that in the living *Moloch* and *Phrynosoma*. The maxilla and lacrymal carry protruding horns. The quadrate appears to be much anteriorly inclined (45°). The maxilla is deep. A long and strong horn is developed on the tabular, and represents the tabular boss.

Type, Coll. Geol. Survey, Elgin Sandstone.

LITERATURE CITED.

- AMALITZKY, V.—“Diagnoses of the New Forms of Vertebrates and Plants from the Upper Permian on North Dvina,” Bull. Acad. Sci. Russ., 1922.
- BOONSTRA, L. D.—“Pareiasaurian Studies. Part III.—On the Pareiasaurian Manus,” Ann. S. Afr. Mus., vol. xxviii, pt. i, 1929.
- BOONSTRA, L. D.—“Pareiasaurian Studies. Part IV.—On the Pareiasaurian Pes,” Ann. S. Afr. Mus., vol. xxviii, pt. i, 1929.
- BOONSTRA, L. D.—“A Contribution to the Cranial Osteology of *Pareiasaurus serridens* Owen,” Ann. Univ. Stellenbosch, vol. viii, Section A, No. 5, 1930.
- BOONSTRA, L. D.—“Pareiasaurian Studies. Part VII.—On the Hind Limb of Two Little-known Pareiasaurian Genera: *Anthodon* and *Pareiasaurus*,” Ann. S. Afr. Mus., vol. xxviii, pt. iv, 1932.
- BOONSTRA, L. D.—“Pareiasaurian Studies. Part VIII.—The Osteology and Myology of the Locomotor Apparatus.—B. Fore Limb,” Ann. S. Afr. Mus., vol. xxviii, pt. iv, 1932.
- BOONSTRA, L. D.—“A Note on the Hyoid Apparatus of Two Permian Reptiles (Pareiasaurians),” Anat. Anz., Bd. 74, 1932.
- BOONSTRA, L. D.—“A Study in Evolution: The Phylogenesis of the *Pareiasauridae*,” S. Afr. Journ. Sci., vol. xxix, 1932.
- BOONSTRA, L. D.—“Paleobiologiese Beskouinge oor 'n Uitgestorwe Reptielgroep (*Pareiasauridae*),” S. Afr. Journ. Sci., vol. xxix, 1932.

- BROOM, R.—“On an Almost Perfect Skeleton of *Pareiasaurus serridens* Owen,” Ann. S. Afr. Mus., vol. iv, pt. ii, 1903.
- BROOM, R.—“A Comparison of the Permian Reptiles of North America with those of South Africa,” Bull. Amer. Mus. Nat. Hist., vol. xxviii, pp. 197–234, 1910.
- BROOM, R.—“On Four New Fossil Reptiles from the Beaufort Series, South Africa,” Rec. Alb. Mus., vol. ii, 1913.
- BROOM, R.—“Further Observations on the South African Fossil Reptiles,” Amer. Mus. Journ., vol. xiv, 1914.
- BROOM, R.—“Catalogue of Types and Figured Specimens of Fossil Vertebrates in the American Museum of Natural History. II.—Permian, Triassic, and Jurassic Reptiles of South Africa,” Bull. Amer. Mus. Nat. Hist., vol. xxv, 1915.
- BROOM, R.—“Pareiasaurian Nomenclature,” Ann. Mag. Nat. Hist., ser. viii, vol. xvii, 1916.
- BROOM, R.—“On Some Points in the Structure of the Pareiasaurian Skull,” P.Z.S., vol. i, 1924.
- BROOM, R.—“On a New Species of *Anthodon* (*A. gregoryi*),” Amer. Mus. Novitates, No. 448, 1930.
- BROOM, R., and HAUGHTON, S. H.—“On the Skeleton of a New Pareiasaurian (*Pareiasuchus peringueyi*),” Ann. S. Afr. Mus., vol. xii, pt. i, 1913.
- HARTMANN-WEINBERG, A.—“Zür Systematik der Nord Düna Pareiasauridae,” Palaeontologische Zeitschrift, Berlin, Bd. 12, 1930.
- HAUGHTON, S. H.—“Pareiasaurian Studies. Part II.—Notes on Some Pareiasaurian Brain-cases,” Ann. S. Afr. Mus., vol. xxviii, pt. i, 1929.
- HAUGHTON, S. H., and BOONSTRA, L. D.—“Pareiasaurian Studies. Part I.—An Attempt at a Classification of the *Pareiasauria* based on Skull Features,” Ann. S. Afr. Mus., vol. xxviii, pt. i, 1929.
- HAUGHTON, S. H., and BOONSTRA, L. D.—“Pareiasaurian Studies. Part V.—On the Pareiasaurian Mandible,” Ann. S. Afr. Mus., vol. xxviii, pt. ii, 1930.
- HAUGHTON, S. H., and BOONSTRA, L. D.—“Pareiasaurian Studies. Part VI.—The Osteology and Myology of the Locomotor Apparatus.—A. Hind Limb,” Ann. S. Afr. Mus., vol. xxviii, pt. iii, 1930.
- NEWTON, E. T.—“On Some New Reptiles from the Elgin Sandstones,” Phil. Trans. Roy. Soc. (Lond.), B, vol. clxxxiv, pp. 473–489, 1893.
- OWEN, R.—“Catalogue of the Fossil Reptilia of South Africa, etc.,” Publ. British Museum, London, 1876.
- SEELEY, H. G.—“Researches on the Structure, Organization, and Classification of the Fossil Reptilia. II.—On *Pareiasaurus bombidens* (Owen), etc.,” Phil. Trans. Roy. Soc. (Lond.), B, vol. clxxix, 1888.
- SEELEY, H. G.—“Researches on the Structure, Organization, and Classification of the Fossil Reptilia. VII.—Further Observations on *Pareiasaurus*,” Phil. Trans. Roy. Soc. (Lond.), B, vol. clxxxiii, 1892.
- SUSHKIN, P. P.—“On the Modifications of the Mandibular and Hyoid Arches and their Relations to the Brain-case in the Early Tetrapoda,” Pal. Zeitschrift, Bd. viii, Heft 4, 1927.
- VERSLUYS, J.—“Das Streptostylie-Problem und die Bewegungen im Schädel bei Sauropsiden,” Zool. Jahrb. Suppl., xv, pp. 545–716, 1912.
- WATSON, D. M. S.—“On the Skull of a Pareiasaurian Reptile, and on the Relationship of that Type,” P.Z.S., vol. i, 1914.
- WATSON, D. M. S.—“On the Nomenclature of the South African Pareiasaurians,” Ann. Mag. Nat. Hist., ser. viii, vol. xiv, 1914.



EXPLANATION OF PLATES.

PLATE I.—*Pareiasaur Skulls in Lateral View.* $\times \frac{1}{4}$.

- Fig. 1. *Bradysaurus baini*. This is drawn from the type in the British Museum, but was checked and augmented by reference to South African Museum specimens (Nos. 3533, 4347, 4999, 5002, 5127, 9104, 9105), and the specimen in the Tübingen Museum.
- Fig. 2. *Bradysaurus seeleyi*. Drawn from the type and co-type in the British Museum, but checked and elaborated by reference to S.A.M., Nos. 5624, 9115, 9121, 9137, and 9168.
- Fig. 3. *Bradysaurus vanderbyli*. Drawn from the type in the South African Museum (No. 3718) and two other specimens (Nos. 8941 and 9169).
- Fig. 4. *Bradysuchus whaitsi*. Drawn from Broom's published photograph of the type in the American Museum (No. 5567).
- Fig. 5. *Nochelesaurus alexanderi*. Drawn from the type in the South African Museum (No. 6239).
- Fig. 6. *Nochelesaurus strubeni*. Drawn from a South African Museum specimen (No. 5019).
- Fig. 7. *Dolichopareia angusta*. Drawn from the type in the South African Museum (No. 6238), but checked by reference to No. 3717.
- Fig. 8. *Brachypareia rogersi*. Drawn from the neo-type in the South African Museum (No. 5012) and checked by No. 5340.
- Fig. 9. *Brachypareia watsoni*. Drawn from the type in the South African Museum (No. 6240).
- Fig. 10. *Embrithosaurus schwarzi*. Drawn from the type in the South African Museum (No. 8034) and incorporating some details elucidated by Watson in the Hottentots River specimen.
- Fig. 11. *Anthodon serrarius*. Drawn from the South African Museum specimens (Nos. 4020 and 10074) and incorporating the details elucidated by Watson in the type in the British Museum.
- Fig. 12. *Pareiasuchus peringueyi*. Drawn from the type in the South African Museum (No. 2337), with additional details from No. 2367.
- Fig. 13. *Pareiasuchus nasicornis*. Drawn from the type in the South African Museum (No. 3016).
- Fig. 14. *Pareiasaurus serridens*. Drawn from the neo-type in the Geological Museum of the University of Stellenbosch.
- Fig. 15. *Scutosaurus karpinskii*. Drawn from the published photograph by Hartmann-Weinberg.
- Fig. 16. "*Pareiasaurus*" *horridus*. Drawn from a cast in the British Museum.
- Fig. 17. *Elginia mirabilis*. Drawn from the published illustration of Newton. Newton's determination of the sutures are doubtful.

Fr. =frontal.	P. Orb. =postorbital.
Jug. =jugal.	Pr. Fr. =prefrontal.
Lac. =lacrymal.	Pr. Mx. =premaxilla.
Mx. =maxilla.	Qu. Jug. =quadratojugal.
Na. =nasal.	Sq. =squamosal.
Pa. =parietal.	Tab. =tabular.
P. Fr. =postfrontal.	

An



R.M



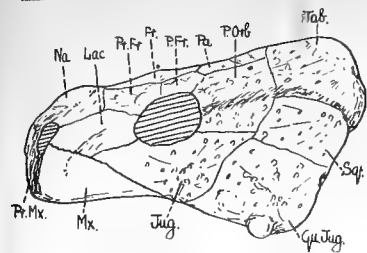


FIG. 1.

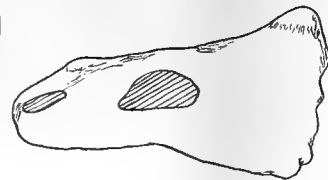


FIG. 4.

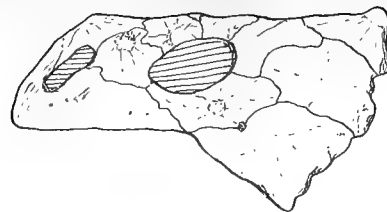


FIG. 7.



FIG. 12.



FIG. 15.

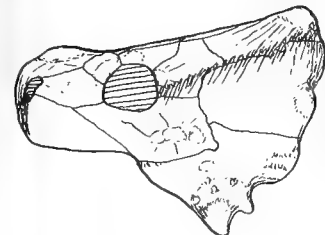


FIG. 2.

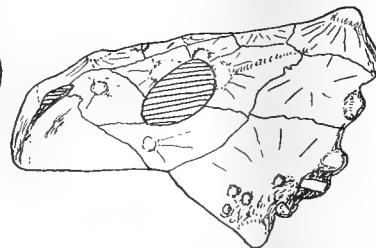


FIG. 5.

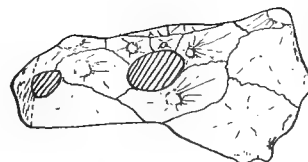


FIG. 8.

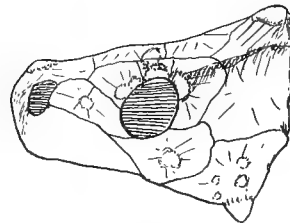


FIG. 10.

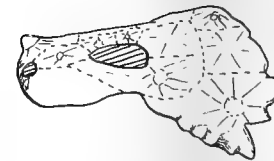


FIG. 13.

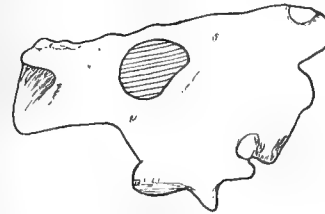


FIG. 16.

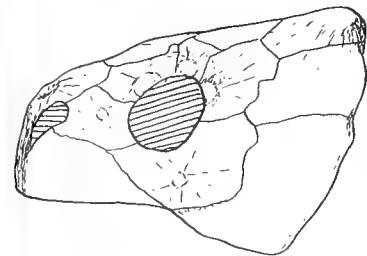


FIG. 3.

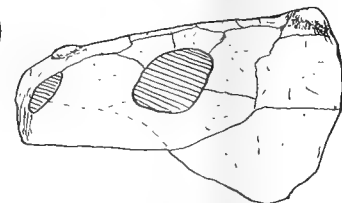


FIG. 6.

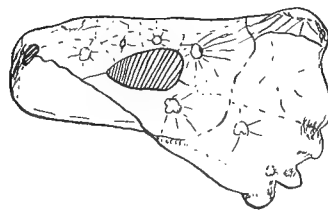


FIG. 9.



FIG. 11.

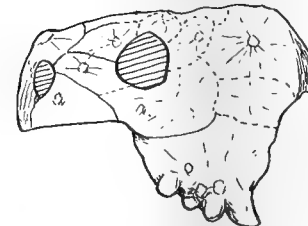


FIG. 14.



FIG. 17.



PLATE II.—*Pareiasaur Skulls in Dorsal View.* $\times \frac{1}{6}$.

For details of specimens examined see explanation to Plate I.

- Fig. 1. *Bradysaurus bairdi*.
 Fig. 2. *Bradysaurus seeleyi*.
 Fig. 3. *Bradysaurus vanderbyli*.
 Fig. 4. *Bradysuchus whaitsi*. Drawn from a sketch kindly supplied by Dr. Broom and a photograph by the American Museum.
 Fig. 5. *Nochelesaurus alexanderi*.
 Fig. 6. *Nochelesaurus strubeni*.
 Fig. 7. *Dolichopareia angusta*.
 Fig. 8. *Brachypareia rogersi*.
 Fig. 9. *Brachypareia watsoni*.
 Fig. 10. *Embrithosaurus schwarzi*.
 Fig. 11. *Anthodon serrarius*.
 Fig. 12. *Pareiasaurus serridens*.
 Fig. 13. *Pareiasuchus peringueyi*.
 Fig. 14. *Pareiasuchus nasicornis*.
 Fig. 15. "*Pareiasuchus*" *horridus*.
 Fig. 16. *Elginia mirabilis*. Newton's determination of the sutures are probably incorrect.

Fr.	=frontal.	P. Orb.	=postorbital.
Jug.	=jugal.	Pr. Fr.	=prefrontal.
Lac.	=lacrymal.	Pr. Mx.	=premaxilla.
Mx.	=maxilla.	P. Pa.	=postparietal.
Na.	=nasal.	Qu. Jug.	=quadratojugal.
Pa.	=parietal.	Sq.	=squamosal.
P. Fr.	=postfrontal.	Tab.	=tabular.

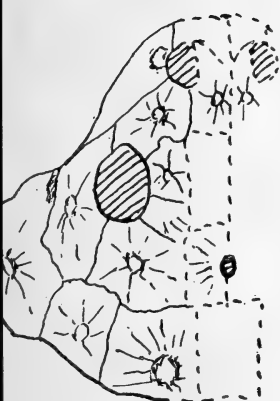
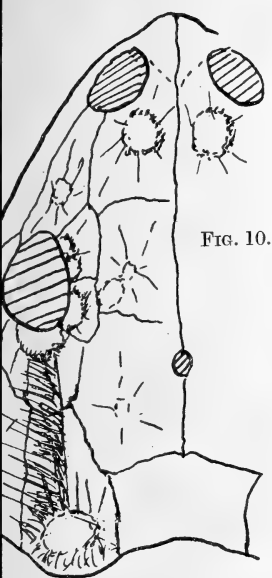


FIG. 1.

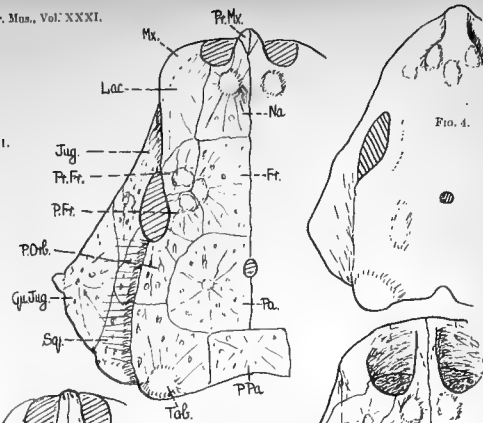


FIG. 4.

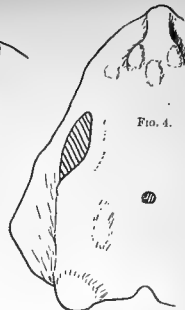


FIG. 2.

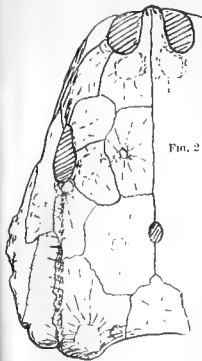


FIG. 3.

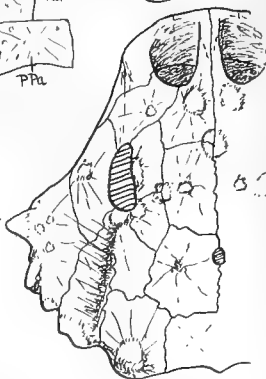


FIG. 5.

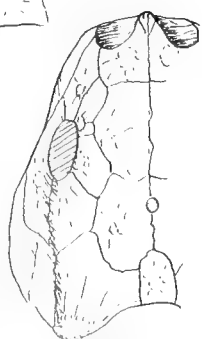


FIG. 6.

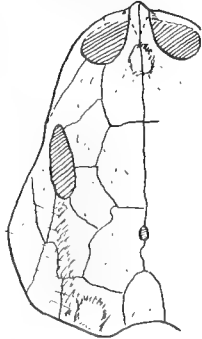


FIG. 7.

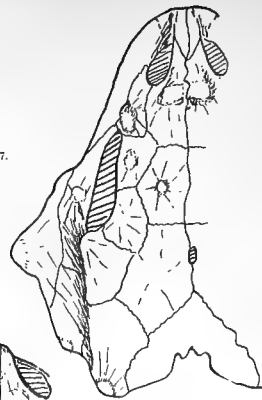


FIG. 8.

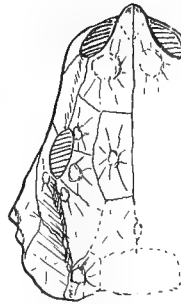


FIG. 9.

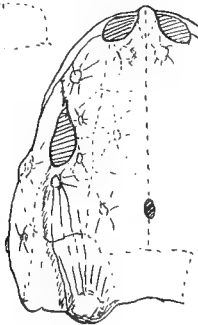


FIG. 10.

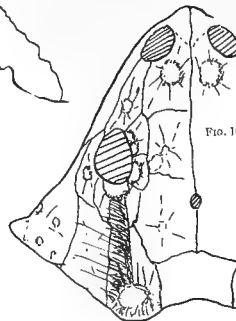


FIG. 11.

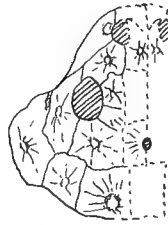


FIG. 12.

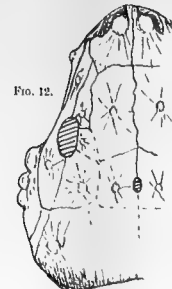


FIG. 13.

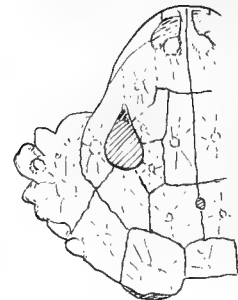


FIG. 14.

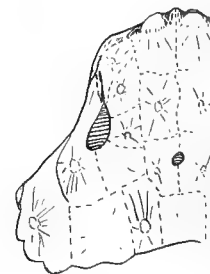


FIG. 15.



FIG. 16.



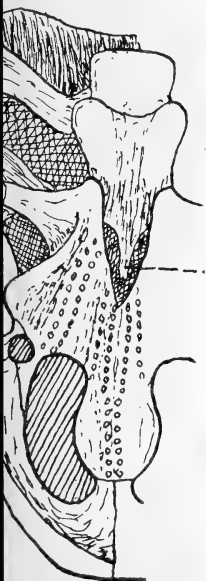
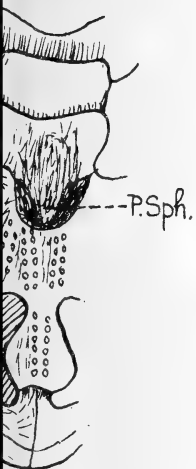


PLATE III.—*Pareiasaur Skulls in Ventral View.* $\times \frac{1}{8}$.

For details of specimens examined see explanation to Plate I.

- Fig. 1. *Bradysaurus bairdi*.
 Fig. 2. *Bradysaurus seeleyi*.
 Fig. 3. *Bradysaurus vanderbyli*.
 Fig. 4. *Nochelesaurus strubeni*.
 Fig. 5. *Brachypareia rogersi*.
 Fig. 6. *Embrithosaurus schwarzi*.
 Fig. 7. *Anthodon serrarius*.
 Fig. 8. *Pareiasuchus peringueyi*.
 Fig. 9. *Pareiasuchus nasicornis*.
 Fig. 10. *Pareiasaurus serripedus*.
 Fig. 11. *Scutosaurus karpinskii*. Details published by Sushkin are incorporated.
 Fig. 12. *Koalemasaurus acutirostris*. Drawn from the type in the Albany Museum.
 Fig. 13. *Dolichopareia angusta*.
 Fig. 14. *Dolichopareia angusta*. Dorsal view of the palate of the type (S.A.M., No. 6238).

A. Pter.	=anterior ramus of the pterygoid.
B. Oc.	=basioccipital.
B. Sph.	=basisphenoid.
For.	=foramina in the premaxillary processes.
For. Qu.	=foramen quadrati.
Int. Pter. Slit.	=interpterygoid slit.
Jug.	=jugal.
L. Pter.	=lateral ramus of the pterygoid.
Mx.	=maxilla.
Pal.	=palatine.
P. Oc.	=paroccipital.
P. Sph.	=parasphenoidal rostrum.
P. Par.	=postparietal.
Pr. Fr.	=prefrontal flange.
Pr. Mx.	=premaxilla.
Pr. Vo.	=prevomer.
Pr. Ot.	=pro-otic.
P. Pter.	=posterior ramus of the pterygoid.
Qu.	=quadrate.
Qu. Jug.	=quadratojugal.
Sub. Orb. Vac.	=suborbital vacuity.
S. Oc.	=supraoccipital.
Sq.	=squamosal.
Tab.	=tabular.
Trans.	=transversum.
T. St.	=tubercle for attachment of stapes.



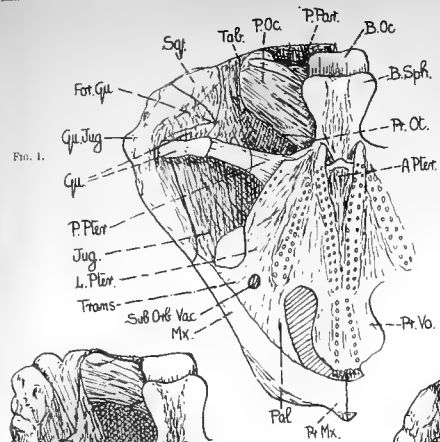


FIG. 1.

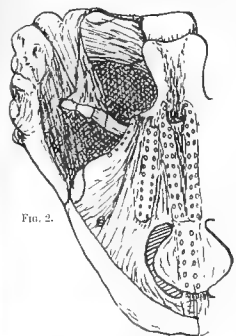


FIG. 2.

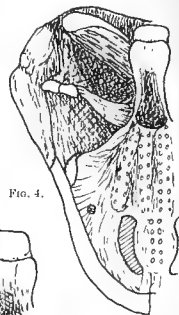


FIG. 4.



FIG. 3.

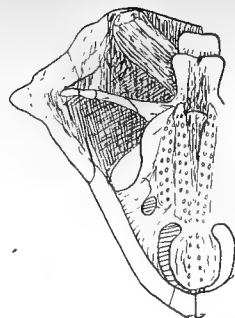


FIG. 6.

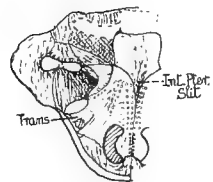


FIG. 7.

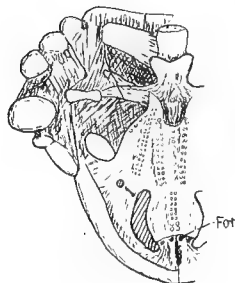


FIG. 8.

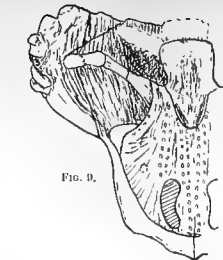


FIG. 9.

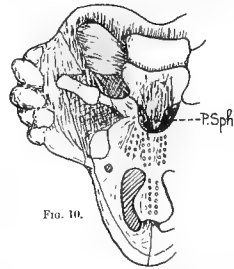


FIG. 10.

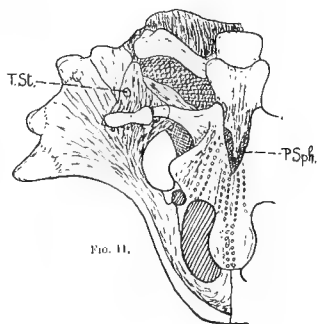


FIG. 11.



FIG. 12.

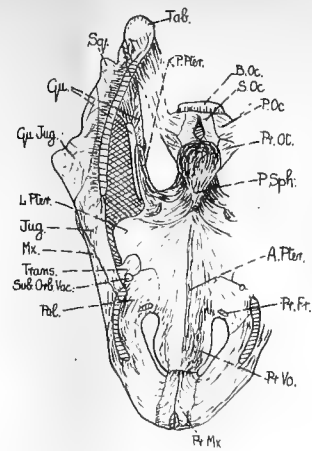


FIG. 14.

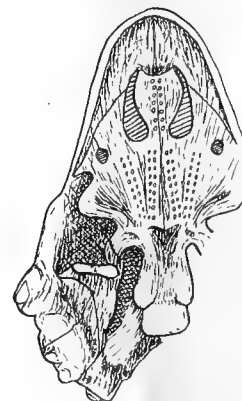


FIG. 13.



PLATE IV.—*Pareiasaur Skulls in Occipital View.* $\times \frac{1}{6}$.

For details of specimens examined see explanation to Plate I.

- Fig. 1. *Bradysaurus bairdi*.
 Fig. 2. *Bradysaurus seeleyi*.
 Fig. 3. *Bradysaurus vanderbyli*.
 Fig. 4. *Nochelesaurus alexanderi*.
 Fig. 5. *Nochelesaurus strubeni*.
 Fig. 6. *Dolichopareia angusta*.
 Fig. 7. *Brachypareia watsoni*.
 Fig. 8. *Embrithosaurus schwarzi*.
 Fig. 9. *Pareiasuchus peringueyi* (No. 2337).
 Fig. 10. „ „ (No. 2367). After Haughton.
 Fig. 11. *Scutosaurus karpinskii*. After Hartmann-Weinberg and Sushkin.
 Fig. 12. *Pareiasaurus serridens*. From Annals of the University of Stellenbosch.

B. Oc. = basioccipital.
 B. Sph. = basisphenoid.
 Ex. Oc. = exoccipital.
 For. Mag. = foramen magnum.
 For. Qu. = foramen quadrati.
 P. Oc. = paroccipital.
 Pp. = postparietal.
 P. Pter. = posterior ramus of the pterygoid.
 P.T.F. = post-temporal fenestra.
 Qu. = quadrate.
 Qu. Jug. = quadratojugal.
 S. Oc. = supraoccipital.
 Sq. = squamosal.
 Tab. = tabular.

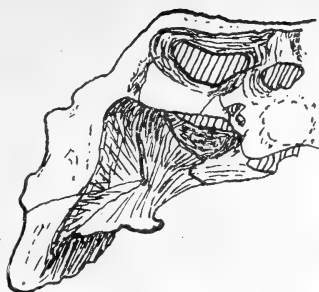
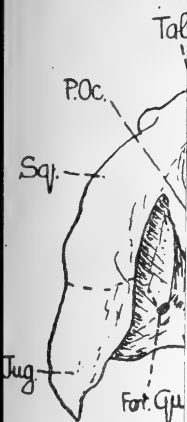


FIG. 10.



FIG. 11.



FIG.



FIG. 12.

FIG.

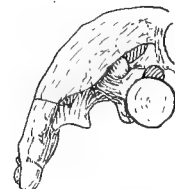
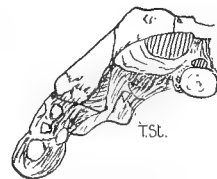
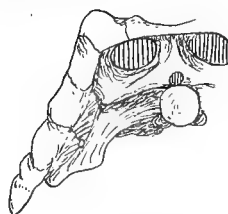
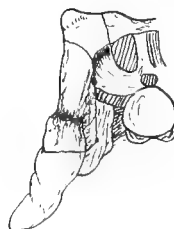
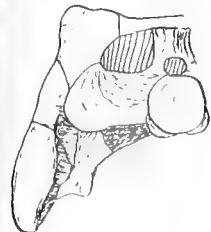
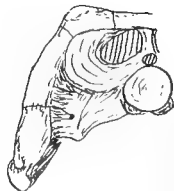
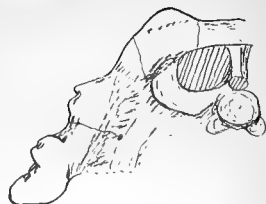
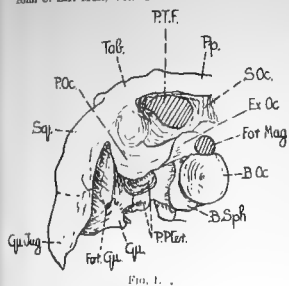




PLATE V.—*Pareiasaurian Teeth in External View.* $\times \frac{1}{2}$.

- Fig. 1. *Bradysaurus bairdi*. 5th left tooth.
Fig. 2. *Bradysaurus seeleyi*. 1st left tooth.
Fig. 3. *Bradysaurus vanderbyli*. 3rd right tooth.
Fig. 4. *Nochelesaurus alexanderi*. 6th left tooth.
Fig. 5. *Nochelesaurus strubeni*. 5th left (mandibular) tooth (after Broom).
Fig. 6. *Dolichopareia angusta*. 8th left tooth.
Fig. 7. *Brachypareia rogersi*. 8th right tooth.
Fig. 8. *Brachypareia watsoni*. 14th right tooth.
Fig. 9. *Embrithosaurus schwarzi*. 9th right tooth.
Fig. 10. *Anthodon serrarius*. 6th or 7th left tooth (after Owen).
Fig. 11. *Propappus omocratus*. 3rd or 4th right tooth.
Fig. 12. *Pareiasuchus peringueyi*. 5th right tooth.
Fig. 13. *Pareiasuchus nasicornis*. 4th right tooth.
Fig. 14. *Pareiasaurus serripes*. 6th right tooth.
Fig. 15. "*Pareiasaurus*" *russowii*. 3rd right mandibular tooth (from Haughton).



FIG. 1.



FIG. 2.



FIG. 3.



FIG. 4.



FIG. 5.



FIG. 6.



FIG. 7.



FIG. 8.



FIG. 9.



FIG. 10.



FIG. 11.



FIG. 12.



FIG. 13.



FIG. 14.



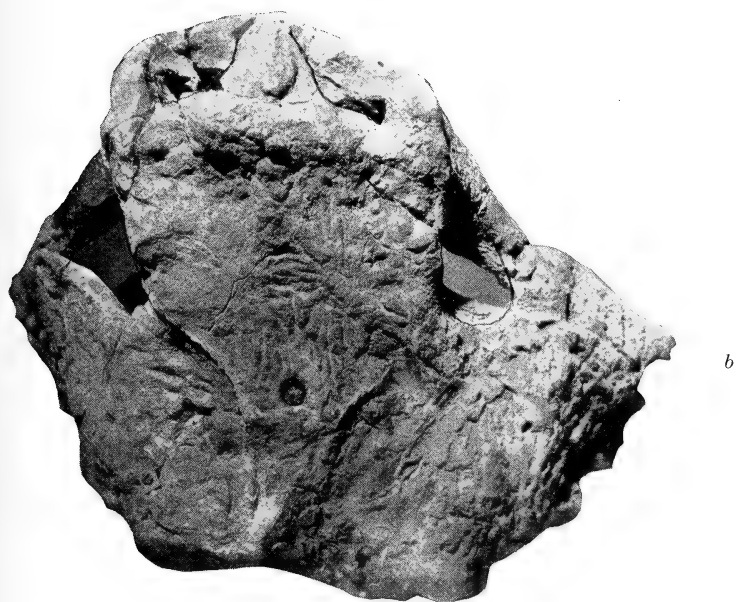
FIG. 15.

PLATE VI.

Bradysaurus bairdi . . . S.A.M., No. 5002. $\times \frac{1}{4}$.

(a) Lateral view.

(b) Dorsal view.



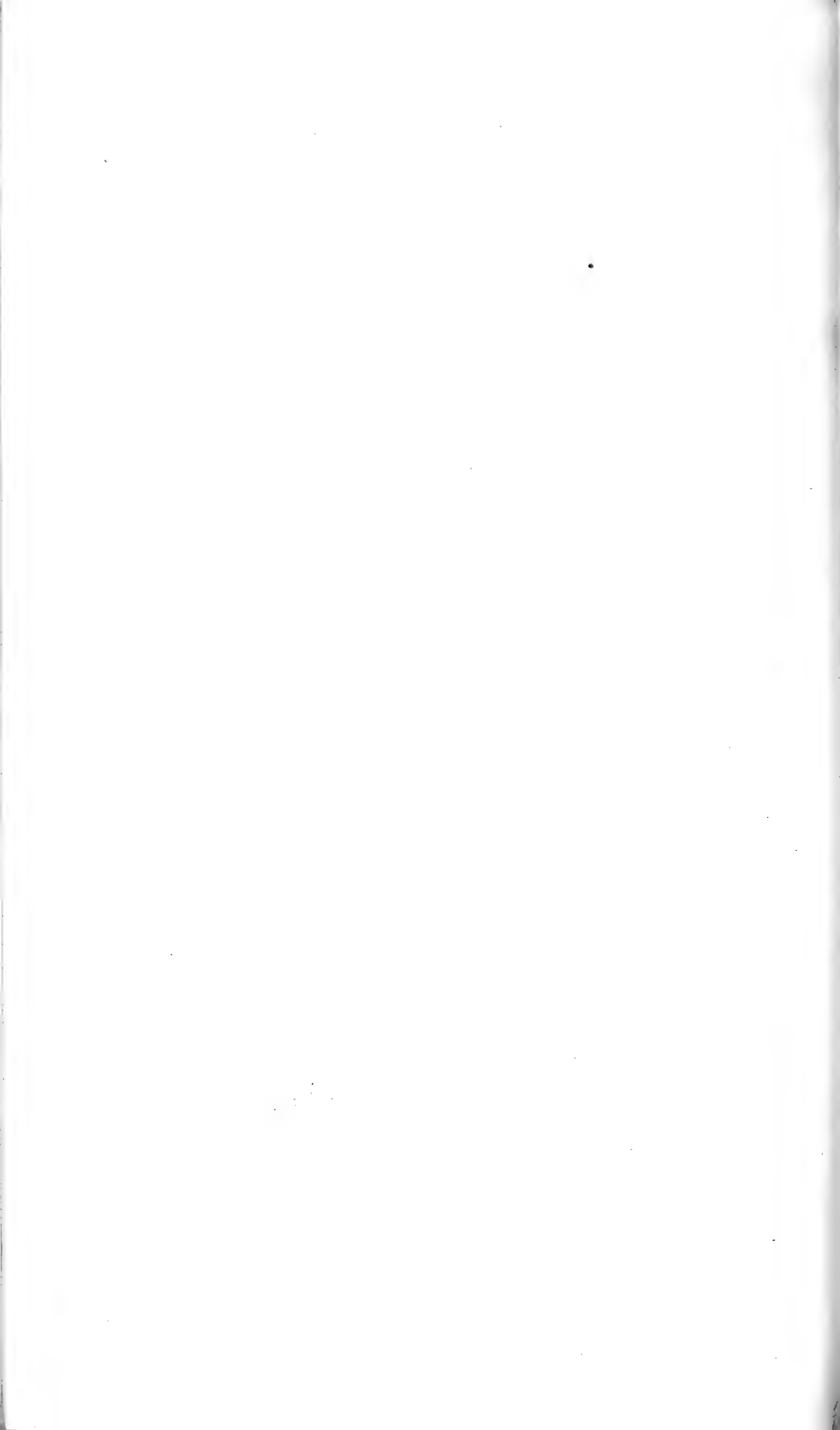




PLATE VII.

Bradysaurus seeleyi . . . S.A.M., No. 9137. $\times \frac{1}{3}$.

(a) Lateral view.

(b) Dorsal view.





PLATE VIII.

- (a) *Bradysaurus seeleyi* . S.A.M., No. 9137. Occipital view. $\times \frac{1}{4}$.
(b) *Bradysaurus vanderbyli* S.A.M., No. 3718. Ventral view. $\times \frac{1}{4}$.





PLATE IX.

Bradysaurus vanderbyli . S.A.M., No. 3718. $\times \frac{1}{4}$.

(a) Lateral view.

(b) Dorsal view.

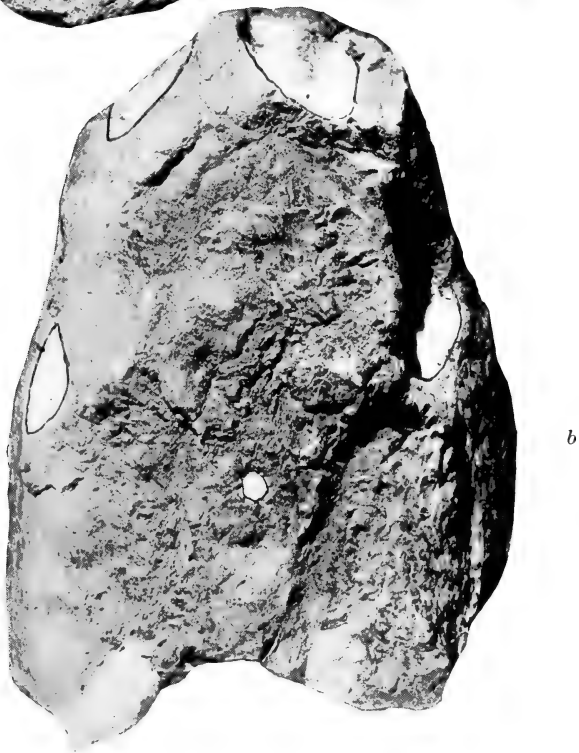
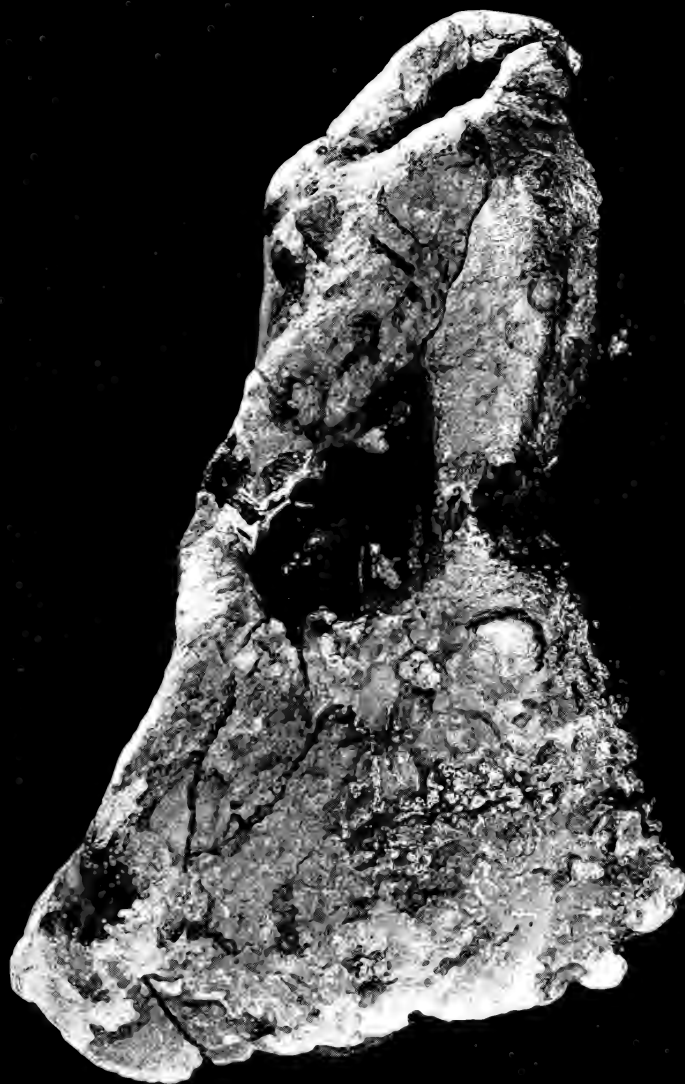




PLATE X.

Bradysuchus whaitsi . . . Amer. Mus. Nat. Hist., No. 5567. $\times \frac{3}{2}$.
Lateral view. Photograph kindly supplied by the
American Museum.



Neill & Co., Ltd.

PLATE XI.

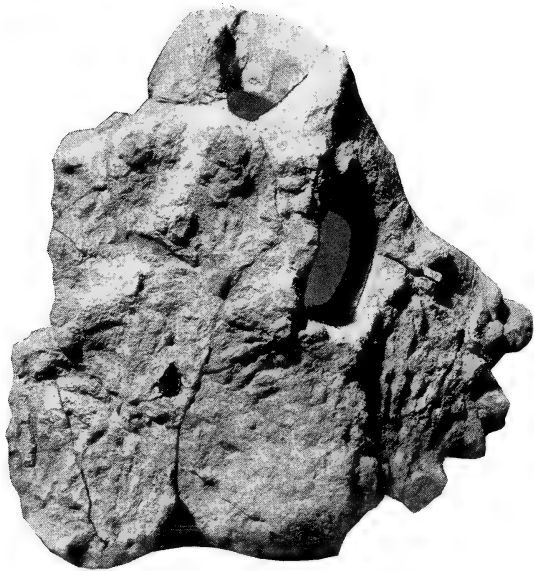
Nochelesaurus alexanderi . S.A.M., No. 6239. $\times \frac{1}{4}$.

(a) Lateral view.

(b) Dorsal view.



a



b



PLATE XII.

Nochelesaurus strubeni . S.A.M., No. 5019. $\times \frac{1}{4}$.

(a) Lateral view.

(b) Dorsal view.

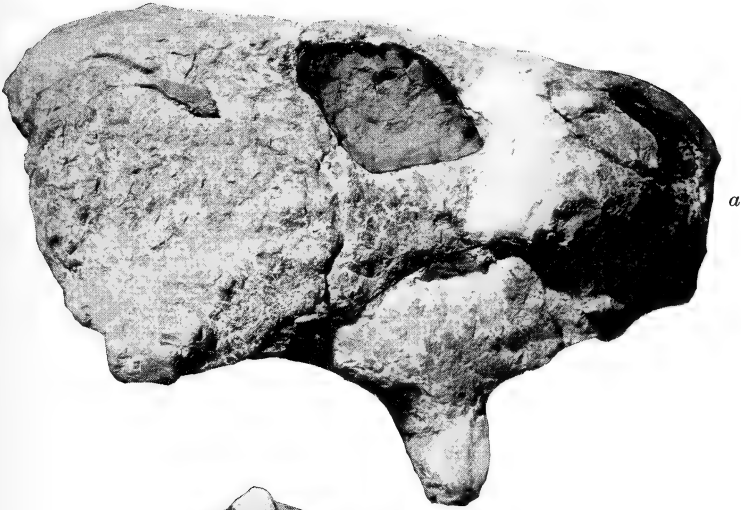


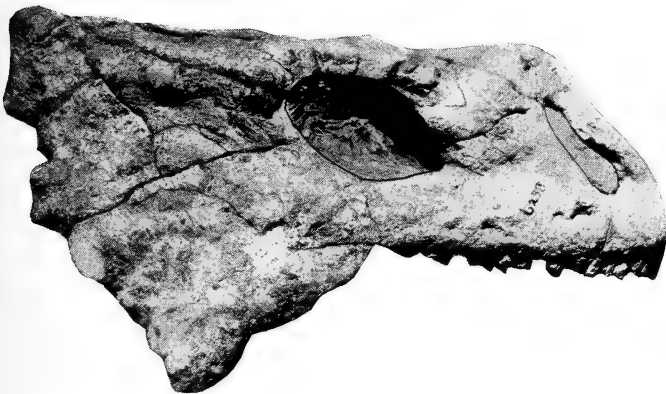


PLATE XIII.

- (a) *Nochelesaurus strubeni* . S.A.M., No. 5019. Occipital view. $\times \frac{1}{4}$.
(b) *Dolichopareia angusta* . S.A.M., No. 6238. Lateral view. $\times \frac{1}{4}$.



a



b

PLATE XIV.

Dolichopareia angusta . S.A.M., No. 3717. $\times \frac{1}{4}$.

(a) Dorsal view.

(b) Ventral view.

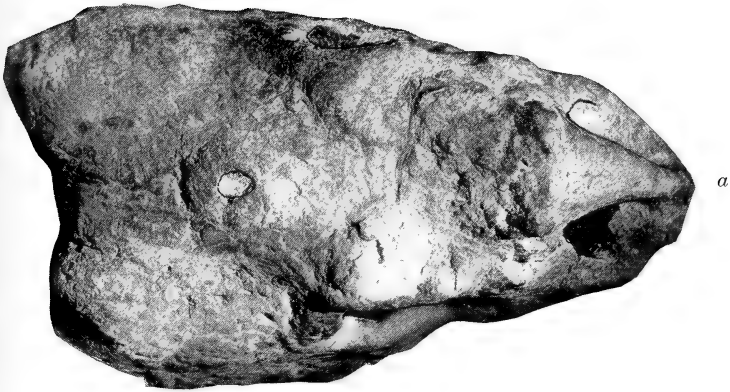
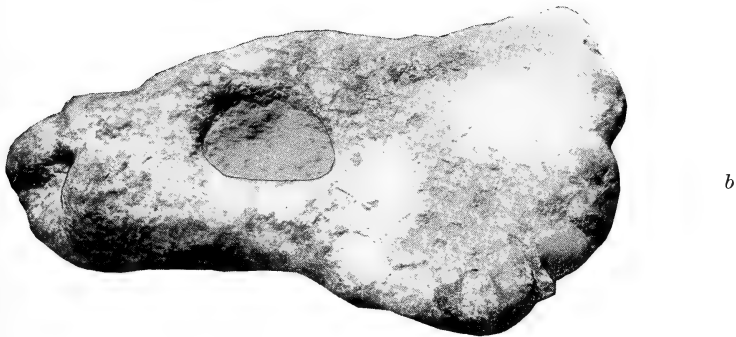


PLATE XV.

<i>Brachypareia rogersi</i>	. $\times \frac{1}{4}$.
(a) Lateral view.	. S.A.M., No. 5012.
(b) Lateral view.	. S.A.M., No. 4350.



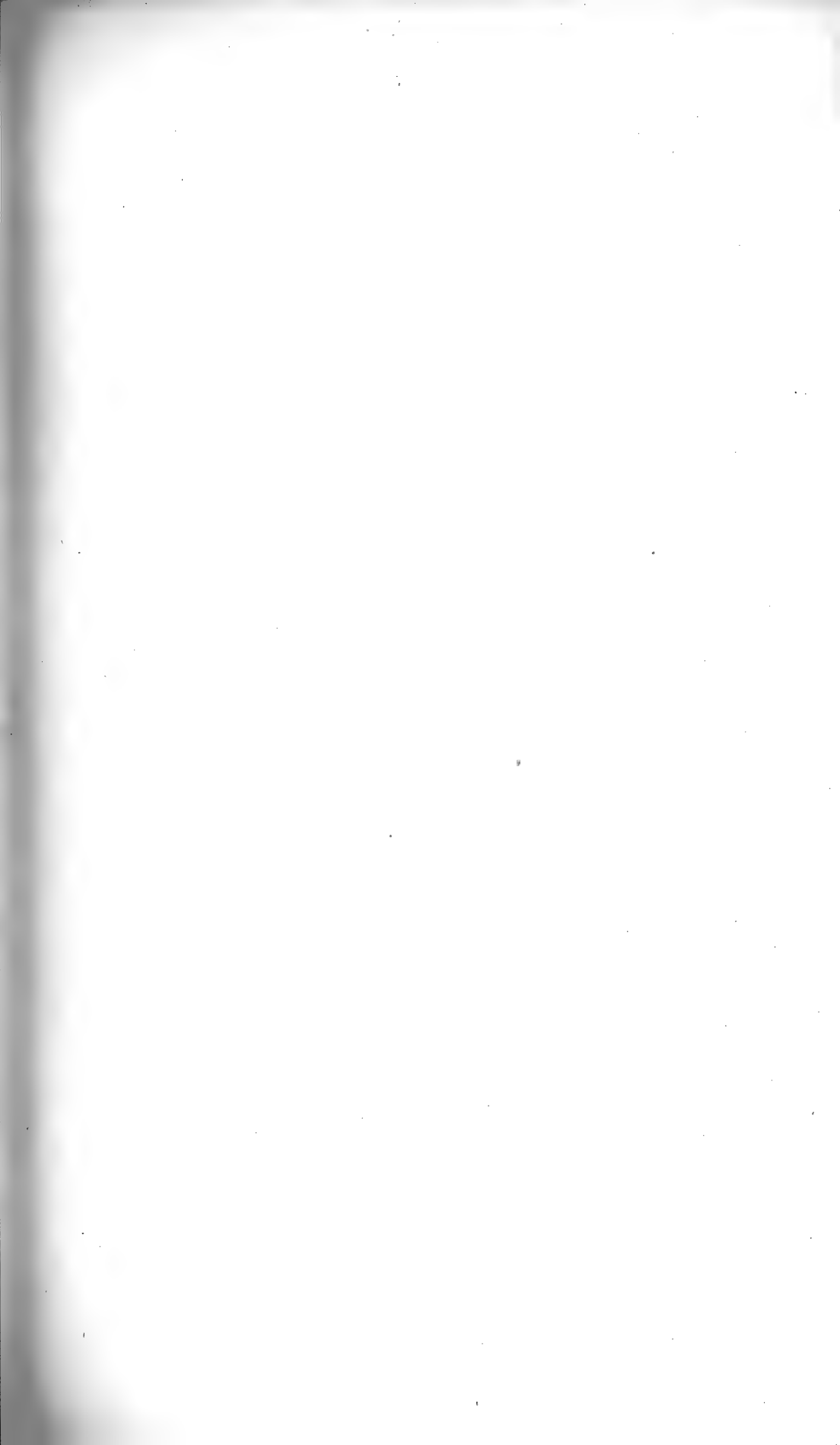


PLATE XVI.

Brachypareia watsoni . . . S.A.M., No. 6240. $\times \frac{1}{4}$.

(a) Lateral view.

(b) Dorsal view.

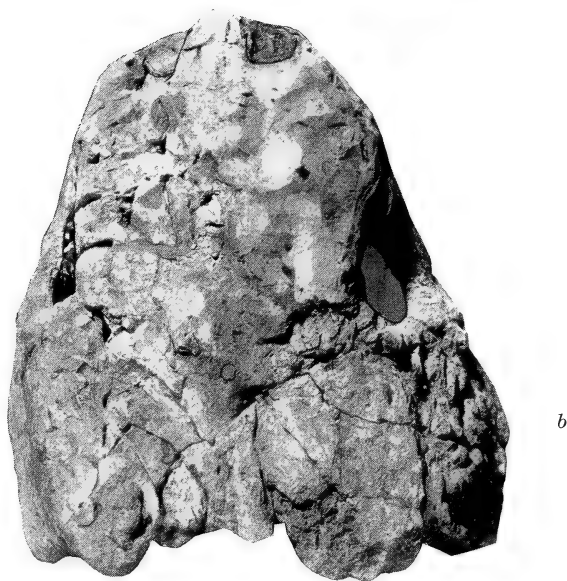




PLATE XVII.

Embrithosaurus schwarzi . S.A.M., No. 8034.

(a) Lateral view. . $\times \frac{1}{4}$.

(b) Occipital view. . $\times \frac{1}{3}$.



a



b



PLATE XVIII.

Pareiasuchus peringueyi . S.A.M., No. 2337. $\times \frac{1}{4}$.

(a) Lateral view.

(b) Occipital view.



a



b



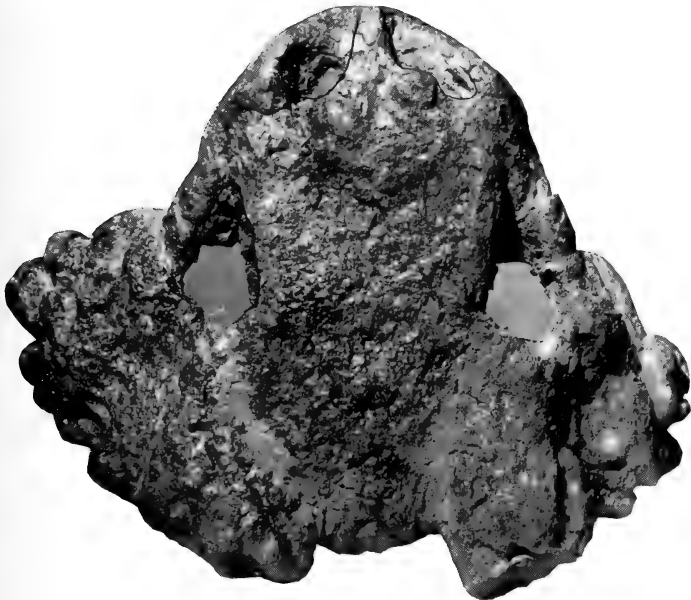


PLATE XIX.

Pareiasuchus peringueyi . S.A.M., No. 2337. $\times \frac{1}{4}$.

(a) Dorsal view.

(b) Ventral view.



a



b

PLATE XX.

Pareiasuchus nasicornis . S.A.M., No. 3016. $\times \frac{1}{4}$.

(a) Ventral view.

(b) Dorsal view.



a



b

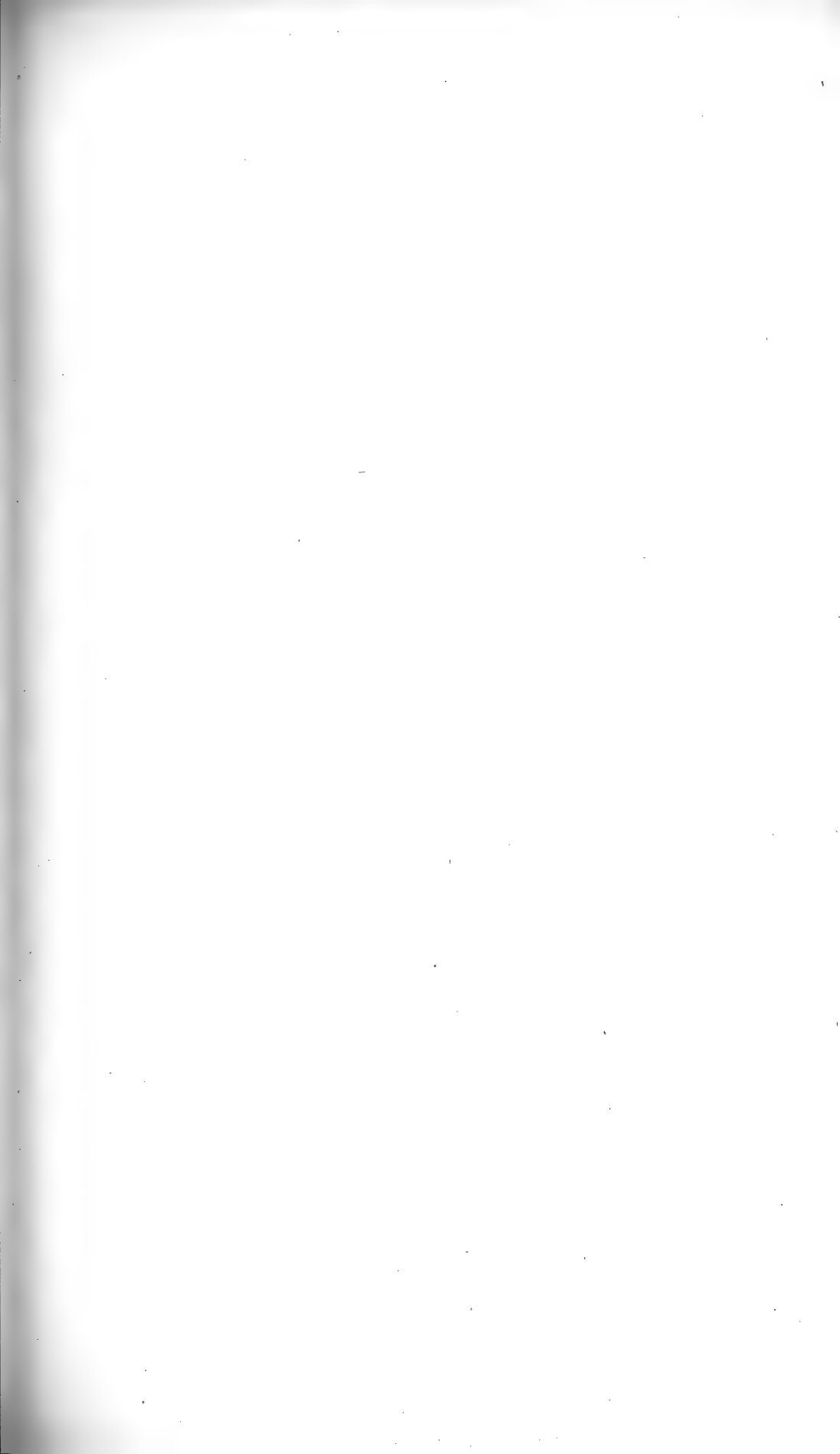


PLATE XXI.

- (a) *Pareiasuchus nasicornis* S.A.M., No. 3016. Lateral view. $\times \frac{1}{4}$.
(b) *Anthodon serrarius* . S.A.M., No. 10074. Lateral view. $\times \frac{2}{5}$.

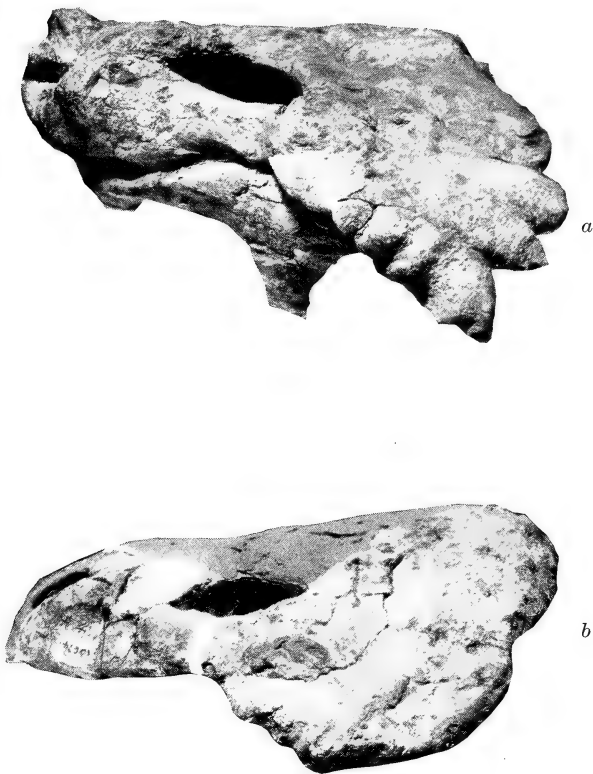
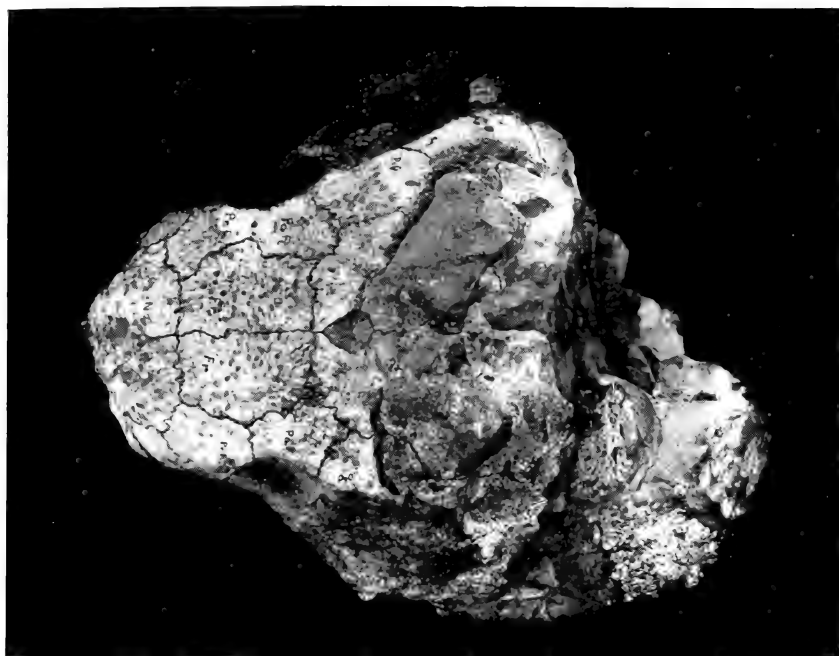




PLATE XXII.

- (a) *Anthodon serrarius* . Amer. Mus., No. 7001. Dorsal view. $\times \frac{1}{3}$.
Photograph kindly supplied by the
American Museum.
- (b) *Pareiasaurus serridens* . Geol. Mus. Univ. Stellenbosch. Lateral
view. $\times \frac{1}{3}$.



a



b

Pareiasaurian Studies.

Part X.—*The Dermal Armour*.—By LIEUWE D. BOONSTRA, D.Sc.,
Department of Palaeontology, South African Museum.

(With Plates XXIII–XXVII.)

INTRODUCTION.

THAT the Pareiasaurs possessed a more or less extensive armour of bony scutes of dermal origin has been noted by a number of authors. Seeley gave the first and also the most complete account of the armature in the genus *Bradysaurus*. Broom described it in *Propappus* and *Brachypareia*, and referred to it in *Embrithosaurus* and *Anthodon*; publishing jointly with Haughton, a brief reference was made to the scutes of *Pareiasuchus*. Subsequently Watson used the nature of the armature as a generic character. Amalitzky and Hartmann-Weinberg have considered the nature of the scutes as of specific as well as of generic value in the case of the Russian Pareiasaurs.

In the body of this paper an attempt is made to gather together our knowledge of the Pareiasaurian armour in order to obtain a general idea of the appearance and the defensive abilities of the Pareiasaurs as a whole, and, secondly, to determine the specific and generic differences (if any), and, as a further development of the same theme, to see whether there is any progressive or retrogressive development of the armature. The large number of new specimens now in the South African Museum, together with those already partly known, fully justifies such an attempt being made. Wherever possible the verbal description is accompanied by photographs.

Genus BRADYSAURUS.

1888. Seeley, H. G., Phil. Trans. Roy. Soc., vol. clxxix, B 22, p. 91.

1892. Seeley, H. G., Phil. Trans. Roy. Soc., vol. clxxxiii, B 76,
pp. 345, 346.

1908. Seeley, H. G., P.Z.S., vol. ii, pp. 605-607.

1914. Watson, D. M. S., Ann. Mag. Nat. Hist., vol. xiv.

The dermal ossicles in the three species of this genus are very similar (Pl. XXIII; Pl. XXIV, fig. 1); the scutes preserved are roughly circular or oval in outline; the external surface is relatively smooth; in *Br. vanderbyli* they are practically devoid of any ornamentation; in *Br. baini* the scutes are convex, curving down from a thickened centre which in some scutes appears like an incipient boss; there are no distinct radiating ridges; in *Br. seeleyi* the central boss appears to be somewhat more distinct, and the surface somewhat pitted. There is also very little difference in the size of the scutes, viz. *Br. baini* ($50 \times 50-45 \times 12$ mm.), *Br. seeleyi* ($57-35 \times 50-30 \times 10-7$ mm.), *Br. vanderbyli* ($48 \times 47 \times 7$ mm.).

The above facts appear to exhaust the dissimilarities. From the available facts the following composite account, which includes some of Seeley's observations, of the arrangement of the armour appears to be correct for all three species. "No indications of large dermal bones are preserved. Three rows of scutes appear to have extended down the median line of the back." "The median row was placed on the summits of the neural spines and above the interspaces between them. In contact with these, laterally, there is a pair of scutes extending transversely outward; so that in the antero-posterior direction three scutes may be counted corresponding to each vertebra. And the effect is a median longitudinal strip of close-set scutes, flanked by two lateral rows." From the large number of specimens in the South African Museum it appears that the scutes were in more close contact above the scapulae and the sacrum than along the rest of the back and on the tail. Above the ribs, *i.e.* on the flanks of the animal, the scutes seem to have been little developed, and this also applies to the upper portions of the limbs. No small stud-shaped or conical ossicles have been found in this genus, and they probably did not exist.

In this connection it is perhaps significant to note that in the other large genera (*Dolichopareia* and *Nochelesaurus*) of the Tapinocephalus zone no scutes have been found. It must be admitted that of these genera we only know a few specimens, not very fully preserved, but the absence of scutes in the specimens known seems to indicate a lesser development of armour than in the more highly evolved forms of the younger horizons.

Genus KOALEMASAURUS.

No dermal scutes are preserved in association with the type skull in the Albany Museum. Associated with a skull and vertebral column referred by me to this genus there are, fortunately, a few scutes. Although it is impossible to ascertain the extent of the armature from this scanty material, the nature of an individual scute can be described. The scutes preserved (Pl. XXIV, fig. 2) are small ($45 \times 32 \times 7$ mm.), oval in outline, smooth, with only a slight indication of a central knob and a hardly perceptible rugous radiation.

The possibility exists that the scantiness of the number of scutes preserved is due to the fact that the specimen is immature, and to the same cause the smoothness of the scutes may be ascribed.

Genus BRACHYPAREIA.

1912. Broom, R., Ann. S. Afr. Mus., vol. vii, p. 323.

1914. Watson, D. M. S., Ann. Mag. Nat. Hist., vol. xiv.

Unfortunately no scutes are known of *Brachypareia watsoni*—only the skull of the type specimen being preserved. The description that follows thus only refers to *Brachypareia rogersi*. A very large number of dermal scutes of various sizes and shapes are preserved in association with the type specimen (Pl. XXIV, fig. 3). There is a perfect gradation from fairly large ovoid or circular ossicles, whose outer surfaces are ornamented with a central knob from which fairly strong ridges radiate, through a series of smaller circular ossicles with a strong central knob, but with only feeble ridges radiating from it, standing on a base and presenting the appearance of a depressed collar stud, to small globular ossicles about the size of large peas, and with apparently no surface ornamentation. In all the ossicles, with the exception of the globular ones, there is on the external surface a foramen entering the interior of the bone and cut into the side of the knob. It communicates with a small foramen opening on the internal surface. From the plate a better idea can be obtained of the relative sizes and shapes than from any verbal description.

The number of ossicles preserved, in addition to this gradation in a series in point of size and ornamentation, allows one to draw the following conclusions, viz. that all along the back, from the neck to the proximal dorsal surface of the tail, there must have been rows of ossicles (two or three per rump segment) with contiguous edges. The flanks, withers, and quarters were apparently studded with the

circular stud-shaped ossicles; the upper portions of the limbs, the extremity of the tail, and the lateral parts of the belly must have housed the smaller globular ossicles; the belly, throat, and those parts affected by the movements of the limbs would have been practically free of dermal armour.

Genus EMBRITHOSAURUS.

1903. Broom, R., Ann. S. Afr. Mus., vol. iv, pl. xvi.

1914. Watson, D. M. S., Ann. Mag. Nat. Hist., vol. xiv.

Although Broom only mentioned the dermal ossicles of *Embrithosaurus* in his explanation to a plate, a series, above the 6th, 7th, and 8th presacral vertebrae, is very well preserved *in situ* and merits a fuller description.

Above the spinous process a large (50 × 50 mm.) and thick (20 mm.) scute is situated (Pl. XXV, fig. 1); it has a very large and strong central boss of irregular shape, but no ridges radiate from it towards the periphery. Both anteriorly and posteriorly this scute articulates with a smaller smoother scute, which overlies the interspace between the spinous processes; laterally there lie two rows of scutes, each row has two scutes per segment—one lying on the postzygapophysial ridge and the other in the interspace; these scutes articulate with each other and with the median row of scutes. These lateral scutes are smaller (50 × 40 mm.) and thinner (15 mm.), have a more circular boss from which a few ridges commence, but do not reach the periphery; the edges are serrate. A still smaller scute (35 × 22 × 5 mm.), apparently from the flank, is preserved. It is oval in outline, has a slightly thickened centre, rugose near the edges, and serrated edge.

In summary one can thus state that above the withers of the animal there were five rows of articulating ossicles, that it is probable that some of these rows extended along the whole length of the back, and that the flanks were in all probability studded with smaller and smoother scutes.

Genus ANTHODON.

1930. Broom, R., Amer. Mus. Novitates, No. 448.

Although Broom has described the specimen of *Anthodon* in the American Museum of Natural History as a new species, I have seen fit to doubt that it is distinct from Owen's species. The nature of the dermal armour in a specimen in the South African Museum, which

certainly belongs to Owen's species, is so similar to that of the American Museum specimen that my doubt as to the validity of Broom's species appears to have further justification.

Broom has stated that the back of *Anthodon* was "covered by a bony carapace formed by large articulating bony scutes." From a number of dermal ossicles found overlying the sacral region of one of the South African Museum specimens, it becomes evident (Pl. XXV, fig. 2; Pl. XXVI, fig. 1) that at least some of the scutes are firmly articulated to each other, so that in ventral view (Pl. XXVI, fig. 1) the line of articulation is only indicated by a digitating suture similar to those found between some cranial bones. A small foramen is also to be noted opening on to the ventral surface.

The scutes are of medium size ($64-54 \times 45-40 \times 11$ mm.), roughly circular in outline, and are strongly ornamented on the outer surfaces, the central knob stands out very distinctly—this being due to the fact that it does not grade into the base, but is partly demarcated from it by an encircling moat traversed by radiating ridges. Relative to this moat the peripheral edge is somewhat raised and thickened; at the articulation with adjoining scutes the edge is deeply serrate.

Genus PAREIASAURUS.

1914. Watson, D. M. S., Ann. Mag. Nat. Hist., vol. xiv.

Watson has shown that the pelvis described by Owen as that of *Dicynodon tigriceps* belongs to the type of *Pareiasaurus serripedus*. With it are associated scutes which would appear to have formed an extensive armour. "The whole of the dorsal surface of the pelvis between the crests of the ilia is covered with very large scales which are of the *Propappus* type, but differ in their more definitely pitted ornament and much larger size." Associated with the neo-type skull in the University of Stellenbosch there are a number of scutes preserved, and I also have a specimen in the South African Museum with a number of scutes (Pl. XXVI, fig. 2).

Three sizes ($67-53-47 \times 58-45-40 \times 25-20-15$ mm.) of ossicles are preserved. Each ossicle has a strong central boss from which strong ridges alternating with deep grooves radiate towards the periphery. The foramen, entering the interior of the bone on one side of the boss, is constant. A small foramen also opens on the internal surface of the scute. The scutes of *Pareiasaurus* are very similar to those of *Pareiasuchus*.

There is evidence (Pl. XXVI, left bottom pair) that some of the

lateral scutes overlying the ribs have their serrated edges interlocking, and if this is the case in a series of scutes a carapace of mosaic pattern would be formed, but it does not appear that a very great degree of rigidity would result as there appears to be a possibility of relative movement at the "sutures."

The scutes overlying the ribs have their longer diameter directed dorso-ventrally and the shorter antero-posteriorly. There is, furthermore, reason to believe that, as in the case of the dorso-median scutes, the lateral scutes on the flanks were also regularly arranged in rows.

Genus PAREIASUCHUS.

1913. Broom, R., and Haughton, S. H., Ann. S. Afr. Mus., vol. xii, p. 25.

Dermal scutes are present in the type specimens of both species. Those of *Pareiasuchus peringueyi* have been described by Broom and Haughton in the following words: "Dermal ossicles occur all along the back, between the proximal parts of the ribs, especially in the neck, and around the pelvis. The scutes are smaller than those of *Propappus*." Those of *P. nasicornis* have as yet not been described. Although only a limited number of bony scutes are preserved there is sufficient evidence available to enable one to state that fairly large ($65-40 \times 55-30 \times 15-10$ mm.) scutes were present, in at least three rows, all along the back, and that they appear to have been especially well-developed above the shoulder-blades and the sacrum; as preserved, some of the scutes are in contact along their edges, and it is thus legitimate to assume that the armour consisted of rows of scutes in contact with each other. As is apparent from the illustration (Pl. XXVII, fig. 1), the scutes vary in size, shape, and external ornamentation. All the preserved scutes are rugose; they have a central knob from which strong ridges radiate; the foramen on the side of the knob is constant, but in one case the foramen is open to the periphery and forms a notch.

Genus PROPAPPUS.

1908. Broom, R., Ann. S. Afr. Mus., vol. iv, pp. 358, 359.

1914. Watson, D., M. S. Ann. Mag. Nat. Hist., vol. xiv.

Although only a few scutes of *Propappus parvus* are preserved in the one known specimen, it appears that the armour differs substantially from that of *Propappus omocratus*.

The armour of *Propappus omocratus* was first described by Broom : "*Propappus* must have had the whole back and probably sides covered with a carapace of bony plates somewhat after the manner of the crocodile. They vary in size from plates 50 mm. in diameter to little bony nodules about the size of peas. The larger ones have a central boss and irregular radiating ridges. At the edges they overlap each other, and it seems probable that the carapace was not quite rigid. It extended at least as far out on the sides as 300 mm. from the middle line. There is no evidence of any plastron."

Some additional remarks may be appended (Pl. XXVII, fig. 2) : there is evidence that along the median line in each rump-segment one scute overlay the spinous process, one lay between the spinous processes, and lateral to these one lay on the postzygapophysial ridge, and one in the interspace between this and the next ridge. Broom records an overlapping of the scutes, whereas to me there appears to be an articulation at the edges.

Only a few scutes of *Propappus parvus* are preserved (Pl. XXVII, fig. 2). Judging from these the scutes appear to be more oval (60–50 × 37 mm.) and flatter (8 mm.) than those of *Pr. omocratus*; the central boss is weaker and the ornamentation much weaker—the radiating ridges being only distinct at the edges of the scute.

Genus SCUTOSAURUS.

1922. Amalitzky, V., Bull. Acad. Sc. Russ.

1930. Hartmann-Weinberg, Pal. Zeitschr., Bd. xii.

In 1922 Amalitzky, in his brief "diagnoses," mentioned the dermal armour of the Russian Pareiasaurs. In *Scutosaurus Karpinskii*, "star-shaped dermal plates are situated above the spinous processes of the vertebrae, two or three rows of similar plates lie on the sides of the body. There are also plates distributed, without apparent order, over the whole body (fig. 8) (from the illustration these ossicles look very similar to those of *Pareiasaurus* L.D.B.); the belly was covered with small conical bosses."

"*Pareiosaurus*" *tuberculatus* has "three rows of star-shaped dermal plates on the sides of the neck; in the tail region the plates are boss-like."

In 1930 Hartmann-Weinberg stated that the osseous scutes of *Scutosaurus* are of various shapes and sizes. The ornamentation is similar to that of the skull; they lie closely applied to each other to form a heavy carapace.

Incerta sedis.

1908. Seeley, H. G., P.Z.S., pp. 607-610.

In 1908 Seeley described and figured (text-figs. 125 and 126) a number of scutes which he had obtained from Steenkamps Poort. The evidence afforded by the nature of these scutes appeared to him to justify the creation of a new species, *Pareiasaurus steenkampensis*. From his excellent description and figures it appears that these scutes are very similar to those of either *Brachypareia rogersi* or *Pareiasuchus nasicornis*, but it would be rash, lacking corroborative evidence from the rest of the skeleton, definitely to assign these scutes to either of these forms. These scutes are thus best referred to as simply Pareiasaurian, with the corollary that they definitely do not belong to forms of the genus *Bradysaurus*.

GENERAL.

It is possible, from the above detailed account, to determine the essential characters of the Pareiasaurian dermal armour. One of the most striking features is the apparent correlation that exists between the ornamentation on the dermal cranial bones and that on the dermal ossicles. Most of the dermal cranial bones have a more or less centrally placed boss from which ridges and grooves and bone-fibres radiate, and the sutures between adjoining bones is often of a zigzag nature. Practically the same features are found in the dermal ossicles.

Moreover, in the early forms with moderately smooth skulls the dermal ossicles are found to be fairly smooth, and conversely, the rugose skulls of later forms are accompanied by highly ornamented and closely articulating dermal ossicles. It thus appears to be consistent with the facts to conclude that the Pareiasaurs during their evolutionary history, in addition to acquiring a greater cranial rugosity, developed an armour of more highly ornamented and more closely articulating dermal ossicles.

It would, furthermore, appear that the development of the dermal armour began above the scapulae and above the sacrum, and then extended along the whole back; then along the flanks, and finally above the limbs and possibly also the belly. So also the articulation of the scutes, *inter se*, appears to have followed the same order of development.

There seems to be little doubt that in general the dermal ossicles

were arranged in regular rows running parallel and at right angles to the dorsal median line. The arrangement of a pair of ossicles per vertebral segment and also the position in relation to the ribs seems to indicate that the scutes were more firmly articulated along their lateral margins than along either the anterior or posterior margin, so that it is perhaps more correct to refer to transverse rows of scutes. I imagine the arrangement of the scutes to have been very similar to those of the living *Zonurus*.

Mention has been made of a foramen entering each ossicle on the external surface on the side of the central boss, and also of a much smaller foramen opening on the internal surface. The former opens into a conical pit on the outer surface. In specially prepared sections it is seen that these foramina communicate; I have examined the scutes in the living *Varanus* and *Zonurus*, and find that in the former a nutritive foramen enters on the external surface, whereas in the latter it enters on the internal surface just under the spine. It would thus appear that both foramina in the Pareiasaur scute, in all probability, housed blood-vessels.

Consisting of strong bony ossicles, the Pareiasaur armour was certainly of great biological value to these animals. As has been noted, it is first developed above the most vulnerable spots, and it is significant that the forms surviving up to the end of Lower Beaufort times show the highest development of armour. The last Pareiasaurs, although carrying a greater amount of armour, do not appear to have become more clumsy animals. On the contrary, our studies of the limbs and limb-musculature point to a more upright gait accompanied by greater agility. The development of armour in these animals was certainly an acquisition of a character of decided survival value, and, furthermore, does not appear to have eventually overreached itself.

EXPLANATION OF PLATES.

PLATE XXIII.

- Fig. 1. *Bradysaurus seeleyi* (9168). $\times \frac{2}{3}$. Dermal ossicles above 5th, 6th, and 7th presacral vertebrae. The median and first lateral row of each side are represented.
- Fig. 2. *Bradysaurus baini* (9001). $\times \frac{2}{3}$. Dermal ossicles of the first lateral row above the anterior dorsal vertebrae.

PLATE XXIV.

- Fig. 1. *Bradysaurus vanderbyli* (9169). $\times 1$. Three articulating ossicles above the anterior dorsal vertebrae.
- Fig. 2. *Koalemasaurus acutirostris* (4345). $\times \frac{3}{4}$. Two isolated ossicles.
- Fig. 3. *Brachypareia rogersi* (8453). $\times \frac{3}{4}$. A series of isolated ossicles; the larger ones in the top row come from the median line of the back; the smaller ones in the second row from the flanks, and the lowest row probably low down the flanks and upper portions of the limbs.

PLATE XXV.

- Fig. 1. *Embrithosaurus schwarzi* (8034). $\times \frac{5}{8}$. Ossicles from the median and first lateral row of each side; from above the 6th, 7th, and 8th presacral vertebrae.
- Fig. 2. *Anthodon serrarius* (10074). $\times \frac{3}{8}$. Ossicles of the median and first lateral row; from above the sacrum.

PLATE XXVI.

- Fig. 1. *Anthodon serrarius* (10074). $\times \frac{1}{2}$. On the left is the external view of two closely articulating ossicles. On the right is the internal view of two ossicles very firmly joined—a suture marks the line of articulation. Both sets come from above the sacrum.
- Fig. 2. *Pareiasaurus serridens* (10032). $\times \frac{1}{2}$. A series of isolated scutes; the two top ossicles probably came from the back; the left bottom pair are firmly articulated and overlie a rib and thus come from the flank—the long axes of these two scutes are at right angles to the long axis of the body; the two ossicles in the left bottom corner probably come from lower down the flank.

PLATE XXVII.

- Fig. 1. *Pareiasuchus nasicornis* (3016). $\times \frac{2}{3}$. A set of isolated scutes; the small scute with the notch is remarkable.
- Fig. 2. *Propappus parvus* (2351). $\times \frac{1}{2}$. The two upper scutes belong to this species; the one on the left is seen in internal view, that on the right in external view; in the former a small foramen is to be noted.
- Propappus omocratus* (1058). $\times \frac{1}{2}$. The ossicle on the bottom left corner is from the dorsal median row; that on the bottom right from a lateral row as it overlies a rib; smaller stud-shaped ossicles, similar to those of *Brachypareia*, are also preserved.

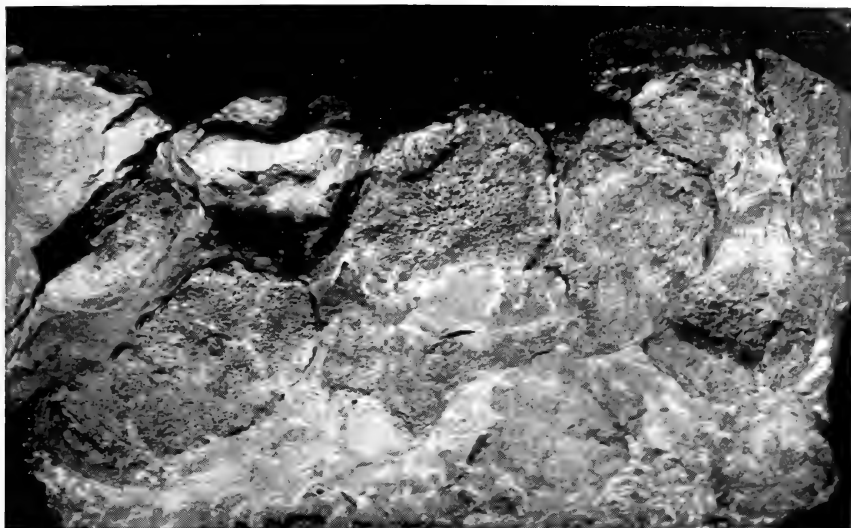


FIG. 1.

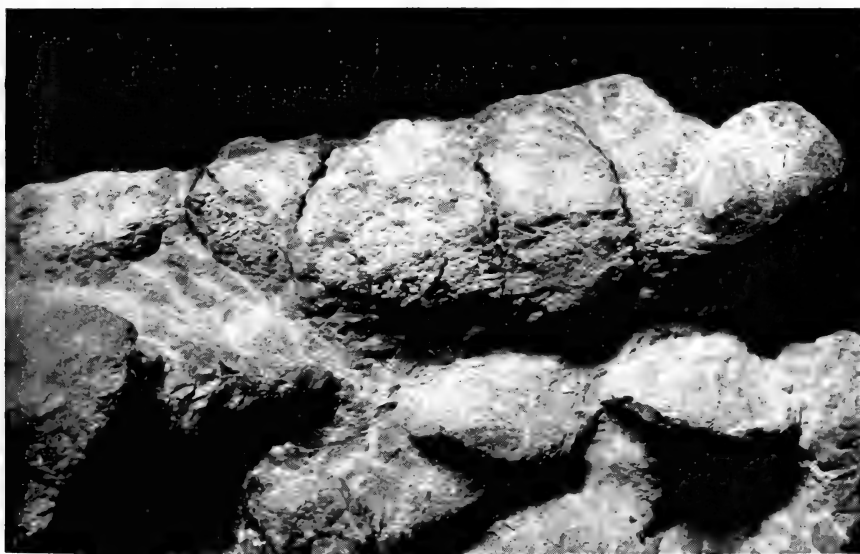


FIG. 2.

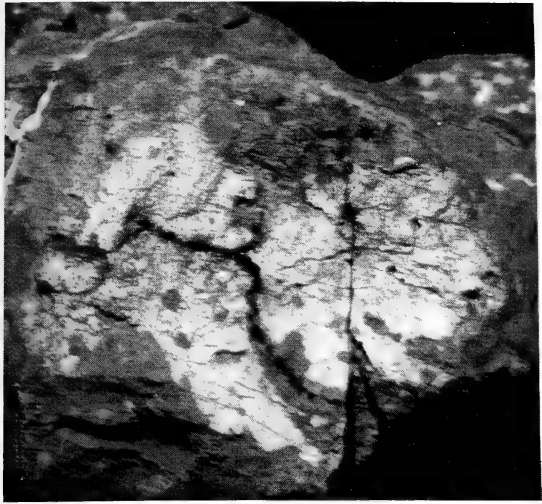


FIG. 1.

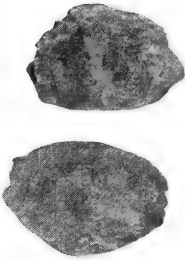


FIG. 2.

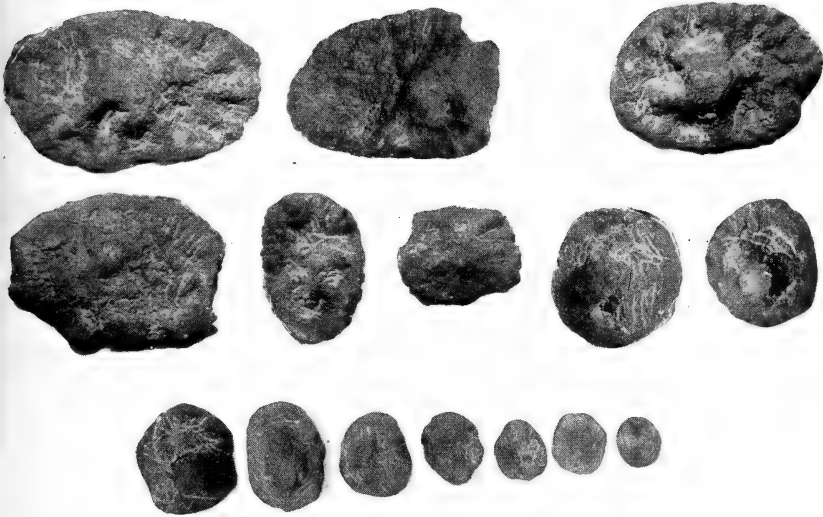


FIG. 3.

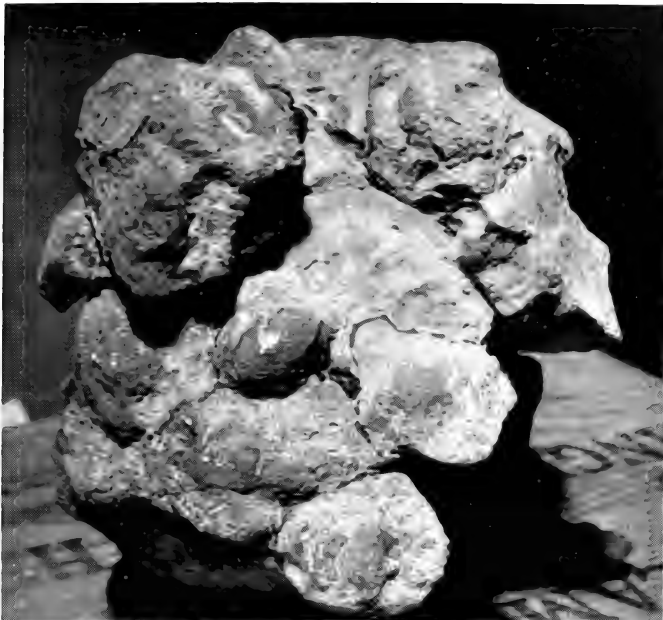


FIG. 1.



FIG. 2.



FIG. 1.

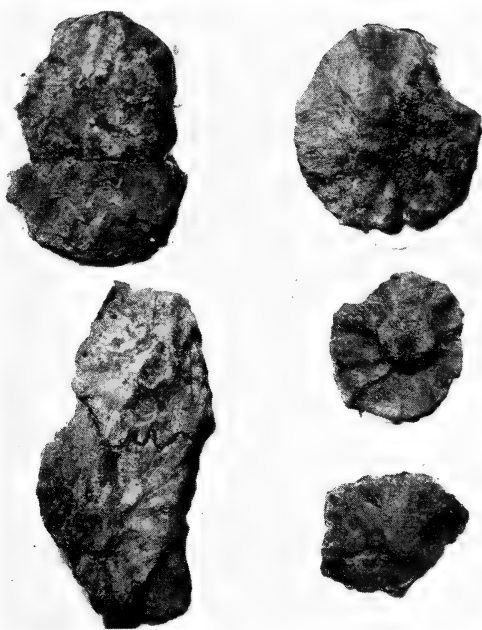


FIG. 2.



FIG. 1.

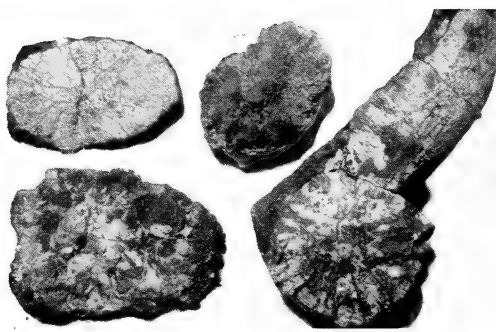


FIG. 2.

Pareiasaurian Studies.

Part XI.—*The Vertebral Column and Ribs.*—By LIEUWE D. BOONSTRA,
D.Sc., Department of Palaeontology, South African Museum.

(With Plate XXVIII and Text-figures 1–7.)

INTRODUCTION.

To Owen (1876) we owe our first description (pp. 9–11) of a Pareiasaurian vertebra. But the vertebra figured (pl. xi) and described as that of *Pareiasaurus bombidens* is that of a Deinocephalian, in all probability *Tapinocephalus*, and not of a Pareiasaur at all.

In 1888 Seeley described (pp. 77–89) and figured (pls. xii, xvii, xviii, and xix) the nearly complete vertebral column of the Palmiet Fontein specimen of *Bradysaurus seeleyi*. According to this author there are 18 presacral, 2 anchylosed sacral, and 9 caudal vertebrae. The presacrals consisted of 9 cervicals and 9 dorsals. Only the first sacral rib supported the ilium. There are 9 pairs of dorsal ribs. “The head of the rib is obviously notched.” “In the last dorsal the rib appears to be almost entirely supported upon the diapophysis, the parapophysis having become very small.”

In 1892 the same author described (pp. 338–345) and figured (pls. xvii, xxi, xxii, and xxiii) the nearly complete column of *Bradysaurus baini*. “There appears to be eighteen presacral vertebrae.” Of these Seeley thought that 10 were cervicals and 8 dorsals. The sacrum consisted of 4 vertebrae—the first a sacro-lumbar, then a true sacral and 2 sacro-caudals. Four sacral ribs supported the ilium—the first two being much more massive than the last two. “Twenty-six caudals are preserved”—but the tip of the tail was lost. The first 4 ribs had, according to Seeley, single facets; in the 5th to the 7th the facet is elongated. From the 5th postsacral vertebra chevrons appear—the first being unpaired, the rest paired.

In the Tamboer specimen of *Bradysaurus seeleyi* there were 19 presacrals, of which 11 were dorsals and 8 cervicals.

In 1893 Newton described (pp. 489–493) and figured (pl. xli) parts

of the vertebral column of *Elginia mirabilis*. There are 4 anchylosed sacrals with ribs—the 1st being much larger and carrying a much stronger rib than the posterior three.

Broom, in 1903, described (pp. 127–130) and figured (pl. xvi) the well-preserved vertebral column of *Embrithosaurus schwarzi*. “There are 20 presacral vertebrae, 2 anchylosed sacrals, and probably 30 caudal vertebrae.” Broom found that no rib articulated with the atlas; a two-headed rib articulated with the axis; in the 3rd, 4th, and 5th cervicals there were two articular surfaces for each rib; in the 6th the two articulatory surfaces became united, and in all the succeeding presacral vertebrae there is only a single articular surface; two sacral ribs give attachment to the ilium—the first is very much the stronger and there may have been a third sacral rib; chevrons were developed.

The incomplete vertebral column of *Propappus omocratus* was described (pp. 353, 354) and figured (pl. xlv) by Broom in 1908, and that of *Brachypareia rogersi* (pp. 323, 324, pl. xix) in 1912.

Broom and Haughton described (pp. 20–22) and figured (pl. v) the vertebral column of *Pareiasuchus peringueyi* and found 19 presacrals, 4 anchylosed sacrals, and 12 caudals; the axis had an apparently single-headed rib; the 3rd, 4th, and 5th cervicals had double-headed ribs; the 6th and all the other presacrals had single-headed ribs; there were 4 sacrals supporting the ilium—the 1st was massive, the 2nd and 3rd weak, and the 4th moderate; from the 7th caudal chevrons were present.

An incomplete series of *Propappus parvus* was described (pp. 44–45) by Haughton. There were apparently 4 sacral ribs; the ribs were single-headed and there were chevrons on the caudal vertebrae.

In 1914 Watson had found parts of the type of *Pareiasaurus serridens* in the cellars of the British Museum. The sacrum consisted of 4 constricted vertebrae. These parts had been described (pp. 40–41) and figured (pl. xxxvi, fig. 1) by Owen as belonging to *Dicynodon tigriceps*. Parts of *Propappus omocratus* were also found by Watson. The sacrum consisted of 4 vertebrae and was originally figured (pl. xxxvi, figs. 2–4 and figure on p. 74) by Owen as *Dicynodon tigriceps* and *Dicynodon*. Watson defines the genus *Bradysaurus* as having 4 sacrals, as also had *Embrithosaurus*.

Haughton and Boonstra, in their paper on the Hind Limb, described and figured the various sacra and their ribs in so far as they acted as supports to the pelvic girdle.

In her description of *Scutosaurus*, Hartmann-Weinberg stated:

“Halswirbel 6, Rumfwirbel 13, Sacralwirbel 4–5, Schwanzwirbel genaue Zahl unbekannt.” 1–3 sacral ribs articulated with the ilium—3–2 probably ligamentously. The cervicals had two-headed and the dorsals single-headed ribs; the postsacrals were provided with chevrons.

GENERAL OSTEOLOGY.

Although there are in the collection of the South African Museum parts of the vertebral column of 46 Pareiasaurs, only a small proportion of these are even approximately complete. Quite a number have the dorsal series complete but very often lack a full series of cervicals, and in all, except one specimen, the postsacrals are not preserved as a complete series.

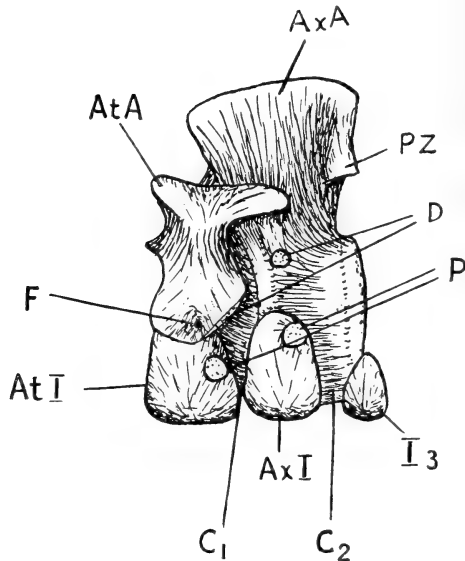
In view of these facts it has been considered advisable to base our general description chiefly on the one column which is known to be practically complete and to use the other material mainly to check any conclusion arrived at. Some of this material belonging to the various species will, of course, be treated of in a subsequent section which deals with the vertebral column from a systemic aspect.

The above-mentioned column (S.A.M., No. 9168) was excavated by the author on the farm Knoffelfontein in the Beaufort West Division and was that of a practically complete animal identified as *Bradysaurus seeleyi*. The skull was disarticulated and the atlantal centrum, intercentrum, and atlantal arch were not preserved. From the axis onwards, however, the column was absolutely complete—the posterior section of the tail was removed in a block of matrix which extended to the last postsacral vertebra so that there is no doubt as to the number of postsacrals. The atlantal centrum, intercentrum, and paired arch are, however, preserved in a specimen of *Bradysaurus vanderbyli* (S.A.M., No. 9169) found by the author at the same locality. These elements are in addition preserved in a specimen of *Nochelesaurus strubeni* (S.A.M., No. 5590) from Abrahams Kraal, Prince Albert, and in a specimen of *Pareiasaurus serridens* (Stellenbosch, No. K. 218) from Houd Constant, Graaff-Reinet, and also, although much distorted, in a specimen of *Nochelesaurus strubeni* (S.A.M., No. 5019) from Blaauwkrantz, Prince Albert, and, incompletely, in the type specimen of *Brachypareia watsoni* (S.A.M., No. 6240) from Abrahams Kraal, Prince Albert.

The column consists of 20 presacrals, to which in all probability another, viz. the pro-atlas, should be added; 4 sacrals with coalesced

centra; and 39 postsacrals. These main divisions can be further subdivided, viz. 4 cervicals 15 dorsals, 4 sacrals, 3 pygals, and 36 caudals.

Cervicals (Pl. XXVIII, Text-figs. 1, 2, and 3).—Although the usual criterion for determining the beginning of the dorsal series, viz. the



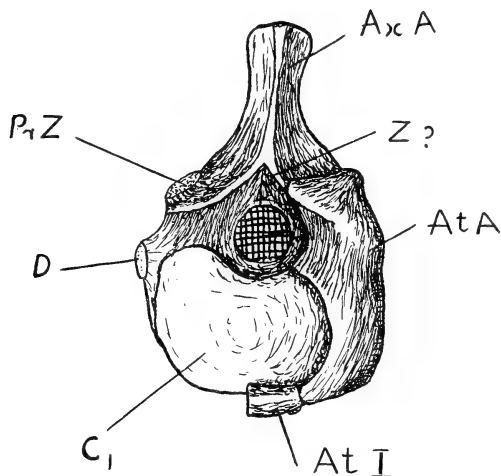
TEXT-FIG. 1.—*Bradysaurus vanderbyli*. S.A.M., No. 9169.
Lateral view of the atlas and axis. $\times \frac{1}{3}$.

- At. A. =atlantal arch, left half.
- At. I. =atlantal intercentrum.
- Ax. A. =axial arch.
- Ax. I. =axial intercentrum.
- C₁. =atlantal pleurocentrum (odontoid).
- C₂. =axial pleurocentrum.
- D. =diapophyses on atlantal and axial arch.
- F. =foramen.
- I₃. =intercentrum between the axis and the 3rd cervical.
- P. =parapophysial facets on the atlantal and axial intercentra.
- PZ. =axial postzygapophysis.

sternum, is absent, there appears to be sufficient other evidence to enable one to state the number of cervicals. The first 5 presacrals carry two separate processes—a diapophysis on the arch and a parapophysis on the centrum or on the preceding intercentrum; articulating with these there are 5 slender dichoccephalous ribs which have the tuberculum and capitulum separated by a deep notch. The characters of the next vertebra—the 6th—show an abrupt change; the diapophysis and parapophysis are fused to form an elongated

vertical transverse process, and articulating with this is a stout and much longer holocephalous rib. This abrupt change is considered to afford sufficient evidence for the delimitation of the cervical series.

The 1st vertebra differs from the rest in retaining certain primitive temnospondylous characters; the 2nd is specialised, as in all reptiles with the exception of *Seymouria*; the 3rd differs from the succeeding vertebrae in its distinctively shaped neural spine; the 4th and 5th



TEXT-FIG. 2.—*Embriothosaurus schwarzi*. S.A.M., No. 8034.

Anterior view of atlas and axis. $\times \frac{1}{3}$.

The left half of the atlantal arch and half of the unpaired atlantal intercentrum have been omitted from the sketch.

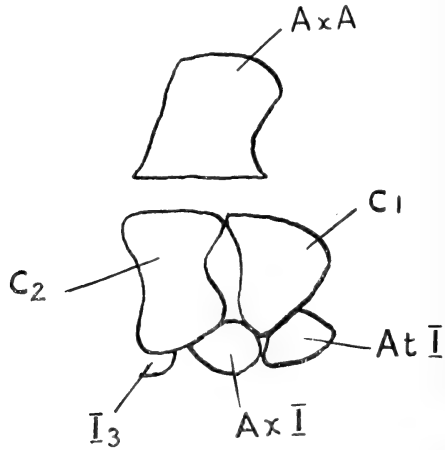
- At. A. =atlantal arch.
- At. I. =atlantal intercentrum.
- Ax. A.=axial arch.
- C₁. =atlantal pleurocentrum (odontoid).
- D. =diapophyses on atlantal and axial arch.
- Pr. Z. =axial prezygapophysis.
- Z.? =an undeveloped zygosphenes?

have nearly all the characters of the dorsal vertebrae and pass gradually into the dorsal series.

Proatlas.—In no specimen has any portion of a proatlas actually been found. The fact, however, that it occurs in all groups of primitive reptiles leads one to entertain the idea of its probable presence. Furthermore, there seems to be some evidence pointing that way, viz. the antero-dorsal extremity of the atlantal arch appears to be very similar to that in the forms possessing a proatlas (e.g. *Ophiacodon* and *Moschops*) and it seems highly probable that a

proatlas was articulated to it; in addition the relations of the occiput with the atlas is such that the dorsal surface of the medulla on emerging from the foramen magnum would be wholly uncovered in the absence of a proatlas. In forms like *Scymnognathus* and *Aelurognathus* this is precisely the function of the paired proatlas. For these reasons it is believed that a proatlas was present in life.

Atlas (Pl. XXVIII, Text-figs. 1, 2, and 3).—The atlas, as in nearly all reptiles, remains temnospondylous; it consists of a paired neural



TEXT-FIG. 3.—*Bradysaurus vanderbyli*. S.A.M., No. 9169. Median section through the atlas and axis. $\times \frac{1}{3}$.

At. I. = atlantal intercentrum.

Ax. A. = axial arch.

Ax. I. = axial intercentrum.

C₁. = atlantal pleurocentrum (odontoid).

C₂. = axial pleurocentrum.

I₃. = intercentrum between the axis and the 3rd cervical.

arch resting in part on a large hemicylindrical intercentrum, and in part on an odontoid-like pleurocentrum; the whole is loosely articulated to the axis. The arch is a bone of complex shape; dorso-posteriorly it carries a process which corresponds to the processes of succeeding vertebrae that carry the downwardly facing post-zygapophyses; it articulates with the prezygapophysis on the axis; dorso-anteriorly it probably gave articulation to a proatlas; ventrally it articulates with the intercentrum; ventro-posteriorly it carries a posteriorly directed facet for the articulation of the tuberculum of the atlantal rib; dorso-medially it articulates with a facet on the odontoid-like pleurocentrum; near its ventro-posterior border it is perforated by a foramen (vertebrarterialis); its ventro-anterior edge

took part in the articulation to the skull; in the median line the two halves of the arch just fail to meet and no spine is developed as is primitively the case (*Seymouria*). The atlantal intercentrum is the largest in the entire column; articulating with the odontoid with its dorsal surface and laterally with the arch, it forms the ventral half of a disc; a posteriorly directed facet for the capitulum of the atlantal rib is situated on its postero-lateral edge. In its most primitive form such a facet is carried on a distinct process (*Seymouria*). All the cervical intercentra are unpaired. In *Procolophon* they are paired.

The pleurocentrum is odontoid-like in shape, but still bears features of an embolomereous pleurocentrum; its posterior surface is deeply concave and it is only in some cases that there appears to be an incipient fusion with the axial centrum ventral to the neural canal; its anterior face is strongly convex—the point articulating with the concavity in the basioccipital, whereas laterally and ventrally the intercalation of the paired arch and the atlantal intercentrum complete the articulation with the skull. It is thus apparent that the movement of the skull relative to the atlas was mainly rotatory.

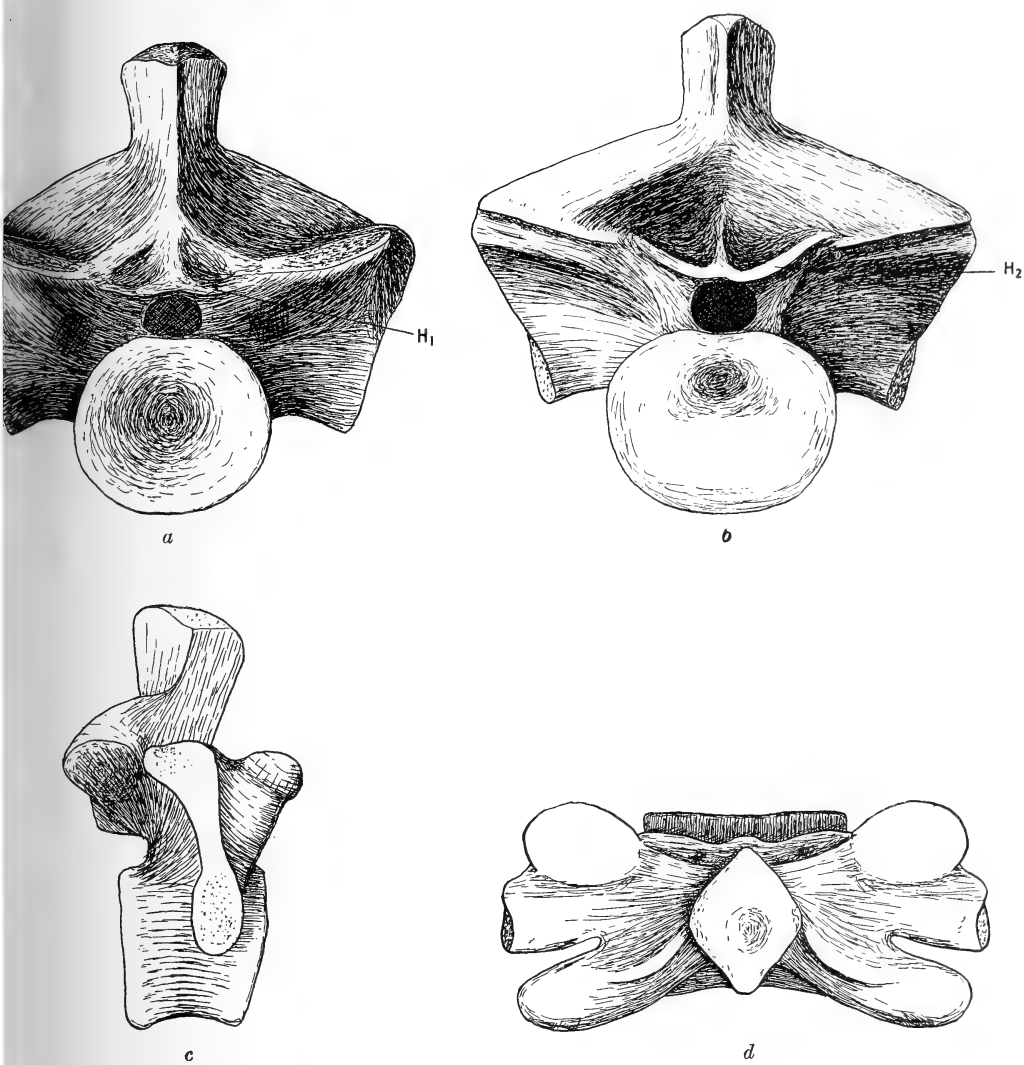
Axis (Pl. XXVIII, Text-figs. 1, 2, and 3).—In the axis the paired neural arch is fused with the pleurocentrum to form the reptilian type of holospondylous vertebra. The two elements of the neural arch are fused and dorsally form an antero-posteriorly elongated comb-like spine, which is distinct from that on all the other vertebrae; antero-dorsally an upwardly directed prezygapophysial facet gives articulation to the atlantal arch; antero-medially at the base of the spine there is a paired flange which may be termed a zygosphenes although there is no corresponding zygantrum; postero-dorsally horizontal upwardly facing postzygapophyses give articulation to the succeeding vertebra; slightly below the junction of arch and centrum there is situated a slightly raised diapophysis for the tuberculum of the rib. The centrum is deeply amphicoelous and anteriorly is freely articulated with the odontoid which in its dorsal part, however, does in some cases show indications of incipient fusion; laterally below the diapophysis the centrum is hollowed out, ventrally there is a slight ridge; on the antero-ventral edge there is no parapophysis for the capitulum of the rib—this facet is carried by the axial intercentrum. The axial intercentrum is smaller than the atlantal, but otherwise similar.

In the nature of its neural spine the axis thus possesses a specialised character, whereas the deeply amphicoelous nature of its centrum without a parapophysis is a primitive character.

3rd, 4th, and 5th Cervicals.—These three vertebrae are very similar; the centra are amphicoelous, laterally excavated, and with a medio-ventral ridge; the diapophysis gradually shifts higher up on to the arch, and the parapophysis is now situated on the extreme anterior edge and gradually shifts higher up on to the centrum; the pre- and post-zygapophyses are well-developed and lie in a horizontal plane; with each succeeding vertebra the processes bearing the zygapophyses extend farther laterally; the centra similarly increase in length. The 3rd vertebra differs from the whole series in having a pointed pyramidal neural spine; the spines following are massive, subquadrate in section, and taller and more slender than the mid-dorsal spines but shorter than the first 3 dorsals. The intercentra of the 3rd, 4th, and 5th vertebrae are smaller than the two previous ones, and the parapophysis has shifted on to the anterior edge of the centrum.

The narrowness across the zygapophyses, the tall spines, and the relatively lower centra produce an appearance of tallness in the last cervicals in comparison with the dorsals, where the massive zygapophysial and transverse processes cause these vertebrae to appear low and squat.

Dorsals (Pl. XXVIII, Text-fig. 4).—The series of 15 dorsal vertebrae present great uniformity in all essential points of structure. Each vertebra consists of an amphicoelous centrum; the anterior and posterior faces are, however, not quite similar, viz. the anterior face is typically symmetrically concave with the centre as deepest point, the posterior face, however, has its upper half concave and its lower half convex; the sides of the centrum are excavated and ventromedially there is no ridge or keel; the neural arch is wide, low, and massive, and carries a low stout spine; the pre- and post-zygapophyses are horizontal and are carried on widely separated processes; the transverse process for the rib is composed of the fused diapophysis and parapophysis, with which is also fused the process bearing the prezygapophysis; the articulatory surface for the rib is better developed in its upper portion, medially it is not over-functional, whereas the lower portion is functional but less developed than the upper portion; the transverse process, and in particular its upper portion, extends farther laterally than the zygapophyses. Medially on the posterior surface of the arch there is a ridge continuous with the postzygapophysial process which appears to be an undeveloped hyposphene facing an equally undeveloped hypantrium on the succeeding vertebra. The differences in the series are of degree; the



TEXT-FIG. 4.—*Dolichopareia angusta*. S.A.M., No. 6238. $\times \frac{2}{10}$.

a=anterior view of a mid-dorsal vertebra.

b=posterior " " "

c=lateral (right) view of a mid-dorsal vertebra.

d=dorsal " " " "

H. 1=undeveloped hypantrum.

H. 2=undeveloped hyposphene.

anterior 3 spines are taller than the middle 2-3, and from there to the last dorsal the spines again gradually increase in height; similarly the transverse process gradually shifts higher up on to the arch in each succeeding vertebra, and also increases in length up to the 9th dorsal and then decreases; the upper portion also progressively shifts in posterior direction, so that whereas in the first dorsals the process stands vertical, in later ones it stands obliquely.

Small intercentra are present throughout the series except in the first 5 dorsals, where they appear to be variable.

As the vertebra immediately anterior to the sacrum bears a rib-facet, there can be no question as to the non-existence of lumbar vertebrae.

Sacrals.—The number of sacrals is 4; although in the majority of cases they are all coalesced, this is not invariably the case. In this specimen (S.A.M., No. 9168) of *Bradysaurus seeleyi* there are 4 vertebrae with coalesced centra; the zygapophyses are still preserved, but could not have allowed any intersacral movement; each bears a rib which is firmly fused mainly to the centrum but also in part to the arch; the first is very massive with an extended surface of attachment to the ilium—its shape is best seen from the illustrations (Pl. XXVIII and text-figs. in the paper on the Hind Limb); the second is much less massive and is a fairly straight rod-like bone with expanded ends; the third is of the same type but more slender; the fourth is still more slender and did not reach the ilium, but was ligamentously attached to it. The sacrals are much lower than the last dorsal; this is due to a decrease in the height of the centrum more than to that of the spines; the spines are less massive and consequently appear taller—the first two are still subquadrate in section whereas the last two have become triangular. The width across the postzygapophyses abruptly becomes much less than across those of the last dorsal.

Pygals.—There are 3 postsacral vertebrae with ribs but without chevrons. The ribs are fairly long and slender and are fused low down on the centrum, apparently only with the parapophyses. The centra are shorter and narrower than in the preceding sacrals, and the neural spines relatively longer and more slender and are laterally compressed. In all the postsacral vertebrae there is no indication of an hyposphene and hypantrum, and all the centra are deeply amphicoelous.

Caudals.—There are 36 caudals, of which the first 31 bear paired chevrons. The caudals differ from the pygals only in matters of degree, viz. in posterior direction they become progressively shorter,

lower, and narrower as regards centra and neural spines, and the fused ribs eventually become wart-like protuberances. The only delimiting feature is the presence of chevrons; these commence with the 4th postsacral; they are paired rod-like elements that articulate with a swollen proximal end to a facet formed on the ventro-posterior edge of the centrum; proximally they enclose a space (haemal canal) through which the vascular elements of the tail pass. The zygopophyses are well developed in the anterior part of the series; they are less rigid than in the dorsals; progressively, however, they become less and less developed until finally they are absent from the 26th postsacral onwards; the last 13 vertebrae articulate only by their centra; the last 4 are reduced to centra by the loss of the spine; in the last 15 postsacral there are no indications of the transverse protuberances to which in the anterior part of the series the proximal ends of the caudal ribs are fused.

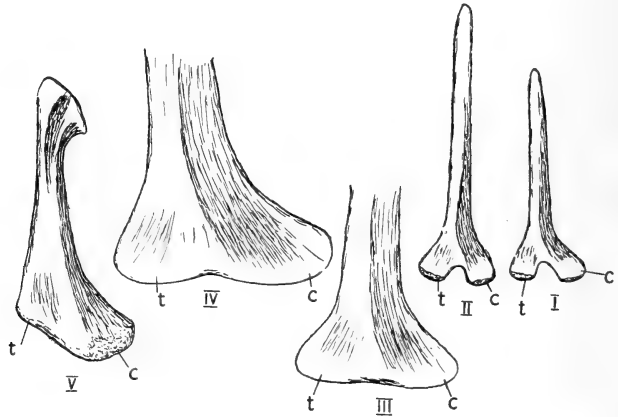
In the one specimen (S.A.M., No. 9168) with a complete vertebral column the presacral part is somewhat longer than the tail. The proportions are: presacrals 13·9, sacrals 2·5, and postsacrals 10·7. It thus appears that the tail is longer and comparatively more slender than it was formerly thought to be.

Ribs (Text-fig. 5).—All the vertebrae—from the axis to the sacrum—bear a pair of ribs. There are thus 20 pairs of presacral ribs. In the 5 cervicals the ribs are fairly short (107 mm. in the 4th), slender, and dichcephalous—the tuberculum being separated from the capitulum by a deep notch. The atlantal and axial ribs have their capitula articulated to a facet on the atlantal and axial intercentrum respectively. In the next three cervicals the capitula articulate with facets on low parapophysial processes situated on the extreme antero-lateral border of the respective centra. From the 6th–20th vertebrae the ribs are stout and longer—a web of bone connects the tuberculum and capitulum so as to produce a holocephalous rib which articulates with the long facet produced by the fused diapophysis and parapophysis. From the 6th to the 10th the thoracic ribs increase in length and in the width between tuberculum and capitulum. From the 11th to the 20th the ribs again shorten and become more curved. These last ribs curve directly downward, whereas the anterior thoracic ribs are directed somewhat posteriorly so that they curve obliquely downwards. The last thoracic ribs have a truncated distal end which is developed into the nature of a facet; in one anterior-thoracic rib the same condition has been observed, and in this case it is articulated to a rod-like element bearing a similar facet. It

MENTS.

<i>Pareiasaurus serridens.</i>	<i>Pareiasuchus</i>		<i>Dolichopareia angusta.</i>	<i>Brachypareia rogersi.</i>	<i>Propappus parvus.</i>	<i>Anthodon serrarius</i>
	<i>peringueyi.</i>	<i>nasicornis.</i>				
201	160	170
..	1020	980
203	150	177	147
..
105
65	45
70	55
40	35
68
95
..
57
43	40
36	33
63	49
75
..
..
..
68
47	45
45	43
70	61
76
173	119	125
65	61	67
71	69	80
45	51	57
87	74	107
166	..	109
80
47
55	48
..	163	130	219	134	113	112
..	..	61	82	55	50	46
..	65	64	100	60	55	43
..	52	64	67	47	55	41
..	128	155	200	121	105	107
..	154	154	223	136	110	109
..	..	42	47	46	42	28
..	..	56	61	45	35	32
..	..	38	84	43	30	33
163	138	106	95
77	54	53	..	65	..	40
86	67	63	..	55	..	39
60	50	49	..	50	..	38
175	159	158	..	110 ?	..	113
120	135	134	..	90	..	83
69	51	50	32
58	53	55	33
50	37	35	29
..
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would thus appear that some of the ribs were segmented. Unfortunately I have no complete series and cannot determine the full nature of this segmentation of the ribs. On the posterior edge of the thoracic ribs an irregular flange is developed to house the insertion of muscles (external oblique abdominal, sacro-spinal, and the intercostals); on the anterior proximal edge a flange received the latissimus dorsi and serratus muscles.



TEXT-FIG. 5.—*Pareiasaur* ribs. $\times \frac{1}{4}$.

- I = atlantal rib.
- II = 5th cervical rib.
- III = 1st dorsal rib.
- IV = mid-dorsal rib.
- V = last but one dorsal rib.
- c = capitulum.
- t = tuberculum.

As has already been mentioned, there are 4 sacral ribs; the first is very strong, having a long surface of anchylosis on the centrum and has a still greater distal expansion which clasps the anterior inner surface of the iliac blade; the succeeding three progressively decrease in size and the 4th appears to be only ligamentously attached to the iliac blade.

The anterior postsacrals have fairly long and slender ribs fused to the parapophysis. These progressively decrease until eventually they are only wart-like protuberances and are finally absent in the last 15 vertebrae.

Systematic.—As is the case in the other parts of the skeleton, the vertebral column of the various genera and species show only differences of degree and not of kind. As a further complication there is

the fact that within a single column there are fairly similar differences between vertebrae in different parts of the series. Unfortunately the column is insufficiently preserved in many species, with the result that some characters which may have been used in a classificatory scheme are only known in some species. The main points of difference are of size, nature of neural spine, proportions of the constituent parts, and some rather indefinite variations in shape.

In our paper on the Hind Limb certain alleged differences in the sacrum were stressed. An examination of additional material seems to indicate that these points are invalid. The Pareiasaur sacrum consists of 4 vertebrae with their ribs, and the differences formerly mentioned are preferably to be ascribed to individual and age variations rather than to specific differences. In the mature Pareiasaur the 4 centra are coalesced and the first sacral rib is the strongest; in immature animals 2-3 centra only may be coalesced. In the genus *Bradysaurus* these variations are very well shown.

Genus BRADYSAURUS.

(Pl. XXVIII.)

There are 5 cervicals, 15 dorsals, 4 sacrals, 3 pygals, and 36 caudals. The dorsals are large and massive, with strong, though not very high, transverse processes. The neural spines are stout and low, with somewhat expanded tops, and are roughly subquadrate in section, but the four sides of the spine are rounded and not separated by very sharp edges.

Genus NOCHELESAURUS.

(Text-fig. 6.)

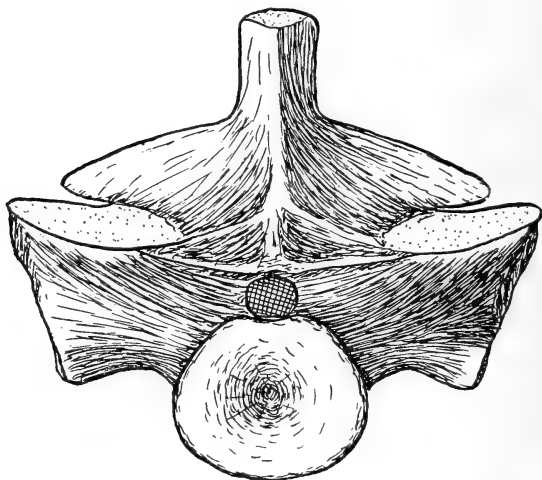
The dorsals differ from those of *Bradysaurus* in their absolute and proportional greater width across the transverse processes and the zygapophyses. The sides of the spines appear to be less rounded and taller than in *Bradysaurus*.

Genus EMBRITHOSAURUS.

Very similar to *Bradysaurus*, except that the last cervicals and first dorsals appear to be taller; the vertebrae are, moreover, slightly smaller and the width across the zygapophyses is proportionally less.

Genus DOLICHOPAREIA.

Very massive neural arch, but with the neural spine taller than in *Bradysaurus*; the two anterior and two posterior faces of the spine are flat and are separated by sharp and prominent edges. The articulatory face on the transverse process is very long, and the width across them is proportionally greater than in *Bradysaurus*, notwithstanding the greater height of the neural spine.



TEXT-FIG. 6.—*Nochelesaurus strubeni*. S.A.M., No. 5590. Anterior view of a mid-dorsal vertebra. $\times \frac{1}{4}$.

Genus BRACHYPAREIA.

The dorsals are smaller ($\frac{3}{5}$) and also relatively less massive than in *Bradysaurus*; centra are deeply amphicoelous; the spine is massive and very low, with fairly flat faces separated by ridges.

Genus PROPAPPUS.

There is a decided difference in the vertebrae of the two species. Those of *omocratus* are very similar to those of *Brachypareia*, but the spines are even lower, whereas in *parvus* the spines are much more slender and consequently do not appear so low as they really are. Moreover, the dorsals of *parvus* are considerably smaller (slightly more than $\frac{1}{2}$ of *Bradysaurus*), and the transverse processes are situated high up on the arch and not partially on the centra, and carry a short articulatory face. The centra are very deeply amphicoelous and in some vertebrae actually notochordal.

Genus PAREIASUCHUS.

There are 5 cervicals, but only 14 dorsals, 4 sacrals, and an unknown number of caudals. The dorsals are smaller than in *Bradysaurus* ($\frac{2}{3}$), but larger than in *Propappus parvus*. The spines are tall and not very massive; the articulatory face on the transverse process is fairly short.

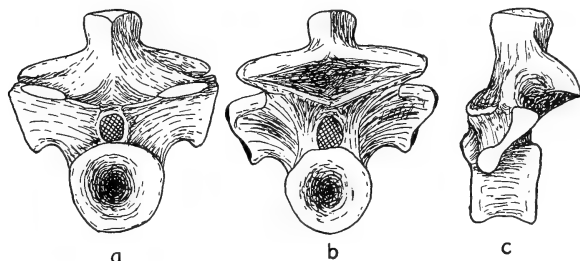
Genus PAREIASAURUS.

The vertebrae are large but not so massive as in *Bradysaurus*. The neural spines are massive and fairly low and are subquadrate in section. The articulatory face on the transverse process is fairly short. In the Stellenbosch specimen the centra of the sacrals are not so much constricted as Watson found in the type material in the British Museum.

Genus ANTHODON.

(Text-fig. 7.)

In the specimen from Dunedin (S.A.M., No. 10074) there is preserved a dorsal vertebra, sacrals, and caudals. The dorsal is small (slightly



TEXT-FIG. 7.—*Anthodon serrarius*. S.A.M., No. 10074. $\times \frac{1}{4}$.

a = anterior view.
b = posterior view.
c = lateral (left) view.

greater than $\frac{1}{2}$ of *Bradysaurus*), comparatively light; the spine is low and fairly slender; the transverse process is situated high up on the arch and the articulatory surface is short. On the whole, the vertebra is very similar to those of *Propappus parvus*. The centrum is notochordal with an hour-glass shaped perforation.

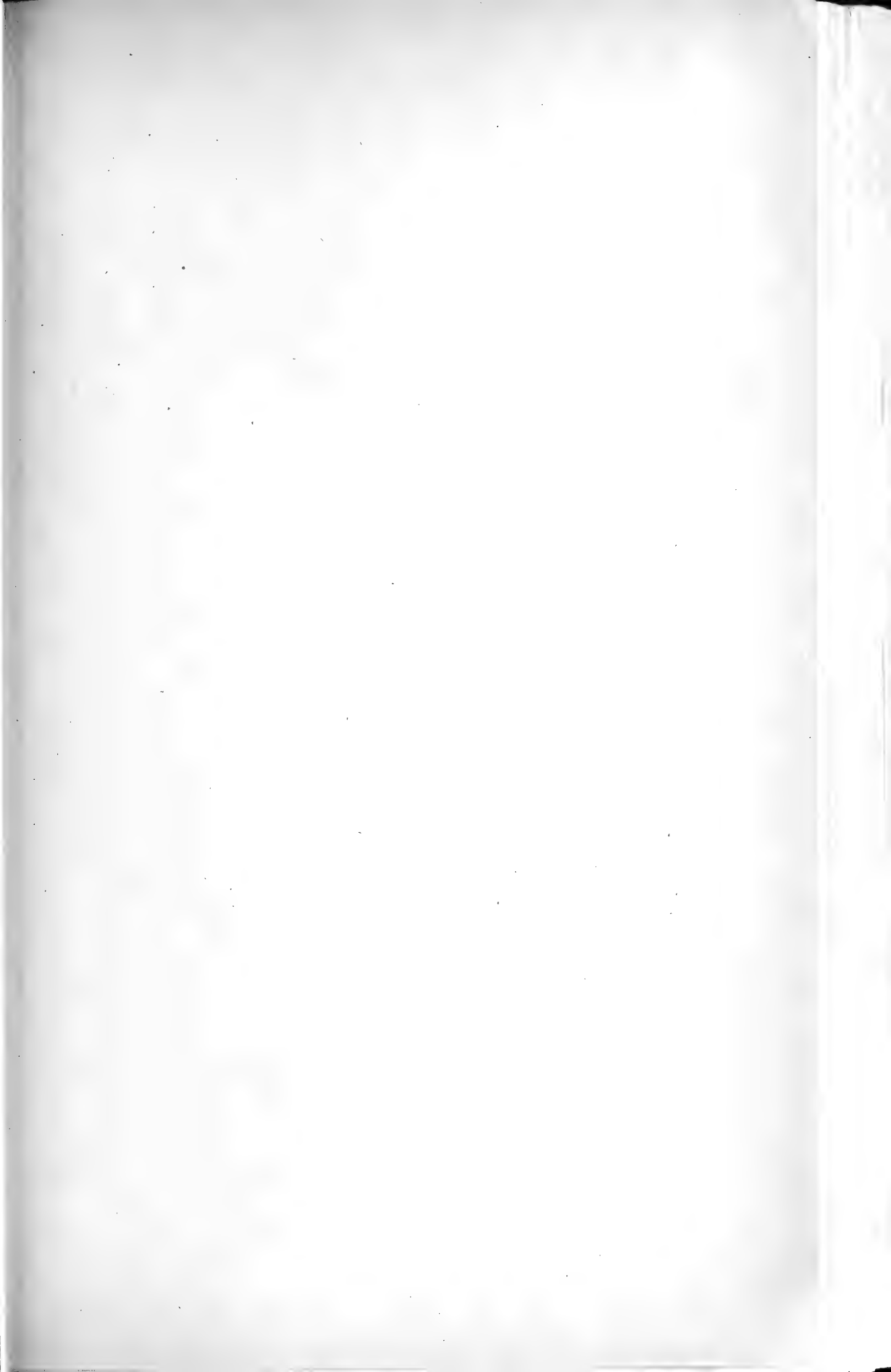
Short Discussion.—If we are correct in stating that the Pareiasaurs possessed 5 cervicals this fact would indicate a definite advance from the primitive embolomere condition where the neck at most consisted of 2–3 vertebrae; and they would occupy an intermediate

position within the assemblage of Cotylosaurs where the number of cervicals appears to vary from 2-9; they also would definitely be less specialised than the Pelycosaurs and the Mammal-like Therapsids where the mammalian number—7—is fairly constant. The atlantal arch shows a definite advance over the Stegocephalian and Seymourian condition in that the development of an atlantal spine does not take place, and in this agrees with higher reptiles. The apparently unfused odontoid is also fairly primitive, whereas the axis shows most of the typical modifications obtaining in all reptiles higher than *Seymouria*. The slender dichoccephalous cervical ribs, which, in the two first segments, articulate with their capitula to a parapophysial facet on the intercentrum, are primitive. In *Seymouria* alone are these more primitive, being carried on definite processes.

It appears that the original number of presacrals in Amniote vertebrates was over 20, probably between 23-25. If this generalisation holds good, the Pareiasaurs have undergone a reduction in this series which does not appear to be paralleled in most other Cotylosaurs, Pelycosaurs, and Therapsids.

The sacrum, consisting of 4 vertebrae with centra mostly coalesced, is more specialised than the primitive condition in which there was only a single element, and also than that of most reptiles in which there are only 2; the Deinocephalia and Anomodontia, however, are often parallel with 3-7 sacrals.

The number of postsacrals—36—is large, though shorter than the presacral series, and is greater than in some Cotylosaurs, *e.g.* *Capto-rhinus* and *Labidosaurus*, indicating a greater functioning of the tail, but less than in others, *e.g.* *Limnoscelis*.



EXPLANATION OF PLATE.

Bradysaurus seeleyi. S.A.M., No. 9168. $\times \frac{1}{6}$.

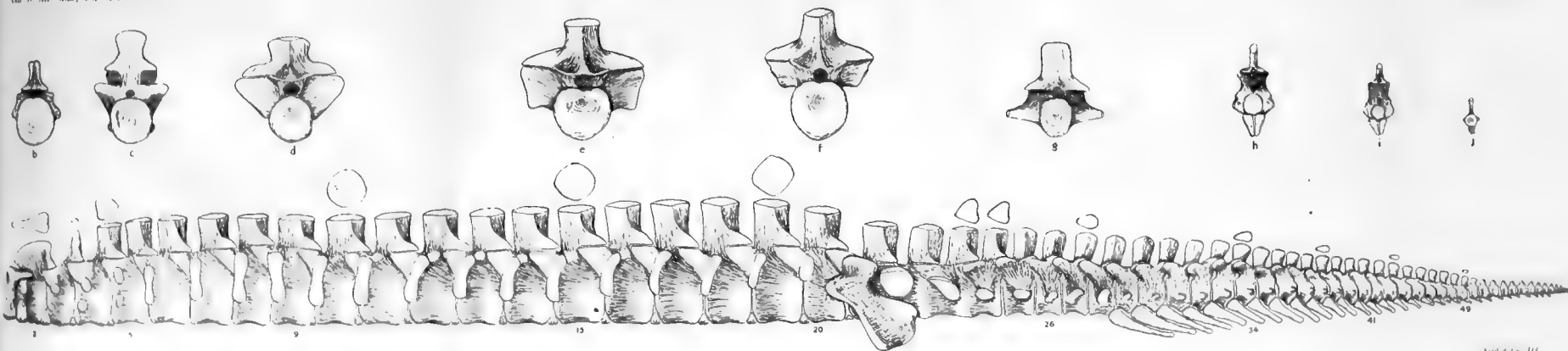
The restoration of the atlas is based on 5 other specimens where this element is preserved.

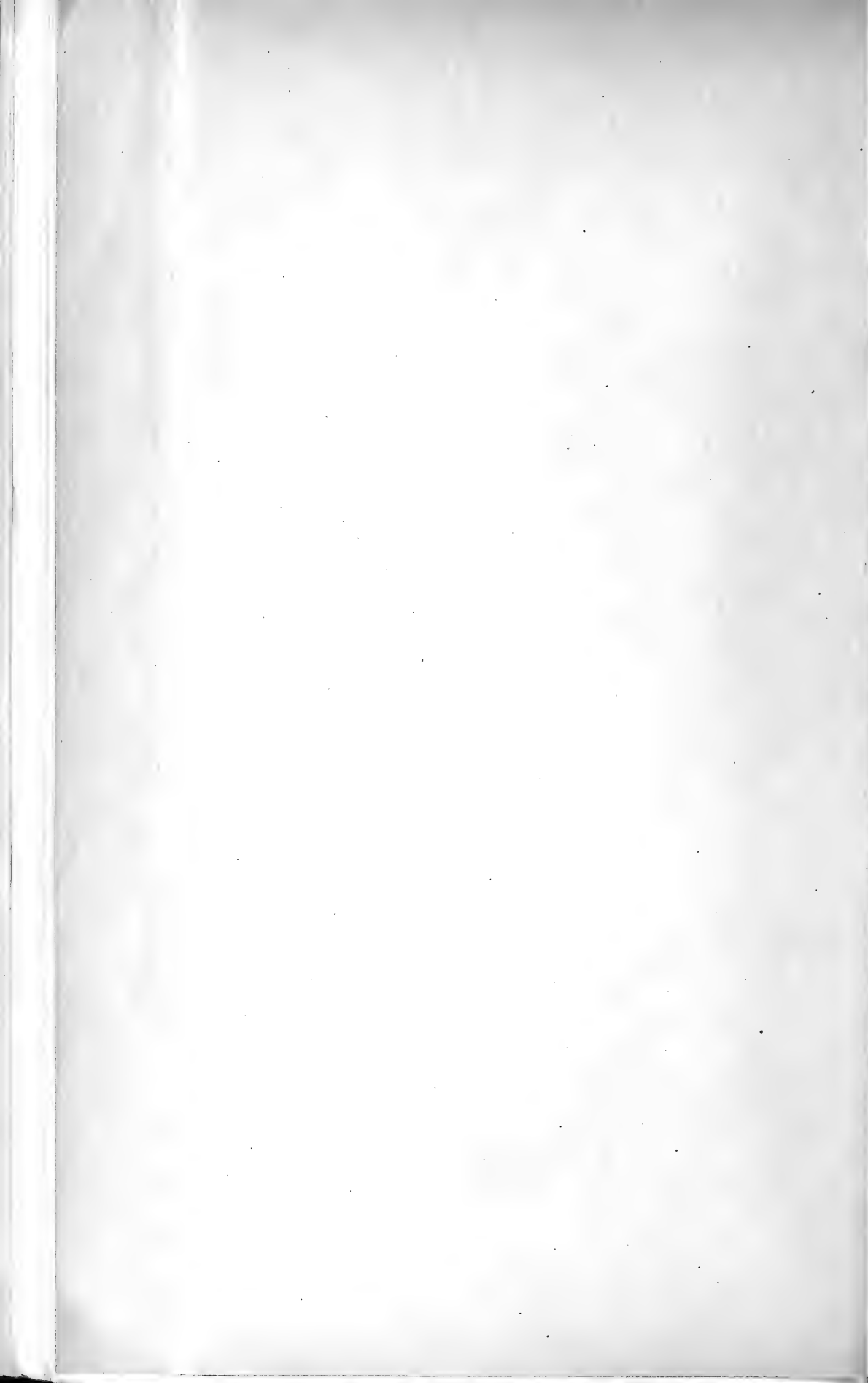
a = Lateral (left) view of the entire column. No attempt has been made to indicate the spinal curvatures. Cross-sections of some of the spines are given.

b = Posterior view of the 2nd vertebra (axis).

<i>c</i> =	"	"	"	5th	"	(last cervical).
<i>d</i> =	"	"	"	9th	"	(4th dorsal).
<i>e</i> =	"	"	"	15th	"	(10th dorsal).
<i>f</i> =	"	"	"	20th	"	(15th dorsal).
<i>g</i> =	"	"	"	26th	"	(2nd caudal).
<i>h</i> =	"	"	"	34th	"	(10th caudal).
<i>i</i> =	"	"	"	41st	"	(21st caudal).
<i>j</i> =	"	"	"	49th	"	(29th caudal).







2. *Fossil Plants from Fort Grey near East London*.—By Prof. R. S. ADAMSON, M.A., Botanical Department, University of Cape Town.

(With 27 Text-figures.)

Introduction.—The flora at present existing in South Africa is one not only of great diversity and interest but has also been the subject of some investigation and speculation in regard to possible origins and relationships. Our knowledge of its past history is at present rather fragmentary.

The fossil plants of the Karoo rocks and of the Cretaceous rocks have been investigated to a considerable extent, but the Tertiary period still represents a largely unknown epoch in South Africa. Fossiliferous rocks of Tertiary or later age are by no means abundant, and such fossils as do occur are poor. This renders the investigation of any favourable examples a most important link in the building of our knowledge. Of the more recent deposits in this country the lignite beds at Knysna formed the subject of a preliminary investigation by Phillips (S. Afr. J. Sci., xxiv, p. 188, 1927). He recorded the occurrence of *Widdringtonia*, *Podocarpus*, and *Curtisia*, all of which are living at present at Knysna. Some fossil wood described by Warren (Ann. Nat. Mus., ii, p. 345, 1912) as *Eugenia cordata* is probably of Tertiary age.

Of the fossils described in this paper no descriptions appear to exist. A brief and rather popular account of the rocks at Fort Grey was given in 1868 by Piers (S. Afr. Magaz., Apr. 1868). He made, however, no investigation and, indeed, treats them rather scurvily, as they are so much less good as specimens than those obtainable from the older rocks.

In view of the fact that several of the fossils here are conspicuous objects it is a little difficult to understand how no collector so far has given any descriptions of them.

The present investigation was suggested by Dr. A. W. Rogers, F.R.S., lately Director of the Geological Survey of South Africa. It was undertaken in the first place with a view to determining the

probable stratigraphical position of the rocks, which form an isolated superficial deposit of quite local occurrence.

Acknowledgments.—Part of the investigation has been carried out with the aid of a grant from the British Association for the Advancement of Science.

I take this opportunity of returning thanks to Dr. Rogers for directing my attention to these fossils in the first case, for supplying me with material he had collected, and for arranging for the sectioning of a number of specimens. I have also to thank Dr. Rogers for his continued interest throughout the work.

I am also indebted to the Director of the South African Museum for permitting me to examine a number of specimens in their collection. I have to thank Dr. J. V. L. Rennie, who spent some time with me in the field, for his assistance both in the collection of the material and for suggestions, geological and other. Finally, I have to thank Professor A. Young of the University of Cape Town for carrying out the sectioning of rock specimens.

Locality.—The fossil-containing rocks occur on the summits of two or three koppies on the south bank of the Buffalo River near Fort Grey, about 12 miles from East London. The portion where most of the material examined occurs is on Farm 36, known as Springfontein. I should like here to express my thanks to Mr. L. W. Gower, owner of the farm, for the readiness with which he granted free access to his land and for his assistance in various ways on visits made to the farm.

The koppies where the rocks occur form part of the dissected penepplain of this region. The fossiliferous rocks are hard and silicious and overlie the Karoo Dolerites which form most of the surface in the region.

The main koppie rises to a height of about 225 m. (750 feet) above sea-level. The top is a flattish area sloping gently to the south, in length about 305 m. (340 yards) and 81 m. (90 yards) in width at its widest part. Except on the south, the ground falls away abruptly in a low cliff at the sides.

Rocks.—These superficial silicious rocks vary both in thickness and in character. On this koppie the rocks thin out from north to south. At the southern end is a small quarry, at one time used for road metal. At this point the rocks form a hard bed about 1·2 m. (4 feet) in thickness, which directly overlies very much weathered dolerite. At the northern end the exact thickness could not be determined with accuracy, as the base of these rocks is nowhere exposed but

covered by a talus deposit. On the cliff at the north end a thickness of 7.5 m. (25 feet) is exposed. The summit of the koppie is about 3.5 m. (12 feet) above the edge of the cliff. Descending, true dolerite soil was first struck about 15 m. (50 feet) lower down than the base of the exposed rocks.

These silicious rocks themselves are of more than one kind, a general threefold division can be recognised; the lowest rocks seen are hard and claylike, blueish when fresh but weathering to a rusty brown or red. Above these is a hard, often flintlike rock with no regular joints and a conchoidal fracture. This rock is grey or purple when fresh, but becomes white with partial weathering. The uppermost part is a brown or red rock which varies from a hard compact chertlike rock to a granular quartzite. In some parts it looks like a sand cemented by amorphous silica. Local bands occur which are almost wholly amorphous silica. On the koppie these uppermost beds overlap the others at the southern limit and occur directly above the basal dolerite. These main divisions can be subdivided, though the subdivisions are more local in character.

Other Localities.—The above description is based on the main koppie on Farm 36. A similar deposit, but of less thickness and containing much fewer plant remains, caps the ridge forming the east boundary of the farm. In this the hard flinty bed seems wanting. A further small deposit occurs as a cap to a rise about $\frac{3}{4}$ mile to the south-east, but this has yielded no fossils.

A general investigation has been made of the surrounding country for other deposits of this kind, but so far without result. Both sides of the Buffalo River were examined and the study continued in a general way southwards to the coast and west to the Keiskama River. The only evidence for other deposits in the neighbourhood was the presence of some loose blocks of quartzite in a field near Need's Camp, but the origin of these was not found.

Material.—The locality was visited in 1930 and again in 1932, and a quantity of material was collected. The bulk of this has been deposited in the South African Museum. In addition some specimens were obtained from Dr. Rogers, and the material in the Museum was examined.

The material consists of fragmentary plant remains which are silicified. The original material has been completely replaced in some, but in others a powdery condition is found which is very fragile and difficult to work with. In no case is there any carbonaceous material or other substance that could be separated from the matrix.

Fossils occur in all the beds, but in the lowest parts are structureless impressions. The hard flinty rock has provided the majority of the workable material. Especially in the uppermost layers plant remains are often in cavities that suggest shrinkage having occurred.

Descriptions.—In the following account the remains are grouped in accordance with their nature; their distribution in the rocks is recorded, but is discussed later.

GYMNOSPERMS.

Wood.—The most prominent fossils are woody axes which are not infrequent. These are of various sizes, varying from small twigs to portions suggesting pieces of large trees.

The woody axes occur in all the beds of rock, and fragments are often found weathered out from the rock in the talus flanking the koppie. Some of these separate specimens have been carried down some distance beyond the limits of the rocks from which they were derived. In size there is considerable variation, from twigs 0.75–2.5 cm. ($\frac{1}{2}$ –1 inch) in diameter up to logs 40 cm. (16 inches) or more. Among the largest specimens measured was a weathered-out portion which consists of about half the original axis and which has a diameter of over 22 cm. Another much decayed and weathered portion had a length of 4 m. 18 cm. and a diameter of 54 cm. In the rock these axes occur in all the beds. Some are erect or ascending, others horizontal. The former give all the impression of being preserved *in situ*, an impression which is further strengthened by the fact that in some cases an axis can be traced through more than one bed of rock. In the quarry at the south end of the koppie these axes are continuous down into very much weathered dolerite. They seem especially abundant at the top of the lowest beds. The examples that are apparently *in situ* are generally not very large; the largest erect stem was a portion 80 cm. (32 inches) in length with a diameter of 18.75 cm. ($7\frac{1}{2}$ inches). Much longer portions of smaller diameter occur.

The external appearance shows a good deal of variation; some are quite smooth, others ridged, or fluted in various ways. Little weight can be put on these external features, as practically none of the specimens are complete. The wood only is preserved, the original outer tissues are wanting. The wood itself in many of them has been eroded before fossilisation took place.

Some of these axes show branching. The branches occur singly, not in whorls.

Structure.—As seen in hand specimens the structure in all the axes is very uniform and certainly that of a Gymnosperm. The wood is made up of uniform-sized tracheids, and is traversed by numerous narrow and shallow medullary rays. In the majority annual rings are not distinctly present and sometimes quite absent.

A few specimens exhibited an appearance of broad rays at intervals between the narrow ones, but more detailed study showed that this was the result of radial splits or cracks that had become filled with silica.

The degree of preservation of the internal structure shows a good deal of variation; in a few, much of the structure is preserved, though generally the finer details, such as pitting on the walls, are faint and ghostlike.

Some thirty specimens have been studied by means of sections or transfer films. To avoid repetition the general features common to all the specimens will be given first, and the details that separate the different kinds of wood later.

The wood is made up of very uniform tracheids, between which are numerous medullary rays which are one cell in width. Among the tracheids are vertical rows of cells filled with a dark material. These cells are rarely well preserved, but appear to have been shorter than the tracheids and represent parenchyma.

In the larger specimens annual rings are not at all distinct and sometimes quite absent. Of 26 transverse sections, 15 showed no signs of annual rings, 7 had very indistinct rings, more obvious in the hand specimen than in the section, 2 had rings that were separated from one another by a single line of smaller tracheids, 1 showed rings of this kind in the outer parts but not near the centre. One specimen had been so much compressed that no conclusions could be drawn.

These differences in the formation or otherwise of annual rings could not be definitely correlated with differences in other structural features.

While annual rings are not distinct, many of the specimens, and especially the larger ones, show a pronounced concentric zonation, which is due to compression. Zones round the axis occur in which the tracheids have become squashed and more or less displaced. These compression zones are readily distinguished from annual rings in a section owing to the distribution of the medullary rays.

The numerous medullary rays are composed entirely of parenchyma; in depth they are most commonly 2–6 cells, though occasionally

deeper rays, 8-12 cells or even 20 cells, occur. An appearance of even deeper rays may be given by the close approximation of numerous small rays (fig. 1).

The tracheids forming the wood show differences in size and thickness of the walls in different specimens. These differences seem largely due to the state of preservation and to the condition of the specimen when preservation took place. In some, pits are easily visible, in others they are very faint or absent. There are bordered pits on their radial walls. The bordered pits are circular, and occur in a single row, or in two rows, when the pits are opposite to one another. In some cases one tracheid may show bordered pits, both paired and single, and in such cases occasional alternating pits are found. The bordered pits may be separate or in contact. In the latter case they may be somewhat flattened along the line of contact. Polygonal pits do not occur (fig. 2).

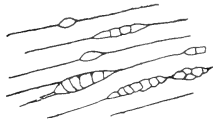


FIG. 1.—Long. tang. sect. wood showing medullary rays. $\times 55$.

Thickened rims, rims of Sanio, between the pits are generally present and sometimes very distinct. In some they seem absent, but as these are the least well preserved the negative evidence is of little value. The pits on the tracheids occur in groups towards the ends of the cells and in the neighbourhood of medullary rays.

No resin canals are present either in the wood or in the medullary rays.

In most of the specimens wood alone is preserved, but in a few the central parts are preserved: both stems and roots occur which show no noticeable differences apart from the primary structures.

In stems the central pith is of small size and parenchymatous with cells rounded in cross-section and not much elongated longitudinally. The primary xylem projects into the pith. No specimen shows any detail in the primary wood.

The roots have a solid core. The primary xylem appears to be 4-arch, but this may be due to compression and poor preservation. Small rootlets associated with the larger axes are 2-arch.

Both in stems and roots the outer tissues are very seldom present and are absent in all the larger specimens. Even where bark is

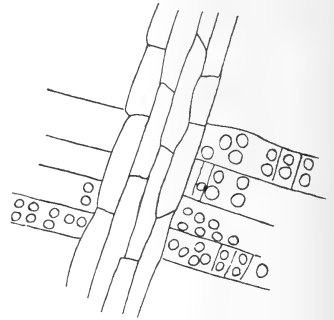


FIG. 2.—Long. rad. sect. wood showing pits. $\times 80$.

found very little detail can be made out. The bark seems to have been thin and smooth. Cork occurred on the surface. There is no evidence for the presence of resin canals.

It is possible to distinguish three types of wood.

The first type, which is much the commonest, has parenchyma scattered among the tracheids without regular arrangement. The rays in transverse section are narrower than the tracheids. Annual rings are never distinct. The tracheids have one or two rows of bordered pits separated by rims of Sanio, and connect to the rays by one or two pits. These field pits are bordered and circular in outline: the central aperture was probably, but not certainly, elliptical (fig. 3).

A few specimens only differ from this type by possessing rays of much larger cells, as wide as or wider than the tracheids.

The second type of wood is less common. The rays are narrow. Not very distinct annual rings are present. The ray cells have three or four rather small field pits (fig. 4). The wood contains less parenchyma, which is often in tangential bands running between the rays.

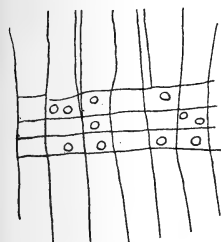


FIG. 3.—Long. rad. sect. *Podocarpus* wood showing field pits. $\times 125$. (Traced from a photograph.)

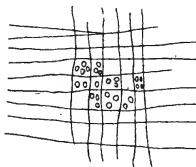


FIG. 4.—Sect. similar to 3 of *Widdringtonia*. $\times 125$. (Traced from a photograph.)

The third type has only been found in small specimens, not more than 5 cm. (2 inches) in diameter. The most obvious character is the presence of well-marked annual rings. These are narrow and separated from one another by zones of very small tracheids forming the autumn wood. Throughout the tracheids are smaller than in the other types, and the appearance is given of a harder more compact wood. In detailed structure the differences are less; a small amount of parenchyma is scattered through the wood, the uniseriate rays are 2-4 cells deep or occasionally 6-8 cells, bordered pits are circular in one row, contiguous but not flattened. Rims of Sanio are indistinct. The field pits are 1-2 and circular. The pith in the centre was of cells with thickened walls.

Branching occurred freely in these stems; several specimens have an irregular structure due to the formation of branches as large as the main axis.

Comparisons.—Of these fossil woods the first type seems to show

a close agreement with *Podocarpus*. There are some points of disagreement: in the fossil the diameter of the tracheids is larger than in recent *Podocarpus* wood, and the bordered pits appear to have a circular aperture while the recent wood has an oblique elliptical one. Both these differences may be explained by lack of perfect preservation.

The second type, characterised by less parenchyma and grouped field pits, is more like *Widdringtonia* than *Podocarpus*. Both these comparisons are supported by other structures, especially leaves and young shoots that occur in the rocks.

STRUCTURES ATTRIBUTABLE TO *Podocarpus*.

Leaves.—In the uppermost portion there occur impressions of lanceolate parallel-sided leaves which have a definite central vein but no lateral or branch veins. None of the impressions are complete, though some show signs of a narrowing at the ends. The largest is 2.8 cm. long and 9 mm. wide. These impressions have no structure preserved.

Another specimen is a silicified fragment of a linear lanceolate leaf. A part only is exposed, 4 mm. long and 1.3 mm. wide. The fragment tapers to one end, which is apparently the base. At the broader part there is a faint ridge in the centre which is about a third the width.

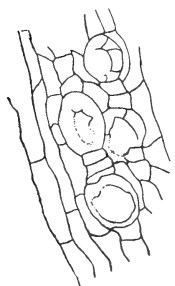


FIG. 5.—Epidermis
of linear leaf.
× 180.

Transfer films show the surface features. The epidermal cells are rectangular, rather elongated along the midrib but not at the sides, where there are rather large stomata arranged in straight rows. The guard cells are sunk below the surface (fig. 5).

This leaf is certainly that of a Gymnosperm, and, except for the very small size, agrees in its characters with *Podocarpus*.

In several sections are fragments of small leaves which are not well preserved. These have a palisade layer occupying about half the thickness. Vascular bundles are generally not visible, but some show a thickening in the middle region. One or two show indications of a hypodermal layer on the upper side.

Seed.—In the upper layers two specimens have been found which may be seeds. The more perfect has been split open. It is rather flattened, about 8 mm. long and 4.5 mm. across. It is pointed at

one end, but not symmetrically so; one side is straight, the other distinctly curved. The widest part is near the base. There is a smooth central mass surrounded by an outer wall. The central mass at its widened base has a sharp conical projection, 0.5 mm. long, opposite the angle of the bulging side. This structure immediately suggests a comparison with the seed of *Podocarpus*. The central mass with its projecting point is the prothallus enclosed by the nucellus with a nucellar beak.

The other specimen, found in proximity, is complete and shows the external surface only. It is 12 by 9 mm., with a rounded outline, very slightly pointed. The surface at the edges where flattening has occurred is slightly grooved.

STRUCTURES ATTRIBUTABLE TO *Widdringtonia*.

In various parts of the upper beds are portions of shoots bearing small leaves in decussate pairs. In the younger parts these leaves are closely appressed, but in older parts they are longer and with free projecting tips. These cupressoid twigs may be silicified, but are more commonly impressions on the rock.

Where the leaves are appressed they appear broadly triangular with a pointed or rounded tip. The spreading leaves are ascending or squarrose: the free portion is



FIG. 6.—Tracing of cupressoid twig. $\times 4$.

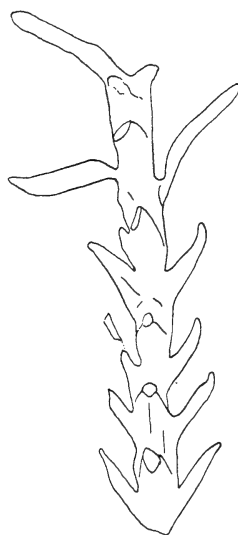


FIG. 7.—Tracing of cupressoid twig. $\times 4$.

flattened on the adaxial side. In the majority of cases the leaves on a twig are of uniform size, but in a few smaller leaves occur at the base (figs. 6 and 7).

Some of the specimens show internal structure. They are undoubtedly Gymnosperms, though details of wood structure are lacking.

The leaves in section are plano-convex, rhomboid, or curved: at the tip nearly circular. Each is traversed by a single vascular bundle which is central or nearer the upper side. In the lower half a large resin canal follows the bundle on its abaxial side (fig. 8).

Palisade tissue is not very regular but is more developed on the abaxial surface. The epidermis is thickened, but there is no hypoderm.

In one specimen traces of stomata of the Gymnosperm type occurred on the adaxial face.

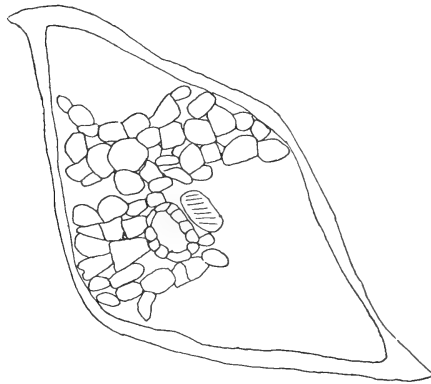


FIG. 8.—T.S. of leaf from cupressoid twig.
× 80.



FIG. 9.—Possible male cone.
× 40.

Possible Cones.—In one section in close proximity to leaves of the cupressoid type there is a rather vague structure that may be a fragment of a male cone. It consists of a short axis bearing three structures that widen to the tips: two are lateral, one seems terminal. Two of these bear hollow structures attached below the expanded tip. The whole structure is about 0.75 mm. in length, and does not show good cellular structure (fig. 9).

In another piece of rock containing cupressoid twigs is a flattened body that may be a cone scale. This is about 2 cm. long, and is blunt-ended and narrowed to its base. The surface is smooth and marked by faint lines that converge towards the blunt apex. The specimen shows traces of cell structure on its surface. The epidermis is composed of small rectangular cells, except along the lines mentioned, where they are elongated. No stomata were visible.

Gymnosperm Roots.—In some parts of the rock there occur numerous roots with characteristic gymnosperm structure. These are from

2-6 mm. in diameter. In transverse section they consist of a central mass of tracheidal wood traversed by narrow medullary rays of parenchyma. The primary xylem in the centre is diarch. There are no resin canals. The outer tissues are present, but are in a poor state of preservation (fig. 10).

All the roots have secondary tissues developed, though in some of the smaller ones the amount is not large. In the larger ones no division of the wood into annual rings is noticeable.

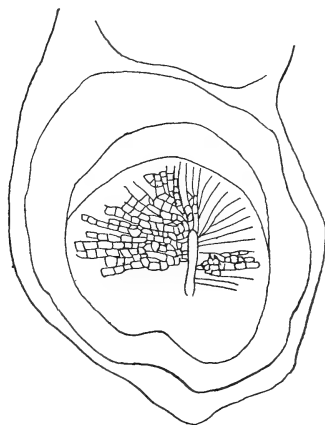


FIG. 10.—T.S. gymnosperm root. $\times 65$.

These roots have not been found in actual connection with any larger axis.

FERNS.

Remains of ferns occur somewhat locally in the rocks. While not generally distributed these remains are abundant in patches, especially in the upper parts of the hard beds.

All the fern remains found are fragmentary and, at present, do not allow of certain identification, or even of clear association of different portions of the plants.

Ferns are represented by stems, roots, petioles, fragments of leaves, and traces of sporangia and spores.

Stems.—Stems of ferns of more than one kind have been found.

Solenostelic Stems.—These are the largest, and, while only found in one portion of the rock, are abundant there.

These stems may be as much as 10 mm. in diameter and are commonly 6-8 mm. They occur generally as short fragments, no piece over 2 cm. in length having been found. In section they appear elliptical, but this seems due to compression.

These stems show typical solenostelic structure, a closed ring stele with a central pith region and a relatively wide cortex outside; the stele is bounded both outside and inside by phloem, pericycle, and endodermis. The xylem is made up of tracheids associated with parenchyma. In longitudinal section the tracheids have scalariform thickenings.

The cortex in some specimens is uniform parenchyma, in others it is differentiated into zones, the inner and outer having thin-walled cells, while the middle region is thick walled. The pith may show the same differentiation, though the thick-walled portion extends to the centre.

At the surface the cells are very thick walled. In the better preserved specimens there are projections from the surface in the form of rows of cells or of groups of 2-3 cells. These represent rammenta, which were abundant.

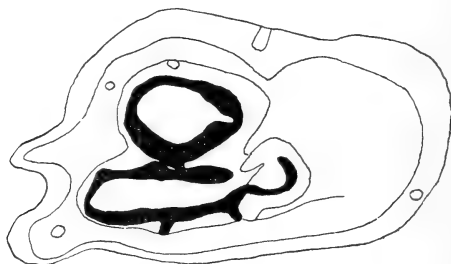


FIG. 11.—T.S. solenostelic fern stem showing branching and departure of leaf trace. $\times 7$.

Some portions show nodes. Here a small gap is formed in the stele: the leaf trace passes out through the cortex in the form of a curved strand.

Branching of these stems occurred. Branching is apparently dichotomous, though one division is distinctly larger than the other. Roots arise in numbers from these axes. No gap is formed in the stele at the departure of the root trace (fig. 11).

Protostelic Stems.—These are more common than the solenostelic stems described above, and are more generally distributed through the upper parts of the rocks, though never so abundant in any part.

These protostelic stems are smaller in size than the solenostelic ones. The largest is 5-6 mm. in cross-section, but 0.75-1.5 mm. is the more general size. Though the diameter is less these stems may occur as continuous axes of 5-6 cm., following a straight course through the rock.

Two types of protostelic axes can be recognised.

First Type.—These are generally larger, 2–3 mm. in diameter as an average. They exhibit a wide cortex and a central stele. The cortex may be uniformly thickened or have the outer and inner parts thick walled and the middle region thinner. The epidermis is smooth, with no trace of rameta.

The central stele, which may be a third or more of the total thickness, has the middle occupied by xylem. This is surrounded by a narrow zone of thin-walled cells, which represents the phloem and pericycle. In no specimen is this zone well preserved. There is a definite endodermis between this zone and the cortex.

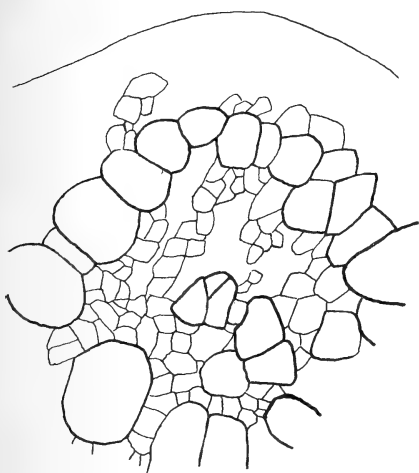


FIG. 12.—T.S. exterior of xylem of protostele showing mesarch protoxylem. $\times 140$.

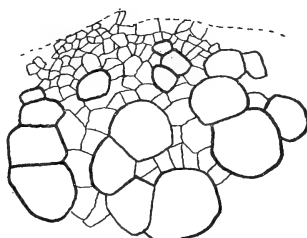


FIG. 13.—Sect. similar to 12 with exarch protoxylem. $\times 140$.

The central xylem is made up of tracheids with scalariform thickenings interspersed with parenchyma. The tracheids may be wide. The protoxylems are mesarch (fig. 12).

One of the largest specimens found includes a node. At one side of the stele is an arc of xylem separated from the main mass by a patch of rather small celled parenchyma, the cells of which are thick walled. In the sections obtained this parenchyma is enclosed by xylem, the arc being attached at the sides to the main mass. At the opposite side, ventral side, of the stele are projections from the xylem that represent root traces.

Second Type.—The stems included here are of smaller size, 1.5 mm. as the average. In general structure they are very similar to the first type, but differ in having the protoxylems exarch (fig. 13). Also

the tracheids in the xylem are differently arranged: instead of being scattered with separating parenchyma they occur in groups with the cells flattened at the points of contact.

Petioles.—These are the commonest fern remains, and in some pieces of the rock are abundant. No case has been found where a petiole is attached to a stem. The examples noticed of nodes in stems have only the leaf traces and not the free portion of the petiole.

These petioles are cylindrical or flattened, and slightly grooved on the upper surface. In diameter they vary from quite small structures to 2–2.5 mm. Portions as much as 3 cm. long have been found.

In structure they are fairly uniform, the stele consisting of a single continuous horse-shoe-shaped band with central xylem. This



FIG. 14. — Outline of fern petiole.
× 9.



FIG. 15. — Outline of fern petiole.
× 9.



FIG. 16. — Outline of petiole with divided stele.
× 9.

band may be simple or the tips may be thickened or bent round in hooks. Where hooks occur at the tips these may be bent over to be parallel with the main portion or spread out at an angle (figs. 14, 15).

Some portions have been found in which the stele is divided up and has the form of an arc more or less curved, sometimes distinctly U-shaped, with two separate strands which themselves may be curved. There is no significant difference in size between those with a continuous stele and those with the divided stele (fig. 16).

It is not possible to associate these petioles definitely with the stems. The different stems occur associated in the same rock. Petioles with divided steles have not been found associated with solenostelic stems.

Roots.—Especially in association with the solenostelic stems small roots are exceedingly abundant. These roots appear unbranched. In section they have a small stele with diarch xylem. The endodermis consists of cells distinctly elongated in the tangential direction. The cortex is thin walled (fig. 17).

Leaves.—The remains of leaves attributable to ferns are exceedingly fragmentary and of little value for purposes of identification.

Some portions occur as impressions which represent fragments of an apparently compound leaf, and probably ultimate segments. These are pinnatifid scraps with forwardly directed rounded lobes. The venation is dichotomous without anastomoses. No cell structure is preserved.

In some of the sections in association with the petioles and fern roots are a number of scraps of leaves. These are thin, flat structures. The epidermis is not distinctly thickened. The mesophyll on the

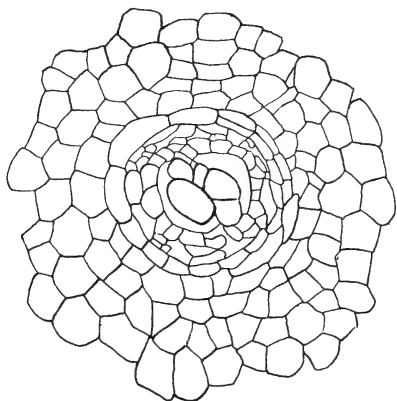


FIG. 17.—T.S. fern root. $\times 80$.

upper side has a rather irregular palisade formation. The preservation is poor and no vascular bundles with structure are present.

Some of these leaf scraps show a downward curving of the margin of the leaf.

Sporangia.—No sporangia or any trace of them have yet been found in direct connection or immediate association with the leaves. All that have been discovered are some poorly preserved specimens lying isolated in the rock containing fern remains. No complete specimen has been found. Some of the sporangia are circular, with a rather massive annulus running round the periphery. The annulus extends about two-thirds round. The appearance suggests an equatorial annulus (fig. 18). Others are more elongated, with the annulus extending half or more longitudinally. These seem to have had a vertical annulus (fig. 19).

Spores.—Some groups of spores showing formation on tetrads occur, but they do not show any distinctive features.

Comparisons.—Owing to the fragmentary nature of these fossils, especially of the leaves and sporangia, detailed comparisons with living plants are difficult.

The protostelic stems of the first type, with mesarch protoxylem, and the pocket of thickened ground tissue at the node, agree closely in size and many details of structure with species of *Gleichenia*. Further support is got from a section of an axis closely associated with one of these protosteles which has the xylem in a ring enclosing a small central area. This is extremely like a section of a petiole of *Gleichenia* formed near a rapidly growing rhizome tip in which the



FIG. 18. — Sporangium with equatorial annulus. $\times 130$.

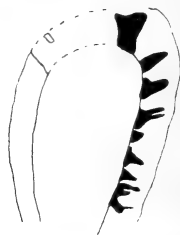


FIG. 19. — Sporangium with vertical annulus. $\times 130$.

stele forms a closed ring. These fossils agree in so many features with *Gleichenia* that generic identity may be accepted.

The identity of the other fern types must remain unsettled at present.

ANGIOSPERMS.

Both monocotyledons and dicotyledons are found, though all are of small size. Most of the fossil material is in the form of isolated scraps which are described if only to give a stimulus to subsequent collectors.

Monocotyledons.

Stems.—Stems of a small monocotyledon are abundant in local areas in the rock. These stems are of two kinds, but as they have been found in attachment they are from the same plant and represent rhizomes and aerial axes respectively.

Rhizomes.—These are cylindrical structures as much as 2–3 cm. long and 2.5–3.5 mm. in diameter: a few reach 5.5 mm. Most are unbranched. They have a characteristic appearance due to furrows on the surface which run both longitudinally and horizontally and divide the surface into rectangular areas which have the longer axis horizontal. In the younger portions scale leaves arise from the

raised areas and enclose the terminal part: these are wanting in older parts.

In section these axes show the characteristic rhizome structure, with a wide cortex and the bundles in a definitely bounded central cylinder which is often less than a third of the total diameter (fig. 20). In the central cylinder are numerous bundles which follow a rather irregular course. The bundles are close at the periphery but more separate and larger in the centre. Each is concentric, amphivasal, with a small phloem. The cells of both phloem and xylem are narrow (fig. 21). The cortex is composed of thin-walled parenchyma cells with rather numerous small spaces between them.



FIG. 20.—Monocotyledon rhizome. $\times 9$.

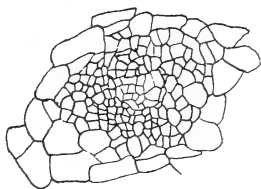


FIG. 21.—Amphivasal bundle from rhizome. $\times 200$.

The epidermis is a very distinct layer. In old portions regular layers of cork occur on the outside.

Scale Leaves.—In section these seem structureless. It is probable that they were dry, shrivelled scales. Near the base they are composed of undifferentiated parenchyma through which run a number of small parallel vascular bundles.

Roots.—Roots are produced in large numbers from the rhizomes. They are found passing through the cortex in all directions and emerge indiscriminately through the raised areas and the furrows. The roots are small, rarely 0.5 mm., and are unbranched. They have a parenchymatous cortex and a relatively wide central cylinder which is medullated and has numerous strands of xylem.

Aerial Stems.—These are slender and slightly compressed and show no trace of division into nodes and internodes and have no appendages. They may be as much as 2 by 1 mm. in section, but are generally smaller, 1.0–1.25 by 0.5–0.75 mm. Internally the cortex is narrow and the central region, with scattered bundles, not sharply separated

from it. The cortex is traversed by strands of subepidermal fibres which are widest outside and extend in almost to the bundle region, so that the palisade-like parenchyma of the cortex comes to the surface along quite narrow lines (fig. 22). The bundles run parallel; each is collateral, not concentric, and is surrounded by a sheath of fibres. The xylem is spiral, reticulate or pitted, with the pits elongated transversely.

General.—These monocotyledons seem to have been plants with scapose aerial stems which grew separately, not in tufts. The structure of the bundles excludes the Gramineae and almost certainly the Cyperaceae also. In the absence of any flowers more certain identification is not possible.

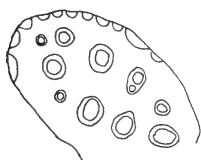


FIG. 22.—Aerial stem of monocotyledon. $\times 14$.

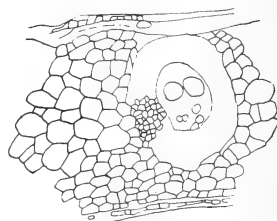


FIG. 23.—T.S. monocotyledon leaf. $\times 75$.

Monocotyledon Leaf.—In a section from a part of the rock remote from that which yielded the plants just described is a portion of a transverse section of a leaf that seems that of a monocotyledon.

The section is incomplete. It shows a slightly curved outline with three vascular bundles. The epidermis is of thick cells, the mesophyll of regular parenchyma with few intercellular spaces. The cells are polygonal and similar on the upper and lower sides. The bundles are embedded. Each has a sheath, 3–4 cells deep, of small cells. The interior is poorly preserved, but towards one side are two large rounded cells that look like vessels (fig. 23).

Dicotyledons.—Scraps of stems and leaves, very numerous roots, and fruit structures have been found. The material does not allow of definite association of the various parts and is in most cases insufficient for identification.

Woody Stems.—These are not abundant and are of small size. They occur in the hard middle layers and in the upper beds. The best preserved are twigs about 5 mm. in diameter. They have a rather thick cortex round the wood, which is characterised by the

presence of large vessels which occur singly or in radially placed pairs. The vessels are surrounded by small thick-walled cells. Medullary rays, 2-4 cells across, traverse the wood (fig. 24). No longitudinal sections are available.

The cortex had fibres in groups. Fibres also occur in the phloem, in which the rays widen out.

Roots.—Roots of more than one kind have been found, and in some parts are exceedingly abundant. None have been found in connection with a stem, so that identification is not possible.

Four types of root can be distinguished.

First Type.—These are much the commonest, indeed they are the commonest fossils. They occur in all the layers. In the lowest, roots are extremely abundant, but are in the form of casts or structureless tracks. In the hard rock, parts consist of very little else than these roots. The roots run in various directions, but are most often vertical and at times are very regularly parallel.

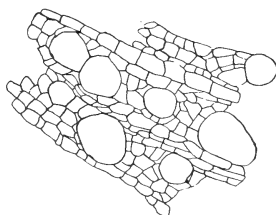


FIG. 24.—Dicotyledon wood. $\times 105$.

There is some variation in size; an average diameter is 2.5 mm., but some are as much as 5-8 mm., and there are many small ones. The smaller ones are often in groups. Branching occurs, but not commonly.

In structure the roots have a small central cylinder surrounded by a wide cortex of rather regular parenchyma in regular radial rows. The cells of the cortex appear rectangular in cross-section and have very small or no spaces between. On the outside there are 5-6 layers of smaller cells with thicker walls. In longitudinal view the cortical cells are rectangular and about 2-3 times as long as wide.

The central cylinder is bounded by a definite layer which is not distinctly thickened. The centre is filled by the xylem, which is made up of rather small cells, very uniform in size. There are no large vessels. Pith is only found in the largest roots. The xylem is typically 5-6 arch, with the protoxylems at the points of the pentagonal or hexagonal column. Small roots and branches have 4-3 protoxylems.

The xylem cells have spiral and reticulate thickenings.

The phloem and pericycle are in most cases torn. They had thin-walled cells.

Many of the larger roots show secondary thickening, but none have

more than the first stages. The secondary xylem is composed of small tracheid-like cells with regular arrangement.

Stretching and some disorganisation of the pericycle and endodermis occur, but in no case is the cortex cast off, nor is there any sign of cork.

In many of the larger roots the cortex is penetrated by smaller ones of the same kind. Three or four of these penetrating roots may be found round the central cylinder of a large root.

Note on the Cortex of Roots.—The very regular large-celled cortex with few intercellular spaces is very characteristic of these roots. This cortex is very different from that usually associated with roots with a wide cortex in which secondary growth takes place slowly and not in much quantity. A much more common arrangement is one of cells that are rounded or polygonal in cross-section.

A comparison of these fossil roots with roots of similar size from living plants has led to the view that the form of the cells in the cortex of the fossils is not the original one but is brought about by alterations in the course of preservation. A careful examination of the cortical cells in well-preserved specimens of fossil roots reveals small projections on the walls and especially on the tangential walls. The projections are lines or ridges running along the walls. Careful tracing of these lines exhibits a framework of a cell pattern of polygonal or rounded cells with intercellular spaces. It may be noted that at times this arrangement is more definite in a photograph than in direct examination.

The formation of the regular rectangular cell appearance from cells with rounded or polygonal outlines would seem to be brought about by shrinkage in preservation combined with some disruption. The frequent breakdown of the phloem and pericycle is further evidence of shrinkage having taken place. To test this some experiments were made on living roots. Roots of *Villarsia ovata* were used as a type of a size similar to the fossils. The cortex in this plant is composed of radial rows of cylindrical cells, rounded in cross-section.

Various methods of shrinkage were tried, most of which were unsuccessful, but one very simple method gave striking results. Sections or pieces of root were placed in a solution of gelatine that was allowed to concentrate and set by evaporation at room temperature. While frequently the contraction of the gelatine caused rupture of the tissues, in some cases an appearance in the cortex very strikingly like that seen in the fossils was obtained. The originally rounded cells have been pulled out and appear rectangular in section and the spaces have been quite obliterated.

Second Type.—These occur in association with the first type of root, but are much less numerous. They are generally of smaller size, 1–2 mm. in diameter. The cortex is less regular and has not the zone of thicker cells on the outside. Correlated with this absence of the thicker cells the cortex generally appears compressed or deformed in various ways. The central cylinder is relatively larger, and is bounded by a definite endodermis of rather large cells. Internal to the endodermis are two or three layers of cells with thin walls. The centre is occupied by a mass of small cells which are apparently xylem mixed with parenchyma. There are no distinct rays or projection from the xylem.

Third Type.—A few examples of another and distinctive type of root have been found. These are small, 1 mm. or less in diameter. The cortex has the cells somewhat thickened. The central cylinder is about one-third the total thickness of the root. The greater part of the central cylinder is occupied by xylem, which here contains large vessels associated with smaller thick-walled cells. The xylem seems to be tetrarch. The peripheral portions of the central cylinder are not preserved. The endodermis appears to have been thick walled.

Fourth Type.—The roots placed here are slender structures about 0.5 mm. in diameter. The central cylinder is very small, with triarch xylem. The cortex is in three distinct layers; an inner zone of small cells, a middle region of large cells with very thin walls, and an outer zone of smaller thickened cells. The middle zone is in most cases poorly preserved and incomplete.

Comparisons.—While identification is not possible, some general comparisons may be made. The first type of root, which is rather thick and has very little secondary growth, seems most like the root of a perennial herb. Roots very similar in their general features occur in some of the Compositae, which have roots which are little branched, with a wide cortex, and with small amounts of secondary growth. The xylem is also composed of small cells.

Leaves.—In the uppermost layers of the rock there are a number of scraps of leaves which have an astomosizing venation. The preservation is poor, and no details of epidermis or of stomata are obtainable. The leaf is represented by a powdery substance which disintegrates at a touch. None of the fragments discovered has a complete outline. There seems to be certainly more than one type of leaf represented. Some have a single midrib with pinnate venation, others apparently more than one main vein. These latter have

smaller veins running across between the main ones and smaller branches forming a reticulation.

Fruits.—In the uppermost layers are found isolated bodies that are fruits and probably fruits of dicotyledons. Most occur as casts or impressions without cell structure.

“Four-chambered Fruits.”—Two specimens have been found of bodies which are almost spherical and smooth externally. These are 2–4 mm. in diameter. Internally they are divided into four equal chambers. The outer wall is $\frac{1}{2}$ mm. in thickness; the partitions, which run at right angles to one another, are thinner; they are slightly thicker at the centre. In one specimen the chambers are empty; in the other, which is silicified, there are indications of contents. Each chamber held one body, probably a seed (fig. 25).



FIG. 25.—
Curtisia fruit.
× 5.

These fruits, both in size and structure, bear a striking resemblance to the “stones” of the drupaceous fruits of *Curtisia faginea*. This resemblance is supported by the identity of cell structure in the outer wall. Tentatively these bodies may be regarded as being the fruits of that tree.

“Two-chambered Fruits.”—These are the commonest of the fruit bodies and are locally abundant in the rock. They are smooth ovoid bodies 8–12 mm. long and 6–8 mm. across. Externally they are slightly pointed at one end and blunt at the other. In many there is a groove running round the fruit longitudinally which gives an appearance of division into two. Internally each is divided into two chambers by a partition which ran longitudinally down the middle. The groove is at the line of junction of the partition and the outside wall.

The partition is complete, but is much thinner at the point and is often broken down there.

The majority of these fruits appear quite empty or are filled with amorphous material. A few, however, have been found which have contents. In each chamber is a body flattened along the septum but convex on the outer side. Near the base of the flat surface is a rounded area which forms the point of attachment. Each of these internal bodies has a rugose surface.

In one piece of the hard rock there is a two-chambered fruit of a different kind. This is a rounded, rather flattened body about 4 by 3 mm. and 3 mm. thick. Broken across it shows a thick wall composed of uniform parenchyma-like cells. There is a partition dividing the interior into two unequal portions. The interior is filled with chalcedony and does not show any certain structure.

MISCELLANEOUS ANGIOSPERM STRUCTURES.

"Smooth Fruits."—These occur in the same rock with the "two-chambered fruits" described above, but are much less abundant. They are nearly spherical and measure 9–12 by 8–9 mm. The ends are rounded, not at all pointed. They were quite smooth both externally and internally. On the inside there is a low ridge projecting inwards. This ridge was not a complete partition, as there is no trace of it on the opposite side. The ridge runs longitudinally, but not quite straight. No contents have been found.

"Flat Fruits."—A few flattened structures, probably fruits, have been found. They are smooth and oval, 6–8 by 4–5 mm. in surface, and 2–3 mm. thick. When broken across they show a distinct thick outer wall enclosing a smooth body with a much thinner wall. No details of structure are available.

"Smooth Seeds."—From various parts of the rock and especially from the uppermost layers there have been obtained smooth ovoid bodies up to 2·5 mm. long and 2–3 mm. across. Some are nearly spherical, others are distinctly pointed at one or both ends. There is a considerable range in size and shape, and it is certain that more than one kind is represented. In some of the best preserved examples a low ridge runs obliquely up the surface on one side for about two-thirds the length.

One specimen, perhaps, justifies further description. This is a smooth ovoid body, 4 by 2·5 mm. The specimen has been partly broken, and the break reveals a distinct double wall. The outer and inner walls are connected by numerous fine strands that run straight across between them.

"Ribbed Seeds."—These are ovoid bodies 3·5 by 2–3 mm., in which the surface is marked by longitudinal grooves or ridges. These occur as impressions. They were bluntly pointed at one end. On the surface the grooves are much wider than the intervening ridges.

In some the grooves and ridges are simple, in others they are interrupted or complicated in various ways.

"Prickly Seeds."—Three examples have been found of ovoid or nearly spherical bodies about 2–3 mm. in diameter which have an unridged surface covered by sharp projecting points. In two of the three specimens these points are irregularly arranged—in the third they are in lines.

Fungi.—Hyphae of a fungus have been found in more than one of the sections in the tissues of other plants. They have been noted in

the Gymnosperm wood and in the roots of ferns and in various unidentifiable fragments. No spores or spore-producing structures have been found.

Structures of Uncertain Affinity.—In the rocks are numbers of plant fragments that cannot at present be assigned to any definite group. Some of these are very fragmentary, but some are quite definite and distinctive. Of these uncertain fossils by far the most abundant and important are leaves that for want of any means of identification are referred to as "Ribbed Leaves" on account of their general appearance.

"*Ribbed Leaves.*"—Locally in the uppermost bed there are large numbers of fragments of parallel-sided leaves which are marked by prominent longitudinal ribs. These occur in a poor state of preservation or as impressions. In one part of the rock they occur in very large numbers; masses of these fragments are found together in layers. The leaves themselves run in all directions. The rock here is hard and does not split along any definite planes, so that it has not been possible to obtain really satisfactory specimens. Not one example has been seen in which a complete leaf is present. The largest piece is 9 cm. in length. In width the pieces are very uniform, about 2-2.5 cm.

These leaves taper at both ends: at the base rather gradually to about 0.75 cm.; more abruptly at the tip, which is rounded but acute.

One specimen has been found which shows what may be the attachment of these leaves to an axis. In this there is a much flattened axial structure, 13.5 cm. long, with the basal parts of leaves attached at either side. There are three leaves on one side and five on the other. The leaves are narrowed to their attachment, but show no sign of any sheath. The leaves are approximately opposite on the axis. The latter tapers: it is 2 cm. across at one end and only 1.25 at the other.

In the leaves themselves the ribs are much more prominent on one side than the other: the ribbed side is presumably the lower.

The flat surface is without stomata. It has an epidermis of elongated lozenge-shaped cells which appear uniform all over. The under surface has numerous stomata arranged in bands in the grooves: there are none on the ridges. The epidermis is made up of elongated lozenge-shaped cells; narrow on the ridges and broader where the stomata occur. The stomata are sunk somewhat below the surface. Each depression is surrounded by 4-6 cells: examples with four, five,

and six cells have been found on one leaf. There are two cells much smaller than those of the general epidermis adjacent to the guard cells which are accessory cells (fig. 26).

The stomata are in lines, but not regularly so.

Sections show a rather thick leaf. The epidermal cells project somewhat. Subepidermal fibres occur along the flat upper surface and on the ridges on the lower surface. Of the interior about two-thirds is occupied by palisade cells. In none of the sections is any definite vascular tissue recognisable. Areas of structureless material represent the positions of veins.

The axis which has probably leaves in attachment is very much compressed and has little definite structure preserved. It appears to be made up of strands running in a matrix, but no certain cell outlines can be made out.

With the material available it is not possible to assign these leaves to any group. The specimen referred to in which attachments occur may be a portion of a stem bearing leaves, or a piece of a large pinnate leaf. A prolonged search failed to give any further specimens that could afford evidence that might decide this point. One specimen with impressions only shows an axis with three leaf bases. There is no indication of any kind of bud on this: the base of the leaf passes into the axis gradually on the lower side; on the upper side the outline curves upwards just at the point of attachment, giving a rounded angle. While the specimen is incomplete and entirely without cell structure it seems to support the possibility of these leaves being pinnae of a compound leaf.

On the other hand, the large numbers of leaf fragments and the great rarity of portions attached to any form of axis is not easily explained if this is the case.

The lack of recognisable vascular structures renders any attempt at identification a matter of mere speculation.

The general appearance and shape are suggestive of monocotyledons, but the absence of a sheath seems against associating them with that group. The epidermal structure seems to eliminate the possibility of a cycadean affinity.

The large mass of these leaves was found in close proximity to a

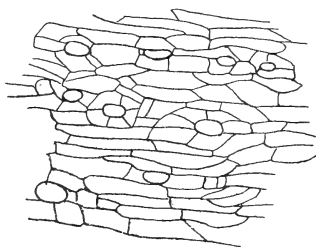


FIG. 26.—Epidermis of ribbed leaf. $\times 140$.

stem which had wood of the type identified as *Podocarpus*, but there is nothing except their positions in the rock to suggest any sort of connection.

Miscellaneous Structures.—(a) In two sections are fragments that represent portions of the wall of a rounded body such as a spore or pollen grain. These are thick bands with, on the outside, a series of sharp projecting points. They are made up of continuous material and not of separate cells (fig. 27).

(b) In close proximity to one of the above is a small portion of tissue with cell structure. This consists of 2-3 layers of parenchyma cells connected to a layer of large columnar cells with walls very much thickened all round. The fragment is probably a bit of a seed coat.

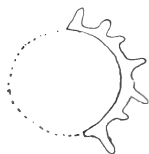


FIG. 27.—Spore-like structure.
× 42.

(c) In one section there occurs an oval body about 1.5 mm. along the longer axis. This has a somewhat irregular wall through which runs a band of thickened columnar cells. The interior is hollow.

Various other scraps and fragments have been found which it is impossible to assign to any group of plants. Most of these are so uncertain in nature that no descriptions are needed.

General Considerations.—The fossil plants described above without doubt represent the remains of a land flora. Not one of the structures is of a nature to suggest an aquatic or even a marsh environment. The roots with their wide large-celled cortex might possibly at first sight seem to be associated with moist conditions, but it has been shown that the cortex here is not in the original condition and that the existing plants that give the most probable comparison are certainly plants of dry land.

The distribution of the roots in the rock would point to their preservation *in situ*. This is supported also by the positions of a large number of the gymnosperm axes which has already been noted. In the quarry at the south extremity of the rocks gymnosperm axes pass down without break from the silicious rock into extremely weathered dolerite below.

As regards the original conditions, this preservation *in situ*, and especially the penetration of the tree-roots into the dolerite, completely rules out any possibility of transportation and redeposit. The origin that is most likely, and which explains most readily the nature and distribution of the fossils, is that the soil in which the plants were living has been impregnated with silica and so con-

solidated. Preservation of the soil would give the explanation for the great abundance of roots and the scarcity and fragmentary condition of the leaves.

The gymnosperm wood also seems to fit in with the soil nature of the rocks. The largest portions, which would be the aerial stems, are prostrate and often in short pieces, while those *in situ*, which are roots, are smaller.

A soil would also explain the apparent complete absence of animal fossils: such animals as were living in the soil would leave no trace behind.

The woody gymnosperms, and especially *Podocarpus*, are of quite general occurrence in the rocks. They occur in all the layers, and are not noticeably more abundant in one than another. The roots, too, are generally distributed through the middle and upper layers. In the basal beds the absence of preserved structure, except in wood, renders it uncertain whether the numerous casts and tracks which occur belong to these roots or to rootlets of gymnospermous trees. On the other hand, the other plants seem very much more local in their distribution. The cupressoid gymnosperm twigs, which are tentatively associated with the less abundant type of wood, are only found in portions of limited extent in the uppermost beds and in the upper part of the hard flinty rock.

Local distribution is still more evident in the cases of the solenostelic ferns, the scapose monocotyledons, and the ribbed leaves. Each of these is abundant where it is found, but the area occupied is very limited. The protostelic ferns, though never abundant, are more widely spread through the rocks, especially in the upper portions.

Relations of Fossils.—In these rocks the gymnosperm wood, even in the most favourable cases, shows signs of alteration and of decay having taken place before silicification. Specimens have been examined from all the beds of rock, and none has been found in which the softer portions, such as the bark, have been preserved. Bark is completely absent in all the larger pieces; and even in small ones, if present, is in a poor state of preservation. In many examples the wood itself shows signs of decay: the outer surface in some is eroded and irregular: radial cracks have been noted above. In one large piece the centre was not closely connected to the outer parts of the wood. Further, the generally found ghostlike nature of the pits on the cell walls and the very poor preservation of the parenchyma of the wood and medullary rays point to decay before impregnation and fossilisation.

In contrast to this condition of the wood, the roots frequently show excellent preservation, not only of the harder parts but also of the much less resistant thin-walled cells of the cortex. Alteration has taken place, but it is of a different kind, occurring in preservation and not previous to it.

It may be noted in this connection that gymnosperm roots of small size, which may occur in the same rock with these other roots, are not nearly so well preserved as the latter.

Several examples have been found in which portions of wood have been penetrated by roots. These may make their way along cracks or even penetrate the wood itself. Sections of such root-penetrated wood show excellent preservation in the roots and a good deal of alteration in the wood.

These various results strongly suggest that changes in the vegetation were occurring previous to fossilisation. The wood decay indicates that the trees were already dead, while the state of the roots and their penetration into wood show a later period of activity. The cessation of activity of the trees previous to fossilisation is supported by the prostrate position and often short lengths of the stem portions and the frequent presence in the uppermost beds of small isolated pieces of woody stems.

Taking all the available data into account, it seems probable that a gymnospermous forest, mainly composed of *Podocarpus*, existed at one time on this site, but was destroyed. On destruction the underground portions remained in position and were eventually preserved before decay had proceeded too far. The upper parts fell and broke up to a large extent. On destruction of the forest, herbaceous plants became exceedingly abundant, as shown by the great numbers of their roots that have been preserved.

The cause of the destruction of the forest is a matter of speculation. There is no evidence for subsidence and waterlogging of the soil which might be an explanation. Another factor that might have operated is fire. Trees killed by fire may remain in position for a long period, and direct regeneration may not occur. It is conceivable that the local abundance of ferns is an indicator of fire. At the present time *Gleichenia polypodioides* may become very abundant locally on burned areas of forest at Knysna (*cf.* Phillips, "Forest Succession and Ecology in the Knysna Region," Bot. Survey S. Afr., xiv, p. 236, 1931).

Age of the Rocks.—The fossil plants that occur here, so far as they can be identified at all, are such as would be expected in a fairly

recent rock. All are types that might be in existence at the present time.

The fossil flora shows a striking difference to that existing in the locality at the present time in the dominance of gymnosperms and the relative paucity of angiosperms. The latter are both less in abundance and smaller in size in the fossil flora.

Whether this difference represents a real difference in the flora as a whole that existed, or is the result of the preservation of a local community of plants, can only be settled by the study of contemporary deposits over a wider area.

At the present day *Podocarpus* occurs in the region, but at this low altitude only as isolated individuals in communities definitely dominated by angiosperms. Continuous forests of this tree, even of small extent, do not occur.

The differences in the fossil flora as compared with the existing one at this altitude point to a not very recent date for the rocks. On the evidence available a Tertiary age is the most probable, though the position in that epoch must await the accumulation of further data.

SUMMARY.

1. Near Fort Grey is a local surface quartzite containing plant fossils. The plant remains are numerous, but fragmentary.

2. The quartzites overlie dolerites.

3. The most abundant fossils are woody stems and roots of a type that is identified with *Podocarpus*. Other gymnosperms are more like *Widdringtonia*.

Leaves, twigs, and possible seeds can be associated also with these trees.

4. Ferns occur rather locally. Some specimens are identified with *Gleichenia*. Other ferns are represented by solenostelic and protostelic stems, petioles, roots, and scraps of leaves and sporangia.

5. Both monocotyledons and dicotyledons occur, the former as rhizomes, aerial stems, and roots; the latter as roots, small woody stems, scraps of leaves, and fruits and seeds. *Curtisia* has been identified by fruits.

The roots are shown to have undergone shrinkage, and some experiments to demonstrate this are described.

6. Some large ribbed leaves of uncertain affinity are described.

7. The general distribution of the plants in the rocks is discussed, and it is considered that the rock represents a solidified soil.
8. The gymnosperm wood is in less good condition than the roots and represents an earlier phase of the vegetation.
9. The fossils are part of a land flora.
10. The rocks are of Tertiary age.

3. *On some Karroo Fishes from Central Africa.*—By S. H. HAUGHTON,
B.A., D.Sc., Hon. Keeper of Palaeontological Collections.

(With Plates XXIX–XXXI and 2 Text-figures.)

Ischnolepis bancrofti gen. et sp. nov.

(Pl. XXIX.)

Co-types.—Two almost complete fish on slab No. 9338 in collection South African Museum; specimen No. 9339 in same collection.

Locality.—Lunsempfwa Valley, N. Rhodesia (lower portion); collected by Dr. Davis, and presented by Dr. J. A. Bancroft. Discovered in “a brown ferruginous shale with a maximum thickness so far found exposed of from 3 to 4 feet. Above this brown shale is a thin bed of a tough calcareous shale showing a peculiar cone-like structure” (Davis). Associated with fossil plants and *Palaestheria*.

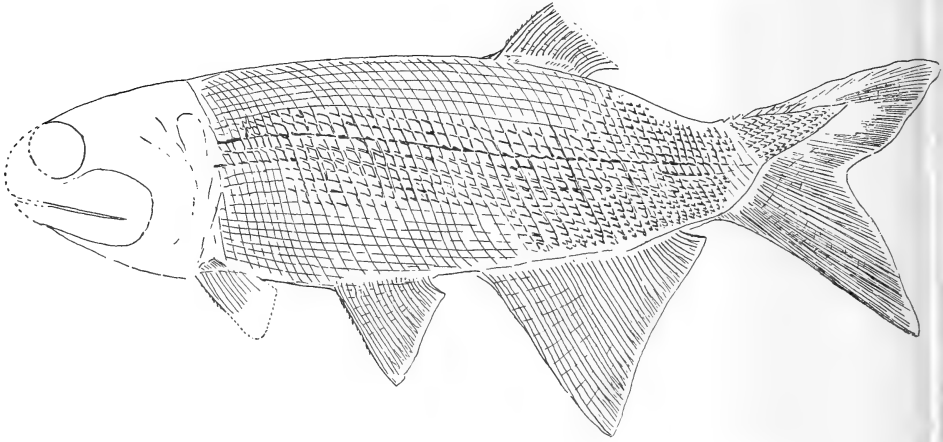
Horizon.—Probably Upper Beaufort or Lower Stormberg.

Generic Characters.—Body fusiform. Mandibular suspensorium oblique, gape moderately wide. Dentition consisting of sharp, well-spaced, delicate, anteriorly directed teeth in front part of mandible and maxilla, and sharp, robust, more closely packed teeth in the hinder two-thirds. Opercular apparatus relatively small; interoperculum well developed. One X-bone present in front of preoperculum. Fins with fulcra, forked distally, articulated except in pectoral; pectoral fin relatively short-based; pelvic fin long-based; dorsal fin remote, opposed to anal, rather high in front, with a moderately elongated base-line; anal fin much extended, high and acuminate in front, its base reaching almost to the lower caudal fork; caudal fin almost equilobate, body lobe not extending to distal end, and fairly blunt-ended. Scales small, rhomboidal, arranged in numerous rows passing slightly sigmoidally backwards from dorsal to ventral margins of body. Lateral line prominent, surrounded by fine tubes.

Specific Characters.—As for the genus. Fish small, up to 75 mm. in length. Head occupies about one-fifth of the entire length, greatest depth of body a little more than length of head, and in neighbourhood of pelvic fin.

Description.—The details of structure are obtained from the study of several specimens and a number of body and head fragments; no specimen is complete enough to show all the features. The arrangement of the bones of the head in the postorbital region is Palaeoniscid. A number of details can be obtained from a specimen that gives an inner view of the bones of this region.

The maxilla has a low suborbital portion and a higher and long postorbital part; the latter has a regularly curved upper border, and



TEXT-FIG. 1.—*Ischnolepis bancrofti*, Htn.
Restoration of body, drawn by Dr. K. H. Barnard.

has no pronounced upper posterior angle such as is seen in *Palaeoniscus*. The upper portion of the postorbital part of the bone is excavate on its inner surface, while the lower half is furnished with a series of small pits, which are elongated in an antero-posterior direction.

The mandible is rather weak, with a pointed anterior end. Its inner surface is apparently ornamented with irregular longitudinal grooves and ridges. It is not possible to determine whether it and the maxilla carry one or two rows of teeth. In the hinder two-thirds of the dentigerous borders the sharp-pointed but robust mandibular and maxillary teeth interdigitate closely; the anterior sharp-pointed slender teeth are more widely spaced.

The preoperculum is of the usual Palaeoniscid shape, with a narrow vertical posterior part forming the hinder boundary of the maxilla, and a deeper upper part lying above the maxilla. The front border of the preoperculum is excavate for the reception of a suborbital element. The long posterior margin meets the suboperculum, the

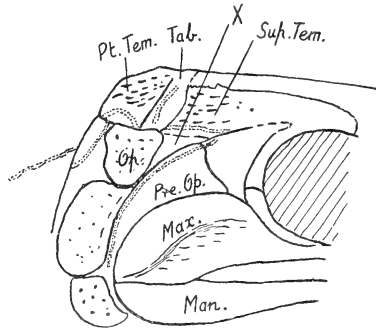
operculum and, superiorly, the supratemporal, and is convex. The bone is pierced, along its posterior border, by the preopercular sensory canal.

The operculum is a relatively small, somewhat triangular, plate, with a rounded ventral apex and a dorsal width nearly equal to its height. The upper anterior corner is of uncertain shape, but it is apparently separated from the preopercular by a small triangular ventral prolongation of the supratemporal, which may be a separate element corresponding to Traquair's bone X.

The suboperculum is larger than the operculum, and is higher than wide. Its anterior border is concave, its posterior and lower borders convex. The upper border is slightly excavate, so that there is a loose junction between the bone and the operculum. The upper anterior corner is acute-angled.

Ventrally to the suboperculum is a smaller reniform bone which probably belongs to the opercular series, and is here interpreted as an interoperculum. It lies behind the hinder end of the mandible, and has the same internal surface ornamentation of small circular pits as the suboperculum and operculum. The branchiostegal rays undoubtedly passed forward from the lower border of this bone; but no specimen shows them in contact with the bone, although their presence is confirmed by one fragmentary example which is seen in ventral view and which presents, on either side of a median triangular bony mass, a series of four or five overlapping branchiostegal plates lying mesial to the mandible.

In his recent paper on "Fossil Fishes from the Karroo System," Brough (P.Z.S., 1931, p. 234) figures the bone which is here described as an interoperculum, but describes it as probably the modified first branchiostegal ray, stating that it "does not correspond to the interoperculum." He also asserts the absence of branchiostegal rays in some Catopterygoid genera, and thinks that they may be absent in all. The specimens from Northern Rhodesia described here as one species usually show no trace of such rays; and their presence is only confirmed by one fragmentary example which is, fortunately, seen in ventral view.



TEXT-FIG. 2.—*Ischnolepis bancrofti*, Htn.
Restoration of posterior part of
skull, lateral view.

The ornamentation of the opercular bones on the external surface presumably consisted of small, rather scattered, low tubercles.

The limits of the membrane bones of the cranial roof are difficult to decipher exactly, but they can be drawn approximately from the positions of the sensory canals that penetrate them, which are preserved as raised tubes on the inner face of the skull.

Above the preopercular the lateral canal runs longitudinally through the supratemporal, which has apparently a ventral triangular portion wedged in between the opercular and preopercular. The supratemporal ("supratemporo-intertemporal" of Stensiö) has a somewhat digitated suture with the parietal and a straight suture with the tabular ("extrascapular" of Stensiö), which lies behind it. This latter carries the transverse tabular canal. The lateral canal cannot be traced in the tabular, which is a short broad bone; but its curved course through the presumed post-temporal ("suprascapular" of Stensiö) can be followed, and its continuation through the upper posterior corner of the supracleithrum to the lateral line of the body.

The shoulder-girdle is not fully displayed in any one specimen, but the cleithral and supracleithral are typically Palaeoniscid. The former is a bent pillar-like bone ornamented with longitudinal ridges; the supracleithral is an expanded plate with a strengthened anterior border. In front of the ventral prolongation of the cleithral, and partly enwrapping it, is a long, pointed triangular clavicle which, in one specimen, seems to be fused with its neighbour in the middle line.

The pectoral fin is small and low down on the body. The fin-rays, which are possibly about 15 in number, are forked distally, and seem to be unjointed throughout their length. There are well-developed small fulcra.

The pelvic fin is considerably larger than the pectoral, with about 20 rays, and is in front of the middle of the body. The rays are articulated near their bases, but apparently not distally. The rays are forked distally, and fulcra are present.

The anal fin has a long base, and in the anterior part is relatively high. The rays number about 50, but the baseosteos are less than half this in number. The rays are forked and, at least in the anterior half of the fin, articulated.

The base of the dorsal fin is about half the length of that of the anal, and the number of fin-rays is about 20. In front of the fin there are a few enlarged pointed dorsal ridge-scales, and prominent fulcra are

developed. The front of the fin is opposite the front of the anal. The fin-rays are forked distally, and articulated throughout their length. The baseoste number only about half the fin-rays.

The caudal fin is deep and fairly deeply cleft, with the lobes about equal to one another and not excessively elongated. The body lobe is fairly long and somewhat bluntly pointed. All the rays of the fin are articulated and branched. At the base of the upper lobe are a number of elongated dorsal ridge-scales, and the anterior border of each lobe is furnished with fulcra.

A typical fish has an estimated length of 75 mm., a greatest depth of body (at pelvic fin) of 16.5 mm., and the length of base of anal fin 17 mm. The body has about 50 transverse rows of scales, which are small and very thin, and are apparently ornamented with two or three irregular longitudinal ridges. The lateral line of the body is enclosed in small tubular bones lying in a continuous longitudinal row, and continues backwards to the base of the caudal fin opposite to the point of bifurcation.

This fish, while bearing some resemblance to the Upper Beaufort genus *Helichthys*, does not seem to fall within the limits of any of the hitherto described Catopterid genera. The combination of characters presented by the head, body, fins, and scales—the small size, the smallness of the scales, the relative positions of the dorsal and long-based anal fins, and the probable presence of a well-defined interoperculum—give it a very distinctive appearance; one or more of these characters can be paralleled in one or another of the genera which have an oblique mandibular suspensorium, but they are not all found in combination in any of the known forms. The description of *Urolepis* given by de Alessandri almost fits the specimens under discussion; but his photographs of typical examples of that genus display distinct points of difference. It thus becomes necessary to found a new genus for these fishes, which can be known as *Ischnolepis bancrofti* gen. et sp. nov., the tribal name being given in honour of Dr. J. Bancroft, to whom the opportunity of studying these specimens is due. For the accompanying drawing of one of the co-types I am indebted to Dr. K. H. Barnard.

Pygopterus (?) sp.

A broken slab and partial counterslab display part of the body of a small-scaled fish in which the axial skeleton is well seen. Although the anal fin is not preserved and only a portion of the dorsal fin

remains, the latter was certainly small compared with the anal and did not arise in front of it.

Above the notochord there is a series of neural arches which diminish in height posteriorly, and whose height in the middle of the specimen is slightly less than the diameter of the notochord. The head of each arch is slightly dilated, and the arches are inclined backwards at about 45° to the axis of the notochord. Above each arch is an elongate slender neural spine whose proximal end only is dilated. The dorsal fin is supported by two rows of interspinous bodies, 12 or 13 in each row. Of these the axonosts are longer than the baseosts; both sets are more elongate than in "*Oxygnathus browni*". Both sets are slender, hour-glass shaped bones, and the length diminishes rapidly in the posterior half. The lepidotrichia of the dorsal fin are far more numerous than these endoskeletal radials.

Haemal arches occur from front to back of the specimen. They are longer than the neural arches, considerably swollen proximally, and only very slightly expanded distally. Each articulates with a long slender haemal spine. The anal fin is supported by a number of elongate endoskeletal radials arranged in a single row, each of which is dilated distally.

The relative sizes of the endoskeletal elements in this fragment are sufficient to differentiate the form from *Oxygnathus browni*, to which it approximates in size. The body scales were obviously small and thin; and the position of the dorsal fin with respect to the anal renders it possible that the fragment falls within the limits of *Pygopterus*.

This description is based on specimen No. 9340 in collection South African Museum, from the lower part of the Lunsempfwa Valley, N. Rhodesia. The slab and counter-slab were collected by Dr. Davis from the beds that yielded *Ischnolepis bancrofti*, and were presented by Dr. J. A. Bancroft.

Cf. *Atherstonia* sp.

(Pls. XXX, XXXI.)

Three specimens, obtained by Dr. Davis from the beds which yielded *Ischnolepis bancrofti* in the lower part of the Lunsempfwa Valley, North Rhodesia, give evidence of the presence of a large Palaeoniscid fish, although they are not complete enough to be generically identifiable. Each will be briefly described.

Specimen 9351 (in coll. S. Afr. Mus.).

Contains part of the head and pectoral fin. Operculum high and narrow, ornamented with irregular, closely set ridges and elongate

tubercles. Suboperculum very much smaller, subpentagonal in shape, as wide as high, ornamented with a central mass of rounded tubercles surrounded by irregularly curving ridges and elongate tubercles.

Branchiostegal rays numerous—23 being preserved ; rays much wider than high.

Pre-operculum long and well developed, situated very obliquely. Bone slightly bent, rodlike posteriorly and expanded anteriorly.

Maxilla large, presumably Palaeoniscid in form.

Dentition (seen on mandible only) consists of stout conical teeth of two sizes, larger and smaller, rather widely spaced.

Pectoral fin incomplete; large, consisting of about 21 rays, of which most show dichotomous forking; fulcra numerous, but small; articulation doubtfully present in anterior rays.

Specimen 9350 (in coll. S. Afr. Mus.).

Slab and partial counter-slab, showing most of the body, lacking the tail and dorsal fin, together with the badly preserved posterior part of the head, and the pelvic and anal fins. Tentatively, it is considered to belong to the same species as the foregoing, although it is rather smaller. Body fusiform. Depth of body about half the length from posterior edge of clavicle to root of tail. Scales rather small with non-denticulated posterior borders, and ornamented with irregular, rather weak, forked, and anastomosing ridges. Continuous series of dorsal ridge-scales.

Pelvic fin rather closer to anal than to pectoral; rays nearly 30 in number, articulated, distally bifurcated; anterior rays longer than fin-base.

Anal fin long-based; rays numerous, articulated.

Position of dorsal fin not exactly determinable, but probably opposite to, or slightly in advance of, anal. It is certainly not behind the anal.

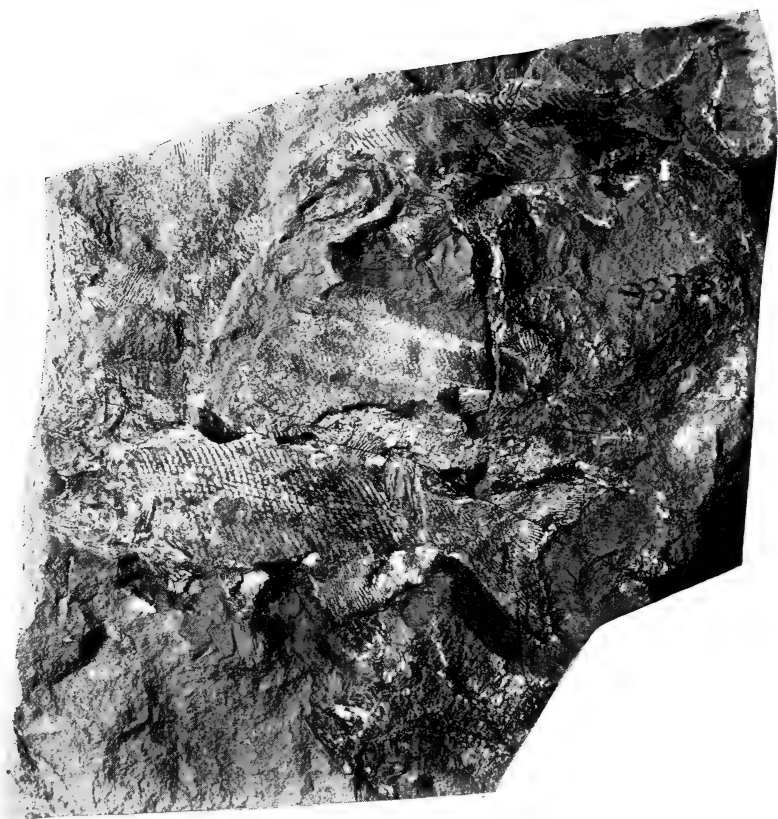
Specimen 9353 (in coll. S. Afr. Mus.).

The greater part of a tail, which probably belongs to this species. Tail strong and forked, upper and lower lobes about equal. Rays strong, jointed throughout their length, dichotomously forked. Dorsal lobe has ridge-scales of medium strength; ventral lobe has rather small fulcra. There are shown five strong haemal spines forming a support for the anterior part of the ventral lobe. The body squamation extends for a considerable distance up the dorsal lobe, and ends in a sharp point.

On account of the uncertainty concerning the position of the dorsal fin, it is not clear whether these specimens belong to that

group of the Palaeoniscidae that contains the genera *Acrolepis*, *Gyrolepis*, *Atherstonia*, *Myriolepis*, and *Oxygnathus*, or to that containing *Pygopterus* and *Urolepis*. It differs from *Acrolepis* in the length of base of the anal fin and in the size of the scales. It agrees with *Gyrolepis*, particularly in the relative narrowness and depth of the operculum and in the nature of the fins; it is larger than most of the described species of that genus, and its scales are smaller and not so deeply overlapping. The dorsal ridge-scales are not so pronounced as in *Atherstonia*, and the body-scales are smaller; the ornamentation on the scales is somewhat similar. *Myriolepis* differs in the possession of smaller scales and in having a short-based anal fin. In *Oxygnathus*, too, the scales are smaller and the body is more elongate.

The generic position of this form is thus rather doubtful. Of those cited, *Acrolepis*, *Atherstonia*, and "*Oxygnathus*" (Broom) are known from deposits in South Africa and Madagascar; and it would seem best temporarily to designate the forms under consideration simply as Cf. *Atherstonia* sp., recognising that there are certain points of difference that mark them off specifically at least from other members of the genus.



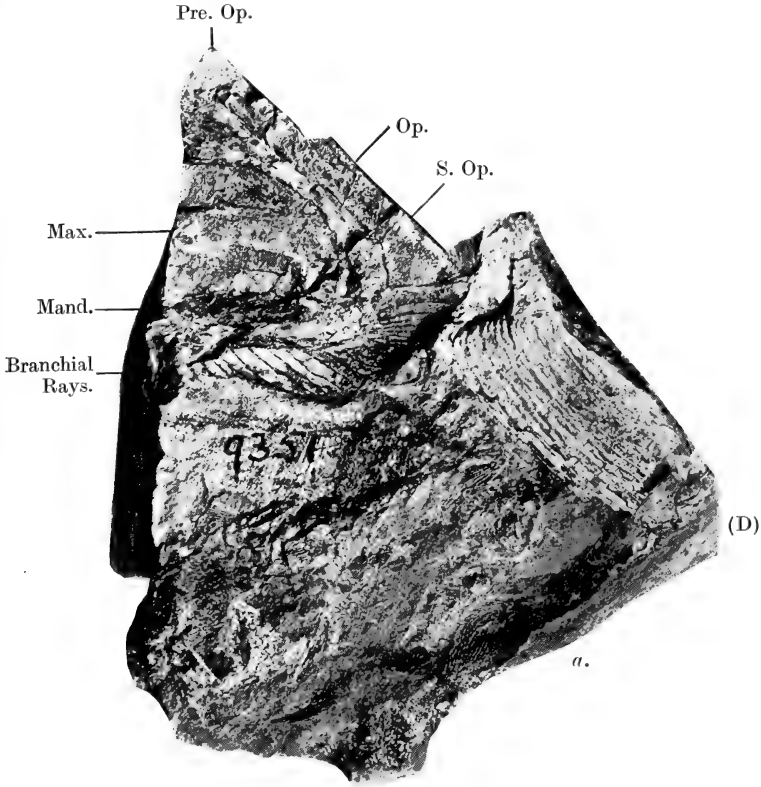
ISCHNOLEPIS BANCROFTI Gen. et Sp. N.

Co-types: Two fish on Slab 9338.

(C)



Cf. *ATHERSTONIA* Sp.
Partial fish, Slab 9350.



Cf. *ATHERSTONIA* Sp.

a. Slab 9351.

b. Slab 9353.

Neill & Co., Ltd.

4. *The Phosphatic Nodules of the Agulhas Bank.* (A Study of Submarine Geology.)—By L. CAYEUX, Membre de l'Institut, Professor at the Collège de France, Paris.

(Translated into English by Dr. S. H. HAUGHTON.)

(With Plates XXXII–XXXV.)

THE cruise of the *Challenger* was responsible for the discovery of phosphate of lime among the marine sediments which are accumulating in our day. According to J. Murray, A. F. Renard,* and L. W. Collet, † the *Challenger* dredged nodules of phosphate of lime on the Agulhas Bank, south of the Cape of Good Hope, on the eastern sides of Japan and of Australia, on the coasts of the Argentine Republic, between the Falkland Isles and the estuary of the Plata, to the west of Chile, and on the coast of Spain. Further, phosphatic nodules have been recovered by the *Blake* ‡ at numerous points on the coast of the United States between Florida Strait and Cape Hatteras, and in the North Pacific. Finally, the German cruises of the *Gazelle* and of the *Valdivia*, § not to mention the important researches of the Department of Agriculture of the Cape, have dredged much phosphatic material on the Agulhas Bank, previously explored by the *Challenger*. In our present state of knowledge it can be said that the three great meridional oceans have each yielded phosphatic concretions.

J. Murray and A. F. Renard (1891) and, above all, L. W. Collet (1905 and 1908) have given detailed descriptions of the nodules

* J. Murray and A. F. Renard, "Deep-Sea Deposits" (Report of the Scientific Results of the exploring Voyage of H.M.S. *Challenger*), 1891, Phosphatic Concretions, pp. 391–400, pl. xx.

† L. W. Collet, "Les concrétions phosphatées de l'Agulhas-Bank," Proc. Roy. Soc. Edin., vol. xxv, 1905, pp. 862–893; "Les dépôts marins, 1908," Les concrétions phosphatées, pp. 194–213.

‡ J. Murray, "Report on the Specimens of Bottom Deposits (Cruise of the *Blake* in the Atlantic, 1877–80)," Bull. Mus. Comp. Zoology, vol. xii, 1885–86, pp. 37–61; A. Agassiz, Three Cruises of the *Blake*, vol. i, 1888, pp. 275–276, and vol. ii, 1888, pp. 281–282.

§ Sir John Murray and Professor E. Philippi, Die Grundproben der Deutschen Tiefsee-Expedition, 1898–99, Bd. xx, 1908, pp. 181–187, pl. xxii.

recovered from the Agulhas Bank. Then Sir John Murray and Professor E. Philippi have devoted several pages to the concretions obtained by the *Valdivia* (1908). J. Murray had previously initiated these studies by a brief description (1885-86) of the phosphatic concretions dredged by the *Blake* on the coasts of South America.

Although, however, phosphatic concretions have been dredged at a number of places, it would seem that, up to the present, but one true deposit has been discovered—that of the Agulhas Bank. To this reason for giving to the subject particular attention I add another—the very great interest which it presents from the theoretical standpoint.

Thanks to the happy intervention of Dr. A. W. Rogers, formerly Director of the Geological Survey of the Union of South Africa, and to the kindness of Dr. E. L. Gill, Director of the South African Museum, to whom I express my acknowledgments, I have had the good fortune to study some specimens of phosphatic nodules dredged, many years ago, by the Cape Government, under the direction of the late Dr. Gilchrist. The material examined came from nine different stations, ranging from 48 fathoms (88 m.) to 56·0 fathoms (1024 m.). A table of stations is given here.*

No. of Sample.	Bearings of Station.	Distance from Coast.	Depth.
1	Lion's Head, S. 82° E.	27 miles = 43·2 Km.	125 fathoms; 229 m.
2	„ N. 63° E.	34 „ = 54·4 „	154 „ 282 „
3	Vasco da Gama Peak, N. 71° E.	18 „ = 28·8 „	230 „ 421 „
4	Hang Berg, N. $\frac{3}{4}$ E.	29 „ = 46·4 „	48 „ 88 „
5	Cape St. Blaize, N. \times E. $\frac{3}{4}$ E.	73 „ = 116·8 „	105 „ 192 „
6	Cape Point, N. 44° E.	38 „ = 60·8 „	315-400 „ 576-731 m.
7	„ N.E. $\frac{3}{4}$ N.	39 „ = 62·4 „	560 „ 1024 „
8	„ N.E. \times E. $\frac{3}{4}$ E.	28 „ = 44·8 „	300 „ 549 „
9	Lat. 36° 34' S., long. 21° 32' E.	..	240 „ 439 „
10	Off Vasco da Gama (specimen from L. W. Collet, P.F. Stat. XI).	25 „	166 „ 304 „

Note.—Lion's Head is a part of Table Mountain, Cape. Vasco da Gama is a headland near Cape Point. Hang Berg is found at Cape Hangklip, on the E. coast of False Bay.

To this material is added a nodule of great interest, dredged from a depth of 166 fathoms (304 metres) at station 10 (Vasco da Gama), which has been given me by Mr. L. W. Collet (see Map).

* The map (Pl. XXXII) indicates the points of origin of my samples, numbered 1 to 9. From my examination, I conclude that all the stations, except 4 and 5, are situated on the slopes S.W. of the Agulhas Bank.

The nodules recovered by the *Challenger* came from two very distinct regions. One group was obtained at 98 fathoms (179 m.) and at 150 fathoms (274 m.) on the edge of the Agulhas Bank; the other at 1900 fathoms (3475 m.), and thus in very deep water, nearly 100 miles S.E. of that Bank.

Those which were sent to the *Challenger* office by Dr. J. D. F. Gilchrist, and studied by L. W. Collet, were taken from depths varying from 80 fathoms (146 m.) to 800 fathoms (1460 m.).

External Characters of Nodules.—The specimens furnished by the Agulhas Bank and its neighbourhood have a striking morphology, seldom comparable with that of the pebbles of our Albian green-sands. Of a form extremely variable in detail, generally rounded but occasionally very angular (Pl. XXXIII, figs. 1–3), the nodules are irregular, mammiliform, ornamented with protuberances, even deeply indented, and—according to L. W. Collet—perforated by numerous holes. Certain of my specimens show a tubercular and scoriaceous appearance. One of them, cut through the middle, shows irregular funnel-shaped cavities reaching to the centre, and representing from a quarter to a third of the total volume.

Representative in an unknown measure of the deposit, these nodules are divisible into two categories. The majority are characterised by an irregular form, and have a colour varying from a blackish-grey to pure black: the others are angular and brownish-yellow in tint. The former are dull, and the latter have a polished and varnished appearance, remarkably pronounced. In other words, the one group resembles concretions, while the other gives the idea of *remanié* rock fragments. These latter, which have on a single face cavities measuring 2 cm. in diameter and 1 cm. in depth, show further, on the same side, tiny perforations resembling cupules, 2 mm. broad, filled with glauconite. These differences of facies do not appear to me at all a function of the bathymetric conditions of the surroundings whence the nodules have been dredged. In this regard, it should be noted that the lightest colours (brownish-yellow) are found at depths of 105 fathoms (192 m.) and of 230 fathoms (421 m.), while the blackish nodules have been dredged from 154 fathoms (281 m.) to 400 fathoms (731 m.) As to the scoriaceous pebbles, I can only say that the most typical of my specimens from this point of view came from the greatest depth, 560 fathoms (1024 m.).

Many nodules carry incrustations of an organic nature, already recorded by L. W. Collet, who has identified corals, bryozoans, worms,

alcyonaria, sponges, and foraminifera with this interesting fact—which I have not been able to observe—that the incrustations can determine the positions of the concretions on the sea-floor and their degree of burial. One part, black and shiny, corresponds to the portion embedded in the sediment, and another—grey—to the incrustations defining the upper zone protruding from the mud. The incrustations visible on my samples, mostly due to bryozoa, are seen sometimes over the whole surface—proof that the nodules have been rolled in every direction—and sometimes over a part only. Several lack incrustations.

According to J. Murray and A. F. Renard, the dimensions of the concretions vary mostly from 1 to 3 cm., and exceptionally reach 4–6 cm. L. W. Collet states that they generally lie between 5 and 10 cm. The largest, dredged from 111 fathoms (304 m.) at 25 km. from the coast (St. 10, Vasco da Gama), measures $23 \times 16 \times 12$ cm. The largest of my specimens does not exceed 7.5 cm. in greatest diameter.

From the descriptions and figures given by L. W. Collet, Sir John Murray and Prof. E. Philippi, it is concluded that the nodules are either isolated or cemented to form a true conglomerate. As far as I can judge from the few indications furnished by the gangue of the nodules, it is formed of greensand more or less consolidated. The latter authors have figured a curious grouping of perforated nodules.*

It must be noted here that, whatever their shape, the nodules have acquired the consistency shown by the hardest pebble of the Albian of the Paris Basin.

Chemical Composition of Nodules.—J. Murray and A. F. Renard have published the following analysis of concretions dredged at Station 142, at 150 fathoms (274 m.), on the edge of the Agulhas Bank:—†

P ₂ O ₅	19.96	per cent.
CO ₂	12.05	"
SO ₃	1.37	"
SiO ₂	1.36	"
CaO	39.41	"
MgO	0.67	"
Fe ₂ O ₃	2.54	"
Al ₂ O ₃	1.19	"
Loss ‡	"
Insoluble residue	17.34	"
						95.89	"
Phosphate of lime	43.57	"

* Sir John Murray and Professor E. Philippi, *op. cit.*, pl. xxii, fig. 1.

† J. Murray and A. F. Renard, *op. cit.*, pp. 392–393.

‡ Not estimated owing to an accident.

An analysis of a nodule dredged by the *Valdivia* * gave:

SiO ₂	26.70 per cent.
Ca ₃ (PO ₄) ₂	36.37 „
CaCO ₃	10.53 „
CaSO ₄	11.26 „
MgCO ₃	4.67 „
Fe ₂ O ₃	5.34 „
Al ₂ O ₃	7.51 „
					<hr/>
					102.38 „

Two analyses of yellow nodules, made by L. W. Collet, showed respectively 37.79 and 46.69 per cent. of phosphate of lime, and 21.09 and 23.70 per cent. of Fe₂O₃. Two other specimens studied by the same author, taken from one and the same station, yielded 48.70 and 52.05 per cent. phosphate of lime.†

Three specimens which I have analysed, without estimating all the elements present,‡ are characterised by the following compositions:—

	(7).	(8).	(10).
SiO ₂	17.20	21.90	13.60
Al ₂ O ₃	3.00	3.00	2.10
Fe ₂ O ₃	6.25	6.25	6.30
CaO	37.20	31.70	38.40
MgO	1.16	1.80	1.44
P ₂ O ₅	19.36	18.47	18.60
Fl	1.19	0.97	1.35
Cl	0.25	0.24	0.32
CO ₂	8.14	4.20	7.93
H ₂ O	5.75	7.20	6.50
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	99.50	95.73	96.54

(7) Dredged at 560 fathoms (1024 m.), Cape Point.

(8) Dredged at 300 fathoms (549 m.), Cape Point.

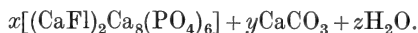
(10) Dredged at 166 fathoms (304 m.), Vasco da Gama.

* Sir J. Murray and Professor Philippi, *op. cit.*, p. 185.

† L. W. Collet, "Les concrétions phosphatées de l'Agulhas Bank," Proc. Roy. Soc. Edin., vol. xxv, 1905, pp. 868 and 870.

‡ In particular, the alkalis ought to figure in a higher proportion in the complete analyses of the nodules from Stations 8 and 10, on account of the frequency of occurrence of glauconite.

The composition of these three nodules leads to the conclusion that the phosphate of lime is a *fluocolophanite*, a mineral to which A. Lacroix attributes a formula susceptible of variation : *



From this composition it can be inferred that, from the chemical point of view, the nodules of the Agulhas Bank are allied to the group of phosphates of the ancient sedimentary series.

These analyses show a remarkable similarity of content of phosphate of lime to those of J. Murray and A. F. Renard, and of Sir John Murray and E. Philippi. The figures of L. W. Collet (values of 46.69, 48.70, and 52.05 per cent. of phosphate of lime), whilst sensibly higher, do not invalidate the conclusion to be drawn from the other analyses, that the nodules of the Agulhas Bank fall within the category of *poor phosphates*.

I would note, without stressing the point, that the figures of phosphoric acid content are of the same order as those of the Albian greensands of the Paris Basin.

MICROGRAPHIC STUDY.

J. Murray and A. F. Renard have described and figured two types of concretions: (1) those found in the greensands of Station 142 of the *Challenger*, dredged at 150 fathoms (274 m.), compounded into aggregates, formed of minerals in the maximum proportion of 2/3, comprising glauconite, quartz, and "silicates," cemented by phosphate of lime, with organisms absent; † (2) those found in the Globigerina ooze, and found at a depth of 1900 fathoms (3475 m.) (Station 143), containing a preponderance of Foraminifera.‡ The occurrence of the latter being independent of the Agulhas Bank, I leave them provisionally aside, but not without remarking on the extraordinary bathymetric dispersion of the nodules in question.

I define here briefly six varieties of nodules, and afterwards shall consider them together.

(1) *Calcareo-phosphatic nodules, very quartzitic*. [No. 1, 125 fathoms (229 m.), Lion's Head, and No. 8, 300 fathoms (549 m.), Cape Point (Pl. XXXIV, fig. 1).]—Blackish nodules, the richest in detrital matter of the whole series. Very uniform in size and scarcely ever exceeding

* A. Lacroix; *Minéralogie de la France*, t. iv, 1890, p. 561.

† J. Murray and A. F. Renard, *op. cit.*, pl. xx, fig. 1.

‡ J. Murray and A. F. Renard, *op. cit.*, pl. xx, figs. 2-4.

0.05 mm. in diameter (No. 8); the quartz grains (*q*) are unequally scattered in the restricted space of a section, of which they form a third, a half, or even more. On the average, they represent less than 50 per cent. of the deposit. Contrary to the state of things in the nodules of the greensand, described by J. Murray and A. F. Renard, glauconite (*g*) may be rare, although one may count several dozen small grains in a preparation (No. 8). In the other nodules (No. 1), the mineral is thinly scattered. The fauna is characterised by the presence of some Globigerinae. The gangue is sparingly developed, and is calcareo-phosphatic.

As can be seen, the rock is far from being a typical greensand.

(2) *Phosphatic or calcareo-phosphatic nodules, very glauconitic, with Globigerinae.* [No. 4, 48 fathoms (88 m.), Hang Berg; No. 3, 230 fathoms (421 m.); and No. 7, 560 fathoms (1024 m.), Cape Point.]—The nodules from Stations 4 and 7, blackish and encrusted with glauconite, show indentations filled with this mineral.

The grains of quartz and of glauconite alternate, but the glauconite has the greater relative volume. In the specimens examined, the quartz forms grains of variable diameter, seldom greater than 0.13 mm., or elements whose diameter is always less than 0.10 mm. The glauconite is distributed in a most irregular manner, being totally absent sometimes, and at others forming by itself the greater part of the pebble. The Globigerinae are widely distributed, so much so that there is very little cement.

Between this type of nodule and the preceding the differences are purely quantitative, and they are linked by transitional varieties.

(3) *Calcareo-phosphatic nodules with Bryozoa and Pulvinulinae.* [No. 9, 240 fathoms (439 m.), S. of Agulhas Bank.]—Nodules of very deep colour, in which the quartz, represented by grains measuring at the most 0.06 mm.–0.07 mm., is noticeably less. Glauconite is, on the average, less widely distributed or rare. Numerous very fragmentary remains of Bryozoa appear, of which at least a dozen can be counted in a section. The Globigerinae are considerably reduced in number, a reduction which is only partly compensated by a very marked increase in Pulvinulinae, which are generally characterised by a very thick test. The amount of gangue material is noticeably increased. The appearance is thus very distinct from that of the preceding types.

(4) *Calcareo-phosphatic nodules, quartzitic, and with abundant Globigerinae.* [No. 3, 230 fathoms (421 m.), Vasco da Gama (Pl. XXXIV, fig. 2).]—These nodules differ greatly from the preceding in their

buff-yellow colour. The quartz-grains (*q*) are more numerous, but do not show the same degree of frequency as in the nodules of the first two categories. Fairly variable, the maximum diameter reaches 0.13 mm., while the minimum may be less than 0.05 mm. Glauconite is only an accessory mineral. The principal characteristic of this type is the abundance of Globigerinae and the presence of spicules of calcareous Sponges. Gangue material is very unimportant.

The matrix of the nodules formed in this way is a passage-deposit to the true Globigerina mud.

(5) *Phosphatic and ferruginous nodules with Globigerinae*. [No. 5, 105 fathoms (192 m.), Cape St. Blaize (Pl. XXXIV, fig. 3).]—These nodules have an angular shape and brown colour, are almost free of quartz (0.05 mm.–0.10 mm.), very poor in glauconite, and particularly rich in Globigerinae. Their cement, which is both phosphatic and ferruginous, has preserved the organisms in an exceptionally beautiful manner. Numbers of these are riddled with perforations filled with oxide of iron. This type of nodule offers most affinity, of all the series examined, with the Globigerina ooze.

(6) *Phosphatic and ferruginous nodules with large benthic Foraminifera and Bryozoa*. [No. 6, 105 fathoms (192 m.), Cape St. Blaize (Pl. XXXIV, fig. 4).]—Although coming from the same station as the foregoing, these nodules have almost nothing in common with them (compare figs. 3 and 4). The organic remains, often so abundant that they touch one another, give to the thin section a very pronouncedly coarse appearance. They consist principally of the remains of benthic Foraminifera with extremely thickened tests, accompanied by accessory pelagic forms, especially Globigerinae, in a very small proportion. There are also fragments of bryozoan colonies and of parts of Echinoderms (plates and spines), both fairly frequent, and some fragments of the shells of Mollusca and of Brachiopoda, to the absolute exclusion of detrital minerals and of glauconite. In this chaotic complex, the pelagic Foraminifera may be arranged in rows. Most of the organisms are riddled with perforations which are filled with phosphate of lime and oxide of iron. Many are incomplete and penetrated by the matrix. Amorphous phosphate of lime and iron peroxide play a very important part both in the fossilisation of the test and in the infilling of the cavities.

To these six categories I add another, very different from the preceding, and constituted of nodules of phosphatic greensand, whose characters will be discussed later (Pl. XXXV, fig. 3).

From the examples thus passed in review, which possibly give an

incomplete idea of the mode of occurrence, it is possible to judge of the variety of phosphate rocks represented in the deposit. These rocks include types obviously terrigenous, such as the *calcareo-phosphatic, very quartzitic, nodules* and also the *phosphatic and ferruginous nodules with Globigerinae*, which resembles pelagic formations. Between these two extremes is ranged a series of intermediate types whose terrigenous characters gradually disappear, step by step. The variety which is characterised by Bryozoa and numerous benthic Foraminifera appears to stand at the border of the complex. I see in it a representative of the numerous bottom deposits of organisms, formed in a terrigenous environment, which never figure in the classification of true marine sediments.

In order to state fully the problem for solution, it is necessary to add that these phosphatic rocks have been dredged from a bottom of *greensand*, and that the specimens which most closely approach a *Globigerina* ooze—although deviating from the normal type by a very small proportion of quartz granules—have been recovered at a depth of only 105 fathoms (192 m.), *i.e.* well outside the actual domain of the *Globigerina* oozes.

As far as I know, no deposit of phosphate of lime in the older sedimentary series contains such a variety of types nor raises a problem of such importance.

ANALYSIS OF THE CONSTITUENTS OF THE NODULES.

The little that we know, up to now, of the constitution of the nodules scarcely allows us to suspect the great interest which is attached to the elucidation of the general history of phosphatic concretions of all ages. Therefore I describe successively all the elements which go to form the nodules, and then discuss the structural details which give an unforeseen picture of the mode of origin.

1. **Minerals.**—From one end to the other of the series analysed, *quartz* shows a great variation in frequency, since the grains may be predominant in the first variety and completely absent in the last. These variations entail only slight changes in the quantity of the elements, without showing a modification in shape. All are angular, with a mean diameter which is always less than 0.10 mm.; hence nearly all the grains would float in water that was only feebly agitated. The angular form of the grains, already noted by J. Murray and A. F. Renard, is a consequence of this. From our point of view, one character of this mineral dominates all the others: *the variations in*

size and in the degree of frequency of the quartz grains are independent of the depth at which the nodules were obtained.

As to the "silicates" mentioned by J. Murray and A. F. Renard, they are undoubtedly related to rather rare felspathic elements, and comprise triclinic feldspars.

Glaucconite.—It must be confessed that the numerous works devoted to this mineral and its history are far from exhausting the subject, as the following data show:—

J. Murray and A. F. Renard have shown, in their description of the Agulhas Bank phosphates, that the glauconite, which has a cryptocrystalline structure like that of the glauconite of older deposits, is present in rounded grains independent of organisms, and as a product of the material filling the interior of numerous Foraminifera, in which it is very common. Their study has been very usefully completed by Messrs. L. W. Collet and G. W. Lee,* who discovered in these same phosphates the variety which I formerly designated † as pigmentary glauconite. Bearing in mind their observations, I shall abstain, as far as possible, from repeating what is already known in this matter.

An analysis by Gümbel ‡ of glauconite from the Agulhas Bank gave the following results:—

SiO ₂	46.90	per cent.
Al ₂ O ₃	4.06	"
Fe ₂ O ₃	27.09	"
FeO	3.60	"
CaO	0.20	"
MgO	0.70	"
K ₂ O	6.16	"
Na ₂ O	1.28	"
H ₂ O	9.25	"
						99.24	"

In preparing for examination nodules from the Agulhas Bank, I have been able to gather new data, some of which concern the glau-

* L. W. Collet, "Les concrétions phosphatées de l'Agulhas-Bank avec une note sur la glauconie qu'elles contiennent par G. W. Lee," *Proc. Roy. Soc. Edin.*, vol. xxv, 1904-1905, pp. 885-893; L. W. Collet and G. W. Lee, "Recherches sur la glauconie," *Proc. Roy. Soc. Edin.*, vol. xxvi, 1906, pp. 266-267.

† L. Cayeux, "Contribution à l'étude micrographique des terrains sédimentaires," *Mém. Soc. Géol. Nord*, t. iv, 2, 1897, pp. 165 and 175.

‡ V. Gümbel, "Ueber die Natur und Bildungsweise des Glaukonits," *Sitz. d. Math. Phys. Clas. d. k. Akad. Wiss., München*, t. xxvi, 1896, p. 545.

conite of the sediments whose age will be discussed later, and others the history of glauconite in general.

(A) Despite the frequent occurrence of glauconite grains on the one hand and of Rhizopods on the other, it has not been possible to find a single glauconite element enclosing a Foraminifer.

(B) The relations between glauconite and Foraminifera give material for interesting observations. In general, the mineral invades all the chambers, but it may avoid one or two, and it is also capable of associating there with phosphate of lime. The chambers once being filled, the glauconitic complex which results either ceases to develop—a state exhibited by absolutely intact shells of Foraminifera filled with glauconite—or the glauconite continues to form. If the latter, then a whole series of results is presented:

(a) Exceptionally the material enters the pores, without any trace of metasomatism.

(b) The glauconite fixes itself in the test, no matter where, in the form of minute globules, free or coalesced, which destroy the microstructure of the shell.

(c) The whole test becomes metasomatised by the glauconite, darker than that of the cells, which admirably preserves the structure, for, curious to state, the pores are not penetrated by it. Globigerinae, fossilised in this manner, yield beautiful tangential sections in the form of a network with very regular mesh, whose distinctness recalls sections of crinoids mineralised by ferruginous compounds.

To these examples of pseudomorphosis of foraminiferal shells by glauconite—which, it must be added, are by no means rare—I add fragments of foraminiferal tests reduced to simple isolated arcs grouped in such a manner that their fragmentation was certainly anterior to their deposition. These too are metasomatised without an infilling of the pores, and yet do not show the slightest impression of glauconite on the matrix. In certain sections, these fragments of shells converted into glauconite are frequent.

This is the first occasion on which I have been able to observe such a disposition to metasomatism on the part of foraminiferal remains without a resultant destruction of their individuality and of their microstructure.

(d) In a variant of this, the whole test is metasomatised and the pores are invaded. Thanks to its darker colour, the surrounding material is perfectly differentiated from that within the shell. As in the preceding case, it is impossible to notice the slightest projection into the matrix, which could lead one to suppose the existence of

a passage between the glauconitic moulds and the grains independent of the Foraminifera.

(e) In a fifth mode of occurrence—which, as in the preceding, involves a substitution of glauconite for carbonate of lime in Rhizopod shells—these appear as moulds, without trace of test. But in many cases there can be seen a thin border, of a very pale yellowish-green colour, which, between crossed nicols, is distinguished by brighter tints than the rest. Actually, there has been metasomatism of the test, and orientation of the glauconite in such a manner as to differentiate it more or less in white light and between crossed nicols.

This example shows that it may be necessary to discriminate casts of Foraminifera which may simulate whole Foraminifera, test included. The absence of such differentiation, which was only observed in a few casts, leads one to assume the existence of elements which originated within the cells of the Foraminifera, and were subsequently extracted from them by a process of mechanical decortication. This is wholly uncertain, and it is possible that the whole question of the interpretation of the glauconitic casts of Foraminifera may be studied anew.

(C) Foraminifera, which are often profusely distributed in the nodules, are not the only organisms more or less altered into glauconite. Leaving aside the Foraminifera, which play the principal rôle in the fixation of the mineral by organisms, we can pass at once to the groups of Brachiopods, Bryozoa, and Mollusca, not pausing at groups which are without interest. In the Bryozoa, glauconite plays a part in the infilling of the chambers; but most of the specimens do not contain it. Some Brachiopod fragments are penetrated by glauconite in the form of irregular globules, which may be free, in groups, or fused together.

(D) Apart from the glauconite grains associated with organic remains, the mineral also acts as a cement. Of this type of occurrence one example only can be cited, which was observed in the most quartzitic nodule of all. In it was found a small stony layer of quartz grains accompanied by feldspars, all bound together by a very pure glauconite which encroached on the neighbouring calcareo-phosphatic cement, both as irregular prolongations and as small completely isolated particles.

Considering the total amount of glauconite of altered appearance, it can be seen that the percentage of this mineral which acts as gangue material reaches a figure that is wholly unknown in the older rocks. Those nodules which are of a brown colour and usually

angular shape possess a brown cement of various shades in which the obvious calcareous islets form but a very small proportion of the whole.

(E) Another variety shows glauconite present in veinlets of very small size, similar to those that have been noted in nodules of Albian age.* It will be seen later that, under certain conditions, glauconite in this form may have a wide distribution.

(F) Not one of the least interesting facts to record is the profoundly altered appearance of glauconite in certain nodules. All things considered, this alteration—real or apparent—falls into two categories which appear to denote two distinct phenomena:

(a) In the midst of a layer rich in grains of very pure glauconite, one may see, *e.g.*, a single and unique grain which is brown at the periphery, or several grains laden with oxide of iron to varying depths, the alteration sometimes reaching the centre and leaving only insignificant traces of the original mineral. Decomposition may affect all, or nearly all, the glauconite grains in a layer, thus freeing oxide of iron which partly remains in place and partly masks the neighbouring cement. The same phenomenon is produced at the expense of glauconite included in the organisms. In both cases, the iron oxide invades the gangue material and produces within it tints of very variable colour, a proof that the decomposition has taken place *in situ*.

(b) This occurrence of glauconite carrying iron oxide, playing the rôle of cement, in angular brown-coloured nodules, is probably connected with another phenomenon. Not a single layer has escaped what appears to be, at first sight, a very characteristic alteration which is developed in varying degree. Some parts, which remain greenish, are partly masked by a little oxide of iron; others have become deep brown, but the colour retains a greenish shade, without the cryptocrystalline structure, so characteristic of the mineral, being destroyed. Gradually the colour turns to dark brown. All this takes place, therefore, as if there were a production, on an unparalleled scale, of glauconite playing the part of cement, followed by a no less general alteration of the mineral, liberating oxide of iron. The phenomenon should be important, since L. W. Collet has found up to 21.09 and 23.70 per cent. of Fe_2O_3 in the yellow nodules.† That is probably an incomplete picture of the sequence of events leading to the present condition of things.

* L. Cayeux, *op. cit.*, p. 181.

† L. W. Collet, *op. cit.*, pp. 869 and 870.

This opinion is founded on the existence in the apparently decomposed glauconitic gangue of grains of absolutely unaltered glauconite. On an hypothesis of one alteration, it is necessary to suppose that glauconite of the second generation is deeply decomposed, whilst that of the first generation, corresponding to the grains, has remained unaltered in all the samples examined. The conclusion, therefore, seems inevitable that the glauconite of the second generation has kept its present nature right from the time of its formation. In other words, for unknown reasons, certain reactions caused the mineral to produce an excess of oxide of iron, and the so-called altered glauconite was in reality, at the time of its formation, nothing but glauconite coloured by oxide of iron.

This question was raised by L. W. Collet, who wrote concerning the yellow nodules of the station Vasco da Gama: "Une idée qui vient naturellement à l'esprit est que cette couleur des nodules jaunes pourrait être due à de l'oxyde de fer provenant d'une décomposition de la glauconie, ou que les conditions n'étant pas satisfaites pour la formation de la glauconie, ou hydrosilicate de fer et de potasse, il se soit formé un hydrate ou un oxyde de fer." * Accepting the fact that a web of typical glauconite is found behind the veil of iron oxide, as is shown by examination between crossed nicols, it appears more logical to admit that the reactions produced glauconite surcharged with peroxide of iron. It is not impossible that this problem likewise affects certain glauconites of the older deposits that appear to have suffered general alteration.

Whatever the solution of this problem may be, the development on a large scale of glauconite as a cement-mineral is certain.

Conclusions.—As will shortly be learned, the details enumerated by no means exhaust all the facies adopted by this mineral in the nodules. However, three salient facts have been ascertained up to the present:

(A) The mineralisation of foraminiferal shells by glauconite is a very rare phenomenon. The specimens analysed here in detail have furnished examples which are incomparably more numerous than those of the sedimentary formations that hitherto have been submitted to micrographic study.

(B) In the light of what the nodules examined have shown, no proof is given that the free grains originate from glauconite primitively englobed in the chambers of Foraminifera. Of the authors who have previously occupied themselves with the problem of glau-

* L. W. Collet, *op. cit.*, pp. 874 and 876.

conite origin, some conclude that all the grains, of whatever kind, have originated in the interiors of organic cavities and, particularly, in foraminiferal chambers. This is, in particular, the opinion of Ehrenberg, W. J. Sollas, Bonney, J. Murray, and A. F. Renard, etc. Others, such as J. Bailey, A. E. Reuss, V. Gümbel, etc., believe in a dual mode of formation.

The hypothesis—often propounded—that the innumerable elements whose shape does not suggest organic origin result from the irregular growth or fusion of casts of Foraminifera receives no support, in spite of the fact that the occurrence yields observations particularly decisive in this respect because of the large number of nodules and of free grains found side by side. No example of a cast passing into an irregular grain has been seen, and no example of an irregular grain enclosing a foraminifer with its chambers obliterated by glauconite. In every case, without exception, the two types of glauconite grains present are entirely independent; my absolute conviction is that, *in this deposit, glauconitic casts remain glauconitic casts, and that grains, whatever their size and form, never originate from them.* Many examples, taken from elsewhere, help to give this conclusion a general application. I add that the development of the epigenic glauconite of the cement and a mode of occurrence on which I shall lay stress later prove, once more, that glauconite can be formed on a large scale independently of organisms.

(C) Incomplete as it is, the preceding study shows the existence of at least two generations of glauconite—one consisting of the free grains and casts of Foraminifera, and the other the epigenetic glauconite of the matrix and the rare veinlets.

2. Organisms.—Beginning with the highest forms, it is necessary only to mention the exceptional presence of splinters of bony tissue, which are usually absent.

To the *Brachiopoda* are assigned a small number of fragments of tests and of entire shells which, on the average, number at the most one example in each section. Both have preserved their structure intact, and the canals may, or may not, be filled with phosphate of lime.

Less rare than the Brachiopods, *Bryozoa*—represented by very fragmentary colonies—do not appear in all the thin sections; their maximum frequency is 20 individuals in one section—a notable proportion, having respect to the size of the débris.

The *Mollusca*, which form the most important group after the

Foraminifera, are chiefly found in the angular brown nodules. There occur some dozens of curved, fragmentary, and usually thin forms with their microstructure preserved.

To the *Echinoids* are assigned some calcareous plates, with a single optical orientation, whose microstructure is almost entirely destroyed, as well as some exceedingly rare spines. All occur in the brown nodules, to the maximum number of a dozen plates in a section.

The very rare *Sponge* spicules observed are calcified. The one example, unique up to the present time, proves that the *solution of siliceous spicules and the replacement by calcite are not necessarily late phenomena posterior to the emersion of the sediments.*

The *Foraminifera*, however, easily surpass the preceding organisms in importance and numbers. Except in the brown nodules with Bryozoa and large benthic Foraminifera, Globigerinae predominate, to the point of forming by themselves the whole Rhizopod fauna. Generally speaking, the Foraminifera are whole and beautifully preserved. With the exception of the brown nodules, rich in bottom-dwelling Foraminifera, the shells, both entire and fragmentary, show no corrosion, and it is impossible to imagine the fragmentation of the Globigerinae otherwise than by mechanical action.

Boring organisms have left profound traces in the brown nodules in the form of numerous irregular tubes filled with phosphate of lime, ferruginous glauconite, or opaque oxide of iron, most of which are probably attributable to sponges. Except for the sponge spicules and the Echinoid remains, all the groups have suffered from their action.

3. Cement.—From the point of view of the constitution of the matrix, the nodules form very dissimilar groups—the brown nodules on the one hand, and the blackish nodules on the other.

(A) By their matrix the latter recall immediately, under the microscope, the phosphatised chalks of the North of France. Although on the average little developed, on account of the profusion of Foraminifera, the cement is generally calcareo-phosphatic, at places phosphatic and calcareous and, very exceptionally, formed of pure phosphate of lime in very restricted areas. In white light, the phosphate of lime is identified by a very pale yellowish tint, which becomes most pronounced as the phosphate content increases and, finally, attains a pale-yellow colour. Under crossed nicols, as a rule the yellowish base becomes charged with very numerous small brilliant and iridescent spots, representing the presence of carbonate of lime,

which are prominent when phosphatisation is feeble but disappear completely in the exceptional layers which are wholly phosphatic. In short, it is necessary to examine but a very limited number of nodules to observe a complete passage from a matrix exclusively calcareous to a cement which is entirely phosphatic. It follows that, on the average, these nodules are rather poor in phosphoric acid.

(B) Actually, the brownish nodules—which differ considerably from the preceding—are far from forming a constant variety. Although limited to two specimens, my studies have shown profound differences between them.

The one which is considered a partly phosphatised *Globigerina* ooze possesses a cement that is essentially glauconitic and more or less haematitised (Pl. XXXIV, fig. 3), enclosing some plates of *Globigerina* mud free from mineralisation, exceptionally converted into mostly crystalline calcite, and others—rather rare—which are on the way to being phosphatised. It is difficult to say if the matrix, which is strongly impregnated with oxide of iron, is not at the same time slightly phosphatised, since the brown base prevents the identification of phosphate of lime.

The cement of those brownish nodules that are rich in large benthic Foraminifera has visible phosphate of lime in preponderance. Sometimes this mineral surrounds uniformly all the perfectly preserved constituents in a yellowish base, which is undifferentiated and full of minute calcareous specks; sometimes it is associated with calcite, which is mostly crystalline, and forms a thin, pure yellow border to all the material which it serves to bind. In this variety the organic remains are corroded and are often almost unrecognisable. It is rather the calcite which actually plays the part of cement.

The same slide shows both these modes of occurrence, to which can be added a third, characterised by a ferruginous matrix (Pl. XXXIV, fig. 4) like that of the preceding specimen, which does not permit one to say that the oxide of iron is intimately associated with glauconite, although this is probable. This ferruginous matrix may also enclose calcite in the form of irregular patches of varying size.

The history of these nodules is thus complicated by a profound alteration of the original constituents of the ooze which have escaped phosphatisation and mineralisation, these constituents having now a crystalline condition comparable with that of the highly recrystallised ancient limestones. There are even true *veinlets of calcite* in the mass, like those found in ancient marbles. These are, it is true, few in

number, and one cannot invoke dynamic alteration to account for them.

Mode of Occurrence of Phosphate of Lime.—At the outset, phosphate of lime plays a double rôle:

(A) It fills the chambers of Foraminifera, the cellular fabric of echinoderm plates, the cells of Bryozoans, etc. Actually, this mode of occurrence is bound up with the following, for the phosphate of lime in the foraminiferal chambers retains traces of calcite which bear witness to epigenetic phenomena. The truth is that, despite appearances, phosphate of lime is not concentrated as such in these spaces.

(B) It is produced on a large scale by alteration of the calcareous matrix of the foraminiferal muds and, on a reduced scale, in the tests of the organisms present.

It follows that, in its two principal modes of occurrence, phosphate of lime is undoubtedly a substitution product.

The phosphate of lime formed at the expense of the cementing material is optically amorphous and lacks any kind of morphological differentiation; it therefore belongs to the group of *colophanite* or, more exactly, of *fluocolophanite*. This is so for all the nodules examined to date. It will be shown later, from a study of aberrant specimens, that a crystalline variety may also occur, but seemingly exceptionally.

Granular phosphate of lime is extremely rare, when it is not completely absent. There are doubtless exceptions to this rule, for J. Murray, examining material dredged by the *Blake*, noted that a concretion, obtained in the Atlantic at Station 317, in lat. 31° 57' S., contained phosphatic grains "similar to the grains found in the phosphate nodules dredged near the Cape of Good Hope and elsewhere by the *Challenger*." *

Finally, the alterations undergone by the parent rocks, converted into poor phosphates, are much less profound than those noted by J. Murray and A. F. Renard in the nodules from the Indian Ocean where, at the same time, are integral substitution, destruction of organic characters, development of zonary structure, and crystallisation of the phosphatic material.†

* J. Murray, "Report on the Specimens of Bottom Deposits," Bull. Mus. Comp. Zool., vol. xii, 1885-86, p. 43.

† J. Murray and A. F. Renard, *op. cit.*, pl. xx, figs. 3 and 4.

ANOMALIES OF COMPOSITION AND STRUCTURE OF NODULES.

Among the nodules of dark colour which arise from quartzitic Globigerina muds are some that are characterised by the presence of inclusions, traces, and incrustations of aberrant constitution, and some by the juxtaposition of two very dissimilar rocks.

1. Nodules with very Glauconitic Inclusions.—(A) Glauconite gives rise to narrow bands with well-defined contours, from which minerals and organisms are absent. These differ from the grains disseminated through the rock by a light brownish colour, indicative of an elimination of peroxide of iron. In this form the mineral presents its true appearance.

This same variety serves as a cement to large grains of glauconite of a normal colour, strikingly different from those that form an integral part of the nodules. Thus it is possible to see well-defined bands formed exclusively of glauconite grains of one shade (*g*), surrounded by a glauconitic matrix of an entirely different shade (Pl. XXXV, fig. 1). Thus there are present two generations of glauconite which have nothing in common, in point of age, with those concerning which question was raised in the study of nodules of normal type. These can, moreover, be seen in a given nodule.

(B) The inclusions are rich in grains of ordinary glauconite, which may form the greater part of them, and often touch one another. Apart from insignificant exceptions, the mineral is very clear, except when it is obscured by the neighbouring plates.

With few exceptions, the inclusions in this category show no trace of Foraminifera or other organisms. Their cement is entirely, or almost entirely, phosphatised and cryptocrystalline, *i.e.* it is a *staffélite*. In general, the phosphate is differentiated as a very clear border round grains of glauconite and of quartz. This differentiation is also observed, but not always, around the islets and bands.

The relations of these inclusions to the neighbouring rock are illustrated by the two following examples:—

In the first, there is a beautifully distinct band of glauconitic phosphate which is bounded on one side by a curved line traversing a large plate without deviation, cutting as with a knife the glauconite grains and phosphatic constituents which it encounters. On the other side, the boundary is irregular and roughened with protuberances and hollows in a manner that is immediately reminiscent of the phenomena of corrosion. Moreover, along this line of separation the

nodule is strongly impregnated with glauconite, just as is frequently found on old hard and corroded floors.

But the relations between these two portions are susceptible of quite another interpretation. The cementing of the two rocks follows, then, a very irregular line, whose limits it is often impossible to fix, and the rocks merge into each other at their junction.

From the study of a number of thin sections it is possible to obtain an idea of the form of this sort of inclusion. They represent, in fact, a product of the partial or complete infilling of cavernous or scoriaceous holes in the nodules. Such of these bands as can be followed throughout their whole development leave the bottom of a hollow in the form of a funnel and penetrate into the heart of the nodules. In short, bands and islets are really the same, and simply represent respectively longitudinal and transverse sections of cavities filled by greensands.

The specimens which favour this type of observation correspond, I believe, to the concretions "*avec fentes remplis d'une substance verdâtre*" which appears to L. W. Collet "*pouvoir être attribuée à de la glauconie.*" *

Nothing is more evident than that this material exhibits an interpenetration of two fundamentally distinct types of rock—an older, not typical, *Globigerina mud* and a true *greensand*, both consolidated. The same contrast exists between the material of the nodules and their mineral incrustations, which do not differ at all from the islets and bands.

Under these conditions it is impossible to escape from the conclusion that *the nodules, formed at the expense of non-typical Globigerina muds, have been removed from the locality in which they were formed and deposited in areas where greensands were being laid down.* From this conclusion is derived another: *In the process, the nodules have been transported from one sediment more pelagic than terrigenous into another plainly terrigenous, and from greater depths to more shallow areas.*

2. Nodule formed of two differing Rocks (Pl. XXXIII, fig. 1, and Pl. XXXV, fig. 2).—Station 10 (Vasco da Gama), situated 25 km. from the coast, has yielded a set of "concretions," among which is the largest known, as well as rolled pebbles of quartzites and schists. In one of the nodules which he has figured, L. W. Collet has clearly distinguished two portions separated by a black line 0.5 mm. thick, one of which is yellowish and characterised by numerous Foraminifera, the other blackish and rich in grains of glauconite.† This nodule, whose

* L. W. Collet, *op. cit.*, p. 867.

† L. W. Collet, *op. cit.*, p. 869 and fig. 3.

greatest diameter is a dozen centimetres, is formed of two distinctly different rocks, joined in such a manner that it would not be correct to say that one serves as a matrix for the other.

On a polished surface (Pl. XXXIII, fig. 1) there can be seen a lower part of clear yellowish colour, darkened above over a width of about 1 cm., and an upper part of very deep tint in which, under the lens, a crowd of little black glauconitic grains can be distinguished.

(A) The yellowish portion (Pl. XXXV, fig. 2, *a*), which was clearly the lower part of the specimen in place and which, according to L. W. Collet, was "formée presque entièrement de coquilles de Foraminifères," must have a variable composition. Actually, sections cut from the same specimen display but a small proportion of *Foraminifera* and, it is interesting to note, an irregular distribution of the organic constituents—a fact which doubtless explains the discrepancies between our observations as to the quantity of *Foraminifera* present. However, as far as I have seen it, the yellowish rock contains a preponderance of fragments of *Bryozoa* and, in addition, *Foraminifera* which are rare or relatively frequent and mostly *Globigerinae*. *Echinoderms* are represented by several plates and one or two echinoid spines, together with a single holothurian spicule. In addition there are some indeterminable fragments. Along certain widespread planes all the organisms are represented by hollow moulds.

The matrix of the rock, which in each section is formed of limestone containing dozens of quartz granules, is more or less penetrated by phosphate of lime and glauconite; it becomes more phosphatic as one approaches the contact of the two rocks. At the point (*b*) and along the suture-line (*c*) it is wholly phosphate and glauconite.

The phosphate of lime, tinted in yellow of differing shades, is clearly cryptocrystalline. In the sections showing the onset of decalcification it is crystalline in the form of short scales bordering the cavities or arranged in very thin zones. Except for a short distance from the line of contact (*c*) carbonate of lime is abundant, even in the most phosphatic portions, in the form of a very large number of small corroded fragments which are identifiable. The phenomenon of epigenesis is clearly marked.

Everywhere glauconite accompanies the phosphate of lime as very scattered grains, and chiefly as pigment. Its partial alteration is concomitant with the yellow coloration of the deposit. The fact that this does not extend to the glauconite of the upper part of the nodule, which is of more recent formation, shows that the decomposition of this mineral dates from far back and that it is of submarine origin.

The dark zone (c), which marks the upper limit of the rock containing Bryozoa and Foraminifera, is characterised not only by the complete disappearance of carbonate of lime, but also by a development of pigmented glauconite on a scale which is unique in my experience. The phosphate of lime and glauconite are intimately associated there. The latter mineral is concentrated in plates, pockets, and bands that are arranged very irregularly. Some clear areas are a kind of discontinuous network formed of anastomosing veinlets, and have no parallel in any known rock. In addition, glauconite metasomatises all the organisms in the zone, such as Foraminifera, Bryozoa, and Echinoderms, showing absolute freshness everywhere. It is here that the most beautiful examples of Foraminifera converted into glauconite can be seen.

The same line of suture (c) can be clearly traced from one end to the other. It is characterised sometimes by a concentration of coloured glauconite whose density may or may not decrease lower down, and sometimes by a concentration of phosphate of lime marked by a particular coloration and transparency. *There is no encroachment of phosphatised limestone beyond this line.* Finally, its shape is marked by a number of irregularities which give it the characteristic shape of a *line of corrosion*.

(B) Beyond this line an entirely different rock appears. This is coarse-grained, crowded with glauconite, much more quartzitic, lacking invertebrate remains, and has a phosphate matrix. The contrast is extremely striking. Here is no trace of pigmentary glauconite or of epigenesis. The mineral forms a crowd of very pure grains of the ordinary type, measuring on the average 1 mm. in diameter, and may preponderate in a good many of the sections (Pl. XXXV, figs. 2 and 3). In all characters this glauconite is identical with that of the incrustations and of the nodules previously described. In addition to the granules which represent quartz in the preceding rock, there are here large grains measuring 0.6 mm. and more (Pl. XXXV, figs. 2 and 3, *q*), of such a kind that, in one and the same section, the diameter of the grains may vary in the ratio of 1 : 30 and even more. This is quite abnormal and necessitates a strongly agitated environment. Organisms are represented only by one or two fragments of bony tissue, with very undulose extinction. The matrix, composed of phosphate of lime which is grey, pale yellow, or deep yellow, is isotropic, or cryptocrystalline, between crossed nicols and nearly always free from fine calcareous inclusions. In its characters this rock might be taken for certain pebbles of the greensands with *Douvilleiceras mammillatum* from the east of the Paris Basin.

It can be noted here that this constitution is a replica of that of the nodules formed exclusively of phosphatised greensand, described with the six types already analysed (p. 112).

This specimen yields good evidence of a great disturbance which has affected the sea-bottom at some time and produced an eroded surface. There are two fundamentally different rocks in contact, one arising from greensands and the other from a bryozoan foraminiferal limestone, two deposits formed in different surroundings. In parenthesis, the term "concretion" does not appear the correct one to designate a rock detached from the junction of two different formations and shaped into a nodule or, more properly, a pebble.

Corrosion of Nodules.—The intrusion of glauconite of the greensands into certain nodules, discussed above, has arisen from true corrosion phenomena which, as a final product, have resulted in the formation of scoriaceous material. The cavities thus created are to-day either empty or have been more or less filled with glauconitic phosphate.

The material at my disposal is of too restricted a nature to elucidate the problem of the corrosion of pebbles. Some nodules have escaped corrosion, but the proportion is unknown; this is the case for those which have been produced from greensand. Some have been affected over their whole surface, resulting in a scoriaceous appearance. Others have been worn on one side only; *e.g.* a brownish, very angular nodule resting on the bottom on a flat face has been corroded and finely perforated on its upper side only. The conclusion is reached that corrosion has affected material that was already detached from the parent rock, *i.e.* the nodules themselves, in which the phenomenon has nothing in common with the grooving shown by one specimen.

It cannot be questioned that all the corrosion is anterior to the penetration of the greensands into the cavities created by it; but it is no less certain that the wearing away was continued after the change in environment which caused the greensands to appear. As witness to this, there is the nodule formed of two distinct rock-types, of which the upper part, characterised by an old phosphatic greensand (Pl. XXXIII, fig. 1), is itself corroded.

At the moment this phenomenon of *submarine corrosion* requires elucidation, especially as to the nature of the environmental conditions that are favourable to it. Possibly an examination of a large number of specimens would throw some light upon it by supplying an answer to one important question—Does a single station provide, at one and the same time, corroded pebbles and pebbles that have escaped corrosion?

Nomenclature of the Phosphatic Material of the Agulhas Bank.—I have purposely refrained from using the term "concretion," since it was first necessary to obtain discriminatory knowledge of the mode of origin of the material. In its general acceptation the term *nodule* does not imply any given mode of origin, while that of *concretion* immediately suggests concentration around one or several points of attraction. Such is the idea that is held—often wrongly—of the mode of formation of flint. Among this material, the only true concretions are the phosphatic greensand nodules. All the rest are referred to a phenomenon of substitution of phosphate of lime for carbonate of lime, a phenomenon which does not obey the same laws as the former and which, moreover, is quite independent of their morphology.

In short, *all the phosphatic materials of the Agulhas Bank, without exception, are nodules, and an unknown fraction of these nodules falls within the category of concretions.*

INTERPRETATION OF THE FACTS, AND CONCLUSIONS.

In describing the material dredged to the south of the Cape of Good Hope which furnished almost the only basis for their study of the mode of formation of phosphatic concretions, J. Murray and A. F. Renard laid emphasis on the important fact that the minerals and organisms of the nodules on the one hand, and of the sediments in which they are included on the other hand, are identical, both in the case of the concretions of the greensands and those of the *Globigerina* mud. This is to say that all the present-day phosphates, and those of South Africa in particular, have been formed *in situ*. In this connection there is no doubt that J. Murray and A. F. Renard studied material, formed in place, that perfectly displayed the characters of the greensands and of the *Globigerina* ooze.

L. W. Collet agreed with their opinion, writing "*Les concrétions phosphatées sont en quelque sorte l'image du fond dans le quel on les trouve.*"* There are certain facts cited by L. W. Collet in his description of the phosphatic concretions of the Agulhas Bank which support this contention. One is the observation that in the concretions "*la quantité de coquilles de Globigérines augmente avec la profondeur de la mer.*"†

It is pertinent here to state that the concretions studied by J. Murray

* L. W. Collet, *Les dépôts marins*, 1908, p. 200.

† L. W. Collet, *Proc. Roy. Soc. Edin.*, vol. xxv, 1905, p. 879.

and A. F. Renard are not the same as the large number of specimens obtained by the Cape Government. Having stated this, it appears to me that a conclusion contrary to that given above is supported by some very convincing evidence and by arguments drawn from the interesting monograph of L. W. Collet on the phosphatic concretions of the Agulhas Bank.

Station 12 (421 m.) of the Agulhas Bank yielded L. W. Collet some nodules rich in Globigerinae, which were frequently whole, and some which "se composent uniquement de grains de glauconie cimentés par le phosphate."* Similarly, Station 7 (146-238 m.)† yielded some very ferruginous nodules of a yellow-brown colour and others "ressemblant extérieurement à de la ponce."‡ The first, according to G. W. Lee, are free from detritic minerals, and the second contain abundant quartz, etc. Lee concludes, logically enough, that "il y a une différence essentielle entre ces deux espèces de concrétions."§

My own observations show that the brownish nodules, dredged at one and the same place, are of very differing characters (p. 112); one type is a consolidated globigerinal mud, the other is formed from a deposit of large benthic Foraminifera with fragments of bryozoan colonies. These two very different rocks cannot have been formed at the same depth.

The existence of cavernous nodules with Globigerinae carrying inclusions from which these tests are excluded, as well as that of the nodule from Station 10 formed of two distinct rock-types, are further evidence on the same lines.

From this assemblage of facts the following conclusions can be drawn:—

(1) All the nodules used in this study and, without doubt, a portion of those studied by L. W. Collet have, at some period of their history, become *remanié*. We shall see later how it is possible to reconcile the presence of nodules formed on the spot with the existence of transported pebbles.

(2) To this idea of *submarine remaniement* can be added another, also formulated for the first time, which concerns the present-day sea-bottom and can be called a *submarine erosion*. The composite nodule, described above, furnishes proof that the bottom of the sea has suffered denudation, and that this erosive action coincided with

* L. W. Collet, *op. cit.*, p. 876.

† This Station 7 is not the same as that given in the table on p. 106.

‡ L. W. Collet, *op. cit.*, p. 877.

§ L. W. Collet, *op. cit.*, p. 878.

a radical change in the nature of the surroundings as well as in that of the sediments. *The phenomena of erosion have acted on the calcareous substratum in the same way as the changes of level of the supra-Cretaceous epoch on the chalky muds of the Paris Basin; hardening of the bottom, impregnation by phosphate and by glauconite, etc., are present in both cases.*

It remains to determine the succession of events that can explain this deposit, a problem that the preceding discussion seems to have obscured, and which necessitates a departure from the domain of facts for a moment.

In my opinion, the problem is essentially dependent on the following important fact: *All the remanié material is derived from deposits that were formed at a greater depth than that at which they were dredged.* This fundamental observation leads to the conclusion that the region in question has been the seat of important bathymetrical changes. Without justifying their opinion, J. Murray and E. Philippi have advanced the idea of an elevation of the sea-floor.* Unless I am in error, *everything points to an uplift of great amplitude, which has raised up limestones of varied types, and even Globigerina oozes.* This change of level, which is to be measured in hundreds of metres, has terminated the deposition of limestones, has inaugurated the formation of greensands, and has induced the phenomena of erosion, of disintegration, transportation, and re-cementation of the material. Phosphatisation enters into this complex of phenomena, of which we find an equivalent in the distant past, always in close connection with the manifestation of great changes. It is, too, from this period that the phenomenon of corrosion, which has shaped a portion of the nodules, dates.

To be more precise, it must be added that the phenomenon is less simple than it appears, for it is complicated both by a delay in movement of the material and by a resumption or continuance of the corrosive action after the change in level, as is shown by the nodule of mixed composition.

Nothing is easier to understand than that this change of level, with its consequences, can explain the *duality of origin* of phosphatic rocks. At the same time as the pre-existing materials have been metasomatised there were formed true concretions at the expense of the greensands that were in course of formation. I shall show later, in examining the more ancient phosphates, that such an association is not unique in the sedimentary series.

Although I believe this to be the true succession of events, it must

* J. Murray and E. Philippi, *op. cit.*, p. 186.

be confessed that it is not wholly clear. One episode of the history in particular remains a puzzle. How did the nodules, or the limestone fragments from which they were formed, become concentrated in one area? This question is all the more important, seeing that rocks formed under differing bathymetric conditions are found to-day gathered together in one place.

Without pretending to give to this problem the answer it deserves, it may be that the solution should be sought in the following direction:—

One finds, on the deep-sea side of the Agulhas Bank, very steep slopes which sink rapidly to depths of 3000 metres and more (see Map, Pl. XXXII). Actually, all the concretions dredged by the *Challenger*, and most of those supplied to L. W. Collet by the Cape Government, came not from the Agulhas Bank proper but from the external slopes. Of the nine stations which supplied the nodules sent to me one only is on the actual Agulhas Bank. It is from this that were obtained the brownish nodules, one of which corresponded to a *Globigerina* mud, and the other to a calcareous clay enclosing numerous benthic Foraminifera and Bryozoa. To clarify the idea even a little, it can be presumed that the different types of limestone from which the phosphatic nodules have been derived outcrop in horizontal beds of the slopes of the plateau which is covered with a mantle of greensands, which is probably very thin. Whatever may be the succession of the deposits it is natural that, following the change of level, an agglomeration will be produced in the talus on the outside of the ridge. Further, it must be supposed that this surface, profoundly eroded during uplift, would enable the dredge to explore different horizons of the complex forming the Agulhas Bank.

Whether this view is acceptable or not, it is indisputable that the *phosphatic nodules of the Agulhas Bank are not dependent on present-day phenomena*, a conclusion contrary to the opinions of J. Murray, A. F. Renard, and L. W. Collet.

Possibly the conclusion, stated thus, is too absolute. It includes all the nodules which do not result from the consolidation of greensands. It applies equally to the nodule formed of two rocks fused together, one of which was derived from phosphatised greensand. Actually, one can show that the nodules formed from metasomatised limestones are not of modern origin, but it is not possible to show this for the concretions that are exclusively built up in consolidated greensands. It is not an objection that the *remaniement* of the fragment detached from the contact of the greensands and the

underlying calcareous beds leads, naturally, to the supposition that those nodules which were produced solely from the greensands date from the same period as the others. If I do not state my conclusions as absolute, it is because I can picture an hypothesis which involves a prolonged period for the genesis of the greensand nodules.

It is not possible to fix the age of the phosphatic materials of the Agulhas Bank from a knowledge of their mode of origin. In this connection it must be recalled that the dredgings have not furnished only phosphatic nodules. L. W. Collet taught that the nodules of the Agulhas Bank are "accompagnés de nombreux restes d'animaux," "consistant en dents de poissons et de squales, os tympaniques de cétacés." * We know also from him that, at a depth of 421 metres (Station Vasco da Gama),† there were dredged, in addition to the concretions, "un grand nombre de fossiles de Lamellibranches et de Brachiopodes, ainsi que des coquilles mortes," and living representatives of several groups "qui témoignent d'une abondance de vie" ‡ in this region. Concerning the fossils, L. W. Collet notes that one finds "tous les modes de passage depuis la coquille morte, blanche, à celle complètement transformée en phosphate de couleur brillante brune." § The same author records the presence of phosphate of lime in the dead shells. Unfortunately, none of the fossils are identifiable.

Now that the problem has been placed on a new basis, the shells ought to furnish material for two interesting observations: (1) If they are corroded, they must date at least from the period of disturbance which determined a radical change in the nature of the sediments. (2) If showing no trace of corrosion, and if they are of the same size and thickness as the living shells or the unfossilised dead ones, then the hypothesis of *remaniement* (derivation) must be discarded, and cannot be used in fixing the age of the deposit.

Sir John Murray and E. Philippi, whose brief account of the phosphates of the Agulhas Bank appeared three years after the publication of L. W. Collet's memoir, wrote: "Es scheint aber sicher zu sein, dass diese Fauna nicht älter als jungtertiär ist . . ." || without furnishing any proof.

The presence of a tooth of *Carcharodon*, probably belonging to the

* L. W. Collet, *Les dépôts marins*, 1908, p. 207.

† This station has furnished nodules rich in Globigerinae, as well as others that are solely composed of grains of glauconite cemented by phosphate of lime.

‡ L. W. Collet, *Proc. Roy. Soc. Edin.*, vol. xxv, 1905, p. 875.

§ L. W. Collet, *ibid.*, p. 876.

|| Sir John Murray and Professor E. Philippi, *op. cit.*, p. 186.

living *C. Rondeletii*, does not settle the question. It is useful to note that Dr. A. W. Rogers, formerly Director of the Geological Survey of the Union, recognised among the material obtained by Dr. Gilchrist a shell of *Aturia* partially enclosed in the phosphate "which," he wrote to me, "reminded me of the *remaniés* fossils in the Cambridge Greensand." This observation would date the deposit in a singular manner, if the hypothesis of derivation (*remaniement*) could be discarded with certainty, for the most recent known forms of *Aturia* appear in the Miocene. But if at least part of the material is derived, then any fixed conclusion is impossible.

Whatever the age of the phosphatic deposits of the Agulhas Bank, it is indisputable that the major phosphatisation which produced them began before the present epoch and after the disturbance which put an end to the deposition of limestones and substituted greensands for them. The change of level is such that it is probably necessary to place it before the Pleistocene period.

The fact, observed by J. W. Collet, that dead shells belonging to living species are encrusted with phosphate of lime does not lead to the conclusion that the phosphatisation has been prolonged until quite recent times. The absence of incrustations of phosphate on living shells rather leads to the supposition that deposition has not continued until now.

Perhaps the problem of the age of the phosphatic nodules could be approached from an entirely different standpoint. Has the change in level shown by these submarine sediments, not far from the coasts, left traces on the dry land? If so, one can foresee the possibility of solving the problem. This aspect of it must be dealt with by those geologists who have such a wide knowledge of that portion of South Africa.

From all that has been learned, it results that *the submarine deposit of the Agulhas Bank constitutes in some way the last phase of an important series of phosphatic deposits which are arranged almost from one end to the other of geologic time.* From this it follows that the deposit in question, that must be considered whenever one seeks to explain the origin of sedimentary phosphates, is far from presenting us with a clear picture of all the factors which play a part in their formation. As far as is known at present, it shows no essential difference from the older phosphatic formations.

It is no exaggeration to say that the preceding study has been unexpectedly fruitful and full of novelty. Apart from the ideas of great changes of level, and of submarine erosion and derivation

which have clearly emerged from it, it has shown the existence of several generations of glauconite and of instructive conditions of fossilisation (calcified Sponge spicules and numerous Foraminifera with glauconitic tests). Moreover, it has made known phenomena, developed in a submarine environment, which ordinarily belong to continental areas, such as decomposition of glauconite, the sometimes widespread crystallisation of carbonate of lime which has escaped phosphatisation, the genesis of true veinlets of calcite, decalcification observed in the composite nodule, and corrosion of numerous nodules. With regard to the problem of genesis, this study has stressed the extreme rarity or absence of microscopic remains of fishes, organisms whose rôle is usually held to be preponderant in the genesis of phosphate nodules. Finally, from the chemical point of view, it has shown the presence of fluorine, and thus created a close connection between the phosphates of the Agulhas Bank and those of earlier times.

Thanks to the material placed at my disposal, this description has assumed the character of a *study of submarine geology* applied, not to an interior sea of reduced depth like the English Channel, but to one of sub-oceanic depths, with both pelagic and terrigenous sediments. From every aspect it is intimately bound up with the geology of emerged formations.

If one separates phosphatic nodules of the Agulhas Bank from those of the present day for the reason that they are older—with the reservation made above in favour of the pebbles that are solely derived from the greensands—the distribution of phosphates of modern origin becomes very restricted. Hitherto, nearly all the evidence of the properties of modern phosphates has been furnished by the nodules of the Agulhas Bank. If these latter are considered as of an earlier origin, all that remains within the category of phosphates of modern origin are the nodules dredged by the *Blake* and the *Challenger* in areas not within the Agulhas Bank; and the conclusions reached for the Agulhas Bank nodules are of such a nature as to suggest doubts as to the true age of the others.

Moreover, the authors who have recorded the existence of phosphatic nodules have scarcely given all the necessary information required. It is impossible to find statements as to their degree of frequency; nor do we know whether we are dealing with petrographic curiosities or with true pebble-beds—a matter of considerable importance. If the former—which is more probable—the existence of a few nodules throws no more light on the genesis of sedimentary

phosphates than does a study of the scattered nodules in the White Chalk of the Paris Basin clarify the problem of the origin of the older phosphates.

Finally, almost nothing is known of the deposits of nodules other than that of the Agulhas Bank. What is known can only justify doubts as to their age. The single nodule, described by J. Murray, which was dredged by the *Blake*,* came from a *hard bottom*, i.e. from unusual conditions of sedimentation. The question arises, Is not this hard bottom evidence of a change of level with all its consequences? That such a question can be asked is enough to show that the value of the nodules dredged by the *Blake* is not known.

Contrary to expectation, the present-day formations throw but little light on the vast problem of the genesis of sedimentary phosphates. To find a solution it is necessary to pin our faith on the past.

* J. Murray, *Three Cruises of the Blake*, vol. i, 1888, p. 276, fig. 189.

EXPLANATION OF PLATES.

PLATE XXXII.

Map of Agulhas Bank area.

PLATE XXXIII.

Morphology of nodules, nat. size.

- Fig. 1. Rounded nodule, formed by two different rocks (see Pl. XXXV, fig. 2).
 Fig. 2. Scoriaceous nodule, Stat. 7, Cape Point, 560 fath. (1024 m.).
 Fig. 3. Very irregular nodule, Stat. 6, Cape Point, 315-400 fath. (576-732 m.).

PLATE XXXIV.

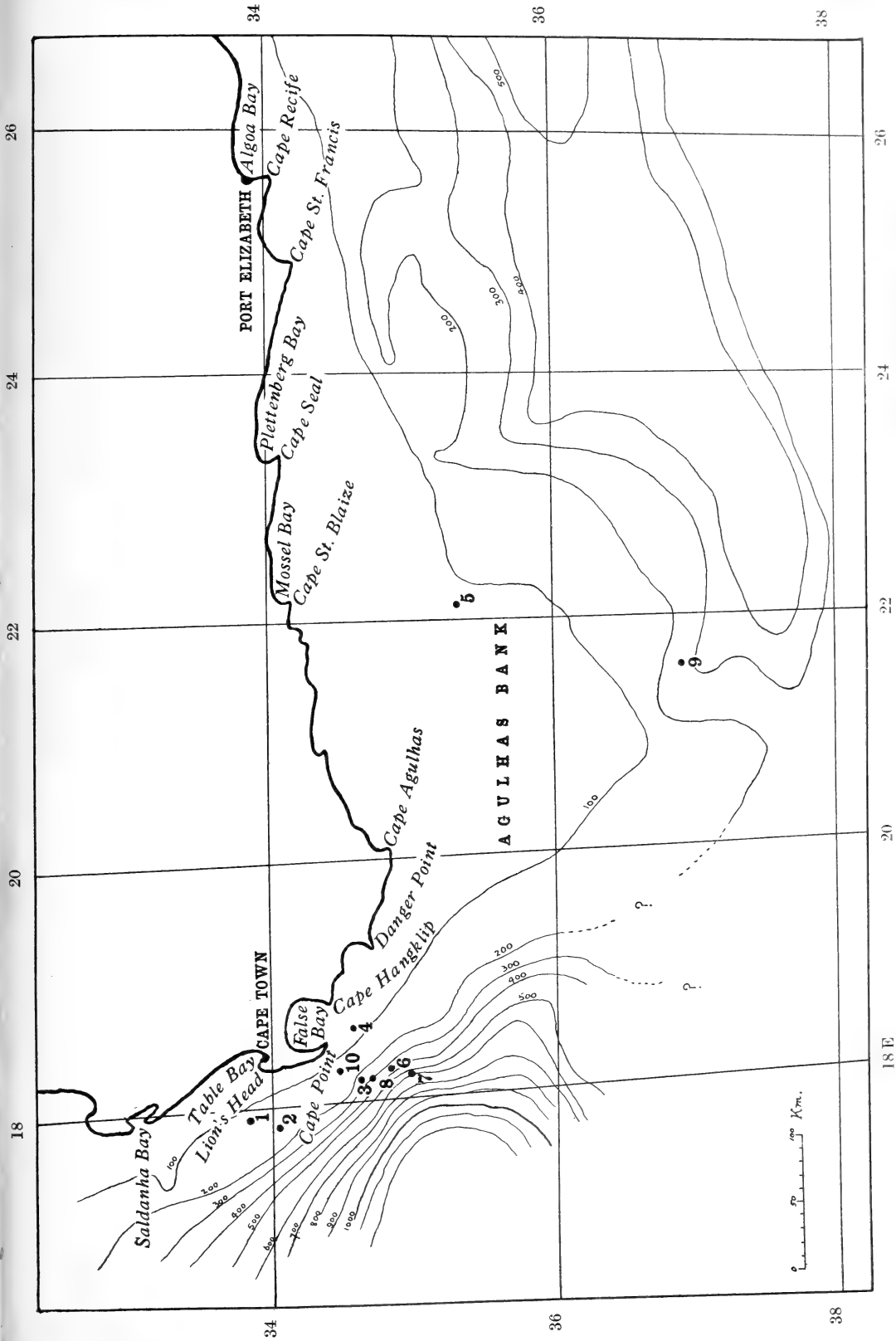
Thin sections of nodules.

- Fig. 1. Calc-phosphate nodule, very quartzitic. Stat. 8, Cape Point, 300 fath. (549 m.). *q*, quartz; *g*, glauconite. ($\times 50$.)
 Fig. 2. Calc-phosphate quartzitic nodule, rich in Globigerinae. Stat. 3, Vasco da Gama Peak, 230 fath. (421 m.). *q*, quartz; *g*, glauconite. ($\times 45$.)
 Fig. 3. Phosphatised and ferruginous nodule, full of Globigerinae. Stat. 5, Cape St. Blaize, 105 fath. (192 m.). ($\times 50$.)
 Fig. 4. Phosphatised and ferruginous nodule, with large benthic Foraminifera. Stat. 5, Cape St. Blaize, 105 fath. (192 m.). ($\times 50$.)

PLATE XXXV.

Thin sections of nodules.

- Fig. 1. Glauconitic layer enclosing grains of glauconite (*g*) in the scoriaceous nodule of Pl. XXXIII, fig. 2. Stat. 7, Cape Point, 560 fath. (1024 m.). ($\times 60$.)
 Fig. 2. Section of nodule formed of two rocks, showing line of contact. Stat. 10, Vasco da Gama, 166 fath. (304 m.). *a*, lower yellowish portion; *b*, band strongly impregnated with glauconite and phosphate, in neighbourhood of contact; *c*, line of contact; *q*, quartz of upper portion. ($\times 45$.)
 Fig. 3. Upper part of same nodule, showing the constitution of a phosphatised greensand nodule. *q*, quartz; *g*, glauconite. ($\times 50$.)



REGION OF THE AGULHAS BANK (based on du Toit, Physical Geography for South African Schools, 1912; and Admiralty Charts). Contours in fathoms.



FIG. 1.

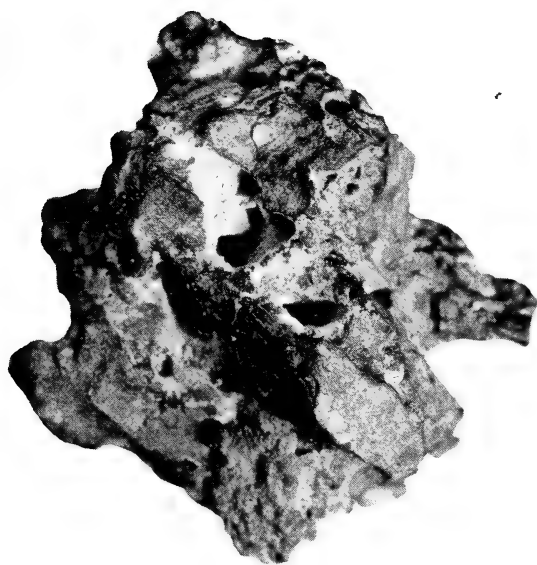


FIG. 2.



FIG. 3.



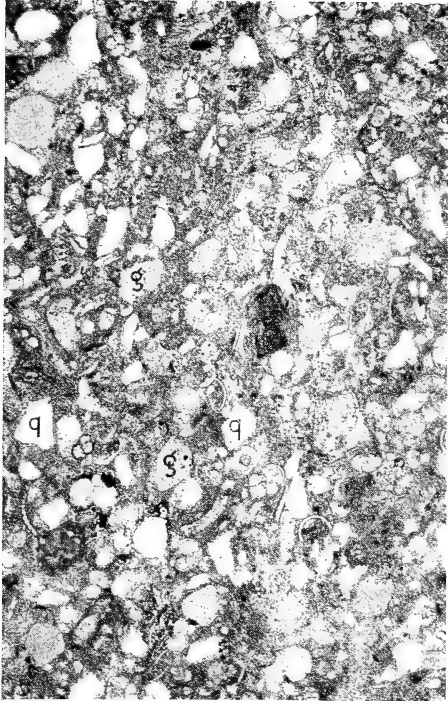


FIG. 1.

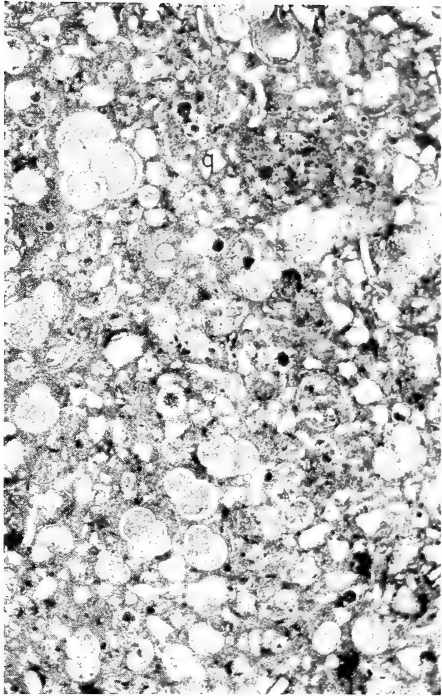


FIG. 2.

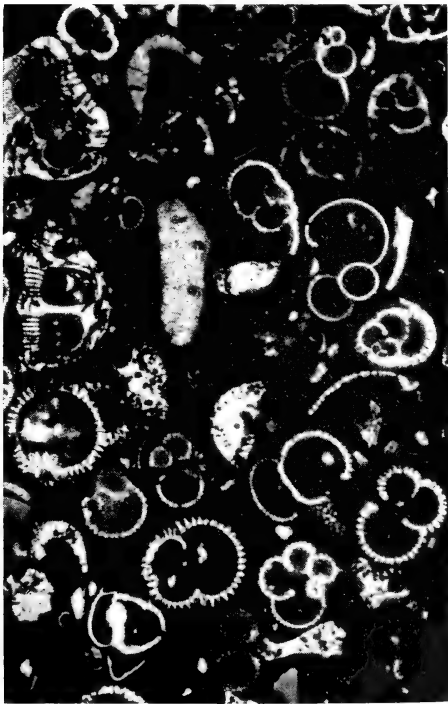


FIG. 3.

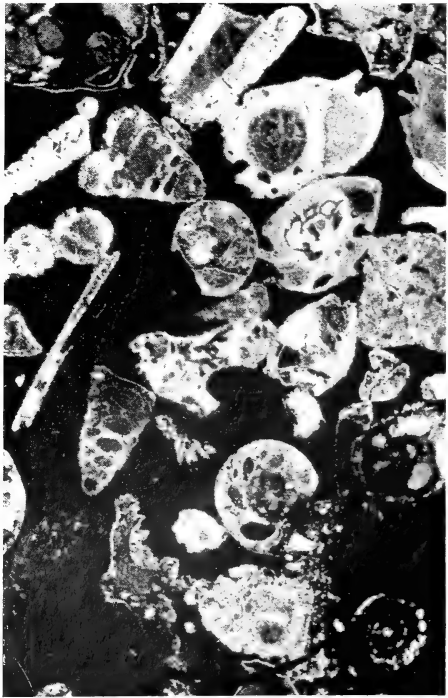


FIG. 4.



FIG. 1.

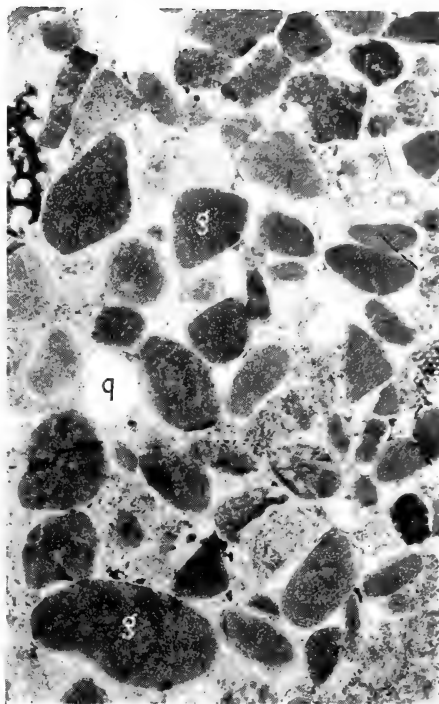


FIG. 3.

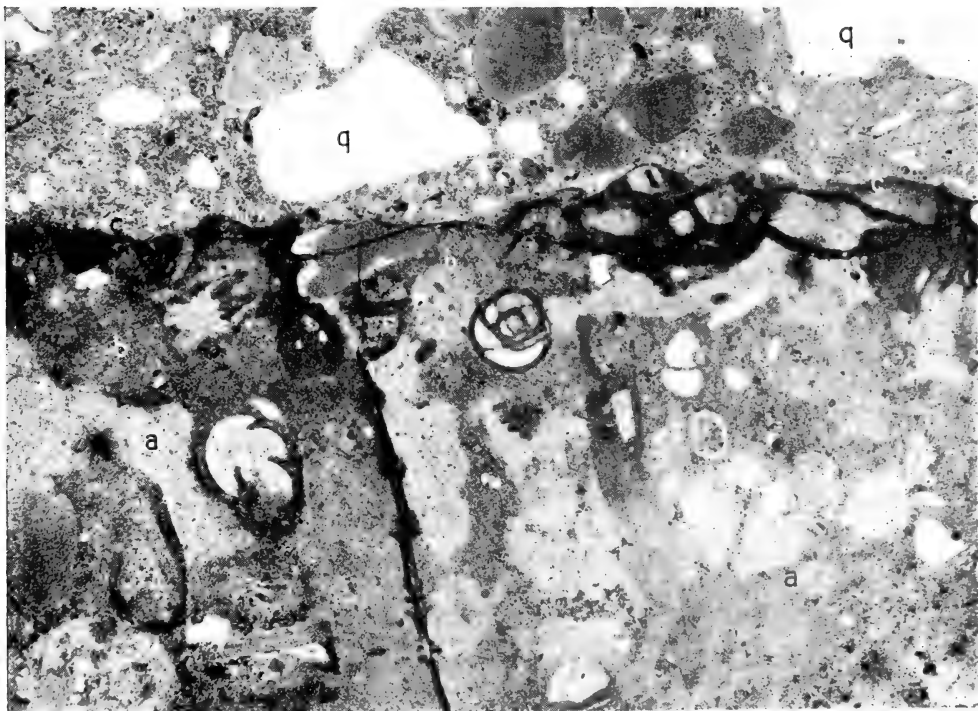


FIG. 2.



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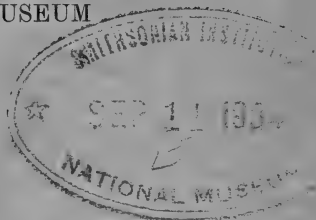
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VOLUME XXXI.

DESCRIPTIONS OF THE PALAEOONTOLOGICAL MATERIAL
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5. *A Contribution to the Morphology of the Gorgonopsia.* By LIEUWE D. BOONSTRA, D.Sc., Palaeontologist to the South African Museum. (With 11 Text-figures.)
6. *Additions to our Knowledge of the South African Gorgonopsia, preserved in the British Museum (Natural History).* By LIEUWE D. BOONSTRA, D.Sc., Palaeontologist to the South African Museum and Queen Victoria Scholar of the University of Stellenbosch. (With 18 Text-figures.)
7. *A Contribution to the Morphology of the Mammal-like Reptiles of the Suborder Therocephalia.* By LIEUWE D. BOONSTRA, D.Sc., Palaeontologist to the South African Museum and Queen Victoria Scholar of the University of Stellenbosch. (With 35 Text-figures.)

ISSUED JULY 1934. PRICE 13s. 6d.

PRINTED FOR THE
TRUSTEES OF THE SOUTH AFRICAN MUSEUM
BY NEILL AND CO., LTD., 212 CAUSEWAYSIDE, EDINBURGH.

5. *A Contribution to the Morphology of the Gorgonopsia.*—By LIEUWE D. BOONSTRA, D.Sc., Palaeontologist to the South African Museum.

(With 11 Text-figures.)

ALTHOUGH the first Gorgonopsian was described as long ago as 1860, and notwithstanding the fact that since then twenty-seven reputed genera and thirty-six species have been recorded from the South African Karroo Beds, our knowledge of these animals was until quite recently practically confined to their cranial morphology. The reason is not difficult to find. The Gorgonopsia were agile beasts of prey that lived on the higher and drier parts of the great Karroo Basin during Upper Permian and Lower Triassic times, so that on death their remains, in order to be entombed in the sediments, had to be transported to the lower-lying areas. During transportation the comparatively slender and more fragile bones of the postcranial skeleton were destroyed, whereas the more compact skull was more often preserved. Hitherto very few parts of the postcranial skeleton have been found in association with skulls. Owen, in 1876, described at length and gave good figures of the humerus of *Cynodraco*. Nothing more was added to our knowledge of the postcranial skeleton until Broom and Haughton, in 1913, jointly described and gave unsatisfactory photographs of the cervical vertebrae, pectoral girdle, and fore-limb of *Aelurognathus tigriceps*. In a later paper, 1913, Broom gave a fuller description, with a figure, of the manus of *Aelurognathus*, and in the same year a short account of the shoulder-girdle of *Scylacops*. In 1921 Watson figured, without describing, the anterior cervicals of *Scymnognathus whaitsi*. Then, in 1927, Pravoslavlev published two important papers on the Gorgonopsia of the North Russian Karroo Beds. Some of these forms had been photographed by Amalitzky, but had never been described. Unfortunately Pravoslavlev's work is in Russian, so that only the text-figures and photographs are intelligible to most non-Russian scientific workers. It would appear, however, that in two genera—*Inostrancevia* and *Amalitzkia*—a practically complete vertebral column, pectoral and pelvic girdles, hind- and fore-limbs lacking only the feet, are known. In 1929 Haughton had the good fortune to obtain from the Rev.

1934

J. H. Whaits a fairly well-preserved shoulder girdle and fore-foot of *Lycaenodontoides*. These were fully described and figured.

In a recent (1930) fairly comprehensive account of the Gorgonopsia, Broom figured and described an imperfect vertebral column, pectoral and pelvic girdles, and the practically complete fore- and hind-limbs of *Lycaenops*. The known parts of *Aelurognathus* and *Scylacops* were also incorporated.

During three collecting trips in the Southern Karroo I had the good fortune to collect a number of Gorgonopsians, which had considerable portions of the postcranial skeleton preserved. This material, augmented by the other previously described specimens preserved in the South African Museum, forms the basis of this communication. The collection consists of:—

(a) S.A.M. Cat. No. 8950. Klein Koedoeskop, Beaufort West. Middle *Tapinocephalus* zone.

A practically complete vertebral column, complete pectoral girdle, imperfect pelvic girdle, and fore- and hind-limb, lacking only some of the digits, are preserved. Unfortunately this specimen is preserved in a very intractable calcareous nodule, so that it has been very difficult to free the various skeletal elements from the matrix without more or less damaging the bone. The skull of this specimen has been described by Haughton under the name, *Hipposaurus boonstrai*. Collector, L. D. Boonstra.

(b) S.A.M. Cat. No. 2342. Dunedin, Beaufort West. Low *Cistecephalus* zone.

This specimen consists of a skull, seven cervical vertebrae, a complete though somewhat crushed pectoral girdle, a good humerus and radius, an imperfect ulna and a nearly complete fore-foot. This is the type specimen of *Aelurognathus tigriceps* described by Broom and Haughton. Collector, S. H. Haughton.

(c) S.A.M. Cat. No. 2343. Dunedin, Beaufort West. Low *Cistecephalus* zone.

Associated with the skull there is an incomplete and crushed pectoral girdle, a good sternum and humerus, and some cervical vertebrae. This is the type of *Scylacops capensis* described by Broom. Collector, S. H. Haughton.

(d) S.A.M. Cat. No. 3329. Oudeberg, Graaff-Reinet. *Cistecephalus* zone.

Associated with a snout, an imperfect pectoral girdle and manus are preserved. This is Haughton's type, *Lycaenodontoides bathyrhinus*. Collector, J. H. Whaits.

(e) S.A.M. Cat. No. 9344. Klein Bloemhof, Richmond. *Cistecephalus* zone.

This specimen consists of a crushed skull; a continuous series of seven cervicals and seven dorsals (the rest of the posterior dorsals are lost), then a series commencing with the last presacral, three sacrals and five caudals; an excellently preserved pectoral girdle with a sternum; two good humeri, a good radius and ulna, and the proximal ends of the ulna and radius of the other side; an imperfect carpus; the left ilium and ischium and part of the right ischium; a good femur, tibia, fibula, tarsus, metatarsals, and some phalanges. For this specimen I propose the name—*Aelurognathus microdon* sp. nov. Collector, L. D. Boonstra.

(f) S.A.M. Cat. No. 9345. Ou Plaas, Richmond. *Cistecephalus* zone.

In this specimen there are preserved: a good, though slightly weathered and crushed, skull; a continuous series of seven cervicals and nine dorsals, together with some isolated dorsals and caudals; a nearly complete pectoral girdle with a sternum; two crushed humeri, a good right radius and ulna, and a crushed left radius and ulna; some isolated carpals, metacarpals, and phalanges. For this specimen I propose the name—*Arctognathoides breviceps* gen. et sp. nov. Collector, L. D. Boonstra.

(g) S.A.M. Cat. No. 10188. Dunedin, Beaufort West. Low *Cistecephalus* zone.

There is preserved a somewhat crushed skull with an excellent palate; a humerus, radius, and ulna; a tibia and fibula; and some crushed vertebrae. I have identified this as a specimen of *Scylacops capensis*, Broom. Collector, L. D. Boonstra.

Skull.

As the main object of this paper is primarily to note the increase of our knowledge of the postcranial osteology of the Gorgonopsia, no detailed account of the cranial morphology will be advanced. In the case of the three skulls of known species, only those points of structure which have hitherto not been fully understood will be mentioned. In the case of the two new forms the account will necessarily be somewhat fuller.

Scylacops capensis (text-fig. 1, *a*, *b*, and *c*).

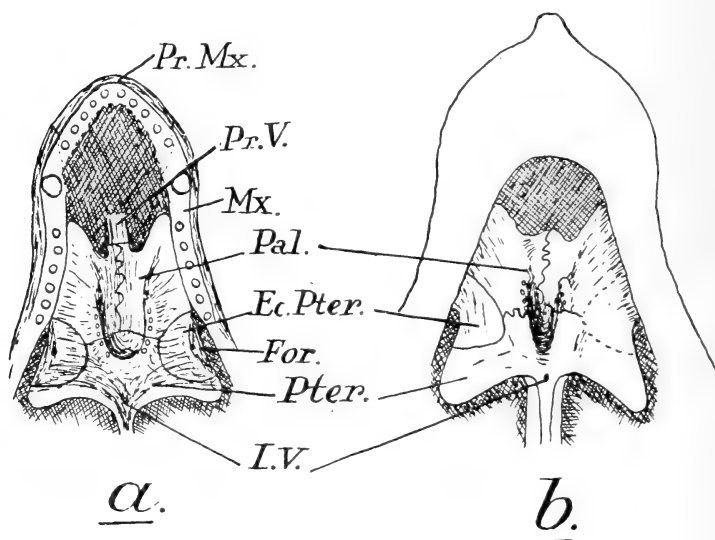
The palate of the type (S.A.M. Cat. No. 3444) has been reconstructed by Broom (Mammal-like Reptiles, fig. 39A). The anterior

part of the palate has now been partly exposed by removing part of the lower jaw, and it has now become clear that Broom's reconstruction is at fault in a number of respects. The median vault formed by the pterygoid and palatine is as figured (fig. 1, c) and the prevomer tapers posteriorly, whereas Broom figured it as swelling out. Anteriorly the prevomer is wide with a median keel and a lateral flange. Unfortunately the palatal process of the premaxilla cannot be exposed without seriously damaging the whole snout. No interpterygoid suture is visible, but posteriorly there is a depression which may be an interpterygoid vacuity. As in *Lycaenodontoides* (fig. 2, a), there is a small foramen in the ectopterygoid. This bone extends right up to the antero-lateral corner of the transverse pterygoid process. In my specimen (S.A.M. Cat. No. 10188), identified as *Scylacops capensis*, the palatine stretches very far forward and meets the palatal flange of the maxilla—a condition reminiscent of some Cynodonts (e.g. *Glochiodontoides*), Deinocephalians (e.g. *Lamiasaurus*), and Therocephalians (e.g. *Whaitsia*). In my specimen the preparietal is a smaller and rounder bone than that of the type. On the ventro-posterior margin of the squamosal a thin wall-like flange of bone is developed, which appears to function as a partial external auditory meatus. In the zygomatic arch the relations of the squamosal and jugal are peculiar, in that the squamosal is clasped dorsally and ventrally by posteriorly directed forks of the jugal; laterally the squamosal appears as a ridge lying intercalated between the two jugal flanges. Neither in the type, nor in my specimen, does the occiput slope so much backwards as Broom figures it (Mammal-like Reptiles, fig. 34D).

Lycaenodontoides bathyrhinus (text-fig. 2, a).

Dr. Haughton has recently removed the matrix from the palate of his type-specimen (S.A.M. Cat. No. 3329), which now shows the structure of most of the anterior half. Two dentigerous ridges limit a fairly deep median vault, which is formed by both the pterygoid and palatines. There is no median pterygoid suture, but posteriorly a small vacuity is present. The ectopterygoids, which do not extend so very far down along the transverse pterygoid flanges, are pierced by a small foramen. The prevomers are separated from the pterygoids by the palatines, which meet along a convoluted suture in the median line. In this it agrees with forms like *Scylacops*, *Aelurosaurus*, and *Arctognathus*. On the whole, the anterior part of the palate of *Lycaenodontoides* is very similar to that of *Arctognathus curvimola*.

Unfortunately it has not been possible to expose the extreme anterior end of the palate, so that nothing can be stated as to the nature of the palatal portion of the maxilla and premaxilla; but it would appear that the palate is on the whole a flat one, without the extraordinary vaulting shown by *Arctognathoides* (fig. 4, c).



TEXT-FIG. 2.

- (a) *Lycenodontoides bathyrhinus*. S.A.M. Cat. No. 3329. Ventral view of anterior part of the palate. $\times \frac{1}{2}$.
 (b) *Arctognathus curvimola*. Type. British Museum Natural History. Ventral view of anterior part of the palate. \times about $\frac{1}{2}$.

For.=foramen in the ectopterygoid.
 Other lettering as in fig. 1.

Arctognathus curvimola (text-fig. 2, b).

Dr. S. H. Haughton kindly let me copy a sketch of the palate of the type in the British Museum, and I quote the following from his notes: "My interpretation of the palate is entirely different from that of Watson. All the sutures are easily visible by wetting the skull; there is *no* interpterygoid suture; but there is a small interpterygoid vacuity. The arrangement of the bones is very similar to that in the form I have called *Arctognathus whaitsi*. The sutures are all plainly visible as convolute lines—and different from the straight cracks which Watson has misinterpreted as sutures. The palate thus agrees with the Aelurosaurids in the separation of the pterygoids

from the prevomers; but differs in the fact that the ectopterygoid does not extend on to the massive pterygoidal transverse process and in the nature of the ridge bounding the median vault." There is thus much similarity between the anterior portions of the palates of *Arctognathus* and *Lycaenodontoides*, but there is some difference in the nature of the median vault and the proportions of the various elements.

The dental formula in *Arctognathus curvimola* is i. 4, c. 1, m. 5, and in *Lycaenodontoides* i. 5, c. 1, m. 6; in the former, the molars are serrated.

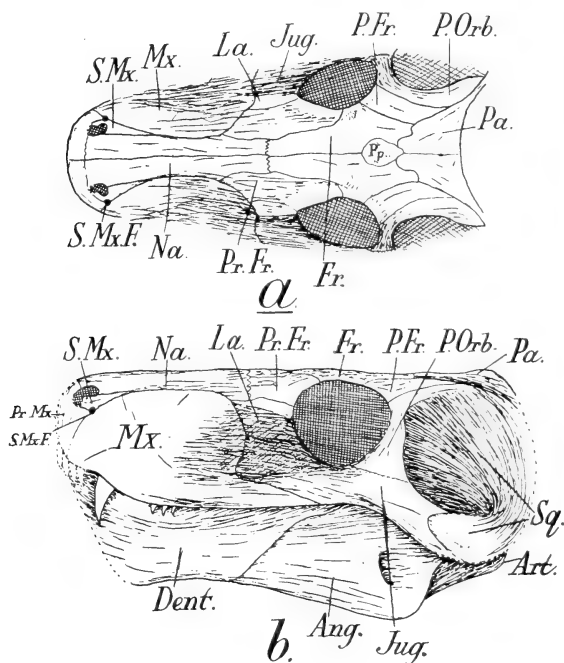
Aelurognathus microdon sp. nov. (text-fig. 3, a, b).

The skull of this new species from Klein Bloemhof is somewhat crushed, and it has not been possible to expose the palate. Although it is much smaller than either *A. tigriceps* and *A. serratidens* it is undoubtedly cogenetic. The general configuration of the different bones is very similar, and it possesses a similar antorbital depression which is slightly overhung by the prefrontal; this depression is as deep as in *A. serratidens*, but deeper than in *A. tigriceps*. As in the other two species of *Aelurognathus*, the snout is high and rounded, and the width of the parietal region is much greater than the interorbital width, whereas, in the closely allied *Scymnognathus*, the width of the parietal region is relatively smaller. The temporal fossae are not wide in dorsal view, and the orbit does not look as much forward and outward as in the case of *Scymnognathus*. This species differs from the two hitherto known, mainly in that it is smaller; having in addition three and not four molars, which are also much smaller. The molars are not serrated, whereas in *A. serratidens* they are. It also approaches *A. tigriceps* more closely in that the pineal foramen is small, whereas in *A. serratidens* it is large; it is situated further posteriorly than in both. The frontal forms a greater part of the upper orbital border than in *A. tigriceps* and a still greater part than in *A. serratidens*. The nasal stretches further posteriorly than in *A. serratidens*, but the frontal is larger than in *A. tigriceps*.

Arctognathoides breviceps gen. et sp. nov. (text-fig. 4, a, b, c, and d).

Although slightly distorted by post-mortem crushing, it has been possible to prepare reliable dorsal, lateral, and ventral views of the skull. The most distinctive feature of this skull is its broad, short, and relatively high snout. In this it bears points of resemblance to *Lycaenodontoides* and *Arctognathus*. The interorbital region is, however, much wider than the parietal region, whereas in *Arctognathus*

it is actually slightly narrower. Furthermore, there does not appear to be such an overhang of the nasals over the nostrils. The nature of the palate is, moreover, totally different from that of these two genera. The massive transverse pterygoidal flanges are situated very far forward. Anterior to these flanges, the palatal roof continues in anterior direction at a much higher level—there being an



TEXT-FIG. 3.

Aelurognathus microdon sp. nov. S.A.M. Cat. No. 9344. \times about $\frac{1}{4}$.

(a) Dorsal view of skull (crushing corrected).

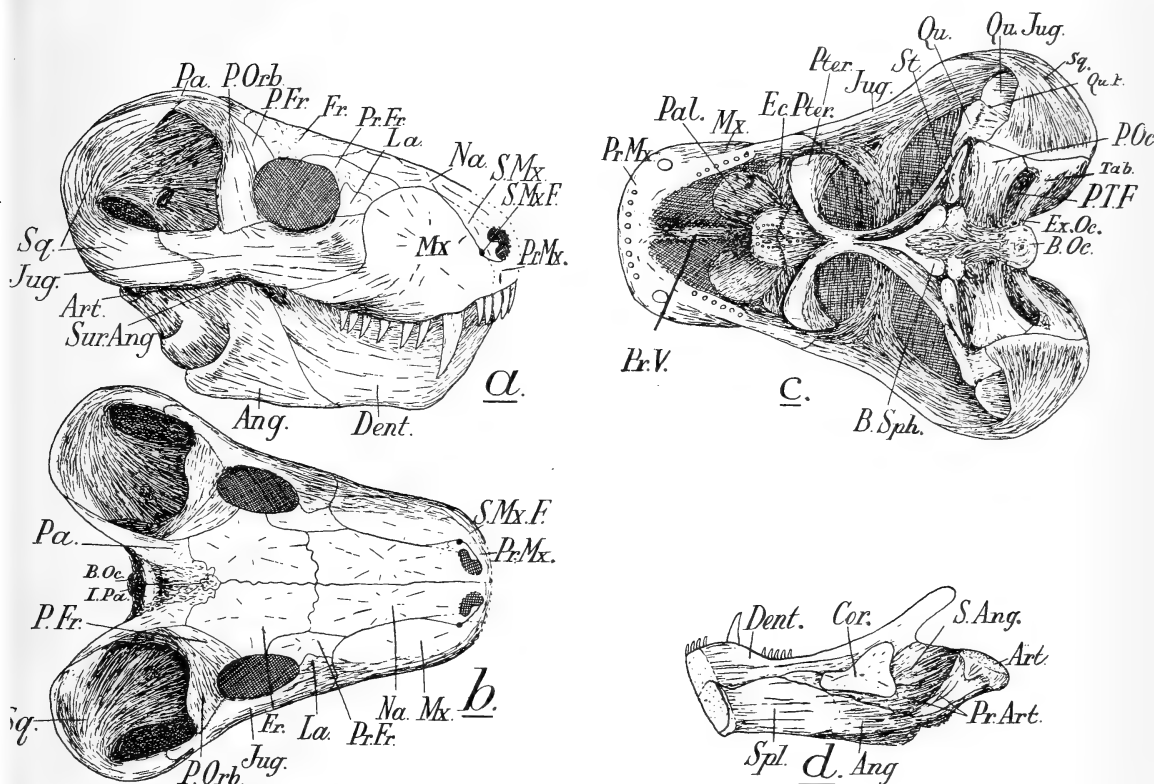
(b) Lateral view of skull „ „

Ang. = angular. Art. = articular. Dent. = dentary.

Other lettering as for previous figures.

abrupt step of about 15 mm. In the median line the anterior portions of the pterygoids and the postero-median portions of the palatines form a very curious rump, which, in its palatine portion, houses a median vault. Laterally and anteriorly there is yet another step of about 15 mm. on to the ventral surfaces of the ectopterygoids, prevomers, and antero-lateral portion of the palatines. Anterior to the transverse pterygoidal flanges, the palate thus contains two successive high vaults. The palate of *Arctognathoides* is thus very

distinctive. In all other Gorgonopsians the palate is in comparison quite flat. The occiput does not slope backwards. The orbits look more outwards than upwards. The snout is square in section. The



TEXT-FIG. 4.

- Arctognathoides breviceps* gen. et sp. nov. S.A.M. Cat. No. 9345. \times about $\frac{1}{4}$.
 (a) Lateral view of skull (crushing corrected). (c) Ventral view of skull (crushing corrected).
 (b) Dorsal view of skull " " (d) Inner view of lower jaw.

Cor. = coronoid. Qu.F. = quadrate foramen. Sur.Ang. = surangular.
 Pr.Art. = prearticular. Spl. = splenial.

Other lettering as in previous figures.

infraorbital bar and zygoma are strong. The lateral ends of the paroccipital bone are directed posteriorly, so that the occiput is concave laterally.

The preparietal is a small irregularly rounded bone. The pineal foramen is very small and situated far posteriorly. The frontals form about half of the upper orbital border. The orbit looks mostly outwards. The temporal fossa is large and roomy.

The dental formula is c. 4, i. 1, m. 6. The molars are large; their posterior edges are distinctly serrated. There is a fairly distinct step in the dental border at the maxilla-premaxillary suture. The lower jaw is typically Gorgonopsian; the mentum is high, strong, and square; the coronoid process of the dentary is strong, but does not project into the temporal fossa as it does in *Aloposaurus*. The coronoid is large. There is one molar less than in the maxilla.

The Chief Measurements.

The measurements given here and in the subsequent tables are all taken by means of a Martin's beam-compass, so that they all represent projections on to a vertical or a horizontal plane, given in millimetres.

	<i>Aeluro- gnathus microdon.</i>	<i>Arcto- gnathoides breviceps.</i>	<i>Scylacops capensis.</i>
	S.A.M. Cat. No. 9344.	S.A.M. Cat. No. 9345.	S.A.M. Cat. No. 10188.
<i>Length :</i>			
(Basioccipital-premaxilla)	197	187	156
(Premaxilla-pineal foramen)	171	155	123
(Pineal foramen-edge of occipital plate)	18	19	23
(Snout—front of orbit)	105	90	84
Length of lower jaw	180?	160	140
<i>Width :</i>			
(Across squamosals)	140?	150	120
(Interorbital)	52	56	40
(Intertemporal)	56	53	44
(Across canines)	60	66	44
(Across quadrates)	99?	122	100
<i>Height :</i>			
(Maxillary edge—median suture)	63	71	30
(Edge of occipital plate—basioccipital)	66	71	39
(Quadrate—median suture)	73	75	43
(Mentum of lower jaw)	?	52	33
Length of molar series	9	35	11
Length of diastema	22	12	10

The Vertebral Column.

Hitherto the complete presacral series was known in only one Gorgonopsian—*Inostrancevia alexanderi*. This has been described by Pravoslavlev, but as his description is in Russian I am not able to appreciate the nature of his account, and, furthermore, am unable to count the number in the series from the photograph published. In *Lycaenops*, Broom found a continuous series of 20 vertebrae, and he believes that this comprises the complete dorsal series, and that, anteriorly, 7 cervicals were lost. Broom stated that this material is badly crushed, and he has been unable to determine the details of the various structural points. In *Aelurognathus*, Broom and Haughton and I have described the cervicals.

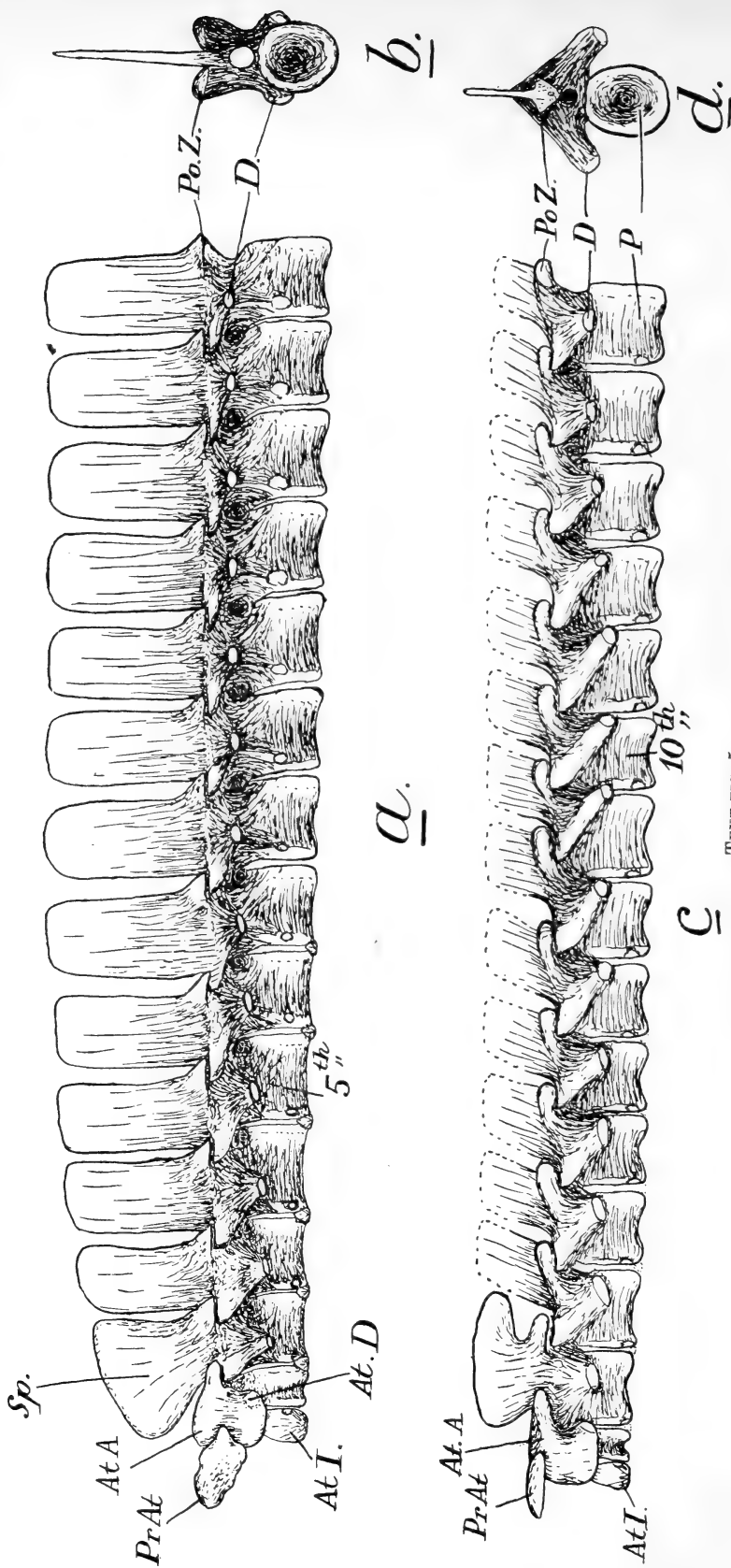
In *Hipposaurus boonstrai* (S.A.M. Cat. No. 8950) I excavated the complete presacral, sacral, and probably also all the postsacral vertebrae. This is the first form from the *Tapinocephalus* zone where anything is known of the postcranial skeleton. This skeleton was preserved in a calcareous nodule which has proved to form an extremely intractable matrix, with the result that, during preparation, the caudals have been seriously damaged and their sequence lost, and even in the presacrals many of the processes have been damaged. In the presacral series there are 28 vertebrae. Of these 7 are cervicals, 15 typical dorsals, and the posterior 6 are perhaps best referred to as lumbar vertebrae. There are 3 sacrals and at least 26 caudals. The total length of the presacral series is 700 mm.; of the sacrals 55 mm., and of the caudals at least 450 mm.

In *Aelurognathus microdon* (S.A.M. Cat. No. 9344, fig. 5, *a, b*) there is present an excellently preserved presacral series of 14 vertebrae, of which the anterior 7 are cervicals; then, probably 12–13 vertebrae are missing, and then there is a further continuous set commencing with the last dorsal, which includes 3 sacrals and 5 caudals.

In *Arctognathoides breviceps* (S.A.M. Cat. No. 9345, fig. 5, *c, d*) a continuous series of the first 16 presacrals and a further number of disarticulated dorsals and caudals are preserved. These vertebrae are all slightly crushed, and in most the tops of the neural spines have suffered from weathering.

The Cervicals.

I have already described the cervicals of *Aelurognathus tigriceps* (fig. 5, *e*) in a short note—"The Cervical Vertebrae of a Gorgonopsian (*Aelurognathus tigriceps*)" in the *Ann. Mag. Nat. Hist.*, Series 10, vol.



TEXT-FIG. 5.

Aelurognathus microdon sp. nov. S.A.M. Cat. No. 9344.

(a) Lateral view of the first 14 presacral vertebrae, \times about $\frac{1}{2}$.
(b) Posterior view of the 5th vertebra, \times about $\frac{1}{2}$.

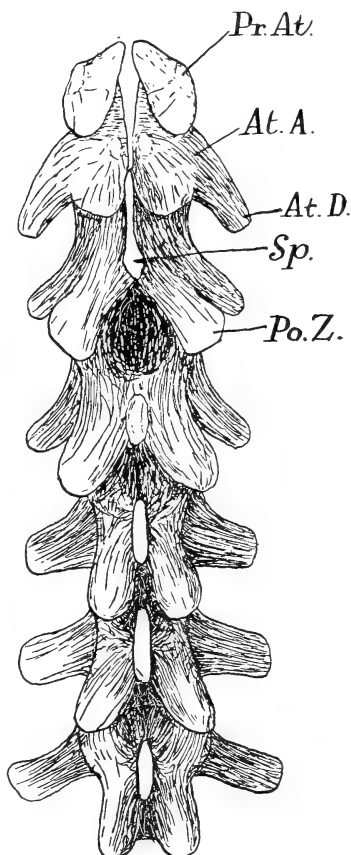
Arctognathoides breviceps gen. et sp. nov. S.A.M. Cat. No. 9345.

(c) Lateral view of the first 15 presacral vertebrae, \times about $\frac{1}{2}$.
(d) Posterior view of the 10th vertebra, \times about $\frac{1}{2}$.

At.A. = atlantal arch.
At.D. = atlantal diapophysis.

Po.Z. = post-zygapophysis.
Pr.At. = pro-atlas.
P. = pleurocentrum.
Sp. = neural spine of the 2nd vertebra.

xii., 1934. The excellent material now at my disposal fully confirms the views expressed in this paper. In *Hipposaurus*, *Aelurognathus*, and *Arctognathoides* the neck consists of 7 vertebrae. In *Hipposaurus* and *Aelurognathus* the shoulder-girdle is preserved in natural relation to the vertebral column so that this important point in the determination of the cervical series is known. In addition the presence of intercentra in the first 7 vertebrae, the abrupt increase in length of the diapophyses in the 8th vertebra, the upward shifting of the parapophysial facet, and the change of the zygapophysial articulation from a horizontal plane to one at 45° , are all points that definitely show that the neck consisted of 7 segments. In all three genera a pro-atlas is preserved, and has the relations as described for *A. tigriceps*; the atlantal arches composed of two unfused halves are essentially the same in the three genera, although they differ somewhat in point of shape and size; the large atlantal intercentrum and unfused atlantal pleurocentrum appears to be constant in the Gorgonopsia. In all three genera the atlantal dichoccephalous rib articulates with a diapophysis on the atlantal arch and with a parapophysial facet on the atlantal intercentrum. In the succeeding vertebrae the parapophysial facet shifts on to the extreme anterior edge of the centrum, and the diapophysial facets are carried on strong ventro-posteriorly directed processes. The zygapophysial articulations are horizontal. All the centra are deeply amphicoelous—practically notochordal. The neural spine of the axis is typically differentiated as in all Therapsids. The shape differs somewhat in



TEXT-FIG. 5, e.

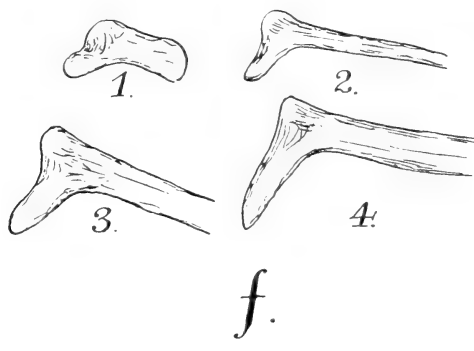
Aelurognathus tigriceps.
S.A.M. Cat. No. 2342.

Dorsal view of the first 6 vertebrae.
× about $\frac{1}{2}$.

Lettering as in fig. 5.

the various genera (fig. 5, *a, c, e*). Only in *Hipposaurus* do the cervicals carry a strong ventral keel to the centra. In *A. tigriiceps* the spine of the 3rd vertebra appears to be rudimentary. This may be pathological, as in none of the others does this condition obtain.

Professor D. M. S. Watson has in his collection at University College a skull and a series of 8 cervical vertebrae of a specimen of *Scylacops capensis* from Wellwood, Graaff-Reinet, which had been presented to him by the South African Museum. The cervical series is in a fairly good state of preservation, and confirms the conclusions arrived at in



TEXT-FIG. 5, *f*.

Aelurognathus microdon. Ribs. \times about $\frac{1}{2}$.

- | | |
|----|--------------------------------|
| 1. | Lateral view of the axial rib. |
| 2. | 4th rib (proximal end). |
| 3. | 7th " " " |
| 4. | 12th " " " |

our study of the neck in *Aelurognathus*, *Hipposaurus*, and *Arctognathoides*, viz. the structure of the pro-atlas, atlantal arches, the odontoid, and the atlantal intercentrum is as described in those forms; the same evidence of the presence of 7 cervicals is present. The anterior cervicals of *Scylacops* agree with those of *Hipposaurus* in that they also have a slight ventral keel developed on the centra.

Watson's skull shows a very good articulation between the basisphenoid and the posterior ramus of the pterygoid; the stapes and the foramen for the 10th nerve are beautifully preserved. The frontal seems to take a greater part in the formation of the orbital border than is shown in the two specimens in the South African Museum.

The Dorsals.

In *Hipposaurus*, where the dorsal series is fully preserved, there are 21 vertebra; in *Lycaenops*, Broom maintained that the 20 elements

preserved comprises the whole dorsal series. In *Hipposaurus* the first 15 elements of the dorsal series are typical dorsal vertebrae. Continuing backwards from the 22nd presacral to the first sacral, the vertebrae decrease considerably in height and width, becoming thereby relatively longer and more slender; the diapophyses also become more slender and weaker, and no indication of a facet for the capitulum of the ribs can be seen, and thus the possibility arises that the posterior ribs were either single-headed or that these vertebrae are really lumbar and possessed no ribs; it is, moreover, remarkable that the first 15 dorsals possess no intercentra, whereas in the posterior presacrals intercentra are developed, nearly as strongly as in the neck. Although Broom, in his reconstruction of *Lycaenops* (Mammal-like Reptiles, fig. 45), figured ribs right up to the sacrum, I am inclined to think that in the Gorgonopsia the vertebrae immediately anterior to the sacrum carried no ribs. This would be in harmony with the rest of the skeleton, which indicates fairly lightly built animals of considerable agility. The absence of ribs in the lumbar region would greatly increase the flexibility of the back—particularly in lateral direction. If I am correct in this point of view the Gorgonopsia would in this respect approach the condition of some Cynodonts (e.g. *Thrinaxodon*), Cotylosaurs (e.g. *Limnoscelis*, *Labidosaurus*), and Pelycosaurs (e.g. *Sphenacodon*).

In the three genera—*Hipposaurus*, *Aelurognathus*, and *Arctognathoides*—the width across the zygapophyses in the dorsal vertebrae abruptly decreases at the transition from the cervicals; the diapophysial processes increase in length and are more horizontally directed, so that the facet is at a higher level than in the cervicals; the parapophysial facets shift higher up on to the centrum, and in *Hipposaurus* are not seen after the 15th dorsal. Continuing backwards the centra progressively increase in length. Whereas in the cervicals the zygapophyses are horizontal, in the dorsals they lie at 45° to the horizontal, which indicates that less lateral movement was possible. The centra are deeply amphicoelous, with a moderate lateral constriction; ventrally the centra are concave in antero-posterior direction, but are not pleurocoelous; no keel is developed. In *Aelurognathus microdon*, where the neural spines are perfectly preserved, they are very tall and laterally compressed, and are very similar to those of *Amalitzkia annae* figured by Pravoslavlev; in *A. tigriiceps* the cervical spines are short and much thicker; in *Arctognathoides* the spines are shorter than in *A. microdon* and slightly less laterally compressed; in *Hipposaurus* they were apparently shorter still, and also somewhat laterally compressed.

Sacrum.

The sacrum is well-preserved in *A. microdon*, but is somewhat crushed in *Hipposaurus*. In the former, three vertebrae contribute to the support of the ilium. Their centra are fairly firmly, although not completely, fused. Each carries a strong sacral rib which emerges from rather high up on the middle of the centrum. Distally the ribs spread out fan-wise to abut deeply on the ilium. The first rib is the strongest, and its distal end stretches very far ventrally—to below the upper half of the acetabulum. The posterior two abut higher up on the ilium. As in Mammals, the ribs abut on the postero-internal surface of the ilium, leaving the anterior part unsupported. In *Hipposaurus* the upper portion of the crest of the left ilium is preserved in its natural position. Here also 3 sacral ribs support it—abutting on the postero-internal surface. Broom's inferences, as to the condition in *Lycaenops*, appear, in the light of this new material, to be substantially correct.

Caudals.

In no specimen are the caudals fully preserved. In *Hipposaurus* there are at least 26. In *Aelurognathus microdon* the first 5 caudals are preserved. The neural spines are lower, shorter, and less compressed than in the dorsals, and the transverse processes are strong and extend as far laterally as the external iliac surface. Judging by the imperfectly preserved tail of *Hipposaurus*, it would appear that in the Gorgonopsia the tail was long and whip-like.

The chief measurements are:

Vertebral Column.

	<i>Aeluro- gnathus tigriceps.</i>	<i>Hippo- saurus boonstrai.</i>	<i>Aeluro- gnathus microdon.</i>	<i>Arcto- gnathoides breviceps.</i>
	S.A.M. Cat. No. 2342.	S.A.M. Cat. No. 8950.	S.A.M. Cat. No. 9344.	S.A.M. Cat. No. 9345.
Length of 7 cervicals. .	270	191	167	180
„ 1st 7 dorsals .	?	155	176	200
Height of Axis .	76	37	57	43
„ 3rd cervical .	56	32	67	41
„ 4th „ .	?	35	71	47
„ 1st dorsal .	?	37	81	57

Vertebral Column—continued.

	<i>Aeluro- gnathus tigriceps.</i>	<i>Hippo- saurus boonstrai.</i>	<i>Aeluro- gnathus microdon.</i>	<i>Arcto- gnathoides breviceps.</i>
	S.A.M. Cat. No. 2342.	S.A.M. Cat. No. 8950.	S.A.M. Cat. No. 9344.	S.A.M. Cat. No. 9345.
<i>Width across Diapophyses :</i>				
(a) Axis . . .	60	34	34	41
(b) 3rd cervical . . .	61	36	36	45
(c) 5th „ . . .	74	38	37	47?
(d) 7th „ . . .	84	40	44	48?
(e) 1st dorsal . . .	?	43	46	49
(f) 5th „ „ . . .	?	45	50	51
<i>Length of Centra :</i>				
(a) Axis . . .	32	26	21	21
(b) 3rd cervical . . .	33	27	23	22
(c) 7th „ . . .	?	22	24	20
(d) 5th dorsal . . .	?	22	27	21
<i>Width across Prezygapophyses:</i>				
(a) Axis . . .	34	25	20	29
(b) 3rd cervical . . .	35	30	22	27
(c) 7th „ . . .	32	24	22	28
(d) 5th dorsal . . .	?	17	21	23
<i>Width of Centrum :</i>				
(a) Axis . . .	27	16	20	26
(b) 7th cervical . . .	34	15	21	23
(c) 5th dorsal . . .	?	14	20	17

The Ribs (fig. 5, f).

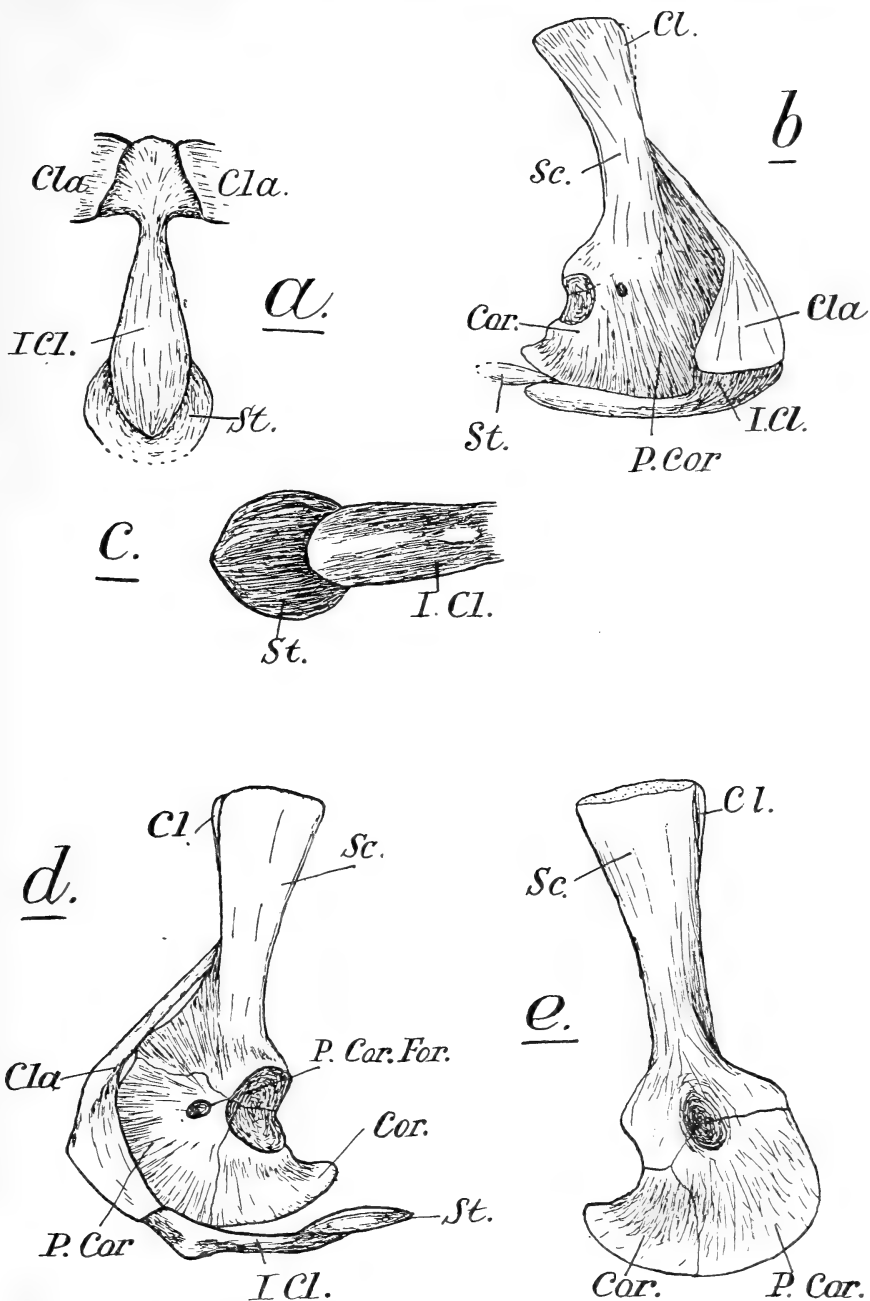
The ribs in all the specimens are very badly preserved. The proximal ends, however, are preserved in quite a number of cases. In all, the dorsal ribs are long and slender—those of *Hipposaurus* are not more than 4 mm. thick; in *Aelurognathus*, however, they are somewhat thicker (12 mm.). In *A. microdon* some of the cervical ribs are preserved—the axial rib is a short, wide, and leaf-like bone, the 4th is already long and has a slender shaft. All the ribs that are preserved are dichoccephalous, the tuberculum and capitulum being separated

by a slight notch; it is, however, possible that the posterior dorsals are single-headed. In no case has it been possible to determine the nature of the junction of the anterior dorsal ribs with the sternum. Broom, in his reconstruction (1930) of the pectoral girdle of *Aelurognathus tigriceps*, indicated three ribs articulating with the sternum. There is, however, no evidence that this is so, although in the sternum of *Lycaenops* he maintained to have noticed three notches on the lateral edge of the sternum, to which an equal number of ribs apparently articulated.

The Pectoral Girdle (text-fig. 6).

The Gorgonopsian breast-shoulder-apparatus is now very well known. It is fully preserved in *Hipposaurus* (from the *Tapinocephalus* zone), in *Aelurognathus microdon*, in *Arctognathoides breviceps*, and somewhat incompletely and crushed in *Aelurognathus tigriceps*, *Lycaenodontoides* and *Lycaenops*. In the Russian forms Pravoslavlev has described it in *Inostrancevia* and in *Amalitzkia*. It consists of a scapular part formed by the three cartilage bones—scapula, coracoid, and procoracoid—and a clavicular part, which consists of three dermal bones—clavicles, cleithra, and an unpaired interclavicle; in addition an ossified sternum is always developed. The scapula is a tall and slender bone with the dorsal part of its blade considerably expanded; it carries no acromion process, and thus no supraspinatus fossa as in mammals and closely related reptiles; it forms half of the simple, posteriorly directed non-“screw-shaped” glenoid cavity; on its ventro-anterior end an extensive plate of bone is developed, which received the m. supracoracoideus. There is no supraglenoid foramen, but internally the scapula forms the dorsal border of the strongly developed subscapular fossa. In the different genera the scapula is very similar, except that in the Russian forms the dorsal expansion of the blade appears to be relatively greater than in the South African forms.

The greater part of the coracoid plate is formed by the procoracoid, which is tall and long (particularly in *Hipposaurus*); the procoracoid foramen is situated immediately anterior to the glenoid and passes through the bone in dorsal direction; the procoracoid just enters the glenoid cavity to form a small part of its extreme anterior border; the coracoid has a well-developed posteriorly developed lip, from which the coraco-brachialis and costo-coracoideus arose; anteriorly the coracoidal plate is closely applied to the internal face of the clavicle, and ventrally it rests on the median stem of the interclavicle.



TEXT-FIG. 6.—Pectoral girdles.

(a) *Hipposaurus boonstrai*. S.A.M. Cat. No. 8950. Ventral view of interclavicle. $\times \frac{2}{3}$.

(b) *Hipposaurus boonstrai*. S.A.M. Cat. No. 8950. Lateral view. $\times \frac{2}{3}$.

(c) *Aelurognathus microdon* sp. nov. S.A.M. Cat. No. 9344. Ventral view of sternum. $\times \frac{1}{3}$.

(d) *Aelurognathus microdon* sp. nov. S.A.M. Cat. No. 9344. Lateral view. $\times \frac{1}{3}$.

(e) " " " " Internal view. $\times \frac{1}{3}$.

Cl. = cleithrum.

Cla. = clavicle.

Cor. = coracoid.

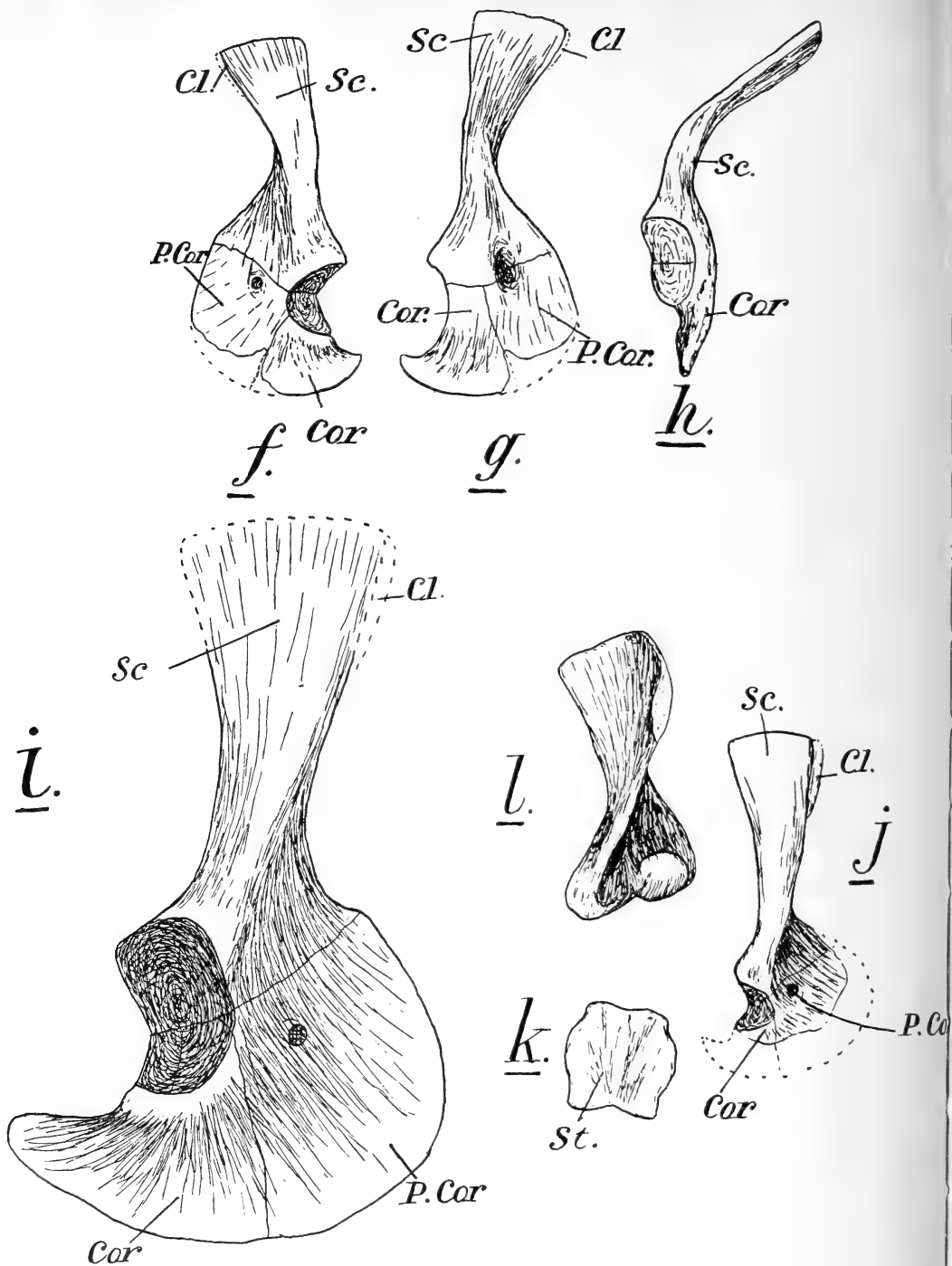
I.Cl. = interclavicle.

P.Cor. = procoracoid.

P.Cor.For. = procoracoidal foramen.

Sc. = scapula.

St. = sternum.



TEXT-FIG. 6.—Pectoral girdles—continued.

- | | | | | |
|-----|---|-----------------------|-------------------------------|------------------------|
| (f) | <i>Arctognathoides breviceps</i> gen. et sp. nov. | S.A.M. Cat. No. 9345. | Lateral view. | $\times \frac{1}{3}$. |
| (g) | " | " | Internal view. | $\times \frac{1}{3}$. |
| (h) | " | " | Posterior view. | $\times \frac{1}{3}$. |
| (i) | <i>Aelurognathus tigriceps</i> . | S.A.M. Cat. No. 2342. | Lateral view. | $\times \frac{1}{3}$. |
| (j) | <i>Scylacops capensis</i> . | S.A.M. Cat. No. 2343. | Lateral view. | $\times \frac{1}{3}$. |
| (k) | " | " | Ventral view of sternum. | $\times \frac{1}{3}$. |
| (l) | " | " | Ventral view of left humerus. | $\times \frac{1}{3}$. |

Lettering as on previous page.

In the older *Hipposaurus* the plate appears relatively larger than in the forms from the *Endothiodon* and *Cistecephalus* zones.

The clavicle is a large bone, being particularly massive in *Lycaenodontoides*; dorsally it has a long process which is applied, very high up, to the antero-internal edge of the scapula; ventrally it has a triangular expansion with a relatively long base; this clasps the lateral expansions of the anterior end of the interclavicle. In *A. tigriiceps*, *A. microdon*, and *Lycaenodontoides* the ventral ends of the clavicles nearly meet and thus hide the anterior end of the interclavicle from ventral view; in *Hipposaurus*, however, the clavicles are widely separated by the interclavicle (fig. 6, *a*).

The interclavicle is a large bone, as long as the coracoidal plate; anteriorly it is expanded, and lies nearly wholly internal to the expanded ends of the clavicles, except in *Hipposaurus*, where in ventral view it is shovel-shaped; posteriorly it is shaft-like for a short distance and then expands to form a long oval extremity, which, lying ventrally to the sternum, supports that element along its anterior half. In *Lycaenodontoides*, *Arctognathoides*, and *Aelurognathus microdon* a strong keel, which is developed on its medio-ventral surface, received the pectoral muscle; in *A. tigriiceps* and *Hipposaurus*, however, there is only a slight ridge on the medio-ventral surface.

The sternum is present in the type-specimens of *Scylacops capensis*, *Lycaenops ornatus*, *Aelurognathus microdon*, *Arctognathoides*, and, in part, in *Hipposaurus*. In *Scylacops* (fig. 6, *k*) it is roughly square, whereas in all the others it is roughly oval in outline. In *Lycaenops*, Broom figured (Pl. XXVIII, 18, 1930) the sternum as an elongated bone which has three notches on either side for the reception of the first three dorsal ribs. In the sterna examined by me no such definite notches have been noticed, but it is possible that the sternal edges were cartilaginous, and the junction with the ribs would in that case not be preserved.

The chief measurements are:

[TABLE

Pectoral Girdle.

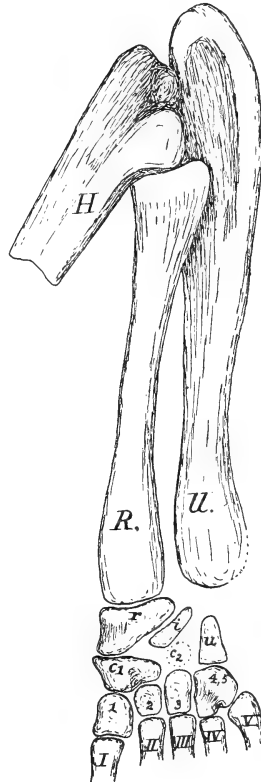
	<i>Hipposaurus</i> <i>boonstrai</i> .	<i>Aelurognathus</i> <i>microdon</i> .	<i>Arctognathoides</i> <i>breviceps</i> .	<i>Scylacops</i> <i>capensis</i> .	<i>Aelurognathus</i> <i>tigriceps</i> .
	S.A.M. Cat. No. 8950.	S.A.M. Cat. No. 9344.	S.A.M. Cat. No. 9345.	S.A.M. Cat. No. 2343.	S.A.M. Cat. No. 2342.
<i>Height :</i>					
Total coraco-scapular	113	178	155	128	230?
Glenoid edge-top of scapula	99	123	116	98	130?
Greatest procoracoidal	42?	57	43	36?	115
Greatest clavicular	78	107	100?	?	163
<i>Length :</i>					
Coracoid plate	77	90	75	55?	143
Interclavicle	105	103	81?	?	210
Sternum	25	54	61	44	?
Blade of scapula	24	52	41	33	65?

Fore-limb (figs. 7-9).

As a whole the fore-limb is fairly light and slender. In *Hipposaurus* the relative length and slenderness of the limb is much greater than in *Cynodraco*, *Aelurognathus*, *Arctognathoides*, *Scylacops*, *Inostrancevia*, and *Amalitzkia*. But, notwithstanding the relative slenderness, the humerus still retains most of the typically primitive reptilian characters, viz. (although constricted in its middle, one can hardly speak of a humeral shaft as it is known in mammals) both the distal and proximal ends are expanded and are twisted around the "shaft" to subtend an angle of about 40°; the proximal articulatory surface is elongated, and, although mainly articulating with the glenoid cavity with its pre-axial corner, there is not much approach to the typical ball-and-socket joint of mammals; the glenoid faces backwards and downwards, so that the humerus no longer stands out practically horizontally as in the primitive Cotylosaurs; the animal, however, does not stand vertically on the fore-limbs, but still hangs somewhat between its supports; the distal articulation

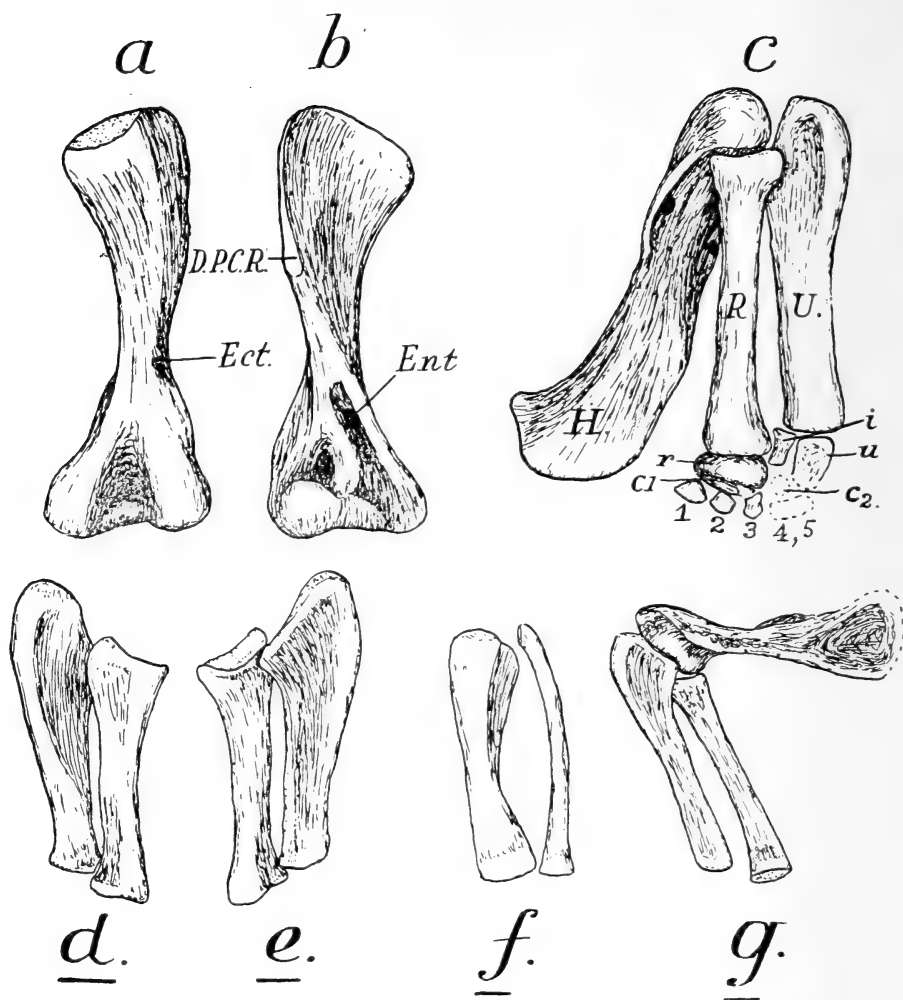
for the radius and ulna is much more terminal than in Cotylosaurs and Pelycosaurs, and the trochlear fossa is quite deep, so as to allow considerable extension of the epipodial; the gait of the Gorgonopsia was thus much more upright than in the more primitive reptiles; the delto-pectoral crest is fairly strong and extends far distally; it is, however, much weaker than in Cotylosaurs, Pelycosaurs, Deinoccephalians, and the higher Cynodonts (*Cynognathus*); in particular it appears that the pectoral muscle was much weaker than in the forms mentioned; the delto-pectoral flange is demarcated from the dorso-proximal surface by a weak anterior dorso-ventral line; distally, the confluent ectepicondylar and supinator flange is strong, indicating strong extensor muscles; on the post-axial side the entepicondylar flange is also quite well developed, indicating strong flexors. Except in point of size there appears to be very little difference in the humeri of the known forms of the Gorgonopsia—*Hipposaurus* is distinct in possessing a long and slender humerus; in *Arctognathoides* the epicondyles are more strongly developed than in the others; the keel on the interclavicle in *Lycaenodontoides*, *Aelurognathus*, and *Arctognathoides* indicates a greater degree of localisation of the pectoralis than in the geologically older *Hipposaurus*.

Proximally, the radius fits fairly firmly in the sigmoid notch of the ulna; proximally, the chief articulation of the epipodial is formed by the radius, which fits on to the rounded capitellum of the humerus; the ulna has a trochlear joint, and its olecranon fits into a deep trochlear fossa when the lower limb is extended; distally, the intercalation of the intermedium further prevents much independent



TEXT-FIG. 7. — *Hipposaurus boonstrai*. S.A.M. Cat. No. 8950. Dorsal view of part of the left fore-limb. $\times \frac{1}{2}$.

- c1, c2 = first and second central.
- H. = humerus.
- i. = intermedium.
- R. = radius.
- r. = radiale.
- U. = ulna.
- u. = ulnare.
- 1-5 = distal carpals.
- I-V = metacarpals.



TEXT-FIG. 8.

Aelurognathus microdon sp. nov. S.A.M. Cat. No. 9344.

- (a) Dorsal view of right humerus. $\times \frac{1}{3}$.
 (b) Ventral view of right humerus. $\times \frac{1}{3}$.
 (c) Anterior view of left fore-limb. $\times \frac{1}{3}$.

Arctognathoides breviceps gen. et sp. nov. S.A.M. Cat. No. 9345.

- (d) Dorsal view of right radius and ulna. $\times \frac{1}{3}$.
 (e) Ventral view of right radius and ulna. $\times \frac{1}{3}$.

Scylacops capensis. S.A.M. Cat. No. 10188.

- (f) Dorsal view of right tibia and fibula. $\times \frac{1}{3}$.
 (g) Anterior view of right humerus, radius, and ulna. $\times \frac{1}{3}$.

c1, c2 = first and second central.

D.P.C.R. = delto-pectoral crest.

ect. = ectepicondylar foramen.

ent. = entepicondylar foramen.

H. = humerus.

i. = intermedium.

R. = radius.

r. = radiale.

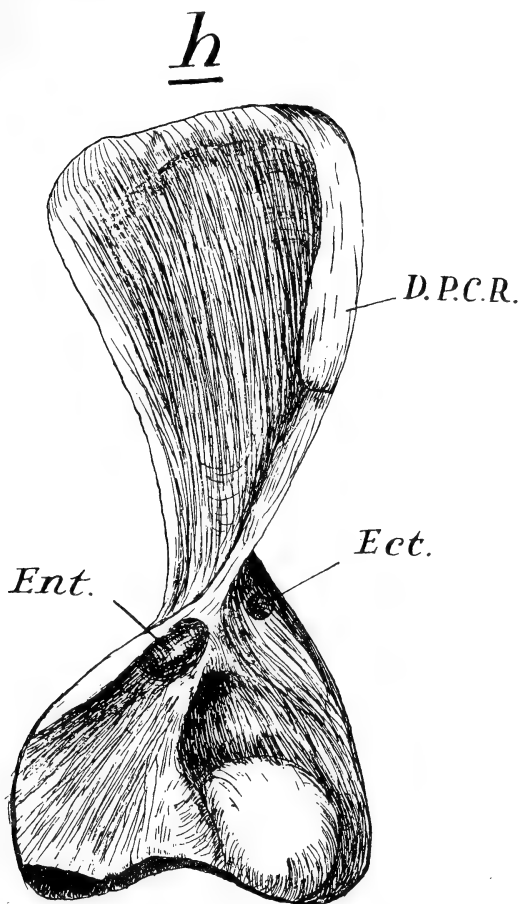
U. = ulna.

u. = ulnare.

1-5 = distal carpals.

movement by either radius or ulna. The proximal post-axial border of the ulna is rugose for a firm insertion of a strong triceps muscle.

The Gorgonopsian manus is known from a number of forms—



TEXT-FIG. 8—continued.

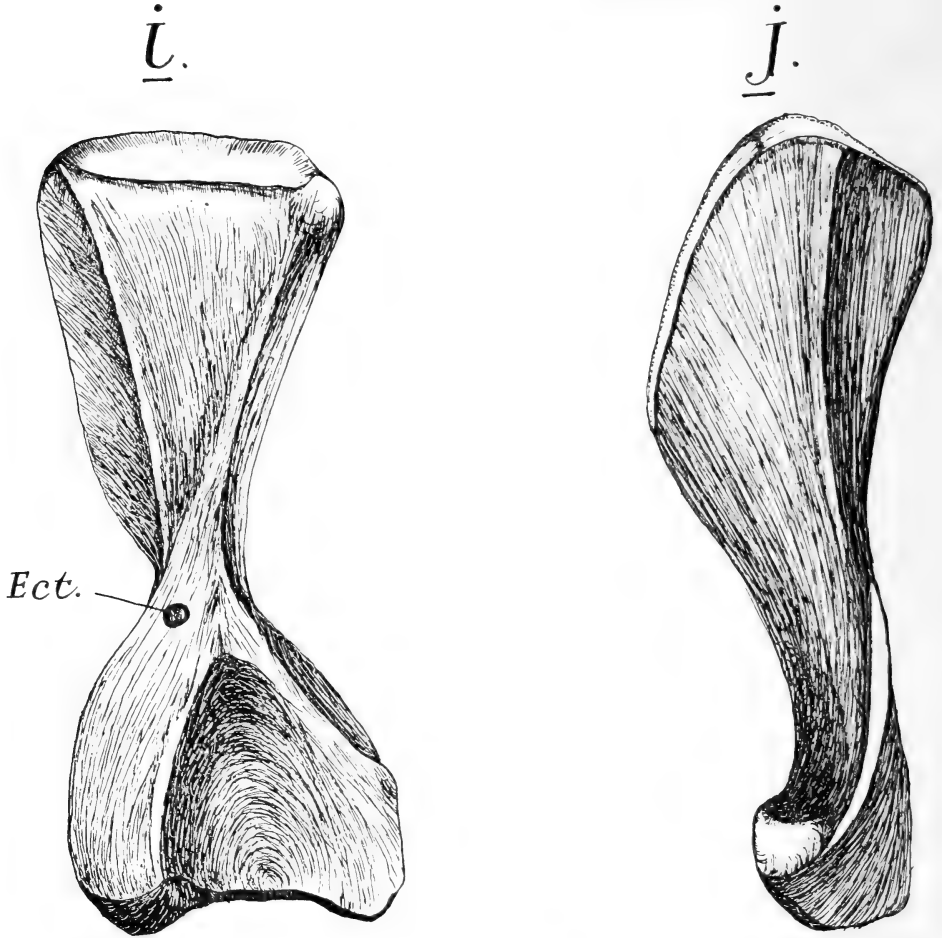
Cynodraco major. B.M.N.H., 47310.

(h) Ventral view of left humerus. $\times \frac{1}{2}$.

Lettering as on previous page.

Aelurognathus tigriceps, *A. microdon*, *Lycaenodontoides bathyrhinus*, *Lycaenops ornatus*, and *Hipposaurus boonstrai*—in which it is either partly, or, in two cases, practically completely preserved. The carpus consists of three rows of elements and has the formula 3, 2, 4 or 5; in the proximal row there are radiale, intermedium, and

ulnare, with a space between them for the perforating carpal canal; in the central row two well-developed centrals are present; in the



TEXT-FIG. 8—continued.

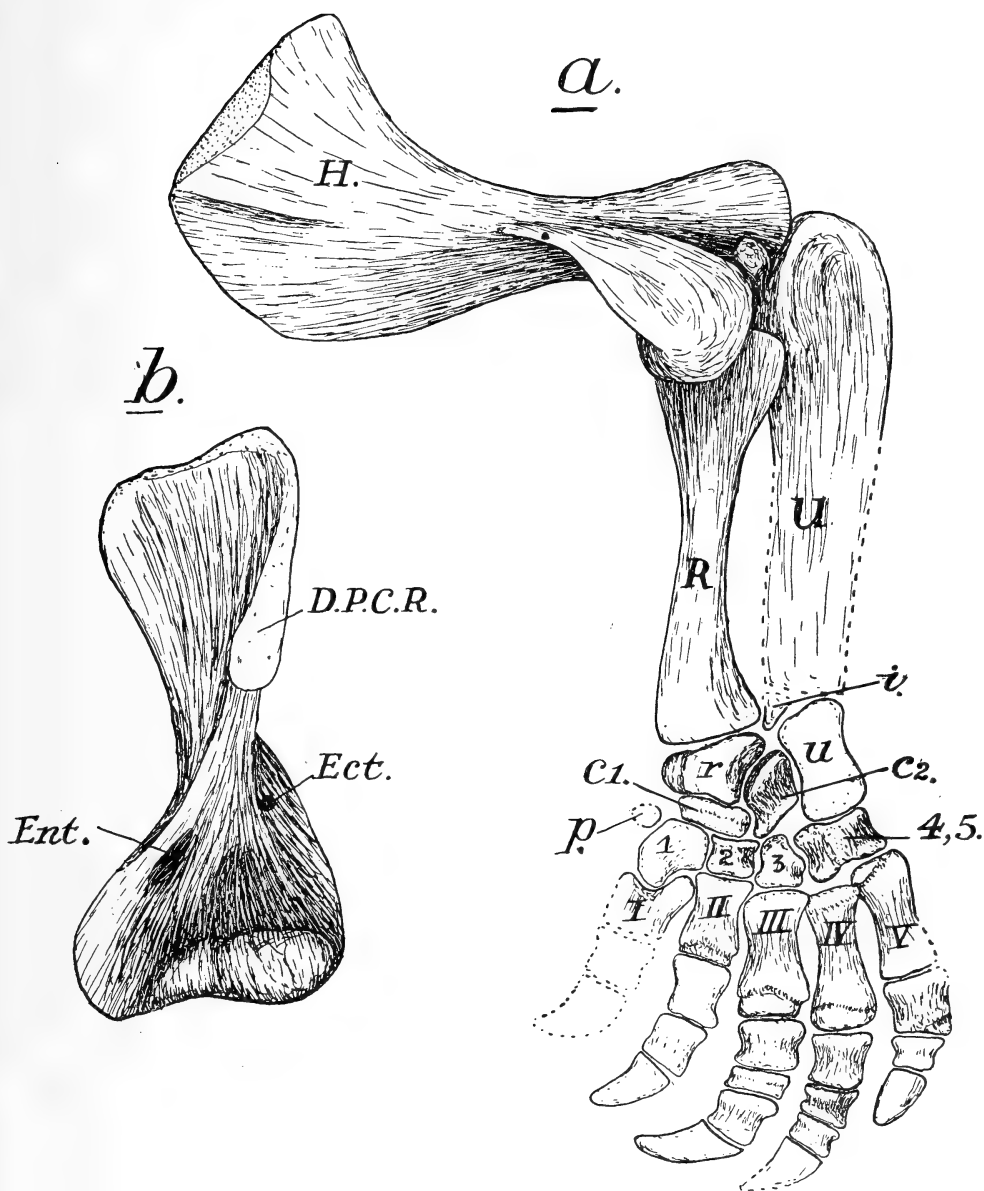
Cynodraco major. B.M.N.H., 47310.

(i) Dorsal view of left humerus. $\times \frac{1}{2}$.

(j) Preaxial view of left humerus. $\times \frac{1}{2}$.

Lettering as on page 160.

distal row there are 4 bones in *Aelurognathus*, *Lycaenops*, and *Hipposaurus*, but in *Lycaenodontoides* the 4th and 5th distals are not fused, so that here 5 bones are present; this was noted by Haughton in *Lycaenodontoides*, and I have re-examined the type-material and find that there is definitely an unfused 5th distal; in *Lycaenops*,



TEXT-FIG. 9.—*Aelurognathus tigriceps*. S.A.M. Cat. No. 2342. $\times \frac{1}{3}$.

(a) Anterior view of left fore-limb.

(b) Ventral view of left humerus.

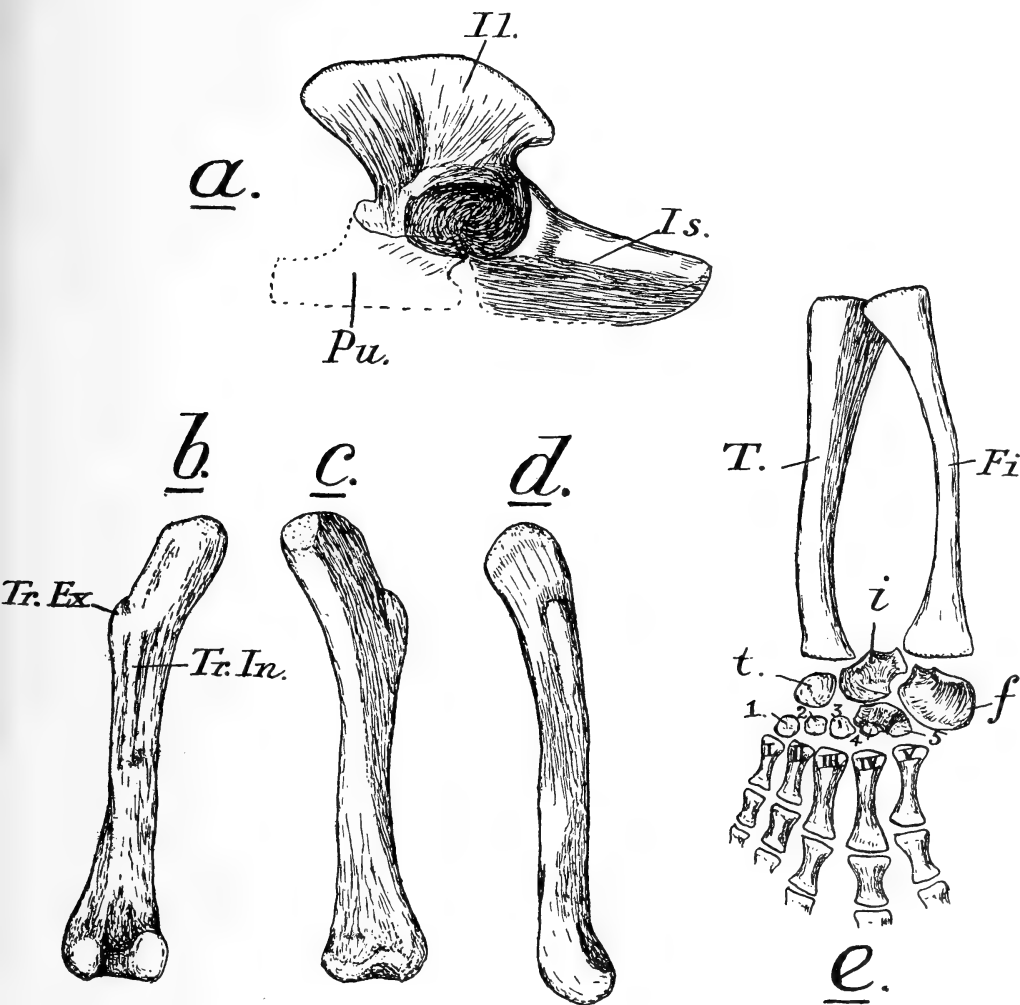
c1, c2 = first and second central.
D.P.C.R. = delto-pectoral crest.
ect. = ectepicondylar foramen.
ent. = entepicondylar foramen.
i. = intermedium.

p. = rudiment of a prepollex (radial
sesamoid).
r. = radiale.
u. = ulnare.
1-5 = distal carpals.
I-V = metacarpals.

Broom has recorded a fully preserved pisiforme, and in *Aelurognathus tigriceps* a piece of bone representing the pisiforme is preserved. In no Gorgonopsian is the whole acropodium preserved; in *A. tigriceps* 4 digits are preserved, in *Lycaenops* 4 digits, some lacking the claw phalanx, and in *Lycaenodontoides* only the 3rd and 4th digits are complete. In *A. tigriceps*, Broom gave the formula 2, 3, 4, 5, 3, and subsequently the same formula was advanced for *Lycaenops*; Haughton has given the formula ?, ?, 3, 3, ? for *Lycaenodontoides*, and an examination of this material shows that Haughton's figures are correct. It is only recently that I have adequately removed the matrix from the beautifully preserved manus of *Aelurognathus tigriceps*. The metacarpals are as figured (fig. 9, a); they have curiously formed ends; distally, in particular, they look very much like epiphyses; the 5th is of complex shape, the 4th squat, and the others elongated; the phalangeal formula I find to be 2?, 3, 4, 4, 3. In the 4th digit the second phalanx is deeply constricted, but very careful preparation has revealed that it is a single bone, and not two separate elements as Broom thought. The question now arises whether Broom is correct in figuring two short elements as the 2nd and 3rd phalanges of the 4th digit in *Lycaenops*. I have not seen this material, but on the facts at my disposal I think that in *Lycaenops* the 4th digit only possessed 4 segments. Both in *Lycaenops* and *A. tigriceps* the 2nd phalanx of the 3rd digit is very short, and it appears probable that in this digit the number of phalanges is undergoing reduction. In this case it is of great interest to note that in *Lycaenodontoides* both the 3rd and 4th digits possess only 3 segments.

The chief measurements are :

	<i>Hipposaurus boonstrei</i> , S.A.M. Cat. No. 8950.	<i>Aelurognathus microdon</i> , S.A.M. Cat. No. 9344.	<i>Arctognathoides breviceps</i> , S.A.M. Cat. No. 9345.	<i>Scylacops capensis</i> , S.A.M. Cat. No. 2343.	<i>Aelurognathus tigriceps</i> , S.A.M. Cat. No. 2342.	<i>Scylacops capensis</i> , S.A.M. Cat. No. 10188.
<i>Length of :</i>						
Humerus	174	159	144?	111	226	90?
Radius	127	111	101	?	162	83
Ulna	147	123	111	?	200?	93
<i>Width across :</i>						
Epicondyles of humerus . . .	44	57	75?	50	113	35
Proximal expansion of humerus	47	61	60	43	121	33?
Minimum of humeral shaft . .	16	17	21	12	32	14
Proximal end of radius . . .	23	28	32	?	51	18
Distal end of radius	17	24	25	?	44	17
Proximal end of ulna	31	38	37	?	65	24
Distal end of ulna	19	21	20	?	?	15



TEXT-FIG. 10.—*Aelurognathus microdon* sp. nov. S.A.M. Cat. No. 9344.

- (a) Lateral view of left half of the pelvis. $\times \frac{1}{3}$.
 (b) Left femur, ventral. $\times \frac{1}{3}$.
 (c) „ „ dorsal. $\times \frac{1}{3}$.
 (d) „ „ posterior. $\times \frac{1}{3}$.
 (e) Left hind limb, dorsal. $\times \frac{1}{3}$.

F. = femur.

f. = fibulare.

Fi. = fibula.

i. = intermedium.

T. = tibia.

t. = tibiale.

Tr.Ex. = external trochanter.

Tr.In. = internal trochanter.

1-5 = distal tarsals.

I-V = metatarsals.

Pelvic Girdle (fig. 10, a).

Hitherto the pelvis of the Gorgonopsia was known in only two forms—*Lycaenops ornatus* and *Inostrancevia alexanderi*. In the former only the ilium is perfectly preserved—both the pubis and ischium have parts missing. In *Aelurognathus microdon* the left ilium is perfect, whereas on the right side only the internal face with the distal ends of the three sacral ribs in position is well shown; the left and part of the right ischia are preserved; only the acetabular portion of the right pubis is preserved. The ilium is vertical, long, and low, and forms more than half of the acetabulum; the main sacral suspension is pre-acetabular; the anterior process of the iliac blade extends far anterior to the acetabulum (strong ilio-femoralis) whereas the posterior process is in line with the posterior edge of the acetabulum (tail extensors of medium strength); the acetabulum is directed outwards. The ischium is long, but the ischial tuberosity does not appear to be strong; the symphysis is weak, but the upper edge is rounded and thickened; it forms less than $\frac{1}{4}$ of the acetabulum, and is not strongly fused with the ilium. The pubis forms considerably less than $\frac{1}{4}$ of the acetabulum; its articulation with the ilium and ischium is weak; it is of great antero-posterior length—in this respect differing greatly from Deinocephalians and Cynodonts. In *Hipposaurus* the crest of the right ilium is preserved, and on the left the ischium and pubis and acetabular portion of the ilium are preserved. Unfortunately, however, the pes overlies most of the left ischium and cannot be removed without destroying it. The ischium and ilium do not differ greatly from that of *Aelurognathus*. The ilium of both these genera differ from that of *Lycaenops*, where the anterior and posterior iliac processes are of equal length. In the pubis of *Hipposaurus* the foramen is not encircled by bone, but is really a notch in the pubis to which the ischium forms the posterior border; medially it appears to be open, and appears to be confluent with its fellow of the other side; unfortunately the specimen is not very well preserved, so that some uncertainty exists. In *Lycaenops* the foramen is also not encircled by bone in the specimen as preserved, but Broom thought that in life a typical pubic foramen was present. In view of the known condition in *Hipposaurus*, it would appear that the Gorgonopsia possessed a pubo-ischiadic fenestra and no pubic foramen (homologous to the “obturator foramen” of Mammals, which includes the real obturator foramen merged with the pubic foramen). The upper border of the pubis is very much thickened in *Hipposaurus*, and from this shaft-like edge a

thin flange of bone proceeds medially to meet its fellow in a very weak symphysis.

The chief measurements are:

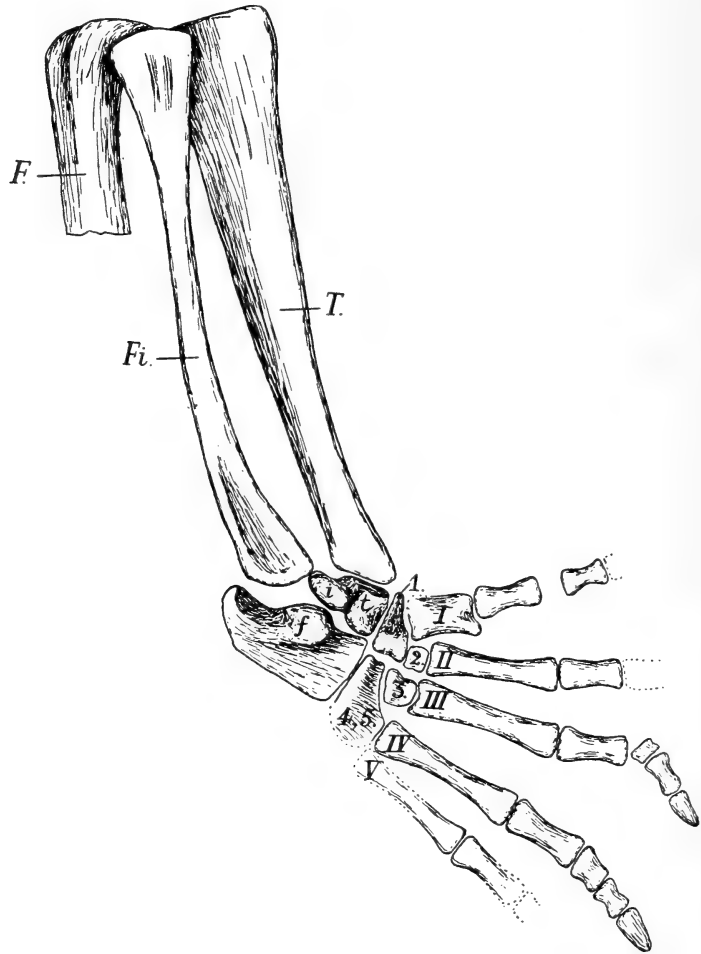
	<i>Hipposaurus boonstrai.</i>	<i>Aelurognathus microdon.</i>
	S.A.M. Cat. No. 8950.	S.A.M. Cat. No. 9344.
Length of ilium	64	102
„ ischium	65	82
„ pubis	56	?
„ acetabulum	32	41
Height of ilium from the acetabular border	?	49

Hind Limb (figs. 10, 11).

In the American Museum of Natural History the pelvis and both hind limbs of a specimen referred by Broom to ? *Aelurosaurus felinus* is preserved. The femur has been figured by Williston (Osteology of the Reptiles, fig. 132, b). In *Lycaenops* the hind limb has been shortly described and only an indifferent figure of the limb has been published, together with a reconstruction of the pes. In *Aelurognathus microdon* a beautiful hind limb, lacking only the distal phalanges, is preserved. In *Hipposaurus boonstrai* the complete right hind limb was preserved, but has unfortunately been damaged in preparation due to the intractable nature of the matrix.

The hind limb is appreciably longer than the fore limb, and as its elements, particularly the femur, are much more slender, an appearance of still greater length is created. The femur is a long slender bone with a long shaft and unexpanded ends, which are only slightly "twisted" on the shaft; the proximal end is directed preaxially, and its articulatory face is rounded (it is more elongated in ? *Aelurosaurus*); There is no "neck," but there is a slight notch on the proximal post-axial edge between the proximal surface and the external (major) trochanter; this trochanter is situated far proximally, and continues distally as a narrow flange for the gluteal muscles; on the ventro-postaxial surface a low ridge represents the internal trochanter, which is much less prominent than in Therocephalians and Cynodonts; there is no intertrochanteric fossa, and the m. pubo-ischio-femoralis externus

must have been weak; distally the condyles are not separated by a deep intercondylar sulcus; on the ventro-distal surface there is a fairly deep popliteal fossa; on the dorso-distal surface there is a slight



TEXT-FIG. 11.—*Hipposaurus boonstrai*. S.A.M. Cat. No. 8950. Right hind limb, dorsal view. $\times \frac{1}{2}$.
Lettering as in previous figure.

depression, so that it would appear that the femora-tibial muscle was weak. It is evident from the points raised in the structure of the femur that in the *Gorgonopsia* the body was not slung in between the hind limbs, but, on the contrary, the gait must have been more or less upright, and the locomotory movements executed with considerable

agility. The epipodial, though long and slender, is shorter than the propodial; the fibula has a long thin shaft with relatively greatly expanded ends, and it has a strong postaxial curvature, and as the tibia also had a slight preaxial curvature the spatium interosseum is great; the tibia has a widely dorso-ventrally expanded proximal end, but its distal expansion is weak; its cnemial crest is not strongly developed; proximally both elements articulate with the distal end of the femur; the articulation of the tibia is the stronger, but the fibula directly receives the femur and does not form a sliding joint on to the postaxial femoral epicondyle; distally the articulation with the tarsus is not a very firm one—a considerable amount of cartilage must have been developed. The tarsus of *Lycaenops* has been described by Broom; he found that the epipodial articulated with only two elements in the proximal row of the tarsus; these he thought were the astragalus and calcaneum; distally, on the radial side a navicular was intercalated between the proximal row and the 4 distal tarsals. In *Aelurognathus microdon* (fig. 10, *a*) I have found 3 proximal elements and 4 distals; the fibula articulates with a large flattened fibulare which is, antero-postaxially, thin and plate-like; intercalated between the ends of the tibia and fibula a remarkably shaped bone, carrying three facets, is present; this I consider to be an intermedium, although it is possible that it is a composite element consisting of a fused intermedium and tibiale; distal to the end of the tibia there lies a pebble-like bone which I have identified as the tibiale, although it must be admitted that it does not actually lie articulated to the tibia and may possibly have fitted in between the intermedium and the distal tarsals and would then have the topographical relations of a centrale (navicular). There are 4 distals, but the shape of the 4th clearly indicates that it is a composite bone consisting of a conjoined 4th and 5th distal tarsal. In *Hipposaurus boonstrai* (fig. 11), which comes from the *Tapinocephalus* zone, there are only two proximal tarsal elements; articulating with the fibula there is a large element of very distinctive shape and having a strong heel-like spur; articulating with the tibia there is a composite element, dorsally carrying two rounded bosses; this element I identify as a conjoined intermedium and tibiale, although I admit the possibility that it may be composed of the intermedium and centrale (navicular). The position I have taken up here gives rise to some points of interest—in the geologically older *Hipposaurus* there are only two elements in the proximal row, whereas in the younger *Aelurognathus* there are three; such a position would be contrary to evolutionary theory. If, on the other hand,

the element identified as the tibiale in *Aelurognathus* is really the centrale (navicular), the same objection could be raised since in *Hipposaurus* there is no centrale (navicular). I see no way of clearing up this difficulty, and am content to await some further discoveries of Gorgonopsian tarsi before deciding one way or the other.

In respect of the distal tarsals of *Hipposaurus* there are also some interesting possibilities. As preserved there are 4 elements; the 4th element, as is generally the case in Therapsids, is large and obviously composite, and includes the 4th and 5th distal tarsals, but as it also stretches proximally to the 3rd distal it appears probable that it may also include a centrale (the 2nd); contrary to the general condition in Therapsids the 1st distal is a large bone, and as it stretches proximal to the 2nd distal tarsal it may be fused to a centrale (the navicular?). According to this view it would appear that in the tarsus of *Hipposaurus* we have some evidence which tends to show that in the ancestors of the Gorgonopsia the tarsus was composed of three proximal elements (tibiale, fibulare, and intermedium), two centrals, and 5 distal tarsals.

In no Gorgonopsian are all the digits preserved; in *Lycaenops* the 1st digit has 2 segments; in *Hipposaurus* the 3rd digit has 4 segments, and the 4th also has 4 segments. Broom's reconstruction of the pes of *Lycaenops*, with the phalangeal formula 2, 3, 4, 5, 3, is, in view of the condition in *Hipposaurus*, probably incorrect. The Gorgonopsian phalangeal formula must, on the facts at our disposal, be taken as 2, 3, 4, 4, 3. The 2nd phalanx of the 3rd digit of *Hipposaurus* is much reduced, and it is probable that in the geologically younger form it is lost, and the phalangeal formula would then be 2, 3, 3, 4, 3.

The chief measurements are:

[TABLE

	<i>Hippo- saurus boonstrai.</i>	<i>Aeluro- gnathus microdon.</i>	<i>Scylacops capensis.</i>
	S.A.M. Cat. No. 8950.	S.A.M. Cat. No. 9344.	S.A.M. Cat. No. 10188.
<i>Length :</i>			
Femur	167 ?	176	?
Tibia	159	136	95
Fibula	162	137	95
4th metatarsal	41	34	?
<i>Width :</i>			
Proximal end of femur	30 ?	32	?
Distal end of femur	33	34	?
Across the trochanter	30 ?	31	?
Proximal end of tibia	26	41	25
Distal end of tibia	20	27	21
Proximal end of fibula	17	27	9
Distal end of fibula	21	25	12

Comparative Morphological Discussion.

Structurally the vertebral column of the Gorgonopsia stands on a higher developmental niveau than that of the Cotylosaurs in that it no longer possesses the heavy neural arches with low and massive neural spines which are so characteristic of these primitive reptiles. The deeply amphicoelous nature of the centra is, however, primitive, and in the structure of the cervical vertebra many temnospondylous characters are retained. This is, however, applicable to most Therapsids. The Gorgonopsian atlantal arches differ from those of Mammals, Cynodonts, and Titanosuchids in remaining separated, and agree in this character with the Tapinocephalids and Anomodonts. The presence of a dichocoelous atlantal rib is of great interest. No extreme adaptive specialisations such as the development of zygosphenes, zygantra, hyposphenes, hypantra, exapophyses have been observed in the Gorgonopsia. The apparent presence of distinct lumbar vertebrae is of interest. Distinct lumbar vertebrae are known in some Cotylosaurs (*Limnoscelis*, *Labidosaurus*), Pelycosaurs (*Sphenacodon*) and Cynodonts (*Thrinaxodon*). The presence of 27 to 28 presacrals is typical of Therapsids, where this number varies between 23 to 28; and 3 sacrals are a good average for Therapsids where this number varies between 2 to 7.

The shoulder-girdle of the Gorgonopsia is typical of primitive reptiles in containing scapula, coracoid, procoracoid, clavicle, interclavicle, and cleithrum; but in many respects shows advanced characters—the cleithrum is rudimentary and the glenoid is a fairly simple posteriorly directed fossa with only a slight indication of its ancestral “screw-shape.” No acromion is, however, developed as in Anomodonts and Cynodonts. In the geologically older *Hipposaurus*, the great length of the coracoidal plate is more Deinocephalian-like (*Jonkeria*) than in the younger *Aelurognathus* and *Arctognathoides*. A well-ossified sternum is present as in Anomodonts and Therocephalians.

The great length of the pubis in *Hipposaurus* and *Lycaenops* is strikingly different from the condition in other Therapsids where the pubis is invariably much shorter than the ischium. In the Deinocephalians and Anomodonts there is a single opening, the pubic foramen, whereas in Therocephalians and Cynodonts there is a large pubo-ischiadic fenestra; although not well preserved in the known Gorgonopsia, it appears highly probable that a pubo-ischiadic fenestra was developed and was probably confluent with its fellow of the other side.

The humerus is a much slenderer bone with less expanded ends than in the Deinocephalians, Anomodonts, and Cynodonts; the deltopectoral crest is also less developed than in these forms. In some Therocephalians, however, the humerus is even more slender and the shaft longer than in the Gorgonopsia.

The epipodial of the Gorgonopsia is long and slender as in the Therocephalians, whereas in the Deinocephalians it is extremely short.

The Gorgonopsian carpus contains three bones in the proximal row, 2 centrals, and 4 or 5 distals, as in the Cynodonts; the phalangeal formula is 2?, 3?, 3, 3, 3? in *Lycaenodontoides*, in *Aelurognathus* 2?, 3, 4, 4, 3, whereas in the Anomodonts it is 2, 3, 3, 3, 2 and in Cynodonts 2, 3, 3, 3, 3.

The femur of the Gorgonopsia is a long slender bone with a long shaft and unexpanded ends, whereas in the Deinocephalians (except in some undescribed material collected by me at Merweville) and Anomodonts it is short with widely expanded ends; in the Therocephalians and Cynodonts the femur is as in the Gorgonopsia; in the former, however, the internal trochanter is much stronger than in the Gorgonopsia.

In the Gorgonopsian tarsus there are 2 to 3 separate elements in the proximal row; in the middle row 0 to 1; in the distal 4; The phalangeal formula of the Gorgonopsia is 2, 3?, 4, 4, 3?.

BIBLIOGRAPHY.

1. BROOM, R., 1910.—“A Comparison of the Permian Reptiles of North America with those of South Africa,” *Bull. Amer. Mus. Nat. Hist.*, vol. xxviii.
2. BROOM, R., 1910.—“Observations on some Specimens of South African Fossil Reptiles Preserved in the British Museum,” *Trans. Roy. Soc. S. Afr.*, vol. ii.
3. BROOM, R., 1911.—“On some New South African Permian Reptiles,” *P.Z.S.*
4. BROOM, R., 1912.—“On some New Fossil Reptiles from the Permian and Triassic Beds of South Africa,” *P.Z.S.*
5. BROOM, R., 1913.—“On Four New Fossil Reptiles from the Beaufort Series, South Africa,” *Rec. Albany Mus.*, vol. ii.
6. BROOM, R., 1913.—“On the Origin of the Mammalian Digital Formula,” *Anat. Anzeiger*, Band 43.
7. BROOM, R., 1913.—“On the Gorgonopsia, a Sub-order of the Mammal-like Reptiles,” *P.Z.S.*
8. BROOM, R., 1913.—“On some New Carnivorous Reptiles,” *Bull. Amer. Mus. Nat. Hist.*, vol. xxxii.
9. BROOM, R., 1913.—“On a Nearly Perfect Skull of a New Species of the Gorgonopsia,” *Ann. S. Afr. Mus.*, vol. xii.
10. BROOM, R., 1914.—Croonian Lecture “On the Origin of Mammals,” *Phil. Trans. Roy. Soc., B*, vol. ccvi.
11. BROOM, R., 1915.—“On some New Carnivorous Therapsids in the Collection of the British Museum,” *P.Z.S.*
12. BROOM, R., 1915.—“Catalogue of Types and Figured Specimens of Fossil Vertebrates in the American Museum of Natural History. II. Permian, Triassic, and Jurassic Reptiles of South Africa,” *Bull. Amer. Mus. Nat. Hist.*, vol. xxv.
13. BROOM, R., 1921.—“On the Reptilian Tarsus,” *P.Z.S.*
14. BROOM, R., 1925.—“On some Carnivorous Therapsids,” *Rec. Albany Mus.*, vol. iii.
15. BROOM, R., 1930.—“On the Structure of the Mammal-like Reptiles of the Sub-order Gorgonopsia,” *Phil. Trans. Roy. Soc., B*, vol. ccxviii.
16. BROOM, R., 1931.—“Notices of some New Genera and Species of Karroo Fossil Reptiles,” *Rec. Albany Mus.*, vol. iv.
17. BROOM, R., 1932.—“The Mammal-like Reptiles of South Africa,” Witherby, London.
18. BROOM, R., and HAUGHTON, S. H., 1913.—“On a New Species of *Scymnognathus* (*S. tigriceps*),” *Ann. S. Afr. Mus.*, vol. xii.
19. HAUGHTON, S. H., 1915.—“On some New Gorgonopsians,” *Ann. S. Afr. Mus.*, vol. xii.
20. HAUGHTON, S. H., 1918.—“Some New Carnivorous Therapsida, with Notes upon the Brain-case in Certain Species,” *Ann. S. Afr. Mus.*, vol. xii.
21. HAUGHTON, S. H., 1926.—“On Karroo Vertebrates from Nyassaland,” *Trans. Geol. Soc. S. Afr.*, vol. xxix.
22. HAUGHTON, S. H., 1929.—“On some New Therapsid Genera,” *Ann. S. Afr. Mus.*, vol. xxviii.

23. HAUGHTON, S. H., 1932.—“On a Collection of Karroo Vertebrates from Tanganyika Territory,” Q.J.G.S., vol. lxxxviii.
24. LYDEKKER, R., 1890.—Cat. Foss. Rept. Amphibia, British Mus., vol. iv.
25. NOPCSA, F. VON, 1923.—“Die Familien der Reptilien,” Fortschr. Geol. Pal., ii.
26. NOPCSA, F. VON, 1928.—“Palaeontological Notes on Reptiles,” Geol. Hungarica, i.
27. OWEN, R., 1860.—“On some Reptilian Fossils from South Africa,” Q.J.G.S., vol. xvi.
28. OWEN, R., 1876.—Cat. Foss. Rept. S. Afr.
29. OWEN, R., 1876.—“Evidences of Theriodonts in Permian Deposits elsewhere than in South Africa,” Q.J.G.S., vol. xxxii.
30. OWEN, R., 1881.—“On the Order *Theriodontia*, with a Description of a New Genus and Species (*Aelurosaurus felinus*),” Q.J.G.S., vol. xxxvii.
31. PRAVOSLAVLEV, P. A., 1927.—“III, IV. Gorgonopsidae,” Akad. Nauk.
32. PRAVOSLAVLEV, P. A., 1927.—“Relation of the Gorgonopsids of Northern Russia to Mammals,” Ann. Soc. Pal. Russe, vol. i.
33. SEELEY, H. G., 1895.—“Researches on the Structure, Organisation, and Classification of the Fossil Reptilia. Part IX, Section I. On the Therosuchia,” Phil. Trans. Roy. Soc., B, vol. clxxxv.
34. WATSON, D. M. S., 1912.—“On some Reptilian Lower Jaws,” Ann. Mag. Nat. Hist., Ser. 8, vol. x.
35. WATSON, D. M. S., 1913.—“On some Features of the Structure of the Therocephalian Skull,” Ann. Mag. Nat. Hist., Ser. 8, vol. xi.
36. WATSON, D. M. S., 1914.—“Notes on some Carnivorous Therapsids,” P.Z.S.
37. WATSON, D. M. S., 1921.—“The Bases of Classification of the Theriodontia,” P.Z.S.

6. *Additions to our Knowledge of the South African Gorgonopsia, preserved in the British Museum (Natural History).*—By LIEUWE D. BOONSTRA, D.Sc., Palaeontologist to the South African Museum and Queen Victoria Scholar of the University of Stellenbosch.

(With 18 Text-figures.)

THERE is preserved in the British Museum (Natural History) a small, though historically important collection of South African Mammal-like Reptiles of the sub-order Gorgonopsia. In all there are thirty specimens. These have been studied by Owen, Lydekker, Seeley, Broom, and Watson, and have been referred to fifteen genera and sixteen species. As will become apparent in the sequel, some of these so-called species cannot be considered to have been founded on valid characters. There are included, one specimen which apparently comes from the *Tapinocephalus* zone, six species from the *Endothiodon* zone, and nine species from the *Cistecephalus* zone. Considered as a whole, this collection consists of very indifferently preserved material. Quite a number are of a very fragmentary and incomplete nature, and some show practically no structure at all; even the best preserved specimens leave much to be desired. A considerable amount of preparation has been necessary, and the following descriptions are, I believe, as full as the nature of the material warrants.

A. Forms from the *Tapinocephalus* zone.

Cyniscodon lydekkeri, Broom.

The type-specimen is the anterior portion of a small right dentary. It was found on the farm Palmietfontein by T. Bain in 1878; but as there are many farms in the Karroo with this name it is not certain that the specimen represents a form from the *Tapinocephalus* zone. It was found in association with some remains of a small Dicynodont, and was referred by Lydekker to *Cynosuchus suppostus*. Broom in 1915 showed that the dentary was apparently that of a Gorgonopsian. The roots of three incisors, one canine, and four small molars are preserved. Broom was of the opinion that in life four incisors were present; I can find no evidence for this supposition; as preserved,

the first incisor is practically on the anterior edge of the bone and there is no room for an additional tooth. There is no diastema anterior to the canine, which has an oval root and lies lateral to the last incisor. Posterior to the canine, there is a diastema of 7 mm.; the three incisors occupy 7 mm.; the canine measures 6 by 3 mm., and the four molars measure 9 mm. The mentum is deep and square; the depth being 19 mm., and the width 20 mm.

At the present time five types of Gorgonopsia from the *Tapinocephalus* zone are known, viz. *Eoarctops*, *Eriphostoma*, *Galesuchus*, *Hipposaurus*, and *Scylacognathus*. Of these *Eriphostoma* is the only one to which the fragment of *Cyniscodon* can be compared. The nature of the mentum is very similar, but the dentition is quite different. Broom compared it to *Aelurosaurus*, but in this form the mentum is sloping, whereas in *Cyniscodon* it is upright; in addition, there is a considerable difference in the nature of the teeth. The relations of this fragment thus remain unknown.

As this fragment throws practically no light on the nature of the Gorgonopsians of the *Tapinocephalus* zone, it seems a pity that a new genus should have been created for such an unimportant fragment with practically no diagnostic characters. An additional name does not increase our knowledge.

Type, B.M.N.H., 49404, Palmietfontein, Beaufort West?, Cape Province.

B. Forms from the *Endothiodon* zone.

From this zone there are in the collection six forms, viz. *Arctops*, *Aelurosaurus*, *Aelurosauroides*, *Gorgonops*, *Leptotrachelus*, and *Scymnognathus*. Most of these are represented by fairly complete skulls, from which a number of structural details has been determined.

Arctops willistoni, Watson.

(Figs. 1-3.)

This type was collected by A. G. Bain in 1857 at Howse Post, near Fort Beaufort, which locality Watson considered to be in the *Endothiodon* zone; the nature of the matrix suggests the older *Tapinocephalus* zone. In either case, *Arctops* is one of the earlier Gorgonopsians. It consists of the posterior two-thirds of a skull, from which the quadrates and quadratojugals have been lost. Watson in 1914 described and figured the occiput and part of the brain-case, with which account I am in agreement. In 1921 figures and a

description of the dorsal, lateral, and palatal surfaces were published. I have since etched all these surfaces with dilute hydrochloric acid

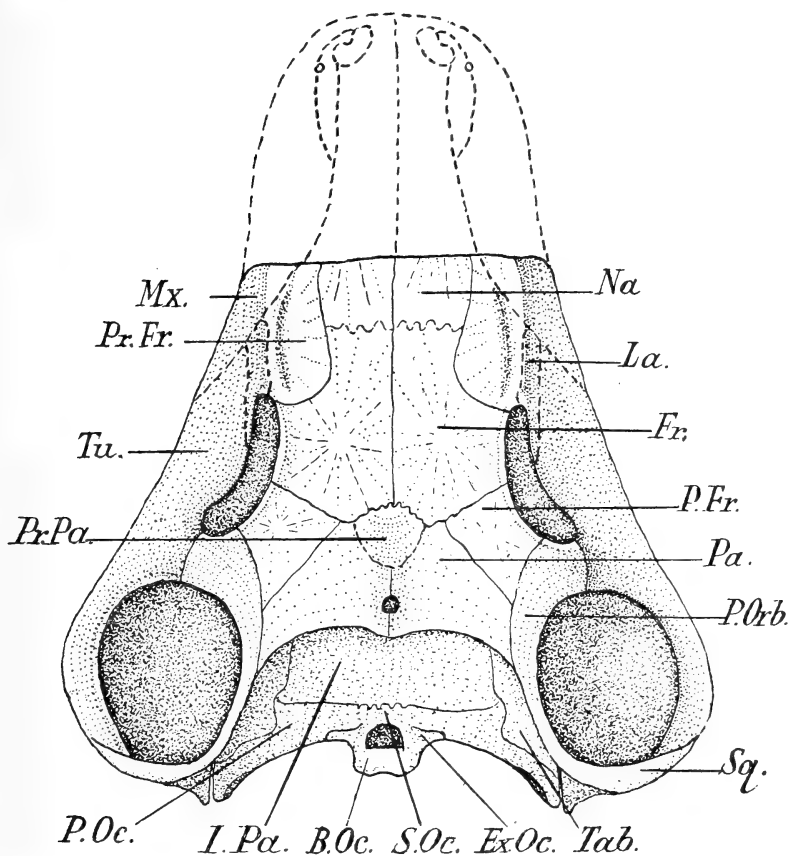


FIG. 1.—*Arctops willistoni*. Type, B.M.N.H., R4099. Dorsal view of the skull. $\times \frac{1}{2}$.

B.Oc. = basioccipital.
Ex.Oc. = exoccipital.
I.Pa. = interparietal.
Fr. = frontal.
Ju. = jugal.
La. = lacrimal.
Mx. = maxilla.
Na. = nasal.
Pa. = parietal.

P.Fr. = postfrontal.
P.Oc. = paroccipital.
P.Orb. = postorbital.
Pr.Fr. = prefrontal.
Pr.Pa. = preparietal.
S.Oc. = supraoccipital.
Sq. = squamosal.
Tab. = tabular.

and developed the brain-case, so that the skull now shows a number of points not determined by Watson. This account is thus purely supplementary.

On the dorsal surface the radiation of the bone-fibres assists materially in determining the limits of the various bones, which are best understood by referring to fig. 1. The short cruciform frontal deserves notice.

On the ventral surface I was able to determine that the palatines meet in the median line, and thus on the palatal surface the pterygoids

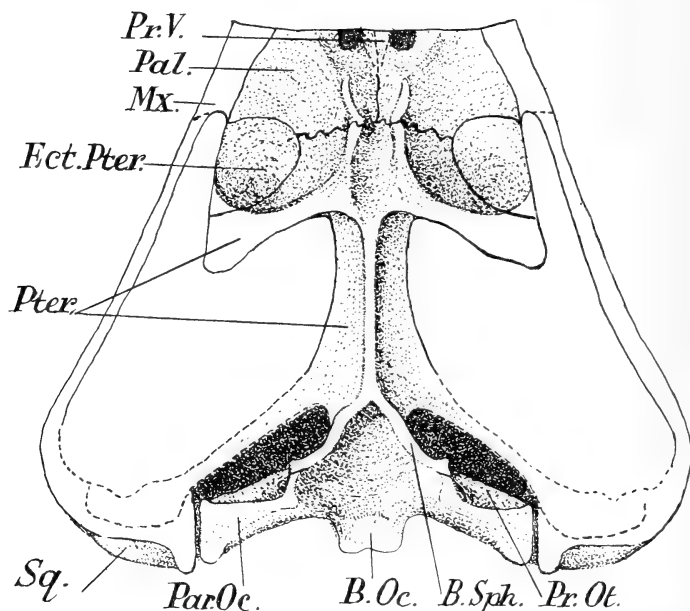


FIG. 2.—*Arctops willistoni*. Type. Ventral view of the skull, modified after Watson. $\times \frac{1}{2}$.

B.Sph. = basisphenoid.
Ect.Pter. = ectopterygoid.
Pal. = palatine.

Pter. = pterygoid.
Pr.Ot. = pro-otic.
Pr.V. = prevomer.

are prevented from meeting the prevomers; on either side of the median line there is a low ridge; enclosed between these ridges is a median groove; just behind the highest part of this ridge the transverse suture, between the anterior pterygoid ramus and the palatines, is clearly seen as a convoluted line lying anterior to a dark line of matrix in a crack, which runs parallel to it and with which it must not be confused; in a parasagittal section the pterygo-palatine suture can also be seen; the suture then continues in lateral direction to meet the ectopterygoidal suture (fig. 2). The ectopterygoid descends to form the anterior corner of the transverse pterygoidal

process, which is much shallower and situated somewhat further posteriorly than in later forms, but it has shifted somewhat forward from the primitive condition. The junction of the prevomers and palatines is not clearly shown, but its nature is indicated in broken lines in the figure. No teeth can be seen on the median palatal ridges, but in analogy with other known forms it is certain that they were present on the palatinal portion of the ridge, but would appear to have been absent on the pterygoidal part. In a longi-

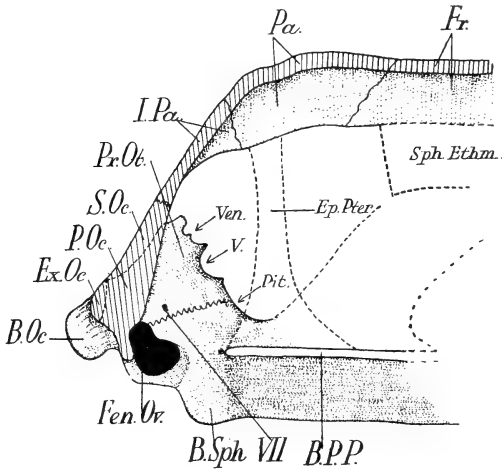


FIG. 3.—*Arctops willistoni*. Type. Lateral view of the right side of the brain-case. $\times \frac{1}{2}$.

B.P.P. = basipterygoid process.	Pit. = pituitary fossa.
Ep.Pter. = epipterygoid.	Sph.Ethm. = sphenethmoid.
Fen.Ov. = fenestra ovalis.	Ven. = venous fossa.
P.Sph. = parasphenoid.	

Roman numerals refer to the foramina for the cranial nerves.

tudinal section, it is seen that the anterior pterygoidal ramus carries a high dorsal keel.

The palate of *Arctops* is thus seen to agree in the essential points of structure with all the forms in which the palate has hitherto been studied, viz. *Scylacops*, *Aelurognathus*, *Arctognathus*, *Lycosaurus*, *Cynariodes*, *Lycaenodon*, *Lycaenodontoides*, and *Arctognathoides*, and, as I hope to show later in this paper, with *Gorgonops*, *Aelurosaurus*, *Aelurosauroides*, and *Scymnognathus*. In all these forms there is no evidence whatsoever of a median unpaired bone in the anterior part of the palate.

The basicranial region is not very well shown; the basisphenoidal

tubera are present as high narrow ridges with a broad deep groove in between; posteriorly, it rests on ridge-like tubera of the basioccipital, and it forms the anterior border of the fenestra ovalis; anteriorly, the limits of the basisphenoidal portion of the median keel and the basipterygoidal processes cannot be determined. Although I have gone to considerable trouble to expose the lateral surface of the brain-case on the right side, the result is rather disappointing. The posterior part of the quadrate ramus of the pterygoid is lost, and portions only of the epipterygoid, which rested on it, can be indistinctly seen; it has also been impossible to expose the sphenethmoidal part of the brain-case satisfactorily. Posteriorly, the broad anterior end of the basioccipital and the widely diverging basisphenoidal tubera produce a roomy floor to the brain-case; the skull is also high in this region, but due to the shortness of the parietal, the frontal with the sphenethmoid attached to its ventral surface lies far back, thus producing an extremely short hind brain. The pro-otic stands on the basisphenoid and lies against the anterior face of the paroccipital in the usual manner; it is, however, an extremely small bone, which stretches very little in anterior direction, and dorsally extends for less than half the height of the occiput. It would thus appear that in *Arctops* a considerable part of the otic region did not ossify. In *Leptotrachelus* and *Scymnognathus* the pro-otic is higher and longer, and, in the forms from the *Cistecephalus* zone (e.g. *Cynariops*), it is very much higher and longer. The lateral opening into the pituitary fossa, the notch for the fifth nerve, and the venous notch above it are situated far back and low down; the latter two openings have no ossified anterior borders as have the later forms. In sagittal section it is seen that the spur of the basisphenoid, forming the posterior border of the pituitary fossa, is well developed. The fenestra ovalis is large and irregular, and is on the level of the basioccipital condyle. Posteriorly, neither the supraoccipital nor the interparietal send flanges to contribute to the walls of the brain-case, as they do in later forms. In the median line the occiput is extremely thin. The parietal sends down two lateral flanges, with which the rod-like epipterygoids presumably articulate. Lying ventral to the frontals, parts of the sphenethmoidal portion of the brain-case can be seen. Unfortunately the epipterygoid is not preserved; if it were rod-like, as in all known Gorgonopsians, the sides of the middle portion of the brain-case would be largely unenclosed by bone, i.e. the *cavum epiptericum* is not yet included within the cranial cavity.

The main morphological features are:

Primitive. Square section of the snout; laterally directed orbits; very small lateral temporal openings; sides straight; basioccipital large; strong paroccipital; fenestrae ovals far apart; basisphenoid massive, but with deep edge-like tubera; pro-otic small; pineal foramen situated far posteriorly; preorbital depression; frontal forms large part of the orbital border; little ossification of the side-walls of the brain-case; wide parietal region.

Advanced. Pterygoid flanges not far posteriorly; skull slightly wider than high; flat laterally-placed basipterygoid processes; maxilla apparently fairly deep; basisphenoidal tubera edge-like; occiput fairly upright, but not concave.

From this summary it is evident that *Arctops*, although advanced beyond the Pelycosaurian and Deinocephalian stage, is one of the more primitive *Gorgonopsians*.

Chief measurements :

Pineal foramen to edge of occipital plate	9 mm.
Width across the squamosals	185 „
Interorbital width	64 „
Intertemporal width	89 „
Width across lateral pterygoid flanges	100 „
Height of snout	60? „
Height of occiput	80 „

Type, B.M.N.H., R4099, Howse Post, Fort Beaufort, Cape Province.

Gorgonops torvus, Owen.

(Fig. 4.)

This is the type species, and was found by A. G. Bain in 1853 at Mildenhalls, near Fort Beaufort. This locality probably is in the *Endothiodon* zone; another specimen, in the American Museum, comes from an undoubted *Endothiodon* zone locality, and we may thus consider *Gorgonops* to be a form from that zone. The type is a good skull which lacks the temporal arches and the mandibles; the occiput and posterior half of the ventral surface are not clearly shown, and in general the surface has been somewhat stripped by former developers.

Owen's lithographs are beautiful illustrations of the outward appearance of the skull as preserved.

Watson's account (1921) of the dorsal and lateral surfaces is correct; anterior to the pineal foramen, a large preparietal, which was not

figured by Watson (fig. 4), is present; his interpretation of the relations of the septomaxilla, maxilla, and the premaxilla is correct.

With regard to the palate, I am in agreement with Watson as to his interpretation of the relations of the premaxilla and the prevomers, and also as to the posterior intercalation of the prevomers; but my

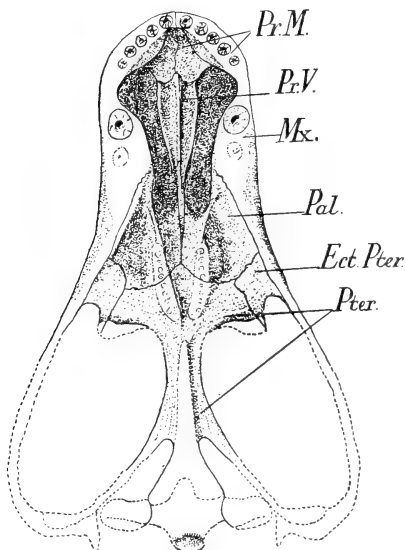


FIG. 4.—*Gorgonops torvus*. Type, B.M.N.H., R1647. Ventral view of the skull, modified after Watson. $\times \frac{1}{3}$.

Pr.Mx. = premaxilla.

interpretation of the relations of the palatines, pterygoids, and ectopterygoids is totally different. The posterior slip-like prolongation of the prevomers is clasped in the median line by the two palatines lying laterally; from the posterior tip of the prevomers a median suture proceeds in posterior direction for a short distance; it then bifurcates and each branch continues in postero-lateral direction, crossing the ridge, that borders the median groove at its lowest part, to meet the ectopterygoid suture. According to this interpretation, the pterygoids are ventrally excluded from the posterior borders of the internal nares; whereas, according to Watson, the pterygoids stretch far for-

ward and are intercalated between the palatines, which do then not meet in the median line. The limits of the ectopterygoids are not clearly visible, but I am inclined to think that they descend further down the pterygoid flanges than figured by Watson.

The ridges bounding the median palatal groove are not well preserved; but although no teeth are visible, in life they were probably present on both the pterygoid and palatal portions of these ridges. Watson has maintained that the roof of the posterior part of the median groove is formed by a distinct element—the vomer—which is, of course, quite distinct from the prevomer. In *Gorgonops* there is no evidence of any posterior limit to this part of the roof of the median vault, which would definitely separate it from the rest of the pterygoid. My interpretation of the palate of *Gorgonops* is thus in agree-

ment with the condition found in the nine *Gorgonopsian* genera mentioned above.

The main morphological features of *Gorgonops* are:

Primitive. Square section of the snout; laterally directed orbits; slightly sloping occiput; tooth row straight and step in alveolar border; very small lateral temporal openings; basioccipital large; posterior position of the pineal foramen; preorbital depression; frontals form large part of orbital border; large postfrontals.

Advanced. Pterygoid flanges not far posteriorly; slightly cupped occiput; sides of skull not straight; snout wider than high; maxilla deep; flat basipterygoid processes laterally placed.

As far as the skull of *Gorgonops* is known, it is quite as primitive as *Arctops*, but as the region of the nostril is absent in the latter, and the brain-case is unknown in the former, further discussion would not be profitable.

Chief measurements:

Length from basioccipital to premaxilla	210 mm.
Length from premaxilla to pineal foramen	170 „
Length from pineal foramen to edge of occipital plate	14 „
Length from premaxilla to front of orbit	111 „
Width across squamosals	120? „
Interorbital width	60 „
Intertemporal width	68? „
Width across the canines	60 „
Width across pterygoid flanges	72? „
Height of snout	50 „
Height of occiput	45 „
Diastema	14 „
Incisor series	34 „

Type, B.M.N.H., R1647, Mildenhalls, Fort Beaufort, Cape Province.

Scymnognathus whaitsi, Broom.

(Fig. 5.)

There are in the collection three specimens of this species, which have been described by Watson. All come from the *Endothiodon* zone of Beaufort West.

In R4052 it is possible to determine from the weathered fragments the nature of the snout and the dental formula (i. 5, c. 1, m. 4 or 5), as fully described by Watson. The material is, however, not sufficiently well preserved to enable one to state with certainty what the relations

of the prevomers, palatines, and pterygoids are. Watson's figure of this part is based on inconclusive evidence, and I have no doubt that better preserved material will show that, in this region, *Scymnognathus* agrees with other Gorgonopsians, viz. that the palatines meet in the median line, that the pterygoids do not meet the prevomers, and that there is no unpaired median bone.

An imperfect weathered axis is the basis on which this element was

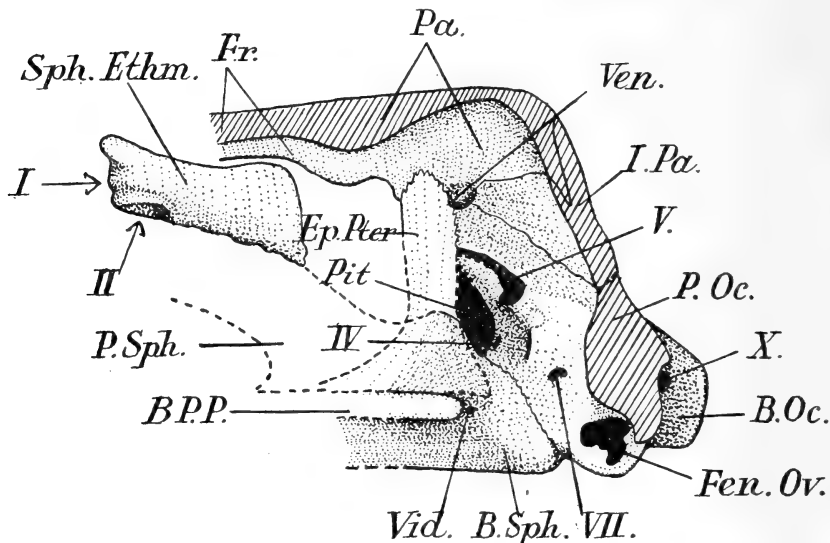


FIG. 5.—*Scymnognathus whaitsi*. B.M.N.H., R4053. Lateral view of the left side of the brain-case, modified after Watson. $\times \frac{2}{3}$.

Vid. = Vidian foramen.

figured by Watson. The anterior cervicals are much better shown in *Hipposaurus*, *Aelurognathus*, and *Arctognathoides* recently described by me, and these show that Watson was correct in his restoration.

Watson's figures of the sectioned snout (49369) are correct. In fig. 12, No. 7, the inner pair of strips labelled "pterygoid" are open to discussion. There is no doubt as to their presence as separate strips of bone; what must be decided is whether they represent the anterior extremities of the pterygoids or not. If they do, it means that the palatines do not meet in the median line and that the pterygoids meet the prevomers, which would be contrary to the condition in at least nine other Gorgonopsia. I believe that the explanation is that they represent a dorsal pterygoidal girder which is not exposed in ventral view.

In R4053 the back portion of the skull is fairly well preserved; the proatlas and the axial centrum are well shown *in situ*; and the structure of the occiput and the greater part of the brain-case can be determined. From the material in the collection I have been fortunate enough to develop the brain-case in three different genera—*Cynariops*, "*Lycaenodon*," and *Arctognathus*—and comparing these to the figure of the brain-case of *Scymnognathus* published by Watson, some very disturbing differences were noticed. Re-examining the specimen in the light of this new knowledge, an interpretation different to that of Watson was arrived at. In the figure it is shown that the pro-otic is a much larger bone than Watson thought; its ventral limit is marked by a suture, which runs from behind the basisphenoidal tubera to the edge of the lateral opening into the pituitary fossa; dorsally, it extends right up to the parietal and interparietal and forms the ventral and dorsal borders of the notch (or foramen?) for the fifth nerve, and the ventral border of the venous fossa; it is this dorsal part that Watson, as I believe in error, considered to be supraoccipital. The foramen for the sixth nerve is extraordinarily large, and lies ventro-posteriorly of the notch for the fifth nerve; it has a depression below it. The foramen for the seventh nerve lies in advance of the fenestra ovalis, and below it is a depression for the geniculate ganglion. In the specimen the basiptyergoid process has been forced upwards, and in the figure its normal horizontal position is restored; behind this process lies an opening—the Vidian foramen.

The chief morphological features are:

Primitive. Laterally directed orbits; sloping occiput; slender epiptyergoid; large basioccipital; fenestrae ovales far apart; basisphenoidal tubera fairly large, but edge-like; step in maxillary border.

Advanced. Snout somewhat broader than high and not square in section; ptyergoid flange has shifted forward; basiptyergoid process laterally situated; parietal enters brain-case; pro-otic fairly large; pineal foramen not posteriorly situated; practically no preorbital depression; frontal forms only small part of orbital border; maxilla deep; paroccipital not massive; basisphenoidal tubera situated more anteriorly than in *Arctops*; squamosals widened, and thus increase in size of temporal openings; occiput concave.

A consideration of all these characters tends to show that *Scymnognathus*, although retaining some primitive characters in common with *Arctops* and *Gorgonops*, does show a definite advance over them.

Scymnognathus sps.

In the collection is a specimen found by Professor D. M. S. Watson in 1915; he did not think it worth describing, but Broom, in a paper; which consists of a number of specific descriptions based on absolutely impossible material, created a new species—*S. parvus*. The type is a weathered skull, very badly crushed; nothing can be made out of the palate, occiput, or lateral surface; on the dorsal surface a few sutures are visible. The dental formula is as for the genus—i. 5, c. 1, m. 4; the posterior edges of the incisors and canines have very definite fine serrations, whereas, on the last molar, which alone is fairly well preserved, there are some indefinite grooves which may be serrations.

I do not think that the specimen is sufficiently well preserved to warrant the creation of a new species; the few characters that can be determined are sufficient only to identify the genus, and there are no valid characters to differentiate it from the other species of *Scymnognathus*.

B.M.N.H., R4139, Kuilspoort, Beaufort West, Cape Province.

There is another specimen consisting of a fragment of a left maxilla, which shows the dental formula—i. 4 or 5, c. 1, m. 3, and has a distinct step anterior to the canine. This has, I believe, been correctly identified by Broom as *Scymnognathus* sp.

B.M.N.H., R3611, Karroo.

Leptotrachelus eupachygnathus, Watson.

(Figs. 6-7.)

Although somewhat distorted, the skull shows a considerable portion of its structure, and this has been fully described by Watson. The dental formula, which is the same as in *Scymnognathus whaitsi*, is i. 5?, c. 1, m. 4 or 5. There is no evidence as to the nature of the crowns, and no definite evidence of a step in the alveolar border as Watson's figure would imply. I have refigured the dorsal aspect of the skull, for, as Watson has admitted, the snout as reconstructed by him is too long and narrow. The position of the pineal foramen has also been determined.

I have refigured the brain-case in order to indicate the position of the basisphenoidal-pro-otic suture, the depression which apparently leads into a venous fossa, and the probable position of the foramen for the sixth nerve. Above the notch for the fifth nerve the bone has

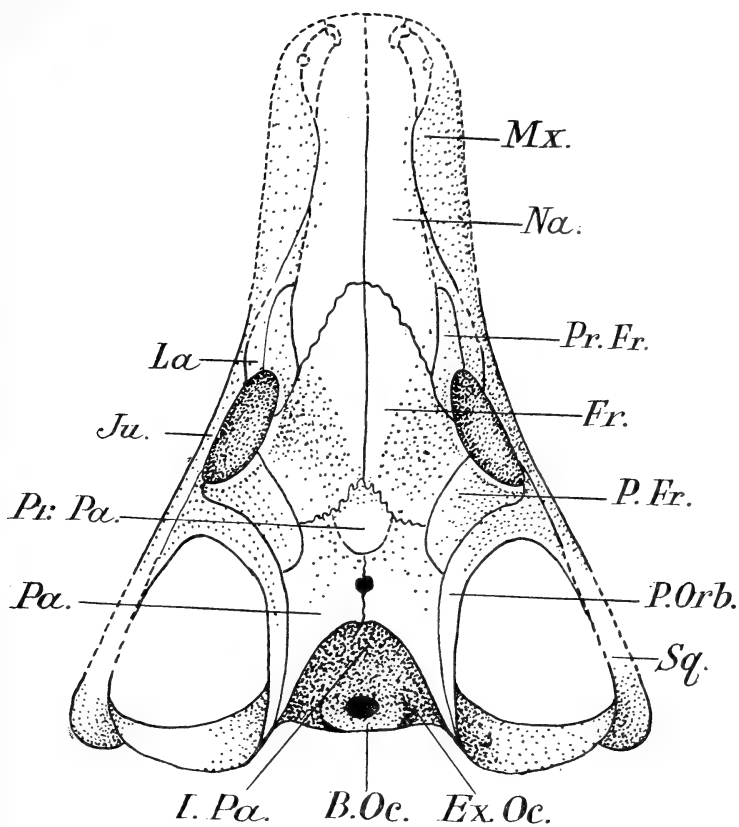


FIG. 6.—*Leptotrachelus eupachygnathus*. Type, B.M.N.H., R4051. Restored dorsal aspect of the skull. $\times \frac{1}{2}$.

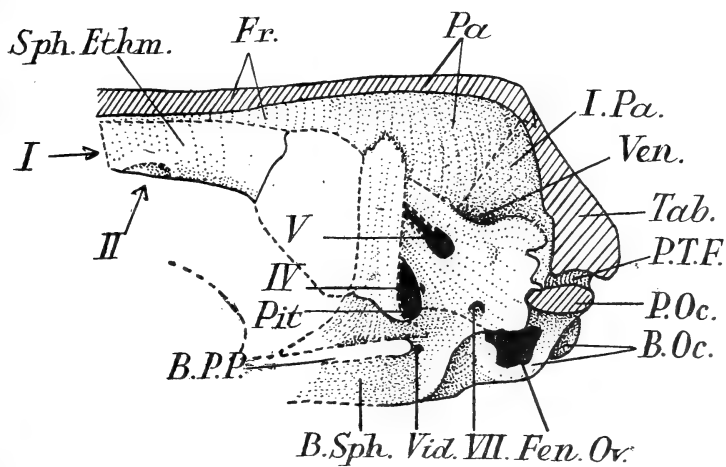


FIG. 7.—*Leptotrachelus eupachygnathus*. Type. Lateral view of the left side of the brain-case, modified after Watson. $\times \frac{2}{3}$.

P.T.F. = posttemporal fenestra.

suffered from crushing and sun-cracking, and it can unfortunately not be determined to what extent the interparietal and supraoccipital contribute to the formation of the lateral wall of the brain-case.

The brain-case of *Leptotrachelus* is thus very similar to that of *Scymnognathus*, and shows, particularly in the size of the pro-otics and the part played by the parietals, interparietals, and to a lesser extent, the supraoccipitals, a stage of development well in advance of that attained by the more primitive *Arctops*. In this form, attention was drawn to the fact that the pro-otic was not developed anterior to the notches identified as pituitary, venous, and fifth nerve openings; in both *Leptotrachelus* and *Scymnognathus* these notches are deeper, *i.e.* more enclosed by the pro-otic. As will be pointed out when dealing with *Cynariops* and "*Lycaenodon*," some of these notches are wholly enclosed by bone in these forms.

The chief morphological features are:

Primitive. Preorbital depression; frontals forming large part of orbital border; apparent step in alveolar border; large postfrontal; large quadrate.

Advanced. Rounded snout, fairly depressed; deeply cupped but upright occiput; squamosal bayed, forming fairly large temporal opening; curiously small basioccipital; basisphenoid far forward; pro-otic fairly large; deep maxilla.

Leptotrachelus is thus very similar to *Scymnognathus* and stands on the same developmental niveau.

Chief measurements :

Length from premaxilla to basioccipital condyle . . .	170 ? mm.
Length from premaxilla to pineal foramen . . .	120 ? „
Length from pineal foramen to edge of occipital plate . . .	24 „
Length from premaxilla to front of orbit . . .	80 ? „
Length of lower jaw	200 „
Width across squamosals	160 „
Interorbital width	50 „
Intertemporal width	60 „
Height of snout	65 ? „
Height of occiput	67 „
Height of mentum of lower jaw	57 „

Type, B.M.N.H., R4051, Hans River, Beaufort West, Cape Province.

Aelurosaurus felinus, Owen.

(Fig. 8, A.)

Owen's original figures excellently illustrate the form and general appearance of the skull, but he mistakenly considered it "mononarial." Lydekker rightly pointed out that in reality the internasal bar was lost. Owen's dental formula—i. 5, c. 1, m. 5—is correct, and Lydekker, in his description and figures, drew attention to the finely serrated

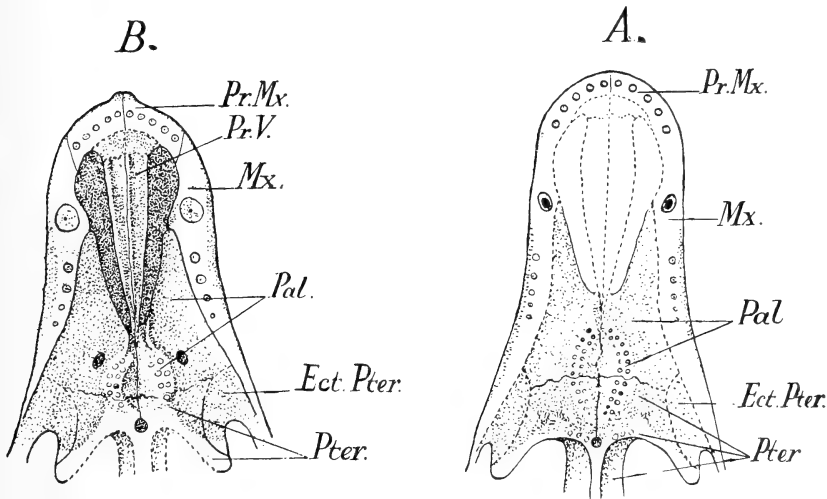


FIG. 8.

A.—*Aelurosaurus felinus*. Type, B.M.N.H., R339.

B.—*Aelurosauroides watsoni*. Gen. et sp. nov. B.M.N.H., R855.

Ventral views of the anterior part of the palate. $\times \frac{1}{2}$.

nature of the posterior borders of both incisors and molars. Seeley's interpretation of the articulation of the lower jaw was at fault, and Broom (1910) showed that in *Aelurosaurus* this structure is typically as in other Gorgonopsians. Seeley correctly noticed teeth on the transverse pterygoidal bar, and also noticed two groups of teeth on the pair of palatal ridges, but failed, as did Broom and Watson after him, to see the transverse suture between them. This suture between the palatine and pterygoid is plainly visible, on the left side, as a dark convoluted line demarcating the two lighter coloured bones. From the ectopterygoid suture, this suture runs medially and crosses the tooth-bearing ridge between the two sets of teeth—an anterior larger set on the palatine, and a set of fewer and smaller teeth on the pterygoid. Unfortunately the ectopterygoid is not

sufficiently exposed, but it apparently stretched for a considerable distance down the transverse pterygoidal flange.

The main morphological features are:

Primitive. Snout higher than wide; laterally directed orbits; slight preorbital depression; frontals form large part of orbital border.

Advanced. Snout rounded; anterior position of pterygoidal flanges; deep maxilla; no step in alveolar border.

The characters shown by *Aelurosaurus*, and also by *Aelurosauroides*, indicate that these two forms occupy a position quite distinct from that of the other forms from the *Endothiodon* zone. It would appear that they represent a branch stock of the *Gorgonopsia*, in which the more advanced characters of the later Gorgonopsians are, as it were, foreshadowed.

Chief measurements :

Length from premaxilla to pineal foramen	80 mm.
Length from premaxilla to front of orbit	55 „
Length of lower jaw	85 „
Interorbital width	22 „
Width of snout	30 „
Width across lateral pterygoidal flanges	35 „
Height of snout	32 „
Height of mentum of lower jaw	31 „
Length of molar series	12 „
Diastema	6 „
Length of incisor series	16 „

Type, B.M.N.H., R339, Gouph, Beaufort West, Cape Province.

Aelurosauroides watsoni, gen. et sp. nov.

(Fig. 8, B.)

This specimen has been regarded by both Lydekker and Broom as *Aelurosaurus felinus*. It consists of the anterior two-thirds of a small skull, and lacks the lower jaw; the outer surfaces are well exposed, and Watson has had the palate developed. I concur in Watson's description and figures, except that, in dorsal view, the preparietal is oval and not squarish and, moreover, agree with him that it is generically distinct from *Aelurosaurus*. In addition to the points enumerated by him, I have been able to determine that the palatines meet in the median line, and thus the pterygoids do not meet the prevomers.

Aelurosauroides agrees with *Aelurosaurus felinus* in its dentition, size, and general shape, but differs in that the snout is rounder and less high. As Watson has already pointed out, the two forms differ very markedly in the relative size and shape of the palatal elements, although they agree in the essential morphological features. Watson's point, that great care must be taken before assigning specimens of Gorgonopsians, which have the same outward appearance, to the same species, without knowing the nature of the palate, therefore deserves full emphasis. The differences in proportion are best understood by referring to the figures; the main are—the shortness and raised nature of the tooth-bearing ridge in *Aelurosauroides*; the relatively shorter prevomers; the great ventral extent of the ectopterygoids, and the more posterior extent of the internal nares.

The main morphological features are:

Primitive. Laterally directed orbits; snout slightly higher than broad; slight preorbital depression; frontal apparently forms a large part of the orbital border.

Advanced. Snout short and somewhat rounded in section; pterygoid not situated far posteriorly; tooth row slightly curved; sides not straight; deep maxilla; no step in alveolar border.

Thus, although retaining some characters which are primitive, *Aelurosauroides* is more advanced than the forms from the *Tapinocephalus* zone, and also than *Arctops* and *Gorgonops*.

Chief measurements:

Length from premaxilla to front of orbit	60 mm.
Interorbital width	22 „
Width of snout	33 „
Height of snout	37 „
Width of pterygoid flanges	35 „
Length of molar series	12 „
Diastema	6 „
Length of incisor series	15 „

Type, B.M.N.H., R855, Gouph, Cape Province.

An Unidentified Specimen.

There is in the collection a specimen, labelled 855a, which lacks the external surface; but its palate can be exposed. Until this is done, it is not possible to state whether it must be referred to *Aelurosaurus* or to *Aelurosauroides*.

C. Forms from the *Cistecephalus* zone.

Eight species from this zone are represented, viz. *Arctognathus*, *Arctosuchus*, *Cerdognathus*, *Cynariops*, *Cynodraco*, *Lycaenodon*, *Lycosaurus*, and *Scylacops*. Careful preparation has produced two good palates and the lateral surfaces of three excellent brain-cases.

Lycaenodon longiceps, Broom.

(Fig. 9.)

The type-specimen consists of two-thirds of a skull; the whole parietal, occipital, and basicranial regions are lost; very little of the palate is present. A short original description was given by Broom in 1925, and in 1930 two figures were published. The dental formula is i. 5, c. 1, m. 6; the very long molar series, measuring 28 mm., is remarkable, as in the *Gorgonopsia* the tooth row is in general very short. A sagittal fracture reveals some points of structure, which were figured by Broom; the dorsal unperforated keel of the prevomers is very strongly developed; the sphenethmoid is a large element, and its shape is probably as figured by Broom; on its antero-lateral surface there is a large foramen for the exit of the second nerve; Broom's figure clearly shows that the palatines meet in the median line and thus prevent the pterygoids from meeting the prevomers. There can be no doubt that this is the usual *Gorgonopsian* condition, and that my interpretation of the palatal aspect of *Arctops*, *Gorgonops*, *Arctognathus*, etc., is correct, and that Watson misinterpreted these relations. Broom's reconstruction of the basicranial portion of the sagittal section, as figured, is based on another specimen, and this will be referred to later. The detailed structure of the anterior part of the palate cannot be determined. Its general shape is, however, of interest; although the skull is a long one, the prevomers appear to be relatively longer, and the palatines do not stretch so far anteriorly, as is usually the case—their anterior borders lie well posterior to the plane of the canines; the median groove is deep, but unfortunately the ridges bounding it are not shown.

The outer surface, although thoroughly cleaned and etched, shows few sutures, as the skull appears to be that of an old animal with closed sutures. The dorsal surface, with the posterior third reconstructed, is shown in the accompanying figure.

The main morphological features are:

Primitive. High, fairly narrow snout; extraordinarily long

straight tooth row, with a step anterior to the canine; preorbital depression; frontals apparently forming a large part of the orbital border; temporal openings apparently small, and parietal region probably very wide.

Advanced. Orbits slightly anteriorly directed; sides of snout not upright; deep maxilla.

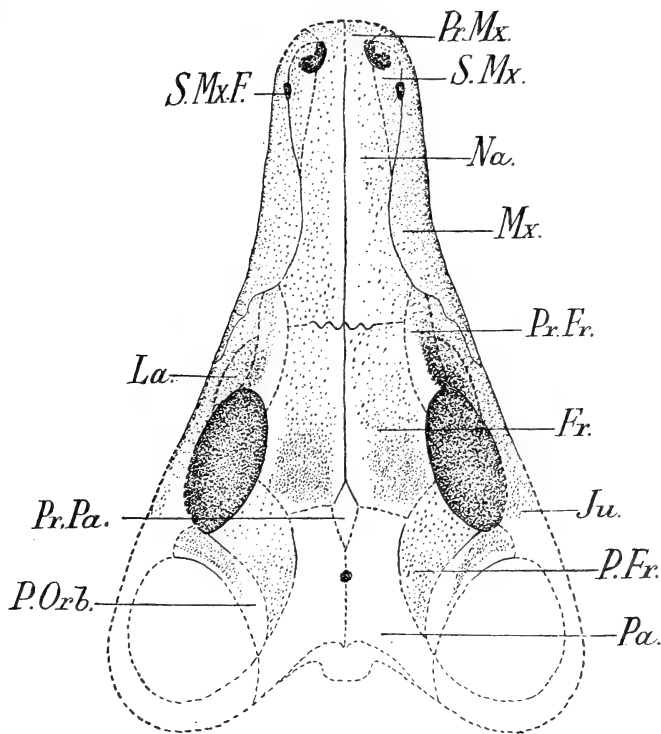


FIG. 9.—*Lycaenodon longiceps*. Type, B.M.N.H., R5700. Restored dorsal view of the skull. $\times \frac{1}{2}$.

As far as the skull of *Lycaenodon* is known, it appears to be very primitive for a form from the base of the *Cistecephalus* zone. The very long molar series is unique amongst all the known *Gorgonopsia*, and, if we are correct in considering this to be a primitive character, then *Lycaenodon* is in this respect the most primitive known Gorgonopsian. The general contour indicates a very broad parietal region, with very small laterally directed temporal openings, and if such is actually the case, then *Lycaenodon* would be less advanced in this region than either *Arctops* or *Gorgonops*.

Chief measurements :

Length from premaxilla to front or orbit	100? mm.
Interorbital width	47 „
Width of snout	38 „
Width across lateral pterygoidal flanges	85? „
Height of snout	46 „
Length of molar series	28 „
Diastema	10 „
Length of incisor series	18? „

Type, B.M.N.H., R5700, Biesjespoort Station, Cape Province.

“*Lycaenodon*” sp.

(Fig. 10.)

In the collection purchased from Dr. Broom, in October 1932, there is included an isolated brain-case, parts of which were figured in 1930 by Broom, and included in his reconstruction of the sagittal section of *Lycaenodon*, and it is stated that it probably belongs to this species, presumably on the fact that it was found at the same locality. The difference in the state of preservation precludes the assumption that it belongs to the same individual, and, as this particular part is not preserved in the type, a comparison is not possible. Until further specimens are found, there is no means of proving that the brain-case is that of *Lycaenodon*; for convenience of reference it will be referred to “*Lycaenodon*” sp.

The whole posterior part of the brain-case and basicranial axis is perfectly preserved, and I have, with great care, completely exposed the brain-case on the left side and removed all but the dorsal extremity of the epipterygoid; the anterior border of the pro-otic and the pituitary fossa have also been freed of matrix. This specimen, before adequate development, was the basis of Broom's (1930) figure showing the relations of the epipterygoid, pterygoid, and the two elements identified as “vomer” and “basisphenoid” respectively, and also of the reconstructed posterior part of his sagittal section of *Lycaenodon longiceps*.

The basisphenoid is a fair-sized bone with edge-like tubera, which underlie the processes sent downwards by the basioccipital, and which form the anterior border to the large irregular fenestra ovalis. From the dorso-anterior corner of the fenestra a slightly digitating suture runs anteriorly, in a plane practically horizontal, to enter the

lateral border of the pituitary fossa. From the tubera the basisphenoid extends, in anterior direction, in the form of a vertical sheet of bone, which laterally carries the horizontal basiptyergoid processes; on the ventral surface this produces the median keel; dorsally, it forms the anterior border of the pituitary fossa. Here it is broken off, but, in life, it apparently stretched forwards and upwards as a median septum. In *Arctognathus curvimola* this

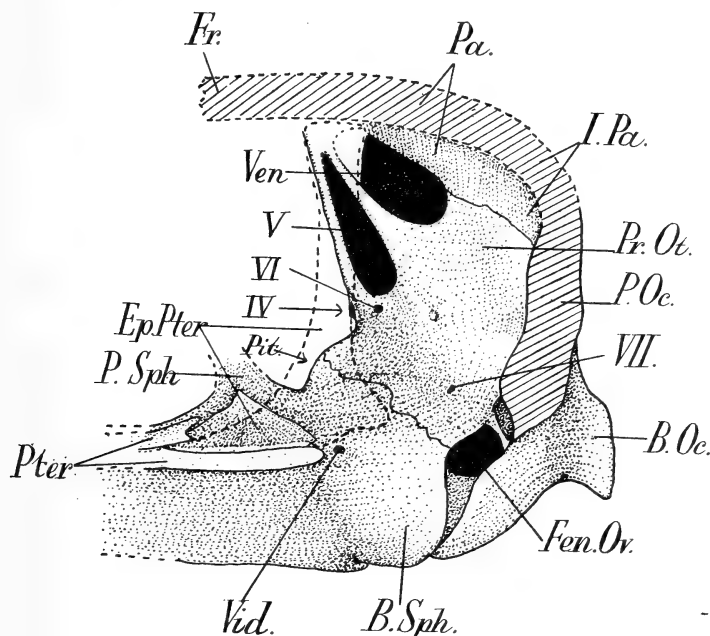


FIG. 10.—“*Lycaenodon*.” B.M.N.H., R5746. Lateral view of the left side of the brain-case. $\times \frac{4}{3}$.

structure is better shown, and this will be discussed further when describing that form. It is evident that this extent of bone cannot all be basisphenoid; the anterior part of the ventral keel, and the antero-dorsal vertical sheet of bone must, for its greater part, be the parasphenoid. The limits of the parasphenoid cannot, however, be determined; the parasphenoid—a membrane bone—appears to have become intimately connected with the basisphenoid, which is, of course, preformed in cartilage.

As indicated in the figure, the flattened, horizontally situated basiptyergoid processes of the basisphenoid are clasped on their dorsal and ventral surfaces by the posterior end of the pterygoid

ramus, which has split into two thin horizontal plates—a long ventral one and a shorter dorsal one. Immediately behind the end of the basipterygoid process a Vidian foramen pierces the bone. It is on the latero-dorsal edge of the ventral pterygoid plate that the epipterygoid stands; from this lateral edge a thin horizontal flange extends medially, and this acts as a base to the epipterygoid. From its base the epipterygoid stretches dorsally as a thin pillar, which is shown in broken lines in the figure.

The pro-otic is a large bone; posteriorly, it is applied to the paroccipital process in the usual manner and forms the antero-dorsal part of the border of the fenestra ovalis; anteriorly, it stretches to the plane of the epipterygoid, which dorsally overlies its extreme antero-dorsal corner. The shape of the pro-otic is best understood from the figure; it forms nearly the whole of the lateral wall of the posterior part of the brain-case. A small foramen for the seventh nerve lies a short distance antero-dorsally to the fenestra ovalis; below it is a shallow depression for the geniculate ganglion; still further antero-dorsally the bone is pierced by a small rounded foramen for the sixth nerve, and under it is a depression; this foramen lies near the edge of a large opening through which the fifth nerve emerged; this opening appears to be a large oval foramen, whose anterior border is formed by the long anterior process of the pro-otic; it is not certain that this opening is bounded antero-dorsally by bone, as a part of the epipterygoid overlies this region; its general shape indicates a large oval foramen completely bounded by the pro-otic; the postero-dorsal border of this foramen is formed by a long process of the pro-otic, similar to the anterior one, which separates it from an equally large foramen lying dorsally to it; this is the large venous foramen.

In anterior view, the edges of both pro-otics have been exposed and it is seen that, above the pituitary fossa, processes are sent inwards by both pro-otics, so as to form a bridge of bone over the pituitary fossa; ventrally, the bridge appears to be supported by a spur of the basisphenoid, which here forms the posterior border of the pituitary fossa; dorsally to this bridge, the pro-otics approach each other closely (3 mm.), so that the brain here emerged through a high and narrow slit. On the anterior face of the pro-otic, just above the bridge, is a small foramen facing directly forwards—this is for the exit of the fourth nerve.

The sphenethmoidal region is unfortunately not preserved.

The basioccipital has a well-developed condyle and has strong downwardly directed processes, on whose ventral surfaces the

basi-sphenoidal tubera are applied; it forms the postero-ventral border of the fenestra ovalis; on its ventral surface lie the two nutritive foramina in their usual position. The foramen for the tenth nerve is overhung by the exoccipitals in the usual manner.

If we are right in our interpretation that in *Arctops* the anterior part of the pro-otic is not ossified, and that the foramen for the fifth nerve is only represented as a shallow notch, and that in *Cynariops* the notch is deeper, but still unenclosed, then "*Lycaenodon*" is a more highly developed form, as here the pro-otic has extended forward to surround the foramen for the fifth nerve. The type of *Lycaenodon* was shown to appear primitive, and it would thus seem that there is an additional reason for regarding this brain-case as not belonging to the genus *Lycaenodon*. The strong basioccipital, much stronger than in *Cynariops*, is, however, a primitive character, which may well be found associated with the characters found in the type of *Lycaenodon*. Until we know more about the relative values of characters styled "primitive" and "advanced," any further expression of opinion will serve no useful purpose.

B.M.N.H., R5746, Biesjespoort Station, Cape Province.

Cynariops robustus, Broom.

(Figs. 11-14.)

The type consists of a good skull, lacking the temporal arches, part of the occiput, and the premaxillaries. After some further preparation, the lateral and dorsal surfaces show the sutures well; the relations of the various elements are best understood by referring to the figures.

The dental formula is i. 5, c. 1, m. 4; on the right side there are three, on the left four, the fourth being small; there is a diastema between the last incisor and the canine, whereas the first molar follows immediately on the canine.

Mr. L. E. Parsons, Technical Assistant in the Geological Department, has prepared the palate and the lateral surface of the brain-case for me, and after some further development and etching, a number of interesting features have become apparent. The structure of the palate is adequately exposed; ventrally, the prevomers have a strong median keel and two lateral flanges on their anterior part; the median palatal groove has deep overhanging ridges, and both the palatine and pterygoid portions bear teeth; the median convoluted interpalatine suture is beautifully shown, and so is the transverse

suture separating the palatine and pterygoid in ventral view; the latter crosses the ridge at its lowest part and then continues in postero-lateral direction to meet the ectopterygoid suture. The posterior limits of the prevomers are not clearly shown, but probably are as indicated in the figure.

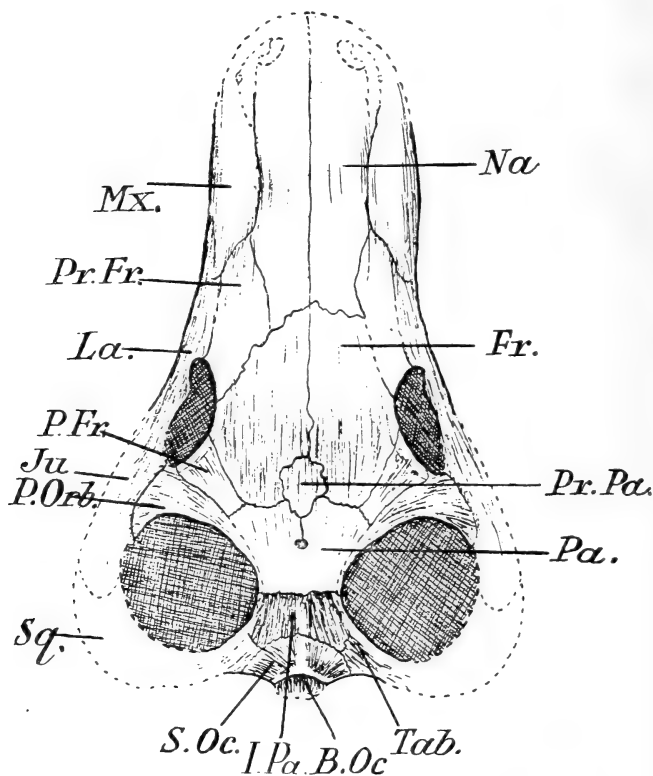


FIG. 11.—*Cynariops robustus*. Type, B.M.N.H., R5743. Dorsal view of the skull. $\times \frac{5}{8}$.

On the left side, the outer surface of the brain-case has been partially exposed; on this side, the epipterygoid is not preserved, but, on the right side, it is practically complete. The epipterygoid has a long base resting on the quadrate ramus of the pterygoid; it then extends dorsally as a very high, narrow, and flattened pillar to meet the parietal; it thus forms the side wall of the *cavum epiptericum* anterior to the pro-otic, with the Gasserian ganglion lying immediately median to it; in lateral view, it lies in front of the lateral opening into the pituitary fossa and, further dorsally, overlies the anterior

border of the large irregular notch for the fifth cranial nerve. The pro-otic is a fairly large bone, whose shape will be better understood from the accompanying figure than from a verbal description. Ventrally, it meets the basisphenoid in a fairly open suture; antero-

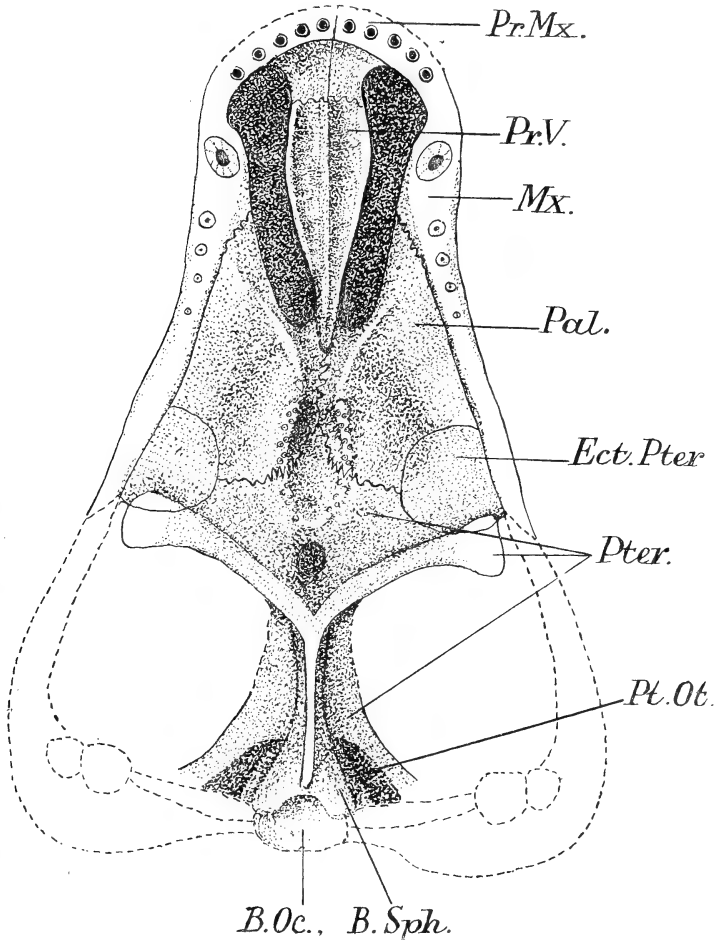


FIG. 13.—*Cynariops robustus*. Type. Ventral view of the skull. $\times \frac{5}{8}$.

ventrally, it forms the posterior border of the fenestra leading into the pituitary fossa; dorsally, it forms the ventral and posterior borders of the notch for the fifth nerve; the anterior pro-otic process is apparently not strongly developed, so that the notch is not deep; further dorsally, the pro-otic forms the ventral border of the large

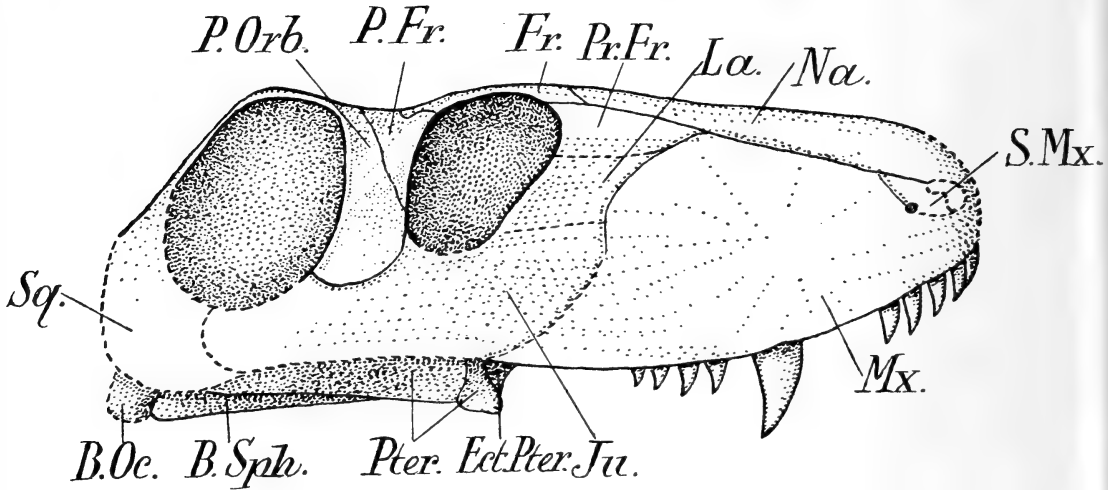


FIG. 12.—*Cynariops robustus*. Type. Lateral view of the skull. $\times \frac{1}{3}$.

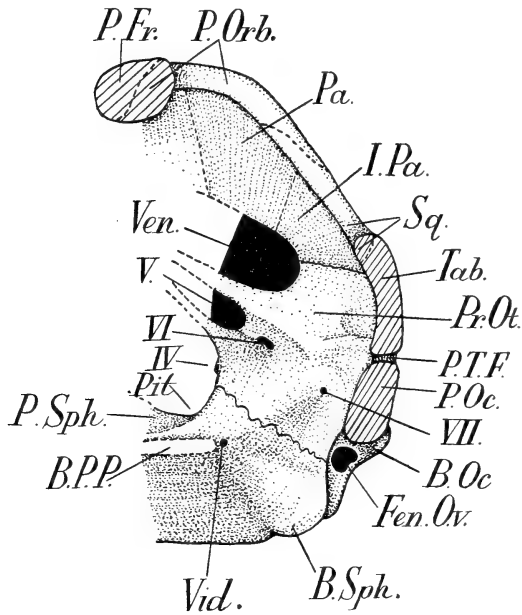


FIG. 14.—*Cynariops robustus*. Type. Lateral view of the left side of the brain-case. $\times \frac{1}{3}$.

venous foramen; but, unfortunately, the extent to which the supra-occipital and interparietal enter the side wall of the brain-case cannot be determined. The fenestra ovalis is seen to lie above and behind the basisphenoidal tubera, and appears to be fairly large. The foramen magnum is extraordinarily large and the basioccipital condyle is remarkably small. Unfortunately I have not been able to determine anything as to the presence of a parasphenoidal rostrum or the nature of the sphenethmoidal portion of the brain-case. The most striking feature about the brain-case of *Cynariops* is its great height and relative narrowness. In this respect it agrees with the fragmentary brain-case of "*Lycaenodon*."

The main morphological features are:

Primitive. Sloping occiput, not cupped; epipterygoid slender; preorbital depression; pro-otic of no great anterior extent.

Advanced. Snout as broad as high and rounded; no step in maxillary border; orbits slightly anteriorly directed; pterygoid flanges anteriorly situated; temporal openings somewhat dorsally directed, but not large; parietal apparently enters brain-case; basi-occipital extraordinarily undeveloped; pro-otic larger than in *Arctops*; frontal forms only small part of orbital border; deep maxilla; short tooth row, but straight; parietal width reduced; paroccipital not massive.

From this summary of characters, it is clear that *Cynariops* is much further advanced than *Arctops*, *Gorgonops*, *Scymnognathus*, and *Leptotrachelus*. In the nature of its brain-case it appears to occupy a position intermediate to *Arctops* and that represented by the brain-case referred to "*Lycaenodon*," and it is in this respect comparable to *Scymnognathus* and *Leptotrachelus*. These two latter genera are, however, in all other respects definitely more primitive.

Chief measurements :

From premaxilla to basisphenoidal tubera	125? mm.
From premaxilla to pineal foramen	97? "
From pineal foramen to edge of occipital plate	8 "
From premaxilla to front of orbit	65? "
Interorbital width	35 "
Intertemporal width	22 "
Width of snout	53 "
Height of snout	45 "
Width across pterygoid flanges	50 "
Height of occiput	45 "
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Length of molar series	19 mm.
Diastema	2 „
Length of incisor series	20 „

B.M.N.H., R5743, Biesjespoort Station, Cape Province.

Lycosaurus pardalis, Owen.

This form has been studied by Owen, Lydekker, Broom, and Watson. In Watson's 1921 account all the evidence is fully stated. The left side is best preserved, and Watson's figure is obviously a mirror image of this side. It is the left, and not the right, ramus of the mandible that is preserved. Although the difference in level between the pre-canine and post-canine edge is considerable, the step is not so abrupt as in *Gorgonops*. The dental formula is apparently i. 5, c. 1, m. 4?; the incisors are serrated, but as the teeth are badly preserved this is not well shown. The coronoid process of the dentary stretched far in dorso-posterior direction.

The main morphological features are:

Primitive. Orbits laterally directed; skull higher than wide; laterally situated nostril; slender epipterygoid.

Advanced. Snout short, rounded but high; section of snout not square; no abrupt step in dentigerous border; maxilla deep; small facial part of septomaxilla.

Although *Lycosaurus* is very inadequately known, it seems certain that it represents a stage somewhat in advance of that reached by the forms described above. As nothing is known of the basicranial axis and the posterior part of the skull, it would be best not to include this form in any morphological series.

Chief measurements:

From premaxilla to pineal foramen	120? mm.
From premaxilla to front of orbit	80 „
Length of lower jaw	130? „
Interorbital width	30? „
Intertemporal width	25? „
Width of snout	43? „
Height of snout	43? „
Height of mentum	44 „
Length of molar series	15? „
Diastema	6 „
Length of incisor series	11 „

Type, B.M.N.H., R1717, Karroo, Cape Province.

1717a, „ „ „

A number of specimens have been referred to *Lycosaurus*, viz.:—

49407. A badly weathered snout, which shows the dental formula
i. 5, c. 1, m. ?. Letjesbosch, Cape Province.

49410. A weathered fragment of snout, which shows the dental
formula i. 5, c. 1, m. 3 + 1?.

R512. Weathered fragment of snout.

Arctognathus curvimola, Owen.

(Figs. 15–17.)

The type is a distorted and weathered skull; the occiput, roof of skull, and temporal arches are very much weathered; part of the palate had been developed, and the teeth of the upper jaw are well preserved on the right side. This type has been studied by Owen, Lydekker, Seeley, Broom, and Watson. Watson's 1921 account is a detailed one, and the sutures of the dorsal and palatal surfaces are indicated in his figures. I have refigured the dorsal surface in order to show the relations of the septomaxilla and its foramen, the maxillo-nasal and the jugo-lacrimal sutures. The septomaxilla is a fairly large bone and the foramen is a fair-sized narrow slit—both larger than described by Watson. The dental formula is i. 4, c. 1, m. 5; the posterior edges of the canine and molars are serrated.

The middle part of the palate was misinterpreted by Watson, who described the pterygoid as a large bone forming the roof of the median groove, carrying the two dentigerous ridges and reaching the prevomers and internal nares. The line of matrix lateral to the dentigerous ridges, taken by Watson to be the pterygo-palatine suture, is a crack. The real suture is plainly visible as a thin, digitating line of matrix, which commences at the antero-median corner of the epi-ptyergoid and then runs medially to cross the dentigerous ridge at its lowest part, then runs obliquely forward and continues in the median line as a well-marked wavy line of matrix. Posterior to the median groove, which has an abrupt hinder edge, there lies a distinct small interptyergoid foramen.

The left side of the skull lacks the temporal arch, and I have succeeded in exposing the lateral surface of the brain-case from this side by removing the displaced portion of the lateral surface. This could have been done sixty years ago as it was a straightforward piece of development, which was accomplished by the use of a small chisel and

hammer only. As now developed, the skull shows all but the anterior quarter of the internal structure in parasagittal view.

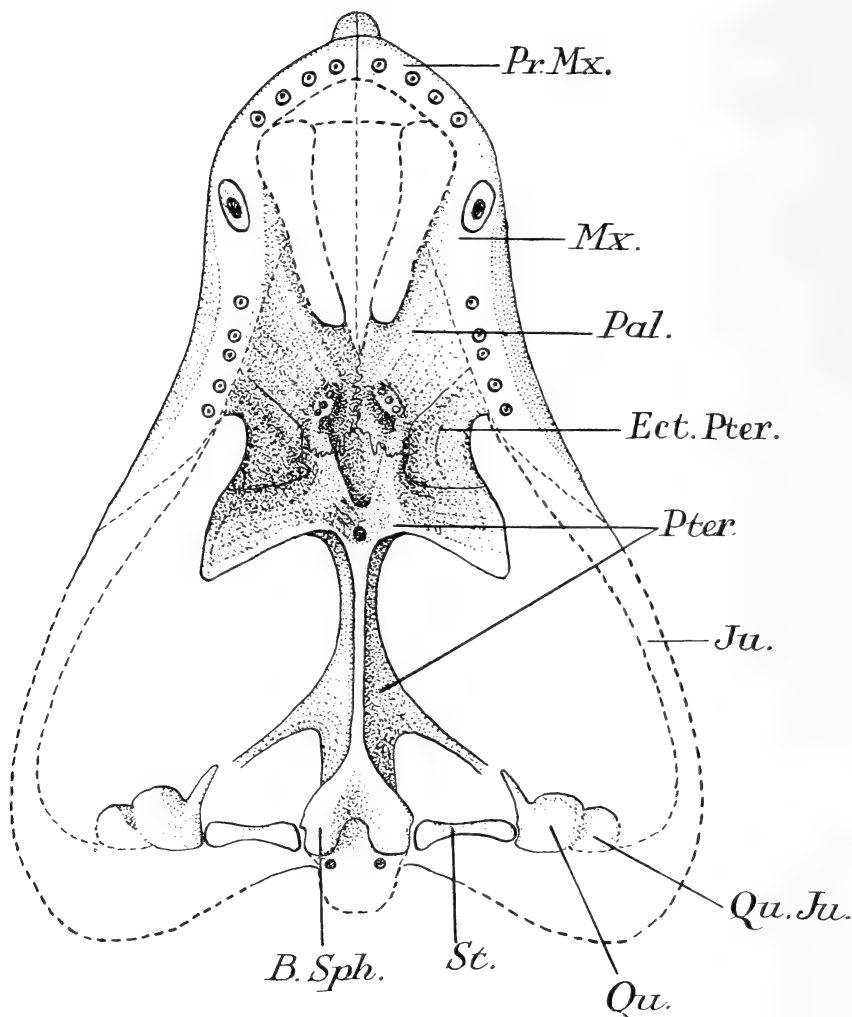


FIG. 15.—*Arctognathus curvimola*. Type, B.M.N.H., 47339. Ventral view of the skull, modified after Watson. $\times \frac{3}{5}$.

St.=stapes.

Qu.=quadrate.

Qu.Ju.=quadratojugal.

The basioccipital condyle and the greater part of the paroccipital have been removed by a fracture; their nature is probably as indicated in broken lines in the figure.

The basisphenoid is present *in toto*. Ventro-posteriorly lie its tubera, which are thin and edge-like; they underlie the ventrally directed processes of the basioccipital and diverge in posterior direction, so that the floor of the hinder end of the brain-case (for the cerebellum) is wide, and the fenestrae ovaes far apart. Anteriorly, the basisphenoid extends as a thin vertical sheet of bone, which laterally carries the horizontal basiptyergoid processes; the ventral part of this sheet forms the posterior part of the keel, which must further anteriorly be formed by the parasphenoid flanked by the pterygoids, but the exact relations of these elements cannot be determined as the fusion appears to be very intimate; the dorsal part of the basisphenoid is anteriorly confluent with the parasphenoid; its free anterior edge lies in the plane of the posterior border of the pituitary fossa and, in life, this edge must have supported the infundibulum; dorsally, the basisphenoid meets the pro-otic along a line running from the fenestra ovalis to the open side of the pituitary fossa.

The outer surface of the pro-otic does not show up too well; posteriorly, it was apparently applied to the anterior face of the paroccipital in the usual manner; ventrally, it rests on the sides of the basisphenoid; anteriorly, its extent is not great; this is rather remarkable for a form otherwise showing many advanced characters; the anterior process of the pro-otic does not extend far, so that the exit for the fifth nerve appears to be only a shallow notch, whereas in "*Lycaenodon*" it is a large oval foramen; the outer surface of the anterior pro-otic process is deeply hollowed out, and this may have housed the Gasserian ganglion; dorsal to the opening for the fifth nerve, the hinder pro-otic process is also short, so that the venous notch has no extensive osseous ventral border. Dorso-anteriorly to the large fenestra ovalis lies a small foramen for the facial nerve, with a slight hollow under it for the geniculate ganglion. Anteriorly, the pro-otic forms the posterior border of the open side of the pituitary fossa and, posteriorly, forms part of the anterior border of the large and irregular fenestra ovalis.

Dorsally, there are indications that both the parietal and interparietal sent down flanges, which contributed to the formation of the side-wall; the anterior part of this parietal flange articulated with the posterior part of the sphenethmoid; it was this relation that apparently led Watson astray, since, what he interpreted as a broad epiptyergoid on the right side is, in reality, the outer surface of the sphenethmoid; the posterior part of the parietal flange articulated with the ascending epiptyergoid.

The epipterygoid is not preserved, but there is no reason to suppose it to be different from that of the other known Gorgonopsia; standing on the pterygoid, it would ascend as a thin bony rod in a plane lateral to the other bones of the brain-case, and acted as a lateral wall for the thalamencephalon, mid-brain, and Gasserian ganglion.

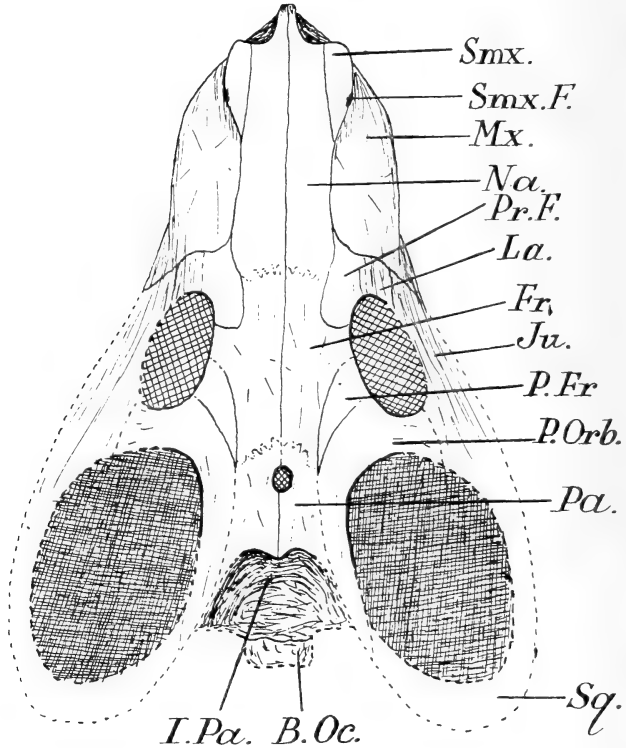


FIG. 16.—*Arctognathus curvimola*. Type. Dorsal view of the skull. $\times \frac{1}{2}$.

The parasphenoid, from where it is indistinguishably fused with the basisphenoid, stretches antero-dorsally as a vertical sheet of bone; at its dorsal edge it appears to split, and in this groove the ventral edge of the sphenethmoid rests; anteriorly, the parasphenoid tapers, and here appears as a vertical slip of bone applied to the lateral surface of the sphenethmoidal part of the interorbital septum.

The sphenethmoidal part of the brain-case is beautifully shown, and it is now evident that the "sphenethmoid" figured in *Scymnognathus*

and *Leptotrachelus* is only a part of that bone. The sphenethmoid in *Arctognathus* is a very large element; its ventral half represents a part of an ossified interorbital septum and rests on the parasphenoid, and, further forward, on the dorso-median keel of the pterygoid. Anteriorly, the interorbital septum is continued forward, but is separated by an unossified portion from the internasal septum. It is thus only the dorsal portion, which has split into two curved sheets of bone, that is preserved in *Scymnognathus* and *Leptotrachelus*. This housed the

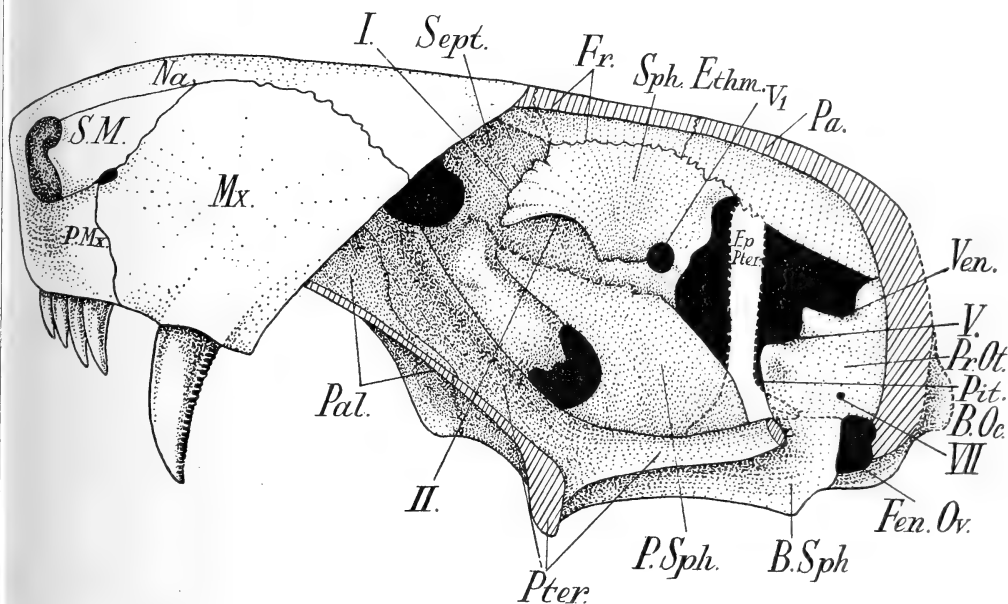


FIG. 17.—*Arctognathus curvimola*. Type. Lateral view of the left side of the brain-case. $\times \frac{2}{3}$.

fore-brain. Dorsally, flanges from the frontal and parietal are sent downwards and these, meeting the dorsal edges of the sphenethmoid, complete the side-wall. Ventro-posteriorly, a large rounded foramen pierces the sphenethmoid; it is directed somewhat forward and outward, and from it may have emerged the ophthalmic branch of the fifth nerve, but the large size makes it more probable that it is really a venous foramen. Ventro-anteriorly, lies a downwardly-directed oval slit between the median septum and the side of the sphenethmoid, through which the second nerve emerged. Anteriorly, the sphenethmoid has a free edge, and anterior to this edge, the median septum

is visible. The olfactory lobes were probably situated in this position. Antero-ventrally to the tapering end of the parasphenoid, the sphenethmoidal part of the interorbital septum is extraordinarily thickened and, in this part, rests on the dorso-median keel of the anterior pterygoid ramus. The thickening is solid, and I can make no suggestion as to its probable function. Posterior to this structure there is a gap, which thus lies between the sphenethmoid, pterygoid, and parasphenoid.

The general plan of all these internal ossifications in the skull of *Arctognathus* is very similar to that which is known in the Dicynodonts from Pearson's account.

The main morphological features may be summarised:—

Primitive. Preorbital depression, but very weak; septomaxilla with large facial exposure and large foramen; epipterygoid apparently rod-like; fenestrae ovals far apart; pro-otic relatively small; fenestra ovalis not situated high up in the brain-case.

Advanced. Snout short and rounded in section; nostril large; orbits not wholly laterally directed; small postfrontal; preparietal small or absent; short, deep maxilla; tooth row short; dentigerous border with a distinctive, ventrally convex curve, with no step; pterygoid flange anteriorly situated; interorbital width reduced; intertemporal width reduced, and fairly large temporal openings; basisphenoidal tubera reduced.

Arctognathus is thus clearly a Gorgonopsian well advanced in the direction of development taken by this group, but it still possesses a number of primitive features. It has been shown that a number of features noted by Watson as advanced were cited on invalid grounds, viz. the septomaxilla and its foramen are large as in other Gorgonopsians and there is no evidence that the epipterygoid is broad. The pro-otic is certainly not very advanced, and stands on the same developmental niveau as do *Scymnognathus* and *Leptotrachelus*; in this respect "*Lycaenodon*" is much more advanced. The nature of the basisphenoid and its relations with the pterygoids and parasphenoid do not show very marked advances over the condition of the earlier Gorgonopsians that have been described above. In the attainment of a short rounded snout and the reduction of the interorbital and intertemporal width, however, *Arctognathus* shows definite advances. The great amount of ossification in the median septum appears to be primitive and will probably be found in the earlier forms when better preserved material is examined.

Chief measurements:

From premaxilla to basisphenoidal tubera	180 mm.
From premaxilla to pineal foramen	126 "
From pineal foramen to edge of occiput	32 "
From premaxilla to front of orbit	91 "
Length of lower jaw	153 "
Width across squamosals	146? "
Interorbital width	36 "
Intertemporal width	38? "
Width of snout	64 "
Width across lateral pterygoid flanges	72 "
Height of snout	56 "
Height of occiput	55? "
Mentum	67 "
Length of molar series	31 "
Diastema	7 "
Length of incisor series	23 "

Type, B.M.N.H., 47339, Kagaberg, Bedford, Cape Province.

Arctognathus ?curvimola, Owen.

In the collection there is a preorbital portion of a skull with part of the lower jaw in position, but with the teeth badly preserved. Owen described it under the name *Lycosaurus tigrinus*; Broom, in 1911, showed that it could not be included in the genus *Lycosaurus*, and proposed the new name *Arctosuchus*, and, in 1932, considered it to be a Therocephalian. The specimen is a very bad type, but there is no doubt that it represents a Gorgonopsian, probably very close to *Arctognathus*. In 1921 Watson maintained that it was specifically identical with *Arctognathus curvimola*. I have etched the right side of the snout, and the maxillo-premaxillary suture now shows clearly; the relations of maxilla, premaxilla, septomaxilla, and septomaxillary foramen and the nostrils are typically Gorgonopsian and do not differ much from the condition in *A. curvimola*. There appear to be four incisors, although the roots of only two are actually preserved; the molars are badly preserved, but probably number five. All the features shown by the fragment thus agree very well with *A. curvimola* and, as no differentiating features can be determined, there is no valid reason to distinguish it by name from *A. curvimola*.

B.M.N.H., R1719, Mildenhalls, Fort Beaufort, Cape Province.

Cynodraco serridens, Owen.

Owen described a number of fragmentary snouts under this name, and another fragment presumably associated with a good humerus under the name of *C. major*. There is no evidence to warrant the separation into two distinct species. Moreover, so little can be determined of the structure that, except for the deep mentum in one specimen, there is very little evidence that the fragments are Gorgonopsians at all. Owen's lithographs show the general appearance of these specimens very well. They are :

Type, B.M.N.H., 47084, Bovey's Farm, Fort Beaufort, Cape Province.

This is a bad piece of snout, which exhibits some features of the incisors; there are five upper incisors with fairly strong and coarse serrations, four lower incisors with similar serrations; the incisors are strong and protruding.

B.M.N.H., 47086, Fort Beaufort, Cape Province.

A mandibular fragment showing the canine of both sides and also four incisors.

B.M.N.H., 47085, Stylkrantz, Graaff-Reinet, Cape Province.

Weathered and fragmentary snout; the fragmentary incisors show fairly coarse serrations on both anterior and posterior edges. The spur of the septomaxilla protruding into the nostril is shown on the right side.

B.M.N.H., 47309, Mildenhalls, Fort Beaufort, Cape Province.

This is Owen's type of *C. major*. It consists of a fragment of mandibular symphysis with both upper canines attached. The roots of four large incisors are seen in section; the serrations on the posterior border of the very large canines are beautifully preserved. The symphysis is deep.

B.M.N.H., 47310, Mildenhalls, Fort Beaufort, Cape Province.

A very good left humerus showing both foramina, well illustrated in Owen's lithograph.

Chief measurements :

Length	260 mm.
Width across the epicondyles	110 „
Width across the proximal surface	105 by 36 mm.
Width across delto-pectoral crest	110 mm.
Maximum width of shaft	36 „
Minimum width of shaft	26 „
Length of delto-pectoral crest	149 „

Cerdogmathus greyi, Broom.

The type is an imperfect dentary; the number of incisors cannot be ascertained, but four seems to be the most probable number; the canine and four molars are badly preserved as casts and, although no serrations can be seen, this evidence is simply negative; Broom is probably right in postulating a low coronoid process, as this would conform with the general contour. The very low, though upright, symphysis and the absence of a diastema stamps the dentary as a distinct type; but one wonders if such a fragment warrants the creation of a new generic name.

Chief measurements :

Probable length of dentary	100? mm.
Height of symphysis	21 „
Length of molar series	13 „
Depth of dentary behind last molar	14 „

Type, B.M.N.H., R2892, Klippoort, Cradock, Cape Province.

Scylacops capensis, Broom.

This specimen consists of the middle third of a skull, which shows the greater part of the structure of that region. Watson's description and figures appear to be correct in every detail. His attitude with regard to the specimen is to be highly commended. The snout is missing and the dentition is thus unknown and, as much of the classification of the Gorgonopsia rests on this character, Watson, although recognising the fact that he had before him a representative of a new genus, refrained from naming it. Instead, he gave a good morphological account, which is of far greater value than a new generic name. Subsequent finds have shown the wisdom of such a procedure. We now have an excellent skull as the type of *Scylacops capensis*, named by Broom, but to Watson must go the honour of the first morphological description.

B.M.N.H., 47098, ?Fort Beaufort, Cape Province.

A Fore-foot of an Unnamed Form.

(Fig. 18.)

Lying on a series of vertebrae, there is a partial right fore-foot of a Gorgonopsian. The fourth digit is fully preserved; the third lacks

only the point of the claw; the fifth has two phalanges preserved; parts of the third, fourth, and fifth metacarpals are present; the fourth and fifth distals are present as a single fused element, to which the distal half of the ulnare is articulated. The foot is typically Gorgonopsian (about two-thirds the size of that of *Aelurognathus tigriceps*), with the distinctive mammal-like epiphysial distal ends to the metacarpals, and with indications of an incipient reduction



FIG. 18.—An unnamed Gorgonopsian. B.M.N.H., R3768. Dorsal aspect of the partial manus. $\times \frac{1}{2}$.

U. = ulnare.

4+5 = fused fourth and fifth distal carpals.

III-V = the third, fourth, and fifth digits.

in the number of phalanges. The fourth and fifth metacarpals articulate with the fused fourth and fifth distals; the second phalanx of the fourth, and, in particular, of the third digit, is very much shortened; the third phalanx is robustly developed.

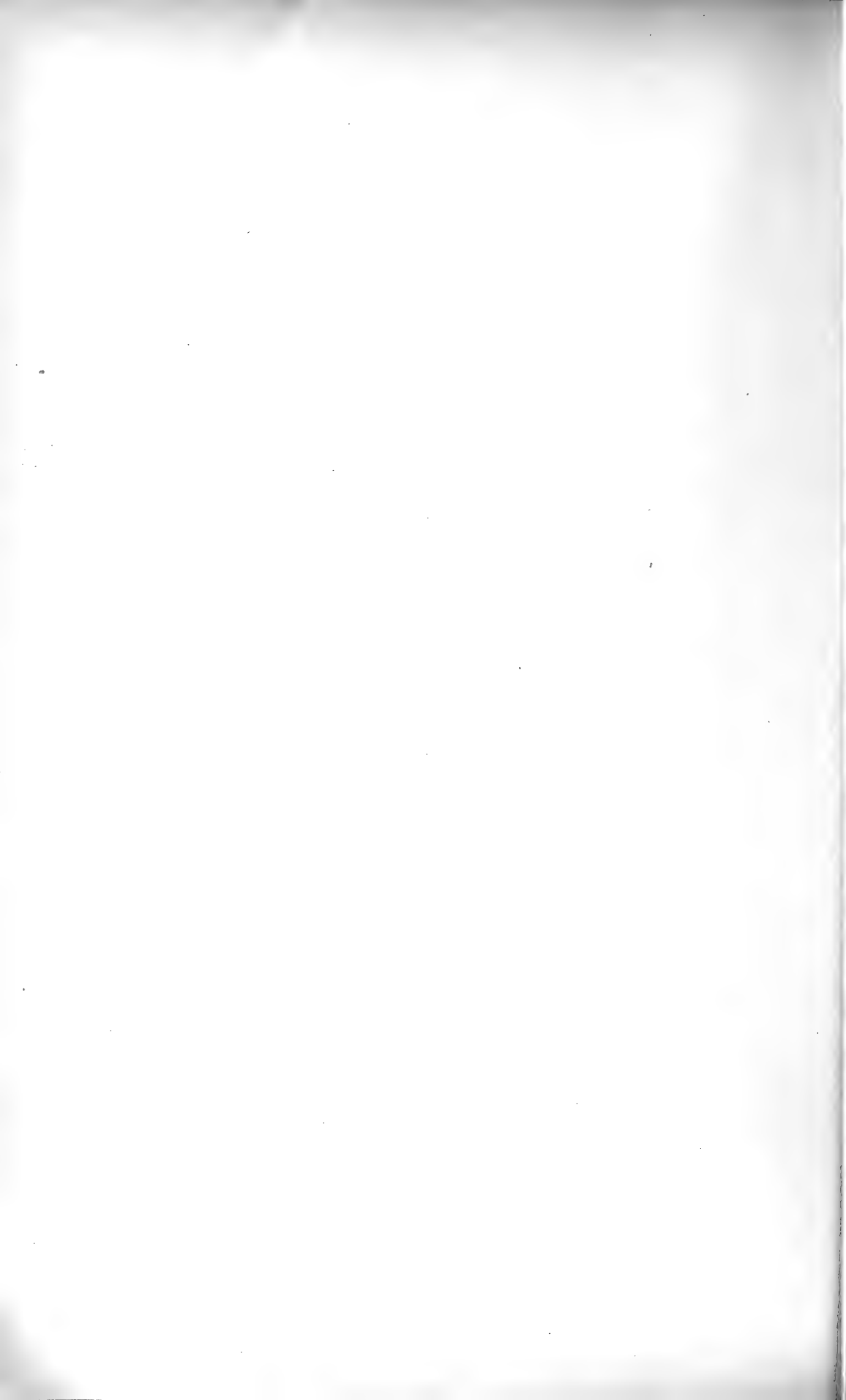
As preserved, the phalangeal formula is—?, ?, 4, 4, 3. If the first and second digits possessed two and three phalanges respectively, the structure of the digits would be exactly as in *Aelurognathus tigriceps* and, as in that form, dorso-ventral movement of the segments *inter se* is well developed with finely modelled articulatory faces.

B.M.N.H., R3768, Oude Klip, Cape Province.

Short Discussion.

In a series of papers on the Therocephalians, Gorgonopsians, Bauriamorphs, and Cynodonts, Watson has argued that one branch of the Therocephalians gave rise to the Bauriamorphs, and that the Gorgonopsians led on to the Cynodonts. With the first conclusion I can concur, but in this study of a limited number of Gorgonopsian skulls two important facts bearing on this question have been established, viz. the nature of the epipterygoid and the relations of the posterior end of the prevomers, and these seem to invalidate Watson's second conclusion. In all the Gorgonopsians I have studied there is no evidence, whatsoever, of a tendency for the original slender rod-like epipterygoid to become widened and intimately incorporated into the side-wall of the brain-case; and in all, where the palate is known, the prevomers have their posterior ends tapering and are here clasped by the palatines and do not meet the pterygoids on the ventral surface. In the Therocephalia, on the other hand, there is very definite evidence of the progressive widening of the epipterygoid and, in this group, the posterior end of the prevomers is expanded and underlies the pterygoid in ventral view. This is also the condition in the Cynodonts. With respect to the nature of the prevomers and the epipterygoid, it seems that the Gorgonopsians must be excluded from the direct ancestry of the Cynodonts; but at this stage it would be premature to maintain that these two characters indicate a Therocephalian ancestry. I am more inclined to think that no known Therocephalian indicates anything more than a parallel development in the two suborders, *Therocephalia* and *Cynodontia*. I do not intend to continue this discussion any further; this can be more profitably done when the various suborders of the Theriodontia are treated monographically, as I hope to be able to do in the near future.

My thanks are due to the officers of the British Museum (Natural History) for permission and facilities to study the material in their charge. I am particularly grateful to Dr. W. E. Swinton for his constant readiness to facilitate my work, and to Mr. Parsons for doing some of the developmental work. Professor D. M. S. Watson's interest was very encouraging, and his critical advice always welcome. To the University of Stellenbosch I am indebted for a small scholarship, which has enabled me to undertake the visit to London. All but three of the figures are by my wife.



7. *A Contribution to the Morphology of the Mammal-like Reptiles of the Suborder Therocephalia.*—By LIEUWE D. BOONSTRA, D.Sc., Palaeontologist to the South African Museum and Queen Victoria Scholar of the University of Stellenbosch.

(With 35 Text-figures.)

Although many genera and species of Therocephalians have been described by Owen, Seeley, Broom, Watson, and Haughton since these forms became known about seventy years ago, very little is known of the cranial morphology. The outer surface of the skull has hitherto been the only structure adequately known; certain features of the palate of *Scylacosaurus*, *Ictidosuchoides*, *Moschorhinus*, *Notosollasia*, and *Whaitsia* have been described by Broom; Haughton has described the palate in *Akidnognathus* and *Whaitsia*, and a longitudinal section of the brain-case of *Alopecognathus*; Watson's account of the palate and basicranial region of the Scaloposaurids has placed our knowledge of this family on a sound footing.

In this paper the results of a study of the Therocephalians preserved in the British Museum (Natural History) are recorded. This collection consists of about twenty distinct types, and in a number of cases it has been possible to determine the structure of the palate and brain-case in addition to the dorsal, lateral, and occipital surfaces. As a number of these specimens are the historical types of Owen, Seeley, and Lydekker, a re-examination will serve as a useful introduction to a monographical account of the Therocephalia, which I hope to undertake in the near future.

The suborder Therocephalia has hitherto been subdivided into five families, viz. *Alopecopsidae*, *Ictidosuchidae*, *Pristerognathidae*, *Scaloposauridae*, and *Whaitsidae*; to these must now be added *Euchamberidae* and *Lycideopsidae*.

The *Pristerognathidae* are represented in the collection by *Alopecodon*, *Cynariognathus*, *Pristerognathus*, *Scylacosaurus*, *Scymnosaurus*, and *Trochosaurus*; *Hyorhynchus* and probably also *Theriodesmus* may be included here. All these forms are from the *Tapinocephalus* zone, and represent the more generalised forms of the Therocephalia, which are on a definitely more primitive stage of development than the more advanced Scaloposaurids, *Whaitsids*, *Euchambersia*, and *Lycideops*.

Alopecodon cf. *priscus*, Broom.

A very much weathered and badly preserved snout with the anterior third of the mandible, showing only the dentition in a very unsatisfactory manner, was, in 1925, made the type of a new species—*Alopecodon minor*, Broom. Broom gave the dental formula i. 7, c. 3, m. 7 or 8. I find seven incisors as described by Broom; the two small teeth, which on account of their different direction may possibly be small canines, but may equally well represent two last incisors differing somewhat from the anterior ones, as there is no evidence that they are implanted on the maxilla; then a large canine, oval in cross-section; then a diastema of 8 mm.; then six closely packed molars followed by an empty socket, to which, medially, there lies a small tooth; the length of the molar series (7) is 24 mm. On none of the teeth are any serrations visible, but they may have been present in life.

Both *A. minor* and *A. rugosus* are bad types. Broom's specific characters comprise only the number of teeth, and as these are badly preserved, it is not a reliable criterion. In *A. priscus* the dental formula given by Broom is i. 7, c. 2 + 1, m. 8?; in *A. minor* i. 7, c. 2 + 1, m. 7 or 8; in *A. rugosus* i. ?, c. ? + 1, m. 7. Considering the nature of the preservation in these three specimens, the dental formulae approximate so closely that, in the present state of our knowledge, it would appear advisable to consider both *A. minor* and *A. rugosus* as examples of *Alopecodon priscus*. It is true that they are considerably smaller forms, but this does not appear to be a sufficiently weighty reason for retaining three distinct specific names, each of which is only represented by a very incomplete skull.

B.M.N.H., R5750, Abraham's Kraal, Prince Albert, Cape Province.

Cynariognathus platyrhinus, Broom.

(Fig. 1.)

This specimen is a weathered snout, which Broom has determined as belonging to the same species as the type snout now in the American Museum. Sufficient of the teeth are preserved in a fair state of preservation to enable one to determine something of the dentition; two anterior and two posterior incisors and a space for another in between are present; there is one large canine, oval in cross-section; then a series of six closely set, fairly small molars; posterior to the sixth, there may have been one or more additional molars. In the lower jaw, a smaller canine followed by eight very closely set molars are visible; there is no diastema as in the maxillary

series; there does not seem to be room for more than three lower incisors. The dental formula would thus be : $\frac{i. 5?, c. 1, m. 6 + 2}{i. 3?, c. 1, m. 8}$. For

the type, Broom has given the following formula : $\frac{i. 6, c. 1, m. 8}{i. 3, c. 1, m. 8}$.

As both specimens are not well preserved, I believe it legitimate to assume that in life the dentitions were probably similar. In the British Museum specimen the posterior border of the incisors, canines, and molars all carry fine serrations. Of the type, Broom stated, "There is no evidence of any serrations, and were they present the specimen would be expected to show some of them."

If Broom's observations are correct, there are thus points of difference between the two specimens. Further evidence, based on more complete and better preserved specimens, is, however, necessary before a new species can legitimately be created.

I have had three slices cut across the anterior part of the snout. These are reproduced here in a slightly diagrammatised form. It is seen that, posteriorly, the prevomers are fused, whereas, anteriorly, the fusion becomes less intimate and finally ceases; the palatine is seen to form a paired dorsal keel in the median line, which is supported by a girder of the anterior pterygoid ramus. Through the weathered right side the dorsal paired keel of the prevomers is seen; this supported the soft internasal septum.

B.M.N.H., R4097, Uitkyk, Prince Albert, Cape Province.

Pristerognathus polyodon, Seeley.

The specimen in the collection is the type of the genus; it consists of a weathered snout, from which very little of morphological interest can be determined. As far as can be ascertained the dental formula

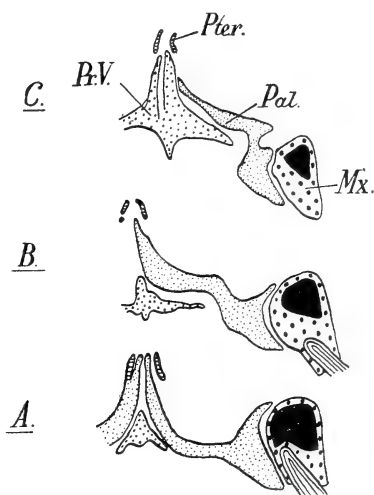


FIG. 1. — *Cynariognathus platyrhinus*. B.M.N.H., R4097. Diagrammatic cross-sections through the snout. $\times 1$.

A. At the level of the fifth molar.

B. " " fourth "

C. " " third "

Mx. = maxilla. Pr.V. = prevomer.

Pal. = palatine. Pter. = pterygoid.

is : $\frac{i. 6, c. 1, m. 3?}{i. 3, c. 1, m. ?}$. The posterior border of the lower incisors bears

fine serrations; in the upper incisors the crowns are lost, but one may assume that they also were serrated; the posterior border of the upper canine (and lower?) carry somewhat coarser serrations. The incisors are fairly large—so is the canine; the molar roots are of the same size as those of the incisors. There is a step on the maxillary border anterior to the canine. The splenial practically enters the symphysis on the ventral surface; further dorsally, it may actually enter it.

Chief measurements:

Length of the six upper incisors	35 mm.
Length of the three lower incisors	17 „
Width of upper canine	14 „
Width of the snout	55 „
Height of the snout	46 „

Type, B.M.N.H., R2581, Cypher, Tamboerfontein, Beaufort West, Cape Province.

Under the number R5753 there is registered a badly preserved shoulder girdle, of which Broom has given good restored figures under the name ?*Pristerognathus minor*. The number R5752 refers to some cervical vertebrae of the same form.

Scylacosaurus sclateri, Broom.

(Figs. 2-5.)

A nearly complete, though slightly weathered, skull, preserved in an extremely intractable matrix, was purchased by the British Museum, in 1912, from J. H. Whaits. This specimen has been referred to the above species. In point of size and arrangement of the external bones of the snout it agrees exactly with the type in the South African Museum. Broom's account (1903) of the dentition of the type gave the dental formula $i. 6, c. 3, m. 7$, incisors without serrations, canine probably with serrations. In 1932, he gave the formula $i. 6, c. 2, m. 7$. In this specimen the incisor series is composed of five small, slender, and closely packed teeth; these are definitely on the premaxilla; behind them are three much smaller teeth; these appear to lie on the maxilla, as in lateral view the premaxillo-maxillary suture lies anterior to them; posterior to a short diastema lies the large canine (20×7 mm.); the molar teeth are of the same size and nature as the anterior incisors; on the right side, a closely set series of seven teeth

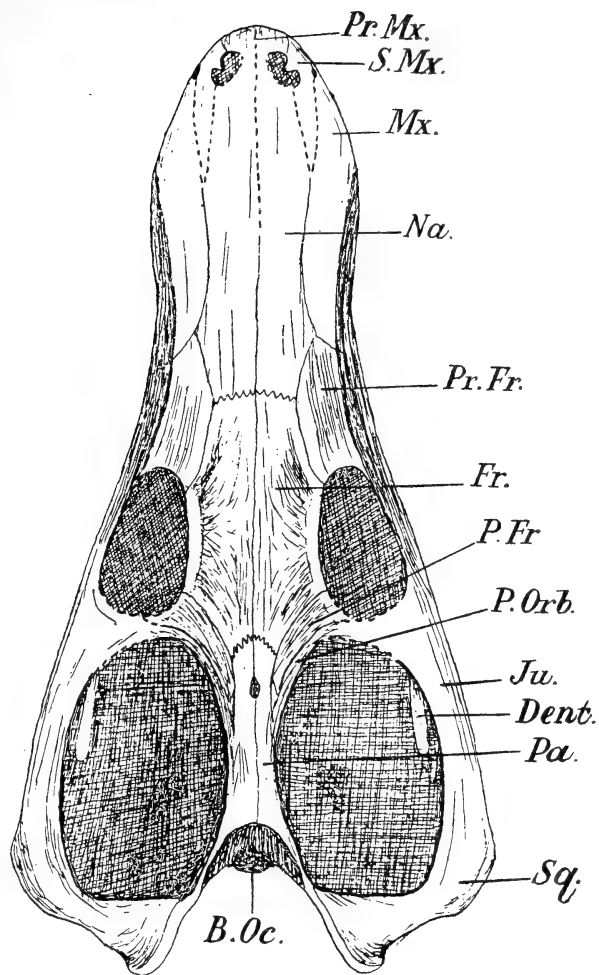


FIG. 2.—*Scylacosaurus sclateri*. B.M.N.H., R4055. Dorsal view of the skull. $\times \frac{2}{3}$.

Abbreviations to this and the subsequent figures.

Ang.	=angular.	Pit.	=pituitary foramen.
Art.	=articular.	P.Oc.	=paroccipital.
B.Oc.	=basioccipital.	P.Orb.	=postorbital.
B.P.P.	=basipterygoid processes.	Pr.Art.	=prearticular.
B.Sph.	=basisphenoid.	Pr.Fr.	=prefrontal.
Cor.	=coronoid.	Pr.Mx.	=premaxilla.
Dent.	=dentary.	Pr.Ot.	=pro-otic.
Ect.Pter.	=ectopterygoid.	Pr.V.	=prevomer.
Ep.Pter.	=epipterygoid.	P.Sph.	=parasphenoid.
Ex.Oc.	=exoccipital.	Pter.	=pterygoid.
Fen.Ov.	=fenestra ovalis.	P.T.F.	=post-temporal fenestra.
F.I.	=foramen incisivum.	Qu.	=quadrate.
F.J.	=foramen jugulare.	Qu.Ju.	=quadratojugal.
Fr.	=frontal.	S.Ang.	=surangular.
I.Na.	=internal nares.	S.M.F.	=septomaxillary foramen.
Ju.	=jugal.	S.Mx.	=septomaxilla.
La.	=lacrymal.	S.Oc.	=supraoccipital.
Mx.	=maxilla.	S.O.V.	=suborbital vacuity.
Na.	=nasal.	Spl.	=splenial.
Pa.	=parietal.	Sq.	=squamosal.
Pal.	=palatine.	St.	=stapes.
P.Fr.	=postfrontal.	Tab.	=tabular.
Pin.	=pineal foramen.	Ven.	=venous foramen.

Roman numerals refer to the cranial nerves.

occupy 23 mm.; on the left side, there are six less crowded teeth, with a gap for one additional tooth, occupying 27 mm.; the dental formula thus appears to be i. 5, c. 1 + 3, m. 7. All the teeth bear fine serrations on the posterior border. The dentigerous border curves upwards anterior to the canine, but there is no step. There are thus some differences in the dentition between the type and this specimen; allowing for the state of preservation and for a certain amount of individual variation, these differences should not restrain us from considering them specifically identical.

Mr. E. L. Parsons, at my request, attempted to display the palate and occiput, but found that the bone was more fragile than the hard

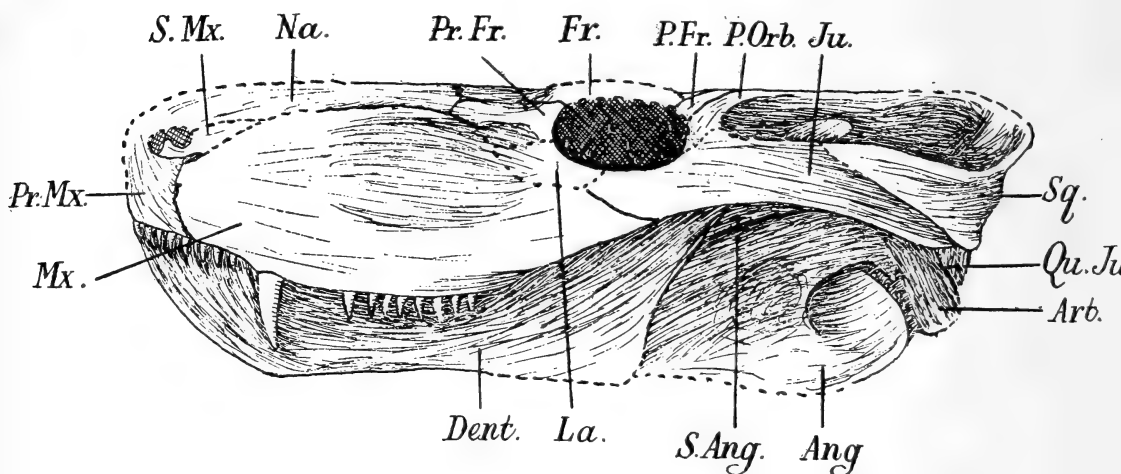


FIG. 3.—*Scylacosaurus sclateri*. B.M.N.H., R4055. Lateral view of the skull. $\times \frac{5}{8}$.

matrix, and had to abandon the attempt. On taking up the specimen again, I decided to make another attempt, and have succeeded in sufficiently exposing the left side of the brain-case and parts of the posterior half of the palate, so as to determine the general structure.

In the accompanying figure, the anterior part of the palate has been drawn from the type-specimen in the South African Museum, as figured by Broom, and the posterior half from the British Museum specimen. The chief points of interest are: the widening of the basisphenoid and the bulge on the paroccipital, which characters are, in some respects, paralleled in the Scaloposaurids; the prevomers have a posterior shovel-shaped expansion, which underlies the pterygoid; the anterior palatal fenestrae are relatively short; the paired tooth-bearing ridge lies wholly on the pterygoid, not, as in the Gor-

gonopsians, partly on the palatine; the suborbital vacuities are large; an interpterygoid vacuity is present; the pro-otics enclose a broader space than in the Gorgonopsians; the auditory groove, formed by a ridge of the squamosal, is well developed.

The brain-case does not show up very well, but is of considerable interest in that it shows that there is a certain amount of parallelism between this Pristerognathid and the Scaloposaurids, and in that it differs considerably from that of another Pristerognathid—*Trochosaurus*.

The basisphenoid is a strong bone with widely separated, ridge-like tubera; lateral to the tubera proper, the basisphenoid extends still further laterally, and here forms a sharp distinctive ridge, which bounds the fenestra ovalis antero-laterally and then continues posteriorly to meet the paroccipital (figs. 4, 5). This sharp ridge is not known in any other Therocephalian, but is present in *Galesaurus* and some Anomodonts. Anteriorly, the basisphenoid carries a ventral keel and, anterior to the plane of the pituitary fossa, carries the horizontal basiptyergoid processes on its lateral face.

Nothing can be determined of the relations of the basisphenoid with the parasphenoid.

The lateral development of the basisphenoid, mentioned above, also occurs in the Scaloposaurids and Bauriamorphs, but if Watson's account is correct, the relations differ somewhat, e.g. the flange does not bear a sharp ridge and, in Watson's figure of *Scaloposaurus*, the fenestra ovalis lies anterior to the paroccipital and lateral to the widened end of the basisphenoid, whereas in *Scylacosaurus* it lies in

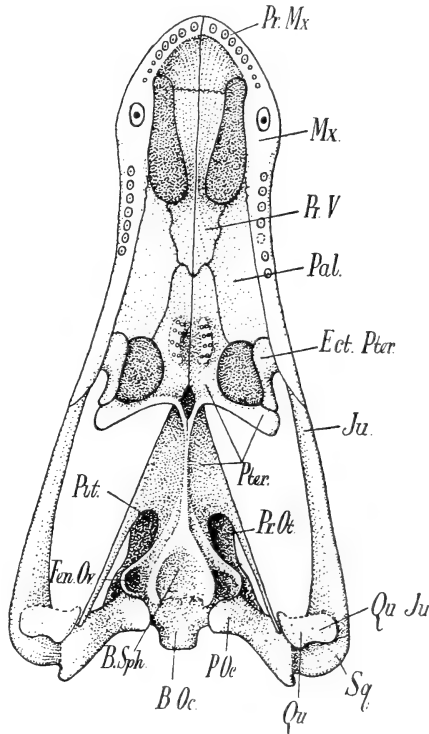


FIG. 4.—*Scylacosaurus sclateri*. B.M.N.H., R4055. Ventral view of the skull. Partly restored after Broom. $\times \frac{1}{2}$.

the normal Therapsid position between the basisphenoid, pro-otic, paroccipital, and basioccipital; in *Scaloposaurus* there does appear to be a hollow filled with matrix in the same position as the fenestra in *Scylacosaurus*, and, moreover, the depression figured by Watson as the fenestra ovalis in *Scaloposaurus* also occurs in *Scylacosaurus*, and here it definitely is not the fenestra ovalis.

The pro-otic is strongly developed; its anterior margin is overlain by the epipterygoid so that the *cavum epiptericum* has not yet been included in the cranial cavity; the ventral part of this bone has been removed and it can now be seen that the posterior border of the lateral opening into the pituitary fossa is formed by the basisphenoid

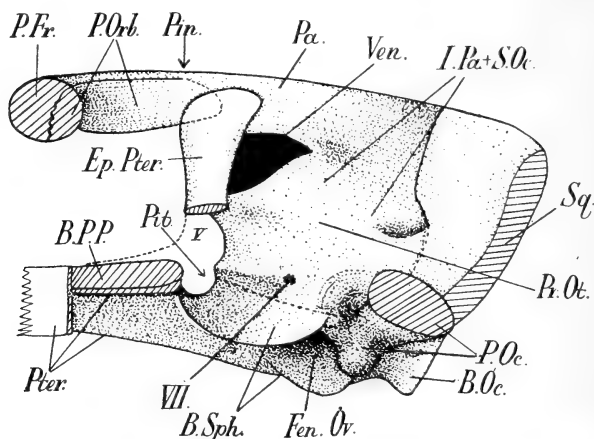


FIG. 5.—*Scylacosaurus sclateri*. B.M.N.H., R4055. Lateral view of the left side of the brain-case. Occiput, basiptyergoid process, and the postorbital bar seen in section. Lower half of epipterygoid removed. $\times 1$.

and pro-otic; in lateral view the epipterygoid obscures the perforation for the fifth cranial nerve; further dorsally lies the large venous fossa found in all Therapsids; the dorsal limits of the pro-otic cannot be determined; here the side-wall is formed by flanges from the parietal, interparietal, and supraoccipital, but their exact relations cannot be ascertained. As far as can be determined, the anterior margins of the pro-otics do not approach each other as they do in some Gorgonopsians.

The epipterygoid is a high bone standing with its elongated base on the quadrate ramus of the pterygoid in a plane immediately lateral to that occupied by the pro-otic, forming a *cavum epiptericum*; it is fairly narrow and flattened, but is proportionately twice as broad as in any known Gorgonopsian, and roughly half as broad as

in the Whaitsids and Cynodonts; dorsally, its inner surface is applied to the parietal, and its outer covered by a flange of the postorbital.

The lower jaw is of the usual Therapsid nature, and its structure is best understood by referring to the figure, where it is shown in lateral view.

Chief measurements :

Length from premaxilla to the basioccipital condyle	. 175 mm.
Length from premaxilla to the pineal foramen	. 118 „
Length from pineal foramen to edge of occipital plate	. 25 „
Length from premaxilla to anterior margin of orbit	. 82 „
Length of the lower jaw	. 160 „
Width across the squamosals	. 93 „
Interorbital width	. 22 „
Intertemporal width	. 9 „
Width of the snout	. 39 „
Height of the snout	. 36 „
Height of the occiput	. 48 „
Width across the lateral pterygoid flanges	. 37 „
Height of mentum of lower jaw	. 33 „
Length of the molar series	. 27 „
Diastema	. 8 „
Length of the incisor series	. 22 „

B.M.N.H., R4055, Fraserburg Road Station, Prince Albert, Cape Province.

Scymnosaurus watsoni, Broom.

(Figs. 6-8.)

The type-specimen consists of the greater part of a large skull, lacking the snout; some vertebrae and ends of limb-bones, from which very little can be determined. The palate was figured, in 1914, by Watson under the name *Lycosuchus*?. In 1915 Broom published outline drawings of the dorsal and lateral aspects, without indicating the constituent bones, and proposed the new name—*Scymnosaurus watsoni*. In 1921 Watson published a fuller account; his figures and account of the internal aspect of the brain-case I find to be correct, and here he corrected his former error in the orientation of the articulatory surfaces for the lower jaw. I have refigured the palatal aspect, as my interpretation of its structure differs considerably from that of Watson. The most obvious error is that he maintained that a median bone, which he called the vomer, was

present in the middle third of the palate, lying between the pterygoids and palatines, and posteriorly separated from the basisphenoidal

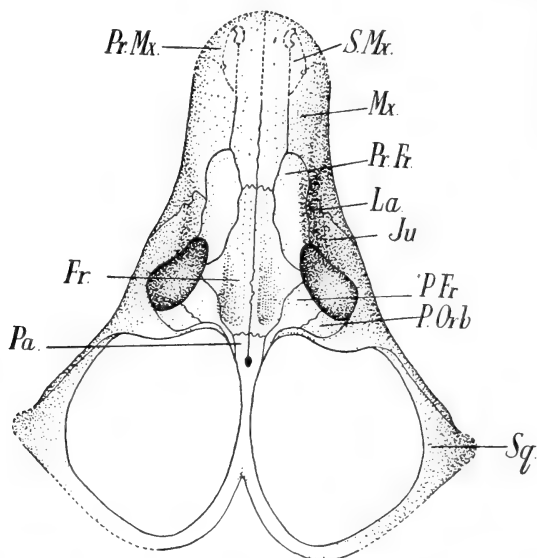


FIG. 6.—*Scymnosaurus watsoni*. B.M.N.H., R4100. Dorsal view of the skull. $\times \frac{1}{4}$.

rostrum by the interpterygoid vacuity and the pterygoids. The long median slip of bone interpreted as "vomer," is really the fused

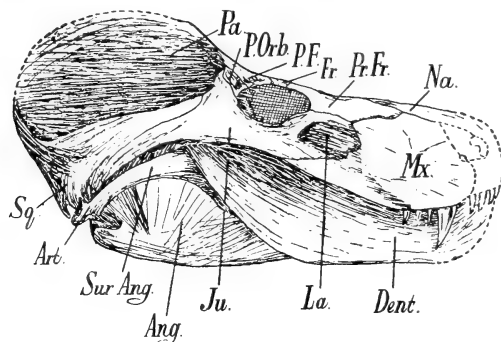


FIG. 7.—*Scymnosaurus watsoni*. B.M.N.H., R4100. Lateral view of the skull. $\times \frac{1}{4}$.

dorsal keel of the pterygoids, on which the median septum rested. The state of preservation of the specimen is, however, such that it is only in the light of our increased knowledge that we are able to

establish the fact that no median "vomer" can possibly be present in this position. From my figure it can be seen that the relation of the prevomers, palatines, pterygoids, and ectopterygoids is typical as in all known Therocephalia.

Attention may here be drawn to the points in which the Therocephalian palate differs from that of the Gorgonopsians.

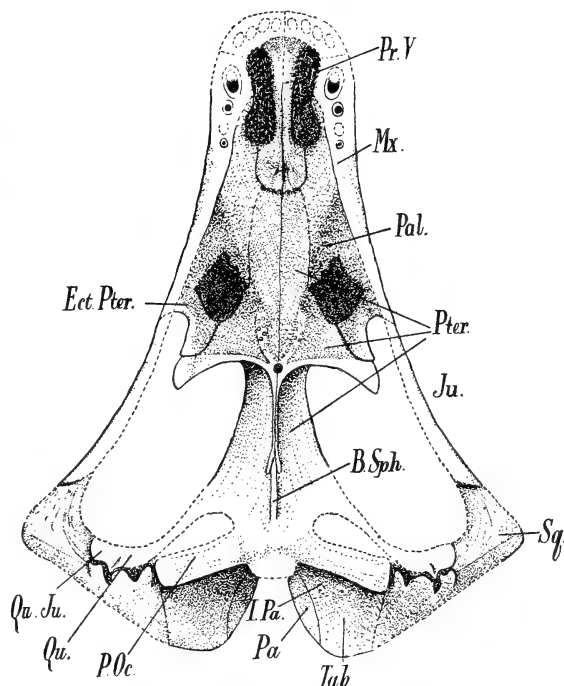


FIG. 8.—*Scymnosaurus watsoni*. B.M.N.H., R4100. Ventral view of the skull. $\times \frac{1}{3}$.

- (a) The internal narial opening is relatively shorter and, in the Whaitsids, is wholly or partly bipartite.
- (b) Posterior to the plane of the nares, the prevomers expand in shovel-shaped fashion and underlie the palatines and pterygoids, whereas in the Gorgonopsians the prevomers end posteriorly as tapering slips of bone, laterally flanked by the palatines.
- (c) The suborbital vacuities are large, and consequently the ectopterygoids are reduced to form their posterior girder-like border.

- (d) The median dentigerous ridges, when present, are carried wholly by the pterygoids.
- (e) The pterygoid has a long anterior ramus, which meets the prevomers; the palatines thus do not meet in the median line, whereas they do in the Gorgonopsians.
- (f) The quadrate ramus of the pterygoid has a straight outer edge, whereas in the Gorgonopsians it is concave.
- (g) The paroccipital bar is a much stronger element.
- (h) The ventral basisphenoidal keel is very deep in nearly all Therocephalians.

I had considerable difficulty in determining the structure of the dorsal and lateral surfaces, but, by a lengthy process of alternately grinding down with a file and etching with acid, the limits of the majority of elements are now visible, and are shown in the accompanying figures. The main points of interest are: the deep preorbital depression; the two grooves on the frontal, which is short and cruciform with only a small entry into the orbital border; the large prefrontal and postfrontal; the deep maxilla; the peculiarly high slip of the jugal on the postorbital bar; the high, thin parietal crest; the somewhat anteriorly directed orbits; the small posttemporal fossae; the epipterygoid, with straight edges, proportionately twice as broad as in the Gorgonopsians.

Chief measurements:

Length from premaxilla to the basioccipital condyle	. 240? mm.
Length from premaxilla to the pineal foramen	. 180? „
Length from pineal foramen to the occipital plate	. 70 „
Length from premaxilla to the front of the orbit	. 110? „
Length of the lower jaw	. 235? „
Width across the squamosals	. 234? „
Interorbital width	. 50 „
Intertemporal width	. 7 „
Width of the snout	. 64 „
Width across the lateral pterygoid flanges	. 94 „
Height of the snout	. 62 „
Height of the occiput	. 105? „
Length of the molar series	. 22 „

Type, B.M.N.H., R4100, Uitkyk, Prince Albert, Cape Province.

Trochosaurus major, Broom.

(Figs. 9-11.)

The type of this species is in the American Museum, and was described by Broom as *Trochosuchus major*. Haughton described a specimen in the South African Museum as *Trochosaurus intermedius*,

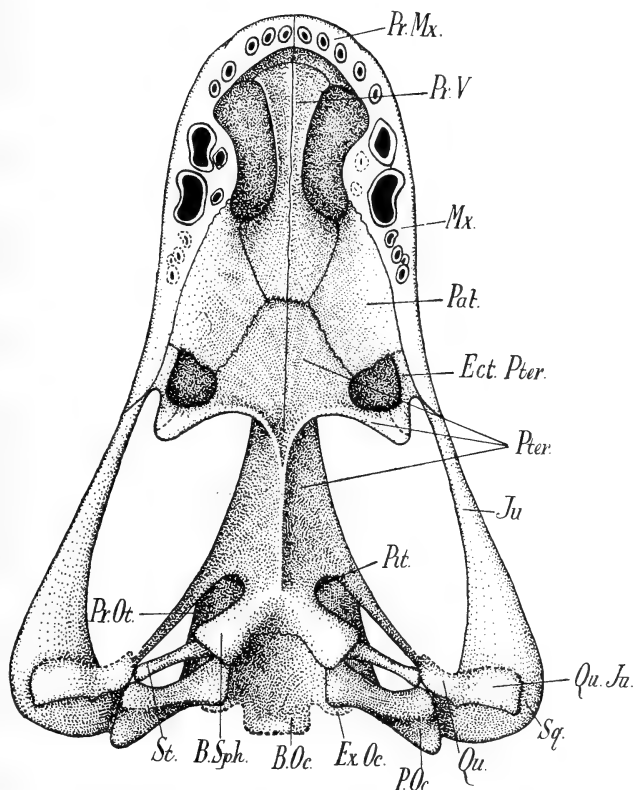


FIG. 9.—*Trochosaurus major*. B.M.N.H., R5747. Ventral view of the skull. $\times \frac{1}{2}$.

and, in 1932, Broom referred his species to Haughton's genus. The specimen in the British Museum formed the subject of the figures of the dorsal and lateral surfaces published by Broom in 1932.

After Mr. Parsons had done the preliminary development, I succeeded in exposing the whole palate, occiput, and the greater part of the lateral surface of the brain-case on the right side.

In the type, Broom found the dental formula to be i. 5, c. 2, m. 3?

the incisors have a strongly serrated posterior border. In the British Museum specimen the dental formula is identical, but here there is, in addition, definite evidence that the molars as well as the canines and incisors are replaced; it is not certain that the last incisor is implanted on the premaxilla.

I find Broom's figures of the dorsal and lateral surfaces correct; in this supplementary account only the palate, occiput, and lateral aspect of the brain-case will be figured and described.

The skull had been fissured, and subsequently weathered at the plane of the lateral pterygoid flanges so that this region is not very well shown; the middle part of the palate is revealed by a frontal fracture; the anterior and posterior portions have been chiselled out.

As shown in the figure, the palatal structure is typically Thercephalian; the paired prevomers separate two short and wide fenestrae—the anterior part of which housed the lower canine, and the posterior functioned as internal nares; the prevomers have a shovel-shaped posterior expansion, which underlies the palatines and pterygoids; the palatines do not meet in the median line; the suborbital vacuities are large, and the ectopterygoids appear to be beam-like structures forming the posterior and lateral borders of these vacuities; the extent to which the ectopterygoids participate in the formation of the transverse pterygoid bar cannot be determined; posteriorly, the deep median keel, formed by the pterygoids flanking the basisphenoidal rostrum, is a prominent feature; the quadrate ramus of the pterygoid has a nearly straight outer edge; the basisphenoidal tubera are very massive and rounded, and diverge greatly and have a deep hollow between them, with the result that the fenestrae ovals are very far apart and the stapes short; there appears to be no evidence of a "vomer" underlying the basisphenoidal tubera. The flat nature of the anterior part of the palatal roof is in strong contrast to the deeply vaulted antero-median part of the palate of the Whaitsids.

In the occiput the structure is adequately shown, only the basi-occipital condyle being lost. In general appearance the low and wide occiput is very similar to that of the Whaitsids, but there are great differences in the proportions of the constituent elements. A curious step above the supraoccipital forces the interparietal on to the dorsal surface; the post-temporal fenestrae are situated very high up and are far apart; the paroccipitals are enormously developed, their distal ends being bipartite, the lower supporting the quadrate and the upper supporting the strongly developed auditory groove

of the squamosal. In posterior view, the quadrate and quadratojugal appear to be unfused, the quadrate is rounded and forms the main articulation, whereas the quadratojugal is exposed on the lateral surface and forms the small outer part of the articulatory surface; the stapes is short; the foramen magnum is small; in section it is seen that, at the plane of the foramen magnum, the dorso-lateral corners of the condyle are formed by the exoccipitals; the foramen jugulare is large; the basioccipital sends two processes ventrally to support the widely separated and massive basisphenoidal tubera; on this specimen I can see no evidence that there are three bones in this region; if, however, these ventrally directed processes really represent the basisphenoid intimately fused to the basioccipital, then the bone lying ventrally to them would represent a parasphenoid.

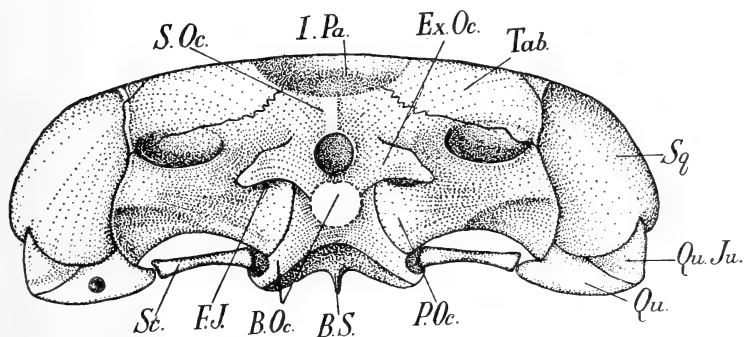


FIG. 10.—*Trochosaurus major*. B.M.N.H., R5747. Posterior view of the occiput. $\times \frac{1}{2}$.

A successfully induced parasagittal fracture has enabled me to get at the brain-case from the right side; this section also reveals the structure of the occiput (fig. 11).

The basisphenoid is seen to be a large bone with very strong posteriorly directed tubera, which rest on the basioccipital processes; the floor of the posterior part of the brain-case is thus very wide; laterally, it forms the ventral and anterior borders of the fenestra ovalis (the stapes is *in situ*), and its rostrum is flanked by the pterygoids; the basiptyergoid processes are horizontal and flattened, and are immovably clasped by the pterygoids; dorsally, it meets the prootic in a long suture and forms the lateral border of the opening leading into the pituitary fossa; anteriorly, it is continued as a median keel, but it has not been possible to determine where the transition into the parasphenoid occurs; the pituitary would lie in the dorsal surface of the basisphenoid.

The pro-otic is a large bone, whose anterior portion is flanked by the epipterygoid; posteriorly, it is applied to the anterior surface of the paroccipital, and in part to the squamosal; antero-dorsal to the fenestra ovalis lies a small foramen for the seventh cranial nerve, and under this there is a small depression for the geniculate ganglion; as, in lateral view, the anterior part of the pro-otic is overlain by the epipterygoid, forming a *cavum epiptericum*, the foramina for the fifth and sixth nerves cannot be seen; dorsally, the pro-otic forms the ventral border of the venous fossa.

Dorsal to the pro-otic, the side-wall of the posterior part of the brain-case is formed by the supraoccipital, interparietal, and parietal; the

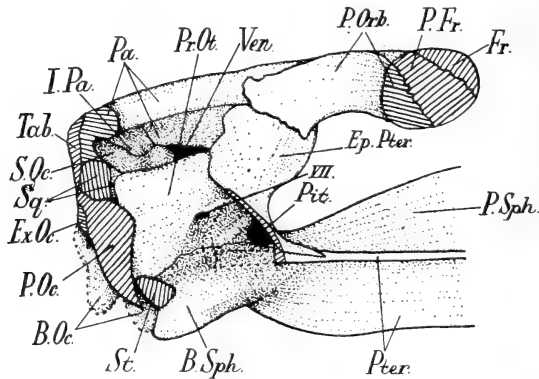


FIG. 11.—*Trochosaurus major*. B.M.N.H., R5747. Lateral view of the right side of the brain-case. Occiput and postorbital bar seen in section; part of the epipterygoid removed to show the pro-otic. $\times \frac{1}{2}$.

relations of these bones are shown in the accompanying figure and requires no verbal description.

The epipterygoid is a large and broad plate of bone, which forms the side-wall of the *cavum epiptericum*; ventrally, it stands on the quadrate ramus of the pterygoid in the usual Therapsid manner; continuing upwards it obscures the lateral opening into the pituitary fossa and the foramina for the fifth and sixth nerves from lateral view; dorsally, it meets the parietal and is flanked by a thin sheet of the postorbital; the epipterygoid is thus seen to be relatively more than twice as broad as that of any known Gorgonopsian, and has the appearance of the relations hitherto known only in the Cynodonts, amongst the Therapsids. It differs from that known in *Scymnosaurus*, *Scylacosaurus*, and *Ictidosuchoides* in that it is not a relatively narrow plate of bone with straight edges, but has a shaft-like middle and

expanded upper and lower ends, a condition reaching its greatest development in the later Whaitsids.

In the nature of the brain-case and the basicranial axis, *Trocho-saurus* differs considerably from that of the other members of the family *Pristerognathidae*. An examination of further material will undoubtedly show that this family includes forms which will eventually have to be arranged in more than one group. It is, moreover, clear that the Therocephalians are, already in the *Tapinocephalus* zone, a well-established group, in which a number of different evolutionary tendencies have been developed.

Chief measurements:

Length from the premaxilla to the basisphenoidal tubera	225 mm.
Length from the premaxilla to the pineal foramen	170 „
Length from the pineal foramen to the edge of the occipital plate	37 „
Length from the premaxilla to the front of the orbit	125 „
Length of the lower jaw	218 „
Width across the squamosals	165 „
Interorbital width	40? „
Intertemporal width	20 „
Width of the snout	85 „
Width across the lateral pterygoidal flanges	80 „
Height of the snout	60 „
Height of the occiput	40 „
Length of the molar series	15 „
Length of the diastema	3 „
Length of the incisor series	40 „

B.M.N.H., R5747, *Tapinocephalus* zone ?, South Africa.

Hyorhynchus platyceps, Seeley.

The incomplete skull shows the structure of the middle third of the roof of the skull; the frontal is short and has a large entry into the orbital border; the postfrontal and postorbital are well developed; the pineal foramen is large; the parietal region is narrow. Although some bones are visible on the palatal surface, I do not quite understand their relations. *Hyorhynchus* is undoubtedly a member of the *Pristerognathidae*, and the few characters that can be determined seem to indicate a close relationship to *Pristerognathus*.

B.M.N.H., R872, Gouph, South Africa.

The *Ictidosuchidae* are represented in the collection by two specimens referred to two genera, viz. *Cerdodon* and *Ictidosuchoides*. *Cerdodon*, which is not well known, is from an uncertain horizon in the Lower Beaufort, whereas *Ictidosuchoides* is known from a good skull, and is from the *Endothiodon* zone.

Cerdodon tenuidens, Broom.

In 1878, T. Bain had collected a calcareous nodule, which contained part of a Therapsid skull; the anterior part of the left side was weathered and showed a portion of maxilla, premaxilla, and dentary. So little could be determined that neither Owen, Seeley, Lydekker, or Watson named it, but, in 1915, Broom produced a generic description, together with a number of others equally valueless. It is a pity that some authors will persist in naming such fragments, which are of no morphological or phylogenetic value whatsoever.

In 1915, Broom gave the dental formula, $\frac{i. 5?, c. 1, m. 7-8?}{i. 3, c. 1, m. 3}$, and in 1932, $\frac{i. 6?, c. 1, m. 5}{i. 4, c. 1, m. 5}$. I find the formula to be, $\frac{i. 4, c. 1, m. 4}{i. 3, c. 1, m. 3}$. The posterior border of the lower molars, which alone have the crowns preserved, are serrated; the incisors are small and slender.

I asked Mr. Parsons to attempt to have a parasagittal section made in order that something more definite may be known of this "type." Unfortunately, this section was not cut true, with the result that very little of the structure could be determined; an additional slice was cut in an attempt to obtain a section along the median line, but also without success. The external weathered surface of the left side, figured by Broom, is thus all that can be determined in this new genus.

Type, B.M.N.H., 49420, Gouph, South Africa.

Ictidosuchoides longiceps, Broom.

(Figs. 12-14.)

In his original description Broom gave the dental formula, $i. ?, c. 3, m. 9$, and maintained that anterior to the large canine there were an additional two teeth implanted in the maxilla. Unable to find these two teeth, and thinking that they may have been lost in transit and through handling, I ground down the anterior maxillary border in order to expose the roots. At the level of the maxillary edge two filled alveoli were found, but no crowns extended beyond the maxillary border; it would thus appear that these two teeth were in the process of eruption. No serrations are visible on the canine or the molars.

Broom found that due to the narrowness and depth of the anterior part of the palate the infilling matrix could not be removed without damaging the maxillary teeth. By careful preparation with a fine

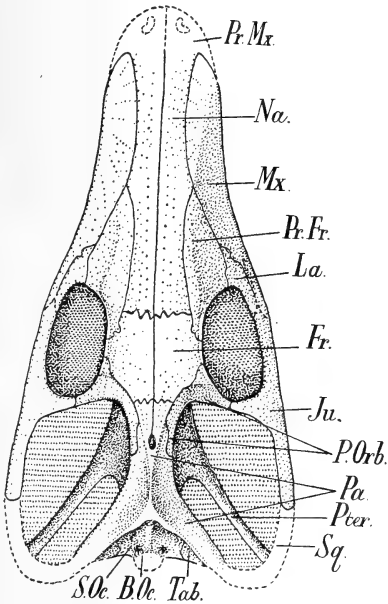


FIG. 12. — *Ictidosuchoides longiceps*. B.M.N.H., R5744. Dorsal view of the skull. $\times \frac{1}{2}$.

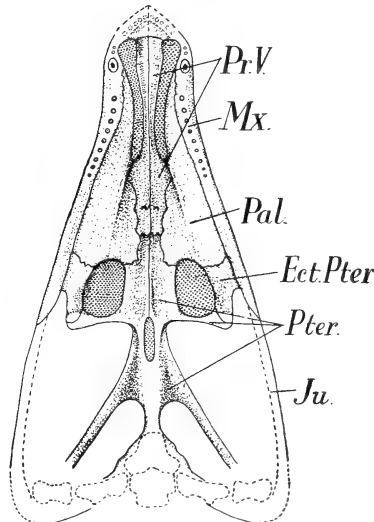


FIG. 14. — *Ictidosuchoides longiceps*. B.M.N.H., R5744. Ventral view of the skull. $\times \frac{3}{4}$.

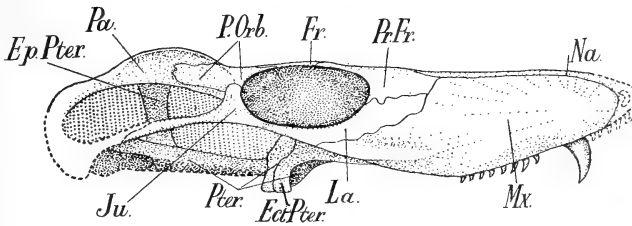


FIG. 13. — *Ictidosuchoides longiceps*. B.M.N.H., R5744. Lateral view of the skull. $\times \frac{1}{2}$.

chisel I have been successful in exposing the whole palate, but, unfortunately, the premaxillaries had fallen out prior to fossilisation, and thus the nature of the junction of the palatal processes of the premaxillaries with the prevomers cannot be determined. An oblique fracture at the level of the last molar reveals that, on the dorsal surface of the unfused prevomers, a pair of ridges are developed, and the groove

in between them must have supported the soft internasal septum. The prevomers are of the usual Therocephalian type; anteriorly, the end is fan-shaped, and posterior to the level of the internal nares, they again expand and underlie the anterior rami of the pterygoids and the median edges of the palatines well behind the level of the last molar.

The interpterygoid vacuity has its posterior margin somewhat indefinitely preserved, but it would appear that it was very similar to that of *Scaloposaurus* and *Icticephalus*. The suborbital vacuities are large, and the lateral border formed by the ectopterygoids are of the narrow beam-like character as in *Scaloposaurus*. The sweep of the quadrate ramus is typical of the Therocephalians, and nothing of the web, which in *Scaloposaurus* and *Icticephalus* connects the lateral and posterior pterygoid rami, can be seen. The basisphenoid, however, appears to be of the same broad nature as in the Scaloposaurids, and, although the specimen is not very well preserved in this region, there does appear to be some evidence that the pro-otic is applied to the sides of the basisphenoid in a manner very similar to that described by Watson in the type of *Scaloposaurus*. Only part of the epipterygoid is preserved; this is very similar to that of *Scylacosaurus* and *Scymnosaurus*, i.e. its dorsal and ventral ends are not expanded, and its sides straight; in this character *Ictidosuchoides* is thus distinct from *Trochosaurus* and the Whaitsids, and more akin to the generalised Pristerognathids.

In the nature of the dentition, the slight flaring-out of the maxillaries, the elongated interpterygoid vacuity, the absence of a postfrontal, the slender inferior temporal and postorbital bar, the apparently widened basisphenoid, and the large suborbital vacuities bounded by a beam-like epipterygoid, *Ictidosuchoides* approaches the Scaloposaurids. The narrow temporal region with its sharp crest, the comparatively long and large temporal fossa, the complete postorbital bar, the confinement of the interparietal to the occipital surface, the large pineal foramen, and the apparent absence of a web of bone connecting the lateral and posterior pterygoid rami, go to show that *Ictidosuchoides* is a form more akin to the more generalised Pristerognathids, but has some parallel characters, which are typical of the Scaloposaurids.

Chief measurements:

Length from premaxilla to the basisphenoidal tubera	. 140? mm.
Length from premaxilla to the pineal foramen	. . 110? "
Length from pineal foramen to edge of occipital plate	. 18 "
Length from premaxilla to front of orbit	. . 75? "
Width across the squamosals	. . . 80? "

Interorbital width	24 mm.
Intertemporal width	10 "
Width of the snout	27 "
Width across the lateral pterygoid flanges	40 "
Height of the snout	22 "
Height of the occiput.	28? "
Length of the molar series	25 "
Diastema	5 "
Length of the three canines	11 "

Type, B.M.N.H., R5744, Bruintjieshoogte, Somerset East, Cape Province.

The family, *Lycideopsidae*, is instituted for the reception of a single crushed skull; this skull cannot be included in any of the existing families without affecting the homogeneity of these groups. The characters distinguishing this from the other families are—extremely long dorso-ventrally depressed skull, with an extremely long molar series (10 teeth), consisting of ill-developed teeth, which may be absent in old age.

Lycideops longiceps, Broom.

(Figs. 15–16.)

In his original description of 1931, Broom gave little more than the dental formula, i. 5, c. 1, m. 8. In 1932, a slightly fuller description and a restoration of the anterior half of the left side was given without the constituent elements being indicated.

Although considerably crushed and sun-cracked, it has been possible to clear the external surfaces and most of the palate of a considerable amount of matrix. The extensive cracking, however, makes it extremely difficult to determine the structure. The dental formula is i. 5, c. 2, m. 10.

i. 0, c. 1, m. 5. The incisors of the upper jaw are very small and rather crowded, and in the lower jaw there are no incisors at all; in the upper jaw two long and slender canines are present, but it would appear that the posterior one is being replaced; in the lower jaw there is only one canine, situated very far anteriorly; the upper molars are exceedingly small teeth, occupying as much as 50 mm.; they are well separated, and appear to be rudimentary; in the lower jaw the molars are also very small, with large interspaces; they occupy 26 mm.; there is a diastema anterior as well as posterior to the canine. Broom is

probably right in thinking that the molars eventually disappear, and that *Lycideops* would in old age be molarless.

The skull has lost the greater part of its posterior third; on the left side, however, the lower jaw is complete and is in articulation with the quadrate and quadratojugal; part of the squamosal is also preserved.

The species is remarkable for its great relative length and consequent slenderness; the snout, in particular, is very long and slender, and was rounded in section; an antorbital depression, if any, must have been shallow; the orbit was large and rounded, directed as much outwards as upwards; the length of the molar series is very great. As far as can be determined, the palate is typically Therocephalian, with

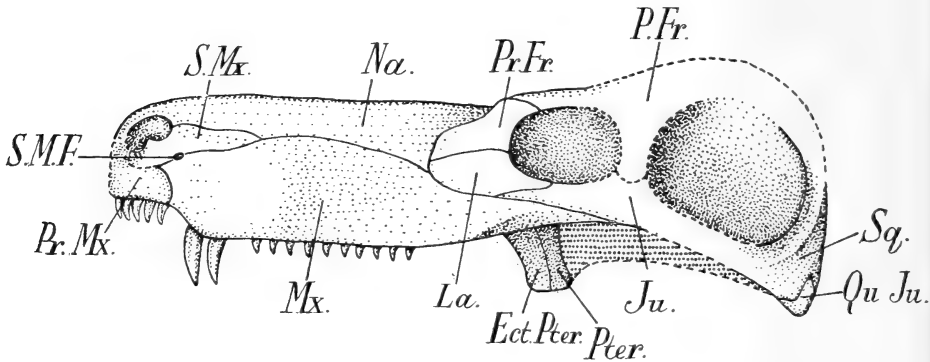


FIG. 15.—*Lycideops longiceps*. B.M.N.H., R5695. Lateral view of the skull, with the distortion corrected. $\times \frac{1}{2}$.

all the elements relatively lengthened; the transverse pterygoidal bar is deep; the suborbital vacuities fairly large; the anterior ramus of the pterygoid is very long; the vacuities for the internal nares are extremely short, absolutely as well as relatively; they are nearly rounded and the anterior part, which received the lower canine, situated very far anteriorly. The lower jaw is very long and slender, and the symphysis is extremely weak; there are no incisors, and the splenial, if present, must have been weak, especially at the symphysis.

This form, with its incipient molar reduction, its depressed form and rounded snout, narrow, transverse pterygoidal bar, and the curved contour of the mandible, has much in common with the Whaitsids. Its great length and the presence of a long molar series, however, excludes it from the Whaitsids proper. *Lycideops* may thus be regarded as a form, which in certain respects foreshadows the Whaitsid structure.

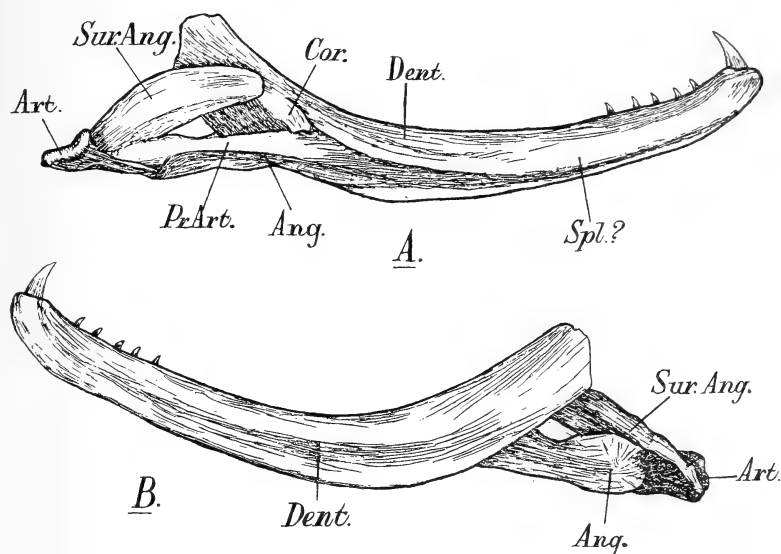


FIG. 16.—*Lycideops longiceps*. B.M.N.H., R5695.

A. Inner view of the left mandible. $\times \frac{1}{2}$.
B. Outer view of the left mandible. $\times \frac{1}{2}$.

Chief measurements :

Length from premaxilla to front of the orbit .	120 mm.
Length of the lower jaw	198 „
Interorbital width	32 „
Width of the snout	40 „
Width across the lateral pterygoidal flanges .	58 „
Height of the snout	30 „
Height of the mentum	12 „
Length of the molar series	50 „
Diastema	13 or 22 mm.
Length of the incisor series	24 mm.

Type, B.M.N.H., R5695, Thaba 'Nchu, Orange Free State.

The family, *Whaitsidae*, is particularly well represented in the collection in the British Museum, viz. a good anterior half of the type-skull of *Moschorhinus kitchingi*, a practically complete skull of the type of *Notosollasia laticeps*, the imperfect skull of the type of *Theriognathus microps*, the excellent type-skull, and an additional snout, of *Whaitsia major*, and the imperfect snout, which is the type of *Tigrisuchus simus*. All these forms fall into a homogenous group,

having all the characters enumerated by Houghton in his original description of *Whaitsia platyceps*. The *Whaitsidae* may be defined as follows: Therocephalians with a broad, depressed, moderately short and rounded snout; large temporal openings; crested parietal region with a small pineal foramen; molars absent or obsolescent; width across the lateral pterygoidal flanges reduced; the anterior palatal vacuity greatly shortened, wholly or partly separated into an anterior foramen incisivum, and a posterior internal narial opening; the anterior part of the palate deeply vaulted with an ingrowing of the maxillaries, which is sometimes met by an outwardly directed swelling of the prevomers; suborbital vacuity variable, absent, small or large; epipterygoid broad, with expanded dorsal and ventral ends; postfrontal absent; very strong paroccipital process; weak, but long, mandibular symphysis and distinctively curved dentary.

Moschorhinus kitchingi, Broom.

(Figs. 17-19.)

Broom's original account and figures are good; but, since I have developed and etched the skull, some additional features can be recorded. Although it is possible that in life six incisors were present, this is by no means "quite manifestly" so; actually, on either side, only five are preserved; on both sides there are no functional molars, but sockets of two are preserved. The dental formula can thus be given as i. 5, c. 1, m. 2?. In the accompanying figures of the dorsal and lateral surfaces a number of additional features are shown; it is evident that the septomaxilla is a much larger bone than Broom thought—its posterior extent, in particular, is very large; the short frontals form only a small portion of the supraorbital border; there is no postfrontal; the lacrymal carries a distinctive tubercle; there is no step in the dentigerous border; the ectopterygoid meets the jugal.

The palate of *Moschorhinus* is essentially similar to that of the other members of the family *Whaitsidae*, but there are some very interesting and illuminating differences in the less basic points of structure; the entire palate is relatively wider than in the other *Whaitsids*, and, due to its absolute greater width and less vaulted nature, creates an impression of still greater width; this is due to the fact that the maxillaries and, to a lesser extent, the palatines do not curve inwards as much as they do in the other *Whaitsids*; in *Moschorhinus* the alveolar edge is fairly straight, whereas in the other *Whaitsids* it sweeps inwards with a medially directed convexity;

on the inner vertical surface of the palatines there is a sharp oblique ridge for the attachment of the soft palate; this is situated half-way up, whereas in *Notosollasia*, *Theriognathus*, and *Whaitsia* it lies on the ventral edge.

The prevomers are of a distinctive shape; anteriorly, they are greatly expanded, and carry only a very low ventral keel on their middle third; a fracture reveals the fact that the premaxillaries

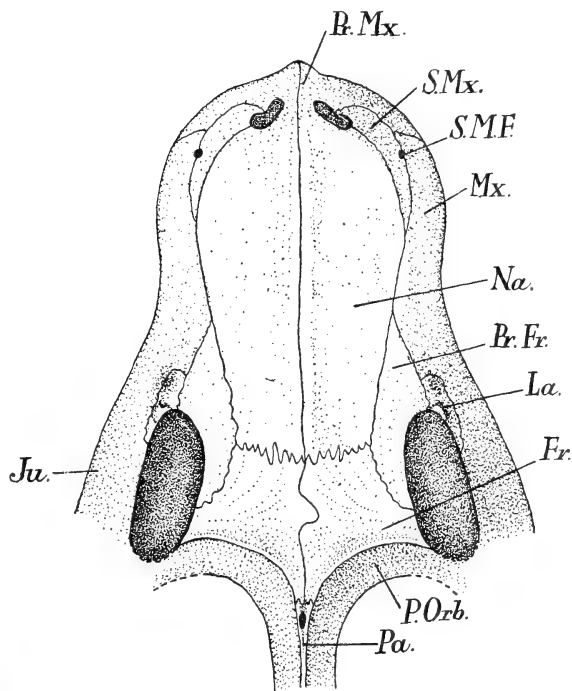


FIG. 17.—*Moschorhinus kitchingi*. B.M.N.H., R5698. Dorsal view of the anterior half of the skull. $\times \frac{1}{2}$.

extend on to the dorsal surface of the prevomers; posteriorly, the prevomers underlie the pterygoids and palatines and present a shovel-shaped outline; they form the greater part of the posterior margin of the extremely short internal nares; there is no ventro-lateral swelling of the prevomers, which in *Notosollasia* and *Whaitsia* divides the anterior palatal vacuities in two unequal parts; in *Moschorhinus* these vacuities are short but wide, and slightly constricted to produce a dumb-bell shape; the whole functioned as internal nares, since the lower canine was received in a depression

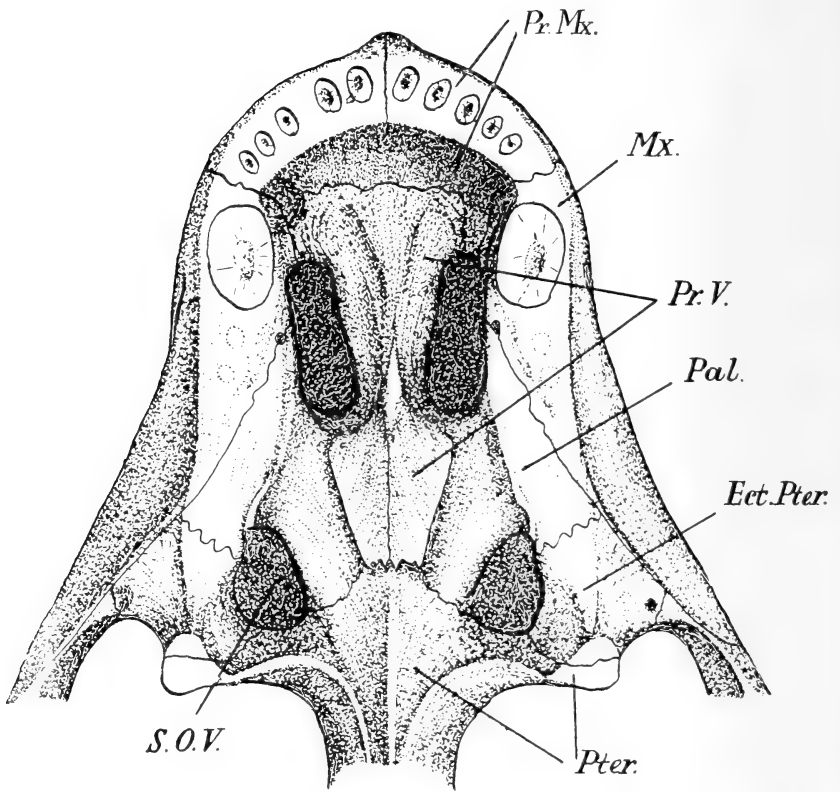


FIG. 18.—*Moschorhinus kitchingi*. B.M.N.H., R5698. Ventral view of the anterior half of the skull. $\times \frac{2}{3}$.

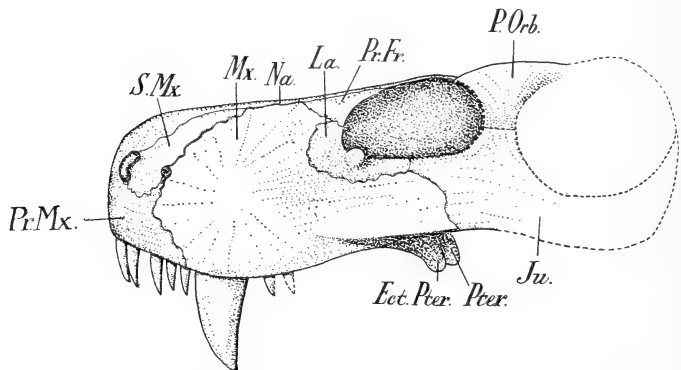


FIG. 19.—*Moschorhinus kitchingi*. B.M.N.H., R5698. Lateral view of the skull; posterior half reconstructed. $\times \frac{1}{3}$.

in the premaxilla, anterior to the vacuity and the upper canine, whereas in *Whaitsia* the anterior part functioned as a foramen incisivum, and the posterior as internal nares; the ectopterygoids are strongly developed; they form the lateral borders of the large suborbital vacuities and, posteriorly, send a strong flange to support the anterior surface of the transverse pterygoidal bar, but do not form the whole corner of this bar as they do in *Whaitsia*, *Theriongnathus*, and *Notosollasia*. The nature of the suborbital vacuities is more akin to that of the Scaloposaurids and the less advanced Pristerognathids, than to that of the other Whatsids, where they are very small or absent; in the Gorgonopsians they are also very small or absent.

The pterygoids are only partly preserved; owing to the size of the suborbital vacuities and the posterior extent of the prevomers, the pterygoids have, anteriorly, a much smaller palatal surface than in the other Whatsids; as is shown in the figure, a very deep but thin median keel is developed on the ventral surface of the anterior rami of the pterygoids—a feature not found in the other Whatsids; lateral to this there lies a deep groove, and then there lies the deep, thin, postero-medially directed flange of the lateral rami of the pterygoids; there is no interpterygoid vacuity. Unfortunately, nothing is preserved of the posterior half of the skull.

The skull of *Moschorhinus kitchingi* throws an illuminating light on the nature of the Whatsids. The broad depressed snout, the apparently large temporal openings, the reduced width of the lateral pterygoidal bar, the absence of the postfrontal, the reduction of the anterior palatal vacuities, the slight inward swelling of the maxillaries and the palatines, and, finally, the reduction of the molar series, clearly stamps it as a Whatsid. The persistence of two molars, the unipartite anterior palatal vacuities, the large suborbital vacuities, and the ectopterygoid not forming the corner of the pterygoidal bar, show this species to be less advanced than the Whatsids—*Theriongnathus*, *Notosollasia*, and *Whaitsia*, and probably indicates the road traversed by these more advanced forms. In an unnamed species of *Moschorhinus*, described by Broom, there are two persistent molars in a skull which is mature; and in the inadequately known *Moschorhinus warreni* there are three upper and four lower molars. We thus appear to have a progressive series showing molar reduction.

The relations of *Moschorhinus*, and thus all the Whatsids, to the other Therocephalians are not very clear; the three specimens of

Moschorhinus are manifestly considerably removed from the less advanced Pristerognathids, and only the discovery of some forms less advanced than *Moschorhinus* will enable one to trace the ancestors of the Whaitsids and also of the parallel family of Scaloposaurids.

Chief measurements :

Length from premaxilla to pineal foramen	145 mm.
Length from premaxilla to front of orbit	93 „
Interorbital width	56 „
Intertemporal width	28? „
Width of the snout	83 „
Width across the lateral pterygoid flanges	90 „
Height of the snout	55 „
Length of the molar series	12 „
Diastema	4 „
Length of the incisor series	40 „

Type, B.M.N.H., R5698, Bethesda Road Station, Cape Province.

Notosollasia laticeps, Broom.

(Figs. 20-24.)

Broom founded this new genus in 1925, and in his description gave little more than the dental formula—i. 4, c. 1, m. 0. In 1932, he gave the formula—i. 5, c. 1, m. 0, and stated that a small secondary palate is formed by the union of the maxilla and a downward development of the prevomers; he could find no suborbital vacuity.

I have spent a considerable time in removing masses of matrix and in etching the skull, which now shows a number of very interesting points of structure.

In the upper jaw there are four well-developed incisors with longitudinal grooves, but with no serrations on either the anterior or posterior edges; these are followed by a very much smaller fifth incisor, which appears to be in the process of eruption; between the last incisor and the canine there is a space of 4 mm.; the canine is a curved tooth of medium size; on the left side there is another canine being absorbed, whereas on the right there is a filled-in alveolus behind the functional canine; posterior to the canines, there are no indications of molars whatsoever. *Notosollasia* thus differs in this character from *Moschorhinus*, where two molar alveoli or even three teeth persist.

The palate of *Notosollasia* is of some interest; anteriorly, the paired prevomers meet the palatal processes of the premaxillaries and form

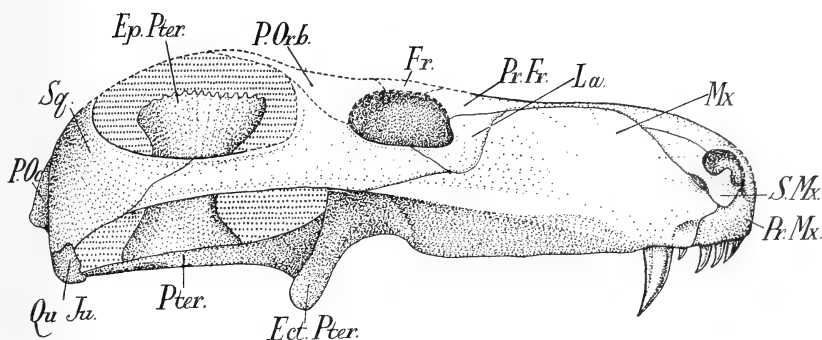


FIG. 20.—*Notosollasia laticeps*. B.M.N.H., R5699. Lateral view of the skull. $\times \frac{3}{4}$.

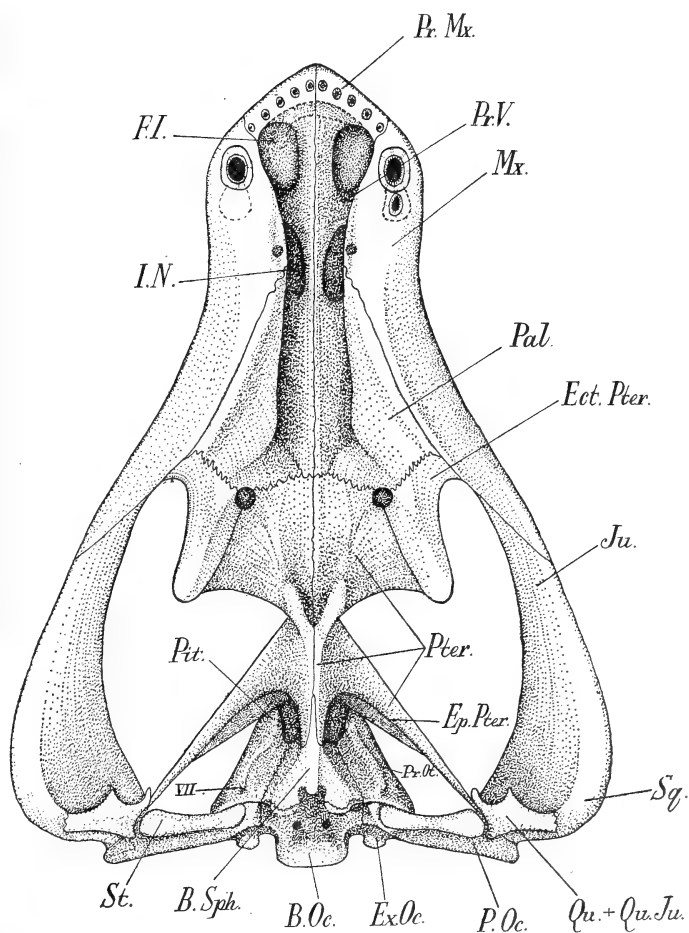


FIG. 21.—*Notosollasia laticeps*. B.M.N.H., R5699. Ventral view of the skull. $\times \frac{1}{2}$.

a comparatively narrow internarial bar, which in life supported a cartilaginous septum dorsally, and which separates two anterior

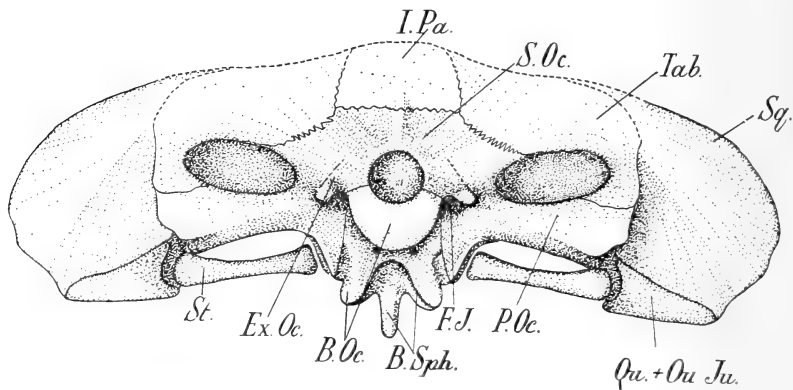


FIG. 22.—*Notosollasia laticeps*. B.M.N.H., R5699. Occipital view of the skull. $\times \frac{2}{3}$.

fenestrae in the palatal roof, in which the lower canines fit. Posterior to the border of these fenestrae the prevomers swell out and become

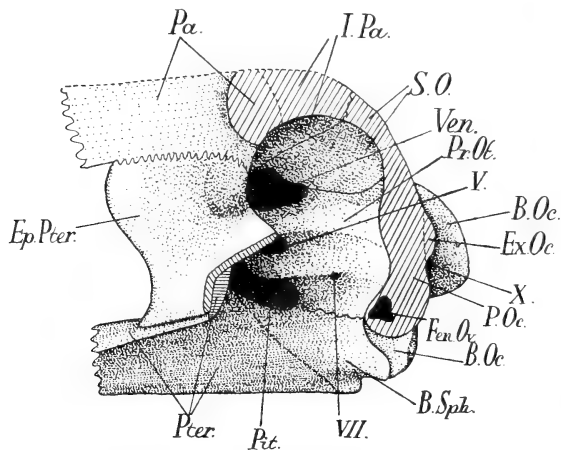


FIG. 23.—*Notosollasia laticeps*. B.M.N.H., R5699. Lateral view of the left side of the brain-case, with the occipital plate seen in section. $\times \frac{2}{3}$.

thickened ventrally as well as laterally, so that they meet the dorso-medially bulging maxillaries; the ventral surface of the prevomers still, however, occupies a plane much dorsal to the alveolar maxillary border. Continuing in posterior direction the prevomers again become narrow, and lateral to them lie the two internal nares; the

prevomers curve round the posterior border of the internal nares and then continue in posterior direction to meet the palatines and the pterygoids, as shown in the figure. The posterior two-thirds of the prevomers carry a high keel on the palatal surface, and on their dorsal surface are supported by a girder formed by the anterior pterygoidal rami (this is clearly shown in a cross-section). The maxillaries curve downwards and inwards to a great extent, and, in addition, are flanked by the palatines, so that the prevomers form the roof of a very narrow, grooved naso-phalangeal passage, which lies at a much higher level than the surface of the antero-lateral portions of the palatines. The relations of the pterygoids, palatines, and ectopterygoids are shown in the figure and are basically as in the less advanced Pristerognathids. The small size of the rounded suborbital vacuities is a feature which appears typical of the Whaitsids (with the exception of *Moschorhinus*), and is in marked contrast to the other Therocephalian families, where it is always large. There are no teeth on the palatines and pterygoids, which is in accordance with the general lack of tooth-development in the Whaitsids. Posteriorly the pterygoid sends out a process, which eventually abuts on the quadrate, and, in the median line, two high flanges form a strong keel, which separate to clasp the anterior prolongation of the basisphenoid, which apparently represents a parasphenoid fused with the basisphenoid proper.

The brain-case and basicranial region have been adequately freed of matrix. The brain-cavity is relatively long, narrow, and low.

The basioccipital forms a strong condyle, and sends two strong ventrally directed processes to support the basisphenoidal tubera; these processes form the posterior border of the foramen ovale; below the level of the foramen magnum there is thus a considerable extent of basioccipital.

The basisphenoid is not very strongly developed; its tubera are unthickened, and they do not diverge much; dorsally, it meets the pro-otic and forms the posterior border of the lateral opening into the pituitary fossa; unfortunately, the relations of the anterior prolongation of the basisphenoid cannot be determined; on the lateral surface of the vertical sheet there are two horizontally placed basi-ptyergoid processes clasped by the pterygoid.

The pro-otic is fairly well developed; antero-dorsally of the fenestra ovalis there lies a small foramen for the seventh nerve; from here a ridge runs anteriorly to the anterior pro-otic process; above this lies the large perforation for the fifth nerve; dorsal to this lies the

posterior pro-otic process, which forms the border of the large venous foramen; anteriorly, the pro-otic is flanked by the broad epipterygoid, and, posteriorly, is applied to the paroccipital and supraoccipital. Dorsal to the pro-otic the side-wall of the posterior part of the brain-case is formed by flanges from the interparietal and parietal.

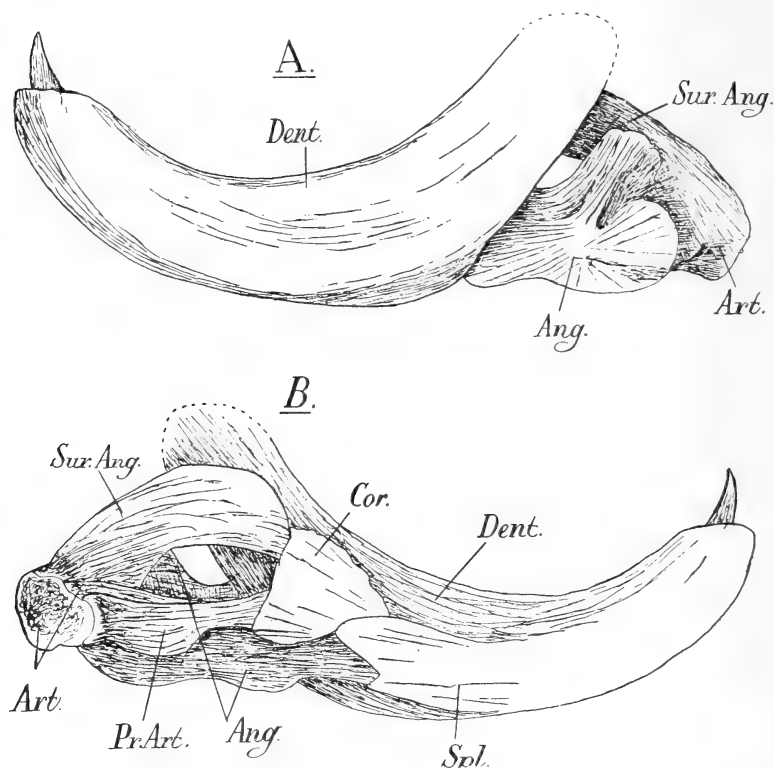


FIG. 24.—*Notosollasia laticeps*. B.M.N.H., R5699.

A. Outer view of the mandible. $\times \frac{1}{2}$.

B. Inner view of the mandible. $\times \frac{1}{2}$.

The epipterygoid is a low, broad bone with greatly expanded ends; it is firmly attached to the quadrate ramus of the pterygoid ventrally, and, dorsally, to the parietal; it encloses a large *cavum epiptericum*.

The greater part of the occiput is preserved; it is low and broad; the post-temporal fenestrae are large and situated low down (contrast *Trochosaurus*); the foramen magnum is small, and attention must be drawn to the great depth of bone ventral to it; the paroccipital bar is strong, and lateral to it the squamosal forms a deep auditory

groove; the exoccipital takes no part in the formation of the condyle, but forms a strong tubercle overhanging the large foramen jugulare; the quadrate and quadratojugal are intimately connected, and the latter is exposed on the lateral surface; the stapes is preserved on the right side in its natural relations; it is a strong bone with expanded ends and constricted shaft; no foramen can be seen.

The lower jaw is of a distinctive shape when viewed from below; at its articulatory end the ramus is very wide; it then sweeps forward in a medially directed curve and, at the level of the canines, it straightens out and forms a long and relatively narrow symphysis. It has not been possible to expose the extreme tip of the ramus; a fracture near the end, however, reveals a large canine, oval in cross-section, and another in the process of eruption; no roots of incisors are visible at this plane, and it does not appear probable that any could be present, as the canines do not leave much room anteriorly for the development of additional teeth; there are no molars. The general arrangement of the constituent bones are typically Therocephalian; their relations are best understood by referring to the accompanying figure (fig. 24).

Chief measurements :

Length from premaxilla to basioccipital condyle	210 mm.
Length from premaxilla to front of orbit	100 „
Length of the lower jaw	185 „
Width across the squamosals	165 „
Width of the snout	60 „
Width across the quadrates	110 „
Width across the lateral pterygoid flanges	65 „
Height of the snout	45 „
Height of mentum of lower jaw	25 „
Length of the incisor series	22 „

Type, B.M.N.H., R5699, Bethesda Road Station, Cape Province.

Theriognathus microps, Broom.

(Figs. 25-27.)

Owen's figures give a good idea of the skull as it was preserved. This author considered the specimen to represent an Anomodont, and Lydekker, subsequently, placed it in the genus *Endothiodon*. Broom, in 1910, gave a good summary of Owen's and Lydekker's accounts and, on a superficial study of the lower jaw, rightly came

to the conclusion that it was a Therocephalian. In 1932, Broom thought it best to regard it as a member of the *Whaitsidae*.

Mr. Parsons has attempted to expose the palate, but found that for the greater part he could not remove the matrix without damaging

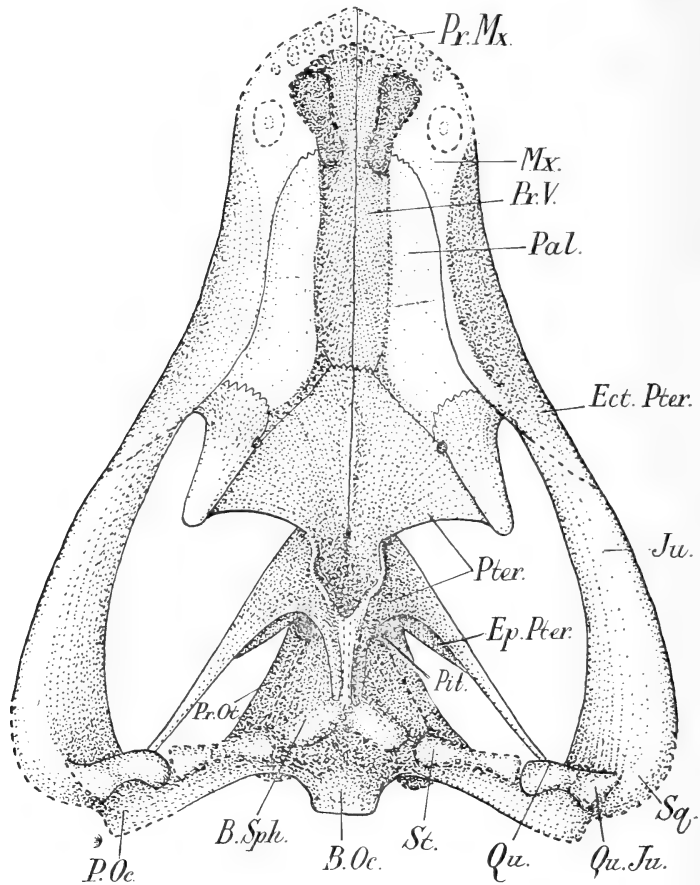


FIG. 25.—*Theriognathus microps*. B.M.N.H., 47065. Ventral view of the skull. $\times \frac{1}{2}$.

the bone. Subsequently, with a hammer and a small chisel, I succeeded in exposing the whole palate and also parts of the occiput. A fortunate fracture exposed the outer surface of the left epipterygoid and proved that the matrix would split very easily. I thus deliberately induced additional fractures, with the result that the entire brain-case can now be studied from a variety of sections—frontal,

sagittal, parasagittal, and cross-sections—and also from some parts where it has been possible to expose the outer surface.

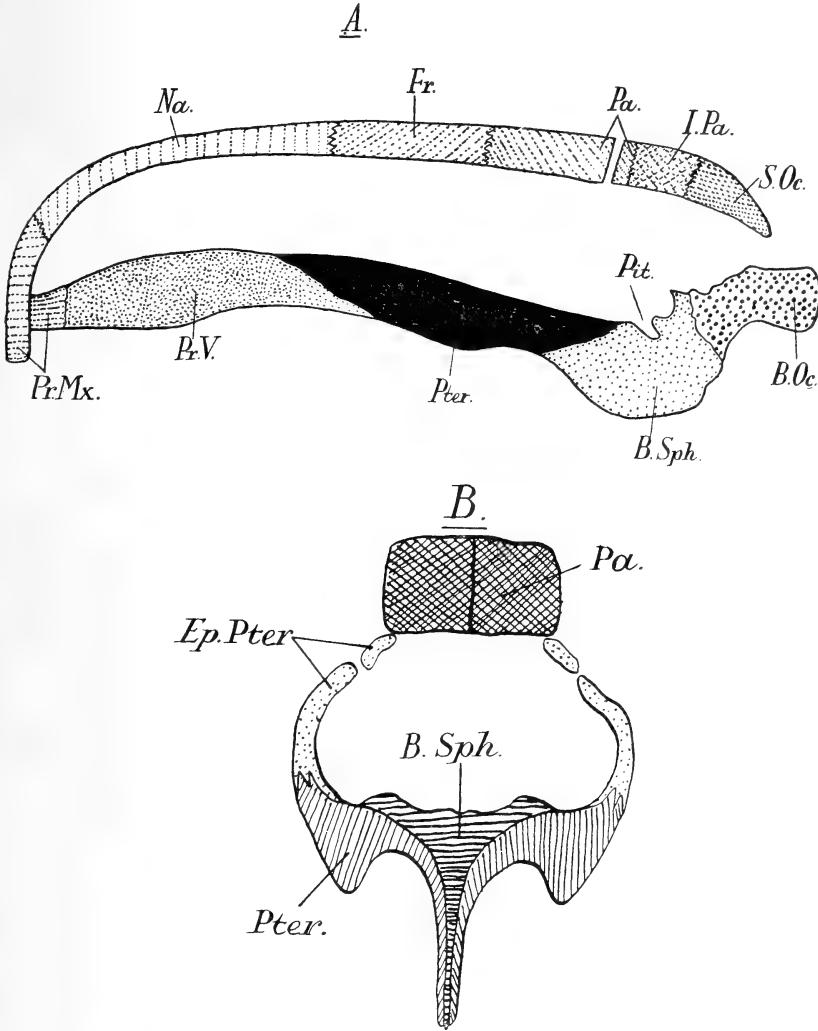


FIG. 26.—*Theriognathus microps*. B.M.N.H., 47065.

- A. Sagittal section, reconstructed from a number of partial frontal, parasagittal, sagittal, and cross-sections. $\times \frac{1}{2}$.
 B. Cross-section through the brain-case, just anterior to the pituitary fossa. $\times 1$.

It is now clear that, basing his conclusions mainly on the molarless nature of the jaws and the structure of the mandible, Broom was

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right in referring this form to the family *Whaitsidae*. The general appearance and arrangement of the various palatal and occipital bones and the structure of the brain-case bear a very close resemblance to that of *Whaitsia*, *Moschorhinus*, and *Notosollasia*.

The anterior end of the snout is missing and nothing can be ascertained as to the nature of the canines and incisors; as both alveolar edges have been perfectly exposed it is possible to state definitely that no molars were present; there are not even indications of alveoli. The dorsal and lateral surfaces have for their greater part been lost, and the occipital surface has also been much damaged.

The palatal surface, although somewhat sun-cracked, is preserved in a sufficiently complete state for its whole structure to be determined. The relations of the constituent elements are shown in the accompanying figure. Although only the posterior borders of the anterior palatal vacuities are preserved, it would appear that they were of the type of those in *Moschorhinus* rather than that of *Notosollasia* and *Whaitsia*, i.e. the whole functioned as internal nares, the canines of the lower jaw being received in hollows antero-laterally to the nares. The prevomers are relatively long and form the median part of the roof of the deeply vaulted anterior half of the palate. On both the dorsal and ventral surfaces the prevomers carry high median keels. Lateral to the prevomers lie the palatines, which form the deep lateral walls to the highly vaulted median part of the palate. The palatines extend laterally to meet the maxillaries at the edentulous alveolar edge; on their medial surface the palatines carry a well-defined ridge, to which in life the soft palate must have been attached; between the prevomers and the soft palate a spacious air-passage was thus developed. The ectopterygoids are remarkable in that they form the strong lateral corner of the transverse pterygoidal bar, whereas, in the normal Therocephalian condition, and also in *Moschorhinus*, they are only supporting flanges to the pterygoids, which themselves form the corners. A small suborbital vacuity is present; this is very similar to that of *Notosollasia*, whereas it is large in *Moschorhinus* and, by both Broom and Haughton, maintained to be absent in *Whaitsia platyceps*, as it is in *Whaitsia major*. The pterygoid is very well developed; it forms a large part of the middle portion of the palate; the lateral flanges are not very strong since the corners of the pterygoidal bar are formed by the ectopterygoids; the posterior rami form, in their anterior part, two diverging flanges, in between which lies a deep groove; continuing posteriorly, these flanges form a very deep keel and clasp between them a similar high unpaired keel

sent forwards by the basisphenoid (basisphenoidal rostrum); the quadrate rami stretch postero-laterally with a straight outer edge (as is typical for the Therocephalia in contradistinction to the Gorgonopsians, where it is curved) to meet the quadrate.

The basioccipital (figs. 25-27) forms the well-developed condyle, and, in a fracture, the processes supporting the basisphenoidal tubera are very well shown; dorso-laterally the exoccipitals support the condyle; the medulla rested on its rather irregular grooved dorsal surface.

The basisphenoid forms two widely separated tubera and, anteriorly, forms the deep vertical keel flanked by the pterygoids;

the basipterygoid processes are horizontal, flat, and immovable; in a sagittal fracture no trace of a median parasphenoidal process is seen extending dorsally, although both the anterior and posterior borders of the pituitary fossa can be seen; it is, however, possible that the anterior part of the bone labelled "basisphenoid" represents a parasphenoid

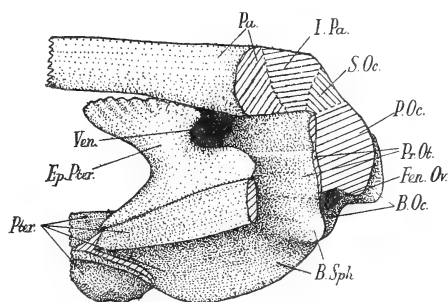


FIG. 27. — *Theriognathus microps*. B.M.N.H., 47065. Lateral view of the left side of the brain-case. $\times \frac{1}{2}$.

indistinguishably fused with it; in a cross-section it is seen that the basisphenoid forms a broad floor for the hind-brain.

The pro-otic is only partly exposed and, as far as can be ascertained, agrees with the condition in *Notosollasia*; it lies against the paroccipital; antero-dorsally, it forms the ventral border of the venous foramen; the foramen for the seventh nerve apparently lies in the usual position; that for the fifth is obscured by the epipterygoid.

The epipterygoid, as in all the Whaitsids, is a large flat element with expanded dorsal and ventral ends; its base on the quadrate ramus of the pterygoid is very long and, as it lies lateral to the *cavum epiptericum*, obscures the foramen for the fifth nerve, whose nature has thus not been determined.

The occiput is depressed; the post-temporal fenestrae are of medium size; the paroccipitals are very massive, with greatly expanded distal ends, which support the auditory ridge formed by the squamosals; they are situated in a plane considerably in advance of the paroccipital processes.

The lower jaw is of the usual Therocephalian structure, but in shape is curved in the distinctive way seen more highly developed in *Notosollasia* and *Whaitsia*. The angular is a strong element with a large exposure externally; the surangular forms the usual curved girder intercalated between the dentary and the articular; the dentary bears no molars; the articular articulates with both quadrate and quadratojugal.

A long slender bone, which is probably a ceratohyal, is imbedded in the matrix lying on the right side of the basisphenoidal keel.

Chief measurements :

Length from premaxilla to the basioccipital condyle	205? mm.
Length from premaxilla to the pineal foramen	150? „
Length from pineal foramen to the occipital plate	30 „
Length from premaxilla to the front of the orbit	90? „
Length of the lower jaw	200? „
Width across the squamosals	165 „
Interorbital width	45 „
Intertemporal width	10 „
Width across the lateral pterygoidal flanges	80 „
Width of the snout	70? „
Height of the occiput	45 „

Type, B.M.N.H., 47065, Stylkrantz, Sneeuwberg, Cape Province.

Whaitsia major, Broom.

(Figs. 28-34.)

Five good skulls of this species are known. The type in the British Museum consists of a very good skull, which is, however, slightly distorted; associated are a right radius, ulna, and manus; the latter was described by Broom as a pes; a humerus is catalogued (R5755) as that of *Whaitsia*, and the nature of the matrix and of the fossilisation is as in the skull; the femur described by Broom is not in the British Museum collection; a snout labelled as *Anteosaurus minor* is obviously that of another specimen of this species: its number is R5748.

Through the courtesy of Dr. W. E. Swinton, Mr. Parsons was asked to do the preliminary clearing of the type skull; I have carried the

development further so that it now shows the greater part of the detailed structure.

The skull is of a large Therocephalian; it is broad and depressed; the intersquamosal width is great and the temporal fossae are, as in all the Whaitsids, thus very wide, but short; the posterior part of the mandibular ramus is very wide, but in anterior direction it curves inwards and forms a narrow, though long, symphysis.

The dental formula is i. 5, c. 1, m. 0; as in *Notosollasia* the incisors carry longitudinal grooves.

The structure of the outer surface is best understood by referring to the figures of the dorsal and lateral surfaces; the parietal crest is thin and fairly high; the pineal foramen is a narrow slit; the frontal is broad, but short, with only a small entry into the supra-orbital border; there is no postfrontal; the dorsal and anterior borders of the orbit are raised into a sharp ridge, which is interrupted above the lacrimo-prefrontal suture; the lacrimal and prefrontal form a deep anterior face to the orbit; there is a small lacrimal foramen; the facial exposure of the septomaxilla is fairly large, and it has two distinctive spurs projecting into the nostril; the two depressions along the maxillo-septomaxillary suture, usually found in Therocephalians, are very well shown.

The occiput is exposed exceedingly well; the basioccipital condyle is strong and kidney-shaped; it sends down two strong processes to support the basisphenoidal tubera; the exoccipitals support its corners without actually coming on to the articulatory surface, and form quite strong processes overhanging the large jugular foramina; the paroccipital processes are strong; the post-temporal fenestrae are of medium size, and are situated low down; the foramen magnum is small; the tabular is a large bone forming a considerable part of the post-temporal edge; the quadrate and quadratojugal lie well below the level of the condyle.

The palate has its posterior half well exposed in the type, where it is, however, distorted; the anterior half is beautifully shown in the duplicate specimen—R5748, and the accompanying figure is a composite one based on both specimens. In the anterior half the important point to notice is the bipartite anterior fenestra; the anterior part received the lower canine, and the posterior functioned as internal nares, posterior to which the palatines form a deep nasophalangeal passage; the partition is brought about by a process of the maxilla growing in dorso-median direction and then overlying a ventro-laterally directed process sent out by the prevomer. In

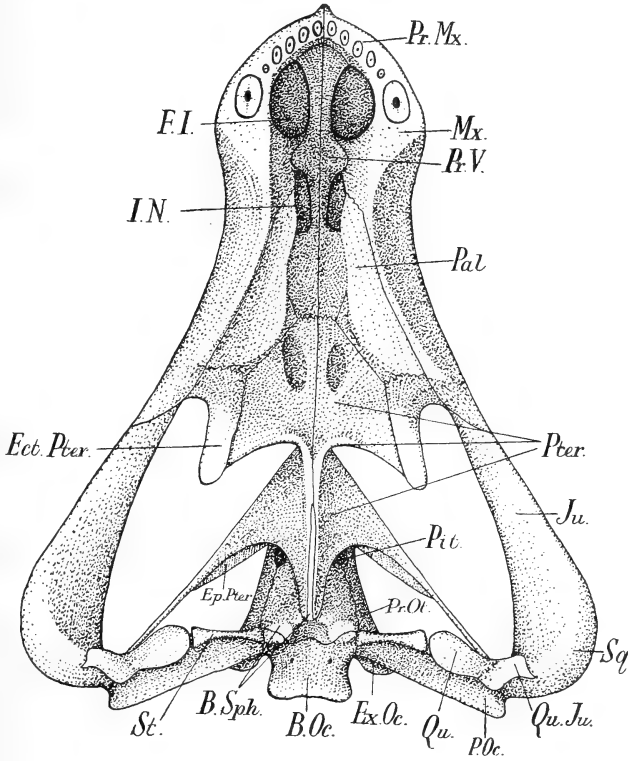


FIG. 30.—*Waitsia major*. B.M.N.H., R5694. Ventral view of the skull. $\times \frac{3}{10}$.

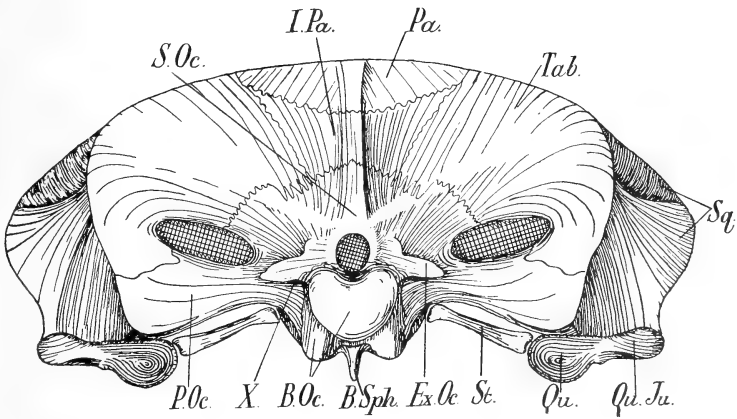


FIG. 31.—*Waitsia major*. B.M.N.H., R5694. Occipital view of the skull. $\times \frac{2}{5}$.

Moschorhinus the swelling of the maxilla inwards has been mentioned, but here there is no outgrowth from the prevomer; in *Notosollasia* the maxilla grows inwards and the prevomer has a lateral process, which meets it so that the vacuity is bipartite, but here the process of the prevomer is in a plane considerably dorsal to the maxillary swelling; in *Whitsia* the maxillary and prevomerine processes lie in the same plane, which lies at an angle of about 45° to the horizontal. In this character these three forms form a morphological series, which is, however, certainly not a direct ancestral one. Posterior to the

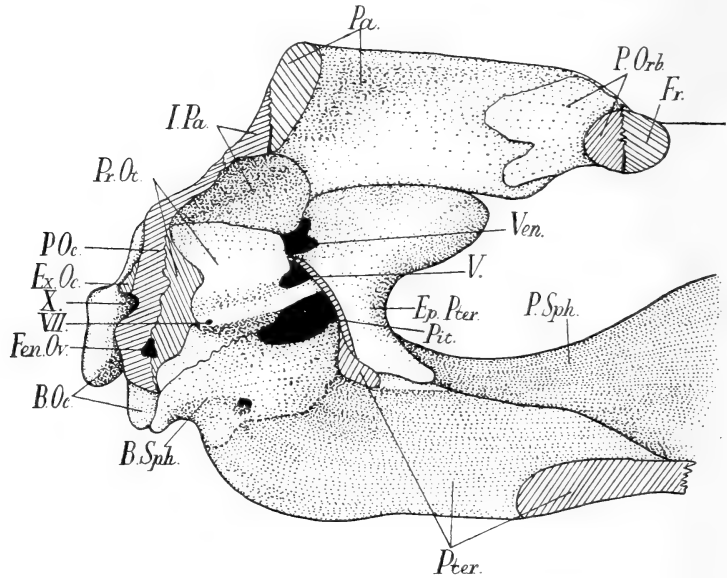


FIG. 32.—*Whitsia major*. B.M.N.H., R5694. Lateral view of the right side of the brain-case. $\times \frac{1}{2}$.

internal nares, the prevomers expand in shovel-shaped fashion and underlie the palatines and pterygoids. On the anterior ramus of the pterygoid there are two large and deep depressions; I can offer no suggestion as to their significance. There is no suborbital vacuity. The ectopterygoids, as in *Notosollasia* and *Theriognathus*, form the corners of the transverse pterygoidal bar, whereas in *Moschorhinus* it is still formed by the pterygoid itself. Posteriorly, the pterygoids form a deep keel in the median line, and here clasp the anterior prolongation of the basisphenoid, which here may have a parasphenoid fused on to its ventral surface. The quadrate ramus has a straight outer edge and is applied to the anterior face of the quadrate. The

basisphenoid is not a very strong bone and its tubera are, for their greater part, formed by the overlying basioccipital processes; it is, however, possible that the bone forming the ventral surface of the tubera is really a parasphenoid, and that the processes supporting it are really basisphenoidal, and not basioccipital; the sagittal fracture in *Theriongnathus*, however, shows a good suture between the basioccipital and basisphenoid, with nothing to indicate that the ventral part of the basisphenoid is really an underlying parasphenoid very closely applied to the basisphenoid proper. In ventral view it is seen that the basisphenoid swells out and meets the pro-otic, which then continues dorsally. The quadrate forms the main articulatory

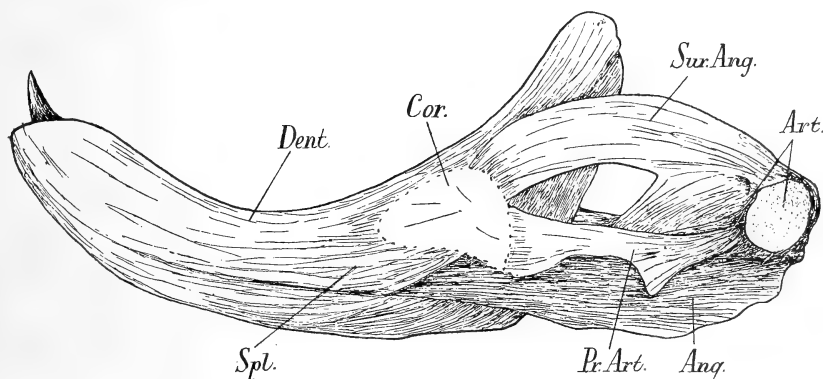


FIG. 33.—*Waitsia major*. B.M.N.H., R5694. Inner view of the right mandible. $\times \frac{1}{3}$.

surface, and the quadratojugal only the lateral corner, which, in lateral view, projects below the level of the squamosals.

The brain-case is beautifully shown in lateral view on the right side; the epipterygoid is a large bone with greatly expanded ends and a constricted waist; it lies in a plane lateral to the pro-otic, and encloses a large *cavum epiptericum*; the pro-otic is well developed; ventrally, it meets the basisphenoid in a suture, which runs from the border of the fenestra ovalis to the lateral border of the pituitary fossa; dorsally, it meets a flange of the interparietal and, posteriorly, is applied to the paroccipital; it has a strong anterior process, which separates the lateral opening into the pituitary fossa from the opening for the fifth nerve; it forms part of the anterior border of the fenestra ovalis and, antero-dorsally to this, is pierced by a foramen for the seventh nerve; a posterior pro-otic process separates the foramen for the fifth nerve from the large venous foramen. From this structure

Aelurognathus, *Arctognathoides*, etc.; the surface for the insertion of the deltoid muscle lies less on the dorsal surface than it does in the Gorgonopsians and Anomodonts; the distal end is greatly expanded, the ectepicondyle being particularly strong; the scar of the scapulo-humeralis posterior and subcoraco-scapularis is very strong, and so is the supinator and extensor crest; the large pit for the

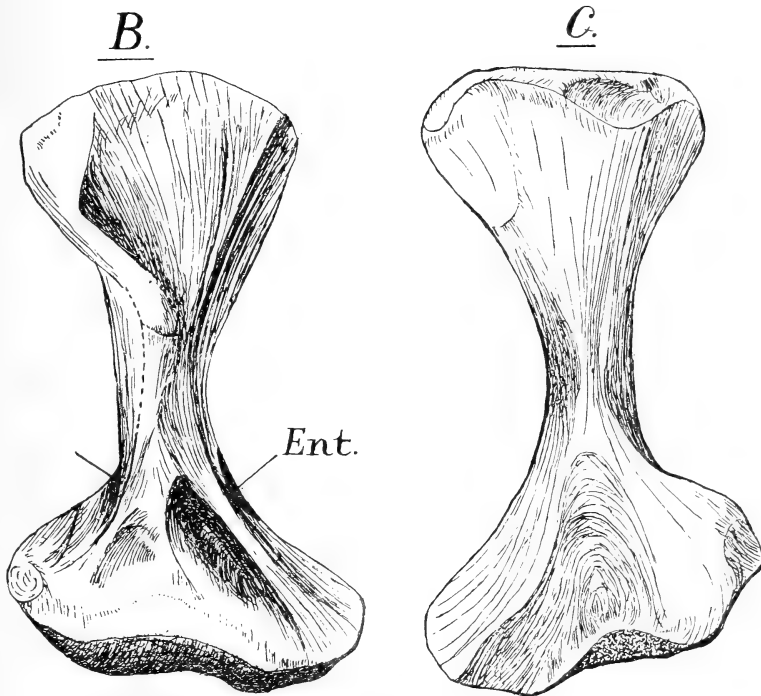


FIG. 34.—*Whaitsia major*.

- B. Ventral view of the right humerus. B.M.N.H., R5755. $\times \frac{1}{2}$.
C. Dorsal view of the right humerus. B.M.N.H., R5755. $\times \frac{1}{2}$.

ent. = entepicondyle.

brachialis indicates a strong muscle of that name; the intertrochanteric fossa is deep, and the coraco-brachialis must have been strong.

The ulna is a very peculiar bone; there is no olecranon process, but the proximal end is greatly expanded preaxially in a manner unknown in any other Therapsid; the bone is somewhat flattened, and this expansion may represent a sigmoid process with a sigmoid notch into which the radius fitted.

The radius has no distinctive characters; it is slightly shorter than

the ulna; as the humerus is also short, the whole fore-limb was short, and the animal could thus not have been very agile.

The carpus is not fully preserved, the intermedium and the greater part of the ulnare being lost; the radiale is a strong, oval-shaped bone, to which, distally, two bones are articulated; the preaxial one is undoubtedly a composite bone consisting of the fused first and second centralia; the central one is the third central; there are four distals; the postaxial one, which articulates with the fourth and fifth metacarpals, represents the fused fourth and fifth distals; the metacarpals have peculiar mammal-like epiphysial ends, also encountered in the Gorgonopsian, *Aelurognathus*; the phalanges have very well-modelled articulatory surfaces with a much better finish than those of *Aelurognathus*. The carpal formula is thus 3, 3, 4, and the phalangeal 2, 3, 3, 3, 3, as in Cynodonts and primitive Mammals, and not 2, 3, 4, 4, 3, as in *Aelurognathus*.

Chief skull measurements :

Length from premaxilla to the basioccipital condyle	305 mm.
Length from premaxilla to the pineal foramen	200 „
Length from premaxilla to the occipital plate.	60 „
Length from premaxilla to the front of the orbit	140 „
Length of the lower jaw	280 „
Width across the squamosals	250 „
Interorbital width	65 „
Intertemporal width	19 „
Width of the snout	85 „
Width across the lateral pterygoid flanges	90 „
Height of the snout	80 „
Height of the occiput	90 „
Length of the incisor series	35 „

Type, B.M.N.H., R5694, Thaba 'Nchu, Orange Free State.

Tigrisuchus simus, Owen.

This very unsatisfactory type consists of a weathered snout, which shows the roots of three large incisors and a large canine on both sides of the upper jaw. This snout has always been considered to represent a species of Gorgonopsian, but recently Broom has recognised it to be a Therocephalian. In comparing it to the Whaitsid skulls in the collection, I was impressed by the similarity in the broad depressed snout, the general shape of the nostril and the septomaxillary, and the broad expanded anterior end of the prevomers. As there appears

to be no character which would exclude it from the Whaitsid family, this fragment had better be included in this group. The specimen is of some morphological interest in that a fracture shows the detailed relations of the premaxilla, septomaxilla, and the prevomers.

Type, B.M.N.H., R1721, Stylkrantz, Graaff-Reinet?, Cape Province.

The family *Euchambersidae* is instituted for the remarkable skull described by Broom as *Euchambersia mirabilis*. The possession of the following characters clearly distinguish this new family from the other Therocephalian families, viz. jugal bar absent; incomplete postorbital bar; the presence of a very remarkable preorbital depression, which leads by a notch into the buccal cavity; the canine has a sharp ridge on its labial surface; there is no maxillary border posterior on the canine, and thus there are no molars.

Euchambersia mirabilis, Broom.

(Fig. 35.)

This remarkable skull was first described by Broom in 1931, and figured in 1932. The skull, though crushed in an oblique direction, is fairly completely preserved; the squamosals, quadratojugals and quadrates have been lost, and the occiput cannot be satisfactorily cleared.

The skull is unlike that of any other Therapsid, but the essential points of structure in the palate, dorsal and lateral surfaces conclusively show that the animal is an aberrant Therocephalian. There are a number of remarkable specialisations, viz. the postorbital and infraorbital bars are incomplete; the infratemporal bar is absent, though it is likely that the squamosal formed an incomplete bar; there is a very large and deep preorbital depression lying in the external surface of the maxilla and the lacrymal; a notch leads from this cavity to the buccal cavity; there are no molars; the canine is of medium size, and has a unique ridge on its labial surface; no incisors are preserved, but, according to Broom, five were present. Broom has suggested that the preorbital depression housed a huge par-otic gland, and Nopcsa suggested that the gland was poisonous, and was connected with the ridge on the canine. Broom's suggestion is untenable, as the depression is preorbital, and the par-otic gland is generally postorbitally situated. It seems more likely that this depression housed an enlarged labial or lacrymal gland. At this

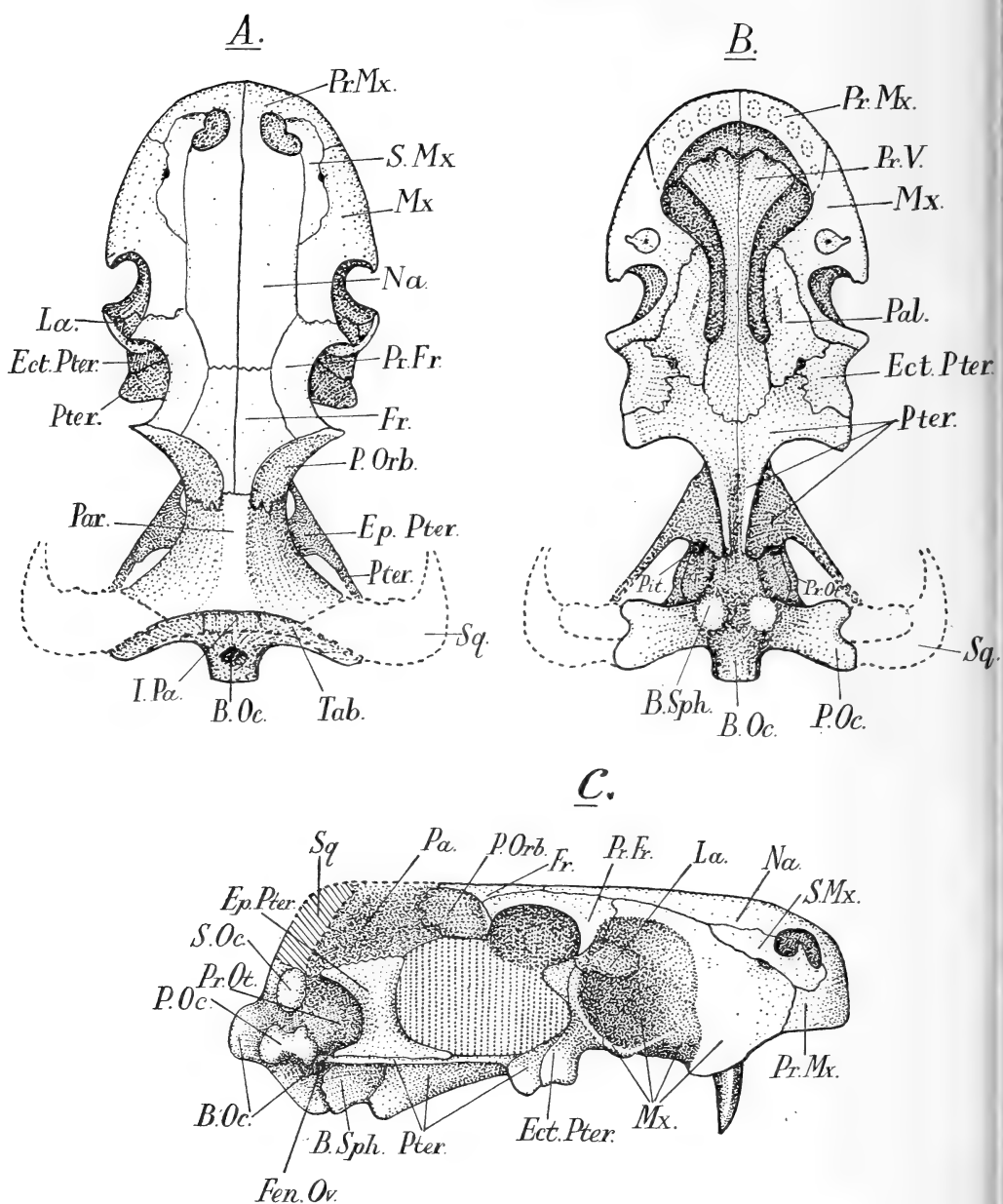


FIG. 35.—*Euchambersia mirabilis*. B.M.N.H., R5696. $\times \frac{3}{2}$.

A. Dorsal view of the skull.
 B. Ventral " "
 C. Lateral " "

point it is of interest to recall the fact that in the Gorgonopsians and Therocephalians there is generally a shallow preorbital depression, which probably housed a gland of some kind; the gland in *Euchambersia* may be the result of the hypertrophy of such a normal supralabial or lacrymal gland.

On the outer surface the important points are: the very large prefrontal, which forms the whole supraorbital border; the small frontal with no entry into the orbital border; the absence of a postfrontal; a minute pineal foramen; the rudimentary jugal forming a little of the preorbital border, but not extending backwards to meet the squamosal or postorbital; the short maxillary border, which does not meet the jugal; the large septomaxilla.

The palate is essentially Therocephalian; the anterior palatal vacuities are unipartite and relatively long; the prevomers are, anteriorly, greatly expanded and, posteriorly, are shovel-shaped, and underlie the pterygoids and palatines; the ectopterygoid does not reach the corner of the lateral pterygoid bar; the median vertical flanges of the posterior pterygoid ramus do not meet along the median line, and laterally flank the basisphenoidal rostrum; if my interpretation, that the basioccipital sends two strong processes ventrally, is correct, then the basisphenoid is a thin bone underlying these processes; on the other hand, if these processes are actually the basisphenoidal tubera, then the thin bone must be a parasphenoid; I find no evidence for the latter view; the paroccipital bar is strong, and is distally grooved to receive the quadrate; dorsal to this the supraoccipital sends a thickened process laterally, and to this a tabular must have been attached; actually, no tabular is, however, preserved; the basioccipital condyle is fairly strong.

The epipterygoid is a moderately slender element, as in the Pristerognathids, *Scylacosaurus*, and *Scymnosaurus*; the pro-otic is not sufficiently exposed to merit a description; the fenestra ovalis is large; there is a great depth of bone ventral to the foramen magnum.

Euchambersia is thus a Therocephalian, which can be derived from an unspecialised Pristerognathid; its evolutionary direction has been along a line quite distinct from that of the Lycideopsids, Whaitsids, and Scaloposaurids; in the main its palate is quite primitive, and so is the epipterygoid; but the extreme specialisation in the occiput, the loss of the postorbital and jugal bar, the development of the peculiar preorbital depression, and the apparently correlated notch leading on to the ridged canine, are all characters with no parallel

in any of the other Therocephalian families. It is of interest to recall that an analogous loss of postorbital and infratemporal bar connected with the development of a poison fang occurs in the *Ophidia*.

Chief measurements :

Length from the premaxilla to the basioccipital condyle .	120 mm.
Length from the premaxilla to the front of the orbit .	55 „
Interorbital width	28 „
Intertemporal width	14 „
Width of the snout	50 „
Width across the lateral pterygoid flanges	45 „
Height of the snout	37 „
Height of the occiput	35 „
Depth of bone below the foramen magnum	23 „

Type, B.M.N.H., R5696, Norval's Pont, Cape Province.

In the family *Scaloposauridae* seven genera have been included, viz. *Akidnognathus*, *Choerosaurus*, *Icticephalus*, *Ictidognathus*, *Ictidostoma*, *Scaloposaurus*, and *Simorhinella*. Three of these are represented in the collection of the British Museum, and they have recently formed the basis of an excellent description by Watson; with the exception of a few supplementary remarks on *Icticephalus*, it is thus unnecessary to go into any details.

The family is of considerable interest in that it ranges throughout Lower Beaufort times without showing any very marked evolutionary changes; *Icticephalus* of the *Tapinocephalus* zone may even be cogenetic with *Scaloposaurus* of the *Cistecephalus* zone. Although occurring as early as the *Tapinocephalus* zone, the Scaloposaurids are, in a number of points of structure, definitely distinct from any of the other Therocephalian families. The Whaitsids, Lycideopsids, and Euchambersids represent three lines of development which are completely divergent from that of the Scaloposaurids. The Pristerognathids are apparently a retarded stock in which a number of primitive features are retained; in one form, *Scylacosaurus*, the nature of the basisphenoid suggests a development parallel to that of the Scaloposaurids. In the Ictidosuchids, *Ictidosuchoides* has been shown to possess some characters also met with in the Scaloposaurids. It would thus appear that the Therocephalians of the Lower Beaufort represent the end branches of a phylogenetic tree, whose main stem must be sought for in pre-Beaufort rocks.

Icticephalus polycynodon, Broom.

In his original description Broom made the following observations: dental formula, i. 6, c. 3, m. 11; all the teeth are unserrated; this new type differs from *Scaloposaurus* in having eleven, and not nine, molars, and in that the postorbital arch meets the jugal.

Watson, in 1931, gave a much fuller account, and with this I am in agreement. I have, however, found that something more can be determined of the dentition. Although very badly preserved, Broom is probably right in assuming the incisors to be six in number; there is a large canine, with one tooth anterior and another posterior to it—all on the maxilla; then there is a diastema of 2 mm.; this is followed by nine molars, although between the fifth and sixth there is an interspace, which may have housed another tooth; the molars are small and progressively decrease in size in posterior direction. In the British Museum specimen the dental formula would thus be, i. 6, c. 3, m. 9–10, which is thus not very different from that of *Scaloposaurus*. If Broom's supposed distinguishing character in the dentition is thus invalid, the only other distinguishing character is the nature of the postorbital bar, and in neither of these two specimens is the nature of the postorbital bar known with absolute certainty. Watson has at great length drawn attention to the great similarity of these two skulls in nearly all, even the most detailed, points of structure. So that one can really only maintain that the type *Icticephalus* of the *Tapinocephalus* zone is represented in the *Cistecephalus* zone by a practically identical animal, *Scaloposaurus*. The older *Icticephalus* has a slightly larger skull, with its snout higher and thus relatively less broad; the orbits look as much outwards as upwards; the mentum of the lower jaw is fairly deep. In the younger *Scaloposaurus* the skull is somewhat smaller; the whole skull, including the snout, is somewhat flattened, so that the snout is relatively broader than high; the orbits look more upwards than outwards; the mentum of the lower jaw is less deep and more sloping. Viewed from in front, *Scaloposaurus* has a more pointed snout and appears rounded in section, whereas in *Icticephalus* it is squarish.

Type, B.M.N.H., R4096, Weltevreden, Prince Albert, Cape Province.

Chief measurements:

	<i>Scaloposaurus</i> .	<i>Icticephalus</i> .
Premaxilla to basisphenoid .	50? mm.	65 mm.
Premaxilla to pineal foramen .	?	59 „
		23

	<i>Scaloposaurus.</i>	<i>Icticephalus.</i>
Premaxilla to front of orbit	28? mm.	34 mm.
Interorbital width	10 "	12 "
Intertemporal width	9 "	8 "
Width of the snout	12 "	16 "
Width across lateral pterygoid flanges	20 "	25 "
Height of the snout	10 "	16 "
Height of mentum of lower jaw	7? "	10 "
Length of the molar series	9 "	14 "

SUMMARY.

1. The palate is figured and described in three Pristerognathids, one Ictidosuchid, four Whaitsids, and one Euchambersid; it can thus be claimed that the main morphological features of this region in the Therocephalians have been established. In the more generalised Pristerognathids, in the slightly more advanced Ictidosuchids, and in the specialised Euchambersids and Scaloposaurids, the palate is comparable in general plan to that of the less advanced Deinocephalians and Pelycosaurids; even in the very specialised Whaitsids, the underlying ground plan is still the same. The Therocephalian palate differs from that of the Gorgonopsians, which occupy the same developmental niveau, but on a parallel plane, in the number of points mentioned; the chief being the nature of the prevomers.

2. The occiput is described and figured in one Pristerognathid and in two Whaitsids; it differs mainly from that of the Gorgonopsians in the very massive paroccipital bar and the large post-temporal fenestra (except in *Scymnosaurus*); in the Scaloposaurids a special process is developed on the paroccipital.

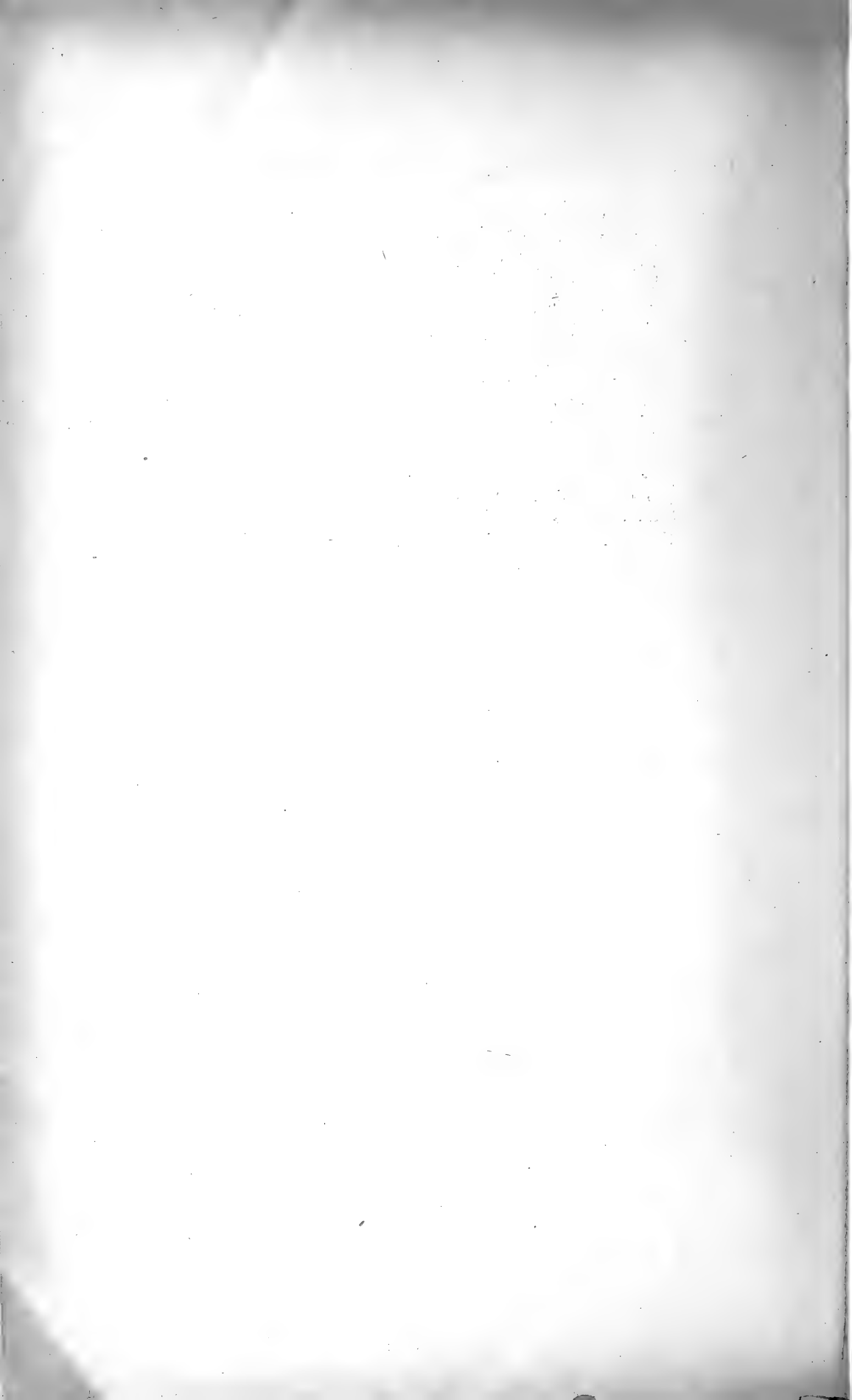
3. Parts of the brain-case are figured and described in two Pristerognathids, in one Euchambersid, and in three Whaitsids; it has become evident that in the Therocephalians there has, in respect of the epipterygoid, occurred a development, which has in some respects been paralleled by the Cynodonts.

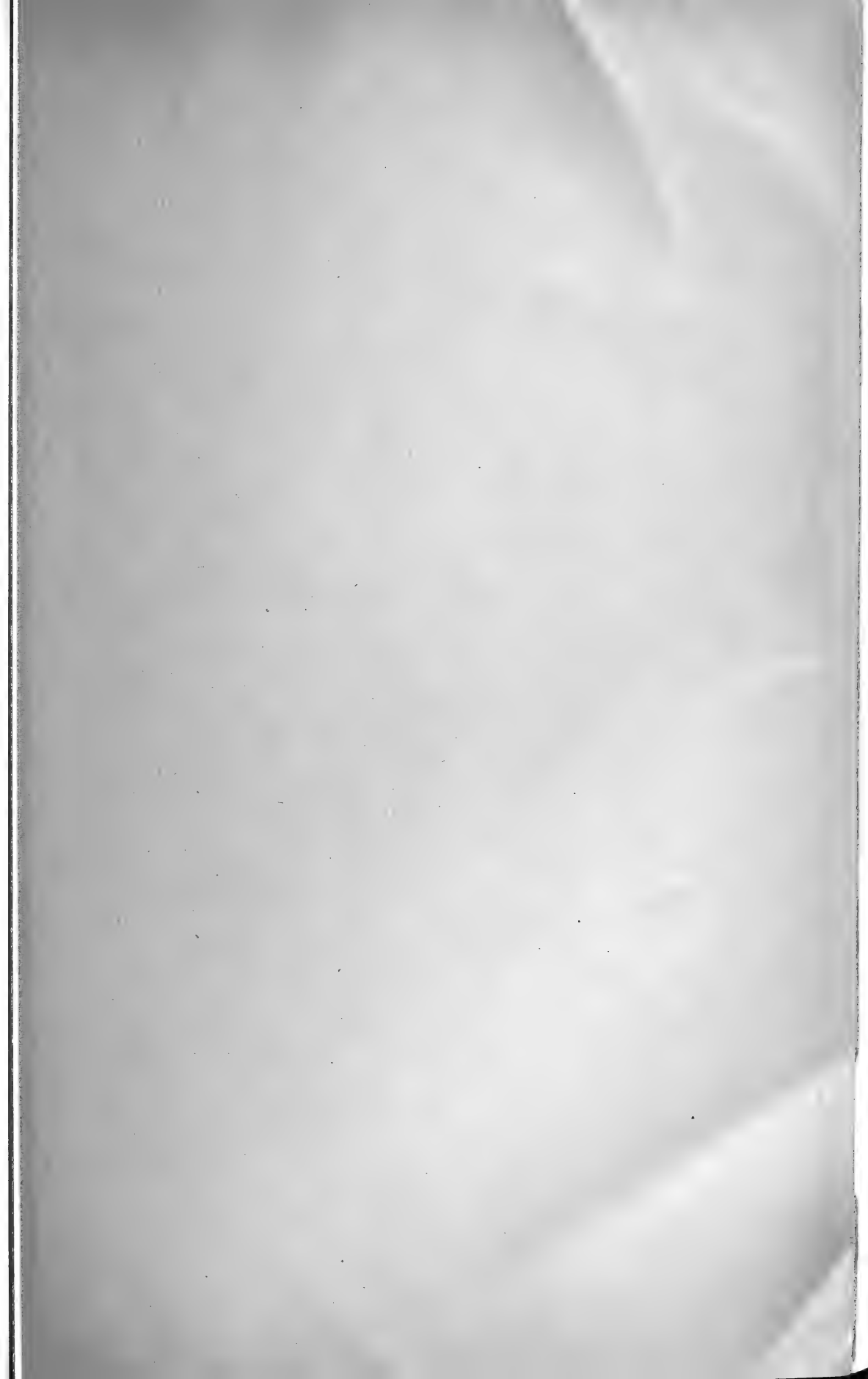
4. The description of a complete fore-limb of *Waitsia* adds to our knowledge of the postcranial skeleton of the Therocephalians, about which lamentably little is as yet known.

5. In the course of this paper it has been shown that the seven families, into which the suborder has been divided, represent distinct evolutionary trends, and that certain similarities in structure do not necessarily imply any close direct relationship, but may simply have

resulted as parallel developments from an original stock possessing common characters and potentialities. The Whaitsids, Euchambersids, and Lycideopsids are families possessing some very definite characters, separating them from each other and from the Scaloposaurids, Alopecopsids, Ictidosuchids, and Pristerognathids; the Scaloposaurids are also quite distinct, but may be a composite family, as there is a discrepancy in one character, viz. in some the postfrontal is present, whereas in others it is absent; finally, the Pristerognathids, although the most generalised group, does contain some forms which possess quite advanced characters, *e.g.* the epipterygoid of *Trochosaurus*. Some subdivision, as, for example, that of Williston, will in time have to be considered seriously.

In conclusion, my thanks are due to the officers of the British Museum (Natural History), in particular to Dr. W. E. Swinton, for affording me the facilities I have enjoyed in my study of the material in their charge. Professor D. M. S. Watson's critical interest has been very encouraging. To the University of Stellenbosch I am indebted for a small grant, which has enabled me to come to London. My wife has been responsible for the execution of the greater number of the figures which illustrate this paper.





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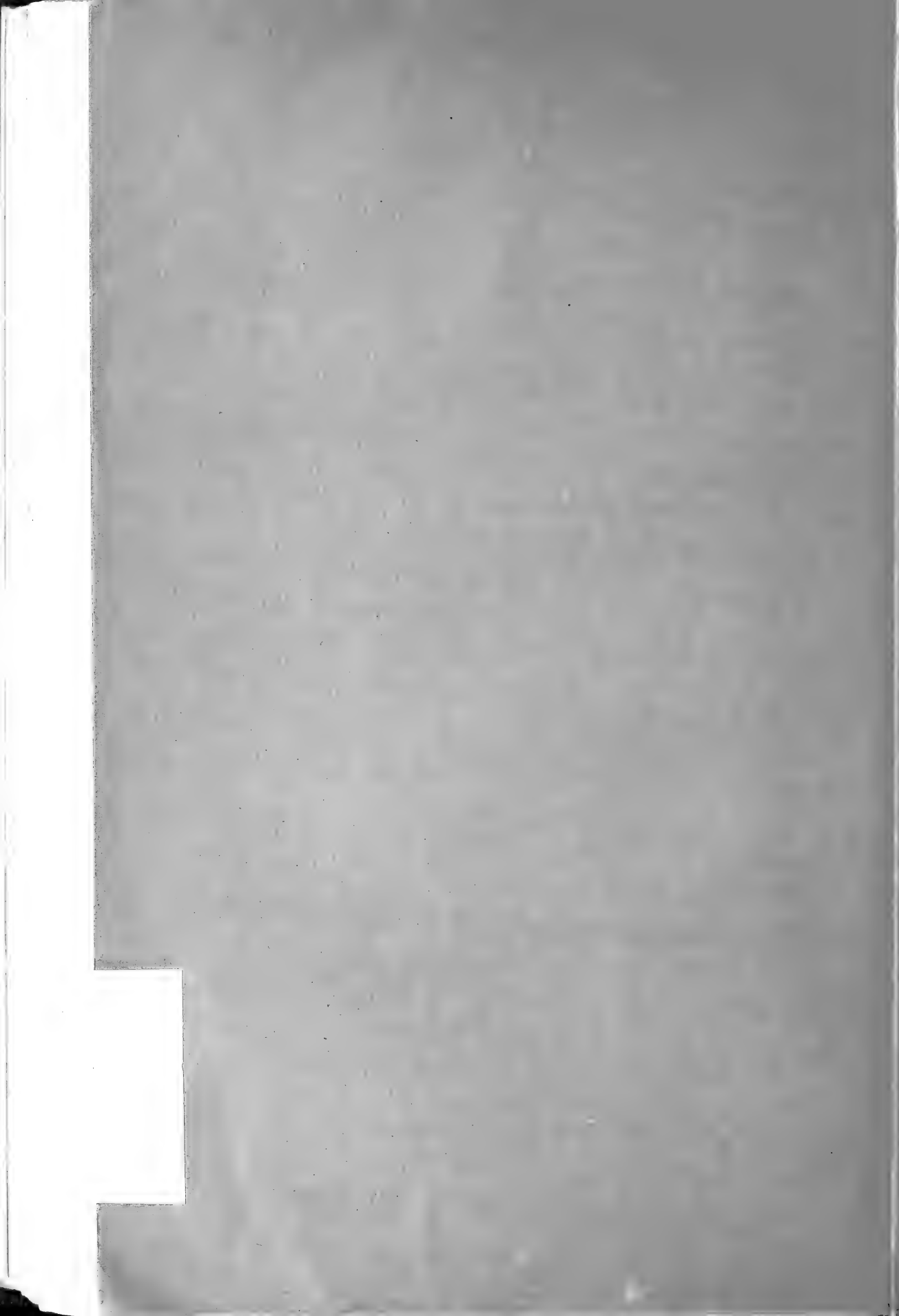
8. *On Placocystella, a New Genus of Cystids from the Lower Devonian of South Africa.* By JOHN V. L. RENNIE, M.A., Ph.D., Department of Geology, Rhodes University College, Grahamstown, South Africa. (With Plate XXXVI.)
9. *Lower Cretaceous Lamellibranchia from Northern Zululand.* By JOHN V. L. RENNIE, M.A., Ph.D., Department of Geology, Rhodes University College, Grahamstown, South Africa. Together with an *Account of the Geology of the Cretaceous Beds and a Preliminary Analysis of the Associated Ammonite Fauna*, by S. H. HAUGHTON, B.A., D.Sc., Director of the Geological Survey of the Union of South Africa. (With Plates XXXVII–LV.)



ISSUED AUGUST 1936. PRICE 17s. 6d.

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GEOLOGICAL SURVEY OF SOUTH AFRICA

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8. *On Placocystella, a New Genus of Cystids from the Lower Devonian of South Africa.*—By JOHN V. L. RENNIE, M.A., Ph.D., Department of Geology, Rhodes University College, Grahamstown, South Africa.

(With Plate XXXVI.)

The class Cystoidea was recorded for the first time from South Africa in 1925, when Dr. F. R. C. Reed described a single specimen from the Bokkeveld Series (Lower Devonian), collected by him at a roadside cutting near Buffelskraal, between De Doorns and Tunnel Siding in the Hex River Pass. The specimen was named *Placocystis africanus* sp. nov. (Reed, 1925, p. 30, pl. iv, fig. 1) and was compared with the Silurian (Wenlock) species *Placocystis forbesianus* de Koninck (see Bather, 1900, part iii, p. 51, fig. xiii) and other representatives of the Anomalocystidae, a primitive but specialised family of echinoderms rare in post-Silurian deposits. In 1928 Dr. L. D. Boonstra and the writer collected two specimens of a cystid in the First or Basal Shales of the Bokkeveld Series at the northern entrance of Gamka Poort in the division of Prince Albert. The writer was able to make an examination of Reed's specimen in the Sedgwick Museum in Cambridge, and to compare directly with it the two specimens here described.

The writer is indebted to the Research Grant Board of the Union of South Africa for financial assistance and wishes to express his thanks to Dr. John Hewitt, Director of the Albany Museum in Grahamstown, for the use of camera and dark room.

Placocystella capensis gen. et sp. nov.

The two specimens from Gamka Poort, here described as *Placocystella capensis* gen. et sp. nov.,* are preserved as moulds, coated with reddish-yellow ferruginous matter, in a greenish micaceous mudstone. In each case what is presumed to be the convex external

* This paper was read at a meeting of the Royal Society of South Africa in 1932, and the generic name appeared in the title of the paper published in the minutes of proceedings in 1934 (Trans. Roy. Soc. S. Afr., xxii, p. lvi). The name *Placocystella* Rennie 1934 is a *nom. nud.*

mould of the concave or right side of the theca is shown, the edge of the convex surface on the hand specimens being reflexed upwards if preserved at all; in the paratype (S.A.M. 9700) the adcolumnal margin is also reflexed upwards, but perhaps as the result of fracture; in the holotype (S.A.M. 9701) the lower margins of the two adcolumnal plates curve downwards, this feature apparently being an original one, and supporting the interpretation of the specimens as external moulds. The preservation is relatively superior, though the column and brachioles are not attached in either case. There is some indication, shown by irregularities of the surface, of slight relative movement of plates subsequent to the death of the animal, but on the whole there has been little compression of the thecae, the majority of the plates being in position and the sutures being very clearly marked. A number of the sutures are preserved as strong raised ridges, such as could have been formed by infilling; the fact that they are raised would also indicate that the specimens are external moulds.

The Holotype of Placocystella (Plate XXXVI, figs. 4-6).—The arrangement of the plates is more distinct in one of the above (S.A.M. 9701) than in the other, and the specimen is accordingly taken as holotype. The moulds of the plates are arranged on a gently convex surface. The periphery is intact except along the adoral margin. The theca is subquadrate in outline, somewhat wider towards the columnal end than towards the oral end, the widest part situated at a little less than one-third of the length of the theca from the columnal end. The theca is distinctly longer than wide. The lateral margins are gently convex, but straightened towards the oral end. The adoral margin is not preserved. The adcolumnal margin is concave for the attachment of the stem. The margin of the lower left lateral marginal plate is abruptly reflexed upwards, the other lateral marginal plates not showing this feature.

The concave side of the theca appears to have been composed of twelve plates, ten of them marginals, with two somatic plates enclosed by them, the twelve arranged symmetrically about a line drawn from front to back. At the columnal end are two large marginals, meeting along the middle line, truncate above against the larger somatic plate, in length somewhat less than one-third of the length of the theca, the sutures between them and the adjacent marginals reaching the lower angles of the theca; towards the lower angles of the theca these plates are truncate, while the columnal margin is fairly deeply embayed for the attachment of the stem,

with the edges of the plates curved downwards within the embayment. On each side are three marginals, subequal, the lower pair subtriangular, the middle and upper pairs subquadrate. At the oral end two smaller marginals meet along the middle line; the one on the right side meets the uppermost right lateral in a suture which is apparently directed towards the right upper angle of the theca, the corresponding suture on the left side being only visible in part. Centrally placed is a large subquadrate somatic plate, bounded below by the adcolumnal marginals and laterally by the two lower pairs of lateral marginals. The second somatic plate is considerably smaller than the other, is subquadrate, and placed along the middle line.

The sutures between the plates, as distinguished above, are for the most part visible as straight ridges or lines of whose nature there can be no doubt. This applies particularly to the sutures between the marginals. The sutures bounding the somatic plates are somewhat disturbed, owing probably to a slight relative movement of the plates, but their positions can be determined with some certainty.

A few of the plates are traversed by ridges, which are not regarded as sutures, since (i) they bear little or no relation to the symmetry of the theca, (ii) they are in some cases much less evident than the sutures, (iii) they often pursue an irregular course across the plates, and (iv) similar features in the paratype are differently placed. Each adcolumnal marginal is traversed by a faint ridge in the anterior-posterior direction, but the position of that on the right is quite different from that on the left, and that on the right is curved in an irregular manner. A similar ridge pursues a somewhat irregular course across the lower corner of the right adcolumnal plate and is continued across the lowermost lateral marginal roughly parallel to its outer margin, almost certainly a fracture from its appearance under the binocular microscope; a ridge is present in nearly the same position on the corresponding marginals of the left side. The smaller somatic plate is traversed by two faint ridges, one curved and almost along the middle line, the other across the upper left-hand corner. The remaining plates are free of these features. The larger somatic plate has a broad raised band placed obliquely across it.

The three marginals on either side are traversed by irregular, relatively broad, wavy, or discontinuous bands placed obliquely to the outer margin of the theca. These may have been original features of the theca.

The stem is absent, as well as the brachioles. The margin of the lowermost lateral marginal on the left side is curved upwards, *i.e.* there is preserved a fragment of that part of the plate which bounds the rim of the theca; the curved fragment is demarcated by a groove (presumably secondary) and traversed by wavy bands.

Dimensions: length 16.5 mm.; greatest width 13.5 mm.; length of adoral margin about 10 mm.

The Paratype of Placocystella (Plate XXXVI, figs. 7-9).—The second specimen from the same locality (S.A.M. 9700) agrees with the first in dimensions and structure and is taken as paratype of the species. The moulds of the plates are arranged on a gently convex surface and the periphery is well preserved. The outline agrees completely with that of the holotype, with the addition that the adoral margin is very slightly convex and the upper corners of the theca are rounded angles of about 115° .

The sutures are for the most part well marked. The sutures between the marginal plates are clearly marked on both sides and correspond exactly with those of the holotype. At the oral end there are only two marginals, that on the left being clearly demarcated by a suture along the middle line and a suture joining the periphery just behind the left upper corner of the theca, the corresponding suture on the right being less defined. The suture between the large central somatic plate and the adcolumnal marginals is only partly seen, and that between the adcolumnals is not well marked. The suture between the two somatic plates is very evident. The theca is in various places traversed by faint incisions or low well-defined ridges, or broader bands, all of which are probably secondary features; noteworthy is the fact that none of these features correspond exactly in position with similar markings on the plates of the holotype.

The margins of the lateral marginal plates are curved upwards, *i.e.* there is preserved the cast of the rim of the theca on either side. The lateral marginal plates are traversed by wavy bands roughly at right angles to the periphery of the theca. In places these appear as short crescentic lines, sometimes continuous with one another. The stem is absent; the adcolumnal margin is reflexed upwards, but apparently as the result of fracture. The brachioles are not present in position, but there is a cast of a cylindrical spine-like body, 8 mm. long, emerging from beneath the theca on the right side. •

Dimensions: length 17 mm.; greatest width 13.5 mm.; length of adoral margin 9 mm.

Affinities.—The specimens described above are similar to but somewhat larger than the type of *Placocystis africanus* Reed (1925, p. 30, pl. iv, fig. 1) from the same formation, from a locality about 100 miles distant. In the latter the column is present in position, and what is apparently a fragment of a brachiole is preserved near the right anterior corner. The theca has much the same proportions as *Placocystella capensis*, but the arrangement of the plates, as interpreted by Reed, is entirely different from that of the corresponding surface of either the new species here described or of *Placocystis forbesianus* de Koninck. Moreover, *Placocystella capensis* differs from de Koninck's genotype in features of sufficient importance to warrant the erection of a new genus.

The holotype of *Placocystis africanus* (see Plate XXXVI, fig. 1) is too poorly preserved to allow of a definite statement as to the relationship of that species with the new species here described. The figure published by Reed is a drawing of the test apart from the matrix on which it is situated, enlarged $\times 2\frac{1}{2}$, giving the impression of an extraordinarily well-preserved specimen; the sutures in the drawing are very well marked and give the author's interpretation of the test, which is described in some detail. The writer examined this specimen, which is in the Sedgwick Museum,* and came to the conclusion that only a few of the markings present could be interpreted as sutures. The specimen is preserved on a piece of mudstone, and has a weathered flaky ferruginous surface. Presumably, from the few sutures present as well as from a comparison with the Gamka Poort specimens, the concave side of the theca is shown, but in a flattened condition. According to Reed this side is made up of some twenty plates arranged for the most part in five transverse series in four vertical rows. The writer came to the conclusion that the arrangement of the plates is to a certain extent very doubtful; that few of the markings accepted as sutures by Reed are either as clearly marked or as regular as his figure indicates; that several of these markings could equally well have been accepted as cracks through the plates or the matrix, or lines due to the partial removal of surface flakes by weathering. Indeed, the whole surface of the thecal portion of the specimen is in a most unsatisfactory condition, rough with ferruginous flakes, and marked by a multitude of relatively coarse and finer lines of a most irregular kind, clearly related to the weathering of the surface. There are, however, several relatively straight lines on the surface, which are quite unmistakably sutures, and it is

* Recently numbered A. 3044.

noteworthy that these correspond in position with the sutures observed in the Gamka Poort specimens. Sutures bounding three marginals on the right side are distinct, the plates having the same shapes and relative positions as in the new species. There is a well-marked suture between the right adcolumnal plate and the somatic plate anterior to it. The lowermost of the three right marginals is traversed by a crack which continues into the matrix, accepted as an additional suture by Reed. Indications of portions of a few other sutures are present. The writer was unable to find evidence suggesting a fundamental difference in structure between the two Bokkeveld species, but as far as the evidence goes, it would appear not more than probable that they belong to the same genus and possibly to the same species. In view of the very great imperfection of the holotype of *Placocystis africanus*, and the absence of any satisfactory evidence as to the arrangement of the plates in the middle and anterior part of the concave side of the test, *i.e.* over about two-thirds of the exposed surface, the writer has thought fit to propose a new specific name for the specimens from Gamka Poort.

Placocystis africanus must certainly be removed from the genus *Placocystis* on either interpretation of the specimen. *Placocystella capensis* is distinguished from *Placocystis forbesianus* chiefly by reason of its almost perfect bilateral symmetry. In *P. forbesianus* (see Plate XXXVI, fig. 2) there are thirteen plates on the concave side, including three adoral marginals; the larger somatic plate is situated on the anterior half of the theca, and the smaller somatic plate is placed towards the left upper corner. The perfect bilateral symmetry in the arrangement of the plates thus distinguishes *Placocystella* from the Silurian *Placocystis* as well as from the early Devonian *Ateleocystis* Billings and *Anomalocystis* Hall (for references see Reed, 1925, p. 31). According to Bather (1900, p. 49) the evidence suggests that the evolution of the family was towards greater bilateral symmetry, and therefore started from the usual sac-like form. *Placocystella* is thus both the most advanced and one of the last representatives of the Anomalocystidae.

REFERENCES.

- BATHER, F. A. (1900). Anomalocystidae, in Lankester's Treatise on Zoology, pt. iii, pp. 49-51.
- HALL, J. (1859). Anomalocystites, in Palaeontology of New York, vol. iii, pp. 132, 133, 145, 146.
- KIRK, E. (1912). "The Structure and Relationships of certain Eleutherozoic Pelmatozoa," Proc. U.S. Nat. Museum, vol. xli, pp. 1-137, pls. i-xi (Anomalocystidae, pp. 21-29).
- REED, F. R. C. (1925). "Revision of the Fauna of the Bokkeveld Beds," Ann. of the S. African Museum, vol. xxii, pp. 27-225, pls. iv-xi (*Placocystis africanus*, p. 30, pl. iv, fig. 1).
- SCHUCHERT, C. (1905). "On Silurian and Devonian Cystidae and Camarocrinus," Smithsonian Misc. Coll., vol. xlvii, pp. 201-272, pls. xxxiv-xliv (Anomalocystidae, pp. 204-208).
- SCHUCHERT, C. (1913). Anomalocystidae, in Maryland Geological Survey, Lower Devonian, pp. 228, 229.
- WOODWARD, H. (1880). "Notes on the Anomalocystidae, etc.," Geol. Mag., N.S., dec. 2, vol. vii, pp. 193-201, pl. vi.

EXPLANATION OF PLATE XXXVI.

Placocystis africanus Reed.

1. Holotype, $\times 2.5$ approx., in the collection of the Sedgwick Museum (A. 3044), re-drawn by Miss E. T. Talbot under the writer's direction.

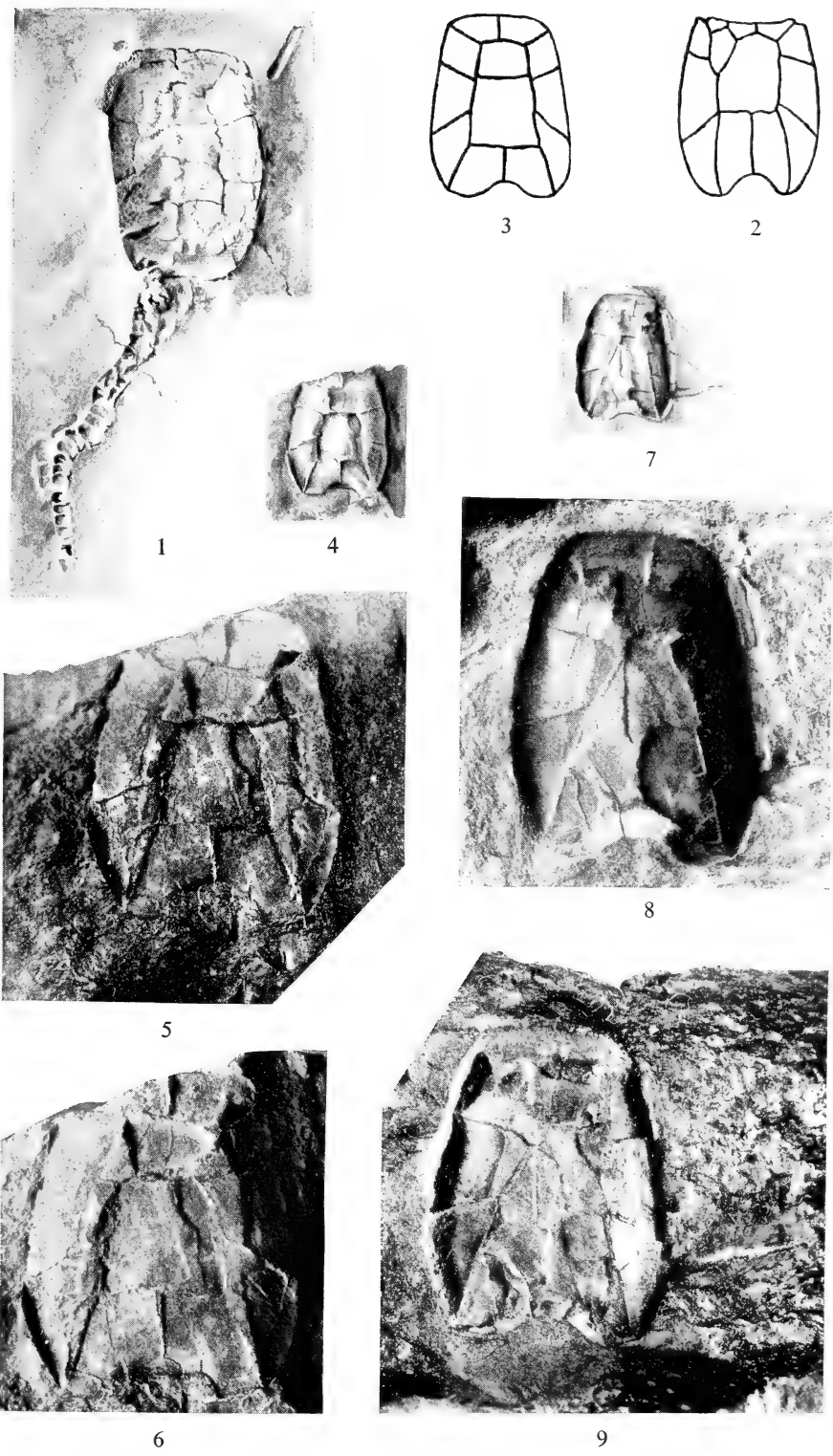
Placocystis forbesianus de Koninck.

2. Concave side of theca, after Bather, modified.

Placocystella capensis gen. et sp. nov.

3. Concave side of theca, showing probable arrangement of plates.
4. Drawing of holotype, natural size.
5. Holotype, S.A.M. 9701, $\times 2.6$.
6. Another photo of holotype, $\times 2.9$.
7. Drawing of paratype, natural size.
8. Paratype, S.A.M. 9700, $\times 2.6$.
9. Another photo of paratype, $\times 2.5$.





E. T. Talbot, del., et J. V. L. R., phot.

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CYSTIDS FROM DEVONIAN OF SOUTH AFRICA.

9. *Lower Cretaceous Lamellibranchia from Northern Zululand*.—By JOHN V. L. RENNIE, M.A., Ph.D., Department of Geology, Rhodes University College, Grahamstown, South Africa. Together with an *Account of the Geology of the Cretaceous Beds and a Preliminary Analysis of the Associated Ammonite Fauna*, by S. H. HAUGHTON, B.A., D.Sc., Director of the Geological Survey of the Union of South Africa.

(With Plates XXXVII–LV.)

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1. INTRODUCTION.

Historical.—In South Africa marine deposits of Cretaceous age are well represented, and have provided the material for a formidable list of palaeontological publications. The deposits are all but confined to the south-eastern and eastern coastal belt, and occur intermittently for a distance of over 700 miles in the Union and extend northwards into Portuguese East Africa. General accounts of these deposits have been given in recent years by du Toit (1926, pp. 292–330), Rogers and Haughton (1929, pp. 143–148), and of the occurrences in Portuguese territory by de Andrade (1929, pp. 147–165).

In the southern part of the Cape Province only the Neocomian is represented, in the Sundays River Beds of the Uitenhage Series, which have yielded a rich fauna, monographed by Kitchin (1908), and including ammonites which have enabled Spath (1930) to deter-

mine the age more precisely as Upper Valanginian. The Neocomian stage has not hitherto been recorded from between the neighbourhood of Algoa Bay and Moçambique, a distance of well over 1600 miles. A few Neocomian species have been reported from the northern part of Portuguese East Africa near Moçambique (de Andrade, 1929, p. 158), and the well-known Tendaguru Formation in Tanganyika has yielded a fine Lower Cretaceous fauna, described by Lange (1914), Dietrich (1933), and other workers.

Between Algoa Bay and East Pondoland, for a distance of about 280 miles, the Cretaceous System is practically absent, and the Karroo and Cape Systems outcrop at the coast. In East Pondoland the Umzamba Beds, almost confined to beach outcrops over some 25 miles of coast, including outcrops at Umpenyati in southern Natal, are characterised by an exceptionally rich fauna of Upper Campanian age, described by Woods (1906), Spath (1921 *a*, 1922), Rennie (1930), and others. The beds here rest directly on the pre-Karoo basement. The same horizon occurs as sub-outcrops farther north at Durban.

Cretaceous beds reappear at the coast near Port Durnford, south of Richards Bay and about 80 miles north of Durban, and stretch continuously northwards through Zululand for about 150 miles, passing into Portuguese territory, where the system is widespread. A considerable portion of the Cretaceous succession is represented in the Cretaceous of Zululand, though much remains to be done before the sequence is thoroughly understood. The beds rest unconformably on the Karroo System and on Old Granite, for a long distance directly overlying the Lebombo Volcanics, and are practically undisturbed, the beds dipping eastwards towards the coast at very small angles. Fossiliferous outcrops occur at certain favourable localities, the greater part of the area covered by the system being hidden beneath recent deposits.

Nearly all the species described up to the present from the Zululand Cretaceous come from two areas, south of the Umfolosi River and north-west of Lake St. Lucia respectively, situated about 40 miles apart, the latter some 35 miles south of the big bend of the Pongola River. The Lamellibranchia described below come from localities north of the big bend of the Pongola River, and between that river and the Swaziland border.

A rich fauna has been described by Etheridge (1904) and Spath (1921, pp. 224-272), with a few additions by Newton (1909) and Rennie (1930, pp. 236-250), from a limited area just south of the

Umfolosi River, including the well-known fossiliferous locality of Umkwelane Hill and the neighbouring localities Lake Itesa (Eteza, Isitesa), and "Railway Cutting between Umfolosi Station and Mill Halt." The work of Spath (*ibid.*, pp. 264-272) has made it clear that the great majority of, if not all, the ammonites are Campanian (and Maestrichtian?), though it is hardly safe to assume the complete absence of Lower Senonian horizons; there is no indication of pre-Senonian species. The beds here are approximately equivalent to the Umzamba Beds in Pondoland, and the transgression of the Senonian over older horizons is evident, for at Umkwelane Hill the Senonian rests directly on Lebombo basalts.

A considerable succession of Cretaceous beds is known from the area north-west of Lake St. Lucia, where fossiliferous outcrops occur along the Umsinene River and its tributary the Manuan Creek (Munyuana), which flow into the north-west corner of False Bay, Lake St. Lucia. Marine fossils have been described by Etheridge (1907), Crick (1907), Newton (1909), Spath (1921, pp. 273-309), Rennie (1930, pp. 236-250), van Hoepen (1929, 1931), and Heinz (1930). According to Spath the ammonite evidence proves the presence of the Middle and Upper Albian, the Cenomanian, the Lower Senonian (Coniacian), and the Upper Senonian (Campanian, including Maestrichtian?) horizons. An account of the succession along the Umsinene River, from above its junction with the Manuan Creek to the shore of False Bay, has been given by van Hoepen (1926), who divided the sequence into seven beds, to which names were given as follows, with suggested correlations:—

7. Umzamba Beds	.	.	Upper Senonian.
6. Itweba Beds	.	.	Middle Senonian.
5. <i>Peroniceras</i> Beds	.	.	Lower Senonian.
4. Munyuana Beds	.	.	Turonian.
3. Skoenberg Beds	.	.	Cenomanian.
2. Umsinene Beds	.	.	} Albian.
1. Ndabana Beds	.	.	

The palaeontological evidence on which these correlations were made has only been published in part by van Hoepen (1929, 1931). The presence of the Turonian has not been recognised by previous workers (Spath, 1921, p. 268; du Toit, 1926, pp. 316, 319), its presumed absence being in conformity with evidence from Angola and elsewhere; the transgression of the Senonian on to pre-Cretaceous formations at Umkwelane Hill and in Pondoland points to a break within

the Upper Cretaceous of Zululand which has not yet been disproved. However, van Hoepen (1929 *a*) insists that there is a practically unbroken sequence from the Aptian to the Senonian, and Heinz (1930) has identified species of *Inoceramus* from the Umsinene River as Turonian. In a later publication van Hoepen (1929 *a*, p. 10) correlates the Ndabana Beds as Aptian, though without giving palaeontological evidence.

A few Cretaceous species have been recorded from localities in Northern Zululand, between the Manuan Creek and the Portuguese border, but practically nothing was known of the succession in this stretch of country until the visits in 1933 of Mr. H. F. Frommurze and Drs. S. H. Haughton and A. W. Rogers, whose collections have afforded material for this paper. Spath (1921, p. 221) has recorded Albian and Senonian ammonites from the Mkusi (Mkuzi) River, and Heinz (1930, p. 685) has recorded from the same area a species of *Inoceramus*, said to be Upper Turonian; this locality, 20 miles north of the Umsinene, forms an interesting link between the Umsinene and Pongola areas. The writer (Rennie, 1930, p. 239) has placed on record the occurrence of the Albian species *Trigonia cricki*, *Neithea quadricostata*, and *Veniella etheridgei* at the Ingwavuma road drift on the Pongola River, as well as *Nordenskjöldia natalensis* and *Pleuromya africana*, Senonian species, at some locality west of the Pongola River.

The Cretaceous of Zululand is continuous with that of the district of Lourenço Marques in Portuguese East Africa, where outcrops occur from the Zululand border northwards as far as the neighbourhood of the point of entry of the Limpopo River into Portuguese territory, a distance of about 300 miles. Outcrops occur on the Maputo (Usutu) River near Catuane, close to the Zululand border, and between Bela Vista and the east coast to the south of Delagoa Bay; Cretaceous beds are known to extend northwards along the eastern flank of the Lebombo Mountains as far as the Limpopo, where they rest on the Lebombo Volcanics and dip eastwards at small angles beneath recent deposits as they do in Zululand. The area is at present being investigated by the officers of the Department of Mines and Industries of Moçambique. It would appear that at least the Aptian, Albian, Cenomanian, and Senonian stages are present. A number of species of Aptian ammonites have been recorded by Kilian (1902), Krenkel (1910), and Spath (1921, pp. 309–318) from Catuane, Powell's Camp, and other localities (de Andrade, 1929, p. 159) in the region south of Delagoa Bay; the Aptian has not hitherto been recorded from farther south in Zululand, unless van Hoepen (1929 *a*, p. 10) is

correct in correlating his Ndabana Beds at the base of the sequence on the Umsinene with that stage; according to Spath the Aptian beds at Catuane, etc., are probably Upper Aptian. From Catuane Spath (1925, pp. 180-196) has also described a number of Upper Albian ammonites, while Cox (1925, pp. 202-207) has described some gastropods from the same locality and horizon. The Senonian stage has been recognised at Incomanini on the Incomati (Komati) River, north of Lourenço Marques, the fauna containing a few species of Lamellibranchia identical with or allied to species in the Umzamba Beds of the Union (du Toit, 1926, p. 327); the Lamellibranchia have not been described, but Cox (1925, pp. 202, 208-215) has recorded a number of Gastropoda of somewhat Tertiary aspect; ammonites appear to be absent. Spath (1925, pp. 196-200) has recorded a Cenomanian ammonite and two Upper Senonian ammonites from Maputoland, the region south of Delagoa Bay.

In the region between the Limpopo and the Zambesi the Cretaceous System is for the most part covered with recent deposits, but beds referable to the system appear here and there, both on the coast and inland. Newton (1924) has recorded both Senonian and Danian faunas from the Cheringoma (Sheringoma) Plateau adjoining the Urema trough, north of Beira; while the Upper Cretaceous species *Lopha* (= *Alectryonia*) *ungulata* was recorded by Newton (1896) from the neighbourhood of Sofala.

Still farther north the Cretaceous is absent for a considerable distance, but Cretaceous beds reappear on the coast south of Moçambique, and can be traced into Tanganyika. From this region Choffat (1903) has recorded Cretaceous beds at Conducia, apparently largely Cenomanian; the Neocomian, Aptian, and Albian stages are said to occur in this region also (de Andrade, 1929, pp. 158-160).

The New Collections from Northern Zululand.—The Lamellibranchia described in this paper come from outcrops in Northern Zululand, situated for the most part on the Pongola River and in the region between the Pongola River and the borders of the Transvaal and Swaziland, not far to the south of the southern boundary of Portuguese East Africa. Prior to 1933 this tract of country was practically unknown from a geological point of view, though it was known that the Cretaceous beds exposed north-west of Lake St. Lucia extended northwards along the lower course of the Pongola and into Portuguese territory. In 1933 Mr. H. F. Frommurze, B.Sc., of the Union Geological Survey, while engaged in irrigation work in this area, collected from fossiliferous Cretaceous beds along the

Mfongosi stream, a tributary of the Pongola, and the collections sent to Cape Town were deemed of such importance that the area was immediately visited by Dr. S. H. Haughton, now Director of the Survey, and Dr. A. W. Rogers, formerly Director of the Survey. Cretaceous outcrops were located over a wide area and an attempt was made to work out the sequence by careful collections of fossils on a zonal basis. Subsequent to their visit further collecting was done by Mr. J. S. Hutt, Surveyor to the Irrigation Department, without reference to localities or horizons; this collection was presented to the Transvaal Museum.

Acknowledgments and Preliminary Remarks.—The Lamellibranchia described below form part of the collections obtained by Mr. H. F. Frommurze, Dr. S. H. Haughton, and Dr. A. W. Rogers, and by Mr. J. S. Hutt in 1933. The writer is very greatly indebted to Dr. S. H. Haughton, Director of the Geological Survey of the Union of South Africa and Honorary Curator of the Palaeontological Collections in the South African Museum in Cape Town, for placing the Lamellibranchia at his disposal for description, and for much useful advice. Dr. E. L. Gill, Director of the South African Museum, and Dr. T. W. Gevers, formerly on the Union Geological Survey, have very kindly forwarded to the writer specimens and literature contained in the collections in Cape Town, while the writer is particularly grateful to Dr. Gill for arranging for the publication of this paper and for help in various ways. Mr. L. R. Cox, of the Geological Department of the British Museum (Natural History), and Dr. K. H. Barnard, Assistant-Director of the South African Museum, have given invaluable help by looking up early references to *Trigonia* not accessible in Grahamstown, and giving their opinions on certain problems of nomenclature; to them the writer is very greatly indebted. The accompanying plates were prepared by the writer, and his best thanks are due to Dr. John Hewitt, Director of the Albany Museum in Grahamstown, for granting every facility in the use of camera and dark room; and for much helpful criticism.

The cost of photographic materials was defrayed by a grant from the Research Grant Board of the Union of South Africa, for which the writer expresses his thanks.

The collections obtained by Mr. H. F. Frommurze have been placed in the South African Museum in Cape Town; those made by Mr. J. S. Hutt in the Transvaal Museum in Pretoria; where individual specimens are referred to, "S.A.M." or "T.M." precede the catalogue numbers. The collections made by Dr. S. H. Haughton and Dr.

A. W. Rogers are in the Cape Town office of the Geological Survey of the Union, at the South African Museum; these are simply labelled with the horizon letter and number, but types and figured specimens at least will be transferred to the collections of the South African Museum in due course. A few specimens from the Albany Museum (A.M.) are also referred to.

In recording localities in the text the number of available specimens from each locality has been indicated by a number in brackets, e.g. Z19 (4) indicates that 4 specimens were collected at horizon Z19. References to published papers have been made by indicating the author's name and the date of publication; a list of references will be found at the end of the paper.

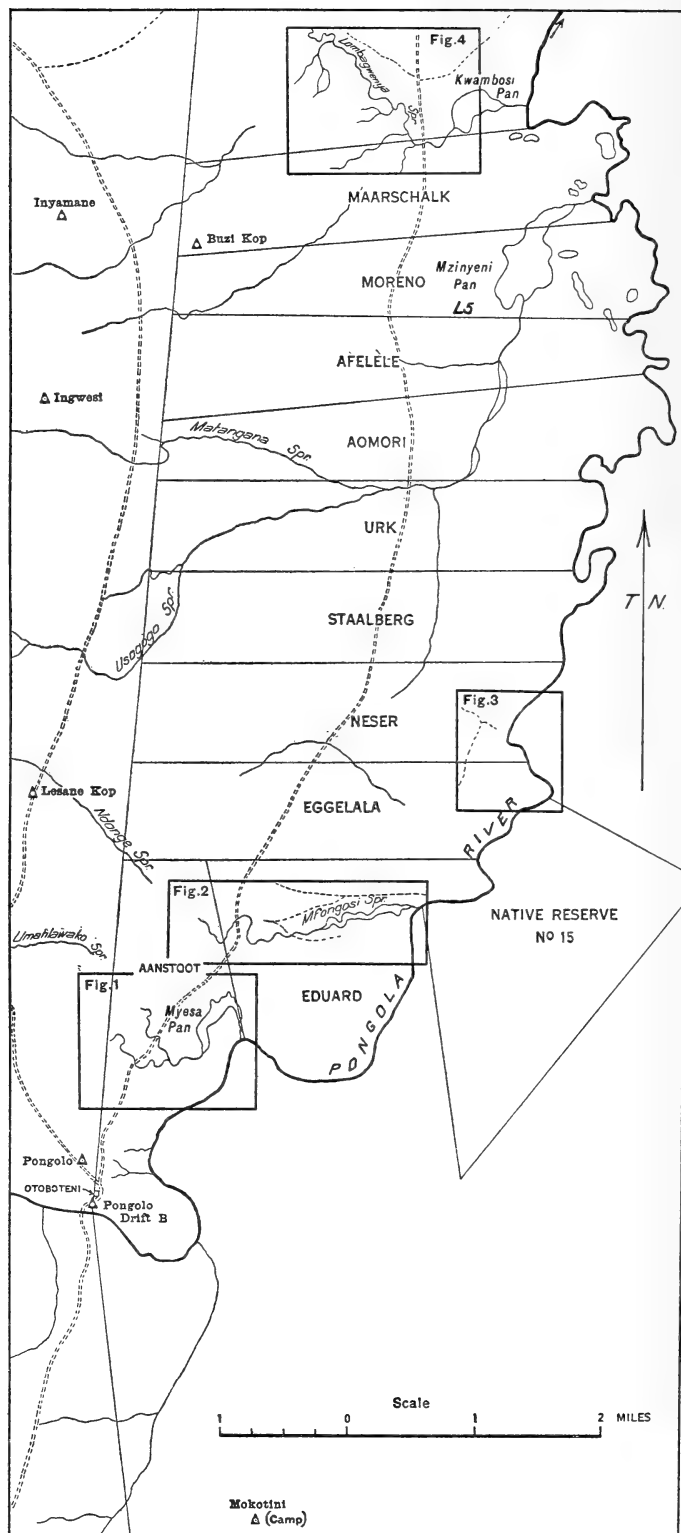
In preparing the descriptions that follow, reference to a number of badly preserved, fragmentary, or otherwise doubtful species of Lamellibranchia has been omitted. It was considered that no good purpose would be served by giving descriptions or figures of these species, either because the locality at which they were collected was not precisely recorded, or because they were found at one locality and horizon only, and therefore fail to be of any value in correlating horizons at one locality with those of another, or because of some uncertainty as to the identity of the genus to which they belong, or because of great imperfection in the preservation of the shells concerned. Included in this category are a number of specimens referable to the *Veneridae*, to *Ostrea*, to *Pecten*, and to a few other genera.

Trigoniae belonging to the section *Scabrae*, which would be referred to the sub-genus *Scabrotrigonia* Deecke, or to the several sub-genera proposed by van Hoepen (1929), have not been specially dealt with here, although several species are represented in the abundant material available. Apart from this group, which will be worked out later, all the recognisable and significant species of Lamellibranchia contained in the collections are described below. A brief reference to the *Scabrae* is included, however.

2. AN ACCOUNT OF THE GEOLOGY OF THE CRETACEOUS BEDS.

(By S. H. Haughton, M.A., D.Sc., Director of the Geological Survey of the Union of South Africa.)

The localities from which the fossils described in the following pages were collected lie in the coastal belt of Northern Zululand, in the magisterial districts of Ubombo and Ingwavuma. This belt is bounded to the west by the Lebombo mountain range, a dissected



penneplaned ridge of Karroo volcanic rocks whose structure and features have been recently described by du Toit (Trans. R. Soc. S. Afr., 1929, vol. xviii, pp. 189-217). The range has an approximately north-south strike, and—in the area visited by the writer—its wonderfully even sky-line is broken only by the deep gorges of the Mkuzi, Pongola, and Ingwavuma rivers. Transecting the range in a west-east direction these streams begin to meander as soon as they leave the foothills of rhyolite and enter the flat coastal plain, the Mkuzi turning in a south-east direction to empty itself into False Bay, the Pongola—joined by the Ingwavuma—flowing northwards into Delagoa Bay.

In addition to these major streams which cut through the Lebombo, a number of smaller tributaries rise on its eastern flanks. Where they, and the bigger streams, flow through the Cretaceous beds they form a number of disconnected deep pools in which hippopotami and crocodiles are to be found.

The actual river-beds lie about 60 feet below the general level of the coastal plain. This plain is capped by a covering of gravel with, in parts, a consolidated calcareous grit of marine origin. Sand, too, is common. The fossiliferous Cretaceous beds are only exposed on the banks of the streams or sides of gullies. The localities investigated are shown on the accompanying plans, and are—from south to north—the Myesa Spruit, the Mfongosi Spruit, the Pongola River with a tributary gully, the Msinyene Pan, and the Lombagwenya Spruit. Small collections were also made south of Pongola Poort at Mokatini Camp and to the south of it.

The investigation of this area by the writer and Dr. A. W. Rogers, F.R.S., was only made possible by the kindness of the Director of Irrigation, who kindly placed all his large-scale contour plans at our disposal, and of Mr. J. S. Hutt, Surveyor-in-Charge of the Lower Pongola Irrigation Survey, whose camp at Otobotini provided us with every comfort, and who placed both his time and local knowledge enthusiastically at our service. Mr. Hutt, both before and after our visit, was active in the collection of fossils, and presented the bulk of his material to the Transvaal Museum. Some of it has been studied, and the results are incorporated in the palaeontological descriptions which follow.

Description of Localities.

1. *Myesa Spruit.*—Very platy rhyolites with a dip of about 10° – 12° in a direction 10° north of east form a cliff just below the drift on

the southern branch of the stream. The contact between the rhyolites and Cretaceous beds is not seen, being overlain by alluvium and gravels.

North of the drift, across the northern branch, buff sandy beds containing gypsum are seen in a roadside hole and in a shallow donga. They contain a band of hard gritty quartzite, which is nodular; on

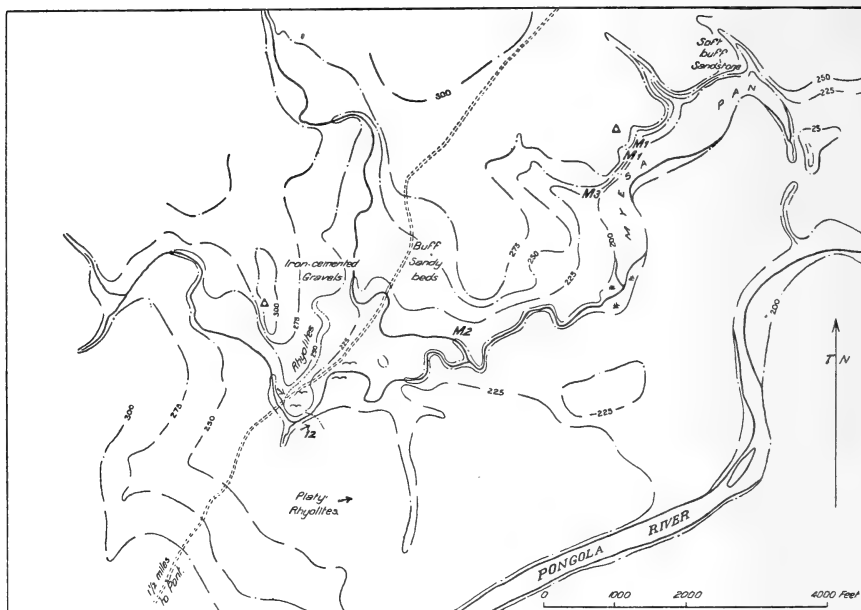


FIG. 1.

the weathered surface this shows masses of fibrous calcite, which may possibly be replaced wood.

At locality M2 are unevenly bedded pebble beds and grits, buff in colour, with a dip towards the south-east. The exposures on the left bank of Myesa Pan (M3 and M4) are poor. They consist of buff soft sandstones with occasional small lenses of hard calcareous grit, which sometimes carry badly preserved shells.

2. *Mfongosi Spruit*.—The most easterly outcrop of rhyolite along this spruit is seen at the point where the river leaves the foothills, some 3·8 miles in a direction west 30° north from the drift across the spruit on the main road. Here the rhyolite is platy and amygdaloidal, and dips at $12\text{--}15^\circ$ in a direction slightly north of east.

Below this the river banks are low and gravel-covered. A few hundred yards downstream there is a short exposure of consolidated boulder beds and gravels which appear to have a slight dip downstream. There is no evidence available as to their age; but none of the recent conglomerates along the rivers appear to be so compacted as these.

The most westerly outcrop of Cretaceous beds occurs on the south branch of the spruit at a point about 2 miles above the drift, measured in a straight line, bearing west 15° north from the drift. This consists of buff-coloured, sandy pebble beds and sandy grits in which no fossils were seen.

Just above the junction of the two branches of the spruit there is a good exposure on the south branch of a thickness of about 30 feet of buff sandstones, grits, pebble-washes, and conglomerate, with a dip of 3° towards the east. In places current-bedded bands show a much higher dip in the same direction. Included in the conglomerate are many rhyolite pebbles, some of agate, and some of sedimentary rocks. The sandstones carry ferruginised badly preserved fossil wood, but no marine fossils were seen.

At the big cliff, on the left bank of the stream above the drift, there is a succession of beds, mostly of buff sandstone with hard lenticular nodules about 55 feet thick. This locality was designated Za. The basal 5 feet contain six thin hard bands filled with fossils, which include *Trigonia obesa*, *Trigonia haughtoni*, and *Trigonia hennigi*, separated by buff sandy joint clays. Two feet above this is a narrow band with the same *Trigonia* species and a Belemnite.

The buff sandstones of the higher part of this succession outcrop at the first cliff above the drift on the right bank of the river. Here some of the gritty sandstone is rather more micaceous than at locality Za; the finer-grained sediments contain fragments of stems; and a few fossiliferous concretions with *Trigonia* occur. On the slope above the cliff (locality Zo) one specimen of a large uncoiled ammonite, *Tropaeum* cf. *gigas*, was discovered, and some fragments provisionally assigned to the genus *Toxoceratoides*.

Below the drift the cliff on the left bank has at its western end sandy shales with rounded and irregular nodules containing a species of *Acanthohoplites* and *Dicroloma* sp. (locality Z1). Then follows a succession of sandy clays with thin bands of fossiliferous limestones (locality Z2) containing *Trigonia obesa*, *Trigonia pongolensis*, *Cardium rogersi*, and *Dicroloma* sp. The highest horizon in this cliff section (Z3) consists of buff argillaceous sandstones with thicker elongate

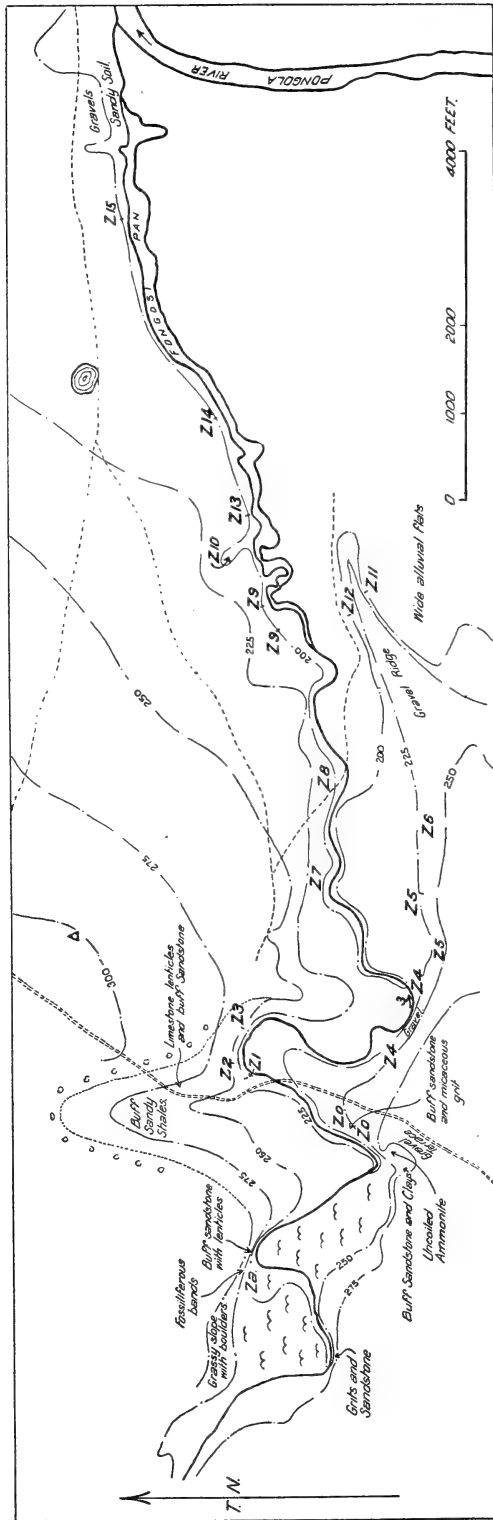


FIG. 2.

lenticles of limestone, and yielded *Trigoniae* of the Scabrae group, *Trigonia obesa*, *Gervillia dentata*, and *Cardium rogersi*.

On the right bank the first cliff is of buff sandy clays, with plant fragments and calcified wood with, at the top, bands of unfossiliferous septarian nodules. This cliff is succeeded by a slope, at the top of which is a fossiliferous limestone (locality Z4), with *Gervillia dentata*, *Pseudavicula* (?) *africana*, *Trigonia obesa*, and *Trigoniae* of the Scabrae group. Many of the shells here were broken before consolidation; further, the limestone carries large mud-pellets and some pebbles.

This fossiliferous limestone dips at a low angle downstream at the top of the next cliff on the right bank. Near the lower end of the cliff it gives place gradually to fossiliferous soft sandstones, which yield a large number of small shells. The limestone is in reality a series of flat lens-like bodies occupying one horizon. Between the lenses the grey marly sandstone is fossiliferous. Shells of the same species as occur in the limestone are also found some 2 feet below it.

Locality Z5 occurs on the slopes below a terrace farther down the right bank of the river and shows outcrops of shelly limestones definitely higher in the succession than those of Z4. From here were collected *Gervillia dentata*, *Pseudavicula* (?) *africana*, *Trigonia obesa*, *Belemnites*, and *Acanthoplites*. Farther along the slope, opposite a cliff of the left bank, dirty buff-coloured, weathering, shelly limestone bands, frequently with spheroidal weathering, become common. This is locality Z6. Logs of heavily bored calcified wood are numerous, and the fauna contains *Gervillia dentata* in large numbers, *Inoceramus concentricus* (?), *Trigonia frommurzei*, *Trigoniae* of the Scabrae group, *Panope gurgitis*, *Acanthohoplites* spp., *Toxocara-toides* sp., and *Ancycloceras* (*Australiceras*) sp.

The higher ground on the right bank of the spruit ends to the east in a narrow gravel-capped spur. Locality Z11 is on the south flank of this spur; locality Z12 on the north. The outcrops are of buff shales and nodular limestone, and the fossils collected include a *Pseudodiadema*, *Acanthohoplites* spp., several large ammonites, *Cucullaea woodsi*, *Pseudavicula* (?) *africana*, *Trigonia obesa*, abundant *Trigonia frommurzei*, *Trigoniae* of the Scabrae group, *Protocardia* cf. *sphaeroidea*, and *Panope gurgitis*.

On the left bank, locality Z7, is a cliff opposite the space between Z5 and Z6. A highly fossiliferous limestone band overlies sandy clays with limestone concretions. *Gervillia dentata*, *Trigonia frommurzei*, and large uncoiled ammonites are very common; *Isognomon* sp. and scabrous *Trigoniae* also occur.

Above the limestone band which delimits the upper part of this succession is a slope formed of soft sandy shales and calcareous shelly concretions. This is locality Z8. Numerous bored logs, some of them 9 feet in length, occur here. Large loosely coiled *Lythceratids*, *Acanthohoplites* spp., *Lytocrioceras*, *Chelonicerias*, *Diadochoceras* sp. nov. aff. *nodosocostatum*, *Tropaeum* cf. *bowerbankii*, *Helicancyloceras* (?), and *Sonneratia* all occur in fair numbers, and the Lamellibranch fauna includes *Trigonia frommurzei*, *Trigonia obesa*, scabrous *Trigoniae*, *Cucullaea woodsi*, *Glycymeris* cf. *griesbachi*, *Gervillia dentata*, *Isognomon* sp. (?), *Exogyra conica*, and *Panope gurgitis*. The band containing this fauna continues for several hundred yards downstream, and is overlain at Z9 by a series of outcrops of ball-like concretions that contain very few fossils, succeeded by outcrops of shelly limestone with minute shells, *Trigonia frommurzei*, *Rhynchonella* sp., *Acanthohoplites*, and *Diadochoceras*. In these beds a log of calcified wood 30 feet long was seen.

A gully running into the spruit at Z10 exposes soft buff shales with numerous logs of wood and a layer of ball-like concretions with sparse, large, flat, involute *Beudanticeras*—like ammonites, *Gervillia dentata* and *Trigonia frommurzei*.

Below this gully the cliff shows bands of highly fossiliferous sandstone and sandy limestone dipping at a low angle eastwards. The upper end of this cliff (Z13) has *Pseudavicula* (?) *africana*, *Trigonia frommurzei*, *Neithea quinquecostata*, *Protocardia* cf. *sphaeroidea*, *Douvilleiceras mammatum*, *Beudanticeras*, and *Puzosia* cf. *stoliczkai*; the lower end (Z14) yielded *Isognomon* sp., *Inoceramus concentricus* (?), and *Panope gurgitis*.

Locality Z15, which is near the lower end of the Mfongosi Pan, yielded a possible new species of *Beudanticeras*.

3. *Pongola River*.—North of the mouth of the Mfongosi Spruit, between the Irrigation Survey points RAF and CRAFT, a short rather wide valley runs into the Pongola River. Along the sides of the valley is a continuous outcrop of a prominent thin band of limestone crowded with shells of *Turritella manuanensis*. This limestone has an apparent slight dip to the north-east. Below it are sandy buff clays with limestone concretions, which are highly fossiliferous, *Dipoloceratids*, *Mortoniceratids*, and *Desmoceratids* being common, particularly at an horizon about 40 feet below the *Turritella* limestone. This limestone and the beds below were numbered Z16, whilst the beds above the limestone on the valley sides were numbered Z17. From Z16 were obtained *Puzosia stoliczkai*, *Hysterocheras* spp.,

Diploceras quadratum, *Deiradoceras* spp., *Pervinqueria* spp., *Gervillia dentata*, *Inoceramus concentricus*, *Scabrotrigonia* spp., *Pholadomya vignesi*, *Goniomya* sp., *Veniella etheridgei*, *Exogyra conica*, *Ostrea* sp., and *Turritella manuanensis*.

The beds Z17 are less fossiliferous, but carry *Adkinsites umsinenense*,

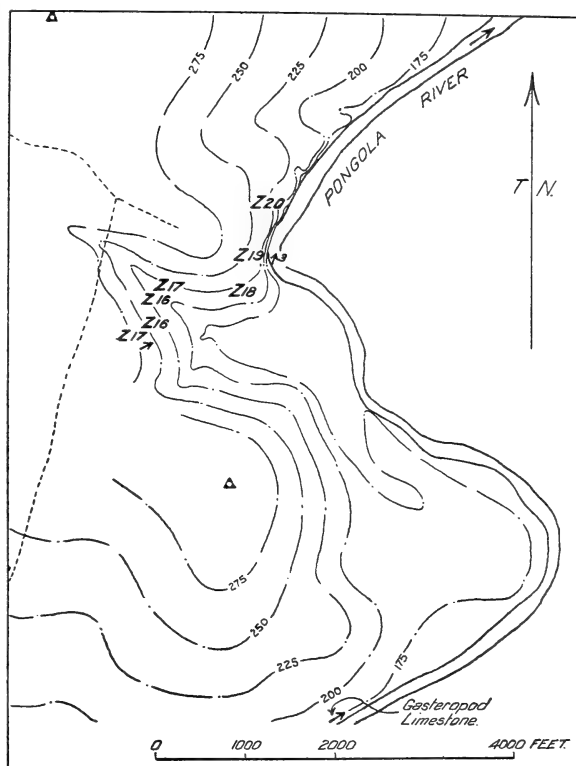


FIG. 3.

Pervinqueria, *Hysterocheras choffati*, *Diploceras cristatum*, and *Phylloceras velledae*.

North of the junction of this valley with the Pongola, on the farm Naser, there is a very fine long cliff-section on the left bank of the river. The section is about 40 feet high, and its upper 5 feet is formed of Tertiary or Recent gravels and sands. The Cretaceous beds consist of a succession of clays and clayey sandstones with limestone bands and bands of nodules, and their apparent dip is at a low angle downstream.

Near the base of the section (Z19) is a prominent thin pebble bed. Below this the clays are highly fossiliferous, *Oxytropidoceras* sp. nov., Nautiloids, *Neithea quadricostata*, *Cucullea woodsi*, *Gervillia dentata*, *Trigonia cricki*, *Protocardia* cf. *sphaeroidea*, *Veniella etheridgei*, *Exogyra conica*, *Turritella manuanensis*, and *Avellana* cf. *incrassata* being the commonest forms present. Above this pebble bed there are definite highly fossiliferous layers with the same Lamellibranchs as in the lower bed (with the exception of *Veniella*), together with small Dipoloceratids and the echinoderms *Hemiaster zululandensis* and *Holaster vanhoepeni*.

Towards the top of this section (Z19) *Puzosia* cf. *bhima* becomes the commonest ammonite, and *Dipoloceras cristatum* is found.

Proceeding northwards the cliff section continues (Z20) and some 25 feet of buff sandy clays and limestone nodules carry abundant *Exogyra*, *Veniella*, *Trigonia*, *Neithea*, and Nautiloids. Ammonites, however, become rather scarce, *Myloceras*, *Puzosia*, and *Dipoloceras* being the only genera collected.

Still farther to the north the cliff becomes lower, and the post-Cretaceous grits and gravels sink considerably in level. The Cretaceous beds are more sandy than to the south, and carry sporadic nodules of calcareous quartzite, some of which are fossiliferous. Fossils are scarce in the buff sandstones. From this locality (Z21) *Holaster*, *Hemiaster*, *Inoceramus concentricus* var. *subsulcatus*, *Pholadomya vignesi*, and *Goniomya* are recorded.

4. *Lombagwenya Spruit*.—The main road from Otobotini to Ndumu crosses this spruit to the west of the Kwambosi Pan, and rises up to the plateau past the Lombagwenya Store. On the slopes down to the spruit, west and north-west of the store, richly fossiliferous outcrops occur; and other exposures of Cretaceous beds occur a short distance below the drift.

Three traverses were made across this fossiliferous slope.

Immediately to the west of the store a thickness of about 125 feet of beds (locality L3) consists mainly of buff sandy marls with calcareous nodules. Near the base are large open-coiled Crioceratids with depressed whorl section and prominent widely spaced ribs passing right across the venter, associated with *Gervillia dentata* and *Trigonia frommurzei*. Just above the bed most prolific in ammonites is a narrow band of sandy clays, below a thin limestone, that contains numbers of *Rhynchonella* and *Terebratula*. The upper 50 feet of beds carry several species of *Douvilleiceras* including typical *D. mamillatum*, *Phylloceras* sp., *Leymeriella* sp.n., *Acanthohoplites* spp., and a new

genus of ammonite. At the top of the slope large Terebratulids occur.

Following the slope to the north-west one encounters blocks of fossiliferous limestone; here and there are low benches formed of limestone outcrops. The buff shaley beds which are intercalated with these are only occasionally exposed in shallow dongas.

The second traverse was made upwards from the southern end

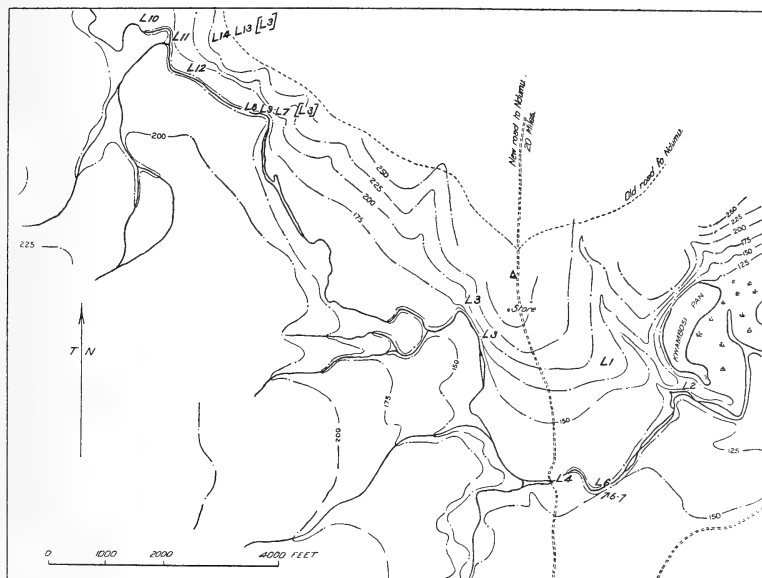


FIG. 4.

of a cliff about 2300 yards north-west from Lombagwenya Store. The cliff is composed of almost unfossiliferous buff sandy clays, showing some false-bedding with fossiliferous limestone nodules (locality L8). *Phylloceras* sp. and *Exogyra conica* (?) occurred here. Just above the crest of the cliff occurred *Megacucullaea* sp., *Trigonia hennigi*, *Tropaeum* sp., and higher up the gully are limestones with large *Ostrea*, *Panope gurgitis*, *Aconeceras* cf. *walshense*, and *Toxocera-toides* of the *royeri* group (locality L9). The next outcrop up the gully (L7) is limestones with *Pholadomya*, *Panope*, *Australiceras* cf. *lampros*, *Lytoceras* cf. *mikadiense*, *Chelonicer* (?), and numerous specimens of a sinistral *Turritites* cf. *emericianus*. At the top of the slope are specimens of the loosely coiled Crioceratids generally similar to those that were found near the base of locality L3.

The third traverse was made beyond the northern end of the cliff. The lowest beds seen here (L10) are buff sandy marls with large lenticles and rounded masses of slightly calcareous sandstone carrying fossil wood. The lenticles sometimes carry shells, especially a medium sized *Chlamys*. Above these beds is a band of shelly limestone (L11) with *Panope gurgitis*, *Aconeceras* cf. *nisus*, *Acanthohoplites* spp., *Leymeriella* spp. Slightly to the south-east, and at about the same height above the river, are shelly sandstones (L12) with *Cucullaea woodsi* (?), *Megacucullaea* sp., *Trigonia hennigi*, but no ammonites. Above these is a band of sandy shale with fragile *Scabrotrigonia*, *Gervillia dentata*, *Ostrea* sp., and *Thetironia* sp., followed by shales with limestone and very abundant fossil wood. Higher is a zone of buff shales with limestone concretions yielding enormous specimens of *Gervillia*, *Trigonia hennigi*, *Ostrea* sp., *Nautilus*, and *Phylloceras*, with fossil wood (L4). Above this is an outcrop of shelly limestone with large loosely coiled Crioceratids, whilst at the top of the slope are numerous weathered, rounded clay nodules (L3†) * of various sizes, many of which are fossiliferous and carry *Isognomon* sp., *Lopha diluviana*, *Tropaeum* cf. *mozambiquense*, *Tropaeum* cf. *arcticum*, *Australiceras*, *Acanthohoplites* of the *roseanus* group.

Exposures of Cretaceous beds occur also below the drift.

On the right bank of the spruit about 150 yards below the drift is an exposure of a thickness of about 30 feet of stiff sandy clays with one layer of hard fossiliferous limestones and some sporadic calcareous nodules (locality L6). These yield *Phylloceras*, *Douvilleiceras*, *Scabrotrigonia*, *Terebratula*, *Exogyra* cf. *conica*, and *Gervillia dentata*.

On the north side of the spruit are low ridges above the alluvial plain. On the slopes of these (L1) are occasional outcrops of weathered calcareous nodules that contain large specimens of *Gervillia dentata*, *Scabrotrigonia*, *Panope gurgitis*, *Glycimeris*, brachiopods, *Douvilleiceras*, and *Oxytropidoceras* (?) sp. juv.

Farther down the spruit a low cliff above the water has buff clays which are highly fossiliferous, but retain the fossils only in the form of internal casts. Fragments of ammonites only were seen here (L2), one small crushed Echinoid, and *Scabrotrigonia* sp.

5. *Msinyene Pan* (locality L5).—The low slopes on the western side of the south end of this pan show few outcrops; but some fossils were collected here which are of interest. Among them was a specimen of a new ammonite belonging to the form already recorded

* Locality L3† is distinct from L3 and may not be the same horizon. L3† is equivalent to [L3] in fig. 4.

from the upper beds of section L3, *Leymeriella* sp., and a species of *Beudanticeras* similar to one found in the highest beds of the Mfongosi Spruit. *Scabrotrigonia* sp. also occurs, and an imperfect shell which Rennie has tentatively assigned to *Neithea quadricostata*.

6. *Mokatini*.—The area to which this name has been given lies between the Pongola and Mkuzi Rivers. Apart from the rhyolite foothills of the Lebombo the country is almost entirely covered by soil and sand, and shows very few outcrops of the Cretaceous beds.

The low ridge which runs south from the Mokatini Irrigation Survey camp, on the south side of the Enseleni road, carries an exposure of a band of very hard shelly limestone from which it is difficult to extract shells (locality Z24). The shells are arranged in layers separated by bands of hard, barren, brown-weathering, fine-grained calcareous quartzite. From here come *Pseudavicula* (?) *africana*, *Scabrotrigonia* sp., and *Thetironia* sp.

About 4 miles to the east of this, and at an altitude about 150 feet lower, is a small exposure of a hard limestone with pebbles and shell fragments and blocks of fossil wood. A little downstream from this a softer shaley bed (Z25) yielded *Trigonarca* cf. *ligeriensis*, *Exogyra conica*, *Trigonia blanckenhorni*, and *Veniella etheridgei*.

3. A PRELIMINARY ANALYSIS OF THE AMMONITE FAUNA.

(By S. H. Haughton, M.A., D.Sc., Director of the Geological Survey of the Union of South Africa.)

Until the ammonite fauna is identified specifically exact determination and correlation of the various horizons present will not be possible. Nevertheless, certain generalisations may be made which are of interest.

1. *Mfongosi Spruit Succession*.—It is estimated that a thickness of 800 feet of fossiliferous beds are exposed along this spruit, the lowest being exposed at locality Za and the highest at locality Z15. On the right bank ammonites were collected at, in ascending order, Zo, Z5, Z8, and Z12; on the left bank at Z1, Z7, Z8, Z9, Z10, Z13, Z15.

The lowest horizon (that at Zo) yielded *Tropaeum* cf. *gigas*, and must lie some 30 feet below Z1, which carries *Acanthohoplites* sp. nov. The presence of *Tropaeum* would seem to indicate the presence of the top of the Lower Aptian or of the lower part of the *martini* zone of the Upper Aptian at Zo.

The assemblage from Z8 includes forms that may be representative of more than one of the European zones. *Tropaeum* cf. *bowerbanki*

is compared with a species that is representative of the middle sub-zone of the Tropaeuman of the Upper Aptian. On the other hand, *Diadochoceras* sp. nov. aff. *nodosocostatum* (ident. L. F. Spath) is compared with a species that is characteristic of the lowest zone of the Albian. It is possible, however, that this apparent mingling may be susceptible of interpretation, as the locality Z8 extends for nearly 1500 feet along the side of the spruit and contains a thickness of some 78 feet of beds. Further collecting may show that each of the critical forms is confined to a definite horizon, and that the intervening *subnodosocostatum* zone may also be present. It is of interest that a species of *Acanthohoplites*, comparable with *A. aschillaensis*, comes from the lower beds at Z9; this species is characteristic of the upper part of the *subnodosocostatum* zone.

At locality Z9 *Acanthohoplites bigoureti* is definitely indicative of the presence of the lowermost Albian (Clansayes horizon); and at Z13 *Douvilleiceras mammillatum* shows the presence of the base of the Middle Albian (*mammillatus* zone). Here again there is a hiatus in the faunal succession as worked out in Europe, corresponding to the Leymeriellan zone of the Lower Albian, which may be represented by the beds at Z10, which contain *Beudanticeras* sp. These beds cannot be more than a few feet thick.

Since no stratigraphic break was visible in the rock succession, it may be accepted that along this section there is a succession of fossiliferous beds ranging from the lower part of the *martini* zone of the Upper Aptian at least to the *mammillatus* zone of the Middle Albian, and that the unfossiliferous beds in the upper reaches of the spruit are Lower Aptian and may range down into the Neocomian. A tentative classification of the beds, according to the locality numbers, is as follows:—

Middle Albian .	<i>mammillatus</i> zone	Z13, Z15.
Lower Albian .	<i>tardefurcata</i> zone (Leymeriellan)	Z10 (?), Upper beds of Z9 (?).
	<i>nodosocostatum</i> zone (Acanthohoplitan)	Z9. Upper part of Z8 (?), Z12.
	<i>subnodosocostatum</i> zone (Parahoplitan)	Lower part of Z9? Lower part of Z8?
Upper Aptian .		$\left\{ \begin{array}{l} \text{Z2 (?), Z3 (?),} \\ \text{Z7 (?).} \end{array} \right.$
	<i>martini</i> zone (Tropaeuman)	Zo, Z1 (?).

2. *Lombagwenya Spruit*.—Beds of approximately similar age to the above occur in this area. The presence of the *mammillatum* zone is evidenced by abundant *Douvilleiceras* in the upper 50 feet of the L3 succession; these upper beds also yielded *Leymeriella*, so that it may be possible to see in them lower *tardefurcata* zone beds and upper *mammillatum* zone beds. The lowest beds in this section contain Crioceratids that are comparable with those of Z7 and Z8.

The assemblage at L11 contains peculiar features, in that *Aconeceras* and *Leymeriella* apparently occur together. Hitherto *Aconeceras* has been considered to be confined to the Gargasian, with the exception of possible representatives from the Bedoulian, but is unrecorded from the Albian; *Leymeriella*, on the other hand, seems to be confined to the upper half of the Lower Albian. It is certain that L11 lies below L3†, in which Gargasian *Ancycloceratids* and *Acanthohoplites* of the *roseanus* group occur. It may be remarked that the association of *Tropaeum* with *Australiceras* both at L3† and at Z6–Z8 tends to throw doubt on Whitehouse's suggestion that the former was a descendant of the latter.

3. *Pongola River*.—In this area the fauna is definitely Middle and Upper Albian. The lowest horizon (basal part of Z19) contains *Oxytropidoceras*, whilst *Manuaniceras* occurs just above the pebble bed near the base of this section. Slightly higher were found *Dipoloceras cristatum*, *Dipoloceras bouchardianum*, and *Puzosia* cf. *bhima*. The *Dipoloceratids* of this assemblage are closely comparable with those from the top of the Middle Albian of England, the *cristatum* sub-zone of the Lower Gault.

Localities Z16 and Z17 contain forms that are indicative of the Upper Albian, such as various species of *Pervinquieria* and *Deiradoceras*. The former ranges in England from the *orbigny* to the *aequatorialis* sub-zones. *Hysterocheras*, which is also fairly abundant here, is typical of the lower part of the Upper Albian. On the other hand, *Dipoloceras cristatum* has also been found at this locality, as has *Adkinsites umsinenense*. The presence of these probable members of the *cristatum* sub-zone fauna in the upper part of this section above the gasteropodous limestone is an anomaly that cannot at present be explained.

4. THE LAMELLIBRANCH FAUNA.

The faunas collected at the localities described above consist mainly of Ammonites and Lamellibranchs, with comparatively few Gastro-

Pods, and rare Echinoids, Belemnites, etc. The Lamellibranchs are described below, and a brief notice of the associated Gastropods is appended.

The assemblage of Lamellibranchs in the collections is remarkable for the high proportion of large, massive, and thick-shelled species, among which several species of *Trigonia* are conspicuous, e.g. *T. obesa*, *T. hennigi*, *T. frommurzei*, as well as *Cucullaea* spp. aff. *kraussi*, *Gervillia dentata*, *Veniella etheridgei*, and *Protocardia* cf. *sphaeroidea*. From the systematic point of view, the chief interest in the faunas is the great diversity displayed by the *Trigoniae*, at least ten species of which are represented, referable to as many as seven sub-genera, including the very remarkable new species *T. frommurzei*, for which the new sub-generic name *Sphenotrigonia* is proposed.

A table showing the distribution of the species at the several localities is appended to this paper.

Though in the last resort the precise identification of the ages of the several horizons must be based on the associated Ammonite fauna, the Lamellibranchs are of some considerable interest. On the Lamellibranch evidence alone, the beds would appear to range from Neocomian to not later than Cenomanian, and are thus largely Lower Cretaceous in age. The presence of the Neocomian is suggested by the occurrence of several species of Lamellibranchs with distinctly Neocomian affinities, but it appears from Dr. S. H. Haughton's preliminary analysis of the Ammonite fauna that these species are actually associated with Upper Aptian and even Lower Albian Ammonites at certain localities. The association of *Trigoniae*, belonging to groups hitherto regarded as exclusively Neocomian and highly characteristic of Neocomian deposits in Central and South America, the Uitenhage Formation and deposits in East Africa and India, with post-Neocomian ammonites, is a remarkable feature of the faunas. As a result of his studies of the southern Neocomian Lamellibranch faunas, Kitchin (1926, p. 467) has emphasised the fact that such Lamellibranch types as the Pseudo-quadrate *Trigoniae*, *Trigoniae* of the groups of *T. conocardiiformis* and *T. v-scripta*, and large *Cucullaeae* of the *C. kraussi* group are confined to Neocomian deposits.* It is therefore somewhat surprising to find species that can be paired off with well-known Uitenhage (Valanginian) species from the Cape Province occurring in Zululand in association with Ammonites of later stages. Dr. Haughton finds it probable that on the Mfongosi "the unfossiliferous beds in the upper reaches of the spruit are Lower

* But see p. 300.

Aptian, and may range down into the Neocomian," but Neocomian Ammonites are wanting in the collections. It is just possible that the Neocomian is represented on the Myesa stream (M1 and M3) and at ZA on the Mfongosi, since the *Trigonia v-scripta* group is there represented by a new species that was not collected at higher horizons, and Ammonites were not found; but in view of the undoubted association of e.g. a Pseudo-quadrate *Trigonia* with Aptian-Albian ammonites on the Lombagwenya and of *T. obesa* with Lower Albian ammonites at Z12, the occurrence of a new species of *Trigonia* belonging to the *T. v-scripta* group cannot be held to prove the presence of the Neocomian at the localities mentioned, and it is thus possible that the Neocomian is not present in Zululand at all.

Cretaceous beds older than the Middle Albian were not known to occur in Zululand until after the publication by Spath (1921) of his paper on the Cretaceous Cephalopoda of Zululand, though it might have been suspected that the Aptian stage, which was known to outcrop just north of the Zululand border, extended farther south. In 1929 van Hoepen published a description of the *Trigoniae* obtained by him on the Umsinene River, and in the same year claimed (1929 a, p. 10) that his Ndabana Beds at the base of the succession at that locality represented the Aptian. The evidence on which that claim was based has not yet been published in full.

From his Ndabana Beds van Hoepen (1929) has only described four species of *Trigonia*, and these have a distinctly Uitenhage aspect, being closely comparable with species occurring in and highly characteristic of Neocomian deposits in Central and South America, and of the Uitenhage Series in the Cape Province. The occurrence of no less than four species of *Trigonia* in the Ndabana Beds that can all be paired off with well-known species from the Sundays River Beds in the Uitenhage Series of the Cape is suggestive of a Neocomian age for the Ndabana Beds, since at least three of these species belong to groups of *Trigoniae* highly characteristic of the southern Neocomian, as Kitchin (1903, 1908, 1926, 1929) has urged, and since also the age of the Sundays River Beds has been determined very precisely by Spath (1930, p. 132) as undoubtedly Upper Valanginian, i.e. well below the top of the Neocomian. The species concerned are as follows: *Megatrigonia obesa* van H. belongs to the group of *T. conocardiiformis* (Krauss), named after a well-known Uitenhage species; *Iotrigonia crassitesta* van H. and *I. inconstans* van H. belong to the group of *T. v-scripta* Kitchin, and are closely comparable with *T. stowi* Kitchin and *T. van* Sharpe

respectively, both characteristic Uitenhage species; *Pisotrighonia salebrosa* van H. is a massive species of the group of the Scabrae distinctly reminiscent of the Uitenhage species *T. kraussi* Kitchin.

The occurrence of the Neocomian in Zululand is further suggested by the new collections of Lamellibranchs from the Pongola area. In addition to *T. obesa* (van H.), a new species belonging to the *T. v-scripta* group (*T. haughtoni*), and a large member of the group of the Scabrae strikingly like *T. kraussi* Kitchin, other characteristic southern Neocomian types are recorded. *T. hennigi* Lange is a very typical pseudo-quadrate *Trighonia*, first described from the *T. schwarzi*-Beds of the Tendaguru Formation in Tanganyika, the Neocomian age of which has been generally accepted (Kitchin, 1908, pp. 46-49; 1926, 1929), though Dietrich (1933, pp. 75-79) would correlate these beds with a succession ranging from Upper Valanginian to Lower Aptian; the species is also closely allied to two characteristic Uitenhage species, *T. herzogi* (Goldfuss) and *T. holubi* Kitchin, as well as to species in the Neocomian of South and Central America, and the Oomia Beds of Cutch. *Trighonia pongolensis* nov. is apparently very closely allied to *T. krenkeli* Lange from the *T. schwarzi*-Beds in Tanganyika. The massive radially costate *Cucullaeae*, collected on the Lombagwenya stream, belong to the group of which *Cucullaea kraussi* Tate from the Uitenhage Series is the type, and which has hitherto been regarded as confined to the southern Neocomian faunas, being reported also from the Neocomian of East Africa and of Madagascar, and from India.

The Zululand species referred to in the preceding paragraphs are closely allied to species belonging to a widespread southern bivalve fauna which Kitchin (1926, p. 467) regarded as probably entirely Valanginian. The association of members of this fauna with Aptian and even Albian Ammonites is, however, recorded above by Dr. Haughton for Northern Zululand, while in India the work of Spath (Geol. Mag., 1935) and Cox (Pal. Indica, 1935) has shown that this fauna survives the Neocomian there also.

1. *Lombagwenya Spruit*.—The whole of the succession on the Lombagwenya stream (L1-L14) carries Lamellibranchs of a distinctly Uitenhage aspect. This is based on the occurrence of the pseudo-quadrate *Trighonia hennigi* in L9, L12, and L14, and of *Cucullaea* spp. aff. *kraussi* in L9 and L12. The occurrence of *Panope gurgitis* in L1, L3, L7, L9, and L11 is not inconsistent with this comparison, since the species ranges from Neocomian to Albian in Europe. In a preliminary identification of species certain Albian or post-Albian

Lamellibranchs appeared to occur at these localities, but in each case the identification was based on doubtful material and no weight can therefore be attached to the record based thereon; *Cucullaea woodsi* from L12 was based on a single incomplete specimen very doubtfully referred to this species; *Aucellina gryphaeoides* (Upper Albian to Turonian) from L6 was based on three rather featureless shells which might belong elsewhere; *Exogyra conica* (Upper Albian and Cenomanian) from L8 was based on two very small specimens that might well belong to another species of the same genus; *Pholadomya vignesi* (Cenomanian) from L7 was based only on a small fragment; *Veniella etheridgei* from L3 was based on a poorly preserved juvenile shell that might belong to another species of *Veniella* or even an unrelated genus; *Neithea quadricostata* (Albian and Cenomanian) from L5 (Msinyene Pan) was based on a juvenile specimen referred only doubtfully to this species. *Lopha diluviana* is recorded from L3†, the record being based on two specimens which belong either to this species or at any rate a very similar form; it is significant that in Europe the species does not appear to occur before the Aptian.

2. *Myesa Spruit*.—The succession on the Myesa stream (M1–M3) could also be compared with the Uitenhage on the Lamellibranch evidence, on account of the occurrence in M1 of *Trigonia haughtoni* and *T. hennigi*, both belonging to groups characteristic of the southern Neocomian, and of the former species in M3. *T. obesa*, which occurs in M1, belongs to a group known previously only from the southern Neocomian, but the species occurs on the Mfongosi stream as high up as Z12, and is apparently associated with Albian Lamellibranchs in Z8, Z11, and Z12.

3. *Mfongosi Spruit and Pongola River*.—The sequence on the Mfongosi stream and the Pongola River below its junction with the Mfongosi appears on the Lamellibranch evidence alone to range from the Neocomian to the Albian, if not to the Cenomanian; the Senonian is absent, but whether the whole succession from the Neocomian to the Albian or Cenomanian is represented does not appear from the Lamellibranch evidence. The localities ZA, Z1–Z3 carry Lamellibranchs suggestive of the Neocomian, the estimate of age being based on the occurrence of *Trigonia haughtoni* and *T. hennigi* in ZA, *T. pongolensis* in Z2, and of *Cardium rogersi* in Z2 and Z3, the last-named species occurring also in association with *T. haughtoni* and *T. hennigi* in M1 on the Myesa.

The horizons represented by Z4–Z14 are not certain from the Lamellibranch evidence. The occurrence of *Trigonia obesa* in Z4,

Z5, Z8, and Z12, and of a large Scabroid *Trigonia* comparable with *T. kraussi* in Z8, is suggestive of a Neocomian age for these horizons, since these species belong to groups of *Trigonia* characteristic of southern Neocomian deposits.* On the other hand, a preliminary identification of species gave certain Albian species as occurring in Z6, Z8, Z9, Z11–Z14. Among the latter is *Cucullaea woodsi*, described by Newton from the Manuan Creek area, and said by du Toit (1926, p. 318) to come from the upper portion of the Manuan Creek (Albian). The record of *Glycymeris griesbachi* (Albian and Cenomanian at Manuan Creek, according to du Toit) from Z8 was based on a single and not very well preserved specimen, and may be incorrect. The record of *Exogyra conica* (Upper Albian and Cenomanian) from Z8 was based on one small shell, and it is possible that it belongs to another species. The record of *Neithea quadricostata* (Albian and Cenomanian) from Z9 was based on an extremely unsatisfactory specimen, an incomplete and juvenile shell. *Neithea quinquecostata*, recorded from Z13, is very long ranged, having been recorded from the Aptian to the Senonian. *Inoceramus concentricus*, a characteristic Upper Albian species in Europe, was apparently satisfactorily determined from Z6 and Z14, but in each case the record is based on one specimen. In determining the horizons of Z4–Z12 the only Lamellibranch evidence which appears to be of possible significance is the occurrence of *T. obesa* at several localities (Z4, Z5, Z8, and Z12), the presumed occurrence of the Albian species *I. concentricus* in Z6, and the fact that *C. woodsi*, which occurs in Z8, Z11, and Z12, occurs also in a typical Albian association in Z19. The horizons present at these localities must be determined on the evidence of the Ammonites.

The localities north of the Mfongosi and below its junction with the Pongola River (Z16–Z21) are, on the Lamellibranch evidence, either Albian or Albian and Cenomanian, no higher horizon being represented. The correlation is based on the occurrence of a number of species which occur in the Manuan Creek area, some of which occur in the Albian and Cenomanian of Europe and elsewhere. *Pholadomya vignesi* occurs in the Cenomanian in Syria, but is said by du Toit (1926, p. 318) to occur in the Albian of the Manuan Creek, while it makes its appearance in Z16 (7 typical specimens), and appears also in Z19–Z21. *Exogyra conica* (Upper Albian and Cenomanian) occurs in Z19 and Z20. *Neithea quadricostata* (Albian and Cenomanian) is represented by fine specimens in Z19 and Z20. *Inoceramus concentricus* (Upper Albian) occurs in Z19, and its variety

* But see p. 300.

subsulcatus in Z16, Z19, Z21. In addition to the above, several species occur which have been described from the Albian-Cenomanian succession on the Manuan Creek and the Umsinene River, *Veniella etheridgei* and the Gastropod *Turritella manuanensis* making their appearance in Z16.

4. *Mokatini*.—The species recorded from Z25, south-east of Mokatini and south of the Pongola River, include *Trigonia blanckenhorni*, *Trigonarca* cf. *ligeriensis*, *Veniella etheridgei*, and probably also *Exogyra conica* (one flat valve), which is very similar to the assemblage recorded by Newton (1909, p. 88) from the north end of False Bay (Zululand), probably Cenomanian in age.

Note on certain Lamellibranchs from the Uitenhage Series.—This opportunity is taken of publishing additional figures of certain Uitenhage species of Lamellibranchs described originally by Krauss (1850), Tate (1867), and Neumayr (1881), but which were not refigured by Kitchin (1908) in his monograph on the fauna of the Uitenhage Series, as well as figures of an adult individual of *Trigonia conocardiiformis*. Additional information with regard to these species is forthcoming, or additional figures are required. These species are referred to in the systematic descriptions of Zululand shells which follow, and only passing reference need be made here. The species concerned are as follows:—

Cucullaea kraussi Tate (see p. 305, Plate XLIV, fig. 2). Additional figures are necessary to show the finer radial ribbing present in addition to the coarse radial costae. The species becomes the type of the new sub-genus *Megacucullaea*.

Gervillia dentata Krauss (see p. 310, Plates LIII-LV), the original figures of Krauss are insufficient to show the form of the species.

Trigonia conocardiiformis (Krauss) (see p. 337, Plate XL, figs. 1-3); the species was well described by Kitchin, but only juvenile and half-grown specimens were figured. A fine adult shell (Alb. Mus. 738) is here figured for comparison with *T. obesa*.

"*Anoplomya*" *lutraria* Krauss (see p. 385, Plate L, figs. 2-4, 7, 10, 11); this species is probably in the synonymy of *Panope gurgitis*. Additional figures are given for comparison with shells from Northern Zululand.

5. DESCRIPTION OF THE SPECIES.

FAMILY ARCIDAE.

Genus CUCULLAEA Lamarck 1801.

Sub-genus *Cyphoxis* Rafinesque 1819.*Cucullaea (Cyphoxis) woodsi* R. B. Newton.

1909. *C. woodsi* Newton: Trans. Roy. Soc. S. Afr., vol. i, p. 31, pl. iv, figs. 4-9.

This species occupies a unique position in the South African faunas, and has been sufficiently well described by Newton. Its occurrence on the Mfongosi stream and neighbourhood is as follows: Z8 (2, typical), Z11 (3, doubtful), Z12 (1), Z19 (35, fine and very typical set). The species was described with a mixed Cretaceous fauna from the Manuan Creek in Zululand, but is said to be from the Albian at that locality (du Toit, 1926, p. 318). As is pointed out below, the typical Cretaceous *Cucullaeae* should be referred to *Cyphoxis* Rafinesque.

Cucullaea Lamarck 1801, *Idonearca* Conrad 1862, and *Cyphoxis* Rafinesque 1819.

According to Gardner (1916, p. 529) and Stewart (1930, p. 74) the genus *Cucullaea* was founded by Lamarck in 1801 (Syst. Anim. sans Vert., p. 116), and the genotype, subsequently designated by Children (Lam. Gen. Shells, 1823, p. 45), is the recent Oriental species *Cucullaea auriculifera* Lamarck, for which the earliest name appears to be *Arca concamerata* Martini, 1777. Stewart states that the Mesozoic species commonly included in *Cucullaea* not only have a much thicker shell than the genotype, but also have diagonal grooves on the ligamental area which are lacking in the latter. According to him it does not seem that the Mesozoic group can be regarded as more than a sub-genus.

The generic name *Idonearca* proposed by Conrad in 1862 (Pr. Ac. Nat. Sci. Philad., p. 289) for the Cretaceous species *C. tippiana* Conrad, has been widely used for the Mesozoic *Cucullaeae*. The type species is usually placed in the synonymy of *C. vulgaris* Morton (Gardner, 1916, p. 529, pl. xx, figs. 8, 9; pl. xxi, figs. 1, 2; Wade, 1926, p. 43,

pl. ix, figs. 3, 4, 6, 7), one of the most common Lamellibranchs in the Upper Cretaceous of the eastern United States. On the other hand, Gardner, Wade, and Dietrich (1933, p. 28) have sunk *Idonearca* in *Cucullaea*, though Gillet (1924, Lamell. Néocom., Mém. Soc. Géol. France) has maintained the distinction. The differences noted by Stewart, together with the fact that the Mesozoic type apparently failed to survive the Lower Eocene, seem sufficient to warrant the retention of a distinct sub-genus for the Mesozoic species.

Stewart (1930, p. 75) states that Pilsbry has found that the name *Cyphoxis* Rafinesque 1819 (Jr. de Physique, vol. 88, p. 427) is an earlier name for Cretaceous *Cucullaeae*, and has accordingly referred Gabb's species to the sub-genus *Cyphoxis*.

Sub-genus *Megacucullaea* sub-gen. nov.

Type.—*C. kraussi* Tate.

The large, massive, radially costate South African Neocomian species *Cucullaea kraussi* Tate appears to be sufficiently distinct from the recent *Cucullaea* and from *Cyphoxis* (= *Idonearca*) for it to be placed in a separate sub-genus. The species was originally described by Krauss (1850, p. 452, taf. 48, fig. 2) as *C. cancellata*, the name being later changed by Tate (1867, p. 161) to *C. kraussi* as the former name was preoccupied. The species was well described by Neumayr (1881, p. 275, taf. 2, fig. 2), who referred to its isolation as a species and to the difference between it and *Cucullaea* (*sensu stricto*), but the species, which is by no means rare in collections from the Sundays River Beds of the Uitenhage Series, does not appear to have been figured since in a palaeontological publication. According to Dietrich (1933, p. 28) the species was placed by Gillet (Lamell. Néocom., 1924) in the genus *Idonearca*, but in a "section spéciale" on account of its peculiar massiveness and strong ribs.

Similar forms have been recorded from East Africa (Lange, 1914, p. 223; Dietrich, 1933, p. 28) as *C. kraussi*, but these do not appear to have been figured. Kitchin (1908, p. 43) has mentioned the occurrence of fragments of a similar *Cucullaea* in the Oomia Beds in India, and Dietrich (*loc. cit.*) states that Gillet has recorded the species from Madagascar. Dietrich also states that *C. neuquensis* Weaver (1931, p. 186) from the Argentine belongs to the same group. The sub-genus appears to be a characteristic element of the southern Neocomian fauna, and is here recorded also from post-Neocomian beds in Zululand.

The genotype is characterised by the following salient features: Shell very large, presumably equivalve, more or less equilateral, roughly triangular in outline, very strongly inflated, longer than high. Shell substance very thick. Anterior and ventral margins rounded, forming a continuous broad curve, coarsely scalloped. Posterior margin relatively short, more or less straight, sloping steeply downwards, and meeting the ventral margin in a rounded postero-ventral angle. A strong, rounded posterior carina, separating a steep concave posterior area from the rest of the valve, persists from the umbo to the postero-ventral angle. Umbonal region broad, very prominent, more or less centrally placed; umbo very strongly incurved, free and projecting, at some distance from the hinge margin, showing very little forward curvature. Hinge line long, straight, a little shorter than the greatest length of the shell. Hinge very narrow except at the two ends, with numerous small transverse teeth for more than half of its length, the central teeth short and vertical, passing laterally into slightly longer oblique teeth; at each end there are three considerably larger teeth approximately parallel to the hinge margin, the upper two long, the lower shorter. Area very large, remarkably wide, triangular, concave; area with numerous (15-18) deeply incised ligament grooves, separated by smooth, flat interspaces and traversing the area more or less parallel to its upper margin. Interior of valves smooth, faintly undulate near the ventral border; muscle impressions large, the posterior a bit sunken but without a raised plate.

Shell surface ornamented with very strong radial costae, numerous radial riblets, and with growth lines. Between the posterior carina and the anterior slope there are several (7 or 8) very strong, relatively sharp costae, triangular in cross-section, separated by broad concave interspaces. In addition there may be a weaker rib in the broad space between the carina and the first of the costae, as well as 2 or 3 weaker ribs on the anterior slope; the posterior area has 2 or 3 weak ribs. Radial riblets very numerous, rounded, separated by rounded interspaces, varying very much in strength, present on all parts of the valve, but tending to be absent from the vicinity of the hinge margin; with full maturity the riblets die out before reaching the ventral border. Growth lines and growth lamellae throughout, tending to form a lattice with the riblets, and giving rise to notches on the crests of the costae.

The most striking characters of the sub-genus, which serve to distinguish it even at a glance from the living genotype of *Cucullaea*

and from *Cyphoxis* (= *Idonearca*), are the very large size, the extraordinary degree of inflation, the very wide area with very numerous grooves, and the prominent radial costae. The genotype of *Cucullaea* is said by Stewart (1930, p. 75) to be thin and without grooves on the area, and judging from Fischer (1887, p. 977, pl. xvii, fig. 14) is a smaller shell with numerous radial riblets, a ventral border very finely scalloped within, a relatively narrow area, a raised plate for the attachment of the posterior adductor muscle, and a less differentiated dentition with the teeth radially arranged. *C. kraussi* certainly cannot be included in *Cucullaea* (*sensu stricto*) in view of the differences above noted, the absence of the raised plate for the posterior adductor ("an essential character of *Cucullaea*"—Arkell, 1930, p. 309), the strongly developed costation and the ponderous form being of importance. The dentition is also different, for in *C. kraussi* the short vertical teeth at the centre of the hinge are transitional into longer oblique teeth which are directed laterally downwards, and there is an abrupt change when the horizontal teeth begin; in the genotype of *Cucullaea* the teeth are directed radially upwards, and the shorter central teeth pass gradually into the rather longer very oblique lateral teeth.

I am not acquainted with the genotype of *Cyphoxis*, but the species presumably has the same general features as the genotype of *Idonearca*, *C. vulgaris* Morton (*vide supra*). The latter is a very characteristic Cretaceous *Cucullaea* and is distinguished from *C. kraussi* in several important respects. In the first place *C. kraussi* is distinguished by its larger size, the great thickness of the shell substance, the extraordinary degree of inflation, the great prominence of the umbonal region, the great width of the area, and the very large number of ligament grooves. In the second place *C. kraussi* is distinguished by the very prominent radial costae which have no counterpart in *C. vulgaris*; the radial costae are present in addition to the much finer, more or less reticulate, ornament of radial riblets and concentric growth lines characteristic of *C. vulgaris* and other species; the costae are correlated with the scalloping of the ventral margin, which in *C. vulgaris* is smooth. In the third place the posterior adductor impression of *C. kraussi* is, according to Neumayr, without the raised plate or radial buttress which occurs in *C. vulgaris* and the *Cucullaeae* generally. In the fourth place *C. kraussi* is distinguished by the relatively smaller teeth, the central teeth being relatively shorter and more than twice as numerous as in *C. vulgaris*. In view of these striking differences the exclusion of *C. kraussi* from

Idonearca, where it was placed by Gillet, is imperative, and a new sub-generic name is proposed.

C. kraussi has not been adequately described or figured, and the opportunity is here taken of publishing an additional figure (Plate XLIV, fig. 2) and of emending the descriptions given by Krauss and Neumayr in the publications cited above. The species was founded by Krauss on a single incomplete left valve, and Neumayr's fine figures were based on a complete left valve, the only specimen in the Holub collection. The original specimen apparently showed no traces of radial riblets, for these were neither mentioned by Krauss nor depicted in the figure; the broad interspaces between the costae were said to be crossed by growth lines which, in groups of 4-8, gave rise to alternate raised bands and furrows, *i.e.* a concentric undulation of the valve surface, giving the surface a latticed appearance. Neumayr noted only in one place on his specimen a fine radial striation, which formed a lattice with the growth lines, which he merely described as strong and somewhat scaly. Well-preserved specimens show that radial riblets, numerous and rounded, are a characteristic feature of the greater part of the shell surface, and these have been described above and are here depicted on the accompanying figure; their absence or rarity in the earlier described specimens is presumably due to their condition of preservation. The concentric undulation of the surface is not usually as regular as depicted by Krauss, and becomes very indistinct towards the ventral border of nature shells.

Cucullaea (Megacucullaea) spp. indet.

(Plate XXXVII, figs. 1-3.)

The sub-genus is represented in the collection made by Dr. S. H. Haughton and Dr. A. W. Rogers by three very imperfect shells having a close general resemblance to *C. kraussi* Tate and undoubtedly closely allied to that species. The specimens, unfortunately, are too incomplete, weathered, or crushed for a satisfactory comparison. The occurrence of the sub-genus in Zululand is, however, of some interest.

The specimens were collected at two localities on the Lombagwenya tributary of the Pongola River, in both cases in association with *Trigonia (Steinmanella) hennigi* Lange: at L9 two fragments of the anterior part of a left valve; at L12 a complete but very weathered and crushed left valve, as well as another weathered left valve preserved partly as an internal cast.

The fragments from L9 are portions of a very large mature, highly inflated, very thick shell, showing a small portion of the area, the terminations of the anterior costae, and a broad marginal band with growth lines only. Finer radial ornament is not preserved, but the fragments could well be portions of a shell of *C. kraussi*. The area is traversed by very numerous parallel ridges and grooves resembling ligament grooves, but these have been produced by weathering, and traces of the more widely spaced ligament grooves are preserved, crossing the former obliquely.

The more complete shell from L12 is at first sight rather different from *C. kraussi* by reason of the fact that the umbonal region is more prominent and the apical angle much less than in that species. An examination shows, however, that the specimen has been badly crushed, so that the anterior slope has been considerably increased and the incurved tip of the umbo pressed down on to the area. To what extent the difference in form noted is original or due to crushing I could not satisfactorily determine. The specimen is badly weathered and not only shows no sign of fine radial ornament but only traces of the growth lines. In front of the posterior carina there are six prominent costae, as in *C. kraussi*, and these appear to have been of the same character as those of the Uitenhage species. On the posterior slope there are four finer radial ribs.

The second left valve from L12, though incomplete, seems to be distinct from *C. kraussi*. The specimen is weathered and the thick shell is preserved only in the anterior third and on the posterior slope, the central portion being in the condition of an internal cast. The cast shows faint, broad, radial undulations and the impression of a narrow, raised, internal rib, which proceeds almost vertically from the posterior side of the umbo for a distance of 30 mm. The general form is identical with that of a medium-sized *C. kraussi* and the posterior slope is similarly ornamented. The radial costae seen at the antero-ventral margin differ from those of *C. kraussi*, in being conspicuously broader; the two uppermost costae at the anterior end are narrow and raised as in *C. kraussi*, but the next three costae are broad and convex and carry on their summits a distinctly demarcated narrow rib or crest; in one case there is a trace of a subsidiary rib on the flank; these costae are followed by a smaller strong rib. The interspaces are more or less deeply U-shaped, are crossed by growth lines, and show traces of radial riblets. The difference in costation is so marked that a distinct species might well

be represented, but the specimen is too poor to be made the holotype of a new species.

Genus TRIGONARCA Conrad 1862

(= TRIGONOARCA Conrad 1867).

Trigonarca cf. *ligeriensis* (d'Orbigny).

1909. *T. ligeriensis* (d'Orb.): R. B. Newton, Trans. Roy. Soc. S. Afr., vol. i, p. 33, pl. iv, figs. 13-18.

Newton figured three specimens, referred to this typically Cenomanian species, from the north end of False Bay in Zululand, where it occurs with *Trigonia blanckenhorni* and *Exogyra conica*. A single imperfect specimen that resembles the above was found in the same association south of Mokatini, Z25.

The original spelling of the generic name is *Trigonarca* (fide Stephenson, 1923, p. 96), and for form *Trigonoarca* used by Woods (1906, p. 288) and Rennie (1930, pp. 169, 240) for South African species is incorrect.

Genus GLYCYMERIS da Costa 1778.

Glycymeris cf. *griesbachi* R. B. Newton.

1909. *G. griesbachi* Newton: Trans. Roy. Soc. S. Afr., vol. i, p. 36, pl. iii, figs. 13-17 (*non G. griesbachi* Etheridge, Saxicavidae).

The type set is from the north end of False Bay in Zululand, where the species occurs with *Exogyra conica* (J. Sow.). The occurrence is as follows, though in every case the shells are imperfectly preserved and the identification is somewhat uncertain: Mfongosi stream Z8 (1); Pongola River below junction with Mfongosi, Z19 (4).

FAMILY ISOGNOMONIDAE (=PERNIDAE).

Genus GERVILLIA Defrance 1820.

Gervillia dentata Krauss.

(Pl. LI, figs. 1, 2; Pl. LII, figs. 1-3.)

(Pls. LIII-LV, from the Uitenhage Series.)

1850. *G. dentata* Krauss: Untere Kreide Kaplandes, p. 458, pl. 1, figs. 1 a-c.

- ?1907. *G. dentata* Krauss: Etheridge, Rep. Geol. Natal, 3, p. 73, pl. i, figs. 13-15.
1908. *G. dentata* Krauss: Kitchin, Ann. S. Afr. Mus., vol. vii, p. 36.
1909. *G. sublanceolata* (d'Orb.): Newton, Trans. Roy. Soc. S. Afr., vol. i, p. 48, pl. iii, figs. 7-10.

Material.—Large *Gervilliae* similar to *G. dentata* Krauss from the Uitenhage formation are of frequent occurrence in the Cretaceous of Northern Zululand. Dr. S. H. Haughton and Dr. A. W. Rogers collected specimens from the following horizons along the Mfongosi stream and neighbourhood, the number of examples being indicated in brackets: Z3 (1), Z4 (3), Z6 (3), Z7 (7), Z8 (10), Z10 (2), Z16 (1), Z19 (4). Mr. H. F. Frommurze collected a number of specimens at the same locality: S.A.M. 10802-10807; whilst Mr. J. S. Hutt collected the specimens numbered T.M. 1661-1666, 1668, 1670-1, 1673, 1678-9, 1682, 1684, 1685, 1687, 1911.*

Remarks.—Krauss figured three examples of this species from the Sundays River Beds of the Uitenhage Series, but the species has not been described by subsequent authors, although examples are not infrequent in collections. The species has a close general resemblance to the European *G. sublanceolata* (d'Orb.) and *G. anceps* Deshayes. R. B. Newton (1909, p. 48, pl. iii, figs. 7-10) described some rather imperfect shells from the north end of False Bay in Zululand, associated with ammonites identified as Cenomanian by Crick (1907), as *G. sublanceolata*, and stated that *G. dentata* is distinguished by its more convex and more robust valves and by the fact that the antero-ventral margin is not concave. With a representative set of *G. dentata* before me (see Plates LIII-LV), including some examples from the cliffs opposite Redhouse on the Zwartkops River (the vicinity of the locality from which came the type specimens), I have found great difficulty in drawing any distinction between that species and the so-called *G. sublanceolata* from False Bay, and it may well be that these, together with the new specimens from the Mfongosi, belong to *G. dentata*.

The figures given by Krauss show the anterior part of the ventral margin very slightly convex, and this point has been used by Newton in drawing a distinction between *G. dentata* and *G. sublanceolata*, though the distinction is of no great magnitude. In fact, the anterior part of the ventral margin is very nearly straight in all the forms here

* The species was also recorded by Dr. S. H. Haughton at the following localities: Z5, L3, L12, L4, L6, L1.

being considered. In the specimens from the Uitenhage Series before me the anterior part of the ventral margin is either very nearly straight or quite distinctly but gently concave, the latter condition being by no means uncommon. In this respect some of the Uitenhage shells agree exactly with the forms figured by Newton from False Bay, as well as with Woods's figures of *G. sublanceolata* from the Lower and Upper Greensands (1905, p. 74, pl. x, figs. 14-16; pl. xi, fig. 1; text-figs. 7 a-c, 8). A very gentle concavity is usually discernible among the Mfongosi specimens also. Since it can scarcely be doubted that the specimens before me from Redhouse are examples of Krauss's species, it is clear that the distinction based on this feature must be dropped.

Newton further states that *G. dentata* is of greater thickness, more robust, and more convex than *G. sublanceolata*. There is little in the figures given by Krauss to warrant this statement, though it would appear that the shell substance is by no means thin in the former. The shells before me show quite a considerable range of variation in respect to massiveness, including both somewhat convex and more flattened forms; the shell substance in one instance is as much as 13 mm. thick in the middle part, though usually very considerably less, so that the valves can in some instances be described as relatively thin.

The shells figured by Newton from False Bay were found in association with *Exogyra conica* (J. Sow.), and with *Glycimeris griesbachi* Newton (Newton, 1909, p. 88), and it is significant that the same association is encountered in Z8 and Z19 on the Mfongosi, though *Gervilliae* extend down into beds of possible Neocomian age at that locality. The specimens from the Mfongosi are in general agreement with those figured by Newton, and must be the same species. The former have been carefully compared with examples of *G. dentata*, and the comparison has failed to reveal any general distinction, though in one or two instances it was noticed that the apical angle was somewhat larger than is the case with either the Uitenhage or Lower Greensand shells, and consequently the posterior wing was relatively broader; this latter condition is, however, by no means general, and in the majority of specimens no distinction can be drawn in this respect.

A number of specimens from Uitenhage and the Mfongosi would appear to be scarcely distinguishable from the specimens of *G. sublanceolata* figured by Woods, the agreement extending to the details of form used in distinguishing the species from its European allies,

the slightly concave antero-ventral margin, the central position of the line of greatest convexity, and the nearly straight posterior margin of the posterior wing, and extending also to the nature and number of the ligament pits and to the dentition. It should be pointed out, however, that *G. sublanceolata* is apparently very closely allied to certain other European species, in particular to *G. anceps* Deshayes, with which it has frequently been confused, and that a satisfactory comparison with *G. dentata* cannot be made without an actual examination of representative sets of these European species.

Only in one particular does there seem to be a constant point of difference between the Uitenhage shells before me and those from Atherfield figured by Woods. In the latter the left valve is distinguished from the right by having a demarcated, antero-ventral area below the pointed umbo; this area is narrow, elongate, and bounded by a linear depression, its length less than one-third of the total length of the valve. In the Uitenhage shells the same distinction between the valves is evident, but the antero-ventral area in the left valve may be of considerable length and width, extending backwards for more than one-third of the total length of the valve, in one instance nearly one-half of the length of the valve. The length and width of this demarcated area varies considerably, though in every instance the contrast with the much smaller feature in the Atherfield shells is noteworthy. The area is convex and is distinguished only in that it is bounded by an impressed line, and in that there is a discrepancy between the growth lines of area and flank. Newton does not mention the feature in the case of the False Bay shells, and the figured left valve was probably too poorly preserved to show it. The shells from the Mfongosi are in general somewhat weathered, and the feature is not easily discerned on that account, though in one or two instances it is apparently indicated, the area in question being relatively wide and persisting for about one-third of the total length of the shell, the shell exactly matching a similar valve from the Uitenhage Series.

The distinctions drawn by Newton between *G. dentata* and *G. sublanceolata* have been shown to be without substance, and if a distinction is to be maintained between these species the difference in the size of the demarcated antero-ventral area will have to be relied on. In every other respect the species would appear to be very similar, and it is significant that Newton, who presumably was able to compare directly the shells from False Bay and Atherfield, did not hesitate to identify the False Bay shells with *G. sublanceolata*. Certain specimens from the Uitenhage Series have this antero-ventral area

so distinctly larger than in the shells from Atherfield, that a specific distinction might well be maintained in spite of general agreement in other respects. The Mfongosi shells appear to agree with certain examples of *G. dentata* in respect to this feature, and to them and the shells from False Bay the name *G. dentata* might well be applied. It must be admitted, however, that the state of preservation of the Zululand material leaves much to be desired and the comparison is not ultimately satisfactory.

The specimens figured by Etheridge (*loc. cit.*) from the Umsinene River in Zululand, though presumably the same species as the other Zululand shells, are too imperfect for fine distinctions to be drawn.

Genus ISOGNOMON Solander 1786

(= PERNA Bruguière 1789).

Isogonomon sp.

Rather imperfect specimens of a large species, sometimes showing the ligament pits, were recovered from the following localities: Lombagwenya stream, L3† (1); Mfongosi stream, Z7 (1), Z8 (1), Z14 (2).

Genus INOCERAMUS Parkinson 1819.

Inoceramus concentricus Parkinson.

1910. *I. concentricus* Park.: Woods, Cret. Lam. England, vol. ii, p. 265, pls. xlv-xlvii.
 1930. *I. concentricus* Park.: Heinz, Ueber Inoceramen Südafrika, Comp. Rendu, 15th Int. Geol. Congress, vol. ii, p. 683, fig. 1.

Heinz collected a single specimen of this well-known species at the Manuan Creek (Munyuana) from an horizon identified by van Hoepen as Albian. According to Heinz the species is a key-fossil of the Upper Gault in Europe. What is almost certainly the same species was collected on the Mfongosi stream and neighbourhood: Z6 (1), Z14 (1), Z19 (1).

Inoceramus concentricus Park. var. *subsulcatus* Wiltshire.

1910. *I. concentricus* var. *subsulcatus* Wilts.: Woods, Cret. Lam. England, vol. ii, p. 268; pl. xlvii, figs. 3-14.

A radially sulcate *Inoceramus*, which appears to be identical with the form described by Woods, is sparingly represented in the collection from the neighbourhood of the Mfongosi stream: Z16 (2), Z19 (1), Z21 (1). The form has not hitherto been recorded from South Africa, though in the collection of the Transvaal Museum there is a well-preserved specimen (T.M. 1284) in an Albian fauna from Catuane, a locality some thirty miles distant on the southern border of Portuguese East Africa.

FAMILY PTERIIDAE.

Genus *PSEUDAVICULA* R. Etheridge, fil., 1892.

Pseudavicula? *africana* R. Etheridge, fil.

1907. *Pseudavicula?* *africana* R. Eth., fil.: 3rd Rep. Geol. Natal, p. 71, pl. xi, figs. 8-11.

Small shells similar to those named by Etheridge from the Umsinene River in Zululand, and referred by him very doubtfully to *Pseudavicula*, are very abundant at certain horizons on the Mfongosi, mostly in an exfoliated condition; these were collected as follows: Z4 (abundant), Z5 (4), Z11 (5), Z13 (several). The same species was also collected at Z24 (abundant) south of Mokatini.

FAMILY MYALINIDAE.

Genus *AUCELLINA* Pompeckj 1901.

Aucellina gryphaeoides (J. de C. Sowerby)?.

1905. *Aucellina gryphaeoides* (J. de C. Sow.): Woods, Cret. Lam. England, vol. ii, p. 72, pl. x, figs. 6-13.

In England this species ranges from Upper Albian to the top of the Cenomanian. Shells referred doubtfully to the species were collected on the Lombagwenya stream at L6 (3). At Catuane on the Zululand-Portuguese East African border the species is present in an Albian fauna preserved in the Transvaal Museum, some of the specimens being very finely preserved (10 specimens, T.M. 1257, 1258, 1265-7, 1295).

FAMILY OSTREIDAE.

Genus EXOGYRA Say 1820.

Exogyra conica (J. Sowerby).

1909. *Exogyra conica* (J. Sow.): R. B. Newton, Trans. Roy. Soc. S. Afr., vol. i, p. 51, pl. xi, figs. 8-10.

1912. *Exogyra conica* (J. Sow.): Woods, Cret. Lam. England, vol. ii, p. 407, figs. 215-242.

Newton figured specimens from the north end of False Bay and from the Manuan Creek in Zululand. The species is said to be Upper Albian and Cenomanian. In the present collections there are examples from the following: Lombagwenya stream, L8 (2, small?); Mfongosi stream, Z8 (1, small?); Pongola River below junction with Mfongosi, Z19 (15, fine set), Z20 (2); south of Mokatini, Z25 (1, flat or right valve, presumably the same species).

The species was also recorded by Dr. S. H. Haughton at localities Z16 and L6.

Genus LOPHA Bolten 1798

(= ALECTRYONIA Fischer de Waldheim 1807).

Lopha diluviana (Linn.).

1912. *Ostrea diluviana* Linn. Woods: Cret. Lam. England, vol. ii, p. 342, figs. 98-138.

This species, which in Europe ranges from the Aptian to the Lower Chalk, is apparently represented in the collections from L3† and Z19. The specimens from L3† (2) on the Lombagwenya stream are of the characteristic elongate type and agree very closely with the English examples figured by Woods. Those from Z19 (4) on the Pongola River below its junction with the Mfongosi stream are short and coarse ribbed, and are referred somewhat doubtfully to the species; they are not unlike *Ostrea milletiana* d'Orbigny from the Gault, a species included in the synonymy of *O. diluviana* by Woods.

FAMILY TRIGONIIDAE.

Genus TRIGONIA (Bruguière 1789) Lamarck 1799.

Genotype *T. sulcata* (Hermann, § Costatae).

During the past decade a number of authors (Deecke, 1925; van Hoepen, 1929; Crickmay, 1930, 1930 a; Marwick, 1932; Dietrich,

1933) have proposed new generic or sub-generic terms for species of *Trigonia* from Jurassic and Cretaceous formations. Several of these are founded on or are applicable to the species described below. In view of the divergent views recently expressed as to the genotype of *Trigonia*, and in view also of the fact that a considerable number of genera, grouped in four sub-families, were proposed for Zululand species by van Hoepen (1929), and the present writer's preference for accepting these terms as of not more than sub-generic value, a general statement of his position will not be out of place.

The Genotype of Trigonia.—The genus was founded by Bruguière (1789, *Encycl. Méth. Vers*, vol. i, p. xiv) with short diagnosis but without mention of species by name, without figures or references. His diagnosis reads: "Coquille triangulaire inéquilatérale, charnière composée de deux grosses dents plats, très saillantes et sillonnées des deux côtés." According to Article 25 *a** of the International Rules of Nomenclature this is sufficient to found the genus if the author has applied the principles of binary nomenclature, which Bruguière certainly has done elsewhere in the same volume. Such a case appears to be covered by Opinion 46,† the last part of which reads: "If it is not evident from the original publication of the genus how many or what species are involved, the genus contains all the species of the world which would come under the generic description as originally published, and the first species published in connection with the genus becomes *ipso facto* the type." From this it would follow that *Trigonia* Bruguière 1789 is valid, and indeed the validity has seldom been questioned. The Rules are ambiguous and the various Opinions contradictory, however, since it might be held that the whole spirit of Article 30 (designation of type species) requires the genus to be accompanied by a *named* species; ‡ if this view is adopted then *Trigonia* would have to be cited from the earliest reference of a named species to the genus.

The name appeared again in 1797 at the top of Plates 237 and 238 § of the *Tabl. Encycl. Méth. Vers*, on which unnamed species of *Trigonia* were figured by Bruguière. Plate 237 consists entirely of shells which we should refer to *Trigonia* (*sensu lato*), but Plate 238

* IXe Congrès Internat. Zool. à Monaco (Rennes, 1914), p. 901.

† *Ibid.*, p. 914.

‡ I am indebted to Dr. K. H. Barnard for pointing this out to me.

§ Stewart (1930, p. 88) and others have failed to mention that the name *Trigonia* heads two plates, and we are indebted to Crickmay (1932, p. 446) for pointing out that the name appears on Plate 238 as well as on Plate 237.

includes in figs. 3 *a, b*, one species which we should refer to *Lima* (*Plagiostoma*) and which would not fall under the diagnosis given by Bruguière in 1789. It may be doubted whether species figured under a generic name but not named specifically have any claim to be considered as genosyntypes to the exclusion of all other species. In the present instance two courses have to be taken into account: (1) the genosyntypes are the unnamed species figured on Plates 237 and 238 of Tabl. Encycl. Méth. Vers, Bruguière 1797, and either the first specific name to be applied to any of these figures becomes the type by monotypy, or it is competent for a subsequent author to designate a genotype from among the several specific names applied to these figures in the interim; (2) the unnamed species figured on Plates 237 and 238 are not necessarily the genosyntypes, and since it is competent for a subsequent author to refer to the genus any named species which would fall under the diagnosis given by Bruguière 1789, the genotype would then be either the first-named species so referred or among the several named species so referred.

Stewart (1930, p. 88) has adopted the former course, for he rejects *T. pectinata* Lam. on the grounds that it is not available, though he erroneously restricts the genosyntypes to the figures on the first of the two plates. The figures on Plate 237 were later given names by Lamarck, and one of these has usually been cited as genotype. The names given were: * *T. nodulosa* Lam. for fig. 4 in 1801 (Syst. Anim. sans Vert., p. 117); and in 1819 (Hist. Nat. Anim. sans Vert., vol. vi, pp. 63-64) *T. scabra* for fig. 1, *T. nodulosa* for fig. 2, *T. navis* for fig. 3, and *T. aspera* for fig. 4; of the latter *T. nodulosa* Lam. 1819 is invalid and *T. aspera* is a synonym of *T. nodulosa* Lam. 1801. It has usually been stated † that *T. nodulosa* Lam. 1801 is the first specific name to be coupled with that of the genus and that according to Opinion 46 (quoted above) this species is *ipso facto* the type. But if it be held that all the unnamed species of Bruguière 1797 are available for subsequent type designation, then it does not follow that the naming of one of them in 1801 excludes the other species as possible types, since it has been held (Opinions 79 and 81) that rigidly construed, Lamarck's 1801 Syst. Anim. sans Vert. is not to be accepted as designation of type species. Stewart (1930, pp. 88-90), who has recently gone very fully into the matter, has accepted the latter position, but has shown that the first valid designation (on the assumption that the genosyntypes are the unnamed species

* Information published by Stewart (1930, p. 88).

† But *vide infra*.

figured by Bruguière 1797) is that of Gray (Proc. Zool. Soc. Lond., 1847, p. 197) who cited *Trigonia* as of Lamarck 1801, so that *T. nodulosa* became the type by monotypy on Gray's interpretation.

It may well be doubted whether specifically unnamed forms can be accepted as genosyntypes, though the Rules and Opinions are not clear on this point. Opinion 35 states that "In determining the type of a genus, the selection must be confined to species included under the generic name in question at the time of its original publication, regardless of the fact whether they were named binomially or not," and, further, Article 30 states *inter alia* that species must be *excluded* from consideration in determining the types of genera "that were not included under the generic name at the time of its original publication." Nomenclature can know nothing of a species unless and until it has a specific name, and where, as in this instance, no named species were included under the generic name at the time of its original publication we must fall back on the first-named species published in connection with the genus. Unnamed figures under a generic title cannot be regarded as a proper indication of species, though the figures of Bruguière 1797 serve to clarify the brief diagnosis of Bruguière 1789. The whole spirit of Article 30 and Opinion 35 is against accepting a genus proposed without a proper indication of species, and Article 30 must have precedence over Opinion 46 which would allow the genus ("If it is not evident how many or what species are involved, the genus contains all the species of the world which would come under the generic description"). The safest course to adopt in the present instance, and the one most in accord with the spirit of Article 30, is to quote the genus as of the first author to indicate a species, with Bruguière 1789 in brackets, thereby giving recognition to the coining of the generic name by the earlier author; assuming for the moment that the earliest use of *Trigonia* with indication of species is Lamarck 1801 (Syst. Anim. sans Vert.), the genus should be quoted "*Trigonia* (Bruguière 1789) Lamarck 1801, genotype *T. nodulosa* Lamarck 1801, type by monotypy." This point of view has been adopted by Marwick (1932, p. 506), who has pointed out that biologists are not unanimous in their treatment of genera based on figures alone, without a specific name, at the time of publication, and has accordingly suggested that the simplest and best course is to treat a genus as not valid until it is published along with a specific name that can be identified. He is inclined to quote *Trigonia* as of Lamarck 1801, unless the uncertainty expressed by certain authors as to the identity of

T. nodulosa Lam. 1801 necessitates falling back on the next earliest reference, which is *Trigonia* Lam. 1804 (Ann. Mus. Nat. Hist., vol. iv, p. 355) with monotype *T. margaritacea* Lam. 1804.

It would appear, then, that unless an earlier reference than Lamarck 1801 can be found, the genotype of *Trigonia* must be *T. nodulosa* Lamarck 1801, whether the genus be quoted as of Bruguière 1789 or Lamarck 1801, and in the former case whether the genotype was fixed by the naming of a species by Lamarck in 1801 or by the subsequent designation by Gray in 1847. This species has indeed been very generally regarded as the type, e.g. by Fischer (1887, p. 994) and Stewart (1930, p. 89), while Cossmann (1912, p. 62) and Marwick (1932, p. 506) have questioned the validity only on the grounds that the species was not well established, and Crickmay (1932, p. 446) admits that he long regarded the species as "monotype."

It follows from the above argument that Children (Lamarck's Gen. Shells, 1823, p. 48) and Stoliczka (1871, p. 310) were in error in accepting the living species *T. margaritacea* Lam. 1804 (= *T. pectinata* Lam. 1819) as genotype. This species can only become the genotype of *Trigonia* if both *Trigonia* Bruguière and *Trigonia* Lamarck 1801 are regarded as not valid, in which case *Trigonia* Lamarck 1804 would have to be accepted, being the next earliest reference. This would only arise if *T. nodulosa* Lam. 1801 were regarded as indeterminable, as Marwick (1932, p. 506) has put forward as a possibility, following Cossmann (1912). The figure on which *T. nodulosa* Lam. 1801 was based is by no means bad, and more recently the original specimen of *T. nodulosa* Lam. 1819 has been figured by Favre (1914, Cat. Illus. Coll. Lam., Mus. d'Hist. Nat. Genève, pl. 35, fig. 253, a, b); the reference is given by Stewart (1930, p. 89), who states that the figures do not differ much from the original figure of *T. nodulosa* Lam. 1801 and that it seems probable that they represent, if not the same species, closely related forms. The species *T. nodulosa* Lam. 1801 is a delicately sculptured member of the Clavellatae, and even if the lectotype cannot with absolute certainty be identified with *T. herberti* Bigot or any other species, its affinities can be expressed within such narrow limits that there could be no doubt as to the meaning of *Trigonia* (*sensu stricto*) by adopting the species as genotype. Marwick (1932, p. 506) has pointed out that the selection of an allied species, *T. clavellata* Sowerby, as neogenotype by Cossmann (1912, p. 62) is quite invalid, and the same opinion is presumably held by Stewart and Crickmay.

We are indebted to Crickmay (1932, p. 446) for bringing to light

an earlier reference than Lamarck 1801, a reference that has apparently been entirely overlooked by previous investigators, and which has necessitated a re-examination of the whole problem. In his *Prodrome d'une nouvelle classification des Coquilles* (Mém. Soc. Hist. nat. Paris, 1799), on pp. 86, 87, Lamarck gives a short diagnosis of *Trigonia*, followed by two references, one to certain named species figured by Hermann in 1781. The diagnosis reads as follows: "*Trigonie. Trigonia. Coq. inéquilatérale, subtrigone; charnière à deux grosses dents plates, divergentes, et sillonnées transversalement,*" and is followed by "*Encycl. t. 237; Naturforsch, 15e livraison, t. iv.*" The first reference is of course to the first plate of Bruguière 1797, and the second has been identified by Crickmay with a plate accompanying a paper by Hermann (Brief über einige Petrefacten, Der Naturforscher, Bd. 15, t. iv, Hall, 1781). On that plate appear 16 figures of several species of Lamellibranchs bearing valid specific names, all *Trigoniae*, except figure 1, which appears to be a *Pholadomya*. The *Trigoniae* (figs. 2-16) are grouped in four species under the generic title "*Venus oder Donax,*" viz. *sulcata*, *tuberculata*, *nodosa*, and *dubia*.* This would appear to be the earliest reference of named species to the genus *Trigonia*, and *T. nodulosa* Lam. 1801 would only be the genotype if we accept the contention that the genosyntypes must be chosen from among the unnamed figures of Bruguière 1797. Two courses are open on the available data—(1) to accept Bruguière 1797 as fixing the genosyntypes, and (2) to accept Lamarck 1799 as fixing the genosyntypes on the ground that it contains the earliest reference to a species by name; the first course would lead to accepting as genotype a Clavellate *Trigonia*, as outlined above; the second course would lead to accepting as genotype a Costate *Trigonia*, *T. sulcata* (Hermann), type by subsequent designation (Crickmay, 1932). The ambiguities and contradictions in the International Code make it difficult to come to a decision on this point, but it would seem, from the arguments set forth above, that the second course is preferable, and the writer accordingly

* I am indebted to L. R. Cox for looking up the references Lamarck 1799 and Hermann 1781 at the British Museum. The figures on Hermann's pl. iv are named as follows:—

Fig. 1. *Cardium tortuosum*.

Figs. 2-4, 9, 10. *Venus oder Donax sulcata*.

Figs. 5, 8. *Venus oder Donax tuberculata*.

Figs. 6, 7, 15, 16. *Venus oder Donax nodosa*.

Figs. 11, 12. *Venus oder Donax dubia*.

Figs. 13, 14. *Venus oder Donax zwischen sulcata und dubia*.

accepts *T. sulcata* (Hermann) as genotype of *Trigonia* (Bruguière 1789) Lamarck 1799. The original figures of the lectotype of this species, a fine representative of the Costatae, have been reproduced by Crickmay (1932, pl. i, figs. 1, 2); these correspond to Hermann's figures 4 and 3 respectively, two views of the same shell.

The writer is not, however, in agreement with the arguments set forth at some length by Crickmay (1932, pp. 447-451) in favour of accepting Hermann's species as genosyntypes, even though the arguments lead to the same result. A fairly clear case seems to have been made out above for accepting these species by reason of priority of reference to the genus, assuming that unnamed figures are not admissible. Crickmay raises two objections against the customary acceptance of *T. nodulosa* Lamarck 1801 (or of *T. margaritacea*) as genotype. The first objection, that the species do not conform strictly to the original generic diagnosis in that they have ovate rather than triangular shells, can scarcely be taken seriously, depending as it does on the use of the word "triangular" in this connection. The older authors apply the terms triangular and trigonal to the majority of the *Trigoniae*, and even if the term is used in a more exact sense it can be used for a considerable range of species in the genus, including many representatives of the Clavellatae, as can readily be seen, *e.g.* by inspecting the plates of Lycett's monograph. Indeed, in many species of Clavellatae the shape is as markedly triangular as in the majority of the Costatae, and in several cases paired species from the two groups can scarcely be distinguished in outline. There are no grounds whatever for the statement that only the Costatae have triangular shells, and *T. nodulosa* might well have been described as triangular by many authors. It does not follow, therefore, that it is probable that Bruguière had the Costatae particularly in mind when founding the genus, and that therefore this group ought to be regarded as typical.

The second objection was raised against the custom permitted by Opinion 46 of the International Code "of genotype selection literally from among *all the species of the world*," in the case of a genus published without species. The restriction suggested by him is novel, but can scarcely be maintained. "It is impossible for a species unknown to the author of the genus to be in any real sense the genotype. Only species named by the time the genus name appeared can possibly have served an author for his conception of his genus. Such previous species are the only concrete things on the basis of which a genus published without species can be known in binomial nomenclature

until species are joined to it. It ought to make no difference that these previous species are not coupled with the genus name until later; they may be *correlated* with it by their agreement with the generic diagnosis. Among them only a genotype ought to be sought." He then proceeds to show that the species of "*Venus* oder *Donax*," published by Hermann in 1781, fall under the diagnosis of *Trigonia* published by Bruguière in 1789, and accepting them as being among the possible genosyntypes, designates one of them as genotype. The argument seems to be based on the assumption that the genotype must be a species known to the author of the genus, but one might ask what guarantee there is that Bruguière was aware of or had particularly in mind Hermann's species when he founded *Trigonia*; it is indeed conceivable that Bruguière had in mind only certain specimens in the collections accessible to him, of unpublished species, and was unaware of the fact that certain previously published species would fall under his generic diagnosis. The essential point in limiting the choice of genotypes is the fact of reference of species by the author at the time of original publication of the generic name; Article 30 and Opinion 35 are quite clear on this point. Article 25 a and Opinion 46 apparently allow a genus to be treated as valid when it is proposed without species, but it may be doubted whether any real knowledge of the genus can be obtained until a subsequent author associates named species with the generic name, and if that is so the subsequent author should be regarded as the real author of the genus.

Crickmay's proposal brings in another difficulty which was not considered by him; if, in a case of this kind, the genotype is among the species described previously under other generic names, the usual priority rules should apply, and the genotype would have to be the earliest or at least among the earliest of such species. It may be doubted whether the species of Hermann 1781 are the earliest species of what we now call *Trigonia*; there may be several earlier species which have not been recognised for what they are, either because of the rarity of the publication in which they appear or because of some doubt as to their agreement with the original generic diagnosis. It would be possible for an author to unearth, successively, older species, some possibly of very doubtful affinities, which in his opinion agree with the original generic diagnosis, and to designate each in turn as genotype—surely a *reductio ad absurdum* !

Crickmay (1932, p. 449) has sought to strengthen his conclusions by stating that the species of Hermann 1781 were reproduced in

Bruguière's plates of 1797. The writer is indebted to Mr. L. R. Cox for the statement that Bruguière's figures are absolutely different from those of Hermann, and that there can be no question of their being copies. The identification of figures on Bruguière's plates with Hermann's species is merely a statement of opinion, and it would seem from a comparison of the figures reproduced by him that he is probably incorrect in some instances. For example, on pl. xi, figures 1 and 2 are said to be copies of Bruguière; pl. cccxxviii, figs. 1 *a*, 1 *b*, which on p. 449, footnote, are said to be the equivalent of Hermann's *sulcata*; it may be doubted whether these figures represent the same species as the figures of the lectotype of *T. sulcata* reproduced on Plate I.

Synonyms of Trigonía sensu stricto.—In 1823 Sowerby (Min. Conch., vol. v, p. 40) substituted the name *Lyridon* (emended *Lyriodon* Bronn) for *Trigonía* on the grounds that *Trigonía* had previously been used for a plant. Since this does not constitute a case of pre-occupation under the existing rules, *Lyridon* is a strict synonym of *Trigonía*, as has been pointed out by Cossmann (1912, p. 62) and Stewart (1930, pp. 88–90). *Lyridon*, and its emendations *Lyriodon* and *Liriodon* are therefore not available for use for the Costatae as has been done by Rollier (Mém. Soc. Pal. Suisse, 1912, vol. xxxviii, p. 65), Deecke (1925, p. 68), Dietrich (1933, p. 32), and others.

Stewart (*loc. cit.*) has pointed out that *Lyrodon* Goldfuss is virtually in the same category as these other emendations, but might be revived, as Goldfuss did not actually say he was renaming *Trigonía*. Stewart accordingly designated as type the Clavellate *T. aspera* Lamarck, which is synonymous with *T. nodulosa* Lam. 1801, in order to make *Lyrodon* Goldfuss an objective synonym of *Trigonía*; but if *T. sulcata* (Hermann) is accepted as genotype of *Trigonía* (following Crickmay 1932), then *Lyrodon* might possibly be revived for the Clavellatae, for it would have priority over *Myophorella* Bayle. But Goldfuss certainly used the term as an objective synonym of *Trigonía* even if he did not explicitly state so, and was clearly following Sowerby and Bronn, hence the term must be a strict synonym of *Trigonía*.

Myophorella Bayle 1878 (Explic. Carte Géol. France, Foss. Princ. des Terr., vol. iv, pl. cxx) was based on two figured species, *M. nodulosa* (Lam.) and *M. muricata* (Roemer), both Clavellatae. The genus was stated to be a synonym of *Trigonía* by Cossmann (1912, p. 63) *ex eodem typo*, which seems to imply the designation of *M. nodulosa* (Lam.) Bayle as genotype. If *T. nodulosa* Lam. 1801 is genotype

of *Trigonia* then *Myophorella* becomes a synonym even if there is doubt as to the identity of the type species. On the other hand, with *T. sulcata* as genotype of *Trigonia* (Costatae), *Myophorella* is available for the Clavellatae with *T. nodulosa* (Bayle) non Lamarck as type (Crickmay, 1932, p. 458).

Classification of the Trigonias.—Until comparatively recently there has been little departure from the position taken up by Agassiz as long ago as 1840 as regards the classification of the *Trigoninae*, and it has been customary to refer the *Trigoninae* to one huge genus without sub-division on a Linnaean basis. Agassiz (1840, pp. 7–10) recognised eight groups of species, to which French names were given and whose “types” were in most cases designated, and these groups were believed to be more or less natural. Lycett (1872–1879) added a ninth group and translated the group-names into Latin plurals, while subsequent authors have admitted additional groups, by sub-division or otherwise, but without seriously modifying the original scheme.

The necessity for smaller units has been pointed out by several recent workers, but it is interesting to compare the views of Lycett and others on this matter. Lycett (*ibid.*, p. 217) had been tempted to sub-divide the genus into a number of distinct genera, but the results of his observations led to the perception of a general resemblance between the several groups of species in features of sufficient importance to induce him to regard them as forming part of one great whole. Cossmann (1912, pp. 81–84) in his essay on the evolution of the *Trigoninae* was impressed by an essential unity among the Mesozoic members of the genus, and after pointing out the important structural differences between these and the post-Cretaceous Australasian species (Agassiz's Pectinatae, Cossmann's genera *Eotrigonia* and *Neotrigonia*), was led to remark “tous les . . . groupes présentent des transitions graduelles d'un groupe à l'autre, ce qui démontre l'unité du système adopté par Agassiz” (*ibid.*, p. 62).

On the other hand, few would agree that the accepted groups are as artificial and indistinctly limited as Cossmann would have us believe, and several recent workers have felt that the time is ripe for sub-division. The matter has been discussed at some length by Crickmay (1932, pp. 443–445), who has emphasised the discrepancy between the comprehensiveness of *Trigonia* and the fine distinctions drawn between genera in the Ammonoidea and other groups, living as well as fossil. Crickmay has also drawn attention to the fact that in the *Trigoninae* the evolution of forms was neither so rapid nor

so adventitious as to obscure the course of phylogeny. The retention of a distinctive juvenile ornamentation in many *Trigoniae* has indeed been of very great value in the determination of relationships and discrimination of natural groups, and has been successfully utilised by Kitchin (1903) and others. Classification based on adult characters alone has certainly led in the past to the proposal of certain groups of a very artificial character, the phenomenon of homeomorphy, whose prevalence has been amply demonstrated by modern palaeontological research in many groups of animals, being well displayed in the *Trigoniae*. It would appear, however, that there are grounds for believing that a number of the narrowly limited genera or sub-genera that have been proposed during the last ten years are more or less natural groups, though homeomorphy is sometimes evident, *e.g.* the distinction between *T. vau* and *T. v-scripta* pointed out by Kitchin (1903, p. 65; 1908, p. 112) based on the character of the juvenile concentric ribbing (see remarks below under *Iotrigonia*). It is evident that an adequate and full conception of the evolution of the *Trigoniae* will only be obtained after a very extensive study of the vertical and horizontal distribution of the *Trigoniae*, and the present tendency to recognise a number of genera or sub-genera cannot but materially assist in the elucidation of the problem.

Deecke, Crickmay, Marwick, and others have proposed the new divisions with the status of genera. To a great extent the distinction between genera and sub-genera is purely arbitrary and has admittedly no legal sanction, but nevertheless the writer favours the use of these new divisions as sub-genera, following the lead given by Dietrich (1933). One cannot but be impressed by the extraordinary constancy of the characters of the dental apparatus of the *Trigoniae* throughout the Jurassic and Cretaceous periods. Alien elements of pre-Jurassic and post-Cretaceous age have rightly been separated as genera, but compared with these the Jurassic and Cretaceous *Trigoniae* form in this respect a unit, if an unwieldy one. The variations in dental characters are confined to differences in the relative sizes of teeth, differences in the robustness of the teeth, differences in the degree of bifidity shown by the left central tooth, and differences in the degree of divergence shown by the teeth, features which in the main are closely linked up with differences of external form. As a consequence genera have been proposed largely, if not entirely, on a consideration of external form and ornamentation, and linkage between recognised groups is frequently indicated by the character of the ornament in the youthful stage. The late Dr. F. A. Bather in his

Anniversary Address to the Geological Society of London on "Biological Classification: Past and Future" (Q.J.G.S., Proc., vol. lxxxiii, 1927, pp. lxxxix-xc) emphasised that classification has a practical as well as a theoretical aim, and that the discrimination of units must not be confused with the practical aim of assortment of units for convenience of reference. The fact of seriation, which is obscured by the multiplication of genera, is more important than the discontinuities which the multiplication of genera is designed to illuminate. It appears to the writer that the acceptance of the new groups of *Trigonia* as sub-genera is to be commended both on practical grounds and for the emphasis it gives to a certain uniformity of structure, however much that uniformity may be disturbed by differences in sculpture. As genera, possibly grouped together as units of higher rank, that fundamental uniformity is no longer reflected in the nomenclature. It may be doubted whether the elevation of the sections of Agassiz and others, virtually sub-genera, into sub-families (van Hoepen, 1929) is warranted on the evidence.

One cannot leave this subject without expressing regret at the tendency, as shown in the choice of generic names and in the designation of genotypes, to ignore the names and types of the groups whose recognition is very largely the result of the patient labours of workers during the nineteenth century. It appears to the writer that it would only be courteous to earlier workers to perpetuate as far as possible the names given by them, as has been done by Deecke. Since the "types" designated by Agassiz and others are in the main well-known species, some of which have been accepted as "types" for the greater part of a century, they should wherever possible be designated types of the new genera or sub-genera. It is therefore to be regretted that van Hoepen (1929) has thought fit to base certain genera on comparatively little-known species from a remote locality, species that do not differ in features of more than specific value from the older "types" of Agassiz, Kitchin, and others, that have been amply described in various publications.

The Generic Names proposed by Deecke.—The writer cannot too strongly deplore the casual way in which Deecke (1925, p. 68) has proposed certain new generic terms for groups of *Trigoniae*, but at the same time it would appear that these highly suitable names must be regarded as validly proposed.

Deecke introduced the terms *Laevitrigonia*, *Scaphotrigonia*, and *Scabrotigonia* for the Laeves or Glabrae, Scaphoideae, and Scabrae respectively, thus perpetuating the groups recognised by Agassiz

and Lycett, but failed to give diagnoses or to designate genotypes. Van Hoepen (1929, p. 3) held these names to be *nomina nuda* and has been followed "in the interest of uniformity" by Stewart (1930, p. 90), as well as by Crickmay (1932, p. 452).

There cannot be the slightest doubt as to Deecke's intention when publishing these names. After referring to the groups of Agassiz by name, Deecke goes on to state: "Steinmann meinte, die alten Agassizschen Gruppen besäßen den Wert von Untergattungen und hat damit wohl für die *Laeves*, *Costatae* und vielleicht für die Scaphoiden recht. Für die Costaten führte Rollier den alten Sowerby-Bronnschen Namen *Lyriodon* als Untergattungsnamen ein und für die beiden anderen wären *Laevitrigonia* und *Scaphotrigonia* durchaus brauchbar. Ihnen liesse sich noch *Scabrotrigonia* anschliessen." The wording of the last two sentences is unfortunate and Crickmay has objected *inter alia* that the names were not *formally* proposed, but the names appear in print and could be interpreted as genera, and must be accepted if there is sufficient indication as to the author's intentions. The names are apparently, though not expressly, tautonyms of Lycett's Latin plurals of three of the group-names proposed by Agassiz. Crickmay implied that the names are accompanied by no indication and are therefore *nomina nuda* in spite of the tautonymy. But there cannot be any doubt whatever, from the brief discussion which precedes the proposal, that Deecke had in mind certain identifiable species-groups when proposing the genera, or that *Laevitrigonia*, *Scaphotrigonia*, and *Scabrotrigonia* were intended for the Glabrae, Scaphoideae, and Scabrae of Agassiz respectively. There is a sufficient indication here of the species-groups to which it was intended that these names should apply, and from Article 25 * and Opinion 1 † of the International Rules it would appear that the names are valid.

The objection raised by van Hoepen and also by Crickmay that the species-groups concerned are heterogeneous does not affect the validity of the proposal, since the genera can be restricted by the subsequent designation of genotypes.

It is interesting to find that Stewart (1930, p. 89) was compelled to admit that there was little doubt as to what these names were proposed for, and had accepted the names and designated types for them in manuscript. His abandonment of the names "in the interest of uniformity," following van Hoepen's rejection, has little to commend it; the rules of nomenclature should be strictly adhered to.

* IX^e Congrès Internat. Zool. à Monaco (Rennes, 1914), p. 901. † *Ibid.*, p. 909.

Deecke's genera have been accepted by Dietrich (1933, p. 35), and Mr. L. R. Cox, M.A., F.G.S., in a letter to the writer, has expressed the opinion that the genera were validly proposed.

It had been the present writer's intention to designate genotypes for Deecke's three genera,* choosing the "types" of the corresponding groups recognised by earlier workers. Dietrich (*loc. cit.*) has rightly designated *T. gibbosa* Sow. type of *Laevitrigonia*, this being the earliest designation that the writer has been able to find. The writer hereby designates *T. navis* Lamarck genotype of *Scaphotrigonia*, and *T. scabra* Lamarck genotype of *Scabrotrigonia*, in the belief that designations have not hitherto been made.

The Generic Names Proposed by van Hoepen.—The rather numerous species of *Trigonia* in the Cretaceous deposits of Zululand in South Africa have been studied by van Hoepen (1929). In his paper twenty-one species and varieties of *Trigonia* from the Umsinene River in Zululand and from Pondoland are arranged under no less than nine genera and four sub-families, while a tenth genus was founded on a species from the Uitenhage Series farther south. The minuteness of some of these sub-divisions may be gauged from the fact that the Scabrae, even after the elimination of the doubtful group *Megatrigonia* (known to others as the group of *T. conocardii-formis*), are represented in South Africa by six genera, and that the lengthy diagnoses of three of these genera are so closely similar as to be virtually identical. The author claims to have made an attempt to classify the Zululand species on a phylogenetic basis (*ibid.*, p. 3), but a perusal of his paper fails to reveal much of phylogenetic significance; the species are well described, but throughout the paper there is a fine disregard for the work of previous investigators, and the author makes no attempt whatever to trace the phylogeny of the groups he distinguishes. Van Hoepen appears to have solved the problem of classification of some twenty species of *Trigonia* by designating half of them genotypes of new genera. Some authors may find it a convenient solution of their taxonomic problems to consider only a small number of local species and make most of them types of distinct genera, but some of the genera thus formed are not likely to have any systematic value when applied elsewhere. Van Hoepen is mistaken if he assumes that the mere multiplication of genera, and consequent increase of a somewhat burdensome nomen-

* The writer had prepared a discussion on the *Trigoniae* in 1930 for a paper on the Cretaceous of Angola, in which designations were made. The paper has unfortunately not yet been published.

clature, has any essential bearing on the subject of phylogenetic relationships.

The novelty of outlook displayed by van Hoepen's work may be judged from the following examples: (1) Kitchin, an experienced worker and acknowledged authority, was scarcely able to separate from *T. ventricosa* (Krauss) (Uitenhage species) certain specimens from the Oomia Beds of Cutch *after a careful examination of numerous specimens from both areas* (Kitchin, 1908, p. 95)—yet van Hoepen, who presumably was relying only on Kitchin's figures and descriptions of the Oomia specimens and not on actual examples, not only gave the latter the new name *Pisotrigonia parva*, but *made the Uitenhage species the genotype of a new and different genus!* (van Hoepen, p. 22); (2) In the Umzamba Beds in Pondoland there is a very abundant small *Trigonia* long known under the name of *T. elegans* Baily; van Hoepen has not only split this species into three distinct species (a step which an examination of some hundreds of finely preserved topotypes shows to be scarcely warranted), but has followed the curious course of designating as genotype of *Linotrigonia*, not the well-known *T. elegans* with which he was familiar, but his new species *L. linifera*, *founded on a fragmentary mould of a left valve* and said to differ from *T. elegans* chiefly in its larger size (*ibid.*, p. 16).

Some of the genera proposed by van Hoepen will prove useful in future work, but it would appear that his fine sub-division of a portion of the older group of the Scabrae can scarcely be maintained. The following are the groups whose Zululand representatives were investigated by van Hoepen:—

(1) *Megatrigonia* (type *M. obesa* van H.) was proposed for a single species that was compared only with the elongate Scabrid *T. rogersi* Kitchin. The sub-genus is equivalent to the previously recognised group of *T. conocardiiformis*, the close resemblance of the species concerned having been overlooked by van Hoepen.

(2) *Iotrigonia* (type *I. crassitesta* van H.) should prove useful for the convergent groups of *T. v-scripta* and *T. vau* distinguished by Kitchin. Van Hoepen, in including both of the latter species in *Iotrigonia*, fails to mention the distinction drawn by Kitchin, and it is not clear as to which group the type species belongs.

(3) The type species of the six genera of Scabrae proposed by van Hoepen are from the Cretaceous of Zululand, the Senonian of Pondoland, and the Neocomian of the Uitenhage basin, and the majority would have been regarded as typical Scabrae by other workers. It is doubtful whether the distinctions made between some of these

genera are of much significance, and one or more of them would be included in the synonymy of *Scabrotrigonia* Deecke. The genera concerned are *Pterotrigonia*, *Acanthotrigonia*, *Linotrigonia*, *Pisotrigonia*, *Ptilotrigonia*, and *Rinetrigonia*. Crickmay (1932, pp. 460-463), in giving brief diagnoses of these genera, has referred to the low status of some of them.

(4) *Rutitrigonia* (type *R. peregrina* van H.) was proposed for a single species from South Africa which was compared with certain European species which have hitherto been included in Bigot's group of the Excentricae. The group-names Glabrae and Excentricae were not mentioned, but it would appear that *R. peregrina* is a fairly characteristic member of the latter group, and *Rutitrigonia* can therefore be used in place of the group name Excentricae. The substitution of the "type" of the latter by a later species from a remote locality must be deplored.

(5) *Pleurotrigonia* (type *T. blanckenhorni* R. B. Newton) is founded on a single isolated species of Costate ancestry and appears to be worthy of retention as a sub-genus.

Names Given to Extra-South African Species by van Hoepen.—Two new specific names were proposed by van Hoepen for species from the northern hemisphere, and as there is some danger that these validly proposed names may be overlooked, reference is made to them here.

Ptilotrigonia crassicosata van Hoepen (1929, p. 26) was proposed for *Trigonia aliformis* d'Orbigny (Pal. Française, Terr. crétacés, vol. iii, 1843, pl. 291, figs. 1-3), following the remark of Lycett that the latter was distinct from *T. aliformis* Park.

Pisotrigonia parva van Hoepen (1929, p. 22) was proposed for the Oomia shells previously regarded by Kitchin as scarcely distinguishable from the South African *T. ventricosa* (Krauss). *P. parva* (Kitchin, 1903, p. 104, pl. x, fig. 4—the other figures were not indicated by van Hoepen) must be very close to *T. ventricosa*, since Kitchin (1908, p. 95) states that the points of difference do not suffice even for the satisfactory recognition of two well-defined local races.*

Sub-genus *Megatrigonia* van Hoepen 1929.

The sub-genus *Megatrigonia* was proposed by van Hoepen (1929, p. 3), with the rank of a genus, united with *Iotrigoia* in the sub-family *Megatrigoiniinae*, for the single species *M. obesa* van

* Cox (Pal. Indica, 1935) says of the Indian shells that "their ornamentation is identical with that of South African specimens, and there is no justification for referring the Indian form to a distinct species . . . far less to a distinct genus."

Hoepen from the Lower Cretaceous of Zululand. The type species was compared only with the superficially similar Uitenhage species *T. rogersi* Kitchin, regarded by Kitchin (1908, p. 101) as a normal if elongated representative of the section *Scabrae* and placed in another sub-family by van Hoepen himself. *M. obesa* and *T. rogersi* can only be remotely related. Van Hoepen overlooked the very striking similarity indicative of close relationship between his *M. obesa* and the well-known and rather isolated Uitenhage species *T. conocardii-formis* (Krauss) (Kitchin, 1908, p. 119, pl. vii, figs. 2-4), and the still greater resemblance to the shells from East Africa identified with the Uitenhage species by Lange (1914, p. 235, pl. xix, fig. 1). The omission is curious, since van Hoepen was presumably familiar with Kitchin's paper, in which the peculiarities of *T. conocardii-formis* are finely described, and which includes excellent figures showing area and escutcheon; the adult shell, however, has not been adequately figured up to the present. The latter species agrees with *M. obesa* in all essential features, and differs only in details such as suffice to distinguish closely allied species; the average field geologist acquainted with the Uitenhage fauna would scarcely have hesitated to apply the Uitenhage name to the Zululand shells.

The sub-generic diagnosis has been given by van Hoepen and summarised by Crickmay (1932, p. 460), and may be stated as follows:—Shell very large, considerably longer than high, highest in the anterior third, the posterior part narrower and produced, roughly pear-shaped in outline. Anterior margin very broadly convex and passing gradually into the convex ventral margin; postero-dorsally concave, the margin nearly straight or concave and rather long; posterior margin short. Umbonal region prominent. Moderately inflated in the anterior half and very gradually becoming flattened towards the posterior. Area smooth and rounded, except in the early neanic stage, and becoming progressively wider when traced to the posterior margin. Escutcheon smooth, lanceolate and deeply concave. Dorsal carinae and longitudinal costellae absent, the former, however, represented by weak folds in the neanic stage. Ornamented on the flank with numerous rounded, oblique costae; the anterior costae massive, smooth to more or less nodose, curving downwards and then forwards; the costae becoming progressively finer towards the posterior, tending to be directed vertically and to be less nodose. Umbo concentrically ribbed in the early neanic stage, the ribs passing on to the area. Dentition strong, the left central tooth very markedly bifid.

The sub-genus occupies a somewhat isolated position among the *Trigoninae*, and is well worthy of recognition. Lycett (1879, p. 210) came to the conclusion that the species *T. conocardiiformis* was undoubtedly associated with the *Scabrae*, but Kitchin (1908, p. 123) stated that definite indications of such a relationship are not to be recognised. The group occurs in Neocomian strata from Tanganyika to South America.

Trigonia (Megatrigonia) obesa (van Hoepen).

(Plate XXXVIII, figs. 1-3; Plate XXXIX, figs. 1, 2.)

1929. *Megatrigonia obesa* van Hoepen: Krytfauna Soeloeland, pp. 4-6, pl. i, figs. 1, 2; pl. ii, figs. 1-3.

Material.—The type set was collected by van Hoepen from his Ndabana Beds on the Umsinene River, Zululand. In the collections from the Pongola area there are about 30 specimens. Mr. H. F. Frommurze and Mr. J. S. Hutt collected 10 specimens along the Mfongosi tributary of the Pongola River (T.M. 1763, 1778, 1781, 1782, 1898, 1909; S.A.M. 10784, 10785). Dr. S. H. Haughton and Dr. A. W. Rogers collected about 20 specimens at the same locality, distributed in the zones as follows, the numbers in brackets referring to the number of specimens found: ZA (2), Z2 (1, juvenile), Z3 (7), Z4 (4), Z5 (1), Z8 (5), Z12 (1). A single specimen was collected farther south on the Myesa stream, MI (1.)

The material includes a number of weathered specimens, but some are fairly well preserved and complete. I have not seen the details of the dorsal area, escutcheon, and dentition, which have been well described by van Hoepen.

Description of the Species.—The following is based as far as possible on the new collection from the Pongola, but is in agreement with that given by van Hoepen; a free translation of portions of van Hoepen's paper is included so as to complete the description.*

"Shell very large, considerably longer than high, highest in the anterior third, the posterior part narrower and produced, roughly pear-shaped in outline. Anterior margin very broadly convex, and passing quite gradually into the less convex ventral margin; the anterior margin with its greatest forward convexity a little below

* Where quotations from van Hoepen are given under the descriptions of the species of *Trigonia*, it is to be understood that the writer has given an English translation.

the middle of the shell; dorsal part of the anterior margin moderately convex to relatively straight and sloping forwards and downwards at a moderately steep angle from the umbo. Ventral margin long, moderately convex in the anterior half, becoming straighter in the posterior half and sloping gradually upwards to meet the posterior margin. Postero-dorsal margin moderately long, gently concave, sloping very gradually towards the posterior. Posterior margin relatively short, less than half the height of the shell, sloping downwards and backwards at a moderately steep angle, meeting the postero-dorsal margin in a rounded, very obtuse angle, and meeting the ventral margin in a rounded angle of about 90° . Umbonal region prominent, the umbo situated between a fourth and a third of the length of the valve from the anterior, strongly incurved and curved a little posteriorly. Moderately to fairly strongly and evenly inflated in the anterior half, very gradually becoming flattened posteriorly, with the greatest slope towards the anterior margin, but not anteriorly truncate.

"There is no marginal carina in the adult. In the neanic stage the marginal carina is represented by a weak fold, which passes posteriorly into a convexity of the valve which becomes progressively wider and more indistinct. At the posterior end of the adult shell the fold is lost in the uniform convexity of the valve. The inner carina is similarly but a weak fold, which becomes indistinct towards the posterior and ends near the upper end of the posterior margin. Between the carinae and nearer the inner carina, from which it diverges a little towards the posterior, runs a shallow longitudinal groove which persists to the posterior margin."

The juvenile ornamentation of the flank passes into that of the adult by gradual increase in the amount of anterior divergence of the costae. In the adult the flank is ornamented with numerous rounded costae, the whole series of costae appearing to radiate from a point just above and behind the umbonal region. On the more inflated anterior half of the shell the costae are relatively strong and widely separated; towards the posterior the costae quite gradually weaken and the interspaces become narrower. The anterior costae are strong, rounded, and with broad concave interspaces 2-3 times as wide as themselves; they slope steeply downwards and forwards in the antero-ventral direction, all more or less convex towards the posterior; in front the costae bend gradually forwards so as to approach the anterior margin at an acute angle, but they may (as in the holotype) bend forwards sufficiently to be roughly perpendicular

to the anterior margin; those costae which approach the anterior part of the ventral margin may bend forwards rather rapidly before reaching the margin, even to the extent of diminishing the width of the interspaces. In old shells the anterior costae fail to reach the anterior and antero-ventral margins, which are then bordered by a band marked only by growth lines; the stage at which the costae cease varies a little from specimen to specimen, some comparatively large shells having little sign of the marginal band or of the relatively abrupt forward bending of the costae near the ventral border. In the mid-region of the valve the costae are weaker, rounded, separated by rounded interspaces about as wide as themselves, and are directed approximately vertically, though convex towards the posterior and tending to bend forwards before reaching the ventral border. Posteriorly the costae are progressively weaker and closer together, and are directed steeply downwards towards the posterior.

The flank is ornamented throughout with growth lines, which cross both costae and interspaces. A certain periodicity in the growth gives rise to a series of quite distinct concentric furrows, commonly 6-8 mm. apart in the middle part of the anterior region of the shell, but closer together towards the margin; these have the effect of constricting the costae at more or less regular intervals, so that the costae are lower and narrower at the crossing of the concentric furrows and raised and swollen between. In some specimens the coarsely beaded character of the anterior costae is much in evidence, while in others (as in the holotype) it is much less marked; the tubercles thus formed may be rounded, oval, or even elongate. Towards the posterior the tuberculation is progressively less noticeable, and the anterior costae gradually lose the tubercles and become narrower as they are traced towards the area.

"In the young shell the ornamentation of the flank consists of sharp concentric ribs, situated close to one another, which begin at the marginal carina, are concave downwards for a very short distance, and rapidly pass into a broad downwardly directed curve which ends at the anterior margin. The ribs are more or less parallel to the ventral margin, but not quite so, one specimen showing that the anterior ends of the ribs make an angle of 6° with the growth lines at under 5 mm. from the umbo." At a slightly later stage, when the initial pseudo-concentric ribs pass into anteriorly diverging costae and gradually increase in thickness away from the area, "a short initial part of the ribs at the marginal carina remains thin. Owing to the bending down of the ribs to continue as very oblique

costae across the flank, the concavity or embayment of the ribs just in front of the carina passes into a sharp bend. This bend does not appear in the later costae, which are added successively on the posterior side as growth proceeds." The posterior costae begin below the margin of the area.

"The ornamentation of the area is poor. In the neanic stage the area is crossed by costellae, which are parallel to the growth lines over the marginal carina, and continue over the area and the inner carina towards the umbo. These costellae disappear, and are replaced by very fine growth lines over the area and escutcheon, before the stage is reached at which the costae lose the sharp bend just in front of the marginal carina. The escutcheon is broad and long, and for the most part concave." The area is devoid of costellae after the early neanic stage and ornamented only with growth lines.

The rather strong dentition, characterised by the markedly bifid left central tooth with the two forks of the tooth diverging at about 90° , has been described in detail by van Hoepen and need not be here repeated.

Remarks.—There is a fair amount of variation in the character of the ribbing in the Pongola specimens. I have individuals before me equally well preserved which differ from one another in the development of the tuberculate character of the anterior costae, varying from shells with coarsely beaded costae to shells with rounded costae slightly constricted at more or less regular intervals. In the holotype the only adult shell whose external features are shown in van Hoepen's figures, the costae appear to be of the latter type, though the original description of the species refers to "the impression of tubercles," and describes their formation.

The rapid bending forward of the costae near the ventral margin is not characteristic of all the specimens before me, and in no case do the anterior costae meet the anterior margin perpendicularly, as is the case in the holotype. In a number of cases the costae which approach the ventral margin bend forward at their lower extremities, while the anterior costae are uniformly curved right up to the anterior margin which they meet at an acute angle; in others the forward bend is not evident, though it is to be presumed that with further growth it would have made its appearance. The stage at which this peculiar feature of the costae appears must vary considerably. In the holotype the forward curvature affects the anterior costae as well, so that these approach the anterior margin at about a right angle.

The variations observed appear to be of such a character as would

be expected within the limits of a species. They apparently have no zonal significance, as far as can be judged from the present collection.

Comparison between T. obesa and T. conocardiiformis (Krauss) *from the Uitenhage Neocomian*.—These two species are very strikingly similar and certainly closely allied (cf. Plates XXXVIII, XXXIX, and XL). They have the same general form and are of about the same size, and agree almost exactly in those characters which might be taken to be of generic or sub-generic value. The general characters of the dorsal area and escutcheon are identical, both having weak marginal carinae, which even near the umbones are hardly more than folds; both are characterised by the restriction of the pseudo-concentric ribbing to the early neanic stage and the complete absence of dorsal costellae on the adult area and escutcheon. The ornamentation of the flank is of the same type and in the juvenile stage all but identical.

The species, however, can be distinguished from each other in several respects, the characters being more or less constant for the two areas. *T. conocardiiformis* (see Plate XL) is invariably relatively less high and more elongate than *T. obesa*, with the umbonal region less prominent, the antero-dorsal and postero-dorsal margins diverging at a larger angle, and the posterior more produced. The anterior costae in *T. conocardiiformis* are less steeply inclined, and are usually more convex towards the posterior, the greater curvature and lesser obliquity enabling them to bend round gradually so as to meet the anterior margin nearly perpendicularly; the *T. obesa*, on the other hand, the most anterior costae tend to be steeper and straighter, and except in those cases where their lower extremities bend forward, meet the anterior margin more acutely. In *T. conocardiiformis* the costae are rounded, crossed by growth lines but otherwise smooth, and only sometimes constricted at irregular or infrequent intervals; in some individuals the costae are of roughly uniform strength for a considerable distance from the umbo; in others there are very broad and very shallow concentric furrows which correspond to constrictions on the costae, so that the anterior costae appear to be made up of a succession of elongate, and less commonly oval or rounded, only slightly raised nodes. In *T. obesa* the constrictions tend to be closer together, and the nodes more rounded and sometimes more raised, very often giving the costae a coarsely beaded character; in *T. conocardiiformis* the earlier oblique costae within 30 mm. from the umbo may show raised nodes towards the anterior margin. The division of the costae into an anterior

and a posterior series as described by Kitchin (1908, pp. 121, 124), a frequent though not an essential character of the Uitenhage species, and one which does not appear to mark Krauss's type, has not been noticed in *T. obesa*.

Comparison with East African Species.—The two shells from the *Trigonia schwarzi*-Beds in Tanganyika ascribed by Lange (1914, p. 235, pl. xix, figs. 1 a, b) to *T. conocardiiformis* (Krauss) represent an unnamed new species which resembles *T. obesa* in certain respects. The species is undoubtedly a *Megatrigonia* from its general form, size, costation, and smooth area and escutcheon, the adult shell having been well figured by Lange, though somewhat briefly described. It appears to be distinguished from *T. conocardiiformis* in being relatively shorter, and has much the same proportions as *T. obesa*; the anterior costae are finer and more widely spaced than in *T. conocardiiformis*, and less steeply inclined than in *T. obesa*. The East African form must be very closely allied to the two South African species and is almost certainly distinct, but as only one specimen has been figured it is difficult to make an adequate comparison.

T. staffi Lange (1914, p. 236, pl. xx, fig. 1), founded on a single right valve from the same horizon, is said by its author to be allied to *T. conocardiiformis*. The dorsal area and escutcheon were not described or figured, and the species may equally well be an elongate member of the Scabrae. Lange states that these two species, together with *T. rogersi* Kitchin (1908, p. 99), belong to the same group, but the wide costellate escutcheon of the latter places it among the Scabrae.

Sub-genus *Iotrigonia* van Hoepen 1929.

The sub-genus was proposed by van Hoepen (1929, p. 6) for certain species from India and South Africa, characterised by the possession of smooth V-shaped costae, namely *T. vau* Sharpe and *T. stowi* Kitchin from the Uitenhage Series, and *T. v-scripta* Kitchin from the Oomia Beds, together with two species from Zululand, *Iotrigonia crassitesta* van Hoepen and *I. inconstans* van Hoepen. *I. crassitesta* was cited as genotype, and the group was ranked as a genus and associated with *Megatrigonia* van Hoepen in the sub-family Megatrigoniinae.

The sub-genus, a brief diagnosis of which has been given also by Crickmay (1932, p. 460), may be described as follows:—

Shell from moderately small to large, considerably longer than high, highest towards the anterior end or in front of the middle, the

posterior much produced and relatively narrow, the anterior rounded or produced, moderately convex. Postero-dorsal margin long, concave to almost straight; ventral margin very long, convex. Flank ornamented with numerous more or less coarse, smooth, V-shaped oblique costae, which tend to become irregular or obsolete towards the ventral margin or the anterior end. Area moderately wide in the adult stage, smooth, separated from the flank by a marginal carinal fold which becomes very broad and indistinct towards the posterior. Escutcheon long, lanceolate, moderately wide, excavated, smooth, separated from the area by a change in slope. Neanic stage with smooth concentric ribs, which pass over on to the area as transverse ribs; transverse ribs if present at all soon disappear from the escutcheon, but persist for some distance on the area; the dorsal carinae near the umbones may be sharply marked, linear, or represented only by blunt folds; there is no median carina. Dentition strong, the left central tooth markedly bifid.

Kitchin (1903, pp. 65-67, 115-117; 1908, pp. 110-119) has pointed out at some length the grounds for believing that the striking similarity in adult features between the Indian and Uitenhage species is due to homoeomorphy and has distinguished between a "Group of *T. vau*" (including *T. stowi*) and a "Group of *T. v-scripta*." Convergence in evolution is indicated in the characters of the neanic stage; the former group has a simple youthful ornamentation of crowded raised lines which extend from anterior margin to postero-dorsal margin without a break, while area and escutcheon are hardly defined, the marginal carina being a blunt fold and the inner carina being more or less obsolete; in the Group of *T. v-scripta*, on the other hand, the youthful sculpture is more differentiated, the ribs on the flank are fewer and more widely spaced and bend obliquely forward at the well-defined marginal carina, to terminate at the delicate linear ridge which represents the inner carina. Nevertheless it should be pointed out that the distinction made by Kitchin, though of importance, does not necessarily indicate descent from very remotely related ancestral stocks, since the youthful ornamentation in the two groups is in a broad way of the same type. The sub-generic term *Iotrigonia* can therefore be used for both groups. The genotype, *I. crassitesta* van Hoepen (1929, p. 7; pl. ii, figs. 4, 5; pl. iii, figs. 1, 2), apparently belongs to the Group of *T. vau*.

It is rather curious that van Hoepen, who set out to classify the Zululand *Trigoniae* on phylogenetic lines (*ibid.*; p. 3), included both *T. vau* and *T. v-scripta* in *Iotrigonia* without any mention of the

remarkable convergence shown by these two species and so well described by Kitchin.

Kitchin (1903, pp. 65-78) has stated that the costation differs materially from the analogous sculpture which characterises the members of the Jurassic Undulatae of Europe, and that the general resemblance is of the remotest kind. The Undulatae are more or less palpably derived from the Clavellatae, doubtless along more than one line of descent, but the ancestry of the Indo-African Neocomian group is by no means certain. Crickmay (1932, p. 457) has proposed a genus *Vaugonia* for a member of the Undulatae, and Dietrich (1933, p. 33) has briefly discussed the convergence shown by these V-costate species. There appears to be some justification for associating *Iotrigonia* with *Megatrigonia*, since both are characterised by a primitive concentric ornament in the neanic stage, by smooth area and escutcheon in the adult stage, and obsolescent marginal and inner carinae, but the adult costation is of quite a different character in the two sub-genera; a remote common ancestor is possible, as originally suggested by Kitchin (1908, p. 122).

The two species described by van Hoepen (1929, pp. 7-9) from the Umsinene River in Zululand are strikingly similar to the two species from the Uitenhage Series. *T. crassitesta* (van Hoepen) appears to be close to *T. stowi* Kitchin (1908, p. 115, pl. vi, figs. 4, 5; pl. vii, fig. 1) and *T. inconstans* (van Hoepen) is very similar to but considerably larger than *T. van* Sharpe (Kitchin, 1908, p. 110, pl. vi, figs. 1-3). Both species were collected at the base of the succession, from van Hoepen's Ndabana Beds, where they were associated with *Megatrigonia obesa*, and a member of the group of the Scabrae reminiscent of the Uitenhage *T. kraussi* though distinct from it. The Ndabana Beds were stated to be Albian by van Hoepen (1926, p. 222) in a preliminary account, but the *Trigoniae* which have been collected belong to groups which are more characteristic of the Neocomian.

Trigonia (Iotrigonia) haughtoni sp. nov.

(Plate XLI, figs. 1-4.)

Material.—The species was collected by Dr. S. H. Haughton and Dr. A. W. Rogers from two neighbouring localities, in both cases in association with *T. (Megatrigonia) obesa* and *T. (Steinmanella) hennigi*. There are five pieces of shelly limestone from MI on the Myesa tributary of the Pongola River, including portions of 10 detached valves, both right and left valves being represented, as

well as a right valve from M3. From ZA on the Mfongosi stream 3 specimens. Several of the valves are more or less complete and in a good state of preservation.

Holotype.—The holotype is the largest of four specimens associated on the same slab from MI, and is a fairly complete and well-preserved right valve. Two of the associated specimens, one a right valve and the other a left valve, show the neanic stage and the dorsal area very finely, and may be cited as paratypes. I have not seen the interior of the valves. The postero-dorsal part of the holotype appears to be damaged.

Description of the Species.—Shell moderately small, considerably longer than high, with the umbo situated at about a third of the length of the shell from the anterior end, umbonal region rather prominent, anterior relatively short and rounded, posterior produced and narrower. Shell in the adult stage moderately and more or less evenly convex; the younger shell relatively more convex. Anterior margin broadly convex, the greatest curvature at or about the middle, merging quite gradually into the long convex ventral margin; postero-dorsal margin moderately long, gently to strongly concave for some distance behind the umbo, meeting the ventral margin in a well-rounded posterior termination. Umbo well incurved.

Area and escutcheon taken together wide, more or less crescentic, broadening rather rapidly at first and very steeply inclined, when traced posteriorly gradually becoming a little narrower and less steeply inclined. Marginal carina represented by a raised, very convex, rounded, smooth fold, which gradually becomes wider and relatively less raised when traced posteriorly; the marginal carinal fold pursues a course which is markedly concave towards the postero-dorsal margin, and also concave upwards when the valve is seen in lateral view; from about 5 mm. to about 20 mm. from the umbo the lower side of the fold is more or less distinct by reason of its conspicuously raised character, and the costae of the flank commence immediately below it; traced posteriorly the fold broadens considerably and is less distinctly limited from the flank. Area narrow, narrower than the escutcheon except near the posterior extremity; up to 5 mm. from the umbo the area is very steeply inclined and slightly concave; beyond 5 mm. from the umbo the area gradually becomes deeply and evenly concave in cross-section, merging below into the convex marginal fold and on the upper side meeting the escutcheon in a raised crest; the median longitudinal furrow is not distinguishable in the general concavity of the area; at the posterior end the marginal fold has broadened out so as to make up the greater

part of the width of the area, this broad, gently convex part being succeeded upwards by a much narrower concave part. The concave area meets the wider but equally concave escutcheon in a broadly V-shaped, sharp-crested inner carina, which pursues a course at first markedly concave towards the postero-dorsal margin. Both the marginal carinal fold and the inner carina gradually become less concave towards the postero-dorsal margin as they are traced backwards; both appear concave upwards when the shell is seen in side view. Escutcheon broad, evenly and deeply concave from the raised inner carina to the raised upper margin, crescentic in shape.

In the neanic stage, up to 5 mm. from the umbo, the ornamentation consists of numerous concentric ribs which extend from the anterior margin to the marginal carinal fold in a uniform curve, meeting the fold almost perpendicularly. At from 2 mm. to 5 mm. from the umbo the ribs on the flank are raised, rounded, and separated by wider concave interspaces. Up to about 2 mm. from the umbo the ribs on the flank curve slightly downwards on crossing the carinal fold and then bend upwards so as to cross the area very obliquely. Between 2 mm. and 5 mm. from the umbo the ribs on the flank are not continuous with the corresponding ribs on the area, the carinal fold being smooth except for growth lines; the ribs on the area are very oblique, slightly less raised, and closer together than the corresponding ribs on the flank. Beyond 5 mm. from the umbo the coarse oblique costae of the posterior series make their appearance, but the primitive oblique ribbing of the area persists to about 10–12 mm., the ribs being less close together than at an earlier stage and becoming confined to the centre of the concave area. Beyond about 5–7 mm. from the umbo the ribs on the area fail to reach the inner carina. At a very early stage the ribs probably pass over on to the escutcheon (?), but at 4–8 mm. from the umbo there are only traces of very fine oblique riblets just above the inner carina, but these do not persist when traced towards the upper margin. The greater part of the area and escutcheon is smooth. The ribs appear to have been smooth, but the inner carina bears traces of very imperfectly developed nodes up to about 15 mm. from the umbo.

The adult shell is ornamented with two series of oblique costae so arranged as to give a V-costate appearance, but the anterior and posterior series do not coincide in numbers of costae. The adult type of ornamentation appears abruptly at about 5 mm. from the umbo when the posterior series makes its appearance; a concentric rib which shows no sign of being divided into a posterior and an

anterior limb is succeeded immediately by the two adult series of inclined costae. The primitive concentric ribbing, however, grades into the anterior series of costae, which are directed steeply postero-ventrally and cross the growth lines at an angle of 15–25°. The anterior costae are rounded, smooth, moderately elevated, and are about twice as numerous as the coarser posterior series; they pursue a nearly straight course from the anterior margin, but are very slightly concave to the postero-dorsal margin. The line of junction of the anterior and posterior series is nearly vertical, but very steeply inclined backwards. The posterior costae are coarser and radiate downwards from the margin of the area, the 4 or 5 costae nearest the anterior being directed very steeply forwards so as to abut against the anterior series; these are succeeded posteriorly by vertical costae, and the shorter costae which follow are directed very steeply backwards. The posterior costae are rounded, convex, smooth, separated by concave interspaces of about the same width as themselves; the 4 or 5 nearest the anterior are very wide and coarse from their junction with the anterior series until close to the area, but become narrow close to the marginal carinal fold; traced posteriorly the costae become progressively narrower and shorter. The costae fail to reach the ventral margin in the adult shell, persisting to about 25 mm. from the umbo in the anterior part.

All parts of the shell are crossed by growth lines.

Dimensions, in millimetres:

	Holotype.	Paratype (left valve).
Length . . .	45	± 24
Height . . .	± 31	19
Thickness . . .	± 7	± 5

Comparison with other South African Species.—This fine little species is quite distinct from each of the four South African species of *Iotrigonia* described up to the present, and does not appear to be very closely allied to any of them. The considerably smaller size and rounded anterior serve to distinguish *T. haughtoni* at a glance from the more elongate, anteriorly produced *T. stowi* Kitchin (1908, p. 115, pl. vi, figs. 4, 5; pl. vii, fig. 1) and *Iotrigonia crassitesta* van Hoepen (1929, p. 7, pl. ii, figs. 4, 5; pl. iii, figs. 1, 2). In outline there is some resemblance to the considerably larger *I. inconstans* van Hoepen (1929, p. 8, pl. iii, figs. 3, 4; pl. iv, figs. 1, 2) and to *T. vau* Sharpe (Kitchin, 1908, p. 110, pl. vi, figs. 1–3). The resemblance, based on size and outline only, is greatest to *T. vau*,

but the species can be distinguished in a number of important respects.

T. vau is larger than *T. haughtoni*. In the former both the anterior and posterior series of costae are inclined much less steeply, and consequently meet in a considerably larger angle; the line of junction of the two series is directed obliquely downwards, and is not as nearly vertical as in *T. haughtoni*. In *T. haughtoni* there are about twice as many costae in the anterior series as in the posterior series, where they meet in the line of junction, whereas in *T. vau* the numbers are nearly the same, the majority of the posterior costae passing with a sharp V into the anterior costae, there being only one or two additional costae on the anterior side. In *T. vau* the posterior costae are all directed forwards, while in *T. haughtoni* the most posterior of the costae are directed steeply backwards. In *T. haughtoni* the marginal carinal fold is more convex and raised than is the case in *T. vau*, the area is relatively wider, the escutcheon is relatively narrower and smaller, the inner carina more strongly developed, and the ribbing of the area more persistent.

As pointed out above, Kitchin has distinguished between a "Group of *T. vau*" and a "Group of *T. v-scripta*," basing the distinction on the characters of the neanic stage. The former group includes the two Uitenhage species *T. vau* and *T. stowi*, both characterised by simple concentric ribbing in the neanic stage and obsolescence of the inner carina; in these species the ribs are linear and crowded, and pass on to the area without interruption. The character of the youthful stage in *T. haughtoni* is such as to suggest relationship with the group of *T. v-scripta* rather than with the two Uitenhage species *T. vau* and *T. stowi*, noteworthy being the fact that in *T. haughtoni* the concentric ribs bend rather sharply upwards at a well-defined carinal angle as they do in the Indian species, whereas in *T. vau* and *T. stowi* they pass over on to the area with only a slight change in direction, the carinal angle being much rounded. The fact that the inner carina is raised and sharp-crested supports reference to the Indian group, since in the Uitenhage species the inner carina is a weak fold. On the other hand, the concentric ribs are as numerous as in *T. vau*, the Indian species being characterised by the possession of a few relatively coarse ribs within 5 mm. from the umbo.

Comparison with other Species.—There is a certain resemblance in general features to *T. v-scripta* Kitchin (1903, p. 70, pl. vii, figs. 6–8; pl. viii, figs. 1–3) from the Oomia Beds of Cutch, but the species differ from one another in details of form and ornament. A note-

worthy distinction is the considerably larger number of concentric ribs in the neanic stage in the new species. *T. haughtoni* has greater juvenile convexity, and other points of distinction are the slightly greater obliquity of the line of junction of the anterior and posterior series of costae, the wider escutcheon and more curved inner carina, the sharp demarcation of escutcheon and area, the steep backward slope of the most posterior costae, and the rather shorter anterior. The species are undoubtedly distinct, but an actual comparison of specimens would be necessary for an exhaustive and adequate comparison.

T. dubia Kitchin (1903, p. 67, pl. vii, figs. 3-5) from the same formation as the above appears to be relatively longer and broader (?) in the posterior region, and the anterior series of costae is concentric or almost so. Dietrich (1933, p. 33, pl. ii, figs. 45, 46) has identified with the Indian species some very imperfect shells, from the *T. smeei* beds in Tanganyika, which resemble the new species in the character of the costation, and in which the anterior series of costae is oblique and probably not parallel to the ventral border; the change from primitive to adult ornamentation is, however, not as sudden as in the new species, there being several concentric ribs more or less sharply bent in the middle. *T. dubia* is imperfectly known, and it is very doubtful whether the East African shells represent the same species.

I have not been able to see the paper containing the description and figures of the East African species *T. kuhni* G. Müller, said by Kitchin (1908, p. 113) to be of Neocomian age. Judging from Kitchin's remarks, the species appears to have been founded on imperfect material.

T. heterosculpta Stanton (1901, p. 20, pl. iv, figs. 16-18) from the Lower Cretaceous of Patagonia is characterised by the fact that the anterior costae terminate against a single vertical posterior rib, and differs from the new species in several other respects.

Sub-genus *Steinmanella* Crickmay 1930.

(= *Transitrigonia* Dietrich 1933.)

The species described below is a typical example of the very distinct Neocomian group of *Trigoniae* long known as the Pseudo-quadratae, a name bestowed by Steinmann (1882) to include two southern species, *T. transitoria* Steinmann from South America and *T. herzogii* (Goldfuss) from the Uitenhage Series in South Africa. Several species

have since been added from South America, as well as *T. holubi* Kitchin from the Uitenhage Series, *T. mamillata* Kitchin from the Oomia Beds of Cutch, and *T. hennigi* Lange from East Africa. In America the group has been recognised as far north as Texas, where the species *T. vyschetszkii* Cragin occurs with certain other Lamellibranchs of Lower Cretaceous affinities in the so-called Malone Jurassic Formation; Kitchin (1926) has set forth very fully reasons for believing that the Lamellibranchs concerned came from Neocomian beds included in that formation. The Pseudo-quadratae have been discussed by Kitchin in several papers (1903, p. 98; 1908, p. 108), and were thought by that author to be confined to the Neocomian (1926, 1929).

To this well-marked group two generic names have recently been applied, *Steinmanella* Crickmay (Nat. Mus. Canada, Bull. 63, 1930), and *Transitrigoia* Dietrich (1933, p. 36). The designated types are very closely allied species, and *Transitrigoia* (type *T. transitoria* Steinmann) is therefore a synonym of *Steinmanella* (type *T. holubi* Kitchin). A brief diagnosis of *Steinmanella* has been given by Crickmay (1932, p. 458) in his "Contributions towards a Monograph of the Trigoniidae."

The sub-genus may be described as follows:—

Shell large, massive, quadrate in outline, compressed. Umbones nearly terminal, weakly incurved. Anterior more or less vertically truncate, the anterior margin sloping steeply downwards from the umbones and meeting the long straight postero-dorsal margin nearly perpendicularly. Posterior high, the posterior margin relatively long. Area very broad, forming with the flank a gentle uniform convexity, with a weak longitudinal furrow above the middle; ornamented towards the umbones with three longitudinal rows of tubercles, representing the marginal and inner carinae and a median carina just below the furrow; ornamented beyond the neanic stage with growth lines which may at some stage pass into coarse, crowded, smooth, concentric costellae. Escutcheon narrow, very elongated, ornamented with irregular oblique rows of coarse tubercles. Flank beyond the neanic stage with widely spaced, oblique, coarsely tuberculate costae, or rows of coarse tubercles. Early neanic stage with relatively strong concentric nodular ribs, which pass from the anterior margin across the flank on to the area and escutcheon. Dentition massive, the left central tooth narrow.

The characters shown by the neanic stage indicate descent from the Jurassic Clavellatae (Kitchin, 1908, p. 109).

Trigonia (Steinmanella) hennigi Lange.

(Plate XLIII, figs. 1-3; Plate XLIV, fig. 1.)

1914. *Trigonia Hennigi* Lange: Tendaguruschichten, p. 238, taf. xix, fig. 3.

1914. *Trigonia transitoria* Steinmann: Lange, *ibid.*, p. 237, taf. xix, fig. 2.

1933. *T. (Transitrigonia) hennigi* Lange: Dietrich, p. 37.

Material.—Twelve specimens identified with this East African species were available for study, of which eleven were collected by Dr. S. H. Haughton and Dr. A. W. Rogers along tributaries of the Pongola River, and one by H. F. Frommurze at an unrecorded horizon on the Mfongosi stream. The later collection of eleven specimens was found at the following localities: Myesa stream, MI, 2 juvenile specimens; Mfongosi stream, ZA, 6 specimens; Lombagwenya stream, one specimen from each of the localities L9, L12, L14. The specimen (S.A.M. 10786) collected by H. F. Frommurze is very finely preserved, and it is probable that it is from ZA. The majority of the shells have the valves closed, and though complete are not well preserved. The interior has only been seen in part. Dr. S. H. Haughton also recorded the species at locality L4.

Description of the Zululand Shells. (1) *External Features.*—Shell large, massive, oblong in outline, longer than high, not much inflated. Dorsal margin long, more than two-thirds of the length of the shell, nearly straight. Anterior margin very gently convex, forming about a right angle with the dorsal margin, at first vertical or very nearly so, then curving very gradually backwards, merging into the convex ventral margin about a much-rounded antero-ventral angle. Dorsal margin meeting the posterior margin in a very obtuse angle. Posterior margin very broadly convex, very obscurely angulated above the middle and meeting the ventral margin in a much-rounded obtuse angle.

Umbones small, pointed, slightly incurved and almost terminal at the antero-dorsal angle. Anterior more or less truncated, with a narrow flattened or only slightly convex anterior face almost at right angles to the plane of the valves, well demarcated from the flank not only by the difference in slope but by the absence of costae. Inflation of valves relatively weak, the greatest convexity above the middle of the valves and towards the anterior.

Dorsal area very wide, marked off from the flank by the absence

of the coarse oblique costae. Marginal carina represented only by a very broad gentle curvature of the valve surface. The area is traversed longitudinally by a well-marked shallow furrow, which persists from the umbonal region to the posterior margin, dividing the area into a narrow upper and a broader lower part, the lower part being 2-3 times as broad as the upper. The escutcheon is rather narrow and elongate, and is separated from the dorsal side of the area by an inner carina, which is well marked within 20 mm. of the umbo; the inner carina when traced posteriorly is gradually replaced by an inconspicuous fold that persists to the postero-dorsal angle. The escutcheon is not much excavated near the umbones, and is slightly convex in the posterior half. There is a short, deep, very narrowly cordate lunule well demarcated from the anterior face by an abrupt change of slope.

(2) *Internal Features*.—Interior of the valves not seen, except for part of the sub-umbonal region of a large left valve, in which there is a very massive, relatively narrow central tooth, projecting to about 12 mm. above the margin, oblique, coarsely grooved on the almost vertical sides, and deeply channelled above; there is also a relatively strong anterior tooth, narrow, slightly oblique, and close to the anterior margin.

(3) *Ornamentation*.—Flank of the shell ornamented with about 8-10 very coarsely tuberculated costae, which pass gradually into finer concentric costae within about 8 mm. from the umbones. Costae oblique, from nearly straight to distinctly or even markedly concave towards the anterior. In some specimens the costae behind the middle of the flank bend forwards rather abruptly at some distance from the ventral margin. In the umbonal region the costae are short and directed antero-ventrally, in the mid-region they are more nearly vertical, and they become progressively shorter posteriorly as the dorsal area widens, the last one or two being directed slightly backwards.

The costae are characterised by bearing very large, prominent, rounded tubercles at frequent and fairly regular intervals; the costae themselves are not much elevated, but are given a strong appearance by the very prominent swollen tubercles. The tuberculation may become a bit irregular towards the ventral, particularly the antero-ventral, border. Anteriorly the costae cease abruptly at the angle limiting the anterior face, so that in anterior view the narrow anterior face appears to be bounded by a row of coarse tubercles. The costae are widely separated by concave interspaces, which are much wider

than the costae in the ventral half. The costae end somewhat abruptly at the margin of the dorsal area, near or a little below the obscure carinal convexity.

The area in the adult stage is concentrically striate and devoid of tubercles, but there are indications of two longitudinal rows of low coarse tubercles which persist to about 30 mm. from the umbo, one row representing the obscure marginal carina and one row representing an obscure median carina just below the longitudinal furrow. The inner carina carries a row of rather prominent rounded tubercles for some distance, but these disappear before the posterior margin is reached. The escutcheon bears several indistinct and very oblique rows of moderately large elongate tubercles.

All parts of the surface are traversed by relatively fine growth lines of varying strength. There is little indication in most specimens that the concentrically striate area changes in character with age; the coarse concentric costellae which characterise the greater part, or at least the later part of the area in other species, do not make their appearance until a very late stage. In S.A.M. 10786 concentric costellae are certainly not developed at 100 mm. from the umbo; the posterior border, however, is too damaged for one to be quite certain that they do not appear at all. In the largest specimen, a weathered right valve from horizon L14, there are indications of concentric costellae at about 120 mm. from the umbo, but I have not been able to trace these across the area owing to the poor state of preservation of the specimen.

Within about 8 mm. from the umbo the costae are relatively prominent, nodular, and concentric, and are continued across the slightly raised marginal carina over the area at least as far as the raised inner carina. On crossing the marginal carina these costae form a distinct V, the apex directed ventrally. Beyond about 5 mm. from the umbo, the concentric costae on the area break up into three nearly contiguous tubercles, which at about 20 mm. are distinguishable as the three divergent longitudinal rows of tubercles representing marginal, median, and inner carinae.

(4) *Dimensions*.—Of the following specimens, whose dimensions are recorded in millimetres, 1 is S.A.M. 10786; 2–6 are from ZA; 7 and 8 are from MI; 9, 10, and 11 are from L9, L12, and L14 respectively.

	(1).	(2).	(3).	(4).	(5).	(6).	(7).	(8).	(9).	(10).	(11).
Length . . .	116	108	104	112	101	119	92	60	125	116	126
Height . . .	76	74	73	84	71	81	72	43	92	81	87
Thickness of one valve	22	21	19	26	17	21	22	11	27	23	27

Comparison with Uitenhage Species.—The Pseudo-quadratae have hitherto been represented in the South African Cretaceous by two species from the Sundays River Beds, the age of which has been shown to be Upper Valanginian by L. F. Spath (1930, p. 132). These are *T. herzogi* (Goldfuss) and the less common *T. holubi* Kitchin, the latter the genotype of *Steinmanella*; both species have been described and figured by Kitchin (1908, pp. 101–110).

The shells in the present collection are quite distinct from the two Uitenhage species, though clearly allied to both. I have been able to compare them directly with the examples figured by Kitchin, including the holotype of *T. holubi*, as well as with several other specimens from the Uitenhage division. The Zululand shells are of roughly the same size as the two Uitenhage species, and agree in having robust, little inflated, sub-quadrate valves, with wide area and coarsely costate flank, besides being strikingly similar in the general character of form and sculpture. They differ, however, from both species in outline, in many details of ornamentation, and notably in the nature of the area in its adult stage. In so far as outline and costation are concerned they represent a species intermediate in character between the two Uitenhage species, exhibiting a combination of features which invites comparison with both of them.

The Zululand shells have the same general proportions as *T. holubi*, and are distinctly shorter than *T. herzogi*, which is the most elongate species in the sub-genus. The ratio of length to height is 1:0.7 in *T. holubi* and in the Zululand shells, and 1:0.55 in *T. herzogi*. In this respect they approach the relatively short *T. transitoria* and other species.

In the character of the anterior part of the shell the Zululand specimens are distinct, but features of both Uitenhage species are recalled. In *T. herzogi* the anterior margin is broadly and evenly convex from the umbones downwards, and merges quite gradually into the ventral margin, with little or no sign of anterior truncation and without a flattened frontal face; the general trend of the anterior margin, which at first is gently convex forwards, is *steeply downwards and backwards* from the umbones. In *T. holubi*, on the other hand, the anterior margin is very slightly convex to almost straight, and is directed vertically from the umbones or *inclined forwards* at a steep angle to meet the ventral margin in a well-rounded but distinct angle; the anterior is markedly truncate, and a narrow, *flattened frontal face* is developed. In the holotype of *T. holubi*, *i.e.* the only specimen figured by Kitchin (1908, p. 103, pl. iv, figs. 2, 2 a), the

anterior margin is inclined forwards at a steep angle, but in other specimens it is directed almost vertically. In the Zululand shells the anterior margin is gently and evenly convex, with about the same curvature as in *T. herzogi*, and the general trend of the anterior margin is very steeply downwards and backwards; the anterior margin meets the ventral margin in a very much rounded, obscure, or almost distinct angle; in the above features these shells resemble *T. herzogi* very closely, though in the latter there is no sign of the antero-ventral angle. On the other hand, the anterior is markedly truncate in these shells, a narrow, flattened, or only slightly convex frontal face being developed as in *T. holubi*; but the frontal face is ornamented only with very oblique growth lines, whereas in *T. holubi* there are coarse folds which blend with the flank costae.

In the character of the costae on the flank of the valves the Zululand specimens are again distinct, features of both Uitenhage species being recalled. In *T. herzogi* the flank is ornamented with almost straight, regular, oblique, coarsely tuberculate costae, with the tubercles close to one another; the costae become somewhat irregular close to the ventral border only; the costae close to the anterior margin are inclined steeply forwards, in the mid-region they are directed vertically, and in the posterior half are inclined steeply backwards. In *T. holubi*, on the other hand, the costae are much less regular, and in the mid-region are broken up into widely separated coarse tubercles; the rows of tubercles or costae are regularly curved forwards when traced downwards from the margin of the area, and are never directed backwards; towards the ventral border the tubercles are crowded, and a tendency to elongation parallel to the shell margin exhibits itself, so that with senility crowded growth ridges are dominant at the ventral border. In the Zululand shells the costae have the general character of those of *T. herzogi*, i.e. they are regularly tuberculate with close-set and evenly spaced tubercles; but the costae are either nearly straight or curve forwards when traced downwards from the area, as in *T. holubi*. It should be pointed out, however, that while the forward inclination of the costae is characteristic of *T. holubi* the costae are not necessarily as irregular or the tubercles in the mid-region as widely spaced as in the holotype of that species. I have before me a specimen (A.M. 2356) from the Sundays River Beds which, while agreeing with the type of *T. holubi* in other respects, has fairly regular costae in the mid-region with the tubercles moderately close to one another; as the specimen differs from the holotype also in that the anterior

margin is vertical, it is, however, possible that it belongs to a distinct variety.

It is in the character of the area, however, that the Zululand shells are strikingly different from both Uitenhage species. In the *Pseudo-quadratae* the early neanic stage of the area is crossed by transverse ribs continuous with those of the flank; these soon pass into a "trituberculate" stage in which the area is characterised by bearing three longitudinal rows of tubercles representing marginal, median, and inner carinae, the area being otherwise smooth except for growth lines. At some distance from the umbo coarse crowded concentric costellae make their appearance and these characterise the adult stage. As Kitchin (1908, pp. 108-110) has pointed out, the *Pseudo-quadratae* pass through a similar sequence of developmental phases, but these phases are not reached by all the species at the same time. In *T. herzogi* the "trituberculate" stage may be seen to pass into the "costellate" stage by the progressive transverse elongation of the tubercles in the three sets, and the change takes place before mid-growth. In *T. holubi* the change takes place after mid-growth and is more abrupt, but the three rows of tubercles persist until the "costellate" stage is reached. In the Zululand shells the marginal and median rows of tubercles die out at some time before mid-growth, while the inner row is more persistent, but the "trituberculate" stage is not replaced by a "costellate" stage, the greater part of the area being merely transversely striate with growth lines; the growth lines are hardly stronger on the area than they are in the intercostal interspaces on the flank. In S.A.M. 10786 the marginal and median rows of tubercles persist to about 40-50 mm. from the umbones and the inner row to about 55 mm., while costellae have not made their appearance even at 100 mm., about 10 mm. from the damaged posterior border. In the larger weathered specimen from L14 there are, however, indications of costellae on the lower side of the area at about 120 mm. from the umbo, and though their character is a little uncertain it would seem that they do make their appearance with senility. This delay in the appearance of the costellae is one of the most noteworthy features of the Zululand shells, and they would appear therefore to be more primitive—though not necessarily earlier in age—than the two Uitenhage species and their allies in S. America and India, in all of which racial degeneracy is in evidence (Kitchin, 1908, p. 110).

Comparison with East African Species and with T. transitoria Steinmann.—The *Pseudo-quadratae* have been recorded from the

Trigonia schwarzi Beds in Tanganyika by Lange (1914, pp. 237-239), who described a new species, *T. hennigi*, as well as certain shells which he identified with the very widespread South American species, *T. transitoria*. One is inclined to be suspicious of the identification of an East African *Trigonia* with a South American species, and the suspicion is perhaps strengthened by the absence of that species from the Uitenhage Series. A comparison of the set of shells before me with the descriptions and figures given by Lange has led me to conclude that Lange's *T. transitoria* should be included in *T. hennigi*, and to accept identification of the Zululand shells with that species.

Lange had four specimens before him, from three separate localities, and three of these specimens were identified with *T. transitoria*. The fourth specimen, which is from a different locality to the others, is a right valve, and was made the holotype of *T. hennigi* Lange in spite of the fact that the upper part of the flank is considerably denuded, as is shown clearly enough in the good photograph provided (*ibid.*, pl. xix, fig. 3). The type of *T. hennigi* is said by Lange to differ from the other specimens in that the rows of tubercles are straight, the ventral margin is less convex, and the inflation of the valves extends further back, and it is stated that there is a smooth region completely devoid of tubercles below the dorsal area. The principal feature which no doubt prompted Lange to recognise a distinction, is the fact that the costae or rows of tubercles are traceable upwards from the ventral margin for not much more than one-third of the total height of the valve, and are not seen to reach the margin of the area in the anterior half of the shell. The figures given fail to bring out any real difference in the curvature of the ventral margin, and the slight difference in the inflation mentioned can hardly in itself be of much significance. The photograph of the type, however, clearly shows that the whole of the upper two-thirds of the anterior half of the valve has suffered severely from either solution of calcite or wear, and that the costae cease as this denuded region is approached. I have no doubt that prior to weathering the costae passed up to the border of the area, as in all other species in the sub-genus, and it is highly probable that they were gently curved. The recognition of this fact removes any real reason for separating from *T. hennigi* the other East African shells studied by Lange (*ibid.*, p. 237, pl. xix, fig. 2), for the figures given are in general agreement in other respects, the outlines being almost identical, and the ornamentation of the same type throughout in so far as it can be discerned.

The East African species *T. hennigi* is then a well-marked type

characterised by the forward curvature of the costae and the slightly receding anterior margin. The anterior margin is very gently convex and almost vertical, but traced downwards becomes considerably more convex as it passes back into the ventral margin.* The costae are slightly curved with forward convexity, but their lower portions may be almost straight, and the shorter posterior costae are not directed backwards. These features as well as the size and proportions of the valves very strongly suggest identity with the Zululand shells, described above. The type of *T. hennigi* is further said to have a completely smooth frontal face perpendicular to the flank, and the area in the adult stage is said to be apparently ornamented only with growth lines, points which characterise the Zululand shells also, though it should be mentioned that on Lange's figure there is some slight indication of concentric corrugation towards the posterior. Lange's "*T. transitoria*" is only briefly described, and it is stated that the broad area is transversely ribbed; on the single figure given the area is unfortunately very worn, but it would appear that coarse costellae are not developed, and the transverse ribs mentioned are almost certainly no more than growth lines. I can find no grounds for separating the Zululand shells from *T. hennigi*, though it is to be regretted that the type of the latter—as well as the other East African shells—are not sufficiently well preserved for a complete comparison to be made.

From *T. transitoria* Steinmann (1882), which has been described from the Neocomian of South America from Patagonia to Bolivia, *T. hennigi* differs in several respects. The former is characterised notably by the larger number of costae and the coarse crowded transverse costellae which characterises the area for the greater part of its length. The difference in character will be readily appreciated by comparing the figure of the finely preserved Zululand shell, S.A.M. 10786 (pl. xliii, figs. 1–3), with published figures of *T. transitoria* (refs. in Lange, 1914, and Kitchin, 1908), and with Lange's "*T. transitoria*" (Lange, 1914, pl. xix, fig. 2).

Comparison with other Species.—The notable absence of costellae on the area, except perhaps with senility, serves to distinguish *T. hennigi* from the rather smaller *T. mamillata* Kitchin (1903, p. 100, pls. ix, x) from the Oomia Beds of Cutch, in which costellae appear at an early stage and are remarkably coarse; in other respects the species are very similar, though the anterior face is less clearly marked off in the Indian species. The absence of costellae serves also to distinguish the species from *T. vyschetskii* Cragin (1905, p. 56, pls. viii,

ix) from Texas, and the South American *T. neuquensis* Burckhardt (see Kitchin, 1908, p. 108), both closely allied to *T. transitoria*.

Sub-genus *Rutitrigonia* van Hoepen 1929.

Three generic or sub-generic terms have recently been proposed for concentrically ribbed *Trigoniae* from the Indo-African region, viz. *Rutitrigonia* van Hoepen and *Pleurotrigonia* van Hoepen (1929, pp. 31-34) for species from Zululand, and *Indotrigonia* Dietrich (1933, p. 30) for the Indian and East African *T. smeei* J. de C. Sowerby. The type species of these three groups have in common the possession of a flank ornamentation of coarse smooth concentric ribs as in the Jurassic Costatae, but are distinguished from the latter in that dorsal ornamentation of a longitudinal character, if present at all, is confined to the neanic stage, the area through the period of middle growth and maturity being either smooth or traversed by concentric costellae. In the type of *Indotrigonia*, as has been pointed out by Kitchin (1903, pp. 39, 42-44, 113) and Dietrich (*loc. cit.*), there is fine evidence of descent from the Costatae in the differentiated juvenile ornament of smooth concentric ribs ceasing posteriorly at a narrow ante-carinal space, beaded dorsal carinae, and fine longitudinal granular ridges on the area. In the type of *Pleurotrigonia* the evidence points likewise to Costate ancestry, as is pointed out elsewhere in this paper; the juvenile stage having concentric ribs, ante-carinal space, and sharp marginal carina, and longitudinal ornament on the dorsal area. *Indotrigonia* and *Pleurotrigonia* are, however, readily distinguishable on adult characters; the smooth area, smooth ante-carinal space, and raised marginal fold of the latter group contrasting strongly with the concentric costation, which in *Indotrigonia* tends to obliterate the distinction between area and flank. These characters, together with the marked posterior extension and anterior truncation in *Pleurotrigonia*, justify the recognition of two sub-genera which presumably represent divergent stocks from a common source.

The species described below, *T. pongolensis* sp. nov., is strikingly similar to, and apparently closely allied to, the East African *T. krenkeli* Lange, which has been compared with *T. smeei* by both Lange and Dietrich, and, indeed, included in *Indotrigonia* by the latter author. The new species differs, however, from the type of *Indotrigonia* in that the costae after the youthful stage do not pass over on to the area, which is smooth, and in the highly significant fact that the juvenile stage is not characterised by a sculpture of Costate type

but by a simple series of coarse concentric ribs which pass uninterruptedly across the area. The same features are described by Lange (1914, p. 231) in the case of *T. krenkeli*, and I have no doubt that these two species are only superficially similar to *T. smeei* and can only be remotely related, and, indeed, may be of quite a different origin. I am well aware that certain other species have been included in *Indotrigonia* or compared with *T. smeei* that differ from that species in important respects. *T. crassa* Kitchin (1903, p. 44, pl. iv, figs. 4-6; pl. v, figs. 1-3) fails to exhibit the primitive Costate ornamentation, though in adult features strikingly like *T. smeei*, and the failure may be ascribed to loss of the Costate characters at such an early stage that they have not been detected, though this is by no means certain. *T. dietrichi* Lange (1914, p. 233, pl. xx, fig. 7) has been included in *Indotrigonia* by Dietrich (1933, p. 32, pl. ii, figs. 38-41), in spite of smaller size, crescentic form, and smooth area, on account of the finely developed juvenile Costate stage described by the latter. The inclusion of *T. crassa* and *T. dietrichi* in *Indotrigonia* is justified in view of the fact that they have in common with *T. smeei* an essentially concentric flank ornamentation of smooth costae and a known or presumed Costate juvenile stage.

With *T. pongolensis* and *T. krenkeli*, however, the position is somewhat different. The fact that in these species an initial concentrically ribbed area soon passes into a smooth condition, which is maintained to full maturity, indicates descent from a type which was concentrically ribbed in the adult stage. It might be the case that we have in these two species a development from forms like *T. smeei*, as has been assumed by Dietrich (*loc. cit.*), but there are several considerations which have led me to believe that they are of quite different origin, and the remarkable similarity between them and *T. smeei* would therefore be a striking example of convergence in evolution. The early loss of the concentric ribbing of the area would point to a remoteness in the supposed relationship between these species and *T. smeei*, which it is difficult to reconcile with the fact that *T. smeei* is known to persist into the Zone of *T. schwarzi* (Lange, 1914, p. 228; Kitchin, 1929, p. 195), from which *T. krenkeli* was derived (Dietrich, 1933, pp. 31-77). The failure of the costae to maintain a course strictly parallel to the ventral border—they bend upwards when traced posteriorly—indicates an evolutionary trend which is not in evidence in *T. smeei*. On the other hand, a primitively concentric ornamentation, with ribs passing from the flank across the area, is characteristic of the neanic stage of other

groups of *Trigoninae*, e.g. *Iotrigonia* (*T. vau*, *T. v-scripta*), *Megatrigonia* (*T. conocardiiformis*) whose relationship to the Costatae has not been suggested. A remote kinship with these groups is possible, in spite of the very different adult features.

T. pongolensis and *T. krenkeli* have several features in common with the species included in the *T. excentrica* Group, for which the sub-generic term *Rutitrigonia* appears to be available. The heterogeneous character of the group of the Glabrae (=Laeves) of Agassiz was realised by Lycett (1872, p. 7) and has been referred to by various workers, e.g. Bigot (1892, *Mém. sur les Trigonies*, *Mém. Soc. Linn. Norm.*, xvii), who proposed the sub-divisions Semi-Laeves, Gibbosae, and Excentricae, the two latter for sub-groups recognised by Lycett. Kitchin (1903, pp. 52, 60-62) has pointed out that the sub-division appears to be a natural one. Deecke's term *Laevitrigonia* (1925, p. 68), proposed for the Glabrae, should be confined to the section Gibbosae, since Dietrich (1933, p. 35) cites *T. gibbosa* Sow. as genotype, this being the first citation of genotype that I have been able to discover. The distinction between the typically Jurassic Gibbosae and the Cretaceous Excentricae has been drawn by the authors cited above and need not be elaborated here.

The term *Rutitrigonia* was proposed by van Hoepen (1929, p. 31) for a new species of the *T. excentrica* Group from the Cretaceous of Zululand, with the rank of a genus and as the sole representative of a sub-family Rutitrigoniinae. The type species, *R. peregrina* van H., is characterised by the following features, which have been briefly summarised also by Crickmay (1932, p. 459):—

Shell moderate in size, inflated and highest in the anterior half, posterior part narrowed and produced. Anterior margin broadly convex, merging quite gradually into the long convex ventral margin; postero-dorsal margin relatively long, concave, sloping gradually, downwards so as to meet the ventral margin in a well-rounded posterior extremity. Flank ornamented with numerous rather fine, smooth, concentric costae. Area relatively narrow, smooth, slightly convex in cross-section, indistinctly demarcated from flank and escutcheon, without a longitudinal furrow; the marginal and inner carinae are represented only by convexities, the former very indistinct; escutcheon rather narrow, concave, smooth. Neanic stage with fine concentric ribs which at first persist as far as the postero-dorsal margin, bending sharply upwards at the margin of the area. Dentition relatively delicate, the left central tooth broad.

The features exhibited by this species are in broad essentials

identical with those of *T. excentrica* Parkinson, as described by Lycett (1872-1879, p. 94), noteworthy being the similarity in outline, the smooth concentric costae, the indistinctly limited smooth convex area, and the fine concentric ribs which are said to cross the entire valve near the umbo, the latter characteristic being displayed in one of the accompanying figures (*ibid.*, pl. xx, fig. 6). The application of van Hoepen's term *Rutitrigonia* to the Excentricae is therefore amply justified, the genotype being, indeed, a fairly typical member of the latter group; it is perhaps to be regretted that the type of the Linnaean group, which now replaces the long-established Excentricae, is a new species from a remote South African locality, and not the English species which gave its name to the Excentricae and which has been very well described by Lycett and others. Van Hoepen (1929, p. 33) cites as species of *Rutitrigonia*, *T. laeviuscula* Lycett and *T. longa* Agassiz, both of which were associated with *T. excentrica* by Lycett (1872-1879, pp. 7, 97). It would appear also that the East African Neocomian *T. schwarzi* Müller (Lange, 1914, p. 231, pl. xix, figs. 4, 5; Dietrich, 1933, p. 35, pl. iii, figs. 52, 53) belongs to *Rutitrigonia*, the concentrically ribbed umbonal region having been finely figured by Dietrich, and the flank and area having the essential characteristics of the Excentricae; the species was placed in the sub-genus *Laevitrigonia* by Dietrich, but has no affinities with the Gibbosae for which that term must be used. The rather similar *T. janenschii* Lange and *T. bornhardti* Müller from East Africa belong to the same group.

It is not without some hesitation that I associate with *Rutitrigonia* the species *T. pongolensis* sp. nov. and *T. krenkeli* Lange. The concentric ribbing of the neanic stage is of such a character in both these species as to exclude them from *Indotrigonia* in spite of adult similarities, and *Rutitrigonia* is the only term available for species of *Trigonia* having features at all like those of these two species. The association of *T. pongolensis* with *Rutitrigonia* seems to be justified for the following reasons: the anteriorly rounded and posteriorly produced form; the concentric smooth costae confined in the adult to the flank; the smooth, moderately wide area without carinae; the narrow smooth escutcheon; the neanic ornament of concentric ribs which pass on to the area. These features include the essential characters of the Excentricae. On the other hand, *T. pongolensis* is distinguished from *Rutitrigonia* in certain particulars. The concentric ribbing in the neanic stage is of a remarkably coarse character, and the ribs do not bend acutely at the lower margin of

the area, as do the very much finer juvenile ribs of *R. peregrina* (which "bend back with a swing to cross the area transversely"), *T. schwarzi* (Dietrich, 1933, pl. iii, figs. 52, 53) and other species. The costation of the flank is of a somewhat different character, for at an early stage the costae assume an obliquity, the most notable feature being the posterior bending up of the costae; in *Rutitrigonia* the costae tend to be approximately parallel to the ventral margin throughout, though it should be pointed out that it has been observed that the costae are in part inclined to the growth lines in several species, e.g. *T. excentrica* (Lycett, 1872-1879, p. 94), *T. schwarzi* (Lange, 1914, pl. xix, fig. 4), so that this distinction must not be regarded as of too great importance. The above-mentioned features, which serve to distinguish *T. pongolensis* from typical *Excentricae*, do not seem to be sufficient to warrant the proposal of a subgeneric name, and the species is included provisionally in *Rutitrigonia* with which it has many features in common. *T. krenkeli* Lange is probably closely related, and is accordingly removed from *Indotrigonia* and also placed provisionally in *Rutitrigonia*.

Trigonia (Rutitrigonia) pongolensis sp. nov.

(Plate XLI, figs. 5, 6; Plate XLII, figs. 5-7.)

Material.—Two specimens collected by Dr. S. H. Haughton and Dr. A. W. Rogers on the Mfongosi tributary of the Pongola River, both from Z2. The holotype is an almost complete left valve which has been developed to show the teeth. The paratype has the valves closed and is somewhat damaged posteriorly, but shows the character of the ribbing in the vicinity of the umbones. Both specimens are comparatively well preserved, but the removal of matrix from the surface has been somewhat difficult and I am not quite certain of the exact character of the inner carina and its neighbourhood.

Description of the Species.—Shell of medium size, considerably longer than high, with the umbo at about a fourth of the length from the anterior end, highest at the umbo, the posterior part slightly narrowed. Umbo moderately prominent, well incurved and distinctly opisthogyrous. Shell evenly and moderately inflated, the greatest inflation being in front of the middle. Anterior margin sloping steeply downwards from the umbo, at first moderately convex, becoming more convex below the middle and then merging gradually into the long, gently convex ventral margin. Postero-dorsal margin relatively long, straight, sloping backwards at a small angle, meeting the inclined

and nearly straight posterior margin in a very obtuse angle. Posterior margin relatively long, meeting the ventral margin in a rounded postero-ventral angle, which at middle growth is very obtuse and much rounded, but which becomes progressively more acute with continued growth; in middle growth the posterior margin is distinctly convex and merges almost gradually into the ventral margin, but the posterior margin becomes almost straight at a later stage; at about 45 mm. from the umbo the posterior margin is about perpendicular to the ventral margin, but at a later stage these margins are inclined at an angle less than 90° .

In front the flank bends down rather rapidly to the anterior margin, so that there is a narrow ill-defined steeply inclined anterior face. Area moderately wide, becoming progressively wider towards the posterior margin, inclined to the flank at an obtuse angle, separated from the flank by a broad convexity of the valve surface, the convexity becoming progressively wider when traced backwards; towards the umbones the area is more steeply inclined. Lower part of the area gently convex, upper part gently concave, there being either no trace of the longitudinal furrow in the posterior part of the area (paratype), or an obscure broad furrow well above the middle (holotype). Escutcheon elongate, narrow, very indistinctly separated from the area by a broad convexity which persists to the postero-dorsal angle.

Juvenile ornamentation of a few extremely coarse, elevated, smooth concentric ribs separated by rather narrower interspaces, the ribs passing over an obscure marginal angle on to the area, bending slightly on doing so. There are about 5 ribs in a distance of 8 mm. from the umbo.

Adult ornamentation of coarse, elevated, rounded, smooth more or less concentric costae, separated by wide concave interspaces. The costae are at first inclined to but later about perpendicular to the anterior margin, and sweep round in a broad curve so as to be nearly vertical as they approach the margin of the area in the middle part of the valve. The costae are slightly inclined to the growth lines at the anterior end, and when traced backwards appear to cut across the posterior part of the valve. The costae cease more or less abruptly at the commencement of the anterior slope, the narrow anterior face having only growth lines. Traced backwards the costae at first pass on to the lower part of the area to die away gradually thereon; at a later stage, 15-35 mm. from the umbo, the costae cease on the marginal fold; with maturity the costae fail to reach the fold. The area and

escutcheon after the youthful stage are ornamented only with growth lines.

Hinge of the left valve with a broad triangular central tooth, deeply embayed below and furrowed on the summit, strongly grooved on the sides. Left anterior tooth nearly vertical, grooved on the posterior side.

Dimensions expressed in millimetres:

	Holotype.	Paratype.
Length	60	60?
Height	44	48
Thickness of one valve .	12	13

Remarks.—Reasons have been given above for referring this species to *Rutitrigonia*. The species appears to be very close to the East African *T. krenkeli* Lange (1914, p. 230, pl. xx, fig. 2) which was included in *Indotrigonia* by Dietrich (1933, p. 31). The latter species was founded on a single imperfect left valve which was said to come from the *T. schwarzi* Beds in all probability; Dietrich recorded the species from the same beds, but has not figured additional examples. Lange described a narrow, smooth, perpendicular, anterior face, and the earlier ribs are said to traverse the area without interruption; the area is said to be smooth for the greater part of its length and traversed by a shallow furrow, while the escutcheon is also smooth. The figure given shows a medium-sized posteriorly produced valve, ornamented with widely spaced strong smooth costae which bend upwards on the broad marginal fold of the area; the area is shown to be steeply inclined, and the escutcheon must be narrow. These features and the figure indicate that *T. krenkeli* and *T. pongolensis* are very closely allied. The species appear to differ only in minor respects, *T. krenkeli* having a much more steeply inclined area and *T. pongolensis* having the ventral and postero-dorsal margins more nearly parallel.

Sub-genus *Pleurotrigonia* van Hoepen 1929.

The sub-genus *Pleurotrigonia* was proposed by van Hoepen (1929, p. 33) with the rank of a genus and as the sole representative of a sub-family Pleurotrigoninae, for the single Zululand species *T. blanckenhorni* Newton (1909, p. 40, pl. v, figs. 1-4). The type species has been described by both authors and a brief diagnosis of the group has been published by Crickmay (1932, p. 459).

The sub-genus is characterised by the following features:—

Shell moderate in size, triangular in outline and not much inflated, with the umbo near the anterior end and the posterior produced. Anterior margin gently convex, with a narrow, elongate, steep, anterior face (lunule) separated from the flank by a well-marked anterior carinal fold. Postero-dorsal margin long, more or less straight, sloping postero-ventrally to meet the ventral margin in a rounded angle. Umbo weakly incurved, not appreciably opisthogyrous. Dorsal area smooth, moderately wide, with an obscure longitudinal furrow, longitudinally ribbed in the youthful stage only; marginal carina sharp and nodose near the umbones, passing posteriorly into a conspicuous, broad, rounded fold, relatively straight. Escutcheon steep, elongate, very narrow; inner carina sharp near the umbo. Flank ornamented with strong, rounded, smooth, concentric costae. Dentition relatively massive, the left central tooth narrow and only obscurely bifid.

Newton was uncertain of the relations of the type species, but suggested that it was an intermediate form coming between the Clavellatae and Costatae. That *Pleurotrigonia* is a derivative of the Costatae, can hardly be doubted on the evidence of better specimens; the smooth concentric costae, the ante-carinal space, the youthful ornament of sharp carinae and dorsal longitudinal ribs are proof of such a relationship; the sub-genus would appear to be an offshoot of the Costatae characterised by the complete disappearance, after the neanic stage, of the dorsal ornamentation of longitudinal nodose carinae and costellae, the marginal carina remaining only as a broad conspicuous fold.

The typically Jurassic Costatae appear to have given rise to a number of divergent types towards the close of that period and in the Neocomian, types having in common a trend towards obliteration of the longitudinal ornamentation of the dorsal area, unaccompanied by any radical departure from the essentially concentric character of the flank sculpture. Derivation from the Costatae is indicated in many cases by the presence of longitudinal carinae and costellae, often nodose, in the early neanic stage. The sculpture of the flank, though remaining essentially concentric, may be variously modified, but the costae do not become typically nodose or tuberculate. This rather heterogeneous group of costate-derivatives, with concentric flank ornament and smooth or concentrically ornamented areas, is particularly well represented in the Oomia Beds of Cutch (Kitchin, 1903, pp. 39–60) and includes the species *T. smeei* J. de C. Sowerby,

the genotype of *Indotrigonia* Dietrich (1933, p. 30). *Pleurotrigonia* falls in the same broad group, though of post-Neocomian age. Some of the Indian species, as well as *Sphenotrigonia* nov., are related types marked in addition by the weakening or even obliteration of the concentric costation, giving rise to extraordinarily smooth *Trigoniae* that would formerly have been placed in the heterogeneous group of the *Glabrae*; the tendency to smoothness with maturity is exhibited also in *Pleurotrigonia*.

Trigonia (Pleurotrigonia) blanckenhorni R. B. Newton.

(Plate XLII, figs. 1-4.)

1909. *T. blanckenhorni* Newton: Trans. Roy. Soc. S. Afr., vol. i, p. 40, pl. v, figs. 1-4.

1929. *Pleurotrigonia blanckenhorni* (Newton): van Hoepen, Kryt-fauna Soeloeland, Trigoniidae, p. 33, pl. vii, figs. 17-19.

Material.—Four left valves, collected by Dr. S. H. Haughton and Dr. A. W. Rogers at a locality (Z25) south-east of Mokatini, south of the big bend of the Pongola River. Two of these shells are complete and three moderately well preserved. The early neanic stage is not present.

Remarks.—The species was founded on three right valves described by Newton as fragmentary, and van Hoepen's account was based on three imperfectly preserved left valves. The species has been well described by these authors in so far as the available material enabled them to do so. The specimens before me agree pretty well with the descriptions and figures given by both authors, and I have little doubt that the same species is represented. The new specimens, however, would appear to be more finely preserved than those hitherto known, and some additional observations can be recorded.

The anterior region is described by Newton as follows: "Anterior margin abrupt, deep, smooth, lamelliform," and the concentric costae of the flank "proceed to within a short distance of the outer margin, where they curve upwards by tapering terminations and become merged in the growth lamellae of the shell." Van Hoepen refers to "a long narrow lunule which begins at the umbo and ends at the lower end of the anterior margin," and the costae "begin at the thickened margin of the lunule or a little in front of it." Neither description is quite adequate and the published figures do not clearly convey the true character of the anterior region. In the specimens

before me the gently convex flank of the valves is separated from a narrow elongate anterior face or lunule by an abrupt change of slope, the anterior face being nearly perpendicular to the plane of the valves and to the surface of the flank. The anterior face forms with the flank a sharp anterior carina, which, like the anterior margin, is only very gently convex forwards, so that the valve is truncate in front. The anterior carina is convex as seen from the front, the anterior face being widest in the middle and narrowing gradually towards both the umbo and the rounded antero-ventral corner. The anterior carina is raised and, in the specimens before me, ornamented with a row of conspicuous, large, elevated, rounded, or pointed tubercles; the tubercles are more or less transversely oval in section, with the longer axes parallel to the lines of growth. In many cases each of the costae merges into a tubercle at the anterior carina, but one tubercle may correspond to two costae, or one of the costae may fail to reach the carina, the corresponding tubercle being absent. These tubercles, a very conspicuous feature of the shells in the present collection, were not mentioned by Newton and van Hoepen, and are barely indicated on the figures, their apparent absence being presumably due to the state of preservation of the originals. The thickness of the shell substance is so great that the anterior carina is not noticeable from within as a fold of the valve; the anterior face is strictly speaking only a widely bevelled anterior margin.

Newton observes that the costae of the flank "proceed from" the marginal carina, and the accompanying drawings bear out the statement to some extent, though it would appear that the earlier costae just fail to reach the carina. Van Hoepen states that the costae "do not reach the marginal carina in our left valves." In the specimens before me the costae near the umbones, 10-15 mm. from the apex, terminate posteriorly in slight swellings, leaving a narrow, concave ante-carinal space, which is crossed by growth lines quite strongly concave towards the ventral margin. Traced ventrally the ante-carinal space becomes progressively wider and relatively shallower, the costae dying out gradually at some distance from the carina, and the growth lines crossing the space become less embayed, while the costae themselves tend to pass into broad weak corrugations.

Newton and van Hoepen were not able to describe the earlier part of the area, the latter merely observing that the marginal carina is at first sharp. One of the specimens in the collection before me shows the following essentially Costate youthful features. The marginal carina is sharp, elevated, and very conspicuous for about

15-18 mm. from the umbo, and at 10-15 mm. is unmistakably ornamented with fine transverse nodes. The area is gently and evenly concave, at least the upper half being ornamented with longitudinal ribs. I have not been able to clean the surface thoroughly for fear of causing damage, but at 10-18 mm. the upper half of the area has unmistakable rounded longitudinal ribs, 3-4 in number, which gradually die away at about 20 mm.; I strongly suspect that the lower half of the area is similarly ribbed. The inner carina is raised and very conspicuous for about 15 mm., and is ornamented with fine, rounded, closely set nodes; at about 10 mm. there is a similar, narrow, raised, similarly nodose costella immediately below the inner carina, and separated from it by a deep narrow furrow, with a suggestion of a similar costella below it; in a perfect specimen it is probable that the area would be found to have a number of raised nodose costellae, which become smooth and finally die out when traced posteriorly at about 20 mm. from the umbo.

The escutcheon is very narrow and at first very strongly marked off from the area by a very abrupt descent of the valve surface, the inner carina being very sharp. Traced posteriorly after 15 mm., the escutcheon and area gradually merge into one another. At first the escutcheon is deeply grooved above the middle, the almost vertical lower part being rather sharply distinct from a very narrow shelf-like upper margin. Newton states that the escutcheon is insignificant, and even in his comparatively large shell only about $\frac{1}{2}$ mm. wide.

The identification of the specimens before me with Newton's types is greatly strengthened by the fact that the former were found associated with *Exogyra* cf. *conica* (J. Sow.) and *Trigonarca* cf. *ligeriensis* (d'Orb.), two species which occur at the type locality, and with *Veniella etheridgei* Newton, a characteristic Albian species from localities farther south.

Sub-genus *Sphenotrigonia* sub-gen. nov.

The new sub-generic term *Sphenotrigonia* is here introduced for a very remarkable new species of *Trigonia* from the Lower Cretaceous of Northern Zululand, having the size and something of the shape of a *coup-de-poing*. The genotype, *T. frommurzei* sp. nov., is described below. The species is characterised by the remarkably long and almost perfectly straight postero-dorsal margin, the long and almost straight central margin, the excessively produced straight and pointed posterior region, the very marked anterior truncation, which

combination of characters gives the shell a very distinct shape like that of a wedge; to these characters is added the complete disappearance of costae and dorsal carinae after the neanic stage. The hinge is in all essentials that of a *Trigonia*.

The unusual form of the species led to the assumption in the field, and until the development of the hinge in suitable specimens had been completed, that a second South African species of the aberrant genus *Seebachia* had been discovered, an interesting comparison, since the genotype of the latter has been placed in the Trigoniidae by certain authors. The general resemblance between *T. frommurzei* and *Seebachia bronni* is indeed very remarkable, in spite of the presence of a number of external features which serve to distinguish them, and a very different dentition having only superficial points in common with *Trigonia*. Since *Seebachia bronni*, until recently the only known species, has not been described since 1881, and is rare in collections, and has been quoted as a member of the Trigoniidae as recently as 1925, it is perhaps opportune to point out the characters which serve to exclude *Seebachia* from that family.*

* The Systematic Position of *Seebachia bronni* (Krauss). The genus *Seebachia* was proposed by Neumayr (1881, p. 274) for a species from the Upper Valanginian Sundays River Beds in South Africa originally described as an *Astarte* by Krauss (1850, p. 449, pl. xlviii, fig. 1, a-e), *A. bronni*. Krauss regarded the species as nearest to *Astarte* but probably the representative of a new genus "between" *Astarte* and *Trigonia*. Neumayr saw in the peculiar elongate form and grooved teeth a great distinction from *Astarte*, and while admitting that the character of the teeth recalled *Trigonia* in certain respects, expressed the opinion that the genus was not closely related to the latter.

Both Krauss and Neumayr gave excellent figures showing the internal and external features, Krauss of both valves, Neumayr of a right valve. These figures, together with the descriptions that accompany them, are sufficient to indicate whether the species has or has not affinities with *Trigonia*. It may be pointed out that there appear to be very few specimens of *Seebachia bronni* in existing collections; in addition to the two specimens known to Krauss, and the sight valve figured by Neumayr, I have been able to trace only three specimens of the species; one in the Albany Museum in Grahamstown (A.M. 2418), a finely preserved specimen with the valves closed from the Sundays River, one in the South African Museum in Cape Town (S.A.M. 4676), from Picnic Bush on the Zwartkops River, a left valve which with much labour was developed to show the dentition; and a specimen in the Geology Department of the University of Cape Town.

That *Seebachia bronni* does not belong to the Trigoniidae is shown clearly enough by the character of the hinge, and is borne out by other characteristics of the shell. In the left valve there are two teeth only, the larger and posterior of the two, which is in the position of the bifid tooth of a *Trigonia*, is oblique, elevated, narrow, and entire. In the right valve there is a large elevated tooth

The sub-genus *Sphenotrigonia* sub-gen. nov. (Type: *T. frommurzei* sp. nov.)

Diagnosis.—Shell large, massive, elongately triangular in outline, highest and most inflated close to the anterior end, and tapering very gradually by diminution in height and thickness to a posterior point. Anterior end markedly truncate, with a more or less vertical carinal fold and anterior margin, and a flattened anterior face. Posterior very much produced, the postero-dorsal and ventral margins very long and straight. Primitive ornamentation of oblique costae

reminiscent of the right anterior tooth of the latter genus and a narrow posterior tooth. Affinities with *Trigonia* were presumably suggested by the circumstance that both sides of the large right tooth and the opposed sides of the left teeth are strongly grooved, and it might be held that *Seebachia* is an aberrant Trigoniid in which (i) the posterior tooth of the left valve has disappeared and in which (ii) the left central tooth has become narrower so as to lose its bifid character, with a loss of the grooves on its posterior side. The remarkable stability shown by the *Trigonia* dentition throughout its Jurassic-Cretaceous existence should put us on our guard against such an interpretation, and it has been pointed out that transversely striate teeth are not the monopoly of that genus (Crickmay, 1932, p. 453).

The hinge apparatus is further distinguished from that of *Trigonia* in a very important way, which, in conjunction with the above features, renders any reference to the Trigonidae out of the question. In *S. bronni* the teeth are situated on a well-developed shelf-like hinge-plate, which has no counterpart in the *Trigoniae*; the difference is particularly evident in the right valve, where in *S. bronni* the large central tooth arises from the hinge-plate and receives no support directly from the floor of the valve cavity as is the case with the large anterior tooth of the *Trigoniae*. In addition *S. bronni* is characterised by a deeply concave lunule and denticulations within the ventral border, features which are not normal to the *Trigoniae*. *Seebachia* has, in recognition of these features, been placed in the Astartidae by various authors, e.g. in Zittel (1913, p. 473), by that authority on the *Trigoniae* the late F. L. Kitchin (1929, p. 194), and by Dietrich (1933, p. 42), who has described a second species from the *T. smeei*-Beds in Tanganyika.

Several authors have followed Stoliczka in including *S. bronni* in the Trigonidae. Stoliczka (1871, p. 312), acquainted only with the paper by Krauss (1850), listed the species in that family as a species of *Remondia*, a genus placed by its author Gabb (1869, p. 270) in the Trigonidae, but which has been clearly shown by Stanton (1897) to be in no way related to that family, having an essentially heterodont dentition with cardinals and laterals. *S. bronni* has nothing in common with *Remondia*, a genus of smaller shells with a different external appearance and quite different dentition, and it is difficult to understand Stoliczka's reference. Yet Cossmann (1912, pp. 59–84) in his work on the evolution of the *Trigoniae* not only accepted *Remondia* as an aberrant offshoot of the *Trigoniae* stock, but quoted *S. bronni* as a species of that genus, and Deecke (1925, pp. 58–59), in his catalogue of the *Trigoniae*, included both *Remondia* and *Seebachia*, which have been clearly shown by authors to belong elsewhere.

and dorsal carinae restricted to the neanic stage; costae slightly oblique, smooth (?), terminating posteriorly in a row of tubercles in advance of the marginal carina; marginal and inner carinae delicately beaded; dorsal area and escutcheon distinctly limited only in the neanic stage, the area with smooth (?) longitudinal costellae above the median sulcus and the escutcheon quite smooth. The greater part of the shell devoid of costae or dorsal carinae, ornamented only with growth lines, and broad concentric undulations towards the anterior end. Dorsal area beyond the neanic stage relatively narrow, passing imperceptibly into the flank, without carinae, ornamented only with growth lines, without escutcheon. Hinge massive, the right posterior tooth very long, and grooved only in the proximal half, with a corresponding very long left posterior socket.

There are not many *Trigonia* with which this well-marked type can be compared. There is a resemblance in certain respects to *Pacitrigonia* Marwick (1932) founded on an upper Senonian New Zealand species, which is ornamented only with growth lines beyond the neanic stage, and is a large posteriorly produced shell, with oblique costae nearly parallel to the posterior ridge or marginal carina only in the neanic stage. The New Zealand species, however, is compressed and does not possess the extraordinarily attenuated posterior and strong anterior carinal fold so characteristic of *Sphenotrigonia*. The area of *Pacitrigonia* is described as smooth and the escutcheon and inner carina are said to be absent, but the neanic stage of these appears to be unknown.

There is a considerable resemblance in general features between *Sphenotrigonia* and *Pleurotrigonia* van Hoepen. In each case the type species is characterised by marked anterior truncation and posterior elongation, a juvenile ornamentation of Costate character with non-nodose ribs, beaded dorsal carinae and ante-carinal sulcus, a relatively narrow area and narrow escutcheon. In *Sphenotrigonia*, however, the costation is essentially a juvenile feature, and the area becomes indistinct, whereas in *Pleurotrigonia* the costation, ante-carinal space, and broadly rounded carina are maintained until the adult stage, though obsolescent with full maturity. The excessively elongate and pointed posterior, very narrow and indistinct area, and smooth surface of *Sphenotrigonia* are peculiar features which appear to justify the proposal of a new sub-generic term for *T. from-murzei*.

The ornamentation of the neanic stage in *Sphenotrigonia* indicates

derivation from the Jurassic Costatae, shown by the beaded dorsal carinae, the longitudinal costellae at least on the upper part of the area, and the oblique smooth (?) costae which appear to be pseudo-concentric within a few millimetres of the umbo. The sub-genus is no doubt related to the heterogeneous assemblage of species, placed by Kitchin (1903) in the convenient group of Costate-derivatives, that are linked together by the possession of Costate neanic features, concentric adult ornamentation, and smooth areas. The marked anterior truncation and extraordinarily pointed posterior are quite unique, however. In some of the Indian species, as in *Sphenotrigonia*, the trend towards obliteration of longitudinal dorsal ornament has been accompanied by a trend towards weakening or even obliteration of the concentric costation of the flank, producing extraordinarily smooth *Trigoniae* which would formerly have been included in or associated with the admittedly very heterogeneous assemblage of more or less smooth species known as the Glabrae. For the Glabrae, Deecke (1925, p. 68) has proposed the sub-genus *Laevitrigonia*, the type of which by subsequent designation (Dietrich, 1933, p. 35) is *T. gibbosa* Sow., a Jurassic species of a very different ancestry to the smooth types here being discussed. *Sphenotrigonia* has very little in common with and is not related to *Laevitrigonia*.

Kitchin (1908, p. 101) has remarked on the tendency to posterior elongation, and loss of sculpture on the adult area, shown by several unrelated types in the Uitenhage and Oomia beds. In no *Trigonia* is the extension of the siphonal end as extraordinary as in *Sphenotrigonia*, and it is rather curious that in the Indo-African Lower Cretaceous the same tendency has produced a similar excessively elongated shell in an unrelated family, the Astartid genus *Seebachia*.

Trigonia (Sphenotrigonia) frommurzei sp. nov.

(Plate XLV, figs. 1-3; Plate XLVI, figs. 1-4; Plate XLVII, figs. 1-4.)

Material.—Nearly 60 specimens of this very remarkable species were available for study. The majority of these are more or less complete individuals with the valves closed and the surface roughened, pitted, or otherwise damaged, the specimens having been collected at the surface after their release from the parent rock by the agents of weathering. A number, however, are comparatively well preserved, and several specimens show very finely the internal characters of the two valves.

The species was collected by Mr. J. S. Hutt and by Mr. H. F.

Frommurze along the Mfongosi tributary of the Pongola River (T.M. 1667, 1669, 1672, 1674-1677, 1680, 1681, 1683, and S.A.M. 10585-10592), the horizons not being noted. In 1933 the locality was visited by Dr. S. H. Haughton and Dr. A. W. Rogers, who collected about 40 specimens along the Mfongosi stream at several horizons. The species appears to be characteristic of several of the localities, and was recorded from each of the localities Z6-Z13. The number of specimens collected from each is indicated in brackets: Z6 (7), Z7 (13), Z8 (10), Z9 (2), Z10 (2), Z11 (1), Z12 (1), Z13 (1).

The species was also found in L3 (3 specimens) on the Lombagwenya stream to the north.

Holotype.—The most complete specimen available is taken as holotype of the species, in spite of the fact that the internal characters are not shown, and although the specimen is from a horizon on the Mfongosi stream not precisely known. It so happens that all the specimens showing the hinge are unsatisfactory in that they are either small or are full-sized specimens very incomplete in the posterior part. The holotype (S. Afr. Mus. 10586) was collected by H. F. Frommurze, and is quite complete even to the tip of the posterior; the valves are tightly closed and in a fair state of preservation, though the flanks are rather badly pitted.

Description of the Species. (1) *External Features*.—Shell large, massive, equivalve, extremely inequilateral, elongately triangular in outline, about twice as long as high, anteriorly very markedly truncate, with the greatest height and thickness very close to the anterior, tapering very gradually from the anterior to a posterior point. Umbones small, situated very close to the anterior end, highly incurved and contiguous or nearly so.

Anterior margin moderately long, approximately vertical, very gently and evenly convex from the umbones to the well-rounded antero-ventral angle. Ventral margin long, about twice as long as the anterior margin, moderately convex in the anterior half, becoming almost straight or even slightly concave in the posterior half. Postero-dorsal margin long, about as long as the ventral margin, remarkably straight throughout its length. Postero-dorsal and ventral margins meeting in a rounded point, the two margins forming an angle of about 30-40°. Postero-dorsal and anterior margins forming an angle of about 70°.

A strong carinal fold runs almost vertically downwards from the umbo to the antero-ventral corner. Carinal fold almost straight, slightly convex towards the anterior, clearly dividing the external

surface of the valve into two regions, which meet at the carinal fold at an angle not much greater than a right angle (about 100°), a narrow anterior region being separated from the broad flank of the valve. Anterior region flattened or gently convex. When closed the two valves are cordate to narrowly cordate in anterior aspect. Carinal fold somewhat sharply to gently rounded.

Greatest convexity of the shell close to or a little posterior to the carinal fold, the thickness decreasing quite gradually from the neighbourhood of the carinal fold to the posterior extremity. When closed the two valves are narrowly wedge-shaped in dorsal, ventral, or lateral aspect. Valves often slightly or very slightly concave in the posterior part, with a very broad and very shallow sulcus running obliquely downwards, corresponding to a slight embayment of the posterior half of the ventral margin. The sulcus and embayment are scarcely discernible in the holotype and other specimens. Broad flank of the valves flattened and only slightly convex in the middle part.

For the greater part of the length of the adult shell the flank passes over to the straight postero-dorsal margin in a broad, rounded convexity devoid of carinae or costae, interrupted only by growth lines and by a persistent, narrow, weak, longitudinal furrow towards the upper side. For a distance of about 20 mm. from the umbo there are two posteriorly directed, finely beaded carinae, demarcating the dorsal area and escutcheon. The marginal carina is narrow, raised, rib-like, and ornamented with conspicuous rounded tubercles for at least 15 mm. from the umbo, giving a beaded appearance; the marginal carina curves obliquely backwards, gently concave towards the dorsal area, for about 20 mm. from the umbo, and passes gradually into a broader fold. For almost the entire length of the shell the area is of constant width and relatively narrow, and is not clearly demarcated from the flank of the shell, except that the broad, rounded convexity has its very much rounded crest, across which the growth lines bend round rapidly, in line with the marginal carina near the umbones. Near the umbones the area is relatively broad and gently concave. The area is divided longitudinally by a distinct groove; near the umbones the groove divides the area into two nearly equal flattened or slightly convex bends; traced posteriorly the upper and lower limits of the area are ill-defined, but the longitudinal groove persists for the greater length of the shell, curving very slightly so as to meet the postero-dorsal margin near the posterior extremity. Near the umbones there is a distinct escutcheon, elongate, narrower than the area, separated from the area by an inner carina similar

in character to and continued posteriorly for the same distance as the marginal carina; the inner carina is narrow, sharp, and beaded, and above it the escutcheon is abruptly excavated, concave, and quite smooth. The ornamentation of the area in the vicinity of the umbones is almost unknown; in the holotype, however, there are quite unmistakably two longitudinal costellae between the furrow and the inner carina. Traced posteriorly the inner carina passes into a broad fold, and for the greater length of the shell no distinction between area and escutcheon is possible, though there is a slight flattening at the valve margin.

There is a very distinct though only slightly excavated lunule, represented by a narrowly cordate shallow depression near the umbones on the anterior face of the valves, demarcated from the remaining part of the anterior region by a change in slope; in adult shells the lunule is about 20 mm. high and 13 mm. in width across the two valves.

The shell material is remarkably thick, 4–8 mm. over the greater part of the valves in the adult and greatly thickened to support the teeth.

(2) *Internal Features*.—Hinge apparatus very strongly developed and situated close to the anterior end, the teeth stout, elevated, and strongly grooved laterally.

In the *left valve* there is a strong central bifid tooth separated by an anterior and a posterior socket from an anterior and a posterior tooth respectively. Central tooth directed obliquely backwards, elevated well beyond the hinge margin, elongate-triangular in shape and shallowly concave along the summit, with the vertical sides diverging and the lower end conspicuously embayed; sides of the tooth approximately vertical and strongly grooved, with 12–15 grooves on the posterior side and 8–10 grooves on the anterior side. Anterior socket elongate, very deep, but narrower than the central tooth, with the lower end closed in by a raised wall joining the bases of the central and anterior teeth. Anterior tooth raised, the posterior side nearly vertical and strongly grooved with 8–10 grooves, the anterior side convex and smooth. Anterior socket, together with the anterior tooth and the anterior fork of the central tooth, supported by a broad convex internal rib, which is continued ventrally for a short distance so as to separate the anterior adductor pit from the valve cavity. Posterior socket moderately deep, rounded, very elongate, up to 40–45 mm. long in the adult, directed posteriorly parallel to the hinge margin, bounded ventrally by an elevated sharp-

crested ridge, which is the prolongation of the posterior fork of the central tooth. Posterior tooth confluent with the nymph, narrow and elongate, its crest appearing as a very narrow ridge against the summit of the nymph, strongly grooved on the ventral side up to about 25 mm. from the umbo. Nymph relatively narrow and with the very narrow ligament groove continued for about 30 mm. from the umbo in the adult.

In the *right valve* there is a very elevated anterior tooth and a very elongate narrow posterior tooth. Anterior tooth large, relatively narrow, directed ventrally but a little obliquely, very elevated, raised well above the hinge margin, up to 12 mm. high in the adult, the sides vertical and diverging at a small angle, both sides strongly grooved with 8-10 grooves. Anterior tooth supported by a broad convex internal rib, which is continued ventrally for a short distance so as to separate the anterior adductor pit from the valve cavity. Anterior to the anterior tooth is a relatively narrow, moderately deep and rather short anterior socket, the anterior side of which is concave and smooth. Between the anterior and posterior teeth is a broad triangular gap in which there is, against the base of the anterior tooth, a narrow shelf formed by a continuation of the supporting internal rib. Posterior tooth very long, up to 40-50 mm. in the adult, narrow, sharp-crested, situated close to and parallel to the hinge margin, with the ventral side free to the floor of the valve cavity, and the dorsal side free only along the summit; end nearest the umbo overhanging and strongly grooved from the summit to the floor of the valve cavity, with corresponding short but strong grooves on the dorsal side up to about 25 mm. from the umbones. Posterior socket reduced to a very narrow and shallow furrow about 25 mm. long separating the elongate posterior tooth from the narrow nymph, its dorsal margin smooth, its ventral margin being the grooved summit of the dorsal side of the posterior tooth.

The *adductor pits* are subequal, close to the valve margins and very deep. Anterior adductor pits oval, extremely deep, situated so close to the anterior margins that the shell is quite thin on their anterior side; pits separated from the valve cavity by the internal supporting rib and the lower part of the anterior tooth. Posterior adductor pits rounded and deep; between each and the posterior end of the hinge is a small accessory pit. Pallial line strongly impressed, simple, at some distance from the ventral margin in the anterior half. Ventral margin smooth within, with a broad, flattened, marginal band along which the valves meet when closed.

(3) *Ornamentation*.—The external sculpture consists almost entirely of concentric growth lines and concentric undulations, the valves consequently appearing to be remarkably smooth for a *Trigonia*. Costae, as well as the dorsal carinae, are strictly confined to the neanic stage, and do not appear beyond about 20 mm. from the umbo. Flanks of the valves with numerous relatively fine growth lines which follow the curvature of the ventral margin and towards the umbo pass obliquely across the costae. The growth lines bend somewhat rapidly across the anterior carinal fold so as to follow straight courses across the anterior face and the lunular depression, inclined very obliquely to the anterior margin. Towards the postero-dorsal margin the growth lines bend round in a broad curve over the dorsal convexity, which represents the lower ill-defined boundary of the dorsal area, and are inclined very obliquely to the margin. In the anterior half the surface of the flank is characterised by a series of about 10 broad concentric undulations, with broad moderately convex crests and concave or broadly V-shaped interspaces, 6–8 mm. apart, representing a more or less regular growth periodicity. These concentric undulations appear only after the neanic stage and may not be maintained towards the ventral margin. The undulations vary in strength from shell to shell, being strongly developed in some, while others are apparently marked by a more or less even surface. The undulations are strongest near the anterior carinal fold and become progressively weaker when traced posteriorly, failing to reach the smooth postero-dorsal convexity; they reach the carinal fold and cross over it on to the anterior face, but then very rapidly disappear, the greater part of the anterior face being crossed only by oblique growth lines.

Near the umbo, in the neanic stage, is a series of regular, relatively elevated, rounded, slightly oblique costae, about 10–12 in number, which are almost parallel to the marginal carina bounding the dorsal area and separated from each other by rounded interspaces of about the same width as themselves. The costae persist to about 20 mm. from the umbo. The costae commence at the anterior carinal fold where they end abruptly, and are a little swollen in some specimens; the costae cease posteriorly in an oblique row of conspicuous tubercles, leaving a rapidly widening smooth oblique band between the costate region and the beaded marginal carina. The costae appear to have been devoid of tubercles or granules along their summits, but this absence may be due to wear.

The beaded marginal and inner carinae have been described above

in connection with area and escutcheon. The beaded character is apparent only in young specimens, the tubercles having been worn away in the adult shells.

(4) *Dimensions* (expressed in millimetres):

S.A.M. No.	10586	10587	10588	10590
Length	137
Height	69	70	65	73
Thickness of one valve	23.5	27	28.5	20
Postero-dorsal margin	128

Remarks.—The degree of inflation of the valves varies very considerably, the holotype being rather narrowly cordate in anterior aspect, while other specimens may be more broadly cordate. The ventral margin in the holotype is straight and there is little sign of the broad shallow posterior sulcus; in other examples the sulcus is quite evident and gives rise to a conspicuous gentle embayment of the ventral margin. These variations were not found to have any zonal significance, but this may be due to insufficiency of material.

Sub-genus *Scabrotrigonia* Deecke 1925.

Trigonia (*Scabrotrigonia*) *cricki* R. B. Newton.

1909. *Trigonia cricki* Newt.: Trans. Roy. Soc. S. Afr., vol. i, p. 38, pl. v, figs. 10–15.

1929. *Ptilotrigonia cricki* Newt.: van Hoepen, Krytf. Soeloeland, p. 24, pl. v, fig. 7; pl. vi, figs. 1–4.

A preliminary examination of the *Trigoniae* of the section Scabrae, which are common throughout the succession and apparently represented by several species, shows that *T. cricki* is represented by a fine set of specimens from Z19 (20) on the Pongola River below the junction with the Mfongosi stream. The type is from the Albian (du Toit, 1926, p. 318) of the Manuan Creek and van Hoepen has recorded the species from the Umsinene River, Umsinene Beds, identified by him as Albian (1926, p. 222). Dr. S. H. Haughton also recorded the species at locality Z20.

Trigonia (*Scabrotrigonia*) cf. *kraussi* Kitchin.

1908. *T. kraussi* Kitchin: Ann. S. Afr. Mus., vol. vii, p. 95, pl. 111, fig. 2.

Large Scabrae comparable with the Uitenhage species *T. kraussi*, and with *T. salebrosa* (van Hoepen) (1929, p. 20, pl. v, figs. 1–6) from

the base of the succession on the Umsinene River, are not common, but Mr. J. S. Hutt collected two specimens (T.M. 1768, 1769) on the Mfongosi stream at an unrecorded horizon, and Dr. S. H. Haughton and Dr. A. W. Rogers found a single specimen at Z8, the three specimens apparently belonging to a new species allied to *T. kraussi*. These will be described in a subsequent communication.

Trigonia (Scabrotrigonia) spp.

Several species are probably represented among the numerous smaller Scabrae in the collection. An apparently undescribed species with exceptionally coarse tubercles is abundant at Z3 (17) and Z4 (30) on the Mfongosi, the material being in excellent condition. The Scabrae will be dealt with in a separate paper.

FAMILY PECTENIDAE.

Genus NEITHEA Drouet 1825.

Neithea quadricostata (J. Sowerby).

1903. *Pecten (Neithea) quadricostatus* J. Sow.: Woods, Cret. Lam. England, vol. i, p. 210, pl. xl, figs. 6, 7.
 1909. *Neithea quadricostata* (Sow.): R. B. Newton, Trans. Roy. Soc. S. Afr., vol. i, p. 55, pl. ii, figs. 18-21.
 1930. *Neithea quadricostata* (Sow.): Rennie, Ann. S. Afr. Mus., vol. xxviii, p. 241, pl. xxx, figs. 10-12.

This well-known Albian and Cenomanian species has been figured from the Manuan Creek in Zululand by Newton and Rennie, and has been recorded (Rennie, *loc. cit.*) from the Pongola River. The present collections include a very fine series of about 50 specimens from Z19 on the Pongola River below its junction with the Mfongosi stream, as well as an incomplete juvenile convex valve from Z9 which apparently represents the same species, and 2 good specimens from Z20. From L5 (Msinyene Pan) comes a juvenile convex valve of a *Neithea* which may be this species.

Neithea quinquecostata (J. Sowerby).

1903. *Pecten (Neithea) quinquecostatus* J. Sow.: Woods, Cret. Lam. England, vol. i, p. 202, figs. on pls. xxix, xl.
 1930. *Neithea quinquecostata* (J. Sow.): Rennie, Ann. S. Afr. Mus., vol. xxviii, p. 179, pl. xviii, figs. 1-5 (references to S. African records).

This species is of common occurrence in the Umzamba Beds (Campanian) of Pondoland and has been recorded from a number of localities in Zululand. In Europe it ranges from the Aptian to the Senonian. A single but quite typical convex valve was collected from Z13 on the Mfongosi, from an horizon certainly not later than Cenomanian.

FAMILY PHOLADOMYIDAE.

Genus PHOLADOMYA G. B. Sowerby 1824.

Pholadomya? luynesi Lartet.

(Plate XLIII, fig. 4.)

1877. *P. luynesi* Lartet: Géol. Mer. Morte, p. 125, pl. xi, figs. 7, 8.
1909. „ „ R. B. Newton, Trans. Roy. Soc. S. Afr.,
vol. i, p. 78, pl. vi, figs. 1, 2.

Newton figured a shell from the Manuan Creek in Zululand and referred it to this species, which is said to occur in the Cenomanian of Syria, though the type is from a higher horizon. There is a single well-preserved specimen from the Pongola River below its junction with the Mfongosi stream, from Z19, which agrees with the shell described by Newton and must be referred to the same species. In the collection of the Transvaal Museum there are further excellent examples of the species (T.M. 1235, 1273, 1274, 1301) in an Albian fauna from Catuane in Portuguese East Africa.

The species has been retained in *Pholadomya* by Blanckenhorn and Newton in spite of the absence of radial ribs, but might be better placed in *Homomya* or even in *Pleuromya*.

Pholadomya vignesi Lartet.

1877. *P. vignesi* Lartet: Géol. Mer. Morte, p. 126, pl. xi, fig. 9.
1909. „ „ *emend.* Blanckenhorn: R. B. Newton,
Trans. Roy. Soc. S. Afr., vol. i, p. 79, pl. vi, figs. 3-6.

Newton has described and figured examples of this species from the Manuan Creek and has remarked on its comparative abundance at that Zululand locality. The present collection includes a number of finely preserved and very typical specimens, whose identity with the shells described by Newton is not open to doubt. These were collected as follows: on the Lombagwenya stream, L7 (1?); in the neighbourhood of the Mfongosi stream, Z16 (7), Z19 (10), Z20 (1), Z21 (1). There are finely preserved examples of this species in the

Albian fauna from Catuane, Portuguese East Africa, in the collection of the Transvaal Museum (T.M. 1275, 1303, 1307-9). In Palestine, Algeria, etc., the species occurs in the Cenomanian, while at the Manuan Creek the species is said to be from the Albian (du Toit, 1926, p. 318).

Genus GONIOMYA Agassiz 1842.

Goniomya sp.

The genus is represented by rather fragmentary specimens probably belonging to the same species as *Goniomya* (species 1) figured by Newton (1909, p. 81, pl. vi, figs. 18, 19) from Manuan Creek in Zululand. These were collected as follows: neighbourhood of the Mfongosi stream, Z16 (1, large), Z21 (1). A rather similar form is present at Catuane (T.M. 1137, 1289), but the poorness of the Zululand material makes comparisons difficult.

FAMILY CYPRINIDAE.

Genus VENIELLA Stoliczka 1871.

Veniella etheridgei R. B. Newton.

1909. *V. etheridgei*, Newt.: Trans. Roy. Soc. S. Afr., vol. i, p. 69, pl. xii, figs. 5, 6.

1930. *V. etheridgei*, Newt.: Rennie, Ann. S. Afr. Mus., vol. xxviii, p. 242, pl. xxxi, figs. 1-3.

This massive and very distinct species is represented in the present collections by a number of specimens, the majority with the valves closed and fairly well preserved. The species was described by Newton from the Manuan Creek in Zululand, and is said by du Toit (1926, p. 318) to be from the Albian. A fine left valve was figured by Rennie from the same locality, and the occurrence of the species with *Neithea quadricostata* on the Pongola River was recorded. The species has been recorded from: on the Lombagwenya stream, L3 (1?, juvenile specimen, poorly preserved); neighbourhood of the Mfongosi stream, Z16 (3, small or broken), Z19 (19, fine typical specimens), Z20 (1); south of Mokatini, Z25 (5).

FAMILY CARDIIDAE.

Genus PROTOCARDIA Beyrich 1845.

Protocardia cf. *sphaeroidea* (Forbes).

(Plate XLVIII, figs. 1-6; Plate XLIX, fig. 9.)

1908. Woods: Cret. Lam. England, vol. ii, p. 195, pl. xxxi, figs. 2 *a*, 2 *b*, 3 *a*, 3 *b*.

Material.—The genus is represented by about twenty fairly well preserved specimens of a large species, from exposures on the Mfongosi stream and on the Pongola River. Mr. H. F. Frommurze and Mr. J. S. Hutt collected five specimens on the Mfongosi (S.A.M. 10788, 10789; T.M. 1790, 1796, 1894). Dr. S. H. Haughton and Dr. A. W. Rogers collected three specimens on the Mfongosi, one specimen from each of the localities Z11, Z12, Z13; and ten specimens from Z19 on the Pongola River below its junction with the Mfongosi.

Remarks.—These large shells are very similar to the English Aptian *P. sphaeroidea* (Forbes), which has been well described and figured by Woods (*loc. cit.*). The type is from the *Perna*-Bed (lower Aptian) of the Isle of Wight. The English species has been described by Woods as follows, and the description applies equally well to the Zululand specimens: "Shell stout, large, much inflated, higher than long, slightly inequilateral. Anterior and ventral margins rounded. Posterior margin truncated, forming angles with the postero-dorsal and ventral margins. Umbones prominent, with a small forward curvature, and an inconspicuous carina extending to the postero-ventral angle and limiting the flattened postero-dorsal area. Ornamentation consists of regular, broad, flat concentric ribs separated by narrow grooves. On the posterior area strong growth ridges are present."

Woods figures only two specimens, and I have found it difficult to make a satisfactory discrimination between these and the Zululand set. There is also a considerable resemblance to *P. rothpletzi* Krenkel described recently by Dietrich (1933, p. 51, taf. vi, figs. 89-91) from the *Trigonia schwarzi*-Beds in the Tendaguru Formation of Tanganyika. The latter species is said by Dietrich to be very closely allied to *P. sphaeroidea*, but to be distinguished by slightly narrower ribs and less pointed umbo. From the measurements given by Woods and Dietrich for the two species, it would appear that the East African and English shells cannot be separated by reason of any conspicuous

difference in size or proportions. The ratio of length : height for *P. sphaeroidea* is from 1:1.02 to 1:1.26, the corresponding figures for *P. rothpletzi* being 1:1.03 to 1:1.06, which is within the range given for the former species.

The Zululand shells are remarkable for the great relative height attained by several individuals. In one of the specimens before me (T.M. 1894) the height exceeds the length by a considerable amount (1:1.48); taken by itself one would be inclined to regard the specimen as distinct from *P. sphaeroidea*, but in the remaining 18 specimens, however, the ratio of length : height works out at from 1:1.11 to 1:1.21, which is well within the range given above for *P. sphaeroidea*. In proportions there is a very striking resemblance of some of the shells before me to the shell from the Upper Greensand of Haldon (Upper Albian) figured as *Protocardia* sp. by Woods (1908, p. 196, pl. xxxi, fig. 4), and it is unfortunate that the ornamentation of the latter is so poorly preserved; this shell is said by Woods to resemble in shape the higher forms of *P. sphaeroidea* (from the Lower Greensand), but to have a narrower and more curved umbo and a more distinct carina. The record made by Jukes-Browne (Woods, *loc. cit.*) of *P. sphaeroidea*, from the zone of *Pecten asper* (L. Cenomanian) of Wiltshire, was possibly based on a shell of this type. On the whole, the umbonal region is narrower and more pointed in the Zululand shells than in the two Lower Greensand shells figured by Woods, and there is a closer approximation to the Upper Greensand shell in the form of the umbonal region, but there is an approach to the broader umbo of *P. sphaeroidea* in some specimens. In the type specimen of *P. rothpletzi* the umbo is broader than in any of the Zululand shells.

The concentric ribbing of the English and Zululand shells is essentially the same in character, flat, broad ribs with narrow grooves separating them. In the examples of *P. sphaeroidea*, figured by Woods, there are 5-7 ribs in 10 mm. in the middle part of the shell, judging from the figures which are presumably approximately natural size. In the type of *P. rothpletzi*, again judging from the figure, there are about 7-8 ribs in 10 mm., the grooves being slightly wider than in Woods's figures. In the Zululand shells the number of ribs is usually about 8 or 9 in a distance of 10 mm. at about 50-60 mm. from the umbo, but in one instance (S.A.M. 10788) the number of ribs in that distance is only 5. In *P. sphaeroidea* and in the Zululand shell S.A.M. 10788 the ribs are remarkably broad and flat, while in the majority of the Zululand shells the ribs are relatively

narrower and separated by wider grooves, and a little more rounded, thus resembling those of *P. rothpletzi*.

It would appear from the above facts that there are no very striking features which can be used as a means of discriminating between the English, East African, and Zululand shells, and it may well be the case that we are dealing here with sets belonging to a single, if somewhat variable, species. The peculiarly short Zululand shell (T.M. 1894) mentioned above can be safely regarded as an extreme case, an abnormal individual in which great relative height and more pointed umbonal region are correlated, since no less than 18 associated specimens of the same general character, and undoubtedly conspecific with it, have relatively longer shells. It should be pointed out that the characters of *P. sphaeroidea* were judged on the basis of the two figures given by Woods, and that an examination of an adequate set of this species might disclose grounds for a more emphatic expression of opinion as to relationship with the Zululand shells.

P. sphaeroidea and *P. rothpletzi* are Lower Aptian and Neocomian respectively, while the Zululand shells * occur in association with Albian species. The imperfectly preserved shell figured by Woods from Haldon is Upper Albian.

A feature of the Zululand shells † not mentioned by Woods for *P. sphaeroidea* is the presence of a tooth-like tubercle within the left valve at the postero-ventral corner; with the growth of the valve the tubercle gives rise to a very slightly or scarcely raised internal rib corresponding in position to the posterior carina. The tubercle fits into a slight embayment of the corresponding margin of the right valve, the embayment being rounded, about 1 to 1.5 mm. in depth, and distinctly visible when the valve is viewed from beneath.

Dietrich (*loc. cit.*) included *P. rothpletzi* and *P. sphaeroidea* in a new sub-genus *Tendagurium*, under *Cardium*, the type of the sub-genus being another East African species *C. propebannianum* Dietrich, which is ornamented only with fine growth lines over the whole surface. It is doubtful whether these two species are closely related to the latter, and they are accordingly retained under *Protocardia*.

* Etheridge (1907, p. 77, pl. iii, figs. 6, 7) gave the new name *Protocardium ? cinctutum* to a very imperfect shell from the Umsinene River and suggested affinity with *P. sphaeroidea*, probably rightly.

† Denudation of the carina gives rise to a double impressed line in many of the specimens studied.

Dimensions of representative Zululand shells, expressed in millimetres:

	—	T.M. 1790.	T.M. 1796.	T.M. 1894.	S.A.M. 10788.	S.A.M. 10789.
Length . . .	56	52	55	± 54	± 71	75
Height . . .	68	60	61	± 80	81	84
Thickness of one valve . . .	23	20	21	28	29	33

Genus *CARDIUM* Linnaeus 1758.

Cardium rogersi sp. nov.

(Plate XLIX, figs. 3-8.)

Material.—The species is founded on about 28 specimens, the majority more or less complete. For the most part the specimens are well covered with matrix, but a number were cleaned up sufficiently well to show the external features and the hinge. Mr. H. F. Frommurze collected several specimens on the Mfongosi stream (S.A. Mus. 10791-10796). Dr. S. H. Haughton and Dr. A. W. Rogers collected the species as follows: Mfongosi stream, Z2 (17), Z3 (1); Myesa stream, M1 (2). The holotype (S.A.M. 10791) and figured specimens are for the most part taken from the earlier collection of Mr. Frommurze, in that the general preservation is superior, and in spite of the fact that the horizon is not precisely recorded.

Description.—Shell moderate in size, about as high as long, relatively stout, very convex, slightly inequilateral. Umbones very prominent, highly incurved. Hinge line long, nearly as long as the greatest length of the shell, nearly straight. Anterior margin convex, passing obliquely downwards in a broad curve to merge gradually into the convex ventral margin. Posterior somewhat truncate, the posterior margin nearly vertical, the upper and lower parts convex, the middle part concave, meeting the ventral margin in a broadly rounded postero-ventral angle. Valve evenly convex, the posterior slope becoming steeper than the anterior, with the postero-dorsal corner forming a wing which is separated from the posterior slope by a broad concavity.

Dentition relatively strong, the two cardinals in the left valve close together under the umbo, the lower or anterior cardinal conical and prominent, the upper or posterior cardinal smaller; laterals in left valve prominent, oval in section, the anterior more prominent than the posterior?, situated at some distance from the cardinals. Anterior and ventral margins crenulate within, with numerous short grooves

transverse to the margins; at the postero-ventral angle these pass into stronger marginal incisions, the posterior margin being coarsely denticulate.

Ornamentation essentially radial, that of the posterior slope being considerably coarser and different from that of the rest of the valve, the two areas being sharply demarcated after the period of early middle growth, the line of demarcation being a little more than one-third of the length of the valve from the posterior margin. Flank with numerous incised radiating lines, separated by relatively wide flat interspaces; on partially decorticated surfaces a very fine concentric ribbing comes in, giving a minutely reticulate surface. Towards the anterior the radial incisions widen and the shell becomes ornamented with very faint radial riblets. The posterior area is ornamented with about 20 strong, raised, sharp, radial ribs, separated by deep U-shaped grooves, the ribs corresponding to the teeth on the posterior margin.

Dimensions, in millimetres:

	S.A.M. 10791.	S.A.M. 10792.	S.A.M. 10793.	From Z2.
Length	37	31	35	38
Height	39	29	..	39
Length of hinge (approx.) .	27	25	26	27
Thickness of one valve .	17	12	16	71

Remarks.—The species is quite distinct from any South African Cardiidae hitherto described.

FAMILY VENERIDAE.

Genus *PTYCHOMYA* Agassiz 1842.

Ptychomya robinaldina (d'Orbigny).

(Plate XLIX, figs. 1, 2.)

1844. *Crassatella robinaldina* d'Orbigny: Pal. Franç. Terr. Crét., vol. iii, p. 75, pl. cclxiv, figs. 10–13.

1907. *Ptychomya robinaldina* (d'Orb.): Woods, Cret. Lam. Engl., vol. ii, p. 179, pl. xxvii, figs. 24–26.

The record of this species from Northern Zululand is based on a single specimen (S. Afr. Mus. 10812) collected by Mr. H. F. Frommurze on the Mfongosi stream, the precise horizon not being noted. The specimen consists of the two valves firmly closed. The whole surface is denuded, the dorsal part badly so, so that the umbonal part

is deceptively inconspicuous and some allowance must be made for rounding of the marginal angles. Nevertheless the salient characteristics of form and sculpture are unmistakably indicated, and I see no reason for regarding this shell as distinct from the Lower Greensand specimens described and figured by Woods. The shell is of the same size and general proportions as in the English examples and is ornamented in the same way. The posterior part of the shell is very much worn, but the ribs in that part were clearly stronger and more widely separated than elsewhere, while the postero-dorsal margin bears unmistakable traces of coarse ridges and crenulation. The main portion of the flank bears ribs of exactly the same character and about the same in number as the English shells. Towards the anterior a chevron arrangement of the ribs is just discernible in spite of wear.

There are certain features which might suggest some distinction between this shell and the two specimens figured by Woods, but these appear to be of little importance. The umbones appear to be less conspicuous and there is a greater rounding of the postero-dorsal angle, while the valves appear to be less convex when seen from above; to a large extent these differences may be assigned to the denuded character of the specimen. The anterior part is very slightly narrower and more produced than in the English shells, the umbones being placed a little farther back. The chevron arrangement of the anterior ribs forms a pattern which does not precisely agree with that of either of the shells figured by Woods, but the latter has pointed out that there is a considerable range of variation in this respect, as in other species of lamellibranchs having an analogous sculpture.

P. complicata (Tate) (1867, p. 160, pl. ix, fig. 8), referred to the genus by Dames (Kitchin, 1908, p. 27), was founded on a very small shell from the Sundays River Beds which appears to differ in the details of sculpture.

P. kitcheni Lange (1914, p. 242, pl. xvii, fig. 6), from the *Trigonia schwarzi*-Bed in Tanganyika, is less elongate, and finely ribbed in the posterior part, besides differing in other details. Dietrich (1933, p. 53) has shown that this species is identical with the previously described *P. hauchecornei* Müller from the same area, and has placed it as a variety of *P. robinaldina*.

According to Dietrich (*loc. cit.*) the genus ranges from the Neocomian to the Upper Cretaceous, and Kitchin (1926, p. 460) has pointed out that it forms a characteristic element of the southern Neocomian faunas.

FAMILY uncertain.

Genus THETIRONIA Stoliczka 1871.

Thetironia sp.

Imperfect shells apparently belonging to the same species were collected from L12 (1) on the Lombagwenya stream, and Z24 (1) south of Mokatini.

FAMILY SAXICAVIDAE.

Genus PANOPE Ménard de la Groye 1807.

(= PANOPEA and PANOPAEA of authors).

Panope gurgitis (Brongniart).

(Plate L, figs. 1, 5, 6, 8, 9.)

(Figs. 2-4, 7, 10, 11 from the Uitenhage Series.)

1850. *Anoplomya lutraria* Krauss: Unt. Kreide Kaplandes, p. 447, pl. xlvii, fig. 1.

1907. *Myopsis?* *africana* Etheridge: 3rd Rep. Geol. Surv. Natal, p. 81, pl. i, figs. 9, 10.

1907. *Glycymeris?* *griesbachi* Etheridge: *Ibid.*, p. 81, pl. iii, fig. 9 (non *Glycymeris griesbachi* Newton, Arcidae).

1908. *Pleuromya lutraria* (Krauss): Kitchin, Ann. S. Afr. Mus., vol. vii, pp. 158, 159.

1909. *Pleuromya africana* (Etheridge): Newton, Trans. Roy. Soc. S. Afr., vol. i, p. 84, pl. viii, figs. 1-3.

1909. *Panopea gurgitis* (Brongniart): Woods, Cret. Lam. England, vol. ii, p. 222, figs. on pls. xxxv, xxxvi.

Non *Pleuromya africana* (Etheridge): Rennie, Ann. S. Afr. Mus., vol. xxviii, p. 186, pl. xx, figs. 8-10, 1930.

Material.—The collections include about 30 specimens indistinguishable from this well-known European species. These were collected by Dr. S. H. Haughton and Dr. A. W. Rogers at the following localities: Myesa stream, M1 (several, imbedded in hard limestone); Lombagwenya stream, L1 (1), L3 (2), L7 (4), L9 (2), L11 (1); Mfongosi stream, Z6 (1), Z8 (1), Z9 (4), Z11 (1), Z12 (3), Z14 (1); Pongola River below junction with Mfongosi, Z19 (1), Z20 (1).

Remarks.—The shells before me from the Pongola area do not appear to be distinguishable on external characters from certain forms which Krauss, Etheridge, and Newton have described and

figured under other names from South African Lower Cretaceous deposits. I have been unable to find satisfactory reasons for separating the species named by these authors from the well-known European *Panope gurgitis*, accepting this species in the wide sense adopted by Woods in his monograph of the Cretaceous Lamellibranchia of England.

Krauss (*loc. cit.*) long ago described and figured certain shells from the Zwartkops River, Sundays River Beds, as *Anoplomya lutraria* gen. et sp. nov., said to have the habit of a *Lutraria* (Mactridae), but to be close to *Panope*, though differing from the latter in certain respects. Krauss was led to institute a new genus for the species on the grounds that the cardinal teeth were assumed to be absent; a peculiar strong crenulation of the dorsal margin of each valve near the umbo was described and figured. I have not been able to find specimens of this species, which are not uncommon in collections, showing the hinge completely exposed, but from a comparison of Krauss's figures and fine specimens of *Panope natalensis* Woodw. from a raised beach at Port Elizabeth, I have no doubt that Krauss's specimens possessed the hinge structure characteristic of the genus *Panope*. In that genus the solitary prominent cardinal tooth of each valve is situated close to the hinge margin and immediately below the umbo, while posterior to it the strong elongate nymphal structure projects well beyond the hinge margin; the crenulation of the dorsal margin figured by Krauss for each valve corresponds exactly in outline with the projecting tooth and nymph of *Panope*, and Krauss was clearly in error in his interpretation of these structures; in his fig. 1 b, the right valve is apparently slightly out of place, so that the right tooth and nymph appear to overlap the margin of the left valve. According to Kitchin (1908, p. 159) and Etheridge (1907, p. 82) *Anoplomya* has been quoted as a synonym of *Pleuromya*, but Kitchin, Newton (1909, p. 85), and other authors have included *Panope gurgitis* in *Pleuromya*. According to Woods (1909, p. 225) *Panope* is distinguished from *Pleuromya* by having a well-developed tooth, contiguous but not overlapping dorsal margins, and a well-developed external ligament; in a specimen of *A. lutraria* before me (A.M. 3840) the hinge of the right valve is sufficiently exposed to show a deeply impressed ligament groove and a projecting but relatively short nymph, which, with the interpretation of Krauss's figures given above, supports reference of *Anoplomya* to *Panope*. It is significant that Kitchin (*loc. cit.*, p. 158) associated *A. lutraria* with forms referred by Woods to *P. gurgitis*, and I have failed to

find any distinction between a number of specimens from the Sundays River Beds (in Albany Museum Coll.) and the numerous examples figured by Woods from the lower Greensand of Atherfield. Both the typical and plicate (var. *plicata* (J. de C. Sow.)) types are represented, the distinction being insufficient to warrant recognition of two species, since the forms grade into one another, as Woods has pointed out.

Glycimeris? *griesbachi* Etheridge (1907, p. 81, pl. iii, fig. 9), from the Umsinene River, not to be confused with another Zululand shell of the same name in *Glycymeris* da Costa (*G. griesbachi* Newton, 1909, p. 36), was founded on very imperfect material that could very well have been referred to *P. gurgitis*.

Myopsis? *africana* Etheridge (1907, p. 81, pl. i, figs. 9, 10), from the same locality, was distinguished as a separate species from the above in part by reason of the shorter anterior and more distinct anterior carina. The figured specimen is very imperfect, and it would appear that the postero-dorsal margin is broken away, giving the specimen a spurious appearance of narrowing towards the posterior, an appearance which in part led the author to identify with it two shells from the Upper Senonian of Pondoland (Rennie, 1930, p. 186, pl. xx, figs. 8-10). The latter species is certainly not a form of *Panope gurgitis*, the posterior being narrow and almost pointed, and reference to *Pleuromya* appears to have been correct. The type of *M.?* *africana* is ornamented with radial lines of granules as in some of the shells of *P. gurgitis* figured by Woods, and reference to the latter is highly probable. The shell figured by Newton (1909, p. 84, pl. viii, figs. 1-3) from the Manuan Creek as *Pleuromya africana* (Eth.) was compared with forms included in *P. gurgitis* by Woods, and appears to be indistinguishable from the latter species.

It is apparent from Woods's monograph that *Panope gurgitis* is a very variable species and that a number of unnecessary names have been proposed for European material from different localities. The variation is in respect of the strength of the concentric folds, and in the details of outlines and form. Fine radial granulation, formerly used to distinguish *P. neocomiensis* from *P. gurgitis*, appears in good specimens of the latter. The South African species referred to above cannot be distinguished in form from this variable species, and fine radial lines of granules were noted by Etheridge and Newton in some of the shells before them. In the present collection the material is either weathered or embedded in hard limestone, but the reference to *P. gurgitis* is justified on external characters; the

specimens are fairly typical, those from L7, L9, and L11 being somewhat plicate and relatively short.

In Europe the species ranges from Neocomian to Upper Albian. *P. lutraria* from the Sundays River Beds is Upper Valanginian. In the collection of the Transvaal Museum there are two fine specimens of *P. gurgitis* (T.M. 1261, 111) from Catuane, the horizon being Upper Albian (Spath, 1925, p. 180), one specimen being very typical, the other more distinctly plicate.

GASTROPODA.

The comparative scarcity of Gastropods is a feature of the faunas. Small shells belonging to *Dicroloma* are found at several horizons, and those from localities L9, Z1, and Z2 appear to belong to the same species. The well-characterised species *Turritella manuanensis* Newton (1909, p. 25, pl. viii, figs. 16, 17), described from the Manuan Creek, is represented in the collections by a number of specimens from the neighbourhood of the Mfongosi stream: Z16 (many, more or less weathered), Z19 (10), Z20 (2); the species is said by du Toit (1926, p. 318) to be from the Albian. Rather imperfectly preserved shells, probably identical with the form described by Newton (*ibid.*, p. 30, pl. viii, figs. 6-8) from the Manuan Creek as *Avellana* cf. *incrassata* (J. Sow.), were found at two localities, L1 (1) and Z19 (2), at the latter locality associated with Albian species. On the Mfongosi stream a number of specimens similar to *Pterodonta inflata* d'Orb. were collected at Z2 (12), but whether this Cenomanian species is really represented is doubtful.

6. REFERENCES.

- AGASSIZ, L. (1840).—Mémoire sur les Trigonies.
 ARKELL, W. J. (1930).—"The Generic Position and Phylogeny of Some Jurassic Arcidae," Geol. Mag., vol. lxvii, pp. 297-310, 337-352, pls. xiv-xvi.
 CHOFFAT, P. (1903).—"Le Crétacique de Conducia," Comm. du Serv. Géol. du Portugal, Contrib. conn. Géol. des Colonies Port. d'Afrique.
 COSSMANN, M. (1912).—"Essai sur l'évolution des Trigonies," Ann. de Paléont., t. 7.
 COX, L. R. (1925).—"Cretaceous Gastropoda from Portuguese East Africa," Ann. Tvl. Mus., vol. xi, pp. 201-216, pls. xxxviii, xxxix.

- CRAGIN, F. W. (1905).—"Palaeontology of the Malone Jurassic Formation of Texas," U.S.G.S., Bull. 266, 172 pp., pls. i-xxix.
- CRICK, G. C. (1907).—"Cretaceous Fossils of Natal, Part iii," Third Rep. Geol. Surv. Natal, pp. 161-250, pls. x-xv.
- CRICKMAY, C. H. (1930).—"The Jurassic Rocks of Ashcroft, British Columbia," Univ. Calif. Publ., Geology, vol. xix.
- CRICKMAY, C. H. (1930 a).—"Fossils from Harrison Lake Area, British Columbia," Bull. 63, Nat. Mus. Canada.
- CRICKMAY, C. H. (1932).—"Contributions toward a Monograph of the Trigonidae, (1)," Amer. Journ. Sci., ser. 5, vol. xxiv, pp. 443-464, pls. i, ii.
- DE ANDRADE, C. F. (1929).—"Esbôço Geológico da Provincia de Moçambique, 232 pp.
- DEECKE, W. (1925).—"Ueber die Trigonien," Pal. Zeitschr., bd. 7, heft 2.
- DIETRICH, W. O. (1933).—"Zur Stratigraphie und Palaeontologie der Tendaguru-schichten," Palaeontographica, Suppl. vii, reihe 2, ii, pp. 1-86, pls. i-xii.
- DU TOIT, A. L. (1926).—"The Geology of South Africa.
- ETHERIDGE, R., jun. (1904).—"The Umkwelane Hill Deposit, Zululand," Second Rep. Geol. Surv. Natal, pp. 71-93, pls. i-iii.
- ETHERIDGE, R., jun. (1907).—"The Umsinene River Deposit, Zululand," Third Rep. Geol. Surv. Natal, pp. 67-90, pls. i-vi.
- FISCHER, P. (1887).—"Manuel de Conchyliologie.
- GABB, W. M. (1869).—"Palaeontology of California, vol. ii.
- GARDNER, J. A. (1916).—"Upper Cretaceous Mollusca, Maryland Geol. Surv., pp. 371-733, pls. xii-xlv.
- HEINZ, R. (1930).—"Ueber Kreide-Inoceramen der Südafrikanischen Union," Comp. Rendu, Session XV, Internat. Geol. Congress, vol. ii, pp. 681-687, 2 pls.
- KILIAN, W. (1902).—"Ueber Aptian in Süd Afrika," Centralb. f. Min., pp. 456-468.
- KITCHIN, F. L. (1903).—"The Jurassic Fauna of Cutch, iii, 2, Lamellibranchiata, Genus Trigonina; Pal. Indica, ser. ix.
- KITCHIN, F. L. (1908).—"The Invertebrate Fauna and Palaeontological Relations of the Uitenhage Series," Ann. S. Afr. Mus., vol. vii, pp. 21-250, pls. ii-xi.
- KITCHIN, F. L. (1926).—"The so-called Malone Jurassic Formation in Texas," Geol. Mag., vol. lxiii, pp. 454-469.
- KITCHIN, F. L. (1929).—"On the Age of the Upper and Middle Deinosaur-Deposits at Tendaguru, Tanganyika Territory," Geol. Mag., vol. lxvi, pp. 193-220.
- KRAUSS, F. (1850).—"Ueber einige Petrefakten aus der untern Kreide des Kaplandes," Nova Acta Acad. Caes. Leop.-Carol. Nat. Cur., vol. xxii, pt. 2.
- KRENKEL, E. (1910).—"Die Aptfossilien der Delagoa-Bai," Jahrb. f. Min., 1, pp. 142-168.
- KRENKEL, E. (1910 a).—"Die Untere Kreide von Deutsch-Ostafrika," Beitr. z. Pal. u. Geol. Oesterr.-Ungarns, 23.
- LANGE, E. (1914).—"Die . . . Lamellibranchiaten . . . der Trigonina Schwarzi-Schicht . . .," Wiss. Ergeb. Tendaguru-Exped., 1909-1912," bd. iii, heft 4, pp. 186-289, taf. xv-xxii.
- LARTET (1877).—"Explor. Géol. Mer Morte.
- LYCETT, J. (1872-1879).—"Mon. British Fossil Trigoninae, Mon. Pal. Soc.
- MARWICK, J. (1932).—"A new Trigonina from Canterbury," Rec. Cant. Mus., vol. iii, pp. 505-509, pl. lxvii.

- NEUMAYR, M. (1881).—In Holub and Neumayr, "Ueber einige Fossilien aus der Uitenhage-Formation in Süd-Afrika," Denkschr. d. k. Akad. Wiss., Math.-Nat. Classe, bd. xlv, p. 267.
- NEWTON, R. B. (1896).—"On the Occurrence of *Alectryonia unguata* in S.E. Africa, with a notice of previous researches on the Cretaceous Conchology of Southern Africa," Journ. Conch., vol. viii, p. 147.
- NEWTON, R. B. (1909).—"Cretaceous Gastropoda and Pelecypoda from Zululand," Trans. Roy. Soc. S. Afr., vol. i, pp. 1-106, pls. i-ix.
- NEWTON, R. B. (1924).—Appendix to paper by E. O. Teale on "The Geology of Port. E. Africa between the Zambesi and Sabi Rivers," Trans. Geol. Soc. S. Afr., vol. xxvi, pp. 141-159.
- RENNIE, J. V. L. (1930).—"New Lamellibranchia and Gastropoda from the Upper Cretaceous of Pondoland, with an Appendix on some Species from the Cretaceous of Zululand," Ann. S. Afr. Mus., vol. xxvii, pp. 159-260, pls. xvi-xxxi.
- ROGERS, A. W., and HAUGHTON, S. H. (1929).—Handb. Region. Geol., vol. vii, 7A, S. Afr., pp. 143-148.
- SPATH, L. F. (1921).—"On Cretaceous Cephalopoda from Zululand," Ann. S. Afr. Mus., vol. xii, pp. 217-321.
- SPATH, L. F. (1921 a).—"On Upper Cretaceous Ammonoidea from Pondoland," Ann. Durban Mus., vol. iii, pp. 39-57.
- SPATH, L. F. (1922).—"On the Senonian Ammonite Fauna of Pondoland," Trans. Roy. Soc. S. Afr., vol. x, pp. 113-147.
- SPATH, L. F. (1925).—"On Upper Albian Ammonoidea from Portuguese E. Africa, etc.," Ann. Tvl. Mus., vol. xi, pp. 179-200.
- SPATH, L. F. (1930).—"On the Cephalopoda of the Uitenhage Beds," Ann. S. Afr. Mus., vol. xxviii, pp. 131-157, pls. xiii-xv.
- STANTON, T. W. (1897).—"On the genus *Remondia* Gabb, a Group of Cretaceous Bivalve Molluscs," Proc. U.S. Nat. Mus., vol. xix, pp. 299-301, pl. xxvi.
- STANTON, T. W. (1901).—Rep. Princeton Univ. Exped. Patagonia, 1896-99, vol. iv, pt. i, Marine Cretaceous Invertebrates.
- STEINMANN, G. (1882).—"Die Gruppe der Trigonidae Pseudo-quadratae," Neues Jahrb. f. Min., bd. i, p. 219.
- STEPHENSON, L. W. (1923).—"The Cretaceous Formations of North Carolina," N. Carol. Geol. Surv., vol. v, pt. i, pp. 1-402, pls. i-c.
- STEWART, R. S. (1930).—"Gabb's California Cretaceous and Tertiary Type Lamellibranchs," Special Publ. iii, Acad. Nat. Sci. Philad., pp. 1-314, pls. 1-17.
- STOLICZKA, F. (1871).—"Cretaceous Fauna of S. India: Lamellibranchia," Pal. Indica.
- TATE, R. (1867).—"On some Secondary Fossils from S. Africa," Q.J.G.S., vol. xxiii, p. 139.
- VAN HOEPEN, E. C. N. (1926).—"Oor die Krytafsettinge van Soeloeland," S. Afr. Journ. Sci., vol. xxiii, pp. 216-222.
- VAN HOEPEN, E. C. N. (1929).—"Die Krytafsettinge van Soeloeland, 1, Trigoniidae," Pal. Nav. Nas. Mus. Bloemfontein, deel 1, stuk 1, pp. 1-38, pls. i-vii.
- VAN HOEPEN, E. C. N. (1929 a).—Internat. Geol. Congress, Session XV, guide book, Durban-Zululand excursion, pp. 10-18.

Lower Cretaceous Lamellibranchia from Northern Zululand. 391

- VAN HOEPEN, E. C. N. (1931).—"Voorlopige beskrywing van enige Soeloelandse Ammoniete," Pal. Nav. Nas. Mus. Bloemfontein, deel 1, stuk 2.
- WADE, B. (1926).—"The Fauna of the Ripley Formation, Tennessee," U.S.G.S. Prof. Paper, No. 137.
- WEAVER, C. E. (1931).—"Palaeontology of the Jurassic and Cretaceous of West Central Argentina," Mem. Univ. Washington, No. 1 (not seen).
- WOODS, H. (1899-1913).—Mon. Cretaceous Lamellibranchia England, Mon. Pal. Soc.
- WOODS, H. (1906).—"The Cretaceous Fauna of Pondoland," Ann. S. Afr. Mus., vol. iv, pt. vii, pp. 275-350.
- ZITTEL, K. (1913).—Text-book of Palaeontology, English edition, ed. C. R. Eastman.

EXPLANATION OF PLATES.

The figures are approximately natural size unless otherwise stated; in the majority of cases the figures are very slightly reduced.

PLATE XXXVII.

FIGS.	PAGE
1-3. <i>Cucullaea</i> (<i>Megacucullaea</i>) spp.	308
Lombagwenya stream, Northern Zululand.	
1. Left valve from L12.	
2. Fragment of anterior part of large left valve from L9.	
3. Weathered and crushed left valve from L12.	



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LAMELLIBRANCHIA FROM NORTHERN ZULULAND.

Cucullaea (*Megacucullaea*) spp.

PLATE XXXVIII.

FIGS.

PAGE

1-3. *Trigonia (Megatrigonia) obesa* (van Hoepen) 333

Mfongosi stream, Northern Zululand.

1. Specimen from Z3, dorsal view.
2. The same, anterior view.
3. „ right valve in lateral view.



Photo : J. V. L. R.

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LAMELLIBRANCHIA FROM NORTHERN ZULULAND.
Trigonia obesa.

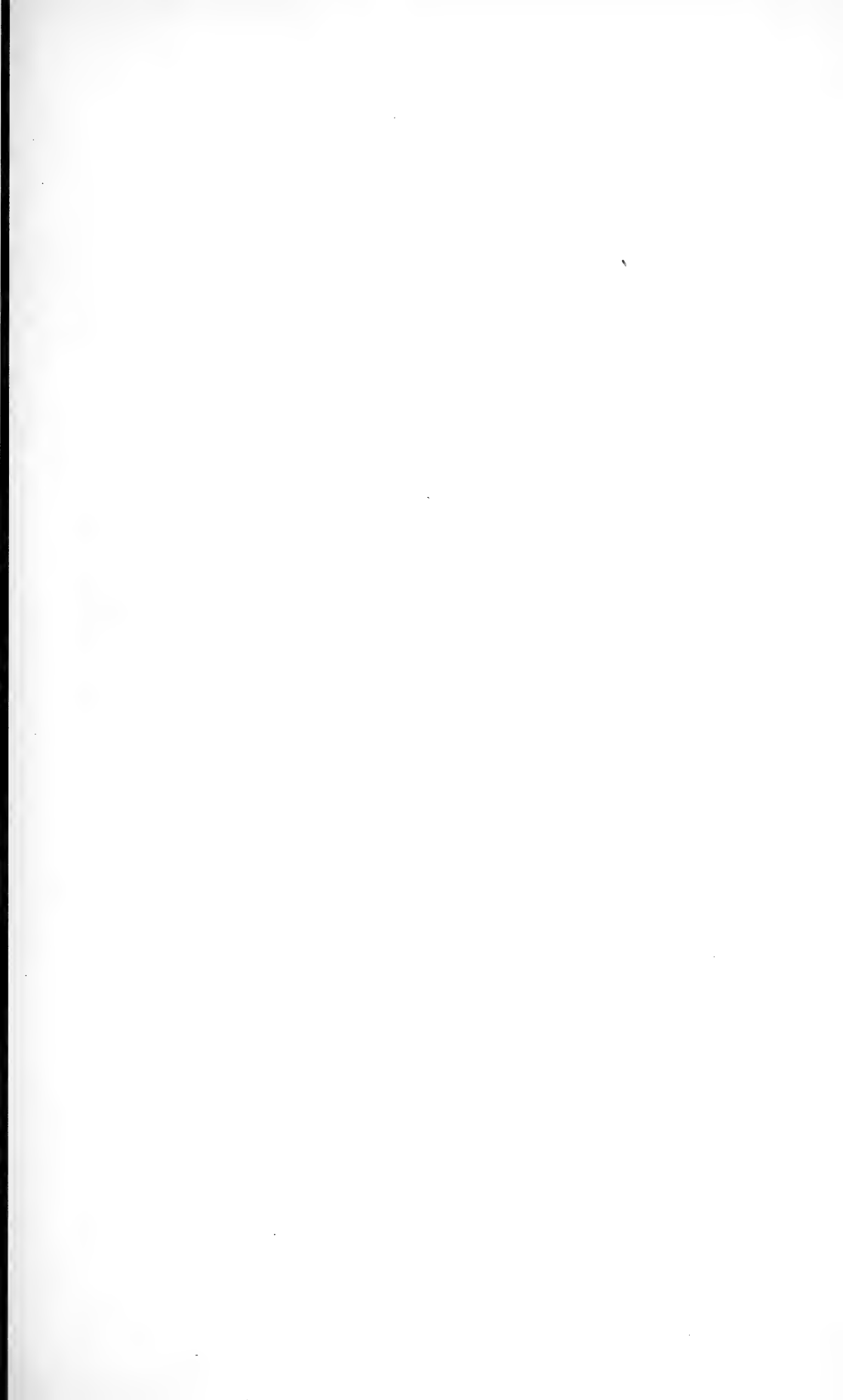


PLATE XXXIX.

FIGS.

PAGE

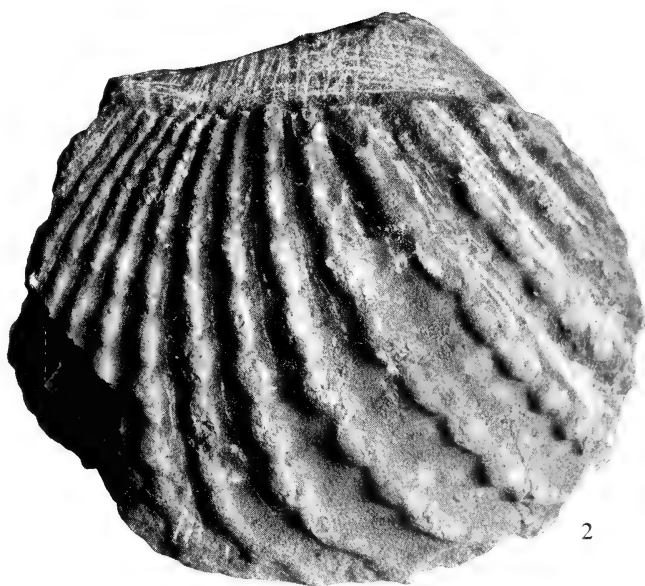
1, 2. *Trigonia (Megatrigonia) obesa* (van Hoepen) 333

Mfongosi stream, Northern Zululand.

1. Left valve from Z3 seen in lateral view.
2. Right valve from Z3 seen in lateral view.



1



2

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LAMELLIBRANCHIA FROM NORTHERN ZULULAND.

Trigonia obesa.

PLATE XL.

FIGS.	PAGE
1-3. <i>Trigonia (Megatrigonia) conocardiiformis</i> (Krauss)	337

Sundays River Beds, Uitenhage Series, Cape Province.

1. Specimen from Sundays River, collected by Dr. W. G. Atherstone, Albany Museum 738, left valve seen in lateral view.
2. The same, dorsal view.
3. „ anterior view.

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LAMELLIBRANCHIA FROM THE UTENHAGE SERIES.
Trigonia conocardiformis.

Photo: J. V. L. R.

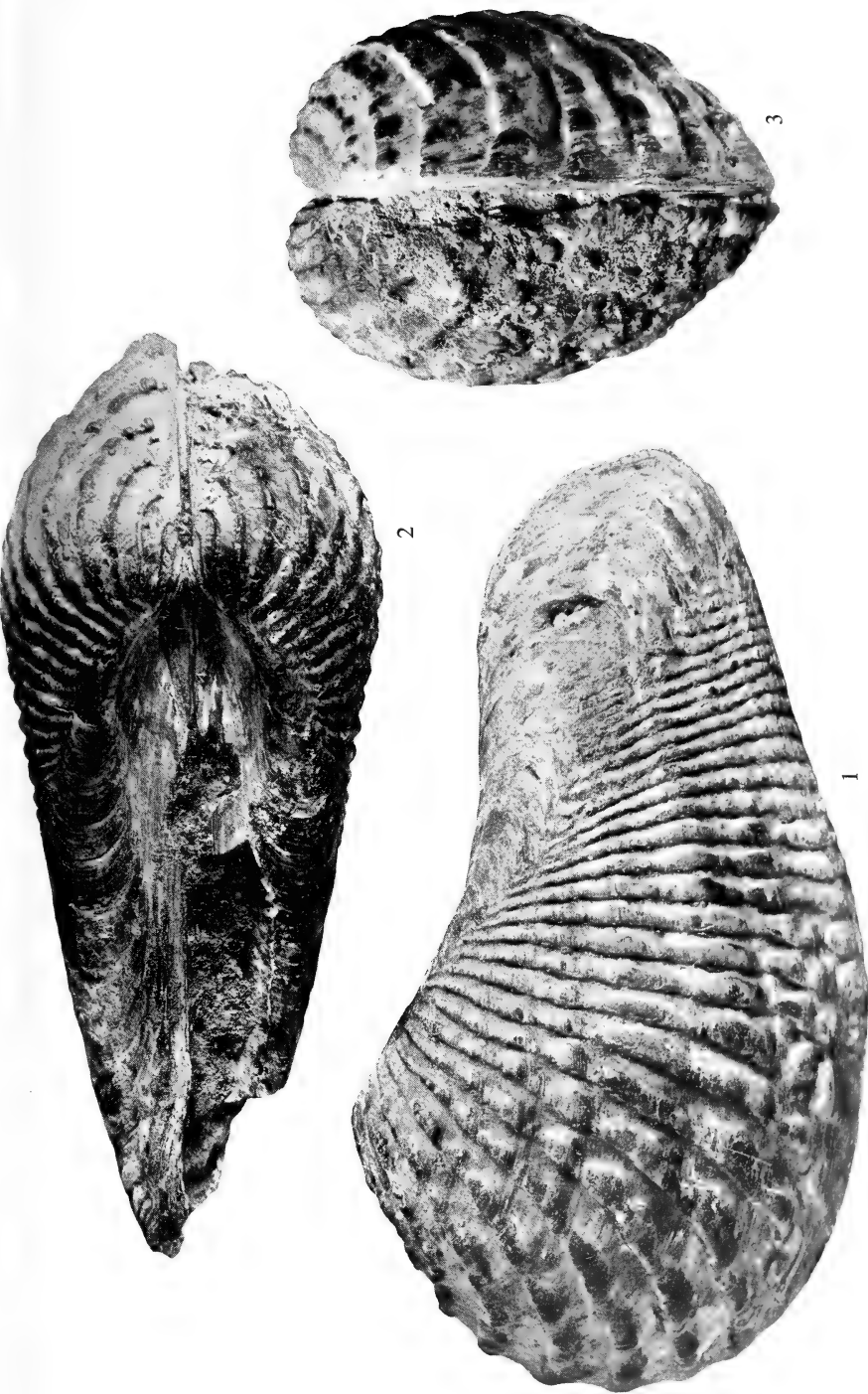


PLATE XLI.

FIGS.	PAGE
1-4. <i>Trigonia (Iotrigonia) haughtoni</i> sp. nov.	340
Myesa stream, Northern Zululand.	
1. Hand specimen, with holotype and paratypes from M1; the holotype, the larger right valve on the right side of the specimen; paratypes, a left valve below and a damaged right valve on the left side of the specimen; natural size. (Figs. 2-4 are enlargements of these.)	
2. Paratype, right valve, dorsal view to show area and escutcheon, $\times 2.65$.	
3. Paratype, left valve, slightly oblique dorsal view to show area and escutcheon, $\times 2.5$.	
4. Holotype, right valve, seen in lateral view, $\times 2$.	
5, 6. <i>Trigonia (Rutitrigonia) pongolensis</i> sp. nov.	359
Mfongosi stream, Northern Zululand.	
5. Paratype from Z2, left valve seen in lateral view.	
6. The same, dorsal view.	

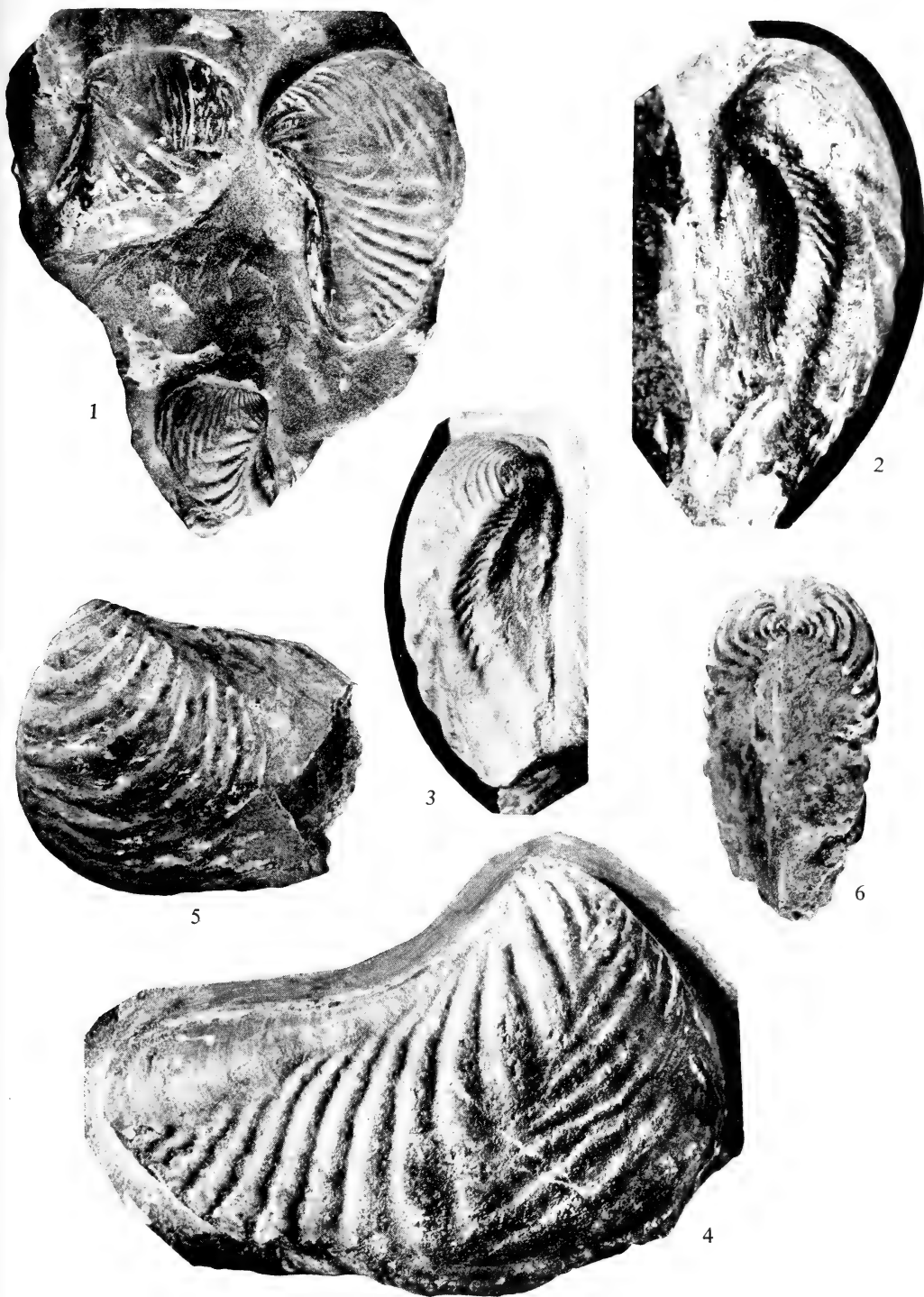


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LAMELLIBRANCHIA FROM NORTHERN ZULULAND.

1-4. *Trigonia haughtoni*.

5, 6. *Trigonia pongolensis*.

PLATE XLII.

FIGS.		PAGE
1-4.	<i>Trigonia (Pleurotrigonia) blanckenhorni</i> R. B. Newton	363
	South of Mokatini, Northern Zululand.	
1.	Left valve from Z25, umbonal region enlarged $\times 2$ approximately, to show beaded marginal carina and traces of costellae on the area.	
2.	The same, anterior view, natural size.	
3.	„ seen in lateral view, natural size.	
4.	„ oblique dorsal view, $\times 2$ approximately.	
5-7.	<i>Trigonia (Rutitrigonia) pongolensis</i> sp. nov.	359
	Mfongosi stream, Northern Zululand.	
5.	Holotype, left valve from Z2, seen in lateral view.	
6.	The same, dorsal view.	
7.	„ hinge, $\times 2$.	

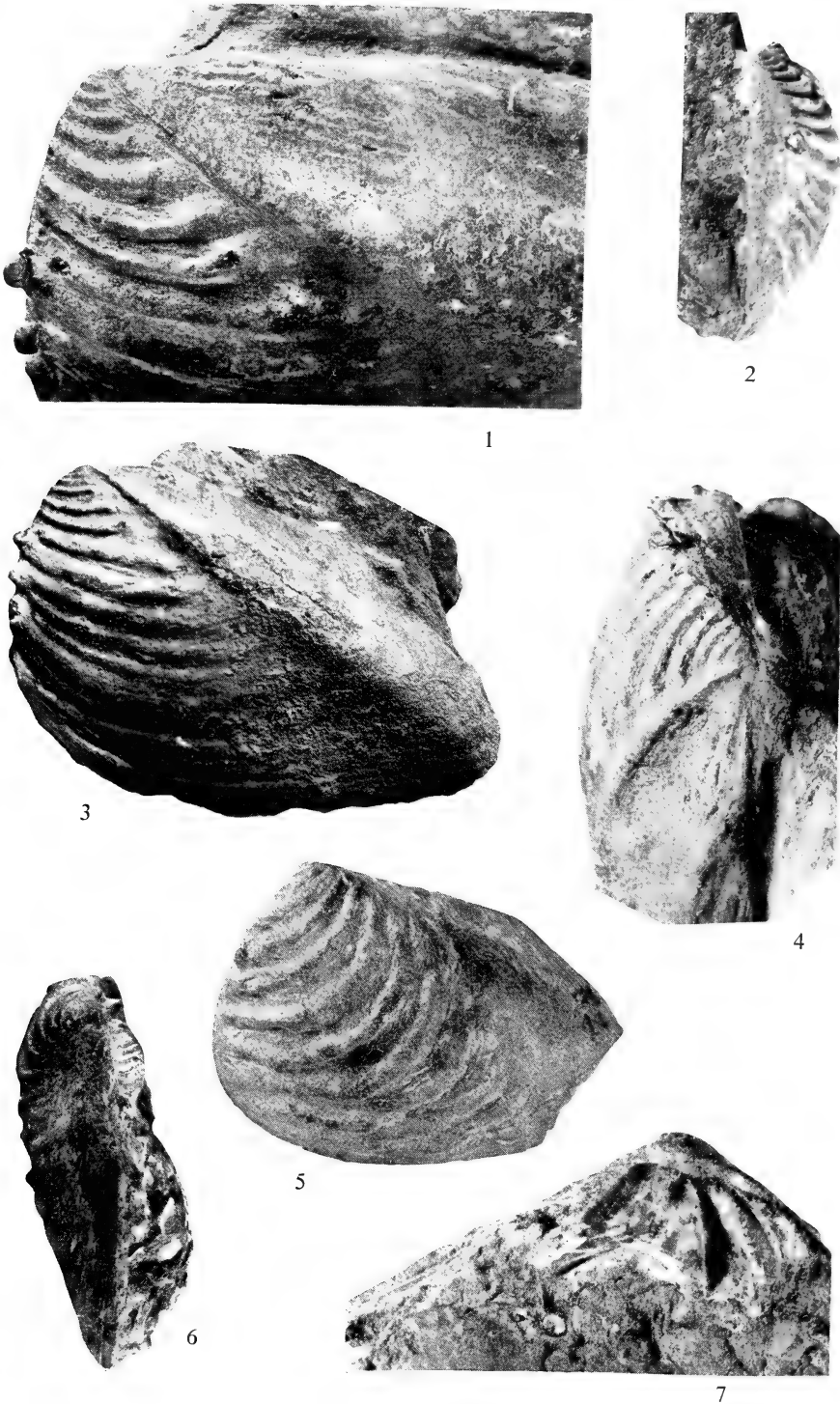


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LAMELLIBRANCHIA FROM NORTHERN ZULULAND.

1-4. *Trigonía blanckenhorni*.

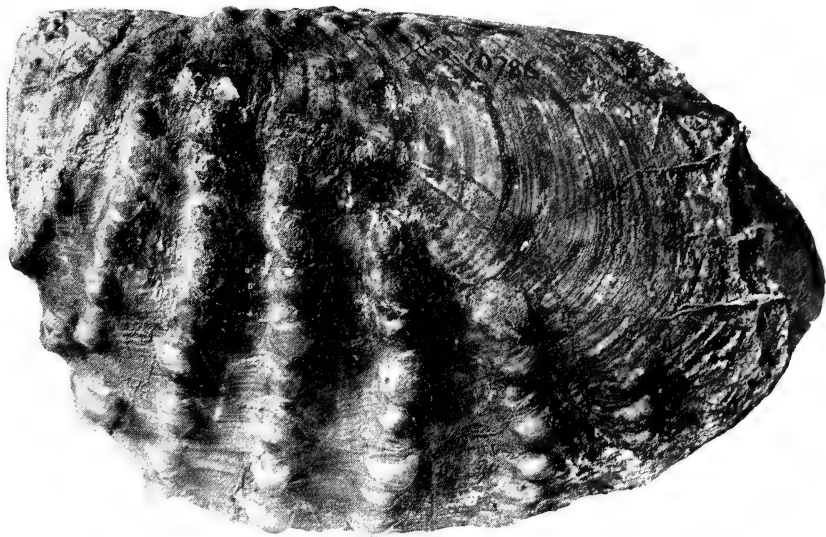
5-7. *Trigonía pongolensis*.





PLATE XLIII.

FIGS.		PAGE
1-3.	<i>Trigonia (Steinmanella) hennigi</i> Lange	347
	Mfongosi stream, Northern Zululand.	
	1. Specimen S. Afr. Mus. 10786, left valve seen in lateral view.	
	2. The same, dorsal view.	
	3. „ „ anterior view.	
4.	<i>Pholadomya luzynesi</i> Lartet	377
	Pongola River, Northern Zululand.	
	4. Specimen from Z19, left valve seen in lateral view, natural size.	



1



2



3



4

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LAMELLIBRANCHIA FROM NORTHERN ZULULAND.

1-3. *Trigonía hennigi*.

4. *Pholadomya luznesi*.



PLATE XLIV.

FIG.		PAGE
1.	<i>Trigonia (Steinmanella) hennigi</i> Lange	347
	Lombagwenya stream, Northern Zululand.	
	Specimen from L14, right valve seen in lateral view.	
2.	<i>Cucullaea (Megacucullaea) kraussi</i> Tate	305
	Sundays River Beds, Uitenhage Series, Cape Province.	
	Portion of right valve from Zwartkops River, Albany Museum 792, collected by Dr. W. G. Atherstone, to show radial ornamentation.	

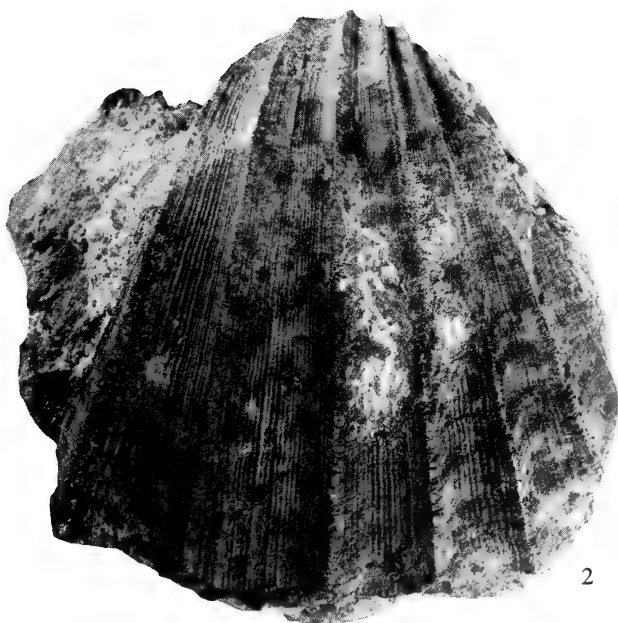


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LAMELLIBRANCHIA FROM NORTHERN ZULULAND AND THE UITENHAGE SERIES.

1. *Trigonia hennigi*.

2. *Cucullaea* (*Megacucullaea*) *kraussi*.

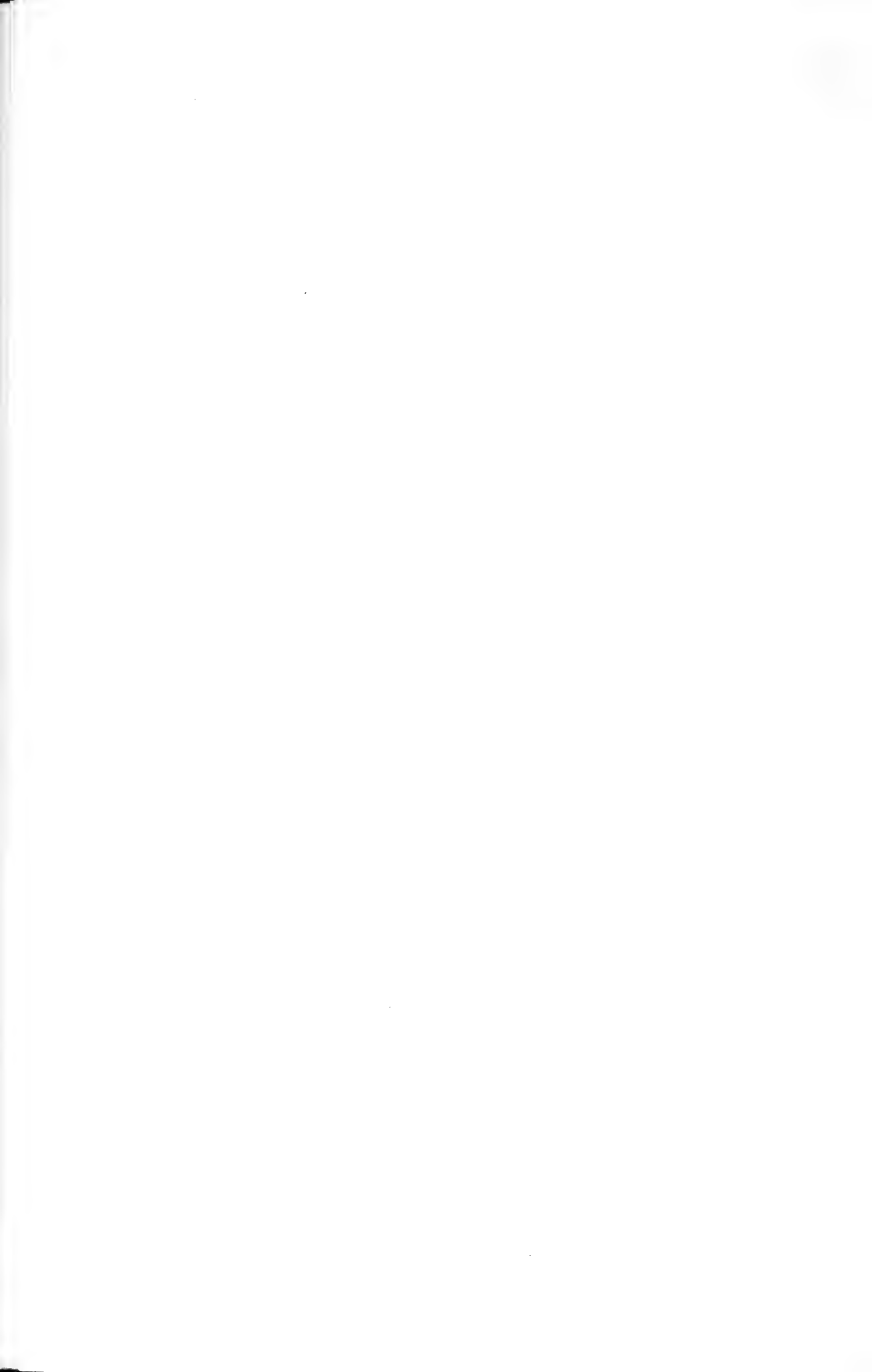




PLATE XLV.

FIGS.

PAGE

1-3. *Trigonia* (*Sphenotrigonia*) *frommurzei* sub-gen. et sp. nov. 367

Mfongosi stream, Northern Zululand.

1. Holotype, S. Afr. Mus. 10586, left valve seen in lateral view.
2. The same, dorsal view.
3. The same, anterior view (the gentle lunular depression does not show up in this photograph).

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LAMELIBRANCHIA FROM NORTHERN ZULULAND.
Trigonia frommurzei.

Photo : J. V. L. R.



PLATE XLVI.

FIGS.	PAGE
1-4. <i>Trigonia</i> (<i>Sphenotrigonia</i>) <i>frommurzei</i> subgen. et sp. nov.	367
Mfongosi stream, Northern Zululand.	

1. Left valve, S. Afr. Mus. 10591, seen in lateral view; a considerable part of the posterior end is missing.
2. Anterior part of an immature left valve from Z7, interior view to show the dentition.
3. Specimen S. Afr. Mus. 10588, anterior view.
4. Same specimen as fig. 3, dorsal view; a considerable part of the posterior end is missing.

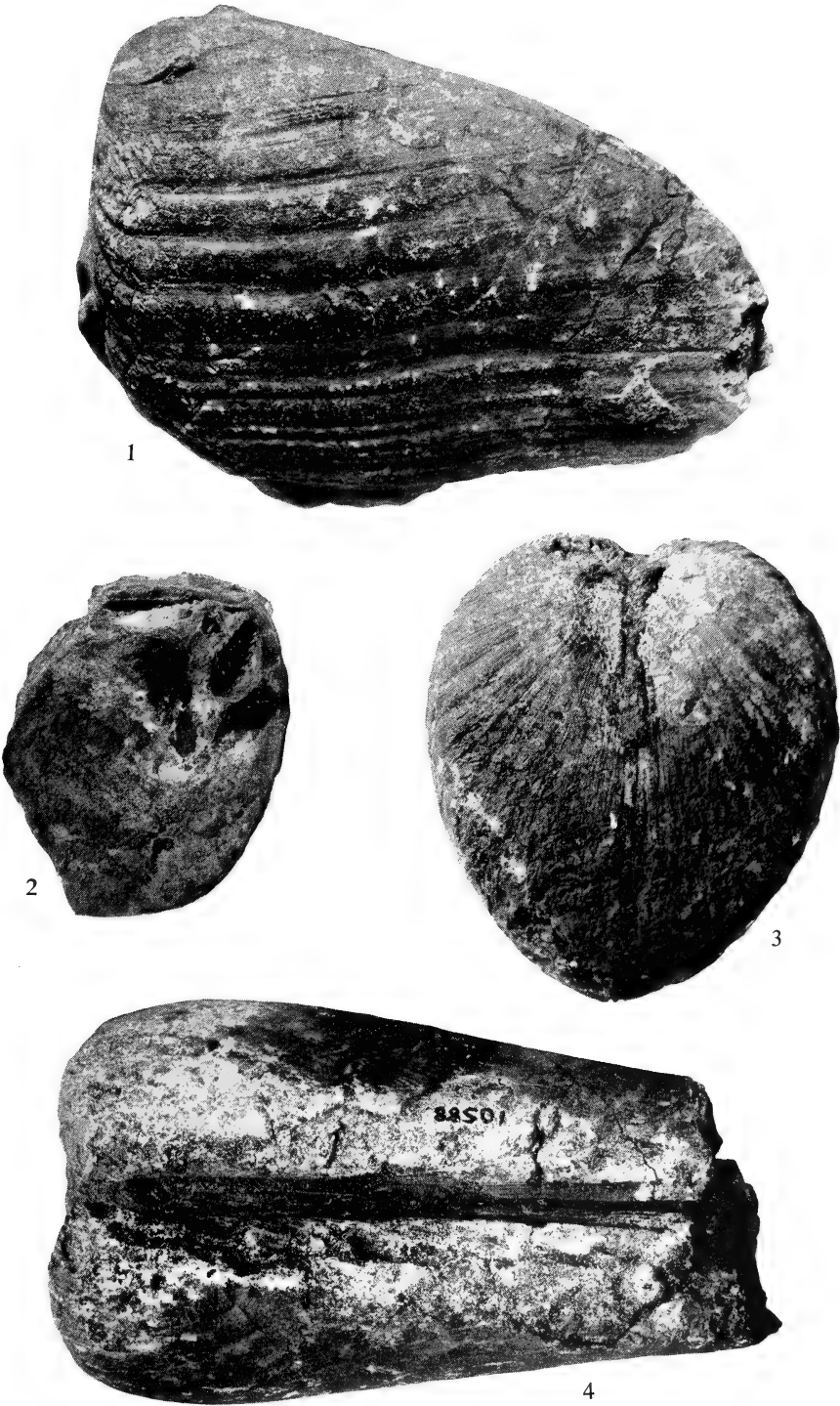


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LAMELLIBRANCHIA FROM NORTHERN ZULULAND.
Trigonia frommurzei.

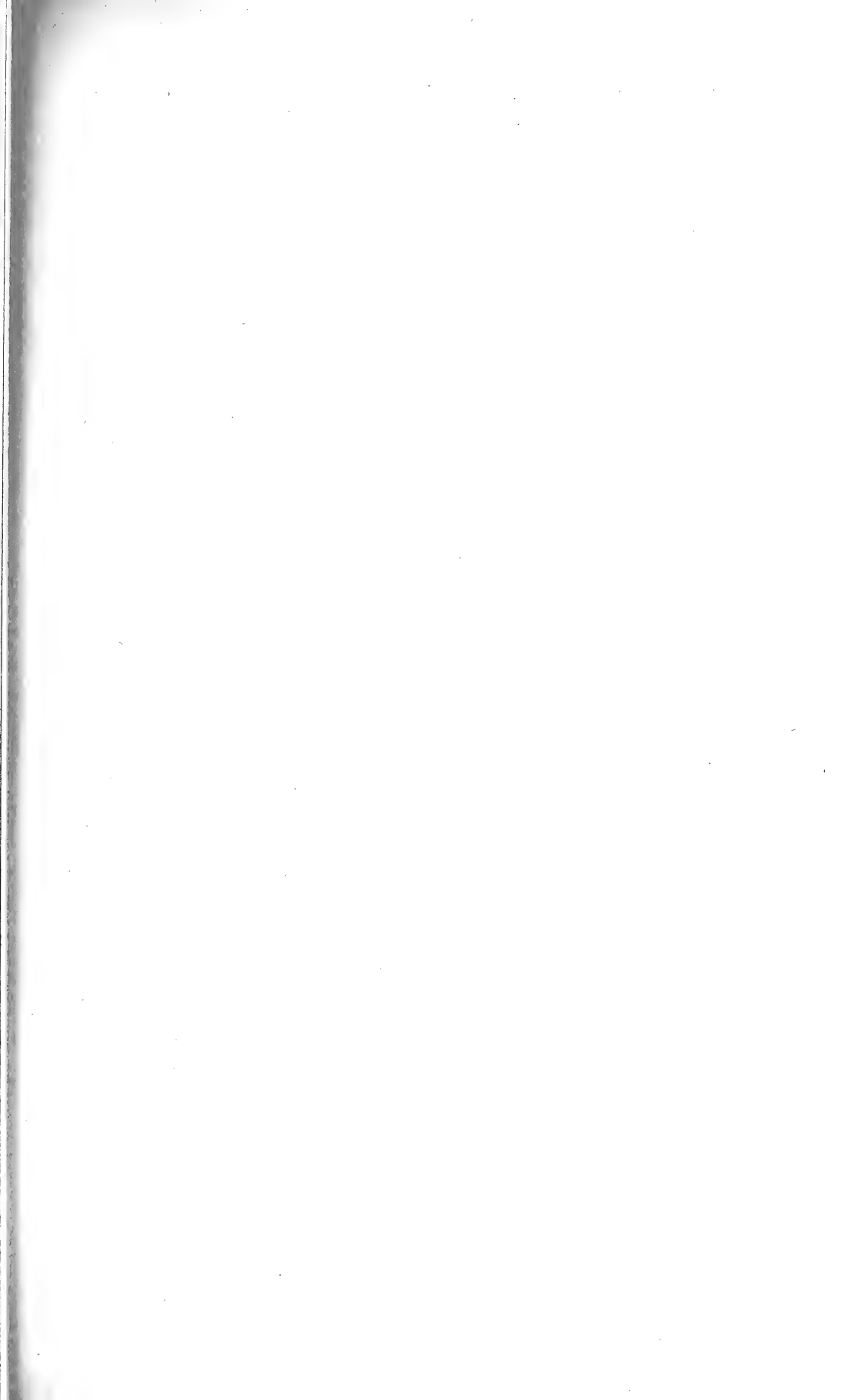


PLATE XLVII.

FIGS.

PAGE

1-4. *Trigonia* (*Sphenotrigonia*) *frommurzei* subgen. et sp. nov. 367

Mfongosi stream, Northern Zululand.

1. Anterior part of a mature left valve from Z13, interior view to show the dentition; a considerable part of the posterior end is missing.
2. Anterior part of an immature left valve from Z7, the same specimen as Plate 10, fig. 2, oblique dorsal view to show the juvenile costae and beaded carinae, $\times 2$ approximately.
3. Right valve from Z8, anterior view.
4. The same specimen as fig. 3, interior view.

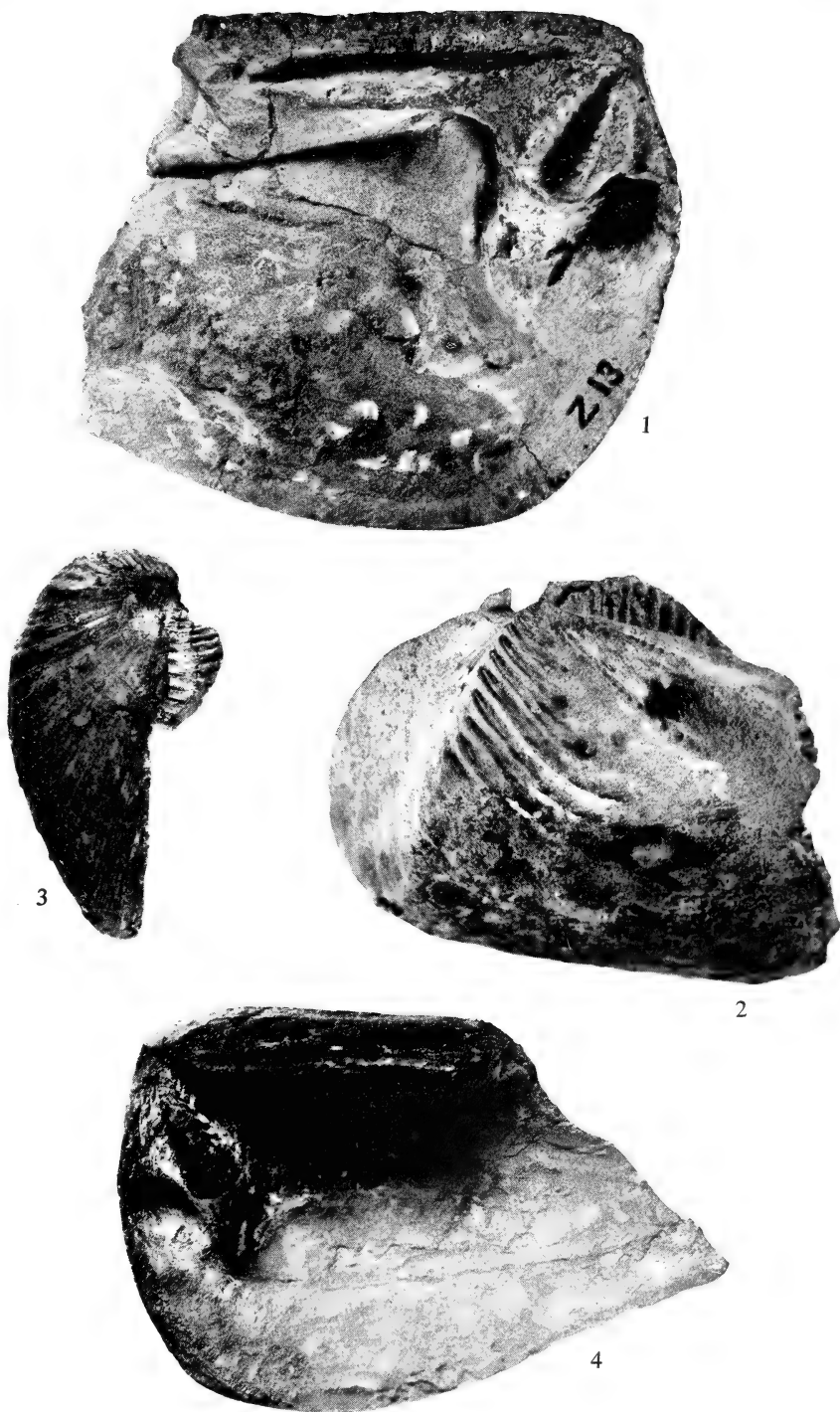


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LAMELLIBRANCHIA FROM NORTHERN ZULULAND.

Trigonium frommuerzei.



PLATE XLVIII.

FIGS.	PAGE
1-6. <i>Protocardia</i> cf. <i>sphaeroidea</i> (Forbes)	379
Mfongosi stream, Northern Zululand.	
1. Left valve from Z19, seen in lateral view.	
2. Same specimen as fig. 1, interior view; note tubercle at margin, postero-ventral corner.	
3. Same specimen as fig. 1, dorsal view.	
4. Right valve, Tvl. Mus. 1796, seen in lateral view.	
5. „ „ Tvl. Mus. 1894, seen in lateral view.	
6. „ „ from Z19, seen in lateral view.	

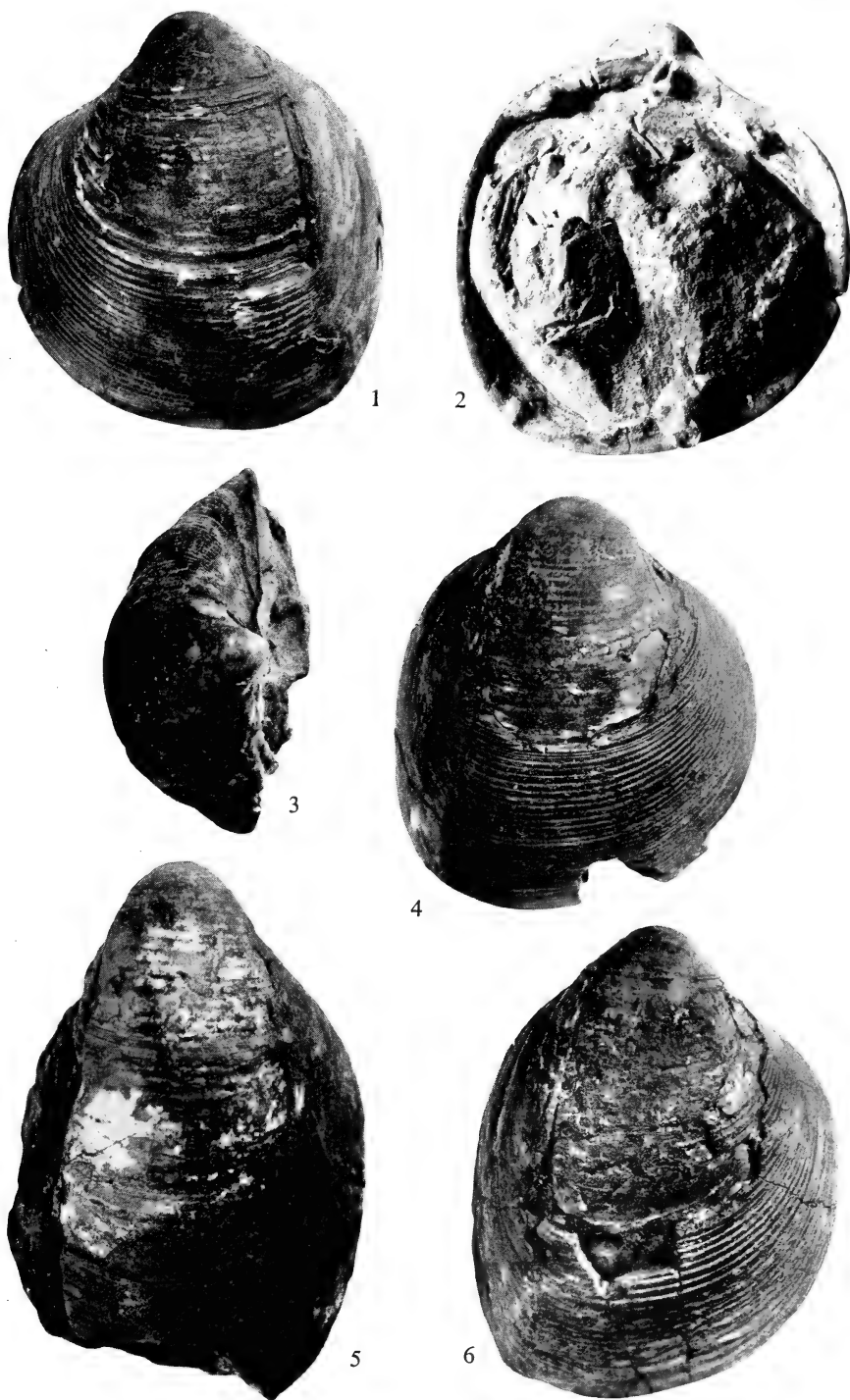


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LAMELLIBRANCHIA FROM NORTHERN ZULULAND.

Protocardia cf. *sphaeroidea*.

PLATE XLIX.

FIGS.		PAGE
1, 2.	<i>Ptychomya robinaldina</i> (d'Orbigny)	383
	Mfongosi stream, Northern Zululand.	
	1. Specimen S. Afr. Mus. 10812, left valve seen in lateral view; very worn specimen, the chevron arrangement of the anterior ribs scarcely but unmistakably preserved.	
	2. The same, dorsal view.	
3-8.	<i>Cardium rogersi</i> sp. nov.	382
	Mfongosi stream, Northern Zululand.	
	3. Holotype, a left valve, S. Afr. Mus. 10791, seen in lateral view.	
	4. Left valve from Z2, interior view.	
	5. Left valve, S. Afr. Mus. 10792, interior view; the subumbonal portion of the hinge has been fractured and depressed slightly.	
	6. Same specimen as fig. 5, seen in lateral view.	
	7. Holotype, same specimen as fig. 3, dorsal view.	
	8. Right valve, S. Afr. Mus. 10793, seen in lateral view; a considerable part of the ventral and posterior borders missing.	
9.	<i>Protocardia</i> cf. <i>sphaeroidea</i> (Forbes)	379
	Mfongosi stream, Northern Zululand.	
	9. Large left valve, S. Afr. Mus. 10788, seen in lateral view.	

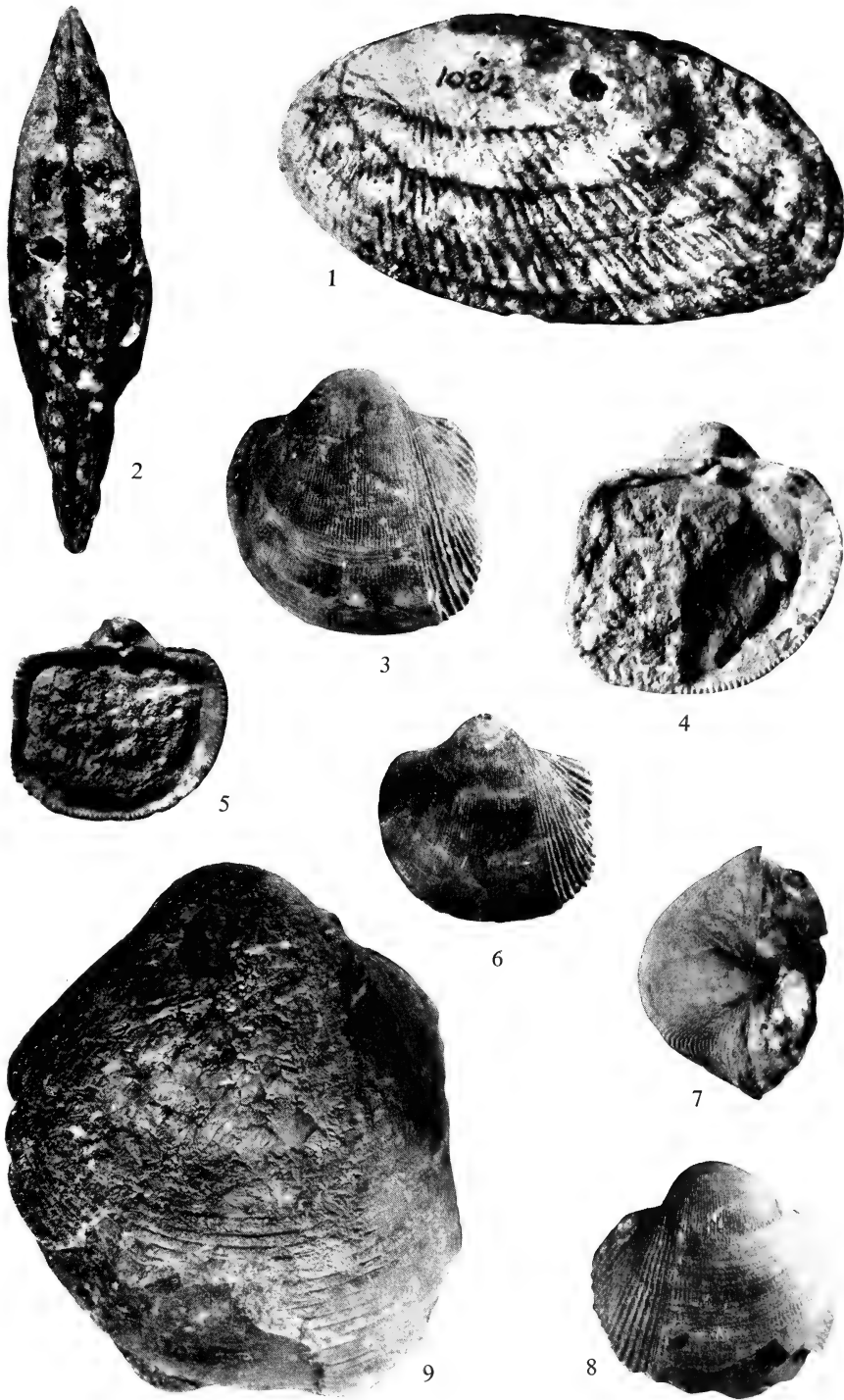


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LAMELLIBRANCHIA FROM NORTHERN ZULULAND.

- 1, 2. *Ptychomya robinaldina*. 3-8. *Cardium rogersi*.
9. *Protocardia* cf. *sphaeroidea*.



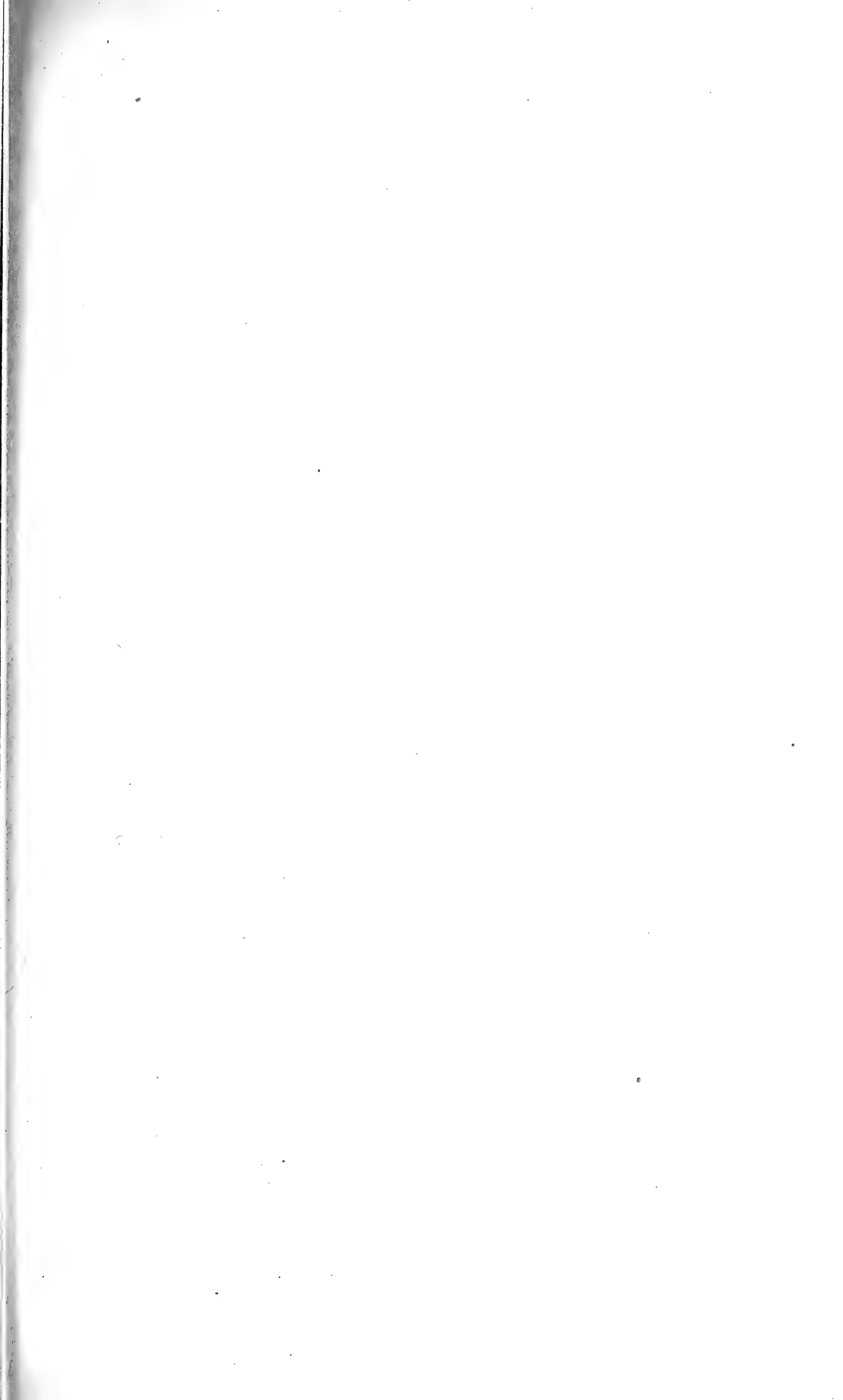


PLATE L.

FIGS.	PAGE
1-11. <i>Panope gurgitis</i> (Brongniart)	385

Figs. 2-4, 7, 10, 11 are specimens of "*Anoplomya lutraria*" Krauss from the Uitenhage Series.

Figs. 1, 5, 6, 8, 9 from Northern Zululand.

1. Specimen from the Lombagwenya stream, Northern Zululand, L7, right valve seen in lateral view.
2. *A. lutraria*, specimen from Zwartkops River, Uitenhage Series, collected by Dr. W. G. Atherstone, right valve seen in lateral view; probably a topotype of Krauss's species. In Alb. Mus. Coll.
3. The same specimen as fig. 2, dorsal view.
4. *A. lutraria*, specimen from Redhouse, Zwartkops River, Uitenhage Series, collected by Mrs. T. V. Paterson, left valve seen in lateral view; probably a topotype of Krauss's species. In Alb. Mus. Coll.
5. Specimen from the Lombagwenya stream, Northern Zululand, L7, portion of right valve seen in lateral view.
6. Right valve from Mfongosi stream, Northern Zululand, Z9, seen in lateral view.
7. *A. lutraria*, specimen from Zwartkops River, Uitenhage Series, collected by Dr. W. G. Atherstone, right valve seen in lateral view; probably a topotype of Krauss's species. In Alb. Mus. Coll.
8. Specimen from the Mfongosi stream, Northern Zululand, Z12, left valve seen in lateral view.
9. The same specimen as fig. 8, dorsal view.
10. *A. lutraria*, specimen from Uitenhage Series, probably part of set Albany Museum 3634-7 collected by Prof. E. H. L. Schwarz at Addo on the Sundays River, seen in lateral view.
11. The same specimen as fig. 10, dorsal view.

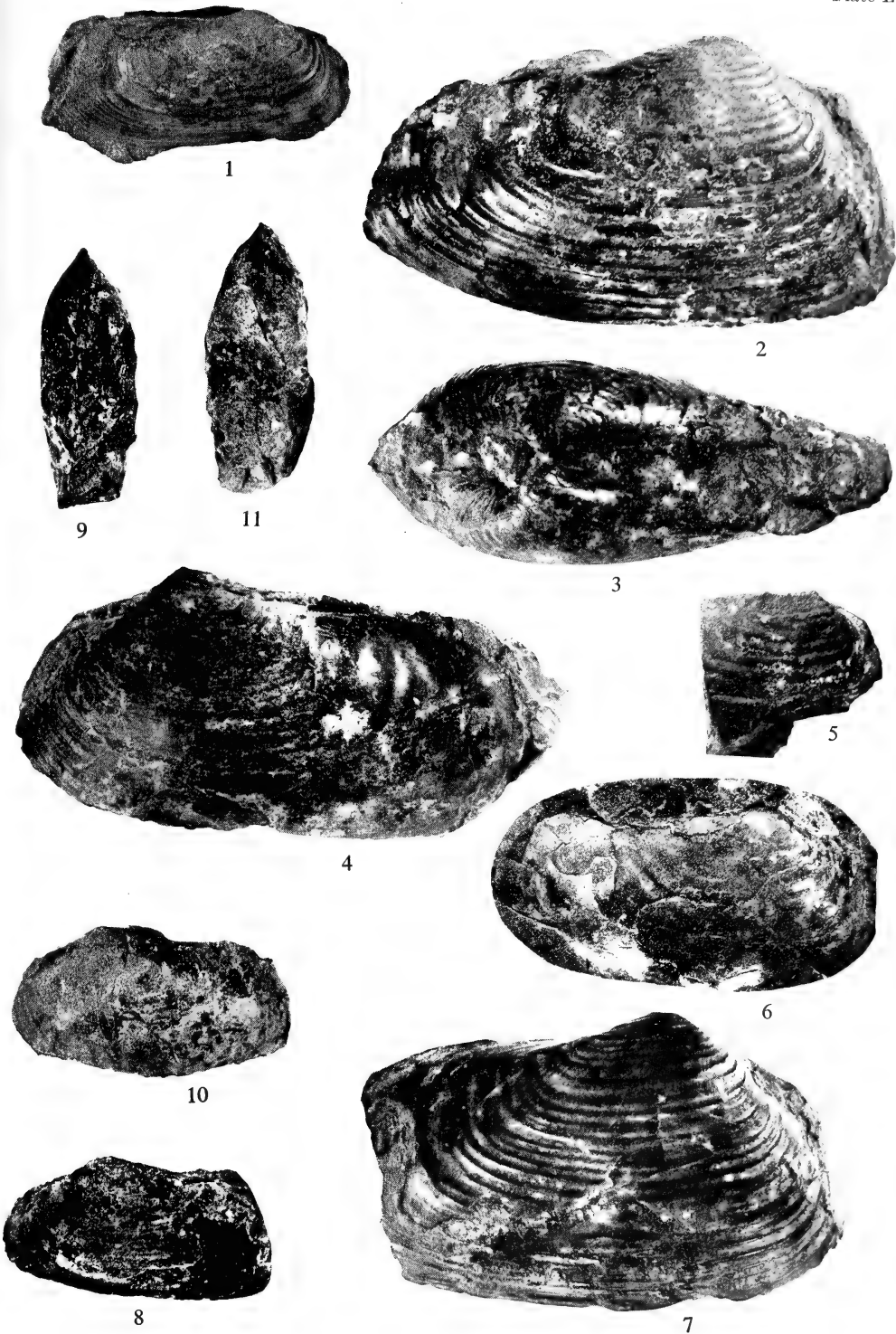


Photo : J. V. L. R.

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LAMELLIBRANCHIA FROM NORTHERN ZULULAND AND THE UITENHAGE SERIES.
Panope gurgitis.



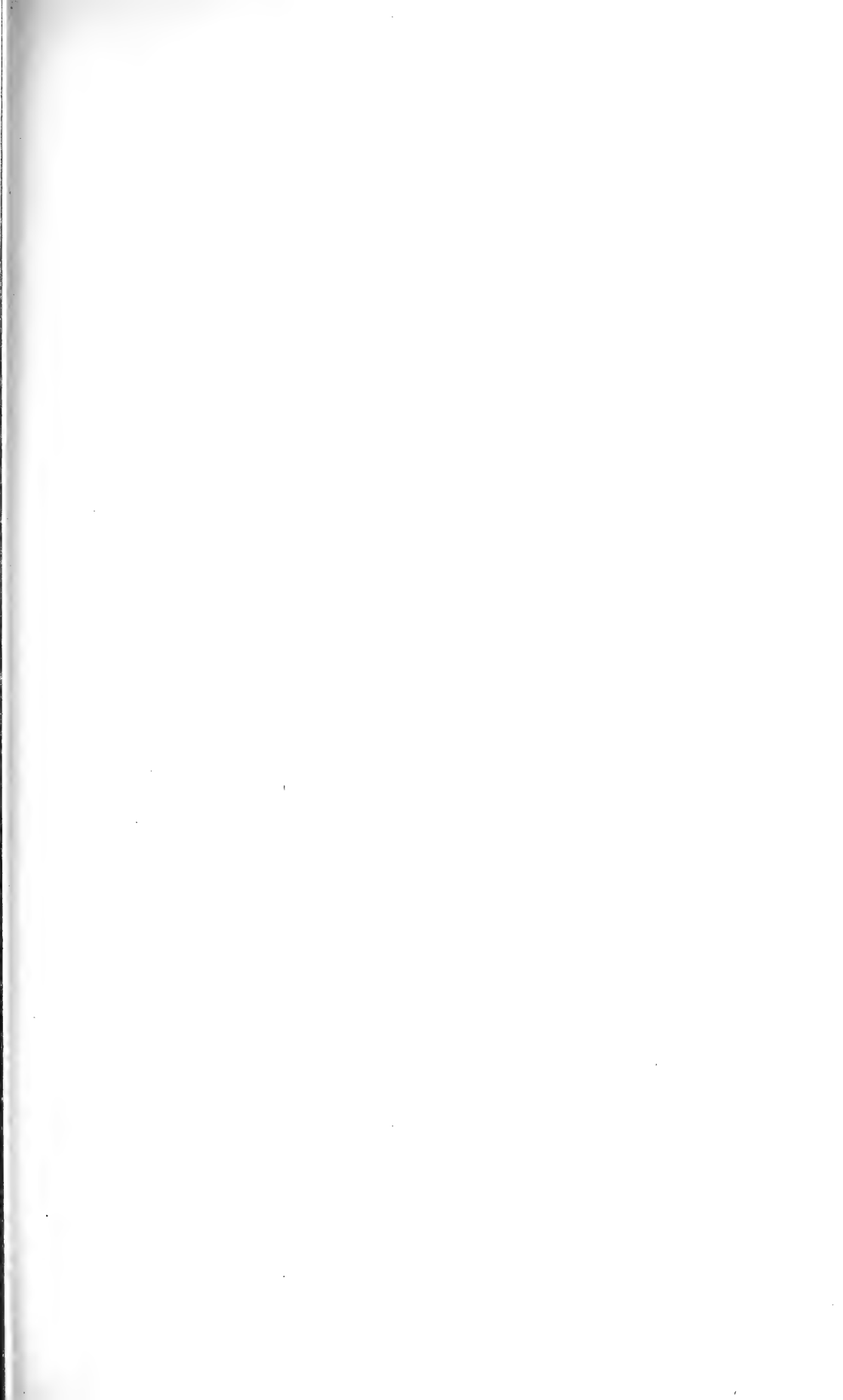


PLATE LI.

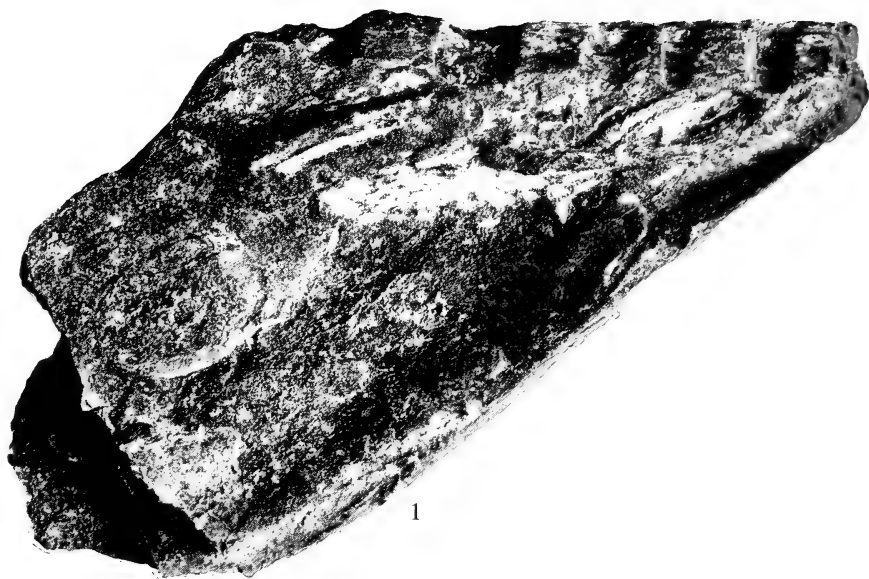
FIGS.

PAGE

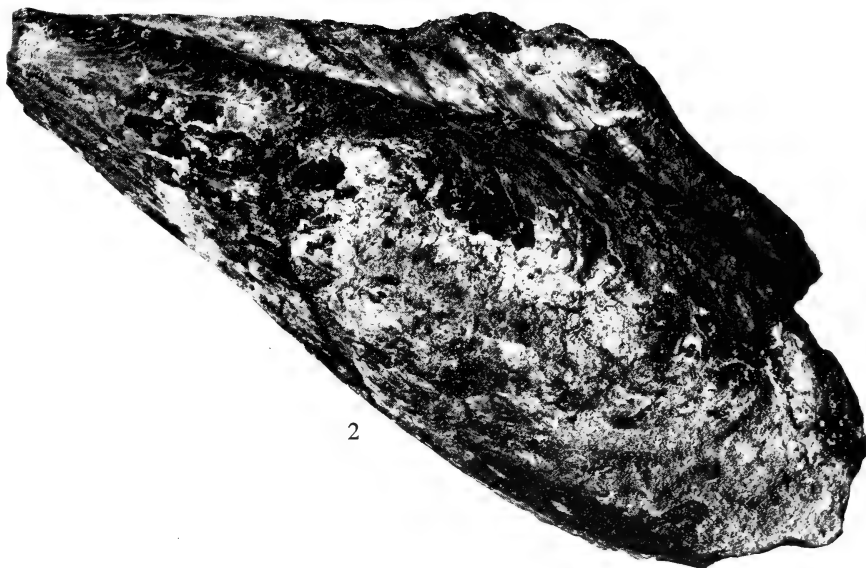
1, 2. *Gervillia dentata* Krauss 310

Mfongosi stream, Northern Zululand.

1. Left valve, interior view, S. Afr. Mus. 10807.
2. The same, seen in lateral view.



1



2

Photo : J. V. L. R.

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LAMELLIBRANCHIA FROM NORTHERN ZULULAND.

Gervillia denatata.



PLATE LII.

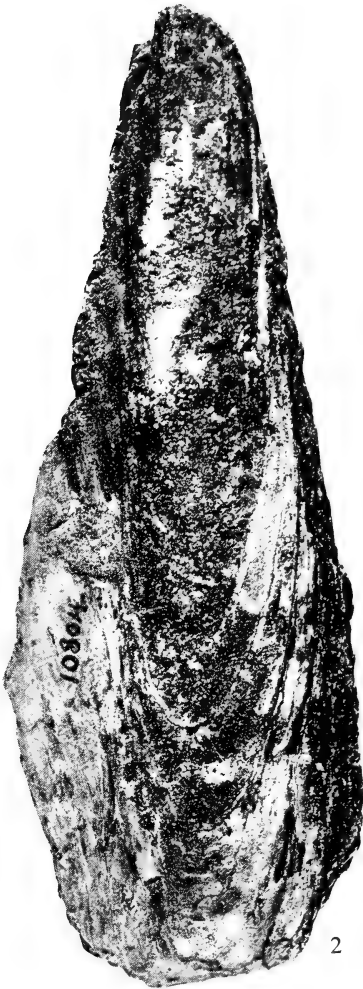
FIGS.	PAGE
1-3. <i>Gervillia dentata</i> Krauss	310

Mfongosi stream, Northern Zululand.

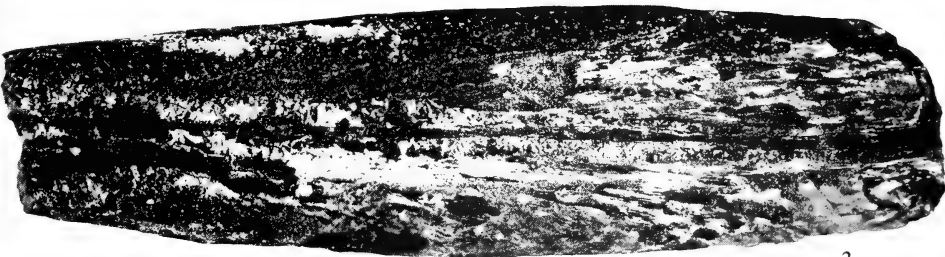
1. Specimen S. Afr. Mus. 10802, right valve seen in lateral view.
2. Specimen S. Afr. Mus. 10804, right valve seen in lateral view.
3. The same specimen as fig. 2, dorsal view.



1



2



3

Photo : J. V. L. R.

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LAMELLIBRANCHIA FROM NORTHERN ZULULAND.
Gervillia dentata.





PLATE LIII.

FIGS.	PAGE
1-3. <i>Gervillia dentata</i> Krauss	310

Sundays River Beds, Uitenhage Series, Cape Province.

1. Specimen from the Sundays River, collected by Dr. W. G. Atherstone, Albany Museum 822, left valve seen in lateral view, reduced $\times 0.83$ approximately, showing the demarcated anterior area.
2. The same, dorsal view, reduced $\times 0.83$ approximately.
3. Specimen from the Sundays River, collected by Dr. W. G. Atherstone, Albany Museum 810, anterior portion of left valve, showing the demarcated anterior area.

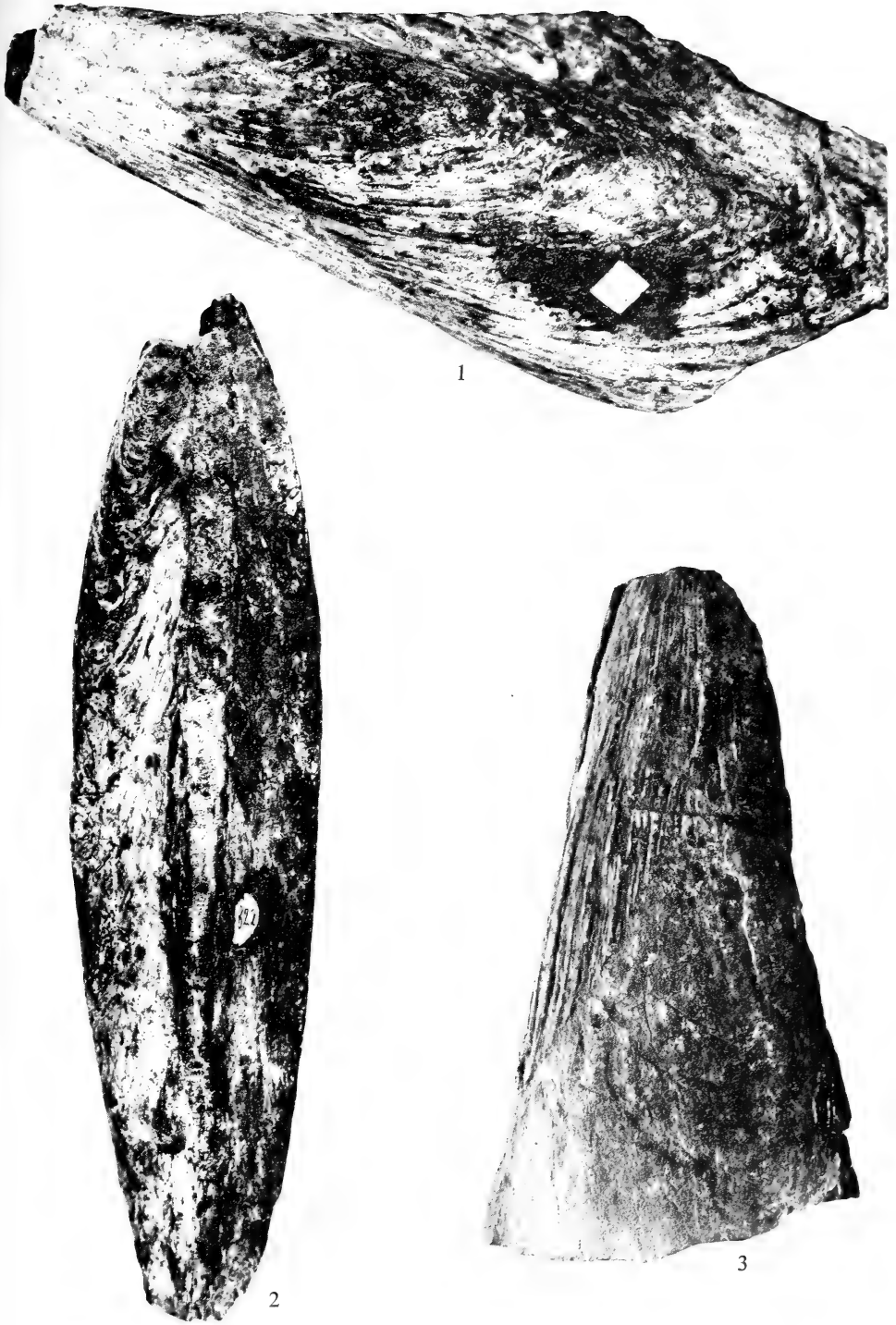


Photo : J. V. L. R.

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LAMELLIBRANCHIA FROM THE UITENHAGE SERIES.
Gervillia dentata.



PLATE LIV.

FIGS.	PAGE
1, 2. <i>Gervillia dentata</i> Krauss	310

Sundays River Beds, Uitenhage Series, Cape Province.

1. Right valve from the Sundays River, collected by Dr. W. G. Atherstone, Albany Museum 823, seen in lateral view, the posterior part missing.
2. The same, interior view.

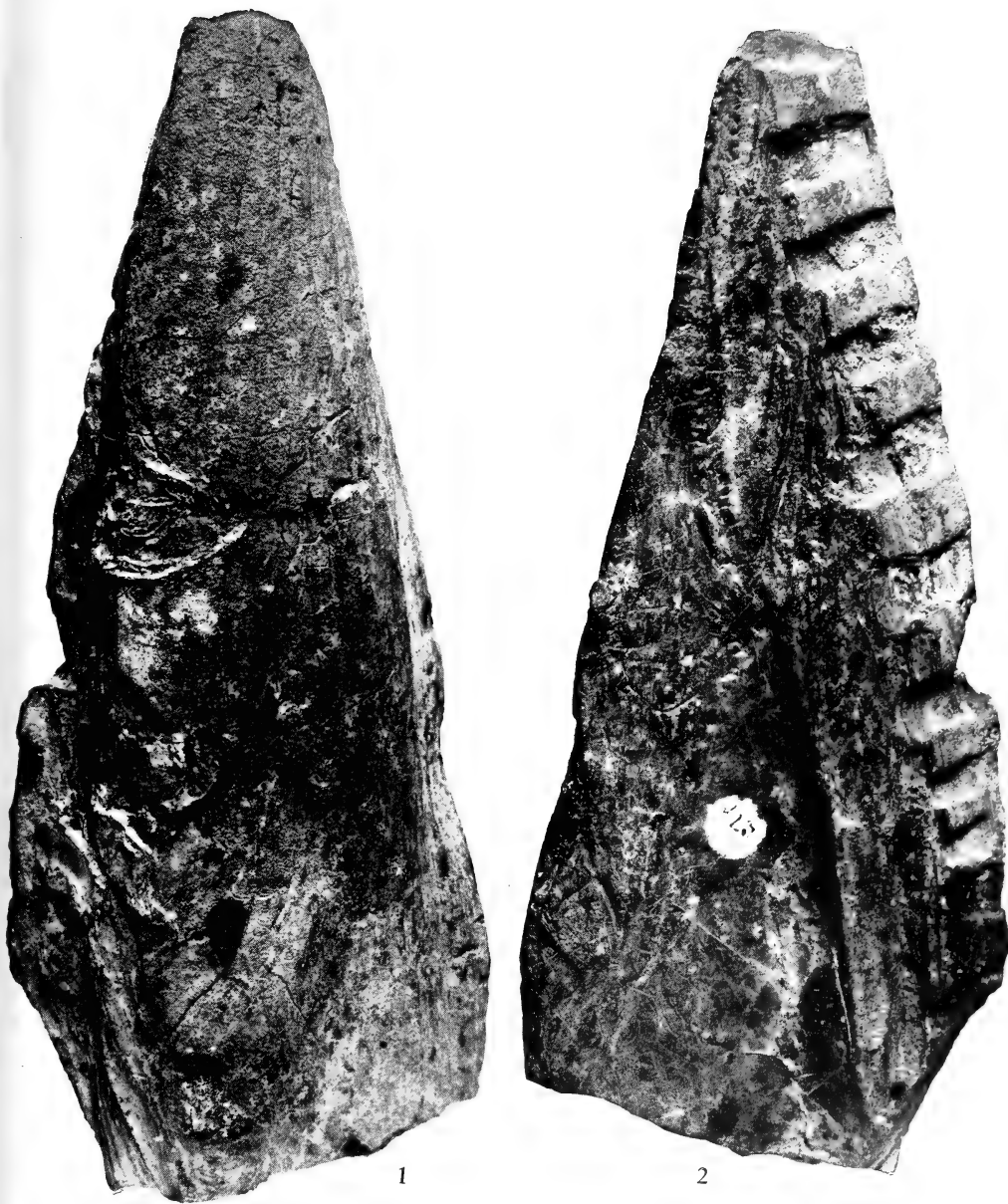


Photo: J. V. L. R.

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LAMELLIBRANCHIA FROM THE UITENHAGE SERIES.

Gervillia dentata.

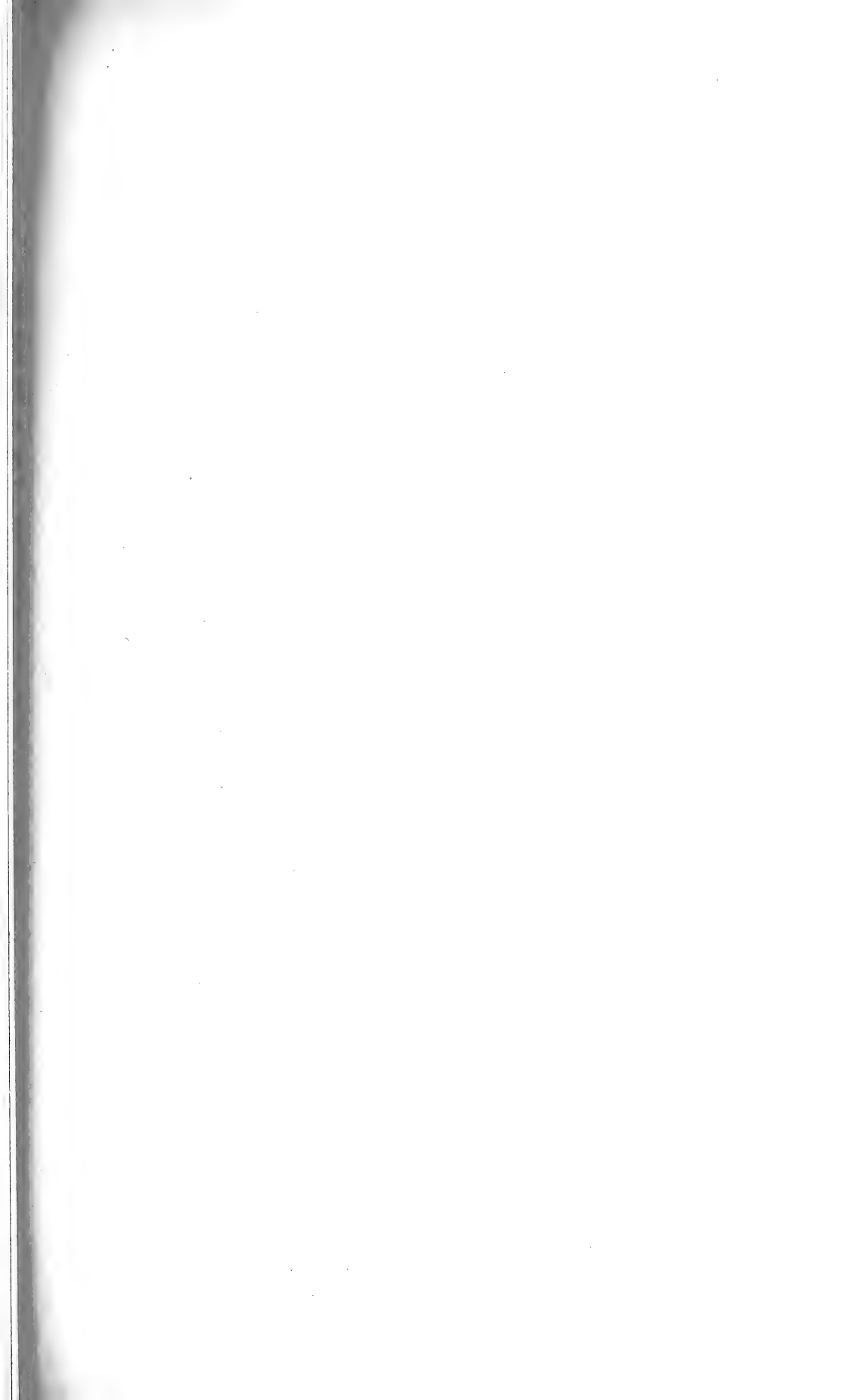


PLATE LV.

FIGS.	PAGE
1, 2. <i>Gervillia dentata</i> Krauss	310

Sundays River Beds, Uitenhage Series, Cape Province.

1. Right valve from the Sundays River, collected by Dr. W. G. Atherstone, Albany Museum 827, reduced $\times 0.7$ approximately, seen in lateral view.
2. The same, interior view.

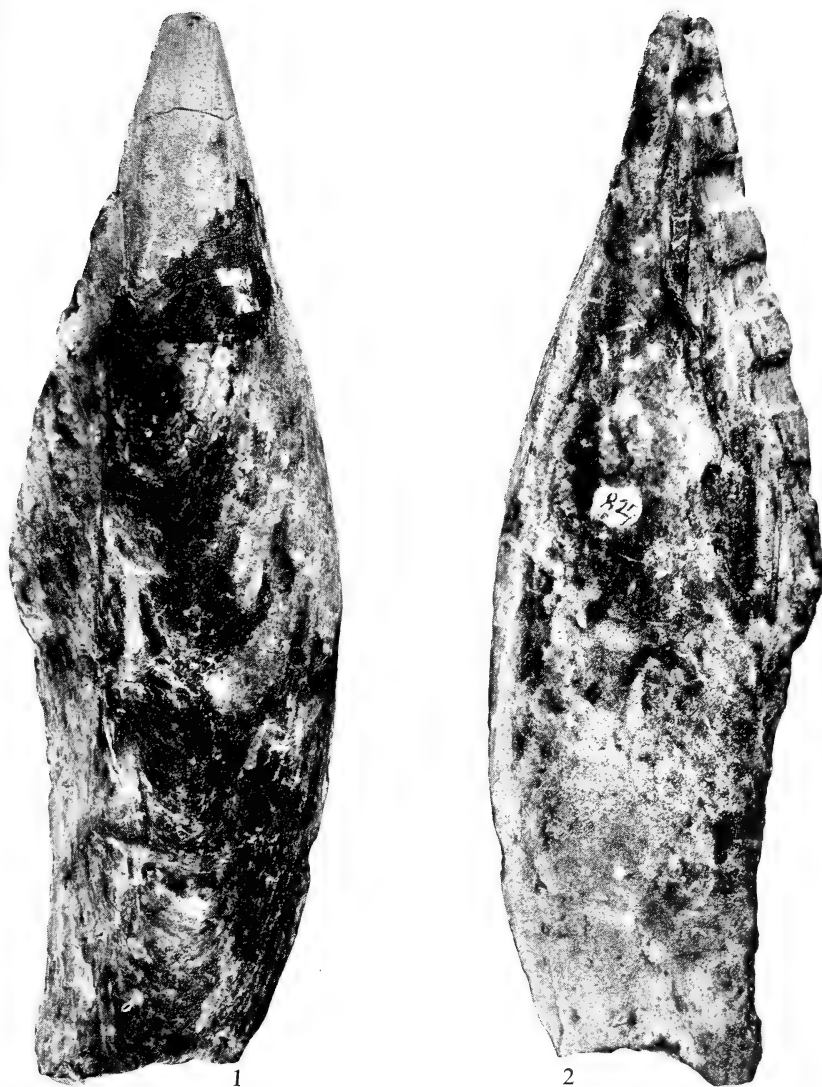


Photo : J. V. L. R.

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LAMELLIBRANCHIA FROM THE UITENHAGE SERIES.

Gervillia dentata.



HERN ZULULAND.

gwenya and Msinyene Pan.										Moka-tini.	
4.	L5.	L6.	L7.	L8.	L9.	L11.	L12.	L14.		Z24.	Z25.
<i>Cucullae</i>							?				
"					×		×				
<i>Trigona</i>											×
<i>Glycyne</i>											
<i>Gervillia</i>		×					×				
<i>Isognom</i>											
<i>Inoceran</i>											
"											
<i>Pseudav</i>										×	
<i>Aucellin</i>		?									
<i>Exogyra</i>		?		?							×
<i>Lopha d</i>											
<i>Trigonia</i>											
"											
"											×
"					×		×	×			
"											
"	×	×	×		×					×	×
"											
"											
<i>Neithe</i>		?									
"											
<i>Pholado</i>											
"				?							
<i>Goniomy</i>											
<i>Veniella</i>											×
<i>Protocan</i>											
<i>Cardium</i>											
<i>Panope</i>				×		×					
<i>Thetiron</i>							×			×	
<i>Turritel</i>											
<i>Avellana</i>											
<i>Dicrolon</i>						×					

7. TABLE SHOWING DISTRIBUTION OF SPECIES IN LOWER CRETACEOUS DEPOSITS, PONGOLA RIVER AREA, NORTHERN ZULULAND.

	Mfongosi.																					Pongola.						Myasa.		Lombagwenya and Mainyene Pan.														Moka-tini.	
	Za.	Z1.	Z2.	Z3.	Z4.	Z5.	Z6.	Z7.	Z8.	Z9.	Z10.	Z11.	Z12.	Z13.	Z14.	Z15.	Z16.	Z17.	Z18.	Z19.	Z20.	Z21.	M1.	M2.	L1.	L2.	L3.	L3+.	L4.	L5.	L6.	L7.	L8.	L9.	L10.	L11.	L12.	L14.	Z24.	Z25.					
LAMELLEBRANCHIA.																																													
<i>Cucullaea</i> (<i>Cyphozia</i>) <i>woodsi</i>	x	.	.	.	x			
" (<i>Megacucullaea</i>) <i>spp.</i>			
<i>Trigonarca</i> cf. <i>tigerianensis</i>			
<i>Oligomyria</i> cf. <i>grisebachii</i>			
<i>Gervillia dentata</i>			
<i>Isochomon</i> sp.			
<i>Inoceramus concentricus</i>			
" <i>concentricus</i> var. <i>subcylindrus</i>			
<i>Pseudoculinis africana</i>			
<i>Cucullina grypharoides</i>			
<i>Eryogma conica</i>			
<i>Lophia diluviana</i>			
<i>Trigonia</i> (<i>Micatrigrionia</i>) <i>obesa</i>			
" (<i>Isotrigriona</i>) <i>haughtoni</i>			
" (<i>Rutitrigriona</i>) <i>panglossensis</i>			
" (<i>Pleurotrigriona</i>) <i>blanchhorni</i>			
" (<i>Steinmannella</i>) <i>kennigi</i>			
" (<i>Sphenotrigriona</i>) <i>fromiaurzei</i>			
" (<i>Scabutrigriona</i>) <i>spp.</i>			
" (") <i>crickii</i>			
" (") cf. <i>kraussi</i>			
<i>Neothoa quadricostata</i>			
" <i>quingocostata</i>			
<i>Phaladonys</i> ? <i>luyensis</i>			
" <i>luyensis</i>			
<i>Goniomya</i> sp.			
<i>Venusella thridgii</i>			
<i>Prodcardia</i> cf. <i>sphaeroides</i>																															



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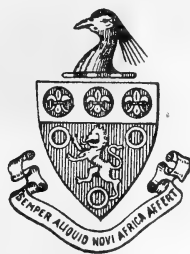
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VOLUME XXXI. 72.4

DESCRIPTIONS OF THE PALAEONTOLOGICAL MATERIAL
COLLECTED BY THE SOUTH AFRICAN MUSEUM AND
THE GEOLOGICAL SURVEY OF SOUTH AFRICA.

PART IV, containing:—

10. *A Critical Revision of the Quaternary Perissodactyla of Southern Africa.*—By H. B. S. COOKE. (With 31 Text-figures.)

Title Page and Index to Volume XXXI.



ISSUED DECEMBER 1950. PRICE 14s.

PRINTED FOR THE
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AND THE
GEOLOGICAL SURVEY OF SOUTH AFRICA
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10. *A Critical Revision of the Quaternary Perissodactyla of Southern Africa* *.—By H. B. S. COOKE, M.A., D.Sc., F.G.S., F.R.Met.S., F.R.S.S.Afr.

(With 30 Text-figures.)

INTRODUCTION.

THE study of fossil mammals in Southern Africa has been far from systematic and, with a few rare exceptions, writers have been more concerned with placing new species on record than with studying the fauna and revising our knowledge in the light of later discoveries. The first fossil mammal known to have been found in this region is the giant "*Bubalus*" *bainii*, whose horns and damaged skull were recovered in 1839 by the remarkable civil engineer and naturalist Andrew Geddes Bain from alluvial deposits of the Modder River, Orange Free State. The material was described only in 1891 by the British palaeontologist Seeley, and the next record of a fossil mammal appeared in 1906 when Dr. R. Beck described a mastodon tooth from the gravels of the Vaal River. In the following year another German scientist, Professor E. Fraas, gave a further account of this tooth and commented on other remains from the gravels. Also in 1907, the celebrated American palaeontologist Professor W. B. Scott described a collection of fossil mammals from the coast of Zululand. Two years later Dr. Robert Broom made the first of his long series of contributions to mammalian palaeontology in South Africa with his descriptions of a new antelope from alluvial deposits at Caledon and of a new giant horse from a limestone fragment washed up on the beach near Maitland, in the south-western Cape. In 1913 Broom described an assemblage of mammalian fossils from the thermal springs at Floris Bad, and in later years he described several new mammals from the Vaal River gravels and various open sites.

In the past twenty-five years the initiative in the description of South African material has passed from the hands of outside experts like Seeley, Scott and Fraas to those of local workers such as Broom,

* Manuscript submitted in January 1946. Appendix added in October 1950.

Haughton, Dart, van Hoepen, Middleton Shaw and others. During this period a considerable body of material has been collected, but much of it has remained largely unstudied and undescribed unless something obviously new was noticed by the individuals through whose hands it passed. Even then it has been for the most part only the new genera and species which were described, and the fauna as a whole has received little attention. Van Hoepen has large collections from his site at Cornelia which still await description, the South African Museum at Cape Town and the McGregor Museum at Kimberley have hundreds of specimens collected over a long period, and other museums have smaller quantities of undescribed material. Since its inception in 1934 the Archaeological Survey of the Union has acquired notable collections as a result of the activities of several collectors, and little of this material has been described or considered as a whole.

During the years 1935-36 a joint survey of the Vaal River basin was carried out by Messrs. P. G. Söhnge and D. J. L. Visser of the Union Geological Survey, and Professor C. van Riet Lowe, Director of the Archaeological Survey, and during the survey much fossil material was recovered from various horizons in the deposits. The results of the geological and archaeological investigations were published in 1937, under the title "The Geology and Archaeology of the Vaal River Basin", as Memoir No. 35 of the Union Geological Survey, and it was intimated in the letter of transmittal of this Memoir that the fossil material collected would be described at a later date. Through the courtesy of the Director of the Geological Survey all this material was placed in the hands of the present writer for examination and report.*

It soon became apparent that a description merely of the material comprising this collection would be of little value, since it would not include all the species recorded from the deposits, and also because there occur in Pleistocene deposits other than those of the Vaal River basin many species which are likely at any time to be found within this area. For example, a tooth found at Christiana by a student and brought to the writer while this account was in course of preparation has been identified as belonging to a species hitherto recorded only at Cornelia in the Orange Free State. It was also only too obvious that the study of our fossil mammals had been far from systematic and that, with the notable exceptions of Haughton and Shaw, writers had been concerned more with placing new fossils on record than with comparative studies and revision of our knowledge in the light of

* See Appendix.

further discoveries. There exists a very considerable confusion of nomenclature and a multiplicity of specific names which renders the task of description of additional material virtually impossible unless it is accompanied by an amount of concurrent specific revision which would obscure the value of any account of the faunal assemblages. Indeed, it appears that until the material already described has been reviewed and new assessments made of the described species, it is of little value to proceed with the many other problems which our fauna presents.

In the course of his investigations on the cave deposits, Broom has to a certain extent reviewed and revised the Primates, Insectivora, Rodentia and Carnivora. Furthermore, these orders furnish the bulk of the cave fauna, and are virtually unrepresented in the material from open sites. Most of the fossils recovered from the Vaal River basin, surface deposits and other open sites belong to the Perissodactyla, Proboscidea and Artiodactyla. It has accordingly been decided that before the undescribed material can profitably be dealt with, the described species of each of these three important orders of mammals in Southern Africa must be critically reviewed. The present paper considers the first, and perhaps the most important, of these orders.*

As much as possible of the material from the Vaal River basin and elsewhere in the possession of the various museums in Southern Africa has been obtained on loan and examined in addition to the large collection in the Archaeological Survey. Dr. Broom has also been kind enough to make his material available to the writer. With the exception of those specimens which are in other countries, the type specimens of every species have been studied and are figured in the present account. Many of these figures have been drawn by the writer from the original specimens where the published figures are considered inadequate or unsuitable; others are reproductions of the original figures. As far as is possible new fossil material has deliberately not been introduced in this paper, as the purpose is to revise the specific descriptions from type material or from such other specimens as can with reasonable certainty be identified with the types. These descriptions are for the most part new, and are based on a fresh assessment of the original specimens interpreted in relation to the wider assortment of material now available and considered against a background of comparative researches upon the characteristics and variability of related living forms. It is hoped that this revision and

* See Appendix.

correlation of scattered data may help to place our knowledge of these fossil mammals in Southern Africa on a firmer basis than has hitherto been the case, and serve to evaluate the characters of the revised species in a form which may facilitate future identification and comparison.

MATERIAL.

As a result of the conditions which prevailed in Southern Africa in the Quaternary, the fossil remains which have survived are mainly teeth, though skull fragments, loose bones and horn cores are sometimes found under suitable circumstances. Almost all the described fossil mammalian species from this region have been named on teeth, and in the present account the descriptions of species generally give only their dental characters. Complete skulls are so rare that they need not be considered, and the identification of isolated bones is not yet possible, largely owing to the complete absence of whole or even partial fossil skeletons.

The majority of the published descriptions have been rather unsystematic and often scanty. It has therefore been considered generally advisable not to quote the original account but to use it and the specimens in the preparation of a new description. Where quotations are given, however, the quoted material is indicated by the usual signs. The type specimens of each extinct species are figured and, in the descriptions given in the text, it has accordingly been possible to give an account of the features of the *species* which may be used for identification rather than a mere list of the characteristics of the *particular specimen* or specimens. An attempt has also been made here to give a definition of the generic characters of any extinct genus which has not been defined by its founder separately from the description of the genotype species. Where the genus is represented only by a single species, or perhaps by two species, this generic definition obviously may require considerable future revision, but some care has been taken to select as generic characters only the most outstanding features which differentiate the material from related types.

The synonymy given for each species is as full as possible and, it is hoped, includes reference to all the specific designations given to fossil representatives of each described species. In the case of living species, however, the synonymy gives the reference to the type description only, and the further synonymy of the living forms can

be found in the ordinary zoological sources: * the names applied to petrified specimens now assigned to these living forms are, however, given as fully as possible. The accepted specific names of all species living within historic times are followed by an asterisk, to avoid their confusion with species extinct prior to historic times and known only as fossils.

In the descriptions of dental characters the nomenclature of the Cope-Osborn scheme has been followed as far as possible, in accordance with the generally accepted information available. Since there appears, however, to be some lack of uniformity in the conclusions regarding the homologies of the cusps, and there is occasionally some doubt regarding the application of certain terms, the terms applied in the present account are shown in a diagram of a typical member of each family described, or are clearly defined in the text.

For convenience and brevity the customary abbreviations are used to denote molar, premolar, canine and incisor teeth. Milk teeth are, on the whole, of little value for specific identification owing to their considerable variability and the uncertainty of the relationship between their characters and those of the permanent dentition. They are accordingly considered only when absolutely necessary.

In some cases a species is regarded as unrecognisable owing to the inadequacy of the material upon which it is founded or defined, and thus becomes a *species insuff. descr. aut inquirenda*. It may nevertheless be the case that a specimen which has been regarded as in itself inadequate for the creation of a species may be capable of reference to more adequate material.

The numbers assigned by the various museums to the type and other specimens mentioned in this text are given wherever possible, together with an abbreviation indicating the museum concerned, viz.:

Arch. Sur.	Archaeological Survey, University of the Witwatersrand, Johannesburg.
Dept. Anat.	Department of Anatomy, Medical School, University of the Witwatersrand, Johannesburg.
M.M.K.	McGregor Memorial Museum, Kimberley.
Nas. Mus.	Nasionale Museum, Bloemfontein.
S.A. Mus.	South African Museum, Cape Town.
Tvl. Mus.	Transvaal Museum, Pretoria.

* The most up-to-date synonymy is that given in "A Checklist of African Mammals", by G. M. Allen, Bull. Mus. Comp. Zool. Harvard, vol. lxxxiii, 1939.

ORDER PERISSODACTYLA.

THE RHINOCEROSSES.

Amongst the fossil mammalia, the rhinoceroses are only very scantily represented in Southern Africa. Two supposedly extinct forms have been mentioned, each only from a single site, but petrified specimens indistinguishable from the two living species have been recovered from various superficial deposits. These latter specimens are probably not of any very great antiquity, but rhinoceros species are in any case not subject to rapid changes.

The two living forms belong to different genera, and both their skulls and their teeth are quite distinct. The square-lipped or white rhinoceros is quite considerably larger than the hook-lipped or black rhinoceros, as can be seen from the drawings of their respective skulls (fig. 1). The lower jaws are sharply distinguished, that of the black rhinoceros having a deep compressed symphysis as compared with the depressed and rather spatulate symphyseal region of the mandible in the white rhinoceros. The horns have been found isolated and again differ widely in form. Incisor and canine teeth are rudimentary or absent in both species.

The cheek teeth in the rhinoceroses comprise four premolars and three molars arranged in a continuous series and having essentially the same structure, though the first premolar is considerably more simplified and is shed early. The lower third molar is also simple, and does not possess the third lobe so characteristic of the horses and most artiodactyls. The premolars are somewhat smaller than the true molars, the second premolar and first premolar particularly being smaller than the more uniform succeeding teeth. Structurally the teeth differ from those of the horse in being rather low crowned and in possessing strong, distinct roots, but their essential composition is similar to that of the equine cheek teeth. The normal order of eruption of the permanent dentition appears to be M^1 , Pm^1 , Pm^2 , M^2 , Pm^3 , Pm^4 , and lastly M^3 , and is thus somewhat different from that of the horses.

The cheek teeth of the rhinoceroses are lophodont in form, *i.e.* the rows of cusps tend to become fused into ridges. In the upper teeth the two main outer cusps form a ridge known as the *ectoloph*, two anterior cusps form the *protoloph* and two posterior ones the *metaloph*. In the lower teeth three triangularly arranged cusps unite to form a crescentic *metalophid*, and posterior to this two cusps form an arcuate

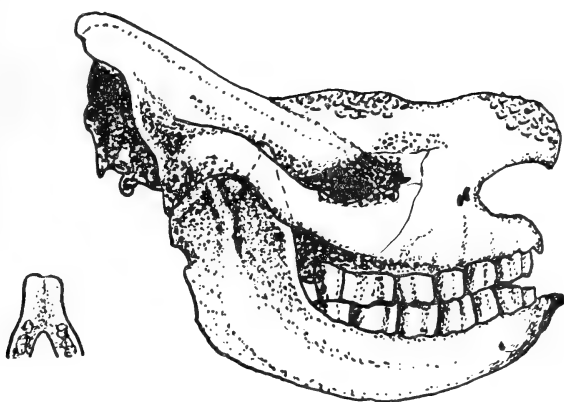
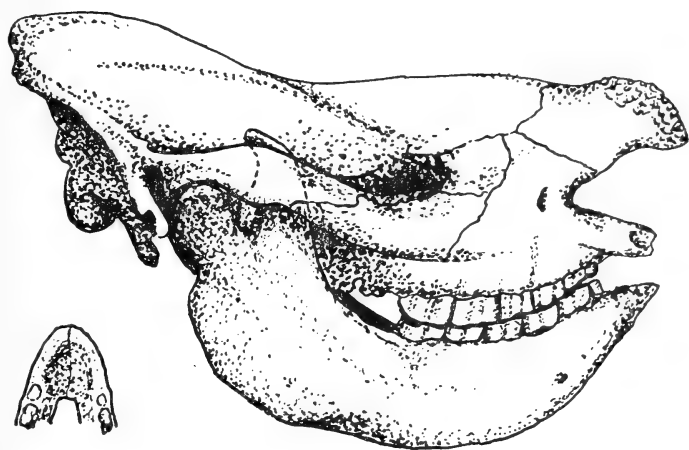


FIG. 1.

Above: Lateral view of skull of *Ceratotherium simum** (Burchell) and plan view of spatulate symphyseal region of the lower jaw. (After Sclater.)

Below: Lateral view of skull of *Diceros bicornis** (Linnaeus) and plan view of the compressed symphyseal region of the lower jaw. (After Owen.)

hypolophid ridge. With wear the enamel is rapidly removed from the top of these ridges and an area of dentine surrounded by enamel is exposed. This can be clearly seen in fig. 2, in which typical upper and

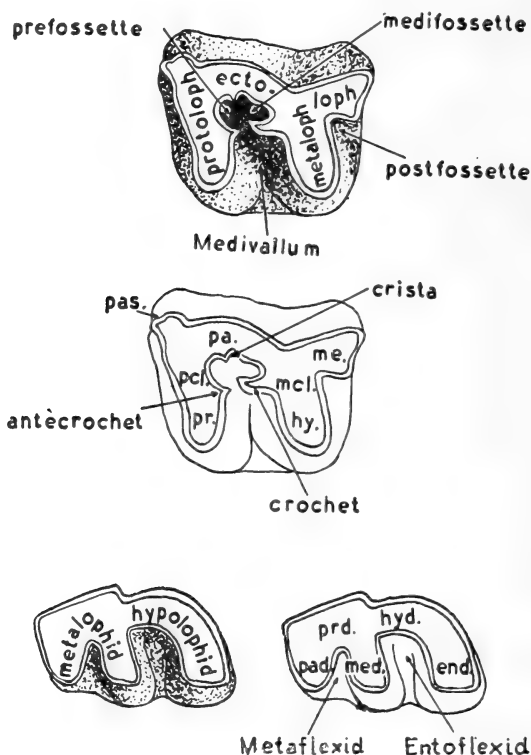


FIG. 2.—Molar elements (following Osborn) of the upper and lower cheek teeth of the Rhinoceros group.

Abbreviations.

Upper teeth: *pas*, parastyle; *pa*, paracone; *me*, metacone; *hy*, hypocone; *pr*, protocone; *pcl*, protoconule; *mcl*, metaconule.

Lower teeth: *prd*, protoconid; *hyd*, hypoconid; *pad*, parastylid; *med*, metaconid; *end*, entaconid. (Original.)

lower first molars are shown indicating the nomenclature used for the cusps, folds and ridges (following Osborn). The valley between the protoloph and metaloph appears to have received no name, and is here termed the medivallum by analogy with the corresponding valley in horse teeth. For the two inlets in the lower teeth the terms "metaflexid" and "entoflexid" are here suggested for convenience

in description, as the same terms have been proposed by Stirton (1941) in the lower teeth of the horses.

Owing largely to a lack of sufficient material, it has unfortunately not been possible to gain any reliable idea as to the constancy or variability of the tooth characters within the series in the rhinoceroses. From the limited material examined, however, it does appear that while the essential structures are reasonably constant, the effect of attrition alters the pattern of the grinding surface to such a degree that identification may be made most difficult. As wear proceeds, the ridges widen and obliterate the intervening valleys, at first fairly slowly, but afterwards very rapidly, until ultimately a uniform tract of dentine may be produced. The crochet, antecrochet and crista which project into the medivallum are generally more prominent in early wear, and are reduced in size as this valley is narrowed. In some species the crochet and crista may unite and isolate the medifossette as an accessory valley, leaving the prefossette as the terminal portion of the medivallum. The postfossette may also become isolated by closure of the posterior enamel border. In the lower teeth the chief effect of attrition is to reduce the size of the two flexids, the metaflexid in particular tending to disappear with wear. Fusion of the metaconid and entaconid may also lead to the complete isolation of the entoflexid as an accessory valley.

FAMILY RHINOCEROTIDAE.

Genus *DICEROS* Gray 1821.

Genotype: *Rhinoceros bicornis** Linnaeus.

*Diceros bicornis** (Linnaeus).

*Rhinoceros bicornis** Linnaeus 1758. Syst. Nat. Ed. (10), i, p. 56.

Opsiceros simplicidens (pars) Scott 1907. 3rd Rep. Geol. Surv. Natal and Zululand, pp. 258-259, pl. xvii, figs. 4, 5.

Diceros whitei (pars) Chubb 1907. Geol. Mag., V, vol. iv, pp. 447-448.

The horns of the black rhinoceros are almost invariably two in number, but exceptionally as many as five have been recorded. The anterior horn has a height of about forty-five to sixty centimetres on the average and has a basal diameter fifteen to twenty-five centimetres. The rear horn is about one-third to one-half the length of the anterior one and has a diameter only a little less than its height. The record horn lengths are about double the average figures. Both horns are rather blunt and curve very slightly posteriorly.

In the upper jaw the first premolar is very small and exhibits no

structures which can be said to be recognisable as persistent. The third molar is triangular in form, the metaloph, being reduced to a small posterior prominence only, and this tooth is very variable in pattern in wear and is of little value for specific identification. The remaining three premolar and two molar teeth are generally more consistent, and are essentially similar in structure, though the premolars differ slightly from the molars. In the premolars the anterior wall of the protoloph is fairly straight and makes an angle of about 75° with the ectoloph, whereas in the molars the protoloph initially makes almost a right angle with the ectoloph, and then curves somewhat posteriorly. The protoloph and metaloph are roughly parallel or slightly divergent and with the ectoloph give the appearance of the Greek letter π . The ectoloph itself is not straight, but has an outer wall incurved or grooved between the paracone and metacone and also has a shallow groove behind the parastyle. The parastyle itself is commonly anteriorly grooved and projects very little in front of the protoloph. The antecrochet is apparently absent, and the crista is very small and disappears rapidly with attrition. A crochet is always present in the earlier stages of wear, and in the normal dentition increases progressively in size from the second premolar to the second molar. It tends to become rounded with increased wear, and may disappear completely before the medivallum is obscured. In no case has isolation of the medifossette been observed in this species except in the third molar. The postfossette is somewhat obliquely V-shaped, tending to be U-shaped with wear as a result of the expansion of the hypocone lobe of the metaloph, and then becomes isolated as an oval valley. The dimensions vary considerably with wear, the breadth across the grinding surface increasing as attrition proceeds. The height above the basal cingulum increases progressively with the successive teeth, and a typical second molar in early wear has a height of about 50–55 mm. The breadth at the base of the second molar is about 60 mm., but in normal wear the grinding surface measures only some 45 mm. transversely. The size and characters can be seen from the scale drawings in fig. 3. Two typical upper dentitions are shown, one in fairly early wear, the other well worn and lacking the first premolar.

The lower teeth have little to distinguish them from the very generalised form of most rhinoceros teeth. The first premolar is greatly simplified in form, but the remaining teeth, including the third molar, are similar in structure. The anterior and antero-external walls of the metalophid are markedly flattened, and make an

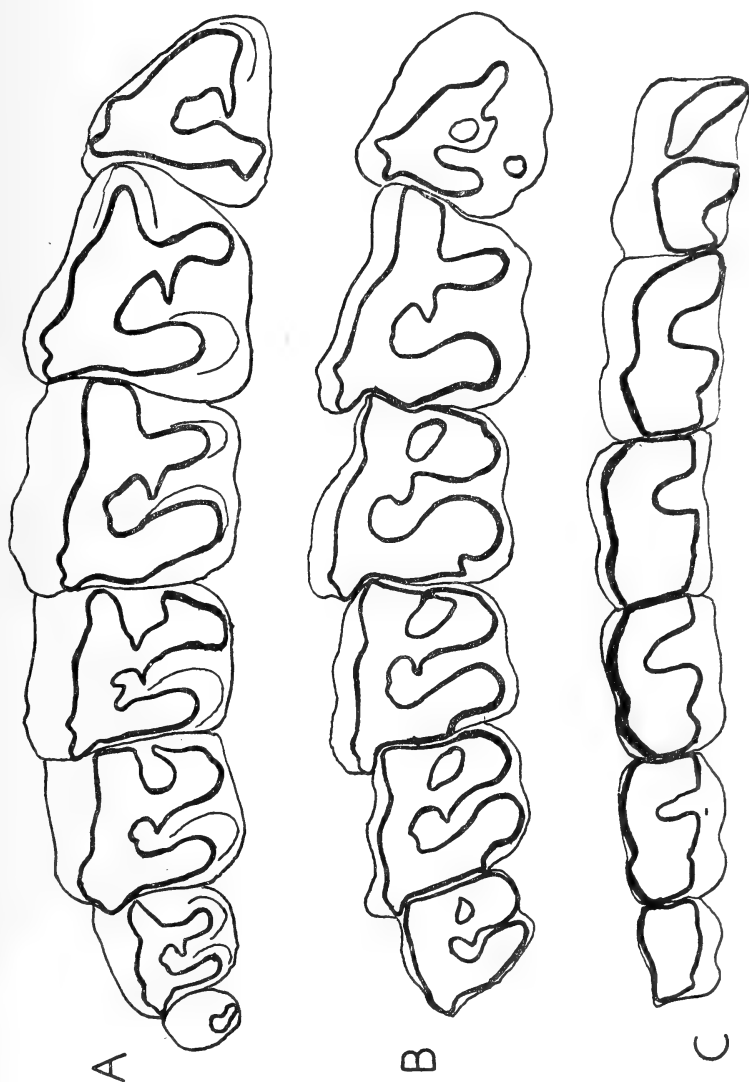


FIG. 3.—Two left upper dentitions (A and B) of *Diceros bicornis** (Linnaeus) and a right lower dentition (C) of the individual B. One-half natural size. (Original.)

angle with each other of about 100° or a little more. A fairly marked groove separates the outer wall of the metalophid from the curved hypolophid wall. The inner walls of the metaconid and entaconid are somewhat flattened. The metaflexid is a good deal smaller than the entoflexid and is rapidly reduced to a shallow V-shaped notch. The height of a normal second molar is about 50 mm. The lower teeth of a typical specimen are shown in fig. 3, and belong to the same individual as the upper dentition figured immediately above it.

Referred Material.

Apart from the petrified specimens from superficial deposits in various parts of Southern Africa which obviously belong to this species, two of the teeth from Zululand which Scott (1907) very tentatively referred to his species *Opsiceros simplicidens* do not appear to warrant distinction from the living *Diceros bicornis**. The type LM² of Scott's species manifestly is not that of *D. bicornis**, but the two heavily worn teeth (M¹ and Pm⁴) do not differ appreciably from correspondingly worn teeth in old individuals of the living black rhinoceros. Scott himself realised the close similarity, and suggested that these two teeth did not actually belong to his new species. The specimens themselves have not been seen by the present writer, but natural size photographs kindly supplied to the writer by Professor Scott, together with the admirable description, form an adequate basis for the conclusion reached above.

Genus CERATOTHERIUM Gray 1868.

Genotype: *Rhinoceros simus** Burchell.

*Ceratotherium simum** (Burchell).

*Rhinoceros simus** Burchell 1817. Bull. Sci. Soc. Phil. Paris, F. 1, 2, p. 97.

Opsiceros simplicidens Scott 1907. 3rd Rep. Geol. Surv. Natal and Zululand, pp. 257-258, pl. xvii, fig. 3.

Rhinoceros scotti Hopwood 1926. Occ. Papers No. 2, Geol. Survey, Uganda, pp. 16-17, fig. 3.

The white rhinoceros possesses a long and rather slender anterior horn which attains a height of about ninety centimetres and, exceptionally, as much as a hundred and fifty centimetres.* The second or rear

* Southern race: $62\frac{1}{4}$ inches. Rowland Ward's Records of Big Game, 9th ed., 1928, p. 446.

horn is small and does not usually attain a height exceeding twenty-five centimetres. The anterior horn is normally more slender than that of the black rhinoceros.

In the upper jaw the first premolar is small and is shed early, but the other premolars differ notably from the molars, for in the former the medivallum becomes rapidly enclosed by fusion of the protocone and hypocone, the form of the metaloph being consequently also affected. From *Diceros bicornis** they differ most markedly in the arcuate, posteriorly curving protoloph, and in the early fusion of the well-developed crista with the crochet to form an isolated medifossette. Due to the posterior curving of both protoloph and metaloph the π -like shape of the teeth is very distorted and not nearly as noticeable as in *D. bicornis**. The form of the ectoloph is also different, being rather more undulate in *Ceratotherium simum** with a distinct outward bulge at the paracone. The parastyle is more pointed and is not apparently grooved, but there is a groove immediately behind it. The postfossette becomes isolated with wear as a result of closure of the posterior enamel. As in *D. bicornis** this isolation of the postfossette is not a constant feature and is generally less marked in the molars than in the premolars. The teeth are higher crowned than those of the black rhinoceros, a typical second molar in normal wear measuring about 75 mm. above the indistinct cingulum. Fig. 4 shows (half natural size) two upper dentitions, one in very early wear with the third molar only just erupting and the fourth premolar coming into use, the second dentition being in a more advanced state of attrition.

The lower teeth are somewhat difficult to distinguish from those of the black rhinoceros. The anterior and antero-external walls of the metalophid make an angle with each other close to 90° instead of the obtuse angle found in *D. bicornis**. The metaflexid appears to be more persistent in the white rhinoceros than in the black, and the enclosure of both metaflexid and entoflexid with advanced wear is a common feature. The height of a typical second molar above the cingulum is about 60 mm. The lower dentition of the same individual as the more worn upper dentition figured is shown in fig. 4.

Referred Material.

Petrified specimens of this species have been found in various superficial deposits in the coastal region and in the interior. A portion of an anterior horn is also recorded from a cave deposit near Kuruman, Cape Province (Malan and Cooke, 1941).

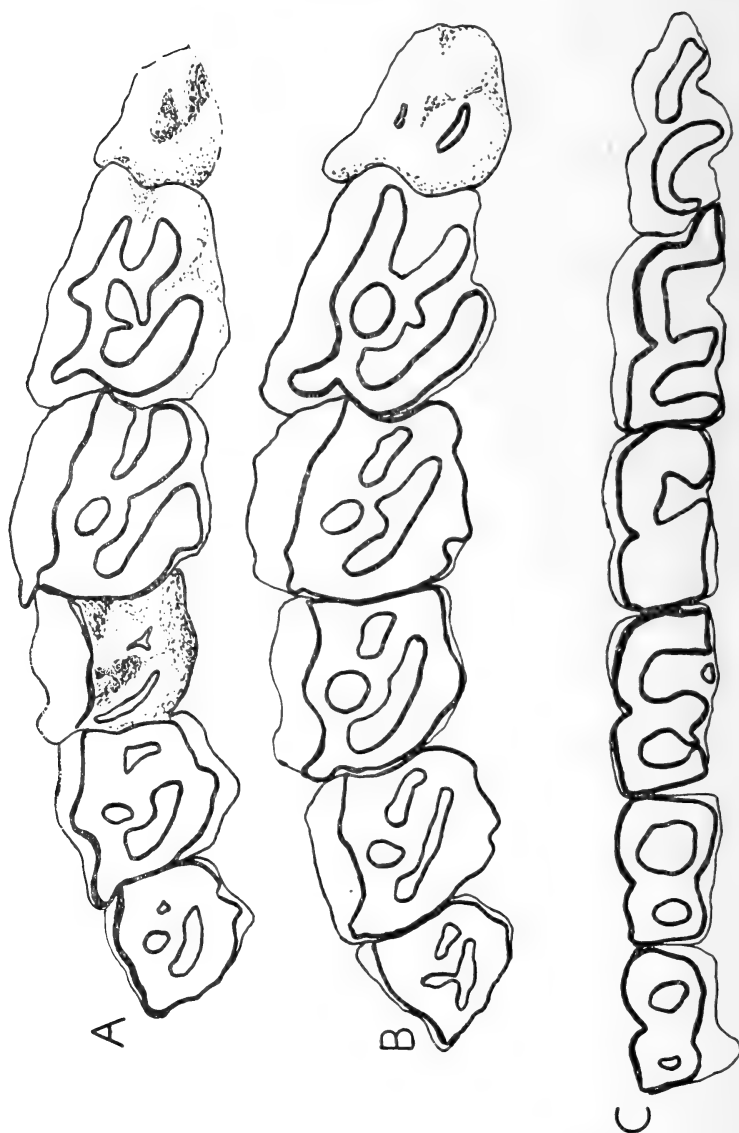


FIG. 4.—Two left upper dentitions (A and B) of *Ceratotherium simum** (Burchell) and a lower right dentition (C) of the individual B. One-half natural size. (Original.)

W. B. Scott reported in 1907 the discovery of a supposedly extinct species in fossiliferous marine clays from the Zululand coast, and he named this species *Opsiceros simplicidens*, with an unworn upper left second molar as the type. Scott compares this tooth with the corresponding one of *Diceros bicornis**, and states that the differences are "clearly of specific value". The distinctive characters are stated to lie, *inter alia*, in the much stronger recurving of the protoloph and in the much better development of the crista, which "fuses with the anticrochet so as to enclose a small and apparently shallow fossette". (Scott here used the term 'anticrochet' in error for crochet, as his figure shows, and in this follows an error previously made by Osborn in describing the Perissodactyla of White River (Scott and Osborn, 1890).) The characters which Scott used to differentiate the species from *D. bicornis** are exactly those which distinguish the white rhinoceros. A skull of the latter species in the South African Museum possesses a second molar in much the same state of development, and the dimensions and appearance of this tooth correspond very closely to the data and figure furnished by Scott. There can thus be little doubt that *Opsiceros simplicidens* is a synonym of *Ceratotherium simum**, a fact which Scott would undoubtedly have realised had comparative material of this rather rare species been available to him.

In 1926 Hopwood recorded an upper left second molar from the Kaiso beds of Uganda and assigned this specimen to Scott's species. He also pointed out that the name *R. simplicidens* was preoccupied and proposed *Rhinoceros scotti* as a substitute. There seems no doubt of the correctness of the reference of this specimen, and equally there is little doubt of its similarity to teeth of the living white rhinoceros. *Rhinoceros scotti* is thus also apparently a synonym of *Ceratotherium simum**.

DISCARDED SPECIES.

Diceros whitei Chubb.

Diceros whitei Chubb 1907. Geol. Mag., V, vol. iv, pp. 447-448.

Diceros whitei Hopwood 1928. Rhodesian Man and Associated Remains.

A supposedly new species of rhinoceros was described very briefly by E. C. Chubb in 1907 in a "List of Vertebrate Remains" from the Broken Hill Cave. It was founded on two limb bones (a right tibia and a right humerus) which had been excavated by Mr. Franklin

White and presented by him to the Rhodesian Museum. This species was also mentioned by A. T. Hopwood in the British Museum memoir on Rhodesian Man, and is there said to be "closely allied to *D. simus*". In view of the uncertainty of the generic position of the species *whitei*, the material was obtained on loan from the Rhodesian Museum, Bulawayo, and permission was obtained from Mr. Chubb to amplify his preliminary description and to figure the specimens. In his brief account Chubb remarks on the scantiness of the comparative material available to him, and this lack and the seeming association of the two bones appears to have resulted in an error in the distinction of the material. The tibia is certainly that of a rhinoceros, though comparison with recent skeletons shows no notable differences in size or in other characters from the corresponding bone in the living *Diceros bicornis**. The humerus, however, differs very considerably from both the living rhinoceroses, and it would appear that it is an artiodactyl and not a perissodactyl humerus, the differences formerly regarded by Chubb as of specific distinctness being actually too great for that possibility to be upheld. The compressed narrow olecranon fossa is a normal artiodactyl feature unlikely to occur in a rhinoceros, and the deltoid ridge and deltoid tuberosity are also much more artiodactyl than perissodactyl. With these views Mr. Chubb now expresses his agreement.

On comparison with various living artiodactyls, the closest resemblance is found between the fossil humerus and that of the living Cape Buffalo. There is no great difference in length, but the fossil bone is somewhat more massive, with the attendant minor modifications consequent upon its greater weight-supporting requirements. Otherwise, however, there is a very close agreement in every character, and it seems highly probable that the fossil humerus belongs to a member of the Buffalo group. It may possibly belong to the extinct "*Bubalus*" *bainii* Seeley, or to "*Bubalus*" *andersoni* Scott.

The species *Diceros whitei* appears, therefore, to have been founded on a humerus which is not that of a rhinoceros and on a tibia which does not warrant distinction from the living *D. bicornis**, so that *D. whitei* must be regarded as incorrectly founded.

THE HORSES.

There have been described at various times from Southern Africa more than twenty-five species belonging to this family, some based on upper and some on lower teeth, but of these not more than half can be

regarded as valid. The position was first reviewed by Haughton in 1931 when the twenty then existing species were reduced to eleven, and in general the present writer is in agreement with these conclusions. Haughton divided the members ascribed to the genus *Equus* into two groups, which he terms the "quagga" group and the "zebra" group on the parallelism of certain characters with those in the teeth of the two living species, the bontequagga and the mountain zebra. Unfortunately these characters in the recently extinct true quagga are very different from those in the living bontequagga and the two group terms must therefore be abandoned.

The relationships indicated by Haughton's work are of great interest and, in order the better to appreciate the definitive characters of the teeth in the extinct forms, the writer has carried out an extensive examination of skulls and teeth of the living forms and of the recently extinct true quagga. As a result of this work it is possible to distinguish on dental characters from this material three undoubted species: *Equus zebra**, the living mountain zebra, *Equus quagga**, the recently extinct true quagga, and *Equus burchellii**, the living bontequagga or Burchell's zebra. Since zoologists have been greatly at variance on the status of these forms, and since all three species occur in the fossil state, the results of the investigation have already been considered fairly fully (Cooke, 1943). These observations also throw some light on the morphological characters and variations encountered in equine species and are of great value in considering the fossil finds. To some extent they repeat and amplify the work of Gidley (1901), and in the present examination a general agreement was found with the conclusions outlined by him.

For convenience of reference the nomenclature of the important elements of the molar teeth of the Equidae (following Osborn) is given here in diagrammatic form (fig. 5). The specimens figured are upper and lower fourth premolars, and show the appearance of the cusps on the unworn crowns and the enamel patterns of the teeth in normal wear. The two enamel islands in the upper cheek teeth have long been known as the pre- and postfossettes, but the partial islands, or inlets, in the lower teeth have until recently received no name. The terms advocated by Stirton (1941) are used here. They are respectively "metaflexid" for the anterior and "entofolexid" for the posterior partial islands of the lower cheek teeth. (These terms have already been suggested for the analogous parts of the rhinoceros teeth.) It is also proposed here to call the posterior groove which lies between the hypocone and the hypostyle in the upper teeth the "hypoglyph",

and the groove anterior to the protocone the "protoglyph". These terms are preferred to "hypoconal groove" and "preprotoconal groove" used by Stirton.

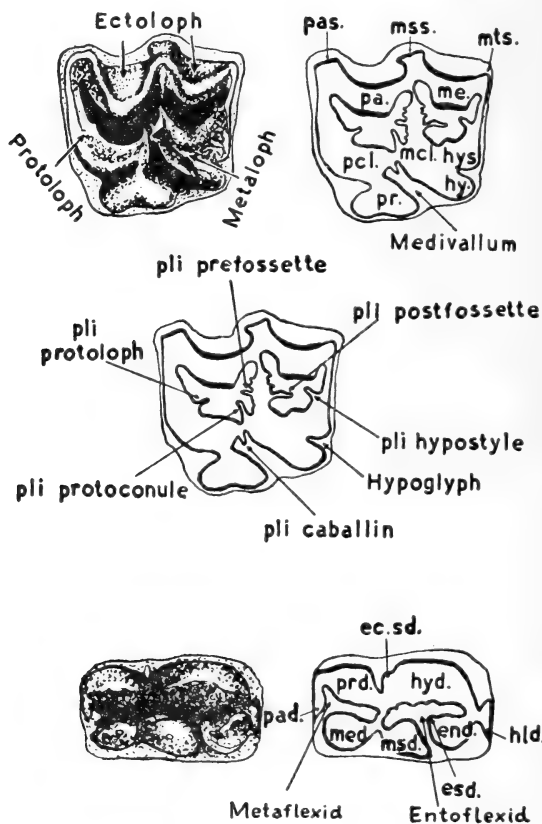


FIG. 5.—Molar elements (following Osborn) of the upper and lower cheek teeth of the Horse group.

Abbreviations.

Upper teeth: *pas*, parastyle; *mss*, mesostyle; *mts*, metastyle; *pa*, paracone; *me*, metacone; *hy*, hypocone; *pr*, protocone; *pcl*, protoconule; *mcl*, metaconule; *hys*, hypostyle.

Lower teeth: *prd*, protoconid; *hyd*, hypoconid; *med*, metaconid; *end*, entacoid; *pad*, parastylid; *msd*, metastylid; *hld*, hypoconulid; *ec.sd.*, ectostylid (fold or ridge); *esd*, entostylid. (Original.)

Distinction between Zebra, Quagga and Bontequagga.

The writer has examined a large number of skulls of these three species in the past few years, though skulls of the recently extinct

quagga are rare and difficult to obtain. Owen (1869) figured one in a little known paper, there is a cast in the Transvaal Museum, one skull in the Kingwilliamstown Museum and several in the McGregor Museum, Kimberley. Based on an examination of this material the chief distinguishing features have been analysed (Cooke, 1943).

From the point of view of classification it would appear that the three species are quite distinct. The bontequagga or Burchell's zebra, while showing skull characters intermediate between the other two forms, is sharply distinguished in dental characters. There can thus be no doubt that the bontequagga is very distinct from the true zebra despite the many similarities of form and colouring which have caused much dispute amongst zoologists with respect to the relationship of the two forms. It differs to an equal degree from the true quagga, and can under no circumstances be regarded as a variety of this form. The specific designation *quagga** must therefore be restricted to the historically extinct true quagga, and the bontequagga or Burchell's zebra must receive the full specific name *burchellii**, to which may be appended, if it is considered necessary, the varietal names *wahlbergi**, *transvaalensis**, etc., though these varieties cannot be distinguished on skeletal or dental grounds as far as the present writer is aware.

The Degree of Constancy and Range of Variability of the Tooth Characters.

Aside from the examination of a large number of skulls of the zebrine group of horses to determine their distinctive features, an attempt has been made to estimate the range of variation found within each species and hence to estimate the value of each possible factor in specific determination. A number of skulls of *Equus caballus** and *Equus asinus** have also been used for this purpose, and reference has been made in addition to many published figures of equine dentitions to ascertain how widely the generalised conclusions may be applied. The factors appear from this examination to follow certain definite trends, a knowledge of which greatly enhances the value of the specific identification of individual finds of isolated teeth. It must be stated however that, despite this knowledge, a fossil species which is named purely on dental characters may well be a "form" species only, as there is a certain amount of overlap in the extreme variations of certain species. The first upper true molar of *Equus quagga**, for instance, may be almost identical with that of *Equus zebra** under certain conditions of variation.

One of the difficulties which besets the worker on the fossil Equidae is the fact that almost all the finds consist only of isolated teeth. Complete dentitions are very rare and are consequently of immense value. It is of the utmost importance therefore to ascertain correctly the position occupied by the isolated teeth in the former jaw in order correctly to evaluate the determinative characters. By far the most satisfactory method is that of direct comparison with a known complete dentition. The angle of wear and degree of antero-posterior curvature are the chief guides in the estimation as to whether a particular tooth is, for example, a fourth premolar or a first molar. Fig. 6 gives an indication of the general shape of the teeth in *Equus burchellii**, and figs. 6 and 19 show the form in some large extinct equines.

The second premolar is at once distinguishable by being rather pointed anteriorly, and the third molar shows a posterior tapering. The last erupted tooth of the series at any given age shows this posterior taper, however, so that in early wear such a tooth might possibly be a second or even a first molar. The rather sharp curvature of the true third molar should, however, facilitate the distinction of this tooth. In the lower teeth the premolars typically have a larger entoflexid than the molars, and the outer groove between hypoconid and protoconid extends further towards the inner groove between metaconid and metastylid in the true molars than it does in the premolars. In the upper teeth the first true molar normally has a rather narrow mesostyle, but otherwise the degree of curvature and angle of wear form the only guide to the position of the tooth in the series.

The factors which affect the characters of each cheek tooth in an individual of a species are: (A) The position of the tooth in the series, (B) the degree of attrition, and (C) variability within the species. The factor of sex does not appear to exert any appreciable influence on the cheek teeth, though the canines, which are usually prominent in the male, are vestigial or absent in the female. The generalised conclusions regarding the three main factors given above may therefore be discussed in turn.

A. THE POSITION OF THE TOOTH IN THE SERIES.

(a) *In the Upper Teeth.*

1. The anterior and posterior teeth (second premolar and third molar) show decidedly different forms of enamel pattern due to their tapering nature and are very variable in character. They are of the least possible value in specific determination, as the prefossette

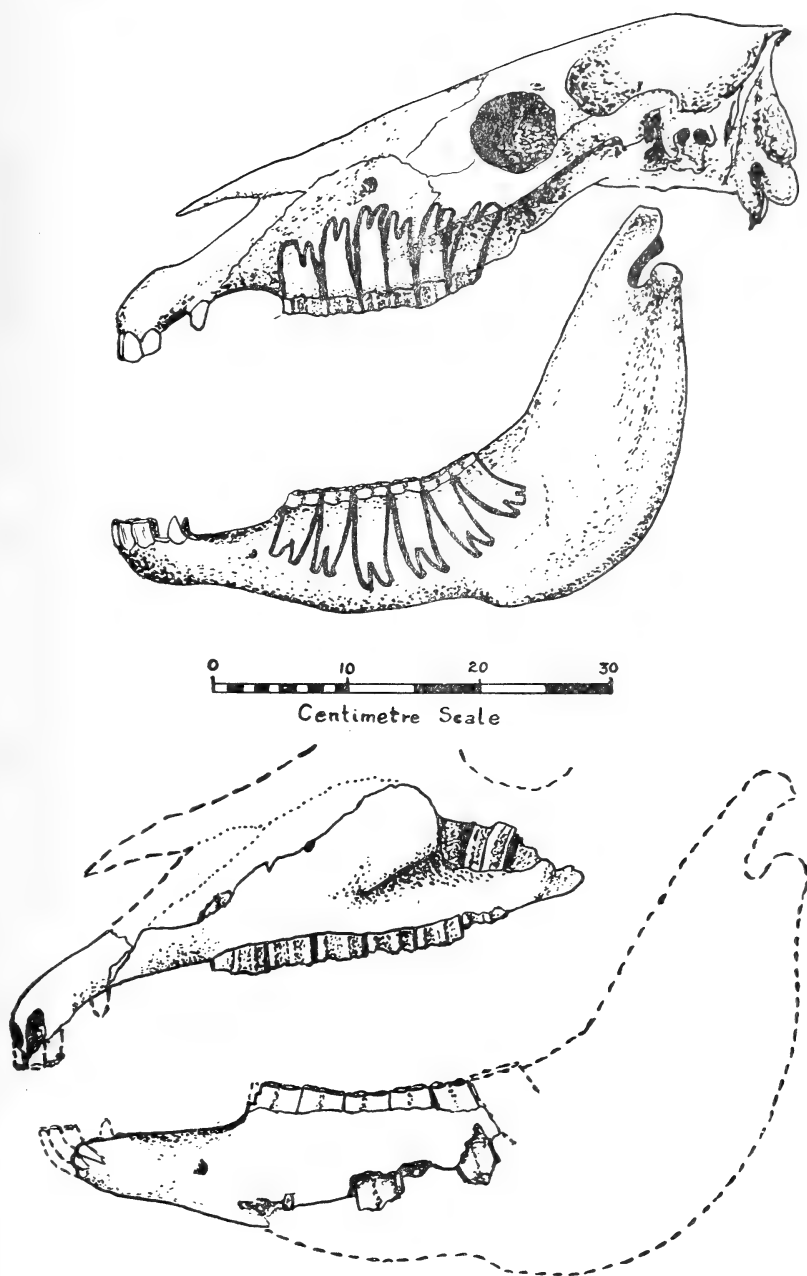


FIG. 6.

Above: Lateral view of skull of *Equus burchellii** (Gray) showing the shapes of the cheek teeth. (Original.)

Below: Lateral view of fragmentary remains of skulls of large extinct equines; Maxilla of *Equus fowleri* Wells, and mandible of *Equus plicatus* (van Hoepen). (Original.)

in the second premolar and the postfossette in the third molar are subject to considerable distortion.

2. In transverse breadth, measured from mesostyle to protocone, the third and fourth premolars are approximately equal, and the first and second molars usually slightly narrower (by perhaps 5–10 per cent.) than the preceding teeth. The second premolar and third molar are always narrower than the other premolar or molar teeth respectively, but bear no constant ratio of relative size.

3. The fourth premolar presents the most complex and the first molar the simplest enamel folding.*

4. The protocone is shortest (antero-posteriorly) in the second premolar and longest in the third molar. The length of the protocone either increases progressively in each succeeding tooth of the series or else the first molar has a smaller protocone than the fourth premolar, and the second molar has one about the same length as in the fourth premolar.

5. The mesostyle is generally reduced in width in the molars as compared with the premolars.

6. The pli-protoloph and pli-hypostyle may be lacking in the first molar though present in the remaining teeth.

7. The pli-caballin may be present in the premolars yet absent in the molars, and may occur in the fourth premolar only.

8. The hypoglyph is often absent in the third molar.

(b) *In the Lower Teeth.*

1. As in the upper teeth, the second premolar and third molar are of sub-triangular form and show departures from the normal enamel pattern. The changes are not always so great as to prevent specific identification, but they are the least useful teeth of the series for this purpose.

2. In transverse breadth the premolars are wider than the molars by about 5–10 per cent. The second premolar may, however, be as narrow as the first molar. The third molar bears no reliable ratio of width to the other molars, and in the second molar the posterior breadth is less than the anterior due to the reduction in size of the hypoconid.

* The normal order of eruption of the cheek teeth is M^1 , M^2 , Pm^2 , Pm^3 , Pm^4 , and lastly M^3 , though the order of the last two may exceptionally be reversed. In a normal dentition, therefore, the first molar in addition to possessing an initially less complex character is also the most worn tooth.

3. The entoflexid has a larger lobe in the premolars than in the molars, this being generally of greatest antero-posterior length in the second premolars.

4. The outer groove between protoconid and hypoconid is deeper in the molars than in the premolars and sometimes meets the internal groove between metaconid and metastylid.

(c) *Relation between Upper and Lower Teeth.*

Of great interest and value is the hitherto apparently unrecognised fact that the breadth over the enamel in the upper teeth bears a fairly constant ratio to the breadth of the lower teeth over the enamel. This ratio is approximately 1:0.6 for the third and fourth premolars to 1:0.55 for the first and second molars, and is apparently subject to a variation of only about 5 per cent.

B. THE DEGREE OF ATTRITION.

I. *Changes in Dimensions.*

The effects of the degree of wear (or age) on the cheek teeth have been well described by Gidley (1901), and the following selected quotations from his paper are illustrative of his findings in this regard.

1. "When a molar or premolar tooth first comes into use, the face, as well as the sides of the crown, is completely covered with enamel which folds in and out, and (though somewhat hidden by cement) presents the same general appearance as that seen in the much more primitive forms *Anchitherium* and *Meshippus*. Soon the enamel on the tips of the cones and along the ectoloph wears through, and small patches and ridges of dentine surrounded by a border of enamel are exposed. As the tooth is further worn away, these patches and irregular ridges broaden and rapidly lengthen until when about one-half to three-quarters of an inch of the crown has been worn away they have all become united by narrow isthmuses, and the fundamental tooth pattern of the horse is presented." "From this point . . . the triturating surface presents a gradually less complex pattern of enamel folding as the tooth crown is worn away, until in the very much worn tooth the simplest pattern of enamel folding is presented" (fig. 7).

2. "The antero-posterior diameter of the first premolar (p_2)* remains about the same for the whole length of the crown, except that sometimes it narrows slightly near the roots."

* Actually the true second premolar according to present usage.

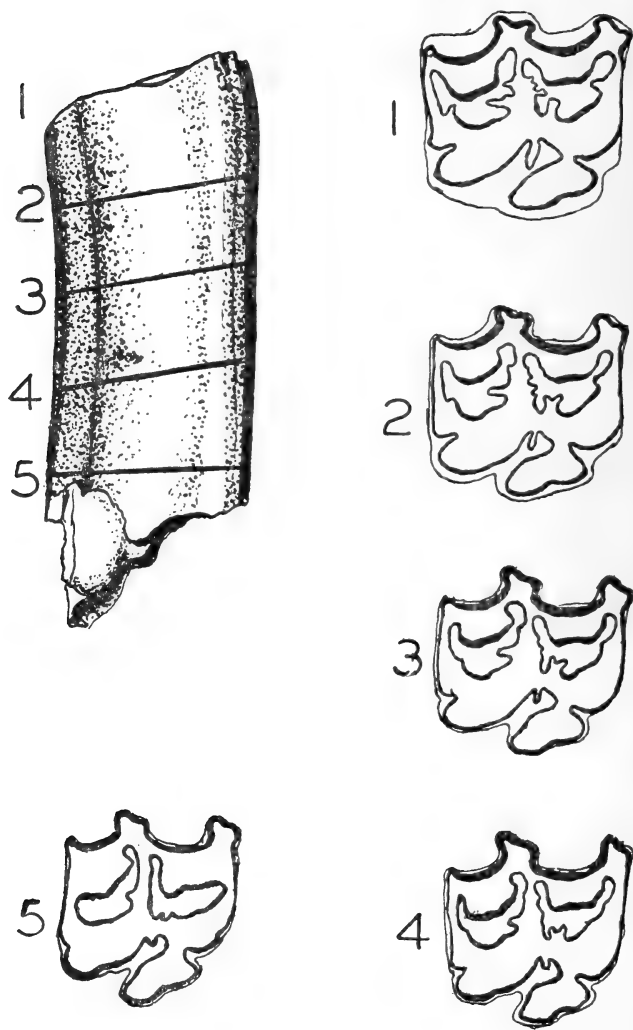


FIG. 7.—Sectioned right upper fourth premolar of adult male *Equus caballus** Linnaeus, illustrating changes in enamel pattern which would result from various stages of attrition. Natural size. (Original.)

3. "The antero-posterior diameter of the last molar (m^3), however, is relatively small at first, and increases continually as the tooth is worn away."

4. "The antero-posterior diameter of the grinding surfaces of all

the intermediate teeth are greater at the stage when the tooth has just fully come into use; . . . from this point the antero-posterior diameter diminishes very rapidly for a short distance and then continues to diminish more gradually to the roots of the tooth."

5. After the tooth has just come fully into use "the transverse diameters of p^3 to m^2 inclusive remain about the same, diminishing slightly near the roots; p^2 gradually diminishes while m^3 increases in transverse diameter as the crown wears away."

6. "The antero-posterior diameter of the protocone in all the teeth of the series remains the same for the whole length of the crown."

7. "Owing to the very slight variation of the transverse diameters of the crowns of p^3 to m^2 inclusive . . . and to the great shortening of their antero-posterior diameters, the ratio of these diameters is very different in old and in young individuals of the same species. Thus in the little worn condition . . . the antero-posterior diameter is always greater than the transverse. As the crown wears away . . . a stage is reached where the two diameters are about equal, then, as the antero-posterior becomes still more shortened, the transverse exceeds it. In every series this variation in ratio seems always to be more advanced in m^1 and m^2 ."

The present writer has not observed any conflict with these views. The transverse diameter (or "breadth") of the crown and the antero-posterior diameter ("length") of the protocone do, however, decrease to a very slight degree with wear, though their ratio remains constant. Gidley made no comments on the precise effects of wear on the complexity of the enamel folds, and the present writer has therefore attempted by means of serial sections of a number of teeth to ascertain which folds are most affected by wear and which least. As a result, the following generalisations, though based on comparatively little material, appear to be possible.

II. *Changes in Enamel Complexity.*

(a) *In the Upper Teeth.*

1. The pli-protoloph may disappear completely when the tooth is as little as half worn, and is always the most affected of the fossette folds.

2. The pli-hypostyle and pli-prefossette suffer rapid reduction in size but have not been observed actually to disappear.

3. The secondary small plications in the regions of the pre- and postfossette folds proper disappear rapidly if they are of an angular or saw-tooth nature, but may survive a considerable degree of wear if they have the form of rounded loops.

4. The pli-protoconule and pli-postfossette are the least affected of the fossette folds.

5. The hypoglyph becomes shallower with wear but does not normally disappear.

6. The pli-caballin does not disappear with wear in the premolars unless initially very small, but may do so in the molars.

7. The halves of the ectoloph become slightly flattened with advanced wear.

(b) *In the Lower Teeth.*

1. The folding of the entoflexid lobe may be very complex in the earliest stages of wear, but becomes rapidly simplified and does not normally survive the half-worn condition of the tooth.

C. VARIABILITY WITHIN THE SPECIES.

I. *Transverse Diameter of the Crown.*

As Gidley has shown, the transverse diameters over the enamel of the teeth (excluding the second premolar and third molar) are subject only to relatively slight variation within a species. In a series of ten skulls of *Equus caballus** ranging from a large draught horse to a small Texas pony, he notes a difference in the transverse diameter of the second molar of only 2.5 mm. or about 10 per cent. In the third premolar of the same individuals, however, his figures show a difference of 4.5 mm. or nearly 20 per cent., and this range of variation agrees with the present writer's findings in the case of the zebrine group. In the many skulls of *Equus burchellii**, *Equus zebra** and *Equus quagga** which have been examined, the extreme variations in transverse diameter amount to about 20 per cent. of the mean value, but at least 70 per cent. of the specimens in each species are very close indeed to this mean value. The transverse diameter of the cheek teeth is thus subject to a variation of about plus or minus 10 per cent. from a predominant mean value, and this value is therefore a useful characteristic of a species (except in the anterior and posterior teeth). The same relative figures apply to the lower teeth.

II. *Length and Form of the Protocone.*

(a) The form of the protocone, and particularly the *relative* anterior and posterior development or elongation, is a very constant character in a species.

(b) The absolute length of the protocone is subject within a species to a variation of as much as 30 per cent. between corresponding teeth. In general, the ratio of the length of the protocone to the transverse diameter of the crown is not affected by wear, and this ratio (which we may term the "protocone ratio") is not quite as variable as the absolute length of the protocone. In *Equus caballus** the average value of the protocone ratio

$$\frac{\text{length of protocone}}{\text{transverse diameter of crown}}$$

is 0.48 in the fourth premolar; in the corresponding tooth of *Equus asinus** 0.41; *Equus burchellii** 0.41; *Equus zebra** 0.40; *Equus quagga** 0.44. Though subject to a variation of plus or minus 15 per cent., and thus having no precise significance since values would overlap considerably, the protocone index might be a useful indication of the relative development of the protocone in a species. It must be remembered, however, that in addition to variation between corresponding teeth, the value of the protocone ratio will change from the second premolar to the third molar. In *Equus caballus** average figures are p^2 0.38, p^3 0.45, p^4 0.48, m^1 0.47, m^2 0.52, m^3 0.62.

III. The Enamel Folds.

A wide variation is found in the degree of complexity of the enamel folding within a species, but the following generalisations appear from the writer's investigations to be applicable to the upper teeth.

1. The caballine fold is not infrequently absent in particular teeth of an individual of a species which normally shows a strong caballine fold. Even though in some species it is apparently never present, it has no precise value.

2. The pli-protoloph is of very variable development and unless very strong is of no specific value.

3. The degree of development of the pli-hypostyle and pli-prefossette, and the secondary plications of the latter, is variable and of slight value only.

4. The pli-protoconule and pli-postfossette appear to be of very constant development and their presence or absence can be considered as of diagnostic importance.

5. In some species the hypocone shows a consistent slight bulge into the medivallum, giving it the appearance of a partial isolation from the metaconule, and this character seems to be of some determinative value.

6. The flattening of the inner wall of the protoconule appears to be a character of minor diagnostic value in some species.

7. The depth of the hypoglyph is a moderately constant feature.

IV. *The Ectoloph and Styles.*

1. Except in the second premolar and third molar, the nature of the halves of the ectoloph, more particularly the anterior one, is of fairly constant character, being either concave inwards as seen in *Equus caballus** and *Equus burchellii**, or else flattened or even convex as in *Equus asinus**, *Equus zebra** and *Equus quagga**.

2. The three styles, parastyle, mesostyle and metastyle, show quite a considerable range of variation in detail within a species in addition to the difference shown between premolars and molars. The characters of the metastyle are of no specific value, and neither the absolute size nor the grooving of the parastyle and mesostyle are entirely constant characters though they may be useful ones. The degree of isolation of the mesostyle and parastyle from the walls of the ectoloph or their easy confluence with them, however, appears to be a valuable specific character. Owing to the normal relative reduction in size of the styles in the true molars, their isolation is less apparent in these teeth than in the premolars.

V. *The Lower Teeth.*

To quote from Gidley, "the characters of the lower teeth are, in general, affected in the same way as the upper, and seem to be of even less value in determining the species". With these conclusions the present writer is in agreement, in that the very simplicity of structure of the lower teeth deprived them of many of the characters which might be of value in making distinctions. The range of normal variation within a species thus permits of considerable overlap between what are actually different species (as is only too clearly seen in the zebrine group of horses), and thus absolute size must be the chief determinative factor. Other useful, though not entirely constant characters, are (a) the shape of the outer walls of protoconid and hypoconid, (b) the shape and degree of separation of metastylid and metaconid, (c) the size and form of the metaflexid and entoflexid lobes, (d) the relative size of the stylids and conids, (e) the development of the ectostylid fold* in the hypoconid.

* Called "pli-caballinid" by Stirton (1941).

GENERAL CONCLUSIONS.

As a result of the examinations made, second premolars and third molars cannot be regarded as providing adequate material for determination, and no species founded on a second premolar or a third molar can be regarded as valid. If second premolars and third molars are known in a species from certain association with determinable teeth, corresponding teeth showing close agreement can then be assigned to the species with fair certainty. On general grounds of size and complexity, isolated second premolars and third molars may be referred to a species as "cf. species".

In the remarks which follow, only the third and fourth premolars and the first and second molars are regarded as exhibiting characters of value in specific determination.

The position of the tooth in the series affects two main characters as follows:—

1. The transverse diameter of the crown, measured over the enamel, is about 5 per cent. greater in premolar than in molar teeth.

2. The enamel pattern is somewhat more complex in the premolar than in the molar teeth, the fourth premolar showing the most complex and the first molar the simplest enamel folding. The mesostyle is somewhat reduced in size in the upper molars, and the entoflexid lobe is smaller in the lower molars than in the premolars.

Bearing in mind the position of the tooth in the series, and the effect upon it of the above factors, the following generalisations may be made with regard to the definition and identification of equine species:—

1. The transverse diameter ("breadth") measured across the enamel is a character of considerable value in determination. The normal departure in size is not more than 10 per cent. and the maximum variation 20 per cent. *If the transverse diameter of a tooth departs by more than 20 per cent. from the measurement of the type, it cannot be regarded as belonging to the same species.* If several teeth of a species are known, the possible range which would exclude a specimen will be further reduced and a departure of 15 per cent. may be regarded with suspicion. It must be remembered, however, that different species overlap in point of size, and that *size alone* is not a sufficient basis for determination.

A. In Upper Cheek Teeth.

The following factors may be regarded as of reasonable constancy and value in determination:—

1. The relative anterior and posterior development and form of the protocone. (The *absolute* size of the protocone is subject to a variation between premolars and molars of as much as 20 per cent.)
2. The form of the ectoloph and styles.
3. The presence or absence of the pli-protoconule and pli-postfossette and their degree of development.

The following factors may be regarded as of confirmatory value:—

- (a) The partial isolation of the hypocone (or the lack of such isolation).
- (b) The protocone ratio (subject to a variation of 30 per cent.).
- (c) The *presence* of any or all of the following folds, though their *absence* cannot be regarded as significant:—
 - (i) Pli-hypostyle.
 - (ii) Pli-caballin (particularly in true molars).
 - (iii) Pli-protoloph (least reliable).
- (d) The form of the inner wall of the protoconule.
- (e) The depth of the hypoglyph.

B. In Lower Cheek Teeth.

The following factors may be regarded as of reasonable constancy and value in determination:—

1. The shape of the outer walls of the protoconid and hypoconid.
2. The relative development, degree and mode of separation of the metastylid and metaconid.

The other factors which, though variable, may be regarded as of confirmatory value are:

- (a) The size and shape of the entaenid.
- (b) The relative sizes of the stylids and conids (if unusual).
- (c) The development of the ectostylid ridge or fold in the anterior wall of the hypoconid.
- (d) The size and form of the metaflexid and entoflexid lobes.

FAMILY EQUIDAE.

Genus *EURYGNATHOhippus* van Hoepen 1930.

Genotype: *Eurygnathohippus cornelianus* van Hoepen.

Broad mandibular symphysis with the four first and second incisor teeth large, anteriorly flattened and arranged almost in a straight line, each incisor showing the cup or "Mark"; the third incisors small and lying behind and in contact with the second incisor. (The cheek teeth are unknown.)

Eurygnathohippus cornelianus van Hoepen.

Eurygnathohippus cornelianus van Hoepen 1930. Pal. Nav. Nas. Mus. Bloemfontein, II, 2, pp. 23-24, figs. 20-22.

Type: Anterior portion of lower jaw with incisor teeth. Nas. Mus., No. C.679. (Fig. 8.)

Locality: Uitsoek, near Cornelia, Orange Free State.

Horizon: The "Cornelia" Beds of van Hoepen (1930A).

The following is a translation of van Hoepen's description:—

"There is preserved the anterior portion of the lower jaw. The four incisors are long and broad. The teeth lie deep in the antero-central part of the jaw and their grinding surface is practically horizontal. The teeth are anteriorly flattened. The first incisor has an indistinct groove along the centre of its anterior or lower surface. The second incisor has two such grooves. On the inner surface each tooth has two surfaces, ribbed parallel to the height, which meet in a blunt corner and a thick ridge. The canine is approximately one-third the width of the other teeth; unfortunately both are broken off. The four big incisors each show a large cup or mark, entirely surrounded by enamel and also completely filled by cement. The enamel on the front of the tooth is thick, but on the back it is thin. The two small canines show no mark; they are broken off very low down."

The present writer conjectured on the possibility of the teeth, which van Hoepen regarded as canines, being in point of fact reduced third incisors, and this suggestion was independently put forward by Dr. L. H. Wells to the writer. The writer and Dr. Wells have had the opportunity, through the courtesy of Dr. van Hoepen, of examining the type specimen, and are of the opinion that this is probably the case and that the specimen is that of a female individual, consequently lacking canine teeth. This reduction of the third incisors is not quite such a startling supposition as would be their complete absence,

though, as Dr. van Hoepen has said, it is but a step in that direction. The jaw thus clearly belongs to a horse, presumably a very large one,

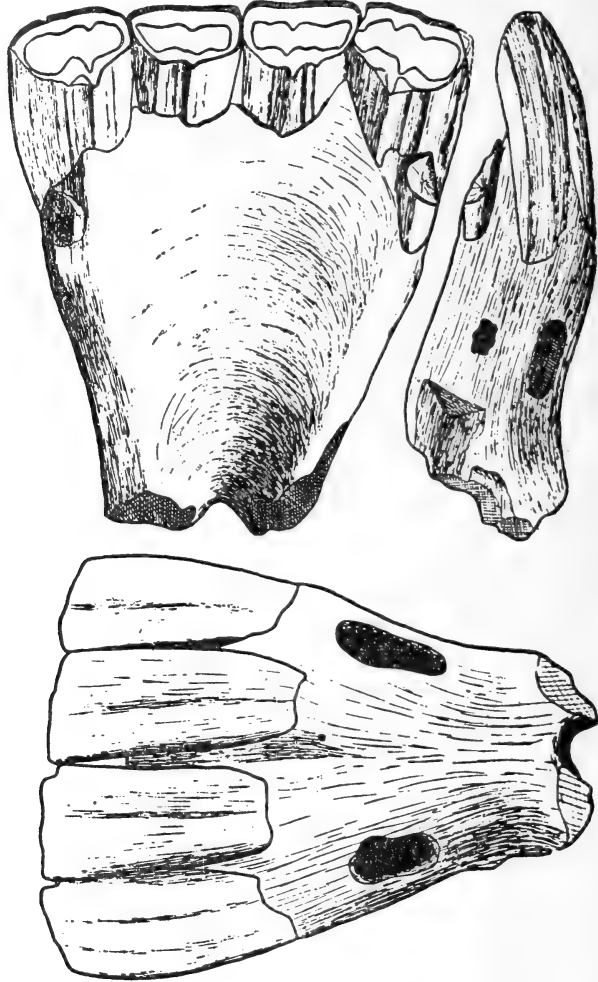


FIG. 8.—Upper, right lateral and lower views of anterior portion of mandible of type of *Eurygnathohippus cornelianus* van Hoepen. Two-thirds natural size. (From van Hoepen.)

but there is some difficulty in absorbing it into *Equus*. Van Hoepen's genus must stand in the mean time, and if "third incisor" be substituted for "canine", his description cannot be bettered.

Genus NOTOHIPPARION Houghton 1932.

Genotype: *Notohipparion namaquense* Houghton.

Rather low-crowned heavily cemented hypsodont lower cheek teeth with an extra antero-external cingulum fold or column, either isolated or fused with the parastylid,* present in all the permanent cheek teeth except the second premolar, and a deep groove separating the strongly developed metaconid and metastylid. The upper dentition is unknown.

Notohipparion namaquense Houghton.

Notohipparion namaquense Houghton 1932. Ann. S. Afr. Mus., xxviii, pp. 421-423, fig. 5.

Cotypes: Series lower Pm_2 , Pm_3 , Pm_4 , M_1 and M_3 of the left side and lower M_2 of the right side. S.A. Mus., No. 9982. (Fig. 9.)

Locality: "40 miles east of Springbok in Namaqualand . . ."

Horizon: "from a granite gravel 60 feet down in the surface limestone".

Measurements:

	LPm_2	LPm_3	LPm_4	LM_1	RM_2	LM_3
Breadth . .	16 mm.	17 mm.	17 mm.	16 mm.	14.5 mm.	12.5 mm.
Length . .	29.5 mm.	27 mm.	26 mm.	23 mm.	24 mm.	29 mm.
Height . .	14.5 mm.	17.5 mm.	25 mm.	23 mm.	30 mm.	34 mm.

The following is Houghton's description of the material:—

"The lower teeth upon which this new genus is founded, indicate a stage of equine evolution not hitherto discovered in South Africa. They consist of a series from pm^2 to m^1 , together with m^3 of the left side, and pm^4 , m^1 and m^2 and a part of m^3 of the right side, obviously of the same individual. As preserved the teeth are all low, the height not being much greater than the length. The main features can be distinguished from the drawings given. In all the teeth the metastylid column is separated from the metaconid column to the base of the crown, and the former projects further inwards than the metaconid or the entaonid, whilst its posterior flange overlaps the anterior border of the entaonid. The antero-external cingulum fold [protoconid fold] is prominent to the grinding surface, being fused with the parastylid in pm^3 and m^1 , but still separated from it in pm^4 , m^2 and m^3 . In pm^4 of the right side (but not of the left), in m^1 and m^2 , there

* As defined by Osborn. Stirton (1941) replaces this by "paralophid" and uses "parastylid" for the antero-external column. Such reapplication of an existing name is too confusing to be accepted. Dr. L. H. Wells has suggested to the writer that this extra fold might be termed the "protoconid fold".

is an ectostylid pillar, which near to the root fuses with the wall of the hypolophid to form an ectostylid ridge. Enamel fairly wavy. Teeth heavily cemented" (pp. 421, 422).

"Unfortunately nothing is known of the sequence of gravels and limestone encountered in the well from which *Notohipparion namaquense* was obtained, and but little light can be thrown upon its age. The valleys of Namaqualand seem to have suffered a progressive infilling with sand from Upper Cretaceous times onward; but the process was, in all probability, not a continuous one and further study will probably reveal breaks in the sedimentation. In so far as comparison is possible, *Notohipparion* would seem to represent an early Pliocene stage of equine evolution" (p. 425).

In view of the fact that teeth of another member of the *Hipparion* group occur in the Vaal River gravels associated with well-made stone implements, it would appear that these forms have survived in this region until a much later time than elsewhere. Though *Notohipparion* is quite possibly a Pliocene form, it need not necessarily be "early Pliocene" as Haughton suggests, and it is included here since its horizon is so uncertain and since it may have a bearing on the undoubted Pleistocene forms.

Genus *STYLOHIPPARION* van Hoepen 1932.

Genotype: *Stylohipparion steytleri* (van Hoepen).

(= *S. hipkini* van Hoepen).

High-crowned rather narrow hypsodont lower cheek teeth with a strongly developed isolated pillar external to the ectostylid, possessing no external groove between hypoconid and hypoconulid, having narrow protoconid and hypoconid and small rather widely separated metaconid and metastylid.

High-crowned upper cheek teeth with isolated oval protocone and possessing a small flange on the antero-internal side of the parastyle.

Stylohipparion steytleri (van Hoepen).

Hipparion steytleri van Hoepen 1930. Pal. Nav. Nas. Mus. Bloemfontein, II, 2, pp. 21-23, figs. 14-19.

Stylohipparion hipkini van Hoepen 1932. Pal. Nav. Nas. Mus. Bloemfontein, II, 3, pp. 31-32, figs. 14-17 and 18-20.

Stylohipparion steytleri van Hoepen 1932. *Ibid.*, pp. 33-35, figs. 21-23.

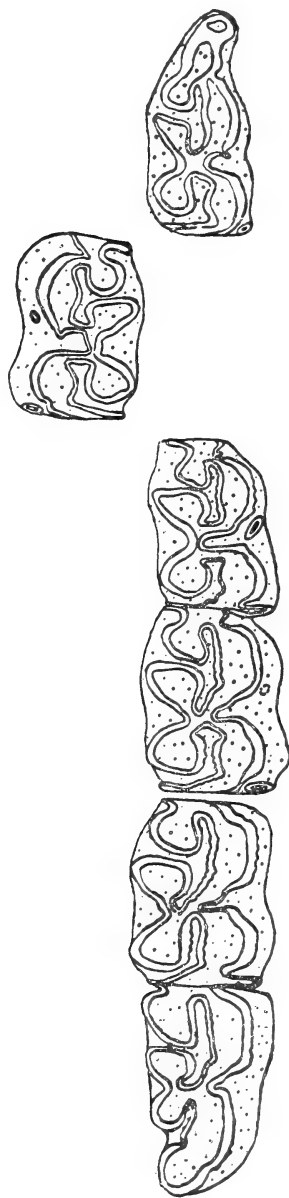


FIG. 9.—Series of lower cheek teeth of the type of *Notohipparion namaquense* Haughton. Natural size. (From Haughton.)

Type: Upper M^1 or M^2 of the right side. Nas. Mus., No. C.558.
(Fig. 10.)

Locality: Uitsoek, near Cornelia, O.F.S.

Horizon: The "Cornelia Deposits" of van Hoepen.

Measurements:

Breadth . . .	22 mm.
Length . . .	22 mm.
Height . . .	54 mm.

Paratypes: Upper M^3 of the left side. Nas. Mus., No. C.555.
(Fig. 10.)

Lower M_1 and M_2 of the left side. Nas. Mus., No.
C.556. (Fig. 10.)

Measurements:

	LM^3	LM_1	LM_2
Breadth . .	18 mm.	10(12) mm.	10.5(12.5) mm.
Length . .	21 mm.	broken	21 mm.
Height . .	66 mm.	32 mm.	41 mm.

(The figures in brackets include the accessory outer column.)

Upper Teeth.

The halves of the ectoloph are concave inwards though the posterior half may be flattened. The metastyle is small and the mesostyle and parastyle narrow, the latter having an unusual anterior flange or groove. The protocone is isolated and oval in shape with a somewhat flattened interior face. A small tongue projects into the medivallum towards the protocone. The hypocone is very small, being less than one-third the size of the protocone. A deep, sometimes double protoconule fold is present and, with the prefossette folds, tends to isolate the postero-internal corner of the prefossette. Protoloph, hypostyle and postfossette folds are present and are of moderate depth. Secondary plications are present in the region of the prefossette fold and appear to be persistent.

Lower Teeth.

Protoconid and hypoconid are rather narrow transversely and have slightly flattened or even concave outer walls. An ectostylid ridge or fold is present in the anterior wall of the hypoconid, and external to this is a stout oval pillar arising from the cingulum and reaching

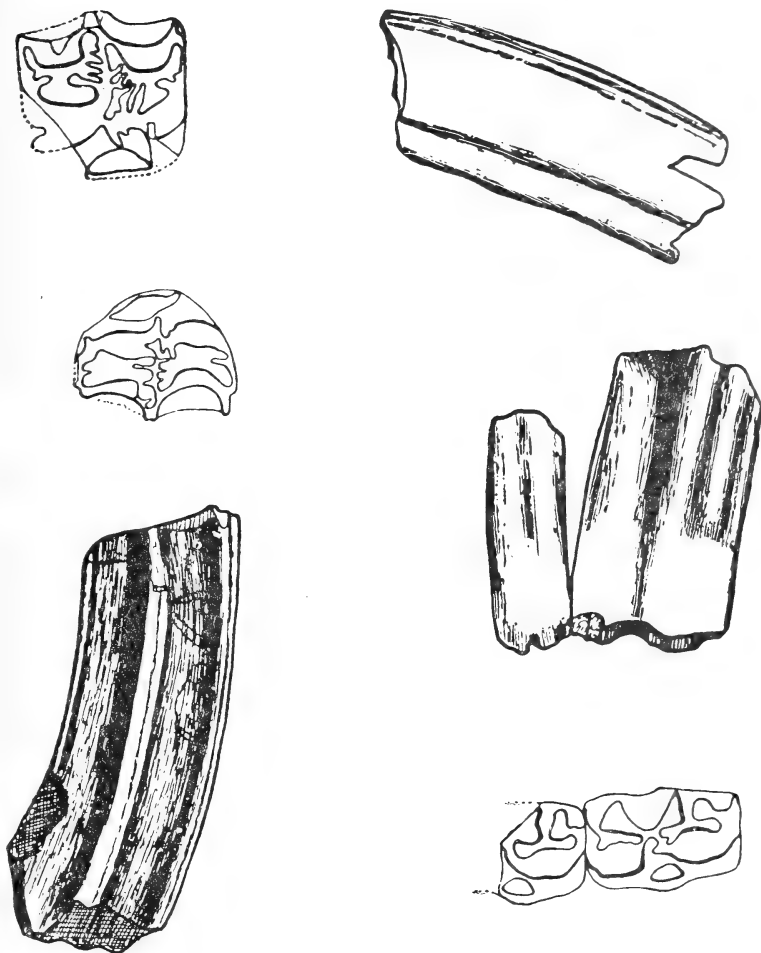


FIG. 10.—*Stylohipparion steytleri* (van Hoepen).

Top: Type upper right second (or third) molar; crown and anterior views.

Left: Paratype upper left third molar; crown and outer lateral views.

Right: Paratype lower left first and second molars; inner and crown views.

All natural size. (From van Hoepen.)

almost to the unworn crown. There is no external groove marking off hypoconid and hypoconulid. The entaconid is small, and the metaconid and metastylid are rather small and widely separated by a rounded groove. The entoflexid lobe is only slightly longer than the

metaflexid lobe, and folding in their walls is slight or lacking, a small notch in the anterior of the entoflexid lobe being sometimes present.

Referred Upper Teeth.

An upper second (or possibly third) molar of the left side has been recovered from the Vaal River deposits at Christiana, probably from Younger Gravels. This specimen (Arch. Sur., No. 113) is considerably worn, but retains all the characters shown by the less worn type and paratype.

Referred Lower Teeth.

Five lower teeth, being a series from LPm_3 to LM_3 from the type locality, were referred to this species by van Hoepen (1932), and the enamel pattern of four of them is shown in fig. 11.



FIG. 11.—Referred series of lower left cheek teeth of *Stylohipparion steytleri* (van Hoepen). Crown views. Natural size. (From van Hoepen.)

The following are the dimensions of these teeth (as preserved):—

	LPm_3	LPm_4	LM_1	LM_2	LM_3
Breadth . .	15 mm.	12 (14) mm.	12 mm.	11.5 mm.	9 mm.
Length . .	25 mm.	28 mm.	22 mm.	24.5 mm.	23 mm.
Height . .	64 mm.	74 mm.	69 mm.	73 mm.	38 mm.

A lower second molar from the type locality was described by van Hoepen in the same paper (1932) as the type of a new species, *S. hipkini*. The specimen (Nas. Mus., No. C.797) is very little worn and thus exhibits an entirely uncharacteristic pattern. Its height is 81 mm., and 15 mm. below the exposed grinding surface the dimensions of the tooth are: breadth 12.5 mm., length 26.5 mm.; in the middle of the tooth the corresponding dimensions are 13 mm. and 22 mm. A left second premolar is provisionally referred to this new species, but there does not appear to exist any valid reason for separating either of these teeth from the earlier species.

Two lower teeth recovered by Broom from the Kromdraai Cave have been referred by the present writer to this species but they have not yet been described.

Genus *EQUUS* Linnaeus 1758.

Genotype: *Equus caballus** Linnaeus.

*Equus burchellii** (Gray).

*Asinus burchellii** Gray 1824. Zool. Journ., 1, p. 247, pl. 9, figs. 1, 2.

*Equus quagga wahlbergi** of most authors.

Equus platyconus van Hoepen 1930. Pal. Nav. Nas. Mus. Bloemfontein, II, 1, pp. 4-5, figs. 3-5.

Equus simplicissimus van Hoepen 1930. *Ibid.*, p. 6, fig. 7.

Equus simplicissimus van Hoepen 1930. Pal. Nav. Nas. Mus. Bloemfontein, II, 2, p. 21, figs. 12, 13.

Kraterohippus elongatus van Hoepen 1930. Pal. Nav. Nas. Mus. Bloemfontein, II, 1, pp. 7-8, fig. 9.

Equus lylei Dreyer 1931. "New Fossil Mammals and Man", p. 30, pl. v, fig. 9; pl. vi, figs. 6, 7, 8; pl. vii, fig. 8.

The general dental formula is the same as in *Equus caballus**, but the vestigial first upper premolar, which is normally lacking in *E. caballus** and in most other members of the genus, is frequently present in *E. burchellii** and is shed only comparatively late in life. The upper incisor teeth closely resemble those of *E. caballus**, but the lower incisors all typically lack the cup or mark so characteristic of the common horse. This cup is normally formed as a result of closure of two posterior folds of the tooth, and its incomplete formation is well seen in many specimens of *E. asinus**. In *E. burchellii** it is completely absent in the lower I_3 , partially formed in I_2 and partially or completely formed in I_1 , but even if present in I_1 is so shallow as rapidly to disappear with wear. A typical specimen is shown in fig. 12. This feature is not characteristic of either *E. zebra** or *E. quagga**, though in the latter species the cup is often absent in the lower third incisor, and is not as deep as in *E. caballus**. The retention of the vestigial first premolar and the nature of the incisor teeth may both be regarded as rather primitive characteristics.

The upper cheek teeth are a good deal smaller than those of *E. caballus**, and the dimensions of a typical complete dentition (Tvl. Mus., No. 173, fig. 13c) in normal wear are:

	Pm ²	Pm ³	Pm ⁴	M ¹	M ²	M ³
Breadth	22 mm.	24 mm.	24.5 mm.	23 mm.	23 mm.	21 mm.
Length	35 mm.	24 mm.	23.5 mm.	20.5 mm.	21 mm.	23 mm.

The breadth variation noted in Pm³-Pm⁴ is 22-26 mm. and in M²-M¹ is 21-25 mm.



FIG. 12.—Lower incisor teeth of *Equus burchellii** (Gray) to show the characteristic absence or reduction of the cup or "mark". Natural size. (Original.)

The halves of the ectoloph are concave from without inwards and curve smoothly into the styles, though the mesostyle may overhang slightly. The parastyle is commonly obliquely flattened anteriorly in the premolars but less commonly so in the true molars. This and the mesostyle are sometimes grooved externally for a small extent below the grinding surface. The metastyle is small and not prominent. The protocone is elongate, oval in form (proportionally narrower than in *E. caballus**), and the portion anterior to the junction with the protoconule comprises about one-third of the total protocone length (except in Pm^2 where the anterior extent is very small in all species of *Equus*). The hypocone is not large and frequently shows a slight bulge into the medivallum, giving to it the appearance of a tendency towards isolation from the metaconule. The caballine fold is typically absent, but may be present in some individuals, particularly in the premolars. The fossette folds are generally small except for a well-developed pli-protoconule and a fairly good pli-postfossette. The pli-hypostyle and pli-prefossette are very variable in development, but the pli-protoloph is usually present and often fairly deep. The crown patterns of three typical dentitions are shown in fig. 13.

The lower teeth are also a good deal smaller than those of *E. caballus**. The dimensions of the lower teeth (fig. 14) in the individual for which the measurements of the upper teeth have already been given are:

	Pm_2	Pm_3	Pm_4	M_1	M_2	M_3
Breadth . . .	12.5 mm.	13.5 mm.	14 mm.	12 mm.	11.5 mm.	11 mm.
Length . . .	28 mm.	25 mm.	24 mm.	22 mm.	23 mm.	27 mm.

The breadth variation noted in Pm_3 - Pm_4 is 12-15 mm. and in M_2 - M_1 is 11-14 mm.

The outer walls of the protoconid and hypoconid are both flattened or even concave inwards, and the ectostylid fold in the hypoconid is small or even absent. The entaonid is small and somewhat quadrate in form. The metaconid is oval, and is separated from the metastylid by a fairly sharp-pointed groove. The metastylid itself is rather small, pear-shaped and bluntly pointed. The metaflexid lobe is smaller than that of the entoflexid, and the outer walls of the entoflexid may show some folding which does not persist with advanced wear.

Referred Fossil Material.

Petrified specimens of this species are of common occurrence in cave deposits, in superficial deposits, in river gravels and elsewhere. Such

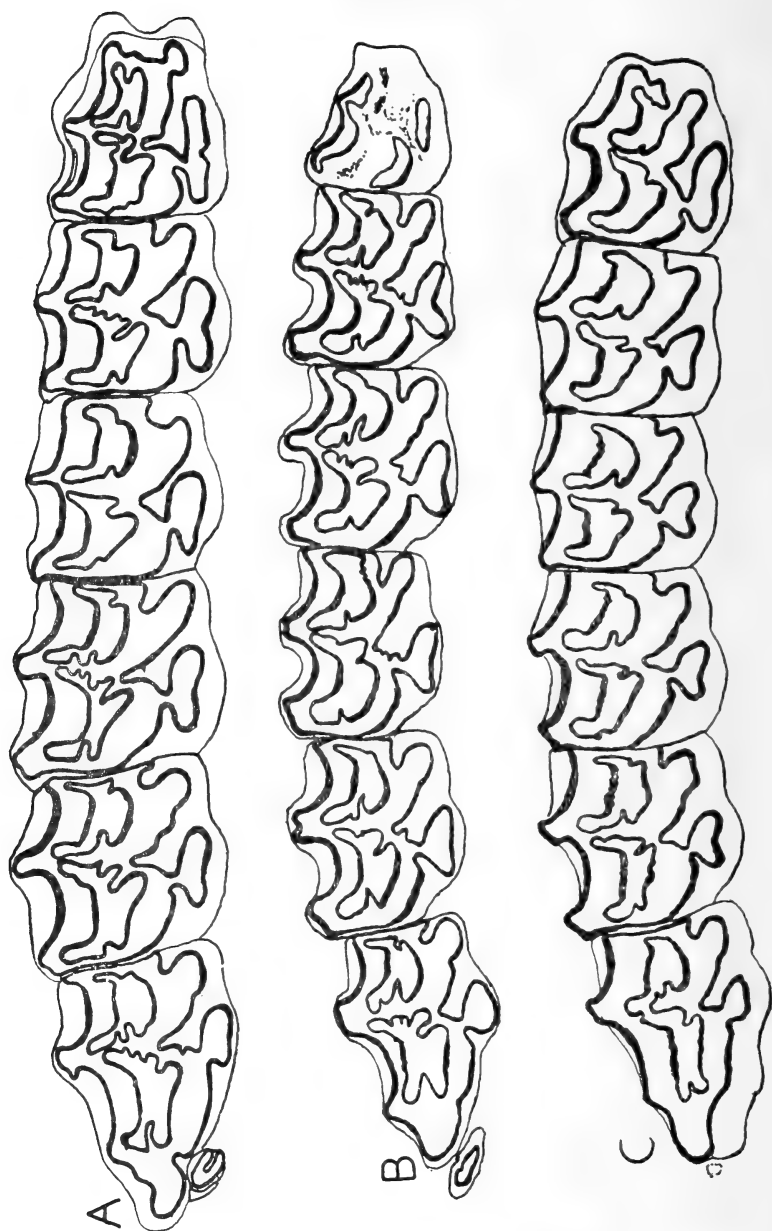


FIG. 13.—Left upper cheek teeth of *Equus burchellii** (Gray). The upper dentition C belongs to the individual figured in fig. 14, C. Natural size. (A, after Owen; B and C original.)

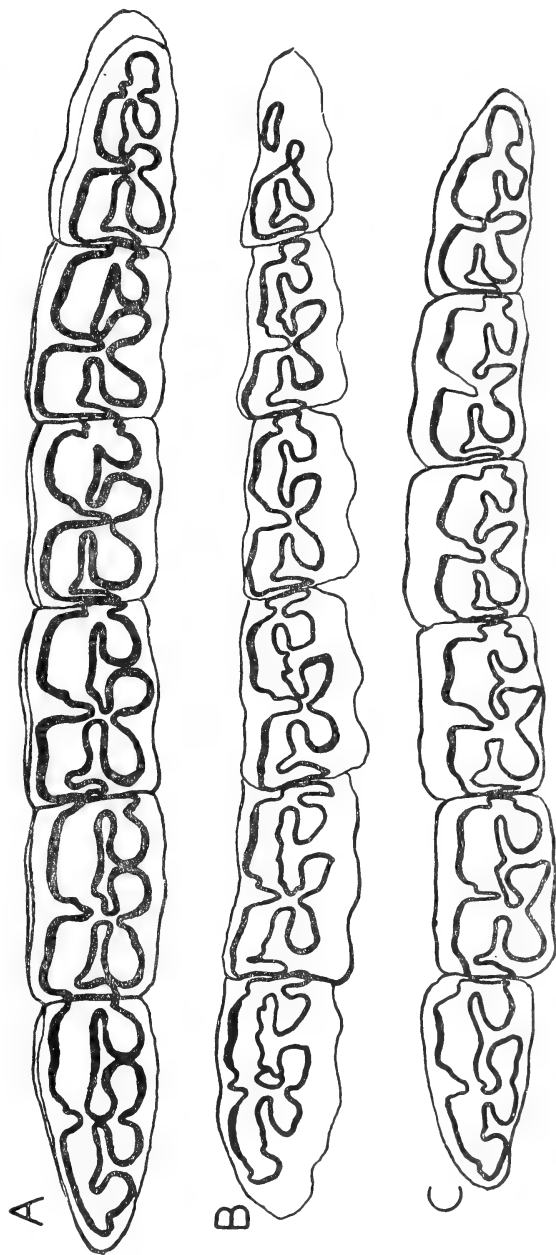


FIG. 14.—Right lower cheek teeth of *Equus burchellii** (Gray). The lower dentition C belongs to the individual figured in fig. 13, C. Natural size. (A, after Owen; B and C original.)

material does not always seem to be of very great antiquity and is quite possibly only of Upper Pleistocene Age.

The species *Equus platyconus* van Hoepen and *Kraterohippus elongatus* van Hoepen have already been regarded by Haughton (1932) in his revision as probable synonyms of the living Burchell's zebra, and there seems no reason to doubt the correctness of this conclusion. *Kraterohippus elongatus*, moreover, is founded on a broken upper Pm², almost certainly incorrectly restored and is valueless as a type. *Equus simplicissimus* van Hoepen also appears to fall well within the range of variation of the living species and does not warrant distinction.

Equus lylei Dreyer, founded on well-mineralised material from the springs at Floris Bad, was regarded by Haughton as falling within the range of variation of the living species. This is certainly the case, most of the specimens from the type and neighbouring areas, however, lying close to the lower size limit of the species. Their enamel characters are quite typical and the material does not apparently require specific distinction, though a varietal or sub-specific separation may prove to be justified.

Mineralised specimens of *Equus burchellii** occur in the deposits of the Vaal River basin.

*Equus zebra** Linnaeus.

*Equus zebra** Linnaeus 1758. Syst. Nat., Ed. 19, 1,

The incisor teeth have been considered under *E. burchellii** above.

The upper cheek teeth differ very little in size from those of *E. burchellii**, though on the average they are possibly a millimetre broader than the average bontequagga. The halves of the ectoloph are almost straight or even slightly convex, and the parastyle and mesostyle are somewhat abruptly marked off from the ectoloph walls. These features are less apparent in the true molars than in the premolars. The protocone is sub-triangular rather than oval, and the portion anterior to its junction with the protoconule is less than one-third of the protocone length. The parastyle is commonly flattened anteriorly but is not as obliquely directed as in *E. burchellii**. The hypocone is only a little smaller than the protocone. A caballine fold is often, but not consistently, present. The fossette folds are all small, and even the pli-protoconule and pli-postfossette may be virtually lacking. The pli-protoloph is typically absent or extremely small.

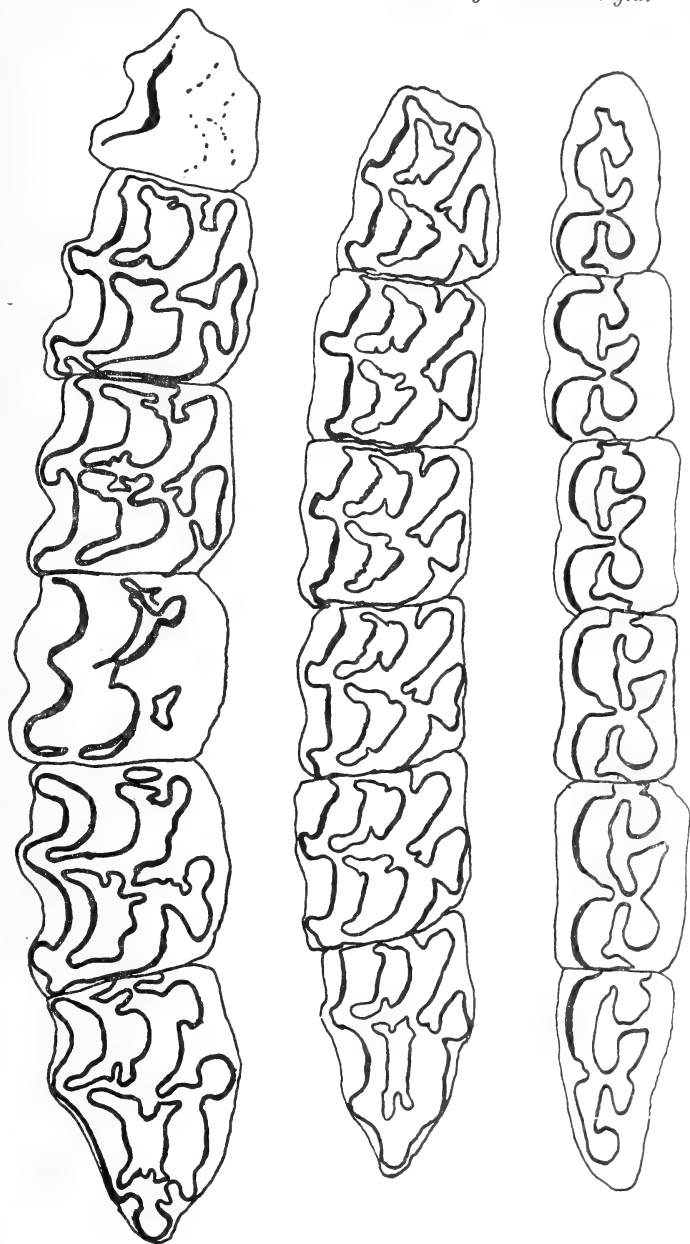


FIG. 15.—Two left upper and a right lower series of cheek teeth of *Equus zebra** Linnaeus. Natural size. (Original.)

The lower teeth are also comparable in size with those of the bontequagga. The outer walls of the protoconid and hypoconid are convex and well rounded, and the ectostylid fold is small or lacking. The entaenid is rounded, as also is the metaenid, but the metastylid is pear-shaped and rather pointed. The groove separating metaenid and metastylid is somewhat pointed. The metaflexid and entoeflexid lobes are simple.

Two upper and a lower dentition are shown in fig. 15.

Referred Fossil Material.

The only petrified specimens certainly to be ascribed to this species were recovered from the Cango Caves near Oudtshoorn, but the remains of zebrine skulls are not uncommon in the older dune sands of the coastal belt in the Cape Province.

*Equus quagga** Gmelin.

*Equus quagga** Gmelin (Linnaeus 1788). Syst. Nat., Ed. 13, 1, p. 21.

*Equus quagga** Cooke 1941. S. Afr. J. Sci., xxxvii, p. 307.

*Equus quagga** Shapiro 1943. S. Afr. J. Sci., xxxix, p. 117.

(non *E. quagga quagga** Dreyer 1931. "New Fossil Mammals and Man", p. 33.)

(non *E. quagga** var. Haughton 1932. Ann. S. Afr. Mus., xxviii, p. 424.)

*Equus quagga** became extinct in 1872 before most museums had commenced the collection of skeletal material from Southern Africa, and only a cast in the Transvaal Museum, taken from a skull in the possession of the Stuttgart Museum, represents a specimen actually known to be that of the true quagga. This individual was very young, and the cast is not of great value for identification purposes. Fortunately the great Richard Owen, in the "Philosophical Transactions of the Royal Society of London" for 1869, gives natural size figures of the dentition of a good adult specimen at that time in the Royal College of Surgeons. Dr. Robert Broom, while in London many years ago, made drawings of the teeth of a quagga in the British Museum collections, and these agree with those given by Owen in all characters. Some old skulls and jaws in the McGregor Museum, Kimberley, and in the collections of the Kingwilliamstown Museum, agree closely with the figures published by Owen and with

the manuscript drawings given to the writer by Dr. Broom, and as these skulls were collected in a region certainly at one time overrun by quagga, this material may with fair certainty be taken to represent the species. Furthermore, the characters which Owen remarks as distinguishing the quagga from the other two South African species, are present in these skulls.

From the limited material available, it would appear that the teeth of this species do not differ very markedly in size from those of the zebra and bontequagga. The largest and smallest upper dentitions in the McGregor Museum collection (fig. 16, B, C) have the following dimensions over the enamel:—

	Pm ²	Pm ³	Pm ⁴	M ¹	M ²	M ³
Breadth .	21.5 mm.	22.5 mm.	22.5 mm.	20.5 mm.	20.0 mm.	19.5 mm.
Length .	30.5 mm.	23.5 mm.	21.5 mm.	20.0 mm.	19.5 mm.	20.5 mm.
Breadth .	23.0 mm.	27.0 mm.	26.5 mm.	24.5 mm.	24.0 mm.	19.5 mm.
Length .	32.5 mm.	24.5 mm.	24.5 mm.	21.5 mm.	21.5 mm.	23.5 mm.

Owen's figure gives measurements only slightly smaller than the dimensions of the larger dentition, so that it would appear that the average quagga dentition was a little larger than the normal bontequagga, and the range in breadth is somewhat greater as well, being 22–27 mm. for Pm³–Pm⁴ and 20–25 mm. for M¹–M².

The halves of the ectoloph are almost straight or even slightly convex, and are abruptly marked off from the parastyle and mesostyle by an acute angle, though this character is suppressed in the third molar and not clear in the second premolar. The external face of the parastyle, unlike that in *E. burchellii** and *E. zebra**, is not directed in an oblique angle anteriorly but lies roughly parallel to the axis of the row of cheek teeth. The protocone is elongate oval or somewhat triangular in form, and commonly has an almost median indentation in its inner wall, giving a rather bilobate appearance. The junction of the protocone with the protoconule is only slightly anterior to the middle of the protocone. The hypocone is small and the hypoglyph is rather variable. The caballine fold is normally absent. The fossette folds are all small, even the pli-protoconule and pli-postfossette being commonly reduced to a small notch only. Nevertheless the pli-protoloph and pli-hypostyle are both normally visible, though the pli-prefossette is typically small or absent. The crown patterns of three upper dentitions are shown in fig. 16.

The lower teeth are comparable in size with those of *E. burchellii**, two typical dentitions measuring:

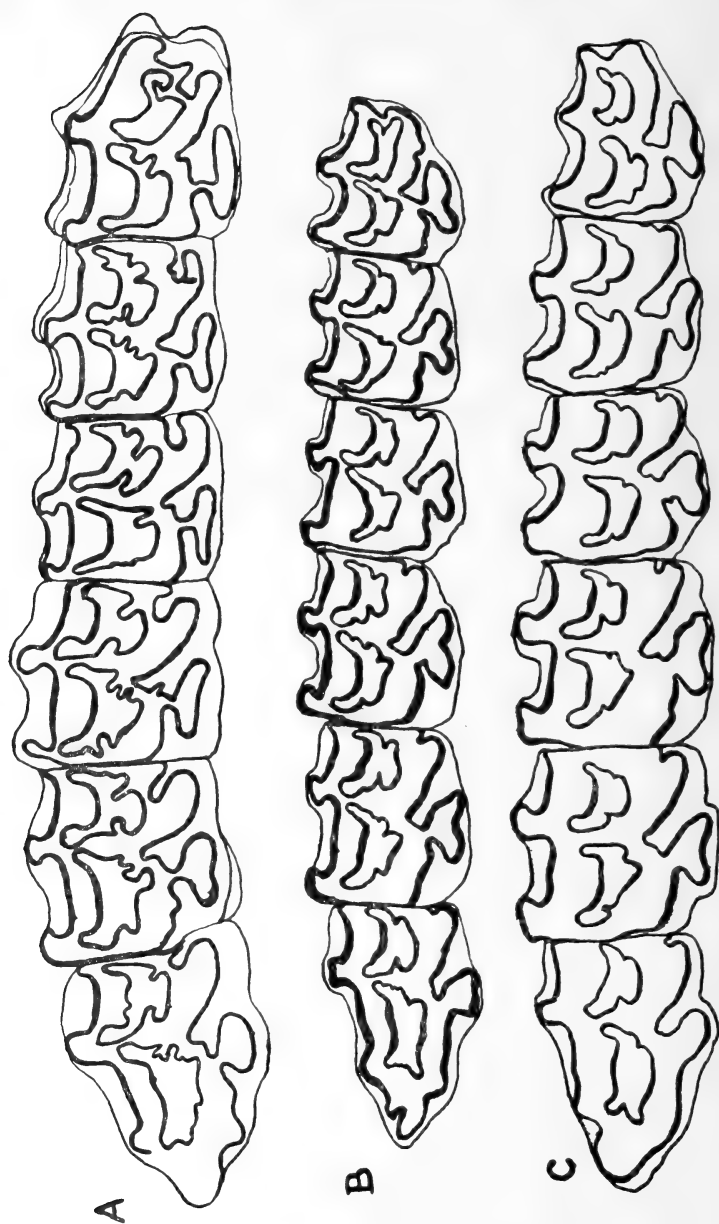


FIG. 16.—Left upper cheek teeth of *Equus quagga** (Gmelin). Natural size.
(A, after Owen: B and C original.)

	Pm ₂	Pm ₃	Pm ₄	M ₁	M ₂	M ₃
Breadth .	13.0 mm.	14.0 mm.	14.5 mm.	12.5 mm.	12.0 mm.	11.5 mm.
Length .	27.5 mm.	25.0 mm.	24.0 mm.	22.5 mm.	22.0 mm.	26.0 mm.
Breadth .	13.0 mm.	14.0 mm.	14.0 mm.	12.5 mm.	12.0 mm.	11.0 mm.
Length .	31.5 mm.	26.5 mm.	26.0 mm.	23.5 mm.	24.0 mm.	23.5 mm.

Owen's figure agrees very closely in dimensions with those of the latter species. The probable range in breadth may be estimated as 12–16 mm. for Pm₃–Pm₄ and 11–15 mm. for M₁–M₃.

In character the lower teeth resemble those of *bontequagga* rather than *zebra*, for the outer walls of the protoconid and hypoconid are somewhat flattened, the latter more so than the former. The ectostylid fold is often present. The metaconid is rounded or oval, and is separated from a pear-shaped metastylid by a rounded groove. The entaonid is rounded to quadrate and notably larger in the premolars than in the molars.

Three dentitions are shown in fig. 17.

Probably largely in consequence of the confused ideas which have hitherto existed regarding the characters of the teeth of *Equus quagga**, none of the teeth referred to by various authors as "*E. quagga*" or "*E. quagga quagga*" can be regarded as actually belonging to Gmelin's species. These so-called "*quagga*" teeth are mainly those of *E. burchellii** (Gray) but, remarkably enough, none of the fossil teeth described under other names can be regarded as belonging to *E. quagga** either, so that it would appear that this recently extinct species has not hitherto been recognised to any notable degree in our fossil collections. This species is represented by material in the McGregor Museum, Kimberley, derived from surface deposits at Koffiefontein, Orange Free State. It has also been recorded from a cave near Kuruman (Cooke, 1941), from Bankies, O.F.S. (Shapiro, 1943) and appears to be present in the deposits of the Vaal River valley. Doubtless more material will be recognised in due course.

Equus capensis Broom.

- Equus capensis* Broom 1909. Ann. S. Afr. Mus., vii, pp. 281–282.
Equus capensis Broom 1913. Bull. Amer. Mus. Nat. Hist., xxxii, p. 437, fig. 1.
Equus capensis Broom 1928. Ann. S. Afr. Mus., xxii, p. 441, fig. 2, A.
Equus cawoodi Broom 1928. *Ibid.*, pp. 443–444, fig. 3, A.
Equus gigas van Hoepen 1930. Pal. Nav. Nas. Mus. Bloemfontein, II, 1, pp. 2–3, fig. 1.
Equus capensis Dreyer 1931. *Ibid.*, pp. 36–37, pl. vii, fig. 5.
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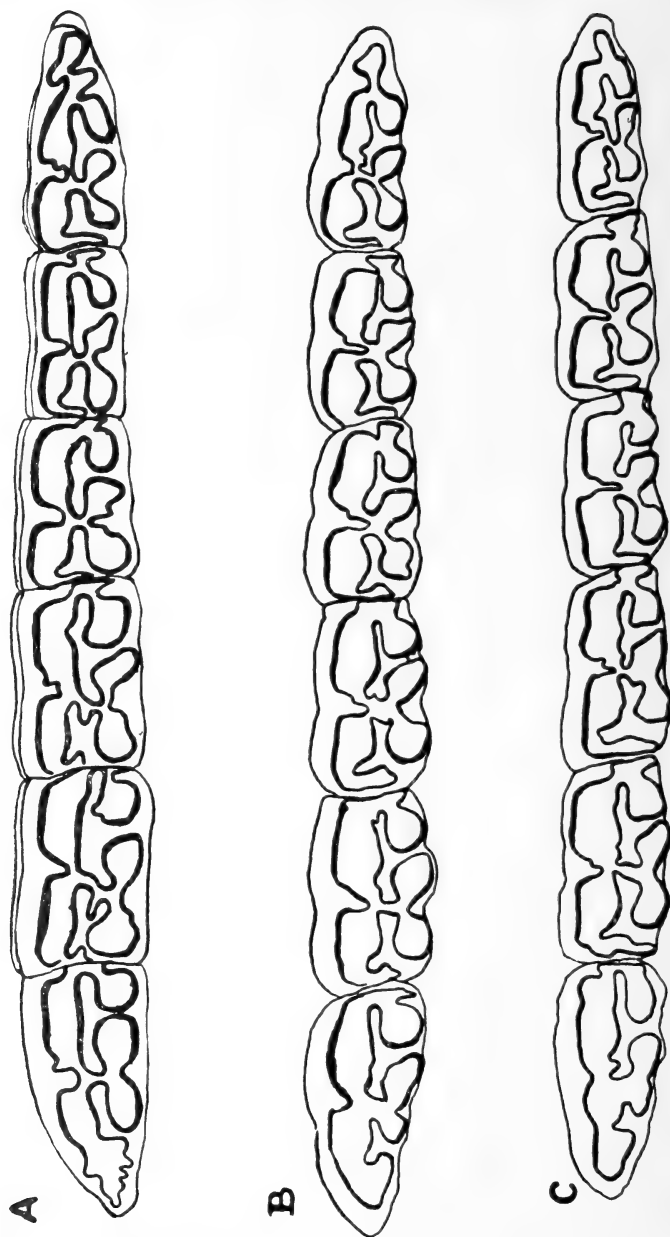


FIG. 17.—Right lower cheek teeth of *Equus quagga** (Gmelin). Natural size.
(A, after Owen; B and C original.)

Equus westphali Dreyer 1931. *Ibid.*, pp. 36-37, text-fig.

Equus capensis Haughton 1932. *Ann. S. Afr. Mus.*, xxviii, pp. 410-412, fig. 2.

Equus capensis Cooke 1939. *S. Afr. J. Sci.*, xxxvi, pp. 413-414, fig. 2.

Equus capensis Cooke 1941. *S. Afr. J. Sci.*, xxxvii, pp. 308-311, figs. 4, 5.

Equus capensis Wells and Cooke 1942. *Trans. Roy. Soc. S. Afr.*, xxix, pp. 228-229, fig. 12.

Equus capensis Shapiro 1943. *S. Afr. J. Sci.*, xxxix, pp. 117-178.

(non *E. carwoodi* van Hoepen 1930. *Pal. Nav. Nas. Mus. Bloemfontein*, II, 1, pp. 3-4, fig. 2.)

(non *E. carwoodi* Dreyer 1931. "New Fossil Mammals and Man", pp. 26-29, pl. vi, figs. 8-12; pl. v, fig. 2.)

(non *E. capensis* Broom and Le Riche 1937. *S. Afr. J. Sci.*, xxxiii, pp. 769-770, fig. 1.)

(non pars *E. capensis* Cooke 1939. *S. Afr. J. Sci.*, xxxvi, pp. 413-414, fig. 2a.)

Type: Series lower left P_2 , P_3 , P_4 , M_1 , M_2 embedded in limestone and damaged on the inner sides. *S.A. Mus.*, No. 658. (Fig. 18.)

Locality and Horizon: Beach debris, Yzerplaats, Maitland, Cape Province.

Measurements:

	LP_2	LP_3	LP_4	LM_1	LM_2
Breadth (damaged)	?	15+ mm.	15+ mm.	14+ mm.	14+ mm.
Breadth (as restored)	?	19.5 mm.	18.5-19 mm.	18 mm.	17.5 mm.
Length	? 30 mm.	? 35 mm.	34.5 mm.	31 mm.	30 mm.
Height	? 75 mm.	87 mm.	103 mm.	92 mm.	94 mm.

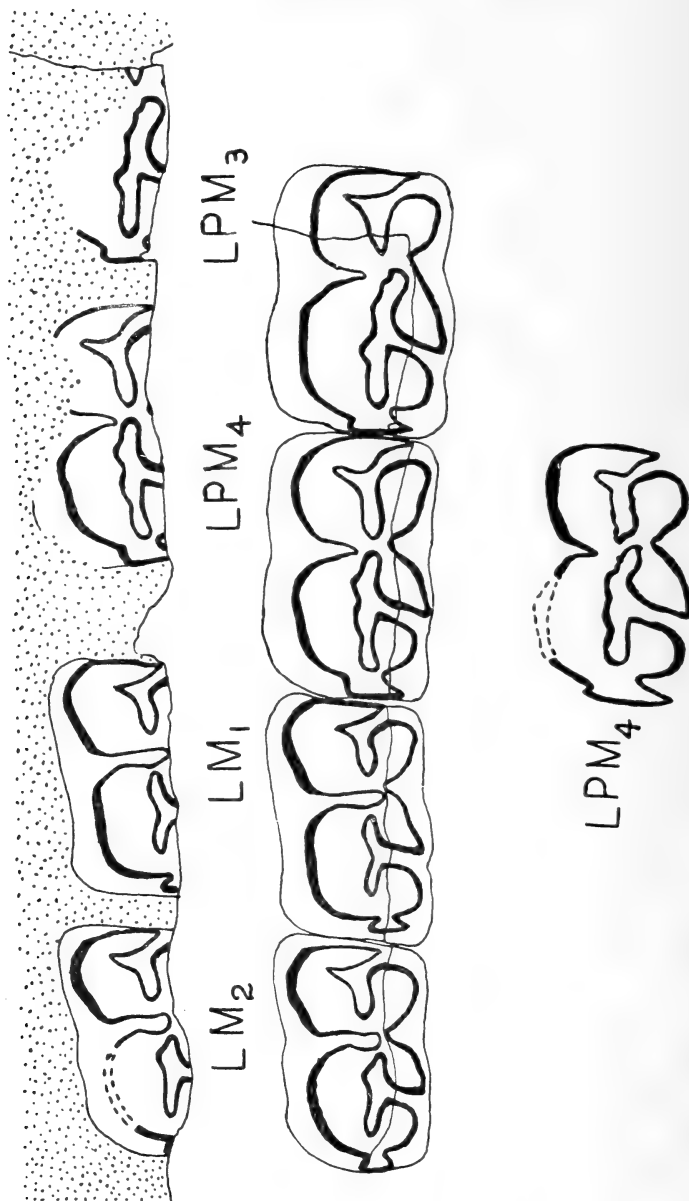
Neotype (Haughton 1932): Lower left fourth premolar. *S.A. Mus.*, No. 2821. (Fig. 18.)

Locality: Saldanha Bay.

Measurements:

	LPm_4
Breadth	18.5 mm.
Length	33.0 mm.
Height	92.0 mm.

The type of this species was first described by Broom in 1909 but was not figured until 1928. It comprises a damaged series of teeth embedded in a slab of sandy limestone found on the beach at Yzerplaats, Maitland district, Cape Province. It would appear that this limestone represents a former land deposit now lying below sea-level

FIG. 18.—*Equus capensis* Broom.

Top: Crown view of the type series of left lower cheek teeth as embedded in the limestone matrix. (Original.)

Centre: Restoration of crown patterns of type series. (Original.)

Below: Enamel pattern of neotype lower left fourth premolar. (From Haughton.)

All natural size.

as a result of late crustal warping. While it is impossible to arrive directly at an estimate of the age of the original deposit, this must antedate the warping which itself is most probably the final crustal warping occurring between the development of the "major emergence" and the "minor emergence" raised beaches. The dating of this event is difficult, but the writer has elsewhere (Cooke, 1941 *b*) suggested that it coincides approximately with the existence of the Stellenbosch industry and may be broadly Middle Pleistocene.

If this estimate is not far wrong, the *Equus capensis* bearing limestone belongs most probably to the Middle Pleistocene, and the general affinities of the teeth also support a Middle Pleistocene age.

The teeth themselves are exposed on a fractured surface of the slab, and the inner portions of each tooth have been lost. The series belongs to the left lower jaw and lacks the third molar, but the second premolar is completely embedded and the anterior portion of the third premolar partly covered by limestone. The patterns of the grinding surfaces are consequently visible only in part of the third premolar, the fourth premolar and the first and second molars, but all the teeth are well exposed in their inner lateral aspects. Broom figured a restoration of these four teeth in 1928, but many features of the drawing are faulty, and the restored portions probably incorrectly given. Fig. 18 shows an accurate drawing of the enamel patterns as they appeared in the slab in 1940, though possibly the specimen is now less perfect than in 1928. Nevertheless, Broom's restoration fails to show the distinct flattening of the hypoconid outer wall, gives incorrectly the shape of the visible portions of the entaconid and simplifies the irregularities in the entoflexid. As Haughton has pointed out: "In his restoration of the missing portions he has shown the metaconid, metastylid and entoconid as being rounded in outline, his restoration of the metastylid in particular differing considerably from the somewhat triangular or pointed form seen in *Equus caballus*." It is impossible from the specimen to see any grounds for maintaining this restoration, and in the light of all the available evidence a new restoration is now given which is probably not far from the truth (fig. 18).

In form these teeth resemble those of the true quagga rather than the other living species, but they are notable for their very large size, far exceeding the dimensions of any living type. The protoconid and hypoconid are well developed, and the outer wall of the latter is more markedly flattened than in the former. The protoconid projects, in the molars at least, beyond the outer wall of the hypoconid, giving a

somewhat lopsided appearance to many of the teeth. The ectostylid fold in the hypoconid wall is small or completely lacking. The hypolophid is quite distinctly marked off from the hypoconid. The entaconid is quadrate to semi-lunate in form with a distinctly angular antero-internal corner ("entostylid"). The metastylid is pear-shaped and somewhat pointed (if the restoration or evidence from the neotype and other specimens can be assumed to be correct). The metaconid is oval and is separated from the metastylid by a pointed groove. The outer wall of the entoflexid is irregular or wavy in the premolars and slightly concave in the molars. The simplicity of the molars as compared with the premolars, and also the rather great disparity of form and size, is striking in some of the series available. The range in breadth for the premolars appears to be about 18.5 to 22 mm. and for the molars 17.5 to 21 mm.

Amongst the large number of lower teeth referred to this species, the best preserved and most valuable series is shown in Fig. 19. These teeth come from a thermal spring at Vlakkraal near Bloemfontein, Orange Free State, and have been described by Wells and Cooke (1942). Their individual dimensions are as follows:—

	Pm ₂	Pm ₃	Pm ₄	M ₁	M ₂
Breadth	18.5 mm.	19 mm.	19.5 mm.	17 mm.	17.5 mm.
Length	38 mm.	34 mm.	34 mm.	29 mm.	30.5 mm.
Height (excluding roots) .	56 mm.	62 mm.	74 mm.	58 mm.	51 + mm.

The teeth are thus very slightly smaller than those of the type series, but there can be little doubt regarding their close agreement in all essentials. This series also illustrates very well the lateral aspects of the teeth and their normal angles of wear, and is very useful as an aid in determining the position of an individual tooth in a series.

The upper teeth of *Equus capensis* are so far not certainly known, but from the normal relationships between upper and lower teeth the expected breadth of the uppers would be 29 to 35 mm. for the premolars and 27 to 33 mm. for molars. Broom (1913 *b*, 1937), Dreyer (1931) and Haughton (1932) have referred large upper teeth to *E. capensis*. New species within the correct size group have also been erected by Broom (1928), van Hoepen (1930), Dreyer (1931) and Wells (1941). All these finds have been on open sites where association is virtually valueless, but material described by the writer (Cooke 1941 *a*) and by Wells and the writer (1942) from sealed sites may elucidate the problem.

In a large collection of equine remains from the Wonderwerk Cave

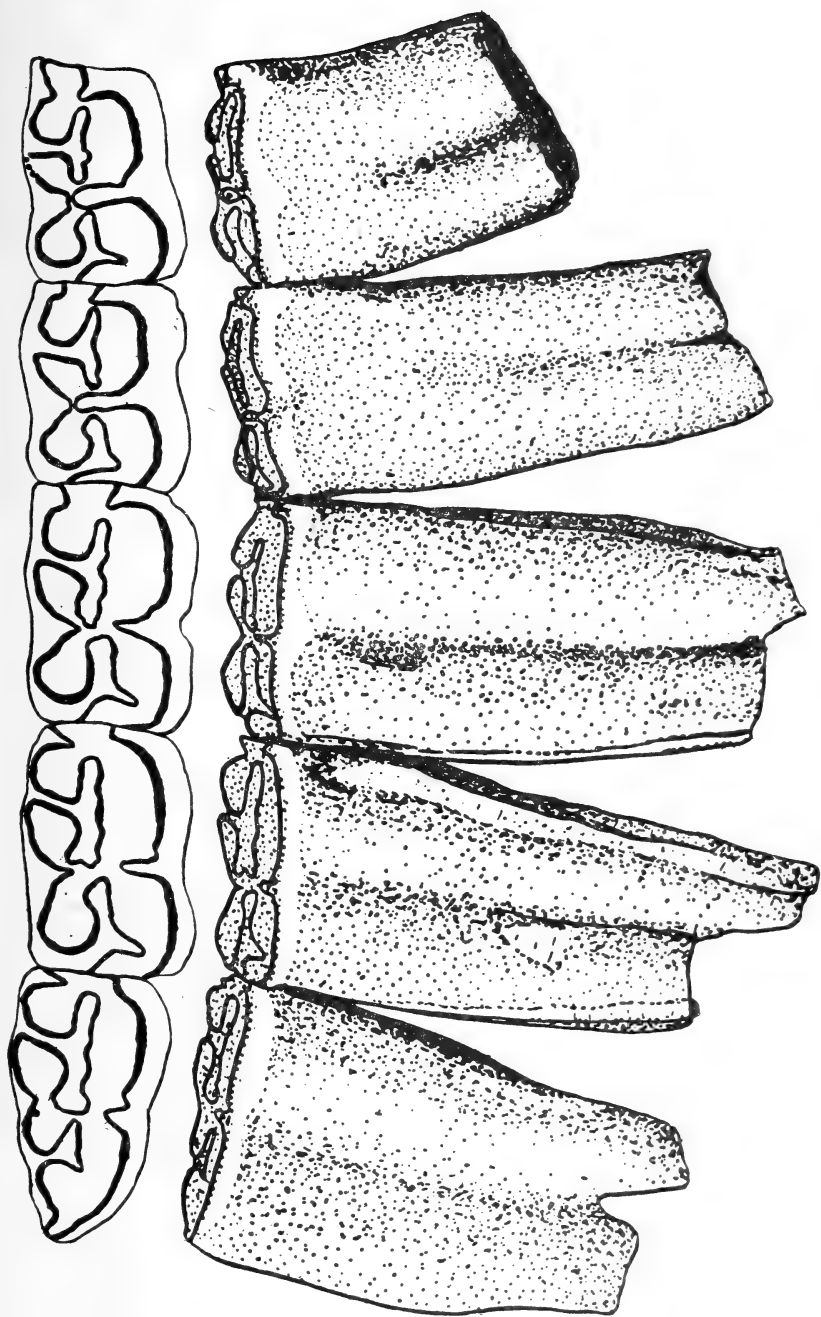


FIG. 19.—Fine series of lower left cheek teeth referred to *Equus capensis* Broom. Outer lateral and crown views. Natural size. (From Wells, Cooke and Malan.)

in the Kuruman district, twelve teeth (upper and lower) were immediately distinguished by their great size. Five are lower teeth which agree in pattern with those of *E. capensis*, though they are very slightly smaller than the type. The associated upper teeth can hardly belong to a different species, and these are closely comparable with the type of *Equus cawoodi* described by Broom (1928) from the Vaal River gravels. The type of *E. cawoodi* (which is most probably a Pm^3 and not a Pm^4 as Broom states) is little worn, and agree in almost every detail with a little worn LPm^4 from Wonderwerk. The Wonderwerk LPm^4 was sectioned, and on its sectional surface showed a very considerably simplified pattern agreeing very well with the uppers referred to *E. capensis* by Broom (1913) and one referred to that species by Haughton (1932). Additional material from Wonderwerk described by Wells (1943) confirms this view. The large upper teeth associated with the fine lower series from Vlakkraal are very worn, but they agree in all essentials with *E. cawoodi* and there can be little doubt that the two species are synonyms. Shapiro (1943) dissented from this view, but his argument was based chiefly upon the material erroneously referred to *E. capensis* by Broom & le Riche and now falls away, as he himself would doubtless agree.

The type RPm^3 of *E. cawoodi* (M.M.K., 3711) has the following dimensions (fig. 20):—

Breadth, on grinding surface (which is very little worn)	31.5 mm.
Breadth, 3 cm. below grinding surface	32 mm.
Length	33 mm.
Height	80 mm.

It may conveniently be taken as a neotype of the upper dentition of *E. capensis*.

The form of the upper dentition of *E. capensis* (as now understood) is very similar to that of *E. burchellii**, of which it is virtually an enlarged version. The halves of the ectoloph are concave inwards and curve easily into the styles, except for a distinct tendency for an anterior overhang of the mesostyle. The parastyle is obliquely flattened anteriorly in the premolars but less noticeably so in the true molars. The metastyle is small. The hypocone is moderately small but the hypoglyph may be rather deep. The caballine fold is sometimes present but may often be absent. The pli-protoconule and pli-postfossette are well marked, but the pli-protoloph and pli-hypostyle are very small and may disappear completely with wear. The pli-prefossette and secondary small postfossette are distinct in

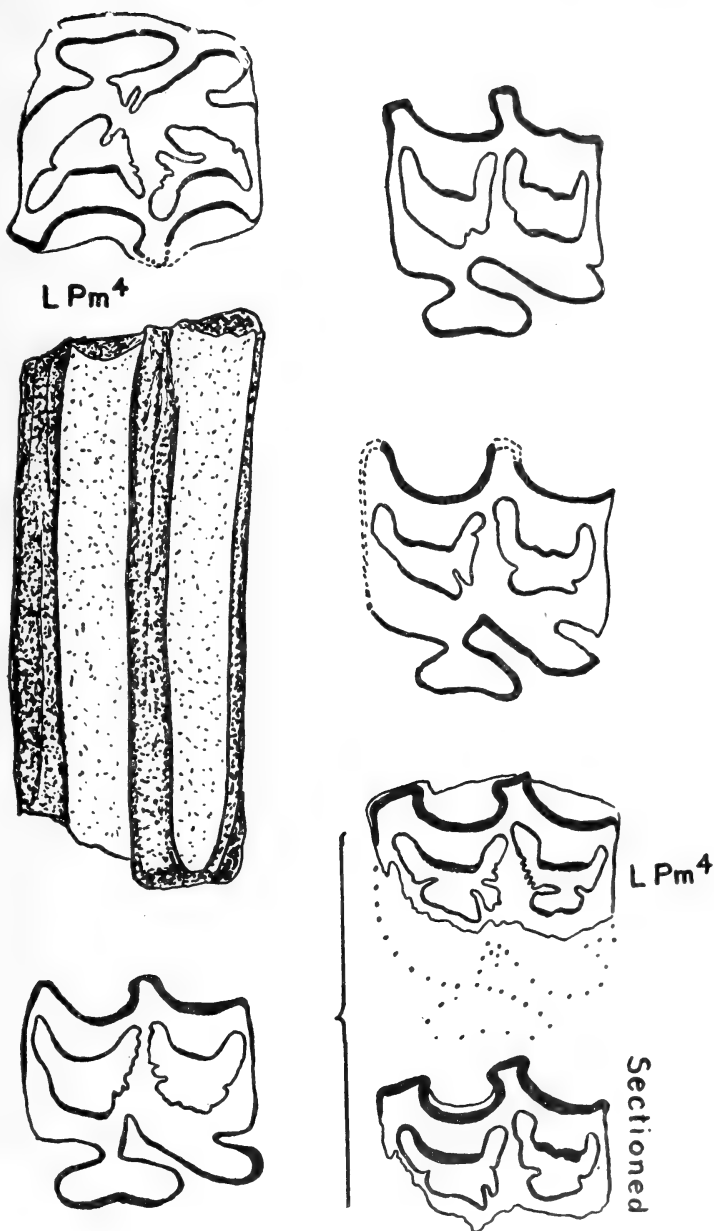


FIG. 20.—*Equus capensis* Broom.

- Upper left:* Crown and outer lateral views of neotype upper right third premolar. (Original.)
- Upper right:* Enamel pattern of two referred upper left fourth premolars from Saldanha Bay. (After Broom.)
- Lower left:* Enamel pattern of referred upper left second molar from Bloembosch, Darling. (After Haughton.)
- Lower right:* Original crown and sectioned enamel pattern of a broken, little worn, referred upper left fourth premolar from Wonderwerk. Sectioned surface approximately 2 cm. below crown. (From Cooke.)

All natural size.

very early wear but vanish rapidly with abrasion. The protocone is elongate oval in form, with rather more than one-third of its total length lying anterior to the junction with the protoconule. The range in size is, as far as observation goes, that deduced from the dimensions of the lowers.

Fig. 20 shows the form and pattern of the neotype (previously the type of *E. carwoodi*), the two teeth referred to the species by Broom (1913), that referred to it by Haughton (1932), and the sectioned damaged tooth from Wonderwerk. Fig. 21 gives the pattern of part of a series from Wonderwerk, two teeth from Floris Bad and one from the Vaal River gravels. These figures give a good idea of the characters and variations of the species.

The series of milk molars and two molars described by van Hoepen (1930 *a*) as *Equus gigas* do not appear to warrant specific distinction and may be referred to *E. capensis*. The upper teeth from Vlakkraal agree with those from Floris Bad to which Dreyer gave the name *E. helmei*, a species which Haughton (1932) regarded as a synonym of *E. carwoodi*. This is accordingly a synonym of *E. capensis*, as also is *E. westphali*, which Dreyer erected on lower teeth of large size from the Vaal River gravels at Pniel.

The tooth which van Hoepen (1930 *a*) referred to *E. carwoodi* and subsequently (1930 *b*) to a new species *E. louwi* does not appear to be *E. capensis*, but rather *E. kuhni* Broom. The same incorrect identification appears to apply to Dreyer's *E. carwoodi* (1931) and to the specimen described and wrongly figured by Broom and le Riche (1937). The smaller of the two right lower fourth premolars referred by the present writer (Cooke 1939) to *E. capensis* seems in the light of later knowledge to belong to *E. harrisi* Broom.

Equus kuhni Broom.

Equus kuhni Broom 1928. Ann. S. Afr. Mus., xxii, p. 444, fig. 3, B.

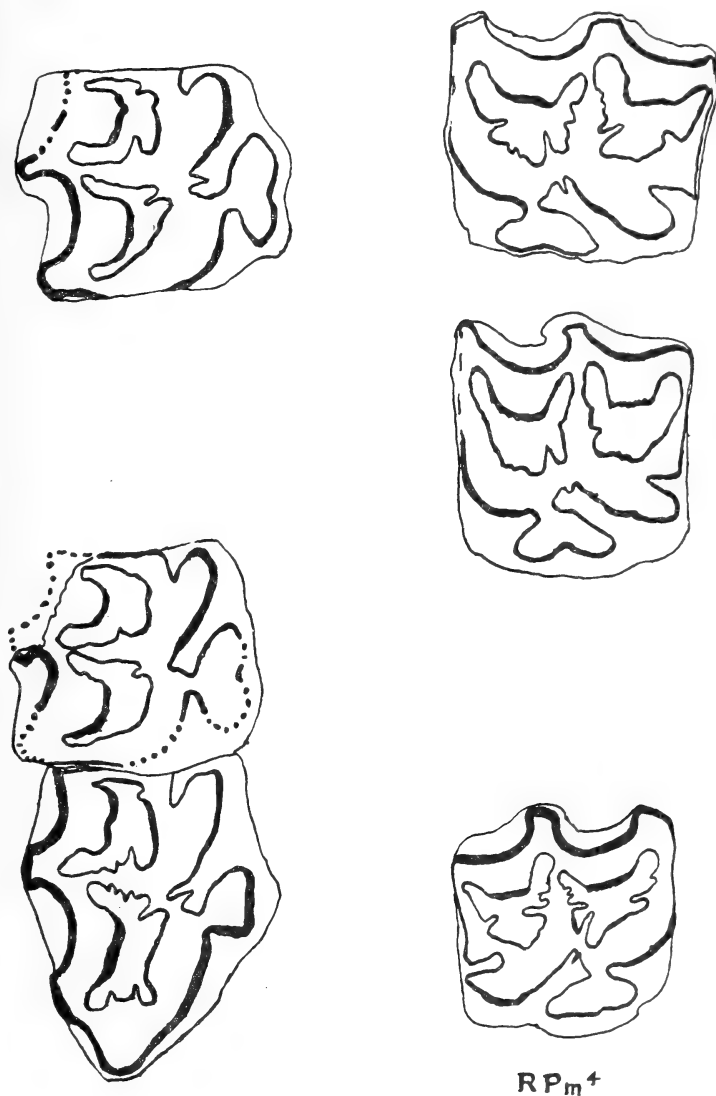
Equus carwoodi van Hoepen 1930. Pal. Nav. Nas. Mus. Bloemfontein, II, 1, pp. 3-4, fig. 2.

Equus louwi van Hoepen 1930. Pal. Nav. Nas. Mus. Bloemfontein, II, 2, pp. 19-21, figs. 6-11.

Equus kuhni Haughton 1932. Ann. S. Afr. Mus., xxviii, p. 414.

Equus kuhni Cooke 1941. S. Afr. J. Sci., xxxvii, pp. 307-308, fig. 3.

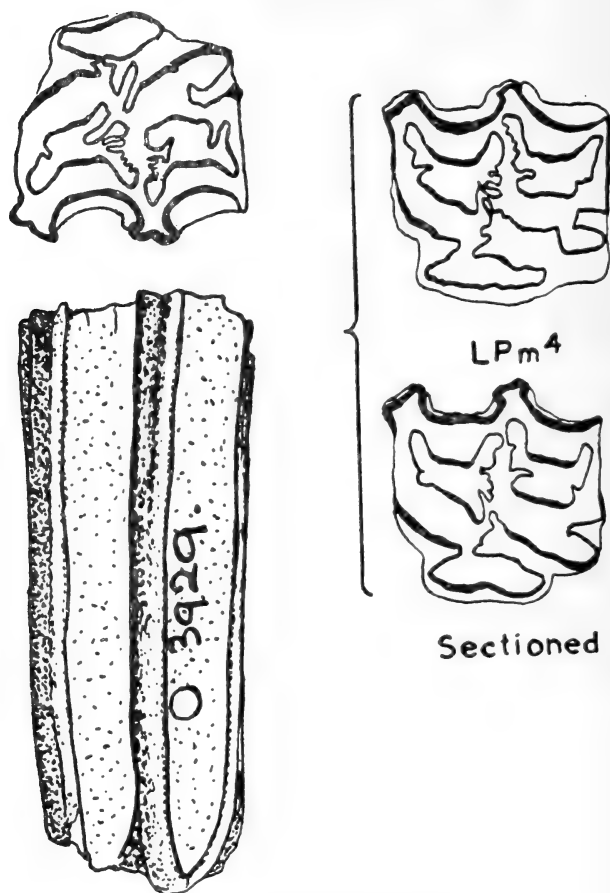
Equus capensis Broom and Le Riche 1937. S. Afr. J. Sci., xxxiii, pp. 769-770, fig. 1, A.



RP_m⁺

FIG. 21.—*Equus capensis* Broom.

- Left:* Part of incomplete series of referred left upper cheek teeth from Wonderwerk Cave. (From Cooke.)
- Top right:* Referred left upper fourth premolar and second molar from Florisbad. (After Dreyer.)
- Lower right:* Referred upper right fourth premolar from Vaal River gravels at Austin's Rush, Barkly West. (Original.)
- All natural size.

FIG. 22.—*Equus kuhni* Broom.

Left: Type upper right fourth premolar. (Original.)

Right: Neotype upper left fourth premolar from Wonderwerk Cave, showing pattern on little worn crown and on surface sectioned 2.5 cm. below the crown. (From Cooke.)

Natural size.

Type: Upper Pm⁴ of the right side. M.M.K., No. 3929. (Fig. 22.)

Locality: Pniel, Vaal River.

Horizon: ? Vaal River gravels.

Measurements:

		RPm ⁴	2 cm. below crown
Breadth	.	29.5 mm.	28.5 mm.
Length	.	31.0 mm.	30.5 mm.
Height	.	79.0 mm.	

Neotype: Upper Pm⁴ of the left side. Arch. Sur., No. 143. (Fig. 22.)

Locality: Wonderwerk Cave, Kuruman District.

Horizon: Disturbed cave deposits.

Measurements:

			LPm ⁴	2.5 cm. below crown
Breadth	.	.	27.5 mm.	28 mm.
Length	.	.	29.5 mm.	28.5 mm.
Height	.	.	77.0 mm.	

The type of this species, like that of *E. cawoodi*, is little worn; indeed the specimen is so little abraded that the protocone is not yet properly connected to the protoconule. The pattern it presents is thus not typical, and it has been necessary to create a neotype which has been sectioned to show the simplified pattern consequent upon more advanced wear. The marked grooving of the mesostyle does not extend far down the tooth. It is also apparent in the type that the smooth and deep concavity of the two halves of the ectoloph is a feature of the early state of attrition and that further wear would show these to be a little more flattened.

The upper teeth are intermediate in size between those of *E. capensis* and *E. quagga**, the breadth in Pm³-Pm⁴ being about 27-30 mm., and in M₁-M₂ about 26-29 mm. The halves of the ectoloph are concave with a slight flattening of the inner face, and the parastyle and mesostyle are prominent and somewhat abruptly marked off as in *E. zebra**. The anterior face of the parastyle is obliquely flattened and commonly slightly grooved in the premolars. The protocone is elongate oval with a flattened or a "bilobed" inner wall. Its junction with the protoconule is not much in front of the middle of the protocone. The hypocone is small and has the appearance of a tendency towards isolation, as the hypoglyph is unusually deep in many specimens and there is also commonly an indentation in the wall of the medivallum between the hypocone and the metaconule. The caballine fold is usually present and may be quite strongly developed. The pli-protoconule is well developed and often deep, as also is the pli-postfossette. The pli-postfossette is usually clearly shown and secondary plications are common. The pli-hypostyle and pli-protoloph are very variable in development and the former is sometimes well marked.

The lower teeth are not certainly known, but from the normal size relationship between upper and lower teeth they should range from 16.5 to 19 mm. for Pm³ to Pm⁴ and 15.5 to 18 mm. for M¹ to M². The species, *E. harrisi* Broom lies in the correct size group, and there is a

strong probability that *E. kuhni* is the upper dentition of that species.

In 1937 Broom and le Riche described and figured certain teeth which they referred to *E. capensis*. The Bothaville material has not been seen by the present writer, but the Sterkfontein specimens were amongst those lent to him by Broom. The lower jaw described by Broom and le Riche from Sterkfontein have the incisors and a second premolar present, and in size these exceed those of the living horses, but are otherwise not specifically identifiable. They might belong to *E. capensis*, *E. kuhni*, *E. harrisi* or *E. plicatus*. The upper palate and teeth from Sterkfontein were not found in association with the lower jaw.

This upper jaw is well embedded in the typical rather hard cave matrix, and it has proved impossible to clean the specimen properly in the normal manner. The occlusal surface of some of these teeth had been ground down by Broom to expose the enamel pattern, and the pattern of the first right molar was figured in the paper cited (fig. 1, A, p. 770) and measurements given. When the present writer examined the material, however, it was realised that the ground surface was very oblique to the plane of normal wear with a consequent distortion and exaggeration of breadth. The whole specimen was accordingly carefully ground down parallel to the palate and the dentition exposed as it would appear in early wear. The surface of the specimen (Tvl. Mus., No. 682) with the patterns now exposed is shown, natural size, in fig. 24. The dimensions are:

	RPm ²	RPm ³	RPm ⁴	RM ¹	RM ²	RM ³
Breadth .	29.0 mm.	? 29 mm.	? 30 mm.	27.5 mm.	? 27 mm.	? 26 mm.
Length .	36.5 mm.	29.5 mm.	30 mm.	30.5 mm.	29.5 mm.	? 28 mm.

The whole character of the teeth places the specimen in the species *E. kuhni*, of which it is an excellent example.

The molar originally referred by van Hoepen (1930 a) to *E. cawoodi*, and later (1930 b) cited as the type of a new species *E. louwi*, is a very typical tooth of *E. kuhni*, as also are the other teeth ascribed to *E. louwi*. Haughton (1932) has already suggested that this species is a synonym of *E. kuhni*, and this view is confirmed.

The teeth which Dreyer (1931) refers to as "*Equus kuhni simplex*" are difficult to refer with certainty, but the "wholly unfossilised fourth premolar dug up at Glen Craig, Grahamstown", looks remarkably like *E. zebra**, while the one from Pniel is too small to be *E. kuhni* and agrees excellently with little worn teeth of *E. burchellii**. The partly fossilised first and second molars "dug up by Mr. S.

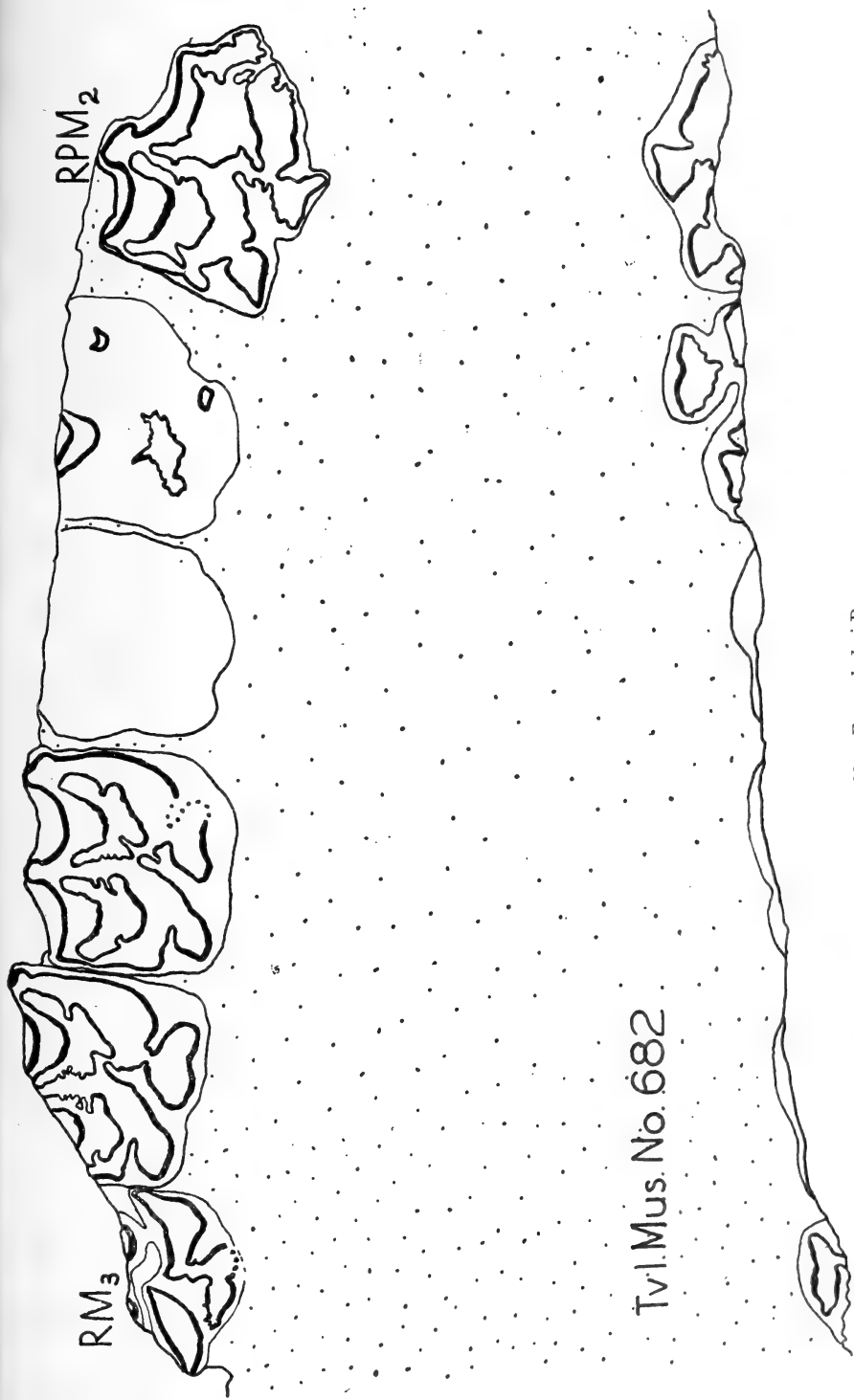


FIG. 23.—*Equus kuhni* Broom.
Palatal view of referred specimen from Sterkfontein Cave, embedded in matrix and with enamel patterns of upper cheek teeth exposed by grinding and polishing the rock. Natural size. (Original.)

Kinneard in Grahamstown", however, agree excellently both in size and character with *E. kuhni* and may certainly be assigned to that species.

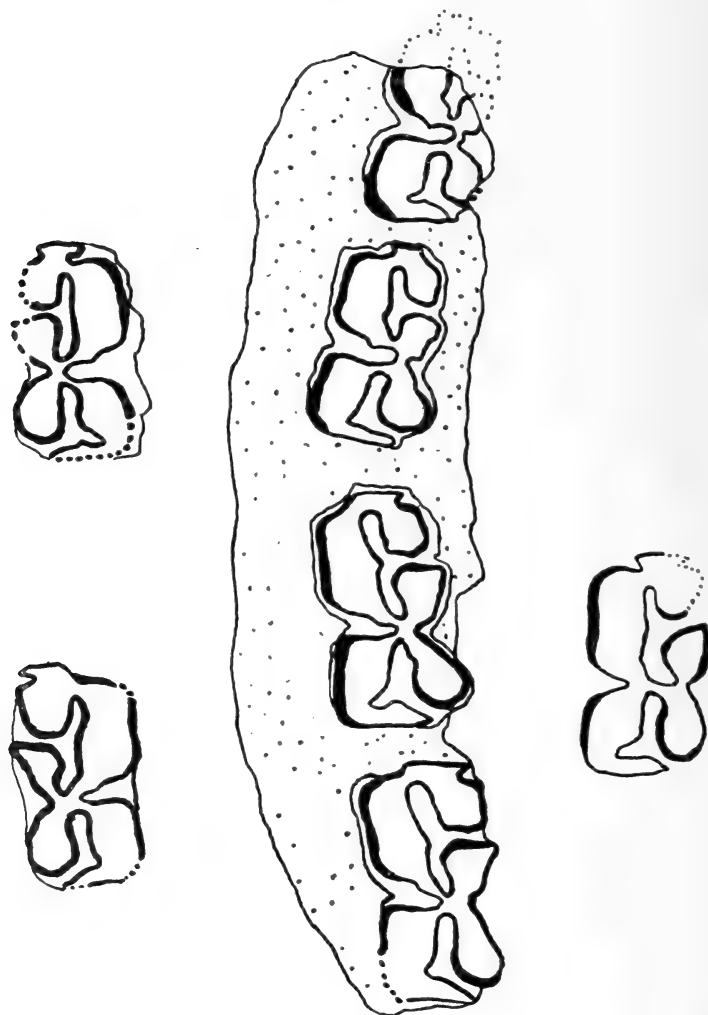


FIG. 24.—*Equus harrisi* Broom.

Top: Type left lower second molar and fourth premolar. (Original.)

Centre: Referred right lower cheek teeth from Sterktontein Cave. (Original.)

Below: Referred right lower fourth premolar from the Vaal River gravels at Pniel. (From Cooke.)

All natural size.

Equus harrisi Broom.

Equus harrisi Broom 1928. Ann. S. Afr. Mus., xxii, pp. 441, fig. 2, B.
Equus (Sterrohippus) harrisi (pars) Haughton 1932. Ann. S. Afr. Mus.,
 xxviii, pp. 412-413.

Equus capensis (pars) Cooke 1939. S. Afr. J. Sci., xxxvi, p. 413,
 fig. 2, A.

(non *Equus harrisi* Dreyer 1931. "New Fossil Mammals and Man",
 pp. 23-25, pl. vi, figs. 13, 14; pl. vii, figs. 11, 12.)

Lectotypes: Left lower M₂ and Pm₄. M.M.K., No. 3939. (Fig. 24.)

Locality and Horizon: "Diamond gravels of the Middle Terrace at
 the bend near Barkly West."

Measurements:

	LM ₂	LPm ₄
Breadth	16.5 mm.	17.5 mm.
Length	29.5 mm.	30.5 mm.
Height (excluding roots)	37.0 mm.	45.0 mm.

The species is a good deal larger than *E. burchellii**, which it somewhat resembles, and it is smaller than *E. capensis*. The type specimens are very much worn, and this fact makes specific identification with less worn specimens rather difficult.

A feature of the species is its relatively greater antero-posterior compression compared with corresponding teeth in *E. capensis*. In the premolars, the entoflexid lobe is simpler and smaller than in *E. capensis*. There is also a marked tendency in the premolars for the indentation between hypoconid and hypolophid to be very small or absent. The outer walls of the well-developed hypoconid and protoconid are flattened or even slightly concave inwards, the ectostylid fold in the hypoconid wall being small or lacking. There is a strongly developed entaenid of rounded or quadrate form. The metaconid is relatively large and elongate antero-posteriorly, while the metastylid is smaller and pear-shaped. The valley between metaconid and metastylid is bluntly pointed.

Good material of this species is difficult to find, but an excellent series discovered by Broom in the hard limestone of the famous Sterkfontein Cave was given to the writer for identification and is figured here (fig. 24) for the first time.* It is unfortunately impossible to remove these teeth from their matrix, but the available dimensions are:

	RPm ₃	RPm ₄	RM ₁	RM ₂
Breadth	17.5 mm.	18 mm.	16.5 mm.	16 mm.
Length	33.0 mm.	32 mm.	28.5 mm.	? 28 mm.

* Also see Appendix.

A lower right fourth premolar from Pniel was identified and figured in error by the present writer (Cooke, 1939, p. 413, fig. 2) as belonging to *E. capensis*. This tooth (Arch. Sur., No. 5) is now assigned to *E. harrisi* and is refigured here. Its breadth is 17 mm., its length 30.5 mm. and its height 74 mm.

The lower right fourth premolar (M.M.K., No. 4066), figured by Haughton (1932, p. 415, fig. 3, B) and referred by him to *E. simplex* van Hoepen, probably belongs to this species, as also may the associated right first molar (M.M.K., 4047).

Referred Upper Teeth.

In his original paper Broom (1928) refers to this species a right upper Pm⁴ from the same locality. Considering the nature of this deposit, the fact of an associated occurrence is only of very slight value in connecting the specimens. On a basis of size relationship between upper and lower teeth, the upper Pm⁴ corresponding to the type lower tooth of this species should be about 28 or 29 mm. broad. The associated specimen referred by Broom has a transverse diameter of 31 mm. which, though not certainly outside the possible range, is rather on the large size. In view of these considerations the reference of this upper tooth to *E. harrisi* cannot be regarded as satisfactory, and the tooth is therefore provisionally made the type of a new species *Equus broomi* described below.

Van Hoepen (1930 a) referred this specimen to a new genus and species *Sterrohippus robustus* which he created on a second premolar. A second premolar cannot be regarded as forming adequate material for the type of a species, nor does there appear to be grounds for separating the genus from *Equus*. His specific name could not be retained as a species of this latter genus, as it is preoccupied by *Equus robustus* from the Pleistocene of Europe. *Sterrohippus robustus* is therefore regarded as incorrectly founded and invalid.

The upper teeth of *Equus harrisi* must for the moment be regarded as unknown until they are found in a good association with recognisable lower teeth. The rather poor lower teeth found in apparent association with upper teeth assigned to *Equus kuhni* Broom agree fairly well with those of *E. harrisi*, but there is as yet insufficient material to warrant identification with that species. The upper teeth of *E. kuhni*, however, are in precisely the right size group and it is very possible that *E. kuhni* represents the upper dentition of *E. harrisi*. The association of the two species in the Sterkfontein group of caves may also be significant.

Equus plicatus (van Hoepen).

Kolpohippus plicatus van Hoepen 1930. Pal. Nav. Nas. Mus. Bloemfontein, II, 1, pp. 8-10, fig. 10.

Equus plicatus Dreyer 1931. "New Fossil Mammals and Man", pp. 33-35.

Equus plicatus Haughton 1932. Ann. S. Afr. Mus., xxviii, p. 417.

Type: Lower series Pm_2 to M_1 of the right side. Nas. Mus., No. C.425. (Fig. 25.)

Locality: Tierfontein, near Port Allan, O.F.S.

Horizon: Not given in description; probably surface deposits.

Measurements: The measurements cited in the type description do not agree with the text-figure, but it appears that the breadths given are total breadths and not just the width across the enamel. The dimensions given below give the breadth over the enamel, estimated by enlarging the illustration in van Hoepen's paper to agree as well as possible with the various measurements he cites. The text-figure of the type series given here is the one derived in this way:

	RPm_2	RPm_3	RPm_4	RM_1
Breadth . . .	17.5 mm.	17.5 mm.	15 + mm.	15.5 mm.
Length . . .	38.0 mm.	33.0 mm.	30 mm.	27.0 mm.
Height . . .	68.0 mm.	81.0 mm.	89 mm.	79.0 mm.

+ very little worn.

The lower teeth are larger than those of *E. quagga** and smaller than those of *E. capensis*, agreeing in size with those of *E. harrisi*, which they otherwise closely resemble. The probable range of breadth in Pm_3 to Pm_4 is about 15.5 to 19 mm., and in M_1 to M_2 14.5 to 17.5 mm. The outer walls of the protoconid and hypoconid are flattened or even concave inwards in the premolars; in the molars the protoconid may be convex. A strong ectostylid fold is present in the anterior part of the hypoconid wall in the premolars, but this fold is small or even absent in molars. The metaconid is rounded, and is separated from the bluntly pointed metastylid by a pointed groove. The entaenid is quadrate and smaller than the metaconid. The lobe of the ento-flexid is complicated in the premolars by strong—or at least well-marked—crimping of the inner wall of the hypoconid. The molars are much simpler than the premolars and cannot be easily distinguished from those of *E. harrisi*.

Van Hoepen's reference of the type teeth to a new genus does not

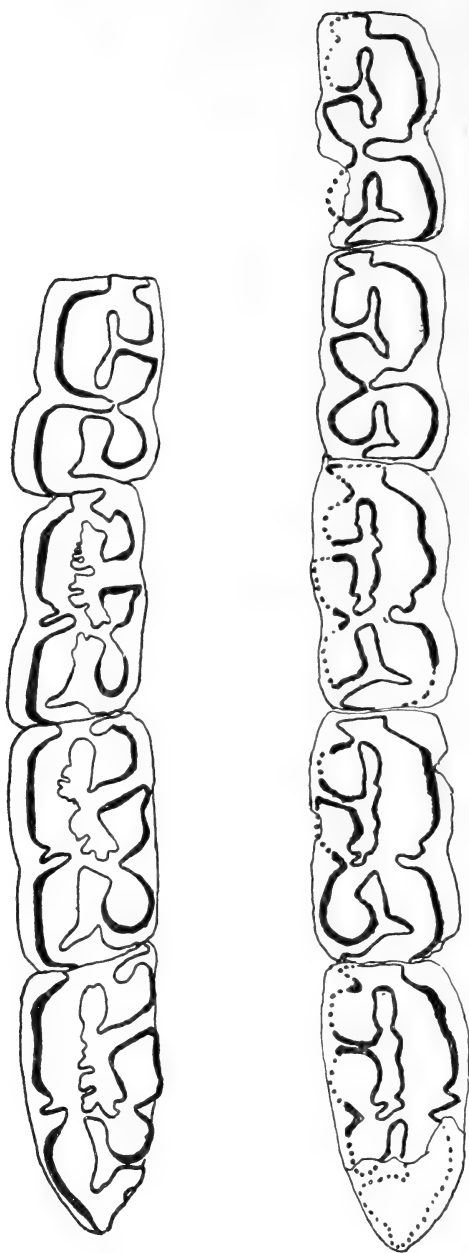


FIG. 25.—*Equus plicatus* (van Hoepen).

Left: Crown view of type series of right lower cheek teeth. (After van Hoepen; modified.)

Right: Crown view of series of lower left cheek teeth from damaged lower jaw from Koffiefontein, Orange Free State. This jaw is shown at the bottom of fig. 6. (Original.)

Natural size.

appear justifiable and even if the species is valid, it must be placed in *Equus*.

A fine series of teeth in a damaged left lower jaw from Koffiefontein, O.F.S., may be referred to this species with considerable certainty. The jaw (M.M.K., No. 4345) is shown in fig. 6 in comparison with a skull of *E. burchellii** and the enamel pattern of the teeth is shown in fig. 25. The inner side of the dentition is slightly damaged but the dimensions over the enamel are given below:

		LPm ₂	LPm ₃	LPm ₄	LM ₁	LM ₂
Breadth	.	17 mm.	17.5 mm.	17.5 mm.	16.5 mm.	15.5 mm.
Length	.	38 mm.	33 mm.	33 mm.	29 mm.	29 mm.

It would appear very probable that the differences between the dentitions ascribed to *E. harrisi* and to *E. plicatus* are not really of specific value. The type teeth of *E. harrisi* are very worn indeed, and it is difficult to assess the probable appearance of the teeth of this species in early wear. There can, however, be little doubt that teeth of *E. plicatus* in advanced wear would be indistinguishable from those assigned to *E. harrisi*.

The upper teeth are not known from a certain association. There is a strong probability that the upper dentition of a skull from the same locality (Koffiefontein) as the lower jaw described above may be that of *E. plicatus*. This upper dentition has been described by Wells as *E. fowleri*, and in the absence of a certain association the merging of these two species must remain an open question.

Equus fowleri Wells.

Equus fowleri Wells 1941. Trans. Roy. Soc. S. Afr., xxviii, pp. 301-306, fig. 1, pl. lv.

Cotypes: "Portions of skull and isolated tooth catalogued as No. 555 in the collection of the Department of Anatomy, University of the Witwatersrand, Johannesburg." (Figs. 6 and 26, A. B.)

Locality: Koffiefontein, O.F.S.

Horizon: "At a depth of about 18 inches in surface soil overlying shale."

Material: This comprises "the greater part of the right maxilla and palatine bone with Pm²-M³ in position and perfectly preserved, the right maxilla containing an unerupted I³ and part of the left maxilla lacking teeth". "The presence of the socket for C suggests that the individual is a male." "The remains are those of an individual not quite fully grown."



FIG. 26.—*Equus foudleri* Wells.
 A. Crown pattern of right upper cheek teeth of type.
 B. Crown pattern of cotype left upper first molar from the type locality.
 C. Enamel pattern on sectioned surface 15–20 mm. below crown of cotype Lm¹ shown in B.
 D. Crown pattern of referred upper right second molar.
 All natural size. (From Wells.)

Measurements:

<i>Skull:</i> Length of upper jaw	About 44.5 cm.
Breadth across the first molars	16.5 cm.
Length of Pm ² -M ³	20.6 cm.
Diastema between Pm ² and I ³	Approximately 11 cm.

Teeth:

	Pm ²	Pm ³	Pm ⁴	M ¹	M ²	M ³
Breadth	29 mm.	31 mm.	31 mm.	30 mm.	29 mm.	24 mm.
Length	44 mm.	35 mm.	32 mm.	32 mm.	33 mm.	32 mm.
Length of protocone	13 mm.	14.5 mm.	15 mm.	13.5 mm.	15 mm.	15 mm.
Height (ex. roots)	56 mm.	66 mm.	70 mm.	64 mm.	74 mm.	76 mm.

The following account is based on the type description, much being directly or indirectly quoted from Wells' paper.

The dimensions of the skull exceed those of many specimens of *E. caballus** and considerably exceed those of the zebrine horses. The lateral aspect of the maxilla in its upper portion, below the naso-maxillary suture, shows a marked hollowing. This region thus presented a form seen in the asses and in the quagga group, but not in the caballine horses nor, to any marked degree, in the mountain zebra.

The teeth are large, being intermediate in size between those of *E. capensis* (*E. caroodi*) and *E. kuhni*, both of which they somewhat resemble. The halves of the ectoloph are deeply concave inwards, and curve rather sharply into the styles with a tendency for the mesostyle to overhang anteriorly. Both parastyle and mesostyle are prominent and massive, especially in the premolars, and are more or less conspicuously grooved. The protocone is elongate, and its connection with the protoloph is established very near its anterior extremity, so that the elongation appears to affect chiefly the posterior lobe. The medial wall of the protocone is sinuous, with an ill-defined median groove. In Pm³ and Pm⁴ the protocone has a remarkably oblique direction, and these two teeth in the type show an unusual prominence of the hypostyle.* The caballine fold is well developed and may be duplicated. The enamel of the fossettes is irregularly crimped and its secondary plications are numerous but relatively coarse. The pli-protoloph and pli-hypostyle are well developed in early wear. The pli-protoconule is unusually complex and even in M¹ is duplicated. The pli-postfossette is also rather complex, but the pli-prefossette is simpler, though small secondary folding may be present.

Another tooth found half a mile distant from the skull fragments at a depth of five feet in similar soil has been referred to this species.

* This is almost certainly a feature of early wear.

It is an upper left first molar and shows all the characteristics of the type, but is from a different individual, also young. The measurements of this tooth are:

Breadth	30 mm.
Length	32 mm.
Height (excluding roots)	65 mm.

The pattern it presents is a little more complex in its secondary plication than that of the type (fig. 26, B). A section has been made through the tooth 15–20 mm. below the grinding surface, where the pattern is somewhat simplified but remains essentially the same (fig. 26, C.)

In the McGregor Museum there occurs a right upper M² (M.M.K., 4342) also from Koffiefontein which Wells refers to his species (fig. 26, D). It is more worn than the corresponding tooth of the type and is a little smaller, its dimensions being:

Breadth	28.5 mm.
Length	29.5 mm.
Height (excluding roots)	76 mm.

The styles are narrower than in the type and are very indistinctly grooved, and the pli-hypostyle is single though remarkably large. These differences, however, are not outside the expected range of variation of such a species and the tooth is referred to *E. fowleri*.

As has been stated above, the lower jaw which agrees so well with the type of van Hoepen's *E. plicatus*, was found also at Koffiefontein, and this dentition is of a suitable size to correspond with *E. fowleri*. There is thus a good possibility that these names are synonymous, but such a decision must await confirmation from a better association.

It also seems very likely that *E. fowleri* is merely a somewhat abnormal variant of *E. kuhni*, and that, in fact, *E. kuhni*, *E. harrisi*, *E. plicatus* and *E. fowleri* represent only a single species.*

Equus sandwithi Haughton.

Equus sandwithi Haughton 1932. Ann. S. Afr. Mus., xxviii, pp. 419–421, fig. 4.

Cotypes: Upper right Pm² and Pm³ and incomplete M³.

Upper left Pm³ and Pm⁴.

Lower right M₁ and incomplete Pm₃.

Lower left M₁ and M₂.

S.A. Mus., Nos. 6577 and 6578. (Fig. 27.)

Locality: Usakos, South-West Africa.

* Also see Appendix.

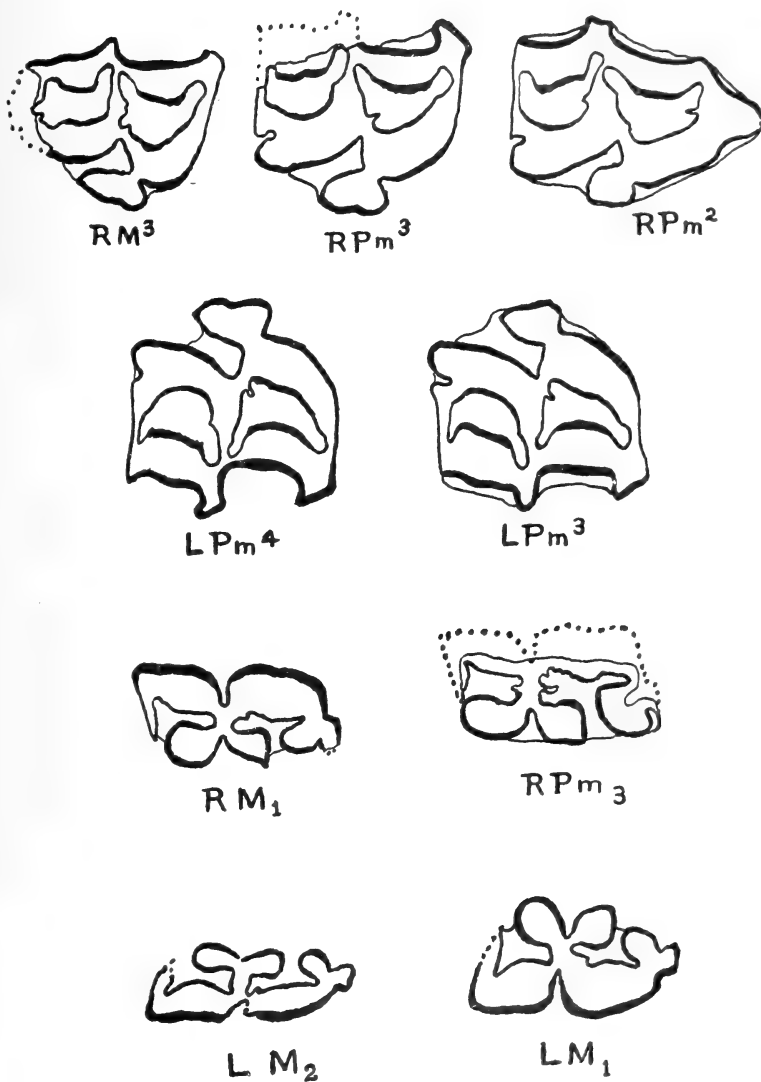


FIG. 27.—*Equus sandwithi* Haughton. Cotype upper and lower cheek teeth.
Natural size. (Original.)

Horizon: In a bed of hard clay and sand 10 feet thick underlying 8 feet of surface limestone.

Measurements:

<i>Upper</i>	RPm ²	RPm ³	RM ³	RPm ³	LPm ⁴
Breadth . . .	26.5 mm.	28 (?) mm.	24.5 mm.	29 mm.	32 mm.
Length . . .	35 mm.	28.5 mm.	29 (?) mm.	29 mm.	29 mm.
Height (ex. roots) . .	56 mm.	54 mm.	67 mm.	53 mm.	57 mm.
Length of protocone . .	7 mm.	10.5 mm.	11 mm.	9 mm.	10 mm.
<i>Lower</i>	RPm ₃	RM ₁	LM ₁	LM ₂	
Breadth (Est.) . . .	16-17 mm.	15 mm.	16 mm.	11.5 mm.	(14.5)
Length . . .	30 mm.	29.5 mm.	29 mm.	29 mm.	
Height (ex. roots) . .	70 mm.	78 mm.	65 mm.	77 mm.	

Haughton's measurements differ slightly from those given above, the explanation lying in the fact that the breadth quoted here is measured directly across the tooth and not along the rather sloping surface of wear. The tooth which Haughton describes as a lower left third molar is here regarded as a lower left second molar in very early wear. The very narrow enamel surface is a feature of early wear, and the crown is 3 mm. wider half an inch below its present surface.

The upper teeth of this species resemble those of *Equus zebra** but are a good deal larger and present an even simpler enamel pattern. The halves of the ectoloph are flattened or even bulge outwards near their centres. The parastyle and mesostyle are strongly developed and well demarcated. The mesostyle is rather narrow, and the parastyle has an oblique flattened face which may be grooved. The protocone is abnormally small, being proportionally even shorter than in *E. zebra**. This shortness is due to the very small development of the anterior prolongation. The fossettes are large and lunate. They are almost devoid of folding, only the pli-protoconule being distinct while the other folds are almost indistinguishable. The pli-caballin is absent. The hypoglyph is shallow. The protoconule shows marked antero-internal flattening.

The lower teeth are unusual in shape, as they present an anterior face which is oblique to the axis of the tooth instead of directly transverse to it. This is due to the posterior deflection of the point of the parastylid and its anterior face. The walls of the protoconid and hypoconid are rounded or slightly flattened and the ectostylid fold is inconspicuous or absent. The entaenid is moderately small in the molars. The metaconid and metastylid are normally large and pear-shaped, but their attitude may be distorted by the relative compression of the interior side of the tooth. The anterior part of the entoflexid tends to be slightly or moderately folded.

The ratio of size of molars and premolars is rather unusual, as the molars appear relatively to be abnormally small and narrow both in upper and lower dentitions. The type LPm^4 owes its unusual width at least in part to the abnormal projection of the mesostyle, but it appears that the expected range in breadth would be 28–33 mm. in Pm^3 and Pm^4 and 26–29 mm. in M^1 and M^2 , with the anterior and posterior teeth notably narrower. The same applies to the lower teeth, in which the range in Pm_3 and Pm_4 may be 15–18 mm. and in M_1 and M_2 13–17 mm.

Referred Material.

Haughton (1932) assigned to *E. sandwithi* two lower teeth from the Vaal River gravels at Sheppard Island. These teeth were discovered by van Riet Lowe but were lost in the library fire at the University of the Witwatersrand in 1931.

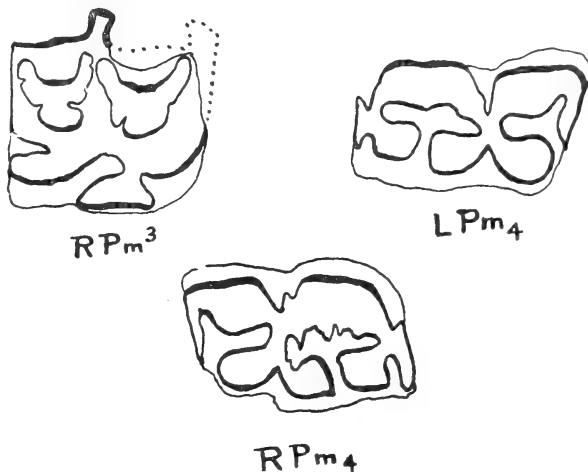


FIG. 28.—*Equus sandwithi* Haughton. Referred upper and lower cheek teeth from the Kromdraai Cave. Natural size. (Original.)

Amongst the material collected by Broom in the Kromdraai Cave deposit there occur several teeth which appear to belong to this species. Most of the teeth, both upper and lower, are damaged and difficult to clean, but a selection of the better ones is shown in fig. 28.

Equus poweri Cooke.

Equus poweri Cooke 1939. S. Afr. J. Sci., xxxvi, pp. 412–414, fig. 1.

Type: Upper right first molar. Arch. Sur., No. 3. (Fig. 29).

Locality: Pniel, Vaal River.

Horizon: ? Younger gravels of Vaal River.

Neotype: Upper left first molar. Arch. Sur., No. 213. (Fig. 29.)

Locality: 35-foot shaft, Lot 197, Windsorton.

Horizon: Younger gravels of Vaal River.

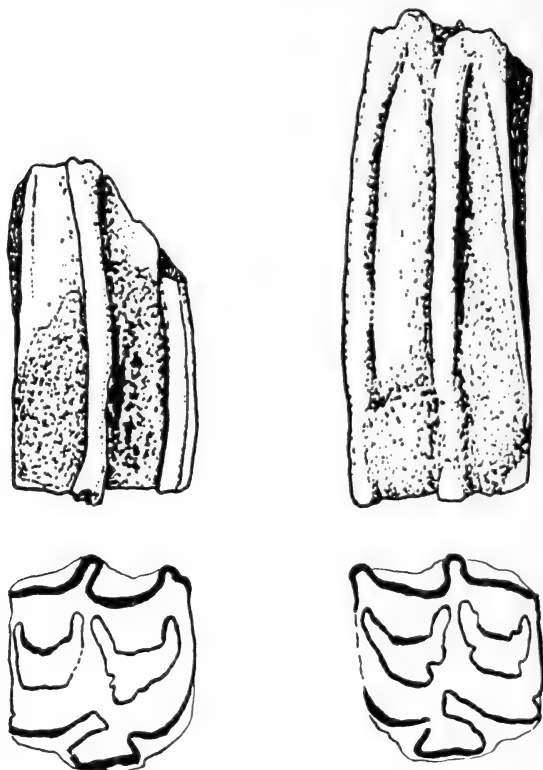


FIG. 29.—*Equus poweri* Cooke.

Left: Type right upper first molar. Outer and crown views.

Right: Neotype left upper first molar. Outer and crown views.

Natural size. (Original.)

Measurements:

	Type RM ¹	Neotype LM ¹
Breadth . . .	27 mm.	26 mm.
Length . . .	24 mm.	23 mm.
Height . . .	44 mm.	64 mm.

This species resembles *Equus sandwithi*, but appears to be very slightly smaller and to differ in several particulars. The halves of the

ectoloph are moderately flattened or bulge outwards near their centres, and the parastyle and mesostyle are well demarcated. Though prominent, the mesostyle is not nearly as well developed as in *E. sandwithi*. The protocone is very small, but the anterior lobe is proportionately larger than in *E. sandwithi* and more like *E. zebra** in this respect. The fossette are large and simple, the post-fossette being subrectangular in shape and not lunate as in *E. sandwithi*. The pli-protoconule is small and the hypostyle and protoloph folds are present only as small notches. The medivallum is small and narrow and devoid of any trace of a caballine fold. The protoconule shows a well-rounded antero-internal face and is not flattened as in *E. sandwithi*. The hypoglyph is very shallow and may disappear altogether towards the base of the tooth.

The estimated dimensions fall a millimetre below those of *E. sandwithi*.

Equus broomi sp. nov.

Equus harrisi (pars) Broom 1928. Ann. S. Afr. Mus., xxii, pp. 442-443, fig. 2 (B₃).

Type: Upper right fourth premolar. M.M.K., No. 3939 c. (Fig. 30.)

Locality: The Bend, near Barkly West.

Horizon: "Middle Terrace" of the Vall River gravels.

Measurements:

					R ^P m ⁴
Breadth	31 mm.
Length	32 mm.
Height	62 mm.
Length of protocone	9 mm.

This tooth, which is badly battered, was assigned by Broom to the species *E. harrisi* on account of the association of the specimen with the two lower type teeth of that species. This association is not a good one in view of the very disturbed nature of the deposit, and the upper tooth seems somewhat large to be correctly associated with the lowers. It is therefore given a new name here until certain associations settle the problems of the relations between the various species named on upper and on lower teeth.

The resemblance of this species to *Equus sandwithi* is strong, almost the only marked difference, apart from the greater size, being the shape of the ectoloph, which is smoothly concave in both halves and is only slightly overhung by the parastyle. The protocone is very short and

unusually rounded. The hypocone projects into the medivallum as a slight bulge but the hypoglyph is small. The fossettes show more folding than is the case in *E. sandwithi*, the pli-protoloph, pli-postfossette and pli-PROTOCONULE being distinct though small, and

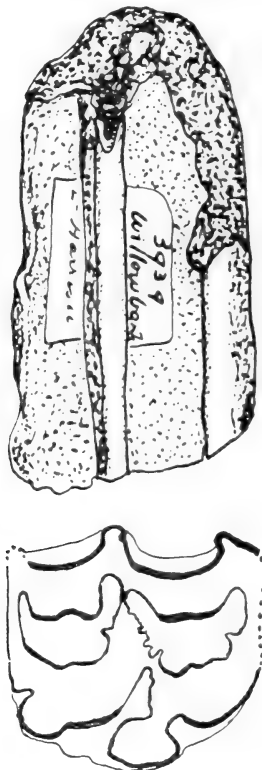


FIG. 30.—*Equus broomi* sp. nov. Outer lateral and crown views of the type upper right fourth premolar of *Equus broomi* sp. nov.; formerly referred to *Equus harrisi* Broom. Natural size. (Original.)

there is a certain amount of minor folding in the posterior wall of the prefossette.

The specimen on which van Hoepen created the new genus *Sterrohippus* and species *robustus* might belong to this species, but van Hoepen's specimen is a second premolar which cannot be regarded as forming adequate material for specific identification. There is no reason to support the generic status of *Sterrohippus*, which is indistinguishable from many species of *Equus*, and the specific name *Equus*

robustus is preoccupied and cannot be retained. *Sterrohippus robustus* is therefore regarded as invalid.

Incertae sedis.

Equus simplex van Hoepen 1930. Pal. Nav. Nas. Mus. Bloemfontein, II, 1, p. 5, fig. 6.

Type: Upper right first molar. (Nas. Mus., No. 284).

Locality: Koffiefontein, O.F.S.

Horizon: ? Surface.

Measurements:

			RM ¹
Breadth . . .			30 mm.
Length . . .			29 mm.
Height . . .			89 mm.

The type specimen has not been seen by the writer, and it is not possible from the drawing to assign the tooth with certainty to any particular species. If the dimensions given in the text of the type description are correct, the tooth may belong to *E. capensis* as suggested by Haughton (1932). Otherwise from the text-figure it resembles *E. kuhni* more closely than *E. capensis*, so that the position (or the validity) of this species is uncertain.

GUIDE TO EQUINE SPECIES.

Incisors.

A. Very broad mandibular symphysis with large, anteriorly flattened first and second incisors and reduced third incisors. (Upper incisors unknown.)

Eurygnathohippus cornelianus v. Hoep.

B. Incisors of the normal (i.e. *Equus caballus**) type possessing the cup or "mark" in the upper jaw but lacking it in the lower jaw.

*Equus burchellii** (Gray).

C. Incisors of the "normal" type with the cup or "mark" present at least in the first and second incisors of both jaws.

? *Equus quagga** Gmelin.

*Equus zebra** Linn.

? *Equus capensis* Broom.

? *Equus kuhni* Broom.

? *Equus fowleri* Wells.

D. Incisors unknown.

Equus harrisi Broom.*Equus plicatus* (v. Hoep.).*Equus sandwithi* Htn.*Equus poweri* Cooke.*Equus broomi* Cooke.*(Equus simplex* v. Hoep.)*Notohipparion namaquense* Htn.*Stylohipparion steytleri* (v. Hoep.).

Upper Cheek Teeth.

A. Protocone isolated; parastyle anteriorly flanged.

Stylohipparion steytleri (v. Hoep.).

(Pm. ? 19-24 mm. M. 18-23 mm.) *

B. Protocone attached.

1. Breadth less than 27 mm.

(a) Ectoloph halves concave; parastyle obliquely flattened anteriorly.

*Equus burchellii** (Gray).

(Pm. 22-26 mm. M. 21-25 mm.)

(b) Ectoloph halves flattened.

*Equus zebra** Linn.

(Pm. 22-27 mm. M. 21-26 mm.)

*Equus quagga** Gmelin.

(Pm. 22-27 mm. M. 21-26 mm.)

2. Breadth greater than 27 mm.

(a) Ectoloph halves concave; parastyle usually flattened.

Equus capensis Broom.

(Pm. 29-35 mm. M. 27-33 mm.)

Equus kuhni Broom.

(Pm. 27-30 mm. M. 26-29 mm.)

Equus broomi Cooke.

(Pm. 28-33 mm. M. 27-32 mm.).

Equus fowleri Wells.

(Pm. 29-33 mm. M. 28-32 mm.)

(b) Ectoloph halves flattened; parastyle prominent.

Some *E. kuhni* premolars.

* These dimensions are range of breadth.

Equus sandwithi Htn.

(Pm. 28-33 mm. M. 26-29 mm.)

Equus poweri Cooke.

(Pm. ? 26-29 mm. M. 25-28 mm.)

C. Position uncertain.

Equus simplex v. Hoep.

D. Upper cheek teeth unknown.

Equus plicatus (v. Hoep.).

Equus harrisi Broom.

Notohipparion namaquense Htn.

Eurygnathohippus cornelianus v. Hoep.

Lower Cheek Teeth.

A. External ectostylid column present.

1. Strong protoconid fold or pillar; metaconid and metastylid strong.

Notohipparion namaquense Htn.

(Pm. 15-16 mm. M. 14-17 mm.)

2. Protoconid fold weak or lacking; metaconid and metastylid small.

Stylohipparion steytleri (v. Hoep.).

(Pm. 11-15 mm. M. 10-13 mm.)

B. No external ectostylid column.

1. Face of parastylid oblique; metaconid and metastylid strong.

Equus sandwithi Htn.

(Pm. 15-18 mm. M. 13-17 mm.)

2. Face of parastylid normal.

- (a) Breadth less than 15 mm.

*Equus zebra** Linn.

(Pm. 12-15 mm. M. 11-14 mm.)

*Equus burchellii** (Gray).

(Pm. 12-15 mm. M. 11-14 mm.)

*Equus quagga** Gmelin.

(Pm. 12-15 mm. M. 11-14 mm.)

(Some molars of *E. plicatus* resemble *E. quagga**.)

- (b) Breadth greater than 15 mm.

Equus harrisi Broom.

(Pm. 17-20 mm. M. 16-19 mm.)

Equus plicatus (v. Hoep.).

(Pm. 15.5–19 mm. M. 14.5–17.5 mm.).

Equus capensis Broom.

(Pm. 18.5–22 mm. M. 17.5–21 mm.)

C. Lower dentitions unknown.

Eurygnathohippus cornelianus v. Hoep.

Equus kuhni Broom.

Equus fowleri Wells.

Equus broomi Cooke.

Equus poweri Cooke.

REFERENCES.

- ALLEN, G. N., 1939. "A Checklist of African Mammals", Bull. Mus. of Compar. Zool. Harvard, vol. lxxxiii, pp. 1–763.
- BECK, R., 1906. "*Mastodon* in the Pleistocene of South Africa", Geol. Mag., Decade V, vol. iii, pp. 49–50.
- BROOM, R., 1909. "On the Evidence of a Large Horse recently Extinct in South Africa", Ann. S. Afr. Mus., vol. vii, pp. 281–282.
- , 1913 a. "Note on *Equus capensis*", Bull. Amer. Mus. Nat. Hist., vol. xxxii, pp. 437–439.
- , 1913 b. "Man Contemporaneous with Extinct Animals", Ann. S. Afr. Mus., vol. xii, pp. 13–16.
- , 1928. "On Some New Mammals from the Diamond Gravels of the Kimberley District", Ann. S. Afr. Mus., vol. xxii, pp. 439–444.
- , 1937. "New Pleistocene Mammals from Limestone Caves of the Transvaal", S. Afr. J. Sci., vol. xxxiii, pp. 750–768.
- BROOM, R., and LE RICHE, H., 1937. "The Dentition of *Equus capensis* Broom", S. Afr. J. Sci., vol. xxxiii, pp. 769–770.
- CHUBB, E. C., 1907. "List of Vertebrate Remains" in "On an African Occurrence of Fossil Mammalia associated with Stone Implements", by F. P. Mennel and E. C. Chubb, Geol. Mag., Decade V, vol. iv, pp. 447–448.
- COOKE, H. B. S., 1939. "On a Collection of Fossil Mammalian Remains from the Vaal River Gravels at Pniel", S. Afr. J. Sci., vol. xxxvi, pp. 412–416.
- , 1941 a. "A Preliminary Account of the Wonderwerk Cave, Kuruman District. Section II.: The Fossil Remains", S. Afr. J. Sci., vol. xxxvii, pp. 303–311.
- , 1941 b. "A Preliminary Survey of the Quaternary Period in Southern Africa", Bur. of Archaeology, Arch., Ser. iv, pp. 1–59.
- , 1943. "Cranial and Dental Characters of the Recent South African Equidae", S. Afr. J. Sci., vol. xl, pp. 254–257.
- (See also WELLS, COOKE and MALAN, 1942; MALAN and COOKE, 1941.)

- DREYER, T. F., in DREYER, T. F., and LYLE, A., 1931. "New Fossil Mammals and Man from South Africa", Dept. Zool. Grey. Univ. College, Bloemfontein.
- FRAAS, E., 1907. "Pleistocene Fauna aus dem Diamantseifen van Süd-Afrika", Zeit. d. Deutsch. geol. Gesell., vol. lix, pp. 232-243.
- GIDLEY, J. W., 1901. "Tooth Characters and Revision of the North American Species of the Genus *Equus*", Bull. Amer. Mus. Nat. Hist., vol. xiv, pp. 91-141.
- GREGORY, W. K., 1934. "A Half-Century of Trituberculy: the Cope-Osborn Theory of Dental Evolution", Proc. Amer. Phil. Soc., vol. lxxiii, No. 4, pp. 169-317.
- HAUGHTON, S. H., 1932. "The Fossil Equidae of South Africa", Ann. S. Afr. Mus., vol. xxviii, pp. 407-427 (February 1932).
- HOPWOOD, A. T., 1926. "Fossil Mammalia" in "Geology and Palaeontology of the Kaise Bone Beds", Occ. Paper No. 2, Geol. Survey of Uganda.
- , 1928. "Mammalia" in Rhodesian Man and Associated Remains, London: British Mus. (Natural History), pp. 70-73.
- LE RICHE, H., 1937. See BROOM, R., 1937.
- LINNAEUS, C., 1758. *Systema Naturae*, 10th Edition.
- LOWE, C. VAN RIET, 1937. See SÖHNGE, VISSER and LOWE, 1937.
- MALAN, B. D., and COOKE, H. B. S., 1941. "A Preliminary Account of the Wonderwerk Cave, Kuruman District", S. Afr. J. Sci., vol. xxxvii, pp. 300-312.
- MALAN, B. D., 1943. See WELLS, L. H., 1943.
- OSBORN, H. F., 1907. *Evolution of Mammalian Molar Teeth*. New York: Macmillan & Co.
- (See also SCOTT and OSBORN, 1890).
- OWEN, R., 1869. "Description of the Cavern of Bruniquet and its Organic Contents. Part II. Equine Remains", Phil. Trans. Roy. Soc. London, vol. clxix, pp. 535-557.
- ROMER, A. S., 1933. *Vertebrate Paleontology*. Chicago: University of Chicago Press.
- SCOTT, W. B., 1907. "Mammalian Remains from the Coast of Zululand", Third and Final Report, Geol. Survey Natal and Zululand, pp. 251-262.
- SCOTT, W. B., and OSBORN, H. F., 1890. "Preliminary Account of the Fossil Mammals from the White River and Loop Fork Formation contained in the Museum of Comparative Zoology. The Perissodactyla", by H. F. Osborn, Bull. Mus. Comp. Zool., vol. xx, No. 3.
- SEELEY, H. G., 1891. "On *Bubalus bainii* (Seeley)", Geol. Mag., vol. viii, pp. 199-201.
- SHAPIRO, M. M. J., 1943. "Fossil Mammalian Remains from Bankies, Kroonstad District, O.F.S.", S. Afr. J. Sci., vol. xxxix, pp. 176-181.
- SHAW, J. C. M., 1938 a. "The Teeth of the South African Fossil Pig (*Notochoerus capensis* syn. *meadowsi*) and their Geological Significance", Trans. Roy. Soc. S. Afr., vol. xxvi, pp. 25-37.
- , 1938 b. "Growth, Changes and Variations in Warthog Third Molars and their Palaeontological Importance", Trans. Roy. Soc. S. Afr., vol. xxvii, pp. 51-94.
- SÖHNGE, P. G., VISSER, D. J. L., and LOWE, C. VAN RIET, 1937. "Geology and Archaeology of the Vaal River Basin", Geol. Mem. 35, Geol. Survey of the Union of S. Afr.
- STIRTON, R. A., 1941. "Development of Characters in Horse Teeth and the Dental Nomenclature", Journ. of Mammalogy, vol. xxii, pp. 434-446.

- VAN HOEPEN, E. C. N., 1930 *a.* "Vrystaatse Fossiele Perde", *Pal. Nav. Nas. Mus. Bloemfontein*, II, pp. 1-11.
- , 1930 *b.* "Fossiele Perde van Cornelia, O.V.S.", *Pal. Nav. Nas. Mus. Bloemfontein*, II, pp. 13-24.
- , 1932. "Die Stamlyn van die Sebras", *Pal. Nav. Nas. Mus. Bloemfontein*, II, pp. 25-37 (September 1932).
- , 1940. "Oor die tande van die Equinae: 1. Die snytande van die Onderkaak", *Tydskrif vir Wetenskap en Kuns*, vol. i, pp. 101-114.
- VISSER, D. J. L., 1937. See SÖHNGE, P. G., 1937.
- WELLS, L. H., 1941. "A Fossil Horse from Koffiefontein, O.F.S.", *Trans. Roy. Soc. S. Afr.*, vol. xxviii, pp. 301-306, pl. lv.
- WELLS, L. H., COOKE, H. B. S., and MALAN, B. D., 1942. "The Associated Fauna and Culture of the Vlakkraal Thermal Springs, O.F.S.", *Trans. Roy. Soc. S. Afr.*, vol. xxix, pp. 203-233.
- WELLS, L. H., and MALAN, B. D., 1943. "A Further Report on the Wonderwerk Cave, Kuruman. Section I: Archaeology, by B. D. Malan. Section II: Fauna, by L. H. Wells", *S. Afr. J. Sci.*, vol. xl, pp. 258-270.
- ZITTEL, K. A. VON, 1925. *Text-book of Palaeontology*. Vol. III. "Mammalia", ed. by Sir A. Smith Woodward. London: Macmillan & Co.

APPENDIX

(With Fig. 31.)

In the five years which have elapsed since this account of the Perissodactyla was written, certain additional information has come to light which, while it does not involve any important alteration of the views already expressed, nevertheless requires to be added in order to bring the work reasonably up to date.

Firstly, the description of the fossil mammals of the Vaal River deposits, mentioned in the Introduction to the present account, has appeared as Memoir 35 (III) of the Geological Survey of the Union of South Africa and it contains a certain amount of stratigraphic information on the distribution of the Equidae in those deposits (Cooke, 1949 *b*). In addition, revisions of the Suina (Cooke, 1949 *a*) and of the Proboscidea (Cooke, 1947) have been published as companion studies to the present one.

Secondly, a perissodactyl family new to this region has been recorded through the discovery of an undoubted Chalicotherium in the cave breccia of the Makapan valley (George, 1950). The type is a left upper second molar and there are also a number of other cheek teeth and an ungual phalanx. The type molar and the phalanx are illustrated here (fig. 31). Chalicotherium remains have previously been reported from the Kaiso beds of Uganda (Andrews, 1923) and from south Serengeti in Tanganyika (Dietrich, 1942), but the Makapan specimens appear distinct and were described as a new species tentatively placed in *Metaschizotherium* as *M. transvaalensis*. The resemblance to the Tanganyika species *M. hennigi* is fairly close and it is considered by Miss George that both species certainly belong to the same genus, whether or not this is really *Metaschizotherium*.

Thirdly, a new species of fossil equine has been erected by Broom (1948) based on material from a cave breccia in the Sterkfontein area about half a mile south-west of the site known as "Bolt's workings". The type of this species, *Equus zietsmani*, comprises an imperfect lower jaw with the incisors, most of the cheek teeth of the right side and some of those of the left side, and part of the left maxilla. The lower series from P_2 to M_2 can be well reconstructed and is figured by

Broom, as also is the damaged upper series from P^4 to M^3 (the latter tooth being a mere fragment). The lower series agrees very well with that shown in fig. 24 of the present text and referred to *E. harrisi*. The upper series resembles that illustrated in fig. 23, which was referred to *E. kuhni*, and also shows features suggestive of *E. fowleri*. In view of these resemblances and especially as the teeth shown in figs. 23 and 24 were also from the Sterkfontein group of breccias, it is likely that only a single species is represented by the three lots of specimens. It remains to be considered what that species is.

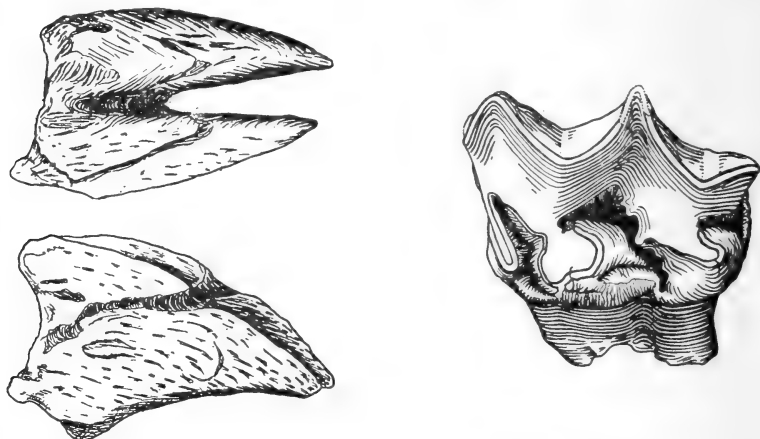


FIG. 31.—*Metaschizotherium* (?) *transvaalensis* George.

Top left: Anterior view of ungual phalanx.

Lower left: Side view of ungual phalanx.

Right: Crown view of type left upper second molar.

All natural size. (From George.)

It has already been suggested in the present revision (p. 464) that *Equus fowleri* and *E. kuhni* may be synonyms and that the corresponding lower dentitions may be represented by *E. plicatus* and *E. harrisi*. This idea lacked confirmation due to the absence of associated upper and lower dentitions but Broom's new material goes a long way towards correcting this deficiency and greatly strengthens the probability that all five species are identical. It may now be considered that *E. fowleri*, *E. plicatus*, *E. harrisi* and *E. zietsmani* are synonyms of *Equus kuhni*.

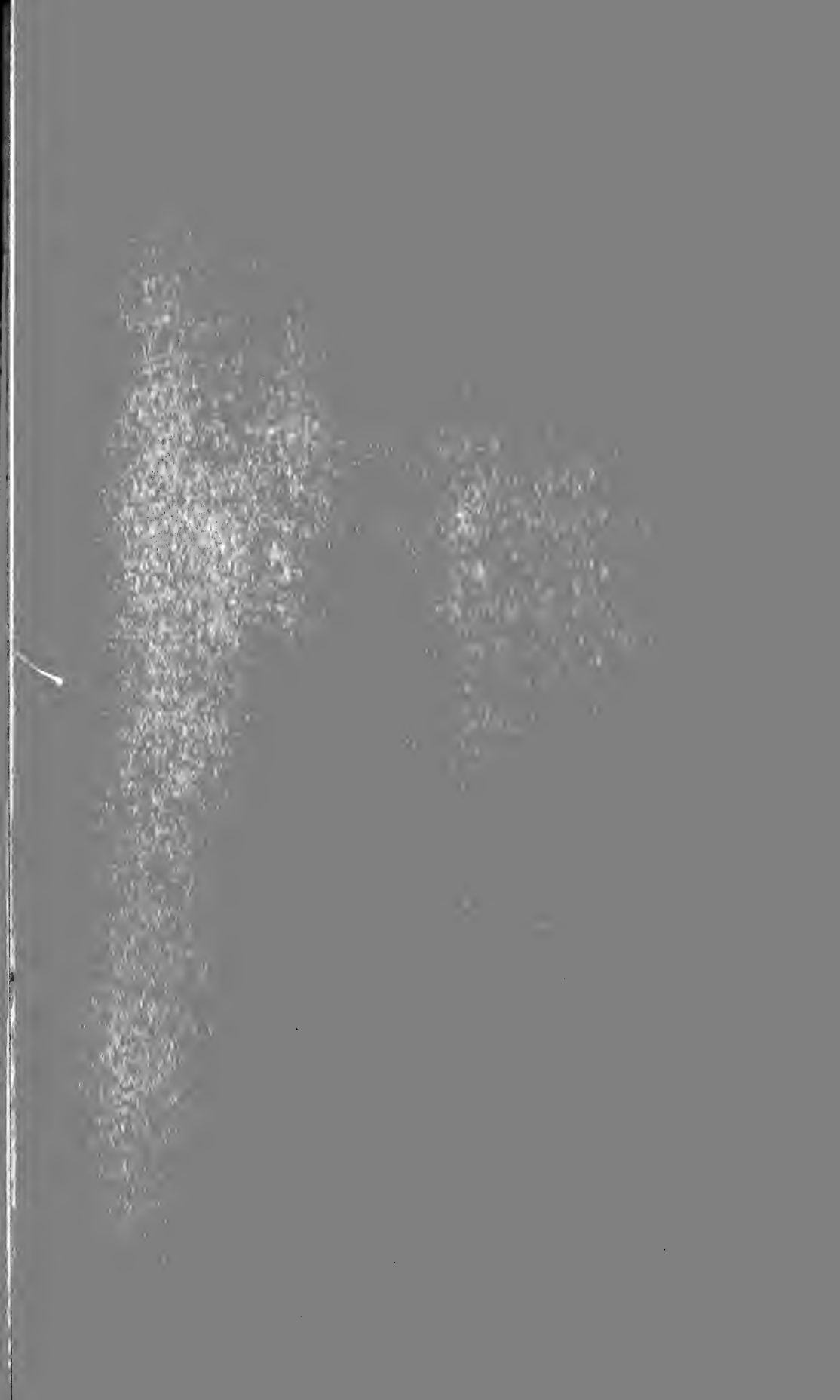
Some additional confirmation of the above conclusion can be obtained from a study of the dental characters of the living Grevy's

Zebra of East Africa. It was suggested to the writer by Dr. L. S. B. Leakey that the South African *Equus kuhni* was, in fact, *Equus grevyi*. Through the courtesy of Dr. Leakey the writer had the opportunity, while in East Africa, of studying a small collection of Grevy skulls and it is clear that there is a close resemblance between the teeth of the living animal and the fossil material referred to *E. kuhni*. Individual teeth, but not whole dentitions, exhibited characters recalling *E. fowleri*, *E. plicatus* and *E. harrisi* and the suggested identity of the four fossil species thus receives a measure of confirmation. There can be no doubt that the fossil *E. kuhni* (and its presumed synonyms) is closely related to *E. grevyi* and the relatively small differences which have been noted could be dismissed as due to individual variation. For the present, however, it is felt that it will be better to retain the designation *E. kuhni* for the fossil material until additional skeletal material is available to support the absorption of *E. kuhni* into *E. grevyi*.

REFERENCES.

- ANDREWS, C. W., 1923. In *Nature*, 10th November 1923.
BROOM, R., 1948. "Some South African Pliocene and Pleistocene Mammals",
Ann. Tvl. Mus., vol. xxi, pp. 23-25.
COOKE, H. B. S., 1947. "Variation in third molars of the living African Elephant
and a Critical Revision of the Fossil Proboscidea of Southern Africa", Amer.
J. Sci., vol. ccxlv, pp. 434-457, 492-517.
—, 1949 a. "The Fossil Suina of South Africa", Trans. Roy. Soc. S. Afr.,
vol. xxxii, pp. 1-44.
—, 1949 b. "Fossil Mammals of the Vaal River Deposits", Geol. Mem. 35 (III),
Geol. Survey of the Union of S. Afr., pp. 1-109.
DIETRICH, W. O., 1942. In *Palaeontographica*, Band xciv, Abt. A, 94.
GEORGE, M., 1950. "A Chalicotherium from the Limeworks Quarry of the Makapan
Valley, Potgietersrust District", S. Afr. J. Sci., vol. xlvi, pp. 241-242.





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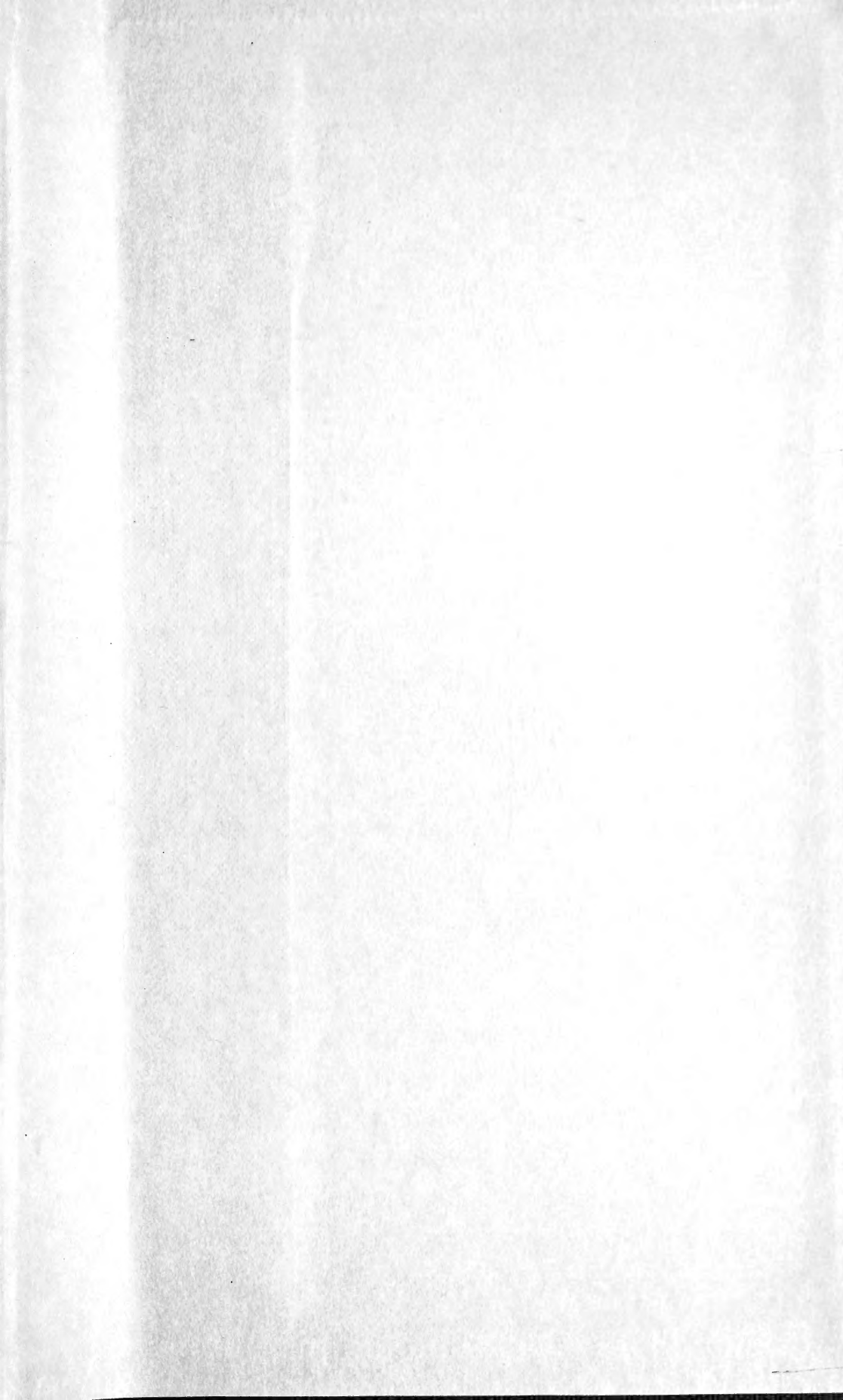
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