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THE CRANIAL MORPHOLOGY OF THE DICYNODONT GENUS *LYSTROSAURUS*

By

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Cape Town Kaapstad



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M. A. CLUVER

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(With 77 figures)

[MS. accepted 12 November 1970]

CONTENTS

	PAGE
Introduction	156
Material and techniques	158
Section I. The cranial anatomy of <i>Lystrosaurus</i>	
Neurocranium	
Braincase and occiput	162
Sphenethmoid complex	175
Visceral arch skeleton	
Palatoquadrate	181
Stapes and hyoid apparatus	183
Dermocranium	
Snout region	184
Palatal region	199
Skull roof	201
Squamosal and quadratojugal	203
Sclerotic plates	204
Mandible	205
Section II. The jaw musculature and masticatory cycle in <i>Lystrosaurus</i>	
The jaw musculature	207
The masticatory cycle	210
Section III. The atlas-axis complex and cervical and occipital musculature in <i>Lystrosaurus</i>	
Morphology of the atlas-axis complex	214
Musculature of the atlas-axis complex and occiput	216
Section IV. Evolutionary sequence leading to the <i>Lystro-</i> <i>saurus</i> grade of dicynodont development	
Comparison of the skulls of <i>Lystrosaurus</i> and typical Permian dicynodonts	
Depth of skull	221
Shortening within the skull	223
Relationships of the brain	226
Adductor musculature	227
Derivation of the <i>Lystrosaurus</i> skull proportions	231
Section V. Variation in the skull of <i>Lystrosaurus</i> and the taxonomy of the genus	
Skull variation within the genus	236
The sexual dimorphism problem	238
Effects of age and distortion on the skull form	240

	PAGE
The species of <i>Lystrosaurus</i>	242
Speciation in <i>Lystrosaurus</i>	254
<i>Lystrosaurus</i> from India, China and Russia	256
Section VI. The origin of <i>Lystrosaurus</i> from a Permian ancestor and its relationships with some other Triassic dicynodont genera	257
Conclusions	
The basicranial axis	261
The soft structures of the snout	263
The jaw and neck musculature	263
Adaptive changes in the skull	264
Division of the species	265
Relationships with other dicynodont genera	265
Summary	266
Acknowledgements	267
References	268
Abbreviations	272

INTRODUCTION

Numerically, the major part of the therapsid fauna of the Karoo system is made up by the infraorder Dicynodontia, herbivores which are represented abundantly throughout the entire succession. The Dicynodontia form part of the suborder Anomodontia (*sensu* Watson & Romer, 1956; Romer, 1966) and are believed to have diverged from the suborder Theriodontia early in the history of the Therapsida. In the following descriptions the term *dicynodont* refers to therapsids within the infraorder Dicynodontia, while *dicynodontid*, *endothiodontid* and *lystrosaurid* refer respectively to members of the families Dicynodontidae, Endothiodontidae and Lystrosauridae. This terminological procedure is in accordance with Romer's (1966) classification.

It is generally accepted that the success of the Dicynodontia is at least in part due to their unique masticatory apparatus, involving horny upper and lower beaks, extremely long and powerful temporal muscles, and an antero-posterior sliding action between the quadrate and articular. While modifications in the cranial anatomy have taken place during the course of dicynodont evolution, and have resulted in rich diversity, the basic masticatory cycle has been retained and improved throughout.

Thanks to the abundance of specimens available for study, the gross anatomy of most dicynodont groups is reasonably well known, although poor preservation, crushing and distortion remain obstacles in any study of Karoo fossils. Again, the numerous duplicate specimens now available in most dicynodont collections make serial grinding and sectioning of selected specimens possible, and these techniques have provided a wealth of additional information regarding the finer anatomy of several species.

Although far removed from the direct line of evolution leading to the first mammals, the dicynodonts make up the bulk of the therapsids, and this

abundance makes them very useful to any investigation involving evolutionary trends among therapsids. Knowledge of such trends in a group whose evolutionary history spans a long, uninterrupted period of time through the Permian and Triassic periods, is essential to organization of Karoo therapsids into faunistic entities. Again, as the finer anatomy of the Dicynodontia becomes more fully understood, and more accurately related to stratigraphical occurrence, it should become possible to establish a detailed dicynodont phylogeny which, when correlated with geographical distribution, will provide useful information regarding continental connections and therapsid migrations during the Permian and Triassic.

At the close of the South African Permian the period of dicynodont diversity so characteristic of the *Tapinocephalus*, *Endothiodon* and *Cistecephalus* zone times came to an end. In the first zone of the Lower Triassic, the *Lystrosaurus* zone, only one dicynodont, *Lystrosaurus* itself, is common, the only other member of the infraorder being the very poorly represented *Myosaurus*. *Lystrosaurus*, taken with the associated *Prolystrosaurus*, therefore comprises a distinct, well-defined stage in dicynodont development, and is well represented in the shales of the *Lystrosaurus* zone. As even a superficial study will show, the genus had soon become successfully adapted to a new environment of fresh-water lakes and streams, and had radiated into several morphologically distinct groups of species.

The following have been the main objectives of this study.

Firstly, an in-depth survey of the cranial anatomy of *Lystrosaurus*, seen purely as a therapsid genus, should add to our knowledge of the therapsids as a whole. Since an abundance of specimens in a good state of preservation was available for this study, and since the majority of these could be extensively prepared, it has been possible to describe the morphology in considerable detail. In this way evidence bearing on several problems of therapsid evolution has come to light.

Secondly, since the Lystrosauridae are a widespread, successfully adapted group with a clearly defined temporal occurrence, a comparative study of the morphology illustrates the manner in which evolutionary processes have acted to produce a skull form adapted to fulfil certain new needs without prejudicing the effectiveness of other essential functional qualities. *Lystrosaurus* is therefore considered first purely in terms of comparative anatomy, and then in terms of functional anatomy, the two aspects being subsequently correlated in an attempt at determining both the most likely Permian ancestor of *Lystrosaurus* and the evolutionary pathway followed to produce *Lystrosaurus* from such an ancestor.

Thirdly, an attempt has been made to assess the relationships which *Lystrosaurus* as a faunal entity bears to preceding and succeeding dicynodont groups. Anatomically, the lystrosaurids represent a departure from the standard pattern found in Permian dicynodonts, themselves a diverse assemblage. Moreover, they are at first glance manifestly distinct from any of the later

Triassic genera, and thus represent an intermediate faunal stage within the Karoo succession, in which the Dicynodontia were represented by one obviously highly specialized genus only (if we disregard the rare and poorly known *Myosaurus*). However, the present investigation indicates several points of structural agreement between the cranial morphology of *Lystrosaurus* and that of the later dicynodonts.

Finally, although any taxonomic division depending entirely on cranial morphology must of necessity be far from conclusive, several anatomical features uncovered during the course of this investigation appear to bear on the taxonomy of the genus. These points are discussed and a tentative division of the various species of the genus is set out.

In 1859 the first specimen of *Lystrosaurus*, from the Beaufort Beds of Colesburg, Cape Province, was described by T. H. Huxley as *Dicynodon murrayi*. In 1860, however, Richard Owen realized that forms allied to Huxley's *D. murrayi* should be placed in a separate genus, for which he proposed the name *Ptychognathus*. By 1890, when Lydekker pointed out that *Ptychognathus* was preoccupied and therefore invalid, six species of *Ptychognathus* had been described by Owen, in 1860, 1862 and 1876. Lydekker introduced the name *Ptychosiagum* for the group, but in 1898 Seeley showed that the specimen described by Cope in 1870 as *Lystrosaurus frontosus* was in fact a species of *Ptychognathus*, and that, should the latter name be invalid, all the species should be placed under the generic name *Lystrosaurus*.

At present 24 South African species of *Lystrosaurus* have been described, as well as a supposedly ancestral genus, *Prolystrosaurus*, with two species.

MATERIAL AND TECHNIQUES

Although a large number of specimens of *Lystrosaurus* in the collections of the South African Museum and the National Museum, Bloemfontein, provided the information needed for the section on the comparative anatomy of the group, the descriptions are based mainly on the following specimens, chosen for their fine preservation, undistorted state, or suitability for sectioning:

Lystrosaurus murrayi

Nat. Mus. No. C.282	. .	Skull & mandible
C.6457	. .	Skull, mandible & neck
C.211	. .	Skull & mandible
C.228	. .	Skull & mandible
S.A.M. No. 1336	. . .	Sectioned skull & mandible
K.1495	. . .	Skull & mandible

Lystrosaurus declivis

Nat. Mus. No. C.150	. .	Skull, mandible & postcranial scraps
C.403	. .	Skull & mandible

Nat. Mus. No. C.391	. .	Skull lacking mandible
C.171	. .	Skull lacking mandible
S.A.M. No. K.1284	. . .	Sectioned skull & mandible

Lystrosaurus curvatus

Nat. Mus. No. C.299	. .	Skull lacking mandible
S.A.M. No. K.90	. . .	Sectioned skull & mandible

Lystrosaurus mcCaigi

S.A.M. No. K.1116	. . .	Skull lacking mandible
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Lystrosaurus sp. indet.

S.A.M. No. K.1496	. . .	Snout
11180	. . .	Braincase

In addition to these specimens of *Lystrosaurus*, the following Permian dicynodonts were frequently referred to as comparative material:

B.P.I. No. 2642	<i>Emydops</i> skull & mandible
S.A.M. No. 10137	<i>Palemydops</i> skull lacking mandible
5600	Braincase
11075	Braincase
6550	Tuskless dicynodont, with mandible, lacking skull roof
10081	Sectioned tuskless dicynodont, lacking mandible
6043	Dicynodont, comprising posterior skull roof, occiput & mandible
8784	<i>Dicynodon</i> , skull & mandible

Three specimens of *Lystrosaurus* were serially sectioned for the purposes of this investigation, i.e. S.A.M. Nos 1336, K.90 and K.1284. Specimen No. K.1284 proved to be the best preserved and least distorted of the three, and provided more reliable information than the other two specimens, which were used mainly for comparative and verification purposes.

For sectioning, a mounted diamond saw with a constant mechanical feed was used, and satisfactory transverse sections were obtained in all three cases. A constant thickness of the specimen, representing the thickness of the blade, is lost for each section cut, but it was found that, the specimen being of sufficient size, no information was lost since the skull, in practice, can never be sectioned at a perfect right angle to the median plane. Consequently, what fine structures are missing or incomplete on one side of each section face are usually present in complementary fashion on the other side.

In two cases it was necessary to embed the specimen prior to sectioning. Two embedding materials were used, Alabastone plaster and Epoxy resin, it being found that the plaster was too friable for easy handling of the sections

and that the resin tended to cause clogging of the blade during sectioning.

In addition to these three specimens of *Lystrosaurus*, a tuskless dicynodont, S.A.M. No. 10081, was embedded in polyester resin and serially sectioned. This series was of value in comparisons between *Lystrosaurus* and earlier dicynodonts.

Mechanical preparation of the specimens was in many cases facilitated by the relatively soft nature of the rock matrix, and its clean separation from the often well-preserved bone. In addition, the high percentage of carbonate in the matrix of several specimens permitted the successful use of 10% acetic acid in the final stages of preparation. The acid technique was especially effective in making areas such as the interior of the braincase and snout available for examination.

Reconstructions of the sectioned specimens were obtained by plotting points directly from the section faces on to a grid, constructed so as to make provision for the section thickness and the loss through sectioning. As in conventional reconstructions, making use of the method introduced by Pusey (1939), lateral and parasagittal views presented no difficulty. However, orientation of the skull for comparable dorsal and ventral views is complicated by the peculiar proportions of *Lystrosaurus*, and by the tremendous variation expressed in the number of recognizable species of the genus. For example, an orientation that provides a useful dorsal view in one species may result in an anterodorsal view in another species.

Theoretically, the most suitable horizontal reference plane is the ventral inner surface of the braincase, formed by the basioccipital, since this can be regarded as a conservative region, but this plane proved unsuitable for the alignment of complete skulls. A number of other planes, based upon structures within the skull which appear to be constant in shape and position within the genus, were investigated. The one selected as most practical extends from the most ventral, median point of the foramen magnum to the ventral, median surface within the external naris. These points can be determined accurately and easily in both sectioned and entire skulls, and, since the position of the nostril is apparently not affected by the deepening and shortening of the skull in *Lystrosaurus*, and since the reference plane has a more or less constant relationship with the basioccipital surface within the braincase, the plane could be used in comparisons between *Lystrosaurus* and its Permian predecessors.

All dorsal and ventral views illustrated in this work are orthoprojections on to this plane, reproduced either from graphic reconstructions of sectioned specimens, or from pantograph drawings of total specimens. In the case of the graphic reconstructions, the two basic points of the reference plane were determined in the lateral reconstructed view of the specimen and then connected to form the reference line in the skull. A second grid, having the reference plane as a base, was then constructed with a section thickness similar to that of the first grid. A line, representing the sagittal median line of the skull, is then drawn across the second grid, parallel to the reference line. In order to recon-

struct a dorsal projection, for instance, any point seen in a transverse section is plotted on to the first grid, as though to produce a lateral projection, and its position determined in relation to the second grid. The distance of the point from the midline of the section face is then determined, and the point is plotted an equal distance from the line representing the skull midline on the second grid. The procedure in plotting such a point is illustrated in Figure 1.

In a case such as in Figure 1, where the midline of the skull is not vertical to the base line, compensation can be made by constructing a new base line at right angles to the skull midline.

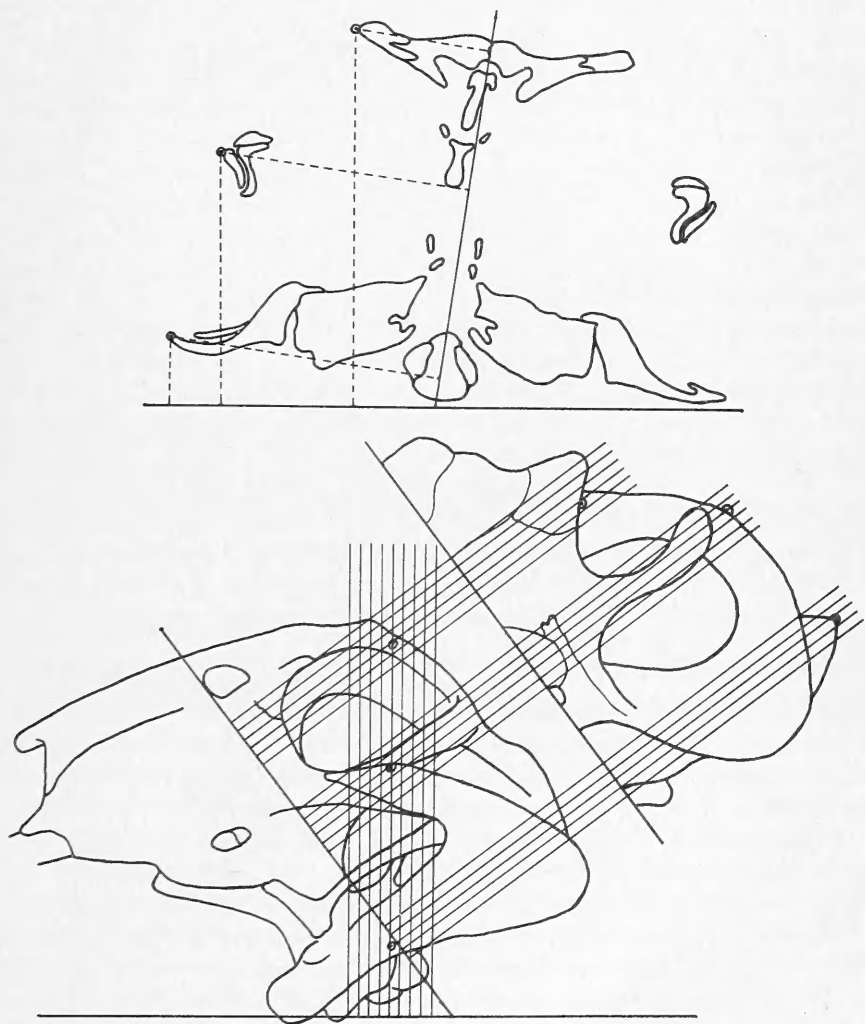


Fig. 1. Method for construction of a dorsal projection onto a hypothetical reference plane from serial sections.

The advantage of this method lies in the ease with which uniformly aligned skulls can be compared. Although essential in an animal such as *Lystrosaurus*, similar methods can be used to advantage in other groups.

SECTION I. THE CRANIAL ANATOMY OF *LYSTROSAURUS*

In spite of the wide range of variation in the skull proportions within the group, all the specimens of *Lystrosaurus* at my disposal appear to have retained a set of certain basic, common morphological characters, making a subdivision of the genus into its various species unnecessary for the purposes of this section. The following morphological description therefore holds good for the genus as a whole.

It has proved possible, by making use of sectioned and incomplete specimens, to determine the precise relationships between the neurocranium and the dermal bones of the skull. Consequently, the descriptions have been divided into sections dealing with the neurocranium, the visceral arch derivatives and the dermocranium. In all cases, however, the relationships between these three developmentally distinct osteological systems have been indicated, in order to illustrate the concept of their functional unity. For this reason the skull has been described regionally, again in an attempt at illustrating how several elements are integrated to produce a single major feature in the skull. It was felt that in the case of *Lystrosaurus*, where the skull has undergone several major changes in proportion and structure during its evolution from a Permian ancestor, this approach was especially pertinent.

THE NEUROCRANIUM

The neurocranium is represented by the braincase-occiput complex and the anterior sphenethmoid ossifications. In the snout region a few impressions on the inner surfaces of the dermal bones provide some indication of the extent of the unpreserved cartilaginous nasal capsule.

The braincase and occiput

The study of this region in both conventionally prepared and sectioned specimens has been greatly facilitated by the fact that the various elements of the *Lystrosaurus* braincase do not fuse with one another as is the case in most other dicynodonts, and there is consequently very little doubt as to the exact relationships they bear to one another. Thus the petiotic in Olson's (1944) sectioned specimens is in *Lystrosaurus* clearly divisible into prootic and opisthotic.

As in other dicynodonts, the braincase is formed by the exoccipitals posteriorly and ventrally, the basioccipital and basisphenoid ventrally, the opisthotics and prootics laterally and the supraoccipital dorsally (Figs 2, 3, 4, 5).

The posterior portion of the braincase floor is formed by the broad concave dorsal surface of the exoccipital condyles, which meet over the condylar portion of the basioccipital (Figs 3, 12).

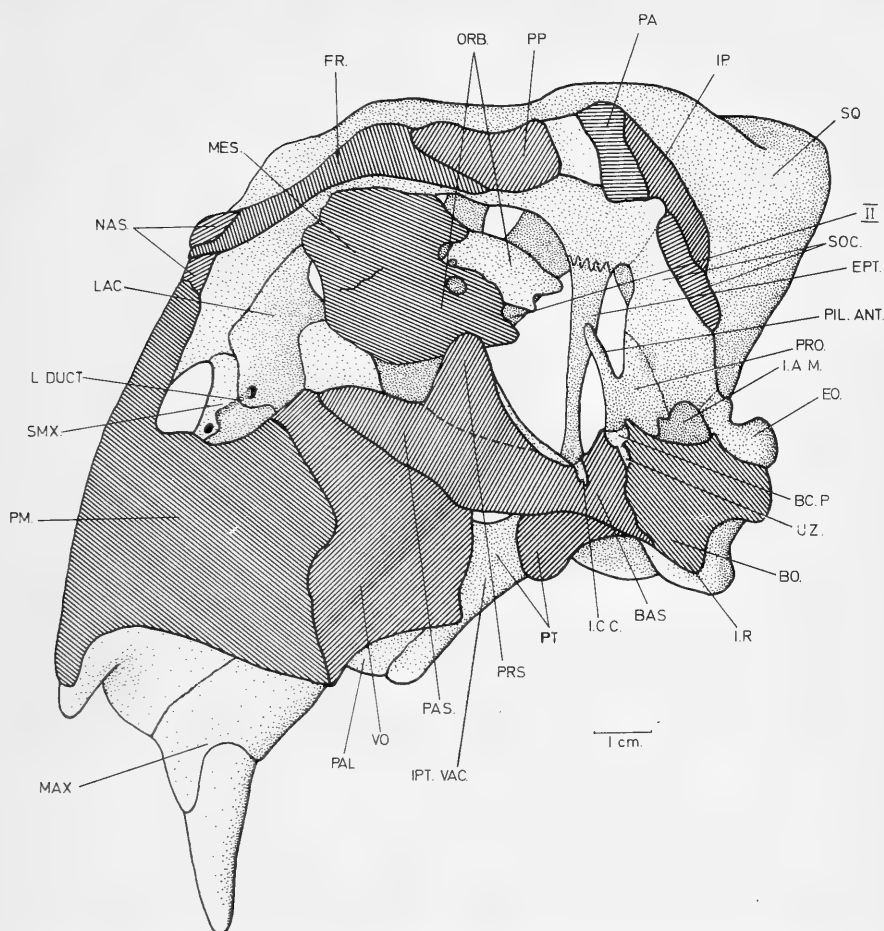


Fig. 2. *Lystrosaurus declivis*. S.A.M. No. K.1284. Parasagittal view of the skull, reconstructed from serial sections.

From this floor each exoccipital extends dorsally for a short way to form a lateral border for the foramen magnum. Dorsally it terminates on the occipital surface as a process for articulation with the proatlas (Fig. 9a) and dorso-medially to the condyle it is pierced by two foramina for the hypoglossal nerve.

The exoccipital-opisthotic meeting is one of the few obscure lines of contact in the skull. In one specimen (S.A.M. No. 11180), however, faint indications of a line of fusion on the occiput near the foramen magnum (Fig. 10b) make it clear that the exoccipital did not extend as far laterally as in *Pristerodon* (Barry, 1967). The large jugular canal lies between the exoccipital and opisthotic, and dorsally to this foramen and just within the cranial cavity the opisthotic-exoccipital suture is distinct (Fig. 9a). Posteriorly each exoccipital forms a prominent exoccipital condyle, which projects beyond the basioccipital

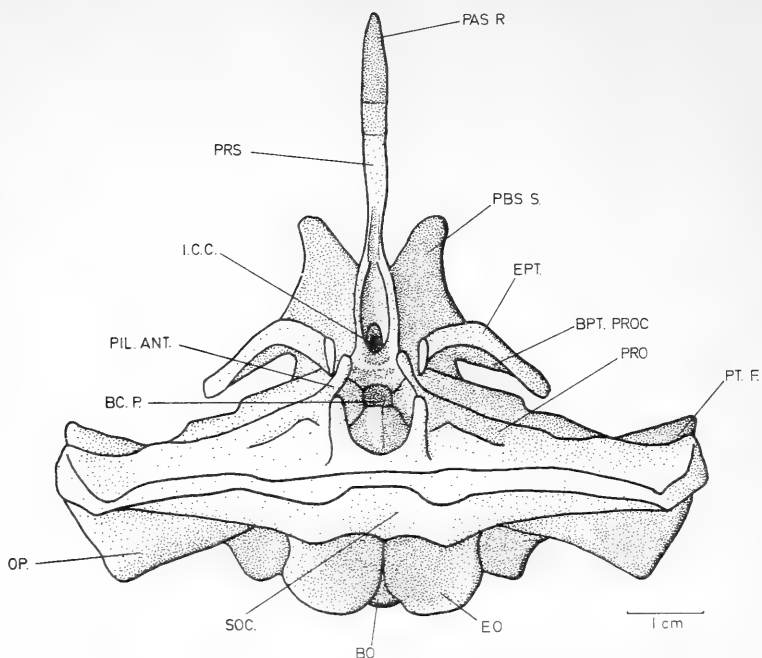


Fig. 3. *Lystrosaurus declivis*. S.A.M. No. K.1284. Neurocranium in dorsal view, reconstructed from serial sections.

condyle, so that functionally a system exists which in some ways resembles the mammalian double condyle. Van Hoepen (1913) and Von Huene (1931) mentioned this feature in *Lystrosaurus*, while Jaekel (1904) found that in *Oudenodon pusillus* the basioccipital tends to become reduced. Olson (1944) states that the dicynodonts parallel the cynodonts in their tendency to form a double occipital condyle.

Anteriorly the floor of the braincase is formed by the dorsal surface of the saddle-shaped *basioccipital* (Figs 10a, 12). This surface has a raised median crest, low posteriorly and rising up anteriorly to form the posterior lip of a cup-like depression, the basicranial pit, lying between the basioccipital and basisphenoid (Fig. 12: BC.P.). Laterally the basioccipital meets the opisthotic and prootic, and between these three bones the long, ventrally directed auditory canal is contained (Figs 9a, 10a: A.C.). This canal widens as it opens on the basioccipital-basisphenoid tuber as the fenestra ovalis (Figs 4, 9a, 10a). Internally, the dorsal opening of the auditory canal is enlarged to form an auditory vestibule (Figs 9a, 10a, 12). Behind the vestibule a groove in the basioccipital leads into the jugular foramen. The direction of the groove seems to indicate that the jugular vein did not enter the vestibule, as it did in Olson's (1944) serially sectioned dicynodonts, but passed medially to it. The jugular foramen itself is separated from the posterior portion of the vestibule by a bony wall (Fig. 10a).

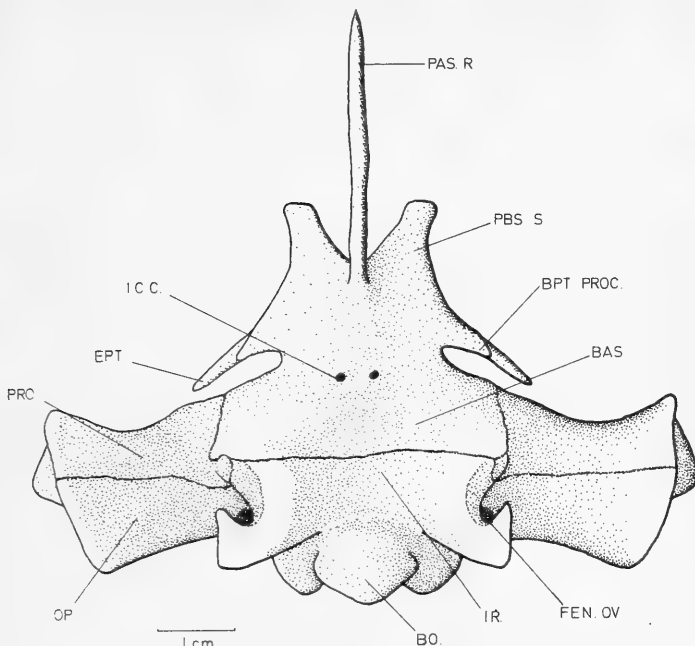


Fig. 4. *Lystrosaurus declivis*. S.A.M. No. K.1284. Neurocranium in ventral view, reconstructed from serial sections.

In front of the vestibule the basioccipital comes into broad lateral contact with the prootic, the suture between the two bones being visible on the anterior wall of the vestibule and auditory canal (Fig. 9). High up on the wall of the vestibule the two bones divide over a short distance to form a small pocket (Fig. 12: P.). It is not known whether this recess housed any specific structure.

Anteriorly, as mentioned above, the basicranial pit lies between basioccipital and basisphenoid. This pit lies in the same area of the braincase floor as the unossified zone described by Olson (1944) and Boonstra (1968) in other therapsids. In sections (Fig. 2) it can be seen that the pit in *Lystrosaurus* is continued ventrally for some distance as a similar unossified zone between the basioccipital and basisphenoid. Olson (1944) states that the unossified zone is a rudimentary basicranial fenestra, and therefore a primitive character. Barry (1967) has found a depression in the floor of the braincase of *Pristerodon*, which may be homologous with the unossified zone, and which, Barry states, could represent a filled-in fenestra basicranialis posterior. These views regarding the homology of the unossified zone are supported by the fact that in the adult *Cordylus* (Van Pletzen, 1946) a fenestra is present in the base of the braincase, in the position of the fenestra basicranialis posterior of *Lacerta* (Gaupp, 1898).

The basioccipital is deepest in the region of the auditory canal. Ventrally, between the two lateral tubera, a transverse intertuberal ridge is formed (Figs 2, 4, 24). This condition is unusual, as in all other dicynodonts (with the

exception of *Dicynodon gilli*, S.A.M. No. 4008, where the basioccipital is deepened as in *Lystrosaurus*) the area between the ventral edge of the basioccipital condyle and the foramina of the internal carotid arteries is flat.

Immediately in front of the intertuberal ridge in *Lystrosaurus* the basioccipital meets the parabasisphenoid complex. Posteriorly it forms the median part of the occipital condyle, and is dorsally overlapped by the exoccipital condyles.

The auditory capsule is formed by the *prootic* anteriorly and the *opisthotic* posteriorly, while the supraoccipital completes the structure dorsally (Figs 5, 9a, 10a). Both prootic and opisthotic extend laterally to form the paroccipital process and make contact with the squamosal. The opisthotic (=paroccipital of some authors) abuts against the quadrate laterally and, on the occipital surface, forms the medial border of the posttemporal fenestra (Fig. 10b). Dorsally it meets the supraoccipital in a straight suture, and its dorsolateral corner, above the posttemporal fenestra, is overlapped posteriorly by the squamosal. The entire anterior face is covered by the prootic. Medially the opisthotic forms the lateral wall of the jugular canal, separating the canal from the vestibule, and descends alongside the basioccipital to form the posterolateral wall of the fenestra ovalis.

The prootic is in the main a flat bone, lying against the anterior surface of the opisthotic and occipital plate. Laterally it extends to meet the ventral flange of the squamosal, and forms the anterior half of the paroccipital process

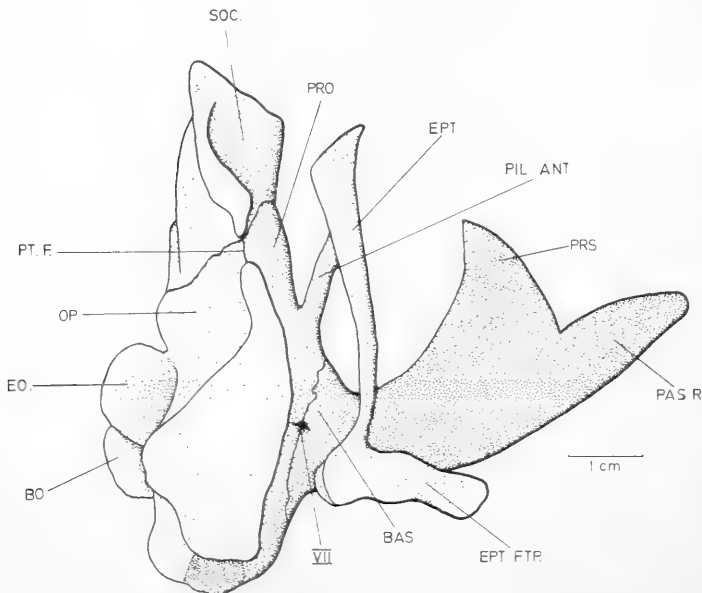


Fig. 5. *Lystrosaurus declivis*. S.A.M. No. K.1284. Neurocranium in lateral view, reconstructed from serial sections.

and the medial border of the posttemporal fenestra. Medially it forms the anterior portion of the braincase and terminates anteromedially as the upright pila antotica. The prootics do not meet in the midline (Figs 2, 55b) and a dorsum sellae, overlooking a sella turcica, as was found in the pelycosaurs and therapsids described by Romer & Price (1940) and Olson (1944) respectively, is not present. Boonstra (1968) finds that the prootics meet in the dinocephalians and therocephalians, but not in the *Tapinocephalus* zone dicynodonts.

The hypophyseal region in *Lystrosaurus* will be discussed more fully at a later stage.

Anteriorly the prootic meets the basisphenoid, and the suture between these two bones runs down from the base of the pila antotica to the lateral rim of the fenestra ovalis (Figs 4, 5). Halfway down the prootic-basisphenoid suture a ledge is formed, covering a distinct recess into which the canal of the facial nerve opens (Figs 5, 11). The ledge is in the same position as the otic ledge of lizards (Romer, 1956), and Boonstra (1934a) has described a similar pocket surrounding the facial foramen in the Gorgonopsia, suggesting that it housed the geniculate ganglion.

A dorsomedial process of the prootic projects up against the anterior face of the supraoccipital, and between them the two bones form a shallow notch in the side-wall of the braincase (Figs 9a, 10a: V.N.). A similar, usually deeper notch has been described in dicynodonts by various authors, and probably stood in connection with the vascular system of the head (see below).

No true floccular fossa (sub-arcuate fossa of Cox, 1959) is found in *Lystrosaurus*, but a shallow depression is present on the inner face of the prootic in some specimens. Sollas & Sollas (1913) and Olson (1944) described deep pockets for the flocculus in various dicynodonts, but Boonstra (1968) found

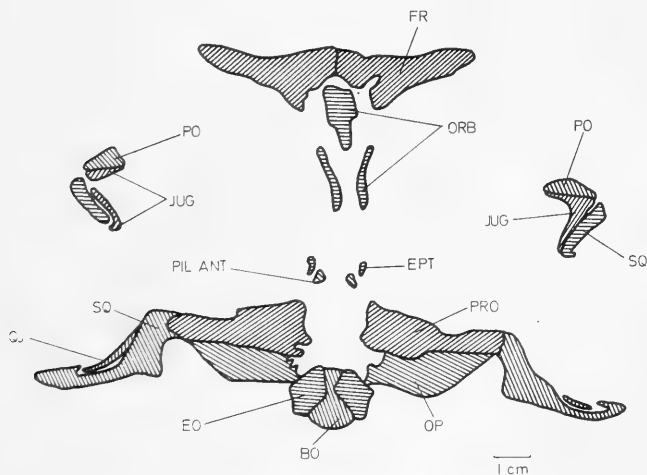


Fig. 6. *Lystrosaurus declivis*. S.A.M. No. K.1284. Frontotransverse section through frontal region and braincase.

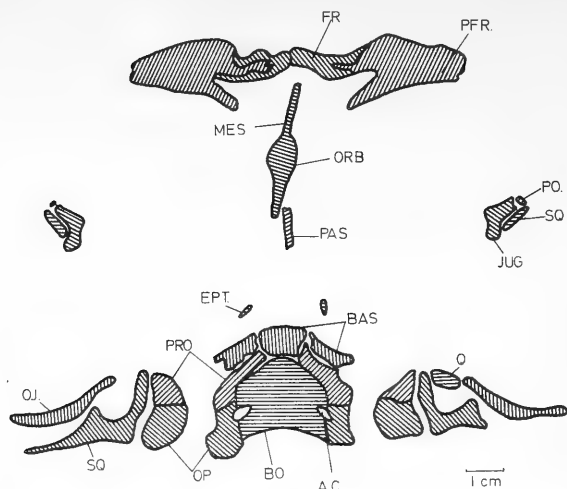


Fig. 7. *Lystrosaurus declivis*. S.A.M. No. K.1284. Frontotransverse section through basicranial axis and skull roof.

only a shallow fossa in the Dinocephalia, while Camp & Welles (1956) state that the fossa is absent in the Triassic *Kannemeyeria*, *Placerias* and *Stahlekeria*. This lends support to Olson's (1944) view that the fossa decreased in depth and importance during the course of therapsid evolution.

The vestibule, lying between the opisthotic, prootic and basioccipital, opens into the sacculo-cochlear recess, which in turn communicates widely with the cranial cavity through the internal auditory meatus. Olson (1944) states

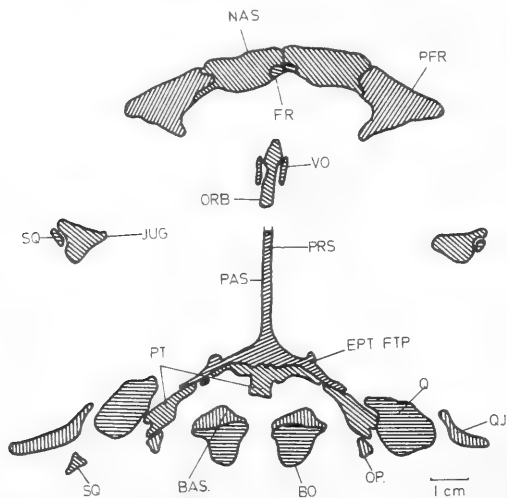


Fig. 8. *Lystrosaurus declivis*. S.A.M. No. K.1284. Frontotransverse section through skull base and nasal region.

that the fenestra rotunda in his sectioned specimens opened into the jugular foramen, and, although the canal for the jugular vein is posteriorly separated from the vestibule, this is probably the case in *Lystrosaurus* too. No division of the recess into a saccular and cochlear part is apparent in *Lystrosaurus*, although a ledge (Figs 9a, 10a: L.) at the level of the ampulla of the anterior ascending semicircular canal might possibly indicate the junction of the sacculus with the utriculus. The utriculus extends dorsally into the supraoccipital to meet the crus communis canalium. Three distinct recesses (Fig. 9a: A.AMP.REC., P.AMP.REC.) at the internal openings of the semicircular canals indicate the positions of the ampullae. The anterior two ampullary recesses are contained within a large, common depression (Figs 9a, 10a: A.AMP.REC.). The anterior and posterior vertical canals run dorsally through the prootic and opisthotic respectively, meeting in the supraoccipital to form the crus communis canalium, which in turn leads into the utriculus.

The *supraoccipital* provides a roof for the braincase and otic capsules, and forms the dorsal margin of the foramen magnum and most of the dorsal half of the occiput. It meets the opisthotic in a straight suture and dorsally to the foramen magnum is overlaid by the interparietal. Laterally it lies beneath the tabular and squamosal and anteriorly it is covered by the dorsal part of the

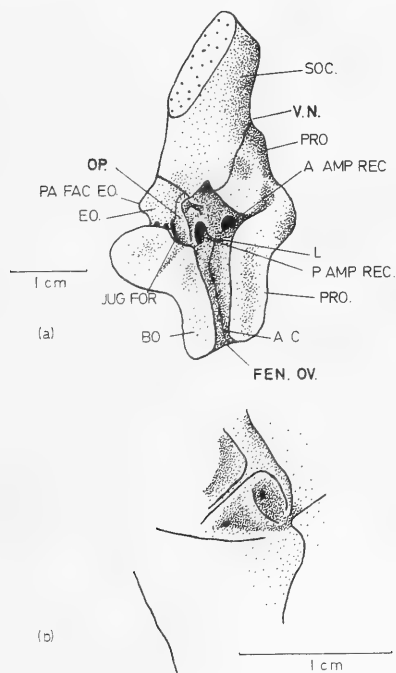


Fig. 9. *Lystrosaurus* sp. S.A.M. No. 11180.
(a) Inner view of left otic capsule.
(b) Detail of left anterior ampullary recess.

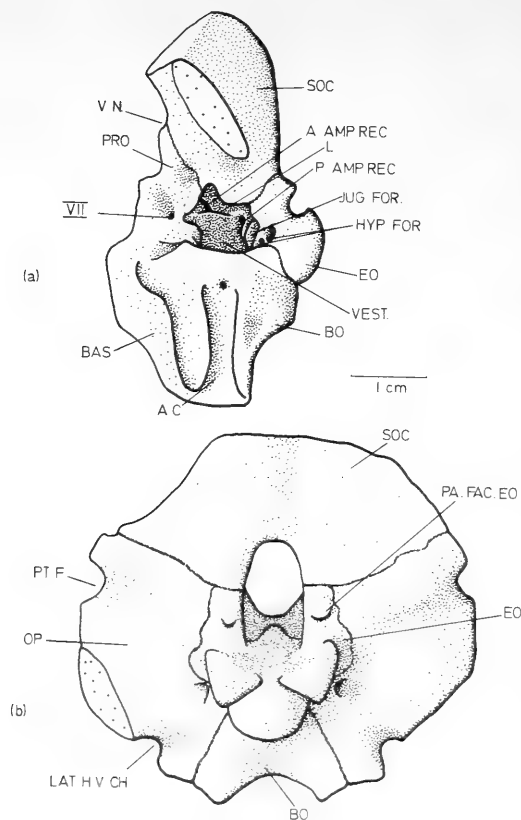


Fig. 10. *Lystrosaurus* sp. S.A.M. No. 11180. (a) Inner view of right otic capsule and basioccipital and (b) braincase in occipital view.

prootic. Above the notch formed between it and the prootic, the supraoccipital provides a partial side-wall to the braincase behind the pineal foramen, this side-wall being covered laterally by the ventrally descending wing of the parietal. The supraoccipital terminates dorsally as an abruptly truncated dorsal process, similar to that of the pelycosaurs (Romer & Price, 1940). The unfinished surface of the anterior edge of this process suggests that the supraoccipital was continued forward as cartilage beneath the inner parietal surface.

The dorsal edge of the supraoccipital forms the base of two tunnels running out laterally onto the occiput, from each side of the interior of the braincase (Fig. 13). Each tunnel lies under the parietal anteriorly, and under the interparietal, tabular and squamosal posteriorly and laterally, and opens out onto the posterior occipital face laterally to the tabular of its side. Watson (1960) and Cox (1959) have described similar channels in *Diictodon* and *Kingoria* respectively, ascribing a nutrient function to them.

This canal and a system of grooves on the prootic and supraoccipital

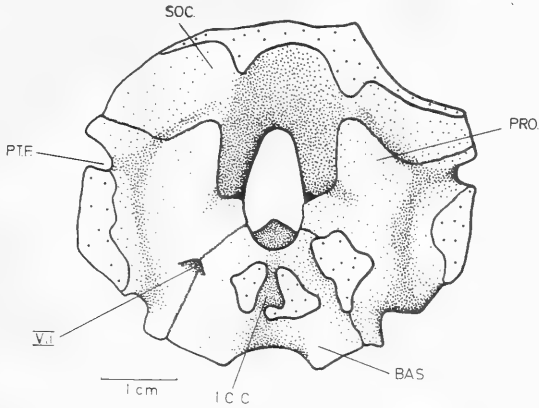


Fig. 11. *Lystrosaurus* sp. S.A.M. No. 11180. Braincase in anterior view.

(Fig. 11) indicate the probable course of veins which drained the deep structures of the head. The exact nature and extent of these blood-vessels is necessarily vague, but the following inferences can be made.

The ventral surface of the paroccipital process is characteristically excavated between the fenestra ovalis and the distal end of the process. The dorsal surface of the stapes is similarly excavated and a clear-cut tunnel (Figs 14, 15: LAT.H.V.CH.) is thus formed, continuing forwards as a groove running anterodorsally over the ventral and anterior face of the prootic, in the direction of the facial foramen. The tunnel and groove are in the position of the lateral head vein of living reptiles (Goodrich, 1930; Dendy, 1909).

The posttemporal fenestra is excavated in such a way as to form a channel running anteromedially from the occiput onto the face of the prootic. In one

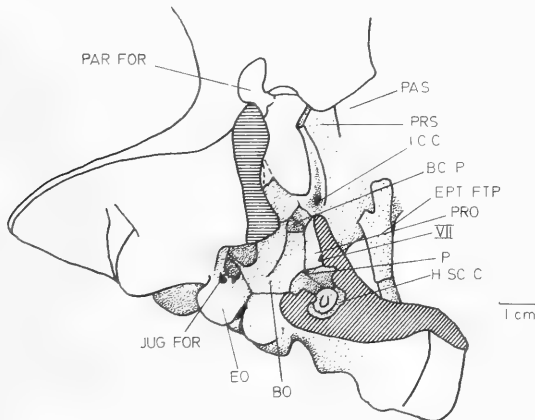


Fig. 12. *Lystrosaurus murrayi*. Nat. Mus. No. C.6457. Dissected braincase in dorsolateral view.

specimen a deep groove in the occiput leading into the fenestra provides strong evidence for a vein passing through the fenestra. A shallow groove runs dorsally up the face of the prootic from the lateral head vein channel to meet the groove from the posttemporal fenestra. This groove is then continued dorsally along the line of contact between the prootic and supraoccipital to the notch between the two bones in the side-wall of the braincase (Fig. 10a: V.N.). This dorsal part of the system of grooves is distinct and deeply excavated in some specimens. Olson (1944) does not believe that the dorsal notch in the braincase, which is well developed in some therapsids, stood in connection with the venous system, stating that the notch was formed between supports for the orbitosphenoid complex. The condition in *Lystrosaurus* is, however, clearly due to the presence during life of a blood-vessel. A similar explanation was proposed by Agnew (1959) in *Dicynodon grimbeeki*, while Boonstra (1934a, 1934b) figures a venous fossa between the supraoccipital and prootic in the Gorgonopsia and Therocephalia, and states that this is a feature of all therapsids.

Using very similar grooves in the skull of the dicynodont *Kingoria*, Cox (1959) reconstructed a system of veins which is comparable with that proposed

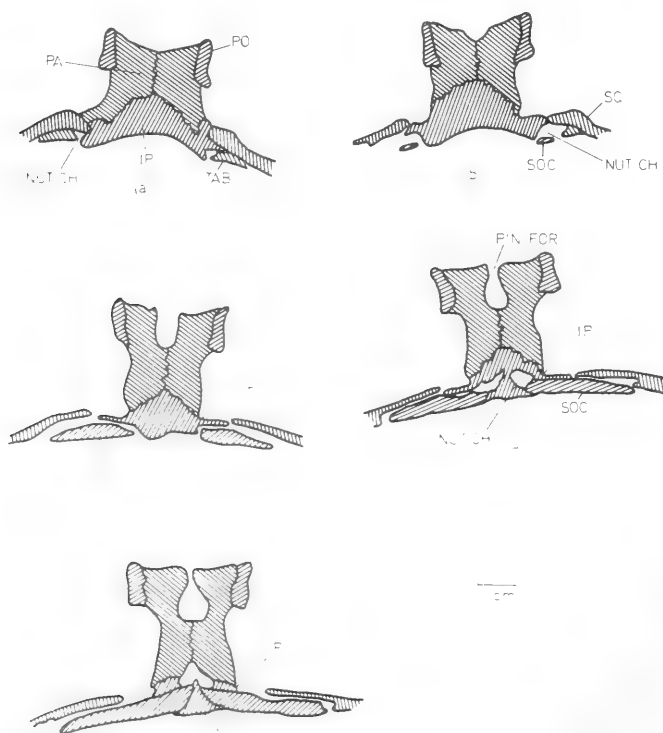


Fig. 13. *Lystrosaurus declivis*. S.A.M. No. K.1284. Consecutive sections, from posterior (a) to anterior (e) of the dorsal braincase and occiput showing the relationships of the occipital nutrient channels.

by Watson (1911, 1913) for *Diademodon*. The posttemporal fenestra probably served as a passage for the v. capitis dorsalis, which in modern reptiles such as *Sphenodon* (Dendy, 1909; O'Donoghue, 1920) drains the occipital musculature and passes forward to enter the braincase in front of the auditory capsule. In *Lystrosaurus* the groove leading to the venous notch in the prootic therefore marks the passage of this blood-vessel into the cranial cavity, as is also thought to be the case in the Pelycosauria (Romer & Price, 1940).

A different function for the posttemporal fenestra has been proposed by Ewer (1961) and Barry (1967), namely, that a slip of the adductor musculature passed through the fenestra and was attached to an adjacent area of the occipital face. However, available evidence, especially in recent reptiles, weighs against this theory.

Within the cranial cavity the v. capitis dorsalis probably met the v. cephalica posterior of its side. This latter vein is the lateral branch of the median longitudinal sinus (Dendy, 1909; Swain, 1968). The v. cephalica posterior would then have continued down to emerge from the skull through the jugular foramen together with cranial nerves IX, X and XI. The size of this foramen suggests that *Lystrosaurus*, in common with other dicynodonts, possessed a fairly large jugular vein.

The v. capitis lateralis passed back above the basiptyergoid process, between the epiptyergoid laterally and the pila antotica medially, and through the pterygo-paroccipital foramen to leave the skull through the channel between the stapes and the paroccipital process, along with the hyomandibular branch of the facial nerve. The shallow groove on the prootic below the post-

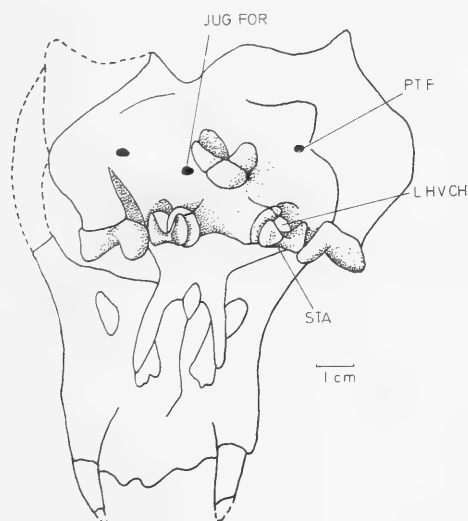


Fig. 14. *Lystrosaurus declivis*. Nat. Mus. No. C.403, Ventral occipital region in posterolateral view. showing stapes and lateral head vein channel.

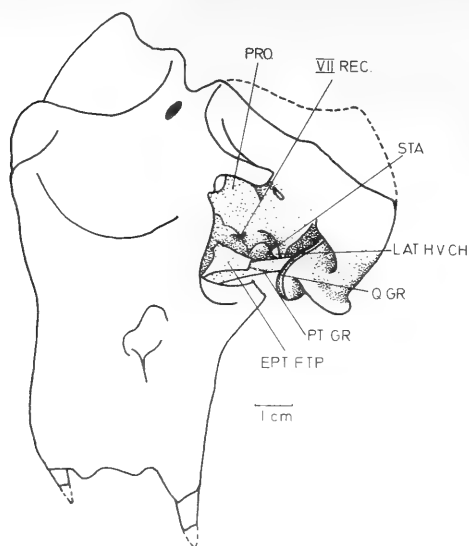


Fig. 15. *Lystrosaurus declivis*. Nat. Mus. No. C.403.
Anterolateral view of braincase, showing stapes
and lateral head vein channel.

temporal fenestra probably indicates a connecting sinus between the v. capitis dorsalis and the v. capitis lateralis, providing an alternative route for venous blood from the occiput.

In *Lystrosaurus* the gutter in each dorsolateral quarter of the occiput, between the supraoccipital and tabular and leading into the back of the cranial cavity, probably stood in connection with drainage of the occipital musculature, as did the v. capitis dorsalis. A vein leading into the gutter from each side of the occiput would emerge from between the supraoccipital and parietal into the cranial cavity and join the v. cephalica posterior of its side. There are thus altogether four forward groups for blood draining from the occiput. Most of this blood was carried by the jugular vein, but a portion would have reached the v. capitis lateralis via the connecting sinus and would have left the skull dorsally to the stapes.

In *Lystrosaurus* the anterior part of the braincase floor, between the two pilae antoticae, is formed by the *basisphenoid*, which is ventrally indistinguishably fused to the parasphenoid. The prootica do not meet in the midline and no true sella turcica, as is found in *Dicynodon*, is present in *Lystrosaurus*, where the entire hypophyseal region has been affected by shortening of the skull base. The possible relations of the hypophysis and dorsum sellae will be discussed in a later section.

In ventral view (Figs 4, 24) the basioccipital-parabasisphenoid suture is characteristically distinct on the anterior slope of the intertuberal ridge. The paired carotid canals enter the basisphenoid ventrally, immediately behind the

interpterygoidal plate, and dorsally emerge together in the small fossa posterior to the vertical presphenoidal plate.

Common to all species of *Lystrosaurus* is a shortening of the skull base anterior to the basioccipital. Thus the presphenoid ossification, usually far forward in dicynodonts, lies immediately in front of the internal opening of the internal carotid arteries in *Lystrosaurus*, obscuring some of the relations between parasphenoid and basisphenoid (Figs 2, 12). However, it is clear that a well developed basiptyergoid process makes contact with the footplate of the epiptyergoid laterally (Figs 3, 4: BPT.PROC.), and that a broad parabasisphenoid sheet extends forward to just behind the interpterygoidal vacuity. This sheet is in close contact with the interpterygoidal plate below. The lateral wing-like portions of the sheet are homologous with the parasphenoidal wings described and figured by Barry (1967) in *Pristerodon* and by Olson (1944). The palatine branch of the facial nerve is contained between the parabasisphenoid sheet and the interpterygoidal plate (Figs 22a, 24). This canal has been found in therapsids by Boonstra (1934a), Parrington & Westoll (1940), Olson (1944), Camp & Welles (1956) and Cox (1959). The nerve entered the ventral surface of the skull laterally to, and in advance of, the internal carotid foramina, and, passing between parasphenoid and pterygoid, emerged anterior to the interpterygoidal fossa and footplate of the epiptyergoid.

Dorsally the parabasisphenoidal plate supports a median, septal ossification, the presphenoid. This latter bone is ventrally and laterally supported by the cultriform process of the parasphenoid, which extends up dorsally from the interpterygoidal vacuity and terminates anteriorly as a process clasped between the posterior, diverging wings of the vomer (Figs 2, 28). In acid-prepared and sectioned specimens it can be seen that the presphenoid is covered laterally for some way by the parasphenoid. In typical dicynodonts (such as the specimen illustrated in Figure 34a) the parasphenoid, while also supporting the presphenoid, is only slightly grooved along the dorsal surface. The high, thin dorsally extended wings on either side of the presphenoid in *Lystrosaurus* represent a different condition altogether, and is the result of the skull-deepening process undergone by the genus.

The sphenethmoid complex

There is considerable uncertainty regarding the homology of the various elements of the sphenethmoid complex, and the terminology used by different morphologists has confused the issue to an even greater extent. For this reason the structure of the complex in *Lystrosaurus* will be dealt with before entering into a discussion on the most suitable terminology.

In *Lystrosaurus* there are three median ossifications of the braincase anterior to the basisphenoid (Figs 2, 28). The most posterior of these is the postero-ventrally situated presphenoid (mentioned previously), which is a vertical plate clasped ventrally and laterally by the cultriform process of the parasphenoid (Figs 12, 17), and which meets the basisphenoid posteriorly. Its

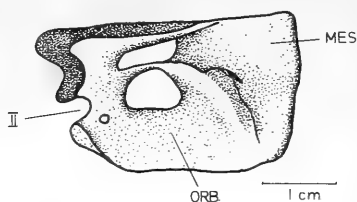


Fig. 16. *Lystrosaurus murrayi*. Nat. Mus. No. C.6457. Sphenethmoid complex in right lateral view.

surface displays a coarser histological texture than the surrounding and clearly distinguishable parasphenoid. Its posterior edge, above and in front of the hypophyseal region, is excavated to form a trough, while its dorsal edge is grooved in a manner suggesting that the ossification was continued dorsally as cartilage. Anteriorly the wings of the parasphenoid project dorsally past this groove (Fig. 17).

The anterodorsal structure situated beneath the frontals (Figs 2, 28: MES., ORB.), is more complicated and consists of two separate ossifications. The posterior ossification is a median keel which bears two lateral wings extending upwards to make contact with the longitudinal ridges on the inner surface of the frontals. (Figs 16, 28: ORB.). The median keel is of irregular thickness and is fenestrated. The trough formed by the lateral wings in all probability corresponds to the embryonic planum supraseptale (Romer & Price, 1940) and housed part of the olfactory lobes of the brain. On the posterior edge of each wing is a notch, representing the anterior border of the optic foramen (Figs 16, 28: II). The remainder of the posterior margin is excavated to form a groove, suggesting that the ossification was continued posteriorly in

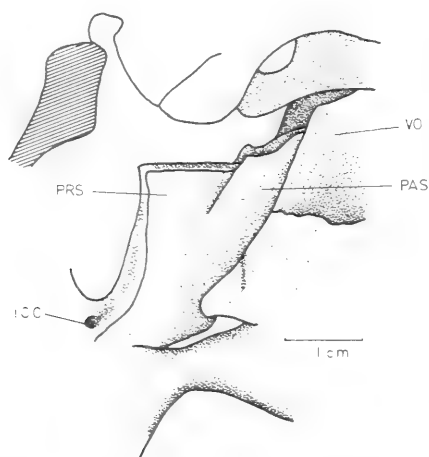


Fig. 17. *Lystrosaurus murrayi*. Nat. Mus. No. C.6457. Presphenoid in right lateral view.

cartilage. In this way a complete optic foramen was probably formed. The ventral edge of the bone, similarly excavated, was probably connected by a sheet of cartilage to the anterodorsal edge of the presphenoid, to form a possibly complete interorbital septum. Cox (1959) has suggested a comparable condition in *Kingoria*.

Anteriorly the trough-shaped ossification makes close contact with a third structure, a median sheet of bone (Figs 2, 16: MES.) extending up to the inner surface of the frontals. This septum is of constant thickness over the greater part of its extent, but dorsally it is laterally expanded beneath the surface of the frontals, forming a roof for, and a partition between, the olfactory nerve bundles.

The two anterodorsal ossifications, lying up against the skull roof, can be clearly distinguished from each other in acid-prepared and sectioned specimens. Basically the complex resembles that of other dicynodonts, but there is wide disagreement in the terminology used by different authors. Seeley (1898) called the entire anterodorsal structure, beneath the frontals, the orbitosphenoid, Broom (1904) called it the ethmoid and Sollas & Sollas (1913) used the terms ethmoid or mesethmoid. The latter supposed the bone to be the forerunner of the mammalian cribriform plate and pointed out that its relations with the olfactory nerve and the rest of the basicranial axis make it very similar to the mammalian mesethmoid. They regard a ventral ossification, anterior to the fossa hypophyseos of their sectioned *Dicynodon* and in the same position as the posteroventral ossification in *Lystrosaurus*, as an anterior extension of the basisphenoid. Broom (1926, 1927) agreed with Sollas & Sollas (1913) on this latter point, and regarded the entire anterodorsal structure as being homologous with the mammalian presphenoid. He concluded that there were three elements in the basicranial axis of all therapsids, *Dicynodon* being representative of the group. These elements were basioccipital, basisphenoid and presphenoid. In 1927 he pointed out that certain mammal groups had only three elements in the basicranial axis, and other groups four. The first groups he collectively called Palaeotherida, which he supposed had inherited the therapsid condition directly. The second group, the Neotherida, he regarded as having secondarily obtained a new element, the mesethmoid, anteriorly in the basicranial axis.

However, Olson (1944), studying sectioned specimens of all four therapsid infraorders, concluded that there were four elements in the basicranial axis, these being basioccipital, basisphenoid, a presphenoid lying in the central stem anterior to the fossa hypophyseos, and an anterodorsal element beneath the frontals which he tentatively identified as a mesethmoid. The dorsolateral wings, which enclose the forebrain, he called the orbitosphenoid, showing that this was not part of the basicranial axis. He also showed that the presphenoid in dicynodonts may lie relatively far back and make contact with the basisphenoid. In cases where the presphenoid made contact with the mesethmoid in gorgonopsians and therocephalians there was no fusion between the elements. He concludes that the presphenoid ossified from the fused trabeculae,

the mesethmoid from the internasal septum of the trabeculae, and the orbitosphenoid from the preoptic pillar and planum supraseptale. The primitive mammalian condition, Olson states, is one where all four elements are present, while some groups of mammals secondarily lost the mesethmoid early in their evolution.

In his work on the cranial development of certain primitive mammals Roux (1947) followed Broom's (1926, 1927) interpretation of the therapsid basicranial axis. He concluded that in those Chrysochloridae which he investigated three basicranial elements were present, i.e. basioccipital, basisphenoid (which extended far forward), and, as Broom (1927) showed, a median element which arose far forward in the skull. This latter element, which lay in the position of the mammalian mesethmoid and in the same position as in Broom's (1926) *Dicynodon*, Roux called the presphenoid. Roux points out that the Palaeotherida are not a natural group and that two or three elements assist in the formation of the anterior ossification. Furthermore, the new median element in the Neotherida does not arise anterior to the presphenoid as would be expected, but in fact between the presphenoid and basisphenoid. The latter bone is now restricted to the lamina hypophyseos posteriorly. Roux, having found that the new element arises from paired centres in the orbitosphenoid, concludes that there are only three unpaired median ossifications in the basicranial axis of all vertebrates.

Camp & Welles (1956) follow the terminology of Camp (1942) in their description of certain Triassic dicynodonts. They call the dorsal trough-shaped ossification, in contact with the ventral frontal surface, the frontosphenoid, while they term the ventral median keel the septosphenoid. The postero-ventral element, in contact with the basisphenoid, they call presphenoid. They state that the septosphenoid may be equivalent to the mammalian mesethmoid, but Camp (1956) rejects this on the grounds that it lies below the cerebrum and forms an interorbital septum. He disagrees with the term orbitosphenoid on the grounds that this bone must ossify from the metoptic root and should therefore enclose an optic foramen. This is not the case in any dicynodont.

Agnew (1959) reviews the question of the sphenethmoid homology, and points out that Camp's (1956) argument is not necessarily valid since the orbitosphenoid ossification in the amphisbaenid *Monopeltis* (Malan, 1946) invades the planum supraseptale, the dorsal part of the interorbital septum and the posterodorsal part of the nasal septum. Agnew agrees with the interpretation of the basicranial axis as set out by Roux (1947) and calls the entire median portion of the sphenethmoid complex in *Dicynodon grimbeeki* the presphenoid, with a possible rudimentary mesethmoid between the anterior portions of the lateral orbitosphenoid wings. However, the posterior portion of Agnew's presphenoid is in the same position as the anterior basisphenoidal extension of Broom (1926) and Roux (1947).

Cox (1959) calls the entire anterodorsal complex in *Kingoria* a sphenethmoid, and states that it is not divided into orbitosphenoid and mesethmoid

ossifications. He maintains that a structure in *Kingoria*, similar to the presphenoid of Olson's (1944) sectioned specimens, is merely an anterior ossification of the basisphenoid, lying in the cultriform process of the parasphenoid. Ewer (1961) agrees with this view, but Barry (1967) finds a division in the anterodorsal structure in *Pristerodon*, and calls the posterior portion, including the lateral wings, the orbitosphenoid. For the anterior, clearly independent ossification, he uses the term septosphenoid of Camp (1942). He states that the wings of the orbitosphenoid should be regarded as the ossified planum supraseptale.

For an interpretation of the elements in *Lystrosaurus* it must be decided whether the posteroventral element is indeed independent of the basisphenoid. In *Lystrosaurus* this element fuses with the basisphenoid in the region of the internal carotid canal as a result of shortening of the skull-base in this region. Camp & Welles (1956) find the same phenomenon in *Placerias*, but state categorically that macerated specimens show that the posteroventral element is independent of the basisphenoid. In his sectioned therapsid specimens Olson (1944) found that the posteroventral ossification may be completely free of the basisphenoid or only partly fused to it. Agnew (1959) found the element to be independent in his sectioned *Dicynodon*. Against this evidence the interpretations of Sollas & Sollas (1914), Broom (1926) and Cox (1959) must fall away. The instances they cite could, it seems, be due to apparent fusion between the posterior element and the basisphenoid.

The second point is the nature of the anterodorsal structure, below the frontals. Sollas & Sollas (1914), Cox (1959) and Ewer (1961) regard it as a single ossification. However Olson (1944) found in his sectioned specimens that it consists of a posterior orbitosphenoid and an anterior, sometimes ventral, mesethmoid. Camp & Welles (1956), Agnew (1959) and Barry (1967) all divide it into two elements, but use different terminologies. Moreover, in the present investigation it was found that in both acid-prepared and sectioned specimens of *Lystrosaurus* a clear-cut line of fusion divides the complex into an anterior plate-like septum and a posterior trough-shaped portion.

There are thus three median elements in the *Lystrosaurus* basicranial axis anterior to the hypophyseal region: the posteroventral one, immediately in advance of the basisphenoid, the anterodorsal one enclosing the forebrain and extending ventrally as a short, fenestrated interorbital septum, and, anterior to this, the anterodorsal plate-like septum extending up to the inner frontal surface and dividing the olfactory tracts.

For the posteroventral element the term *presphenoid* seems the most acceptable, as it ossifies from the fused trabeculae and from the interorbital septum arising from the trabeculae. Furthermore, it is in the position of the rudimentary interorbital septum found in the developing *Ornithorhynchus* (De Beer, 1937). This conclusion is supported by the definition of Bellairs (1949: 492), viz. '... the term presphenoid may be restricted to the trabecular ossifications in contact with the basisphenoid behind', and by Haines (1950) who regards the

term presphenoid as denoting the bone usually ossified from presphenoid and orbitosphenoid centres.

The trough-shaped, anterodorsal element, lying beneath the frontals, seems equivalent to the planum supraseptale of reptiles (Barry, 1967) and the broad preoptic root and adjacent orbital cartilages of mammals (De Beer, 1937). There can be little doubt that the optic nerve emerged through the notch in the posterior border of the bone (Sollas & Sollas, 1914; Olson, 1944). This being so, the ossification is anterior to the optic foramen and must therefore include the preoptic root. Camp & Welles (1956) object to the term orbitosphenoid for this bone on the grounds that the orbitosphenoid ossifies from the metoptic root. However, Boonstra (1934a) has described and figured a sphenethmoid with a complete posterior foramen in the gorgonopsian *Arctognathus*, this foramen being in the position of the notch in *Lystrosaurus* and other dicynodonts. Moreover, Malan (1946) has shown that the orbitosphenoid in *Monopeltis* invades the planum supraseptale and the dorsal part of the interorbital septum. The term *orbitosphenoid* would therefore seem to be suitable for the ossification in *Lystrosaurus*. It is important to note that this bone in *Lystrosaurus* descends ventrally as a septum. This must be regarded as a secondary invasion by the preoptic roots into the basicranial axis, such as was observed by Roux (1947) in the orbitosphenoid of developing embryos of primitive mammals. In crocodiles and lizards (Bellairs, 1949) the orbital cartilages, from which the orbitosphenoid ossifies, also meet in the midline. It is interesting to note that no metoptic root is developed in the marsupials, and no true foramen opticum is formed (De Beer, 1937).

The anterior, septal portion of the anterodorsal structure is more difficult to identify. Olson in his (1944) investigation into the therapsid infraorders tentatively calls it mesethmoid, but Camp (1956) rejects this possibility in the dicynodonts because the bone does not form part of the nasal septum, does not carry the olfactory lobes in its posterior extension and lies between the cerebral hemispheres and forms the interorbital septum. In *Lystrosaurus*, however, these are not the relations of the anterior element, which lies entirely anterior to the cerebrum, forms no part of the interorbital septum and appears to have been intimately associated with the olfactory nerve bundles. Its nearest counterpart appears to be the *mesethmoid* of mammals and it deserves to be referred to as such. Agnew (1959) finds a small median ossification in *Dicynodon grimbeeki* which he calls the mesethmoid.

If the above argument is valid, Roux's (1947) statement that there are never more than three centres of ossification in the basicranial axis of all vertebrates is unacceptable, since he bases his assumption on Broom's (1926, 1927) interpretation of *Dicynodon*. Roux did find that the new median basicranial element in those primitive mammals which he investigated is not a true median ossification but a fusion in the midline of centres arising in the orbitosphenoid. However, the findings of De Beer & Woodger (1930) regarding the strictly median, trabecular origin of the interorbital septum of the rabbit

suggests that some mammals have in fact retained a posterior part of the reptilian median septum, equivalent to the therapsid presphenoid. Haines (1950) has described the ossified interorbital septum in a variety of mammals, showing that this bone is in contact with the mammalian presphenoid, which he defines (p. 585) as '... the bone in the adult skull, separate in most mammals, which is usually ossified from presphenoid and orbitosphenoid centres. It corresponds to the "presphenoid part" of the sphenoid bone of man.'

The basicranial axis of *Lystrosaurus* therefore comprises four separate elements, viz. the basioccipital, basisphenoid, presphenoid, and mesethmoid as primary median ossifications. The preoptic roots of the orbitosphenoid have secondarily invaded the basicranial axis.

In some mammal groups, such as the insectivores described by Roux (1947) it seems that both presphenoid and interorbital septum are absent, and that only the orbitosphenoids may secondarily invade this region.

THE VISCERAL ARCH SKELETON

Palatoquadrate

The *epipterygoid* (Figs 2, 22a, 28) is a long, narrow rod lying between the quadrate ramus of the pterygoid and the descending lateral wing of the parietal. Dorsally the slightly broadened upper tip makes contact with the inside of the descending lateral parietal flange in an interdigitating suture. Ventrally the shaft curves down and back to merge with the footplate. The footplate lies on the lateral edge of the quadrate ramus of the pterygoid, is flattened anteriorly to its junction with the dorsal shaft, and makes medial contact with the parabasisphenoid complex (Figs 3, 4). Its anterior extent varies within the genus. In the larger forms it extends well forward as a pterygoid process (Fig. 5) while in the smaller forms it is generally limited. *Anteosaurus* (Boonstra, 1968) and *Kannemeyeria* (Barry, 1965) have long anterior processes. Ewer (1961) discussed a strip of bone lying anterior to the footplate of the epipterygoid in *Daptocephalus*, and in view of the condition in *Lystrosaurus*, appears to be correct in her interpretation of its being an anterior prolongation of the epipterygoid.

Posteriorly the footplate is sharply truncated and the posterior edge, excavated in the form of a groove, faces backwards along the quadrate ramus of the pterygoid towards the quadrate (Fig. 18). The footplate does not reach as far back as in *Dicynodon grimbeeki* (Agnew, 1959) or *Pristerodon* (Barry, 1967).

The quadrate (Fig. 19) is clasped between the paroccipital process medially and the quadratojugal laterally. It consists of a broad, anteriorly convex, medial plate, which curves down ventrally to form the medial condyle, and a wide sheet extending laterally from the plate to provide a base for the quadratojugal and to form the lateral condyle.

The lateral condylar surface is only slightly rounded and lies mainly in the horizontal plane. The ventral surface of the inner condyle is more rounded and is separated from the outer condyle by a vertical articular surface. A deep

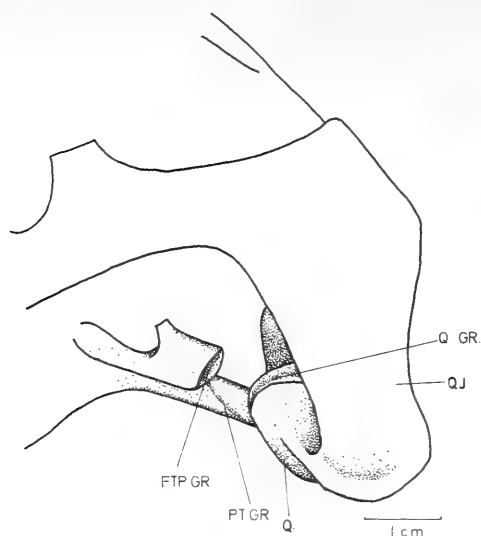


Fig. 18. *Lystrosaurus murrayi*. Nat. Mus. No. C.6457. Left quadrate region in lateral view.

notch is thus formed between the two condyles, into which the articular fits. The anteroposteriorly directed quadrate foramen (Figs 18, 22a), which possibly transmitted a nerve to the lower jaw, as Romer (1956) suggested for *Seymouria*, lies between the quadrate and quadratojugal. The inner surface of the quadrate bears a smooth facet for the reception of the posterior end of the quadrate ramus of the pterygoid (Figs 19a, 19b). Dorsally to the pterygoid facet the groove widens into a notch, facing forwards along the quadrate ramus (Figs 8, 19a, 19b), while the anterior surface of the inner arc-like edge of the quadrate bears a groove, unfinished in periosteum, above its inner condylar portion. These two features of the quadrate strongly suggest the existence during life of a connecting strip of cartilage between the quadrate and the sharply truncated footplate of the epipterygoid, to form a single palatoquadrate complex. Support for this view is provided by a recessed facet on the lateral side of the quadrate ramus of the pterygoid (Figs 15, 18), between

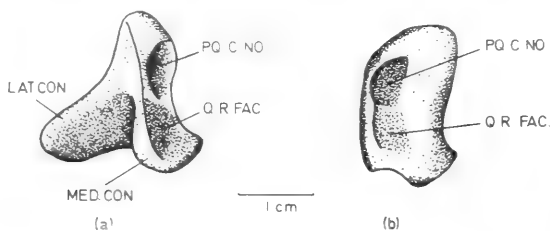


Fig. 19. *Lystrosaurus* sp. S.A.M. No. K.1495. Right quadrate in (a) anterior and (b) medial view.

the footplate and quadrate, presumably indicating that the palatoquadrate cartilage was closely apposed to the pterygoid. The well-defined hollow, unfinished in periosteum and lying above the facet for the quadrate ramus on the medial surface of the quadrate, probably received a medial projection of this cartilage.

White (1939) has found evidence for a palatoquadrate cartilage in *Seymouria*, while Barry (1965, 1967) showed that a similar cartilaginous connection between quadrate and epipterygoid existed in *Pristerodon*, where the quadrate is notched in a fashion very similar to *Lystrosaurus*. In both *Pristerodon* and *Dicynodon grimbeeki* the footplate of the epipterygoid extends far back, almost reaching the quadrate.

Stapes and hyoid apparatus

The stapes (Figs 14, 15, 20) is short and squat. It is deeply excavated dorsally, and a large, clear-cut channel is closed off between it and the paroccipital process. The stapedial footplate has a short dorsal process extending up the fenestra ovalis. Ventrally the medial half of the stapes is cut away into a distinct facet, which appears to be unique among dicynodonts. Barry (1968) suggests that the facet provided attachment for a portion of the hypobranchial skeleton.

Laterally the stapes is dorsoventrally flattened and bears two articular facets. The ventral facet makes contact with the ventromedial surface of the quadrate, and the dorsal facet meets the ventrolateral extremity of the paroccipital process. This latter stapes-opisthotic contact has previously been found

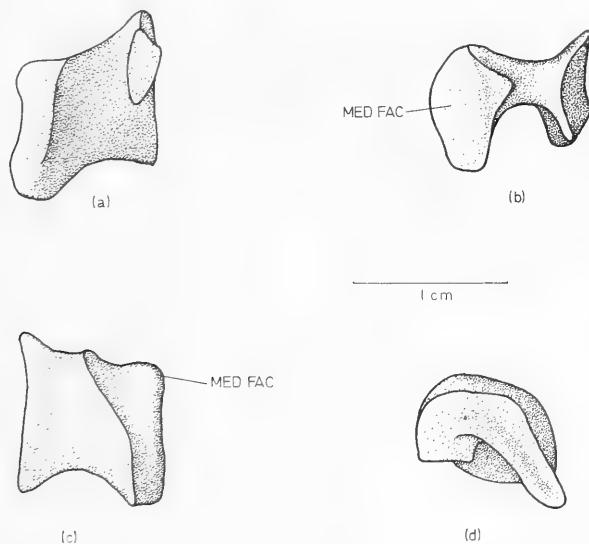


Fig. 20. *Lystrosaurus declivis*. Nat. Mus. No. C.403. Left stapes in (a) dorsal (b) posteroventral (c) ventral and (d) lateral views.

by Boonstra (1965) in the dinocephalian *Struthiocephalus* and by Cox (1959) in *Kingoria*. A well-defined anteroposteriorly directed groove separates the two facets and possibly transmitted a blood-vessel or nerve. There are no indications of an extrastapedial process such as found by Ewer (1961) in *Daptocephalus* or of a sharp 'tympanic' opisthotic process such as is found in *Kingoria* (Cox, 1959), and it seems unlikely that a tympanum was present in life.

In several specimens of *Lystrosaurus* a pair of short, curved rods (Fig. 21) was found, usually in the pterygoid region of the skull. Barry (1968) considers that they are ossified ceratohyals. They are often found in association with the stapes, and a strong possibility exists that in life they articulated with the median, ventral facets of the stapes (Barry, 1968). Other records of preserved portions of the hypobranchial skeleton in dicynodonts are a basihyal in *Pristerodon* (Barry, 1967) and a pair of rods in *Kingoria* and *Daptocephalus* (Cox, 1959; Ewer, 1961).

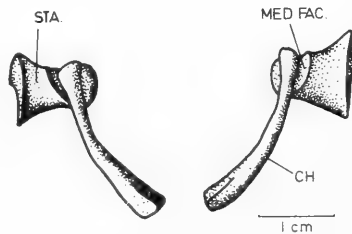


Fig. 21. *Lystrosaurus declivis*. Nat. Mus. No. C.403. Stapes and ceratohyals in articulation, ventral view.

THE DERMOCRANIUM

The snout region

The snout and adjacent skull roof are the most variable portions of the *Lystrosaurus* skull, but several characteristics of the region are common to all variants and can thus be used for diagnosis of the genus. The snout is always strongly developed and ventrally extended, but the nasal apertures have not accompanied this ventral growth and remain relatively high in the skull. In some forms the snout curves down smoothly from the frontal surface, while in others the anterior surface of the snout is a remarkable flat plane, separated from the frontal plane by a transverse frontonasal ridge.

The *premaxilla* has an extensive facial portion, more extensive than in any *Dicynodon*, and forms a large part of the snout (Figs 22a, 27). The variation in degree of development of the snout is caused directly by increase or decrease in the extent of the premaxilla and maxilla. Besides this quantitative variation, there are also marked differences in the shape and form of the premaxilla within the genus. Thus in species with moderately developed, smoothly downturned snouts, and with no transverse nasal ridge, the outer surface of the pre-

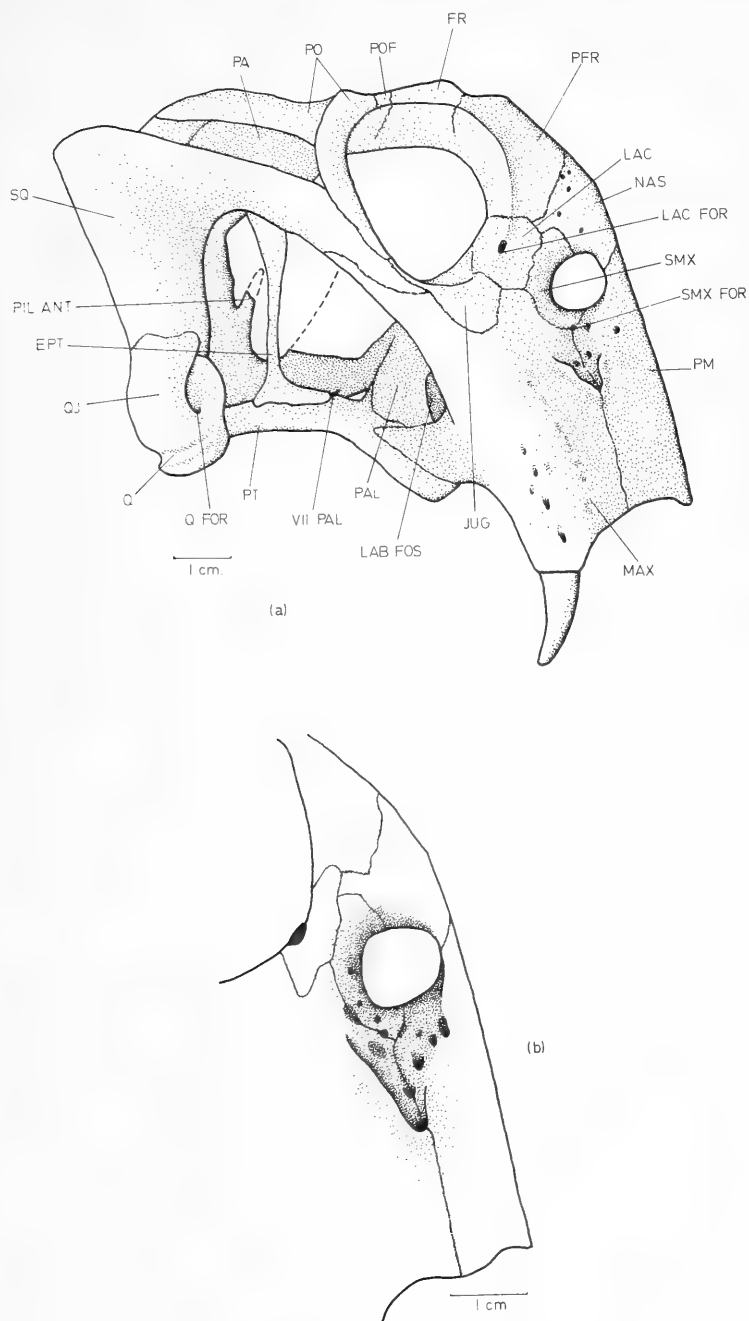


Fig. 22. *Lystrosaurus declivis*. Nat. Mus. No. C.403. (a) Skull in lateral view. (b) Right external nasal aperture.

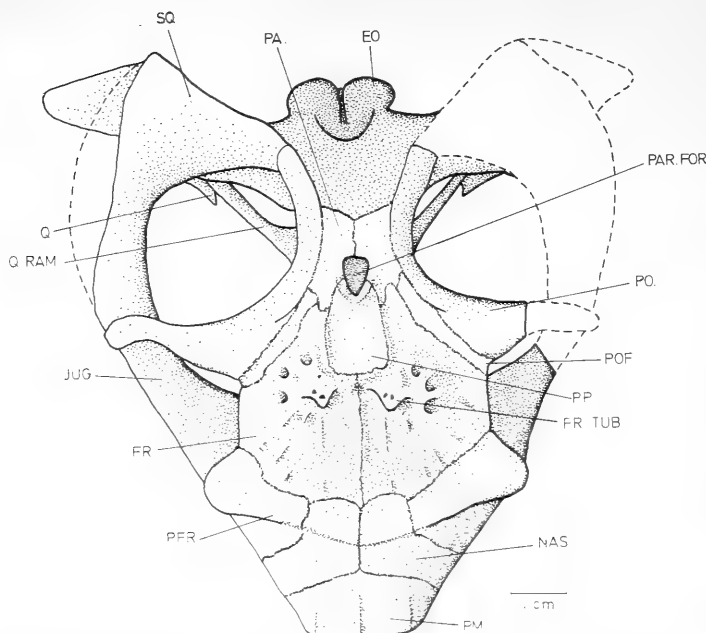


Fig. 23. *Lystrosaurus declivis*. Nat. Mus. No. C.403. Skull in dorsal view.

maxilla is smooth and gently rounded from side to side to merge into the lateral maxillary surface of the snout (Figs 27, 36). On the other hand, those forms with more strongly developed snouts and with frontonasal ridges, have a characteristic longitudinal ridge running medially down the anterior surface of the premaxilla (Fig. 26). This ridge may be knife-edged in some specimens and is of variable extent. It may occur high up on the nasal process of the premaxilla only, or it may run the entire length of the bone. Furthermore, the anterior surface of the premaxilla in these forms is, with the exception of the longitudinal ridge, perfectly flat and straight. This plane, unique among dicynodonts, meets the lateral surface of the snout at a sharp angle. The snout as a whole may be relatively narrow in these species, with a correspondingly narrower and more compact palatal region of the premaxilla.

The nasal process of the premaxilla extends dorsally between the nasals and almost up to the frontonasal ridge, where present. It forms the anterior border of the nasal aperture, and meets the septomaxilla in the floor of the aperture. Ventrally to this it meets the maxilla in a straight suture which runs down to the rim of the palate.

The ventral rim of the palate is sharp and extended relatively far ventrally, and reflects the nature and extent of the unpreserved horny beak. The deeply recessed, dome-shaped palatal portion of the premaxilla bears three prominent longitudinal ridges (Figs. 24, 25). The median ridge is the largest and extends from the anterior portion of the choana, where it meets the vomer

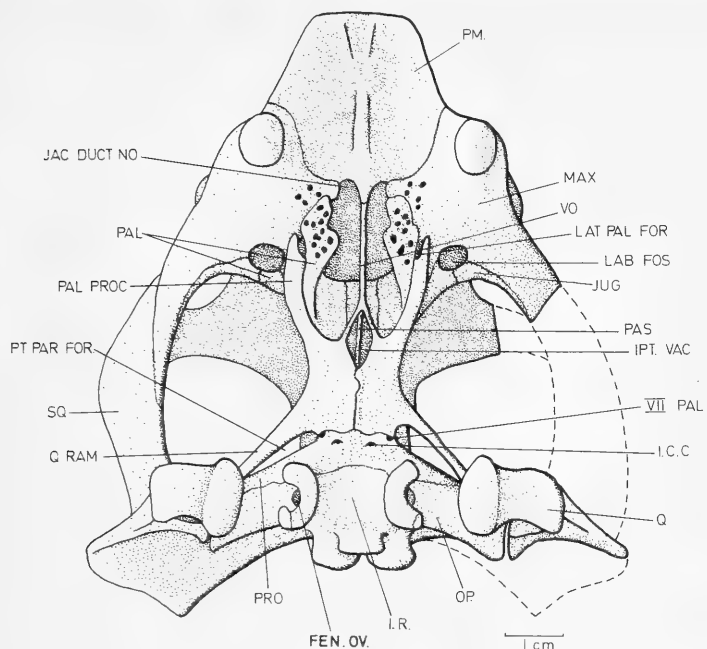


Fig. 24. *Lystrosaurus declivis*. Nat. Mus. No. C.403. Skull in ventral view.

in a complex suture, to a point just behind the descending palatal rim. Posteriorly the ridge is high and sharp, but flattens out anteriorly. On each side of the ridge is a narrow, deeply incised channel, opening out on to the palatal surface at the tip of the ridge.

The lateral palatal ridges lie on the anterior descending rim of the palate, each arising laterally to the anterior tip of the median ridge and terminating as a ventral projection beyond the level of the rest of the premaxillary rim. Each ridge is cut down the middle by a single channel, similar to those alongside the median ridge. It seems probable that these grooves housed nutrient blood-vessels running between the bony ridges and a layer of horn. The presence of horn on the ridges is further suggested by the porous, roughened surface of the bone. The extent of the horny beak on the palate will be more fully discussed in a later section.

Posteriorly the premaxilla divides the nasal passages as a median septum, and terminates as a sharp blade enclosed by the diverging anterior wings of the vomer (Figs 2, 28, 35). Van Hoepen (1913) mentioned this suture in *Lystrosaurus latirostris*, and Barry (1967) found a similar interdigitating contact in *Pristerodon*. The increase in size of the premaxilla in *Lystrosaurus* as compared with other dicynodonts, is reflected in the great dorsoventral extent of this posterior sheet. The ventral half of the premaxilla-vomer suture is more complicated, there being a median septum of the vomer extending between two diverging internal premaxillary processes. Furthermore, a lateral fold of

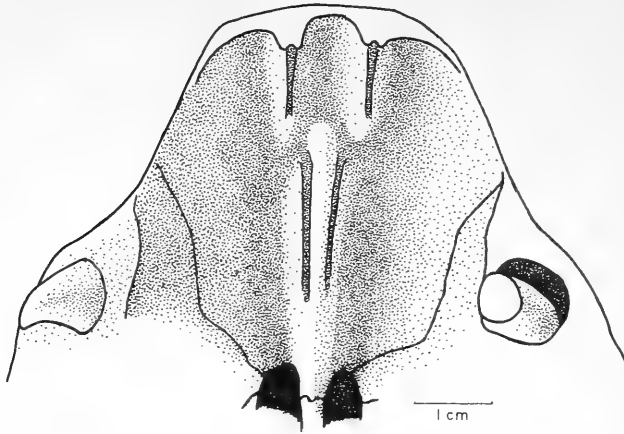


Fig. 25. *Lystrosaurus curvatus*. Nat. Mus. No. C.299. Premaxillary portion of palate in ventral view.

the premaxilla overlaps the anteroventral corner of the diverging vomerine wing. In this way a very firm, interlocking suture is formed between the premaxilla and vomer (Figs 28, 35).

The relative extent of the *maxilla* varies with the size of the premaxilla. It meets the latter bone anteriorly, the septomaxilla and lacrimal dorsally, and overlaps the jugal posterodorsally. Ventrally it is extended as a strong caniniform process which carries the single canine tusk, while a posterior process extends as part of the zygomatic arch to below the middle of the orbit. The line of the zygomatic arch is prolonged downwards to the caniniform process as a pronounced lateral thickening of the snout, the tusk and surrounding portions of the palate being thus powerfully buttressed by the entire zygoma. The lateral thickening of the snout has a rough, pitted surface, suggesting a covering of horn extending up from above the tusk. The posterior part of the sharp palatal rim is formed by the ventral edge of the maxilla in front of the tusk (Figs 24, 26). This, the sharpest part of the palatal rim, slopes down and back to lie flush against the inner surface of the tusk, and is always well developed, regardless of tusk size.

In the palate the maxilla separates the premaxilla from the palatine and forms the lateral border of an anterior notch in the choana. Laterally to this it covers the palatine and the anterior palatal process of the pterygoid by its posterior pterygoid process, the anterior part of which forms the ventral border of the labial fossa (Figs 24, 31).

In the region of the maxillo-palatine contact in the palate, at the base of the caniniform process, the surface of the maxilla is pitted and scored by grooves similar to those found on the premaxillary palatal surface. This appears to be a continuation of a similar pitted surface on the anterior expanded end of the palatine, and indications are that the palatine and adjoining maxilla

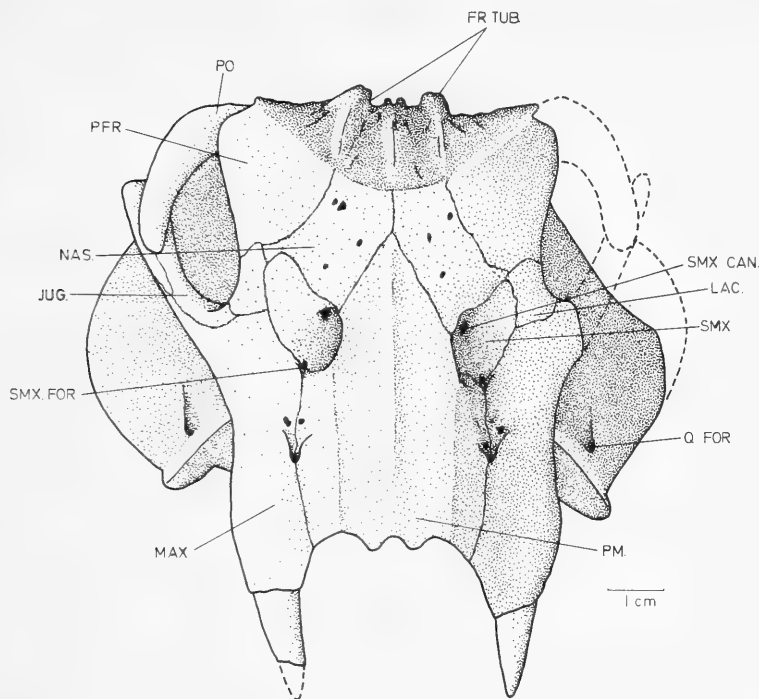


Fig. 26. *Lystrosaurus declivis*. Nat. Mus. No. C.403. Skull in anterior view.

were covered by a layer of horn. That the dicynodont palatine was provided with such a covering has long been recognized (Watson, 1948). It is interesting to note that the area of the maxilla next to the palatine in *Lystrosaurus* is in the same relative position as the postcanine tooth-bearing region in endothiodonts, so that in *Lystrosaurus* the functions of a row of teeth have apparently been taken over by a horny pad. Watson (1960) has found nutrient foramina and a boss around the canine tusk in several dicynodonts, and Cox (1959) has described similar roughened areas on the maxilla of *Kingoria*.

The relative tusk size in *Lystrosaurus* varies considerably. Generally it can be said that those species with frontonasal ridges and more strongly developed snouts possess relatively larger tusks than those species with smoothly rounded, weaker snouts. Wear facets are found in most cases, and are especially marked in forms with large tusks. These facets are confined to the inner surface of the tusk and are clearly the result of wear against the mandibular beak. Absence of other facets and wear marks makes it unlikely that the tusks were used for regular digging or scratching purposes. This conclusion is in agreement with Sollas & Sollas (1914) and Watson (1960). The possibility does nevertheless exist that the tusks, especially of larger individuals, were used as offensive or defensive weapons. No traces of replacement teeth were found, and the presence of concentric growth rings, visible in sections, suggest con-

tinued tusk growth throughout life, such as described by Camp & Welles (1956) in *Placerias*.

The *nasal* forms the dorsal border of the nasal aperture, meets the septomaxilla, lacrimal and prefrontal laterally, and makes contact with the frontal dorsally. In forms with smoothly rounded snouts the nasals diverge posteriorly, whereas in species with transverse frontonasal ridges this is not the case, and the suture between nasals and frontals is straight and transverse. This difference is obviously associated with the presence or absence of the ridge. Along half of their extent the nasals meet in the midline, but ventrally they are separated by the nasal process of the premaxilla. The outer surface of the nasal is smooth but perforated by several large nutrient foramina, and forms a low, rounded boss over the nasal aperture. Together the nasals form the middle portion of the frontonasal ridge when this is present.

The nasal apertures are situated relatively high in the skull, and close in front of the orbits. The nasal provides a roof for each aperture and the premaxilla forms the anterior wall and anterior part of the floor. The septomaxilla closes the opening from behind. A depression in the side of the snout below the nasal opening contains several pits and ridges, and its ventral boundary is a strong ledge of the maxilla (Figs 22a, 22b). Ewer (1961) found a comparable condition in *Daptocephalus*, where the septomaxilla displays a complex of

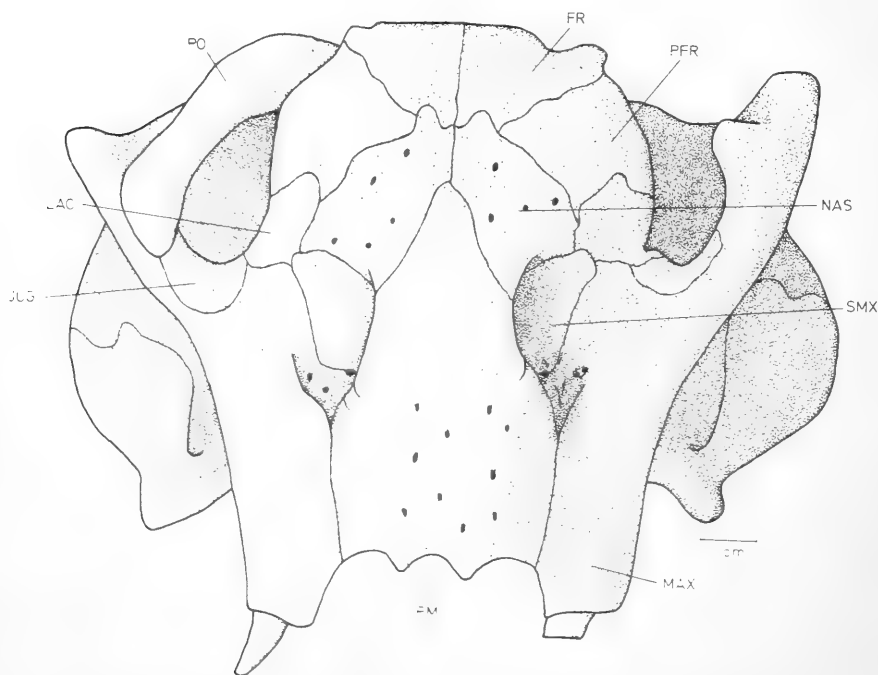


Fig. 27. *Lystrosaurus curvatus*. Nat. Mus. No. C.299. Skull in anterior view.

rugosities and depressions, and she speculates on the possibility of this bone forming the base of a muscular mechanism whereby the fleshy nostril could be closed when the animal was feeding off submerged plant matter. There is a very strong likelihood that a similar mechanism was present in the semi-aquatic *Lystrosaurus*, a possibility first mentioned by Watson (1912). In this connection it is interesting to note that whereas in *Daptocephalus* the roughened, pitted area is confined to the septomaxilla, in *Lystrosaurus* the adjoining premaxilla and maxilla contribute towards the formation of ledges and tuberosities. It thus seems that whatever the nostril-closing device present in *Daptocephalus* was, it was enlarged and probably more important in the aquatic *Lystrosaurus*.

Brink (1951) thought it likely that *Lystrosaurus amphibius* possessed a fleshy nostril which extended dorsally along the snout up to the prefrontal boss. Although no deep groove in the nasal, such as described by Brink, was found in any of the skulls examined during the course of this study, it is interesting

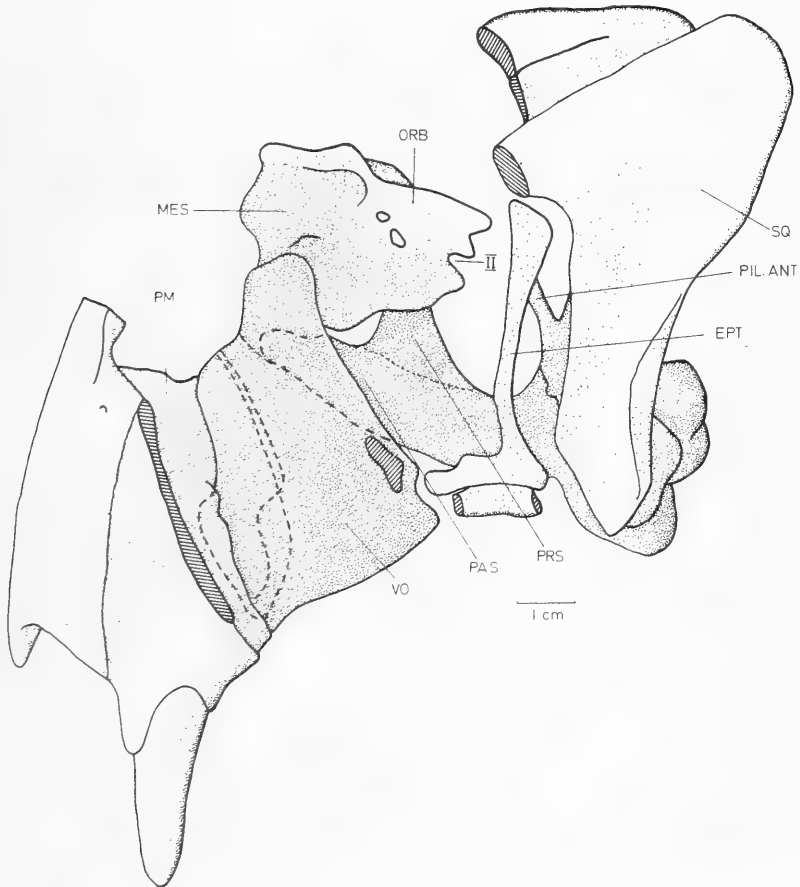


Fig. 28. *Lystrosaurus declivis*. S.A.M. No. K.1284. Lateral view of median septum of the skull, reconstructed from serial sections.

to note that in all specimens the nasal is pierced by numerous large nutrient foramina.

The *septomaxilla* is distinct on the outer surface of the skull behind the nasal opening. The septomaxillary foramen is contained between the maxilla and the ventral edge of the septomaxilla. Posteriorly the septomaxilla meets the lacrimal over a short distance. Van Hoepen (1913) stated that a thin sheet-like portion of the maxilla separated the septomaxilla from the lacrimal in *Lystrosaurus latirostris*, but that beneath this the two bones met. It seems likely that this character is variable and of little significance. A short, wide canal (Figs 26, 29, 32: SMX.CAN.) traverses the body of the septomaxilla and runs medially to open out on the median edge of the bone. The possible function of this canal is discussed below.

The *lacrimal* is an extensive bone and bears complicated relations to the surrounding bones of the snout. Between the jugal and prefrontal it forms the anteroventral border of the orbit and the lateral border of the large fenestra leading from the orbit into the nasal cavity. It terminates anteriorly as a process enclosed by the maxilla and on the outer surface of the snout meets the septomaxilla in a short suture. A short lacrimal duct pierces the lacrimal at the anteroventral corner of the orbit and opens into the nasal cavity close behind the septomaxilla-lacrimal suture (Figs 29, 32).

Serially sectioned and acid-prepared specimens made possible a detailed study of the inner nasal cavities, usually inaccessible in conventionally prepared specimens. The inner surface of the nasal is smooth but pierced by several large foramina. However, the surface of the frontals just behind is unfinished in periosteum, and two distinct ridges are formed, one on each side of the midline. Each ridge has a flat ventral surface and is continued forward on to the nasal of its side (Fig. 30: FR.R.). Both Van Hoepen (1913) and Barry (1967) have found similar ridges in *Lystrosaurus* and *Pristerodon* respectively. Barry (1967) supposes that the ridges supported cartilaginous or membraneous structures of the nasal capsule, and tentatively identifies that part of the mesethmoid (Barry's septosphenoid) which expands laterally beneath the frontals with the sphenethmoidal commissures of recent reptiles. However, it seems more likely that the ridges on the frontals and nasals were associated with a pair of cartilaginous sphenethmoidal commissures, as suggested by Romer & Price (1940) in the Pelycosauria. In recent reptiles (Malan, 1946) and mammals (Roux, 1947) these bars of cartilage are closely applied to similarly ridged frontals.

Alternatively, the pair of frontonasal ridges in *Lystrosaurus* may have supported a pair of turbinals, within a posterior extension of the nasal cavity. Kemp (1969a) has suggested that this was the case in the Gorgonopsia, Therocephalia and Cynodontia, where a more extensive system of ridges is found within the nasal cavity. Kemp further maintains that the above-mentioned ridges in the pelycosaurs are evidence of the presence of turbinals in primitive synapsids.

As shown earlier, the premaxilla terminates posteriorly as a deep septum

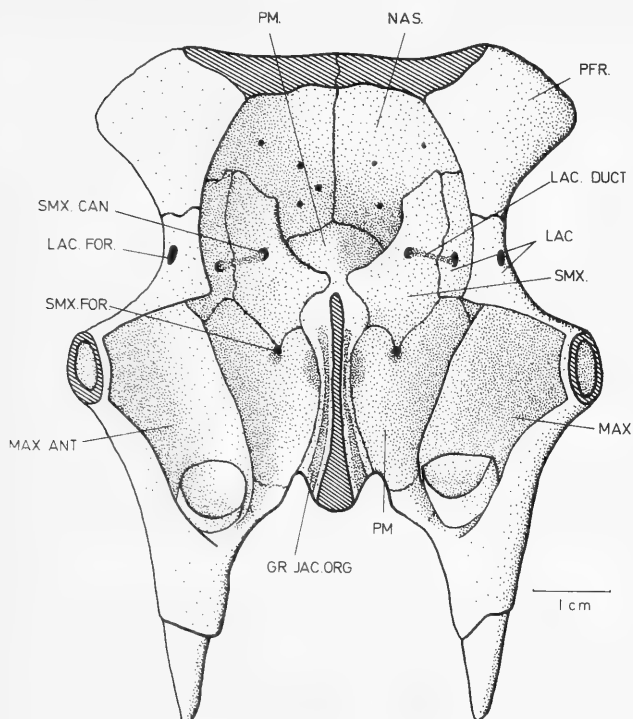


Fig. 29. *Lystrosaurus* sp. S.A.M. No. K.1495. Inner surface of the snout cavity in anterior view.

dividing the nasal cavity and meeting the vomer behind. The dorsal edge of this septum is flat anteriorly, but posteriorly, where it is clasped by the anterior vomerine flanges, it is excavated to form a sulcus. Kemp (1969a) has described a similar sulcus in the dorsal edge of the gorgonopsian vomerine median septum, and suggests that it received the ventral edge of the cartilaginous nasal septum. He goes on to demonstrate that, this being the case, the nasal capsule in gorgonopsids was probably situated high in the snout, and communicated with the internal choanae by means of a choanal tube.

In *Lystrosaurus* the deepened snout has resulted in the internal choanae lying relatively far ventrally to the external nares and the level of the dorsal edge of the premaxillary septum. If the nasal capsule of *Lystrosaurus* resembled that of gorgonopsians, as seems likely, any choanal tube passing down to the choana would have been of considerable length, and would have been supported posteriorly by the median processes of the palatines, as Kemp thought was the case in the *Gorgonopsia*.

Within the nasal cavity the premaxilla is longitudinally grooved on either side of the median septum, so that a furrow is formed leading from a point near the nasal aperture to the anterior notch of the choana (Figs 29, 35). The

posterior part of the furrow is especially deep and clear-cut. It seems very probable that the furrow served to transmit the duct of Jacobson's organ. Camp & Wells (1956) found a similar groove leading from a depression in the snout of *Placerias* and mentioned the possibility of this being evidence for the presence of Jacobson's organ. Pearson (1924) also found indications of the organ in *Kannemeyeria*. In a sectioned dicynodont (S.A.M. 10081) a similar groove opening into the anterior choanal notch was found alongside the premaxillary septum.

In recent reptiles the duct of Jacobson's organ opens into the anterior part of the choana, and in mammals, where the primitive choana has been eliminated by the secondary palate, it passes into the oral cavity through the naso-palatine foramen (foramen incisivum) which lies between the premaxilla and maxilla (Goodrich, 1930; Stadtmüller, 1936).

This reconstruction of the duct of Jacobson's organ in *Lystrosaurus* is at variance with Brink's (1960) deductions regarding the septomaxillary region of a sectioned therocephalian, *Akidnognathus parvus*. Brink, in the first place, maintained that the morphology of this region in therocephalians is different from that of the same region in dicynodonts, but comparison of Figures 29 and 32 with Brink's (1960) Figure 36 shows that the two regions are essentially similar in *Akidnognathus* and *Lystrosaurus*.

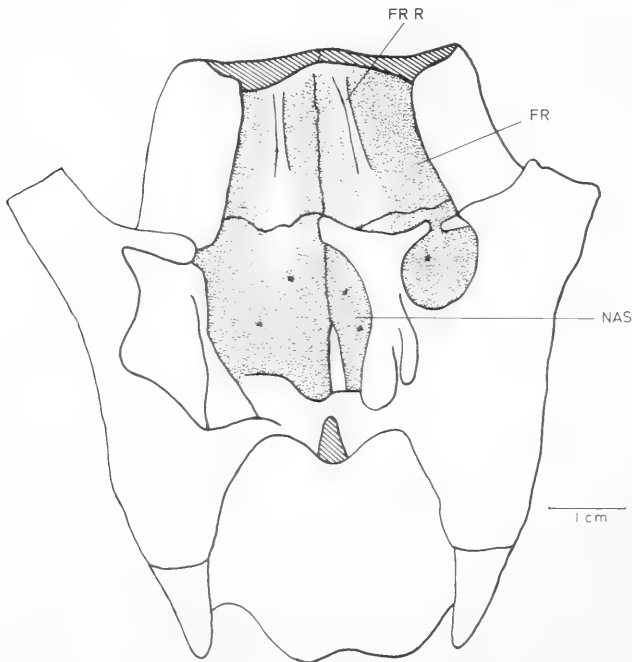


Fig. 30. *Lystrosaurus* sp. S.A.M. No. K.1495. Ventral view of inner frontal and nasal surfaces.

Examination of the grooves and foramina in *Akidnognathus* led Brink to conclude that the duct of Jacobson's organ had departed from its primitive reptilian orientation and now opened in a new position near the external aperture of the nasal passage, through the canal in the septomaxilla. This, Brink supposed, was a result of the developing secondary palate, which had cut off the duct's opening into the oral cavity and thus prevented the organ from functioning as a 'taste' organ. With its new opening at the entrance of the nasal passage the organ could perform the functions of a primitive taste and olfactory organ.

However, as stated above, in typical mammals the organ of Jacobson still opens into the oral cavity through the naso-palatine foramen, and has no direct relations with the nasal chambers. Broom (1895, 1896a, 1896b) has described Jacobson's organ in a variety of mammals and has shown that in groups as diverse as the rodents, the horse, camel and giraffe, as also in the marsupial *Aepyprymus*, the organ does in fact open into the nasal capsule, but in these cases the new disposition of the duct is due to aberrations in the palatal structure, such as, for instance, enlargement of the premaxilla in the horse, whereby the ventral portion of the naso-palatine duct is obliterated. Furthermore, the internal opening of the duct in these forms is close to the organ itself, and never in the vicinity of the external naris.

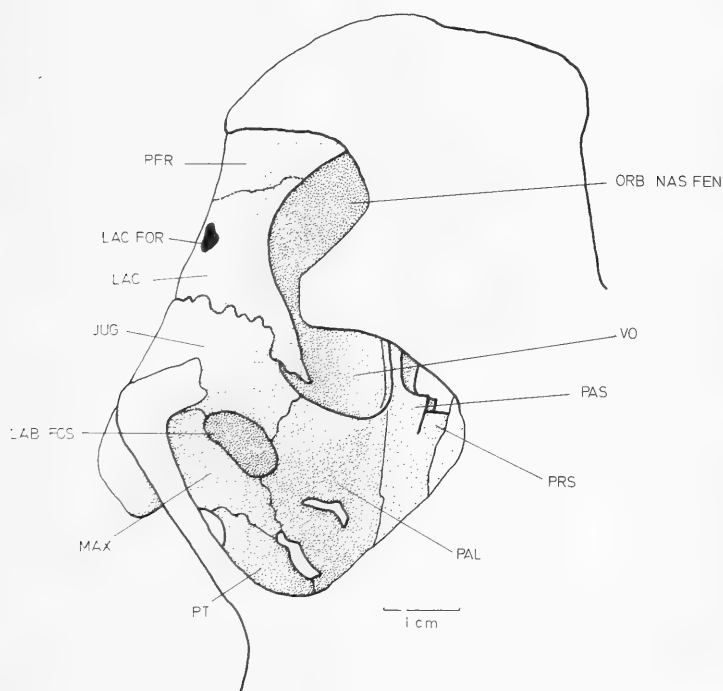


Fig. 31. *Lystrosaurus murrayi*. Nat. Mus. No. C.6457. Posterodorsal view of labial fossa region.

The direct connection of Jacobson's organ with the interior of the nasal capsule in certain mammals must, it seems, be regarded as secondary and uncharacteristic of the class as a whole, since in all other marsupial and placental mammals investigated by Broom, Jacobson's organ opens into the oral cavity via the naso-palatine duct. With all factors taken into consideration, it seems most likely that the organ was present in therapsids, and that its duct opened into the choana. In a recent (1969a) publication, Kemp has come to a similar conclusion regarding Jacobson's organ in the *Gorgonopsia* he investigated. In the dicynodonts the development of the extensive palatal portion of the premaxilla resulted in a backwards displacement of the duct which, however, still opened into the choana. The difference in the position of the duct's opening into the oral cavity in the two therapsid groups in which a functional secondary palate was developed, namely the cynodonts and dicynodonts, is illustrative of the different means whereby a backwards displacement of the internal nares was accomplished in the two groups. While in the cynodonts the bony secondary palate was formed by medial extensions of the maxillae and palatines, enclosing an anterior naso-palatine foramen, in the dicynodonts simple posterior enlargement of the premaxilla took place.

Laterally to the groove for the duct of Jacobson's organ in *Lystrosaurus* the surface of the maxilla is smooth and concave to form a floor and anterior wall for the nasal cavity. The deepening of the snout has resulted in this portion of the maxilla lying at a steep angle, instead of more or less horizontally as in dicynodonts such as *Kingoria* (Fig. 54). A deep recess, such as found by Watson (1960) in a dicynodont snout, in the anterolateral corner of the nasal chamber at the junction of the septomaxilla and maxilla, opens out on to the outer surface of the snout through the septomaxillary foramen (Figs 22a, 32: SMX. FOR.).

Cox (1959) found three foramina in this region in *Kingoria*. Two of these hold the same morphological relationships with the maxilla and septomaxilla as does the septomaxillary foramen in *Lystrosaurus*. The third pierces the septomaxilla and is equivalent to the septomaxillary canal in *Lystrosaurus*. Cox mentions the possibility of one of these foramina serving the duct of Jacobson's organ, but in the light of the above evidence for a different pathway for this duct, his alternative interpretation, that the ducts of the lateral nasal and lacrimal glands were transmitted to the outer snout surface through the foramina, is more acceptable. In *Lystrosaurus* the canal traversing the septomaxilla is large enough to carry a lacrimal duct the size of which is indicated by the bony lacrimal canal. This latter canal enters the nasal cavity at the same level and close behind the septomaxillary canal. A distinct sulcus runs between the two openings (Figs 29, 32: LAC.DUCT), making it virtually certain that the lacrimal duct left the skull through the septomaxillary canal.

Kemp (1969a) has concluded that in the *Gorgonopsia* the lacrimal duct, after entering the nasal cavity, passed into the maxillary sinus and then opened into the choana, as in typical recent reptiles. In *Lystrosaurus* and other dicyno-

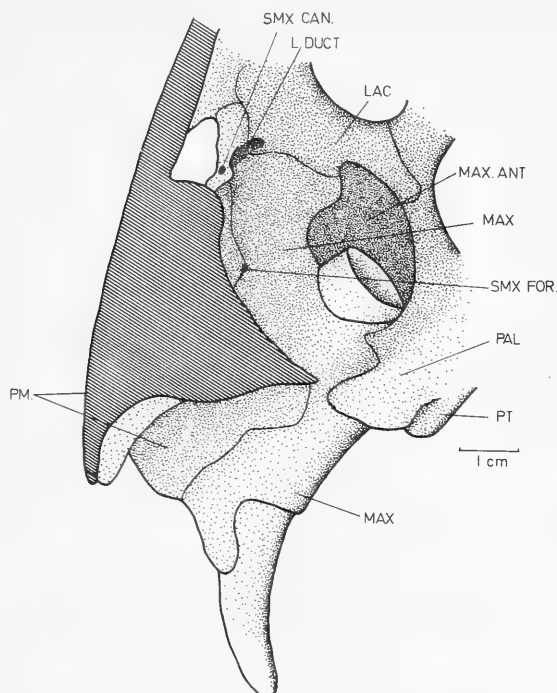


Fig. 32. *Lystrosaurus declivis*. S.A.M. No. K.1284. Interior of snout in medial view. Reconstructed from serial sections.

donts, however, the duct enters the nasal cavity dorsally and anteriorly to the maxillary antrum, making it unlikely that the course postulated by Kemp was followed in these animals. Moreover, the close association between the nasolacrimal duct and septomaxilla in *Dasyops* (Fuchs, 1911) suggests that the duct in therapsids other than *Lystrosaurus* passed through, or close to, the septomaxilla.

The smaller septomaxillary foramen, between the septomaxilla and maxilla, in this case probably served to transmit the duct of the lateral nasal gland, which in recent reptiles opens into the vestibule at this point (Pratt, 1948) and serves to moisten the nostril. The septomaxillary foramen is a feature of the Gorgonopsia, Therocephalia and Dinocephalia (Boonstra, 1934a, 1934b, 1968). In the Squamata, the septomaxilla has abandoned its primary position as a surface bone of the snout and migrated medially to form a roof for Jacobson's organ, and loses its association with the duct of the lateral nasal gland.

Laterally the nasal cavity leads to an extensive maxillary antrum, which surrounds the root of the tusk in the base of the zygomatic arch (Figs 29, 32, 33, 35: MAX. ANT.). Anteriorly the antrum is bounded by the maxilla and lacrimal, and laterally and posteriorly by the jugal. Dorsally the antrum leads into two blind pouches, one reaching forward to near the lacrimal canal, and

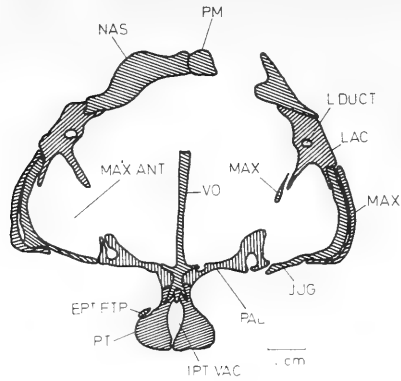


Fig. 33. *Lystrosaurus declivis*. S.A.M. No. K.1284. Frontotransverse section through posterior part of nasal cavity.

one running posteriorly a short way into the zygomatic arch. The posterior wall of the maxillary antrum, consisting of jugal, lacrimal and palatine, is excavated to form the labial fossa.

The function of the maxillary antrum is not one associated with the presence of a large canine tusk, as is shown by the condition in two dicynodonts, S.A.M. 10081 and 6550 (Figs 34a, 54a), which are tuskless and yet possess well-developed antra. In three sectioned dicynodont specimens examined by Agnew (1959) the antrum was absent in two and present in the other. This variable occurrence in closely related animals makes it unlikely that the antrum contained important glandular tissue, and it seems probable that Watson (1960) was correct in his supposition that the space was filled by a diverticulum of the respiratory passage. Such a diverticulum, containing a pair of turbinals,

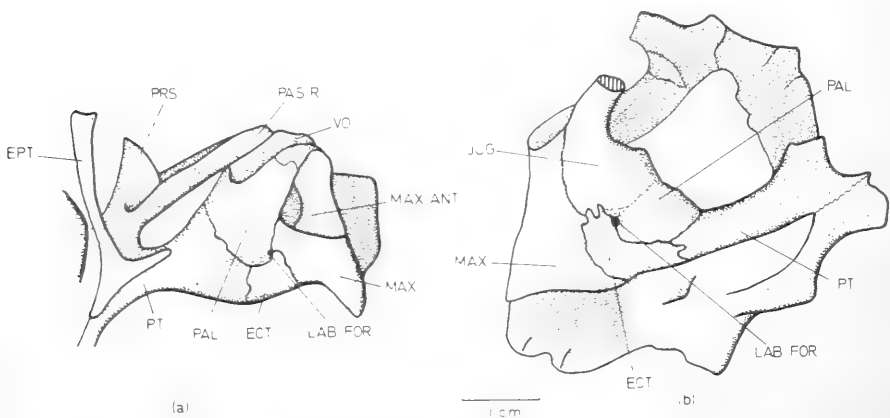


Fig. 34. (a) Dicynodont sp. S.A.M. 6550. Partial snout and basicranial axis in posterolateral view. (b) Dicynodont sp. S.A.M. 10377. Snout in posterolateral view.

has been proposed by Kemp (1969a) in the maxillary sinus of the Gorgonopsia.

Ewer (1961) showed that the labial fossa occurs in *Lystrosaurus*, *Daptocephalus*, *Kannemeyeria* and *Aulacephalodon*, but not in *Dicynodon* or the endothiodontids. It appears that the labial fossa is not a new structure in these genera, as a foramen in a position homologous to the Triassic *Lystrosaurus* and *Kannemeyeria* labial fossa is present in the snouts of two tuskless *Cistecephalus* zone dicynodonts, S.A.M. 6550 and 10377 (Figs 34a, 34b). The foramen very likely served to transmit nutrient blood-vessels into the snout, and the enlargement of the foramen into the labial fossa is probably related to the increase in size of the snout in Triassic dicynodonts and the advanced *Aulacephalodon* and *Daptocephalus*.

The palatal region

There is no ectopterygoid in *Lystrosaurus*. Morphologically the position of the ectopterygoid is taken up by the pterygoid process of the maxilla. Whereas in *Daptocephalus* the ectopterygoid forms part of the ventral margin of the labial fossa, in *Lystrosaurus* this portion of the labial fossa border is formed by the maxilla only. The possibility exists that the pterygoid process of the maxilla represents an ectopterygoid.

The *palatine* is in the main a curved vertical sheet of bone. It forms the lateral and posterior wall of the choana, and its anterodorsal border separates the maxillary antrum from the nasal cavity. It meets the median vomerine septum medially and extends up as a transverse sheet to form the ventral border of the large fenestra leading forward from the orbit into the nasal cavity (Fig. 31: ORB. NAS. FEN.). Above the labial fossa it is clasped between the jugal and lacrimal.

The *vomer* (Figs 2, 28, 33, 35) is a median sheet of bone, bifurcated anteriorly and posteriorly, and extending upward from ventrally in the choana to make a brief contact with the mesethmoid. Anteriorly it is firmly interlocked with the premaxilla, as described above, while the posterior bifurcation clasps the parasphenoidal rostrum dorsally and forms the anterior border of the interpterygoidal fossa ventrally. The dorsal tip of the posterior bifurcation loosely surrounds the ventral edge of the mesethmoid.

The *parasphenoid*, intimately fused to the basisphenoid, has already been referred to in the description of the neurocranium. Deepening and shortening of the skull has transformed the cultriform process of this element from the long low bar of typical dicynodonts to a narrow trough with high, thin sides (Fig. 17). The essential relationships between parasphenoid and presphenoid are retained, however, and the latter is tightly clasped between the high ascending wings of the parasphenoidal rostrum. In dicynodonts such as *Dicynodon grimbeeki* and *Pristerodon* the rostrum is grooved for the reception of the sphenethmoid complex or a cartilaginous extension of it; in *Lystrosaurus* there is a deep trench in the parasphenoid anterior to the presphenoid, which in all likelihood received a similar cartilaginous extension of the sphenethmoid.

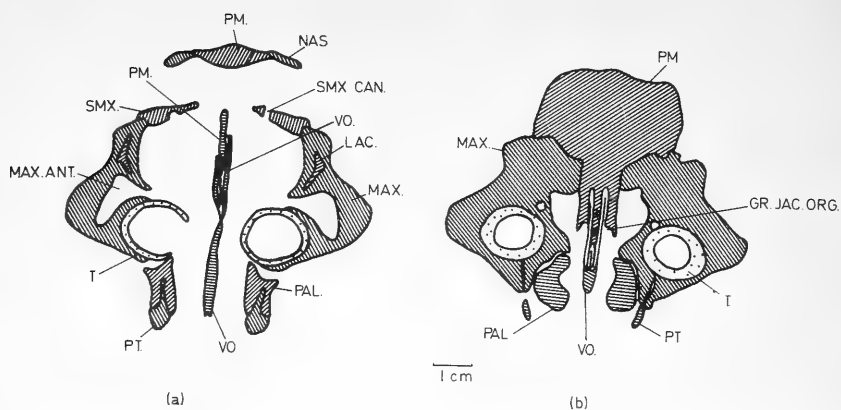


Fig. 35. *Lystrosaurus declivis*. S.A.M. No. K.1284. (a) Frontotransverse section through external nasal aperture and nasal cavity. (b) Frontotransverse section through ventral part of snout and nasal cavity.

The *pterygoid* can be reduced to three processes: an anterior palatine process, a broad median plate-like process which meets its fellow of the other side behind the interpterygoidal fossa (vacuity), and a posterior quadrate ramus (Fig. 24). The anterior palatine process is inserted between the palatine medially and the posterior pterygoid process of the maxilla laterally. Between the palatine and pterygoid is a canal running from the palate to close behind the labial fossa (Fig. 24: LAT.PAL.FOR.). Cox (1959) found a similar canal between the palatine and ectopterygoid of *Kingoria*, and supposes that it is the reduced equivalent of the large lateral palatal fenestra of reptiles (Versluys, 1936). In this connection it can be mentioned that a large suborbital fenestra lies between the ectopterygoid, pterygoid and palatine of the *Therocephalia*, but it is not found in the *Gorgonopsia* (Boonstra, 1936a, 1936b). Versluys (1936) states that a broad lateral palatal fenestra occurs in cotylosaurs and pelycosaurs, and that it probably transmitted a branch of the trigeminal nerve.

The median pterygoid processes meet to form a strong pterygoidal plate which is closely applied to the ventral surface of the parabasisphenoid, enclosing a canal for the palatine branch of the facial nerve (Figs 22a, 24). The quadrate ramus is a flat bar extending laterally to insert between the quadrate and the paroccipital process (Fig. 8). A smooth facet is developed on the medial surface of the quadrate for this contact. Along its anterior dorsal surface the process carries a section of the epipterygoid footplate. Between the epipterygoid footplate and the quadrate, the lateral surface of the pterygoid is grooved (Figs 15, 18), suggesting that a sheet of cartilage connecting the epipterygoid and quadrate (see section on the visceral arch skeleton) lay closely applied to the pterygoid in this region.

Between the quadrate ramus of the pterygoid and the prootic-opisthotic portion of the braincase a large opening, the pterygo-paroccipital foramen of Watson (1911) and Cox (1959) is formed (Fig. 24: PT.PAR.FOR.). Romer &

Price (1940) state that this passage in pelycosaur is equivalent to the cranioquadrate foramen of Goodrich (1930). Technically this would also be correct in a therapsid such as *Lystrosaurus*, since, if the posterior portion of the footplate of the epipterygoid and the quadrate were connected by a band of cartilage, as seems likely, the passage would have been situated between the braincase and palatoquadrate.

The skull roof

Lystrosaurus species may be grouped into two categories on the basis of variation in the shape of the skull roof, which is here considered to include *nasals*, *frontals*, *prefrontals*, *preparietal* and *parietals*. In one group the skull roof is smooth and flat (Figs 27, 36), and gently rounded anteriorly to merge into the anterior surface of the snout. In these forms, as previously mentioned, the flat anterior surface of the snout is rounded off at each side and longitudinal ridges are absent. In the second group the frontals are thickened to form a pair of raised bosses from which a system of grooves and ridges radiate (Figs 23, 26). These latter are especially well exposed in acid-prepared specimens. In such specimens it is also clear that a large number of nutrient foramina, not found in the smooth-skull types, penetrate the frontal bosses. The nature of the bone structure here is remarkably similar to that of the anterior expanded portion of the palatine.

The presence of these bosses, ridges and foramina, which are reminiscent of those found on the horn-forming bony tissue of recent mammals, points to the possible existence during life of a fairly thick horny pad covering the frontals, and which perhaps formed a pair of knob-like projections over the bosses. Less well-developed tuberosities are also found on the anterior portions of the parietals and preparietal. There is no such roughening of the skull surface on the nasals or prefrontals, but a curved, transverse frontonasal ridge, referred to above, is present over these bones, separating the dorsal skull roof from the snout, which in these forms slopes down abruptly from the dorsal fronto-parietal portion of the skull roof. The anterior surface of the snout is perfectly straight and flat, but bears a longitudinal median ridge. In contrast to the smoothly rounded skull types, the snout falls away laterally at a sharp angle, so that it presents a square-cut anterior appearance (Fig. 26). Smooth bosses may sometimes be formed by the prefrontals on the anterodorsal borders of the orbits. These are never large in the group with smoothly rounded skull surfaces, but may become prominent in specimens with nasal ridges and sculptured frontal surfaces.

The inner surface of the frontal is extended down as a ventral ledge which makes contact with one of the two dorsally diverging wings of the orbitosphenoid. Anteriorly the ledge becomes a ridge which is continued on to the inner surface of the nasal (Fig. 30), and which, as stated above, appears to have supported a sphenethmoidal commissure. Between the diverging wings of the orbitosphenoid the inner frontal surface is recessed to accommodate the cere-

bral hemispheres. In parasagittal view (Fig. 2) of the sectioned specimen (S.A.M. K.1284) it can be seen that the frontals are continued forward in the median line between the nasals to emerge briefly on the anterior surface of the snout in front of the frontonasal ridge. This unusual condition was not observed in any other specimen.

The *preparietal* (Figs 23, 36) is large and broad, and extends to behind the frontal bosses, where these are present. There is considerable variation in the shape of this element, and while in some specimens it is wide and blunt anteriorly, in others it terminates as a sharp process between the frontals. In those specimens with frontal tuberosities a low boss on the preparietal surrounds the anterior border of the pineal foramen.

The *postfrontal* lies in the posterodorsal corner of the orbit, and extends back between the frontal and postorbital to reach the parietal. In dorsal view (Figs 23, 36) it is a thin splint of bone, but on the ventral surface of the skull roof it is a broad sheet underlying the postorbital.

The *parietals* surround the posterior half of the pineal foramen and each extends forward as a wedge of bone between the preparietal and frontal. In sections (Figs 2, 13) it can be seen that the parietal lies partly in the occiput and meets the dorsal edge of the supraoccipital. These two bones contain between them the canal and gutter described earlier. On the occiput the parietal is completely covered by the thin interparietal. Laterally a sheet of the

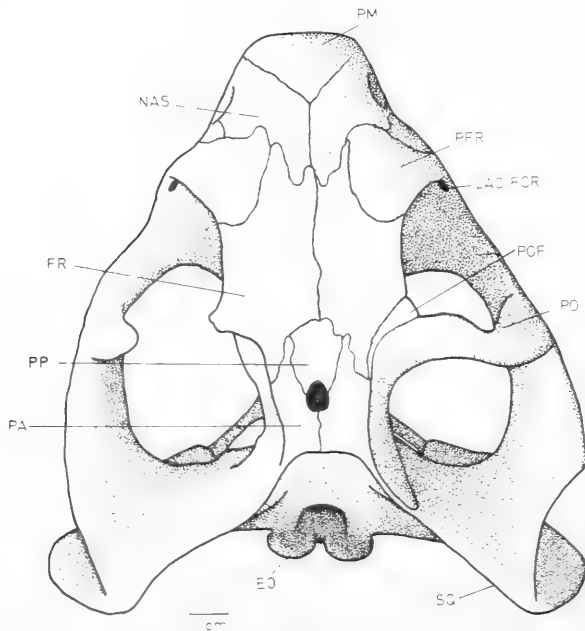


Fig. 36. *Lystrosaurus curvatus*. Nat. Mus. No. C.299. Skull in dorsal view.

parietal descends medially to the postorbital as a lateral wall for the dorsal portions of the brain (Figs 13, 22a). Ventrally this sheet meets the dorsal tip of the epipterygoid.

On the occiput (Figs 13, 37) the *interparietal* covers the parietal, the dorsal half of the supraoccipital and appears briefly in the medial wall of the temporal fossa between the parietal and squamosal (Fig. 13). Laterally it meets the thin *tabular* of each side (Figs 13, 37). The tabular covers the posterior extension of the parietal and posteriorly lies apposed to the squamosal.

Lystrosaurus is characterized by its extremely short temporal fossa, the fossa and orbit being roughly the same size. The zygomatic arch is consequently short and stout relative to skull depth. The *jugal* extends backwards and up from the anteroventral border of the orbit, and lies medially to the squamosal and dorsally to the maxilla in the zygoma. Posteriorly it terminates as a dorsal process which supports the ventral portion of the postorbital.

The *postorbital* curves back posteriorly to form the dorsomedial border of the temporal fossa. Here it overlies the parietal and squamosal and is excavated ventrally to form a deep notch between the skull roof and the descending wing of the parietal. This notch probably served as an attachment point for part of the inner adductor muscle mass. In some of the larger forms of *Lystrosaurus* the postorbital carries a pronounced boss behind the orbit.

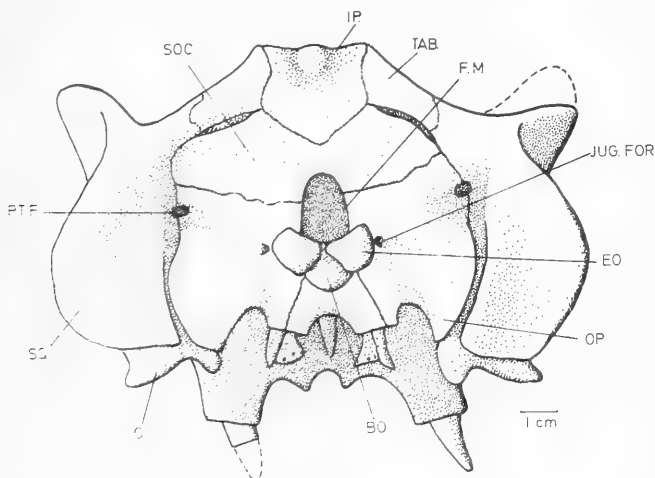


Fig. 37. *Lystrosaurus curvatus*. Nat. Mus. No. C.299. Skull in occipital view.

The squamosal and quadratojugal

The large, triradiate *squamosal* provides attachment areas for the jaw adductor musculature and portions of the neck musculature, and is consequently strongly developed. A ventral flange forms the lateral border of the occiput, lying alongside the supraoccipital and opisthotic and enclosing the

posttemporal fenestra. Ventrally this flange buttresses the quadrate from behind and, above the quadrate, forms the area of origin of a lateral division of the adductor muscle mass (see p. 207). The anterior, zygomatic ramus forms the lateral border of the temporal fossa and terminates below the orbit between the jugal and maxilla. The dorsomedial ramus constitutes the posterior boundary of the temporal fossa and provides attachment for the inner portion of the jaw adductor muscle mass. Within the temporal fossa the squamosal overlaps the supraoccipital and prootic over a small area.

The *quadratojugal* is a fan-shaped bone applied to the anterior face of the lateral squamosal flange (Figs 6, 7, 22a). Ventrally the quadrate is clasped between the squamosal and quadratojugal. The quadratojugal meets the quadrate above the lateral articular condyle, closing off the quadrate foramen.

Sclerotic plates

Although numerous specimens of *Lystrosaurus* were examined in the course of this study, and a great many well-preserved skulls extensively prepared, in only one case were traces of sclerotic plates encountered. In the course of clearing the orbits of S.A.M. K.1402, a series of three sclerotic plates was uncovered in the left orbit, and a similar series of two plates in the right orbit (Fig. 38).

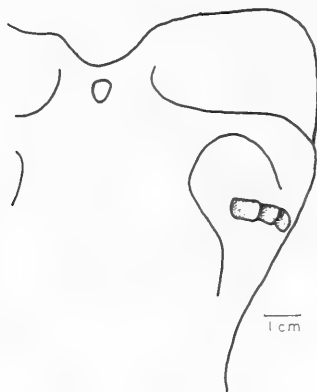


Fig. 38. *Lystrosaurus* sp. S.A.M. No. K.1402. Anterodorsal view of skull showing sclerotic plates.

Huxley (1859) found impressions of sclerotic plates in the type specimen of *Lystrosaurus murrayi*, and believed that not more than four or five plates were present. Among other dicynodonts sclerotic plates have been found in *Dicynodon* by Sollas & Sollas (1916) and Agnew (1959). Among therocephalians these plates are preserved in *Scaloporphinus* and *Zorillodontops* (Cluver, 1969) and in *Ictidosuchops intermedius* (Crompton, 1955).

THE MANDIBLE

The mandible of *Lystrosaurus* conforms closely to the standard dicynodont pattern as described by many authors, including Watson (1948) and Ewer (1961).

The *dentary* is powerfully constructed and, as in the case of several other edentulous dicynodonts, is built up dorsally to the height of the tips of the mandibular teeth of endothiodontids such as *Emydops*. In dorsal view the symphyseal region is square and bounded laterally by two ledges, each ledge being an anterior continuation of the jaw ramus of its side (Fig. 39b). The two ledges, termed dentary tables by Crompton & Hotton (1967), are separated by a rounded, median channel. Each lateral ledge has a slightly concave dorsal surface and is continued forward as a spiny process on the anterior edge of the mentum. On the lateral surface of the symphyseal region are two well-defined grooves (Fig. 39a), leading down and back from the anterior tip of the jaw, and each being bounded anteriorly by a sharp, narrow ridge.

The curved anterior surface of the symphysis, the lateral symphyseal surface, as well as the dorsally situated lateral ledges, are perforated by numerous nutrient foramina, such as are found in bone underlying a layer of horn

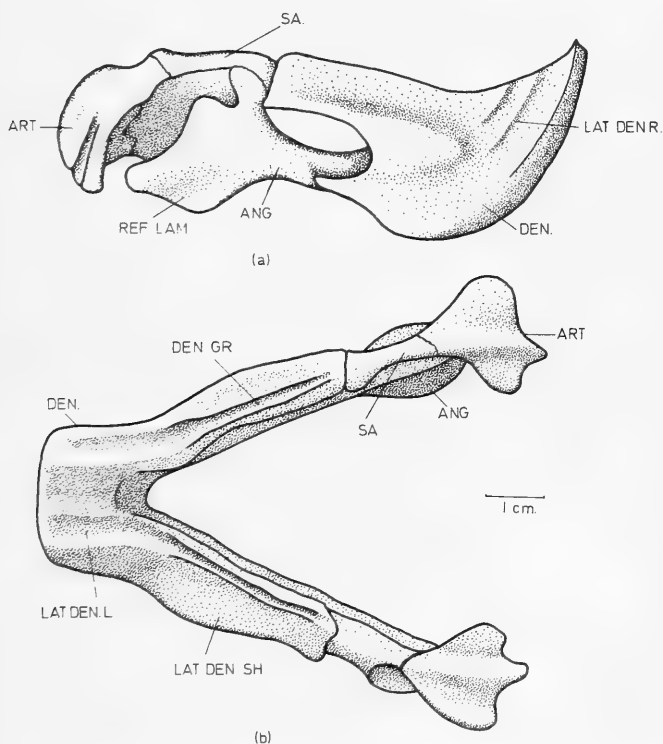


Fig. 39. *Lystrosaurus declivis*. Nat. Mus. No. C.403. Mandible in (a) lateral and (b) dorsal view.

in recent reptiles, and it is safe to conclude that a horny beak covered most of the symphyseal block, with possible pad-like thickenings on the lateral surfaces and the dorsal dentary tables. Anteriorly the beak probably terminated as two sharp lateral processes, separated by a median cleft.

Behind the symphysis each lateral ledge is continued on to the ramus of its side, and the slightly concave dorsal surface of each ledge becomes a deep, thin-walled groove in the dorsal edge of the dentary. This part of the dentary is not perforated by nutrient foramina. Below the groove the dentary is expanded laterally to form a shelf (Fig. 39) lying above the mandibular fenestra.

The *articular* is divided into two condyles, a large lateral condyle and a smaller, thin median condylar shelf, projecting from below the level of the lateral condyle. The lateral condyle is divided into an anterior, concave section and a posterior, convex portion. Below the posterior condylar facet the articular is continued ventrally as a broad retroarticular process (Figs 39a, 40). A lateral recessed area (Fig. 39a) lies between the lateral rim of the articular condyle and the reflected lamina of the *angular*. This recess is continued forward some distance beneath the reflected lamina itself. The articular is similarly undercut beneath the median condyle (Fig. 40). There seems little doubt that both these areas served for attachments of the jaw musculature.

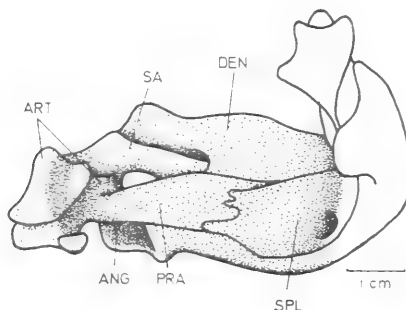


Fig. 40. *Lystrosaurus murrayi*. Nat. Mus. No. C.6457. Inner surface of left ramus of mandible in posterolateral view.

Medially the articular is abruptly truncated, and was clearly continued forward as cartilage into the Meckelian fossa as Meckel's cartilage. A similar condition has been described by Barry (1967) in *Pristerodon*, and Watson (1948) in *Dimetrodon*. The medial border of the Meckelian fossa is formed by the *prearticular*, which posteriorly lies closely apposed to the medial surface of the articular. Anteriorly the prearticular meets the *splenial* (operculum of Van Hoepen, 1913). The *surangular* is of normal dicynodont pattern. As is the case in all other dicynodonts, the coronoid bone is lacking.

SECTION II. THE JAW MUSCULATURE AND MASTICATORY CYCLE IN *LYSTROSAURUS*

THE JAW MUSCULATURE

There is no indication that the changes in skull proportions undergone by *Lystrosaurus* have resulted in a departure from the general composition of the jaw musculature as reconstructed in other dicynodonts by various morphologists. Cox (1959) and Ewer (1961) have discussed the cranial muscles of *Kingoria* and *Daptocephalus* respectively, Watson (1948) has reconstructed those of *Dicynodon*, and Crompton & Hotton (1967) have discussed these muscles and their function in *Emydops* and *Lystrosaurus*.

It is generally accepted that two main groups of jaw muscles found in living reptiles were present in dicynodonts, namely the capiti-mandibularis and pterygoideus groups. In *Lystrosaurus* it is clear that the capiti-mandibularis group was divided into two large adductor muscles, one arising inside the temporal arcade and the other on the lateral flange of the squamosal and posterior part of the zygomatic arch. Crompton & Hotton (1967) call these two muscle masses the *medial* and *lateral external adductor* muscles, terms used by Brock (1938) and equivalent to the capiti-mandibularis superficialis medialis and lateralis of Adams (1919).

In Crompton & Hotton's (1967) reconstruction, the medial adductor arose from the posterior and median borders of the temporal fossa and inserted in the dorsal dentary groove (Fig. 41a). The lateral adductor, which arose from the lateral flange of the squamosal and ventrolateral surface of the zygomatic arch behind the level of the postorbital, inserted on the lateral ledge of the dentary above the mandibular fenestra (Fig. 41b).

Ewer recognized the presence of a temporalis and masseter muscle attaching to the dentary in *Daptocephalus*. In her reconstruction, the temporalis muscle inserted on the lateral shelf and on the rear of the dentary, while the masseter muscle, recognized also by Parrington (1955), inserted on the reflected

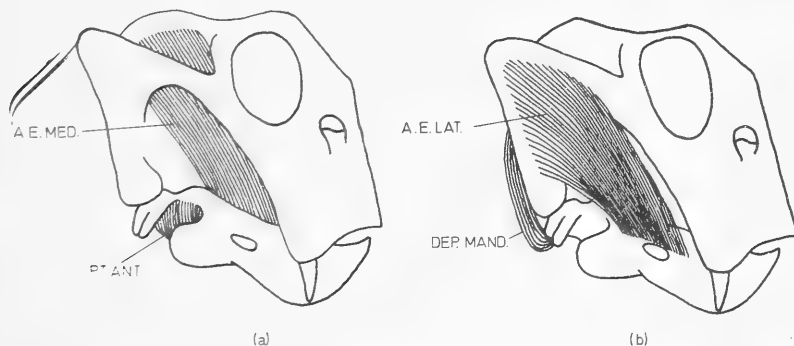


Fig. 41. *Lystrosaurus declivis*. Nat. Mus. No. C.403. Skull in lateral view with (a) adductor externus medialis and pterygoideus anterior and (b) adductor externus lateralis and depressor mandibulae muscles restored.

lamina of the angular. Ewer (1961) supposed that the groove in the dorsal edge of the dentary indicates a posterior extension of the horny beak, and that the two blade-like projections of the beak thus formed would slice food in the mouth against horn-covered tubercles on the palate during the masticatory stroke.

Although such a dentary groove is present in *Lystrosaurus*, no position of the lower jaw exists in which more than only the very anterior portion of the groove is in the vicinity of any horn-covered region of the palate. With the mandible in the most protracted position possible, the deepest portion of the dentary groove lies far posterior to the caniniform process and laterally to the pterygoid. A posterior, double-bladed extension of the horny beak would therefore be useless during the masticatory cycle, and it is far more likely that the inner portion of the adductor mass inserted in the sulcus.

Of interest in this connection is the unusual condition of the dentary in an incompletely preserved *Cistecephalus* zone dicynodont, S.A.M. 6043 (Fig. 42) (Cluver, 1970). This specimen includes an incomplete mandible, which in some respects resembles that of *Kingoria* (Cox, 1959). There is no separate groove in the dorsal edge of the dentary, but the lateral dentary ledge, normally found in dicynodonts, is flared out far laterally and forms the lateral border of a deep fossa, which extends forwards for a short way as a pocket in the dentary. It seems likely that the insertion areas of the entire adductor muscle mass lay in this excavation. The fossa most probably arose by loss of the outer sharp rim of the dentary groove of typical dicynodonts, with consequent merging of the dentary groove with the lateral mandibular shelf. Thus the dorsal edge of the dentary, above the fossa, is a thin sharp plate, similar in all respects to the inner wall of the dentary groove in typical dicynodonts.

The fact that disappearance of the typical dentary groove in this specimen was accompanied by extension of the lateral dentary shelf suggests that the insertion area of the lateral adductor muscle was displaced laterally, so that

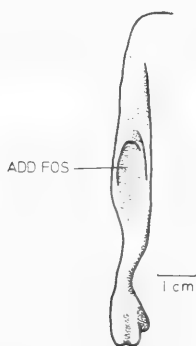


Fig. 42. Dicynodont
sp. S.A.M. No. 6043.
Left ramus of mandible in dorsal view.

accommodation of the inner division of the muscle mass was possible. The condition in this specimen thus indirectly lends weight to the theory that an inner division of the adductor muscle inserted on the dorsal edge of the dentary in typical dicynodonts.

Furthermore, the dentary fossa in S.A.M. 6043 has two main surfaces, a median outward-sloping surface, and a lateral inward-sloping surface. It is conceivable that the lateral external adductor muscle was attached to the lateral surface, and the medial external adductor to the inner surface.

It seems unlikely that a masseter muscle was present in therapsids other than possibly the cynodonts. Barghusen (1968) has maintained that, for functional reasons, a masseter was not present in *Dimetrodon* or primitive therapsids, and possibly arose for the first time in cynodonts. Using data derived from studies by Haines (1934) and Zierler (1961) on muscular extension and contraction, he has shown that in *Dimetrodon* a masseter muscle with the origin and insertion proposed by Watson (1948) and Fox (1964) would be capable of only limited stretch, insufficient to meet the requirements of a reasonable, effective jaw gape. Crompton & Hotton (1967) have similarly maintained that the postulated areas of attachment of such a muscle in dicynodonts are not convincing, and show that the action which would be produced by such a muscle does not conform with the general nature of the dicynodont masticatory cycle.

In this section the external adductor musculature proposed by Crompton & Hotton (1967) has been followed.

In *Lystrosaurus* the *anterior pterygoideus* muscle of the pterygoideus group arose from the lateral surface of the pterygoid and, in the absence of the ectopterygoid, probably also from the posterior pterygoid process of the maxilla, which has taken the position of the ectopterygoid. The direction of the muscle fibres was posterior and ventral, and they passed around the ventral edge of the articular to reach their attachment area in the lateral recess in front of the articular condyle and beneath the reflected lamina (Figs 41a, 43).

In addition to the anterior pterygoideus muscle, a second member of the adductor internus musculature, namely the *posterior pterygoideus* muscle of Parrington (1955) was probably present in *Lystrosaurus*. Arising from the moulded ventral surface of the interpterygoidal plate, and quadrate ramus of the pterygoid, this muscle would have inserted in the excavated area under the median condyle of the mandible (Fig. 43).

Watson (1948) considered that the retroarticular process of therapsids served as an attachment for the pterygoideus musculature and that a depressor mandibulae muscle was absent, the jaw being lowered by other muscles, perhaps the sublingual group. However, Parrington (1955) has convincingly shown that a depressor mandibulae was very likely present in therapsids, and that the retroarticular process of pelycosaurs was retained in later synapsids. Subsequent morphologists have followed Parrington's view, and Barry (1967) showed that in certain Chelonia, where the retroarticular process is very poorly

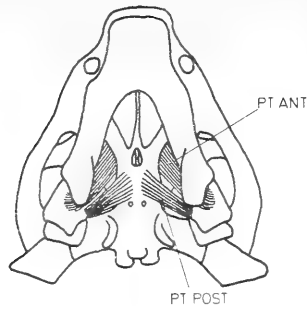


Fig. 43. *Lystrosaurus declivis*. Nat. Mus. No. C.403. Ventral view of skull with pterygoideus anterior and posterior muscles restored.

developed, a strong depressor mandibulae muscle was nevertheless present, so that the small size of the process in dicynodonts need not necessarily be indicative of a weak or non-existent depressor mandibulae muscle. Moreover, it appears that in some endothiodontids, such as a well preserved *Emydops* sp. (S.A.M. 10153) a well-developed, ventrally directed retroarticular process is present.

It may therefore be accepted that the depressor mandibulae muscle in *Lystrosaurus* inserted around the ventral edge of the retroarticular process and found its origin on the lateral squamosal surface of the occiput (Fig. 41b). Cox (1959) and Ewer (1961) have given contrasting areas of origin for this muscle, Ewer suggesting that the origin was low down on the lateral squamosal flange, as in recent reptiles, rather than on the dorsolateral, posteriorly projecting corner of the squamosal, as in Cox's reconstruction of *Kingoria*. The posterior, lateral surface of the lateral squamosal flange above the quadrate does not seem to have served as an attachment area for any of the occipital muscles, and in *Lystrosaurus* the depressor mandibulae very likely originated here, as suggested by Ewer. Thus reconstructed (Figs 41b, 51), the muscle is of considerable length and capable of accommodating fore-and-aft movement of the mandible.

THE MASTICATORY CYCLE

In his study of the Dicynodontia Watson (1948) concluded that the lower jaw of these animals was capable of extensive anterior-posterior displacement, so that from a forward, protracted position where the posterior articular condyle surface lies up against the quadrate, the mandible can be pulled back into a retracted position in which the quadrate lies in the anterior concave facet of the articular condyle. Watson supposed that a back-and-forth propalinal movement of the lower jaw when in the drawn-up position would serve to crush food in the mouth. However, Crompton & Hotton (1967) have shown that only a retractive power stroke could have been useful in mastication of food already in the mouth. Thus the mandibular teeth of *Emydops* are posteriorly

serrated and anteriorly rounded. Furthermore, they show fairly conclusively that the force provided by the anterior pterygoideus muscle, and exerted by the mandibular teeth on the palate during a forward stroke, would have been infinitely smaller than the dislocatory forces at work on the jaw joint. In contrast to this, a very powerful and extremely effective masticatory force was exerted by the external adductor muscles during a retractive stroke.

Crompton & Hotton (1967) have also given an exhaustive functional analysis of the various components of the muscle forces potentially present within the masticatory apparatus of both *Emydops* and *Lystrosaurus* during a typical masticatory cycle. The following description of such a cycle has been largely drawn from their account.

The lower jaw, when drawn up against the palate and retracted so that the quadrate rests in the anterior articular facet, could be lowered by contraction of the depressor mandibulae muscle and, perhaps simultaneously, drawn forwards (protracted) by the pterygoideus muscles. The articular would then eventually come to lie with its posterior articular facet up against the anterior condylar surface of the quadrate (Fig. 44a). At this stage the median condyle of the articular is separated from the inner condyle of the quadrate.

With the mouth now opened to give the greatest possible gape (see p. 232), the external adductor muscles are able to draw the mandible up and back, i.e. they effect both elevation and retraction (Figs 44b, 44c). If the pterygoideus muscles maintained their pull on the posterior part of the mandible, elevation alone would have taken place, and retraction would have started only when these muscles relaxed. As Crompton & Hotton (1967) have pointed out, the anterior tips of the upper and lower beaks in *Lystrosaurus* can approach each other only after a certain amount of retraction has taken place, and it is likely that in *Lystrosaurus* jaw elevation and retraction took place as a single movement. In the first stages of retraction the inner condyle of the lower jaw comes into contact with the median quadratic condyle, but as the jaw moves back, the two surfaces part once more. Retraction ceases when the quadrate slips into the anterior recess of the articular.

Of interest here is that in *Emydops*, where so-called 'beak bite' could take

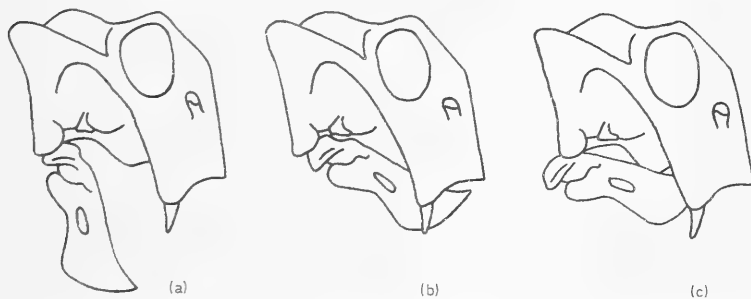


Fig. 44. *Lystrosaurus declivis*. Nat. Mus. No. C.403. Skull in lateral view with mandible in (a) depressed and protracted (b) adducted and (c) retracted positions.

place when the mandible was in the fully protracted position, a third facet on the articular condyle, above the retroarticular process, permitted the quadrate to buttress the mandible while only the vertical component of the external adductors drew the jaw up to give a nip between the upper and lower beaks at the front of the mouth (Crompton & Hotton, 1967). In *Lystrosaurus*, where anterior contact between the upper and lower beaks was not possible, no such facet on the articular is present.

The following account of the relationships between the occlusal surfaces of the upper and lower jaws during jaw elevation and retraction differs in several respects from that given by Crompton & Hotton (1967).

Figures 45, 46 and 47 illustrate a restoration of the upper and lower horny beaks of *Lystrosaurus*, to show the relationships between various pad-like thickenings and cutting edges during the masticatory cycle. As the mandible is drawn up from the protracted, depressed position, the horny pads on the lateral surface of the symphysis move past the sharp, blade-like edge of the palatal rim in front of the caniniform process (Figs 26, 46, 47) in a slicing action. The extensive development of this portion of the palatal rim in all specimens, irrespective of tusk size, indicates the importance of this slicing stage of the masticatory cycle. The pads on the lateral symphyseal surface move up deeper into the recessed palatal dome as retraction begins, with the dorsal edge of the dentary riding against the maxilla in the notch between the caniniform process and the anterior tip of the pterygoid. The degree of intermeshing which takes place between the anterior edges of the mandible and premaxilla as they approach each other at the beginning of retraction depends on the thickness of horn covering the two edges. In the case of *Lystrosaurus* the anterior biting edges on the premaxilla and dentary would have to be extended fairly considerably in horn to be able to meet effectively. The two laterally placed terminal projections of the dentary beak would move back along the palate laterally to the two anterior palatal ridges of the premaxillary palatal rim, drawing food back into the mouth.

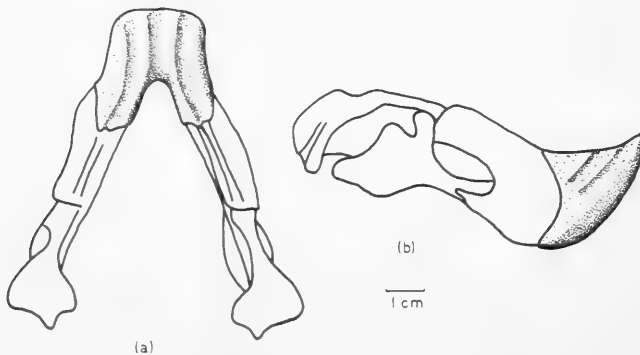


Fig. 45. *Lystrosaurus declivis*. Nat. Mus. No. C. 403. Mandible with restored horny beak in (a) dorsal and (b) lateral view.

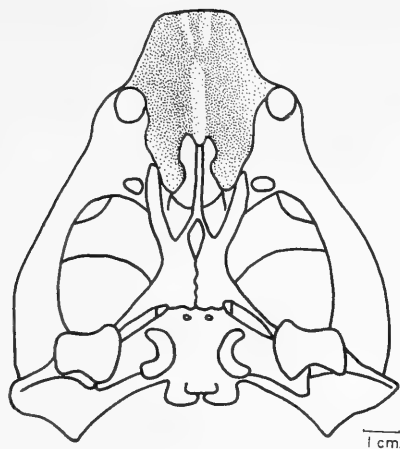


Fig. 46. *Lystrosaurus declivis*. Nat. Mus. No. C.403. Ventral view of skull with horn-covered area on palate restored.

Crompton & Hotton (1967) state that the lower jaw does not approach the dorsal palatal roof during the masticatory cycle, and that the cycle is adapted for slicing only. However, examination of several well-preserved skulls and mandibles (see also Cluver, 1970) has shown that as retraction continues, the lateral horny pads on the lateral symphyseal surface pass behind the caniniform process, and that the pads on the dorsal dentary tables, on each side of the dorsal symphyseal surface (Fig. 45a), move up against the horn-covered areas on the palatines and surrounding portions of the maxilla (Fig. 46). The median palatal ridge of the premaxilla (Fig. 46) now fits neatly into the

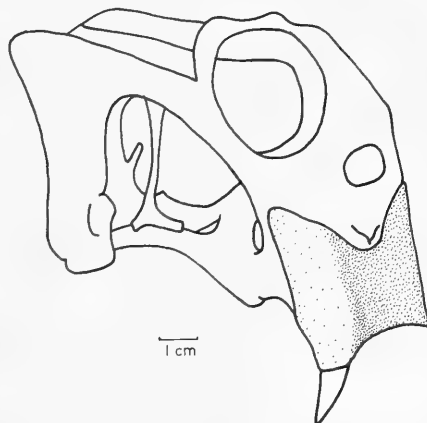


Fig. 47. *Lystrosaurus declivis*. Nat. Mus. No. C.403. Lateral view of skull with horn-covered areas on snout restored.

median groove in the anterior edge of the mentum. At this stage grinding and crushing of the food within the mouth would have taken place, until such time as retraction ceases with the quadrate resting in the anterior recess of the articular condyle. It is interesting to note that in *Lystrosaurus* the horny extension from the palatine on to the maxilla is in the same relative position as the postcanine maxillary teeth of *Emydops*.

The masticatory cycle of *Lystrosaurus* is thus a combination of slicing, which takes place in front of the caniniform processes, and crushing, which takes place in the mouth at the level of the palatal horn layers on the palatine and adjoining maxilla.

SECTION III. THE ATLAS-AXIS COMPLEX AND THE CERVICAL AND OCCIPITAL MUSCULATURE IN *LYSTROSAURUS*

MORPHOLOGY OF THE ATLAS-AXIS COMPLEX

The atlas of *Lystrosaurus* is of the normal therapsid tripartite type, consisting of an intercentrum and two neural arches.

The intercentrum (Fig. 50) is a semicircular, wedge-shaped element, with an anterior concave facet for articulation with the basioccipital, and a posterior facet which meets the odontoid process of the axis. The neural arches (Fig. 48) are well separated in the midline. Each is a complex structure, with the main body of the bone bearing anteromedial and posteromedial articular facets for the exoccipital and odontoid respectively. The body of the bone is extended far laterally and posteriorly as a broad, vertical, wing-like transverse process. Dorsally to this process the bone is narrowed down to a short neck, as is the case in the typical neural arch. Dorsally the arch broadens to provide a proatlantal facet in front and a rudimentary postzygapophysis behind. Laterally to the postzygapophysis the atlas is produced laterally and slightly dorsally

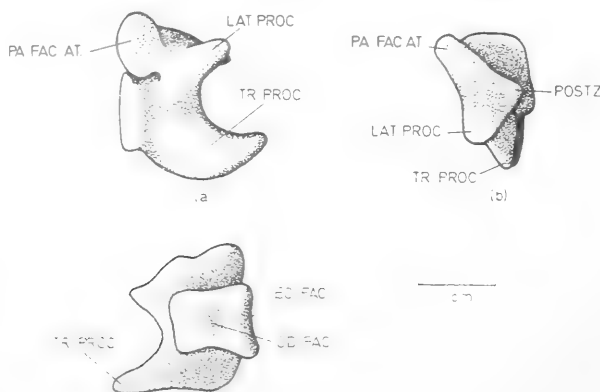


Fig. 48. *Lystrosaurus murrayi*. Nat. Mus. No. C.6457. Atlas neural arch in (a) left lateral (b) dorsal and (c) medial views.

as a short process above the atlantal wing. Between this process (Fig. 48: LAT.PROC.) and the dorsomedial edge of the neural arch a flat shelf is formed.

The *Lystrosaurus* atlas compares well with those which Cox (1959) and Ewer (1961) have described in *Kingoria* and *Daptocephalus* respectively. Cox (1959) has attempted to show that the dorsolateral process on the atlantal arch is homologous with the neural spine of typical vertebrae, and that the neural spine present on the atlas of *Seymouria* (White, 1939) is equivalent to the backwardly-directed spiny process lying laterally to the atlantal postzygapophysis of *Ophiacodon* and *Dimetrodon* (Romer & Price, 1940). Cox also points out that Brink & Kitching (1954) have figured a similar process in *Prorubidgea*, while Brink (1955) has restored a similar spine in *Diademodon*, although Jenkins (1968) states that the neural arch of cynodonts is spineless.

Against Cox's theory it can be pointed out that the new process, lying laterally to the postzygapophysis, is morphologically in a totally different position to that of the neural spine in *Seymouria*, and that there is no spine of any sort in *Captorhinus*, so that there are no known connecting stages illustrating the migration of the spine to its new position. Furthermore, in the primitive pelycosaur *Petrolacosaurus* (Peabody, 1952) again no atlantal spine is found, and Peabody states that the arch is very like that of *Ophiacodon* and *Dimetrodon*, except that there is no process lateral to the postzygapophysis, but '... a longitudinal ridge occurs in the demi-arch ... which suggests incipient development of such a spine' (p. 19). Moreover, certain inferences regarding attachments of the atlas-axis musculature make it unlikely that the process is homologous with the neural spine of *Seymouria*. These inferences will be discussed later.

A pair of curved *proatlas* elements is present in *Lystrosaurus*, each proatlas extending from the facet on the atlantal neural arch to an articular tubercle on the exoccipital alongside the foramen magnum.

The axis in *Lystrosaurus* (Fig. 49) is of fairly typical dicynodont pattern. The prezygapophysis is reduced to the same extent as the postzygapophysis

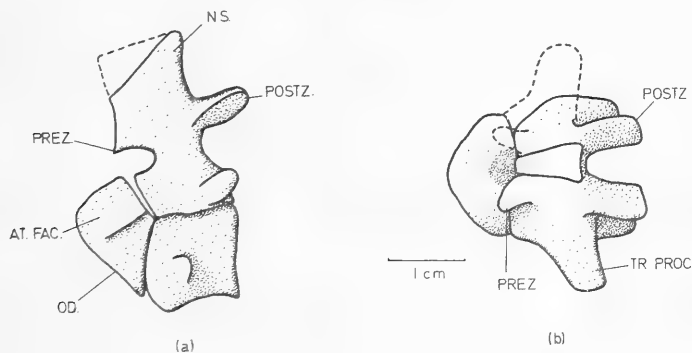


Fig. 49. *Lystrosaurus murrayi*. Nat. Mus. No. C.6457. Axis and odontoid in (a) left lateral and (b) dorsal views.

of the atlantal arch. The odontoid portion of the axis, representing the atlas centrum, is clearly demarcated from the axial centrum by a distinct suture.

THE MUSCULATURE OF THE ATLAS-AXIS COMPLEX AND THE OCCIPUT

Literature dealing with the probable nature of the muscles arising from the atlas-axis complex and inserting on the rear of the skull comprises several sometimes conflicting accounts. Muscle scars are few and indistinct, and uncertainty regarding the proportion of reptilian as opposed to mammalian qualities in the occipito-cervical region makes the problem a vexed one.

Evans (1939) has given a comprehensive review of the occipital and neck muscles in living reptiles and mammals, and has attempted to restore this musculature in fossil reptiles and amphibians. Briefly, three major groups of muscles are present in the cervical region of reptiles and mammals. These are the Iliocostalis system, the Longissimus system and the Transversospinalis system. In mammals the first group loses its insertion on the skull, and is confined to the cervical vertebral series.

The *longissimus capitis* muscle of the longissimus system originates from the prezygapophyses of the cervical vertebrae and inserts on the squamosal and parietal in reptiles and on the mastoid process in mammals. In *Lystrosaurus* this muscle probably inserted on the dorsolateral part of the occiput, beneath the posterior flange of the squamosal (Fig. 51).

The *semispinalis capitis* muscle probably inserted on the occiput below the longissimus capitis muscle. The semispinalis capitis is part of the transversospinalis system, and arises from the transverse processes of the anterior thoracic vertebrae and the postzygapophyses of the cervical vertebrae.

Also belonging to the transversospinalis system are the rectus and obliquus capitis muscles (Fig. 50). In reptiles a *m. rectus capitis posterior (dorsalis) major* arises from the axis neural spine and below it a *m. rectus capitis posterior (dorsalis) minor* may originate from the axis neural spine or the atlantal neural arch. Both muscles insert on the dorsal part of the occiput, near the midline. A *m. rectus capitis lateralis* originates on the transverse process of the atlas and inserts on the occiput. Also in reptiles, a *m. obliquus capitis magnus* originates on the axial neural spine and the dorsal surface of the atlas neural arch, and inserts on the opisthotic occipital surface. A *m. obliquus capitis minor* (Jenkins, 1968), the equivalent of the *m. obliquus capitis inferior* of Evans (1939), originates from the dorsal surface of the axial neural arch and inserts on the atlantal postzygapophysis.

In mammals the organization of the musculature in this region has been considerably altered to accommodate extensive rotation of the now ring-shaped atlas on the odontoid peg of the axis. The obliquus capitis magnus muscle is lost, and an obliquus capitis caudalis muscle (Jenkins, 1968) originates on the axial spine and inserts on the wing of the atlas. An *obliquus capitis cranialis* muscle originates on the wing of the atlas and inserts on the occiput. These

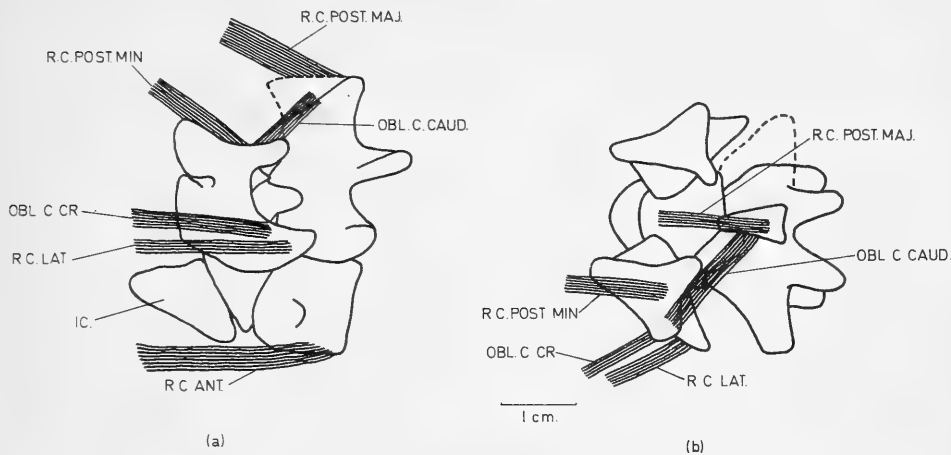


Fig. 50. *Lystrosaurus murrayi*. Nat. Mus. No. C.6457. Atlas-axis complex with restored musculature in (a) lateral and (b) dorsal views.

muscles, which Evans (1939) calls the obliquus capitis superior and inferior, serve respectively for rotation of the atlas about the axis, and extension of the head at the occipito-atlantal joint.

The restoration of the rectus and obliquus capitis muscles in a therapsid such as *Lystrosaurus* is complicated by uncertainty as to the number of 'mammalian' features evolved in the genus, such as, for example, the amount of rotation possible at the atlanto-axial joint. Since the Dicynodontia became a distinct group early in the evolution of the therapsids, and are phylogenetically very distant from the ancestral mammal stock, any so-called mammalian characteristics most probably evolved independently, and should be regarded as parallels to similar qualities in, for example, the cynodonts. Of importance in this connection is the basically reptilian interpretation by Jenkins (1968) of the cynodont atlas-axis complex and the associated musculature.

Cox (1959) has also chosen an essentially reptilian reconstruction of the atlas-axis musculature in the dicynodont *Kingoria*, supposing that the primitive obliquus capitis magnus muscle was present between the axis and occiput. However, Ewer (1961) states that the obliquus capitis magnus muscle was probably not present in any of the therapsids, and that *Daptocephalus* was capable of fairly extensive rotatory movements at the atlanto-axial joint. In *Lystrosaurus*, judging by the rudimentary condition of the pre- and postzygapophyses of the axis and atlas respectively, some degree of rotation did take place at this joint, and since the obliquus capitis magnus muscle would have impeded this motion, it was probably not present, at least not as an important muscle.

Cox (1959) maintained that if the process on the atlantal arch, lateral to the postzygapophysis, is homologous with the neural spine, the m. obliquus capitis minor (inferior of Cox) would have inserted on it, and the m. obliquus capitis superior would have originated on it, since these muscles would origin-

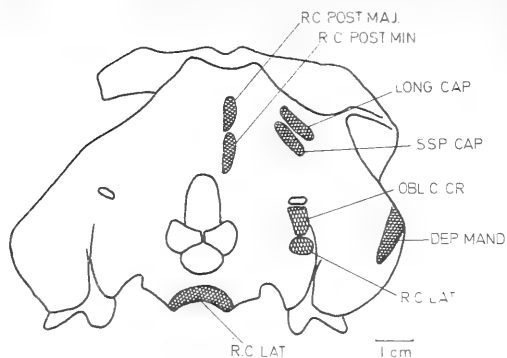


Fig. 51. *Lystrosaurus declivis*. Nat. Mus. No. C.403.
Occipital view of skull showing areas of occipital musculature insertion.

ally have been part of the interspinalis muscles running between successive vertebral spines. Fusion of this atlantal neural spine with the transverse process of the atlas would, according to Cox, produce the mammalian condition, where the obliquus capitis caudalis and cranialis muscles insert and originate on the enlarged atlantal transverse process.

If Cox's theory were correct, signs of this transition would be expected in the atlas-axis complex in cynodonts, since these therapsids are accepted as being closely related to the forms which gave rise to the first mammals. However, the neural arch of the cynodont atlas bears no process equivalent to the spine in *Lystrosaurus* and *Kingoria* (Jenkins, 1968) and the transverse wing retains its primitive vertical position, in contrast to the more horizontal orientation of this process in mammals. Jenkins (1968) has for several reasons preferred to regard the cynodont atlas-axis complex as reptilian, rather than as closely foreshadowing the mammalian condition, as Evans (1939) thought was the case.

Cox's theory is thus further weakened, since as the cynodonts have a primitive transverse process, the neural spine would be expected to be present to provide attachment for the two obliquus capitis muscles. It seems more likely that in the therapsids the m. obliquus capitis caudalis inserted on the dorsal surface of the atlantal neural arch and 'spine', near the postzygapophysis, and that the m. obliquus capitis cranialis originated on the wing-like transverse process, as reconstructed by Ewer (1961). If this view is correct, *Lystrosaurus* had retained a basically reptilian atlanto-axial musculature, with, however, the loss of the m. obliquus capitis magnus. To accomplish more effectively the modest degree of rotation between the atlas and axis, as indicated by the reduced zygapophyseal articulation between the two bones, the atlas developed a process laterally to the postzygapophysis for the insertion of the m. obliquus capitis caudalis. In this way the muscle gained a larger oblique component of force, enabling it to function more effectively as a rotator muscle. However, this mechanism was still much less effective than the mammalian condition, where

the m. obliquus capitis caudalis is inserted on the enlarged and posteriorly directed atlantal wing, and runs in a dorsoventral direction, rather than the posterodorsal-anterioventral direction of dicynodonts.

By this analysis the 'atlas spine' of Cox may be termed simply the dorsal process of the atlas, which, together with the necessity for rotating the atlas about the axis, probably arose in therapsids to accommodate the lateral migration of the insertion of the m. obliquus capitis caudalis from its original position on the postzygapophysis of the atlas (where the equivalent muscle in recent reptiles is still inserted).

The large, vertically orientated atlantal wing of *Lystrosaurus* suggests that it provided a relatively large surface of origin for muscles running anteriorly and laterally. This surface is directed at the region of the occiput below the posttemporal fenestra. The m. obliquus capitis cranialis (Figs 50, 51) arose on the atlantal wing and would very likely have inserted on the opisthotic below the posttemporal fenestra. This region in *Lystrosaurus* is depressed over a fairly large area. The m. rectus capitis lateralis, also arising from the atlantal wing, would have inserted below the m. obliquus capitis cranialis. These two insertion areas are similar to those suggested for these muscles by Ewer (1961) in *Daptocephalus*, and for the m. obliquus capitis magnus by Cox (1959).

The restoration of the rectus capitis muscles (Figs 50, 51) poses fewer problems. A m. rectus capitis anterior (ventralis) would have arisen from the ventral surfaces of the centra of the atlas and axis, and inserted on the base of the skull, in *Lystrosaurus* probably also on the rear of the intertuberal ridge. The m. rectus capitis posterior (dorsalis) was probably divided into minor and major components. The latter arose from the axis neural spine and inserted dorsally on the occiput near the midline. The former muscle probably found its origin on the flat dorsal surface of the atlas behind the articulation between atlas and proatlas, inside the insertion of the m. obliquus capitis caudalis on the dorsal process of the atlas. This muscle, passing dorsally over the curved proatlas, inserted on the occiput below the m. rectus capitis posterior major. These areas of origin and insertion are similar to those proposed by Ewer (1961), although Ewer found indications of a rectus capitis posterior medius having separated from the major component on the axis spine.

Thus reconstructed, the occipital and cervical osteology and musculature of *Lystrosaurus* represent a modified reptilian pattern rather than a primitive mammalian one. Departure from the typical reptilian condition is seen in the loss of the obliquus capitis magnus muscle and the incipient rotation between atlas and axis, with accompanying reduction in the zygapophyseal articulation.

These changes are probably correlated with the characteristic morphology of the lystrosaurian occipital condyles, where the basioccipital has receded below the posteriorly projecting exoccipital condyles. This modification of the typical reptilian condition, where the condyle is a single rounded process, is not confined to *Lystrosaurus* among dicynodonts (Olson, 1944), and suggests that rotation at the occipito-atlantal joint was reduced. Probably concomitant

with the changes taking place at this joint was the reduction of the zygapophyseal articulation between atlas and axis, with consequent changes in the atlanto-axial musculature.

Because of the many uncertain factors involved, the above reconstruction is naturally far from conclusive, but, as it stands, it does account for all the individual muscles which are generally supposed to have been present in this region in therapsids, and provides an explanation for the several osteological innovations.

SECTION IV. THE EVOLUTIONARY SEQUENCE LEADING TO THE *LYSTROSAURUS* GRADE OF DICYNODONT DEVELOPMENT

In previous sections several references have been made to the way in which the characteristic skull form of *Lystrosaurus* differs from that of earlier, Permian dicynodonts. In this section, differences in morphology between a typical *Lystrosaurus* skull and that of typical, earlier dicynodonts will be used as a basis for an attempted comprehensive explanation, in terms of functional anatomy, for the changes within the evolutionary sequence which culminated in *Lystrosaurus*.

At this point *Lystrosaurus* is considered purely as a stage in dicynodont evolution advanced over the typical Permian stage. In a later section the relationships of *Lystrosaurus* to other Triassic groups of dicynodonts, and its origin from a Permian ancestor, will be discussed.

In this section illustrations comparing *Lystrosaurus* with earlier dicynodonts are based on the following specimens:

Lystrosaurus declivis

S.A.M. K. 1284 Sectioned skull & mandible

Nat. Mus. C. 403 Skull & mandible

Emydops sp.

B.P.I. 2642 Skull & mandible

Dicynodon sp.

S.A.M. 8784 Skull & mandible

Two skull measurements were used as constants in the illustrations. Generally, skulls were compared with skull lengths over the reference plane (see Material and techniques) brought to a constant, but in some cases, where it was thought necessary to use a measurement unlikely to have been affected by the adaptive changes in the *Lystrosaurus* skull, the interquadrate length, being the distance between the outer edges of the lateral quadratic condyles, was used.

In comparisons involving the jaw adductor musculature, a line representing the axis of the lower jaw has been selected. This is the line connecting the anterior tip of the dentary with the point of contact between the articular and quadrate.

COMPARISON OF THE SKULLS OF *LYSTROSAURUS* AND TYPICAL PERMIAN DICYNODONTS

Depth of skull

In both lateral and parasagittal view it is apparent that, when compared with earlier dicynodonts, the skull in *Lystrosaurus* has become deeper overall. When the skulls are brought to the same basic length (Fig. 52) this effect is accentuated, since *Lystrosaurus* has also undergone shortening of the basicranial axis. In Figure 53, however, the skulls of *Lystrosaurus* and *Dicynodon* have been drawn to the same interquadrate length. Here it is clear that the skull roof in *Lystrosaurus* is higher than in *Dicynodon*, and that the *Lystrosaurus* snout is produced farther ventrally. The mandible in *Lystrosaurus* thus lies at a greater angle to the reference plane of the skull than in other dicynodonts.

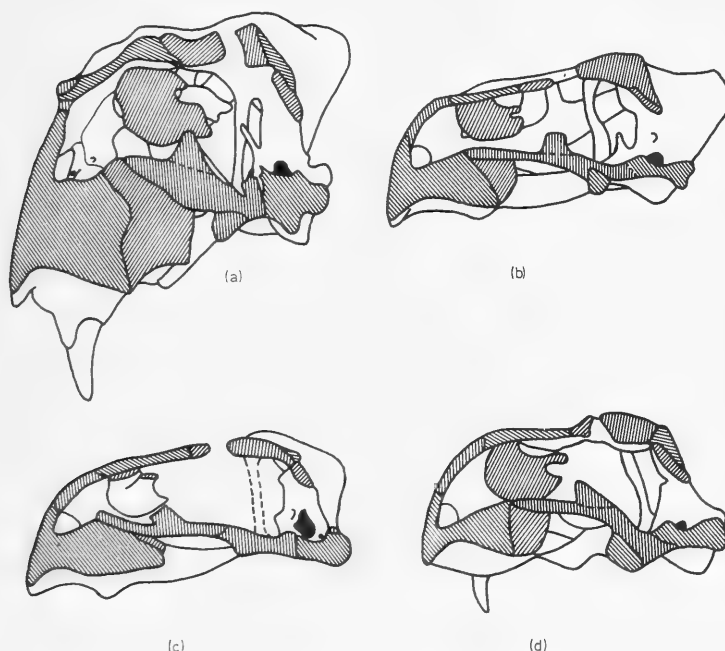


Fig. 52. Comparison of the skull of *Lystrosaurus* with those of Permian dicynodonts. (a) *Lystrosaurus declivis*, S.A.M. No. K.1284; (b) *Dicynodon* sp. S.A.M. No. 10081; (c) *Dicynodon grimbeeki* (after Camp & Welles, 1956); (d) *Dicynodon* sp (after Boonstra, 1968).

The deepening of the snout below the level of the basicranial axis is in effect a lowering of the palate and feeding plane. As can be seen in Figures 52 and 53, this deepening has taken place below the level of the nostril, the position of which, in both *Lystrosaurus* and *Dicynodon*, remains on a more or less constant level in relation to the basicranial axis. In consequence, the premaxilla in *Lystrosaurus* is greatly enlarged and deepened, and the vomer now forms a deep

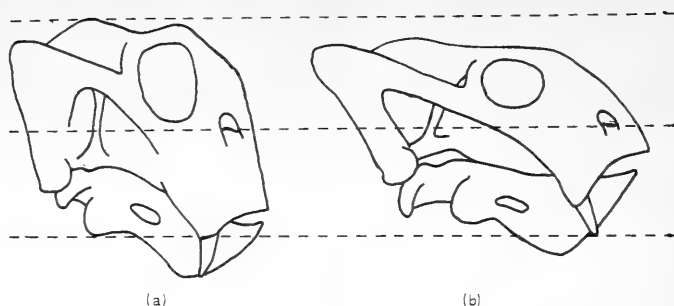


Fig. 53. Comparison of the skull of *Lystrosaurus* with that of a Permian dicynodont. (a) *Lystrosaurus declivis*, Nat. Mus. No. C.403; (b) *Dicynodon* sp., S.A.M. No. 8784.

septum. The deepest part of the skull is at the level of the canine tusks and the vomer-premaxilla suture.

The very deep snout and enlarged premaxilla have necessitated a new orientation of the nasal passages (Fig. 54). In typical dicynodonts the palatal plate of the premaxilla is thin and horizontally disposed, and the respiratory passages lie in an anteroposterior direction, with the choanae only slightly below the level of the nostril. In *Lystrosaurus* the premaxilla is enormously thickened below the nasal aperture, thus displacing the internal nares far ventrally. The direction of the respiratory passages thus became dorsoventral rather than anteroposterior. Furthermore, a choanal tube leading from the nasal capsule to the internal nares, such as was suggested for the *Gorgonopsia* by Kemp (1969a), would, in comparison with other dicynodonts, have been considerably elongated in *Lystrosaurus*.

The remainder of the skull has not followed the deepening of the snout to the same extent, with the result that the palate of *Lystrosaurus* is divided into two planes which meet at an angle at the level of the caniniform processes. The

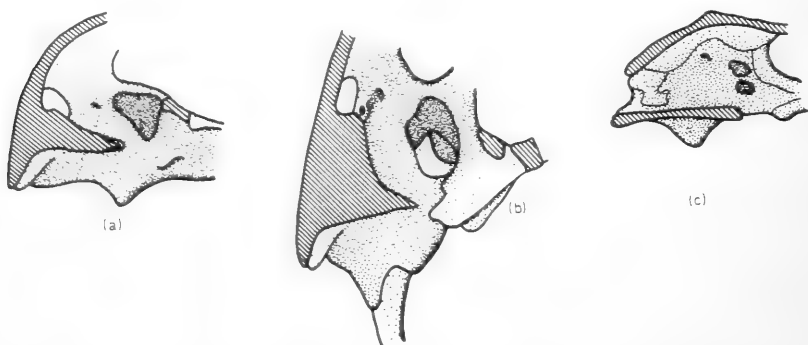


Fig. 54. Comparison of the snout of *Lystrosaurus* with that of Permian dicynodonts. Parasagittal views of (a) *Dicynodon* sp., S.A.M. No. 10081 (from serial sections); (b) *Lystrosaurus declivis*, S.A.M. No. K.1284 (from serial sections); (c) *Kingoria nowacki* (after Cox, 1959).

anterior plane is formed by the palatal surface of the premaxilla and slopes up and forwards. The plane of the choana, which is formed by the ventral surfaces of the palatines and pterygoids, posteriorly slopes up and backwards (Figs 2, 52, 54). With the skull held parallel to the reference plane, the choana faces backwards and down rather than purely ventrally as in more primitive dicynodonts.

Shortening within the skull

Watson (1912) recognized that the characteristic skull form of *Lystrosaurus* was achieved, at least in part, by shortening of the skull, instead of downturning of the face on the rest of the skull, and stated that in this way the animal retained lengthened temporal muscles, enabling it to swing back its shortened jaw through practically 90°.

Again in lateral and parasagittal view, it is immediately seen that considerable shortening of the skull has taken place in *Lystrosaurus* in comparison with other, earlier dicynodonts. The postpineal region of the skull roof and the temporal fossae are much shorter than in other dicynodonts, and sectioning reveals that the basicranial axis, including basioccipital, basisphenoid and parasphenoid, is greatly reduced in length. Thus in Figure 52 the presphenoid in both *Dicynodon grimbeeki* and the S.A.M. dicynodont lies well in advance of the internal openings of the internal carotid arteries in the hypophyseal region. In *Lystrosaurus* on the other hand, the presphenoid lies immediately anterior to the carotid artery canals and hypophyseal region, and above the interpterygoid suture. Similarly, the orbitosphenoid in *Lystrosaurus* lies just anterior to the parietal foramen and internal carotid canal and directly above the presphenoid, whereas in *Dicynodon* and *Emydops* this ossification is situated far forward in the skull.

The shortening of the basicranial axis has brought about changes in the hypophyseal region. In typical dicynodonts the sella turcica is shallow and extends some way back from the internal openings of the carotid canals. In two mechanically prepared braincases of *Cistecephalus* zone dicynodonts, S.A.M. 5600 and 11075 (Fig. 55a) the sella turcica is relatively deep and there is a dorsum sellae formed by the basioccipital. In *Lystrosaurus* (Fig. 55b) on the other hand, there is no impression on the basisphenoidal floor of the braincase behind the internal carotid canal. Furthermore, shortening of the basicranial axis has resulted in compression of the hypophyseal region as a whole, so that the internal carotid canals open into the braincase just anterior to the pilae antoticae of the prootics. If the hypophysis filled the sella turcica in *Dicynodon*, as it seems to have done, and if the relative size of the hypophysis is the same in *Lystrosaurus* and *Dicynodon*, then the hypophysis of *Lystrosaurus* could not have maintained the relationships with the braincase which were present in *Dicynodon*. Either the hypophysis extended far dorsally and retained a very small area of contact with the basisphenoid, or it was partially contained in the basicranial pit (Figs 2, 12, 55) between the basisphenoid and basioccipital. This pocket, which

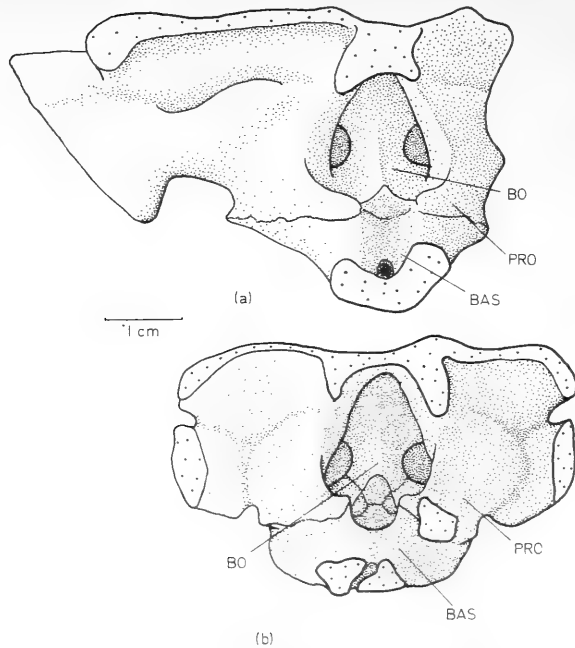


Fig. 55. Comparison of the hypophyseal region of *Lystrosaurus* and a Permian dicynodont. (a) Dicynodont sp., S.A.M. No. 5600; (b) *Lystrosaurus* sp., S.A.M. No. 11180. Anterodorsal views.

is continued ventrally as an unossified zone, is a constant feature in *Lystrosaurus*, and its shape strongly suggests that it housed a soft body of some kind. If the pit did indeed house a portion of the hypophysis, the basioccipital would have formed a dorsum sellae.

Boonstra (1968), however, suggested that in his sectioned *Dicynodon* the sella turcica (and therefore the hypophysis) was small. If this were so in *Lystrosaurus*, and the hypophysis did not reach back to the basicranial pit, then the basisphenoid would have formed a floor for the body behind the internal carotid opening. In this case no distinct sella turcica was present in *Lystrosaurus*.

In ventral view the shortening of the skull has caused the changes in the pterygoid region illustrated in Figure 56. When the skulls of *Emydops* and *Lystrosaurus* are brought to the same basal length, it can be seen that the choana, including the interpterygoid fossa or vacuity of *Lystrosaurus* is slightly shorter than in *Emydops* (*Lystrosaurus* 32·6% of basal length, *Emydops* 36·7% of basal length). The chief difference between the two types in this region is, however, the structure of the interpterygoid vacuity and the position of the parasphenoid and vomer. In the endothiodontid genera *Emydops* and *Palemydops* the posterior portion of the relatively broad median plate of the vomer is recessed into the choana and lies far above the level of the ventral pterygoid and palatine border of the choana. The interpterygoid vacuity is wide and extends far

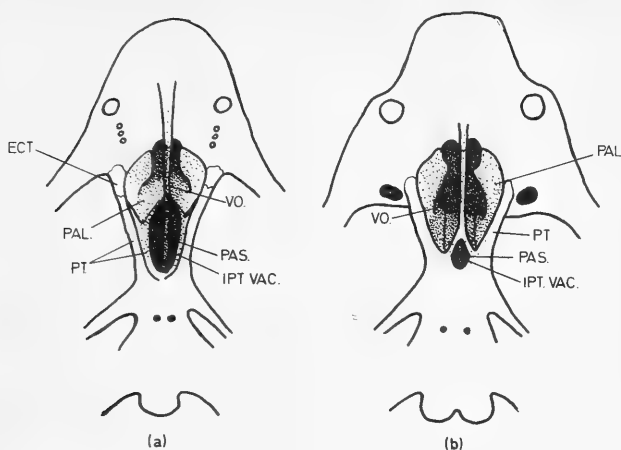


Fig. 56. Comparisons of palates of (a) *Emydops* sp., B.P.I. No. 2642; (b) *Lystrosaurus declivis* Nat. Mus. No. C. 403.

forward, terminating between two posteriorly diverging plates of the vomer, which lie medially to the anterior flanges of the pterygoids. This condition is similar to that found in *Dicynodon grimbeeki* (Agnew, 1959). Dorsally to the interpterygoidal vacuity runs the parasphenoidal rostrum, visible in ventral view as a broad bar forming an incomplete roof for the interpterygoidal vacuity.

In *Lystrosaurus* the entire palate has migrated ventrally to accompany to some extent the downgrowth of the snout. This ventral migration is more pronounced anteriorly than posteriorly, so that the plane of the choana (see above) lies at an angle to the premaxillary palatal surface. The vomer, accompanying the pterygoids and palatines, has become a thin vertical sheet of bone, lying approximately in the same plane as the lateral borders of the internal nares. Furthermore, with reduction in the length of the basicranial axis, the interpterygoidal vacuity has become a shortened and lanceolate fossa, clearly demarcated by the vomers in front and the interpterygoidal plate behind. In ventral view the interpterygoidal fossa has therefore become distinct and well separated from the internal nares.

According to Cruickshank (1967) the 'interpterygoidal space' of *Lystrosaurus* is retained as a typical feature in later Triassic dicynodonts such as *Tetragonias* and *Kannemeyeria*, this being one of the factors which led him to believe that a species of *Lystrosaurus* might have given rise to these later dicynodont groups. In a further (1968) publication dealing with this region in dicynodonts, he maintained that Triassic dicynodonts, with the *Lystrosaurus* type of interpterygoidal vacuity, can be separated from their Permian predecessors by comparison of the length of the interpterygoidal vacuity relative to the length of the internal nares. He found that in Permian dicynodonts the length of the vacuity was always greater than 60% of the internal nares, while in Triassic forms it was always less than 60%. The possible significance of these

points will be more fully discussed at a later stage.

Together with these changes in the *Lystrosaurus* palate, the parasphenoidal rostrum has lifted above the dorsal opening of the interpterygoidal fossa to extend dorsally as a pair of thin vertical sheets of bone closely surrounding the presphenoid. In lateral view a fenestra is visible between the dorsal border of the pterygoid and the ventral edge of the parasphenoid.

In spite of the deepening of the parasphenoid and vomer, and the shortening that has taken place in this region, the basic relationships between the two bones in Permian dicynodonts are still maintained in *Lystrosaurus*, and the parasphenoid rostrum is clasped between the diverging wings of the vomer in the same way as in *Pristerodon* (Barry, 1967) and other dicynodonts (Fig. 52). However, in *Lystrosaurus* the line of contact in the median plane between vomer and parasphenoid is at an angle of approximately 40° to the reference plane of the skull, whereas in typical dicynodonts the line of contact is parallel to the reference plane.

Relationships of the brain

In Figure 57 the endocranial casts of a Permian dicynodont and of *Lystrosaurus*, reconstructed from serial sections, have been compared. Olson (1944) and Boonstra (1968) have figured similar endocranial casts.

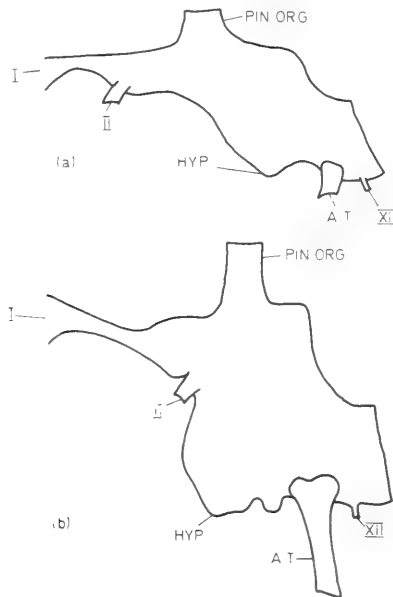


Fig. 57. Comparison of endocranial cast of (a) *Dicynodon* sp., S.A.M. No. 10081 (from serial sections); (b) *Lystrosaurus declivis*, S.A.M. K1284 (from serial sections.)

In typical dicynodonts the brain appears to have filled the posterior portions of the braincase and, in front of the prootics, extended up to the pineal foramen and down to the sella turcica. Anterior to this the cerebral hemispheres were supported by the lateral flanges of the orbitosphenoid, and the olfactory tracts extended far forwards on each side of the mesethmoidal septum. In an endothiodontid such as *Emydops* the brain lay more or less horizontally from medulla oblongata to the cerebral hemispheres. In *Lystrosaurus* the deep, shortened skull necessitated a dorsoventral expansion of the brain in front of the prootics, reaching the pineal organ dorsally and the hypophysis ventrally. Anterior to this the new, relatively dorsal position of the orbitosphenoid and its proximity to the pineal organ indicates that the cerebral hemispheres were located far dorsally in relation to the medulla oblongata, and relatively closer to the hypophysis-pineal organ plane. The brain thus assumed an S-shape, and was higher than it was long. This S-shape is also apparent in Edinger's (1955) illustration of a *Lystrosaurus* endocranial cast.

The adductor musculature

As a result of the changes in proportion undergone by the skull, the external adductor musculature in *Lystrosaurus* underwent changes which produced a new distribution of forces during the masticatory cycle. Crompton & Hotton (1967) have stated that there is no difference in the angle of pull of the adductor muscles on the mandibular axis in *Emydops* and *Lystrosaurus*, but all the specimens at my disposal indicate that in *Lystrosaurus* there was an increased vertical component of force during the masticatory cycle. In Figure 58 lateral views of *Emydops*, *Dicynodon* and *Lystrosaurus* are illustrated, in each case with the mandible in the adducted position. Alongside each skull is a reconstruction of the external adductor muscle masses as they would have appeared with the mandible in this position. It is immediately clear that the average angle of pull by the adductors on the jaw axis becomes progressively more vertical in the series *Emydops*—*Dicynodon*—*Lystrosaurus*. Comparison between several specimens of *Lystrosaurus* shows that within the genus the average angle of pull remains virtually constant.

The condition in *Dicynodon* may be explained fairly simply by reference to Figures 58 and 59. In Figure 58 the skulls of *Emydops*, *Dicynodon* and *Lystrosaurus* have been brought to the same basal length, and it can be seen that in comparison with *Emydops* the *Dicynodon* skull has been slightly deepened overall below the reference plane, the mandible being consequently ventrally displaced. Any such displacement would automatically result in an increased vertical angle of pull by the adductor muscles. Thus in Figure 59 the average angle at A is 18°, as compared with 25° at A₁.

In *Lystrosaurus* (Fig. 58) the skull has deepened to an even greater extent below the reference line. The quadrate is relatively lower than in *Emydops* or *Dicynodon*, and the snout has dropped ventrally to a considerable extent. The lowering of the anterior palatal region would theoretically increase the oblique

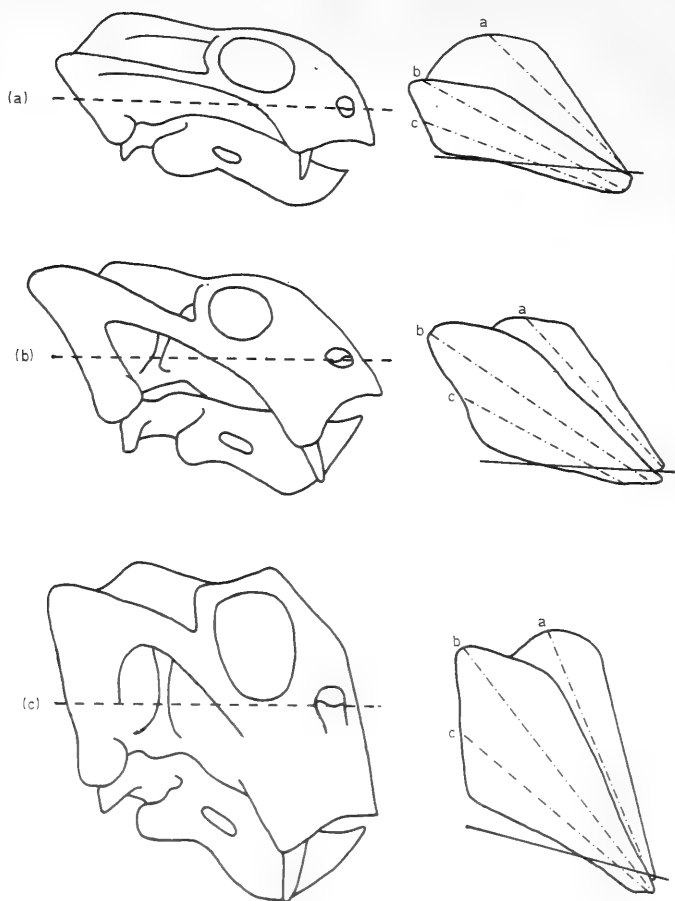


Fig. 58. Comparison of skull and adductor musculatures of (a) *Emydops*, (b) *Dicynodon* and (c) *Lystrosaurus*.

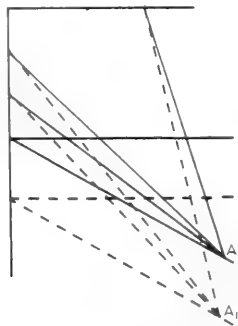


Fig. 59. Schematic representation of the effect on the adductor musculature of simple lowering of the jaw axis.

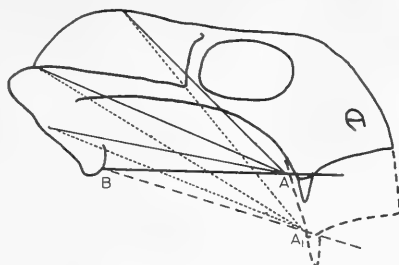


Fig. 60. Schematic representation of the effect on the jaw adductor musculature of snout deepening in *Emydops*.

component of force on the dentary when the jaw approaches the adducted position.

In Figure 60 the skull of *Emydops* is illustrated, with three hypothetical lines of force exerted by the external adductor muscle on an anterior hypothetical point, A, on the jaw axis BA. If the snout is produced ventrally, rotating the jaw axis 15° and without any shortening or deepening of the orbitotemporal region taking place, then the average angle of pull by the adductor muscles at point A on the axis decreases from 25° to 17° , and the vertical component of force exerted during jaw elevation is considerably decreased, while the horizontal component, responsible for retraction, is proportionally increased. If it were necessary for the animal to preserve a minimum vertical component in the total external adductor force in order to ensure a certain minimum amount of pressure from the mandible against the palate, then it is conceivable that shortening of the posterior moiety of the skull could take place to compensate for the lowering of the palate. In Figure 61 the effect of lowering the palate

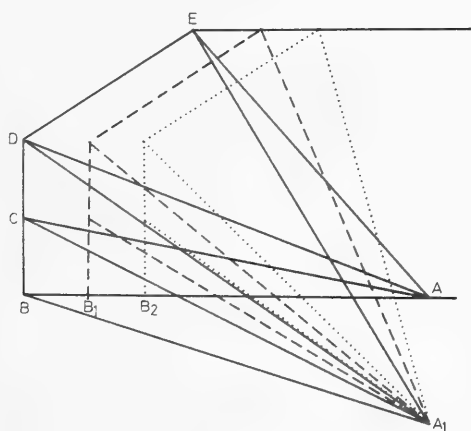


Fig. 61. Schematic representation of the effect on the dicynodont jaw adductor musculature of snout deepening (A—A₁) and skull shortening (B—B₂).

from A to A_1 is diagrammatically illustrated, as well as how shortening of the posterior half of the skull in the sequence $B-B_1-B_2$ compensates for this effect. If A is dropped to A_1 , the average angle (26°) of CA, DA and EA on the jaw axis BA changes to a value of 23° at A_1 on the line BA_1 . There is thus a considerable change in the position of A, but a small change in the average angle of pull on the jaw axis.

If B migrates to B_1 the average angle at A_1 becomes 25° , while if B_1 moves to B_2 the angle becomes 26° . It is therefore clear that a substantial forward migration of B is necessary to cancel the 3° difference in the angle of pull caused by dropping A to A_1 . In terms of skull morphology this means that a substantial lowering of the snout produces a small increase in the oblique component of the external adductor musculature, which in turn can be compensated for only by a fairly substantial forward migration of the posterior areas of adductor muscle attachment (Fig. 62).

However, if forward migration of the posterior areas of attachment of these adductor muscles involves a forward displacement of the quadrate (as indicated in Figure 62), the jaw axis would undergo a series of new orientations, which could be compensated for only by an increase in the height of the muscle attachment areas. This skull deepening would assist in producing the original angle of pull by the adductors on the mandibular axis, but would considerably increase their length. This lengthening effect is shown in Figure 62, where simple dropping of the snout results in an average increase of 20% in the muscle length. If shortening of the temporal region takes place, the average length of the muscle fibres returns to the original value, but now the distribution of long and short fibres is changed. Thus, in the primary stage of Figure 62, before lowering of the palate or skull shortening took place, the posterior, more oblique fibres were longer than the anterior, more vertical fibres. After lowering of the palate and skull shortening, precisely the reverse is the case.

The characteristic skull proportions of *Lystrosaurus* were arrived at by deepening of the snout, and lowering of the anterior palatal region, and shortening and deepening of the temporal region. Combinations of the various effects on

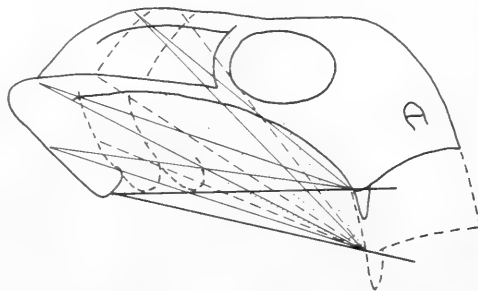


Fig. 62. Schematic representation of the effect on the jaw adductor musculature of snout deepening and skull shortening in *Emydops*.

the adductor musculature in the above hypothetical cases of skull shortening, skull deepening, etc., should therefore be found to apply to *Lystrosaurus*.

Simple shortening of the skull in *Lystrosaurus* would help to compensate for deepening of the snout, and, together with deepening of the posterior part of the skull, would return the average angle of pull by the adductor muscles on the dentary to the original value. However, as shown above, additional deepening of the postorbital region of the skull resulted in an increased vertical component in the adductor mass.

The distribution of long and short fibres in the external adductor muscles in *Lystrosaurus* and *Emydops* has been illustrated in Figure 63, where the mandibles have been drawn to the same length. With the jaw in the adducted position, it is apparent that in *Lystrosaurus* the more anterior muscle fibres, which exert a more vertical pull on the mandibular axis, have become lengthened in comparison with the same fibres in *Emydops*. Analysis of the adductor muscle reconstructions in Figure 58 shows that in *Lystrosaurus* the most oblique fibres, represented by the line c, are shorter than the most vertical fibres, represented by line a. In *Dicynodon* and *Emydops* these two sets of fibres are of approximately the same length. In *Lystrosaurus*, therefore, the longest fibres of the adductor muscles exert force on the dentary at a greater angle than in *Dicynodon* or *Emydops*.

Using these anatomical and functional comparisons, it should be possible to arrive at a logical evolutionary sequence of events leading from some ancestral Permian dicynodont form to a typical species of *Lystrosaurus*.

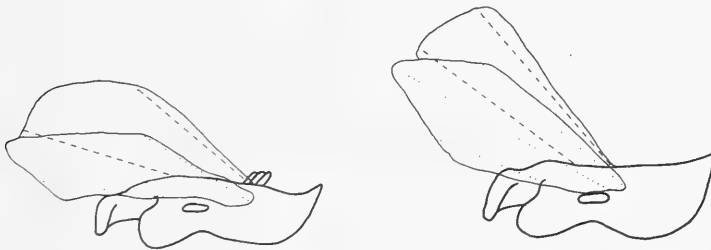


Fig. 63. Comparison of long and short fibres of the jaw adductor musculature of *Emydops* and *Lystrosaurus* with jaws in adducted position.

DERIVATION OF THE *LYSTROSAURUS* SKULL PROPORTIONS

It is generally accepted that *Lystrosaurus* led an aquatic or semi-aquatic mode of life, and incomplete ossification of the tarsalia and the retention of embryonic cartilage between the elements of the neurocranium can be regarded as indications of this. Watson (1912) reconstructed *Lystrosaurus* as a creature capable of strong swimming action, on the grounds that the extended ischium provided attachment for strong and extensive ischio-femoral muscles, and considered that the shallow lower part of the pelvis indicates that the animal did not

require strong adductor muscles to support the weight of its body. Flexibility of the vertebral column also suggests arching of the back during the stroke of the hind limb.

Furthermore, it seems most probable that the characteristic skull form of *Lystrosaurus* was arrived at primarily in response to a need for lowering the feeding level of the skull deeper into the aquatic medium. Since the type of masticatory cycle found in *Lystrosaurus* is essentially similar to that found in earlier dicynodonts such as *Dicynodon feliceps* (Crompton & Hotton, 1967) this change was probably not related to an entirely new diet, but rather to the changed accessibility of a semi-submerged food source.

This primary impetus in the evolution of *Lystrosaurus* resulted in snout deepening, which took place below the level of the nasal aperture and chiefly involved the premaxilla, maxilla and vomer. In this way the premaxillary portion of the palate was produced far ventrally, with the deepest portion of the skull being at the level of the caniniform process. With the condyle-nostril plane of the skull horizontally aligned, the portion of the premaxillary palate anterior to the caniniform process faces antero-ventrally, while the choana, behind the caniniform process, faces posteroventrally. The nasal capsules became modified to allow a new orientation for the nasal passages, which in *Lystrosaurus* ran vertically from the nasal aperture to the choana.

However, any tendency for such lowering of the feeding plane would have two immediate results. First, the mandible, when adducted, would lie at an angle to the reference plane of the skull, in a position equivalent to incomplete adduction in *Emydops*. In the second place the angle of pull by the external adductor muscles on the jaw axis would become smaller, i.e. the direction of pull would become more oblique. The consequence would be a reduction in the arc through which the mandible could be rotated during the masticatory cycle, that is, the mandible would have been capable of providing a very limited gape only.

This is because there is a maximum possible gape in dicynodonts, reached when the external adductor muscles start exerting pull through and behind the quadrate-articular contact (Fig. 64). The extent of the gape is determined by the origin and insertion of the various fibres of the external adductors. In the masticatory cycle the jaw could be swung down by the depressor mandibulae muscle until the extended fibres of the posterior part of the adductor muscles came close to the quadrate-articular contact, and thus began to lose their efficiency as jaw elevators. If the mandible were dislocated through the adductor fibres pulling behind the condylar contact, tremendous stresses would be exerted on the jaw joint and the major part of the muscle mass rendered ineffective. It is clear that the lateral external adductor muscles would be the delimiting factors in the gape size, since, with their origins close to the quadrate and their insertions well below the dorsal edge of the mandible, they would be the first fibres to approach the quadrate-articular contact during jaw depression.

In Figure 65 *Emydops* and *Lystrosaurus* are represented with their jaws depres-

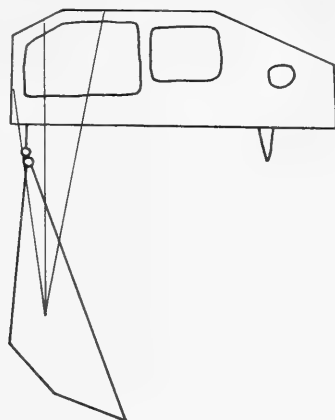


Fig. 64. Model of hypothetical dicynodont illustrating factors which determine maximum gape.

sed to the maximum possible extent, as determined by the lateral external adductor muscle. The lines CX, DX and EX are hypothetical lines of traction exerted by fibres of the lateral external adductor muscle on the jaw axis AB. Angle FGH represents the extent to which the tip of the premaxilla has descended below the reference plane.

As shown above, lowering of the snout in a dicynodont results in a relatively depressed position of the mandible when adducted. If there were no changes involving the areas of origin of the adductor externus muscles, a very limited gape would result. To counteract this effect, deepening and shortening of the temporal region took place in *Lystrosaurus* simultaneously with the deepening of the snout. Deepening of this posterior part of the skull served to provide higher points of origin for the adductor muscle fibres, and shortening meant that these points of origin came to lie relatively closer to the ventral insertion areas. In this way the adductors became less obliquely inserted on the mandible when in the adducted position, and could allow the mandible to be swung relatively further back than in a form such as *Emydops*, and still retain sufficient moment on the jaw axis to be able to elevate the jaw rapidly and effectively.

Figure 65 shows some interesting comparative values for *Emydops* and *Lystrosaurus* when both are seen with the mandible in the maximum depressed position. In *Emydops* the antero-ventral tip of the premaxilla lies 6° below the condyle-nostril reference plane of the skull (i.e. angle FGH = 6°). *Lystrosaurus* has lowered its premaxilla to 14° below this. To compensate for the lowering, the mandible in *Lystrosaurus* has been allowed to drop 11° below the jaw of *Emydops*, to make possible a maximum gape (H—B) of 47° , in which position the average angle of pull by the lateral external adductors on the mandible is 39° . In *Emydops* the maximum gape (H—B) was 48° , and in this

position the average angle of pull by the lateral external adductor muscle was also 39° .

If both skulls are aligned along the same reference plane, both mandibles can be rotated back to make possible an equally large gape, but because of the relatively low position of the palate in *Lystrosaurus*, the mandible had to be swung relatively farther back, and consequently allowed *Lystrosaurus* to execute forward scooping movements with the jaw during the first stages of elevation.

With the jaw in the position of maximum gape, the temporal muscle fibres are stretched to the greatest possible length required by the masticatory cycle. This length is well within the maximum to which a muscle fibre can stretch. Haines (1934) has shown that a human muscle fibre can contract by about 57% of its extended length, i.e. a fibre can stretch by about 132% of its contracted length. Haines (cited by Parrington, 1955) later confirmed these values by means of tests on dog muscle fibres. Parrington (1955) has calculated the extent to which fibres of the jaw adductor muscles would have to stretch to allow sufficient gape in the *Gorgonopsia*, and by making allowance for the possible presence of non-contractile tendons in the total muscle length, has assumed that the muscles could extend by 80% of their total contracted length.

Using the value of 80% possible extension, it can be calculated that in animals such as *Lystrosaurus* and *Emydops*, the external adductor muscles, which inserted far forward on the mandible and were thus of considerable length even when fully contracted, were theoretically capable of far greater extension than required for maximum gape, as illustrated in Figure 65. The same is true of fibres of the anterior pterygoideus muscle.

Ewer (1961) supposes that the increase in height of the posterior part of the skull in *Daptocephalus* is an adaptation for increasing the length of the tem-

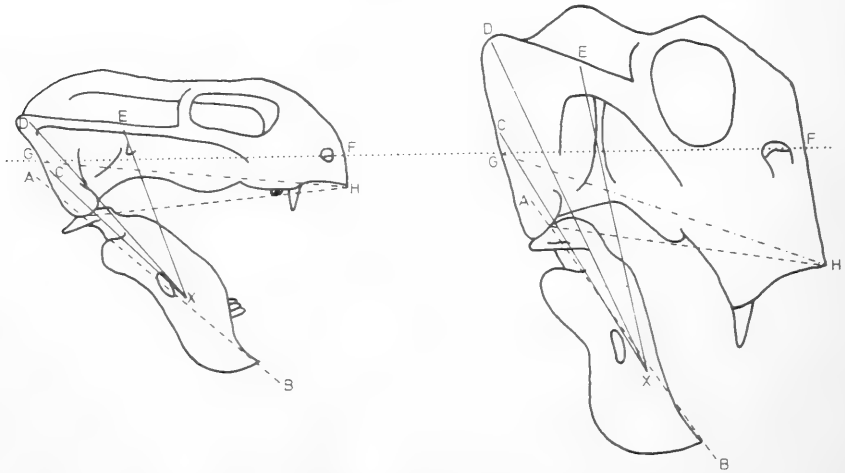


Fig. 65. Comparison of the skulls of *Emydops* and *Lystrosaurus* with mandibles in the position of maximum gape.

poral muscle fibres, to allow the jaw to be opened adequately. However, if the above values for muscle contraction and extension are accepted, the adductor muscles in any dicynodont are of sufficient length, due to their anterior insertion on the dentary, to provide an adequate gape without additional lengthening being necessary.

The distinctive skull proportions of *Lystrosaurus* therefore probably arose as a result of a new aquatic or semi-aquatic mode of life, involving changed accessibility of the food source. The consequent lowering of the feeding level in the skull was of necessity accompanied by shortening and deepening of the temporal region of the skull, to provide the necessary new positions of origin of the temporal external adductor musculature. The maintenance of a constant maximum gape was of overriding importance in this regard.

SECTION V. VARIATION IN THE SKULL OF *LYSTROSAURUS* AND THE TAXONOMY OF THE GENUS

The far-reaching and obviously very successful changes which produced *Lystrosaurus* from a dicynodont ancestor have resulted in a skull form remarkably different to that of other dicynodonts. Moreover, within the broad framework of cranial features which characterize the genus, are several variations in both proportion and structure, indicating that the success of the new skull form did not prevent the genus from radiating into several species in which the skull pattern is modified. To date 24 South African species of *Lystrosaurus* have been described, and a problematical associated genus, *Prolystrosaurus*, with two species, has been created.

The first specimen of *Lystrosaurus* was described in 1859 by Huxley as *Dicynodon murrayi*, but Owen (1860) recognized that new forms similar to *D. murrayi* warranted the formation of a new genus, *Ptychognathus*. This genus included the new species *declivis*, *latirostris* and *verticalis*. In 1862 he further described *P. alfredi* and in 1876 added *P. boopis* and *P. depressus*, and described a new species of *Dicynodon*, *D. curvatus*, which Broom in 1932 placed into the genus *Lystrosaurus*.

It became apparent, however, that the name *Ptychognathus* had been pre-occupied by Stimpson in 1858 for a crustacean, and Lydekker in 1890 introduced a new name, *Ptychosiagum*, for all the specimens of *Ptychognathus*. However, Seeley (1898) maintained that if the name *Ptychognathus* should be withdrawn, only *Lystrosaurus* (Cope, 1870) could take its place since *Lystrosaurus frontosus* was clearly a *Ptychognathus*. Seeley further proposed two subgenera for *Ptychognathus* (or *Lystrosaurus*). These were *Rhabdotocephalus* (*Rhabdotocephalus* of Broom, 1932, and Brink, 1951), with type species *R. mcCaigi*, and *Mochlorhinus*, with type species *M. platyceps*.

Broom (1903) used the generic name *Lystrosaurus* when describing some specimens in the Albany Museum, and in 1907 he introduced a new species, *L. andersoni*. *L. oviceps* (Haughton, 1915) and *L. putterilli* (Van Hoepen, 1915)

were the next new species, and in 1916 Van Hoepen further described *L. breyeri*, *L. jorisseni*, *L. jeppe*, *L. theileri*, *L. wageri* and *L. wagneri*.

In 1917 Haughton maintained that *Dicynodon strigops* of Broom (1913) was related, and ancestral, to *Lystrosaurus*, and placed it, together with a new species, *natalensis*, in a separate genus, *Prolystrosaurus*. Broom in 1940 described *L. rubidgei* and in 1941 *L. bothai*, while Brink (1951) and Toerien (1954) described *L. amphibius* and *L. primitivus* respectively.

There have been several attempts at arranging these species into natural groups, and various synonymies have been declared among them. In 1907, Broom suggested the division of the genus into two branches, one to accommodate the large forms such as *L. mcCaigi*, *L. platyceps* and *L. andersoni*, and the other to include the smaller species. In 1932 he again stressed the need for reorganization of the genus, and pointed out that any collection of *Lystrosaurus* specimens can be divided into males and females, according to the presence or absence of ridges and bosses on the skull roof. He placed nearly all the previously described species under *L. murrayi*, but allowed *L. curvatus* (*Dicynodon curvatus* of Owen, 1876), *L. platyceps*, *L. mcCaigi* and *L. andersoni*. He mentioned the possibility of *L. platyceps* being the female of *L. mcCaigi*, but figured another specimen as the presumed female *mcCaigi*. He claimed that Haughton (1917) had based his genus *Prolystrosaurus* on the crushed skull of a young female, probably of *L. murrayi*.

In 1951 Brink enlarged on Broom's (1907) proposal for the separation of the larger species from the smaller ones. He added *L. putterilli* and the new *L. amphibius* to the larger forms and stated that these species were characterized by the extent to which the dorsal orbital borders protruded above the general level of the skull roof. The smaller species such as *L. murrayi*, *L. declivis* and *L. verticalis* fell into a separate branch. He regarded *L. oviceps* as the most primitive species of the genus, connecting *Lystrosaurus* with *Dicynodon*. He recognized 12 South African species of *Lystrosaurus* and suggested that, since *Prolystrosaurus* did not represent a natural ancestor of *Lystrosaurus*, but was in fact probably allied to *L. murrayi*, the species *strigops* and *natalensis* be referred to *Lystrosaurus*. Brink at the same time merged the species *alfredi*, *depressus* and *boopis* with *Lystrosaurus declivis*, and the species *frontosus*, *jeppe*, *jorisseni*, *theileri*, *wageri*, *wagneri* and *latirostris* with *Lystrosaurus murrayi*. He included *L. breyeri* under *Lystrosaurus oviceps*.

SKULL VARIATION WITHIN THE GENUS

The organization of this genus into different species involves the problem of separation of variations which could be random or due to sex, age or distortion from those which could be regarded as specific differences. The success of any such attempt must depend on the number of specimens available for comparison, and on their state of preservation. Ideally, only perfect, undistorted specimens should be considered, but it is unfortunately true that such specimens are rare in even the best collections. Added to this is the fact that it

is very often impossible to determine whether a skull is distorted in some way without almost complete preparation of the specimen. However, present information, based on the anatomical evidence of the previous section, does permit some conclusions to be drawn.

The genus *Lystrosaurus* can be defined as follows:

Small to large dicynodonts. A single pair of tusks in both sexes. Snout steeply downturned, with extensive premaxillary development. Nostril situated relatively high in the skull. Orbit large, temporal fossa greatly shortened. Post-pineal region of the skull table short. Exoccipital condyles projecting further posteriorly than basioccipital condyle. Prominent ventral transverse ridge between the basioccipital tubers. No floccular fossa. Characteristic pit-shaped unossified zone between basioccipital and basisphenoid. Trabecular region anterior to the hypophyseal region short. Presphenoid immediately anterior to the internal carotid canals. Vomer and premaxilla form deep median septum. Labial fossa present. Ectopterygoid absent. Pterygoid meeting maxilla. Sharp cutting edge on the maxilla anterior to the canine tusk. No notch or break in profile on maxillary margin. Zygomatic arch steeply inclined. Choanal plane at angle to premaxillary palatal plane. Excavated facet on stapes.

While all specimens share the above characteristics, the following variations appear to be significant:

1. Extent of premaxillary and maxillary snout development.
2. Size of tusk.
3. Presence or absence of transverse frontonasal ridge.
4. Presence or absence of frontal tuberosities and bosses.
5. Presence or absence of prefrontal bosses.
6. Presence or absence of longitudinal ridges on the snout.
7. Nature of frontonasal suture.
8. Nature of transition between frontal and nasal planes.

On the basis of several of these variations two skull types can be distinguished:

A	B
1. Strongly developed snout	Moderately developed snout
2. Large canine tusks	Weak canine tusks
3. Frontonasal ridge	Frontonasal ridge absent
4. Frontal tuberosities	Frontals smooth
5. Prefrontal bosses	Prefrontal bosses absent or weak
6. Longitudinal snout ridges	Snout smooth
7. Frontal and facial plane meet at angle	Frontal and facial planes smoothly rounded

Species with typical type A skulls include *L. declivis* and *L. murrayi*, while species with the cranial features listed under B include *L. curvatus* and *L. platy-*

ceps. Basically the skulls in both groups are similar, and the differences are due to a greater or lesser degree of modification of common structures, without change in the fundamental and characteristic skull form. As shown in succeeding pages, no formal systematic status should be conferred on these 'species groups'.

THE SEXUAL DIMORPHISM PROBLEM

The fact that all specimens of *Lystrosaurus* examined fall naturally into either one or the other of the two 'species groups' suggests two possibilities, namely, that either there were two distinct lines of development within the genus, or that a fairly consistent type of sexual dimorphism was present in most or all of the species.

The possibility of two phylogenetically distinct groups being present within the genus has been pointed out by Seeley (1898), Broom (1907) and Brink (1951). Seeley recognized that the nature of the junction of the facial surface with the dorsal interorbital surface of the skull permitted a separation to be made. He stated that whereas in *Ptychognathus* the facial or snout surface was separated from the dorsal skull surface by an angular ridge, in *Mochlorhinus* the two surfaces were smoothly rounded into each other. *Rhabdotocephalus* differed from both of these in that the facial surface of the skull met the skull roof at an angle, but without a transverse ridge.

Seeley's (1898) suggestion has merit in that the factors he used to divide the genus appear to be valid. At that time, however, the taxonomic value of the groups must have been uncertain, and Seeley's proposed subgenera did not meet with much support (Broom, 1903). In the case of *Rhabdotocephalus* (*Lystrosaurus mcCaigi*) lateral compression could have obliterated any transverse ridge, and have produced instead the singular sharp longitudinal ridges on the anterior frontal surface.

As shown above, Broom (1907) proposed that the large forms of *Lystrosaurus* be separated from the small ones, and Brink (1951) enlarged on this idea. However, the criteria used by Brink to distinguish groups of species, i.e. size and the height of the dorsal border of the orbit above the skull roof, are not reliable, and may well be explained in terms of age or distortion. Lateral compression of the frontal region of the type skull of *L. mcCaigi*, for example, has produced artificially raised supraorbital ridges. Furthermore, Brink did not separate the ridged skulls from the smooth, and both types are included in each of the two groups in his scheme of the interrelationships of the species. He regards *L. oviceps* as the most primitive member of the genus, but further preparation of the type skull of this species has revealed considerable crushing, and the species is probably allied to *L. declivis*.

On the other hand, there is also a case for the possibility of the skull differences being due to a fairly constant sexual dimorphism within the genus. This has been suggested by Broom (1932) and Tripathi & Satsangi (1963). The possibility is strengthened by the fact that the characters used to differentiate between the two groups are similar to those which distinguish male and

female individuals of recent animal species. Thus Cave & Steel (1964) showed that sexual differences in the skull of the *Colobus* monkey were differences in the relative development of existing structures, and that sex could be determined by comparing the size of the supraorbital ridges, canine tooth, presence or absence of a sagittal crest and the shape of the palate. Ashton & Zuckermann (1950) found that the sexes of the great apes differed in the size of the canine, and Ashton (1956) showed that sexual dimorphism entered after puberty, when the new canine appeared and especially rapid growth of the temporal and nuchal muscles took place in the male. The degree of sexual dimorphism in the various primate groups varies considerably (Ashton, 1956; Hooijer, 1952). Similar dimorphism occurs in the elephant (Perry, 1954, 1955) and the mountain sheep (Geist, 1966).

The possible effects of sexual dimorphism on the cranial osteology of dicynodonts were recognized by Owen in 1860 and 1876 when he discussed the relationships of the tuskless *Oudenodon* with *Dicynodon*. Broom (1912) concluded that the presence or absence of tusks in *Diaelurodon whaitsi* and *Dicynodon bolorhinus* was due to sexual dimorphism, and in 1932 suggested the possibility of sexual differences in several dicynodont species, among them *Dicynodon vanderbyli* and *Dicynodon whaitsi* and, as shown above, stated that any group of *Lystrosaurus* specimens can be divided into males and females on the nature of the skull roof.

In 1957 Barry gave the problem a new approach and pointed out that on evidence from recent mammals (Fraser, 1938; Ashton & Zuckermann, 1950; Ashton, 1956) sexual dimorphism is not characterized by complete suppression of any factor in one of the sexes, but rather that common characters are emphasized and more pronounced in one sex and reduced in the other. He found that in the specimens of *Dicynodon grimbeeki* he investigated the males have strong tusks, while tuskless specimens, previously regarded as females, still retain a tooth bud in the maxilla. These apparently tuskless specimens may equally well be immature males. Only individuals with weak snouts and tusks may with any reasonable certainty be regarded as females. This view is apparently supported by the specimens of *Dicynodon jouberti* which Broom (1905) and Boonstra (1948) had previously divided into males and females according to the degree of canine tusk development.

Tripathi & Satsangi (1963) supported Broom's (1932) division of *Lystrosaurus* into males and females, and in their definition of *L. murrayi* state:

'Skull table highly variable, in male individuals fronto-nasal ridge well developed, frontals ridged either by prominent tubercles or transverse ridge; female skulls smooth with almost almond-shaped preparietals, tending to be circular in adult individuals; in males a bony outgrowth arises from the preparietal to meet the frontal tubercle' (p. 16).

Neither Broom (1932) or Tripathi & Satsangi (1963) recognized that there is a variation in tusk size, and that this variation is correlated with the

differences in the nature of the skull roof.

There is clearly considerable support for the theory of sexual dimorphism among dicynodonts and thus for Broom's (1932) division of *Lystrosaurus* specimens into males and females. However, essential for the feasibility of the theory is that collecting at any given locality should reveal specimens of both types of *Lystrosaurus* in comparable numbers and in more or less close association with each other.

The Commonage at Harrismith, Orange Free State, presents a favourable test locality. Various sites at this locality form part of the same horizon, and specimens of *Lystrosaurus* are especially abundant and well preserved. Many beautiful skulls have been obtained here in the past, mainly by the late Mr. A. W. Putterill.

In early 1969 a field trip into the Karoo included a short period at Harrismith. Some excellent skulls, many with associated postcranial material, were recovered, and these were subjected to preliminary preparation in order to ascertain the number of specimens representative of each of the two groups of *Lystrosaurus*. It was found that of 20 skulls thus examined, 16 fell into group A (Broom's males) and only one into group B (Broom's females). Of three skulls of more uncertain affinities, one probably belongs in group A and the other two in group B.

Furthermore, of 14 good skulls from Harrismith in the collection of the National Museum, Bloemfontein, only three definitely resort under group B and would classify as females. Again, subjecting 20 identifiable skulls in the South African Museum collection from Skerpioenkraal, Middelburg, to the same process showed that only three specimens fell under group B (Broom's females).

Even though other localities in the *Lystrosaurus* zone should be found to yield both types of *Lystrosaurus* in equal or near-equal numbers, the presence of only a few localities such as Harrismith, where one variety greatly outnumbered the other, must cast doubt on Broom's (1932) conclusions, while the consistent preponderance of supposedly male over supposedly female specimens in the areas tested is another factor difficult to explain. Furthermore, *Lystrosaurus* has, in previous sections, been shown to be a basically primitive therapsid genus, having retained a large proportion of reptilian characteristics, and the presence here of a consistent and morphologically clear-cut sexual dimorphism would surely be unusual. Therefore, until continued intensive collecting shows that both types of *Lystrosaurus* are found in most localities where groups of contemporaneous individuals occur, it seems safest to assume that the two groups characterized on p. 237 represent phylogenetically distinct 'species groups' within the genus.

EFFECTS OF AGE AND DISTORTION ON THE *LYSTROSAURUS* SKULL FORM

Since size of specimens of *Lystrosaurus* varies over a fairly wide range, the question of the influence of age on the nature of the skull morphology arises.

Kitching (1968) has illustrated a convincing growth series of a species of *Lystrosaurus*, here considered to be *L. curvatus*. The smallest specimens in this series, B.P.I. 407 and 408, have a basal length of 42 mm and 45 mm respectively, and tusks have not yet erupted. Comparable in size to these rare little skulls are two specimens, S.A.M. 3531 and K.1396, in which tusks have not yet erupted. The former appears to be very similar to B.P.I. 408, while the damaged prefrontal region of the latter makes a diagnosis impossible.

It is impossible to place such small specimens into either of the 'species groups' on p. 237, since differences such as smooth frontal and prefrontal regions or transverse frontonasal ridges and frontal bosses appear to be established at a slightly later age, represented by three specimens available for this study, namely, S.A.M. K.1362, Nat. Mus. C.211 and T.M. R.19 with basal lengths of respectively 73 mm, 84 mm and approximately 90 mm. Specimen No. K.1362 has a newly erupted tusk and with its smoothly curved skull roof is clearly distinguishable from the other two specimens, with larger tusks, clear frontonasal ridges and frontal bosses. K.1362 (Fig. 67) is here considered to be *L. curvatus*, while C.211 (Fig. 75) and R.19 are regarded as specimens of *L. murrayi* and *L. declivis* respectively. (See also pp. 250 and 247.)

Moreover, individuals with smoothly curved skull roofs are known which are larger than many individuals with frontonasal ridges and frontal bosses. Thus, for example, the basal length of the skull of Nat. Mus. C.205, *L. curvatus*, is 192 mm, making it well over twice the size of a specimen with frontal bosses and frontonasal ridge such as Nat. Mus. C.211.

Minor changes in the skull, such as a change in the relationships of the nasals, may be attributable to age, and are discussed in the succeeding section, but it seems unlikely that age is a factor in the determination of the major differences in skull proportions within the genus.

While determining the skull form in the various species of *Lystrosaurus*, special attention was paid to the possible effects of distortion. It was found that in the majority of apparently well preserved specimens distortion could be detected in the anteroventral orbital border, the postorbital—jugal—maxilla contact in the zygomatic arch, the premaxilla—nasal contact and in the relative positions of the presphenoid and orbitosphenoid. Thus in dorsoventral crushing there is usually telescoping of the lacrimal, prefrontal and jugal in the region of the lacrimal canal, together with ventral displacement of the orbitosphenoid on to or alongside the presphenoid. At the same time it is usually apparent that the nasals have slipped down behind the nasal process of the premaxilla, this being reflected in distortion of the nasal aperture.

In another common type of crushing the skull roof has been forced forward relative to the skull base. This is often difficult to detect, since only careful and extensive preparation reveals any sign of distortion, these being, in the main, forward displacement of the ventral tip of the postorbital over the jugal and maxilla, and the anterior position of the orbitosphenoid relative to the presphenoid. Anteroposterior crushing is usually indicated by distortion in the palate,

while lateral compression generally results in folding back of the posterior squamosal flanges.

Analysis of imperfections such as these will usually indicate the nature of distortion suffered by a particular skull, and allow a tentative reconstruction of the original shape to be made. However, in this study use was made as far as possible only of skulls which were either uncrushed or had undergone easily interpreted distortion. The sphenethmoid complex was regarded as the main indicator of distortion, and in all cases of doubt the presphenoid and orbito-sphenoid were exposed in order to determine their relative positions.

THE SPECIES OF *LYSTROSAURUS*

Lystrosaurus curvatus (Owen)

(Figs 27, 36, 37, 66, 67)

Dicynodon curvatus Owen, 1876.

Lystrosaurus curvatus Broom, 1932.

Lystrosaurus wageri, jorisseni & theileri Van Hoepen, 1916.

Type specimen: B.M.N.H. R.3792

Locality: Cradock, C.P.

Morphologically, this species appears to be the closest to the Permian dicynodonts. The snout, while typically lystrosaurian, is not as far ventrally produced as in some species of *Lystrosaurus*, and frontonasal and premaxillary ridges and frontal bosses are absent. Among dicynodonts these latter features appear to be confined to some of the more specialized species of *Lystrosaurus*.

The skull roof is smooth and the premaxillary plane curves over in a smooth arc to meet the frontoparietal plane. Although a transverse frontonasal ridge as such is absent, slight indications of a fold on the prefrontal may be present.

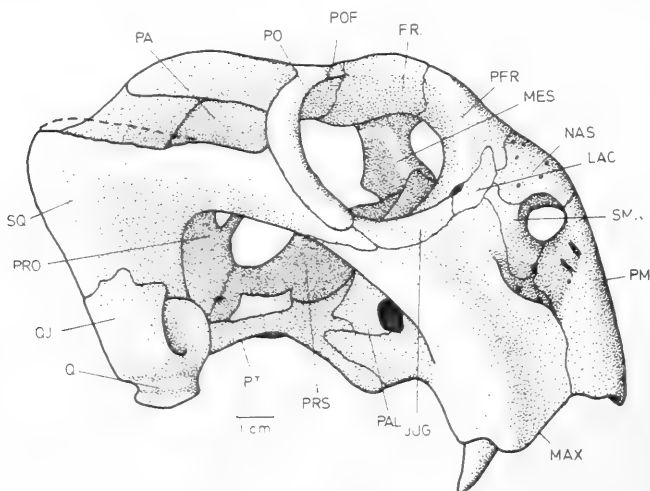


Fig. 66. *Lystrosaurus curvatus*, Nat. Mus. No. C.299. Skull in lateral view.

Frontal protuberances are absent and, in comparison with other species of *Lystrosaurus*, snout and tusk development are not strong. The suture between frontals and nasals lies on the roof of the skull in the general frontoparietal plane and in the majority of specimens is irregular (Fig. 36). Each nasal continues posteriorly as a process between the two anterior diverging processes of the frontal of its side. In a small percentage of individuals, however, the frontonasal suture is almost straight and transverse.

Typical in this species is the shape of the ventral ramus of the squamosal, which in all lystrosaurids is flared out laterally to provide a large area of origin for the lateral external adductor muscle mass. In *Lystrosaurus curvatus* this flange is produced posteriorly as well as laterally so that in a lateral ortho-projection the occipital condyles are concealed behind the squamosal (Figs 66, 67).

L. wageri, *zorisseni* and *theileri* have smoothly rounded skull roofs and are best included under *L. curvatus*. It was not possible to determine whether these forms show the posterior projection of the squamosal.

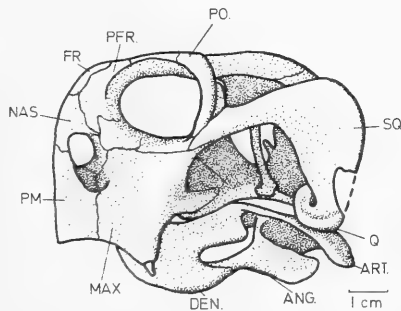


Fig. 67. *Lystrosaurus curvatus*, S.A.M.
No. K.1284. Skull in lateral view.

Lystrosaurus bothai Broom

Lystrosaurus bothai Broom, 1941.

Type specimen: Rubidge Collection.

Locality: Rygerspoort, Cradock District.

This species appears to be related to both *Lystrosaurus curvatus* and the next species, *L. platyceps*. The skull is not ridged and the snout is more strongly developed than in *L. curvatus*, but less than in *platyceps*. Broom (1941) thought that the species resembled *platyceps* in the nature of the frontals, while Brink (1951) thought that it compared with *curvatus*. The relatively narrow interorbital width in *L. bothai* is certainly reminiscent of *L. curvatus*, as is the frontonasal suture, where the frontal extends down between the posterior process of the nasals.

The broad, anteriorly blunt preparietal in *L. bothai* is found in both *L. curvatus* and *L. platyceps*.

Lystrosaurus platyceps Seeley
(Figs 68, 69)

Lystrosaurus (Mochlorhinus) platyceps Seeley, 1898.
Lystrosaurus andersoni Broom, 1907.

Type specimen: Albany Museum.

Locality: Bethulie, Orange Free State.

This species is apparently the most advanced of those species with smooth, *Dicynodon*-like skulls. The snout is relatively deeper than in either *L. curvatus* or *L. bothai*. In lateral view the anterior facial surface is only very slightly convex and the transition between facial and frontal planes is more abrupt than in *curvatus* or *bothai*, although there is no ridge or angular, sharp division between the two planes.

A feature of *Lystrosaurus platyceps*, setting it apart from *L. curvatus*, is the inclusion of the entire nasal within the premaxillary facial plane, suggesting that deepening of the snout, which involves the maxilla and premaxilla in *L. curvatus*, has proceeded to the extent of involving the nasal in *L. platyceps*. That this is probably not an age phenomenon is shown by the fact that the four specimens of *L. platyceps* examined (e.g. S.A.M. 706 and T.M. R.27) were smaller than several specimens of *L. curvatus* investigated.

Lystrosaurus andersoni is included here on account of its smooth skull roof and the inclusion of the nasals in the facial plane.

Resemblances between *L. platyceps*, *L. curvatus* and the apparently intermediate *L. bothai* include the broad, approximately rectangular preparietal, the interdigitating frontonasal suture, the lack of a transverse frontonasal ridge and the absence of longitudinal ridges on the snout. These three species can also be regarded as primitive in that, while they display the specializations of

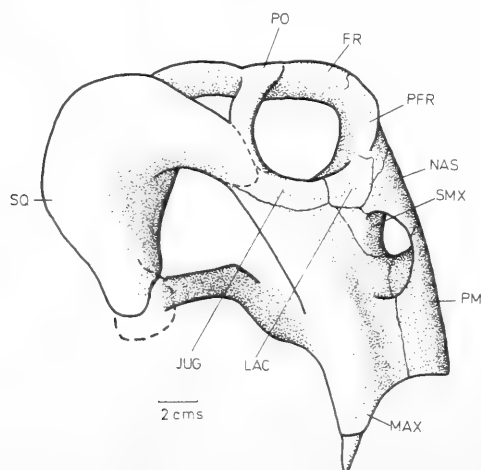


Fig. 68. *Lystrosaurus platyceps*. S.A.M. No. 706. Skull in lateral view.

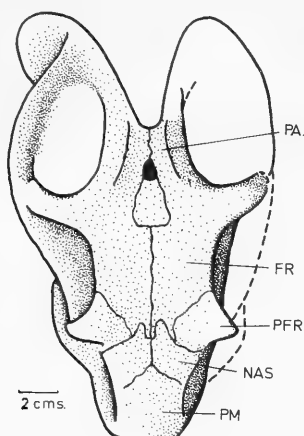


Fig. 69. *Lystrosaurus platyceps*.
S.A.M. No. 706. Skull in dorsal
view.

Lystrosaurus, they have retained the smooth, gently rounded skull roof which is characteristic of Permian dicynodonts. They comprise group B on p. 237.

In the following species of *Lystrosaurus* there is a departure from this condition and the skulls are characterized by the presence of certain pronounced bosses and ridges on the snout and skull roof. These species comprise group A on p. 237.

Lystrosaurus oviceps Haughton
(Figs 70, 71)

Lystrosaurus oviceps Haughton, 1915.

Lystrosaurus breyeri Van Hoepen, 1916.

Type specimen: S.A.M. 641.

Locality: Tarka River, Cradock District.

L. oviceps may be regarded as the most primitive of those species which possess transverse frontonasal ridges and frontal bosses. It is the only species in this group in which the facial surface of the premaxilla is not flat, and the smoothly curved snout, sloping back to the frontonasal ridge, is reminiscent of *L. curvatus*. The snout is, however, very strongly developed and bears a prominent median longitudinal ridge. Since the snout and skull roof merge smoothly into each other, the frontonasal ridge does not divide the facial from the frontal plane. Two frontal tuberosities are present. The frontonasal suture is mainly transverse, and the frontals do not project forward between the prefrontals and nasals, but a short median process formed by both frontals protrudes forward for a short way between the nasals. This type of frontonasal suture resembles that of some specimens of *L. curvatus*.

The type skull has undergone considerable crushing, and the occiput is

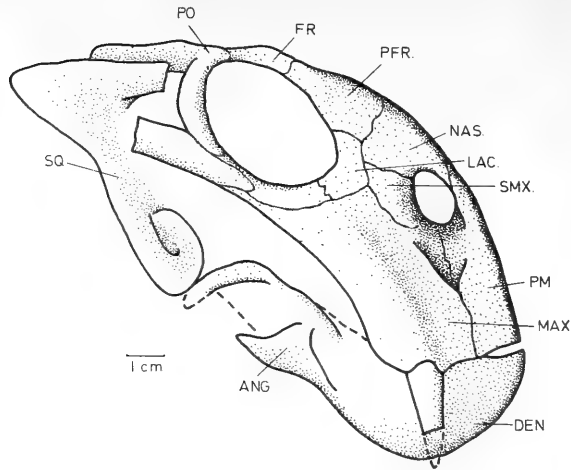


Fig. 70. *Lystrosaurus oviceps*, S.A.M. No. 641. Skull in lateral view.

displaced forward and up. In the undistorted state, therefore, the postorbital region of the skull would have been longer than as illustrated by Haughton (1915). In Figures 68 and 69 the skull is shown in the distorted condition. It seems likely that *L. oviceps* is derived from *L. curvatus*.

Brink (1951) has placed *L. breyeri* of Van Hoepen (1916) under *L. oviceps* and, judging by the illustrations of Broom (1932), this is probably correct.

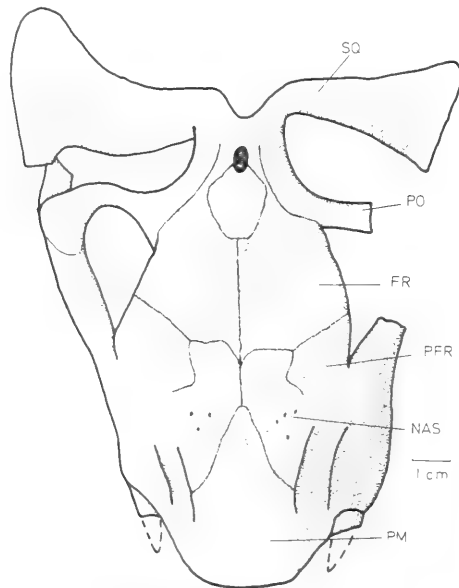


Fig. 71. *Lystrosaurus oviceps*. S.A.M. No. 641. Skull in dorsal view.

Lystrosaurus declivis (Owen)

(Figs 22, 23, 24, 26, 72, 73)

Ptychognathus declivis Owen, 1860.*Ptychognathus latirostris* Owen, 1862.*Ptychognathus depressus* Owen, 1876.*Ptychognathus alfredi* Owen, 1876.*Lystrosaurus wagneri* Van Hoepen, 1916.*Lystrosaurus primitivus* Toerien, 1954.

Type specimen: B.M.N.H. 36221.

Locality: Rhenosterberg.

The skull in this species resembles that of *Lystrosaurus murrayi*, described later, and seems to form a morphological link between it and *L. oviceps*. As in *oviceps*, the snout is directed forward as well as down, but the smoothly curved snout is lost and the anterior premaxillary facial surface in *declivis* is a perfectly flat plane, broken only by a sometimes very prominent longitudinal median ridge.

There is a strongly developed frontonasal ridge and prominent frontal tuberosities. The lateral snout surface lies at a sharp angle to the anterior snout surface, so that in ventral view the premaxillary portion of the palate is rectangular.

A feature of this species, as also of *L. murrayi*, is the division of the skull roof and snout surfaces into three planes: a parieto-preparietal plane which extends over the intertemporal region up to the frontal bosses, a frontal plane which slopes forward and down from the frontal bosses to the frontonasal ridge, and a premaxillary plane, generally referred to as the facial plane, which drops down steeply from the frontonasal ridge. The anterior two-thirds of each nasal is generally included in the plane of the anterior premaxillary surface.

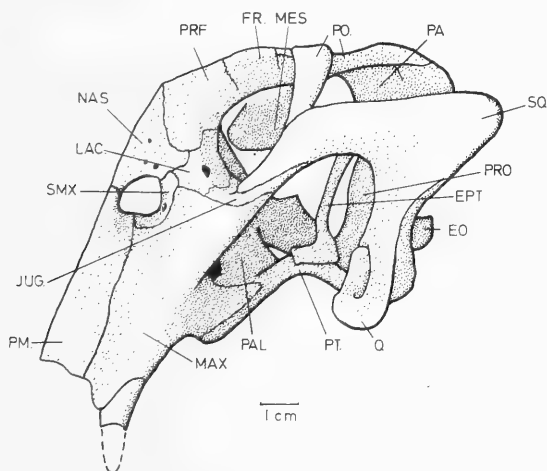


Fig. 72. *Lystrosaurus declivis*. Nat. Mus. No. C.171.
Skull in lateral view.

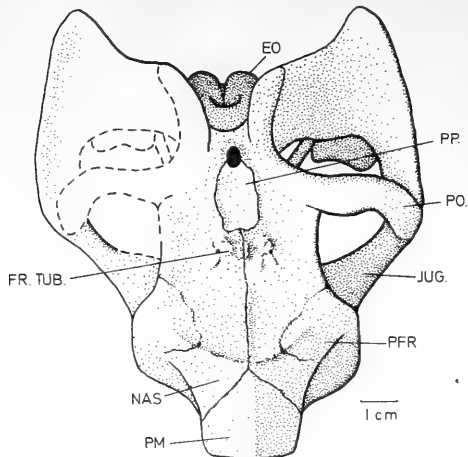


Fig. 73. *Lystrosaurus declivis*. Nat. Mus. No. C.171. Skull in dorsal view.

Included in this species are several specimens (e.g. C.403, Figs 22, 23, 24, 26) which resemble *L. declivis* in all respects excepting the nature of the transition between the premaxillary and frontal surfaces. In these individuals the anterior two-thirds of the nasal is not included in the premaxillary plane, but slopes back to the frontonasal ridge, thus separating the frontal and premaxillary surface planes. These specimens are small and the variation may well be due to age differences. As shown below, a similar size-correlated variation is noted in the species *L. murrayi*.

The frontonasal suture is of the *oviceps* type, with the frontal extending down between the nasal and prefrontal. In a few specimens, however, the frontals protrude forward for a short way between the diverging posterior ends of the nasals. Unlike species such as *L. curvatus*, the ventral squamosal flange faces directly forward, so that in a lateral orthoprojection the occipital condyles are visible (Fig. 72).

Besides the bosses on the frontals and the longitudinal ridges on the snout, several specimens of *L. declivis* display sharp ridges on the skull roof behind the frontonasal ridge. Thus in S.A.M. K.1392 the interfrontal suture is raised considerably to form a median, knife-edged crest, while in S.A.M. 3455 the suture between nasal and prefrontal is similarly elevated. The tusks are strong, with inner wear facets.

Lydekker (1890) placed *L. alfredi* and *L. depressus* under *L. latirostris*, but Brink (1951) seems correct in stating that all three of these 'species' belong under *L. declivis*. All three have frontonasal ridges and strongly developed, longitudinally ridged snouts. Examination of the type skull of *L. primitivus* shows that it is probably a badly distorted *L. declivis*. The specimen has been extensively dorsoventrally compressed, with consequent obliteration of the nasal apertures and foramen magnum.

Lystrosaurus mcCaigi Seeley
(Figs 74a, 74b)

Lystrosaurus (Rhabdotocephalus) mcCaigi Seeley, 1898.

Lystrosaurus mcCaigi Broom, 1903.

Lystrosaurus amphibius Brink, 1951.

Type specimen: Albany Museum.

Locality: Elandsberg, Cradock, C.P.

Although Seeley (1898) referred to this species in the course of a description of *Lystrosaurus platyceps*, Broom (1903) was the first to give an account of the anatomy of the type specimen.

Included in this species are some of the largest specimens of *Lystrosaurus*. The snout is very strongly developed with longitudinal ridging, and the nasals appear to be entirely included in the premaxillary plane. The species resembles *declivis* in that the facial surface slopes forward and down from its junction with the frontal plane. However, the premaxillary plane is much more strongly developed in *mcCaigi* than in *declivis*, the plane in *declivis* being 86% of the skull length over the reference plane, while in *mcCaigi* this figure becomes 103%.

The prefrontals are well developed, although their exact extent is obscured by the lateral compression which the type skull has undergone. However, it is clear that *mcCaigi* differs from all the preceding species in that the prefrontals protrude forward of the midline of the facial surface. The degree of development of these prefrontal bosses and again the lateral compression of the type skull have obscured the transition between facial and frontal planes. No clear frontonasal ridge is apparent in the type specimen, but there is an angular division between the two planes. In three large skulls, namely Nat. Mus. C.228, S.A.M. K.116 and B.P.I. 380, which appear to be specimens of *Lystrosaurus mcCaigi* and which have not suffered lateral crushing, there is a clear frontal ridge, from which the nasals appear to be excluded, across the level of the middle of the orbits, i.e. relatively farther back than in *L. declivis*.

Included under this species is Brink's (1951) *L. amphibius*, which is founded on a laterally compressed skull. The considerable distortion has accentuated the extent of the supraorbital and prefrontal bosses, but it is likely that when allowance has been made for this the specimen would closely resemble *mcCaigi*. Brink (1951) figures two planes in the skull roof of *L. amphibius*, which appear to correspond with the parieto-preparietal and frontal planes. In K.116, which is a well preserved, undistorted skull, these two planes are not differentiated, and a flat skull table leads forward to the prominent frontal ridge. The premaxillary facial plane commences at this ridge. There is no trace in this skull of the grooves which Brink noted in the skull of *L. amphibius*, leading dorsally from the nostril and which he supposed indicated the presence of fleshy external nostrils. Examination of the type skull of *L. amphibius* has shown that these shallow grooves are the result of the extensive lateral compression which the skull has undergone.

A resemblance to *L. declivis* in *mcCaigi* is seen in the extremely prominent

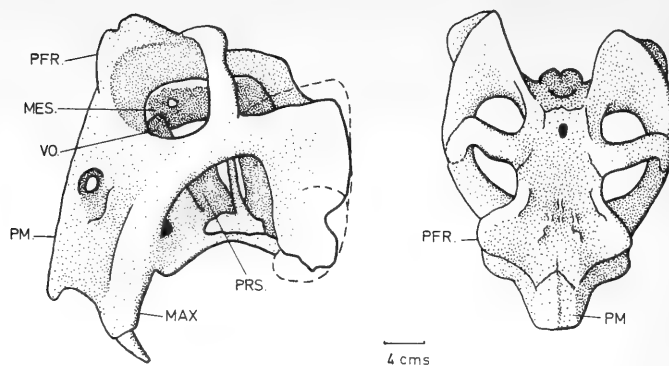


Fig. 74. *Lystrosaurus murrayi*. S.A.M. No. K.116. Skull in (a) lateral and (b) dorsal view.

longitudinal crests in the frontal region. A median crest is formed at the inter-frontal suture, while two laterally situated crests, each lying medially to the prefrontal boss of its side, are probably situated along the nasal-prefrontal suture.

The possibility of *murrayi* representing a large *murrayi* or *declivis* would seem to exist, but Kitching (1969, and personal communication) has found that these large forms of *Lystrosaurus* occur mainly in the lower horizons of the *Lystrosaurus* zone, while *murrayi* and *declivis* apparently persist throughout the entire zone. This suggests that *L. murrayi* is a distinct species which had its main radiation early in *Lystrosaurus* zone times.

Toerien (1953) appears to be correct when he derives the palate of *Lystrosaurus* from that of *Dicynodon*, but the contact between the palatine and the posterior process of the premaxilla which he described in Brink's (1951) *L. amphibius* is certainly due to the lateral compression of the specimen. Premaxillary-palatine contact was not observed in any other *Lystrosaurus* specimen.

Lystrosaurus murrayi (Huxley)

(Figs 75, 76, 77)

Dicynodon murrayi Huxley, 1859.

Lystrosaurus frontosus Cope, 1870.

Ptychognathus boopis Owen, 1876.

Ptychognathus verticalis Owen, 1876.

Lystrosaurus jeppe Van Hoepen, 1916.

Prolystrosaurus strigops Haughton, 1917.

Prolystrosaurus natalensis Haughton, 1917.

Type specimen: B.M.N.H. R.1291.

Locality: Colesburg District, C.P.

The skull in this species is short and deep and in lateral view presents a square appearance. In contrast to the condition in *L. declivis*, the flat anterior surface of the snout lies at right angles to the parieto-preparietal plane. As a result, the orbit lies relatively far forward in the skull.

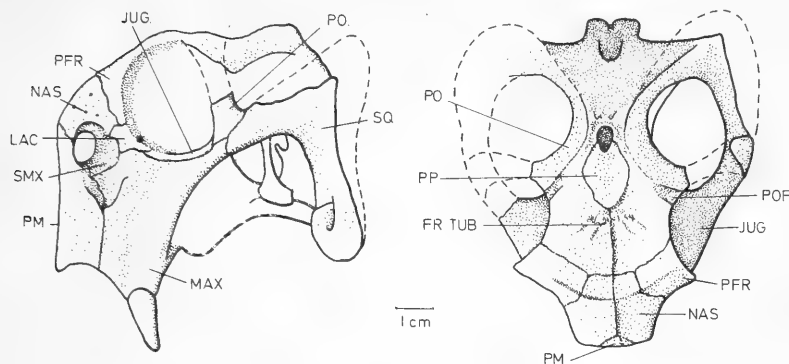


Fig. 75. *Lystrosaurus murrayi*. Nat. Mus. No. C.211. Skull in (a) lateral and (b) dorsal view.

The skull roof is characterized by the presence of a frontonasal ridge, frontal bosses and a radiating system of frontal ridges. In addition, there is a median, longitudinal ridge on the snout. As is the case in *L. declivis*, the dorsal skull roof is divided into a posterior parieto-preparietal plane and an anterior frontal plane, which slopes forward and down from the level of the frontal bosses. The anterior, plane surface of the premaxilla lies at right angles to the parieto-preparietal plane.

A variation, similar to one mentioned in *L. declivis*, occurs in the region anterior to the frontonasal ridge. In smaller individuals, such as C.211 with basal length of 84 mm (Fig. 75), the nasals together form a surface which slopes down from the ridge to meet the premaxillary plane at an angle, while in larger individuals such as C.282 with basal length 112 mm (Figs 76, 77), the anterior

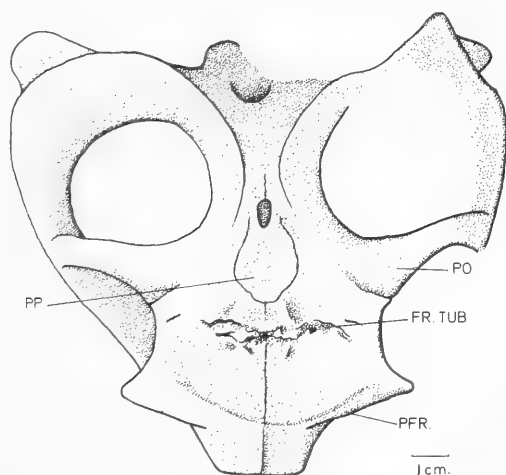


Fig. 76. *Lystrosaurus murrayi*. Nat. Mus. No. C.282. Skull in dorsal view.

two-thirds of the nasals are included in the premaxillary plane, so that the facial plane commences at the frontonasal ridge.

This variation appears to be correlated with the degree of prefrontal development and is probably an age phenomenon. Increase in the size of the prefrontal with increasing age and size appears to result in forward extension of the anterior orbital border, moving the frontonasal ridge forward and rotating the nasals until they come to lie in the premaxillary facial plane. This apparent straightening out of the snout results in the anterior border of the orbit lying relatively farther forward in larger specimens.

Brink (1951) is in error when he states that *L. murrayi* has no transverse ridge separating the facial from the frontal plane, since this was one of the features noted by Huxley (1859) in his description of the type skull. Both Broom (1932) and Brink (1951) have included *L. frontosus* under *L. murrayi*.

Transverse frontonasal ridges are present in *L. verticalis* and *L. boopis*. Lydekker (1890) placed the former under *L. murrayi*, while Brink (1951) included *L. boopis* under *L. declivis*. In 1916 Van Hoepen described six new species of *Lystrosaurus*, which Broom (1932) placed under *L. murrayi*. Brink (1951) stated that of these *L. jeppe*, *L. jorisseni* and *L. theileri* belonged under *L. murrayi*, but that *L. breyeri* is comparable to *L. oviceps*. Examination of these type specimens has shown that while *L. jeppe* is probably a dorsoventrally crushed *L. murrayi* with a frontonasal ridge, the specimens *L. wageri*, *L. jorisseni* and *L. theileri* probably belong under *L. curvatus*, and *L. wagneri* under *L. declivis*.

Haughton in 1917 created a separate genus, *Prolystrosaurus*, for two species,

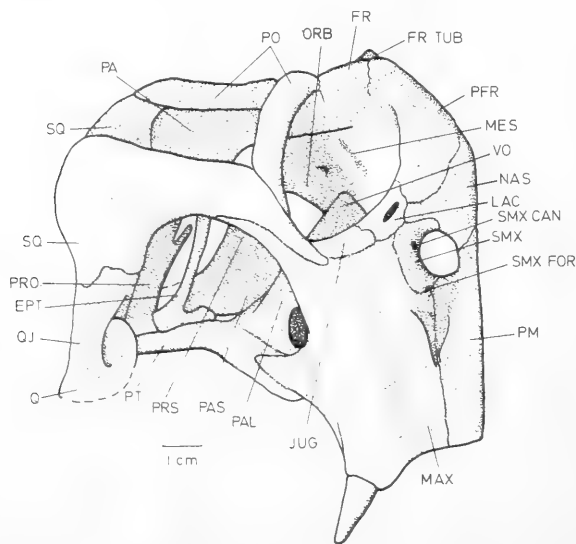


Fig. 77. *Lystrosaurus murrayi*. Nat. Mus. No. C.282. Skull in lateral view.

strigops and *natalensis*, which he claimed were ancestral to *Lystrosaurus*. Broom (1932) referred to these species as variants of *Lystrosaurus murrayi*. Brink (1951) also maintained that the two species were closely related to *L. murrayi*. Personal examination of both the type and co-type specimens of *Prolystrosaurus natalensis* and exposure of the median basicranial ossifications of the co-type showed that both specimens are badly dorsoventrally crushed. This is what Tripathi & Satsangi (1963) had supposed. The type specimen of *P. natalensis* is badly weathered and the nature of the skull roof cannot be determined, but the snout of the co-type specimen bears longitudinal ridges and there are indications of frontal tuberosities on the skull roof. The nasal region of the skull roof is not preserved, making it impossible to determine the presence of a frontonasal ridge. It does none the less seem justifiable to regard *Prolystrosaurus* as being founded on a crushed specimen of *L. murrayi*. It is here proposed that the species described by Haughton (1917) be included under *Lystrosaurus murrayi*.

Lystrosaurus putterilli Van Hoepen

Lystrosaurus putterilli Van Hoepen, 1915.

Type specimen: T.M. R.44.

Locality: Harrismith, Orange Free State.

This species is equal in size, and apparently closely related, to *L. mcCaigi*. Examination of the type skull and a second specimen, T.M. R.47, shows that there is a single parieto-preparietal-frontal plane on the skull roof, terminated by a transverse ridge at the level of the middle of the orbits. This transverse ridge appears to lie posterior to the nasals. The preparietal is large.

This species differs from *mcCaigi* only in the relationships of the nasals, which curve back from the premaxillary facial surface towards the transverse frontal ridge. The prefrontal bosses thus do not protrude forward of the facial plane as is the case in *L. mcCaigi*. At this stage it seems safest to regard *putterilli* as a distinct species.

Lystrosaurus rubidgei Broom

Lystrosaurus rubidgei Broom, 1940.

Type specimen: Rubidge Collection.

Locality: Bethesda Road Station, C.P.

The type skull is considerably crushed (Kitching, personal communication) but the presence of several unusual features seems to justify its retention, at least provisionally, as a separate species. The nasals are entirely included in the premaxillary facial plane. At the same time the frontals and nasals form an interdigitating suture, with the frontals passing far down between the nasal and and prefrontal.

Apparently there is no frontonasal ridge and the species may therefore be allied to *L. platyceps*. Broom (1940) and Brink (1951) regard the forward frontal

extension of the species as unusual for *Lystrosaurus*, but this feature has been found to be common in the branch comprising the smooth-skull-roof types.

SPECIATION IN *LYSTROSAURUS*

Soon after the emergence of the typical *Lystrosaurus* skull form, speciation apparently occurred in two main directions within the genus. One group of species, including *L. curvatus* and *L. platyceps*, retained the smoothly rounded skull roof of its presumably dicynodontid ancestors, while the other group, including *L. declivis*, *L. murrayi* and *L. mcCaigi*, developed longitudinal ridges on the snout, a transverse frontonasal ridge between the facial and frontal planes, and a pair of prominent bosses, with a system of radiating ridges, on the frontals. This second group comprises more species than the first, and the majority of *Lystrosaurus* specimens recovered from the Karoo are included in it.

A certain parallelism exists in the trends shown within the two groups. Thus in both lines of evolution the tendency is for stronger snout development, with *L. platyceps* representing the extreme condition in one group, and *L. McCaigi* the extreme in the other.

In both groups, again, increased snout development is accompanied by a tendency for increased inclusion of the nasal in the facial plane of the premaxilla. The stage of complete nasal inclusion was achieved by only one species in each line, *platyceps* in the one and *mcCaigi* in the other.

L. curvatus appears to be morphologically the most primitive of all species of *Lystrosaurus*, and differs from the typical *Dicynodon* only in the shortening of the basicranial axis and deepening of the snout, basic features of all species of *Lystrosaurus*. While clearly related to *L. bothai* and *L. platyceps*, *L. curvatus* also contains individuals with transverse frontonasal sutures and more strongly developed snouts. These individuals form a morphological link with *L. oviceps*, with a frontonasal ridge and strong tusks. The succeeding species, such as *murrayi* and *declivis*, are characterized by the presence of the frontonasal ridge, frontal bosses and increasingly strong development of the snout, of which the anterior surface is always a flat plane, broken only by a longitudinal ridge.

These features were used in the construction of the following diagrammatic scheme of the morphological relationships between the various *Lystrosaurus* species. This scheme very likely does not represent true phylogenetic relationships, neither do the indicated morphological levels represent horizons within the Triassic. It appears that the primary radiations of *Lystrosaurus* into its various species took place before South African *Lystrosaurus* zone times. Thus a species such as *L. mcCaigi*, which is represented in the scheme as a morphologically advanced species, apparently flourished in basal *Lystrosaurus* zone times, and was poorly represented in later periods. However, on the basis of available information, it was not possible to ascribe any other species with certainty to a particular horizon within the *Lystrosaurus* zone.

In this assessment of the species of *Lystrosaurus*, nine of Brink's (1951) South African species of *Lystrosaurus* are retained, these being *curvatus*, *bothai*, *platyceps*,

oviceps, *declivis*, *mcCaigi*, *murrayi*, *putterilli* and *rubidgei*. The species *andersoni* and *amphibius* of Brink's scheme have been included under *platyceps*, and *mcCaigi* respectively, while the species *verticalis*, *natalensis* and *strigops* have been included under *L. murrayi*.

L. putterilli. Facial plane does not include nasal, which slopes back to frontal ridge.

L. mcCaigi. Facial plane includes entire nasal, slopes down from frontal ridge.

L. murrayi. Facial plane sloping steeply down from ridge, frontal bosses, facial plane at right angles to parietal plane.

L. declivis. Flat facial plane, slopes forward from ridge, nasal partly in facial plane, frontal bosses.

L. platyceps. Snout strong, nasal included in facial plane, snout and skull roof surfaces smooth.

L. oviceps. Weak frontonasal ridge, strong, curved, snout, frontal bosses.

L. bothai. Snout strong, smoothly curved into skull roof, interdigitating fronto-nasal suture.

L. curvatus. Snout relatively weak, skull roof and snout smoothly curved, frontonasal suture interdigitating or transverse.

Permian dicynodontid sp.
Snout weak, snout and skull roof smoothly curved.

LYSTROSAURUS FROM INDIA, CHINA AND RUSSIA

Although the Middle Beaufort beds of South Africa have yielded the vast majority of known *Lystrosaurus* specimens, representatives of the genus have been recovered in areas as far afield as Bengal in India, Sinkiang in China and Luang Prabang in Indo-China (Laos). In addition (Colbert, personal communication; Elliot, *et al.*, 1970) specimens of *Lystrosaurus* have very recently been located in Antarctica. Of these three regions, the Panchet series of the Raniganj coalfields, Bengal, have provided a considerable number of specimens. The first specimens from this area were described as *Dicynodon orientalis* by Huxley (1865), but Lydekker, realizing the true affinities of the form (1879), placed the species successively under Owen's *Ptychognathus* (1887) and his own *Ptychosiagum* (1890). Das Gupta (1922) first used the name *Lystrosaurus* for the Indian specimens.

Tripathi (1960) and Tripathi & Satsangi (1963) have produced recent publications dealing with the fauna of the Panchet series, and have given a comprehensive (1963) account based on a large collection of *Lystrosaurus* from the Panchet beds. They maintain that the Panchet sediments are identical with the Middle Beaufort beds of South Africa, and have identified several South African species of *Lystrosaurus*, namely, *L. murrayi* (*sensu* Broom, 1932), *L. platyceps* and *L. mcCaigi*. In addition, they distinguish a new species, *L. rajurkari*, which they regard as being one of Broom's 'female' specimens, and which appears to be related to the *curvatus-platycephus* group.

The *Lystrosaurus* fauna from Sinkiang province has been described by Yuan & Young (1934), Young (1935, 1939) and Sun (1964). Four species have been recognised, namely, *L. broomi* (Yuan & Young, 1934; Young, 1939), *L. hedinii* (Young, 1935), *L. weidenreichi* (Young, 1939) and *L. youngi* (Sun, 1964).

L. broomi was originally described (Yuan & Young, 1934) as *L. murrayi*, but Young later (1939) considered that its wide geographical separation from the South African Middle Beaufort beds, coupled with the unusual dorsal process of the lacrimal between nasal and prefrontal, pointed to its being a distinct species. Young mentions rough crests on the skull, and indications are that the species has affinities with the *murrayi-declivis* group of South African lystrosaurids.

L. hedinii differs from all other known lystrosaurids in the remarkable embayment in the lateral palatal rim. A resemblance to *L. putterilli*, noted also by Brink (1951), is the apparent presence of a transverse ridge across the middle of the orbits. This species is probably also allied to the *murrayi-declivis* group of South African lystrosaurids.

L. weidenreichi is known largely from postcranial skeletal remains, and comparison with other forms is difficult. *L. youngi* (Sun, 1964) closely resembles the South African *L. curvatus*.

Yuan & Young (1934) state that *Dicynodon incisivum* (Repelin, 1923) from Luang Prabang, Indo-China, is clearly a *Lystrosaurus*, but too poorly preserved for comparisons.

Efremov (1938, 1940) has described *Lystrosaurus klimovi* from the Dongus River, Orenburg Province, U.S.S.R. Although very incomplete, it can be seen that the skull possesses an apparently narrow intertemporal region, while the interorbital region on the other hand appears to be remarkably broad. Efremov (1951) subsequently placed this specimen in a new genus, *Rhadiodromus*.

While the presence of *Lystrosaurus* (including South African species) in India can be explained in terms of Gondwanian affinities, the occurrence of the genus in regions such as Luang Prabang, Sinkiang (and Russia?) points to a geographical distribution which was not confined to within the borders of a southern Gondwana continental mass. The Sinkiang species *broomi* and *hedini*, while possessing structural peculiarities in the skull, are clearly typically lystrosaurian, and there is thus a possibility that *Lystrosaurus* may have arisen in regions to the north of the South African Karoo basin or the Indian Panchet successions.

SECTION VI. THE ORIGIN OF *LYSTROSAURUS* FROM A PERMIAN ANCESTOR AND ITS RELATIONSHIPS WITH SOME OTHER TRIASSIC DICYNODONT GENERA

In the past, various authors have made references to the question of the phylogenetic descent of *Lystrosaurus* from a Permian ancestor, and several dicynodont species have in fact been singled out as possible ancestral forms. Thus Houghton (1917) thought that *Dicynodon testudirostris* foreshadowed *Lystrosaurus* in the lengthening of the premaxilla and maxilla, and the 'bending down' of the snout, and Broom (1932) suggested that since *Dicynodon gilli* of the *Cistecephalus* zone approached *Lystrosaurus* in so many characters, it could very well be close to the ancestral form of that genus. Broom did not elaborate on the lystrosaurian features of *D. gilli*, but the large orbits and slightly shortened temporal fossae are certainly reminiscent of *Lystrosaurus*, and, in addition, the basicranial region resembles that of *Lystrosaurus* in the presence of an intertuberal ridge. However, features which preclude this species from the direct ancestry of *Lystrosaurus* are the contact between the premaxilla and frontals, the small prefrontal and the near-contact between the postorbitals in the intertemporal region.

Toerien (1953, 1955) argued that *Dicynodon* is the most likely ancestor of *Lystrosaurus*, the palate of *Lystrosaurus* being a modification of that of *Dicynodon*, and in 1954 he described a new species of *Lystrosaurus*, *L. primitivus*, which he regarded as being very similar to the Russian *Dicynodon annae*. Camp (1956) similarly suggested that *D. annae* might be close to the ancestry of *Lystrosaurus*.

Comparison of *Lystrosaurus* with other, Permian and Triassic dicynodonts shows that, firstly, some features of the *Lystrosaurus* skull are foreshadowed in various groups of Permian dicynodonts, and secondly, *Lystrosaurus* has several characteristics in common with other Triassic dicynodont groups.

Examples of the first instance are the intertuberal ridge and shortened

temporal fossa in *Dicynodon gilli* and short temporal fossa, steeply downturned snout and overall deepened skull in species such as *Diictodontoides skaios* (Watson, 1960). In *Daptocephalus* the snout is increased in length (as is common in all descendants of *Dicynodon*, including *Lystrosaurus*, cf. Toerien, 1955), and the pterygoid has gained contact with the premaxilla, as is the case in *Lystrosaurus*. A further resemblance to *Lystrosaurus* is the labial fossa in the *Daptocephalus* snout.

In terms of functional morphology, the masticatory cycle of *Lystrosaurus* represents a modification of an essentially similar cycle in *Dicynodon*. In contrast to forms such as *Emydops*, the premaxillary and maxillary palatal rim in both *Dicynodon* and *Lystrosaurus* has been ventrally extended in front of the canine tusk as a sharp cutting blade, against which the lateral surface of the dentary symphysis acts to produce a slicing action during the masticatory cycle.

In the second instance, several points in the cranial anatomy of *Lystrosaurus* indicate that the genus is affiliated to other Triassic dicynodont groups. A review of the exact relationships and evolution of the Triassic dicynodont groups (Cox, 1965) would be outside the scope of this work, and has not been attempted here. Neither is such a review necessary for the present purpose, which is simply to demonstrate various structural similarities between *Lystrosaurus* and some later Triassic dicynodonts.

In *Kannemeyeria*, as shown above, the pterygoid is produced forward to meet the maxilla, in much the same way as in *Lystrosaurus*. More striking is the similarity of structure of the interpterygoidal fossa in *Lystrosaurus* and other Triassic dicynodonts (Cox, 1965) such as *Kannemeyeria*, *Tetragonius njalilus* (Cruickshank, 1967), *Stahlekeria potens* from South America and *Placerias gigas* from North America (Camp & Welles, 1956). In Permian dicynodonts such as *Emydops* and *Dicynodon* the interpterygoidal vacuity is long and extended dorsally to the level of the roof of the choana, whereas in a Triassic form such as *Lystrosaurus* the vacuity is reduced to a small fossa in the basicranial girder, bounded posteriorly by the pterygoids and anteriorly by the vomer. As stated in Section IV, the shortened interpterygoidal vacuity of *Lystrosaurus* is regarded as an advance over the condition in *Emydops* and *Dicynodon*, and is the result of adaptive specializations, principally shortening of the basicranial axis, in the skull.

Camp's (1956) work is of importance here, since he discusses certain features which, he considers, indicate a fairly close relationship between *Kannemeyeria*, *Placerias* and *Stahlekeria*, and which led him to include the three genera in a family, the Kannemeyeriidae. These features include:

- pterygoid-maxilla contact;
- reduction of ectopterygoid;
- reduction of interpterygoidal vacuity.

To these characteristics could be added:

- absence of a floccular (sub-arcuate) fossa;
- posterior position of presphenoid;
- presence of labial fossa.

All six of these features are characteristic of *Lystrosaurus*, the condition of the interpterygoidal vacuity and parasphenoid being especially significant, since it suggests that some shortening of the basicranial axis has taken place in *Kannemeyeria*, *Placerias* and *Stahlekeria*. That this is so is further indicated by the relatively posterior position of the sphenethmoid complex in these genera.

Camp's (1956) illustrations show that in *Stahlekeria* and *Placerias* arching down of the snout on the basicranial axis has taken place. The ventral position of the feeding plane is arrived at in a manner analogous to that in *Lystrosaurus*, since it is the result of simple downwards flexure of the skull axis, which does not involve deepening of the vomer and premaxilla and which carries the nasal opening down with it. In contrast, the nasal aperture in *Lystrosaurus* has retained its primitive position relative to the foramen magnum.

In *Placerias* and *Stahlekeria* the high posterior position of the areas of origin of the adductor musculature is very possibly correlated with the ventral orientation of the snout, in much the same way as deepening and extreme shortening of the *Lystrosaurus* skull has been shown to be the result of ventral displacement of the palate, so that an effective angle of traction on the mandibular axis is maintained. The ventral extension of the quadrate process of the squamosal, effecting a lowering of the suspensorium, may be regarded as a further compensation in *Placerias* and *Stahlekeria*.

In *Kannemeyeria*, where the basicranial axis is shortened but only slightly arched, the parietal, supraoccipital and interparietal are greatly thickened and the areas of external adductor muscle attachment on the squamosal are raised, but the quadrate is not lowered to the same extent as, for example, in *Stahlekeria*, where the skull is least extended above the foramen magnum and the quadrate is in a more ventral position than in the other two 'kannemeyeriid' genera.

There are thus several respects in which *Lystrosaurus* resembles Camp's three kannemeyeriid genera, the most significant of these being shortening of the basicranial axis, pterygoid-maxilla contact, a tendency for ventral displacement of the palate, reduction of the interpterygoidal vacuity and deepening of the posterior moiety of the skull. With regard to the postcranial anatomy, Cruickshank (1964) has noted similarities in the interclavicle of *Lystrosaurus* and later Triassic dicynodonts, and states that in this respect *Lystrosaurus*, while retaining certain features of Permian dicynodonts, also resembles succeeding Triassic dicynodonts. However, the ulna in *Lystrosaurus* does not possess a separately ossified olecranon process, a feature of the later Triassic Dicynodontia (Cox, 1965).

In a later (1967) publication, Cruickshank considers that *Tetragonius njalilus* of the East African lower Middle Triassic is a connecting link in an evolutionary sequence leading from *Lystrosaurus* to *Kannemeyeria*. In support of this view he cites several characters which the genera have in common, namely, similar palatal regions, square shape of the skull in dorsal view, absence of the ectopterygoid, similar ilia, 'W'-shaped naso-frontal suture, large tusks and expanded maxillary flanges. Furthermore, he demonstrates that *Tetragonias*

resembles *Kannemeyeria* in the narrow intertemporal bar, abbreviated post-orbitals, and prespinous fossa in the scapula.

Against this theory is the fact that the main points of similarity between *Lystrosaurus* and *Tetragonias*, i.e. the pterygoid-maxilla contact and the reduced interpterygoidal vacuity, are characters which appear to be widespread among Triassic dicynodont genera and need not indicate a special relationship between *Lystrosaurus* and *Tetragonias*. Furthermore, it seems improbable that any species of *Lystrosaurus*, highly specialized in the very deep median septum in the snout region, the correspondingly deepened premaxilla and the extremely shortened basicranial axis and temporal fenestrae, could give rise to a form like *Tetragonias*, with a weak snout and long temporal fenestrae. Without any information regarding the basicranial axis and the position of the sphenethmoid complex in *Tetragonias*, it is not possible to determine whether shortening or flexure has taken place in this region, although the reduced interpterygoidal vacuity could perhaps be regarded as an indication of such shortening. Certainly, more definite morphological similarities must be uncovered before the idea of a close relationship between *Lystrosaurus* and *Tetragonias* can be fully accepted.

From a comparison of the above groups of Triassic dicynodonts, it seems reasonable to accept that genera such as *Lystrosaurus*, *Kannemeyeria*, *Placerias*, *Stahlekeria* and most probably also *Tetragonias* and *Dinodontosaurus* arose from a single Permian ancestral group, and that these genera, although geographically diverse, retained a basic similarity of skull morphology, in characters such as the presence of a labial fossa, the pterygoid-maxilla contact, shortening of the basicranial axis and interpterygoidal vacuity and a tendency in some for ventral displacement of the palate.

Early in the evolution of this group of Triassic dicynodonts *Lystrosaurus* diverged from the main line of development to become adapted to an aquatic existence. Although a highly specialized and distinct group, it retained several characteristics which were apparent in later survivors of the original basic Triassic stock.

If *Lystrosaurus* can in fact be regarded as a specialized representative of a main line of dicynodont development, the search for its ancestral form can be narrowed down to Permian groups which provide indications of the changes undergone by the Triassic genera. In this connection the Upper Permian dicynodontid (*sensu* Haughton & Brink, 1954; Romer, 1966) genus *Daptocephalus* is of significance. Here the interpterygoidal vacuity is in the process of becoming separated from the choana proper, and is shorter than that of other Permian dicynodonts. This character reflects the tendency in Triassic dicynodonts for reduction of the interpterygoidal vacuity. Furthermore, *Daptocephalus* has a well-developed labial fossa, the presphenoid arises fairly far back in the basicranial axis, and the pterygoid makes contact with the maxilla. The narrow intertemporal bar and long temporal region in *Daptocephalus* make it an unlikely direct ancestor for *Lystrosaurus* at least, but it is very likely that *Daptocephalus* stands near the ancestral stock of the Triassic dicynodonts.

In conclusion it can be said that several features in the cranial anatomy of *Lystrosaurus* had been established in its Permian predecessors, and since several of these features are also characteristic of other Triassic genera, it seems likely that *Lystrosaurus* arose as an early offshoot of a main line of Triassic dicynodont development. Although no specific Permian dicynodont can as yet be pointed out as a direct ancestor of the later dicynodonts, extrapolation back into the Permian of trends seen in Triassic dicynodonts makes it reasonable to assume that such an ancestral form had many of the characteristics of *Daptocephalus*, but had retained a fairly broad intertemporal region.

Whether this hypothetical ancestral form was present in the South African Permian, or whether *Lystrosaurus* and *Kannemeyeria* represent migratory descendants of a geographically distant ancestor, must at present remain uncertain.

CONCLUSIONS

THE BASICRANIAL AXIS

Four elements have been identified in the basicranial axis of *Lystrosaurus*, namely, basioccipital, basisphenoid, presphenoid and mesethmoid. Furthermore, it is concluded that a further ossification, the orbitosphenoid, has secondarily invaded the basicranial axis.

Broom (1927) concluded that the therapsid basicranial axis consisted of three median ossifications only, and divided the mammals into two groups, the Palaeotherida (with three basicranial elements) and the Neotherida (with four basicranial elements). According to Broom, the Neotherida had gained an extra ossification in the basicranial axis. If *Lystrosaurus*, on the other hand, is typical of the therapsids, the premammalian basicranial axis included a presphenoid and mesethmoid anterior to the basisphenoid.

It seems that the critical factor in these considerations is the nature of the bone referred to here as presphenoid. Broom (1927), who was in any case not justified in comparing the Mammalia with a therapsid as aberrant as *Dicynodon* (Parrington & Westoll, 1940), was also mistaken, it seems, in assuming that the presphenoid in *Dicynodon* was a forward extension of the basisphenoid. An apparently similar basisphenoidal extension has been described in the insectivore *Eremitalpa* (Roux, 1947), but the two instances do not appear to be comparable. Thus in *Lystrosaurus* the presphenoid is clearly part of an extensive interorbitonasal septum and was continued dorsally and anteriorly in cartilage. Moreover, this septum is clasped ventrally by the clearly distinguishable cultriform process of the parasphenoid. These two features are clearly reptilian, and the inference must be that the septum arose ontogenetically from fused trabeculae. The dicynodont septum, as exemplified in *Lystrosaurus*, would rather appear to be homologous with the interorbital septum of mammals such as the rabbit and *Ornithorhynchus* (De Beer & Woodger, 1930; Haines, 1950), where the septum arises from fused trabeculae as in *Lacerta*.

This is in agreement with the findings of Olson (1944) and Camp & Welles (1956), who demonstrate that in dicynodonts and other therapsid groups the presphenoid is independent of the basisphenoid and in all likelihood arose in a cartilage derived from the fused trabeculae. From this same cartilage the dorsally situated mesethmoid probably arose. Olson assumes that the mesethmoid of therapsids is lost in some mammal groups (Broom's Palaeotherida).

It may therefore be concluded that Roux's (1947) statement that there are but three centres of ossification in the basicranial axis of all vertebrates is incorrect, and that the four ossifications which appear to be present in the therapsid basicranial axis were inherited by certain mammals, such as those described by De Beer & Woodger (1930) and Haines (1950), where a true interorbital septum, in the position of the therapsid presphenoid, is present. Haines (1950) has shown that a bony interorbital septum is present in several mammals, and defines the mammalian presphenoid as being the bone in the adult skull which, separate in most mammals, ossifies from presphenoid and orbitosphenoid centres.

In a therapsid such as *Lystrosaurus* the orbitosphenoid, arising from the orbital cartilages, has invaded the basicranial axis in the form of a well-developed septum, separated from the presphenoid by cartilage. Roux (1947) has shown that a similar median migration of orbitosphenoid ossification centres occurs in the primitive mammals he investigated. Although the orbitosphenoid bone in therapsids does not generally enclose a complete optic foramen, it has been concluded that (p. 176) the element was continued posteriorly in cartilage, so that the optic notch, in for instance *Lystrosaurus*, would have been closed off from behind to form a complete optic foramen.

Expansion of those portions of the brain supported by the therapsid orbitosphenoid would result in lateral and ventral displacement of this element, with subsequent merging with, or obliteration of, the presphenoidal septum. A fusion between the two elements would result in a compound element with the relations of the mammalian presphenoid as defined by Haines (1950). By this analysis, the dicynodont basicranial axis is of a primitive reptilian pattern.

The validity of this interpretation of the basicranial axis of therapsids as compared with that of mammals is, basically, dependent on the nature of the bone in therapsids referred to here as the presphenoid. If the presphenoid is indeed a discrete element, then the therapsids have four median ossifications in the basicranial axis, one of which may be suppressed in some mammals. On the other hand, if the presphenoid is an anterior extension of the basisphenoid, as Cox (1959) believes, then therapsid structure does not truly foreshadow the condition in mammals.

At present the evidence appears to favour the view that the therapsid basicranial axis is of an essentially reptilian type, with an extensive interorbital septum arising from the fused trabeculae and containing two ossifications anterior to the basisphenoid.

THE SOFT STRUCTURES OF THE SNOUT

The interior of the snout region of *Lystrosaurus* has provided evidence of several of the unpreserved structures of the nasal capsule. It seems likely that the mesethmoid was continued anteriorly beneath the frontal and nasal surfaces as a pair of cartilaginous sphenethmoidal commissures, in a direction indicated by a pair of ridges on the inside of the skull roof. On the other hand, Kemp (1969a) has mentioned the possibility of these ridges in therapsids being evidence for the presence of turbinals.

Furthermore, it seems probable that the ventral edge of the cartilaginous nasal septum was received by the grooved dorsal edge of the premaxillary median septum. This being the case, the nasal capsules were located relatively high in the snout, and a pair of choanal tubes, such as suggested by Kemp (1969a), must have led from the nasal capsules to the oral cavity through the choanae.

In addition, the courses of the ducts of Jacobson's organ, the lacrimal gland and the lateral nasal gland have been suggested. The duct of Jacobson's organ lay in a groove alongside the premaxillary median septum and opened into the choana through the anterior choanal notch between the premaxilla and maxilla. The course of the nasolacrimal duct within the nasal cavity appears to be clearly marked. A deep sulcus leads from the internal opening of the lacrimal canal to the internal opening of the septomaxillary canal, which penetrates the body of the septomaxilla, and it seems certain that the nasolacrimal duct emerged through this canal and opened into the external nasal aperture. Moreover, that this was the case among therapsids generally, is indicated by the close relationship between septomaxilla and nasolacrimal duct in *Dasypus* (Fuchs, 1911).

Furthermore, it is concluded that the maxillary antrum, which is of variable occurrence among dicynodonts, contained a diverticulum of the nasal chamber.

THE JAW AND NECK MUSCULATURE

In order to clarify the nature of the adaptive changes undergone by the *Lystrosaurus* skull, the jaw and neck musculatures were reconstructed and the possible range of movements at the jaw joint and in the neck region determined.

In the jaw musculature, lateral and medial external adductor muscles, anterior and posterior pterygoideus muscles and a depressor mandibulae muscle have been restored. It appears that Crompton & Hotton (1967) are correct in their view that the external adductor muscle mass was divided into lateral and medial groups, and that the medial group inserted in the dorsal dentary groove. There is also the possibility that a portion of the medial group inserted in the normal way in the Meckelian fossa. The masticatory cycle permitted by this musculature would have included slicing, such as proposed by Crompton & Hotton (1967), between the lower and upper beaks in front of the mouth. In addition to the slicing action, this investigation has indicated that

a degree of crushing and grinding between horny pads on the upper and lower jaws took place farther back in the mouth during a later stage of the cycle.

A similar restoration of the musculature in the neck region suggests that *Lystrosaurus* had retained a basically primitive system of occipital and atlanto-axial muscles. However, this essentially reptilian musculature was modified to allow a degree of flexure and extension at the atlanto-occipital joint, as indicated by the posteriorly projecting exoccipital condyles, as well as a certain amount of rotation at the atlanto-axial joint, as indicated by the reduced atlas-axis zygapophyseal articulation. Kemp (1969*b*) has shown on purely mechanical and geometrical grounds that these movements are possible in the specimen of *Lystrosaurus* which he examined.

Comparison of the atlas in *Seymouria*, the pelycosaurs, dicynodonts and cynodonts has shown that the modest degree of rotation between the atlas and axis was most probably accomplished by a lateral migration of the insertion area of the m. obliquus capitis caudalis, resulting in the formation of the dorsal process of the atlas, which Cox (1959) had regarded as the homologue of the neural spine. The m. obliquus capitis cranialis arose from the vertical transverse process of the atlas. Thus, while *Lystrosaurus* was functionally foreshadowing typically mammalian movements in the occipito-cervical region, the musculature involved remained essentially primitive.

ADAPTIVE CHANGES IN THE SKULL

Comparison of the skull of *Lystrosaurus* with the skulls of Permian dicynodonts indicates that shortening of the basicranial axis and deepening of the skull, especially in the snout region, are the main modifications in *Lystrosaurus*. These two processes have affected the orientation and relative position of the nasal capsules and respiratory passages, the position of the presphenoid and orbitosphenoid, the morphology of the hypophyseal region and palate, and the orientation of the brain.

Most significant, however, are the effects of skull shortening and deepening on the external adductor musculature. Lowering of the anterior palatal region in a dicynodont would tend to decrease the arc through which the lower jaw could be rotated back to its maximum gape. Since the size of the gape is determined by the direction and position of fibres of the external adductor muscles relative to the quadrate-articular contact, any disadvantageous reduction of the gape size due to deepening of the snout would have to be compensated for by modifications in the external adductor muscles. Comparisons with *Emydops* and *Dicynodon* have shown that, with the jaw in the protracted, adducted position, the combined retractive forces of the adductor musculature are exerted at a greater angle to the jaw axis in *Lystrosaurus* than in other dicynodonts.

Furthermore, when the skulls of a Permian dicynodont (such as the endothiodontid *Emydops*) and *Lystrosaurus* are compared with the mandibles swung back to the point of maximum gape, as determined by the lateral exter-

nal adductor muscles, it can be seen that the areas of origin of the external adductor musculature in *Lystrosaurus* allow the mandible to be rotated back relatively farther than in Permian dicynodonts. Consequently, although the palatal surface is relatively lower, the size of the gape in *Lystrosaurus* remains comparable to that of typical dicynodonts.

A second effect that simple snout deepening would have on the dicynodont masticatory cycle would be that, due to the steep angle at which the adducted mandible would lie in relation to the reference plane of the skull, the jaw adductor muscles would exert a very oblique tractive force on the jaw axis. Consequently, the tendency for horizontal retraction of the jaw would be vastly increased, at the expense of the vertical component of force, which is especially responsible for the crushing of food against the palate.

These comparisons, taken together with the fact that *Lystrosaurus* was almost certainly committed to an aquatic mode of life, suggest that the characteristic skull proportions in *Lystrosaurus* arose primarily in response to new feeding requirements, which involved a lowered food-gathering level. As a result, deepening of the snout below the level of the nostril took place. Concomitant changes in the orientation of the adductor musculature were essential if a suitable gape and an effective masticatory cycle were to be maintained, and in compensation for snout deepening, shortening of the basicranial axis and deepening of the temporal region of the skull took place. These two changes, effecting an anterior displacement of the areas of origin of the adductor musculature relative to the areas of insertion, ensured that an effective traction force was maintained on the jaw axis, while they at the same time permitted the mandible to be rotated farther back.

DIVISION OF THE SPECIES

Investigation into the pronounced cranial variation within the genus indicates that such variations are due to differences in proportional development of various common structures, and do not affect the basic, functionally integrated skull form. It seems that once the successful adaptive changes had been brought about, speciation in *Lystrosaurus* took place in two roughly parallel directions. While one group of species retained the smooth skull roof of typical Permian dicynodonts, the second group developed prominent ridges and bosses on the snout and dorsal skull roof. In each group there is a tendency for increased deepening of the snout, resulting in eventual inclusion of the nasal into the general premaxillary facial plane.

RELATIONSHIPS WITH OTHER DICYNODONT GENERA

This investigation has shown that *Lystrosaurus* closely resembles later genera of Triassic dicynodonts, which, collectively, are in several respects morphologically distinct from Permian dicynodonts. *Lystrosaurus* appears to have diverged from the main Triassic dicynodont stock very shortly after the emergence of this stock during the Permo-Triassic transition. Although the genus is highly

specialized, features such as the pterygoid-maxilla contact, the presence of the labial fossa, the shortened basicranial axis and reduced interpterygoidal vacuity, as well as the absence of the ectopterygoid and floccular fossa, link *Lystrosaurus* with other geographically widespread Triassic genera such as *Kannemeyeria*, *Placerias* and *Dinodontosaurus*. On the other hand, the South African Upper Permian genus *Daptocephalus* appears to foreshadow the Triassic dicynodont assemblage in that it possesses several of the above-mentioned cranial features, but its narrow intertemporal crest makes it an unlikely ancestor for *Lystrosaurus*.

While the position of *Lystrosaurus* relative to the Permian and Triassic dicynodont assemblages seems reasonably clear, more exact information regarding its geographical region of origin and its most likely ancestor is lacking. Since representatives of the genus are also found in India, Indo-China, northern China and recently Antarctica, it is clear that *Lystrosaurus* was a geographically widespread group, and there is no definite indication of its having arisen in the South African Karoo. Its occurrence in the Panchet rocks of India, which are lithologically very similar to the South African Middle Beaufort beds, suggests that the Indian subcontinent was in close proximity to southern Africa in Eo-Triassic times. However, the presence of *Lystrosaurus* in the Chinese Triassic of Sinkiang shows that the distribution of the genus included areas outside of the Gondwanaland supercontinent. The chances of *Lystrosaurus* actually having arisen in these northern regions appear to be remote, but the fact that in the South African *Lystrosaurus* zone the apparently morphologically advanced species occur mainly in the basal layers certainly does point to a migration into this area. On the other hand, the presence of *Daptocephalus* in the South African Upper Permian indicates that trends which could conceivably have culminated in the appearance of typical Triassic dicynodonts were present in the *Cistecephalus* zone of the Karoo.

SUMMARY

In this investigation attention was paid mainly to the comparative and functional anatomy of the skull of *Lystrosaurus*, a member of the aberrant, herbivorous mammal-like reptiles comprising the infraorder Dicynodontia.

Specimens of *Lystrosaurus* yielded much important information regarding the various braincase and sphenethmoidal ossifications, and allowed a reassessment of the problem of the number of ossifications in the therapsid basicranial axis. The evidence provided by serially sectioned and acid-prepared specimens of *Lystrosaurus* indicates that four such ossifications, namely the basioccipital, basisphenoid, presphenoid and mesethmoid were probably present in therapsids, and that this condition was inherited by the early mammals. In the snout region the positions of the cartilaginous sphenethmoidal commissures and nasal septum have been determined, as well as the courses of the ducts of the lateral nasal gland, Jacobson's organ and the lacrimal gland. It is concluded that in

therapsids the duct of the lacrimal gland penetrated or was closely associated with the septomaxilla, a condition which persists in primitive mammals.

A restoration of the musculature of the neck and occipital region has indicated the likely range of movements possible between the occipital condyles and the atlas, and within the atlas-axis complex. It can be shown that rotation of the atlas on the axis, as well as the dorsoventral flexure of the skull on the atlas, are movements which were acquired parallel to, and independently of, the same range of movements present in the more highly advanced mammal-like reptiles. A similar restoration of the jaw musculature and horn-covered areas of the upper and lower jaws has shown that the masticatory cycle of *Lystrosaurus* included highly efficient food slicing and crushing actions.

A consideration of the adaptive importance of several fundamental morphological characteristics of *Lystrosaurus* permitted a formulation of the evolutionary process by which the characteristic skull form of *Lystrosaurus* was arrived at. This process was shown to be closely connected with the functional requirements of the jaw adductor musculature.

Comparison of *Lystrosaurus* with earlier, Upper Permian dicynodonts, as well as with succeeding Triassic dicynodont genera, shows that *Lystrosaurus* resembles its Triassic successors in several important respects, but retains some primitive features of the Permian groups. It appears that *Lystrosaurus* diverged from the Triassic dicynodont stock at an early stage, and became rapidly adapted to an aquatic or semi-aquatic way of life.

It has been shown that, while pronounced sexual dimorphism may well have been present in several *Lystrosaurus* species, the genus may be more conveniently divided into two parallel groups of species. The less common, and presumably more primitive, of these two groups retained certain characters of their Permian forebears.

The South African species of *Lystrosaurus* have been compared with species from other parts of the world. While the presence of the genus in India, Indo-China and Antarctica can be explained in terms of continental drift, the Sinkiang species of *Lystrosaurus* indicate that the distribution of *Lystrosaurus* included areas to the north of the southern Gondwanaland continental mass.

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ABBREVIATIONS

A. AMP. REC.	— anterior ampullary recess, for ampullae of anterior and horizontal semicircular canals
A.C.	— auditory canal
ADD. FOS.	— adductor fossa
A. E. LAT.	— adductor externus lateralis muscle
A. E. MED.	— adductor externus medialis muscle
ANG.	— angular
ART.	— articular
AT. FAC.	— facet for atlas on odontoid
BAS.	— basisphenoid
BC. P.	— basicranial pit
BO.	— basioccipital
BPT. PROC.	— basipterygoid process
CH.	— ceratohyal
DEN.	— dentary
DEN. GR.	— dentary groove
DEP. MAND.	— depressor mandibulae muscle
ECT.	— ectopterygoid
EO.	— exoccipital
EO. FAC.	— facet on atlas for exoccipital
EPT.	— epipterygoid
EPT. FTP.	— epipterygoid footplate
FEN. OV.	— fenestra ovalis
F. M.	— foramen magnum
FR.	— frontal
FR. R.	— ridges on inner frontal surface

FR. TUB.	—	tuberosities on frontal
FTP. GR.	—	groove in epipterygoid footplate
GR. JAC. ORG.	—	groove for duct of Jacobson's organ
H. SC. C.	—	horizontal semicircular canal
HYP.	—	hypophysis
HYP. FOR.	—	foramen for 12th nerve
I.A.M.	—	internal auditory meatus
IC.	—	intercentrum
I.C.C.	—	internal carotid canal
IP.	—	interparietal
IPT. VAC.	—	interpterygoidal vacuity
I.R.	—	intertuberal ridge
JAC. DUCT NO.	—	notch in palate for Jacobson's organ duct
JUG.	—	jugal
JUG. FOR.	—	jugular foramen
L.	—	ledge in vestibule
LAB. FOR.	—	labial foramen
LAB. FOS.	—	labial fossa
LAC.	—	lacrimal
LAC. FOR.	—	lacrimal foramen
LAT. CON.	—	lateral articular condyle
LAT. DEN. L.	—	lateral dentary ledge
LAT. DEN. R.	—	lateral dentary ridge
LAT. DEN. SH.	—	lateral dentary shelf
LAT. H.V. CH.	—	lateral head vein channel
LAT. PAL. FOR.	—	lateral palatal foramen
LAT. PROC.	—	lateral process on atlas neural arch
L. DUCT	—	lacrimal duct
LONG. CAP.	—	longissimus capitis muscle
MAX.	—	maxilla
MAX. ANT.	—	maxillary antrum
MED. CON.	—	medial condyle of quadrate
MED. FAC.	—	facet on medial end of stapes
MES.	—	mesethmoid
NAS.	—	nasal
N.S.	—	neural spine
NUT. CH.	—	nutrient channel
OBL. C. CAUD.	—	obliquus capitis caudalis muscle
OBL. C. CR.	—	obliquus capitis cranialis muscle
OD.	—	odontoid
OD. FAC.	—	facet on atlas for odontoid
OP.	—	opisthotic
ORB.	—	orbitosphenoid
ORB. NAS. FEN.	—	fenestra between orbit and nasal cavity
P.	—	pocket
PA.	—	parietal
PA. FAC. AT.	—	proatlas facet on atlas
PA. FAC. EO.	—	proatlas facet on exoccipital
PAL.	—	palatine
PAL. PROC.	—	palatine process of pterygoid
P. AMP. REC.	—	ampullary recess for posterior semicircular canal
PAR. FOR.	—	parietal foramen
PAS.	—	parasphenoid
PAS. R.	—	parasphenoid rostrum
PBS. S.	—	parabasisphenoid sheet
PFR.	—	prefrontal
PIL. ANT.	—	pila antotica
PIN. ORG.	—	pineal organ
PM.	—	premaxilla

PO.	—	postorbital
POF.	—	postfrontal
POSTZ.	—	postzygapophysis
PP.	—	preparietal
PQ. C. NO.	—	notch for palatoquadrate cartilage
PRA.	—	prearticular
PRESZ.	—	prezygapophysis
PRO.	—	prootic
PRS.	—	presphenoid
PT.	—	pterygoid
PT. ANT.	—	pterygoideus anterior muscle
PT. F.	—	posttemporal fenestra
PT. GR.	—	groove on pterygoid
PT. PAR. FOR.	—	pterygoparoccipital foramen
PT. POST.	—	pterygoideus posterior muscle
Q.	—	quadrate
Q. FOR.	—	quadrate foramen
Q. GR.	—	quadrate groove
Q.J.	—	quadratojugal
Q. RAM.	—	quadrate ramus of pterygoid
Q. R. FAC.	—	facet for quadrate ramus of pterygoid
R. C. ANT.	—	rectus capitis anterior muscle
R. C. LAT.	—	rectus capitis lateralis muscle
R. C. POST. MAJ.	—	rectus capitis posterior major muscle
R. C. POST. MIN.	—	rectus capitis posterior minor muscle
REF. LAM.	—	reflected lamina
SA.	—	surangular
SMX.	—	septomaxilla
SMX. CAN.	—	septomaxillary canal
SMX. FOR.	—	septomaxillary foramen
SOC.	—	supraoccipital
SPL.	—	splénial
SQ.	—	squamosal
SSP. CAP.	—	semispinalis capitis muscle
STA.	—	stapes
T.	—	tusk
TAB.	—	tabular
TR. PROC.	—	transverse process
U.Z.	—	unossified zone
VEST.	—	vestibule
V.N.	—	venous notch
VO.	—	vomer
I	—	olfactory nerve
II	—	notch for optic nerve
VII	—	foramen for facial nerve
VII REC.	—	recess for opening of facial nerve
VII PAL	—	foramen for palatine branch of facial nerve
XII	—	hypoglossal nerve
B.P.I. No.	—	Catalogue number of the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg
Nat. Mus. No.	—	Catalogue number of the National Museum, Bloemfontein
S.A.M. No.	—	Catalogue number of the South African Museum, Cape Town
T.M. No.	—	Catalogue number of the Transvaal Museum, Pretoria

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