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Triassic Cynodont Reptiles From Antarctica

EDWIN H. COLBERT[1] AND JAMES W. KITCHING[2]

ABSTRACT

Sixteen specimens of cynodont reptiles from the Lower Triassic Fremouw Formation were collected during the austral summer of 1970-1971 in the central Transantarctic Mountains of Antarctica. The fossils are described in the present paper. Fourteen of the specimens are definitely referable to *Thrinaxodon liorhinus* Seeley, a characteristic cynodont from the Lower Triassic *Lystrosaurus* Zone, Middle Beaufort Beds of the Karroo Series in South Africa. Two of the specimens are referred to Cynodontia *incertae sedis*, one of these being a mold in the rock of a heavy mandibular ramus, the other a right zygomatic arch with associated posterior parts of the mandibular rami, other fragments of skull bones and certain postcranial elements, all representing a cynodont considerably larger than a typical *Thrinaxodon*. The presence of *Thrinaxodon liorhinus* in Antarctica constitutes one more element in the chain of evidence indicating that a *Lystrosaurus* fauna, very similar to, if not completely identical with, the *Lystrosaurus* fauna of southern Africa inhabited what is now eastern Antarctica at the beginning of Mesozoic time. The association of the Antarctic-African species, *Lystrosaurus murrayi*, *Lystrosaurus curvatus*, and *Procolophon trigoniceps*, described in previous papers together with *Thrinaxodon liorhinus*, confirms the geological-geophysical interpretation indicating a close ligation between Antarctica and Africa in early Triassic time.

INTRODUCTION

A considerable tetrapod fauna of early Triassic age was collected from the Fremouw Formation in the Transantarctic Mountains during the austral summers of 1969-1970, and 1970-1971. Within this assemblage are 16 specimens representative of the cynodonts, these being among the most-advanced of the mammal-like reptiles. All of these fossils were found during the second field season devoted to searching for Triassic tetrapods in Antarctica, and were collected mainly in the vicinity of the junction between the McGregor and Shackleton glaciers, at approximately latitude 85°13′ S and longitude 174°30′ E.

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The fossils are variously preserved. Some consist of partial articulated skeletons, some of scattered bones, some of skulls and jaws. A number are represented by natural molds in the rocks (the originals having been eroded away) and from these, rubber casts have been made. The fossils are difficult to study because of their fragmented, distorted, or incomplete preservation. Nevertheless they are adequate to afford an insight into this interesting and important segment of Fremouw fauna.

Preparation of the fossils described in the present paper was carried out at the Museum of Northern Arizona, largely by Mrs. Nova Young, and by Miss Camas Lott. The drawings were made by Miss Pamela Lungé and the photographs taken by Mr. Mark Middleton, of the Museum of Northern Arizona staff.

As in previous papers of this series describing Antarctic Triassic tetrapods, we acknowledge the very helpful advice from Drs. David H. Elliot and James W. Collinson of The Ohio State University, members of the field parties involved in the collecting of Antarctic Triassic tetrapods. We are much indebted to the personnel of the United States Navy for logistical support.

We are also deeply indebted to Dr. Farish A. Jenkins, Jr., to the Museum of Comparative Zoology at Harvard University, and to the Bernard Price Institute for Palaeontological Research at the Witwatersrand University, Johannesburg, South Africa, as well as to Dr. Joseph T. Gregory and to the Museum of Paleontology, University of California, Berkeley, for loans of skulls with lower jaws of *Thrinaxodon liorhinus*. Finally, we express our gratitude to Dr. James A. Hopson of the University of Chicago, who not only gave us the benefit of his observations based on protracted studies of *Thrinaxodon* but also provided copies of manuscript notes and sketches, by himself and by Dr. S. Fourie of the University of the Orange Free State. Bloemfontein. All these materials have been of inestimable value for comparative purposes.

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ABBREVIATIONS

AMMM, Alexander McGregor Memorial Museum, Kimberly
AMNH, the American Museum of Natural History
BMNH, British Museum (Natural History)
BPI, Bernard Price Institute, Witwatersrand University, Johannesburg
C, National Museum, Bloemfontein
S, South African Museum, Capetown
TM, Transvaal Museum, Pretoria
UCMP, University of California (Berkeley) Museum of Paleontology

STRATIGRAPHIC RELATIONSHIPS

The stratigraphic relationships of the fossil tetrapods from the Fremouw Formation of Antarctica have been outlined in Colbert, 1974; Colbert and Cosgriff, 1974; Colbert and Kitching, 1974; see also Elliot, Collinson, and Powell, 1972. For those readers who may not have at hand the papers mentioned above, we offer a few summary remarks.

The Fremouw Formation, the lowest unit in the Triassic sequence in the Transantarctic Mountains, may reach thicknesses of some 650 meters. It overlies the Permian Buckley Formation, from which it is separated by a disconformity, and it is succeeded by the Triassic Falla Formation, on top of which is the Prebble Formation. A disconformity separates the Prebble from the succeeding Jurassic rocks.

The Fremouw tetrapods occur at successive levels in the lower part of the Formation, where the sediments are cyclic, with coarse conglomeratic channel deposits at the base and fine floodplain deposits at the top. At McGregor and Shackleton glaciers, where almost all the theriodont reptiles were collected, the fossils were obtained mainly from fine-grained floodplain deposits.

As has been demonstrated in previous papers, the fauna collected in the Fremouw Formation is closely related to the Lower Triassic tetrapod fauna of the *Lystrosaurus* Zone, Middle Beaufort Beds, of the Karroo sequence in southern Africa, for which see Kitching (1968, In Press).

DESCRIPTIONS OF FOSSILS

SYSTEMATICS

CLASS REPTILIA

ORDER THERAPSIDA

SUBORDER THERIODONTIA

INFRAORDER CYNODONTIA

FAMILY GALESAURIDAE

THRINAXODON SEELEY, 1894

Thrinaxodon Seeley, 1894, p. 990.

Type Species. Thrinaxodon liorhinus Seeley.

Horizon and Locality of Type Species. Lower Triassic, Middle Beaufort Beds, *Lystrosaurus* Zone, South Africa. The type is a skull from Thaba 'Nchu, Orange Free State, South Africa.

Generic Diagnosis. Small cynodonts with four upper and three lower incisors, well-developed canines, and large, predominantly tricuspid post-canines with inner cingulum. Skull narrow, with tapering snout, but with wide zygomatic region. Well-developed secondary palate, reduced quadrate, and double occipital condyles. Vagus foramen ventrally placed. Dentary large, with prominent coronoid. Ribs of thoracic and lumbar vertebrae broadly expanded and overlapping. Ilium expanded, ischium long, and pelvis without obturator foramen. Tail short. Limbs slender. Feet with well-developed carpus and tarsus and with phalangeal formulae of 2-3-4-4-3 in the manus and 2-3-4-5-3 in the pes.

Thrinaxodon liorhinus Seeley, 1894

Thrinaxodon liorhinus Seeley, 1894
Ictidopsis elegans Broom, 1912
Ictidopsis formosa van Hoepen, 1916
Thrinaxodon putterilli Broom, 1932
Notictosaurus luckhoffi Broom, 1936
Micrictodon marionae Broom, 1937

(Note. This synonymy follows the synonymy established by Hopson and Kitching in 1972.)

Type. BMNH R 511 a complete skull with lower jaw.

Horizons and Localities. Lower Triassic; Middle Beaufort Beds, *Lystrosaurus* Zone, southern Africa; Fremouw Formation, Transantarctic Mountains, Antarctica. Almost all the Antarctic specimens were collected at a locality designated as *Thrinaxodon* Col, which is approximately 4 km. due south of the southern border of McGregor Glacier at about latitude 85° 13′ S and about longitude 174° 30′ E. This is on the north flank of Mount Kenyon. Two specimens, noted below, were collected at Graphite Peak, where the initial discovery of a Triassic tetrapod was made in Antarctica. This is slightly below the 85th parallel S, and at longitude 172° 30′ W.

Diagnosis. Since this is a monotypic genus, according to the synonymy above, the generic diagnosis applies to the species.

ANTARCTIC SPECIMENS UNDER CONSIDERATION

AMNH 9500, impression of a skeleton in the rock, including portions of the palatal region of the skull, portions of the lower jaw, the presacral vertebrae with ribs in articulation, pectoral girdle with right humerus, radius and ulna and left humerus in articulation, left femur and proximal ends of tibia and fibula. From *Thrinaxodon* Col, Mount Kenyon.

AMNH 9516, impression of a portion of vertebral column with ribs in articulation, consisting of eleven presacral vertebrae and ribs. From *Thrinaxodon* Col, Mount Kenyon.

AMNH 9517, impression of the anterior part of a skull and mandible in the rock. From *Thrinaxodon* Col, Mount Kenyon.

AMNH 9524, impression of a left ilium and femur in the rock. From *Thrinaxodon* Col, Mount Kenyon.

AMNH 9528, two rock fragments containing weathered portions of a skull and of four presacral vertebrae with ribs. From *Thrinaxodon* Col, Mount Kenyon.

AMNH 9529, a weathered fragment of a skull and jaw in rock, consisting of the premaxillae and maxillae with teeth, and certain dentary teeth. From *Thrinaxodon* Col, Mount Kenyon.

AMNH 9534, part of a skull in the rock, considerably crushed and distorted. From *Thrinaxodon* Col, Mount Kenyon.

AMNH 9546, fragment of a right maxilla in the rock. From Graphite Peak, Transantarctic Mountains.

AMNH 9547, posterior part of a skull in the rock, showing the parietal region and the right temporal arcade. From Graphite Peak.

AMNH 9553, impression of foot bones and other miscellaneous bones in the rock. From *Thrinaxodon* Col, Mount Kenyon.

AMNH 9555, impression in the rock of some 10 presacral vertebrae, as well as a few miscellaneous elements. From *Thrinaxodon* Col, Mount Kenyon.

AMNH 9563, a large and somewhat distorted skull and lower jaw, lacking the anteriormost portions. From *Thrinaxodon* Col, Mount Kenyon.

AMNH 9570, part of a skeleton, preserved partially as weathered bones in the rock and partially as impressions. From *Thrinaxodon* Col, Mount Kenyon.

AMNH 9571, part of a skeleton in the rock, preserved as impressions and in part of weathered bones, similar to 9570. From *Thrinaxodon* Col, Mount Kenyon.

At this stage it is probably relevant to draw attention to the similarity and fair abundance with which the genus *Thrinaxodon* occurs at *Thrinaxodon* Col, Mount Kenyon, Antarctica, as well as in the *Lystrosaurus* Zone, Middle Beaufort Beds, South Africa.

Approximately 30 skulls of *Thrinaxodon* (very frequently with skeletal remains attached) have been recovered from the "Old Brickfield" donga or erosion gully on the Harrismith Commonage, whereas 22 specimens of this species have been recovered since 1963, from an erosion gully on a slope, below the Oliviershoek Pass road, Bergville district, Natal. More recently, six skulls with skeletal elements were found in a small localized area on a farm in the Bethulie district, Orange Free State.

The occurrence of fossils is governed by the rate of erosion in these areas, and the genus *Thrinaxodon* is usually confined to a specific horizon within the sediments. This situation is also comparable with the presence of *Thrinaxodon* at *Thrinaxodon* Col in Antarctica.

On a speculative basis the presence of *Thrinaxodon* in Antarctica, which closely resembles occurrences in the South African sediments, seems to indicate that these creatures were either abundant in small localized areas, or lived in colonies or communities, probably in close proximity to the area or site where their remains are found in the sediments. For example, as seen from the figures for *Thrinaxodon* in South Africa as set forth above, 58 specimens have been recovered from three localities, whereas as listed in this paper 14 specimens of *Thrinaxodon* are presently known from Antarctica at two localities (12 at *Thrinaxodon* Col and two at Graphite Peak). Moreover, these fossils result from collecting during one necessarily short field season, an indication that *Thrinaxodon* is probably abundant in Antarctica. Colonizing or living in communities is not uncommon among living lizards (*Gerrhosaurus validus*, etc.) and small mammals (*Procavia*, *Suricata*, etc.).

DISCUSSION

Our present knowledge of *Thrinaxodon* in Antarctica is based on a considerable suite of specimens in varying states of preservation. It is interesting that among all the fossils collected in Antarctica, *Thrinaxodon* is the one form represented by a rather large proportion of natural molds, rather than fossil bone. Most of these molds have yielded excellent latex casts; nevertheless even the best of such casts is not quite the same as a specimen consisting of good fossilized bone for detailed study. For example, whereas the latex cast of the partial skull and lower jaw of AMNH 9517 reveals excellent bone surfaces, the details of some of the teeth leave something to be desired.

The natural mold of the articulated skeleton, AMNH 9500 (see fig. 1), affords good general information for the post-cranial elements of *Thrinaxodon*, but the skull and lower jaw are especially difficult to interpret. Much is missing, so that any comparison with other material is necessarily limited. However, the skull as preserved does indicate its overall size and a few of the characteristic details. In this connection, the cast from a natural mold of the front of a skull with lower jaw, AMNH 9517 (fig. 13), is very helpful.

Several natural molds have yielded some very good casts of ribs, showing the morphological details to perfection. A comparison of a natural mold and the latex cast made from it is shown in figure 5.

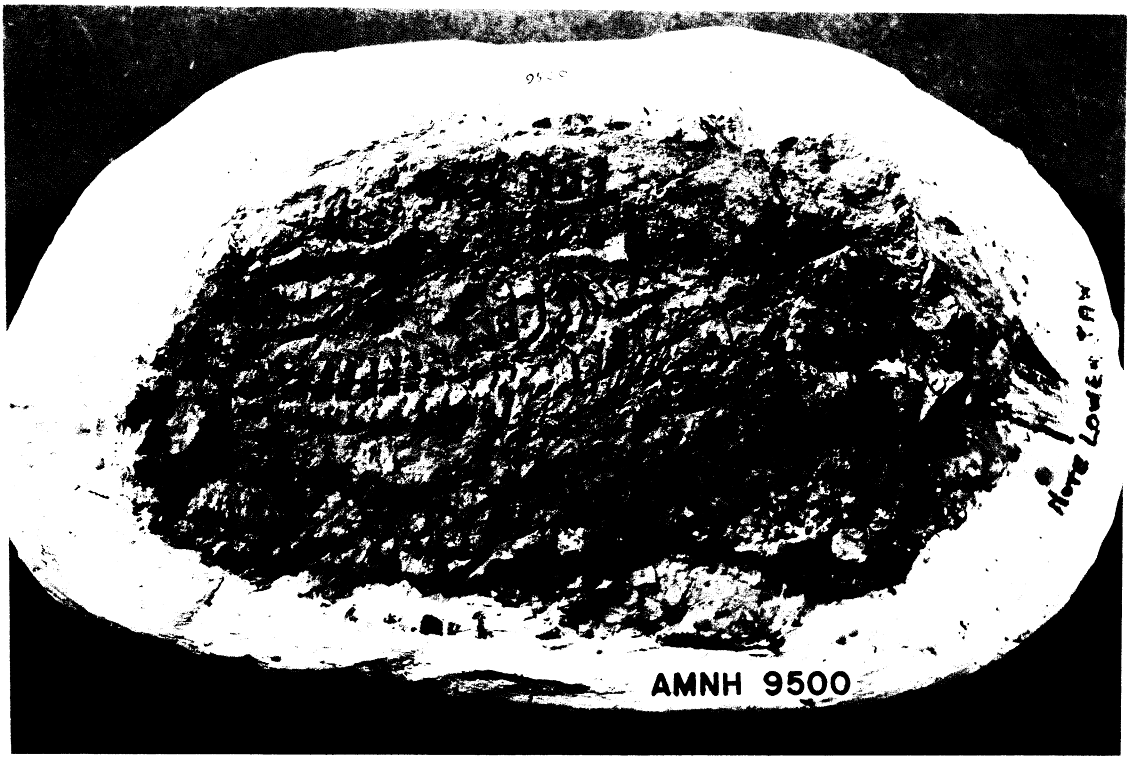

FIG. 1. *Thrinaxodon liorhinus* Seeley. AMNH 9500, natural mold of skeleton in rock. Approximately ×¼.

Bony specimens are less than perfect. The skull and lower jaw, AMNH 9563, shown in figure 10, is somewhat crushed, and parts of it are missing. Nonetheless, careful examination of the specimen does reveal many of the salient features.

We do not intend to convey the impression that the materials are unsatisfactory; they have inadequacies but on the whole they are very valuable. Since these theriodonts are the first to be collected from a continent in which Triassic tetrapods were previously unknown, the abundance and generally satisfactory nature of the fossils are truly remarkable. It seems certain that more and better materials will be found in the future; the evidence indicates that the Fremouw Formation of Antarctica is richly fossiliferous.

With these caveats on record, attention can now be given to a consideration of the fossils.

The Antarctic fossils accord with the definition of the genus *Thrinaxodon* in those features that are to be seen in the new materials. Thus, the skull, broad at the arches, tapers to a rather narrow snout. There are four upper incisors, a large canine, and seven postcanine teeth, these being for the most part tricuspid. The dentary is stout, the coronoid is large, and the postdentary elements are relatively small. There are 27 presacral vertebrae. The thoracic and lumbar ribs are strongly expanded (a galesaurid character), and the ilium is expanded.

An important question is whether the Antarctic materials represent a new species, or whether they can be referred to the African form, *Thrinaxodon liorhinus.* The determination of species among fossil tetrapods is not easy, and judgments as often as not have to be rather subjective. On the basis of the information available, it is our opinion that the Antarctic fossils listed on pages 3-4 are to be equated with *Thrinaxodon liorhinus*, the species characteristic of the *Lystrosaurus* Zone of South Africa. Taken together, we can find no character that definitely separates the Antarctic fossils from those of

Africa. Note that much of the Antarctic material represents large and robust individuals, but this in itself cannot be used to differentiate these fossils as a new species. As measurements indicate, the Antarctic fossils fall within the size range of *Thrinaxodon liorhinus*, as known from South Africa. This is illustrated by the graph, figure 23, in which the lengths and widths of skulls from Africa and from Antarctica have been plotted.

The point has been raised that African materials, as plotted in figure 23, may represent more than one population. Even if so there is no reason to suppose that more than one species, namely *Thrinaxodon liorhinus*, is present in the African *Lystrosaurus* Zone. Therefore, however the graph (based on the simple relationship of two characters) may be analyzed, we believe that it shows specimens belonging to this one species. It should be kept in mind that the diagnosis of *Thrinaxodon liorhinus* depends primarily on the various morphological characters discussed in this paper.

For enumerations of the diagnostic characters of *Thrinaxodon liorhinus*, and classifications of the cynodont and theriodont reptiles, see Haughton and Brink (1954), Romer (1956), Watson and Romer (1956), Piveteau (1961), Romer (1966), and Hopson and Kitching (1972).

The most complete specimen of *Thrinaxodon* in the Antarctic collection is the natural mold of the skeleton, AMNH 9500, seen in ventral aspect, and in articulation as far back as the pelvis. This specimen is illustrated in figures 1-4. The only bony material preserved is in the skull and mandible, which consists of some very fragmentary slivers of the pterygoids, an indistinguishable mass of bone, which is a portion of the right maxilla and nasal as seen in internal ventral view, some very small and fragmentary pieces within the impressions of the jugal arches and the mandibular coronoids, and a small section of the left maxilla with the fragments of a canine and the roots of four postcanine teeth, seen in cross section. Otherwise the specimen consists of reasonably good molds of individual bones, preserved in a fairly hard sandstone. This specimen has been compared with the skeleton of *Thrinaxodon liorhinus*, so thoroughly described by Jenkins (1971) and figured also by Crompton (1973).

The skull and lower jaw do not yield a great deal of information, either from the natural mold or from latex impressions because of the incompleteness of the specimen. Enough is preserved, however, to determine the length of the skull with a fair degree of accuracy, and the width across the arches even more definitely. Most of the vertebral centra are visible, back to the sacrum. The vertebrae, including what are here considered as the tenth presacral through the twenty-seventh, are clearly represented. Two vertebral centra anterior to number 10 are visible, and these are identified as numbers four and seven. Such identifications are based on positions, with due allowances being made for the spaces that would be occupied by missing vertebrae.

In this connection it should be said that the vertebral formula is here considered to contain 27 presacrals. Brink (1954) stated that there are 26 presacral vertebrae, including the atlas, in *Thrinaxodon liorhinus* from Africa, but his restoration of the skeleton of *Thrinaxodon* (1956) shows 27 presacrals. In his paper of 1959 he indicated 27 presacral vertebrae. Also, a review of the literature indicates that 27 is a rather general presacral count among theriodont reptiles, and especially among the cynodonts.

The ribs are present in articulation with the vertebrae, the thoracic and lumbar ribs showing the broadening so characteristic of *Thrinaxodon* and of other galesaurids, for that matter.

The pectoral girdle is partly visible in ventral view, as is the right humerus, radius, and ulna. Unfortunately the right manus is not preserved. The left humerus is partially preserved in the mold.

One sacral centrum is preserved, as well as the left sacral rib associated with it.

The left femur is present, as is a part of the right femur. In addition, the proximal parts of the right tibia and fibula are present.

Returning briefly to the skull in this specimen, although there is little detail to be seen, it is evident that the skull is relatively large—a character shared by *Thrinaxodon* and many cynodonts. Its basilar length, from the premaxillae to the occipital condyles, is equivalent to the combined length of the last eight presacral vertebrae, as preserved in articulation. (These vertebrae all show ample intervertebral spaces, and it could be thought that they may have been separated somewhat, each from the other, during the process of fossilization. We do not think that was the case, however; any separation beyond the spaces normally occupied by the intervertebral discs has been relatively slight.)

Thus the skull appears to show about the same proportion relative to the postcranial skeleton as is the case in *Thrinaxodon liorhinus* as figured by Brink (1954). In Jenkin's reconstruction of the skeleton of *Thrinaxodon liorhinus* (1971), the skull is indicated as being proportionally slightly smaller; in effect about equal to the length of the last seven presacral vertebrae, those elements which Jenkins considered as constituting the lumbar series. It should be noted, however, that Brink's reconstruction is based upon a single associated skeleton, whereas that of Jenkins is based upon a composite of several specimens.

To make another comparison, in the Antarctic specimen the skull is slightly greater in length than double the length of the humerus. In the specimen figured by Brink the humerus is just half the length of the skull.

It is therefore apparent that the proportion of skull to postcranial skeleton is almost the same in the Antarctic fossil as is the case in *Thrinaxodon liorhinus* from Africa. Such differences in proportional size as may exist easily fall within the range of individual variation.

The form of the pterygoids as well as of the basipterygoid in AMNH 9500 is indicated (in a general way) by the natural mold, and both appear to conform in all respects with the same structures in the African *Thrinaxodon.*

Jenkins defined seven cervicals and seven lumbars in his study of the postcranial skeleton of *Thrinaxodon liorhinus*. These in conjunction with 13 dorsal vertebrae make up the 27 presacrals that are characteristic for this cynodont reptile. The cervical series is incomplete in the Antarctic specimen, but in the posterior part of the column there are definitely seven vertebrae that can be considered as lumbars, such an identification being based upon the forms of the associated ribs, which will be described in a subsequent paragraph.

The vertebral pleurocentra are evidently amphicoelous, circular in cross section, and slightly constricted in their middle portions, these being features typical for *Thrinaxodon.* The centra increase in size from the front to the back of the column, indicating a strong lumbar region, but the increase throughout the vertebral column is gradual.

A fragment of a pleurocentrum, the last in the articulated sequence, is here identified as the first sacral because of its association with a very short rib having an elongated distal edge, quite obviously for articulation with the ilium.

The ribs are present on both sides in AMNH 9500, from the ninth presacral rib back on the right side, and from the twelfth rib back on the left side. The first sacral rib, previously mentioned, is also present on the left side.

Thrinaxodon liorhinus is characterized by the remarkable expansion of the ribs in their proximal parts, as is the case in other galesaurids. The materials from Antarctica show this same expansion of the ribs, essentially identical with the manner of rib expansion that so characterizes the African fossils.

In AMNH 9500 the anterior ribs as preserved are only partially exposed; therefore it is not possible to determine the exact nature of the form in each individual rib. It appears, however, that these ribs are relatively slender throughout much of their length, as is the case in specimens known from Africa. However, the seventeenth presacral rib on the right side and the eighteenth on the left side are fairly complete, as are all of the succeeding ribs on both sides, back to the sacral region. In some of these ribs the distal portions are missing, yet preservation is sufficiently good to show the close resemblances between these ribs and the same ribs in skeletons found in Africa.

Jenkins has shown that the thoracic ribs, except for the last one, are characterized by a strong ridge on the ventral surface, each ridge being continuous with the costal shaft distal to the rib expansion, which may be designated as the costal plate. The last of the thoracic ribs would seem to lack such a ventral ridge, and ridges are not present on the lumbar ribs.

In AMNH 9500 well-defined ridges are apparent on the ventral surfaces of the thoracic rib plates, but in this specimen there is a discernible ridge on the last or thirteenth thoracic plate. The lumbar ribs, which take the form of short plates, do lack the ventral ridges.

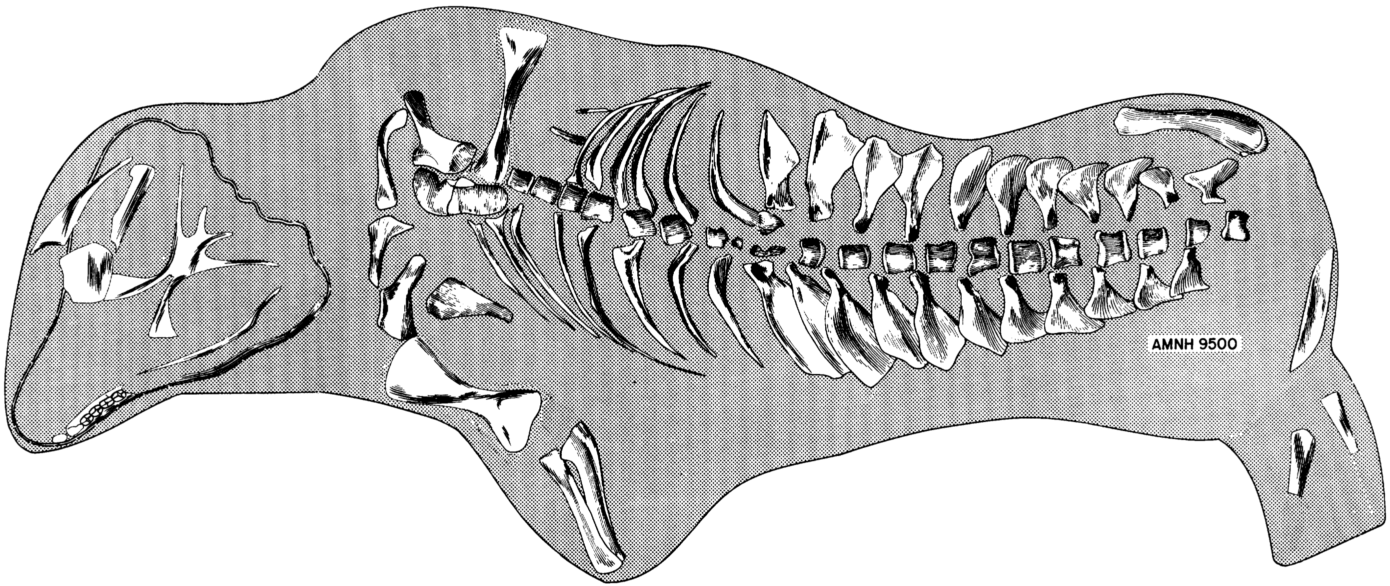

FIG. 2. *Thrinaxodon liorhinus* Seeley. AMNH 9500, drawing made of a latex impression from the natural mold, showing the bones as seen in ventral view. A portion of right maxilla with four teeth and a few other skull and jaw fragments are preserved. ×½.

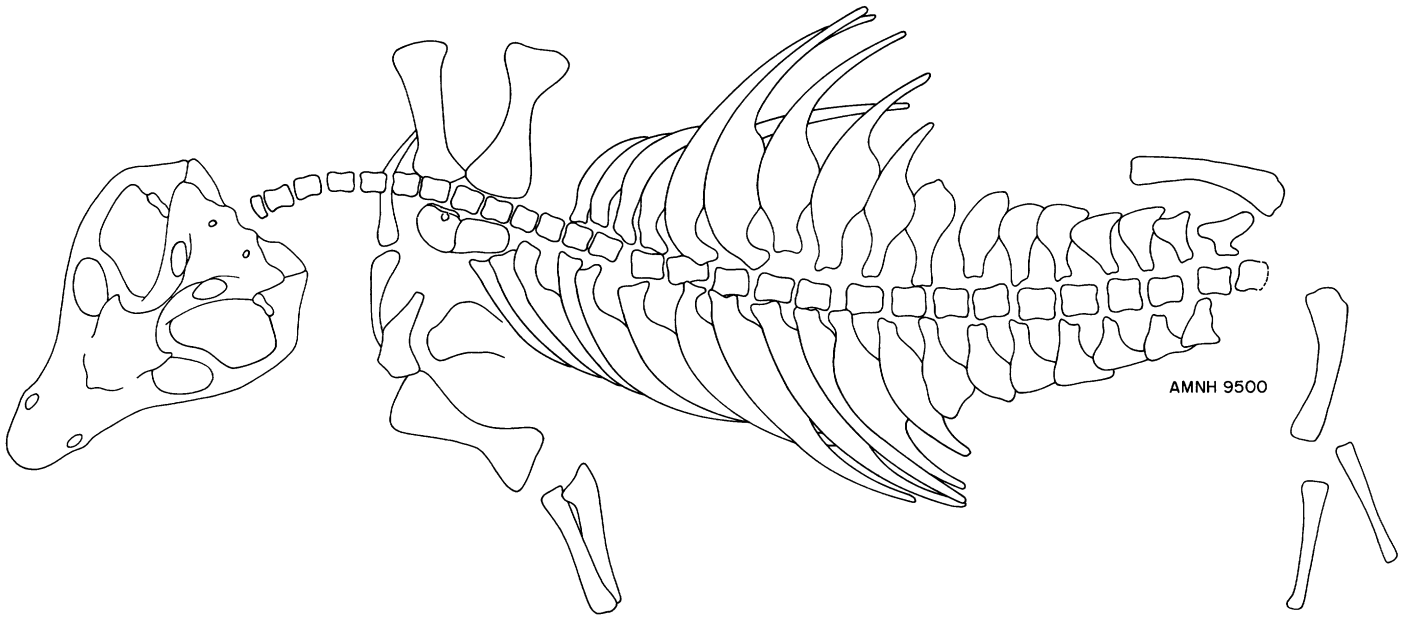

FIG. 3. *Thrinaxodon liorhinus* Seeley. AMNH 9500, restoration in outline of skeleton shown in figure 2, with shape of skull indicated, the left scapulacoracoid and humerus restored, and the ribs restored to their approximate correct lengths. X½.

In African specimens of *Thrinaxodon liorhinus* the largest costal plates are the more posterior ones, namely numbers 11 through 13 in the thoracic series. The costal shafts beyond the expanded plates are long in the more anterior members of the thoracic series and decrease toward the back, being mere spikes on the thirteenth thoracic ribs. The costal shafts in AMNH 9500 are elongated in the anterior thoracic region and they evidently decrease in the progression toward the back of the body. Certainly the last thoracic plate in this specimen seems to end in a short point, comparable with what is seen in African specimens.

In the lumbar region of AMNH 9500 the last five costal plates terminate distally as anteroposteriorly elongated edges, whereas the first two of these ribs are somewhat pointed distally. In Jenkin's restoration of *Thrinaxodon liorhinus* from Africa, the first lumbar costal plate is shown with a slight point, but the second has virtually no such extension. In all, the lumbar plates in the Antarctic specimen seem to be slightly less rectangular than those figured by Jenkins.

Thus there are slight differences in detail between *Thrinaxodon liorhinus* from Antarctica and from Africa in the development of the expanded ribs, as shown in figure 4, but such differences are so small that they are here considered as of no real consequence.

The costal plates in AMNH 9500 overlap, as they do in African specimens. The significance of this overlap has been debated in the literature. Jenkins has suggested that such overlap gives strength to the lumbar region of *Thrinaxodon*, and in general furthers the attainment of a "mammal-like pose" in these mammal-like reptiles.

Supplementary information concerning the ribs in the Antarctic *Thrinaxodon* is afforded by three specimens, AMNH 9516, 9555, and 9571, all preserved as natural molds, from which latex casts have been made, and illustrated in part by figures 5-8. AMNH 9516, from the posterior portion of the presacral region, contains four lumbar vertebrae with ribs on both sides, and in front of these, six vertebrae with thoracic ribs. The lumbar ribs are distally broad; the thoracic ribs show the typical broad costal plates with prominent ventral ridges, terminating in short shafts, these reduced to mere points in the last two of the series.

AMNH 9555 reveals alignments of ribs on the two sides, but with only two vertebral centra in place at the posterior end of the sequence. This specimen evidently comes from the anterior part of the presacral region, because the first nine ribs on the left side do not show significant expansions of costal plates. It may be presumed therefore that some of the anterior, slender ribs are from the cervical region and some from the anterior thoracic region.

AMNH 9571 shows some scattered ribs and some other bones, notably a vertebral spine and portions of limb bones. The vertebral spine is tall, evidently from the anterior part of the presacral series. The ribs have very broad costal plates which narrow quite abruptly to elongated shafts.

The pectoral girdle is present in AMNH 9500, but only parts of it are completely visible. From what can be seen, it would appear that the scapula probably is quite similar to the scapula in *Thrinaxodon liorhinus* from Africa. There does not seem to be an acromion process, and the same is true for African specimens. Although the coracoids are not completely preserved, it is evident that there is a more or less rectangular procoracoid, pierced by a foramen, articulating with an elongated coracoid posterior to it. There are large and rather heavy clavicles as might be expected for, as Jenkins has pointed out, cynodont clavicles are "moderately robust." The interclavicle is not visible.

According to Jenkins, "cynodont humeri more closely resemble those of primitive tetrapods in general and pelycosaurs in particular than those of any therian" (Jenkins, 1971, p. 112), and this applies to the humerus of AMNH 9500. The bone is broad at each end, with a strong deltopectoral crest running down the bone from the proximal end. This crest, which contributes to the great width of the proximal end, is also responsible for the division of the proximal part of the humerus into two planes, intersecting along the bicipital groove. All in all, the deltopectoral crest is a very prominent feature of the humerus. At the opposite end of the bone the articulation is in a single plane, formed by the

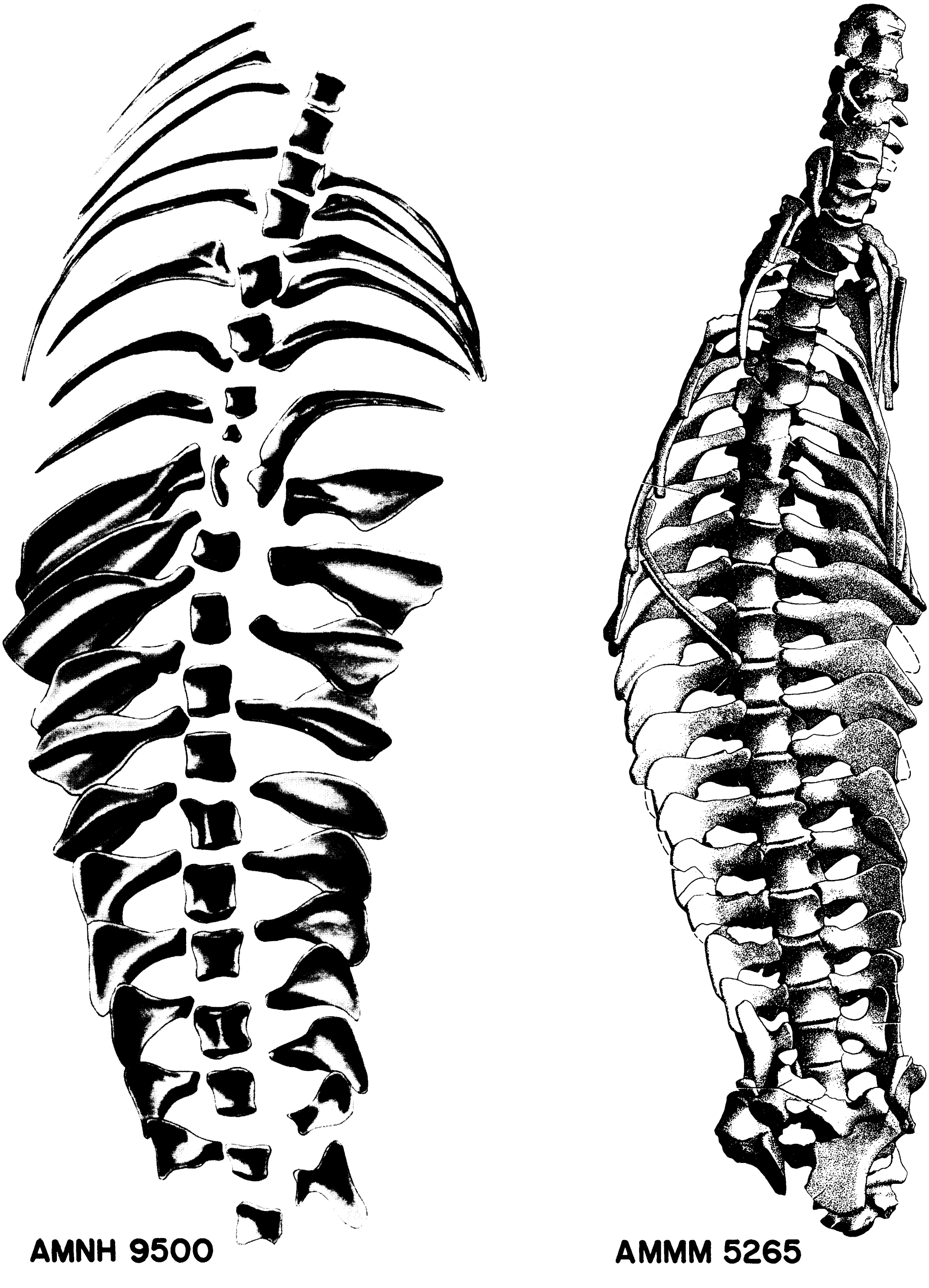

FIG. 4. *Thrinaxodon liorhinus* Seeley. AMNH 9500, portion of skeleton, compared with AMMM 5265, a partial skeleton from South Africa, as figured by Jenkins (1971). × 1.

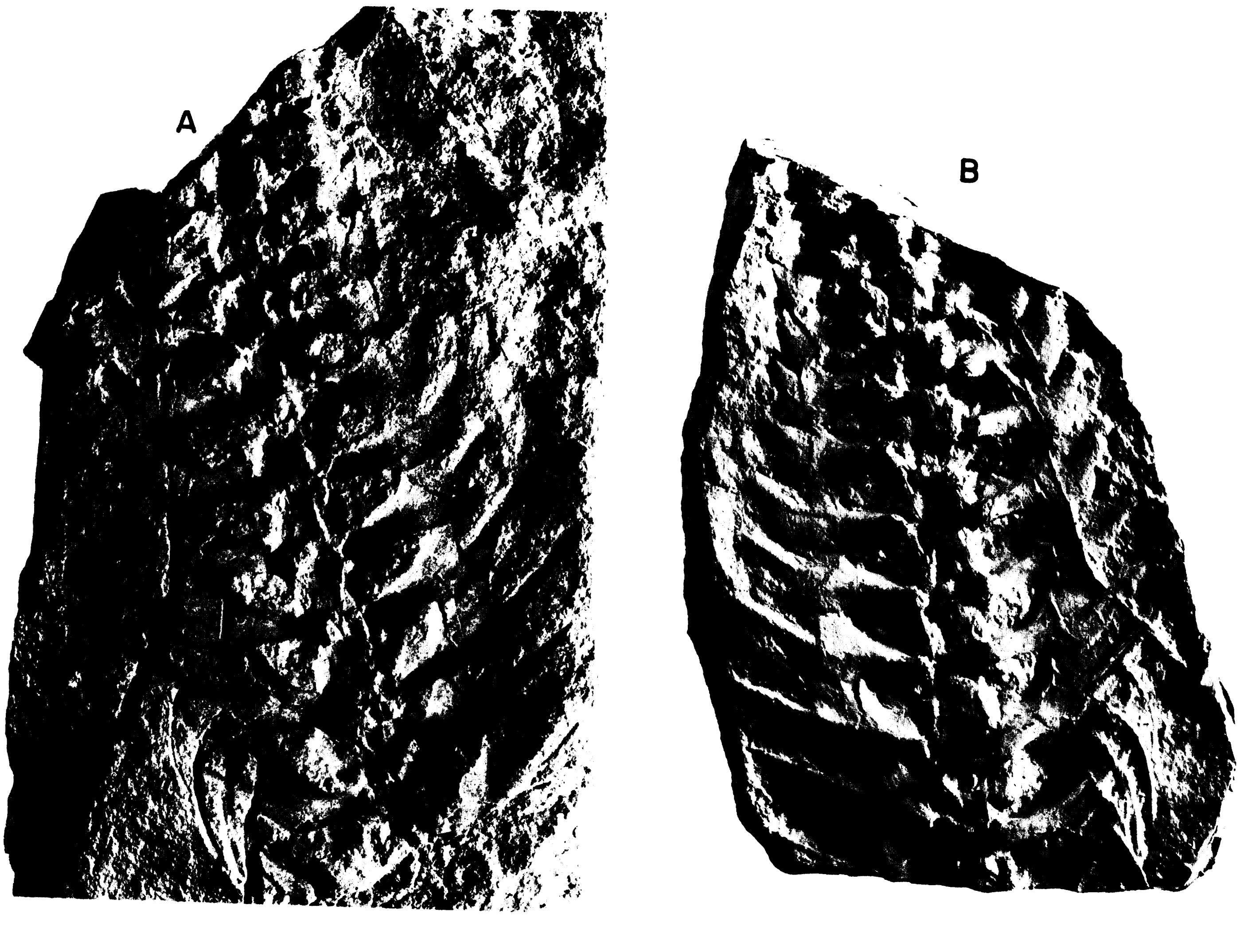

FIG. 5. *Thrinaxodon liorhinus* Seeley. AMNH 9516. A. Natural mold of part of vertebral column with ribs. B. Latex cast from the natural mold. Ventral view. ×1.

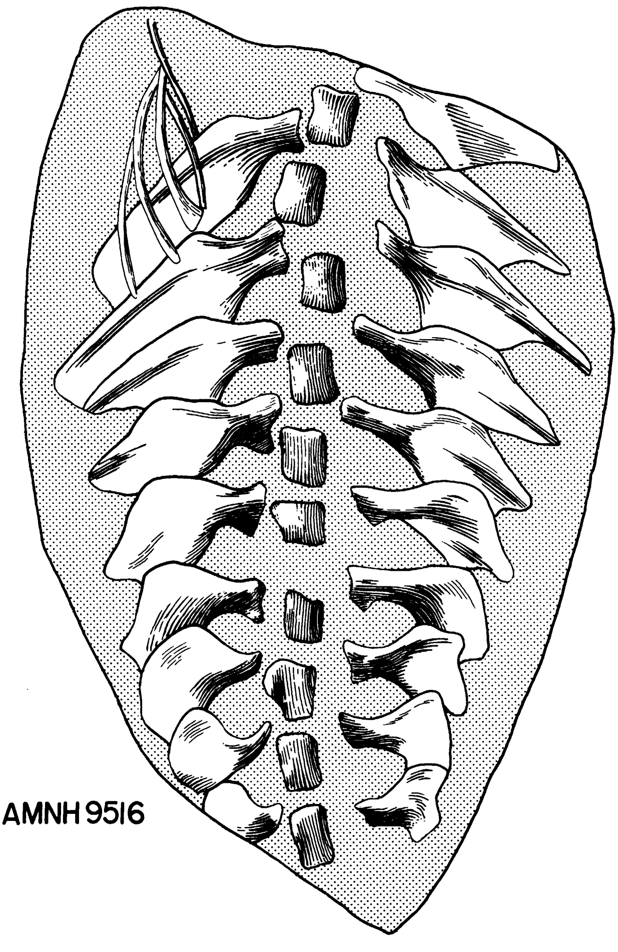

FIG. 6. *Thrinaxodon liorhinus* Seeley. AMNH 9516, portion of vertebral column with ribs. Ventral view. X 1.

flared epicondyles. It seems that the long axes of the two ends of the bone are twisted, as is usual in humeri of this type, but it is difficult from the material at hand to determine the angle of the twist between the two ends of the bone. There is reason to think that entepicondylar and ectepicondylar foramina were present, but these features, so characteristic of *Thrinaxodon*, and of cynodonts in general, cannot be definitely determined in AMNH 9500, because of the manner of preservation. The shaft of the humerus is relatively short.

The right radius and ulna in AMNH 9500 are preserved in position, distal to the humerus. The radius is a comparatively straight and slender bone, expanded somewhat at each end. The ulna is heavier than the radius, the upper end of the bone having its proximal portion curved in such a manner so that the proximal articular facet is at something of an angle to the proximal facet of the radius. The articular lengths of the radius and ulna are somewhat less than the length of the humerus.

The several elements of the pelvis are not preserved in AMNH 9500, but the left femur is nicely exposed in posterolateral view. The bone

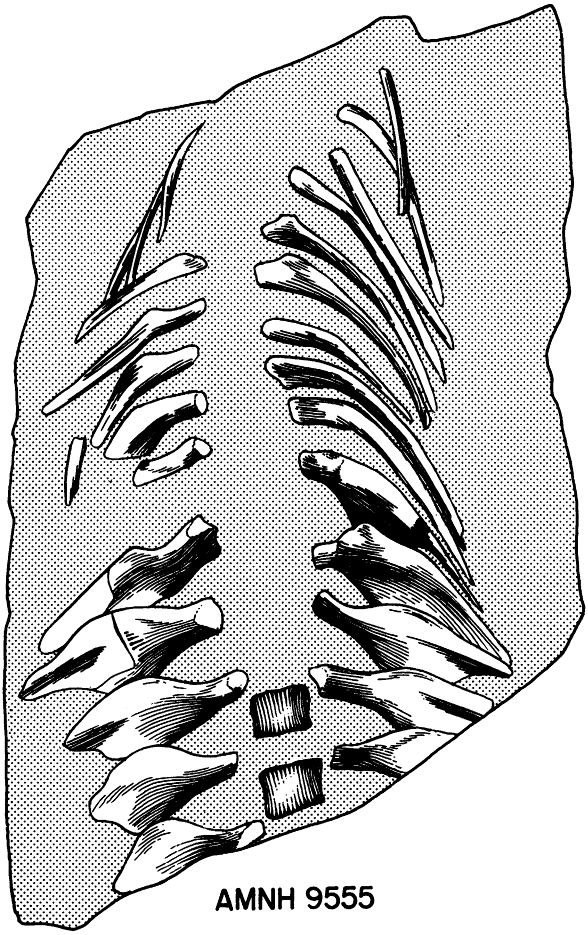

FIG. 7. *Thrinaxodon liorhinus* Seeley. AMNH 9555, portion of vertebral column with two centra and ribs. (Drawn from a latex cast made from a natural mold.) Ventral view. × 1.

is quite comparable with the femur of *Thrinaxodon liorhinus* from Africa, as described and figured by Jenkins. It is about equal to the humerus in length, as is the case in *Thrinaxodon* from Africa. The head of the bone is rather indistinct; Jenkins pointed out that the femoral head in *Thrinaxodon* is unossified. The proximal end of the bone curves dorsomedially, for articulation with the acetabulum of the pelvis. The shaft of the bone is straight, and distally it is somewhat expanded. There appears to be an intertrochanteric fossa on the ventral surface of the bone, between the head and the greater trochanter.

The proximal ends of the right tibia and fibula are barely visible and little is to be said concerning them.

Information concerning the skull of *Thrinaxodon* from Antarctica is best obtained, upon the basis of materials now known, from some of the specimens listed on pages 3-4. Of these, AMNH 9563, a distorted and somewhat broken skull and jaw, is the best specimen, even though it leaves much to be desired. It is supplemented by AMNH 9517, the lower part of the premaxillary-maxillary region with the anterior part of the lower jaw in articulation, by AMNH 9529, a weathered premaxilla-maxilla seen in palatal view, by AMNH 9546, a fragment of a right maxilla, and by AMNH 9547, the posterior part

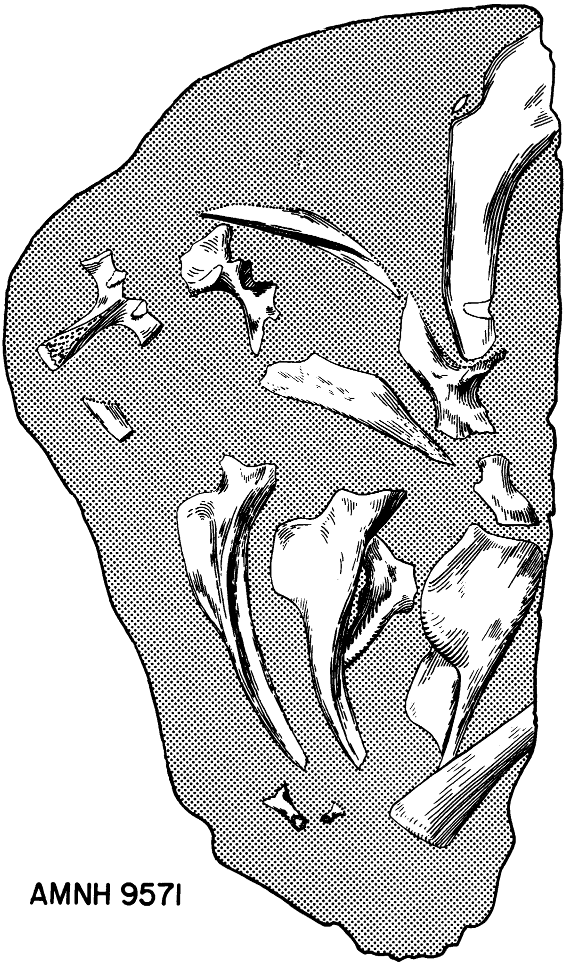

FIG. 8. *Thrinaxodon liorhinus* Seeley. AMNH 9571, latex cast from a natural mold, showing vertebral spine, a portion of another vertebra, several ribs, a part of a limb bone and a part of a lower jaw. X 1.

of a skull in the rock with the parietal region and the right temporal arch, as well as the tip of the right mandibular coronoid in place. Other Antarctic skulls or parts of skulls are in fragmentary and crushed condition. Comparisons of Antarctic materials have been made with African specimens and with descriptions by Brink (1954), Estes (1961), Hopson (1974 personal commun.), and Parrington (1933, 1946).

The skull and jaw, AMNH 9563, represent a rather large individual of the species, but by no means the largest known. Two specimens from South Africa, in the National Museum, Bloemfontein, described by Brink in 1954, are larger. It should be noted that the larger of these two specimens, which would appear to be the largest known *Thrinaxodon* skull, was considered by Brink to belong to a separate species, *Thrinaxodon putterilli*, here considered as a synonym of *Thrinaxodon liorhinus.* Two other specimens in the Bernard Price Institute for Palaeontological Research at the University of the Witwatersrand are comparable in size with the specimen here being considered. These several specimens, as well as others, are plotted on the accompanying graph.

It is possible to delineate many of the bones of the skull and jaw in AMNH 9563, even though the specimen is crushed and broken. So far as can be determined, the bones show essentially the same proportions and relationships that characterize the bones in the skull and jaw of *Thrinaxodon liorhinus* from Africa. The appearance of the skull is shown in figures 9 and 10, the interpretation of the bones in the skull as preserved is presented in figure 11, and a restoration of the skull and jaw in figure 12.

Both Parrington (1946) and Estes (1961) have called attention to the well-developed and fairly numerous foramina on the side of the maxilla in *Thrinaxodon*. Similar foramina are to be seen in AMNH 9563. In addition, there are foramina on the anterior external surface of the dentary in *Thrinaxodon* from Africa, and again, the Antarctic specimen here being discussed shows three nicely developed foramina in this region. Watson (1931), Attridge (1956), and Brink (1957) have interpreted such foramina in the maxilla of cynodont reptiles to be an indication of a mobile snout or a rhinarium or perhaps of vibrissae—all advanced mammalian characters. This interpretation was considered in detail and reinforced by Findlay in 1968. But Van Valen (1960) and Estes (1961) have shown that such is not necessarily the case, for in the modern South American lizard, *Tubinambis*, for example, there is strong vascularization of the maxillary region as an adaptation for the transmission of nerves and blood vessels supplying cutaneous structures.

There is a strong canine tooth in AMNH 9563, and immediately in front of it the tip of an

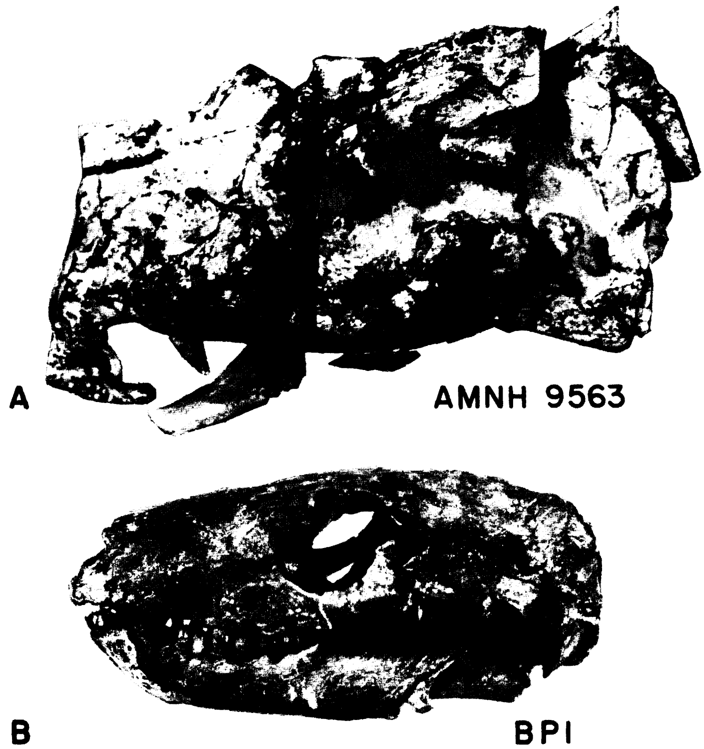

FIG. 9. *Thrinaxodon liorhinus* Seeley. AMNH 9563. A, distorted skull and jaw, compared with B, a specimen from South Africa belonging to the Bernard Price Institute from Palaeontological Research of the University of the Witwatersrand, Johannesburg. Left lateral view. ×1.

erupting tooth. This latter is quite clearly a replacing canine, obviously homologous with the replacing canine as described and figured by Hopson (1964), not a precanine tooth. (*Thrinaxodon* is characterized by the lack of precanine teeth in the maxilla.) An examination of various *Thrinaxodon* skulls from Africa shows that the replacing canine, although initially situated somewhat lingually to the functional canine, shifts its position during development and just before eruption to a location immediately anterior to and in contact with its predecessor.

The Antarctic skull shows a small postcanine tooth, separated by a diastema from the canine, and immediately following that a second postcanine tooth. There is a gap, followed by three more postcanine teeth. The gap is of sufficient size to have accommodated two teeth, so it seems apparent that there were seven postcanine teeth in this specimen—the common number for *Thrinaxodon liorhinus.* The first postcanine is a simple tooth, as is usual in *Thrinaxodon*, whereas the others are tricuspid—a very characteristic *Thrinaxodon* feature. These teeth show the standard tricuspid arrangement, with a large central blade, flanked anteriorly and posteriorly by small low cusps. The postcanine teeth in this specimen are not sufficiently well preserved or exposed to show the cingular cusps that commonly characterize African specimens of *Thrinaxodon* (see Crompton, 1963, 1972).

AMNH 9517, figures 13-15, the ventral part of the premaxilla-maxilla with the lower jaw in articulation, best studied from a latex cast taken from the natural mold in the rock, supplements in certain features what is to be seen in the skull described above. It appears to be perhaps significantly smaller than AMNH 9563, comparable in this respect with a skull from Africa in the University of California collection, UCMP 42866,

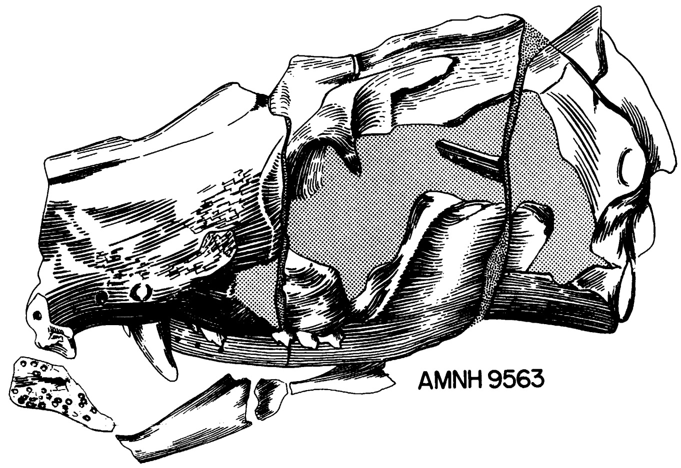

FIG. 10. *Thrinaxodon liorhinus* Seeley. AMNH 9563, distorted skull and lower jaw. Left lateral view. ×1.

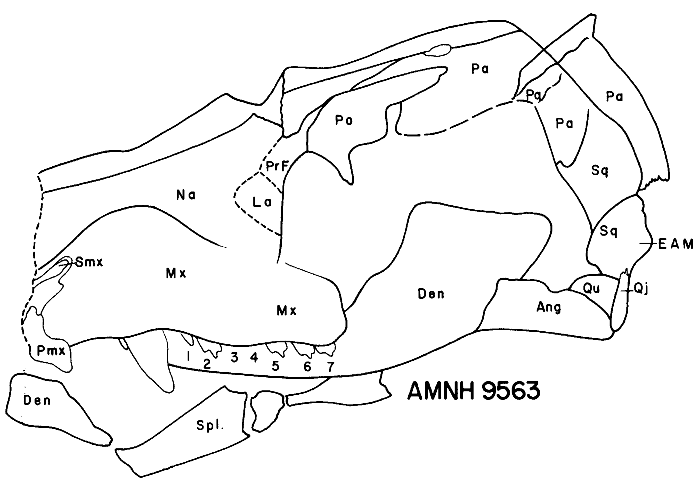

FIG. 11. *Thrinaxodon liorhinus* Seeley. AMNH 9563, skull and lower jaw, interpretation. Left lateral view. ×1. Ang-angular; Den-dentary; EAM-external auditory meatus; La-lacrimal; Mx-maxilla; Na-nasal; Pa-parietal; Pmx-premaxilla; Po-postorbital; PrF-prefrontal; Qj-quadratojugal; Qu-quadrate; Smx-septomaxilla; Spl-splenial; Sq-squamosal; 1-7-upper postcanine teeth.

shown on the accompanying graph, as well as to a skull and jaw from the Bernard Price Institute, University of the Witwatersrand, numbered three on this graph. A satisfactory size comparison is difficult, however, because of the incomplete nature of the Antarctic specimen.

In AMNH 9517, there appears to be a notch in the vicinity of the premaxilla-maxilla suture for accommodation of the lower canine, but this is probably an artifact of preservation. Such a feature does not appear in any of the other known skulls of *Thrinaxodon.*

This specimen shows well-developed foramina in the anterior maxillary region in the vicinity of

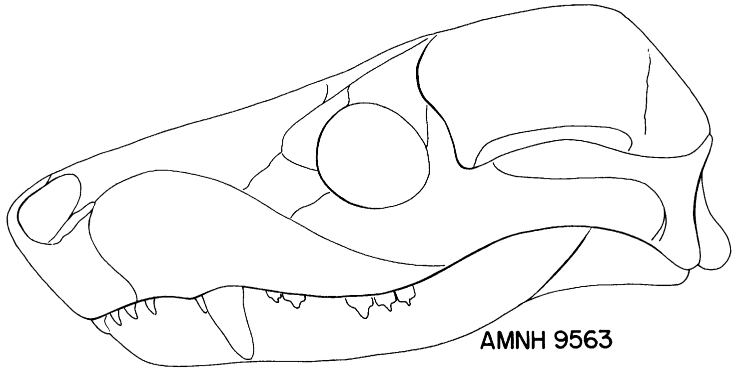

FIG. 12. *Thrinaxodon liorhinus* Seeley. AMNH 9563, restoration. Left lateral view. ×1.

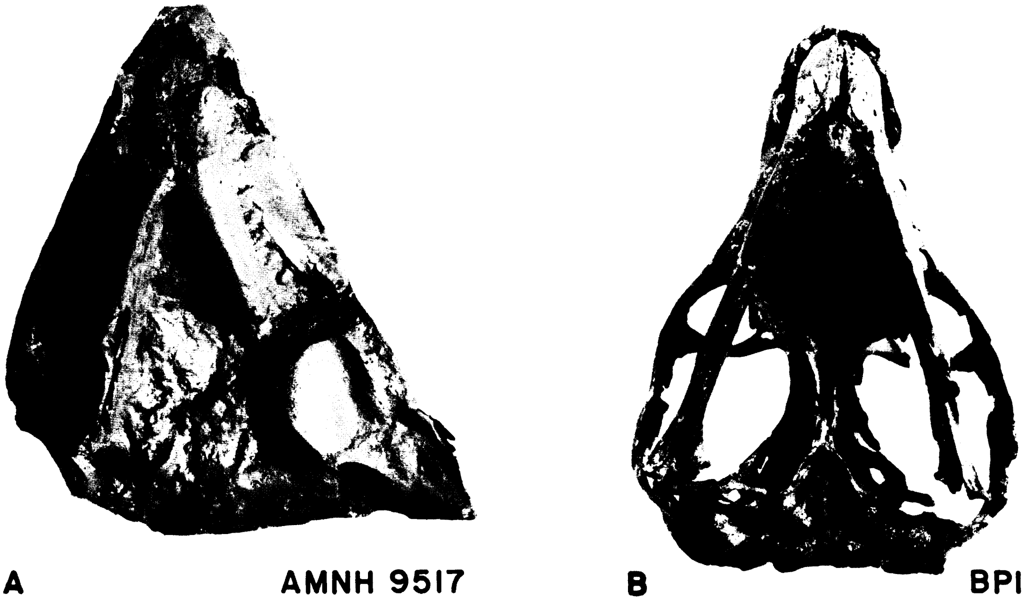

FIG. 13. *Thrinaxodon liorhinus* Seeley. AMNH 9517. A, front of skull and lower jaw (latex cast from a natural mold). Ventral view. ×1.

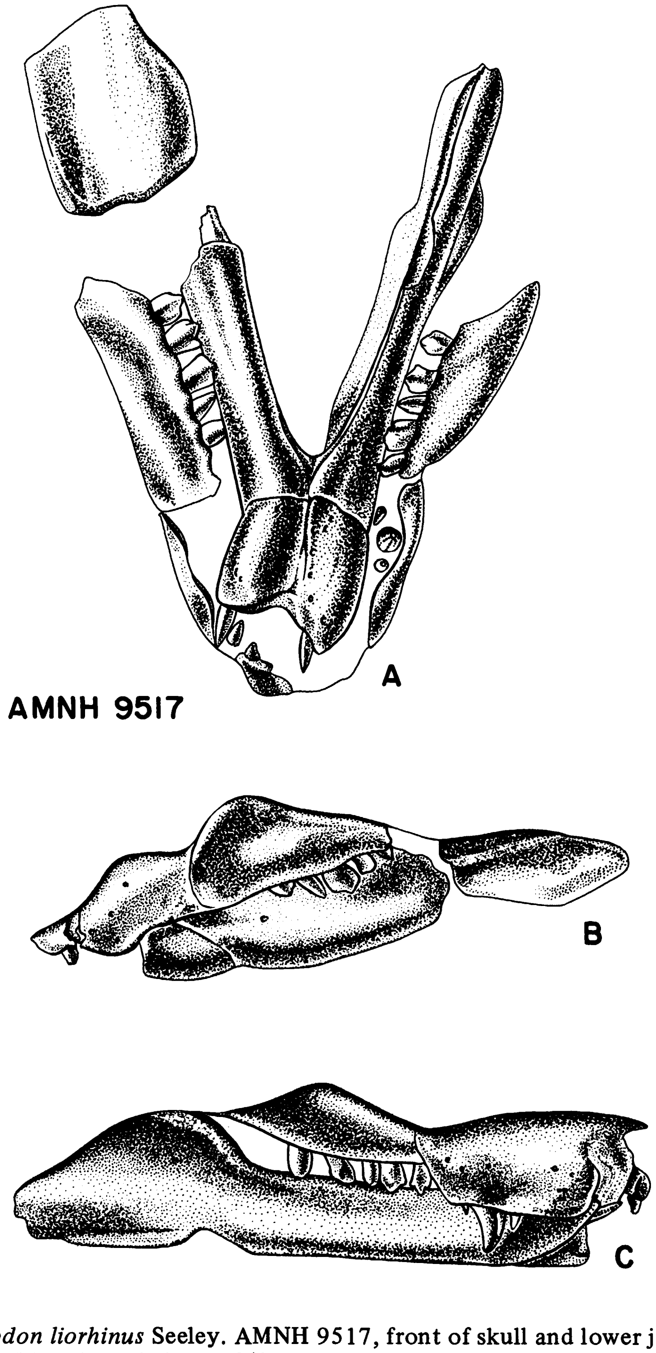

FIG. 14. *Thrinaxodon liorhinus* Seeley. AMNH 9517, front of skull and lower jaw. A. Ventral view. B. Left lateral view. C. Right lateral view. ×3/2.

the canine "bulge," whereas the symphyseal region of the two dentaries is strongly vascularized.

A large canine characterizes this specimen, and in front of it is the tip of the replacing canine, quite similar to the situation seen in AMNH 9563. A single well-developed premaxillary tooth, the last of the series of four, is present on the left side. Five postcanine teeth can be seen on each side in this specimen, and it may be that these represent the full complement of such teeth. Although seven postcanine teeth is the common number in *Thrinaxodon*, some specimens do show five or six such teeth, depending on the stages of replacement. The tricuspid condition of some of these teeth is well-developed. In the lower jaw the postcanine teeth are covered by the overlapping upper series, but the lower left canine is visible, as well as a small median incisor on the right side.

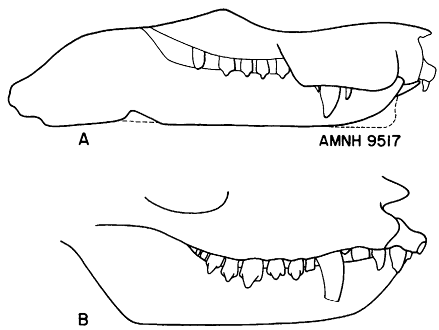

FIG. 15. *Thrinaxodon liorhinus* Seeley. AMNH 9517, outline of front of skull and lower jaws. Right lateral view. ×1.

Our knowledge of the dentition in *Thrinaxodon* from Antarctica is further supplemented by AMNH 9529, figures 16 and 17. This specimen, consisting of a weathered anterior part of the snout, as seen in palatal view, reveals the arrangement of the teeth in spite of its condition. There are four large and well-developed incisors, represented by alveoli and tooth bases separated from a large canine by a diastema. The last of these teeth is the largest of the four. A large replacing canine is present immediately in front of the canine on the left side. The two lower canines are also preserved in this specimen, as are the lower incisors on the left side. These teeth are surprisingly large. Behind the canines and separated from them by diastemata are the postcanine teeth, two of them on the left side showing the tricuspid condition. On the right side there is the root of a tooth immediately lateral to the posterior portion of the lower canine. This is the first postcanine, and its position is a result of the long canine root extending back beneath the anterior end of the postcanine sequence.

FIG. 16. *Thrinaxodon liorhinus* Seeley. AMNH 9529, weathered fragment consisting of premaxillae and maxillae with teeth, and certain dentary teeth. Palatal view. × 1.

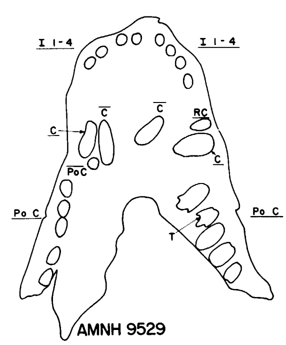

FIG. 17. *Thrinaxodon liorhinus* Seeley. AMNH 9529, interpretation of specimen. Palatal view. ×1. I 1-4, upper incisors 1-4; *C*-upper canine; C-lower canine; *PoC*-upper postcanines; PoC-lower postcanine; *RC*-upper replacing canine; T-tricuspid postcanine.

AMNH 9546 is a fragment of a right premaxilla and maxilla showing four large incisors, the first two represented by alveoli, the last two by broken tooth bases. There are also the bases of a canine and its replacement.

AMNH 9547, figure 18, is a skull fragment, showing the parietal region with the pineal preserved, and the right zygomatic arch. The tip of the coronoid of the mandible is visible, in place.

Two other specimens, again available as latex casts from natural molds, deserve brief mention. AMNH 9524, figure 21, is a right ilium and femur in articulation. The ilium is similar in shape to the same bone of *Thrinaxodon liorhinus* from Africa, being deep, with a broadly rounded anterior edge and diminishing posteriorly to a rounded termination. The femur is long and straight, with a rounded head. It is somewhat longer than the ilium, a characteristic relationship for *Thrinaxodon.*

AMNH 9553, figure 22, shows some foot bones, namely three metacarpals and some phalanges. The proportions of these bones are similar to the same bones in *Thrinaxodon liorhinus* from Africa, as figured by Parrington (1939) and by Jenkins (1971).

In the following table of measurements skull lengths and widths, the latter as measured across the arches, are presented, together with the indices derived from each pair of measurements. It will be seen that in the three Antarctic specimens where such measurements could be made, the indices are rather high, comparable with the upper values among the South African specimens. Otherwise there seems to be no significant differentiation between Antarctic and African fossils. The measurements when plotted on a graph (fig. 23) are positioned [essentially along a regression line], as would be expected within a taxon of species dimensions, with the smallest Antarctic specimen within the loci of the smaller African fossils, and the largest Antarctic specimen well below the range of the largest African specimens, as represented by the two fossils described by Brink in 1954.

In summary it is our opinion that the mate-

TABLE 1
Thrinaxodon liorhinus
(Measurements of skull in Millimeters.)

	Skull Length	Skull Width across Arches	Index
From Antarctica			
AMNH 9500	79.0	58.0	73
AMNH 9563	88.0	62.0[a]	70
AMNH 9570	61.5	46.0	75
From South Africa			
1. UC 42866	68.5	43.0	63
2. From Parrington, 1946	67.5	49.0	72
3. BPI specimen	70.0	49.5	71
4. From Fourie, ms.	73.0	49.5	68
5. UC 40466 From Estes, 1961	73.5	48.0	65
6. C.392 From Brink, 1954	91.5	67.5	74
7. C.393 From Brink, 1954	99.5	73.5	74
8. SAM K377	78.0	53.0	68
9. BPI 4301	84.5	52.5	62
10. BPI 4282	80.5	51.0	63
11. BPI 2776	75.5	46.5	62
12. BPI 2824	90.0	52.0	58
13. BPI 2793	74.0	50.0	68
14. TM 81	80.0	50.5	63
15. TM 80	60.5	30.5	50

[a]Estimated measurement.

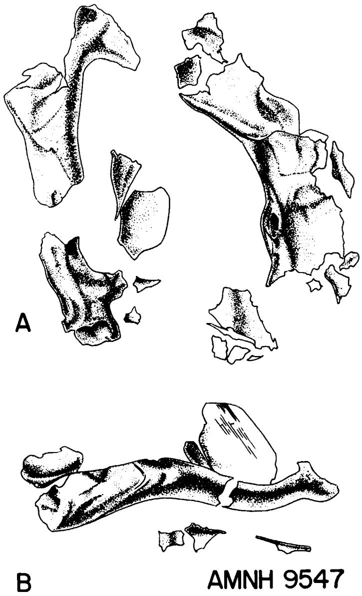

FIG. 18. *Thrinaxodon liorhinus* Seeley. AMNH 9547, portion of temporal region. A. Dorsal view. B. Right lateral view. × 1.

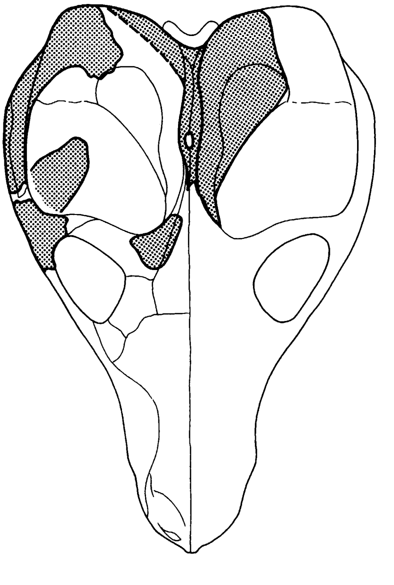

FIG. 19. Diagram of a skull of *Thrinaxodon*, to show those portions preserved in AMNH 9547 (stippled). Not to scale.

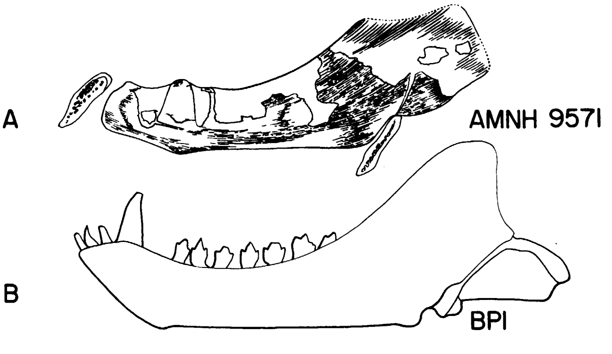

FIG. 20. *Thrinaxodon liorhinus* Seeley AMNH 9571, A, lower jaw. × 1.

rials here described from Antarctica clearly represent the cynodont reptile *Thrinaxodon liorhinus*. Any differences between the Antarctic specimens and comparable specimens from Africa are, we believe, merely those of individual variation. Thus, as in the case of certain other early Triassic reptiles described from Antarctica, the resemblances between such fossils found in the south polar continent and fossils found in southern Africa reach down to the species level.

CYNODONTIA *INCERTAE SEDIS*

AMNH 9523, impression in the rock of a mandibular ramus, containing several teeth. From *Thrinaxodon* Col, Mount Kenyon.

AMNH 9554, fossils in the rock, consisting of a right zygomatic arch, with the back part of the associated dentary and postdentary elements in place, posterior portion of the left dentary and postdentary elements in place, fragments of right pterygoid and of para-

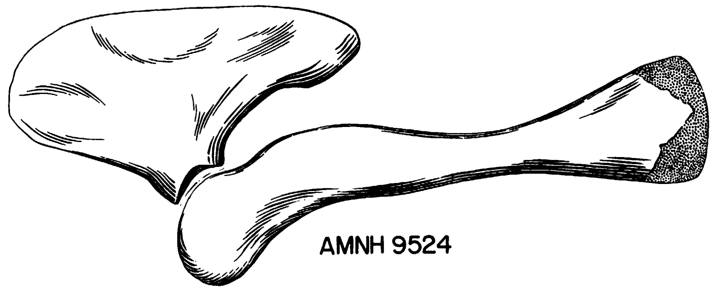

FIG. 21. *Thrinaxodon liorhinus* Seeley. AMNH 9524, latex cast from a natural mold of left ilium and femur. Lateral view. ×1.

sphenoids, atlas intercentrum with right atlantal rib in articulation, five sacral vertebrae in whole or in part, a possible proximal end of an ulna, a possible fragment of a humerus, and possible scapular fragment, proximal end of a tibia, and various bone fragments. From *Thrinaxodon* Col, Mount Kenyon.

An impression in the rock of a mandibular ramus, AMNH 9523, from which a rubber cast was made, has been a very difficult fossil to analyze and identify. As seen in figures 24 and 25, the impression and its cast show the form of the dentary behind the symphyseal region, and some of the teeth. The actual symphysis is lost, the tooth impressions do not show details, and the postdentary elements are missing. Consequently the information to be derived from this specimen is at best scanty and equivocal.

When this specimen was collected one of us (J.W.K.) considered it, upon the basis of a field identification, to be a gomphodont (?) cynodont. This impression, owing in part to the robustness of the dentary and the heavy ascending ramus, has remained, after various comparisons in the laboratory. Indeed, the specimen shows resemblances to some of the broad-toothed cynodonts in the collections of the Bernard Price Institute of the Witwatersrand University in Johannesburg.

Because of its size, the robust nature of the dentary and the very broad, heavy ascending ramus, it seems to us that the specimen must be eliminated from inclusion within *Thrinaxodon.* As preserved the teeth have the appearance of short pegs; it seems possible that in their original state they might very well have been broad teeth of gomphodont type.

Beyond such general remarks, nothing definitive can be said concerning AMNH 9523. One can only hope that at some future date additional fossils will be found in Antarctica which will reveal the true relationships of this presently enigmatic specimen.

AMNH 9554, as seen in figures 26-29, represented by various broken fragments of the skull and jaws, and of the postcranial skeleton, is a remarkably large fossil to be representative of *Thrinaxodon,* even though some of the bones correspond closely with the same elements in *Thrinaxodon liorhinus.* This correspondence applies especially to the coronoid of the dentary, and fragments of the angular and surangular on the right side, and to the coronoid and portions

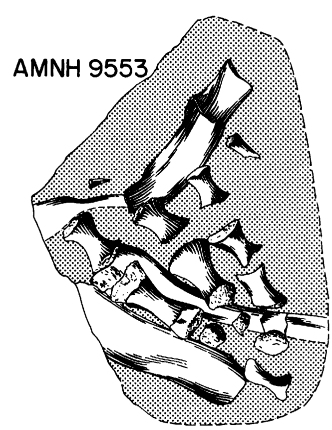

FIG. 22. *Thrinaxodon liorhinus* Seeley. AMNH 9553, latex cast from a natural mold, showing phalanges and fragments of long bones. ×1.

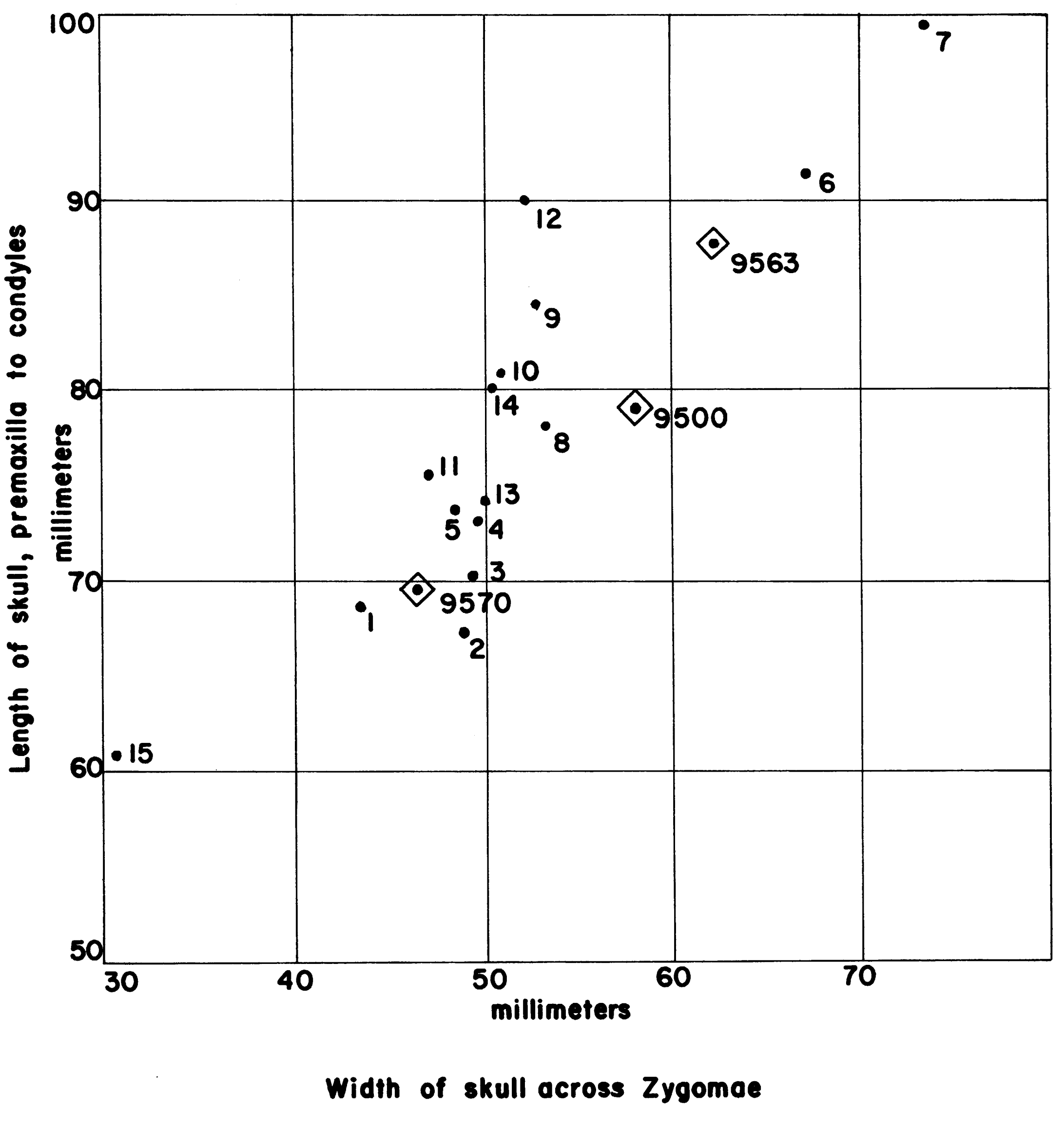

FIG. 23. *Thrinaxodon liorhinus* Seeley. Graph of skull lengths to skull widths, as measured across the arches, of various specimens listed in table 1.

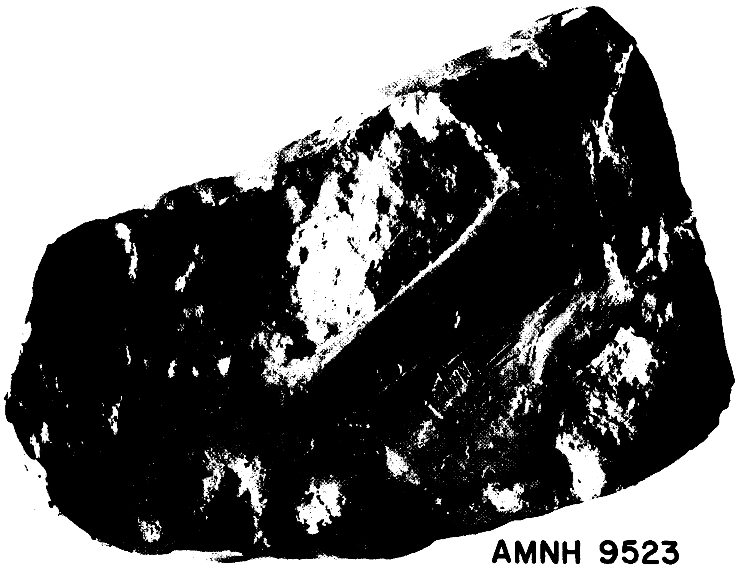

FIG. 24. Cynodontia *incertae sedis.* AMNH 9523, latex cast from a natural mold of a mandibular ramus, with some teeth. Lateral view. X 1.

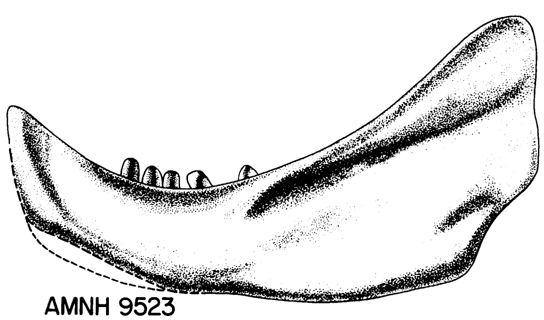

FIG. 25. Cynodontia *incertae sedis.* AMNH 9523, specimen shown in figure 23. X 1.

of the surangular, angular, and prearticular on the left side. (These latter, as shown in figure 28, we consider to have been turned over during the processes of burial and fossilization.)

Can this specimen be a very large *Thrinaxodon liorhinus*? Its very size seems to rule this out, for if it is to be assigned to this species it is by far the largest individual known, with linear dimensions twice those of characteristic *Thrinaxodon* specimens. Is it possibly a new and very large species of *Thrinaxodon*? Or as a third possibility, is this some other galesaurid cynodont?

In the absence of teeth, and because of the very incomplete condition of the skull and jaws, none of these questions can be answered with any degree of satisfaction. Consequently the specimen must be recorded as presently indeterminate within the Galesauridae, and as in the case of AMNH 9523, it is to be hoped that future work in Antarctica will yield the solution to this problem.

CONCLUSION

The presence of *Thrinaxodon liorhinus* in the Lower Triassic Fremouw Formation of Antarctica affords evidence additional to that already published establishing a very close relationship between the lower Triassic sediments of Antarctica and South Africa. As has been shown in previous publications, three other reptilian species, namely *Lystrosaurus murrayi*, *Lystrosaurus curvatus* and *Procolophon trigoniceps* are common to the lower Triassic of the two continents.

Although these identities seem to be well established, there are at the same time certain differences among the fossils of Antarctica and South Africa. Thus, two specimens described in the present paper represent cynodonts, not at the

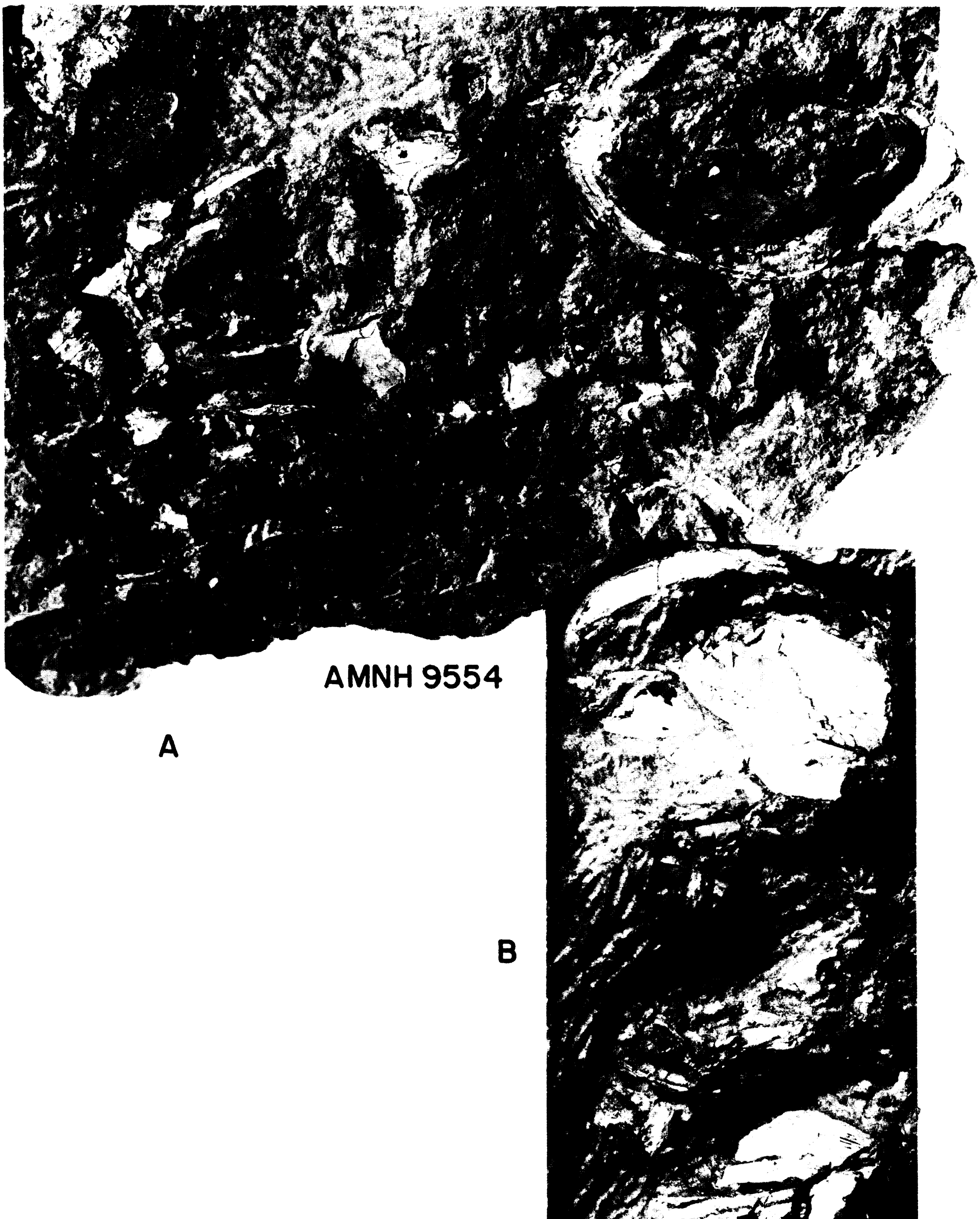

FIG. 26. Cynodontia *incertae sedis.* AMNH 9554. A. Right zygomatic arch, vertebrae and other bones. Dorsal view. B. Portion of right zygomatic arch with associated coronoid portion of dentary and postdentary bones, and posterior part of left dentary and postdentary bones. Ventral view. $\times 1$.

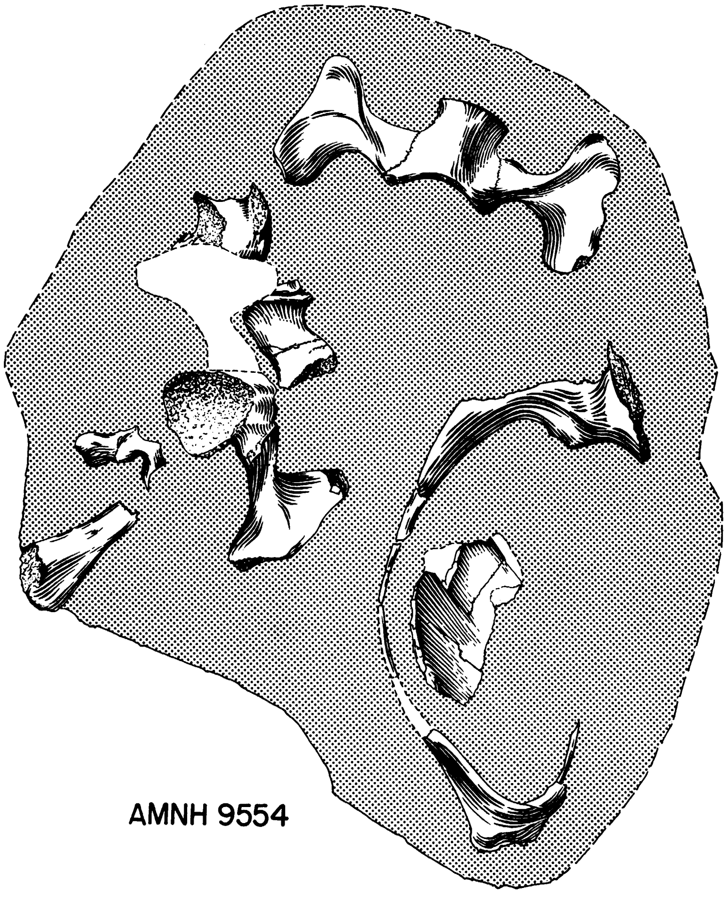

FIG. 27. Cynodontia *incertae sedis.* AMNH 9554, a portion of the specimen shown in (A) of figure 26. Right zygomatic arch with associated coronoid portion of dentary, two sacral vertebrae and other bone fragments. Dorsal view. ×1.

FIG. 28. Cynodontia *incertae sedis.* AMNH 9554, a portion of the specimen shown in (B) of figure 26. Right zygomatic arch with associated posterior portion of dentary and postdentary bones, and posterior portion of left dentary with postdentary bones. Pra-prearticular; Sang-surangular. Ventral view. ×1.

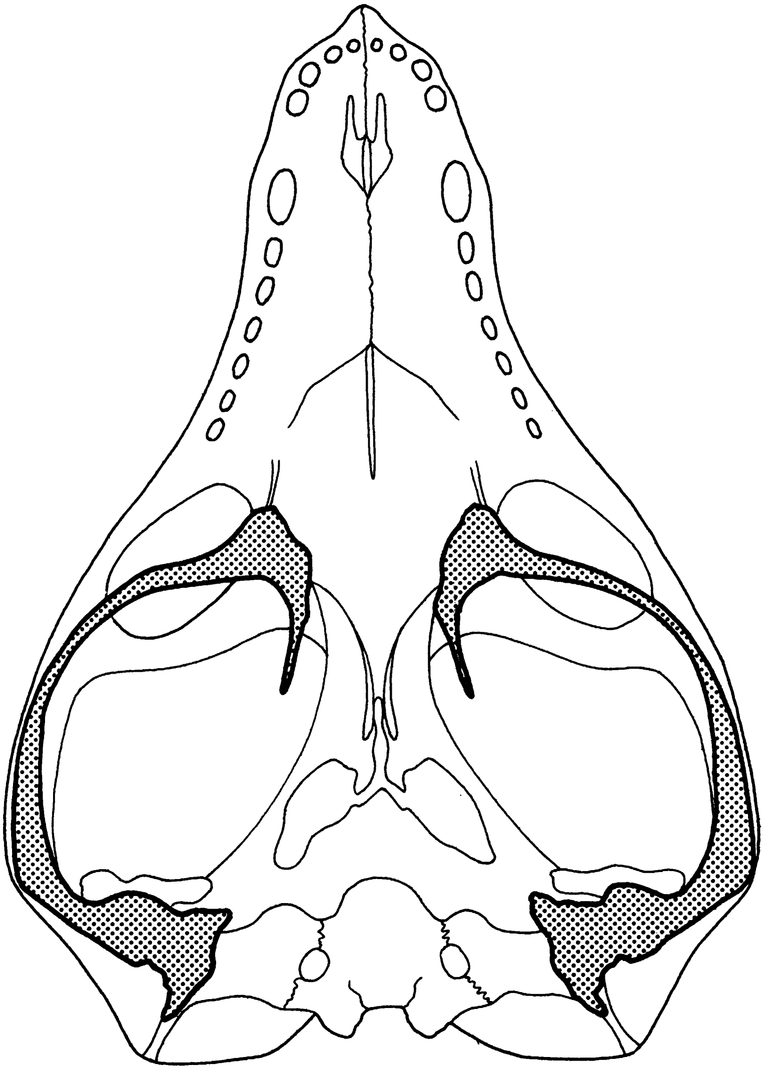

FIG. 29. Right zygomatic arch (dotted) of AMNH 9554, repeated as a left arch, both × 1, and both superimposed over a drawing, after Parrington, of *Thrinaxodon liorhinus* Seeley at twice natural size.

present time generically or specifically identifiable, that are considerably larger and more robust than characteristic *Thrinaxodon*. Such differences are correlative with other differences, notable among the labyrinthodont amphibians, between the Lower Triassic faunas as now known in Antarctica and South Africa.

The resemblances extending down to the level of species and differences involving different genera are not surprising. The fossils from the Fremouw Formation represent the *Lystrosaurus* fauna as it is known in South Africa, but with certain divergences attendant upon the probable distance between the habitats in which the two faunas lived within Gondwanaland. One should not expect complete identities among two faunas that probably were separated by a distance of perhaps 3000 km.

Nevertheless the identities are strong, and these add to the growing evidence that during Triassic time Antarctica was closely connected to South Africa.

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