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NOTE ON THE DISTRIBUTION OF FOSSIL REPTILIA OF KARROO AGE

By S. H. Haughton

Abstract

Reviews briefly the geographical and stratigraphical distribution of reptilia of Karroo age, both within and beyond the confines of the southern hemishpere. Draws attention to the need for further environmental and population studies.

Evidence of the increasing interest which has been taken during the past ten years in the study of Permian and Triassic reptiles is to be found, *inter alia*, in the considerable amount of descriptive work that has been published during that time and in the holding of a Symposium on Karroo reptilia, for the first time in South Africa, on the occasion of the Jubilee meeting of the South African Association for the Advancement of Science held in Cape Town in July, 1962. Although the contributors to this symposium included palaeontologists from countries other than South Africa, the major part of the discussions was focussed on fossils from the South African Karroo basin. It is proposed here to offer a brief review of this reptilian fauna in a wider geographical setting.

Geological Setting. In *South Africa*, the reptilia commonly grouped as the "Karroo reptiles" are found in a succession of strata that has been named the Karroo system and whose age is considered to range from Upper Carboniferous to the top of the Triassic system of the standard European classification and thus to cover a time span of about 100 million years. On stratigraphic grounds this system has been divided into series and stages as follows, from above downwards:

Stormberg Series	Drakensberg lava stage
	Cave sandstone stage
	Red beds stage
	Molteno stage
Beaufort Series	Upper Beaufort stage
	Middle Beaufort stage
	Lower Beaufort stage
Ecca Series	Upper Ecca stage
	Middle Ecca stage
	Lower Ecca stage
Dwyka Series	Upper Dwyka stage
	Tillite stage

The rocks of the Beaufort series have been subdivided into biozones on the basis of the reptilian fossils, and the following subdivision is at present accepted:

Upper Beaufort stage	*Cynognathus* zone
	Procolophon zone
Middle Beaufort stage	*Lystrosaurus* zone
Lower Beaufort stage	*Cistecephalus* zone
	Endothiodon zone
	Tapinocephalus zone

It is possible that further subdivision may be found desirable, since the zone genus *Cistecephalus* appears to be confined to the lower part of the sediments which have hitherto been assigned to the zone that bears its name.

The maximum thickness of the system is about 30,000 feet and the material composing it was obviously laid down in a gradually subsiding basin. Each of the stages, however, in general becomes thinner when traced from its more southerly outcrops northwards. This is particularly so in the cases of the Dwyka series, the Ecca series, and the Molteno stage, and it would seem that material forming them was derived partly from a continental mass lying to the south of the basin and that the basin itself was at its deepest along the northern side of this mass. It also appears doubtful whether any sedimentation took place in Beaufort times over certain areas in the Transvaal where both Ecca and Stormberg beds are still preserved. Apart from the existence of certain invertebrates and fish associated with the Dwyka tillite in South-West Africa and of the swimming reptile *Mesosaurus* in the Upper Dwyka stage, there exists no evidence in South Africa for the incursion of marine conditions into the continental environment in which the Karroo beds were formed..* There is, however, evidence from the rocks themselves of a general climatic change during the long lapse of time in which they were formed, a change that accompanied a marked outburst of reptilian evolutionary trends. Glacial conditions reigned during Dwyka times. After the waning of this ice age, cold humid conditions were succeeded by a warmer humid environment which became more and more arid during Stormberg times. Of course there were fluctuations in the general trend from cold to warm and from humid to arid; but insufficient study has been given to these and to the varying geographic conditions that gave rise to the deposition of sometimes thick arenaceous horizons in what was predominantly, up to the Stormberg series, an argillaceous succession. The almost complete absence of beds of limestone in the Karroo of the type basin is noteworthy.

* Glauconite occurs in the Ecca beds of the southern Transvaal; but this is not necessarily proof of marine conditions of sedimentation.

Palaeontological evidence yielded by both plants and vertebrates dates certain deposits in the Rhodesias and Nyasaland, in Mozambique, in Tanganyika, in Kenya, in Uganda and in the eastern part of the ex-Belgian Congo Republic as belonging to the Karroo system, although the beds in Kenya, Uganda and Congo have not yielded fossil vertebrates. In none of these areas is the succession as complete as in South Africa, but in all of them the deposits are of a continental facies except possibly the *Tangasaurus*-bearing shales of the coastal area of north-eastern Tanganyika and south-eastern Kenya. In Uganda and the eastern half of the Congo only strata assignable to the Dwyka and Ecca series are preserved; in the south-western part of Southern Rhodesia only the Stormberg series appears and in all probability the whole of the central part of this country was a highland undergoing denudation during Dwyka, Ecca and Beaufort times. Rocks, and fossils, of Beaufort age are however preserved in the mid Zambezi-Luangwa trough, in Nyasaland, in south-western Tanganyika and in north-western Mozambique. A basal tillite and sediments which, on the basis of their contained plants and invertebrates, can be correlated with the Ecca series also occur in the northern part of Angola and the Kasai area of the Congo basin.

Outside the continent of Africa continental sediments deposited synchronously with all or part of the Karroo system of South Africa are preserved in Madagascar, India, the eastern half of Australia, Antarctica, Brazil and Argentina, United States of America, Britain, central Europe and the western side of the Ural mountains, various areas in China, and in Indo-China. The southern lands listed and India are parts of Suess' Gondwanaland and in all of them the rock succession has glacial deposits at its base. Reptiles comparable with those of the African Karroo beds are very poorly represented in Madagascar, where there are sporadic marine incursions, and none have thus far been discovered in Antarctica or in Australia although both areas have yielded representatives of the *Glossopters* flora.

Reptilian Distribution. With the exception of Mesosaurids, fossil reptiles have not been found in South Africa below the base of the Beaufort series. At and just above this level the fauna contains a variety of different orders and sub-orders belonging mainly to the sub-classes Anapsida and Synapsida*, the former having a complete bony roof to the post-orbital part of the skull while the latter possesses one temporal opening on each side of the mid-line. These sub-classes are represented by several sub-orders each including a considerable number of differing genera and species. This variety of forms, making its appearance suddenly in the South African stratigraphical succession, suggests strongly that the reptilian fauna of the oldest Beaufort sediments was immigrant. This fauna contained large specialised herbivorous pareiasaurs (Cotylosauria), large herbivorous deinocephalia, large carnivorous titanosuchids, small dicynodonts and endothiodonts, and a few smallish carnivorous therocephalia and gorgonop-

* A. S. Brink considers that the Synapsida should be raised to the level of a class.

sids. In addition there are some little-known forms such as *Broomia* (which Watson considers to be a Sauropsid reptile) and the specialised *Eunotosaurus*. Had this varied assemblage been derived from earlier forms in the Karroo region one would have expected to find such ancestors preserved in Ecca strata which, in the southern part of the Karroo basin in which the oldest Beaufort forms are found, do not differ lithologically to any marked degree from the lowest Beaufort sediments. Indeed, the accepted boundary between the Upper Ecca stage and the Lower Beaufort stage is marked in this area mainly by the incoming of reddish shales, indicating a change in the climatic environment; but even this lithological change is not very widespread. Forerunners of the earliest Beaufort reptiles must be sought elsewhere.

Reptiles that closely resemble the oldest Beaufort forms are known from the Permian deposits of the eastern part of the Russian platform. The stratigraphy and reptilian successions in various parts of this area were described by Efremov and Vjushkov in 1955, and a summary in English of their "Catalogue" was presented in 1957 by E. C. Olson. Lower Permian beds (differentiated as Zone 0) carry pelycosaurs and a diadectomorphid cotylosaur which have no counterparts in the South African fauna. This zone is overlain by a "Deinocephalian Complex" (Zones I and II), the middle and upper portions of which carry primitive pareiasaurids (*Parabradysaurus*), pelycosaurs (some of which are considered by Watson to be intermediate in structure between the dimetrodonts of America and the titanosuchids of the lowermost Beaufort beds), *Deuterosaurus* (allied to the tapinocephalids), *Venjukovia*, which is a primitive form of anomodont with teeth, and a primitive therocephalian (*Porosteognathus*). Anatomically, this fauna appears to be more primitive than the corresponding members of the *Tapinocephalus* zone; but it is more advanced than the fauna of the Lower Permian Clear Fork beds of the United States and of the underlying Wichita beds.

In his paper on *Millerosaurus* Watson (1957) published a table showing the possible derivation of the mammal-like reptiles (anomodonts, tapinocephalids, titanosuchids, gorgonopsids, therocephalids) of the lowermost Beaufort from sphenacodontid pelycosaurs such as *Dimetrodon* through forms that are present in zones I and II of the Russian succession. Watson also suggested a close relationship between *Mesenosaurus* of zone II of Russia and the little-known genera *Broomia* and *Anningia* of the *Tapinocephalus* zone which he considered to be ancestral to the Millerosauria of the top of the Lower Beaufort.

To propound a reason for the apparently sudden appearance of this varied and, in part, advanced fauna in the South African Karroo basin area at the beginning of Beaufort times would demand an incursion into the realms of conjecture. It has to be pointed out that nowhere else in Africa has an assemblage fully comparable with that of the *Tapinocephalus* zone as yet been found, although fossil genera of the zones which lie above it are known from a number of other African areas south of the Equator as well as from the Americas, Europe and Asia. A further fact of importance is the absence of vertebrate remains from the coal-

bearing Ecca deposits of Natal and the Transvaal and of the Rhodesias, which were laid down in climatic conditions that permitted an abundant growth of plants belonging to the *Glossopteris* flora. These conditions were, apparently, inimical to the maintenance of amphibian and reptilian vertebrate life, or else to the entombment of skeletal remains if a fauna did exist there.

However, once established in the southern part of the Karroo basin at the beginning of Beaufort times, some at least of the reptilian orders found an environment favourable to a proliferation of new forms, both specialised and advanced. Both the herbivorous and carnivorous Deinocephalia appear to have died out by the end of *Tapinocephalus* zone times. The cotylosaurian Pareiasauria lingered on, in diminished numbers and somewhat smaller in size, into the *Cistecephalus* zone; but the much smaller cotylosaurian Procolophonia which appear to be close allies of Russian genera occurring in the *Mesenosaurus* beds (*Nycteroleter* etc.), are found in the Lower Beaufort, the Middle Beaufort, and the Upper Beaufort stages. The anomodont Dicynodontia—forms with neither incisor nor molar teeth—flourished in the upper part of the Lower Beaufort stage, being particularly abundant in the beds of the *Cistecephalus* zone which carries a number of very large-skulled forms; but, apart from the specialised genus *Lystrosaurus* of the Middle Beaufort and the characteristic *Kannemeyeria* of the Upper Beaufort, they appear to have reached their climax both in numbers and in species by the end of Lower Beaufort times. During these times the Gorgonopsia and the Therocephalia became the dominant carnivorous forms, both groups being represented by somewhat generalised allies in the lower zones of the Russian Permian; but these, too, suddenly disappeared at the end of the deposition of the *Cistecephalus* zone. This zone is also characterised by the presence of other synapsids probably allied to the Therocephalia—the specialised Whaitsiids without molar teeth, the small Procynosuchia which are the probable ancestors of the later Cynodontia and thus of the Ictidosauria and the mammals, and the small many-toothed Scaloposauria which may have given rise to the *Bauria*-like forms of the Upper Beaufort.

The stratigraphic distribution of the Sauropsids has been discussed at length by Watson (1957). The earliest South African representative of his order Millerosauria is considered to be *Broomia* from the *Tapinocephalus* zone. This is thought to have been pre-dated by *Mesenosaurus* from the Russian deposits, with a lower temporal opening; while the type representatives of the order (*Millerosaurus*, *Milleretta*, etc.) belong to the *Cistecephalus* zone. All are small animals. In the same zone are found the Eosuchia (*Youngina* and its allies), which are advanced in possessing an upper as well as a lower temporal vacuity and, according to Watson, in the absence of a supratemporal bone.

Sauropsida in the Middle Beaufort beds are represented in the South African basin by the genera *Pricea*, *Prolacerta*, *Chasmatosaurus*, and *Elaphrosaurus*. The relationships of the first two have been discussed at some length by Watson who drew attention to the several lizard-like characters possessed by them and con-

sidered them to be capable of immediate derivation from a millerosaurid stock, with an insectivorous mode of life. *Chasmatosaurus* and *Elaphrosaurus* are the earliest of the South African thecodonts and probably from one of them was evolved the large carnivorous Upper Beaufort form *Erythrosuchus*.

Reference may be made here to the existence in late Keuper fissure-fillings of the Mendip hills of Somerset of numerous remains of a gliding lizard that has been named *Kuehneosaurus* by P. L. Robinson (1962). The skull of this form displays considerable resemblance to that of *Prolacerta* and of *Pricea*, particularly in the presence of a ventral process to the opisthotic bone. Robinson considers it evident that these lizard-like animals evolved from an eosuchian stock in Triassic times and that during these times adaptive radiations occurred, one of which led to the peculiar characters of the postcranial skeleton of *Kuehneosaurus*.

Other important Sauropsids of the Upper Beaufort stage include the thecodont *Euparkeria*, a pseudosuchian of an unspecialized type that may have been ancestral to most of the members of this group that evolved so rapidly during Triassic times; the rhynchosaurians *Mesosuchus* and *Howesia* that could have evolved from Middle Beaufort Prolacertilia such as *Pricea;* and a possible rhynchocephalian, *Palacrodon*. These are contemporaneous with the anomodont *Kannemeyeria*, Cynognathidae, Diademodontidae, and bauriamorphs, while procolophonids persisted into the same stratigraphic stage.

The reptilian fauna of the Stormberg series, as known at present, consists predominantly of Sauropsids. The Red beds stage has yielded fragments of some cynodonts, but the most interesting therapsids of the series are the very mammal-like tritylodonts and ictidosaurs. The Sauropsids of the stage show developments in several directions. Both saurischian and ornithischian dinosaurs are present, the more agile forms appearing with the on-coming of the desert conditions under which the Cave sandstone was formed; while *Sphenosuchus* from the Red beds and *Notochampsa* and *Erythrochampsa* from the Cave sandstone can be considered as close allies of the forerunners of the Crocodiles.

Although sediments of Karroo age are known from a number of African regions as far north as Uganda, discoveries of reptilian fossils have been made only in some of these regions. None representative of Beaufort beds has been found in South Africa (outside the main Karroo basin), Bechuanaland, South-West Africa, or the south-western part of Southern Rhodesia, although sporadic finds of dinosaur bones have been made in equivalents of the Stormberg sediments in these areas. This fact has been cited on several instances as suggesting that Beaufort sediments are not present and that there is in these areas a sedimentary hiatus between the top of the Ecca series (when it is present) and the predominantly aeolian deposits of Stormberg age. On the other hand, Beaufort reptiles are found in beds to the east of Wankie in Southern Rhodesia (Sengwe and Busi valleys), whence deinocephalia, endothiodonts and a theriodont have been recovered; in the mid-Zambezi-Luangwa rift; on the western side of Lake Nyassa in the Mount Waller region of Nyasaland; in the Lugno area of the Niassa

province east of Lake Nyassa; and in the Ruhuhu region of southern Tanganyika. Recent collecting in the Luangwa valley has disclosed that, in its upper part, certain horizons of the Karroo succession are very fossiliferous and, although detailed studies of the finds are still in progress, it is clear that the *Endothiodon* and *Cistecephalus* zones of the Lower Beaufort carry therapsids closely comparable with those of South Africa and that probable Upper Beaufort beds carry a characteristic reptilian fauna that may continue into the Molteno stage. Surface collecting of weathered fossils has disclosed the presence of endothiodonts and dicynodonts in the Lugno area of the Niassa province of Mozambique. The Karroo beds of the Mount Waller region of Nyasaland include at least two reptiliferous horizons, the lower of which may be equivalent to part of the *Tapinocephalus* zone while the upper has yielded anomodonts, gorgonopsia and therocephalia that indicate the presence of the upper part of the Lower Beaufort stage.

The most complete sequence of Karroo sediments in Central Africa is that known as the Songea series and is found in the Ruhuhu depression of southwestern Tanganyika. Reptilian fossils have been recorded from two stages in the succession, named by Stockley K6 and K8 respectively, separated one from the other by the apparently unfossiliferous Kingori sandstones (K7). The described material from K6 includes pareiasauria of relatively small size, numerous anomodont species (dicynodonts and endothiodonts), gorgonopsia, therocephalia, and procynosuchids. Some of the species are indistinguishable from forms described from South Africa from both the *Endothiodon* and *Cistecephalus* zones of the Lower Beaufort; additional detailed study with a view to finding stratigraphical relationships between the various species present, as for example between the endothiodonts and the large headed specialised dicynodonts, is very desirable. In the same way, the reptiles recorded from K8 appear to represent a stratigraphically mixed fauna when compared with the succession in South Africa. Dicynodonts characteristic of the *Cistecephalus* zone, *Lystrosaurus* (Middle Beaufort), cynodonts (Upper Beaufort and possibly Lower Stormberg), rhynchocephalia and pseudosuchia (probably both Upper Beaufort and Lower Stormberg) have all been described as occurring in this one stage, together with dinosaurs that are normally characteristic of the Red beds and Cave sandstone. Nowack has pointed out that bones are sporadically distributed in various horizons throughout the stage, and further studies must be made in order that the true reptilian succession here can be compared with that in the South African basin.

Outside of Africa south of the equator, Permian and Triassic terrestrial reptiles belonging to some or all of the orders represented in the African Karroo beds are found in South America (Brazil and Argentinia), the United States, western Europe, Russia west of the Urals, China, Indo-China, and peninsular India. Some of these regions belong to the hypothetical Gondwanaland; others do not.

In South America there are no known reptiles corresponding to those of the Lower and Middle Beaufort of South Africa. Reptiles have, however, been found in the lower part of the Santa Maria stage of the Sao Bento series which

appears to lie either disconformably or unconformably on the next lower (Passa Dois) series of the Santa Catharina system. This Santa Maria stage has yielded a procolophonid (*Candelaria*), some specialised anomodonts such as *Stahleckeria*, which is larger than the Upper Beaufort *Kannemeyeria*, rhynchocephalia, thecodonts and a saurischian in addition to a number of theriodonts. It is possible that not all of these come from the same zone; but there is a general similarity to the fauna of stage K8 of Tanganyika and to the combined faunas of the Upper Beaufort and Lower Stormberg of South Africa. C.L. Camp has expressed the opinion that specimens assigned to the genus *Dicynodon* in the Santa Maria beds are, in so far as they are described, close to the kannemeyeriids; and he has compared in considerable detail species of *Kannemeyeria* from South Africa with the genera *Stahleckeria* (S. America), *Eubrachiosaurus* and *Placerias* (M. to U. Triassic of N. America) and *Sinokannemeyeria* from probably Middle Triassic beds of Shansi province, China. These comprise the only group of dicynodonts that survived into the later Triassic, and were obviously highly specialised herbivores having a very wide geographical distribution.

The apparent absence of Lower and Middle Beaufort reptiles from the South American area is a fact of geographical importance, particularly in view of the abundance of Lower Beaufort fossils in the south-western part of the South African Karroo basin. The Estrada Nova beds, which form the upper part of the Passa Dois series, are considered to be of Permian age; they carry a number of indigenous lamellibranchs, together with ostracods, palaeoniscid and coelacanth fishes, and plants of the *Glossoperis* flora, but have so far yielded no reptilian remains, in spite of the occurrence of mesosaurs in the underlying beds that immediately succeed the tillites.

Although the succession of reptiliferous continental deposits in the United States of America is imperfect, the earliest reptiles are found in beds of Pennsylvanian age (Upper Carboniferous) in New Mexico and Texas, cotylosaurs and pelycosaurs both being represented. Strikingly similar pelycosaurs occur in the Upper Carboniferous of Bohemia. More advanced types of cotylosaurs and pelycosaurs are also to be found in the Lower Permian (Wichita and Clear Fork) of the U.S.A. No reptiles are known from Middle and Upper Permian beds of North America; but, in addition to the anomodonts *Placerias* and *Eubrachiosaurus* to which reference has already been made, the Triassic fauna contains specialised procolophonids (*Hypsognathus*, etc.), rhynchosauria, and pseudosuchians allied to *Aetosaurus* of the Trias of Wurtemburg and to *Stagonolepis* of the Elgin sandstone of Scotland.

The Wolfville formation of the Triassic of the Maritime Provinces of Canada carries disarticulated and abraded reptilian bones which have been mentioned in a paper by G. de V. Klein (*Bull. geol. Soc. Amer.*, lxxiii (1962), 1127). Predominant are small members of the Procolophonidae (4 genera of which 3 are new); next in frequency are pseudosuchians of the family Aëtosauridae and rhynchocephalians (Rhynchosauridae). Small ornithosuchid pseudosuchians

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and small coelosaurian dinosaurs (both rare) are the only carnivorous reptiles represented. The reptilian fauna appears to correlate with that of the Elgin sandstones of Scotland and the Stubensandstein of Germany (late Middle Keuper).

Reference has already been made to the fauna of the lower zones of the Russian deposits that appear to be closely allied and possibly ancestral to the earliest of the South African reptiles. Zone IV of the succession carries a fauna closely comparable with that of the *Cistecephalus* zone, including pareiasaurians that can be compared with *Anthodon*, large gorgonopsians and anomodonts, therocephalians and procynosuchids. Zone V contains the typical Middle Beaufort forms *Lystrosaurus* and *Chasmatosaurus*, an association also known from the higher of two reptiliferous horizons in the Sinkiang province of China, north of Tibet, and from the Panchet beds of India. *Chasmatosaurus* is one of the earliest of the thecodonts but appears to have become adapted to a semi-aquatic environment and to carnivorous habits. Its distribution in time and in space is of great interest. From Zone VI of Russia have come a pseudosuchian and a large anomodont that seems to have similarities to *Kannemeyeria;* while the beds in the south-eastern part of the Shansi province of China that contain *Sinokannemeyeria* and *Parakannemeyeria* have also yielded a cynodont *Sinognathus*. The Lufeng series of the Yunnen province of China contains, in addition to dinosaurs of the types characteristic of the Stormberg series, a skull named *Bienotherium* which shows many points of agreement with the South African *Tritylodon* and with the Ictidosauria, and what Patterson and Olson have described as a triconodontid mammal and have called *Sinoconodon*. Olson points out that tritylodontids are known at present from the Cave sandstone of South Africa, the Lufeng series of Yunnan, from fissure fillings from the Mendip hills of Britain, and from the Kayenta formation of North America.

This necessarily brief review of our actual knowledge of the distribution in time and space of certain reptilian orders and of their relationships one to another is intended to stress the need for further analytical, synthetic and interpretational studies in a field that is of prime importance to an understanding of the evolutionary history of the higher vertebrates. Analytical studies naturally depend on the acquisition of material and yet more material to provide data, not with the prime objective of multiplying generic and specific names but in order to acquire factual knowledge concerning structural variations within populations. Critical taxonomic inquiry is essential to such studies, as are analyses of the stratigraphic range and the geographic distribution of species, genera, and families. Faunal lists can be used to decipher age relationships; but obviously the names occurring in such lists must have a clear morphological significance, a necessity that demands as full a knowledge as possible of all the specimens to which a particular name is given. At the present time, an appreciable number of so-called "species" among the Karroo reptiles have little or no real significance because of the paucity of knowledge concerning them.

The chief objectives of the study of terrestrial reptilia are twofold—geological

and biological. Such complex organisms reflect in detail the ecological conditions under which they existed, their anatomical inter-relationships, and the lines along which changes in structure occurred. The attainment of the geological objective demands data on the succession in time of differing forms, of the nature and mode of formation of the rocks in which the fossil material is now entombed, and of the relations between the mode of preservation and the material in which the fossils are enclosed. This aspect of the study of Karroo reptilia has not progressed as rapidly in Africa as has descriptive anatomy. The subdivision of the Lower Beaufort beds into biozones, for example, still stands in the framework that was laid down some 50 years ago; little attention has been given to detailed examination of the various types of sediment which house the fossil material or to their inter-relationships; comparison of the occurrence of either isolated bones or of partial or complete skeletons with the sedimentology of their surroundings has scarcely been attempted. Few, if any, descriptions of the geological features at fossil-bearing localities have been published, emphasis having been largely placed on the discovery of specimens for incorporation in collections and subsequent description.

While, therefore, it is possible to derive a considerable amount of satisfaction with the progress which has been and is being made by a comparatively small number of devoted students in the field of anatomical studies, that satisfaction has to be coupled with a feeling of discontent regarding the slowness of the advances in knowledge on the more purely geological side, in detailed stratigraphy and sedimentology of the reptile-bearing sediments, in the acquisition of sufficient data to form a basis for a considered interpretation of the conditions that surrounded the deposition of the great thickness of sediments that are known as the Karroo system.

And even on the purely descriptive side, it seems desirable to reconsider such questions as specific definitions and nomenclature. Many of the "species" listed in a bibliography of Permian and Triassic reptiles are founded on individual specimens, few of which are complete or nearly complete skeletons; many of the "type specimens" are describable skulls, many are partial skulls, and some are of such a nature that they are of very little use for comparison with other specimens. A species, as was pointed out by Cuvier in the closing years of the 18th century, is in reality a collection of individuals, a population whose individual members resemble one another although not absolutely identical one with another. The determination of the characters of a species should, as far as it is possible, be based on biometric measurements of a number of individuals in order to decide the mean and the permissible extremes.

More attention, too, should be given to the collection and examination of post-cranial material in order to study evolutionary and adaptive trends in the skeletal structures of reptilian fossils. Had the cave-fillings of the Mendip hills contained only skull fragments of *Kuehneosaurus* no evidence would have been obtained regarding the mode of locomotion of this Triassic lizard-like form and

there would have been no justification for concluding that it had acquired a gliding habit and thus become, in part, freed from the restrictions on movement imposed by pedal locomotion and possibly the first aerial vertebrate.

To obtain a true assessment of the history of reptilian life in Permian and Triassic times, even within the confines of a single sub-continent, demands a concerted concentration on field-work by teams of geologists (stratigraphers and sedimentary petrologists) and collectors and on laboratory work by vertebrate palaeontologists and preparators. Thus far in Southern Africa, these demands have never been fully met; nor will they be met until sufficient financial support is afforded to the few and scattered scientific organisations that are endeavouring to interest themselves in the problem. Of these, the Bernard Price Institute for Palaeontological Research is one; but, in spite of the munificence of its founder, its staff is too small for the tasks that it should be undertaking. Even with so small a staff, however, its annual expenditure exceeds its income, and the desire that it has to expand its activities to try to satisfy the requirements of proper research in vertebrate palaeontology will remain unfulfilled until it can obtain adequate financial backing.