ON THE LYSTROSAURUS ZONE AND ITS FAUNA WITH SPECIAL REFERENCE TO SOME IMMATURE LYSTROSAURIDAE

By J. W. Kitching

In the past, collecting from the middle Beaufort Beds or Lystrosaurus zone has been badly neglected by field workers mainly due to the monotonous occurrence of the genus Lystrosaurus. Collecting has mostly been undertaken in such areas as the Harrismith Commonage, Oliviershoek Pass, Bergville or where there was a good possibility of finding either Thrinaodon, Glochinodontoides or other faunal remains more exciting than Lystrosaurus.

In outline the Lystrosaurus zone follows more or less the same pattern as the main Karroo Basin and the Stormberg series with the shape of a "heel" in the Cradock, Middelburg, and Nauwpoort districts, roughly straightening out towards Bethulie from where the width of the outcrops becomes narrower through the Orange Free State and Natal.

From a point in the Sneeuwberg Range, at Compass Berg, the zone can be followed to Middelburg, Nauwpoort, to the south east of Colesberg, on to Venterstad, Bethulie, Smithfield, Dewetsdorp, Thaba N'chu, Winburg, Senekal, Bethlehem and the Harrismith districts.

In the Harrismith-Bezuidenhouts Pass area the Lystrosaurus zone is overlain by an outlier of the Stormberg series, but it appears again on the Natal side in the Oliviershoek Pass, Bergville and Estcourt districts; it can thence be followed to the west of Nottingham Road to Impendle, Bulwer, Cedarville, Cathcart, Tarkastad and Cradock districts and back to Compass Berg.

In the Rhenosterberg Range to the west of Middelburg, Cape, the Lystrosaurus zone reaches a thickness of 1,000 feet, while in the Nauwpoort-Carlton Siding area a thickness of 1,200 feet was measured. From Nauwpoort the zone thins out considerably towards Venterstad and Bethulie where it is reduced to an overall thickness of about 500 feet. It persists at this thickness through the Orange Free State and Natal, but increases again to about 800 feet in the Tarkastad and Cradock districts.

There is no definite marker such as a consistent band or layer of sandstone anywhere between the top of the preceding Cistecephalus zone and the base of the Lystrosaurus zone, but there is a marked change in colour of the shales, mudstones and sandstones.

At the base of the Lystrosaurus zone the shales and mudstones are normally greenish-grey in colour, above which they alternate with bright coloured reddish-maroon and purple shales and mudstones, with a light bluish-grey medium grained to almost coarse grained felspathic sandstone. In comparison the dark bluish-green shales of the Cistecephalus zone occasionally alternate with red and
purple shales and mudstones, with yellowish, fine to medium-grained felspathic sandstone. In general the *Lystrosaurus* shales and mudstones are more variegated than those of the other zones.

The grey-green, reddish-maroon and purple shales of the *Lystrosaurus* zone are very soft and weather very rapidly. During rainy seasons when they are soaked, they become more like a sticky clay and completely lose their shaly nature. (Shales are defined here according to the "Principles of Physical Geology" by Arthur Holmes, 1944, p. 54.)

Lenticular masses of sandstones are very abundant measuring from eighteen inches to over five feet in thickness, indicating that the *Lystrosaurus* strata were in all probability laid down more rapidly and under wetter conditions than those of the preceding zones. In many areas, the top of the zone is indicated by a thick stratum of sandstone interbedded with thin bands of shale and mudstone.

Other factors that might also indicate a more rapid deposition of the *Lystrosaurus* beds include the presence of a mud pebble conglomerate at the base of almost every sandstone layer. A large proportion of these pebbles or nodules very frequently contain skull and skeletal fragments, most commonly those of the genus *Lystrosaurus*. Also, complete skeletons of *Lystrosaurus*, *Thrinaxodon* and *Lydekkerina* are frequently found completely embedded in hard grey-green calcareous nodules weathering out of the surrounding shales, as if these animals had been completely engulfed in mud.

To determine the top of the *Cistecephalus* and the base of the *Lystrosaurus* zones on the colours of the shales and mudstones only may not be an easy task for the untrained field worker, but through observations in the field the author has found that the genus *Daptocephalus* of the *Cistecephalus* zone is always more abundant where the *Lystrosaurus* zone is in close proximity. In many instances the first *Lystrosaurus* skull has been found *in situ* within 10 feet above the strata from which *Daptocephalus* has been removed.

In areas where there is a certain amount of relief the above can be a very misleading feature because the genus *Daptocephalus* has often been recorded as coming from the *Lystrosaurus* zone when in actual fact it has not been observed that the accompanying *Lystrosaurus* zone fauna has either been washed or has rolled down from the slope or gradient above, the higher strata belonging to *Lystrosaurus* zone.

At the following localities it is known that both the *Cistecephalus* and *Lystrosaurus* zones are exposed:

- Afdeel Native Trust, Polela, Bulwer, Natal.
- Beskuitfontein, Venterstad, Cape.
- Bethulie Commonage.
- Bluegum House, Graaff-Reinet.
- Diepkloof, New Bethesda, Graaff-Reinet.
- Droogefontein, Bethulie.
- Eerstestap (Part of Elswald), Burghersdorp.
- Ennersdale, Estcourt, Natal.
Not only does a lithological change take place at the incoming of the *Lystrosaurus* zone strata, but also in the fauna. The large variety of forms from the preceding *Cistecephalus* zone almost disappears completely except for a few genera such as *Moschorhinus*, *Ictidosuchops*, *Tetracynodon*, *Nanictosaurus*, *Galeophrys* and the amphibian *Lydekkerina*. The abundant and common Dicynodont fauna of the *Cistecephalus* zone is replaced by only two anomodonts—the comparatively large and very abundantly represented genus *Lystrosaurus* and the small *Myosaurus*. The latter is represented by eight well preserved skulls and to date all have come from the old Brickfield Dongas on the Harrismith Commonage.

The diapsid *Chasmatosaurus*, now better known from eight skulls and skeletal elements, eight genera of specialised cynodonts, the two large amphibians *Uranocentrodon* and *Laccocephalus*, and the small comparatively abundant *Lydekkerina huxleyi* constitute the bulk of the known *Lystrosaurus* zone fauna.

To the following brief summary of the *Lystrosaurus* zone fauna are added the genera *Procolophon* cf. *trigoniceps* and *Cyonosaurus* cf. *longiceps*, for the first time.
SUMMARY OF THE LYSTROSaurus ZONE Fauna

Sub-class ANAPSIDA

Order — Cotylosauria.
Infra-order — Procolophonia.
Family — Procolophonidae.
   (1) Procolophon cf. trigoniceps.
   (2) Procolophon sp. — Represented by skull and skeletal remains from Lystrosaurus zone sandstones.
   (3) (Spondylolestes) — Parrington (1948) included this small Procolophonid in his summary of the Lystrosaurus zone fauna, but the type of this genus came from Bethesda Road in the Cistecephalus zone.

Sub-class LEPIDOSAURIA

Order — Eosuchia.
Family — Prolacertidae.
   (1) Pricea longiceps.
   (2) Prolacerta broomi.

Sub-class ARCHOSAURIA

Order — Thecodontia.
Sub-order — Pseudosuchia.
Family — Erythrosuchidae.
   (1) Chasmatosaurus vanhoepeni — Represented by eight good skull and skeletal elements.
   (2) (Elaphrosuchus rubidgei) = Chasmatosaurus vanhoepeni, a juvenile specimen.
   (3) Proterosuchus fergusi. (Type lost.)

Sub-class SYNAPSIDA

Brink (1963) considers that the Synapsids be raised to the level of a class.
Sub-order — Anomodontia.
Sub-family — Pristerodontinae (Myosaurinae).
Myosaurus gracilis—Represented by eight well preserved skulls—all from the Harrismith Commonage. This seems to be an environmental factor. It is generally felt that Myosaurus should be transferred to a new sub-family Myosaurinae, as this species is out of place among the Pristerodontinae, most of which have molar teeth on the alveolar ridges of the maxillae and broad strong maxillae and palatal regions.
Sub-order — Anomodontia.
Family — Lystrosauridae.

(1) Lystrosaurus amphibius.
(2) Lystrosaurus andersoni.
(3) Lystrosaurus bothai = Adult L. murrayi.
(4) Lystrosaurus curvatus.
(5) Lystrosaurus declivis.

Brink (1951) includes the following described forms in *Lystrosaurus declivis* (5) — L. affredi, L. boopis and L. depressus. All of these are imperfectly preserved, being badly crushed and distorted.

(6) Lystrosaurus maccaigi.
(7) Lystrosaurus murrayi.


(8) Lystrosaurus oviceps.

Brink (1951) includes *Lystrosaurus breyeri* in *L. oviceps*.

(9) Lystrosaurus platyceps.
(10) Lystrosaurus primitivus. This skull came from the same horizon as *Lystrosaurus amphibius*, approximately eight feet apart.

(11) Lystrosaurus putterilli. Broom (1932) includes *Lystrosaurus putterilli* in *L. murrayi*, giving no reason for doing so. Kitching (1960) re-examined the type and considered it to be an adult male of *L. murrayi*.

(12) Lystrosaurus rubidgei — The type consists of the anterior two-thirds of a skull; very badly crushed antero-posteriorly and can be either a young *L. amphibius* or an adult male of *L. murrayi*. Broom (1940) when describing *L. rubidgei* suggests that it should be looked upon as coming from the Cistecephalus zone, but the specimen came from lower *Lystrosaurus* zone strata in the old Lootsberg Pass, six miles north of Bethesda Road. This Pass used to be the main road to Middelburg via Blauwater (Blouwater) Siding.

(13) Lystrosaurus verticalis — This species was founded on a very imperfect skull and all its characteristics are close to those of *L. murrayi*.

(14) Prolystrosaurus natalensis — Broom (1932) refers this genus to *Lystrosaurus murrayi*. Brink (1951) refers Prolystrosaurus to the genus *Lystrosaurus* as it is not a natural ancestor to the latter. Cruickshank has recently examined the type in the South African Museum and reported it to be a dorso-ventrally distorted *L. murrayi*.
Large, badly distorted *Lystrosaurus murrayi* (Lystrosaurus rubidgei)
(15) Prolystrosaurus strigops (Dicynodon strigops). Broom (1932) refers this form to Lystrosaurus murrayi. Brink (1951) to the genus Lystrosaurus.

Sub-order — Theriodontia.
Infra-order — Gorgonopsia.
Family — Gorgonopsidae.
   Cyonosaurus c.f. longiceps. (Found in the same horizon as Lystrosaurus, Thrinaxodon and Tetracynodon.)
Infra-order — Therocephalia.
Family — Scaloposauridae.
   (1) Ericiolacerta parva.
   (2) Olivieria parringtoni.
   (3) Tetracynodon darti.
   (4) Scaloposaurus hoffmani.
   (5) Scaloposaurus constrictus. (From unreliable locality.)
Infra-order — Therocephalia.
Family — Whaitsidae.
   (1) Moschorhinus kitchingi.
   (2) Moschorhinus (esterhuizeni) kitchingi.
   (3) Moschorhinus (natalensis) kitchingi.
   (4) Moschorhinus warreni.
Infra-order — Cynodontia.
Family — Procynosuchidae.
   Galeophrys kitchingi.
Infra-order — Galesauridae.
Family — Galesauridae.
   (1) Galesaurus planiceps. (From unreliable locality.)
   (2) Glochinodontoides gracilis.
   (3) Glochinodon detinens—Broom (1932) refers this genus to Galesaurus planiceps: Brink (1954) describes a second specimen referring Glochinodon detinens and the new specimen to Galesaurus.
   (4) Micrictodon marionae.
   (5) Nanictosaurus c.f. kitchingi.
   (7) Nythosaurus larvatus.
   (8) Platycranellus elegans.
   (9) Thrinaxodon luirhinus.
   (10) Thrinaxodon putterilli. (The type of this species is held by a son of the late Mr A. W. Putterill still resident in Harrismith.)

AMPHIBIA

(1) Limnoiketes paludinatus.
(2) Lydekkerina huxleyi. (Most common amphibian in the Lystrosaurus zone).
Over the past twenty years it has been observed that Procolophon skull and skeletal remains occur in conglomerates at the base of three upper Lystrosaurus zone sandstones, on the Harrismith Commonage as well as at Oliviershoek Pass, Excelsior, Wheatlands-Tarkastad, Klipfontein-Bethulie and Joubertsberg-Middelburg, Cape.

In 1964, B. J. Kitching, while examining Lystrosaurus zone strata in the Lootsberg Pass, Graaff-Reinet district, found a well preserved Procolophon cf. trigoniceps in a horizon which also yielded Lystrosaurus murrayi and L. declivis.

It may also be relevant to record at this stage that the genus Procolophon has been found in the Cistecephalus zone at locality 14, in the Upper Luangwa Valley, Zambia.

On a re-examination of the strata on the farms Hales Owen-Cradock and Colton-Dewetsdorp, it was found that in both localities Procolophon skulls occur in nodules at the base of the sandstones well within the Lystrosaurus zone. Some of these nodules also yielded fragmentary Lystrosaurus skull and skeletal remains.

The occurrence of a Cistecephalus zone Gorgonopsid—Cyonosaurus—in the Lystrosaurus zone was an unexpected discovery more especially since it was found high in the Lystrosaurus zone strata, which also yielded a number of Lystrosaurus, Thrinaxodon, Tetracyonodon and Lydekkerina skulls. The skull came from Oliviershoek Pass-Bergville district and was found by Albert Hotton, son of Nicholas Hotton III of the Smithsonian Institution, Washington, D.C., during 1964. The specimen was subsequently described by D. Sigogneau in her D.Sc. thesis (1967).

The nearest Cistecephalus zone strata to the above locality are to be found approximately 30 miles away in the Little Tugela River, Bergville district, or some 45 miles south-east of the Pass on the farm Ennersdale in the Estcourt district. The water-worn texture of Cyonosaurus and the fragmentation of the maxillary and squamosal regions suggests that the skull had in all probability been washed from the Cistecephalus zone strata and had subsequently been re-deposited where it was found in Lystrosaurus zone times.

Seeley, Broom and Watson believe that Lystrosaurus was aquatic, which may account for the wide distribution of this genus. Being able to swim, these creatures could have been carried by streams or floods over large distances with many surviving whole, but some being dismembered and giving rise to the skull and skeletal fragments in the pebble conglomerates.

The sudden appearance of this new form of Anomodont, Lystrosaurus, and its abundance throughout the zone is more indicative of an immigrant form, than of one evolved from a branch of the Lower Beaufort Anomodonts.

From observations in the field and from the records it is obvious that the first forms to appear in the lower Lystrosaurus zone strata are Lystrosaurus murrayi and L. declivis together with such large species as Lystrosaurus amphibius, L. andersoni, L. platyceps and L. maccaigi. These latter species feature less prominently in the upper strata of the zone.
Had the genus *Lystrosaurus* been evolved from a Lower Beaufort Dicynodont then corroborative evidence should have been found among the very large variety of *Cistecephalus* zone Dicynodonts.

Broom (1932) suggested that a species such as *Dicynodon gilli* from the *Cistecephalus* zone could be near to the ancestral type from which the genus *Lystrosaurus* could have evolved. However, although *Dicynodon gilli* is stratigraphically old enough to be ancestral, the frontals in this species meet the premaxillae, a feature not found in *Lystrosaurus*.

Yuan and Young (1934) remarked that some of the Russian Dicynodonts are very *Lystrosaurus*-like. Toerien (1954) described *Lystrosaurus primitivus* from low in the *Lystrosaurus* zone, stating that the specimen shows characters intermediate between *Dicynodon* and *Lystrosaurus* and that it appears to be a late survivor of the earliest Lystrosaurs which were very similar to some of the Russian Dicynodonts.

Broom (1932) considered the Lystrosauridae by far the most difficult genus of South African fossil reptiles with which to deal, and that this group was in great confusion. He then went on to revise the genus *Lystrosaurus*, referring some of the described species to *Lystrosaurus murrayi*. (See summary of *Lystrosaurus* zone fauna.)

In the same paper he also states “that where many specimens of the same genus are found at one locality and in one horizon the presumption should be that most will belong to one species, and that many distinct characters must be evident before a distinct species can be created”. Unfortunately very little notice was taken of this advice, either by himself or by other workers on the genus *Lystrosaurus* or for that matter on various other genera of the mammal-like reptiles.

Brink (1951) again revised the twenty-two already described South African species of *Lystrosaurus*, reducing them to eleven and suggested that the generic name *Prolystrosaurus* should be altered to *Lystrosaurus* as the former is not a natural ancestor of the latter. The strata on the farm Loskop in the Estcourt district lie well within the *Lystrosaurus* zone. He also introduced a new species *Lystrosaurus amphibius* based on a large skull from the lower strata of the zone, with characteristics pointing more clearly to the aquatic features of this genus than any of the previously described species.

Neither of the above authors gave very definite reasons for reducing the number of the described species, but from a recent survey it became evident that the majority of specimens were either badly preserved or distorted and some of them possessed no characteristics sufficiently distinctive to justify their separation into different species.

In recent years, it has become increasingly obvious that more attention should be given to depositional distortion, variations within species and growth stages within the various groups of mammal-like reptiles. Lack of information concerning these features, let alone the badly weathered state or incomplete nature of the material, has been the underlying reason for the creation of a fair number of new genera and species.
In the genus *Lystrosaurus* many skulls are badly distorted, some almost beyond recognition. This distortion can in all probability be attributed to the fragility of the thin bony structure of the skulls, the skull bones being much thinner than is characteristic of Dicynodonts of the same size from the *Cistecephalus* zone. However, the bone could also have been distorted by long periods of submergence in water or in mud, which caused the skulls to become almost plastic or flexible. Yet another, but lesser, cause could have been the contraction of skin, muscle and tendons in cases where the skulls have been exposed to air and sun.

Variations within species, and growth stages, should be very carefully studied. Consideration of these phenomena has been given by work on various lower and upper Beaufort forms, and over the past ten years a number of very immature and intermediate growth stages in *Lystrosaurus* skulls have been collected from different horizons together with adult and already described *Lystrosaurus* species.

For this preliminary description, six of the smallest *Lystrosaurus* skulls yet recorded as well as two intermediate stages have been selected. These can all be referred to *Lystrosaurus murrayi*. In the curvature of the snouts, parietals, pre­parietals and in all other aspects the eight skulls agree completely with *Lystrosaurus murrayi* except that six of the specimens are very immature. All the selected specimens have their lower jaws in place making it difficult to study the palates.

The following tables give the museum numbers, locality, and state of preservation of the eight specimens as well as the principal measurements of the skulls in millimetres.

<table>
<thead>
<tr>
<th>B.P.I.</th>
<th>Mus. No.</th>
<th>Locality</th>
<th>State of preservation</th>
</tr>
</thead>
<tbody>
<tr>
<td>410</td>
<td>Nooitgedacht, Bethulie.</td>
<td>Skull with lower jaw, snout weathered, almost complete skeleton. Skull distorted laterally. Tusks not yet erupted.</td>
<td></td>
</tr>
<tr>
<td>412</td>
<td>Donovan, Bethulie.</td>
<td>Skull with lower jaw, slightly distorted dorso-ventrally. Tusks just erupting.</td>
<td></td>
</tr>
</tbody>
</table>
Skull with lower jaw. Skull distorted ventrally. Tusks not fully erupted.

Undistorted—skull with lower jaw. Tusks fully erupted.

Dorsal view of a growth series of *Lystrosaurus murrayi* skulls.
Side view of a growth series of *Lystrosaurus murrayi* skulls.
<table>
<thead>
<tr>
<th>Maximum skull length</th>
<th>49</th>
<th>50</th>
<th>51</th>
<th>51</th>
<th>61</th>
<th>65</th>
<th>97</th>
<th>143</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum basal length</td>
<td>42</td>
<td>46</td>
<td>±44</td>
<td>—</td>
<td>50</td>
<td>58</td>
<td>83</td>
<td>111</td>
</tr>
<tr>
<td>Maximum skull width across interorbital bars</td>
<td>29</td>
<td>28</td>
<td>±30</td>
<td>±26</td>
<td>41</td>
<td>50</td>
<td>60</td>
<td>97</td>
</tr>
<tr>
<td>Interorbital width Max.</td>
<td>—</td>
<td>16</td>
<td>16</td>
<td>—</td>
<td>18</td>
<td>22</td>
<td>28</td>
<td>65</td>
</tr>
<tr>
<td>Min.</td>
<td>±16</td>
<td>14</td>
<td>15</td>
<td>—</td>
<td>15</td>
<td>20</td>
<td>26</td>
<td>52</td>
</tr>
<tr>
<td>Intertemporal width Max.</td>
<td>10</td>
<td>13</td>
<td>15</td>
<td>—</td>
<td>15</td>
<td>17</td>
<td>19</td>
<td>29</td>
</tr>
<tr>
<td>Min.</td>
<td>8</td>
<td>11</td>
<td>13</td>
<td>12</td>
<td>12</td>
<td>15</td>
<td>15</td>
<td>25</td>
</tr>
<tr>
<td>Snout + orbital length Max.</td>
<td>±29</td>
<td>31</td>
<td>31</td>
<td>—</td>
<td>34</td>
<td>42</td>
<td>73</td>
<td>88</td>
</tr>
<tr>
<td>Min.</td>
<td>±29</td>
<td>30</td>
<td>29</td>
<td>—</td>
<td>40</td>
<td>41</td>
<td>50</td>
<td>103</td>
</tr>
<tr>
<td>Minimum outside width between caniniform processes</td>
<td>16</td>
<td>14</td>
<td>14</td>
<td>13</td>
<td>17</td>
<td>23</td>
<td>35</td>
<td>54</td>
</tr>
<tr>
<td>Maximum length of orbit Max.</td>
<td>±15</td>
<td>15</td>
<td>15</td>
<td>—</td>
<td>17</td>
<td>21</td>
<td>±28</td>
<td>36</td>
</tr>
<tr>
<td>Min.</td>
<td>±15</td>
<td>12</td>
<td>12</td>
<td>—</td>
<td>14</td>
<td>15</td>
<td>26</td>
<td>31</td>
</tr>
</tbody>
</table>

All measurements in millimetres.

Three of the skulls with partial skeletons, B.P.I. museum numbers 409–411, are embedded in a block of grey-green matrix measuring approximately 100 square inches. The skull of specimen 411 is flattened dorso-ventrally with the result that it resembles that of *Lystrosaurus declivis*, but the skeletal parts attached to the three skulls have exactly the same measurements and it is therefore probable that all were born at the same time.

It is at present still difficult to determine whether a specimen is a juvenile or an adult. On re-examining some of the known *Lystrosaurus murrayi* skulls it was found that the intermediate and what was at first thought to be the adult stages of this species have all the characteristics of the large *Lystrosaurus putterilli* which in all probability is an adult male of the former.

It is also difficult to establish when the tusks in *Lystrosaurus* erupt. In five of the specimens, museum numbers 407–411, the tusks have not yet erupted, and there is no swelling of the caniniform processes. In specimen museum number 412 the tusks are just erupting while in the intermediate stage 413 the tusks are not fully erupted.

Although six of the eight specimens mentioned above are immature the skulls and skeletal elements are well developed, the bone well ossified, and there is no marked expansion of the sutures.

In the past it was thought that when sutures tend to part or are expanded that this was an indication that the skull was that of a juvenile. This may be so in some cases, but it now seems likely that the opening of sutures can also be attributed to distortion by submergence in water and mud, or to the length of time that the specimens have been exposed to the air and sun.

On dealing with the mammal-like reptiles, palaeontologists are well aware of their mammalian characteristics in skull and skeletal structures, these being more advanced than those of reptiles. However, for many years there has been
speculation as to whether the mammal-like reptiles were oviparous or viviparous, since no eggs or traces of eggs have yet been found, even where depositional conditions appear to have been favourable. In many instances extremely fragile skull and skeletal elements as well as plant remains have been preserved and for this reason eggs or embryo-like forms ready to be hatched should have also been preserved.
Even when living reptiles lay soft-shelled eggs, these tend to harden or toughen considerably when exposed to the air and sun thus protecting the embryo during incubation which in some instances may last from six to nine months.

Since many well developed immature specimens of various mammal-like reptiles have been recovered from the Beaufort Beds, but as yet no traces of eggs, it could well be possible that live birth had taken place. The type of birth here visualised may have been similar to that found in certain of the living reptiles such as Mabuya, Cordylus and Platysaurus to mention only a few, and where from two to eight young are born alive.
REFERENCES