

---

---

*The Skeleton of Moschops Capensis Broom, a Dinocephalian  
Reptile from the Permian of South Africa*

BY WILLIAM K. GREGORY

---

BULLETIN

OF

THE AMERICAN MUSEUM OF NATURAL HISTORY

VOL. LVI, ART. III, pp. 179-251

*New York*

*Issued July 14, 1926*

---

---



**Article III.—THE SKELETON OF *MOSCHOPS CAPENSIS*  
BROOM, A DINOCEPHALIAN REPTILE FROM THE  
PERMIAN OF SOUTH AFRICA**

BY WILLIAM K. GREGORY

DEDICATED TO THE MEMORY OF SAMUEL WENDELL WILLISTON

PLATES I-XXI; 29 TEXT FIGURES

CONTENTS

	PAGE
INTRODUCTION.....	181
THE SKELETON IN RELATION TO THE HABITS OF <i>Moschops</i> .....	182
VERTEBRÆ.....	188
Vertebral Formula.....	188
Atlas-axis.....	189
Cervicals.....	191
Thoracic Vertebræ.....	191
Sacrales.....	193
Caudals.....	193
RIBS.....	193
PECTORAL GIRDLE AND LIMB.....	196
Scapula.....	196
Coracoid and Precoracoid.....	201
Interclavicle.....	203
Clavicle and Cleithrum.....	203
Teleology.....	203
Origin and Evolution of the Pectoral Girdle.....	205
Structural and Taxonomic Characters of the Pectoral Girdle.....	206
Humerus.....	208
Teleology and Evolution of the Humerus.....	208
Radius and Ulna.....	209
Teleology and Evolution of the Lower Arm.....	211
PELVIC GIRDLE AND LIMB.....	211
Ilium.....	213
Pubis.....	213
Ischium.....	215
Evolution of the Pelvis.....	215
Systematic Characters of the Pelvis.....	217
Femur.....	217
Systematic Characters of the Femur.....	219
Tibia.....	219
Fibula.....	221
MANUS AND PES.....	222
Digits.....	224

	PAGE
SYSTEMATIC RELATIONS OF <i>Moschops</i> AND THE EVOLUTION OF THE SKULL IN THE TAPINOCEPHALIDÆ.....	225
Mechanism of the Jaws and the Origin of the Group.....	225
Growth Changes and Evolution of the Skull.....	227
<i>Moschops</i> and <i>Delphinognathus</i> .....	228
<i>Prigalion</i> .....	230
<i>Lamiasauvus</i> .....	230
Dentition of the Moschopinæ.....	232
<i>Taurops</i> .....	235
<i>Eccasaurus</i> .....	235
<i>Tapinocephalus</i> .....	235
<i>Mormosaurus</i> .....	237
<i>Struthiocephalus</i> .....	240
RÉSUMÉ OF THE SYSTEMATIC RELATIONSHIPS OF <i>Moschops</i> .....	241
Moschosaurinæ.....	241
Moschopinæ.....	241
Tapinocephalinæ.....	241
SUMMARY AND ANALYSIS OF SKELETAL CHARACTERS.....	242
1. Primitive Reptilian Heritage.....	242
2. Comparison with the Pelycosauria.....	243
3. Comparison with the Pareiasauria.....	245
4. Origin of the Dinocephalia from the Gorgonopsian Stem.....	246
5. Comparison with the Dromasauria, etc.....	248
CONCLUSIONS.....	249
LITERATURE CITED.....	250

## INTRODUCTION

In 1910, Dr. Robert Broom brought to The American Museum of Natural History from the Karroo System of South Africa a collection of fossil reptiles, which included, among other valuable specimens, the type and topotypes of *Moschops capensis* Broom (1911, p. 1073). The *Moschops* material was discovered by Doctor Broom himself and by the Reverend J. H. Whaits on the farm of Spitzkop in Moordenaars Karroo, north of Laingsburg, South Africa. The geological horizon was somewhat doubtful but was regarded as "not improbably Upper Ecca Series." "No other determinable remains," Doctor Broom said, "have been discovered in the neighborhood, and it seems probable that were it in the *Pariasaurus* zone some remains of *Pariasaurus* would occur." Another reason he had for assigning the *Moschops* remains to the Ecca formation was that he had previously found there a single *Moschops*-like tooth (Pl. XIX, B), which he had provisionally referred to *Eccasaurus priscus*. The Ecca formation is regarded as of Lower Permian age. On the other hand, both Watson (1914b) and Haughton (1919, p. 12) include *Moschops* in the overlying *Pareiasaurus* (or *Tapinocephalus*) zone of Middle Permian age, which is the zone that has yielded other dinocephalians nearly allied to or identical with *Moschops*.

The type of *Moschops capensis* Broom (Fig. 22B), consisted of a nearly complete skull (A. M. N. H. No. 5550), with a mandible (Pl. XVII, A) which possibly belongs to the same individual, both of which were figured in the type description (Broom, 1911). The topotypes (A. M. N. H. Nos. 5551-5557) include the remains of at least seven or eight skeletons, all apparently belonging to the same species and found within an area of about a rood. As the skulls differ mainly in the degree of thickening of the bones around the temporal fossæ, while the limb bones and girdles differ only in size, Doctor Broom concluded that "the differences are due to age and sex, the larger, thick-skulled forms being males, the more slender skulls females."

During his stay at the Museum, Doctor Broom supervised the cleaning up and preparation of this material by the late Charles Falkenbach, who continued the work of restoring the often fragmentary bones after Doctor Broom's departure. Broom and Falkenbach sorted out from the *Moschops* material three incomplete skeletons, provisionally called A, B and C, according to size. These specimens bore the field numbers 1906A, B, C, and they now bear the catalogue numbers 5551 (=A), 5552 (=B), 5553 (=C).

Mr. Falkenbach's untimely death interrupted the work on the *Moschops* material for several years, until in 1917 Curator Matthew requested me to supervise the mounting of one of the skeletons. In the meantime I had been pursuing studies on the locomotor apparatus of reptiles (1918), which seemed prerequisite for the understanding of the peculiar skeleton of *Moschops*. In 1919, Mr. Charles Christman examined minutely the whole lot of scattered and broken loose bones from the *Moschops* quarry and secured some valuable additional data concerning the ribs and foot bones. After we had critically revised the reconstruction work of our predecessors, the mounting of the middle-sized skeleton (B) was taken up and completed by Mr. Charles Lang. The bones proved very difficult to assemble in a lifelike pose, and the final mount was the result of a long series of trials and corrections. Doctor Matthew frequently examined and discussed our work with us, and Professor Osborn gave us encouragement and helpful criticism.

The mounted skeleton of *Moschops* is a visible token of Doctor Broom's signal contributions to South African palæontology and of his generosity and active friendship for this museum.

The chief objects of the present paper are:

- (1) To describe briefly the *Moschops* skeleton.
- (2) To give our main evidence for reconstructing and mounting the skeleton in the form here illustrated in Plates I, II, VI, VIII, IX.
- (3) To determine, if possible, the systematic status of *Moschops*.
- (4) To determine, if possible, the relationships of various allied genera.
- (5) To summarize the relations of the dinocephalian group to other Permian reptiles.

Great interest in our *Moschops* material was shown by the late Professor Williston, who expressed the hope that it would be fully described. To his revered and inspiring memory this paper is humbly dedicated.

#### THE SKELETON IN RELATION TO THE HABITS OF *MOSCHOPS*

The skeleton as mounted (Pls. I, VI, VIII, IX) represents a massive animal not unlike a walrus in general outline, except that the huge body is carried well raised from the ground by the powerful limbs (Pl. XXI). The beast is shown striding vigorously forward with its small but heavy head lifted above the level of its immense thorax. The vertebral column slopes downward and backward from the head toward the relatively small hind quarters and short tail.

The head is short, and broad across the orbits, which are surmounted by thick and swollen rims of rough bone. The whole cranium is very thick and massive.<sup>1</sup> The occiput is both wide and vertically deep, affording a firm platform for the insertion of the heavy neck muscles. Thus the head is deep posteriorly, but it narrows anteriorly along the dorsal border, widening below toward the broad mouth. The vertically deep temporal fossæ, together with the remarkably stout postorbital and zygomatic arches, doubtless afforded an adequate base for the very powerful temporal muscles. The pterygoid arches, on the under side of the skull, were also very heavy, as well as the angular region of the jaw, so that the pterygoid muscles must have been unusually powerful.

The strong jaw muscles were evidently needed to give effective biting power to the stout and long-crowned teeth, which were arranged in a single series along the margins of the jaws, the teeth longest and heaviest in front, thence grading down in the rear into small teeth with compressed crowns.

In several kinds of extinct reptiles which are supposed to have fed on shelled invertebrates, there are heavy round-topped teeth on the roof of the mouth and on the inner sides of the jaw, but in *Moschops* the form of the dentition is so different that such a diet appears improbable. The teeth near the front of its mouth have a high conical tip and oval base; the crown is long and heavily enameled down to the widely open root. The more posterior teeth, as already stated, are laterally compressed but never have shearing crowns. Thus the characters of the dentition do not indicate a carnivorous diet, but, taken in connection with the great size of the thorax, suggest rather that the animal fed upon great quantities of some relatively tough and innutritious objects, such as cycad stems, which were torn away from their bases by means of the powerful jaw and neck muscles, and then were pierced and broken open by the strong front teeth, the smaller pieces being cut by the compressed rear teeth.

Such a relatively innutritious and presumably vegetable diet requires prolonged activity to supply food enough for the huge body, and so we find the powerful locomotor apparatus well fitted to carry the animal about while feeding. While retaining many skeletal features from the primitive stem reptiles that crawled upon their bellies, *Moschops*, in common with all other therapsids, was already well started on the

---

<sup>1</sup>Nopcsa (1923, p. 50) suggests that the great thickening of the skull bones and other parts was correlated with the enlargement of the pituitary gland, indicated by the enlarged sella turcica in the skull.

road that led to the mammalian type of skeleton, in which a more sustained and effective mode of propulsion was finally attained.

Among the features inherited from the primitive pelycosaurian ancestors were the following:

(1) The primitive dermal pectoral girdle was nearly complete, including vestigial cleithra, large clavicles and a very large interclavicle.

(2) The scapulocoracoid arch consisted of a high scapula and a broad precoracoid, the latter perforated by a large foramen for the supra-coracoid nerve and connected with the true coracoid by a well-defined suture.

(3) In the pelvic girdle and limb, the pubo-ischiadic plate, the tibia and fibula and the proximal tarsals all retained much of their primitive character.

Along with these primitive features of the limbs were many others which indicate that the body could be held well above the ground and the limbs be moved in a manner approaching that of the mammalian limbs. Thus in the fore limb the detailed construction of the humerus shows that *Moschops* could both open out the elbow joint more widely and bring it nearer to the midline in the back-swing than was possible for the primitive crawling reptiles. The enormous pectoral girdle and massive fore limb, with the prominent olecranon of the ulna, indicate great power in lifting the body. Similarly in the hind limb the pelvis approached the primitive mammalian type in the subcircular outline of the acetabulum; in the anteroposterior shortening of the pubis, in the forward growth of the ilium, etc., while the femur was beginning to take on mammalian features in the loss of the primitive trochanteric process on the under side, these and other details indicating that the anteroposterior movements of the femur were gaining in importance as compared with those of adduction, abduction and rotation, which predominated in the crawling ancestors.

The digits of *Moschops* were very short and almost tortoise-like, implying a subdigitigrade posture of the extremities.

The pelvis shows some curious points of remote resemblance to those of modern pinnipeds, as noted by Seeley (1888) in the case of *Phocosaurus*, especially in the anteroposterior shortening of the pubis and ischium and in the anteroposterior extension of the ilium. The pelvis flares outward anteriorly, while the postpelvic region diminishes rapidly in width, so that probably the animal could rest on its massive belly with both hind limbs directed backward after the fashion of a seal.

In considering the probable life habits of the pareiasaurians and the dinocephalians, Haughton (1919, p. 13) states that whenever the bones of the former are found in situ they almost invariably represent nearly complete skeletons, and from this and from the anatomical evidence he concludes that the animals were powerful diggers, that they were herbivorous and that they died where they were found and were covered up with fine mud or silt with sufficient rapidity to insure the preservation of the bones. In the case of the dinocephalians, however, he states that in most cases isolated skulls or isolated portions of the postcranial skeleton occur—sometimes in mudstone and sometimes in sandstone,—that in several cases large portions of skeletons have been found, but they have consisted of disarticulated bones lying scattered over a fairly small area, as if the corpse of the animal had been dismembered and the portions dragged about by beasts of prey. In only a single instance known to him an almost complete skeleton (the type of *Struthiocephalus whaitsi*) was found lying slightly on one side with the head and lower jaw detached from the body. His general conclusion is (p. 14): "There can be little doubt that these animals were land-dwellers and walkers, slow-moving normally on account of their heavy bodies, but capable of raising themselves for the purpose of a rapid dash. The discovery of the complete skeleton of *Struthiocephalus* shows that animal to have died a natural death on some mud-flat. The occurrence of isolated skulls and bones indicates the disarticulation of bodies and the subsequent removal of portions by the action of running water; while the unearthing of almost whole skeletons in a localized patch but with the bones disarticulated, points to cannibalistic feasts on the part of carnivorous forms" [such as the giant titanosaurs or the larger theropods].

Watson (1914c, p. 762) notes as very exceptional the occurrence of parts of a dinocephalian skull in a blue limestone, associated with lamellibranchs.

A review of the chief structural features which seem to be in harmony with the suggestion that *Moschops* and other dinocephalians were more or less fluviatile animals may now be given.

(1) The limbs with their spreading hands and feet and wide fore-and-aft reach would appear to be fairly well adapted for propelling the massive body through the water.

(2) The comparatively slight regional differentiation of the presacral vertebrae, the relatively small size of the neural spines and the immense size of the thorax, as well as the thick cartilaginous epiphyses on the

carpals, tarsals and long bones, rather suggest the conditions in heavy-bodied, semiaquatic reptiles.

(3) The great weight of the head and the massive, bufferlike forehead would seem to be an advantage in an animal that may have dived after its food like a walrus or a manatee.

The function of the pineal eye in relation to the habits is still unknown, but must have been important, on account of the relatively huge size of this structure in dinocephalians. It leads downward through a great vertical passage to the braincase and is much larger than the pineal opening of anomodonts. In *Moschops* (Pl. XV, A) and allied genera it is set at the summit of a protruding eminence or boss on the top of the head—a sort of cyclopean periscope.

Pineal openings in the skull top are found in a great variety of primitive vertebrates, ranging from *Osteolepis* of the rhipidistian crossopterygians, through the varied Amphibia and cotylosaurs, pelycosaurs, therapsids, lizards, *Sphenodon* and others. Thus the primitive function of this organ must have been more or less independent of any particular food habits. Although degenerate and perhaps almost functionless in the modern *Sphenodon* and the lizards, the organ is well known to have the general structure of an eye. Possibly this median eye may have functioned as a phototropic organ. For semiaquatic, diving animals a dorsally-projecting median eye might possibly assist the animal in orienting itself with reference to the surface. In this connection it is noteworthy that the gigantic *Titanosuchus*, which was related to *Moschops*, had a huge skull more or less crocodile-like in general form, with a large central pineal boss.

A rather similar combination of characters is seen on a smaller scale in the very aberrant American pelycosaur (?) *Casea* of Williston. This animal, although of small size, also has a comparatively massive skull with an unusually large pineal opening and large teeth in the front part of both the upper and lower jaws, the lateral teeth diminishing rapidly in size. It also has excessively long dichoccephalous ribs and a swelling thorax. It was regarded by Williston as an "invertebrate feeder."

The general form of the body of *Moschops* shows a certain degree of resemblance to that of the pareiasaurs, which were its contemporaries, but the differences are numerous and fundamental throughout the skeleton. The vertebræ and ribs are widely different; the humerus and femur indicate somewhat dissimilar movements of the limbs, those of *Moschops* being on the whole more mammal-like. The skull-form and dentition contrast in many features with the pareiasaurs, and there is no

reason for supposing that either the food habits or the methods of locomotion were very similar.

In general, *Moschops* gives the appearance of being an aggressive animal, capable of inflicting severe bites and able to take long, quick strides in a sudden lunge toward an adversary. It was probably herbivorous and may have been of littoral, semiaquatic habits (Pl. XXI). Its principal enemies may have been first its relatives the titanosaurs, and secondly, some of the larger therocephalians, certain of which, according to Haughton (1919, p. 14), were as big as a lion.

TABLE I.—SKELETAL MEASUREMENTS OF *Moschops capensis*

Measurements in Meters	Mounted		
	Skeleton 5552 (B),	5553 (C),	5551 (A)
From tip of pmx. to posterior tip of ilium, as mounted.....	1.867	....	....
Length of skull, pmx. to cond.....	....	.323+	.320
Length of vert. column along curve, as mounted..	2.420	....	....
Height at withers, as mounted.....	1.078	....	....
Right scapulocoracoid, length.....	.610	.638 <sup>1</sup>	.545 <sup>1</sup>
Right scapula, top of glenoid to suprascapular border.....	.418	.490	.365
Left scapula, top of glenoid to suprascapular border.....	.465	....	....
Interclavicle, length.....	.485	....	.453 <sup>1</sup>
Left clavicle, length.....	....	....	.308
Right humerus, length.....	.365	.390	.345
Left " " " ".....	....	.390	....
Right humerus, distal breadth.....	.180	.193	....
Left " " " ".....	....	.210	....
Right ulna, length.....	....	....	.248
Left " " " ".....	.275	....	.237
Right radius, length.....	....	.192	.167
Left " " " ".....	.190	.190	.163
Left ilium, length.....	.279	....	....
Right femur, length (axis).....	.330	.347	.310
Left " " " ".....	.352	.370	.310
Right tibia, length.....	.185	.195	.180
Left " " " ".....	.195	....	....
Right fibula, length.....	.200	.200	.190
Left " " " ".....	.185	....	.190

<sup>1</sup>Estimated.

## VERTEBRÆ

Although the skeletons of *Moschops* were found scattered about in confusion, it proved possible for Doctor Broom and Mr. Falkenbach, after the material was cleaned up, to sort it into three chief skeletons of markedly different size, which were called respectively A, B and C. These three, together with that of *Moschognathus whaitsi*, leave little doubt as to the chief characters of the vertebral column in the subfamily Moschopinæ.

VERTEBRAL FORMULA.—Skeleton *Moschops* A (A. M. N. H. No. 5551), the smallest of the three, has a good series of vertebræ. These harmonize with each other in appearance, color and size, and grade from one to the other so well that they have every appearance of being associated both with each other and with the smallest and best preserved skull (A). Of the presacral vertebræ this series includes Nos. 1-3, 6 (?), 7-26 inclusive, 28 (?), 29 (?). Three sacrals and caudal 1 are also represented. The mounted skeleton (B) has a connected series of the first ten vertebræ, which are distinctly larger than those of skeleton A; some fourteen other presacral vertebræ, by reason of their size and other considerations, have been mounted with this series, the missing vertebræ being modeled from those of *Moschops* A; the sacrals also are largely restored from A, but caudals 1, 2, 3, 5 and 6 are present.

With regard to the number of cervicals, it is not known which rib was the first to articulate with the sternum; it may have been either the seventh, the eighth or the ninth. In the type of *Moschognathus* (Pl. VII), the sixth rib surely did not so articulate, as it ends below in a point. The sixth vertebra also is the last to have the diapophysial wall extended ventrad toward the centrum, and it is also at the junction of the opposite curvatures of the neck and back. The fact is that the passage from the cervicals to the dorsals was gradual. The eighth neural spine was markedly longer than the seventh, and the diapophysis of this vertebra is definitely of the dorsal type. We may assign, therefore, to *Moschognathus* from six to seven cervical vertebræ.

Doctor Broom restored the vertebral column of *Moschops* as having 28 presacral vertebræ, but a comparison of series A with those of *Moschognathus whaitsi* seems to indicate that the third presacral (No. 27) is not preserved in the *Moschops* specimens and that the total number of presacrals should be 29 (see below, p. 192). There were three sacrals and an unknown number of caudals, so that the vertebral formula may provisionally be written as C 6-7, D L 21-22, S 3, Cd. ?.

The comparison of this formula with those of other therapsids is as follows:

	Presacrals	Sacrals
<i>Moschops</i> and <i>Moschognathus</i>	29	3
<i>Galechirus</i> (Broom)	28	..
<i>Endothiodon</i> (Broom)	28	..
<i>Cynognathus</i>	28	4

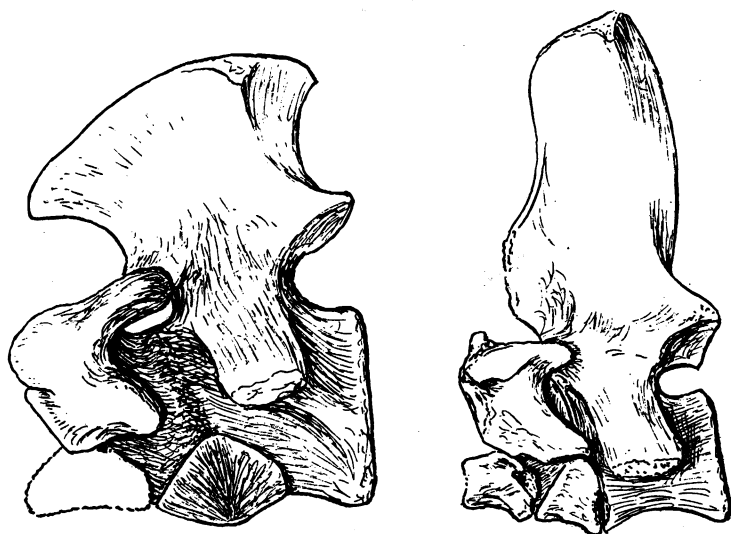


Fig. 1. Atlas-axis complex of *Moschops capensis* and of *Dimetrodon* sp. Both reduced. After Broom, 1914.

Possibly the extra presacral of *Moschops* may have arisen through the spreading apart of the ilia and the setting free of the first sacral ribs.

ATLAS-AXIS.—As Broom has shown (1914a), the atlas-axis complex is of the temnospondyl type characteristic of Permian and other primitive reptiles. The body of the atlas (Fig. 1) consists of a large, vertically deep pleurocentrum, which is suturally united with the body of the axis after the fashion of a mammalian odontoid process. Anteriorly it



Fig. 2 *Moschognathus whaiti* Broom. Cervicals 1-5 of type skeleton, A. M. N. H. 5602.  $\times \frac{1}{2}$ .

bears four facets, the whole forming a convex protuberance. The dorsal pair of convexities articulate with the neural arches of the atlas; the central eminence articulates with the occipital condyle, and the lower sublunate convexity, which is separated on each side by a notch from the upper part, articulates with the enlarged intercentrum of the atlas. The opposite neural arches of the atlas are separated in the midline. Each half consists first of an anteroposteriorly elongate dorsal wing arching over the neural canal and articulating posteriorly with the prezygapophyses of the axis; secondly, of a stout ventral part articulating posteriorly with the odontoid, inferiorly with the large intercentrum of the atlas, and anteriorly with the occipital condyle. Laterally the neural arch of the atlas bears a strong downward and backwardly projecting diapophysis for articulation with the first rib. The construction of the atlas permits some rotation of the head around the vertebral column, and also slight lateral and dorsoventral movements. The pro-atlas is not preserved. The intercentrum between the atlas and axis is unusually large.

**CERVICALS.**—In *Moschognathus* (Fig. 2) there is a marked upward curve in the neck, as the anterior faces of the centra of C 4, 3, 2 are decidedly higher than the posterior ones; there is also more or less tendency toward the opisthocelous condition. In *Moschops* (Pl. II) the neck was also curved upward, but perhaps not quite so sharply. The cervical vertebræ were also shorter than those of *Moschognathus*, especially the axis.

The diapophyses of the cervicals are directed downward, so that the ribs are attached low down on the centra, much below the plane of the zygapophyses. As we pass backward to the fifth, sixth and seventh vertebræ, the tips of the diapophyses, bearing the rib attachments, shift dorsad to about the level of the zygapophyses. The facets for the tubercles of the ribs likewise shift from the lower side of the cervical vertebræ to the base of the neural arch of the lumbar vertebræ.

**THORACIC VERTEBRÆ.**—In *Moschops* A (Pl. III), *Moschops* B (Pl. II) and *Moschognathus* (Pl. VII), the vertebræ diminish in size as we pass backward toward the pelvis, this condition being in harmony with the great size of the pectoral as compared with the pelvic region.

Apart from the atlas-axis complex (see above), the vertebræ are holospondylous, with no observed intercentra. They have large centra, anteroposteriorly short and transversely wide, the dorsal centra having flattened anterior and posterior faces (amphiplatyan). The centra are not pierced by the notochord, at least in adults. The neural arches are

suturally united with the vertebræ (Pls. III, V); their spines are not large and behind the fourth cervical are simple and but slightly differentiated from each other. Those of numbers 7, 8, 9 are short and stout, while in *Moschognathus* (Pl. VII) they are much higher. The spines of the dorsals are also lower than those of *Moschognathus*.

In connection with the dichcephalous characters of the ribs, the dorsal vertebræ have high, prominent diapophyses, buttressed below for the tubercles, and more or less prominent facets on the anterior margin of the centrum, for the heads of the ribs. The larger postzygapophyses of the dorsals face obliquely outward and permit considerable oblique dorsoventral slipping and some lateral movement.

The dorsals grade back into the lumbar region, in which the distance across the diapophyses diminishes rapidly, the greatest interzygapophysial diameter being in the mid-dorsal region. As indicated in Plate VI, the space lateral to the neural arches and dorsal to the zygapophyses affords a broad channel for the axial muscles running to the occiput; this channel becomes narrower as it approaches the sacrum.

The vertebræ immediately in front of the sacrum (Pl. VII) have very short wide flat centra with high and vertically deep diapophyses.

The well-preserved twenty-sixth vertebra of *Moschops* A (Pl. III, C) has very short diapophyses, a low neural spine, and a large facet for the capitulum at the junction of the neural spine with the centrum. The centrum is slightly convex anteriorly, with a slight indication of the remains of the notochordal tunnel. The posterior face is flatter.

Doctor Broom provisionally assigned 28 as the number of presacral vertebræ, but in *Moschops* skeleton A, in which the series is unusually complete, the twenty-sixth vertebra has the centrum very much narrower than that which was identified as the twenty-seventh, and it seems that there is probably a vertebra missing at this point. The one formerly identified as the twenty-seventh, but which I should regard as more probably the twenty-eighth, is well preserved in *Moschops* A and in *Moschognathus* (Pl. VII). The centrum is short anteroposteriorly and very wide transversely. The diapophysial wall is closely united by suture with the rib, in which the head is not separated from the tubercle. The neural spine is very short, low and stout.

In *Moschognathus* the vertebra now identified as the twenty-eighth is shorter anteroposteriorly than in *Moschops*. The centrum is very wide.

The vertebra formerly identified as the twenty-eighth, but which is more probably the twenty-ninth, has a short and transversely wide centrum. The diapophysis is very low and thick, and the greatly enlarged

head of the rib is closely appressed to the side of the centrum and to the diapophysis. The posterior face of the centrum is very wide, flattened above and concavo-convex. Laterally it bears very large flattened facets for the first sacral ribs, which also articulate above these facets with the posterior apices of the first presacral ribs. The neural arch is not preserved in *Moschops* A, but is probably low. The large prezygapophysial facet is strongly convex. In *Moschognathus* (Pl. VII) the corresponding vertebra is greatly shortened anteroposteriorly, and the spine is relatively high.

**SACRALS.**—The sacral vertebræ are preserved in *Moschops* A, C (Fig. 15), and in *Moschognathus*. There are three vertebræ, which are closely appressed and suturally united, and which functioned as sacrals. Of these the first corresponds to the single sacral vertebra of primitive Amphibia; it bears a greatly expanded sacral rib, and consequently has a wide, low diapophysis, articulating with the tubercle, and a wide centrum, articulating by a wide lateral facet with the capitulum. The prezygapophysis was comparatively small and convex and the neural arch very low.

The second and third centra are of similar character, differing in the much smaller facets for the sacral ribs and in the marked backward extension of the postzygapophyses.

**CAUDALS.**—To judge from the comparatively large size of the posterior sacrals and anterior caudals, the tail was not excessively short but of moderate length.

### RIBS

The ribs (Pl. VII) throughout are dichcephalous, but mostly with a thin web of bone joining the tubercle and head. Free ribs were present on all the vertebræ from the atlas to the anterior caudals, inclusive. The large tubercle in all cases articulated with the triangular distal facet of the stout zygapophyses. The more or less elongate head articulated with the anterior part of the centrum, at first low down near the base of the centrum, but gradually rising to near the anterior border of the centrum in the posterior dorsals and lumbar.

The extreme width of the proximal fork between the head and the tubercle increases as we pass backward from the anterior cervicals to the mid-dorsals, and then decreases toward the lumbar region, as shown in the following measurements of the type of *Moschognathus whaitsi*:

## PROXIMAL FORK, TUBERCLE TO HEAD

No. 5—.057M.	No. 13—.085
6—.068 (est.).	15—.090
7—.074 "	20—.069
12—.093	29—.054

A great number of fragments of ribs were found with the *Moschops* skeleton, but even after Mr. Christman's painstaking labors none of them was sufficiently complete to give the length. This deficiency was fortunately supplied by the skeleton of *Moschognathus whaitsi*, which is closely allied to *Moschops* and differs only in minor characters. As the vertebræ of *Moschognathus* are somewhat small, the ribs of *Moschops* were modeled slightly longer and stouter than those of *Moschognathus*, so that they agreed in size with the fragments of the *Moschops* ribs. The lengths of the ribs of *Moschognathus* are as follows:

## LENGTHS OF RIBS, CAPITELLUM TO DISTAL END

Vertebra No. 5—.163M.	Vertebra No. 16—.695 (est.)
6—.240	19—.650 "
8—.400	20—.645 "
9—.483	21—.645 "
10—.508	23—.325 "
12—.570	24—.200 "

The more anterior cervical ribs were short and directed downward, an arrangement conforming to the reduction in size of the visceral arcade in the neck; the cervical ribs had a widely expanded proximal end, the large tubercle being in line with the shaft and the head forking more sharply from the shaft as we pass backward.

The tubercles become smaller and less prominent as we pass caudad to the twenty-third vertebra, when they begin to increase again in size as we approach the sacrum. The longest capitular branch is in the twelfth vertebra, where the distance across the proximal end of the rib is 93 mm. The shafts increase regularly in length except that there is a rather sudden increase between the eighth and ninth vertebræ. The ribs of the sixteenth vertebra are probably the longest, their shafts in *Moschognathus* being estimated at no less than 695 mm. in length.

The ribs of the lumbar region shorten rapidly as we pass toward the sacrum. The two or three posterior lumbar ribs (27, 28?, 29) have slender shafts, but wide proximal forks in which the head and tubercle are continuous and suturally united with the stout diapophysis, articulating below with the whole upper part of the centrum and above with the expanded diapophysial wall.

The first sacral rib (Pl. VII) is of great size and evidently formed the chief support of the pelvis. It is widely expanded distally and ends proximally in a massive head and tubercle. The great convex head articulates with a deep concave facet on the posterior surface of the last presacral vertebra, and with another concave facet on the anterior surface of the sacral vertebra. The head of the first sacral rib articulates with the very thick diapophysial wall of S. 1.

The second sacral rib is intermediate in size, and the third decidedly small. The second sacral rib of *Moschognathus* is much smaller than that of *Moschops*. The coccygeal ribs diminish rapidly in width as we pass caudad. The caudal ribs are not preserved.

The dorsal sides of the sacral and coccygeal ribs doubtless afforded the base for a broad mass of muscles (corresponding to the sacrospinalis + longissimus dorsi mass) running obliquely forward and outward to the posterodorsal borders of the ribs.

The posterior borders of the ribs were flattened toward the proximal end for the insertion of the powerful intercostal muscles. This flattening was continued on to the fork between the capitulum and the tubercle and on to the posterior faces of the diapophyses. The tubercular branch of the fork served as a flying buttress to transmit part of the body weight and muscular stresses to the centrum, also as the short arm of a lever of which the shaft of the rib was the long arm. The dorsal arching of the ribs in the mid-dorsal region probably afforded added room for the lungs, while the excessive length and width of the dorsal ribs provided space for an immense digestive tract.

The ribs of *Moschops* are fundamentally similar to those of the American Permian pelycosaurs, which are dichocoepalous. The stalk of the head, however, is relatively longer in *Moschops*, owing to the greater vertical height of the centra. The ribs of *Moschops* are probably relatively longer in proportion to the size of the animal. Both the ribs and the vertebrae of *Moschops* suggest those of *Casea*,<sup>1</sup> of the American Permian-Carboniferous, but probably the thorax as a whole was much less expanded transversely, since the ribs are less bowed out near the proximal end than in that peculiar reptile, which, according to Watson's view,<sup>2</sup> was probably a cotylosaur.

The tubercles of the *Moschops* ribs are much more distinct and independent than those of *Casea*, in which the tubercles are reduced. In correlation with this the diapophyses of *Moschops* are relatively larger and much more expanded distally.

<sup>1</sup>Williston, S. W., 1911, Pls. XIV-XVIII.

<sup>2</sup>Quoted by Nopcsa, 1923, p. 193.

The first sacral rib of *Moschops* is relatively larger than those of either *Varanosaurus* or *Casea*, and there is greater disparity in the size of the first and second sacral ribs than in *Casea*. These resemblances and differences emphasize the fact that the relationship of *Moschops* either with the pelycosaurs or with *Casea* is only remote and indirect.

#### PECTORAL GIRDLE AND LIMB

The pectoral girdle as a whole (Pl. VIII and Fig. 3) is of the primitive Permian type, in so far as each half of it retains a cleithrum (although greatly diminished), two separate coracoids and a large clavicle, a large interclavicle connecting the two halves. On the other hand, the pectoral girdle of *Moschops* was distinctly modernized in the glenoid region, as discussed below (p. 201).

**SCAPULA.**—A number of scapulæ, some of which have the coracoids attached, are included among the topotypes of *Moschops capensis* (p. 198). Taken altogether they give a fairly accurate contour of the scapulocoracoid. In one, which is associated with the small skeleton A (Fig. 4), the scapular blade is relatively short as compared with that of an adult of skeleton D, this difference perhaps indicating a relatively less expanded thorax in the young animal. The comparative measurements of the *Moschops* scapulæ are given in table I, page 187. In the adults the scapula in side view is a long blade, narrow in the middle, gently expanding at the top and ending below anteriorly in a wide, obliquely-placed sutural contact with the precoracoid plate, and posteriorly in a large downwardly-facing glenoid articular surface for the humerus. Its anterior border bears a vestigial cleithrum above (Fig. 9) and a clavicle below. In one specimen (*Moschops* skeleton A, Fig. 4), in which the clavicle is found adhering to the scapulocoracoid, there is no marked reflection of the anterior border of the scapula in the acromial region, as there is in other *Dinocephalia* figured by Watson (*Rhopalodon*, *Phoco-saurus*). However, in the upper half of the very large scapula (Fig. 6), referred by Broom to *Tapinocephalus*, there is a distinct notch in the anterior border for the clavicular insertion, and below this notch the border is everted into an incipient acromion.

The dorsal border of the scapula is roughened, apparently for the attachment of a cartilaginous suprascapula.

The lower half of the posterior or axillary border is greatly thickened and rounded to receive the dorsal thrusts of the humerus above the glenoid. The upper part of this thick axial column bends gently toward the midline so as to bring the upper bladelike portion in toward the ribs.

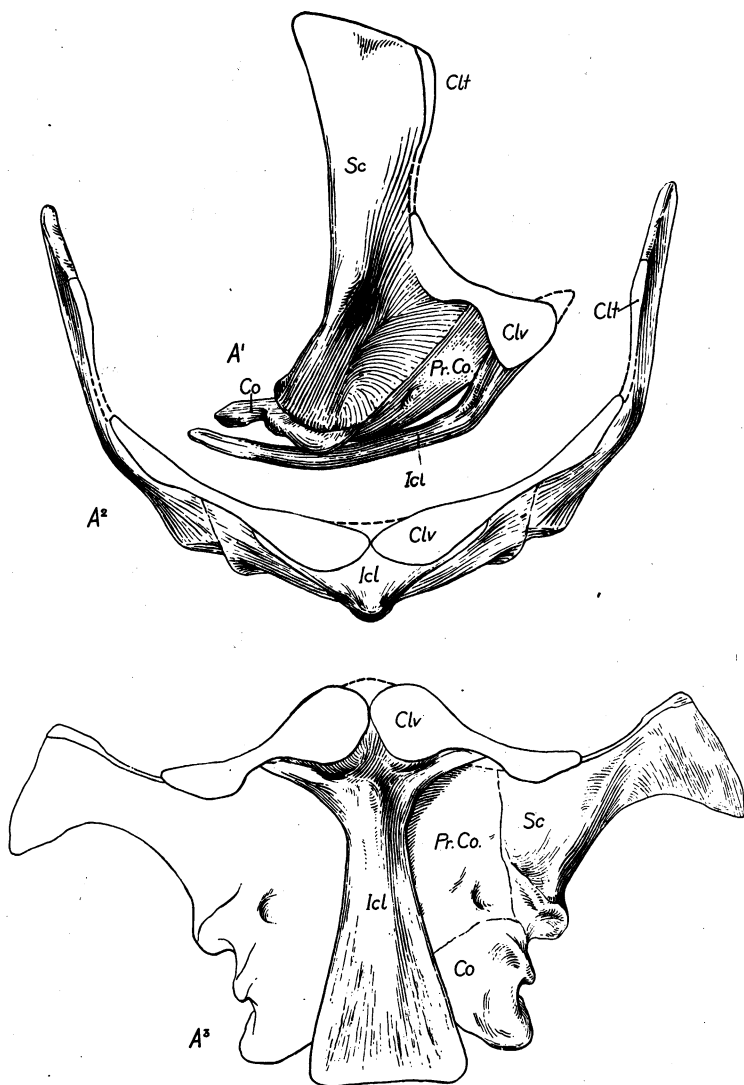


Fig. 3. *Moschops capensis*. Pectoral girdle in side, front and ventral views.

Clavicle and cleithrum from other specimens. Interclavicle and scapulocoracoids from skeleton 'B,' now mounted with bones assembled in somewhat different relations, the width across the scapulae being less.  $\times \frac{1}{4}$ .

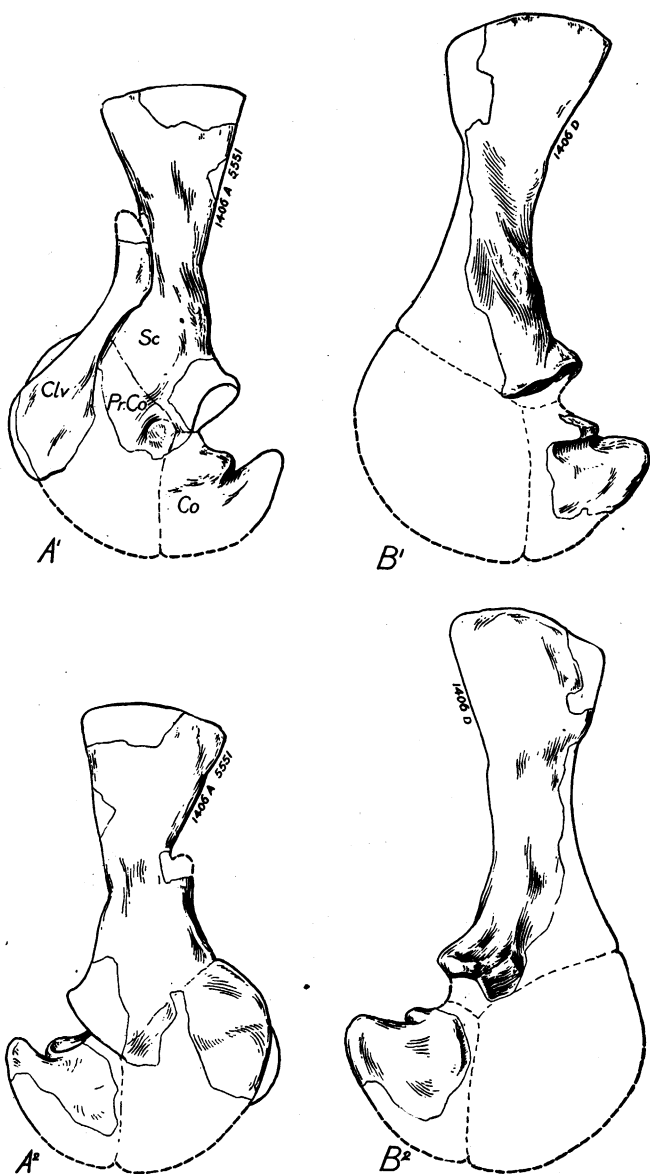


Fig. 4. *Moschops capensis*. Scapulocoracoids, etc., left side.  $\times \frac{1}{9}$ .

A<sup>1</sup>. Outer view, younger individual (skeleton "A"), with clavicle attached.

A<sup>2</sup>. Inner or medial view of same.

B<sup>1</sup>. Outer view of larger individual (1406 "D").

B<sup>2</sup>. Inner view of same.

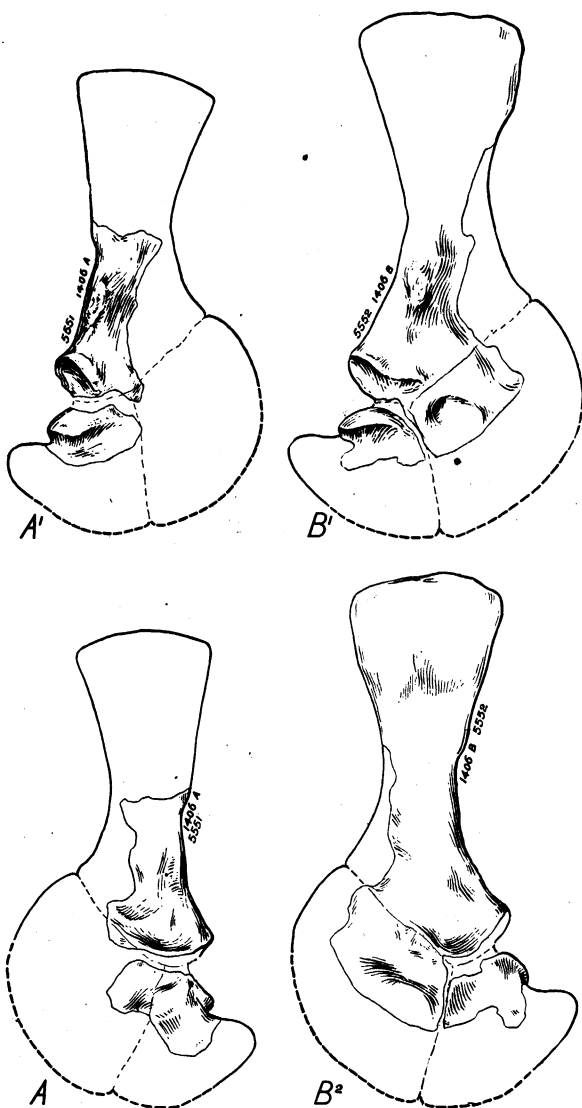


Fig. 5. *Moschops capensis*. Scapulocoracoids, right side.  $\times \frac{1}{9}$ .

- A¹. Outer view of younger individual ("A").
- A². Inner side of same.
- B¹. Outer view of larger individual ("B").
- B². Inner side of same.

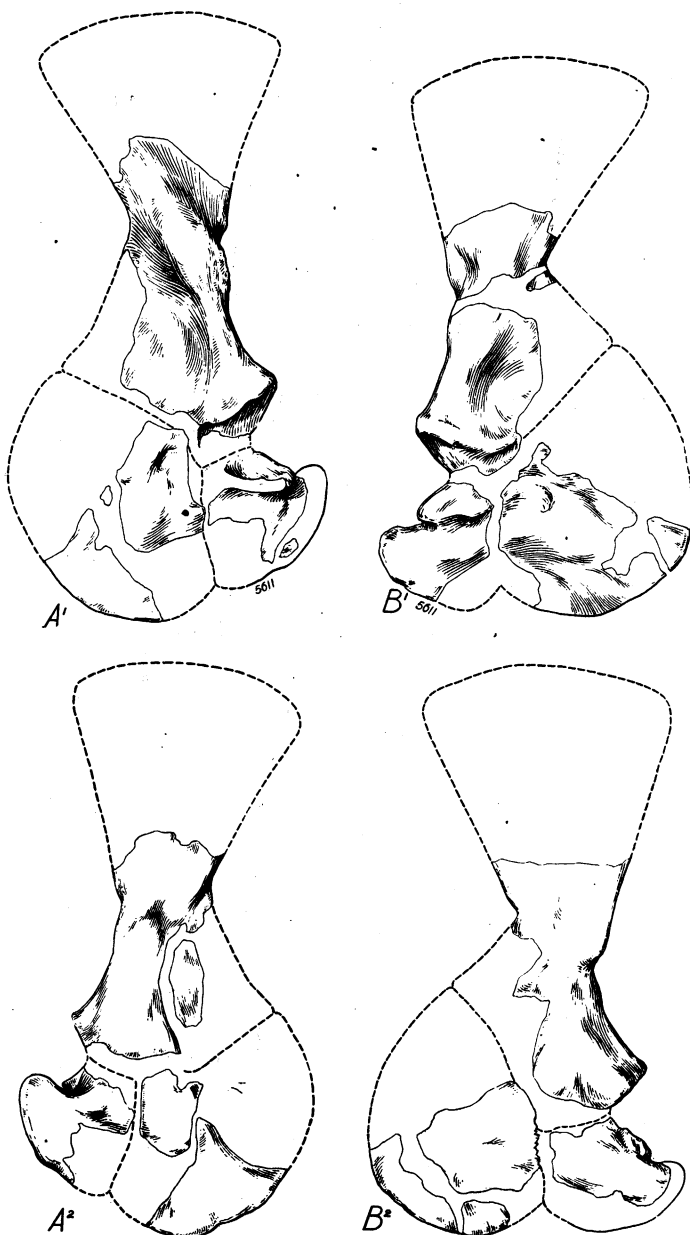


Fig. 6. "*Tapinocephalus*." A. M. N. H. 5611.  $\times \frac{1}{2}$ .

- A¹. Scapulocoracoid, left side, outer view.
- A². The same, inner view.
- B¹. Scapulocoracoid, right side, outer view.
- B². The same, inner view.

In the mounted skeleton of *Moschops*, owing to the flattening of the scapulæ, the blades diverge too widely from the midline (Pl. IX). About three or four inches above the glenoid and just in front of the axial border, there is a prominent tuberosity, probably for the attachment of the long head of the triceps. The front of this tuberosity, the outer side of the blade, is gently concave, running forward into a thin anterior border.

The lower end of the scapula meets the enlarged anterior coracoid, or pre-coracoid, in a long flattened sutural face. Its contact with the posterior, or true mammalian coracoid, is much shorter (Fig. 7).

The glenoid portion of the scapula faces downward, backward and slightly outward. It is ovate in form, wide posteriorly and narrow anteriorly, and lies above and slightly in front of the glenoid surface of the posterior coracoid. Thus, as Watson has shown in his beautiful studies on the limbs of reptiles (1917a), the glenoid of the *Dinocephalia* represents a distinct advance upon the screw-shaped glenoid of more primitive reptiles, in which the glenoid as a whole is more nearly horizontal; the scapular part being chiefly in front of the part formed by the posterior coracoid. The borders and surface of the glenoid are roughened for the articular capsule and its ligaments. The glenoid ends anteriorly in a wide valley between the scapula and coracoid portions, opening toward the anterior coracoid. This is the part with which the humerus articulated in its extreme forward reach.

**CORACOID AND PRECORACOID.**—The very large precoracoid<sup>1</sup> is shaped somewhat like a large sector of a circle, with the apex at the anterior end of the glenoid. The thick anterior border is roughened, probably for the attachment of a cartilaginous rim. In front of the apex is the large precoracoid fossa and the supracoracoid foramen for the

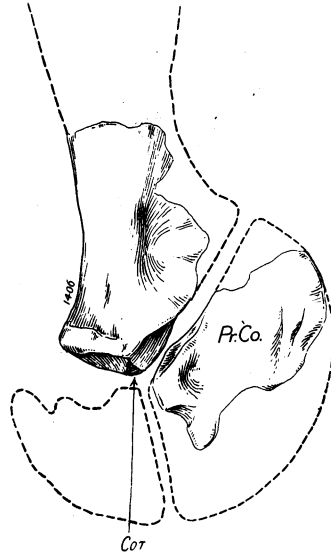


Fig. 7. *Moschops capensis*. Lower end of scapula, showing sutural contacts with the pre-coracoid and coracoid.  $\times \frac{1}{9}$ .

<sup>1</sup>In 1918 I tried to prove (Gregory and Camp, 1918, p. 545) that the anterior coracoid of therapsids was the homologue of the true mammalian coracoid, but since then Romer (1922a) has shown quite conclusively that the posterior coracoid has stronger claims for this homology.

transmission of the supracoracoid nerve. As already stated, only the extreme apex of the anterior coracoid reaches the anterior part of the glenoid fossa. The outer surface of the anterior coracoid is convex, the inner concave. The anterior coracoid meets the posterior coracoid in a conspicuous suture directed ventrally and ending below in a distinct notch. The posterior coracoid, which is much smaller than the anterior

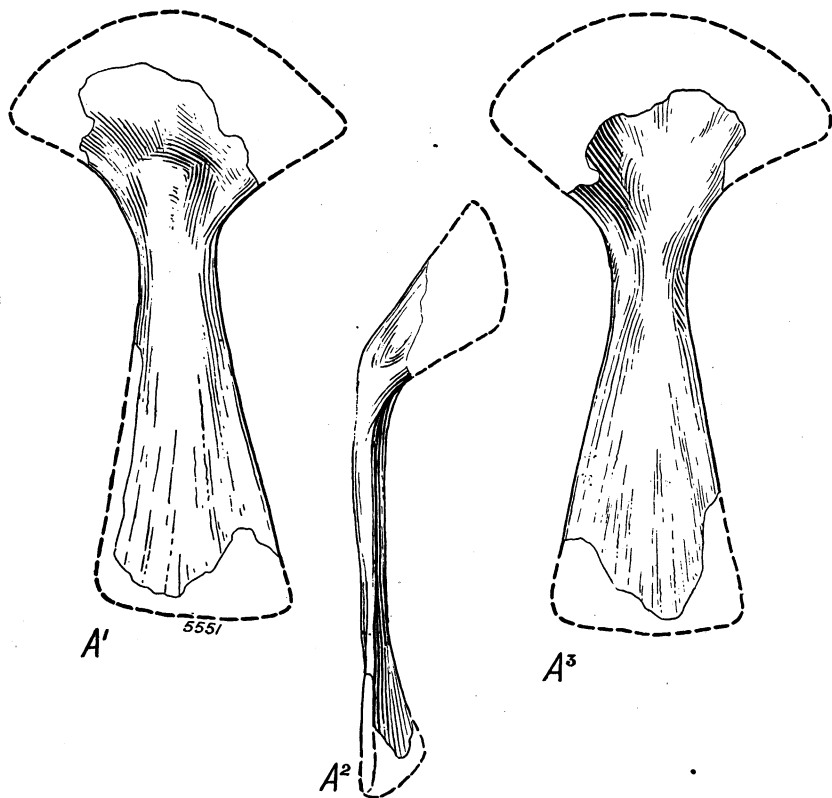


Fig. 8. *Moschops capensis*. Interclavicle of skeleton "A."  $\times \frac{1}{6}$ .

A¹. Ventral view. A². Left side. A³. Dorsal view.

one, ends posteriorly in a prominent coracoid process; the latter lacks the prominent dorsal process for the attachment of the coracoid head of the biceps, which is found in primitive Permian reptiles, but not in therapsids (Romer, 1922a). The posterior coracoid articulates above by a narrow sutural surface with the scapula, on the medial wall of the glenoid fossa, and meets the anterior coracoid in a broad, thick suture. Prob-

ably the medial border of the coracoid plate was received posteriorly in a notch in the sternum, but no trace of the latter structure is known.

**INTERCLAVICLE.**—The large spatulate interclavicle has a widely expanding anterior end and a long stem with posteriorly divergent sides. The anterior end is sharply inclined upward, concave above and broadly convex below, culminating in a prominent median boss. The borders behind the clavicles are thickened and strengthened.

**CLAVICLE AND CLEITHRUM.**—The clavicles preserved in two specimens are thin blades, widely expanded below toward the midline, narrowing dorsally, and with a grooved posterior border overlapping the anterior border of the scapula. At the upper extremity they may have touched the cleithrum. The latter was a small bone ending below in a splint-like process but forming above the anterior angle of the dorsal border of the scapular blade (Fig. 9).

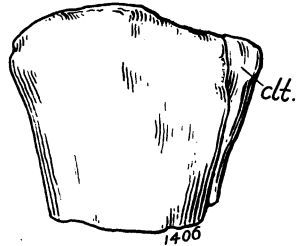


Fig. 9. *Moschops capensis*.  
Upper end of right scapula,  
with cleithrum attached.  $\times \frac{1}{6}$ .

**TELEOLOGY.**<sup>1</sup>—The elements of the pectoral girdle as assembled by us assume positions indicated in plates I, VIII, IX, X, and in figure 3. If the blade of the scapula were thrown sharply forward as it is in monotremes, it would tilt the posterior half of the interclavicle up into the abdomen and rotate the scapular portion of the glenoid into a position in which the humerus would be inclined upward instead of downward. In the position assigned to the pectoral girdle in the mounted skeleton, the anterior part of the interclavicle inclines upward toward the neck and throat. The extreme divergence of the scapulæ from the midline (Pl. IX) is doubtless due to crushing, but even in the existing alligators there is a wide space between the scapulæ and the ribs.

The pectoral girdle, while fundamentally similar to that of Permian reptiles, is more advanced in the shape of the glenoid articular surface; this difference is correlated with the ability to straighten the fore limbs and to lift the body far above the ground, which, as Broom has held, is characteristic of so many South African fossil reptiles.

The pectoral girdle of *Moschops* was of great size and strength, in order to support the heavy head and enormous body and to afford an

<sup>1</sup>This useful old word has perhaps been banished long enough from orthodox scientific literature to have lost much of its former theological aroma, enough to warrant its being welcomed back into the scientific fold. In this paper it stands for the fact that every bone and every part of a bone doubtless served a function about which something may still be learned, if our comparisons be sufficiently broad and intensive and if we be not deceived by false similes.

adequate base for the huge forelimbs. The pectoral girdle was on the whole more primitive in character than that of any surviving reptile.<sup>1</sup> Among existing reptiles the pectoral girdle of *Sphenodon* comes nearest to it and is of great value in determining the relations of the girdle to the backbone and ribs. The pectoral girdle of *Moschops* differed from that of *Sphenodon* in the retention of a vestigial cleithrum, in the relatively greater dorsal extension of the scapular blade (correlated with the great depth of the thorax), in the relatively larger size of the clavicles, in the large size and shovel-like form of the interclavicle, in the greater expansion of the coracoid plate, and in its subdivision by suture into a pre-coracoid and a coracoid. On the whole the musculature of the pectoral girdle must have been similar in plan to that of *Sphenodon* and the lizards, and it has been so restored by Romer (1922b, Pls. XXVII-XXXIV).

The action of the pectoral girdle and its associated musculature in *Moschops* may be summarized as follows: in the standing pose (Pl. IX) the shoulder-girdle as a whole acts as a U-shaped sling between which the body is supported. The sling is not rigid but is composed essentially of a ventral and two lateral pieces tied together by ligaments and sliding upon each other. The weight and pressure of the viscera and thorax prevent the opposite halves of the girdle from collapsing toward the midline. Considering the left half of the girdle, we see (Pl. IX) that in the standing posture it is swung upon the head of the humerus as the main fulcrum. The weight of the body is transmitted through the serratus muscles, acting as living springs, to the upper part of the medial surface of the scapula. But the resulting medial movement of the scapular blade is counterbalanced by the pull of the deltoid, scapulohumeralis anterior and supracoracoideus muscles on the lateral and ventral portion of the girdle. The collapse of the girdle on the ventral surface is prevented chiefly by the action of the abdominal, pectoral and coracobrachialis muscles. Meanwhile the fore-and-aft relations of the scapular blade are maintained, in front by the levator scapulæ, omohyoid and associated neck muscles, and behind by the serratus, the subscapularis, the scapular head of the triceps, the scapulohumeralis posterior and anterior, the latissimus dorsi and the pectoral and abdominal muscles. At every moment the spinal and intercostal muscles prevent the body from collapsing upon the girdle.

On the other hand, when the fore limb is being extended backward the glenoid surface of the scapulo-coracoid blade may be considered as the

<sup>1</sup>For comparative figures of the pectoral girdle of *Moschops* with those of existing reptiles, see Gregory and Camp, 1918, Pl. L.

fulcrum, while the reaction of the ground to the thrust of the arm may be regarded as the resistance. In this case the serratus and other body muscles hold the left half of the girdle in place as a base, while the powerful triceps, the latissimus dorsi, the scapulohumeralis posterior and subcoracoscapularis, together with the flexors of the digits, thrust the ground backward. The opposite halves of the girdle alternately slip upon the interclavicle under the alternating stresses of the opposite limbs. The costocoracoideus and sternocoracoideus on the medial surface of the coracoid assist the serratus and other muscles in these slipping movements.

ORIGIN AND EVOLUTION OF THE PECTORAL GIRDLE.—The pectoral girdle of *Moschops* has recently been figured in comparison with those of typical cotylosaurs, pelycosaurs, therapsids and mammals by Romer (1922*b*, Pls. XXXIII, XXXIV). From these we may see that *Moschops* has inherited from some as yet undiscovered pelycosaur-like ancestors all the elements of the primitive reptilian shoulder-girdle, except that the cleithrum is reduced to a vestige. It also shares with *Dimetrodon*, *Ophiacodon* and their allies the subdivision of the coracoid plate into anterior and posterior moieties.

But *Moschops* had already entered upon the path of evolution leading to the mammalian posture and the ability to run rather than crawl. Its pectoral girdle in fact reflects the advance beyond the pelycosaurian grade in the following characters:

(1) The "screw-shaped" glenoid of the crawling reptiles has been replaced by a modernized type in which the glenoid faces posteriorly, is shortened anteroposteriorly and deepened vertically, and consists of a dorsal moiety borne by the scapula and a ventral moiety on the coracoid, the precoracoid portion of the glenoid being practically eliminated. The way in which this modernization of the glenoid took place is indicated in *Ophiacodon*, as figured by Romer, in which the precoracoid portion of the glenoid is reduced, the glenoid is beginning to face backward and the chief part of it already consists of dorsal and ventral, instead of anterior and posterior, moieties.

(2) In *Moschops* the supraglenoid buttress and supraglenoid fossa, which are prominent features of all more primitive scapulæ, have been reduced to a vestige, so that the great tricripital ridge now forms the posterior border above the glenoid.

(3) The precoracoid is expanded dorsally, carrying with it the area for the supracoracoideus muscle, a condition prerequisite for further improvement in running, as explained by Romer. .

(4) In primitive reptiles there is a prominent process on the postero-superior corner of the posterior, or true coracoid, which Romer has identified as the attachment for the coracoid head of the triceps. In *Moschops* no such process is present, only the ventral posterior process of the coracoid remaining. Romer therefore infers that in *Moschops* the coracoid head of the triceps had already become attached to the latissimus dorsi to form the dorsi-epitrochlearis as in mammals.

(5) On the medial aspect (Romer, 1922*b*, Pl. xxxiv) the scapulocoracoid of *Moschops* differed from that of the primitive reptile *Dime-trodon* especially in the loss of the supraglenoid buttress and in the appearance of the glenoid on the posterior border.

STRUCTURAL AND TAXONOMIC CHARACTERS OF THE PECTORAL GIRDLE.—The *Moschops* pectoral girdle exhibits a fundamental similarity to those of other therapsid reptiles, which alone would be sufficient to indicate its close relationship with them. For they all show the loss of the supraglenoid buttress and fossa and the substitution for it of the powerful tricipital ridge; they show also the “modernized” glenoid, the virtual exclusion of the precoracoid from the glenoid, the dorsal extension of the surface for the supracoracoideus muscle. The clavicles and interclavicle, so far as known, are also fundamentally the same as those of *Moschops*. Especially striking are the resemblances to the pectoral girdles of the small dromasaurian therapsids *Galeops* and *Galechirus*, as restored by Broom (1914*a*, Pl. iv, figs. 33, 34, 35). But *Moschops* and these dromasaurians were decidedly more primitive than the anomodont *Dicynodon* or the cynodont *Cynognathus* in that they did not have a prominent projecting acromial process for the attachment of the clavicle. They were also less mammal-like and more primitive than *Cynognathus* in that the anterior border of the scapula was not reflected laterally and the coracoid plate was of large size, all the foregoing features indicating a less mammalian arrangement of the corresponding muscles.

The shoulder-girdle alone then is sufficient to show that the dinocephalians were a very early offshoot of the therapsid stem.

There is but little material for the comparison of the pectoral girdle of *Moschops* with that of other dinocephalians. Our scapulocoracoids agree in all subordinal characters with that of *Phocosaurus* as figured by Watson (1914 *c*, p. 763), but this seems to have a heavier and thicker scapular blade, with a slight elevation of the anterior border in the acromial region. The precoracoid barely enters the anterior rim of the glenoid. There is an enormous pectoral girdle in the American Museum collection (Fig. 6), referred by Doctor Broom to *Tapinocephalus*, in

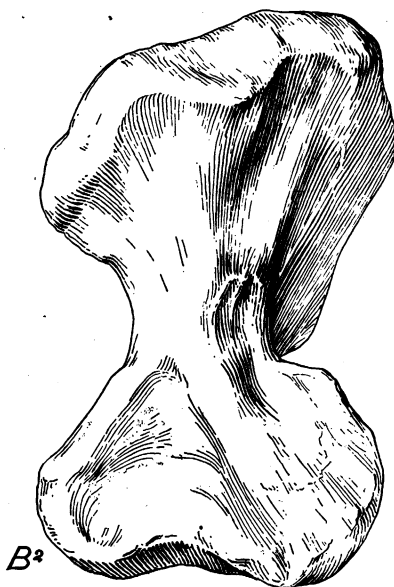
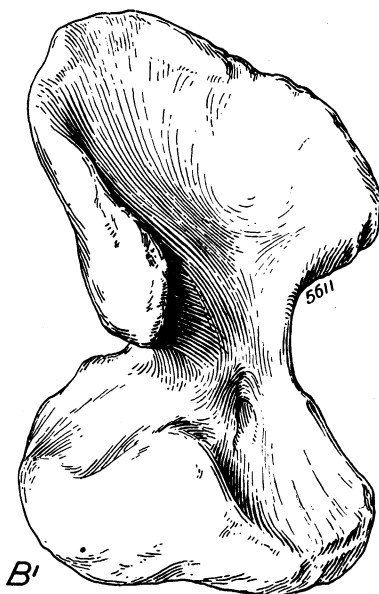
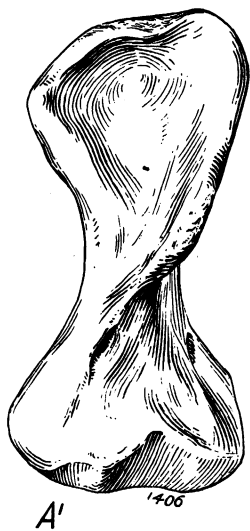


Fig. 10. Humeri of *Moschops* and of "*Tapinocephalus*."  $\times \frac{1}{6}$ .

A¹. *Moschops*, left humerus, front view.  
A². The same, back view.

B¹. "*Tapinocephalus*," right humerus, front view.  
B². The same, back view.

which the scapula widens dorsally much more than in *Moschops*. There is a prominent swelling for the attachment of the scapular head of the triceps, and the acromial region is slightly everted and notched.

**HUMERUS.**—The best preserved humeri (Fig. 10) are those of *Moschops* C. They are fundamentally similar to other therapsid types but are distinguished by the wider expansion of the proximal end and by the wide divergence from the long axis of the strong ridge beneath the medial tubercle or lesser tuberosity.

The head is continuous on one side with the long narrowing summit of the deltopectoral crest, and in the opposite direction with the summit of the internal tubercle, this condition being a modified remnant of the screw-shaped proximal articulation of the humerus in primitive Permian reptiles. The proximal end, however, agrees with the therapsids and differs from that of primitive Permian types in that its general direction is not almost at right angles to the plane of the distal end, but is more nearly parallel with it. The strong development of the deltopectoral crest doubtless implies a corresponding development of the deltopectoral group of muscles, but is equally correlated with the expansion of the fossa for the powerful coracobrachialis brevis on the medial side of the crest. The entepicondylar region, although as well developed as in other therapsids, is not so large and does not project so far in proportion to the length of the bone as in primitive Permian reptiles. The entepicondylar canal is slitlike, instead of forming a wide opening.

The articular surfaces are all very rough and make poor contacts with the other limb elements, thus indicating a condition analogous to that of very large Crocodilia, with persistently growing ends of the limb bones. In *Moschops* C, however, the articular surfaces of the distal end are sufficiently defined to make possible a pretty clear study of the movement of the radius and ulna upon the humerus (see p. 211.)

**TELEOLOGY AND EVOLUTION OF THE HUMERUS.**—Romer (1922b, Pls. XXXV–XXXVII) has given an excellent series of figures in which the humerus of *Moschops* is shown in comparison with those of temnospondyls, cotylosaurs, pelycosaurs and therapsids. From these it will be evident that the *Moschops* humerus differs from the primitive crawling types especially in the following features:

- (1) The humerus is "untwisted," that is, the proximal end is no longer nearly at right angles to the distal end but is inclined to it at a low angle.

- (2) The head or proximal facet tends to be expanded toward the middle of the proximal crest, but not as much so as in recent reptiles and mammals.

(3) The ent- and ectepicondyles are also smaller than in the primitive crawling types.

Watson (1917a) and Romer (1922b, p. 557) have shown that these differences are associated with the changed posture of *Moschops*. "The placing of the distal plane at nearly right angles to the proximal [in primitive crawling types] is correlated with the position of the forearm, which works on a plane which is more nearly parallel to the ground in the more primitive types, as noted by Watson (1917a, p. 13, etc.). When the forearm works in a more nearly vertical position, and one more nearly in the same plane as the long axis of the humerus, the distal plane shifts to preserve its relations, rotating up posteriorly and down anteriorly, hence being more nearly in a horizontal position and more nearly parallel to the plane of the proximal part of the humerus. . . . In the therapsids

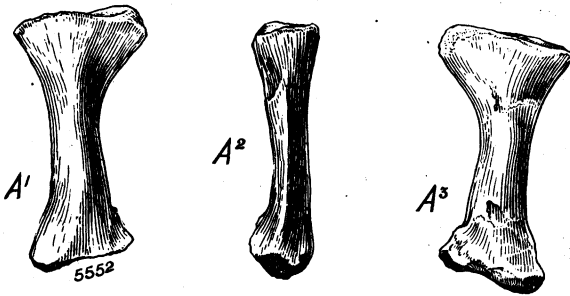


Fig. 11. *Moschops capensis*. Left radius. Skeleton "B."  $\times \frac{1}{6}$ .

A1. Front view. A2. Inner side view. A3. Back view.

the 'untwisting' process is very early and very marked, and tends to an approximation of the two planes. . . ." (Romer, p. 558). Romer also shows that the relative reduction of the epicondyles is correlated with the more vertical position of the forearm, which puts the supporting function more on the radius and less on the extensors and flexors.

The humerus of *Moschops* is fundamentally similar to that of the anomodont therapsid *Dicynodon*, but is less advanced toward the mammalian type than is the humerus of the cynodont *Gomphognathus*. It is distinctly allied with, but perhaps generically distinct from, the humerus of *Prigalion oweni*, which, as figured by Watson (1914c, p. 764), has the very large lesser tuberosity or processus medialis located considerably below the plane of the caput humeri.

**RADIUS AND ULNA.**—The radius (Fig. 11) is a stout bone expanded transversely at both ends. The upper and lower ends look sufficiently

like each other to make it difficult at first to distinguish between them and thus to identify rights and lefts. The wide flattened head of the radius was doubtless appressed to the corresponding facet of the ulna, but in more or less crushed specimens it is difficult to bring these surfaces into articulation with each other and with the capitellum of the humerus at the same time. The proximal surface of the head of the radius has a transversely expanded, warped, concavo-convex facet for the capitellum. The shaft is also flattened anteroposteriorly, being thick and rounded on the ulnar side, flattened on the medial border. The lower end in well preserved specimens has a distinct convexity on the medial side, above the

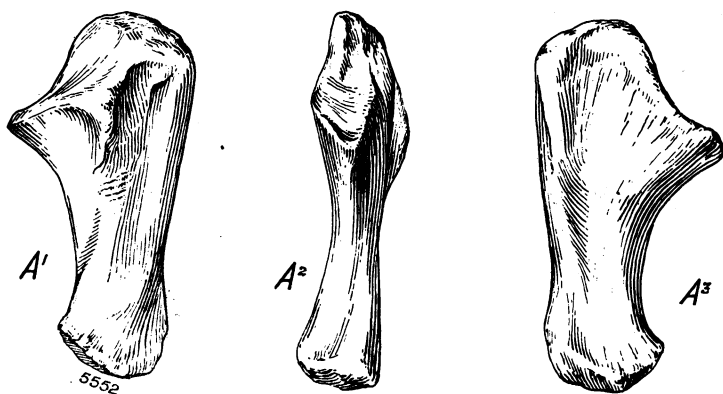


Fig. 12. *Moschops capensis*. Left ulna. Skeleton "B."  $\times \frac{1}{4}$ .

A¹. Anterolateral view. A². Medial anterior view.  
A³. Posteromedial view.

radiale. The lateral part of the head, articulating with the ulna, is bounded below by a strong outwardly-flaring border, which runs obliquely downward and inward to the shaft. The tubercle for the tendon of the brachialis internus muscle on the back of the shaft of the radius is well indicated in *Moschops* A and C.

The radius and ulna, like the other long bones, have the ends very rough and pitted in the fossil state, thus indicating the presence of thick articular surfaces, corresponding to epiphyses, but more like the articular surfaces of very large crocodilian limb bones than like mammalian epiphyses.

The massive ulna (Fig. 12) is distinguished by the huge size of its olecranon, which is probably correlated with the great dimensions of the scapula and the robustness of the triceps. The sigmoid surface, as identified by comparison with that of *Propappus*, affords an extensive contact

with the distal end of the humerus and with the head of the radius. The very prominent coronoid process articulates above with the middle part of the distal facet of the humerus. The ulna terminates below in a very thick, roughened styloid protuberance and a flattened facet for the lateral carpals. The anterointernal border is concave, leaving a space between the radius and ulna which was covered on the anterior face or dorsum by the wide extensors of the hand and on the posterior side by the flexors.

**TELEOLOGY AND EVOLUTION OF THE LOWER ARM.**—Unlike the more primitive American Permian reptiles, and like the other South African therapsids, the *Dinocephalia* could nearly straighten the elbow joint. The capitellum humeri extends from the front, or ventral, face of the bone, around to its distal end, so that at the moment of extreme flexure the head of the radius articulates with the front, or ventral, part of the capitellum, while in extension the head slides around on to the distal end. Similarly the facet for the ulna shows the possibility of a strong flexure and extreme extension; thus the forearm could reach well forward so as to bring the manus near the midline, and it could also reach far backward so as to get a straight thrust forward and upward from the rear of the glenoid.

The radius and ulna of *Moschops* are fundamentally similar to those of the small dromasaurian therapsid *Galeops*, as figured by Broom (1914a, Pl. III, fig. 30), except for their great size, relative width and shortness and great enlargement of the olecranon. The latter is larger than in *Endothiodon*. The ulna referred by Seeley (1889, Pl. xxii) to *Titano-suchus* closely resembles that of *Moschops* and may belong at least to the same family.

#### PELVIC GIRDLE AND LIMB

The pelvis of *Moschops* (Figs. 13–15) is remarkable for its small size in comparison with the pectoral girdle, a condition which is in harmony, first, with the greatly reduced size of the tail, secondly, with the dwindling proportions of the more posterior presacral vertebræ and ribs, thirdly, with the inferior dimensions of the hind limb itself. All this apparently indicates that the backbone of *Moschops* in a walking pose had a considerable slope forward and upward from the ilium.

The next conspicuous features of the pelvis are: (a) the relatively huge size and subcircular contour of the acetabulum, in contrast to the smaller and more triangular acetabulum of primitive Permian reptiles, and (b) the relative shortness of the pubi-ischiadic plate. This again is correlated with the ability to direct the femur forward, to straighten the

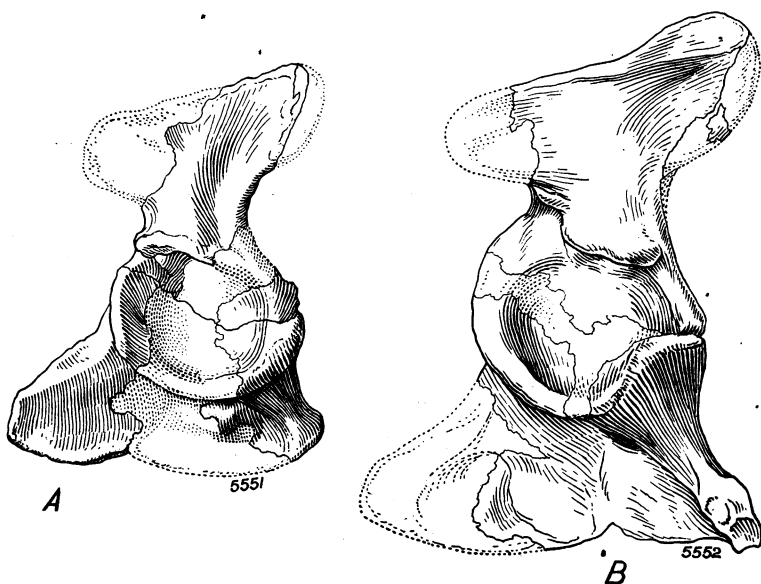


Fig. 13. *Moschops capensis*. Pelvis, right side.  $\times \frac{1}{6}$ .

- A. Younger individual (1406 "A").  
B. Larger individual (1406 "B," the mounted skeleton).

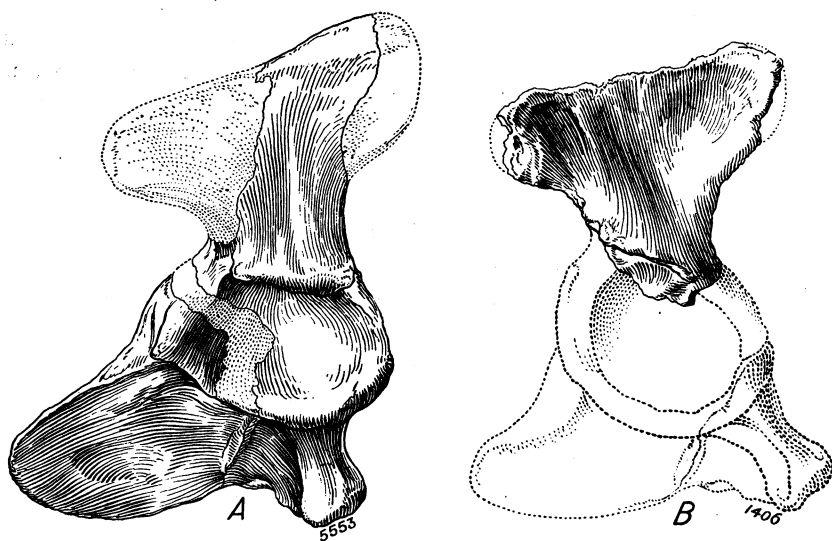


Fig. 14. *Moschops capensis*. Pelvis, right side.  $\times \frac{1}{6}$ .

- A. Large individual ("C").  
B. Ilium, showing the anterior and posterior processes.

knee and to bring the femur well in toward the midline in the forward thrust of the backwardly-extended limb.

**ILIUM.**—As in other therapsids the anterior process of the ilium is directed forward and upward, in contrast with the backwardly-directed ilium of *Casea* and the pelycosaurs. On the other hand, the anterior process of the ilium is not helmet-shaped as it is in the anomodonts, but has a nearly flat superior border. The anterior process diverges laterally behind the widely projecting lumbar ribs. It no doubt afforded a point of support for the powerful iliopubic ligament and for the external oblique abdominal muscles which held up the huge thorax, as well as for the iliocostalis and longissimus dorsi on its medial surface, and for the iliotibialis and iliofemoralis on its outer surface (Romer, 1922b, Pl. XLIV). The posterior process of the ilium is less stoutly developed, in correlation with the reduction of the tail and of its muscles.

On its medial surface the ilium bears a large scar or facet for the expanded first sacral rib, and smaller marks for the second and third sacral ribs. The anterior border in front of the acetabulum rises into a low eminence, the site of the "pectineal tubercle" of monotremes, and possibly serving in *Moschops* for the place of origin of part of the pubi-ischio-femoralis internus muscle. The concave lateral surface of the ilium served for the insertion of the gluteal muscles (iliofemoralis) and its roughened superior border for the extensor iliotibialis. This gluteal area is bounded below by a very prominent projecting rim of the glenoid fossa, which receives the forward and upward thrusts of the backwardly-extended femur. This supra-acetabular rim is also seen in *Cynognathus* and the anomodonts, and is a part of the adaptation for running with the body well raised from the ground.

**PUBIS.**—The pubis is a flat plate everted anteriorly and forming the expanded anterointernal quadrant of the acetabulum. It is perforated by the large pubic foramen (for the obturator nerve). It is not produced anteriorly and is thus unlike that of the primitive Permian reptiles of crawling habit. The pubis ends anteroexternally in a low tubercle (tuberculum pubis) for the attachment of the iliopubic ligament and of the rectus abdominis muscles, and its anterior rim is rounded for the passage of part of the pubi-ischiofemoralis internus muscle. Its concave outer surface doubtless gave origin to the anterior part of the pubi-ischiofemoralis externus muscle.

A slight notch between the pubis and the ischium was probably filled by cartilage in life. The opposite pubes diverge widely, and barely, if at all, meet posteriorly in a median symphysis.

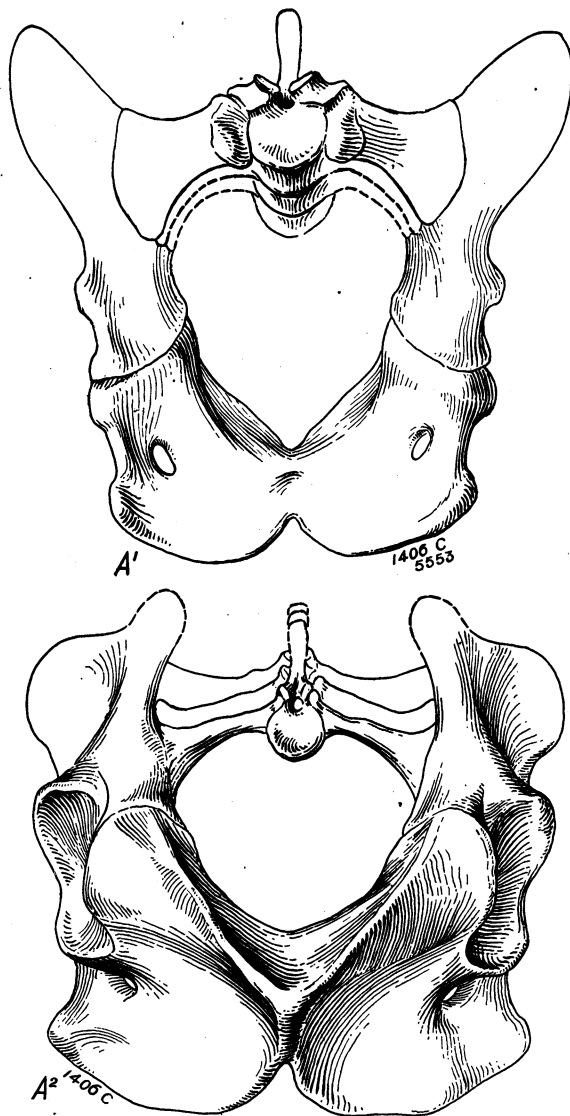


Fig. 15. *Moschops capensis*. Pelvis and sacrum of large individual (1406 "C").  
 $\times \frac{1}{6}$ .  
 A'. Front view, showing pelvic inlet.  
 A². Rear view, showing pelvic outlet.

**ISCHIUM.**—The ischium is relatively short anteroposteriorly, much shorter than in primitive Permian reptiles, perhaps in correlation with the shortness of the tail. The opposite ischia (Fig. 15) meet below in a deep symphysis, forming a median keel and U-to-V-shaped diverging bars, after the fashion of primitive Permian reptiles. The ischia form posteriorly a spout-shaped pelvic outlet. The posterosuperior border is greatly thickened above for the support of the acetabulum and of the stout ilium, but dwindles rapidly below into a narrow crest. The external concave face of the ischium doubtless gave origin to the greater part of the pubi-ischiofemoralis externus or obturator mass; its posterior rim to the long flexors of the lower leg and its posterodorsal rim to the ischio-trochantericus (Romer, 1922*b*, p. 569, etc.).

**EVOLUTION OF THE PELVIS.**—The pelvis has inherited from primitive reptiles the platelike pubis and ischium, the tripartite character of the acetabulum, the outward reflection of the anterior border of the pubis, etc.; but it has advanced in the mammalian direction and in adaptation to a running rather than a crawling posture in the following particulars:

(1) The pubi-ischiadic plate is shortened anteroposteriorly, its length being about seventy to eighty per cent. of the total height of the pelvis, whereas in the primitive dromosaurian *Galepus*, as figured by Broom (1914*a*, Pl. iv, fig. 36), the length of the pubi-ischiadic plate is one and twenty-eight hundredths times the total height of the pelvis; in the primitive gorgonopsian *Inostrancevia*, as figured by Amalitsky, the pubi-ischiadic plate is also relatively much longer than that of *Moschops*.

(2) The acetabulum in primitive reptiles is more or less triangular in outline, but in *Moschops* it is circular and surrounded by a more or less continuous rim, differing from the mammalian acetabulum chiefly in its very large size.

(3) The ilium is produced forward in front of the acetabulum, the posterior process being somewhat reduced, this being the opposite from what occurs in primitive, crawling reptiles.

(4) The opposite halves of the pelvis, instead of uniting below in a narrow V as in temnospondyls, are spread apart so as to make a more capacious pelvic inlet and meet each other below in a shallow and comparatively weak suture.

(5) Conversely, the sacral attachment, instead of being loose and comparatively weak as in *Eryops*, is greatly enlarged and strengthened, thus producing a closer connection between the vertebral column and the pelvic limb.

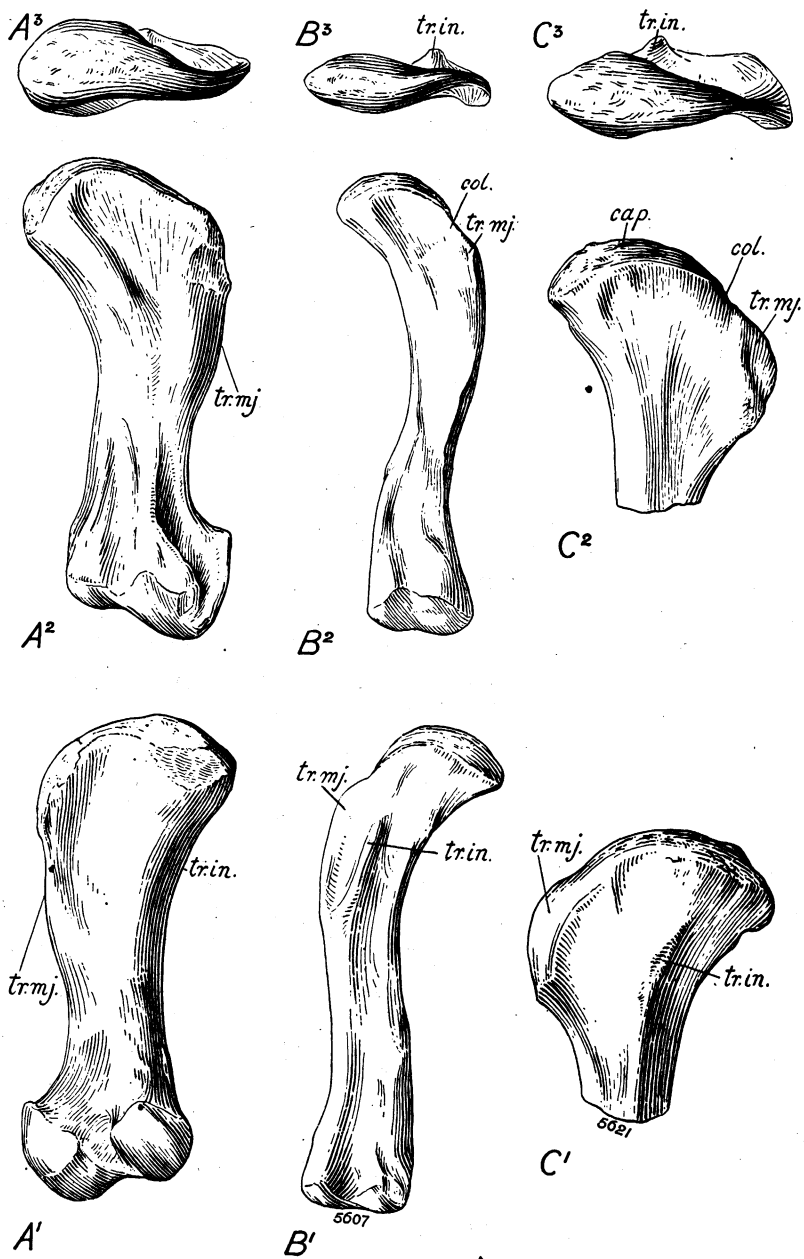


Fig. 16. Comparative series of femora.

A¹. *Moschops capensis*. Back view.  $\times \frac{1}{4}$ .

A². The same, front view.  $\times \frac{1}{4}$ .

A³. The same, top view.  $\times \frac{1}{4}$ .

B¹. *Elurosaurus* (?) (A. M. N. H. No. 5607). Under side.  $\times \frac{1}{4}$ .

B². The same, front view.  $\times \frac{1}{4}$ .

B³. The same, top view.  $\times \frac{1}{4}$ .

C¹. *Cynodont* (?) *Diademodon*, A. M. N. H. No. 5621). Under side.  $\times \frac{1}{4}$ .

C². The same, front view.  $\times \frac{1}{4}$ .

C³. The same, top view.  $\times \frac{1}{4}$ .

SYSTEMATIC CHARACTERS OF THE PELVIS.—The *Moschops* pelvis differs from that of the anomodonts chiefly in that the ilium, although produced forward, has a flattened rather than strongly convex dorsal border and the posterior process is less reduced. It resembles that of the allied tapinocephalid *Phocosaurus* as figured by Seeley (1888, Pl. XXI) and by Watson (1914c, pp. 765, 767), but the ilium of *Moschops* is much higher in proportion to its anteroposterior length. Watson states that in this genus the obturator foramen is absent, and, although our material is not entirely satisfactory, the same is probably true of *Moschops*.

FEMUR.—The femur of *Moschops* (Figs. 16, 17) is in certain respects intermediate between the primitive Permian types on the one hand and the mammalian femur on the other (Gregory and Camp, 1918, Pl. XLVIII; Romer, 1922b, Pl. XLVI). The femur as a whole is fundamentally similar to those of the therocephalian *Ælurosaurus* and of the anomodonts. The external trochanteric margin is prominent and the head is directed inward as in that genus. The great trochanter is represented by a low swelling on the upper third of the lateral border. The bone as a whole is compressed anteroposteriorly and widened laterally, especially in the upper half, somewhat after the manner of the femora of ground-sloths and other mammals with a massive abdominal cavity. In correlation with the reduction of the tail there is little or no fourth trochanter.

The ectocondyle is distinctly larger in the lateral and anterior view, whereas in the more primitive reptilian type the entocondyle is much smaller; in the medial and posterior view, however, the ento- is about equal to the ectocondyle. This modification is correlated with the ability to turn the femur directly forward, and in the extreme forward reach of the foot to bring the greater part of the weight on the medial tuberosity of the tibia.

The posterior surface is very flat, lacking the deep excavation or intertrochanteric fossa, near the proximal end, seen in the primitive Permian reptiles, as well as the Y-shaped trochanteric crest, practically no traces of which remain. The latter condition was probably correlated in part with the small size of the tail and the consequent reduction of the caudifemoralis (coccygeofemoralis) muscles, but the shallowing of the proximal ventral fossa may imply only a corresponding spreading of the insertion area of the pubi-ischiofemoralis externus. There is a broad gastrocnemius fossa near the lower end, above the condyles. The whole distal surface of the condyles and the intercondylar groove are well rounded, permitting the free and full extension of the tibia, whereas in

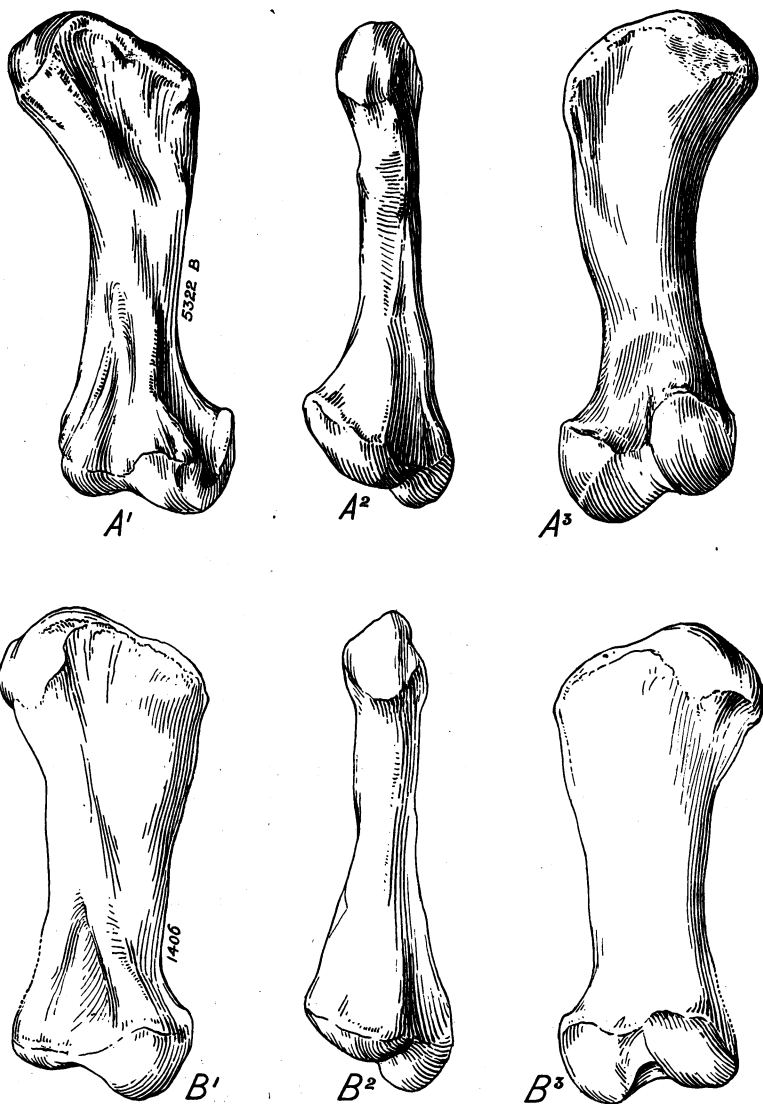


Fig. 17. *Moschops capensis*. Femora.

- A¹. Femur, A. M. N. H. No. 5322-B (in mounted skeleton), front view.  $\times \frac{1}{6}$ .
- A². The same, inner side.  $\times \frac{1}{6}$ .
- A³. The same, under side.  $\times \frac{1}{6}$ .
- B¹. Femur (A. M. N. H.), front view.  $\times \frac{1}{6}$ .
- B². The same, inner side.  $\times \frac{1}{6}$ .
- B³. The same, under side.  $\times \frac{1}{6}$ .

The differences between the more robust femur B and the less robust femur A are mediated by several other femora from the same locality.

primitive Permian reptiles the extension of the tibia was very limited. The lateral surface of the ectocondyle is smoothed for the articulation of the wide head of the fibula. Above the ectocondyle is a deep wide groove lying between the strengthening eminences of the ectocondyle and the lateral border of the femur. From the huge size and strength we may infer that the greater part of its anterodorsal surface was covered by the powerful femorotibialis or vasti muscles inserting on the cnemial process of the tibia, while the ventroposterior surface of the femur was covered chiefly by the adductor and pubi-ischiofemoralis externus muscles.

SYSTEMATIC CHARACTERS OF THE FEMUR.—The femur of *Moschops* differs from that of the pareiasaur *Propappus* (Broom, 1912a, Pl. xx) in its greater length and slenderness, in the greater reduction of the ventral trochanteric crest, in the inward flexure of the head upon the shaft and in the less pronounced divergence of the ecto- and entocondyles. In these and other features the femur of *Moschops* relates to that of *Æturosaurus* and other therapsids, while that of *Propappus* shows evidence of relationship with the cotylosaurian types. The femur of *Moschops* differs from that of the dinocephalian *Pnigalion*, as figured by Watson (1914c, p. 766), in being much less shortened and in having a narrower shaft. The femur of *Titanosuchus ferox* figured by Seeley (1889, Pl. xix) is fundamentally similar to that of *Moschops* but seems to have had the great trochanter farther down on the shaft. Watson (1914c, p. 773) states that the femur of *Titanosuchus* "differs from that of the Tapinocephaloids in its relative slenderness and the lesser size of the trochanter." This is true if the very short femur of *Pnigalion* be taken as representative of the tapinocephaloids. The femora referred to *Moschops* differ considerably in relative breadth but several of them are distinctly less widened than that of *Titanosuchus*. The latter as figured shows a possible vestige of the trochanteric crest on the middle of the under side of the femur.

TIBIA.—The tibia (Fig. 18) is a very short massive bone about half the length of the femur. Its proximal end is greatly dilated, terminating in a broad cnemial protuberance which fitted between the femoral condyles and was doubtless covered with smooth articular surfaces for the condyles. The front of the protuberance formed a cnemial boss for the insertion of the femorotibialis tendon. The articular surfaces between the tibia and the femur were such as to allow considerable twisting of the tibia upon the femur and they also permitted the fullest extension of the tibia on the femur.

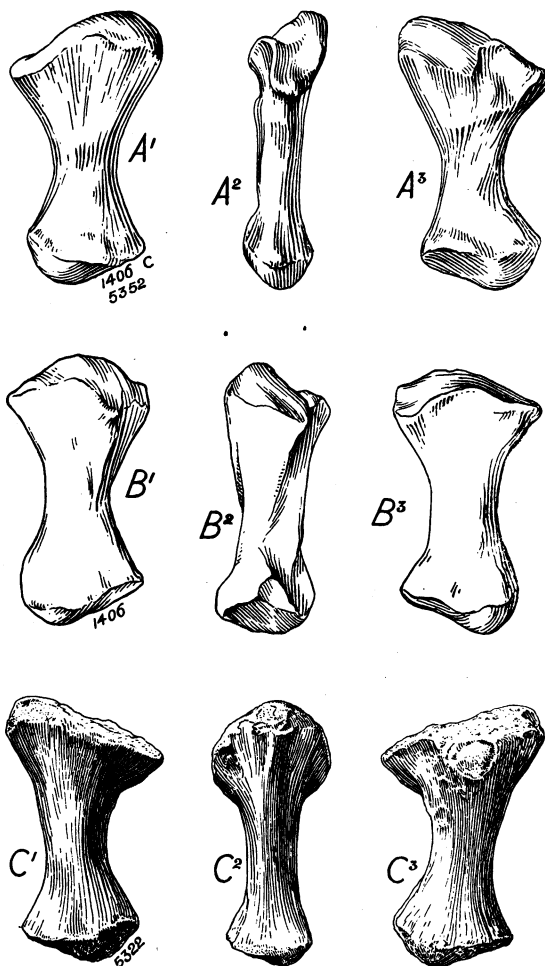


Fig. 18. *Moschops capensis*. Tibiæ.

- A¹. Right tibia, outer view.  $\times \frac{1}{4}$ .  
 A². Posterior view (crushed flat).  $\times \frac{1}{4}$ .  
 A³. Internal view (crushed).  $\times \frac{1}{4}$ .  
 B¹. Another right tibia, more robust but not crushed, probably belonging to the same species, outer view.  $\times \frac{1}{4}$ .  
 B². Anterior or anterointernal view.  $\times \frac{1}{4}$ .  
 B³. Inner view.  $\times \frac{1}{4}$ .  
 C¹. A left tibia (A. M. N. H. 5322) (uncrushed). Outer side.  $\times \frac{1}{4}$ .  
 C². Full front view.  $\times \frac{1}{4}$ .  
 C³. Inner view.  $\times \frac{1}{4}$ .

The cnemial swelling is on the anteroexternal, the distal convexity on the posterointernal side; the latter was probably supported by a cartilaginous tibiale tarsi.

The shaft of the tibia expands toward the distal end, its distal periphery being subcircular on the front and outer side and flattened on the inner side. As in primitive Permian reptiles, the tibia articulated rather with the superolateral than with the proximal surface of the astragalus. The astragalar contact is effected through a prominent protuberance on the medial lower extremity; the lower end of the tibia on the medial side ends in a prominent projection. This is roughened below, perhaps for the attachment of the tarsal ligaments, but probably did not articulate below with a tarsal bone, the true tibiale tarsi not being present in reptiles:

The tibia of *Moschops* somewhat resembles that of primitive Permian pelycosaur in its general configuration, but it is far more massive, with a more projecting cnemial tuberosity and an anteroposteriorly deeper proximal end; the fossa on the outer surface near the proximal end is lacking and the distal end bears a large convexity on its outer or postaxial side.

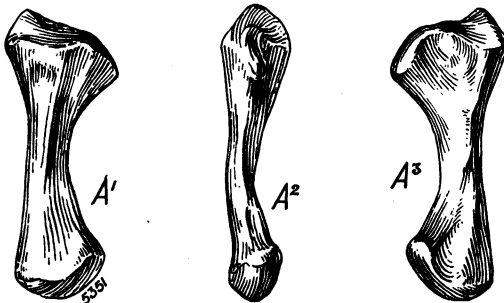


Fig. 19. *Moschops capensis*. Right fibula (A. M. N. H. 5351 "A").

A¹. Outer view.  $\times \frac{1}{4}$ .

A². Front view.  $\times \frac{1}{4}$ .

A³. Inner view.  $\times \frac{1}{4}$ .

The distal convex surface probably articulated with the calcaneum posteriorly and with the astragalus anteriorly. The expanded upper end articulated with the lateral surface of the large external condyle of the femur.

The tibia of *Moschops* is very similar to one figured by Seeley (1889, Pl. xxv) as belonging to an undetermined genus, possibly *Pareiasaurus* or *Tapinocephalus*. A supposed "ulna" figured by Seeley (1889, Pl. xxiii) is a tibia, probably that of *Propappus*, and differs from the *Moschops* type in having a pronounced fossa on the outer side lateral to the cnemial crest and in having the distal surface for the astragalus markedly concave.

**FIBULA.**—The fibula (Fig. 19) is flattened laterally, expanded at both the proximal and distal ends, and has a deeply concave anterior border and a straight to convex posterior border. Its proximal end has a subcrescentic medial articular surface for the ectocondyle of the femur, upon which it slides freely. Outside of this surface is a roughened border

for the attachment of the lateral ligaments. The expanded distal end is thicker than the proximal end, is convex below and roughened for the tarsal ligaments. It articulates both with the astragalus anteriorly and with the calcaneum posteriorly, after the fashion of the fibula of other Permian reptiles, but the facets for these elements are not distinct from the roughened area for the ligaments.

The fibula is essentially similar to that of pelycosaurs although shorter. Its relations with the astragalus and calcaneum also were probably much as in the pelycosaurs.

#### MANUS AND PES

The identification of the carpal and tarsal elements (Pls. XIII, XIV) has proved to be a problem of great difficulty, which I have been unable to solve completely even after many efforts. The difficulty is partly inherent in the fact that there are considerably over a hundred bony elements in the fore and hind feet, each one being either right or left, and presenting six aspects. Secondly, the material available for comparison is unfortunately very restricted, only small forms such as the dromasaurians, small anomodonts and therocephalians being available, while the pareiasaurs and diadectids, although large forms, differ so widely from *Moschops* in the limbs that the foot bones afford but little assistance. Thirdly, the dinocephalian material itself includes the remains of several grades of size from comparatively small animals up to the gigantic "*Tapinocephalus*." Fourthly, the podial elements of *Moschops*, with few exceptions, were nodules of bone with imperfectly ossified peripheries embedded in "cartilage," so that, as they now seldom retain the articular facets, it is usually impossible to find satisfactory contacts between the different elements.

The calcaneum (Pls. XIII, XIV, A) is represented by four subcircular flattened bones similar in general appearance to the calcaneum of the dromasaurian *Galepus*. The outer or upper surface is comparatively smooth and subcircular on the postaxial and distal borders, flattened on the preaxial or medial border. In the middle of the medial border there is a deep groove which is apparently one-half of the astragalocalcaneal canal. Above and below this groove on the medial border are facets for articulation with the astragalus. The very large calcaneum figured in Pls. XIII, XIV, Fig. A, may perhaps belong to "*Tapinocephalus*"; smaller but similar ones very probably belong to *Moschops*.

The element shown in Plates XIII, XIV, Figs. B-C, apparently represents the astragalus. Some of the points in favor of its being an astragalus are as follows:

(1) What I have identified as the front, or dorsum, of the bone agrees in general shape with that of *Galepus*. It has a smaller, well-rounded, supposed upper end and a wide convex lower end. Its upper articular surface is subcrescentic in section, the concavity looking toward the posterior side.

(2) The bone bears on its supposed lateral side a deep groove which when opposed to the corresponding groove in the calcaneum appears to complete the astragalocalcaneal canal.

(3) When these two bones are thus orientated the upper articular surfaces are inclined toward each other in such a way that they appear to form a suitable base for the fibula, while similarly the distal end, which is widely convex, appears to be a suitable surface for the support of the navicular and for contact with the cuboid. The proximal medial articular surface may have been in contact with the distal end of the tibia, although it is far too small for the entire support of the widely expanded tibia, which, as in other primitive tetrapods, was probably supported largely by a cartilaginous element, the true tibiale.

(4) The element in question compares fairly well with the astragalus of the pelycosaurs, which likewise have a prominent notch for the astragalocalcaneal canal, a lateral facet for the tibia, a narrow proximal end for the fibula and a very wide distal end for the navicular and cuboid.

(5) The astragalus more closely resembles that of the anomodont *Lystrosaurus* as figured by Watson (1913, p. 258).

There are at least five of these elements in the collection, three of one side and two of the other side. The considerable differences between the smaller one, with its flattened dorsum and plantar surfaces, and the large ones, with their greatly swollen proximal ends, are perhaps correlated with different age and growth stages.

Another set of bones (Pls. XIII, XIV, Figs. G, H), rights and lefts of different sizes, probably represents the scaphoid, or radiale. The evidence tending to show that these are radialia is as follows:

In the other therapsids available for comparison (which are small forms and therefore perhaps somewhat unsatisfactory guides), the radiale is a relatively large element, of which the front, or dorsum, is nearly as wide as the distal end of the radius, to which it is closely appressed. It is widely convex on the proximal end, the convexity extending on to the dorsum or front surface. It articulates below with the centrals, with the trapezoid, or first distal carpal, and possibly with the cuneiform. In *Moschops* the bone under consideration is likewise a broad element nearly as wide as the distal end of the radius; it has a

broadly convex upper face and bears well-defined facets, two on the lower surface for the centrals, and one on the supposed inner side possibly for the lunar. Moreover the appearance of the supposed proximal surface of this element is similar to that of the distal end of the radius. Nevertheless, none of these bones will fit closely on any of the radii, probably because they were covered with a thick cartilaginous surface. The element in question is apparently not the cuneiform, or ulnare, and it is obviously too large to be any of the centrals or distal carpals. It is wholly unlike any known navicular of the tarsus, and it is almost certainly not the astragalus, for which I at first mistook it.

Several smaller elements with polygonal faces may represent the distal carpals of digits I, II and III of the manus. The larger elements of somewhat similar form (Pls. XIII, XIV, Figs. I, J) may be the fourth distal tarsals.

There are at least six other kinds of mesopodial bones represented in the *Moschops* material, but after many attempts I have as yet failed to identify them.

**DIGITS.**—The digits are represented by a number of very short flattened phalanges and by some of the metatarsals (Pls. XIII, XIV, Figs. K, L). The ungual phalanges (Pls. XIII, XIV, Figs. M–S) were in the form of flattened blunt claws rather than wide-spreading hoofs. In the mounted skeleton the restored unguals are probably too much flattened.

Comparison of the podial elements with those of other animals is naturally limited by the uncertainty of determination of the elements in *Moschops*, but a few points seem reasonably clear.

(1) The astragalus differs from those of the pelycosaurs in the defective ossification of all its borders, but the calcaneum is closer to the type in its flat subcircular contour, in the flattening of the astragalar border and in the presence of the tibial groove for the astragalocalcaneal canal. No doubt the astragalus and calcaneum together articulated with the distal end of the fibula in the fashion characteristic of all Permian reptiles, while the medial side of the astragalus partly supported the tibia.

(2) The astragalocalcaneal complex differed widely from those of the cotylosaurs and pareiasaurs, inasmuch as the astragalus and calcaneum were neither closely appressed as in cotylosaurs, nor fused together as in some pareiasaurs. Thus the tarsus was much more mobile in *Moschops* than in either of these groups.

(3) None of the carpal elements, except possibly those of the distal row, showed any close similarity to those either of the pelycosaurs or of the cotylosaurs with which they were compared.

(4) It may be expected that when better known the carpus will show significant points of resemblance with that of the anomodonts. Meanwhile it may be said that in comparison with the small dromosaurian *Galechirus* and with the primitive theriodont *Theriodesmus*, the carpal elements of *Moschops* are less well ossified and were indeed surrounded by a more or less thick layer of cartilage. The imperfect ossification of the periphery of the bones is not necessarily an indication of aquatic adaptation, as it is in cetaceans and ichthyosaurs, since somewhat similar conditions are found in very large crocodilians, chelonians, dinosaurs and even in small anomodonts. In the case of *Moschops* the peripheries of the podial elements are better ossified in the small skeleton A than in the larger skeletons.

Taken as a whole the manus and pes of *Moschops* are rather similar to those of a gigantic tortoise, with very large mesopodials, very short, broad metapodials and intermediate phalanges, and narrowed ungual phalanges.

#### SYSTEMATIC RELATIONS OF *MOSCHOPS* AND THE EVOLUTION OF THE SKULL IN THE TAPINOCEPHALIDÆ

In considering the relationships of *Moschops capensis* with allied genera, the writer has gradually developed the following general concept of the evolution of the tapinocephalid group of the Dinocephalia. Watson, Broom and Haughton in recent years, and Seeley and Owen in earlier times,<sup>1</sup> have laid the foundations for such an outline through their morphologic and systematic descriptions of the skulls. Broom and Watson have ably discussed not only the remote relationships of the South African Dinocephalia with the stem of the American pelycosaurs but also the probable origin of the dinocephalian group from the Gorgonopsia or primitive theriodont reptiles.

Unfortunately little is known concerning the stratigraphic succession of the Dinocephalia, which range from the *Ecca* beds of the Lower Permian through the *Pareiasaurus* or *Tapinocephalus* zone of the Middle Permian. A review of the group as a whole, however, indicates that there are several grades of organization represented among the various genera.

MECHANISM OF THE JAWS AND ORIGIN OF THE GROUP.—In *Moschops* (Fig. 22B), *Moschognathus* (Pl. XVI), and other dinocephalians, the quadrate, or suspensorium of the lower jaw, is greatly prolonged downward and forward. This has a triple effect: first, it shortens the

<sup>1</sup>See titles in bibliography, pp. 250,251.

jaw and thus brings the fulcrum nearer to the points of resistance lying between the enlarged upper and lower incisors; secondly, it greatly deepens the space occupied by the temporal muscles, and thirdly, by bringing the fulcrum below the level of the teeth it enlarges the angle of insertion of the temporal, masseter and pterygoid muscles on the mandible and thus increases the biting power. A somewhat analogous series of adaptations is seen among the iguanodont dinosaurs, where, perhaps to increase the effectiveness of the power applied to the teeth and to supply vertical space for the high tooth rows, the quadrate suspensorium is greatly deepened, so that the quadrate-articular joint is brought forward and below the level of the teeth.

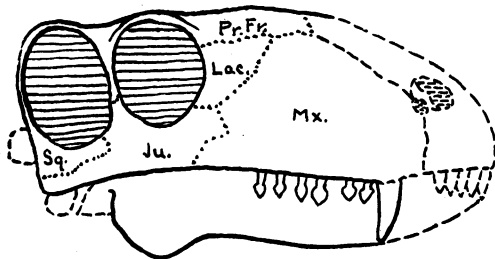


Fig. 20. *Rhopalodon fischeri*. Restoration by Watson (1921) based on figures by Seeley and von Meyer.  $\times \frac{1}{8}$ .

The genus *Rhopalodon* of the Permian of Russia, as reconstructed by Watson (1921, p. 89) from Seeley's data, has not yet effected this important change in the relations of the mandible to the skull. It still has the quadrate-articular joint nearly on a level with the cheek teeth, while the quadrate and squamosal are not produced downward and forward so as to bring the mandibular joint beneath the orbit. This type of skull seems to be near the starting-point of the Titanosuchidæ, which had a long, straight skull without a marked forward displacement of the quadrate-articular joint. On the other hand, the gorgonopsian *Arctops*, as figured by Watson (1921, pp. 37, 38), appears to have taken the initial step towards the tapinocephaloid condition of the temporal region. In the allied *Gorgonops*, the pineal foramen is raised on a column standing above the general level of the parietal region, much as it is in the Tapinocephalidæ, while the large size of the septomaxilla, which divides the anterior nares into two parts, the presence of five incisors, a canine, and in many gorgonopsians, of reduced molars, all afford the common starting-point for the line leading to the Tapinocephalidæ.

GROWTH CHANGES AND EVOLUTION OF THE SKULL.—Apparently the most primitive known South African dinocephalian genus is *Moschosaurus*,<sup>1</sup> in which the postorbital bar is relatively very narrow, while the most advanced genus in this respect is *Mormosaurus*, in which both the postorbital and the zygomatic arches are of enormous width. Similarly *Moschosaurus* has only a beginning of the frontal swellings, which increase in prominence in the *Moschops* series and finally culminate in *Mormosaurus* (Fig. 26B) in an enormous tumescence of the bones above and in front of the orbits.

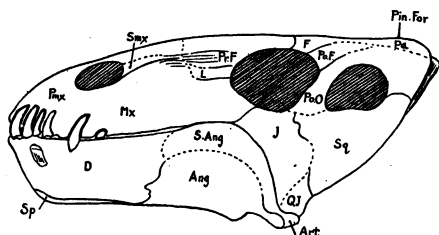


Fig. 21. *Moschosaurus longiceps*. Skull. After Haughton, 1915.  $\times \frac{1}{6}$ .

The evolutionary changes in the tapinocephalid skull are partly recapitulated by the growth changes illustrated in a series of *Moschops* skulls. As shown in the table of measurements (p. 228), the postorbital bar rapidly thickens from youth to old age. The swellings on the frontals above the orbits increase in size, and the broad zygomatic arch connecting the squamosal and quadratojugal with the back and floor of the orbit further increases its width.

Both in the successive growth stage of *Moschops* and apparently also in the evolution of the group, there is a progressive shallowing of the upper jaw. Thus the type of *Moschops capensis* (Fig. 22B), a young skull, has a short and deep face from the orbit to the tip of the premaxilla; *Moschops* A (Pl. XV), a much older skull, has the snout distinctly shallower, while *Moschognathus* (Pl. XVI), *Mormosaurus* (Fig. 24B) and *Struthiocephalus* (Fig. 29) form a progressive morphological series in the shallowing of the snout.

This process is possibly associated with the fact that at a certain stage, illustrated in the type of *Taurops macrodon* Broom (Pl. XX, A),

<sup>1</sup>Broom (1923, p. 663) suggests that the type skull of *Moschosaurus* represents a small and probably immature titanosuchid. If the genera *Scapanodon*, *Dinophoneus* and *Dinartamus* described by Broom in his 1923 paper are really titanosuchids, then perhaps the most conspicuous feature separating the Titanosuchidae from the Tapinocephalidae is the enlargement of the canines in the former, as the two groups are extremely alike in the structure of the skull and of the lower jaw.

TABLE II.—AGE CHARACTERS OF *Moschops*

Measurements in Millimeters	<i>Delphino- gnathus</i>	<i>Moschops</i>				<i>Mormo- saurus</i>
		Type 5550	5551 A	5551 B	5551 C	
Least width of postorb. bar	20	30	55	78	63	99
Least width across parietals at top of temp. fossæ	114	43	81	128	131	144
Least width above middle of orbits	..	120 <sup>1</sup>	103 <sup>2</sup>	135	139	198
Maximum width above and behind orbits	..	178 <sup>1</sup>	165	233	222	..
Maximum width skull across sq.	..	190 <sup>1</sup>	205 <sup>1</sup>	300 <sup>1</sup>	304	432
Ant. post. diam. orbits	70	75	66	..	..	72
Oblique vert. diam. zyg. arch	..	54 <sup>1</sup>	74	..	..	156
Greatest length skull, pmx. to tab.	..	355	360	420 <sup>1</sup>	385 <sup>1</sup>	508
Greatest height skull qu. cond. to tip pineal boss	228	210	257	..	257+	300
Basal length, pmx. to cond.	310+	300	320	..	320+	447
Width occ. above for. mag.	200	..	198	..	..	400
Base occ. cond. to summit occip. plate	160	155	170	160	..	180
Length qj. to pmx. tip	252 <sup>1</sup>	263	282 <sup>1</sup>	..	..	342
Length of snout (pmx. to orb.)	..	178	167	213	..	270
Length of lower jaw	200+	250	..	263	..	..

the large deciduous teeth are all in place, while beneath them are the very deep permanent teeth. The second upper deciduous incisor of *Taurops* was not less than 85 mm. in height, while the third lower permanent incisor, with its lower end still uncompleted, is at least 50 mm. in height. The jaws therefore are correspondingly deep. But after the deciduous set were shed and the permanent teeth were in place, the latter doubtless began to wear down the crowns and to close up the open root canals and thus the size of the basal portion of the teeth would be reduced. Under these conditions the alveolar parts of the jaw would probably become shallower, as they are in the type of *Moschognathus whaitsi* (Pl. XVI).

*Moschops* AND *Delphinognathus*.—The table of measurements shows (p. 230) that *Moschops* is closely allied to *Delphinognathus* (Fig. 22A). One of the chief generic differences was the supposed presence of a large foramen in *Delphinognathus*, separating the quadratojugal from the jugal; but Seeley's carefully executed figure and description (1892) give no

<sup>1</sup>Estimated.<sup>2</sup>Crushed.

indication of the closure of this supposed foramen on the under side, and Broom's restoration of this spot is entirely dotted. It seems possible that the supposed foramen is what Seeley thought it was, a small excavation in the lower border of the jugal, and that it differs only in degree from the slight concavity in this region seen in *Moschops*. The convexity on the lower border of the jugal in front of it may mark the attachment of the tendon of the masseteric portion of the temporal muscle mass. In this case the difference from *Delphinognathus* would be one of degree rather than of kind. The latter genus also differs from *Moschops* in the lesser expansion of the postorbital bar and in the much greater promi-

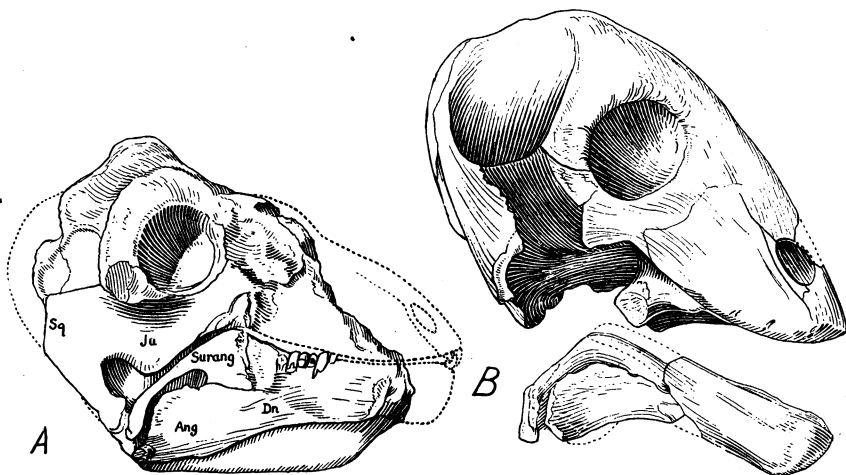


Fig. 22. Comparison of *Delphinognathus* and *Moschops* skulls.

A. *Delphinognathus conocephalus* Seeley. Type skull adapted from Seeley, 1892.  $\times \frac{1}{6}$ .  
 B. *Moschops capensis* Broom. Type skull and lower jaw. A. M. N. H. 5550. Adapted from Broom, 1911.  $\times \frac{1}{6}$ .

nence of the pineal boss. Seeley's figures suggest also that the posterior cheek teeth were larger than those of *Moschops*, but in many respects the relationship of *Moschops* with *Delphinognathus* is close.

The *Moschops* skulls are intermediate in size between the small skull of *Delphinognathus* and the larger forms of the *Tapinocephalus* group, including *Tapinocephalus*, *Mormosaurus* and *Struthiocephalus*. For example, the extreme length of the skull from the tip of the snout to the tabular in the *Moschopinæ*<sup>1</sup> varies from 355 to 402 mm.; in the *Tapinocephalinæ*,<sup>1</sup> from 530 to 580 mm.

<sup>1</sup>See page 241.

TABLE III.—COMPARATIVE SKULL MEASUREMENTS OF *Moschops* AND *Delphinognathus*

Measurements in Millimeters	<i>Delphinognathus conocephalus</i> Type	<i>Moschops capensis</i>		
		Type A. M. 5550	A	C
Length of skull (pmx. to condyle)	310+	300	320	320+
Transv. meas. occiput above for. mag.	200	....	198	....
Vert. meas. base occ. cond. to summit occ. plate	160	155	170	....
Width occ. condyle	40+	48	48	....
Width of quadrate near distal end	40	50	....	....
Transv. width postorb. mass	115	90	95	163
Diam. parietal foramen	20	19	....	....
Measurement from summit of parietal cone to superior margin of zyg. arch	110	135	168	172
Diam. orbit	70	75	65	....
Width postorb. bar	25-20	70-60	55-50 68-57	76-60
Obliq. meas. post. inf. border sq. to lower margin of orbit	75+	100	110	135+
Width subovate notch on lower border zyg. arch between ju. and sq. (Due to unusually strong tubercle for masseteric division of temp. mass.)	Between 20&30	(about 50)	....	....
Length of lower jaw, cond. to symph.	200+	240	....	263
Depth below and behind coronoid	130	100	....	127

*Prigalion*.—This genus (Fig. 23A) is apparently allied with the Moschopinae rather than with the Tapinocephalinae. It is distinguished especially by its relatively narrow occiput. The dentary teeth figured in the top view (Watson, 1914c, pp. 757, 768) seem to agree in principle with those of *Moschognathus*.

*Lamiasaurus*.—The cranium (Fig. 23B) of *Lamiasaurus* (Watson, 1914c, pp. 760, 761) shows that the upper end of the laterotemporal fenestra was excessively narrow. A distinct foreshadowing of this condi-

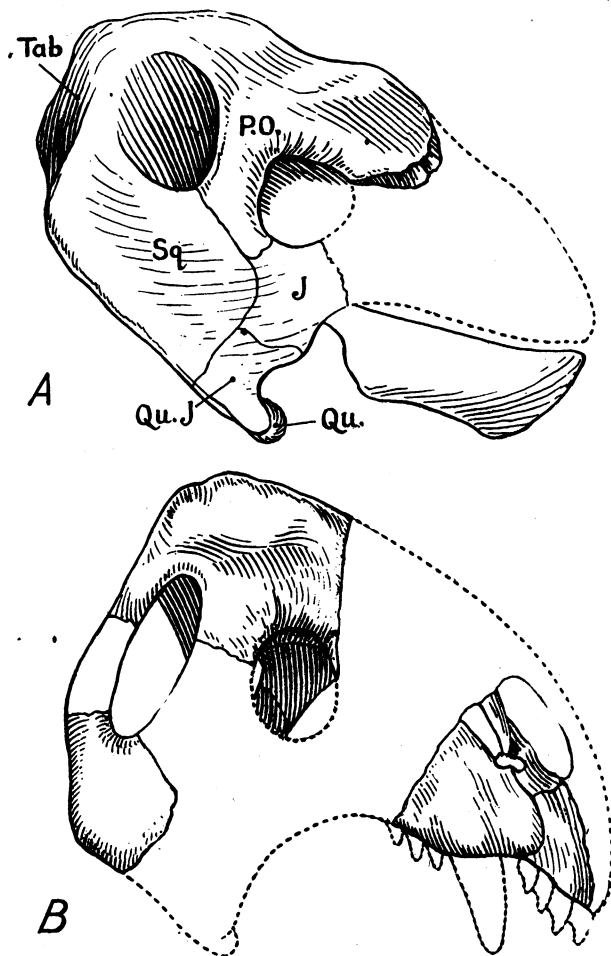


Fig. 23. Comparison of *Pnigalion* and *Lamiasaurus* skulls.

A. *Pnigalion oweni* Watson. Type skull. Adapted from Watson, 1914.  $\times \frac{1}{4}$ .

B. *Lamiasaurus newtoni* Watson. Type skull and wrongly associated snout. Adapted from Watson, 1914.  $\times \frac{1}{4}$ .

tion may be seen in our skull *Moschops* A (Pl. XV), A. The vertex is surmounted by a low but large boss, which apparently represents a combination of the pineal boss with the swollen region above the temporal fenestra. Here again the conditions appear to be derivable from those in the skull of *Moschops* A, and the same is true of the posteroinferior part of the squamosal region. On the other hand, the muzzle assigned to this form differs radically from all definitely known Tapinocephalidæ in the

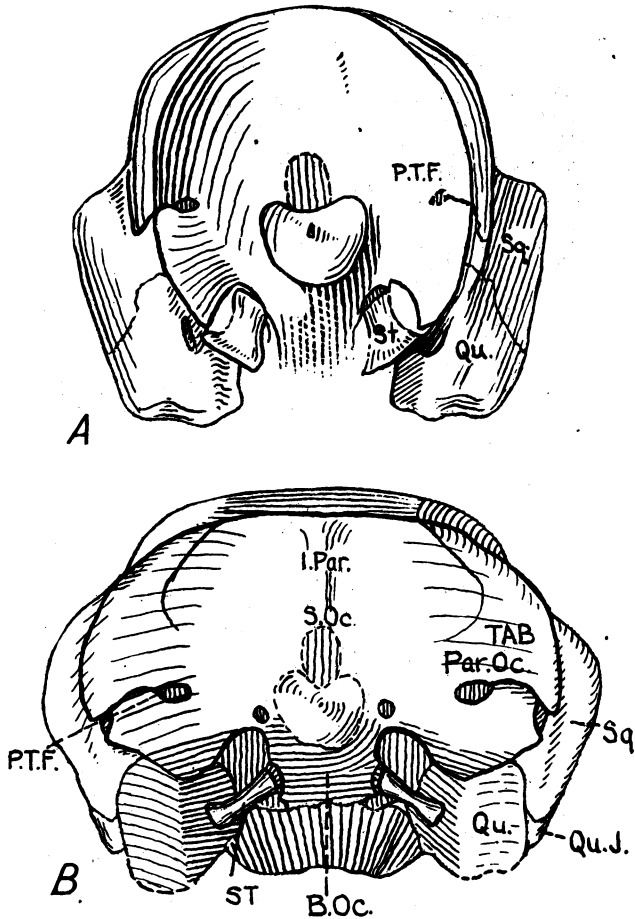


Fig. 24. Comparison of occiputs of *Pnigalion* and *Mormosaurus*.

A. *Pnigalion oweni* Watson. Type skull. Adapted from Watson, 1914.  $\times \frac{1}{6}$ .  
 B. *Mormosaurus seeleyi* Watson. Type skull. Adapted from Watson, 1914.  $\times \frac{1}{6}$ .

great enlargement of the canines (see above, p. 227, footnote) and may therefore belong to a titanosuchid.<sup>1</sup>

**DENTITION OF THE MOSCHOPINÆ.**—Although several skulls and jaws of *Moschops* are in the American Museum collection, their teeth have either dropped out of the sockets or are represented only by broken stumps. The mounted specimen (A. M. N. H. 5552 B), however, has one

<sup>1</sup>Watson (1921) and Broom (1923) have come to the same conclusion. On the other hand, it may well be doubted whether the enlargement of the canine is a reliable criterion for the separation of tapinocephalids and titanosuchids.

of the large anterior teeth adherent to the front border of the orbit. The labiolingual diameter of the crown on the plane of the basal expansion is 20 mm. The height of the crown is comparatively small and the tooth probably belongs to the first or deciduous set. The alveoli indicate that the dental formula of *Moschops* was the same as that of *Moscognathus* and *Taurops* as given below.

When the matrix was removed from the type specimen (Fig. 25 and Pl. XX) of *Moscognathus whaitsi* Broom, it supplemented the facts as to the dentition already known from the type of *Taurops macrodon* Broom (Pl. XX). It also showed that the single tooth to which the name *Eccasaurus* (Pl. XIX) had been applied closely resembled one of the large upper deciduous incisors of *Moscognathus* and that the single known tooth of *Moschops* mentioned above also conformed to the same type. But before considering the systematic status and relationships of these nominal genera, let us first summarize the general, or perhaps subfamily, characters afforded by a comparison of all these specimens with each other.

The teeth belong to two sets, and, at least at present, there is no evidence of more than two sets. The relations of these two sets are the same as those of the deciduous and permanent sets of mammals, that is, the bases of the deciduous teeth become resorbed, while the deciduous teeth fit like caps upon the permanent teeth (Pl. XX). The incisors, canines and premolars are replaced but possibly the molars are not.

The dental formula of *Moscognathus*, *Taurops* and probably also of *Moschops* is approximately:

$$DI\frac{3}{3}DC\frac{1}{1}DP + M\frac{?}{?}\frac{1\frac{1}{2}}{1\frac{1}{2}}; I\frac{3}{3}C\frac{1}{1}P \pm M\frac{?}{?}.$$

The first maxillary tooth is regarded as a canine, although it agrees rather with the incisors in form. The median pairs of upper and lower deciduous incisors (Fig. 25) are relatively small and compressed (see table III). The remaining deciduous incisors are much larger, but their crowns are much shorter than those of the permanent incisors. Some of the latter (known in *Taurops*) are not less than 85 mm. in estimated height from tip to base. They have widely open pulps and the enamel is continued at least two-thirds the way toward the base. In the deciduous incisors (*Moscognathus*) the crowns are shorter; there is a sharp constriction at the neck, and the root canal (shown in one of them) is smaller.

The high tips of the lower teeth fit between the upper teeth, but the expanded lingual basal parts of the upper and lower incisor crowns over-

lap each other. The motion of the jaw is vertical, so that the front teeth have a piercing, tearing and crushing action.

As we pass backward the lingual basal expansion of the crowns increases, while the tips become lower and the whole crown becomes smaller, so that the larger piercing front teeth give place to small, wide, spatulate molars with the cutting edge set obliquely to the alveolar line.

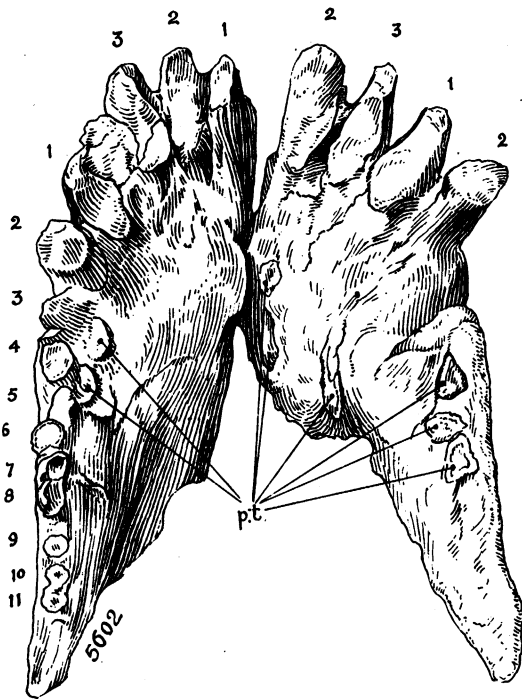


Fig. 25. *Moschognathus whaitsi* Broom. Palate of type. A. M. N. H. 5602. 1, 2, 3, teeth in premaxillæ; 1-11, teeth, or alveoli, in maxillæ; p.t., replacing teeth embedded in alveolar process.  $\times \frac{1}{2}$ .

In view of the fundamental agreement of *Moschops*, *Moschognathus* and *Taurops* in the general morphology of the jaws and teeth, we are confronted with the question whether all these forms may not be congeneric. Indeed if palæontologists had not become accustomed to attaching new names to almost all important specimens of the Permian reptiles, it is doubtful whether these forms would have been separated generically. Nevertheless, after prolonged handling of these specimens my feeling is that Broom's judgment should be accepted at least provisionally, especially in regard to the generic distinctness of *Moscho-*

*gnathus*. Although this genus agrees with *Moschops* in having three teeth in the premaxilla, twelve in the maxilla and probably sixteen in the dentary in use at one time, it differs markedly from *Moschops* in the vertical shallowness of the snout, which distinctly foreshadows that of *Mormosaurus*, and in the unthickened form of the zygomatic bar. The mandible is perhaps not quite so deep as that of a full-grown *Moschops*, but this also may be an age character. *Moschognathus* is also distinguished from *Moschops* by the more slender character of the axis and by other details of the postcranial skeleton.

The series of teeth referred to one individual of uncertain generic reference, figured by Watson (1914c, p. 768), strongly resemble the teeth of *Moschognathus* in so far as they represent the large front teeth with a prominent cusp and oval base, some further back having a widened lingual portion, the molars having compressed and partly serrate crowns. Nevertheless, this resemblance may not imply generic identity with *Moschognathus* in view of the apparent uniformity of the dental characters throughout the Tapinocephalidæ.

*Taurops*.—The muzzle of *Taurops macrodon* Broom (Pl. XX) is larger and more massive than that of *Moschops*, although it has the relatively deep maxilla of that genus. On the other hand, it is distinctly smaller than in any of the Tapinocephalinæ. Again, the dentition is close to that of *Moschognathus*, including the three large teeth in the premaxilla and probably twelve in the maxilla, but the more posterior teeth of the maxilla and dentary are distinctly larger.

*Eccasaurus*.—This genus was originally founded upon a limb bone from the Eccia formation. A single tooth (A. M. N. H. 5625; Pl. XIX, B) provisionally referred to this genus by Broom,<sup>1</sup> resembles the third right upper incisor of *Moschognathus*, but in view of the doubt whether this tooth really belongs to *Eccasaurus*, it would be very inadvisable to cancel *Moschognathus* as a synonym of *Eccasaurus*.

*Tapinocephalus*.—The large snout figured by Owen (1876, Pls. I, II) so closely resembles that figured by Houghton (1913, pp. 40, 41) that we may take the latter skull (Fig. 26A) as a neotype. This form has an enormous tumescence on top of the skull above and in front of the orbit. As noted above, the beginnings of this condition are indicated in *Moschops*, but are never carried very far in that genus. The skull is extremely wide across the squamosals, so that this dimension is equal to the extreme length from snout to tabular. The orbit is small and the

<sup>1</sup>Proc. Zool. Soc., 1912, p. 875.

TABLE IV.—COMPARATIVE MEASUREMENTS OF THE TEETH OF *Moschognathus*,  
*Eccasaurus*, *Moschops*, *Taurops*

Measurements in Millimeters	<i>Moschognathus</i> Type A. M. 5602	" <i>Eccasaurus</i> " A. M. 5625	<i>Taurops</i> Type A. M. 5610	<i>Moschops</i> A. M. 5551B
<i>Premaxillary Teeth</i>				
No. 1, right side, mesiodistal and labiolingual	$\frac{7.8}{17}$			
No. 1, left " " " "	absent		<u>16.2</u>	
No. 2, right " " " "	$\frac{11.6}{25.9}$			
No. "2," left " " " "	$\frac{13}{23}$		<u>13</u>	
No. 3, right " " " "	$\frac{12.3}{25.6}$	$\frac{14}{26}$		
No. "3," left " " " "	$\frac{11.7}{27.3}$		<u>14.3</u>	
<i>Maxillary Teeth</i>				
No. 1, right side, mesiodistal and labiolingual	$\frac{12}{25.3}$		<u>12</u>	
No. 1, left " " " "	$\frac{12.7}{25.2}$			
No. 2, right " " " "	<u>13.2</u>			
No. 2, left " " " "	$\frac{13.8}{17.2}$			<u>20</u>
No. 3, right " " " "				
No. 3, left " " " "			<u>13.8 e</u>	
No. 4, right " " " "	<u>10.6</u>			
No. 4, left " " " "			<u>11.8</u>	
No. 5, right " " " "				
No. 6, right " " " "	$\frac{9.8}{7.2}$			
No. 7, right " " " "	$\frac{10.3}{6}$			
No. 8, right " " " "	$\frac{7.7}{5.7}$		<u>12.2</u>	
<i>Dentary Teeth</i>				
No. 1, right side, mesiodistal and labiolingual	$\frac{17.1}{24.3}$			
No. 2 " " " " "	$\frac{14.2}{21.1}$			
No. 3 " " " " "	$\frac{16.5}{24.7}$			
No. 4 " " " " "	$\frac{11.7}{20 e}$			
No. 5 " " " " "	$\frac{13.5}{18 e}$			
No. 6 " " " " "	$\frac{12.5}{12.6}$			
No. 7 " " " " "	$\frac{10.8}{9.6}$			
No. 8 " " " " "	$\frac{10.2}{7.3}$			
No. 9 " " " " "	$\frac{9.5}{6.5}$			

e=Estimated

opening of the temporal fossa is much restricted. The tooth figured by Watson as ? *Tapinocephalus* (1914c, p. 768, Fig. 16B) is close to those of *Moschops*, *Eccasaurus* and *Moschognathus*.

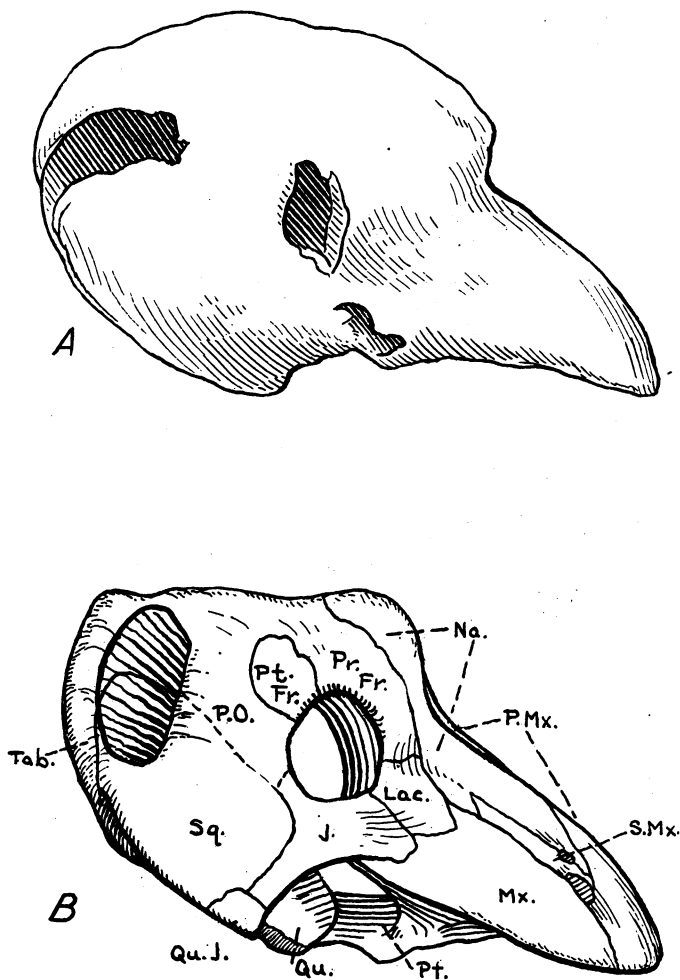
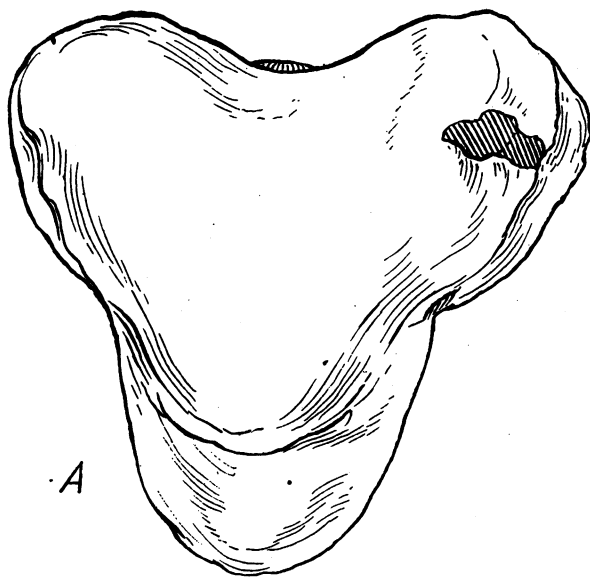


Fig. 26. Comparison of *Tapinocephalus* and *Mormosaurus* skulls.

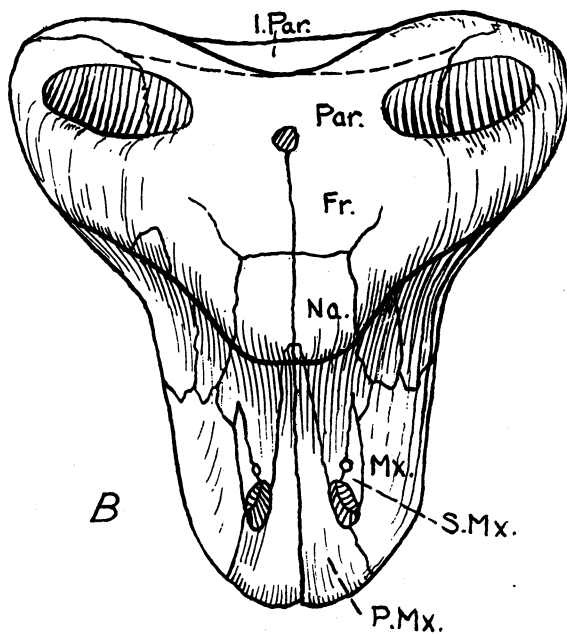
A. *Tapinocephalus atherstoni* Owen. After Haughton, 1913.  $\times \frac{1}{6}$ .

B. *Mormosaurus seeleyi* Watson. After Watson, 1914.  $\times \frac{1}{6}$ .

*Mormosaurus*.—The skull of this form (Figs. 26B, 27B) is admittedly close to that of *Tapinocephalus*, so much so that Broom referred it to the same genus. Allowing for the differences in presentation, the top view



A



B

Fig. 27. Comparison of *Tapinocephalus* and *Mormosaurus* skulls, top view.

A. *Tapinocephalus atherstoni* Owen. After Haughton, 1913.  $\times \frac{1}{6}$ .

B. *Mormosaurus seeleyi* Watson. After Watson, 1913.  $\times \frac{1}{6}$ .

compares rather closely with that of *Tapinocephalus* as figured by Haughton. So far as one can see, the under side of the muzzle (Fig. 28) differs from that of the type figured by Owen chiefly in the narrowness of the posterior extension of the maxilla. Watson, however (1914c, p. 767), states that "*Mormosaurus seeleyi* . . . has an extremely feeble dentition which is quite uniform throughout, so far as can be judged from the

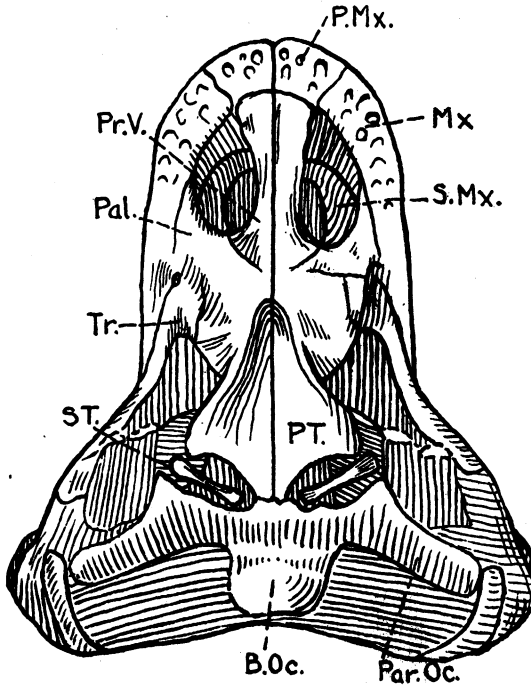


Fig. 28. *Mormosaurus seeleyi* Watson. Under side of type skull. After Watson, 1914.  $\times \frac{1}{6}$ .

usually imperfect crowns of the alveoli. Each tooth seems to consist solely of a cusp which is oval in section and has a closely serrated edge." Apart from this, *Mormosaurus* is close to *Tapinocephalus*. In *Mormosaurus* (Fig. 28) the large premaxillæ and the posteriorly tapering maxilla in the palatal view are substantially like those of *Moschops* and *Moschognathus*. Watson figures two rows of alveoli for the functional and succeeding series of teeth, exactly as in *Tapinocephalus*, *Moschops* and *Moschognathus*. Most of the dimensions of *Mormosaurus*, as deduced from Watson's carefully executed drawings, are compatible with the

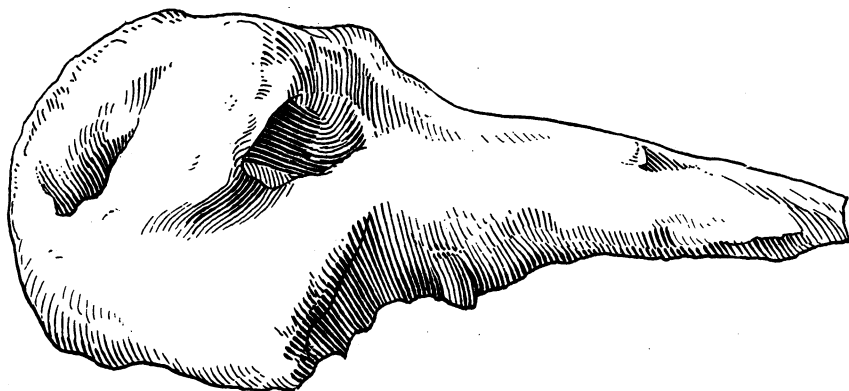


Fig. 29. *Struthiocephalus whaitsi* Houghton. Adapted from Houghton, 1915.  
 $\times \frac{1}{6}$ .

view that this genus is closely related to *Tapinocephalus*. In the side view (Fig. 26B) the nasal tumescence of *Mormosaurus* is essentially similar to that of *Tapinocephalus*, so that under the older standards of palæontology these forms would probably be referred to the same genus.

*Struthiocephalus*.—The skull of *Struthiocephalus* (Fig. 29), as noted above, is distinguished by its great length in proportion to its width and by its relatively long snout. It seems to be related especially to *Mormosaurus*.

TABLE V.—COMPARATIVE SKULL MEASUREMENTS OF THE GENERA OF TAPINOCEPHALIDÆ

Measurements in Millimeters	<i>Moschosaurus</i>	<i>Delphinognathus</i>	<i>Moschops</i>	<i>Prigalion</i>	<i>Tapinocephalus</i> (Haughton)	<i>Mormosaurus</i>	<i>Struthiocephalus</i>
Length skull, pmx. to cond.		310+	300–320+		435	447	515
Extr. length tip snout to tab.	340		35 5–420 <sup>1</sup>		530	508	580
Length, qj, to tip pmx.	246	252 <sup>1</sup>	263–282		290+	342	420
Extr. breadth, across sq.			190–304	372	530	432	355
Height, condyle to top occiput.		160	155–170+	210		180	
Height, qu. cond. to tip pineal boss	260	228	210–257+	336		300	260?
Length, ant. bord. orb. to tip snout	180		178–167		264 <sup>1</sup>	270	325±
Least width skull above mid. orbits	80		120–139			198	
Ant. post. diam. orbit	66	70	65– 75			72	95
Least super. inferior meas. of zyg. arch (from lower border ju. to lower border l. t. f.)	60	66	54– 74+	150	180	156	
Meas. lower border orb. to back qj.	72	108	100–112+	144	144?	123	
Least width post. orb. bar	15	20	30– 78	42		99	
Max. height l. t. f. above sq.	36		130	120		126	
Length of lower jaw, condyle to symphysis	215	200+	250–263				

RÉSUMÉ OF THE SYSTEMATIC RELATIONSHIPS OF MOSCHOPS

In conclusion, the systematic relationships of *Moschops* with the other genera of Tapinocephalidæ may provisionally be epitomized as follows:

MOSCHOSAURINÆ.—Skull long. Postorbital bar narrow, cranial vertex not swollen. No nasofrontal tumescence. *Moschosaurus*.<sup>2</sup>

MOSCHOPINÆ.—Skull short, snout deep. Postorbital bar progressively widened. Cranial vertex swollen. Opposite nasofrontal swellings not united into a median tumescence. *Delphinognathus*, *Moschops*, ?*Moschognathus*, *Taurops*, *Prigalion*, *Lamiasaurus*.

TAPINOCEPHALINÆ.—Cranium wide, snout shallow. Postorbital and zygomatic bars excessively wide. Opposite nasofrontal swellings united into a large median tumescence. *Tapinocephalus*, *Mormosaurus*, *Struthiocephalus*.

<sup>1</sup>Estimated.  
<sup>2</sup>See footnote on page 227.

It will be observed that these provisional "subfamilies" represent grades of organization, not phylogenetic series, which are as yet unknown in the group. But in these days, when "genera" have replaced species, the subfamily must often serve for the old genus, if the classification is to express resemblances as well as differences.

#### SUMMARY AND ANALYSIS OF SKELETAL CHARACTERS

1. PRIMITIVE REPTILIAN HERITAGE.—In the foregoing description I have frequently referred to the specialized and advanced characters of the skeleton of *Moschops* and other dinocephalians, but it should not be forgotten that we are dealing with reptiles of the Lower and Middle Permian and that at that immensely remote epoch *Moschops* preserved, underneath its special habitus, a large number of extremely primitive characters from the dawn of reptilian life in the Carboniferous. They are as follows:

- (1) The *Moschops* skull, so far as known, apparently retained all but four of the primitive tetrapod skull elements, these four being the intertemporal, the supratemporal, the interfrontal and the mesopterygoid.
- (2) It retained the pineal eye common to all primitive vertebrates.
- (3) The septomaxilla is undiminished.
- (4) The palate is of fairly primitive type, with undiminished quadrate.
- (5) The pterygoid ramus of the quadrate and the quadrate ramus of the pterygoid are large.
- (6) The occipital condyle is single and pierced by the notochord.
- (7) The neurocranium is of primitive reptilian type.
- (8) The occiput retains the dermosupraoccipitals (interparietals) and large tabulars.
- (9) The mandible includes the full complement of primitive elements, and the postdentary elements are not reduced.
- (10) In the postcranial skeleton the atlas-axis complex is of the primitive temnospondyl type.
- (11) The other vertebræ are holospondylous, mostly amphiplatyan.
- (12) They are apparently pierced by the notochord in immature specimens.
- (13) They show also but little regional differentiation from the third cervical to the posterior lumbar.
- (14) The sacrum consists of one enlarged sacral rib followed by two or three smaller ones.

(15) The ribs are dichcephalous, the tuberculum articulating with the diapophysis, the capitulum with the anterior part of the centrum.

(16) Fewer primitive reptilian characters are found in the limbs but the pectoral girdle has the full complement of primitive tetrapod elements, although the cleithrum is reduced to a vestige.

(17) The humerus has expanded distal and proximal ends,

(18) a relatively short shaft,

(19) prominent ent- and ectepicondyles and

(20) an entepicondylar foramen.

(21) The radius and ulna are short stout elements not closely appressed to each other but forming a very broad forearm.

(22) The carpals are of large size and many in number.

(23) The phalangeal formula is not known, but may be expected to approximate that of primitive reptiles.

(24) The pelvis has a primitive pubi-ischiadic plate.

(25) All three elements meet in a triradiate suture in the acetabulum.

(26) The pubis has a prominent tubercle on its anterolateral border.

(27) The femur, although much modified, has the oval head continuous with the great trochanter and

(28) the ectocondyle larger than the entocondyle.

(29) The tibia and fibula are short bones widely-spreading at the distal end and the fibula is strongly bowed.

(30) The proximal tarsals consist of a much enlarged intermedium or astragalus and a subcircular fibulare or calcaneum.

(31) Astragalus and calcaneum are separated by a tarsal foramen; the true tibiale, as in most primitive reptiles, had probably already become reduced and cartilaginous.

(32) The remaining tarsals, while not exactly identified, so far as known were of primitive reptilian type.

(33) The manus and pes were very probably pentadactylate.

2. COMPARISON WITH THE PELYCOSAURS.—There are important characters shared by the dinocephalians with the American pelycosaurs or some of them. Broom (1910, 1914a) and Watson (1914a, pp. 178, 179) have made out a strong case for the common origin of the therapsid stem and that of the pelycosaurs. Williston was so well assured of this that at one time he proposed to unite the two groups under Cope's term *Theromorpha*. Among the special points of resemblance between the *Moschops* group and the pelycosaurs, we may recall the following:

(1) The skull is of the compressed type, originally carnivorous, with teeth mostly confined to the marginal bones and with a single temporal

fenestra, bounded chiefly by the postorbital, the parietal and the squamosal.

(2) The occiput, as figured by Watson (1914*b*), is substantially similar to those of *Theropleura* and *Varanosaurus* and includes a single broad interparietal (or fused dermosupraoccipitals) and broad tabulars.

(3) The relations of the columella to the quadrate are also similar to those in *Theropleura*, but this is probably a primitive reptilian character, known also in the captorhine cotylosaurs.

(4) The mandible of *Moschops*, as Broom has shown, is closely comparable with the pelycosaur type in the complex topographic relations of its numerous elements, the dentary having a long ascending process and the angular a special notch (for the pterygoid muscle?).

(5) The atlas-axis complex agrees closely with that of the pelycosaurs, and

(6) the same is true of the holospondylous vertebræ with high diapophyses and dichoccephalous ribs.

(7) The pectoral girdle and limb are readily derived from the more progressive pelycosaur types, but are in many respects more advanced, and

(8) the same is true of the pelvic girdle and limb.

The chief differences between *Moschops* and the pelycosaurs in the skull are conditioned by its relatively gigantic size and quite different specialization of the dentition, and in the limbs by the various characters connected with the ability to raise the body well off the ground and to walk or run rather than crawl. These differences have been fully discussed by Rome (1922*b*) and noted in detail above, but special reference may be made to

(1) the advanced type of glenoid,

(2) the reduction and loss of the supraglenoid buttress and fossa,

(3) the loss of the process for the coracoid head of the triceps, and

(4) the upward spreading of the area for the supracoracoideus.

(5) In the humerus we recall the tendency for the capitular surface to be limited to the middle of the proximal end,

(6) the untwisting of the opposite ends,

(7) the reduction of the distal epicondyles and,

(8) the reduction or loss of the ectepicondylar foramen.

(9) The pelvis, too, shows a marked advance beyond the primitive pelycosaur type, in the forward growth of the ilium,

(10) in the shortening of the pubis and ischium and

(11) in the circular form of the acetabulum.

(12) The femur is highly specialized in the reduction of the V-shaped trochanteric ridge on the lower side and

(13) in the flexure of the head upon the shaft.

3. COMPARISON WITH THE PAREIASAURS.—Romer (1922*b*) has noted a number of points in which the pareiasaurs differ from the American cotylosaurs and resemble the contemporary South African reptiles in the adaptations of the limbs, and he suggests (pp. 588, 589) that these resemblances may not all be due to parallelism but to a possible remote common origin of the therapsids and pareiasaurs, from some early cotylosaurian group apart from the American cotylosaurs and pelycosaurs, which are much more primitive in limb structure. But, admitting the many resemblances between the two, I am nevertheless more impressed by the differences between them.

(1) The skull and mandible of the pareiasaurs are certainly extremely different from anything found in the therapsids but present some striking points of agreement with such varied cotylosaurs as *Diadectes*, *Pantylus*, *Procolophon*.

(2) The vertebræ of *Propappus* are of cotylosaurian rather than therapsid type, with broad and massive neurocentra.

(3) The pectoral girdle is not inconsistent with rather close relationship with *Diadectes*.

(4) Even the humerus of *Propappus*, while paralleling that of *Moschops* in the many features associated with the raised posture of the limbs, differs in the much more symmetrical form of the bone as viewed from the rear, and

(5) in the ball-like character of the capitellum.

(6) The radius and ulna differ considerably from those of *Moschops*.

(7) The pelves of pareiasaurs and of *Moschops* appear to differ substantially.

(8) The femur of *Propappus* has not suffered the strong reduction of the Y-shaped medial trochanteric crest.

(9) Its head is not sharply flexed on the shaft.

(10) But the most profound difference is found in the proximal part of the tarsus, the astragalus and calcaneum being conjoined in *Propappus*.

In short, the straightening of the limbs in pareiasaurs may have been the only way in which they could get their feet down below the level of the immense abdomen, and it is this straightening perhaps which has brought about the chief resemblances to *Moschops* in the glenoid, humerus and femur. I am therefore inclined to agree with Watson (1914*a*, pp. 179, 180), who, after pointing out a number of important differences

between *Pareiasaurus* and the therapsids, concludes that "so far from being at all closely related to the Therapsids, *Pareiasaurus* represents an extremely different branch of the early reptilian stock, any resemblance which it bears to them being simply due to convergence."

#### 4. ORIGIN OF THE DINOCEPHALIA FROM THE GORGONOPSIAN STEM.

—There never has been any doubt that *Moschops* and its allies are true therapsids, and it has been noted above that they appear to have inherited from primitive gorgonopsians not only the general habitus of the skull but also many such palæotelic features as the following:

(1) The large size of the septomaxilla which divides the primitive anterior nares into dorsal and ventral openings;

(2) the large size and posterior position of the pineal foramen;

(3) the platelike form of the occiput, with its large fused interparietals and large tabulars exposed almost entirely on the nuchal surface;

(4) the low position of the opening to the internal ear (Haughton);

(5) the detailed form and relations of the cylindrical stapes to the base of the skull and to the quadrate;

(6) the general arrangement of the elements of the palate;

(7) the single occipital condyle;

(8) the arrangement of the elements of the mandible (which is fundamentally similar in *Moschops* and in the Gorgonopsia, but differs in the dentigerous part);

(9) the detailed form and arrangement of the elements of the atlas-axis complex;

(10) the fundamentally similar character of the vertebræ and dichoccephalous ribs. The girdles and limbs of *Moschops* have also doubtless been derived from those of some primitive gorgonopsian type which probably had

(11) two separate coracoids,

(12) the anterior being nearly excluded from the glenoid;

(13) a humerus of slightly "twisted" type;

(14) a large coracobrachialis fossa;

(15) an asymmetrical development of the distal end;

(16) a femur with flattened shaft;

(17) a much reduced ridge on the under side,

(18) with a flattened oval head flexed upon the shaft, and

(19) with the great trochanter represented by a long swelling on the outer border;

(20) carpus and

(21) tarsus large;

(22) astragalus and calcaneum large and subcircular;

(23) digits short.

(24) Some of the phalanges much reduced and tending toward the mammalian formula.

*Moschops* and its tapinocephalid allies may be regarded as gigantic and highly specialized semi-aquatic gorgonopsians, of some peculiar food habits that are not very well understood but must have required the plucking and breaking up of some very resistant objects such as mussel-shells or cycad cones. As a result of these specializations:

(1) The front teeth became very large.

(2) The skull became very massive.

(3) The articulation of the jaw with the skull was moved down below the plane of the cheek teeth in the manner explained on pages 225, 226. The pterygoids, already meeting below the interpterygoid space in the ancestral gorgonopsian, probably

(4) lost the median crest and

(5) became secondarily thickened and widened.

(6) No median crest was developed on the basisphenoid. The post-orbital, which formerly may have joined the squamosal above the temporal fossa,

(7) lost this connection as the fossa deepened and gained contact with the parietal.

The primary running adaptations already acquired by the gorgonopsian ancestors were retained but were now overlaid by such secondary effects of gigantism as

(1) the great increase in the size of the pectoral girdle,

(2) the expansion of the coracobrachialis fossa and

(3) tricipital areas of the humerus,

(4) the development of a huge olecranon on the ulna,

(5) the further shortening and spreading of the digits,

(6) the great increase in depth of the pelvis,

(7) the anteroposterior shortening of the pubi-ischiadic plate,

(8) the great thickening and shortening of the femur,

(9) the virtual loss of its Y-ridge,

(10) the shortening and thickening of the tibia. The effect of gigantism is also seen in

(11) the delayed ossification of the ends of the limb bones and

(12) of the articular surfaces of the carpals and tarsals, which reminds us of similar conditions in the larger dinosaurs, such as *Triceratops* and the Sauropoda. I do not therefore regard the differences that

separate the Dinocephalia from the Gorgonopsia as of more than subordinal value, and I have yet to find a character which will definitely exclude the Dinocephalia from derivation from the more primitive gorgonopsians.

5. COMPARISON WITH THE DROMASAURIA, ETC.—The Dinocephalia also appear to be closely related to the Dromasauria; indeed it is not inconceivable that if Broom's figure of the skull of *Galechirus* is correct, the latter may represent a stage in the derivation of the Dinocephalia from the stem of the Gorgonopsia.

- (1) Its dentition as figured is suggestive of a pre-dinocephalian stage.
- (2) Its enlarged septomaxilla is exposed on the face and
- (3) has similar relations with surrounding elements except that it is in contact with the lacrymal as a result of the forward displacement of the anterior border of the orbit.
- (4) The large circular orbits might be expected in an early dinocephalian stage, the enlargement of the snout being secondary.
- (5) The quadrate-articular joint is depressed.
- (6) There is a marked concavity of the lower border of the jugal.
- (7) In the top view the large pineal foramen and
- (8) the breadth of the preorbital region are suggestive.
- (9) The mandible has a quite similar arrangement of all its elements.
- (10) The characters of the notochordal vertebræ of *Galechirus* are much more primitive than those of *Moschops*.
- (11) The pectoral girdle, as noted above, shows important and fundamental agreements.
- (12) The ulna has an olecranon.
- (13) The carpus and
- (14) the tarsus appear to afford an ideal starting-point for the conditions in *Moschops*.

It would be no objection to the above to show that the dromosaurians also in other features recall the anomodonts: the latter have paralleled the dinocephalians in some respects, but after a primitive shortening up of the skull, as in *Galeops*, they became beaked and underwent marked changes in the temporal region; as they did not become herbivorous or molluscivorous, they kept and developed the running characters of the skeleton, acquiring high, monotreme-like features in the pectoral girdle.

The skeletal characters of the Dinocephalia appear to be relatively far removed from those of the Therocephalia, Bauriamorpha and Cynodontia, which represent successive approximations to the mammalian grade, but also starting from the gorgonopsian level.

## CONCLUSIONS

1.—Although the several topotype skeletons of *Moschops capensis* were more or less intermingled, a critical re-study of the material tends to confirm Dr. Broom's judgment in sorting out from the material three chief specimens of different sizes. Another single associated skeleton (the type of *Moschognathus whaitsi*) affords corroborative evidence as to the general proportions and appearance of a male *Moschops*, as shown in the mounted skeleton here described.

2.—A detailed study of the limbs and girdles plainly shows that *Moschops* had advanced far beyond the most primitive known reptiles in the ability to lift the body well off the ground and to assume the position shown in the mounted skeleton.

3.—The question of the exact nature of its food is left open, but the food must have had a resistant covering, as of the rhizomes of ferns and the stems of calamites, and must have been ingested in enormous quantities, as indicated by the huge size of the abdominal cavity.

4.—The animal was probably of littoral or semiaquatic habits (Pl. XXI).

5.—A detailed analysis of the osteological characters leads to the view that the Dinocephalia, along with the whole therapsid stem, were derived from unknown relatives of the pelycosaurs; that their resemblances with the pareiasaurs is largely due to convergence; that the Dinocephalia were derived from a primitive gorgonopsian stem and that possibly the Dromasauria represent in some respects an intermediate stage, allied on the one hand to the Dinocephalia and on the other to the Anomodontia.

6.—Leaving out of account the Russian dinocephalians, which are not very well known, the South African Tapinocephalidæ are here divided into two provisional subfamilies: (1) the **Moschopinæ**, including the allied genera *Delphinognathus*, *Moschops*, *Moschognathus*, *Taurops*, *Prigalion*, *Lamiasaurus*; (2) the **Tapinocephalinæ**, including *Tapinocephalus*, *Mormosaurus* and *Struthiocephalus*.

## LITERATURE CITED

- BROOM, R. 1909. 'The Skull of *Tapinocephalus*.' Geol. Mag., N.S., Dec. 5, VI, pp. 406-402.
1910. 'A Comparison of the Permian Reptiles of North America with those of South Africa.' Bull. Amer. Mus. Nat. Hist., XXVIII, pp. 197-234. [Dinocephalia, pp. 206-207; the Pelycosauria compared with the Therapsida, pp. 228-231.]
1911. 'On some New South African Permian Reptiles.' Proc. Zool. Soc. Lond., pp. 1073-1082. [*Moschops capensis* described, pp. 1073-1075, Pl. LXII.]
- 1912a. 'On a new species of *Propappus*, and on the Pose of the Pareiasaurian Limbs.' Ann. So. Afr. Mus., III, pp. 323-330, Pls. XIX-XXI.
- 1912b. 'On Some New Fossil Reptiles from the Permian and Triassic Beds of South Africa.' Proc. Zool. Soc. Lond., pp. 859-876. [Description of *Taurops macrodon*, pp. 859-860, Pl. xc. Figure of *Eccasaurus priscus* tooth, Pl. xc, fig. 3.]
- 1914a. 'A further Comparison of the South African Dinocephalians with the African Pelycosauria.' Bull. Amer. Mus. Nat. Hist., XXXIII, pp. 135-141.
- 1914b. Croonian Lecture: 'On the Origin of Mammals.' Philos. Trans. Roy. Soc. Lond., Ser. B, CCVI, pp. 1-48. [Dinocephalia, p. 10, Pls. I, II.]
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.' [Geological horizons of Dinocephalia, p. 107; Dinocephalia, pp. 111-115.]
1923. 'On the Structure of the Skull in the Carnivorous Dinocephalian Reptiles.' Proc. Zool. Soc. Lond., pp. 661-686.
- GREGORY, WILLIAM K., AND CAMP, C. L. 1918. 'Studies in Comparative Myology and Osteology, No. 111.' Bull. Amer. Mus. Nat. Hist., XXXVIII, pp. 447-563.
- HAUGHTON, S. H. 1913. 'On a skull of *Tapinocephalus atherstoni* Owen.' Ann. So. Afr. Mus., XII, Part 1, pp. 40-42.
- 1915a. 'On a new Dinocephalian from the Gouph.' Ann. So. Afr. Mus., XII, pp. 52-54, Pl. x. [*Struthiocephalus whaitsi*.]
- 1915b. 'On a New Type of Dinocephalian (*Moschosaurus longiceps*). ' Ann. So. Afr. Mus., XII, Part 3, pp. 78-81.
1919. 'A Review of the Reptilian Fauna of the Karroo System of South Africa.' Trans. Geol. Soc. So. Afr., XXII, pp. 1-25.
- NOPCSA, BARON FRANZ. 1923. 'Die familien der Reptilien.' Fortschritte der Geol. u. Paläont., Heft 2.
- OWEN, R. 1876. 'Descriptive and Illustrated Catalogue of the Fossil Reptilia of South Africa in the Collection of the British Museum, London,' pp. 1-88, Pls. I-LXX. [Palate of *Tapinocephalus*, Pls. I, II.]
- PEARSON, HELGA S. 1924. 'A Dicynodont Reptile Reconstructed.' Proc. Zool. Soc., Part 3, pp. 827-855. [Received too late for discussion in the text.]

- ROGERS, A. W., AND DU TOIT, A. L. 1909. 'An Introduction to the Geology of Cape Colony,' 8vo. London. [Fauna and flora of the Karroo system.]
- ROMER, A. S. 1922a. 'The Comparison of Mammalian and Reptilian Coracoids.' *Anatom. Record*, XXIV, No. 2, pp. 39-47.
- 1922b. 'The Locomotor Apparatus of Certain Primitive and Mammal-like Reptiles.' *Bull. Amer. Mus. Nat. Hist.*, XLVI, pp. 517-606, Pls. xxvii-xlvi.
- SEELEY, H. G. 1888. 'Researches on the Structure, Organization and Classification of the Fossil Reptilia, II. On *Pareiasaurus bombidens* (Owen) and the Significance of its Affinities to Amphibians, Reptiles and Mammals.' *Philos. Trans. Roy. Soc. Lond.*, CLXXIX, B, pp. 59-109, Pls. xii-xxi. [Description of the pelvis designated *Phoco-saurus megischion*, pp. 91-94, Pl. xxi.]
1889. 'On the Anomodont Reptilia and their Allies,' *Idem*, CLXXX, pp. 215-296. [Limb bones referred to *Titanosuchus ferox*, pp. 261-268, Pls. xix-xxv.]
1892. 'On *Delphinognathus conocephalus* (Seeley) from the Middle Karroo Beds, Cape Colony, preserved in the South African Museum, Capetown.' *Quart. Journ. Geol. Soc.*, XLVIII, pp. 469-475, August.
1894. 'Further Evidences of the Skeleton in *Deuterosaurus* and *Rhopalodon*, from the Permian Rocks of Russia.' *Idem*, CLXXXV, pp. 663-717, VIII.
- WATSON, D. M. S. 1913. 'The Limbs of *Lystrosaurus*.' *Geol. Mag., N.S.*, X, pp. 256-258.
- 1914a. 'On the Skull of a Pareiasaurian Reptile, and on the Relationship of that Type.' *Proc. Zool. Soc. Lond.*, pp. 155-180.
- 1914b. 'The Zones of the Beaufort Beds of the Karroo System in South Africa.' *Geol. Mag. N.S.*, Decade VI, I, pp. 203-208.
- 1914c. 'The Dinocephalia, an Order of Mammal-like Reptiles.' *Proc. Zool. Soc. Lond.*, pp. 749-786, Pls. iv-v.
- 1917a. 'The Evolution of the Tetrapod Shoulder Girdle and Forelimb.' *Journ. Anatomy*, LII, Part 1, pp. 1-63.
- 1917b. 'A Sketch Classification of the Pre-Jurassic Tetrapod Vertebrates.' *Proc. Zool. Soc. Lond.*, pp. 167-186. [Classification and relationships of the Dinocephalia, pp. 175, 183.]
1921. 'The Bases of Classification of the Theriodontia.' *Proc. Zool. Soc. Lond.*, 1921, pp. 35-98. [Affinities of the Dinocephalia, pp. 88-93.]
- WILLISTON, S. W. 1911. 'American Permian Vertebrates.' [Osteology of *Seymouria*, *Varanosaurus*, *Casea*.]

PLATE I

*Moschops capensis* Broom. Skeleton, partly restored, A. M. N. H. No. 5552. Mounted by Charles Lang, 1919.  $\times \frac{1}{12}$ . Restored parts in lighter color.

The astragalus as restored is probably too large. The partly restored ischium should have been produced posteriorly. Details of manus and pes conjectural.

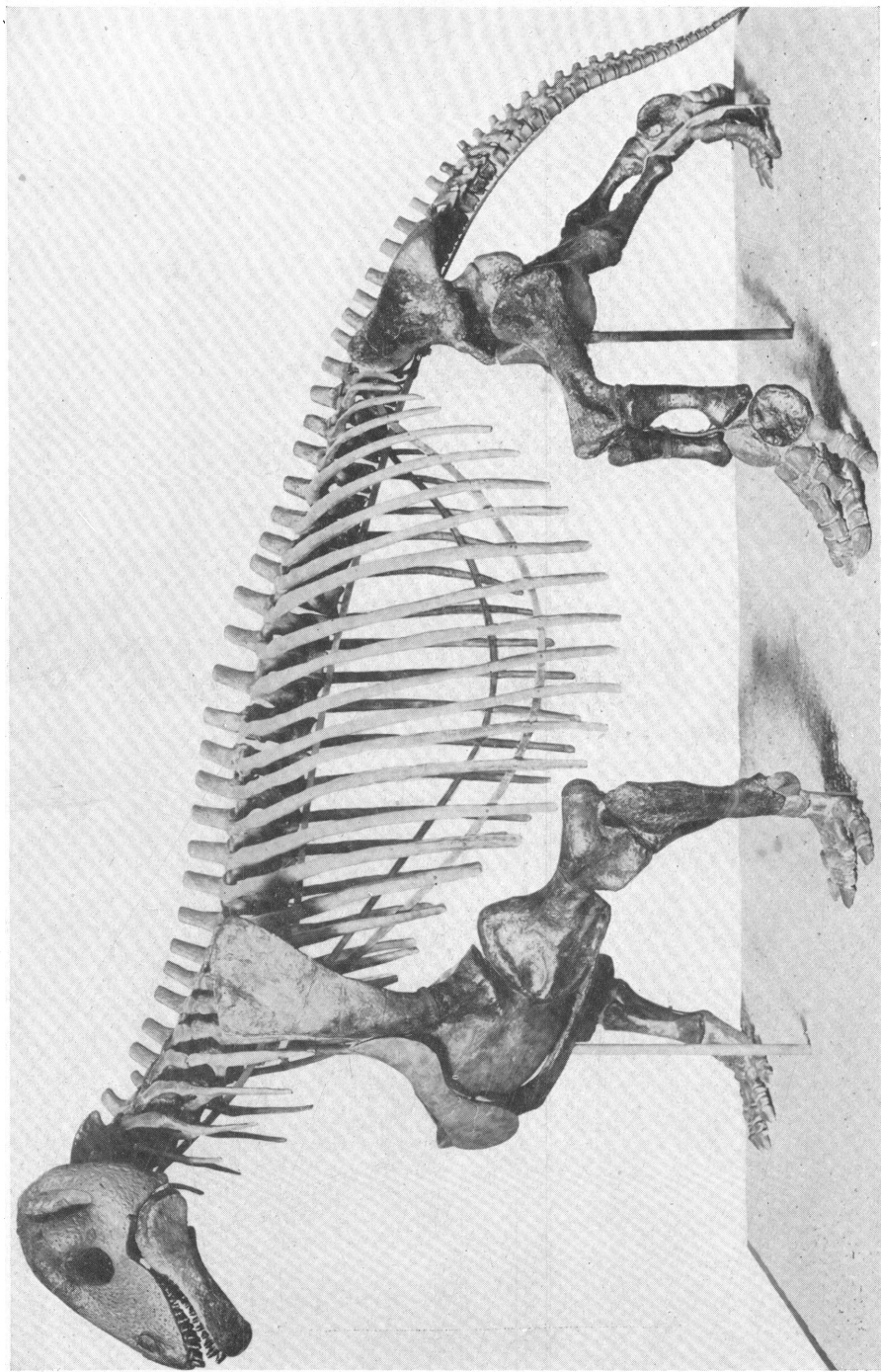


PLATE II

*Moschops capensis*. Vertebral column of mounted skeleton.  $\times \frac{1}{8}$ .  
Restored parts in light color.  
The partly restored ischium should have been produced posteriorly.

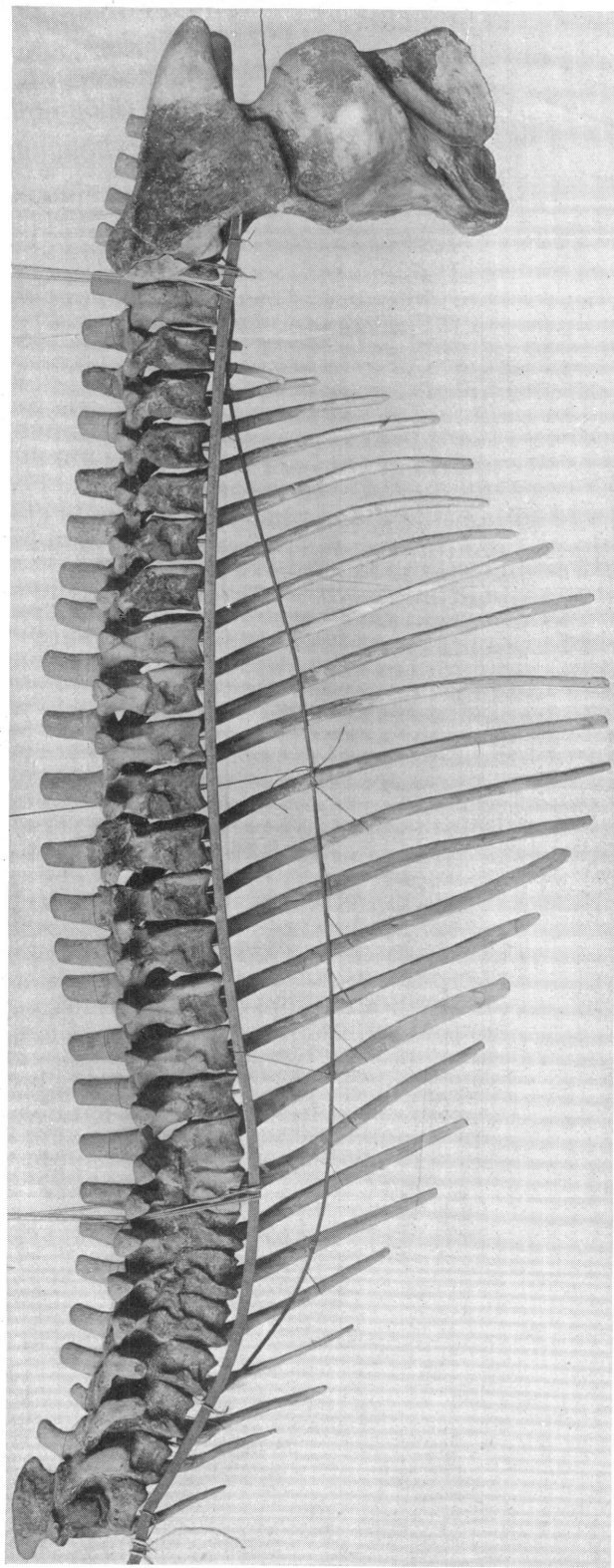


PLATE III

*Moschops capensis*. Vertebrae of skeleton "A" (5551), front view.  $\times \frac{1}{2}$ .

- A. Seventeenth vertebra. D. First presacral (twenty ninth ?).  
B. Twenty-fourth vertebra. E. Fourth (?) caudal.  
C. Twenty-sixth vertebra. F. Ninth (?) caudal.

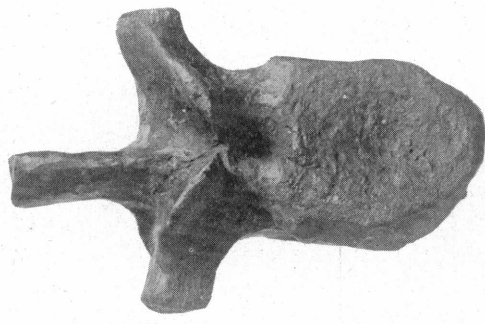
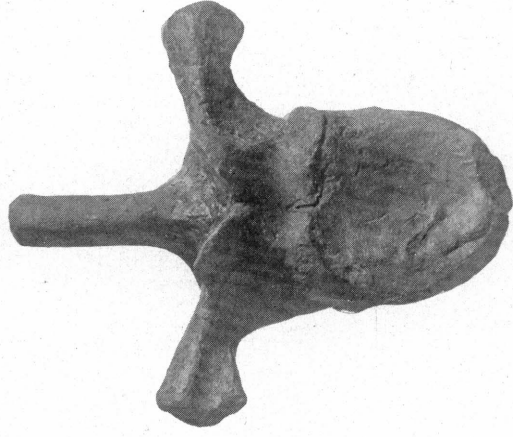
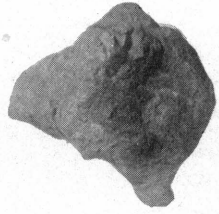
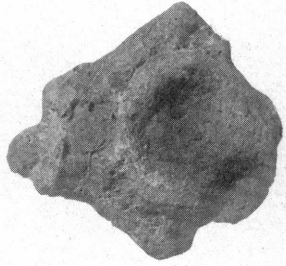
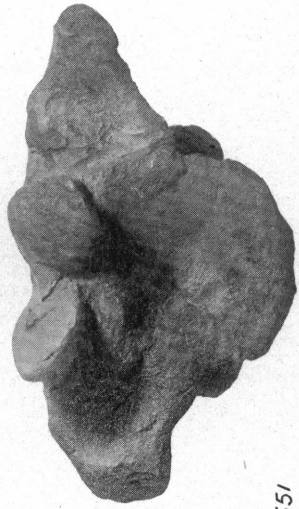
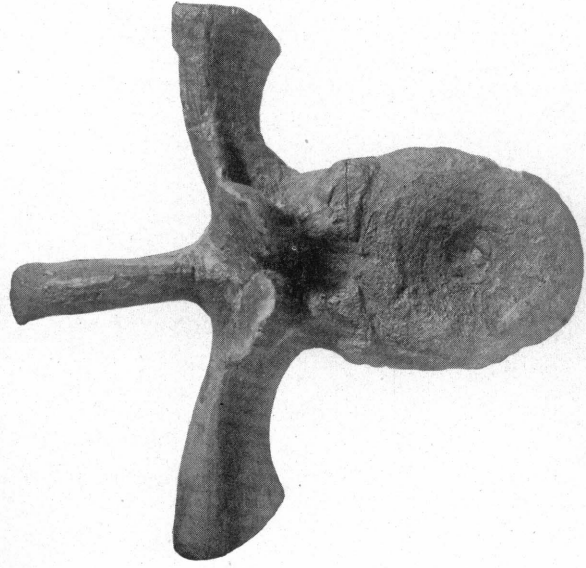


PLATE IV

*Moschops capensis*. Vertebrae of skeleton "A" (5551), left side view.  $\times \frac{1}{2}$ .

A. Seventeenth vertebra. D. First presacral (twenty-ninth ?).

B. Twenty-fourth vertebra. E. Fourth (?) caudal.

C. Twenty-sixth vertebra. F. Ninth (?) caudal.

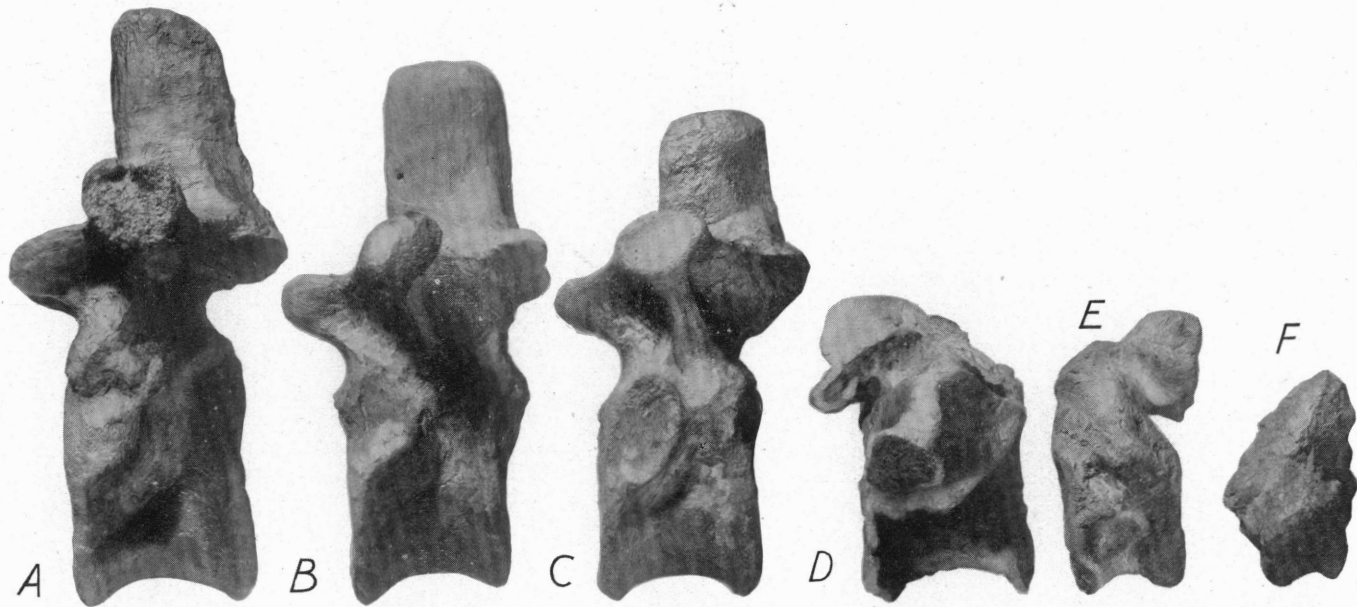


PLATE V

*Moschops capensis*. Vertebrae of skeleton "A" (5551), rear view.  $\times \frac{1}{2}$ .  
A. Seventeenth vertebra. D. First presacral (twenty-ninth ?).  
B. Twenty-fourth vertebra. E. Fourth (?) caudal.  
C. Twenty-sixth vertebra. F. Ninth (?) caudal.

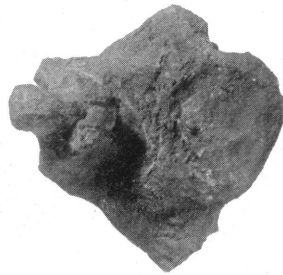
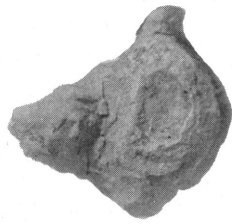
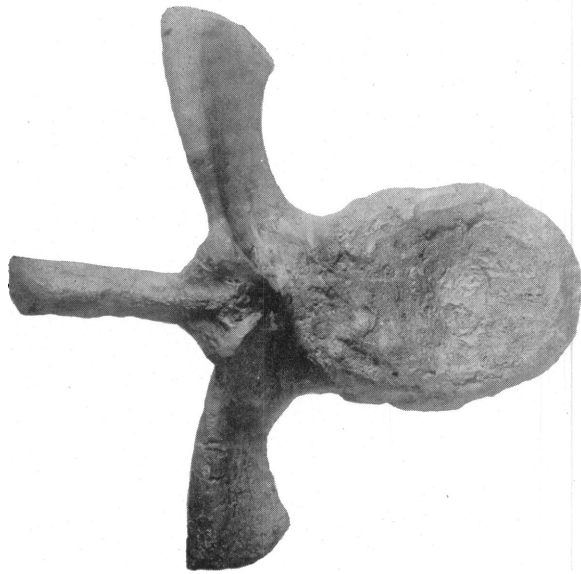
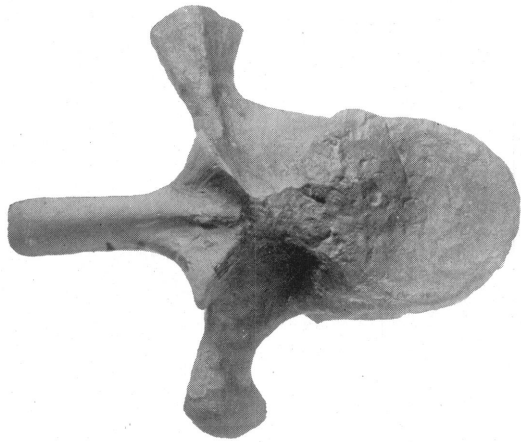


PLATE VI

*Moschops capensis*. Mounted skeleton, rear view.

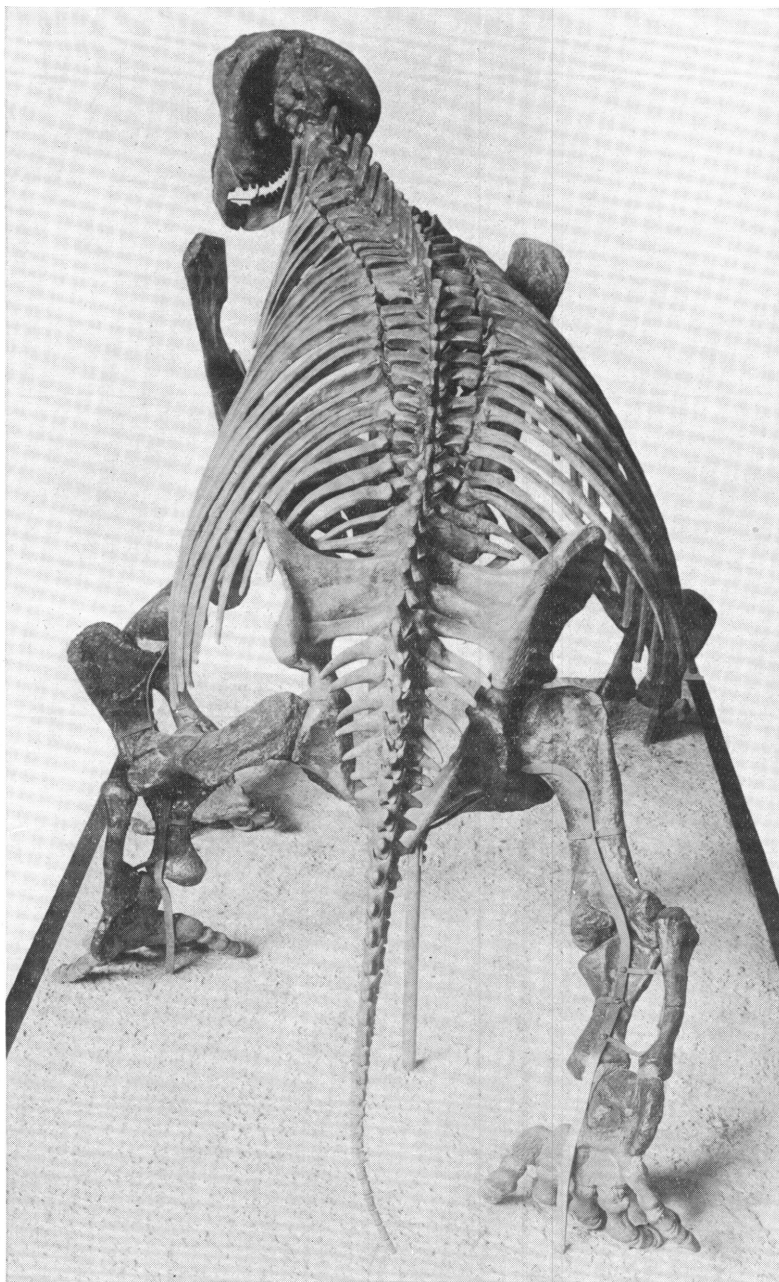
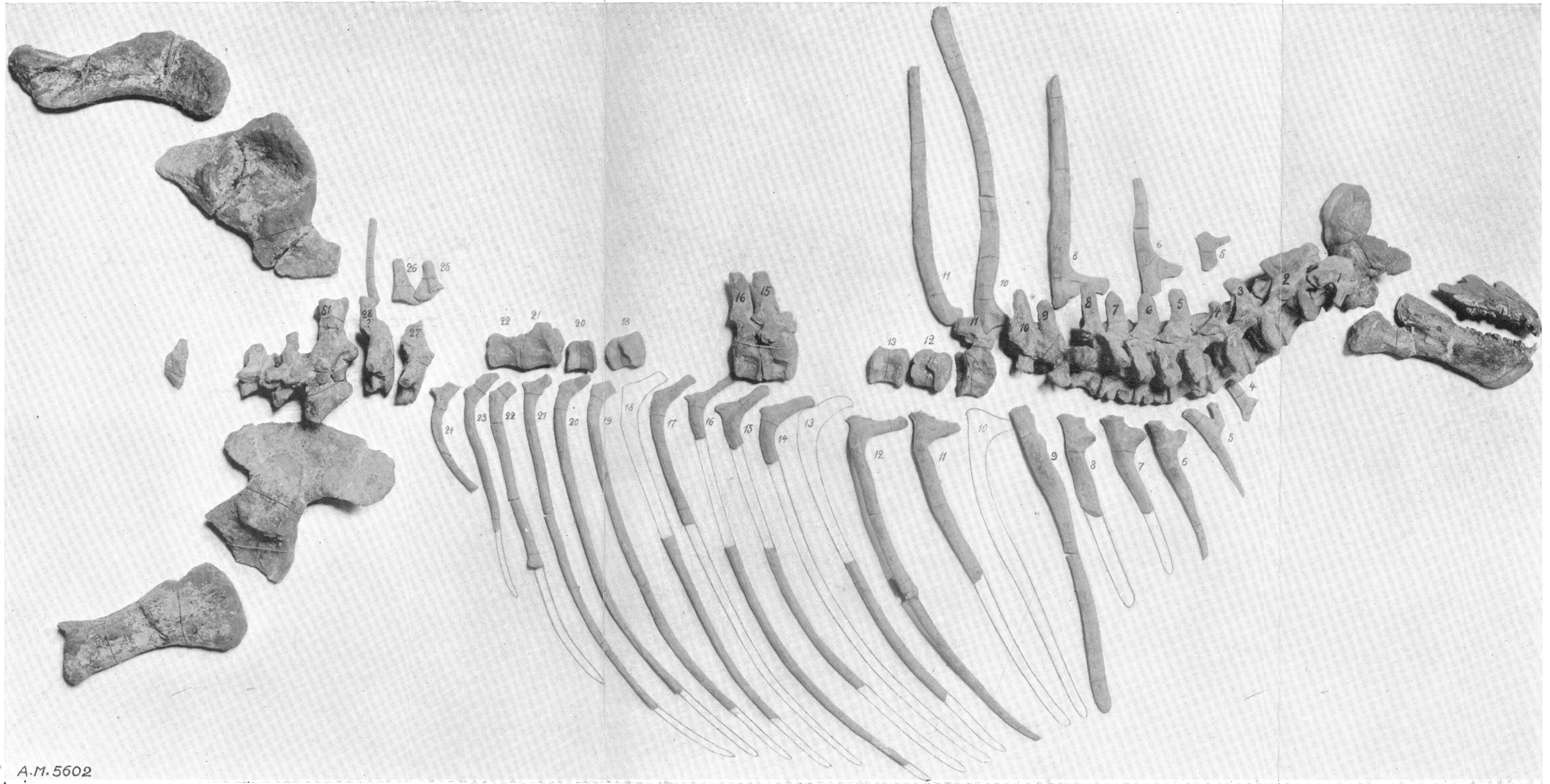


PLATE VII

*Moschognathus whaitsi* Broom. Type skeleton, A. M. N. H. 5602.  $\times \frac{1}{4}$ .



A.M. 5602

PLATE VIII

*Moschops capensis*. Right side, oblique view, showing the relations of the pectoral girdle. Manus restored.

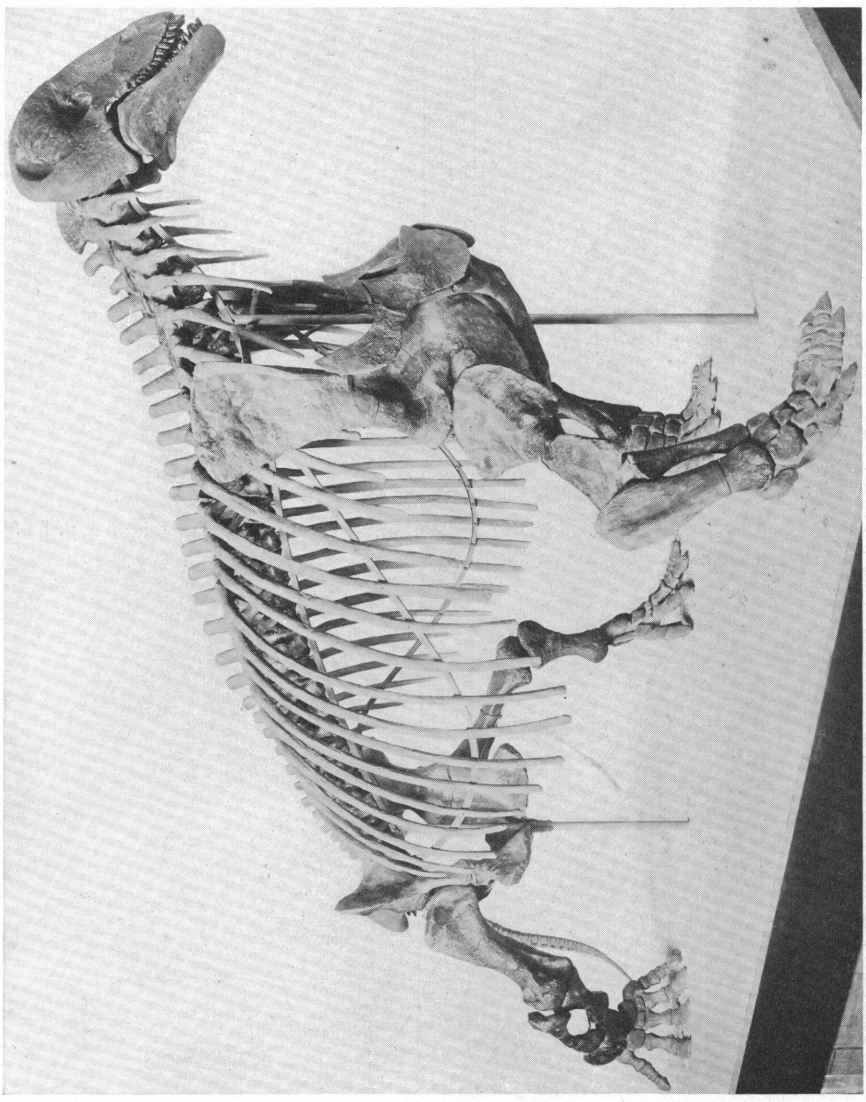


PLATE IX

*Moschops capensis*. Mounted skeleton, front view. The scapulæ probably diverge somewhat too much above.

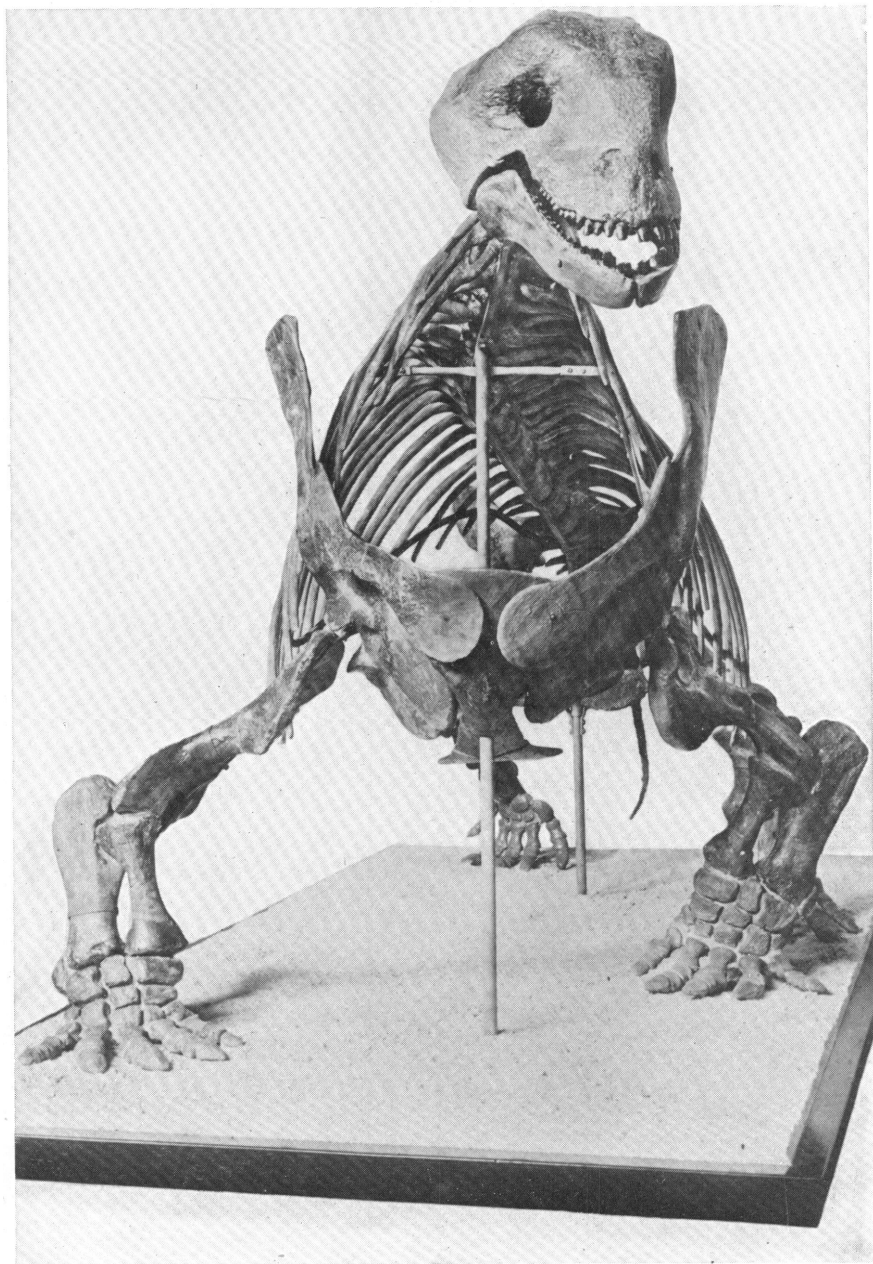


PLATE X

*Moschops capensis*. Pectoral girdle, rear view.

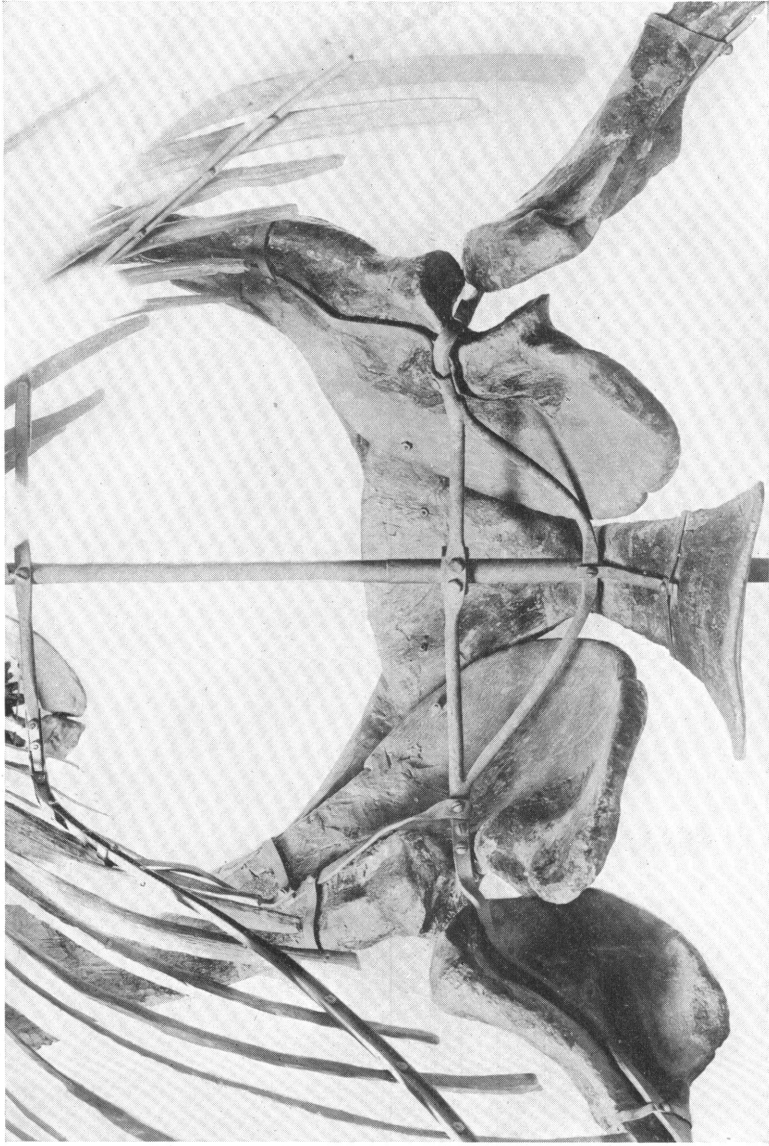


PLATE XI

Comparative views of tibiae.  $\times \frac{1}{4}$ .

- A. *Propappus rogersi* Broom, right tibia (cast), front view.
- B. *Diadectes* sp., right tibia, front view.
- C. *Theropleura retroversa* Cope, right tibia, front view.
- D. *Eryops megacephalus* Cope, right tibia, front view.
- E. *Moschops capensis* Broom, left tibia, front view (the concavity is due to crushing).
- F. *Moschops capensis*, right tibia, rear view (badly crushed).
- G. *Moschops capensis*, right tibia, front view.
- H. *Moschops capensis*, right tibia, front view.
- I. *Moschops capensis*, left tibia, rear view.
- J. *Moschops capensis*, right tibia, front view.

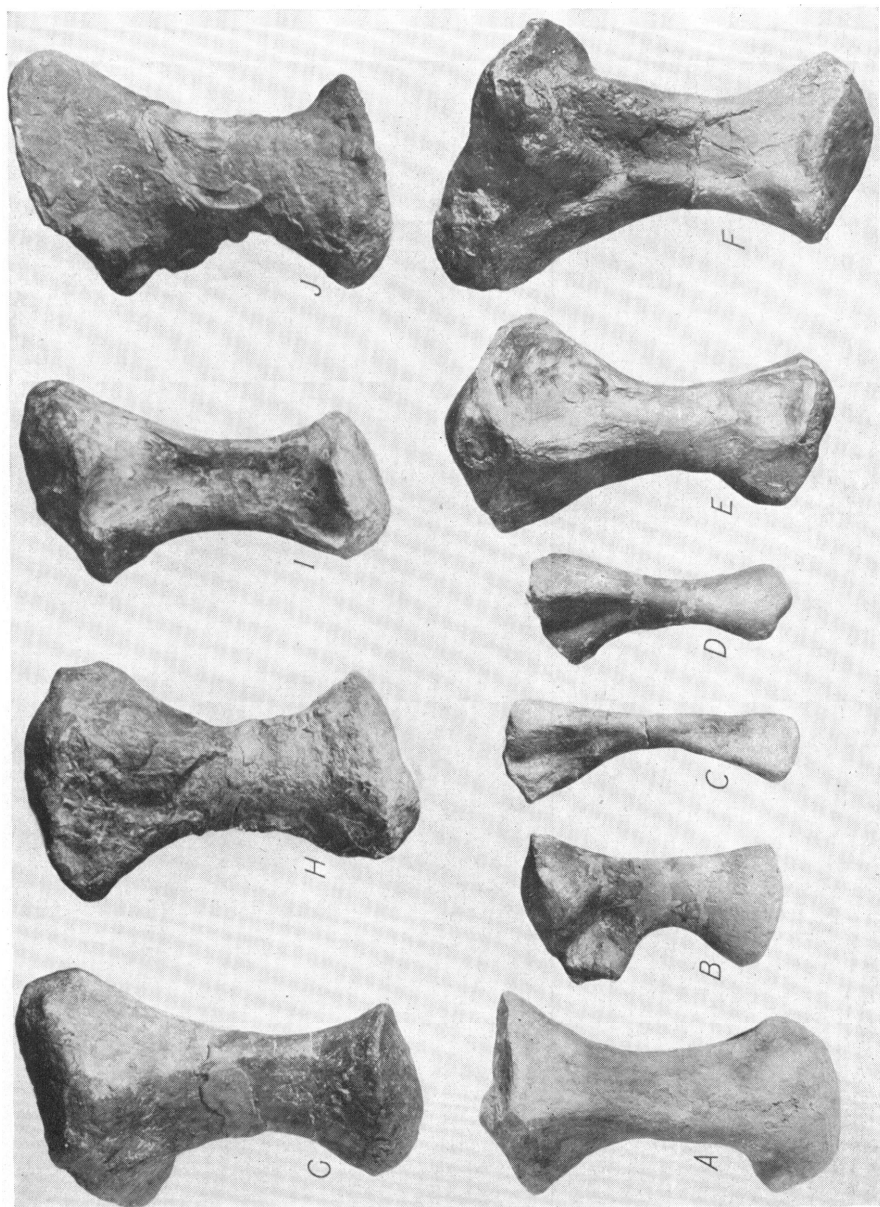


PLATE XII

Proximal ends of tibiae shown in Plate XI.  $\times \frac{1}{4}$ .

The front of the tibia faces downward.

A. *Propappus rogersi*, right tibia (cast).

B. *Diadectes* sp., right tibia.

C. *Theropleura retroversa*, right tibia.

D. *Eryops megacephalus*, right tibia.

E. *Moschops capensis*, left tibia (crushed).

F. *Moschops capensis*, right tibia (crushed).

G. *Moschops capensis*, right tibia (uncrushed).

H. *Moschops capensis*, right tibia (somewhat crushed).

I. *Moschops capensis*, left tibia (crushed).

J. *Moschops capensis*, right tibia (somewhat crushed).

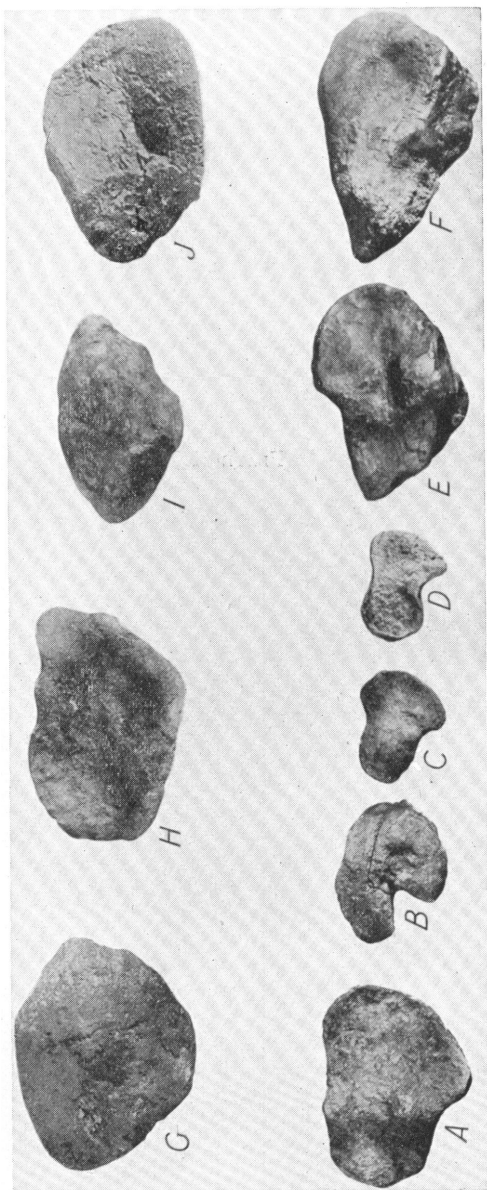


PLATE XIII

*Moschops capensis*. Bones of the manus and pes. All  $\times \frac{1}{3}$ .

A. Calcaneum of large animal, possibly *Tapinocephalus*.

B, C. Opposite astragali.

D. Astragalus of skeleton "A."

E, F. Opposite astragali.

G, H. Opposite radiaia (?), probably belonging with skeleton "A." The supposed radial surface is on the lower side of the figure.

I, J. Opposite tarsalia four (?), belonging with skeleton "A."

K, L. Metapodials.

M-S. Ungual phalanges.

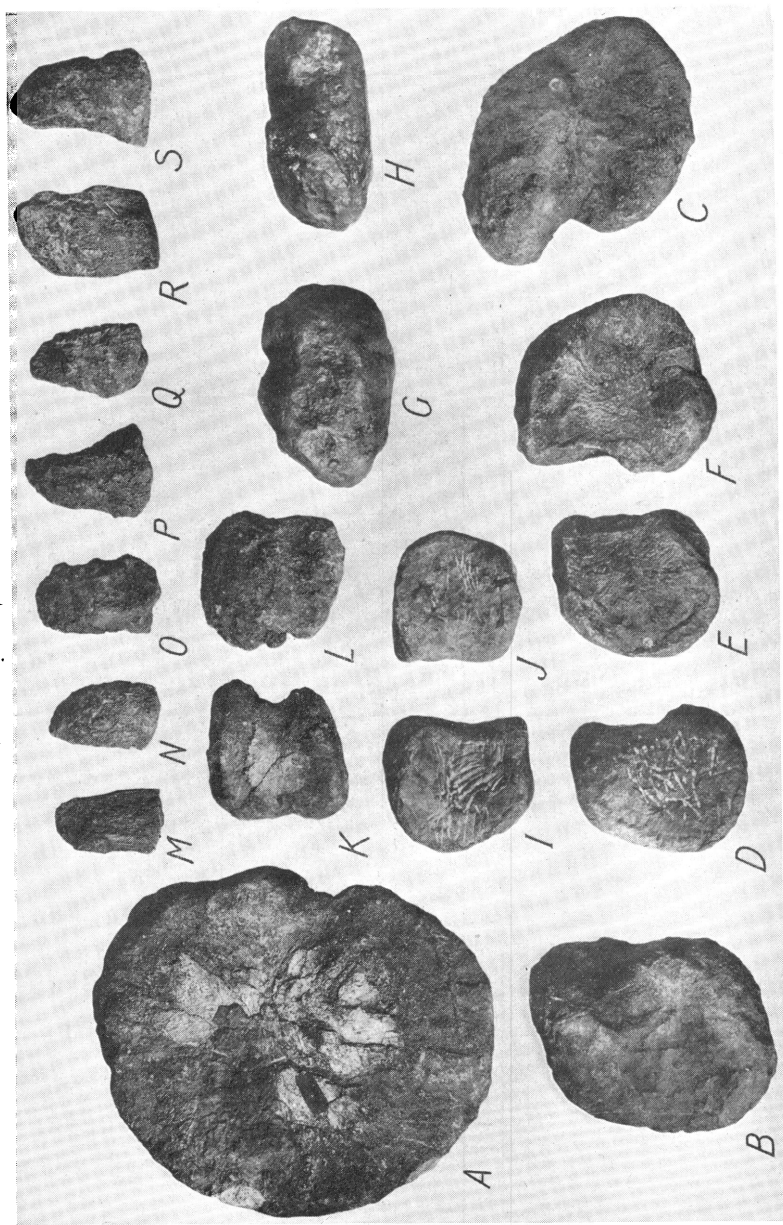


PLATE XIV

Same specimens as in Plate XIII, but turned over to show reverse side. All  $\times \frac{1}{3}$ .  
(In both G and H the supposed radial side is turned upward.)

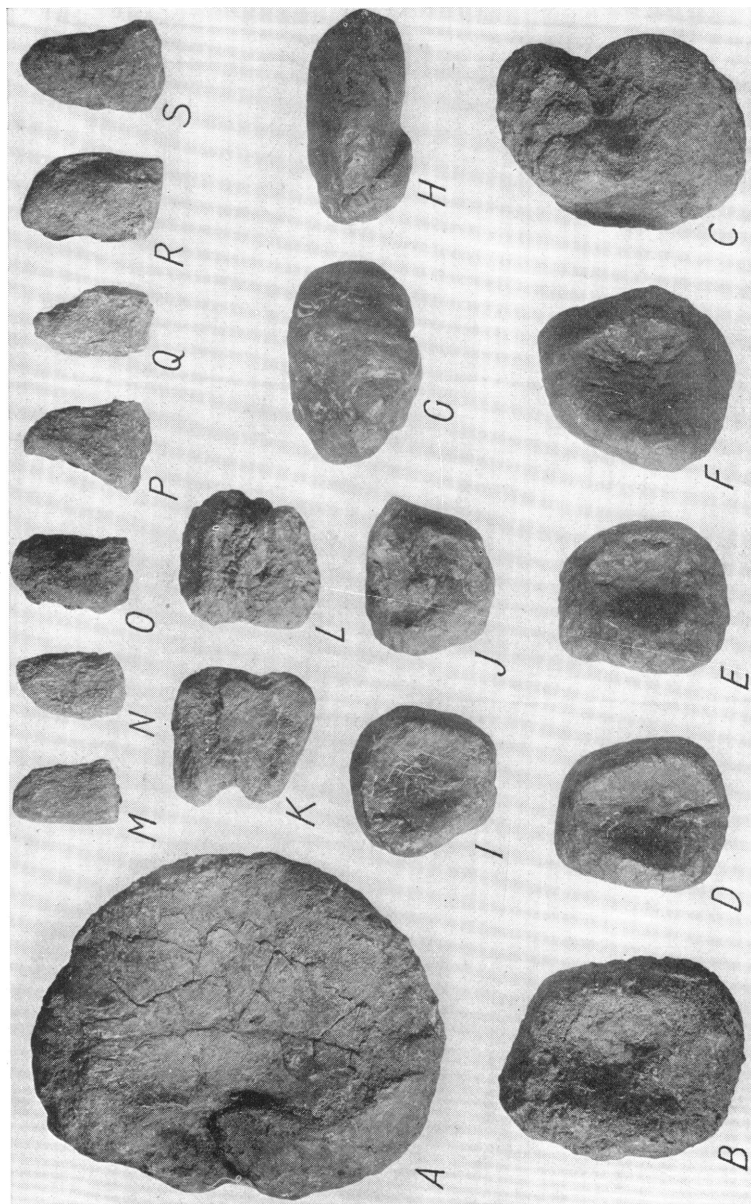


PLATE XV

*Moschops capensis* skulls.  $\times \frac{1}{3}$ .

A. Right side of skull "A," A. M. N. H. 5551.

B. Palatal view of type skull, A. M. N. H. 5550.



PLATE XVI

*Moschognathus whaitsi* Broom. Type skull and lower jaw, A. M. N. H. 5602.  
×  $\frac{2}{5}$ .



PLATE XVII

Jaws of *Moschognathus* and *Moschops*. Right side, outer view.  $\times \frac{3}{8}$ .

A. *Moschops capensis* Broom. Jaw of type, A. M. N. H. 5550.

B. *Moschops capensis* Broom. Jaw of skeleton "C," A. M. N. H. 5553.

C. *Moschognathus whaitsi* Broom. Jaw of type, A. M. N. H. 5602.

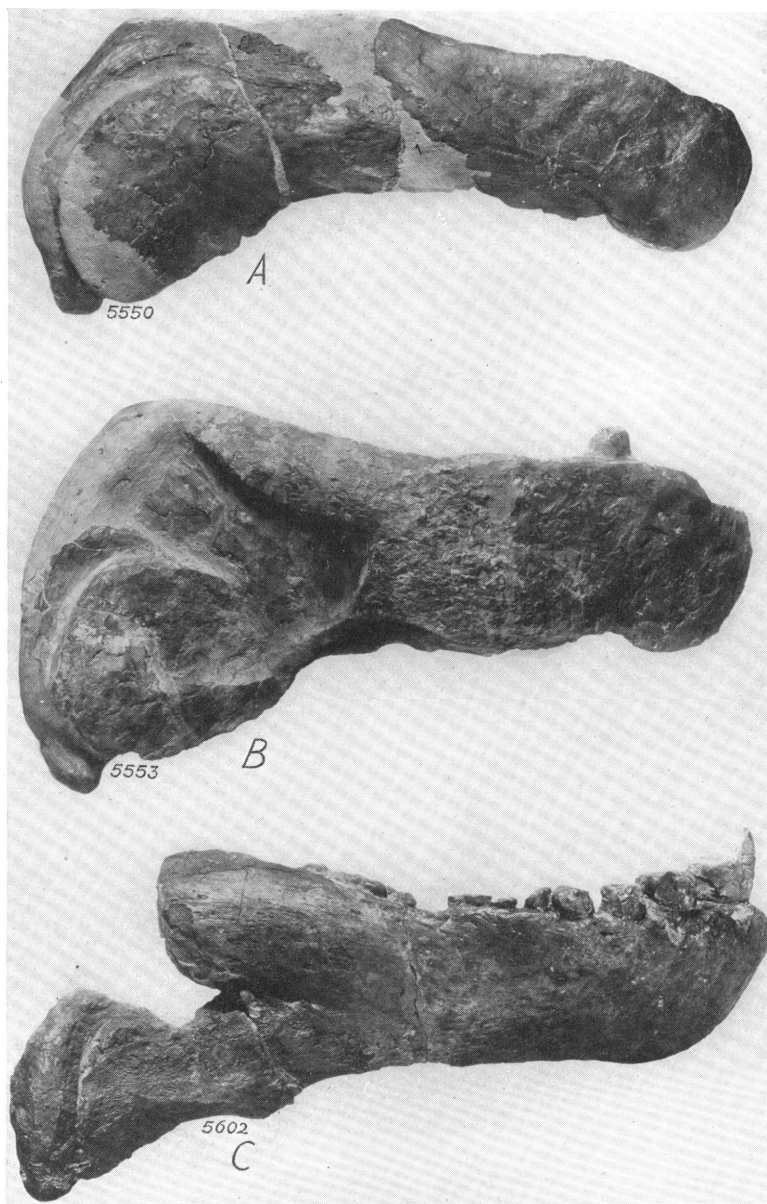


PLATE XVIII

Jaws of *Moschognathus* and *Moschops*. Right side, inner view.  $\times \frac{3}{8}$ .

A. *Moschops capensis*. Jaw of type, A. N. M. H. 5550.

B. *Moschops capensis*. Jaw of skeleton "C," A. M. N. H. 5553.

C *Moschognathus whaitsi*. Jaw of type, A. M. N. H. 5602.

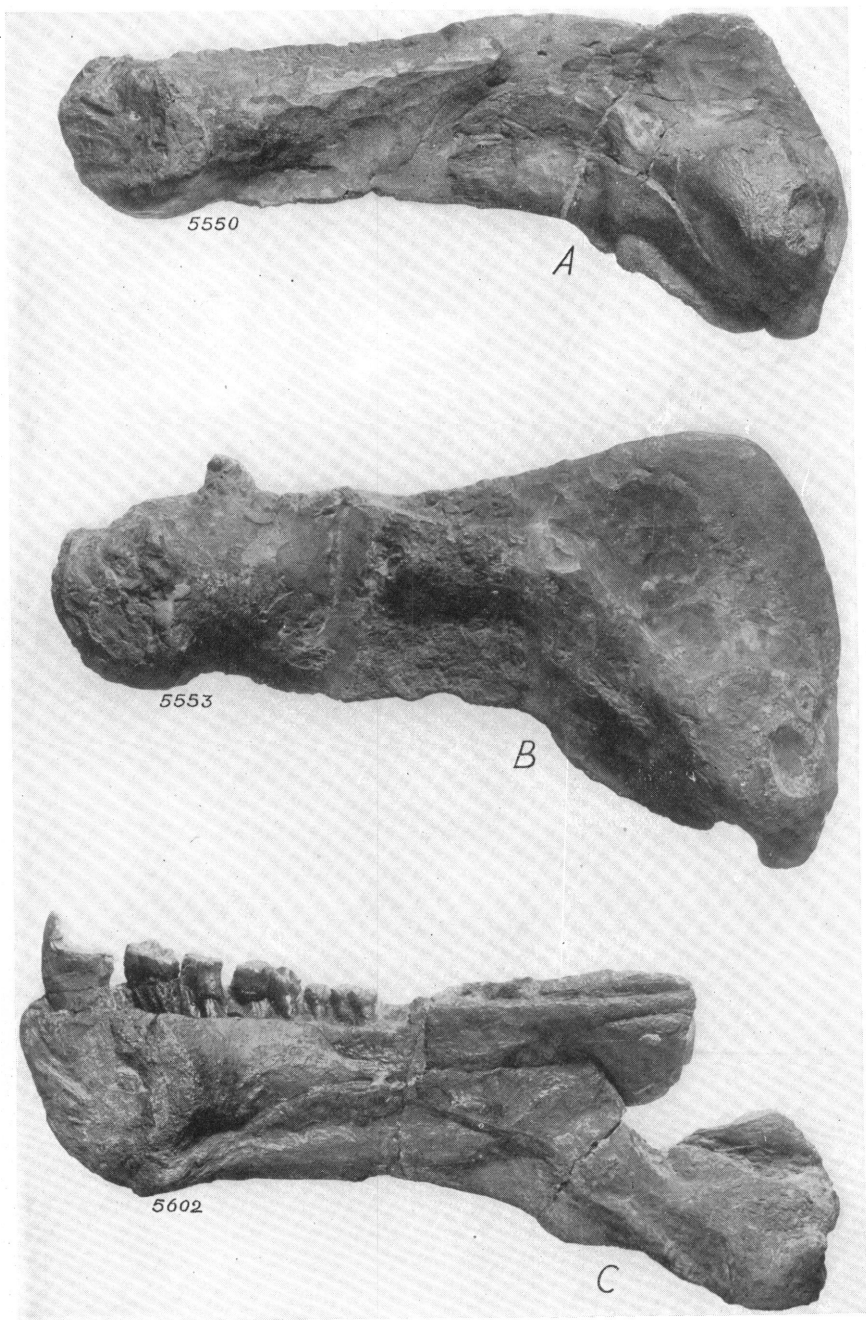


PLATE XIX

Teeth of *Eccasaurus* and *Moschognathus*.  $\times 1$ .

- A<sup>1</sup>. Second right dentary tooth of *Moschognathus whaitsi* Broom, type jaw,  
A. M. N. H. 5602. Occlusal surface.  
A<sup>2</sup>. The same, "mesial" or anterointernal face.  
A<sup>3</sup>. The same, "distal" or posteroexternal face.  
B<sup>1</sup>. Third right premaxillary tooth of *Eccasaurus priscus* Broom, A. M. N. H.  
5625. Occlusal surface, showing basal cingulum and median ridge.  
B<sup>2</sup>. The same, "mesial" or anterointernal face.  
B<sup>3</sup>. The same, "distal" or posteroexternal face.



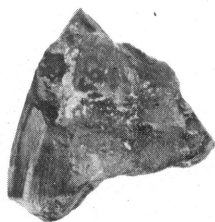
*A'*



*B'*



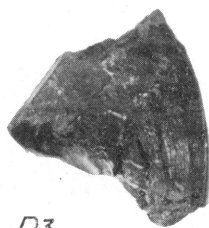
*A<sup>2</sup>*



*B<sup>2</sup>*



*A<sup>3</sup>*



*B<sup>3</sup>*

PLATE XX

Deciduous and replacing dentitions of *Taurops* and *Moschognathus*.  $\times \frac{1}{3}$ .

A. *Taurops macrodon* Broom. Type snout, A. M. N. H. 5610. d, deciduous teeth; p, permanent teeth lying in the jaws, the outer wall of which is broken away.

B<sup>1</sup>. *Moschognathus whaitsi* Broom. Type jaw, right half, A. M. N. H. 5602.

Occlusal view, showing the replacing teeth (p) beneath the deciduous set; m, posterior molars apparently belonging with the deciduous set, but possibly without successors.

■ B<sup>2</sup>. The same, inner side, showing the tips of the replacing set (p) beneath the partly resorbed bases of the deciduous set (d).

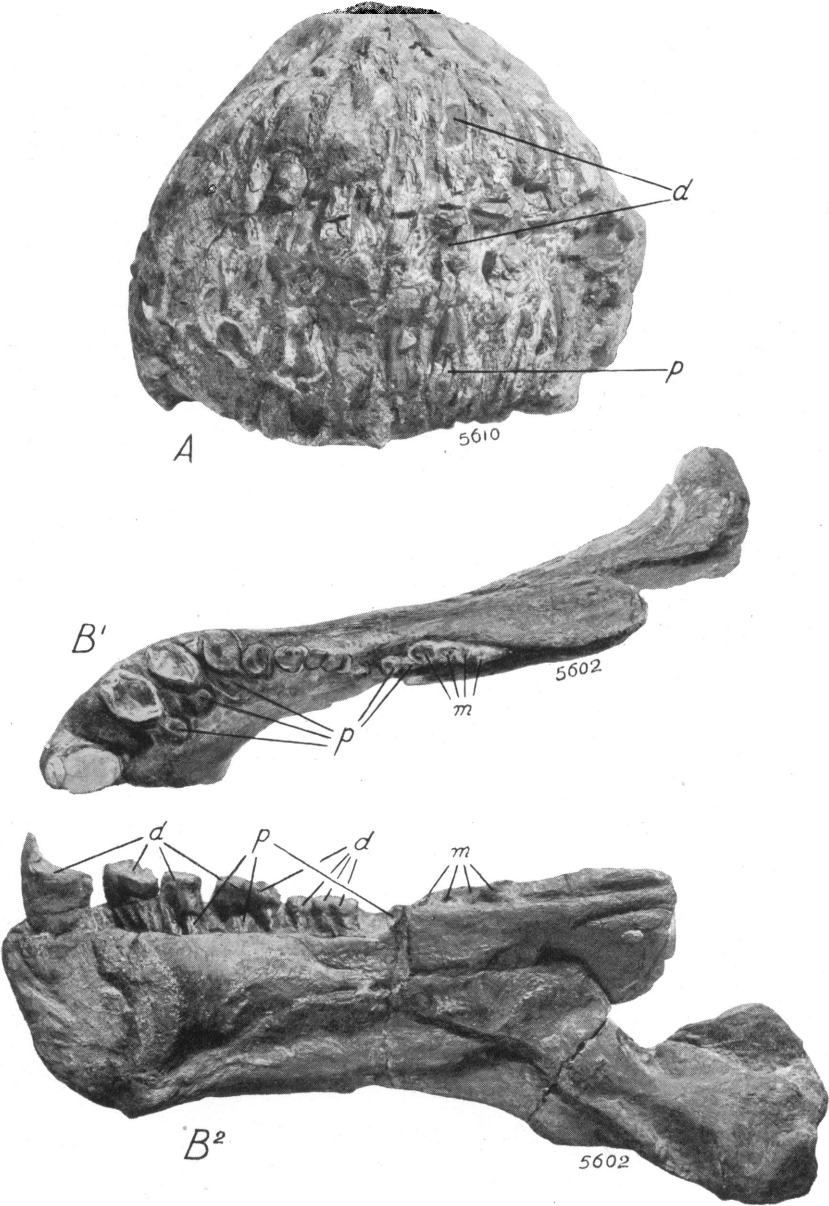


PLATE XXI

*Moschops capensis* Broom. Restoration by Mrs. E. Rungius Fulda.







# PUBLICATIONS

OF

## THE AMERICAN MUSEUM OF NATURAL HISTORY

---

### MEMOIRS

- Volume I. Zoölogy and Palæontology.
- Volumes II-VIII. Anthropology.
- Volume IX. Zoölogy and Palæontology.
- Volumes X-XIV. Anthropology.
- Volumes II, IV, V, VII, VIII, X-XIV, and an Ethnographical Album form Volumes I-X of the Memoirs of the Jesup North Pacific Expedition.

### MEMOIRS—NEW SERIES

- Volumes I and II. Zoölogy and Palæontology.
- Volume III, part 1. Entomology.
- Volume III, parts 2-3. Palæontology.

### BULLETIN

- Volumes I-XXIV, XXV, parts 1 and 2, and XXVI-LI.

### NOVITATES

- Numbers 1-205.

### ANTHROPOLOGICAL PAPERS

- Volumes I-XVIII; XIX, parts 1-5; XX; XXII; XXIII, parts 1-6; XXIV, XXV; XXVI, parts 1, 2; XXVII.

### MONOGRAPHS

- A Review of the Primates. By D. G. Elliot. 3 volumes.
- Hitherto Unpublished Plates of Tertiary Mammals and Permian Vertebrates. By E. D. Cope and W. D. Matthew.

### NATURAL HISTORY

- Journal of The American Museum of Natural History
- Volumes 1-XXV. The Journal is a popular record of the progress of The American Museum of Natural History, issued bimonthly.

HANDBOOKS. Numbers 1-11.

GUIDE LEAFLETS. Numbers 1-61.

ANNUAL REPORTS. First (1869) to Fifty-sixth (1924).

A more detailed list, with prices, of these publications may be had upon Application to the Librarian of the Museum.