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PERMO-TRIASSIC "LIZARDS" FROM THE KARROO

by

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ABSTRACT

Three genera of sauropsid reptiles from the Permo-Triassic beds of South Africa — *Saurosternon* Huxley, *Paliguana* Broom and *Palaegama* Broom — were originally described as lizards, or the immediate ancestors of that group. Restudy of these forms confirms that they are close to the ancestry of later Mesozoic and Cenozoic squamates. The skull is somewhat primitive, but in size, proportions and function extremely similar to that of *Kuehneosaurus*. The pectoral girdle is lacertoid in the proportions and orientation of the clavicles and interclavicle; the anterior margin of the scapulocoracoid is fenestrate, and the articulating surface of the glenoid is very short. A sternum is present and one specimen shows ventral connections between the ribs and the sternum. In *Saurosternon*, the forelimb can be seen as very similar to that of living lizards, with special epiphyseal articulating surfaces on the proximal end of the humerus and distal end of the ulna. The pelvic girdle remains primitive, but the rear limb is close to the pattern in lizards. The fifth metatarsal is not obviously hooked, and all five distal tarsals are retained, but the proportions and functions of the ankle presage the condition in living lizards. Epidermal scales are present. Following Romer, these forms are all included in the Family Paliguanidae. They are placed in the Suborder Lacertilia, provisionally in the Infraorder Eolacertilia.

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INTRODUCTION

The lacertoid habitus has been an extremely important way of life throughout the history of the Class Reptilia. The earliest of all reptiles were small lizard-like forms, and the assumption of this pattern was probably basic to the emergence of the group from the labyrinthodont amphibians (Carroll, 1969). Today, the Lacertilia are the most successful reptiles in terms of number of species and habitus diversity.

This suborder is characterized by having a streptostylic quadrate and total elimination of the lower temporal bar. Animals already exhibiting these features and otherwise close to the ancestry of the modern forms are known from the Upper Triassic (Robinson, 1967). Despite the relatively early appearance of these forms, they are already completely lacertoid in their general anatomy and some genera are extremely highly specialized in having enormously elongated ribs which served to support a gliding "wing", as in the living genus *Draco*. Clearly, lizards had a long previous history.

It has long been accepted that true lizards had evolved from Permo-Triassic eosuchians originally possessing a diapsid skull configuration, by the reduction of the lower temporal bar and the freeing of the quadrate. The genus *Prolacerta* from the *Lystrosaurus* zone of South Africa illustrates an intermediate stage in this process. This genus has long figured prominently in considerations of the origin of lizards as a result of the careful descriptions of the skull by Parrington (1935) and Camp (1945). Genera other than *Prolacerta* have been described from the Karroo as lizards or their antecedents, but curiously have been largely ignored since their original descriptions. *Paliguana* and *Palaeagama* were both described by Broom (1903 and 1926), yet they do not figure in more recent considerations of the origin of squamates (e.g. Robinson, 1967). These forms, in both cases represented solely by the type specimens, have been re-examined as part of a general study of primitive sauropsids from the Karroo. In addition, the type of *Saurosternon bainii* (Huxley, 1868) and one other previously undescribed specimen have been studied. All are found to ex-

hibit a number of important characteristics typically associated with squamates. These specimens are significant in demonstrating that lacertoid forms had evolved by the late Permian or early Triassic, independently and in advance of the pattern shown by *Prolacerta*.

A major difficulty in working with this material is the lack of reliable or precise information on the locality or geological horizon of the specimens. Some have no field data at all. What information is available suggests that all are from the late Permian to early Triassic — *Cistecephalus, Daptocephalus* and *Lystrosaurus* zones.

All of the known specimens from South Africa are described here. Aside from *Prolacerta*, there are only four, collected over a period of 100 years. They are clearly very rare elements in the Karroo fauna, possibly as a result of living in an environment not normally leading to fossilization. It is somewhat surprising that lizard-like forms should be so uncommon in the Karroo, especially over such a long period of time. Small size and fragility of skeleton may contribute to the rarity of recognizable fossils, and small insectivorous therapsids may have successfully filled the role of lizards at this time, at least in this region. The paucity of diapsids of any type in the early Karroo beds strongly suggests some general bias against this group (perhaps climatological). The morphological diversity of the few known forms also suggests that we are seeing only a small portion of their total radiation.

At the beginning of this study, it was assumed that Permo-Triassic fossils would represent a comparatively primitive stage in the origin of lizards and exhibit few of the specializations evident in the late Mesozoic and Tertiary genera. Closer examination revealed a host of specific similarities with later forms. There may be some question as to whether the genera from the South African Karroo should be included within the Suborder Lacertilia, but they are certainly members of the group that was ancestral to later lizards.

Unfortunately, the fossil record of lizards is very incomplete throughout the Mesozoic and Tertiary. Determination of the interrelationships of the various living families must be based to a large extent on the anatomy of modern forms and their geographical distribution. The fossil record may confirm or weaken phylogenetic schemes based on the latter criteria, but does not in itself form the primary basis for classification within the group (Camp, 1923; Estes, 1970). It is evident that the basic diversification of lizards was well underway by the end of the Jurassic and Camp indicates that the origin of the various major types was considerably earlier. Gekkonids and iguanids have both been considered as exemplifying the most primitive of modern lizards. From the standpoint of the skull, however, there can be no question but that the configuration common to the iguanids is closest to that of primitive diapsids. Their current geographic distribution supports an early origin, although this is apparently not confirmed by positive evidence of an ancient fossil record. In comparing the skeletons of the South African forms with a wide range of living lizards, overall similarities are greatest with the iguanids and it is with this group that the most detailed comparisons have been made.

Because it is the most completely known of the Karroo "lizards", *Palaeagama vielhaueri* will be described first.

PALAEAGAMA VIELHAUERI Broom

(Figs. 1, 2 and 3)

The type and only specimen, No. 3707 in the McGregor Museum, Kimberley, is a nearly complete skeleton exposed in ventral view. Broom reported that it had been discovered by Mr. P. F. Vielhauer at Kinira in the Mount Frere District. According to Dr. Kitching (personal communication), the horizon is most probably the Eotriassic *Lystrosaurus* zone, although the specimen might have come from the Uppermost Permian *Daptocephalus* zone. It is surely not from higher in the section than the early Triassic. The specimen is in a slab of fine-grained argillaceous sandstone. It consists of the greater portion of the skeleton, in some parts split through with the fracture of the rock. The skull roof is preserved, visible in ventral view. Although the restorations are shown in customary dorsal and lateral views, the specimen shows primarily the internal surface of the bone. The external surface can be seen only where the bone has been lost and a cast could be made to recreate the original surface. The most obvious feature is the relatively great size of the orbits and the corresponding shortness of both the snout and cheek region. This, together with the similarity in size, gives this skull a very similar appearance to *Kuehneosaurus* (Robinson, 1962) and *Icarosaurus* (Colbert, 1970), the only described Upper Triassic lizards. Although the cheek region as a whole is not well preserved, the jugal is well exposed on both sides. The left jugal is nearly complete, lacking only the end of the dorsal process. The ventral margin of the bone is slightly crushed, but with no substantial portion missing. The posterior margin is complete on both sides, demonstrating the complete absence of a posterior process. As restored, this margin slopes posteriorly at an angle of approximately 10° from the vertical. Much of the bone of the right jugal is lost. An impression shows much of its original anteroposterior extent, but the ventral margin is missing, except posteriorly. No trace of either quadratojugal is evident, but the nature of preservation of this area is too poor to assume that it was originally absent.

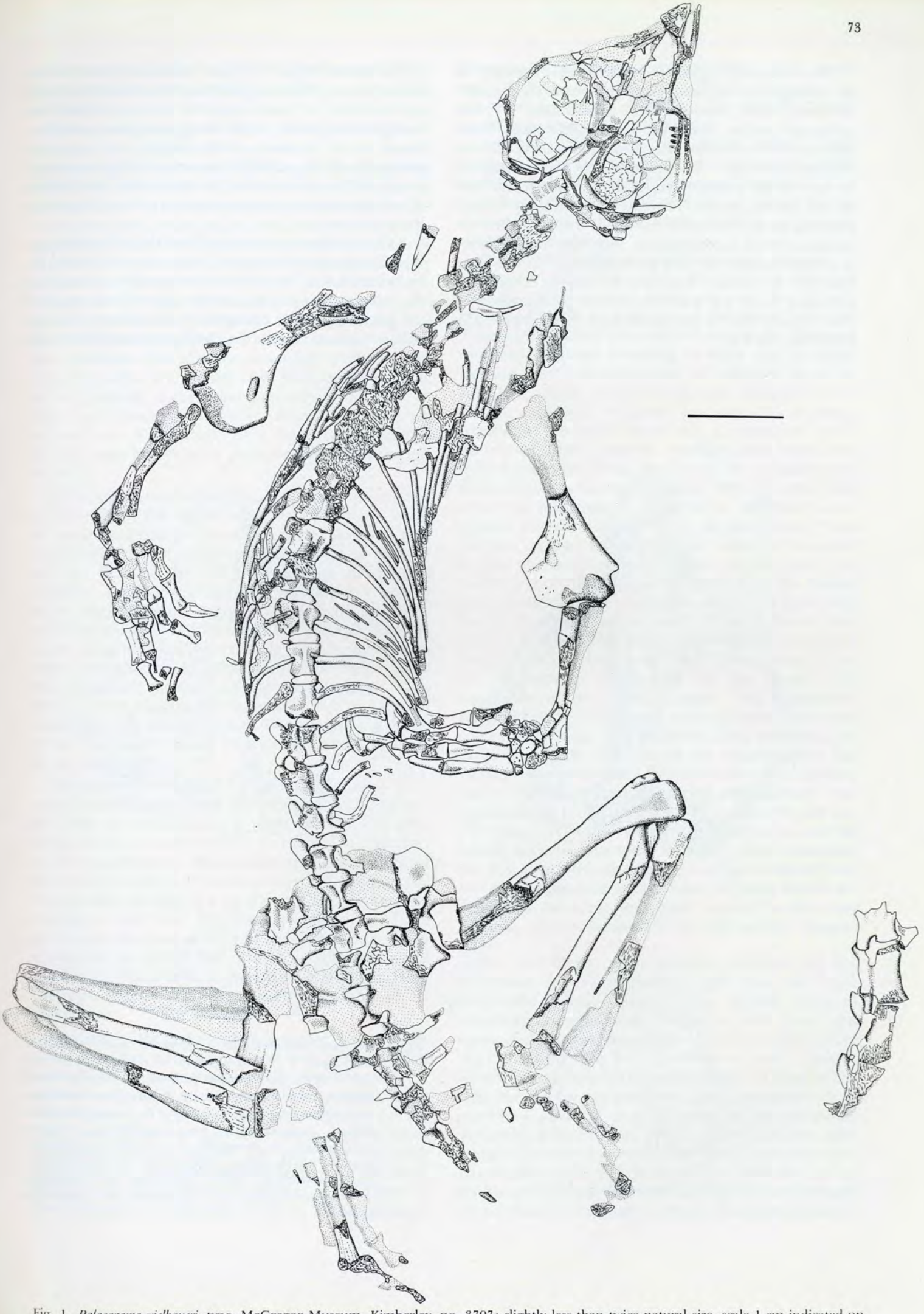


Fig. 1. *Palaeagama vielhaueri*, type, McGregor Museum, Kimberley, no. 3707; slightly less than twice natural size, scale 1 cm indicated on figure.

The temporal region is astonishingly modern in its anatomy. The elements are somewhat disarticulated and portions are represented by impressions rather than the actual bone, but comparison with a modern lizard discloses their identity without question. On both sides, the squamosal can be seen to be a simple strap-shaped bone, much as in the genus *Iguana*. There is definitely no ventral process, as in *Prolacerta*, nor even the posterior extension seen in *Kuehneosaurus*. As preserved, the bone is oriented more or less perpendicular to the long axis of the skull, but this is clearly unnatural, resulting from the anteroposterior compression of this region. The bone must have been essentially horizontal in life.

The postorbital is a flat triradiate bone as in *Keuhneosaurus*; the margin is in contact with the jugal and borders the lower temporal opening in nearly a straight line, rather than being conspicuously embayed as in *Prolacerta*. Unfortunately, the posterior extremity of the posterior process of the postorbital is covered by other bones on both sides, precluding determination of its exact manner of attachment to the squamosal.

The quadrate is represented on the left side by an impression and bone scrap in the shape of a vertically oriented rod. It terminates dorsally adjacent to the paroccipital process and the lateral extremity of the parietal. This is presumably the anterior margin of the tympanic crest. The configuration of the jugal

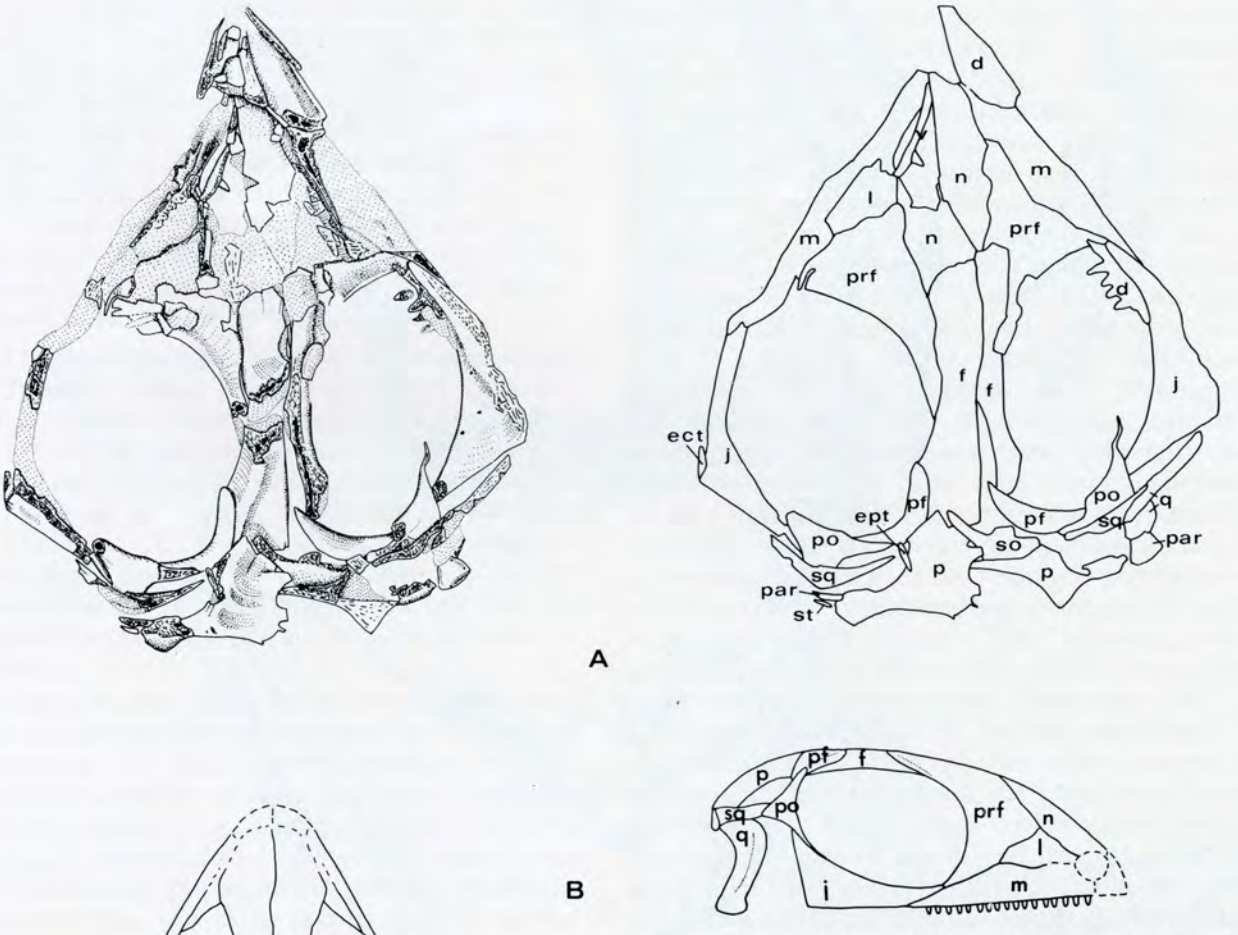


Fig. 2 *Palaeagama vielhaueri*, type. A. detail of ventral surface of skull roof, × 3. B. restoration of skull, in dorsal and lateral views, based almost entirely on the medioventral surface; teeth restored on the basis of the lower jaw, ×2. Abbreviations: d — dentary; ect — ectopterygoid; ept — epipterygoid; f — frontal; j — jugal; l — lacrimal; m — maxilla; n — nasal; p — parietal; par — paroccipital process; pf — postfrontal; po — postorbital; prf — prefrontal; q — quadrate; so — supraoccipital; sq — squamosal; st — supratemporal.

and squamosal indicates that the quadrate was freely movable; the streptostylic condition was fully achieved.

The parietal resembles that of *Kuehneosaurus* except for the slightly shorter extent of the lateral process and the presence of a large pineal opening midway in the length of the bone. A small fragment of bone at the end of the lateral process may be the supratemporal, retaining a primitive position comparable with that of *Youngina*. The ventral surface of the parietal is markedly concave. No postparietals or tabulars are preserved. At the end of the lateral extremity of the right parietal is a small portion of a discrete ossification. Although the fragment is too small to identify on the basis of its anatomy, its position indicates that it is the distal end of the paroccipital process. On the left side, just beyond the end of the parietal, is the other paroccipital process, in this case clearly identifiable despite its peculiar orientation. A fragment of a large supraoccipital may be seen beneath the anterior margin of the left parietal.

Breaking through the edge of the right parietal at the margin of the upper temporal opening is a rod of bone that can be identified by its position and orientation as the epipterygoid, similar to that of modern lizards. The frontals are long narrow rectangular bones, considerably thickened ventrally where they enter the margins of the orbit and buttress the pre- and postfrontals. The frontals, like the other circumorbital bones, lack the ornamentation seen in *Keuhneosaurus*. The postfrontal has a large area expanded medially on the orbital margin. The nasals are as long as the frontals, but considerably wider and very much thinner. The telescoping of the bones in this area makes their exact lateral limits difficult to establish.

The posterior margin of the prefrontal is preserved in the bone on both sides. It apparently reached the level of the maxilla, at least on the left side, eliminating the lacrimal from the margin of the orbit, at least superficially. More anteriorly, the pattern of the roofing bones is difficult to interpret. Much of the bone itself is missing, but enough remains to preclude making a clear cast. The bones in the area of the prefrontal, lacrimal and nasal have been extensively telescoped on the left side. The lacrimal appears as a small area of bone between the prefrontal and maxilla. The top of the snout is obscured by the bones of the lower jaw.

Nothing of the premaxillae is visible. Little of the bone of either maxilla is preserved, but much is represented as an impression. On the left side, the ventral margin lies at the limit of the matrix so that the curvature of the bone may be seen where it extends medially at the base of the teeth, but the teeth themselves are not visible. The posterior extremity of the maxilla is represented by bone on both sides; here it is considerably wider than that of *Kuehneosaurus*. It extends only a short distance posterior to the anterior margin of the orbit. At the end of the snout, the bone itself is present but obscured by other elements. The maxilla curves medially to be exposed dorsally.

Nothing of the palate is preserved, unless a small piece of bone medial to the posterior end of the right jugal is a fragment of the ectopterygoid.

A short section of the dentary is preserved, indicating the presence of small, peg-like, apparently sub-pleurodont teeth.

The postcranial skeleton is in general primitive — eosuchian rather than lizard-like in most observed features. The cervical vertebrae are very poorly preserved. After completion of the whole specimen drawing, the small amount of bone in this area was removed and the resulting cavities cast in latex. Despite their incompleteness, it is immediately obvious that these vertebrae are not elongate as are the cervicals of *Prolacerta* but are, if anything, somewhat shorter than the succeeding trunk vertebrae. Their general configuration resembles that of primitive living lizards and the Jurassic genus *Eichstattosaurus* (Cocude-Michel, 1963, pl. xxx). The count in this region is somewhat difficult to establish, but there appear to be 23 presacrals. There are two sacrals; six caudals are visible in sequence behind the sacrum, and remains of five more are visible a short distance away. Judging by the related species, the tail was probably originally a great deal longer. Except for the cervicals, in which the impression of the dorsal surface is exposed, the column is visible primarily in ventral view. Intercentra are visible throughout the length of the trunk. The zygapophyses are widely spaced and apparently relatively flat. There is no evidence that the neural spines were long. The anterior trunk vertebrae are extremely badly crushed. In the remainder of the column the arches of the vertebrae are crushed down on the centra, obscuring the normal configuration of the pedicle and the transverse process. The bases of the centra show rounded keels, with the lateral surfaces markedly concave. The intercentra are thin crescents whose length is approximately one half that of the centra. They bear no facets for rib articulation. Between the last two isolated caudals may be seen the dorsal part of an incomplete haemal arch.

The ribs of the most anterior cervicals are not preserved, or, as in lizards, they may not have originally been present. The second cervical vertebra, however, does exhibit a well developed transverse process. Assuming a correct count of cervical vertebrae, the first rib preserved is the fourth. which is long, with a cylindrical shaft. In most of the ribs, neither the proximal nor distal extremity is well preserved, making determination of the nature of the heads and the total length difficult. Where adequately preserved, two distinct heads may be seen. Cartilaginous ventral extensions of the ribs in the central portion of the trunk are visible on the right side. A maximum length is attained at approximately

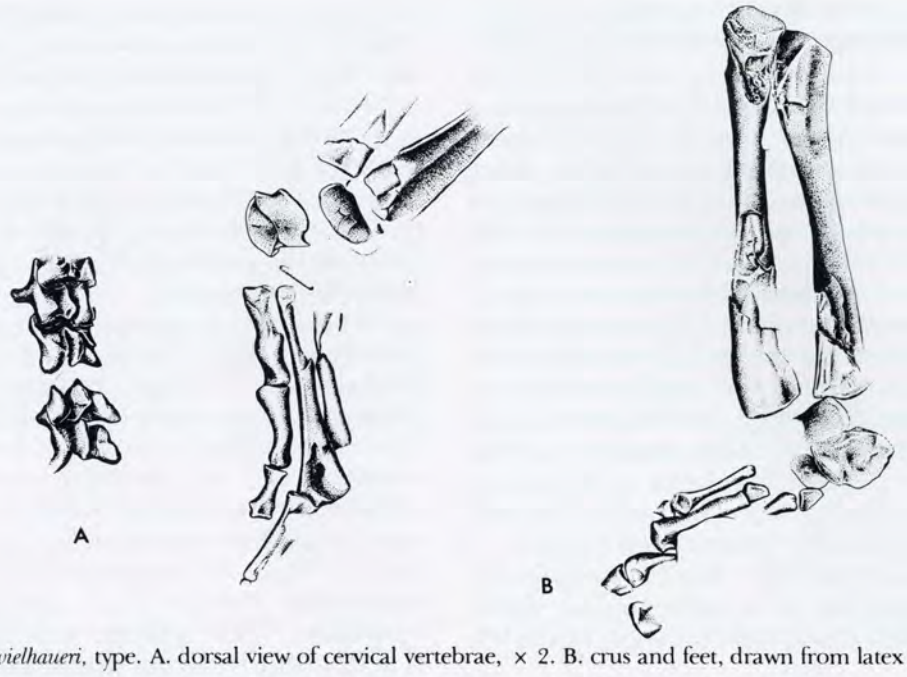


Fig. 3. *Palaeagama vielhaueri*, type. A. dorsal view of cervical vertebrae, × 2. B. crus and feet, drawn from latex casts, ×2.

the 12th rib. The length decreases sharply behind the 17th. The last presacral rib is a narrow rod, apparently shorter than the centrum. The penultimate is not preserved. The antepenultimate is as thick as those more anterior and approximately twice the length of the centra. The anterior sacral ribs are well exposed ventrally. They are not fused to the vertebrae. A shallow constriction demarcates the barely separate heads. The distal end is not greatly expanded and does not curve ventrally to provide a large area for attachment with the illum. Such a narrow sacral attachment is common in modern lizards. Only a small portion of the second sacral rib is visible on the left side. The distal portion resembles that of the first. The ribs of the first three caudals can be seen as fused to the transverse processes and extending horizontally at right angles to the long axis of the tail. They are dorsoventrally flattened. No ribs are preserved more posteriorly.

The most notable feature of the shoulder girdle is the presence of an ossified sternum posterior to the coracoid. The outline of the structure is not well defined, but it must have been the length of at least three centra. The scapulocoracoid is very poorly preserved. There appears to be a narrow anterior projection from the scapula, suggestive of the lattice-like margin seen in the lizards. This cannot be established with any certainty, however. The dermal shoulder girdle is also represented only by fragments, establishing that the plates of the clavicles were narrow, as was the stem of the interclavicle.

The humeri are represented only by impressions proximally, but much of the shaft of the right and the distal portions of both are present as bone. In contrast to late Triassic lizards, the distal ends of the shafts are expanded, much as in romeriids and captorhinids, with a long slit-like entepicondylar foramen and a short supinator process. Only the ventral surface of the area of distal expansion is exposed, showing large areas of unfinished bone for the articulation of the ulna and radius. The ulna and radius are poorly preserved, but clearly short and slender. There is only a slight ossification of the olecranon. The distal elements of the left wrist are well exposed, but the proximal bones are badly crushed and broken, making establishment of the margins impractical. Much better preservation of the area would be necessary to establish any significant features, since there are few dramatic changes in the wrist from romeriids to true lizards. In both hands, only the first four digits are exposed. The first three are almost completely preserved, but only the proximal two phalanges of the fourth. The terminal phalanges are large curved claws. As a unit, the hand is surprisingly massive in appearance.

The puboischiadic plate is largely preserved as an impression. It is generally plate-like in appearance. There is no evidence of ossification where the pubis and ischium would have joined, but it is quite possible that this area was deformed by the sacral ribs and so was not preserved in the plane of the block as it is exposed. There are certainly no clear margins indicating the presence of a thyroid fenestra, as is the case in the late Triassic lizard *Icarosaurus*. On the right side, a small circular obturator foramen is visible. The girdle extends the length of five vertebrae. The ilium is a broad blade of indeterminate length extending posterodorsally.

The femur is the length of seven trunk vertebrae. The head is robust, with the internal trochanter descending ventrally as an extension from the shaft. The distal elements of the rear limb are almost as long as the femur, the tibia and fibula both reaching

93% of its length; both are lightly built bones. The feet are unfortunately represented only by scraps of bone and poor impressions of the dorsal surface (Fig. 3). The astragalus and calcaneum are clearly large, flat, more or less square bones, as in the romeriids and the primitive eosuchian *Galesphyrus*, in contrast to the shorter thicker elements seen in true lizards. Little of the distal tarsals is visible and nothing worth describing. Between the two feet, most of the metatarsals can be reconstructed. The bones are long, with the fifth almost certainly not hooked, in contrast to Broom's interpretation, but substantially shorter than the fourth.

Ventral scales can be seen, scattered among the more posterior ribs. Their configuration resembles that of other small primitive reptiles.

PALIGUANA WHITEI Broom

(Fig. 4)

A second form known from the skull alone, *Paliguana whitei*, was described by Broom in 1903 and discussed again in 1925. It is in the collection of the Albany Museum, Grahamstown, No. 3585. It comes from Donnybrook, between Tarkastad and Queenstown. According to Kitching (personal communication), the specimen may be either Upper Permian or Lower Triassic since strata of both the *Daptocephalus* and *Lystrosaurus* zones are exposed in this area. The bone is soft and white, the matrix a red sandy clay. Very little preparation was attempted, beyond that initiated by Broom. The skull remains essentially as he saw it. The present interpretation differs only in details from that offered by Broom in 1903. The restorations given in his 1925 paper are, however, quite different. The present interpretation owes much to comparison with the Upper Triassic lizard *Kuehneosaurus*. The two forms are of almost exactly the same size and agree in most significant anatomical details.

The outlines of almost the entire skull roof and jaws are apparent, but most of the bone in the antorbital region has gone, leaving only an impression, and the tip of the snout is totally missing. Bones are present in the area of the palate, but so badly broken that no description is possible. The

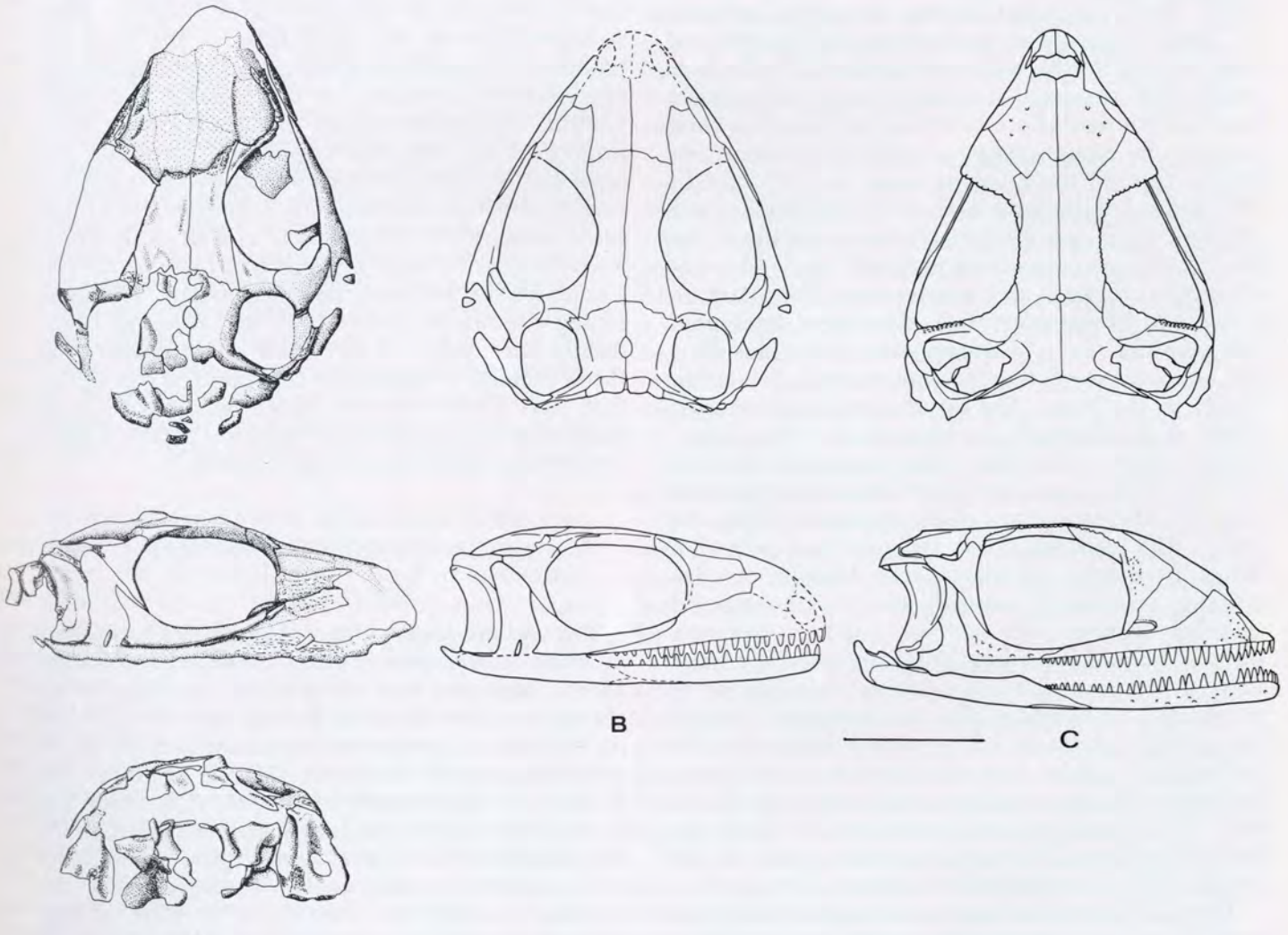


Fig. 4. *Paliguana whitei*, type, Albany Museum, Grahamstown, no. 3585. A. skull in dorsal, lateral and posterior views. B. restoration of skull in dorsal and lateral views. C. skull of the Upper Triassic lizard *Kuehneosaurus*, from Robinson. All × 2.

right lower jaw is present, but shows no details. Fortunately, the temporal region is quite well preserved. The parietals differ from those of *Kuehneosaurus* in the presence of a large pineal opening midway in their length, but are otherwise similar in configuration. A long process extends posterior to the upper temporal opening to make contact with the squamosal laterally. Posteriorly, this process is recessed, probably for a small supratemporal, a bone that has this general position in captorhinomorphs, eosuchians and many lizards. Medially there are two pairs of small quadrangular bones exposed on the occipital surface of the parietal. They surely represent vestiges of both postparietals and tabulars — bones lost in all typical squamates. Little of the actual bone of either squamosal is present, but most of the outline is retained as an impression of the right side, together with traces of the bone. It is in the form of a narrow band, inserting on the anterodorsal surface of the posterior process of the parietal posteriorly, and extending across the dorsal surface of the quadrate. Anteriorly it is overlapped by the posterior bar of the postorbital. There is no evidence of the great extension down over the quadrate shown by Broom (1925, Fig. 5), although it does extend farther than in *Kuehneosaurus*. The postorbital and postfrontal have essentially the same configuration as in that genus. The quadrate is a large bone, of typically lacertoid configuration. Laterally, the bone has been pierced by weathering or earlier preparation. Broom figured the bone as entire in 1903, but in 1925 indicated the bone in front of this opening as a quadratojugal, restoring that bone as L-shaped, the ventral process connecting with the jugal. There is no support for such an interpretation. The quadrate is exposed in posterior view, showing a configuration very like that of *Kuehneosaurus*. A rounded crest for attachment of the tympanum runs the entire height of the bone. The dorsal surface is rounded where it fits beneath the squamosal. The paroccipital process must have fitted against the medial surface of the quadrate just beneath the parietal. The articulating surface of the quadrate is not exposed. The jugal has a very long anterior extension beneath the orbit. There is a very short process extending posteriorly beneath the lower temporal opening. Between this and the quadrate is a tiny piece of bone that Broom (1903) identified as a fragment of the lower jaw. It is just as plausibly interpreted as a rudiment of the quadratojugal. Despite the possible remnant of a quadratojugal and the presence of a short posterior process of the jugal, the temporal region is functionally very similar to that of *Kuehneosaurus* and *Icarosaurus*, in both size and proportions. The area is much closer to the pattern of true lizards than it is to that of *Prolacerta*.

In occipital view can be seen poorly preserved exoccipitals and otic-paroccipital bones. The posterior portions of the pterygoids are visible ventrally. The frontals are long paired rectangular bones, much as in *Kuehneosaurus*, except that their orbital margin is smooth rather than crenulated. The prefrontals have a large dorsal exposure, but probably do not extend ventrally on to the maxilla in front of the orbit as in the Upper Triassic lizards. Only the posterior portion of the nasals are represented, and that only by an impression of the inner surface. There is no evidence of the premaxilla, nor of either the position or configuration of the external nares. The lacrimal, lacking the surface layer, is exposed on the right side. As preserved, it shows a narrow rectangular shape, extending halfway between the orbit and the end of the snout.

Only the broken inner bone of the posterodorsal portion of the maxilla is visible on the right side. A small peg-shaped tooth is present adjacent to the lower jaw. A dentition similar to that of *Kuehneosaurus* has been restored on the basis of it.

The jaw is slender and has a short retroarticular process. No other features are evident.

Palaeagama and *Paliguana* are the only genera from the Karroo that provide evidence of the skull roof of forms directly ancestral to lizards. There is no evidence that either of these forms is any younger than the *Lystrosaurus* zone, at the base of the Triassic, yet the basic pattern is fundamentally the same as that exhibited by Upper Triassic lizards. What primitive features they do exhibit — the large size and posterior position of the pineal opening and the retention of remnants of the tabular and postparietal — are not related to the important functioning of the temporal region. Of particular importance is the relative shortness of the temporal region as recently discussed by Robinson (1973). The great similarity in proportions as well as in size to *Kuehneosaurus* strongly suggests that these forms had a functionally lacertoid jaw mechanism. This is in strong contrast to *Prolacerta*, which, although structurally intermediate between the diapsid pattern of the eosuchian *Youngina* and the lacertoid configuration, has much different skull proportions from *Kuehneosaurus*; details of the temporal region suggest a much less lizard-like jaw mechanism.

SAUROSTERNON BAINII Huxley

(Figs. 5, 6 and 7)

The earliest description of a lizard-like form from the Karroo was that of *Saurosternon bainii* (Huxley, 1868). The only known specimen consists of an almost complete skeleton, lacking only the head and part of the tail, preserved in counterpart blocks of very fine-grained sandstone (British Museum No. R.1234). It was discovered by Mr. Bain from Styl Krantz, Sneeuwberg, South Africa. According to Dr. Kitching, both *Cistecephalus* and *Daptocephalus* zones are exposed in this area. Whichever bed the specimen came from, it is Upper Permian in age. When originally described, the counterparts were essentially mirror images of each other; the bone was split through the middle with little if any of the

original surface exposed. Consequently, Huxley's illustrations show little more than the outline of the bones. Mr. Croucher at the British Museum (Natural History) very kindly prepared the specimen by etching away the bone in hydrochloric acid, leaving the matrix as a high fidelity mould of the original surface. This was cast with silicon and latex rubber. The detailed anatomy of the specimen has been studied from these casts.

The casts of the counterparts represent primarily dorsal and ventral views of the animal. The overall appearance is similar to that of the type of *Palaeagama*. Although there are structural differences that may be used to support the retention of the previously indicated taxonomic difference, several areas of particular significance are not comparably preserved in both specimens. The specimen of *Saurosternon* is certainly less mature, with correspondingly less complete ossification of the distal end of the humerus and most of the other articulating surfaces of the limb bones.

The body is spread out flat, with the tail curving around the front of the block. The forelimbs are bent back with the hands inserted into the rib cage; the rear limbs are strongly flexed, with the feet drawn in just behind the pelvis. The preservation of the individual bones is exceedingly good in this specimen. So good, in fact, that it is necessary to base this description largely on comparisons with living forms. Some primitive features correspond with those seen in *Sphenodon*, but more extensive comparison is possible with lizards. The greatest similarity was found with the common iguanid, *Iguana iguana*, but comparison was also made with a variety of other forms representing many of the living families. Among iguanids, the greatest similarity in proportions was found not with forms of the same size but with animals of considerably greater linear dimensions. For its size, *Saurosternon* has noticeably stouter limbs than modern equivalents, although the detailed structural similarity is very close.

The cervical vertebrae as well as the skull are missing in this specimen. Ten vertebrae are exposed between the pectoral girdle and the sacrum. Presumably, up to 12 had been present more anteriorly. Five can be glimpsed above the puboischiadic plate. From comparison with *Palaeagama* and modern lizards, it is probable that the last of these is the first caudal, although it might be the more posterior of the two sacrals. No trace of the vertebrae in this region can be seen in dorsal view. Twenty-one caudal vertebrae can be seen in articulation behind the pelvis. Extending around the opposite side of the block, over the left shoulder, can be seen 10 distal caudals. Assuming that the tail had been coiled evenly about the body, that the length of the intervening segments was intermediate between those of the extreme ends of the tail, and that no appreciable gaps developed during preservation, there would be 35—40 vertebrae in this area, for a total caudal count approaching 70.

The general configuration of the vertebrae resembles more that of sphenodontids than lizards. Throughout the trunk and sacral region, large intercentra, with proportions similar to those in *Sphenodon*, are apparent. The centra are notched to receive them. They are presumably still deeply notochordal. Laterally, the centra are deeply constricted near the base, but the ventral surface remains rounded rather than keeled. There is no trace of the neurocentral suture. The transverse processes extend a very short distance laterally from the pedicles and slope anteroventrally to the margin of the centra. The articulating surface is essentially flat and faces straight laterally. The neural arches are crushed down into the neural canal, making detailed observation of this surface difficult. The neural spines are short and triangular, with the apex above the posterior zygaphophyses. Anteriorly, the spine continues as a low ridge, passing beneath the preceding arch. Here it bifurcates, as in some lizards, to form laterally facing accessory articulating processes. These are also developed in *Sphenodon* (Hoffstetter and Gasc. 1969). The zygapophyses themselves appear to be quite steeply angled, but this is difficult to quantify due to crushing. In contrast to primitive eosuchians such as *Galesphyrus* and *Youngina*, the zygapophyses are close to the midline, as in most lizards.

As in lizards, sphenodontids and advanced eosuchians, the anterior caudal ribs are indistinguishably fused to the transverse processes. These fused structures extend at essentially right angles to the tail. Those of the most anterior exposed caudals, the first or second of the series, extend at a slight angle anterior to the transverse plane. The next several extend slightly posteriorly. These prominent processes extend for only about five segments. Short pointed ribs are evident to the end of the anterior portion of the tail as preserved. The apparent break in the pattern of the ribs is probably a result of preservation, rather than being natural.

Although not all of the anterior caudal centra are ideally preserved, enough are sufficiently well exposed to indicate the absence of any tail-break mechanism in the portion of the tail where it might be expected.

Intercentra are present anterior to the first centrum behind the ischium. More posteriorly, well developed haemal arches are present in the anterior portion of the tail. The length of the centra does not appreciably shorten even in the terminal caudals, but the height and width are greatly reduced and the zygapophyses become almost indistinguishable.

The shoulder girdle presages the lacertoid condition to a striking degree. The dermal elements are similarly reduced, with the plate of the interclavicle reduced to a narrow bar. The similarity of this bone to that of the monitor was noted by Huxley. In iguanids, the lateral processes angle posteriorly at

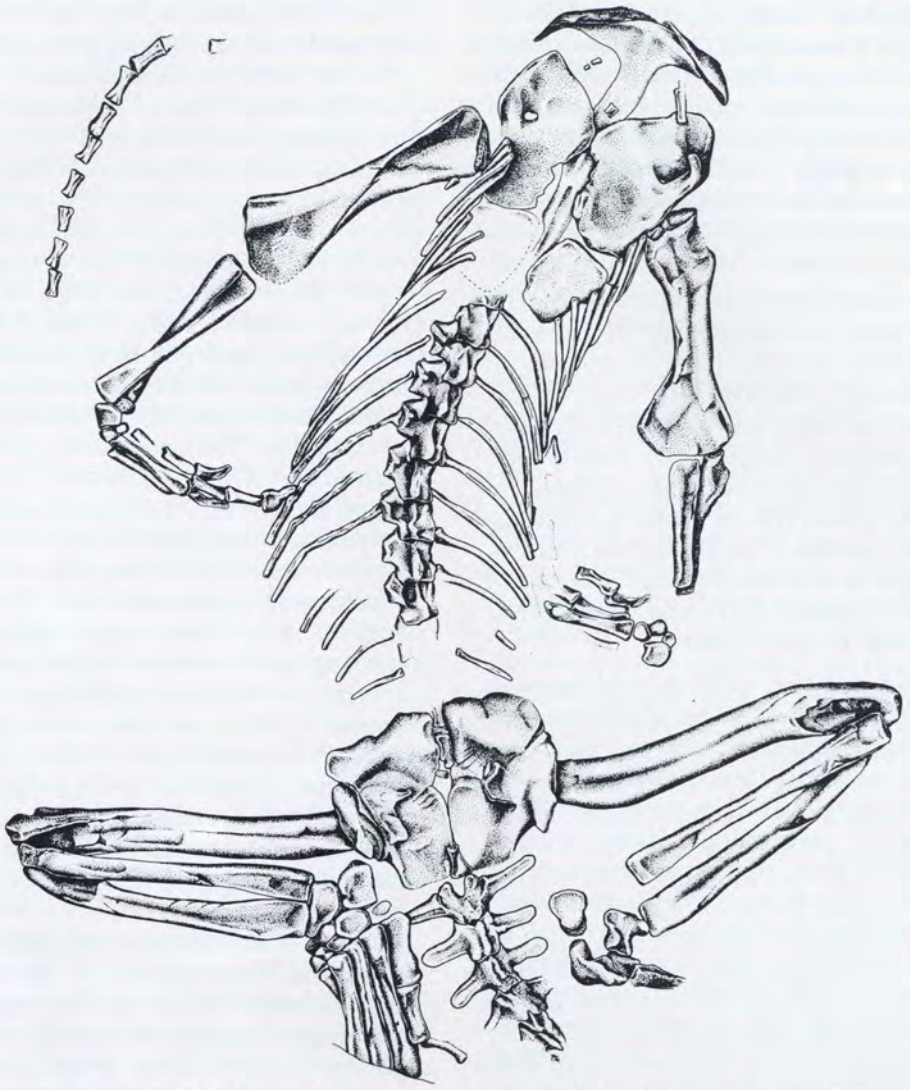


Fig. 5. *Saurosternon bainii*, type, British Museum (Natural History), no. 1234; dorsal view, drawing based on latex cast, ×2.

about 25° to the transverse plane. The angle is approximately 15° in *Saurosternon*. In both forms, there is a midventral ridge extending from the area of the clavicular attachment back to the level of the sternum. In both, the stem extends posteriorly nearly, but not completely, to the posterior limit of the sternum. The clavicular blades are very narrow. Since the specimen is flattened into almost a single plane, it is difficult to reconstruct the original angle of the blades. Their appearance above the dorsal surface of the interclavicle suggests, however, that as in lizards they were angled dorsally from the level of the interclavicle. Only the very base of the shaft is preserved. No trace of the cleithrum is preserved. There is no way to judge whether this element had been eliminated by this stage in the origin of lizards.

Only the ventral portion of the scapulocoracoid is present. This area is very important, however, in showing the inception of lacertoid characteristics. Lizards typically have a fenestrated structure anteriorly in contrast to a more or less continuously ossified anterior portion of the scapulocoracoid of most Paleozoic forms. In the latter group, the anterior margin may be smooth, but is more often irregular as a result of incomplete ossificaton; there are never narrow extensions of tissue between large openings. In *Saurosternon*, there is a large gap ventrally behind the plate of the interclavicle. The margin of this area is clearly defined, but across it are narrow, poorly ossified rods of tissue, clearly comparable to those seen in lizards. *Saurosternon* appears more primitive than iguanids in the lesser extent of the fenestration and possibly in the lower degree of ossification of the separate bars.

In lizards, the scapula and coracoid tend to be separately ossified. Although only the base of the scapula is preserved in this specimen, there is no evidence of a suture separating it from the coracoid. Making allowance for dorsoventral crushing, the glenoid appears essentially like that of iguanids. The shortness of its articulating surface is in marked contrast to the great extent common in Paleozoic reptiles. The scapular portion has been crushed into the ventral plane, but the orientation of this portion of

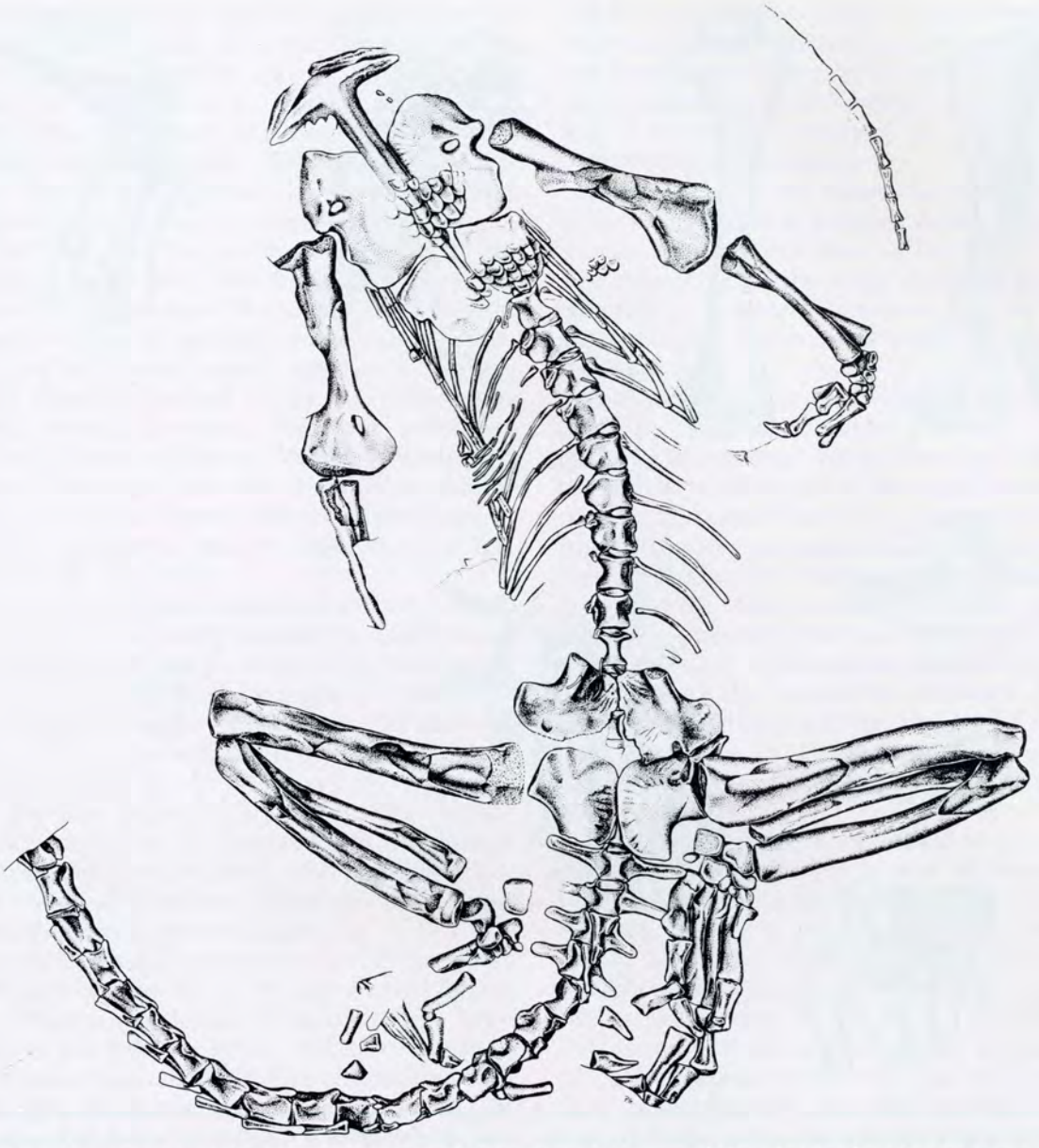


Fig. 6. *Saurosternon bainii*, type, British Museum (Natural History), no. 1234; ventral view, drawing based on latex cast, ×2.

the glenoid was probably obliquely posteroventral, as well as somewhat lateral. There is, as in iguanids, a small opening just anterior to the supraglenoid buttress. Anteromedial to the glenoid is a large coracoid foramen, again as in iguanids. Medially, the configuration of the area appears more primitive, with this foramen opening into a substantial subcoracoscapular fossa.

Saurosternon exhibits a substantial but paired sternum. This bone extends the length of slightly more than two vertebral centra. It has essentially the same proportions and dimensions as those of some modern lizards. The relationship of the coracoid and the sternum is very similar, with a slight gap between them laterally and a larger space medially. The apparent immaturity of the specimen indicates the possibility that the sternum might be co-ossified in an adult. The sternum does appear median in the slightly larger but generally similar specimen from the Albany Museum collection (Fig. 8). The ventral surface of the sternum in *Saurosternon* is somewhat obscured by overlapping scales, but there do not appear to be the lateral projections for the attachment of the ventral extremities of the ribs as seen in modern lizards and also in the Permo-Triassic eosuchians *Tangasaurus* and *Kenyasaurus* (Harris and Carroll, 1975). Cartilaginous ventral extensions of the sternal ribs may not have been well developed in this form, in contrast to the condition seen in *Palaeagama*. Considering the preservation of other delicate structures in this area, their absence in the fossil probably indicates that they were not substantial elements in the living animal.

The humerus is essentially lacertoid, although with some retention of primitive features. In comparing this and other limb bones, it is important to



Fig. 7. *Saurosternon bainii*, type, details of appendicular skeleton, compared with modern lizard. A. *Saurosternon*, dorsal view of humerus (dotted line indicates extent of articulating surface, based on the nature of the glenoid), × 3. B. *Iguana iguana*, dorsal view of humerus, × 1.5. C. *Saurosternon*, medial and lateral views of left carpus, × 4.5. D. *Saurosternon*, restoration of carpus in dorsal view, × 4.5. E. *Saurosternon*, head of left femur, posterior view (dotted line indicates probable extent of articulating surface based on condition in modern lizards), × 3. F. *Iguana iguana*, head of left femur, posterior view (dotted line indicates extent of articulating surface), × 1.5. G. *Saurosternon*, left foot, ventral view, × 4.5. H. *Iguana iguana*, left foot in dorsal view, showing epiphyses, × 2. Abbreviations: a — astragalus; c — calcaneum; cen — centrale; i — intermedium; lc — lateral centrale; mc — medial centrale; p — pisiform; r — radiale; R — radius; U — ulna; u — ulnare; 1-5 — distal carpals and tarsals; i-v — metacarpals and metatarsals.

keep in mind that the ends are incompletely ossified; it should therefore be matched with an immature lizard, or one in which the epiphyses have been removed. In lizards and *Sphenodon* there is a ball-shaped proximal articulating surface of the humerus, extending from the general proximal surface of the bone, and of much less anterior-posterior extent. Such a structure is not visible in this specimen, but such a head must have been present in the living animal since the total width of the proximal end of the humerus is much greater than the available articulating surface of the glenoid. There is some crushing, which probably accentuates the width of the shaft. It is certain that the area of distal expansion is wider than in lizards, since posteriorly the entepicondyle surrounds the entepicondylar foramen so that this opening, as in *Sphenodon,* opens ventrally well anterior to the margin of the bone. Dorsally it is revealed, as in that genus, by a diagonal slit on the margin of the bone. Anteriorly there is a narrow groove running parallel to the margin at the distal extremity indicating the presence of a small ectepicondylar foramen. Except for the reduction in the posterior extent in living forms, the distal portion of the humerus is essentially like that of iguanids.

The ulna and radius are directly comparable with those elements in iguanids, if lack of the epiphyses is taken into consideration. Even without the olecranon, the proximal articulating surface of the ulna slopes ventrally toward the humerus. The shaft of the ulna is slim and about 70% the length of the humerus. Distally it is flattened in the plane of the carpus. More proximally, the shaft is laterally compressed. In living lizards, the distal epiphysis of the ulna develops as a convex head for a ball and socket joint between that bone and the ulnare. This pattern has already evolved in *Saurosternon*. In ventral view, the distal end of the left ulna is concave at the tip, apparently showing the end of the bony shaft. On the dorsal surface, however, the bone continues slightly more than a millimetre longer in tissue that is slightly differentiated in surface detail from that of the shaft. For some reason, the acid preparation removed this epiphyseal area on the dorsal surface, but not ventrally (Fig. 7C).

There are relatively few features for comparison, but the radius is essentially indistinguishable from that of an iguanid. It has a slender shaft; the proximal end is a flat oval at right angles to the shaft. Distally the bone is slightly flattened in the plane of the carpus. The distal articulating surface forms a gently convex arc.

All of the left carpus is preserved. The medial elements are visible in the ventral block, the lateral in the dorsal. The overall pattern and detailed structure of the individual bones closely resemble those of *Sphenodon* and primitive living lizards.

The pisiform lies adjacent to the end of the ulna; it is small, nearly spherical, with only a small finished bone surface anterodorsally. The ulnare is a large oval with an extensive anterior surface of finished bone; the posteroproximal face is concave, for articulation with the specialized surface at the end of the ulna. As in lizards, the radiale is a flattened oval of unfinished bone. There is a small diamond-shaped intermedium which has a very limited surface for articulation with the radius and none with the ulna. It is much smaller than the intermedium of fossil and living sphenodontids. A primitive feature is the presence of a relatively large medial centrale, similar in shape and directly beneath the radiale. A smaller spherical bone can be identified as a second centrale.

The first distal carpal is a tiny spherical bone, occupying less than half the proximal surface of the first metacarpal as in iguanids. The second distal carpal is considerably larger than the first. The third distal carpal is partially obscured beneath the other elements. The fourth distal carpal is the largest, and a small area of the dorsal surface is of finished bone. The fifth distal carpal is a small sphere with no finished surface. Comparison of this carpus with that of specific lizards is difficult due to the presence in the latter group of ossified epiphyseal elements at the proximal ends of the metacarpals and elsewhere. There were apparently no such elements in the fossil, but smaller distal tarsals resemble those elements in their size and position and it is possible that confusion might arise in differentiating between small elements of the central series, distal carpals and metacarpal epiphyses in both fossils and prepared lizard skeletons.

In *Saurosternon,* the length of the metacarpals increases in primitive fashion from the first to the fourth, with the fifth close to the length of the first. The remainder of the hand resembles that of large iguanids in its general structure, but on neither side are enough of the distal elements preserved for restoration.

In ventral view, the pelvic girdle can be seen to be basically primitive, with a nearly continuous puboischiadic plate. Ventrolaterally, the margin of the pubis is thickened to form an anteriorly facing process that ends bluntly in a surface of unfinished bone. This area, conspicuous in many primitive reptiles, served for the attachment of abdominal muscles and tendons. On the dorsal surface, the anterior margin — the only portion of the pubis that is ossified in lizards — is much thickened in this form. In *Saurosternon,* the obturator foramen pierces this thickened portion near the margin of the ischium. The area that in lizards remained open as the thyroid fenestra is still ossified, but the bone is quite thin.

A diamond-shaped unossified area characterizes the juncture of the pubis and ischium. This may have marked the initial development of the thyroid fenestra, but it is equally probable that this area would have been ossified at a more mature stage. It is difficult to determine the natural orientation of the pubis because of crushing. In modern lizards, the major surface of this bone is angled obliquely from the transverse plane so that the largest surface faces anterodorsally. In primitive reptiles, the surface of the bone faces predominantly dorsomedially. In this flattened specimen, it is difficult to determine whether the large dorsal exposure is entirely natural, or if the bone has been twisted as well as flattened during preservation. The symphysis between the pubes appears to extend at least half the length of these bones, in contrast to its very narrow extent in small iguanids, but the length of the symphysis is quite long in larger modern forms such as *Varanus*.

The ischium approaches the lacertoid configuration in its short posterior extent, but the anterior border is certainly not recessed where it might have bordered a thyroid fenestra, in contrast to even the Triassic lizard *Icarosaurus*. Only the bases of the ilia are preserved. This area resembles that of lizards, but there are likewise no distinguishable differences from more primitive forms. In sum, this pelvis shows no specifically lizard-like features in advance of the general eosuchian pattern.

Like the humerus, the femur resembles that of a lizard in which the epiphyses are not ossified. Comparison with an iguanid femur in which these elements are lost shows almost no distinguishing

features. The proximal end of the femur of *Saurosternon* has a large oval area of unfinished bone, ridged at the margins, that must have been covered in life by an extensive, hemispherical, cartilaginous or bony articulating surface, as in modern lizards. Posteroventrally the bone extends as an internal trochanter, arising gradually from the general ventral surface of the bone. The shaft is slightly sigmoidal, with the articulating surfaces twisted relative to one another. The posterior portion of the distal articulating area has an unfinished surface, suggesting the original presence of a bony epiphysis.

The bony shafts of the tibia and fibula are both 20 mm in length, 85% that of the femur. In a specimen of *Iguana iguana* of comparable size, the tibia is 90% the length of the femur. The general proportions, configuration and relative size of these elements resemble those of iguanids; the only notable exception is the relatively smaller size of the proximal head of the tibia in *Saurosternon*. This bone also lacks the proximal crest expressed on the posteromedial margin of the shaft in many lizards. No epiphyses are ossified on either the tibia or fibula. The configuration of the ossified extremities of these bones closely resembles that in lizards. There is no evidence bearing on the presence or absence of proximal ossifications or cartilaginous developments such as the patella or the epiphysis of the fibula. Distally, the configuration of the ventral surface of the proximal tarsals suggests the presence in the living animal of a triangular epiphyseal extension of the fibula such as that seen in an iguanid. The configuration of this area in more specialized lizards such as varanids, however, is not comparable with that of *Saurosternon*.

The left tarsus, with all of the elements in nearly their natural positions, is visible in both dorsal and ventral views. At first glance, it appears to lack all the specializations characteristic of lizards. The fifth metatarsal is not hooked, and all five distal tarsals are retained, along with a substantial centrale. The astragalus and calcaneum are clearly not co-ossified. Comparison with a series of more primitive reptiles, captorhinomorphs and eosuchians, as well as primitive lizards, indicates that the tarsus as a unit was functionally approaching the lacertoid condition. This is particularly noticeable if we consider proportions. Although exact measurements are impractical as a result of the angular contact between the elements, the ratio between the posterodistal extent of the tarsus and the length of the crus shows a general decrease from primitive romeriids, through the primitive eosuchian *Galesphyrus* to *Saurosternon* and later lizards.

In primitive reptiles, romeriids, captorhinids and primitive eosuchians such as *Galesphyrus,* the astragalus and calcaneum are large flat elements, with the articulating surfaces for the tibia and fibula broad, sharply separated and at a considerable angle to one another. In *Saurosternon,* the astragalus and calcaneum are relatively extensive dorsally, with the perforating foramen still evident at the margin of the calcaneum. Ventrally, the extent of the bones is much less. The articulating surface for the fibula is in the shape of a very open V, formed equally by the astragalus and calcaneum. Dorsally, the calcaneum appears as a flattened oval. The astragulus is basically triangular in dorsal view, with the dorsomedial margin sloping toward the centrale. The surface for articulation with the tibia is separated from that for the fibula by a considerable gap. In ventral view, the two surfaces appear to be confluent. Dorsally, the centrale appears as a narrow, more or less flat plate; ventrally, none of the surface is finished bone. Proximally, the bone is deeply grooved so as to be closely integrated with the astragalus. It is probable that the two bones functioned as a unit, presaging the condition in true lizards where the centrale is not retained as a discrete element. The fourth distal tarsal articulates broadly with both the astragalus and calcaneum proximally, with the centrale medially, and both the fifth distal tarsal and the fifth metatarsal laterally. The nearly spherical third distal tarsal fits into the mediodistal surface. Much of the ventral surface of the fourth distal tarsal is flat, finished bone. The remainder of the distal tarsals are rounded and show no finished surfaces. This suggests that the surrounding elements moved over them with extensive flexure of the foot. The extent of the first distal tarsal seems great in this specimen, but this is a result of displacement, with the proximal articulating surface extensively exposed in ventral view. In its natural orientation, this bone would have appeared as only a narrow oval. The second is a tiny spherical structure. The third is in the form of a somewhat larger, laterally compressed oval. The fifth is also a small oval element, occupying much less than the total articulating surface of the fifth metatarsal. The presence of distal tarsals one, two and five may be considered to be a primitive condition, distinguishing this form in a clear and obvious way from modern lizards. Close examination of lizards of various families reveals epiphyses in essentially the same position as these distal tarsals. Although the similarity in position does not in itself necessitate accepting homology between these elements, it would certainly be difficult to differentiate the epiphyses from small distal tarsals in fossil members of living lizard groups. The homology of traction epiphyses with originally distinct ossifications within tendons has been suggested by Parsons (1908). Most pressure epiphyses presumably evolved from cartilaginous tissue primitively associated with the growing extremities of the bones, but comparison with traction epiphyses raises the possibility that epiphyses of the metatarsals and metacarpals have evolved from distal tarsals and carpals.

Of the left foot, the first metatarsal is incomplete and the remainder of the first digit is missing. The remainder of the metatarsals are closely appressed and overlapping throughout their length. The proximal ends would have overlapped when the bones were in their normal position. The third and fourth

metatarsals appear to be of approximately equal length. The fifth is about half this length. It is not conspicuously hooked, as this configuration has been specified by Robinson (1975). The proximal articulating surface is somewhat expanded, and proximally it is tilted slightly medially where it is in articulation with the fourth distal tarsal. The proximal end appears to be somewhat bent medially from the long axis of the bone. It is possible that the fifth digit was strongly divergent in the living animal, but it seems doubtful that the role of the fifth metatarsal as a "heel bone" was far developed in this form. There is no evidence for the development of either the outer process or either of the plantar tubercles.

Distally, the foot is incomplete: of the second digit, there is only the proximal phalanx; of the third, the first and second phalanges and the base of the third; of the fourth digit, only the first phalanx. The fifth digit has two phalanges in place. The right foot is badly scattered, but the individual elements are well preserved. One of the terminal phalanges shows a well developed tubercle for a flexor tendon. The ventral surface is keeled and sharply recurved.

A scattering of typical primitive reptilian scales can be seen adjacent to the ribs at the level of the distal end of the right humerus. Individually they are long and narrow, pointed at one end and thinner and flatter at the other. Of much greater interest is the presence of epidermal scales. These can be seen covering the ventral surface of the sternum, with a few lying more laterally. The size and pattern of the scales is essentially similar to those of some living lizards, e.g. *Sceloperus*, of similar body size. They are diamond-shaped and overlapping, and appear quite thick. Presumably they were preserved initially as impressions and contain no bone.

ALBANY MUSEUM 4133

(Fig. 8)

Despite a fairly thorough search for lizard-like forms in the major South African museums in 1972—73, only one previously undescribed specimen was located. This one, in fact, does not add appreciably to our knowledge, since it has no horizon, locality or collector data, and shows no anatomical features not seen in other specimens. It consists of a natural cast of the trunk region in ventral view, including much of the pectoral girdle and the anterior portion of the puboischiadic plate. It is preserved in a fine-grained sandstone, from which casts can readily be made. The specimen is catalogued as no. 4133 in the Albany Museum, Grahamstown.

The portion preserved measures 94 mm in length, 20% greater than the comparable portion of the type of *Saurosternon bainii*. Apart from size, there are few features to differentiate the two specimens. The distal ends of the humeri appear poorly ossified, even in the larger specimen, suggesting that it had not reached maturity. The sternum, however, appears to be a unitary structure, rather than paired as is that of *Saurosternon*. The bone is in two pieces, but this is apparently a result of crushing against the overlying vertebrae, and does not appear to have taken place at the midline. The Albany Museum specimen does not show the anterior processes extending from the margin of the scapulocoracoid, as reported in the smaller form. The glenoid and other features of the scapulocoracoid are of lacertoid configuration. Ventral extensions of the sternal ribs are not preserved, nor are processes of the sternum for their attachment. Only a few intercentra are exposed, but they were presumably present the full length of the column.

THE PALIGUANIDAE AND THE ORIGIN OF LIZARDS

Of the four lizard-like forms described from the South African Karroo, three have been named as the types of monotypic genera. It is very difficult to evaluate taxonomic distinctions where one genus, *Paliguana*, is a disembodied head, and another, *Saurosternon*, a headless body. *Palaeagama* is represented by an essentially complete skeleton, but the skull is extremely poorly preserved, and the specimen certainly represents a much more mature individual than that by which *Saurosternon* is known. Many differences in detail of structure and proportions might be cited between the latter two specimens, but at least some may be related to degree of ossification and maturity. The difficulty of evaluating the possible taxonomic diversity of these specimens is compounded by the absence of firm stratigraphic data. The probable distribution in both Upper Permian and Lower Triassic might justify recognition of specific or even generic distinction between forms, even if they were morphologically quite similar. A further problem is that we have almost no notion of the probable diversity among lizard-like forms of this age. Most of the modern infraorders had probably differentiated by the end of the Jurassic, but it is impossible to suggest how far this process might have proceeded by the early Triassic. Whether one or three genera should be recognized, it seems reasonable to include all these forms in a single family, Paliguanidae, a practice followed by Romer (1956).

The genera discussed here have long been included within the Eosuchia, but with the acceptance that they possessed some characteristics suggestive of affinities with lizards. The current work has shown a multitude of very significant similarities with primitive lizards. In terms of size, proportions and functional characteristics, the skull of *Paliguana* and, to the extent that it is known, that of *Palaeagama* are essentially similar to those of *Kuehneosaurus* and *Icarosaurus*. The postcranial skeleton demonstrates a

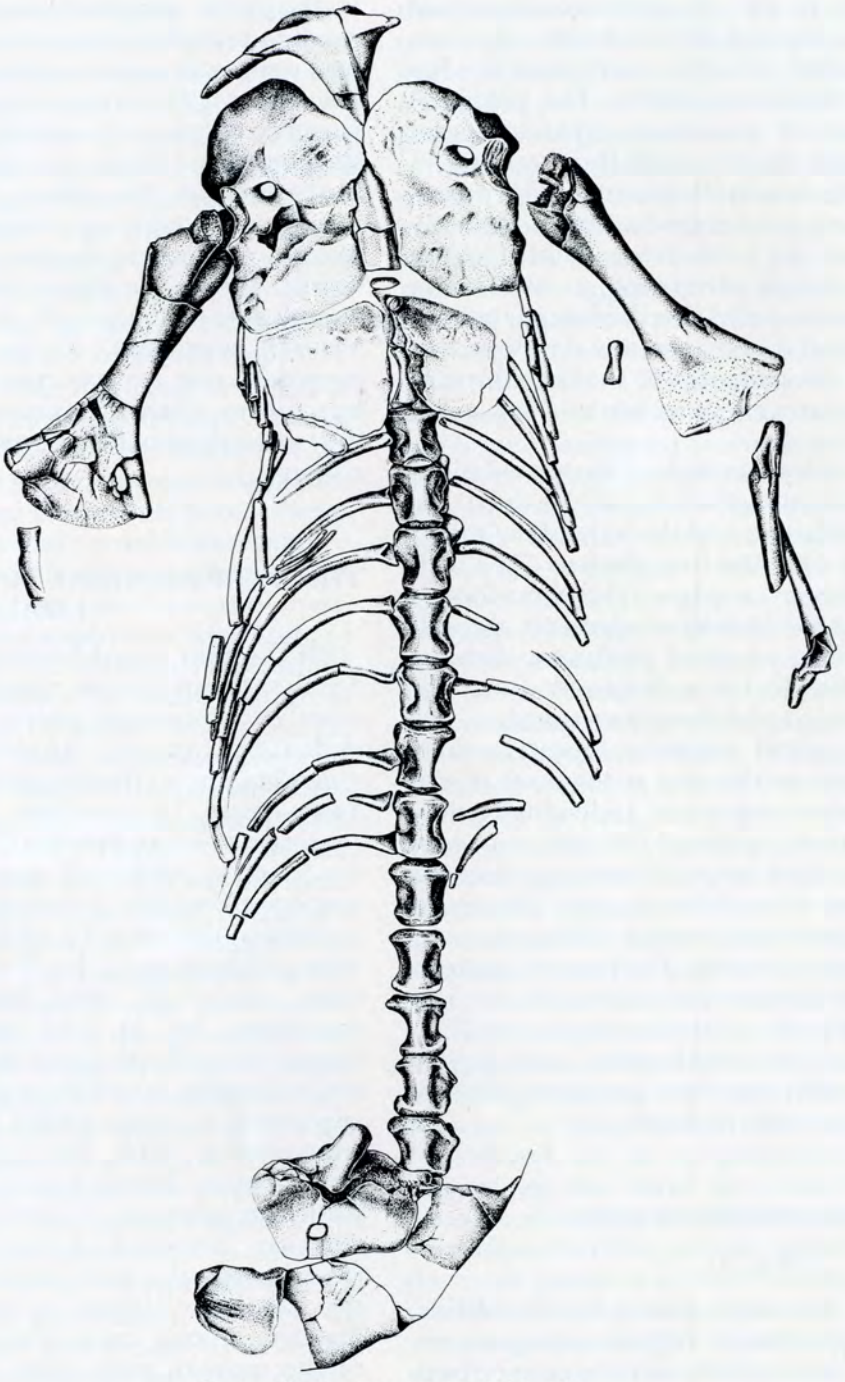


Fig. 8. Albany Museum no. 4133, ×2.

striking mosaic of primitive and lacertoid characteristics. The vertebral column resembles closely that of *Sphenodon,* but shows no features that would not be expected in an ancestor of lizards. In this, it contrasts strongly with *Prolacerta*, in which the cervical vertebrae are of an entirely different nature from those seen in any primitive lizards. The structure of the pectoral girdle and forelimb is comparable even in small details with that of iguanids. The only primitive feature is the retention of the entepicondylar foramen. The configuration of the glenoid and the necessity of a special epiphyseal articulating surface of the humerus are especially striking, as is the nature of the articulation between the ulna and the ulnare.

The pelvic girdle does not appear to show any specializations above the eosuchian level, but the femur, tibia and fibula are almost identical with those of primitive lizards. The tarsus is basically primitive in retaining all the eosuchian elements, but the overall proportions and the functional relationships of the units approach the lacertoid condition. Squamate epidermal scales are present.

The detailed similarities of the paliguanids with primitive living lizards and, as far as they are known, primitive Mesozoic squamates, are so numerous that it may be assumed that they are very closely related. It seems almost impossible for such a complex of characteristics to have evolved in this family if it

were not intimately associated with the ancestry of Mesozoic and Cenozoic lizards.

Although there are some features, such as the structure of the pelvic girdle, and some aspects of the foot structure, of the Paliguanidae that are eosuchian rather than lacertoid in their configuration, the overall anatomy of these forms is that of a very primitive lizard. It is thus suggested that they be included in the Suborder Lacertilia. Since published descriptions of members of the otherwise most primitive lizard infraorder, Eolacertilia, are limited to the highly specialized gliding genera *Kuehneosaurus* and *Icarosaurus,* it is difficult to determine whether the Paliguanidae should be included within this group. In so far as comparable parts of the skeleton are known, the Paliguanidae fit most of the criteria outlined by Robinson and Colbert.

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