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Kitching, J. W.

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THE STRATIGRAPHIC DISTRIBUTION AND OCCURRENCE OF SOUTH AFRICAN FOSSIL AMPHIBIA IN THE BEAUFORT BEDS

by

J. W. Kitching

ABSTRACT

A short account is given of the distribution and occurrence of fossil amphibians from the Beaufort succession, based on analyses of specimens in various South African and overseas institutions. Their occurrence is based on the re-examination of all the localities which have yielded amphibian remains to date and on field observations during the course of collecting.

Attention is drawn to the paucity of fossil amphibians throughout the Beaufort palaeontological record. Possible causes of this paucity are discussed.

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INTRODUCTION

South African fossil Amphibia have been described by various authors (Huxley, 1859; Owen, 1884; Lydekker, 1889; Broom, 1903–1948; Watson, 1913–1962; Haughton, 1915 and 1925; Von Huene, 1931; Broili and Schröder, 1937; Boonstra, 1940; Parrington, 1950; Kitching, 1957, and others) whose efforts were mainly confined to the morphology and taxonomy of the various families represented in the Beaufort succession — ranging from the Upper Permian (*Tapinocephalus* zone) to the lower part (Anisian) of the Middle Triassic (*Cynognathus* zone).

The majority of described species are either incomplete, fragmentary or distorted and in many instances inadequately prepared. Thus comparison with many better preserved but undescribed specimens is almost impossible, thereby causing confusion in fossil amphibian classification. Unreliable or vague locality data also hamper the assignment of specimens to specific zones.

An assessment has been made, wherever possible, of all the described and undescribed amphibian material housed in South African and overseas institutions. The largest collections are housed in the South African Museum, Cape Town, the Transvaal Museum, Pretoria, the Bernard Price Institute for Palaeontological Research, Johannesburg and the National Museum, Bloemfontein. In many instances only preliminary identifications have been attached to undescribed and new material.

A total of 450 specimens were recorded on a catalogue card system; to this 50 specimens were added which appear to lack an adequate record. The total of 500 specimens represent between 3,33 and 3,84 per cent of the total number of between 13 000 and 15 000 fossil reptiles which have been recovered to date from the Beaufort sediments. The assessment together with the locality data have been placed on record in the Bernard Price Institute for Palaeontological Research and will be available for reference purposes to all interested persons.

STRATIGRAPHICAL DISTRIBUTION AND OCCURRENCE

General

Nine families of fossil amphibians are recognised from the *Tapinocephalus* zone sediments upwards: the rhachitomous Rhinesuchidae, Rhytidosteidae, Lydekkerinidae, Uranocentrodontidae, Microphol idae, Trematosauridae, Laidleriidae and the more advanced Capitosauridae and Brachyopidae.

In the Lower Beaufort, which is divided into the *Tapinocephalus, Cistecephalus* and *Daptocephalus* zones, the predominant family is the Rhinesuchidae with the possible appearance of the first member of the Uranocentrodontidae in *Laccosaurus watsoni* Haughton (1925). At this stage it is most probably relevant to point out that no amphibian remains have as yet been recorded from the *Daptocephalus* zone in Natal where the *Tapinocephalus* and *Cistecephalus* zone sediments are missing. Based on lithological and palaeontological evidence the *Daptocephalus* zone sediments in Natal may have been deposited under different climatic and environmental conditions from those represented in the main Karoo basin, or alternately they may even have been deposited in a smaller separate basin (Kitching, in prep.).

In the *Lystrosaurus* zone (Middle Beaufort) the families Rhytidosteidae, Lydekkerinidae, Uranocentrodontidae and Micropholidae are well represented, while the Trematosauridae, Laidleriidae, Capitosauridae and the Brachyopidae are mainly confined to the *Cynognathus* zone (Upper Beaufort).

From field observations and from the records of collected material the distribution of the fossil Amphibia from the Beaufort succession seems to be erratic when compared with the more even distribution of the large variety of fossil reptilian forms.

Few amphibian skull and skeletal fragments were observed within the *Tapinocephalus, Cistecephalus* and *Daptocephalus* (Lower Beaufort) mudstones and sandstones although such elements are not uncommon in the clay-pebble conglomerates at the base of the upper *Lystrosaurus* zone sandstone horizons and in bone-beds and lenticular fine-grained sandstone bands within the *Cynognathus* zone succession.

Most of the *Tapinocephalus* zone specimens such as *Rhinesuchus whaitsi* Broom (1908) and the "aberrant" *Rhinesuchoides tenuiceps* Olson and Broom (1937) came from the lower horizons of the zone. These were all embedded in hard bluish-gray mudstones and were found in close association with various fossil reptilian forms.

Fossil amphibian remains are rare in the *Cistecephalus* zone with its very abundant fossil reptilian fauna and are represented by four species of *Rhinesuchus* together with *Phrynosuchus whaitsi* Broom (1913) which, due to its state of preservation, can be regarded as a *nomen dubium*. More recently, Chernin and Kitching (1977) reassessed the latter species and considered it to be a juvenile *Rhinesuchus* sp. It also came from an inadequately defined locality where both the *Tapinocephalus* and *Cistecephalus* zones are exposed. To judge from the adhering matrix the specimen was probably recovered from the upper horizons of the *Tapinocephalus* zone.

The few amphibians recovered from the *Cistecephalus* zone invariably occur either in the unstratified or massive mudstones and are usually found closely associated with various fossil reptilian forms.

During the deposition of the *Daptocephalus* zone sediments the number of fossil amphibians increased slightly but their occurrence is sporadic.

On the adjoining farms Ferndale, Doornplaas (Rust) and Poortjie in the Graaff-Reinet District, a number of amphibians, including *Laccosaurus watsoni* Haughton (1925), were recovered as single isolated specimens from the same fossiliferous horizon, low in the *Daptocephalus* zone. Romer (1947) synonymises *Laccosaurus* with *Uranocentrodon senekalensis* van Hoepen (1917). If this synonymy is accepted then this species heralds the first appearance of the family Uranocentrodontidae. Romer also synonymises *Laccocephalus insperatus* Watson (1919) with *Uranocentrodon*. This can most probably be accepted, as the specimen came from a locality in the Orange Free State where the *Daptocephalus* zone beds are much attenuated and probably belong to the upper horizons of the zone.

"Lydekkerina kitchingi" Broom (1950), a specific name at present of uncertain validity, is in all probability a rhinesuchid. Specimens of this "species" have been recovered from the adjoining farms Ringsfontein and Beeldhouersfontein in the Murraysburg district, Cape Province. The specimens from the latter farm were found at a lower elevation than those from the former.

On the farm Ringsfontein, the type and paratype of *"L. kitchingi"* were found in close association with *Muchocephalus muchos* Watson (1962) and, according to the skull sculpture and general morphology of the former, the two species could be synonymous, the one being a juvenile of the other. The inadequately prepared state of the specimens has contributed to this confusion.

On the farm Beeldhouersfontein, 92 *"L. kitchingi"* skulls with associated skeletal remains were recovered from an unstratified mudstone horizon approximately 4 × 2 m in extent and up to 20 cm thick. This horizon is overlain by about 1,5 m of sandstone. When the specimens were excavated it was obvious that the *"Lydekkerina"*-bearing mudstone extends farther laterally under the overlying sandstone. Many of the skulls show various types and degrees of distortion. The animals most probably died in a small shallow pool that was gradually drying-up or were trapped in a small pool by the incoming sands which now form the overlying sandstone.

The *Lystrosaurus* zone (Middle Beaufort) fossil amphibians show a noticeable increase in the number of specimens although their distribution is also sporadic, with greater concentrations of certain species

in specific areas. Most of the specimens seem to have been recovered from the middle and upper horizons of the zone or where the sediments assigned to the zone are much attenuated, as, for example, on the Harrismith Commonage and vicinity, where the *Lystrosaurus* zone has a maximum thickness of 63 m in comparison with approximately 362 m in the Noupoort–Middelburg (Cape) area. The increase in the number of amphibians is deceptive unless one considers the various fossil reptilian forms, especially the abundant genus *Lystrosaurus*, which have either been collected from or were left *in situ* in the same horizons and areas that yielded the amphibians.

Of all the amphibian families represented in the *Lystrosaurus* zone the Lydekkerinidae are the most abundant and widely distributed areally, ranging from the Harrismith District to the inadequately defined type site in the Edenburg District, Orange Free State, and thence south to Bethulie. A number of well preserved specimens have also been recovered from *Lystrosaurus* zone exposures in the Bergville and Estcourt Districts of Natal.

Of the 189 *Lydekkerina huxleyi* (Lydekker, 1890) specimens on record, 163 were recovered from a number of localities on the Harrismith Commonage and from a few localities in close proximity to the town, while seven specimens are on record from the type locality of *Lydekkerina huxleyi* in the Edenburg District which has not been relocated since the discovery of the type.

There are at least two distinct horizons exposed on the Harrismith Commonage which yield the genus *Lydekkerina* together with various fossil reptilian forms, the most abundant of which is the genus *Lystrosaurus*. From the same horizons there are also four problematic species : *Broomulus dutoiti* (Broom, 1930), *Putterillia platyceps* Broom 1930, *Lydekkerina putterilli* Broom 1930 and *Limnoiketes paludinatans* Parrington 1948, each based on a single type specimen, the first three of which are very badly preserved and inadequately prepared specimens. They were also found in close association with *Lydekkerina huxleyi*.

Members of the genus *Rhytidosteus* are rare but, together with the more abundant genus *Micropholis*, have a fairly wide distribution ranging from Middelburg, Cape, to the Harrismith districts. *Micropholis* is frequently found is close association with the cotylosaurian genus *Procolophon* in a hard, red siltstone matrix which occurs locally in the Middelburg and Steynsburg Districts, Cape Province.

In contrast with the common occurrence of the fossil amphibians in the mudstones assigned to the *Tapinocephalus, Cistecephalus* and *Daptocephalus* zones (Lower Beaufort) it has been observed that the *Lystrosaurus* zone forms could occur in unstratified purple mudstones, gray-green calcareous concretions within the mudstones, and in sandstone horizons.

Those specimens found within the purple mudstone are frequently encased in a thin layer of calcareous matrix. In addition almost complete skeletons of a variety of fossil forms including small amphibians are often found encased in hard light gray-green or variegated calcareous concretions which weather out of the surrounding mustone.

All the known *Uranocentrodon senekalensis* skulls with their associated skeletal remains come from a sandstone quarry near the top of the *Lystrosaurus* zone in the Senekal District, while a few of the known *Rhytidosteus* specimens were also recovered from sandstone horizons.

Certain sedimentary structures within the *Cynognathus* zone contain more fossil amphibian and reptilian fragments than has been observed in any of the other zones. These fragments occur in varying sizes and possibly represent the remains of an abundant fauna of which complete skulls and skeletal elements are now found in less abundance.

The fragmentary remains are commonly found in local bone beds within the mudstones, in clay-pebble conglomerates or lenticular sandy mudstone. In many instances abundant fragments of amphibians and fossil reptilian remains are also found in brown-weathering fine-grained calcareous sandstone lenses which form bone conglomerates. Here exceptionally rounded and eroded fossil fragments have been found together with less rounded and eroded specimens in the same conglomerate. The state of preservation is probably due to the degree of fluvial reworking and distance of transport.

Fossil fragments found in both the clay-pebble and bone conglomerates of the *Cynognathus* zone indicate fragmentation of skull and skeletal remains prior to deposition, probably during periods of seasonal or prolonged droughts, when the skeletons were exposed to warm semi-arid weathering conditions.

Many of the better preserved specimens such as *Batrachosuchus browni* Broom, *Batrachosuchus watsoni* Haughton, *Laidleria gracilis* Kitching and a few others from the *Cynognathus* zone came from lenticular sandstones, while a few better preserved *Parotosuchus* specimens came from unstratified mudstones or perimeters of localised bone beds within the mudstones.

The following is a brief summary of the labyrinthodonts from the various biozones of the Beaufort sediments from the bottom upwards:

Tapinocephalus zone

	Number of Specimens
Rhinesuchus whaitsi Broom 1908	10
Rhinesuchoides tenuiceps Olson and Broom 1937	1
Rhinesuchoides tenuiceps Synonym: *Rhinesuchus avenanti* Boonstra 1940	1

Also see Watson, 1962, p. 257.

Rhinesuchus whaitsi. Synonym: *Rhinesuchus beaufortensis* Boonstra 1940. See Watson, 1962 This specimen is from an inadequately defined locality. Both the *Tapinocephalus* and *Cistecephalus* zones are exposed in the Beaufort West District.	1
Rhinesuchus sp. Preliminary identification.	9
Total	22

Cistecephalus **zone**

	Number of Specimens
Rhinesuchus africanus (Lydekker 1890). Synonym: *Eryops africanus* Lydekker 1890	3
Rhinesuchus capensis Haughton 1925	1
Rhinesuchus broomianus Von Huene 1931	1
Rhinesuchus rubidgei Broom 1948	1
Rhinesuchus sp. Preliminary identification	13
"Phrynosuchus whaitsi" Broom 1913 = *Rhinesuchus* sp. Chernin and Kitching 1977.	1
Total	20

"Phrynosuchus" is based on a single badly preserved skull and partial skeleton which is almost completely preserved as an impression. The specimen also came from a locality where both the *Tapinocephalus* and *Cistecephalus* zones are exposed on the farm Droogvoets, Fraserburg, Cape Province. To judge from the adhering matrix it seems possible that the specimen came from the *Tapinocephalus* zone sediments.

Daptocephalus **zone**

	Number of Specimens
Laccocephalus insperatus Watson 1919. (Romer, 1947 synonymises this species with *Uranocentrodon senekalensis).*	1
Laccosaurus watsoni Haughton 1925. (Romer, 1947 and Watson, 1962 synonymise this species with *Uranocentrodon)*	1
Laccosaurus sp. (*Uranocentrodon* sp.) Preliminary identification	4
Muchocephalus muchos Watson 1962 (Considered to be a *nomen dubium* — possibly a distorted *Rhinesuchus*).	1
Muchocephalus sp. (*Rhinesuchus* sp.) Preliminary identification	2
Rhinesuchus sp. Preliminary identification	11
"Lydekkerina kitchingi" Broom 1950. This species is at present of uncertain validity — possibly a rhinesuchid.	96
Total	116

Lystrosaurus **zone**

	Number of Specimens
Rhytidosteus capensis Owen 1884	1
Rhytidosteus sp. Preliminary identification	9
Uranocentrodon senekalensis van Hoepen 1917 Synonyms: *Myriodon senekalensis* van Hoepen 1911, *Rhinesuchus major* Broom 1912, *Rhinesuchus senekalensis* Haughton 1915 and 1925.	5
Lydekkerina huxleyi (Lydekker 1890). Synonym: *Bothriceps huxleyi* Lydekker 1890	129
Lydekkerina sp. Preliminary identification.	59
Lydekkerina putterilli Broom 1930. (Parrington, 1948, p. 438 considers this species to be possibly a young individual of the rhinesuchid genus *Uranocentrodon).*	1
Broomulus dutoiti (Broom 1930). Synonym: *Lydekkerina dutoiti* Broom. (Romer, 1947 considers this species to be generically identical with the badly preserved type skull of *Putterillia platyceps* Broom 1930)	1
Putterillia platyceps Broom 1930. Badly preserved and distorted type skull and another two equally badly preserved specimens identified by Broom as paratypes.	3
Limnoiketes paludinatans Parrington 1948	1
Micropholis stowi Huxley 1859 (*Petrophryne granulata* Owen 1876).	30
Kestrosaurus dreyeri Haughton 1925 (Also see Welles and Cosgriff, 1965).	1
Total	240

Cynognathus **zone**

	Number of Specimens
Parotosuchus albertyni (Broom 1904). Synonym: *Cyclotosaurus albertyni* (See Romer, 1947; Welles and Cosgriff, 1965).	1
Parotosuchus africanus (Broom, 1909). Synonym: *Capitosaurus africanus* (See Romer, 1947; Welles and Cosgriff, 1965).	4
Parotosuchus haughtoni (Broili and Schröder, 1937). Synonym: *Capitosaurus haughtoni* (See Romer, 1947).	1
Wetlugasaurus magnus Watson 1962. (Welles and Cosgriff, 1965, transfer this specimen to *Parotosuchus* sp.)	1
Parotosuchus dirus sp. nov. Chernin, this volume.	1
Parotosuchus cf. *dirus*. Preliminary indentification based on an almost complete lower jaw and skull fragments in the National Museum, Bloemfontein.	1

Parotosuchus sp. Preliminary identifications based on fragmentary skull material.	20
Trematosuchus kannemeyeri (Broom 1909). Synonym: *Trematosaurus kannemeyeri* Broom (See Watson, 1919).	1
Trematosuchus sobeyi (Haughton 1915). Synonym: *Trematosaurus sobeyi* Haughton. This specimen came from a locality where both *Lystrosaurus* and *Cynognathus* zone strata are exposed.	2
Microposaurus casei Haughton 1925	1
Laidleria gracilis Kitching 1957	1
Batrachosuchus browni Broom 1903	1
Batrachosuchus watsoni Haughton 1925	1
Batrachosuchus sp. Based on lower jaws in the collection of the University of California (See Welles and Estes, 1969).	5
Total	41

DISCUSSION

Since 1856, various authors have drawn attention to the paucity of fossil amphibians, fishes and invertebrates throughout the Beaufort sediments. From the above analysis this paucity becomes even more obvious when compared with the abundant and diversified fossil reptilian fauna from these sediments, and in many instances from the same localities.

Some of the fossil amphibian localities cover large areas, not only horizontally but also vertically. In the majority of cases the amphibian localities are widely separated areally and only a few isolated occurrences within the *Daptocephalus* and *Lystrosaurus* zones have yielded a number of mainly small amphibians. These localised occurrences are responsible for the increase in the number of specimens recorded from a specific biozone. In general the fossil amphibian occurrences can be described as being isolated, sporadic or inconsistent and highly localised in three or four instances.

The scarcity of fossil amphibians, fishes and invertebrates raises such questions as: (1) have these creatures been overlooked during the course of collecting?; (2) is it an accident of preservation?; or (3) have adverse climatic and environmental conditions been responsible for this scarcity?

Over the past 30 years or more large areas of the Beaufort sequence have been carefully examined both horizontally and vertically by several workers with the result that a considerable number of both small and large fossil reptilian forms were recovered, compared with the very small number of amphibians.

With the long periods of desiccation and deposition of the Beaufort sediments which must have taken place it is generally accepted that there must have been a considerable number of accidents of preservation not only affecting the amphibian fauna but also a large variety of other creatures inhabiting the Beaufort basin during Permo-Triassic times.

Among the abundant fossil reptilian fauna that has been recovered from the sediments there are a large number of small, very frail skulls with some delicate skeletal elements attached. If these frail skull and skeletal structures are compared with the almost solid bone structures of both small and large fossil amphibians, especially with that of their occipital and snout regions, it seems reasonable to assume that more amphibians should have been preserved if these creatures were abundant.

Climatic and environmental conditions are important because the fossil fauna from the Beaufort beds, when considered as a *whole,* contains representatives of a large variety of forms which must have lived together, under the same prevailing climatic and environmental conditions, the vast majority of these creatures having been highly developed terrestrial forms.

Bain (1856), Watson (1913), Von Huene (1925), Case (1926), Du Toit (1948), Romer (1961), Colbert (1963), Keyser (1966), Kitching (1957, 1977) and others have drawn attention to the possible climatic and environmental conditions that may have prevailed during the deposition of the Beaufort succession and, except for small differences of interpretation, all seem to agree in general that the climatic conditions most probably ranged from moderately wet to arid.

From more recent lithostratigraphical, sedimentological and palaeontological evidence, together with careful field observations, it seems that there have been long periods of desiccation under hot semi-arid conditions during the deposition of the *Tapinocephalus, Cistecephalus* and lower half of the *Daptocephalus* zones, especially in the main Karoo basin. The semi-arid conditions could have been intensified to give rise to arid conditions by prevailing warm winds, as in some instances parts of the strata seem to have been wind-laid. (Also see Du Toit, 1948.)

More amenable conditions most probably prevailed during the deposition of the upper *Daptocephalus* zone sediments while the sediments assigned to this zone in Natal were most probably deposited under warm and wetter conditions, as evidenced by the sedimentary structures and the relative abundance of well preserved fossil plant remains, in many places.

Although there seems to be evidence that wetter climatic conditions existed during the deposition of the *Lystrosaurus* zone, there also seem to have been seasonal or prolonged droughts which can be deduced from the purple and red mudstones, the small rosette-shaped inclusions, and the abundance of calcareous concretions (most probably due to leaching), some of which very frequently contain almost complete skeletons of a variety of fossil vertebrates.

During the course of this investigation it was found that a large number of now separated lydekkerinid skulls with associated skeletal elements from the Harrismith Commonage could be joined to-

gether although each specimen had a separate catalogue number. These animals were in all probability trapped together in gradually drying, localised shallow pans or pools. This is not an uncommon occurrence in the Harrismith area and at one known locality in the Bethulie District. At the time that these specimens were collected this type of occurrence may not have been noted or considered to be important with regard to possible past climatic and environmental conditions.

To date no fossil fishes or invertebrates have been recovered from sediments at present assigned to the *Lystrosaurus* zone, but the probable occasional wetter conditions could have stimulated the growth of the large *Dadoxylon* trees which occur as silicified trunks of varying sizes in many places within the *Lystrosaurus* zone sediments. Complete fossil leaves are very rare but leaf impressions have been noted in the sandstones.

From both lithological and sedimentological evidence it seems that the *Cynognathus* zone sediments were deposited in a considerably reduced basin, based on the areal extent of the sediments at present assigned to the zone, and under much drier conditions than envisaged for the preceding *Lystrosaurus* zone. The more consolidated greenish-gray, as well as the unstratified dark-red to maroon mudstones, the abundance of calcareous concretions and the not uncommon rosette-shaped inclusions, may be indicative of drier conditions or prolonged droughts.

The many fragmentary mudstone conglomerates containing bone fragments indicate considerable channel scour systems and deposition of the reworked clasts and fragmentary fossil amphibian and reptilian remains. In a few instances almost complete vertebrate skulls have been recovered from these mudstone conglomerates.

Bone conglomerates are not uncommon in the sediments assigned to the *Cynognathus* zone and occur in brown-weathering fine-grained calcareous sandstone lenses with an abundance of bone fragments of varying sizes. A large percentage of the preserved bone is that of fossil amphibians including the remains of the genera *Parotosuchus* and *Batrachosuchus*. Lung fish *(Ceratodus)* dental plates have also been recovered from these structures. The bone fragments show various degrees of rounding. It has been observed that the bone conglomerates occur at different elevations and are normally localised, measuring between 6 and 20 cm in thickness, and were in all probability deposited by shallow perennial streams.

The deep cracking and marked sub-periosteal flaking or peeling could be attributed to exposure during hot dry conditions. This is frequently seen on many fossil reptilian skulls and skeletal remains and has also been observed on a number of fossil amphibian skulls, causing great difficulty in distinguishing sutures. This damage suggests exposure for some time, prior to deposition, to hot dry conditions which caused the sutures to expand and the skull bones to crack.

Such conditions may also have been responsible for the extremely fragmentary state of skull and skeletal elements found in many horizons throughout the succession. The fragments normally occur in varying sizes and shapes and can in many instances be closely compared with present-day fragmentation of animal remains that have been exposed to the natural elements for long periods, the fragmentation being more rapid under hot and dry conditions.

If it is acceptable that the Beaufort sediments were deposited over broad, low-gradient floodplains drained by wide shallow impersistent rivers and transient shallow lakes and pools, and that possible hot semi-arid conditions prevailed at times, then the areally wide distribution of the abundant fossil reptilian fauna seems indicative of the floodplains having often been dry, thus allowing these creatures to move about freely.

Under hot semi-arid conditions the amphibians may have been restricted in their habitat by their temperature tolerances as in present-day amphibians. These creatures had no internal temperature-control systems and their body temperature was controlled by the temperatures of the environments in which they lived. The amphibians could also have been confined to gradually drying shallow lakes or pools and perennial streams due to other morphological and physiological limitations.

Thus the adverse climatic and environmental conditions may have played a major role in controlling the distribution of the fossil amphibians and certain adaptations were most probably responsible for their survival and evolution throughout the Beaufort succession. From the distributional pattern and paucity of their remains, especially postcranial, it seems almost impossible to assign the fossil amphibians to specific niches such as shallow and deep water forms, as has been suggested (Chernin, 1977).

Various authors have drawn attention to the paucity of plant remains in the Beaufort sediments and it seems logical to assume that the climatic and environmental conditions that adversely affected the amphibians were to a certain extent also responsible for the paucity of fossil plant remains. This paucity is especially marked in the main Karoo Basin. In a few instances it was mentioned that the sediments contain an abundance of fossil plant material, but no mention has been made of their state of preservation. Fragmentary plant remains are not uncommon, but it should be stressed that *one* entire plant can, under natural conditions, become highly fragmented and can also shed many leaves.

Most of the plant remains from the above area are fragmentary "stem" remains ranging from 5–20 cm in length and approximately 2–6 cm in thickness, except for the silicified "trunks" of *Dadoxylon* and possibly other forms which occur in varying lengths

and thickness in places within the upper horizons of the *Daptocephalus* zone and at different elevations within the *Lystrosaurus* zone, more commonly in the Orange Free State and Natal. In the Lower and Upper Beaufort well preserved leaves have been found in localised areas, but occur most commonly as impressions in the fossil vertebrate-bearing horizons and sandstones where they are widely scattered. Well preserved leaves are exceptionally rare in the *Lystrosaurus* zone.

The paucity of plant remains may not only be due to arid conditions and their low preservation potential, but also to the depletion of the flora by the considerable number of herbivorous reptiles of varying sizes which are known to have been present during the deposition of the Beaufort sediments.

CONCLUSION

Examination of all the amphibian types housed in various South African institutions revealed that many of these were inadequately prepared, badly preserved and distorted with the result that such forms as *Putterillia platyceps, Broomulus dutoiti, Lydekkerina putterilli, "Lydekkerina kitchingi", Rhinesuchus rubidgei, Rhinesuchoides tenuiceps* and others should be considered *nomina dubia* until further preparation and morphological studies have been undertaken.

A number of well preserved amphibian skulls were also noted in the various collections and it is important that these specimens should be thoroughly prepared and described, as this will assist greatly in clarifying the taxonomic classification of the South Africa fossil Amphibia. Where relevant an endeavour should also be made to establish paratypes for those holotypes in overseas institutions, and where a species is based on a single specimen.

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Figure 1. Dorsal view of inadequately prepared type of *Rhinesuchus beaufortensis* Boonstra.

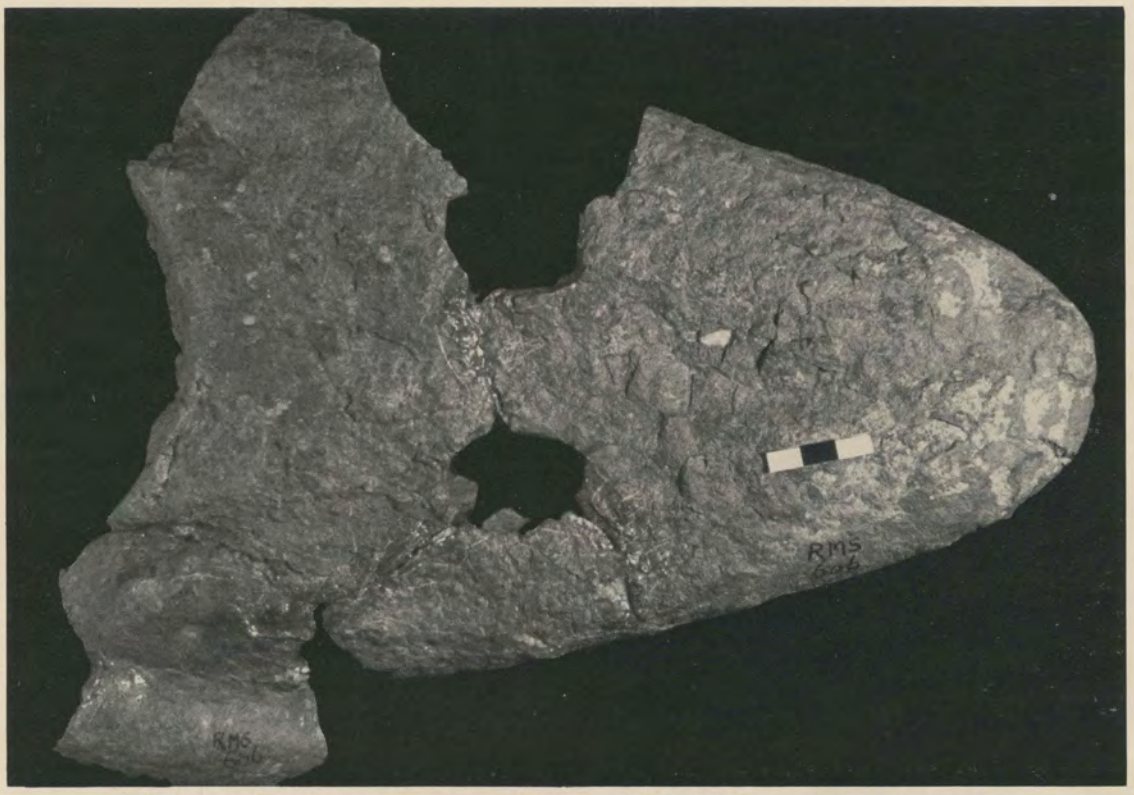


Figure 2. Dorsal view of unprepared rhinesuchid skull from the *Tapinocephalus* zone.

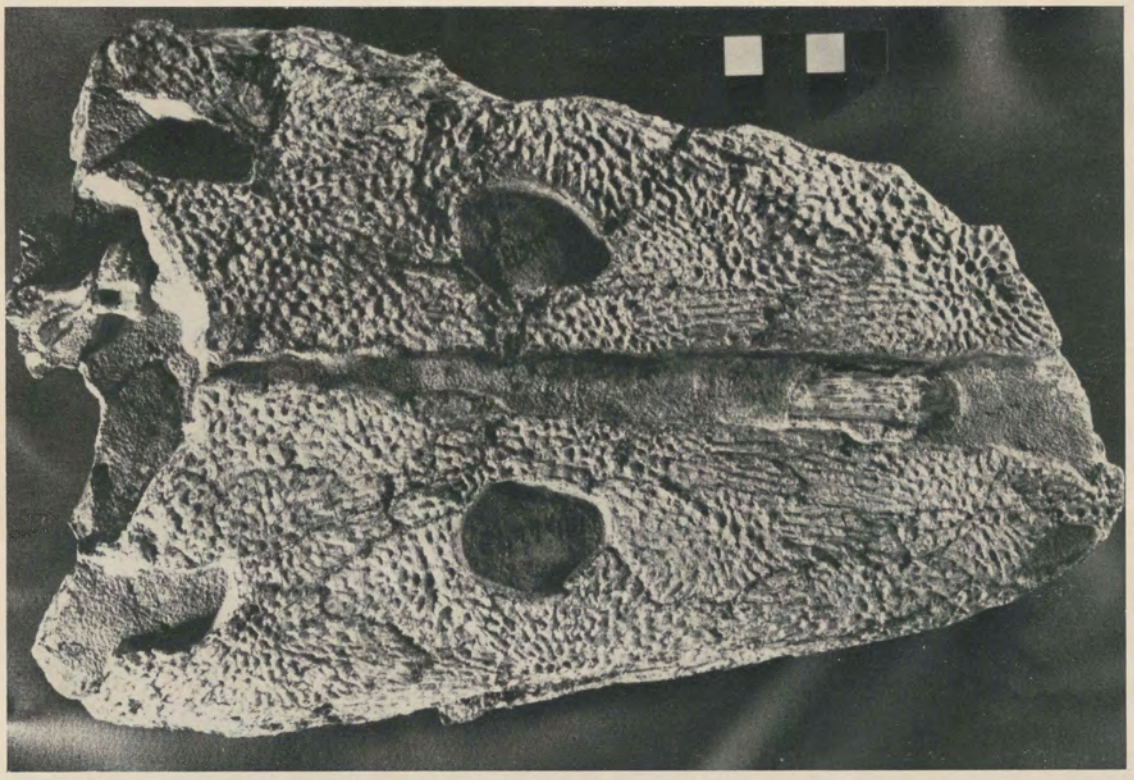


Figure 3. Dorsal view of undescribed rhinesuchid skull from the *Daptocephalus* zone. Note deep prefossilization crack through median suture.

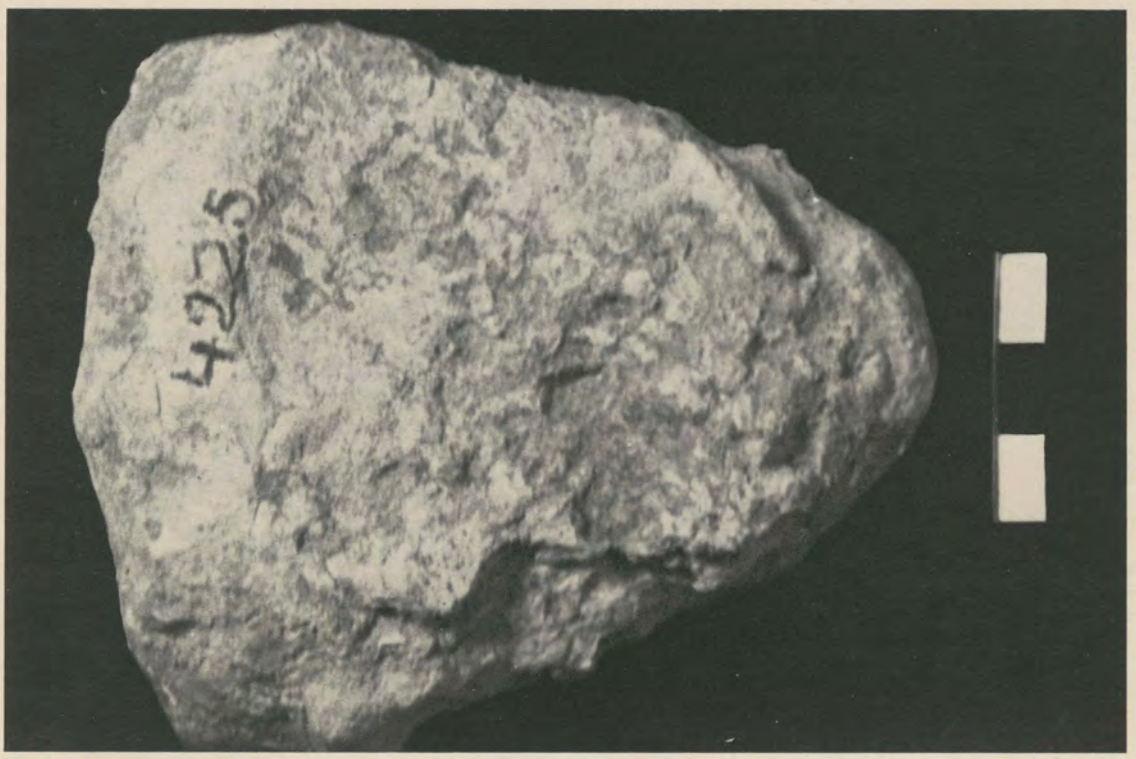


Figure 4. Complete lydekkerinid skull encased in a thin layer of calcareous matrix.

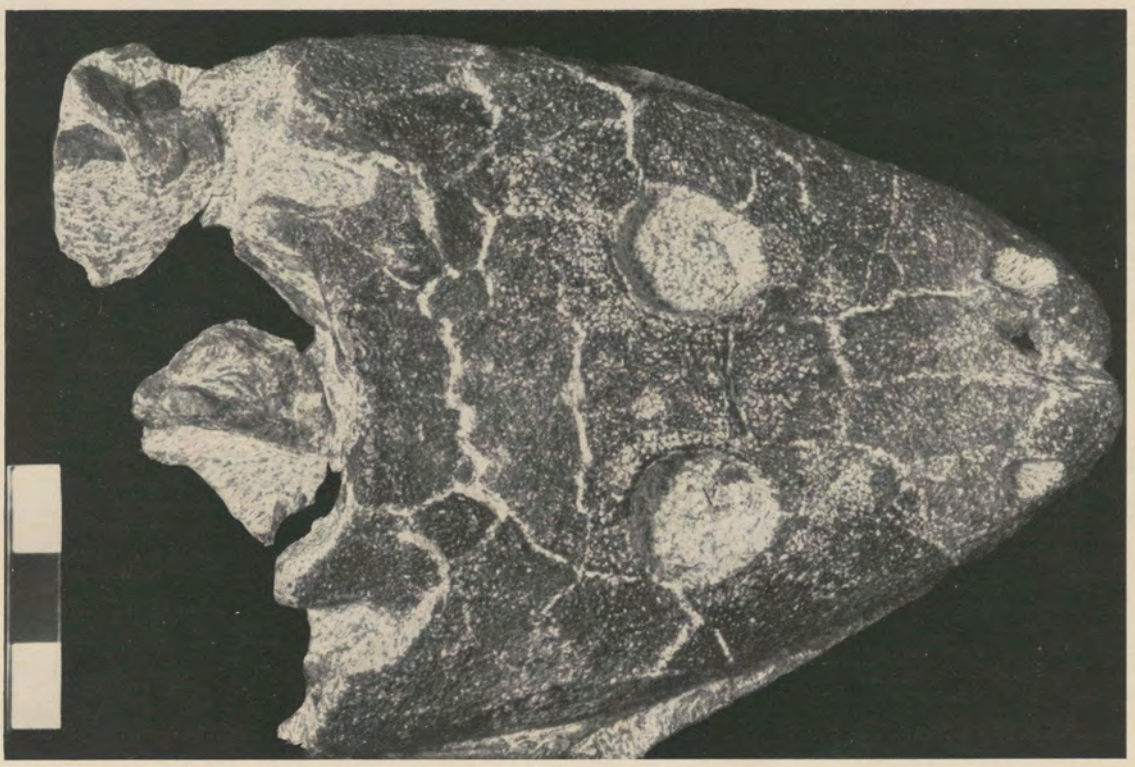


Figure 5. Complete *Lydekkerina huxleyi* (Lydekker) skull after thin layer of calcareous matrix has been removed.



Figure 6. Block of calcareous mudstone from a small localised "pool" on the Harrismith Commonage containing the remains of seven lydekkerinids and a *Lystrosaurus murrayi*. Arrows indicate nasal region of the latter genus.



Figure 7. Block of fine-grained sandy mudstone containing irregular mudstone and fossil bone fragments from the *Cynognathus* zone. Arrow indicates part of the skull roof of a fossil amphibian.



Figure 8. Block of bone conglomerate containing fossil amphibian and reptilian fragments of varying sizes and shapes from the *Cynognathus* zone.