

THE ORIGINS AND CLASSIFICATION OF TRIASSIC DICYNODONTS

by

A. W. KEYSER and A. R. I. CRUICKSHANK

ABSTRACT

The problem of the classification of the Triassic Dicynodontia, a notoriously difficult group of fossil Therapsida, is reviewed in depth and Cox's classification is revised accordingly. From this a suite of characters emerges which serves to define the unified character of the larger Triassic genera, the Kannemeyeriidae Huene, typified by *Kannemeyeria* Seeley. These characters are: large size, with skulls normally exceeding 25 cm in overall length and often being more than 50 cm; possession of a long snout and palatal region, with concomitant shortening of the temporal openings; short fenestra medio-palatinalis, which migrates out with the limits of the choanal depression in some late forms, and may or may not have raised flap-like margins; dorsally deepened intertemporal bar; fused anterior elements in the braincase; a reflected lamina of the angular which is close to or contacts the lateral condyle of the articular; (associated with the latter case, the quadrate foramen is seen to disappear); the forward growth of a pterygoid process of the quadrate; the epityergoid with a dorsal process on the anterior footplate; an intertemporal region always narrower than the interorbital; highly reduced postfrontals; absence or extreme reduction of the ectopterygoid; a short "x"- or "v"-shaped interclavicle; a separately ossified olecranon ulnae.

Using these characters, Triassic dicynodonts can be seen to be derived from a form similar to *Rhachiocephalus dubius* Boonstra, which is shown to be close to the genera *Daptocephalus* and *Dinanomodon* of *Daptocephalus* zone age (uppermost Permian). Because of this relationship, a new genus is created for *Rhachiocephalus dubius*, viz. *Odontocyclops*, which is of *Cistecephalus* zone age (Upper Permian). *Daptocephalus* is believed to be ancestral to the newly defined, broad-snouted, subfamily Dinodontosaurinae and *Dinanomodon* is believed to be ancestral to the narrow-snouted, subfamily Kannemeyeriinae Lehman emend. The very large Upper Triassic genera are classified in the subfamily, *Stahleckerinae* non sensu Lehman. The very late Triassic subfamily, *Jachelerinae* Keyser, is retained. *Lystrorhynchus*, *Myosaurus* and *Kompsosaurus* are included in the final revised classification of Triassic dicynodonts which is seen to be made up of 26 genera and 47 species.

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I. INTRODUCTION

The last decade or so has seen a virtual "explosion" in the number of genera and species of Triassic Dicynodontia. New forms have come from all the Gondwana fragments, except Australia, as well as Russia and China.

In many ways there is great morphological similarity between the various species and a broad subdivision into "blunt-nosed" and "narrow-nosed" forms was demonstrated by Cox (1965). Some of the more specialised Late Triassic forms do not appear to fit into such a broad classification, however, and these, e.g. *Ischigualastia*, *Stahleckeria* and *Placerias* are in retrospect difficult to place in either of these two groups. In this paper they are regarded as forming a distinct group separate from the others.

Most of the newly discovered species more or less coincide with the *Shansiodontidae* as understood by Cox (1965), e.g. *Shansiodon* Yeh, *Tetragonias* Cruickshank,

Dolichuranus Keyser and *Vinceria* Bonaparte. *Dinodontosaurus* von Huene also appears to fall into this group which certainly no longer deserves to be called "primitive" as was done by Cox (1965) in his classic paper on the Triassic Dicynodontia. This "shansiodont" group then actually constitutes a distinct "natural" group of broad-snouted Triassic Dicynodontia, separate from the *Stahleckeridae* as defined by Cox (op. cit.). In the authors' opinion there are far too many generic names in the "shansiodonts" and it is possible that only two genera with many species will be ultimately used as research progresses. These are *Shansiodon* and *Dinodontosaurus*. It is most unfortunate that so little is known about the detailed morphology of *Shansiodon*. Thus we do not propose to base any higher taxon on this latter genus.

The narrow-snouted forms constitute a smaller group of Triassic Dicynodontia, the genus *Kannemeyeria* occupying

a possible central position in this group. The familial name Kannemeyeriidae has been proposed for this group by Cox (1965) in a different sense to that of Von Huene (1948). In the authors' opinion, far too many generic names also exist in this group.

The greater number of Triassic Dicynodontia seem now to be better placed in either one of these two groups. The genus *Jacheleria* Bonaparte is regarded as being the type of a quite distinct fourth grouping of very specialised late Triassic forms.

II. THE ORIGIN OF TRIASSIC DICYNODONTS

A. General

The Triassic Dicynodontia have a number of features in common which are not found in most of the Permian genera. They are characterised by a shortening of the post-orbital part of the skull (as has been noted by many authors, e.g. Crompton and Hotton, 1967; Cox, 1965; Cruickshank, 1967; Keyser, 1974), which probably resulted from a more dorsal origin of the jaw musculature as an adaptation to a diet dominated by the plant genus *Dicroidium* and various cycads (Keyser, 1974).

A shortening of the back half of the skull with a concomitant increase in the length of the snout is not found in any of the Permian genera except *Daptocephalus* and *Dinanomodon*, which occur in the uppermost Permian *Daptocephalus* Zone of the Beaufort Group of South Africa.

Concomitant with the shortening of the rear of the skull, several other characters appear in Triassic Dicynodontia which are not found in most of their Permian counterparts. These are, among others, the marked shortening of the fenestra medio-palatinalis (interpterygoid vacuity or space) and the development of a dorsal process on the pterygoid ramus of the epipterygoid.

It was, therefore, decided that Permian dicynodonts which display these advanced features should be re-examined as possible ancestors of the Triassic forms; as most of the Lower Triassic genera are tusked, only tusked Permian genera need to be considered.

Several large dicynodont skulls in the collection of the Bernard Price Institute for Palaeontological Research display reduced fenestrae medio-palatinales and are tusked. These specimens are from the Madumabisa Mudstone Formation in the Luangwa Valley, Zambia. They were all collected at Locality 4 (Kitching, 1963) at which the genus *Cistecephalus* also occurs. In these, several features can be demonstrated which could indicate that the species they represented is possibly ancestral to the genus *Daptocephalus*. All these specimens can be referred to *Rhachiocephalus dubius* Boonstra. Among the advanced features to be seen in this dicynodont are a shortened fenestra medio-palatinalis and an epipterygoid with an incipient dorsal process on the pterygoid ramus.

However, as this species shows few of the characters seen in combination in the genus *Rhachiocephalus* (Keyser, 1969, 1974) it is necessary to reassess its taxonomic position and to redescribe its cranial anatomy in more detail than did Boonstra in 1938.

B. *Odontocyclops dubius* (Boonstra) gen. nov. formerly *Rhachiocephalus dubius* Boonstra, 1938

Diagnosis

Large Dicynodontia (skull length often more than 60 cm) with canine tusks in most specimens. Nostril placed high up in the snout far from alveolar border. Intertemporal region about the same length as the distance from the postorbital arches to the tip of the snout. The nasal bosses well-developed and elongate; completely confluent with the pre-frontal bosses and give the dorsal surface of the snout a concave appearance. Intertemporal region broad with a wide portion of the parietals visible between the postorbitals which extend back to meet the squam-

osals. Palatal structure similar to that of *Daptocephalus* with extensive contact between the palatines and the pre-maxilla. Fenestra medio-palatinalis placed far back in the choanal depression and is about one third the length of the choanal depression. The footplate of the epipterygoid has a long anterior extension.

Holotype: Specimen 11313, South African Museum, Cape Town.

Type Locality: "Luangwa Valley", Zambia. Locality 4 (Drysdaal and Kitching, 1963) is probably the type locality.

Horizon: Upper Madumabisa Mudstone (Upper Permian: *Cistecephalus* Zone)

Referred Material: 4 Skulls in the collection of the Bernard Price Institute for Palaeontological Research. Collector, J. W. Kitching.

This species was first described by the late Dr L. D. Boonstra in 1938. The holotype consists of a large tusked skull that was badly damaged during excavation and preparation. The greater part of the specimen is embedded in a block of plaster of Paris. The only features that can be identified and used in the identification of the species are the presence of tusks, the elongate nasal bosses and the broad intertemporal region. Since the original description, no other specimens have been referred to this species in the literature. Boonstra referred his original material to the genus *Rachiocephalus*.

Eighteen species of large tuskless dicynodonts are known from the Beaufort Group of South Africa. These were reviewed by Keyser (1975) who concluded that it was impossible to distinguish the various species on the material that is available at present and that only the name *Rhachiocephalus magnus* (Owen) should be used.

It has since then come to light that the type of *Platycyclops crassus* Broom has a pterygoid process of the quadrate which serves to remove it from the genus *Rhachiocephalus* (Keyser, 1974).

Rhachiocephalus dubius Boonstra (1938) displays a number of features that serve to distinguish it from the other species of the genus *Rhachiocephalus*. The species *dubius* has large tusks, labial fossae and peculiar nasal bosses. It lacks the prominent ridges on the caniniform processes as well as the median longitudinal ridge that is so characteristic of *Rhachiocephalus*.

Unfortunately, most of the fossil vertebrates from the Madumabisa Mudstone are preserved in an extremely refractory ferruginous mudstone that mainly consists of haematite. This matrix defies ordinary mechanical and chemical methods of preparation. This accounts for the fact that so little is known about the rich and varied therapsid fauna from the Luangwa Valley.

Measurements in mm

Specimen No.	Total length	Basal length	Inter-orbital width	Inter-temporal width
BPI 3585	561	392	111	100
BPI 3419	—	382	119	80
BPI 3586	589	421	111	83
BPI 3589	424	27	83	56

The specimens show a wide variation in proportions, size of tusks and many other features. These differences must be considered to be due to individual variation and post-mortem deformation. The four specimens are regarded as a sample of a fossil population because they were found close to one another at the same stratigraphic level in the Upper Madumabisa Mudstone and have a number of features in common that are of rare occurrence

in other dicynodont species. These are:

- (a) The possession of elongate nasal bosses.
- (b) The concave dorsal surface of the snout.
- (c) The occurrence of a small boss on the lateral surface of the lacrimal.
- (d) Wide intertemporal region that widens posteriorly.
- (e) Short fenestrae medio-palatinales with raised margins.

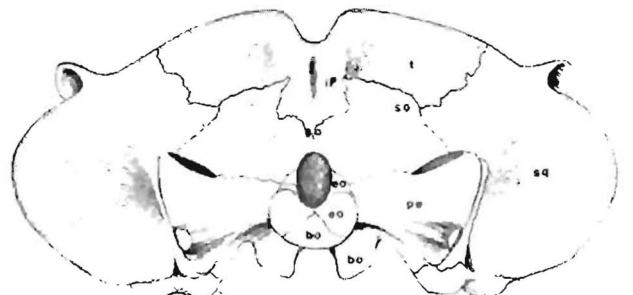
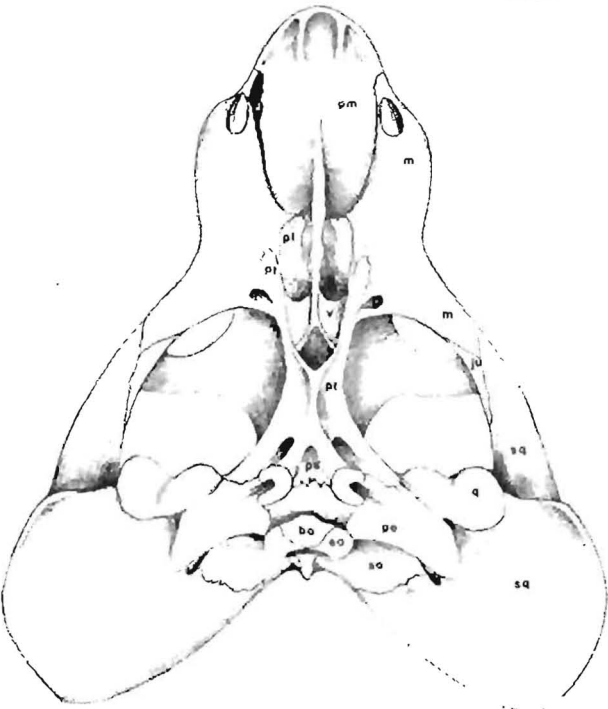
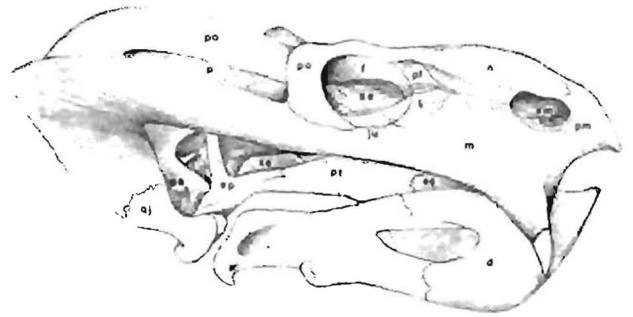
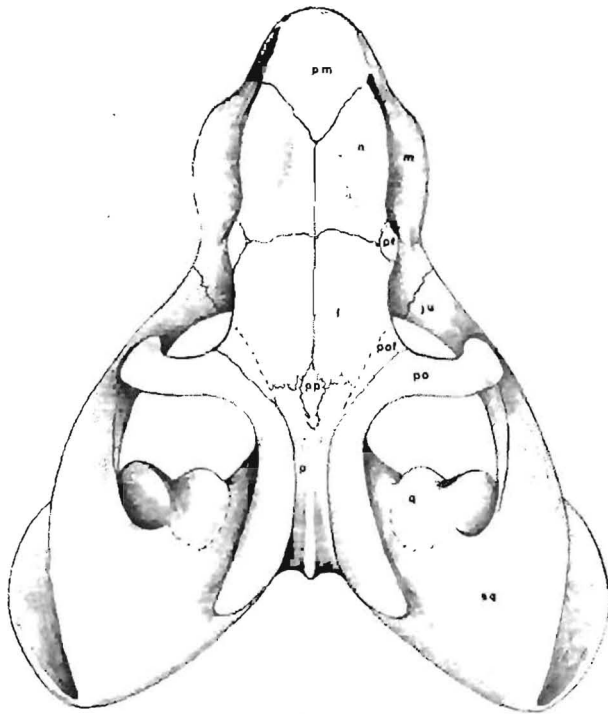
The authors, therefore, feel justified in considering the four specimens as belonging to the same species. The material was prepared by mechanical methods.

The Skull

Dorsal and Lateral views (Figs. 1 and 2)

The general shape of the skull is very similar to that of

Oudenodon and *Rhachiocephalus*. Sutures are difficult to trace because of the massive nature of the bones; the anterior and dorsal surfaces of the premaxilla are concave medially. There is no medial longitudinal ridge on the dorsal surface of the premaxilla as is found in many other anomodonts. The concave dorsal surface of the premaxilla is continued posteriorly on to the dorsal surface of the nasals. Posterior to the nares externi the nasals form large elongate nasal bosses which are continued posteriorly on to the prefrontals. The entire dorsal surface of the snout therefore appears to be concave. It can be expected that this feature will be exaggerated by post-mortem deformation because of the mechanical strength of the elongate nasal bosses, which will be more resistant to compression than the thinner bones along the midline of the snout.



Figures 1-4

Odontocyclops dubius (Boonstra) gen. nov. B.P.I.F. No. 3589. Viewed in dorsal, lateral, palatal and occipital aspects respectively. (Scale 0.25 approximately)

The lacrimals form a small part of the side of the snout but do not reach the posterior margins of the nares externi, and the septomaxillae are firmly sutured to the maxillae.

The occurrence of canine tusks is highly variable in the four specimens that were studied. Specimen BPI 3585, which is the second largest specimen in the series, has no erupted tusks and this has small caniniform processes as are found in *Rhachiocephalus*. One of the caniniform processes was broken off accidentally and showed an unerupted canine in the maxilla. Specimen BPI 3589 has a small erupted canine on one side only. Both the other specimens are tusked. Specimen 3586, the largest in the series, has caniniform processes that are much larger than those of specimens with smaller tusks. The caniniform processes are relatively much smaller than those of later genera such as *Daptocephalus* and *Kannemeyeria*.

The interorbital region is slightly wider than the intertemporal region, and widens posteriorly. A wide strip of the parietals is exposed between the postorbitals posterior to the parietal foramen.

The parietal foramen is placed fairly far forward on the intertemporal bar close to a line drawn between the postorbital arches. The parietal foramen is elongate. A low boss is formed on the preparietal which forms the anterior margin of the parietal foramen.

The zygomatic arches bow out laterally to give the skull a similar shape to that of *Rhachiocephalus*.

It is difficult to determine whether the skull was as flat as that of *Rhachiocephalus* or higher, like that of *Daptocephalus*, as all specimens are deformed. The general impression is that the skull was slightly higher than that of *Oudenodon bairdi*.

Ventral view (Fig. 3)

The anterior part of the palate is not as deep as in many other dicynodont genera such as *Diictodon* and *Daptocephalus*. This feature is, however, highly variable in this series of skulls because of the great variability encountered in the size of the caniniform processes.

The relationships of the bones in the palatal region are very similar to that found in *Daptocephalus*.

The premaxilla displays the two anterior palatal ridges with a deep groove between them as is found in most Dicynodontia. The posterior median palatal ridge is continuous with the vomer posteriorly and is highest at the level of the anterior choanal slits. The premaxilla forms the greater part of the secondary palate. The palatines do not constitute as great a part of the secondary palate as is the case in forms such as *Oudenodon* and *Rhachiocephalus*. There is extensive contact between the premaxilla and the palatines.

The palatines have a similar configuration to the condition found in *Daptocephalus*. They form the lateral walls of the anterior choanal slits and constitute part of the dorsal wall of the choanal depression.

The margins of the fenestra medio-palatinalis (interpterygoid vacuity) are very variable in the series of specimens. In specimen BPI 3585 the fenestra is nearly half as long as the choanal depression. In the other three specimens the fenestra is about one third the length of the choanal depression and placed far back in it. The fenestra is laterally bounded by the divided posterior plates of the vomer, which project ventrally below the roof of the choanal depression, thus bringing the opening of the fenestra to the level of the pterygoids. A similar condition is found in *Daptocephalus*.

The condition of the fenestra in *Odontocyclops* and *Daptocephalus* closely approximates that found in Triassic Dicynodontia and contrasts sharply with the long fenestra without raised margins encountered in most other Permian Dicynodontia.

The pterygoids meet the maxilla at a point midway along the choanae. The ectopterygoids separate the ptery-

goids from the maxilla on the external sides only of the palatine rami of the pterygoids. The pterygoid girder is much narrower than is found in *Daptocephalus*.

In general it can be said that the relationships of the bones on the ventral side of the skull are very similar to those found in *Daptocephalus* and that the differences found can mostly be related to the relatively larger intertemporal region of *Odontocyclops*.

The epipterygoid has an unusual feature that is not encountered in many other Permian Dicynodontia, in that the footplate has a long anterior extension that extends forward and meets the presphenoid part of the sphenethmoid. This part of the epipterygoid differs from the condition found in *Daptocephalus* where an additional dorsal process is formed on the anterior ramus of the epipterygoid. In most Permian dicynodonts the anterior ramus of the epipterygoid is very short.

Remarks

In Zambia, the genus *Odontocyclops* nov. is found associated with the zone fossil *Cistecephalus microrhinus* Owen. *Cistecephalus* is never associated with specimens of *Daptocephalus* in the Karoo Basin. It can, therefore, be assumed that locality 4 in the Madumabisa Mudstone is older than the *Daptocephalus* zone of South Africa. This can be substantiated too by the presence there of a large number of small endotheriodonts which are rare in the *Daptocephalus* zone.

The genus *Odontocyclops* has many features in common with *Daptocephalus* and can, therefore, be considered as a possible ancestor to that genus. These are:

- The small posteriorly placed fenestra medio-palatinalis of which the vomers form the raised margins.
- The anterior process of the footplate of the epipterygoid.
- The large posterior extension of the premaxilla in the secondary palate.
- Reduction of the ectopterygoid.
- The high placement of the external nares in the snout and the sutural contact of the septomaxilla with the maxilla.
- The small size of the parietal foramen and the lack of a large bony boss surrounding the foramen.

In the above features, *Odontocyclops* shows agreement with the genera *Daptocephalus*, *Dinanomodon* and the Triassic dicynodonts. The features in the above list are shared with very few other Permian Dicynodontia. In some respects *Odontocyclops* retains a number of primitive characters that are more typical of Permian Dicynodontia. These features may be termed primitive as they are of rare occurrence in the more advanced Triassic Dicynodontia. Those particularly relate to the general proportions of the skull. The intertemporal region is long and the snout is short, which indicates that the temporalis musculature still functioned like that in typical Permian genera, such as *Rhachiocephalus* and *Oudenodon*. The intertemporal region is relatively very broad when compared with the Triassic genera.

Notwithstanding the many characters possessed by *Odontocyclops* which make it an attractive ancestor to *Daptocephalus*, the following features show it to be, in fact, too specialised to be the actual ancestor, viz. the concavity of the dorsal surface of the snout, the broad intertemporal region and the very large size of the forms presently known. The ancestor of *Daptocephalus* must, therefore, have been a form similar to *Odontocyclops dubius* but without the above specialisations.

In general it can be said that Triassic Dicynodontia are characterised by having long snouts and short crested intertemporal regions. Functionally this means that the main mass of the adductor musculature was more dorsally placed (Crompton and Hotton, 1967). A large number of

other specialisations that occur in few of the Permian dicynodonts also occur, many of which are already found in two genera from the *Daptocephalus* zone of the Beaufort group — *Daptocephalus* and *Dinanomodon*.

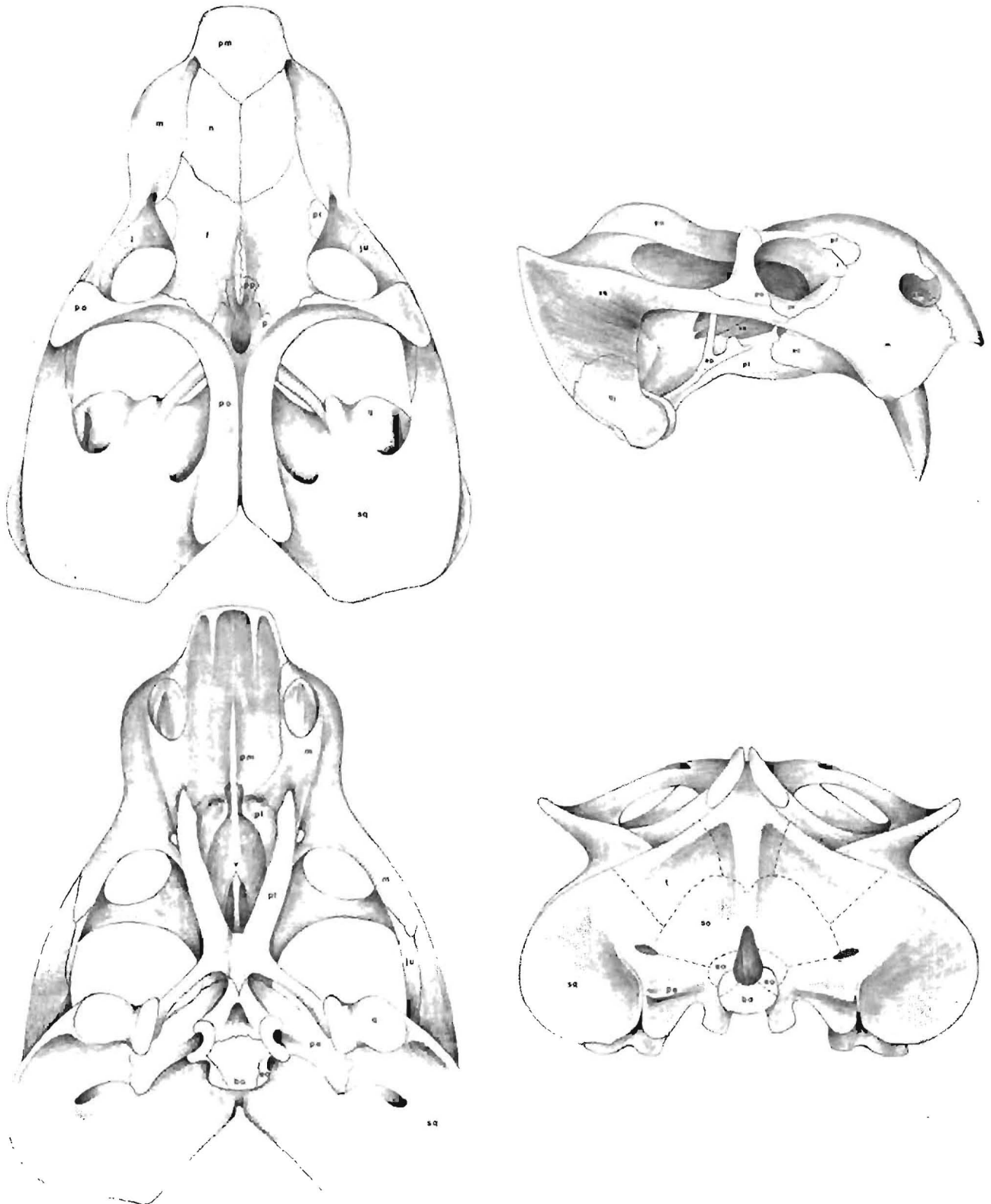
C. Genus *Daptocephalus* Van Hoepen, 1934

Type Species: Daptocephalus leoniceps (Owen), 1876

The cranial morphology of the genus *Daptocephalus* has been well described by Ewer (1961) and redescription of

the morphology would entail needless repetition. Only the more salient features need be pointed out here as *Daptocephalus* is in many ways morphologically intermediate between *Odontocyclops* and many of the dinodontosaurine dicynodonts of the Triassic (see below). The specimen described by Ewer was laterally compressed. The figures given here are of a less distorted specimen of the Geological Survey collection, No. R31.

The stratigraphic occurrence of the genus also fits in



Figures 5–8

Daptocephalus leoniceps (Owen). Geol. Survey No. R.31. Viewed on dorsal, lateral, palatal and occipital aspects respectively. (Scale 0.25 approximately)

with this interpretation as the *Daptocephalus* zone occurs above the strata that contain *Cistecephalus* (age of *Odontocyclops*) and immediately below the lowermost Triassic strata of the *Lystrosaurus* zone (Kitching, 1971, 1977). Features of *Daptocephalus* that can be regarded as advanced with respect to the Permian, and leading on to the Triassic dicynodonts, are the following:

1. Relatively long snout with large caniniform processes.
2. Long secondary palate formed mainly by the premaxilla with the palatines contributing very little to the secondary palate.
3. Pterygoids meet the maxillae anteriorly. The ectopterygoids are small, thin elements separating the pterygoids from the maxillae on the lateral sides of the palatine rami of the pterygoids.
4. The fenestra medio-palatinalis is relatively small (smaller than that of *Odontocyclops*) and placed far back in the choanal depression. The lateral margins of the fenestra consist of raised plates of the vomer that extend ventrally to the level of the ventral surface of the pterygoids.
5. The "pterygoid girder" is much wider than in *Odontocyclops* and almost as wide as the girder in *Kannemeyeria*.
6. The temporal fossae are much shorter than those of *Odontocyclops*.
7. The intertemporal region of *Daptocephalus* is narrow and forms a sharp crest with the postorbitals meeting in the midline behind the parietal foramen. The postorbitals are long and meet the squamosal posteriorly.
8. There is no boss surrounding the parietal foramen which is relatively small.
9. There is no medial longitudinal ridge on the dorsal surface of the premaxilla as is seen in many Permian dicynodonts, e.g. *Oudenodon* and *Rhachiocephalus* or the Triassic kannemeyeriines.

Some broad-snouted specimens of *Daptocephalus* from the northern part of the Karoo Basin in the Orange Free State and Natal (*Daptocephalus* zone) that are being studied by Dr J. W. Kitching of the Bernard Price Institute for Palaeontological Research, may prove to be a new species of *Daptocephalus* which could be intermediate between *Daptocephalus leoniceps* and *Odontocyclops*.

Casts of *Dicynodon annae* that have been received from Russia without any locality data, in the British Museum (Natural History) and the Palaeontological Institute in Tübingen, closely resemble *Daptocephalus leoniceps*. The genus *Jimusaria* from Shansi, People's Republic of China, also appears to have the same level of organisation as *Daptocephalus*. Small specimens of a very *Daptocephalus*-like anomodont occur in the *Cistecephalus* zone of the Lower Beaufort near Pearston in the Cape Province, but their true identity has not yet been elucidated (Kitching, pers. comm.).

It is also possible that the generic name *Daptocephalus* could become a junior synonym of the genus *Dicynodon*. There can, however, be no certainty about this until such time as the genotype of the genus *Dicynodon*, *Dicynodon lacerticeps*, has been studied adequately. It is possible that it could be a young individual of the species that is currently known as *Daptocephalus leoniceps*.

D. Genus *Dinanomodon* Broom, 1938

Type species: Dinanomodon rubidgei Broom, 1938

This genus differs from *Daptocephalus* principally in the very peculiar specialisation of the tip of the snout. In *Dinanomodon* the tip of the snout is pointed, with a prominent ridge on the dorsal surface of the premaxilla, so that it looks very much like the inverted bow of a boat. If only the type of *Dinanomodon rubidgei* had been known this peculiarity could have been considered to be due to lateral compression of the tip of the snout in a *Daptocephalus*-like skull. However, several other specimens are known from

the *Daptocephalus* zone in the Graaff-Reinet district and along the Orange River in the Orange Free State, which are now housed in the National Museum, Bloemfontein. There can, therefore, be no reasonable doubt that the condition of the snout in *Dinanomodon rubidgei* is, in fact, natural.

The relationships of the various elements on the ventral surface of the skull are so similar to those found in *Daptocephalus* that description would be mere repetition.

Despite the beak-like anterior tip of the premaxilla, the anterior palatal ridges are developed in exactly the same way as in *Daptocephalus*. The fenestra medio-palatinalis is also very small. The anterior ramus of the footplate of the epityergoid also has a dorsal process as is found in *Daptocephalus*.

The intertemporal region is very narrow and the postorbitals meet in the midline. The intertemporal region is relatively longer than that of *Daptocephalus*.

The more pointed snout found in *Dinanomodon* with the prominent medial ridge on its dorsal surface, indicates closer relationship with the younger genus *Kannemeyeria* rather than with the *Dinodontosaurus* group of Triassic Dicynodontia.

It has proved almost impossible to provide a view of the occiput of *Dinanomodon rubidgei* owing to the very damaged state of the type and the fact that it is embedded in plaster of Paris. A subjective assessment of the occiput of this species indicates that it may have some resemblance to that of the Upper Triassic form *Ischigualastia*.

E. Genus *Dinodontosaurus* Romer, 1943

Type species: Dinodontosaurus turpior (Huene)

Four species of this genus have been described and the genus *Chanaria* Cox (1968) is possibly a junior synonym of *Dinodontosaurus* (see Keyser, 1974).

Dinodontosaurus resembles *Daptocephalus* in many respects. The sutural relationships of the bones on the palatal surface are essentially the same as in this genus. The relative length of the snout and, consequently, the length of the secondary palate is much longer in *Dinodontosaurus*. Both genera have much reduced, laterally placed ectopterygoids.

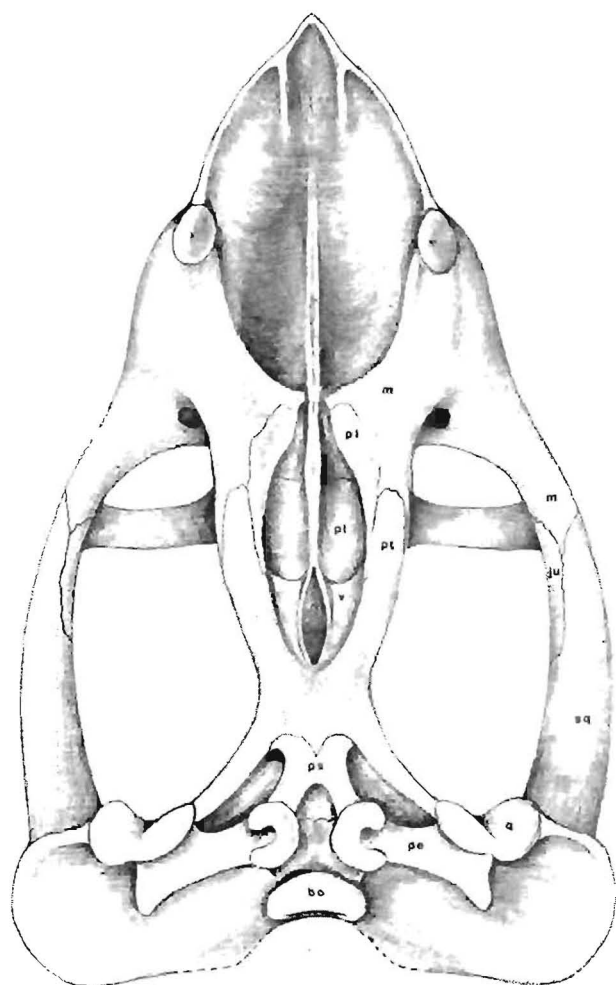
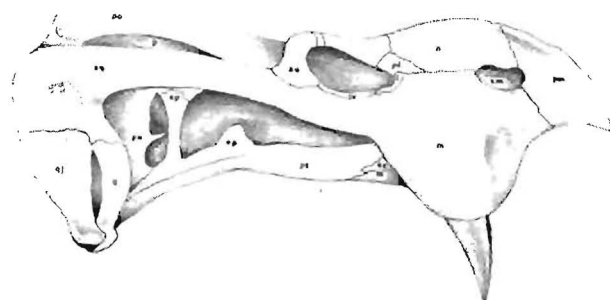
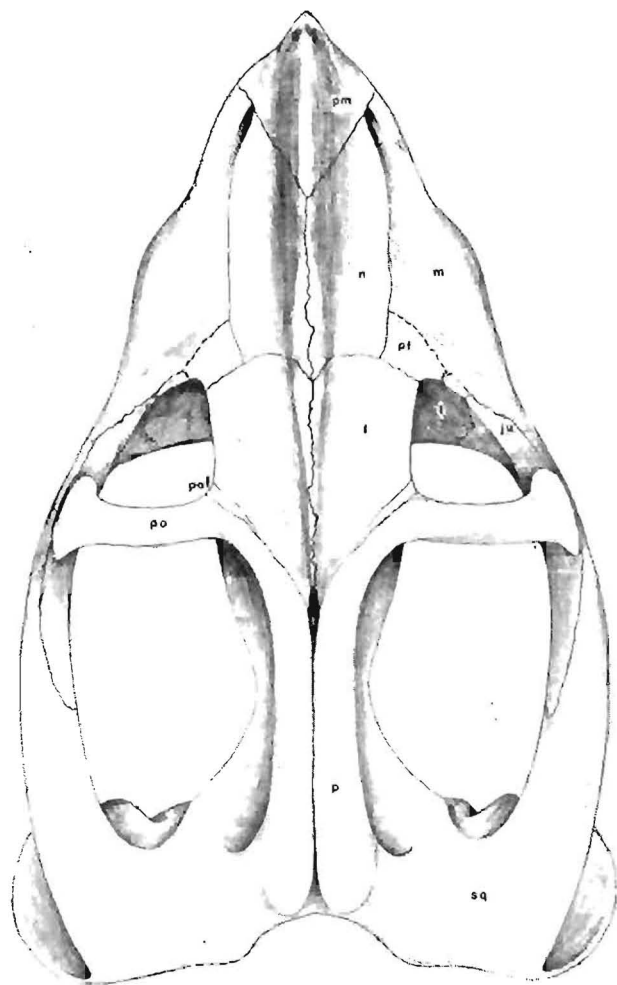
The skull of *Dinodontosaurus* is much higher than that of *Daptocephalus*, but the most noticeable feature that distinguishes the two genera is, however, the very short intertemporal region and temporal fossae of *Dinodontosaurus*. The great relative length of the snout in this genus is concomitant with the shortening of the interpterygoid region.

The high skull with short intertemporal fossae was certainly developed to achieve a more vertical placement of the adductor musculature and led to a greater reduction in the length of the postorbitals which do not extend farther posteriorly than the parietal foramen, in contrast to the condition in *Daptocephalus* where the postorbitals meet the squamosals above the occipital plate.

The fenestra medio-palatinalis is even further reduced in *Dinodontosaurus*. The development of very large canine tusks, from which the genus derives its name, has led to the formation of very deep caniniform processes with sharp anterior edges. This trend seems associated with the shortening of the temporal fenestrae as these features are all intimately linked with mastication.

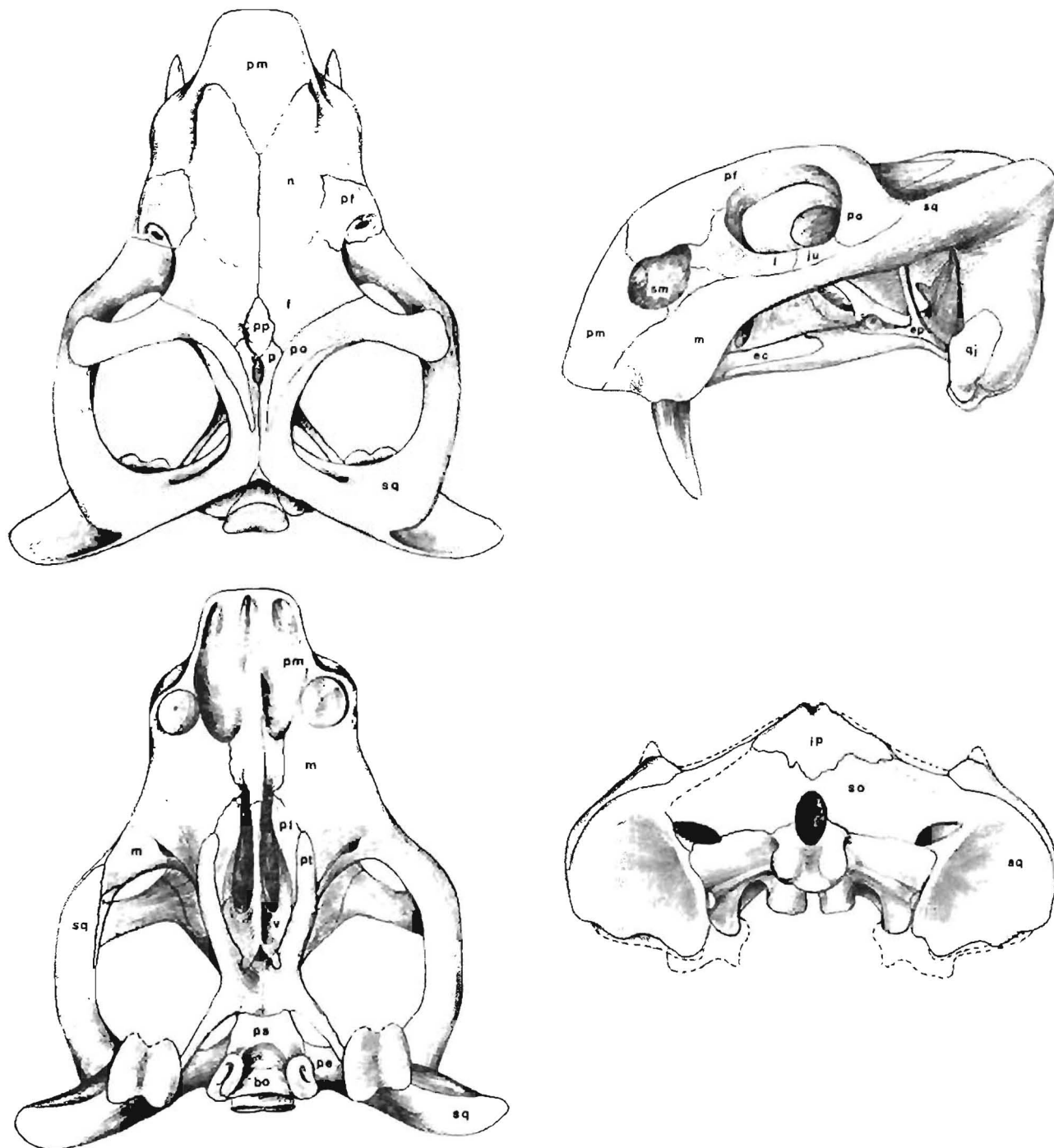
The dorsal process of the anterior ramus of the epityergoid is thickened and is developed into a small boss.

Thus the genus *Dinodontosaurus* can be regarded as typical Triassic dicynodonts which possess all the characters associated with the advanced types of the Upper Triassic. It occurs in the Santa Maria Formation of Brazil and the Ischichuca and Ischigualasto Formations of the Ischigualasto Basin of Argentina (Bonaparte, 1971). These formations are generally considered to be Upper Triassic in age.



Figures 9–11

Dinanomodon rubidgei Broom. Rubidge Collection No. 9. Viewed in dorsal, lateral and palatal aspects respectively. (Scale 0,25 approximately)



Figures 12-15

Dinodontosaurus turpior (Huene). Reconstructed from various sources. Viewed in dorsal, lateral, palatal and occipital aspects respectively. (Scale 0,166 approximately)

F. Genus *Kannemeyeria* Seeley

Type species: *Kannemeyeria simocephala* (Weithofer), 1888

Kannemeyeria was the first Triassic dicynodont to become known to science. The osteology of the genus is well known through the work of Pearson (1924). This genus can be regarded as typical of a large group of Triassic Dicynodontia and, as reviewed above, has been variously referred to either the Family Kannemeyeriidae von Huene or Cox, or Subfamily "Kannemeyeroiinae" Lehman.

The most notable features of the skull in this genus are the high, crested intertemporal region and the pointed anterior tip of the snout.

The intertemporal region is relatively short and the occiput fairly low and wide when compared to a form like

Dinodontosaurus. The postorbitals extend behind the parietal foramen and barely meet the squamosals. The high intertemporal crest indicates that at least the adductor externus medialis muscles functioned in a more vertical direction than was the case in most other dicynodonts.

As is found in all of the Triassic genera the fenestra medio-palatinalis is very small and placed far back in the choanal depression. The footplate of the epipterygoid is expanded in an anterior direction and has a prominent dorsal process.

The anterior tip of the premaxilla is pointed almost as much as that of *Dinanomodon*. This stands in sharp contrast to the condition seen in *Dinodontosaurus* and *Dolichuranus* and in the latter two genera there is no prominent

medial ridge on the dorsal surface of the premaxilla. In *Kannemeyeria*, as in *Dinanomodon*, this ridge is very strongly developed, with the function of adding mechanical strength to the sharp point of the premaxilla. This adaptation is not necessary for a broad square snout like that of *Dinodontosaurus*.

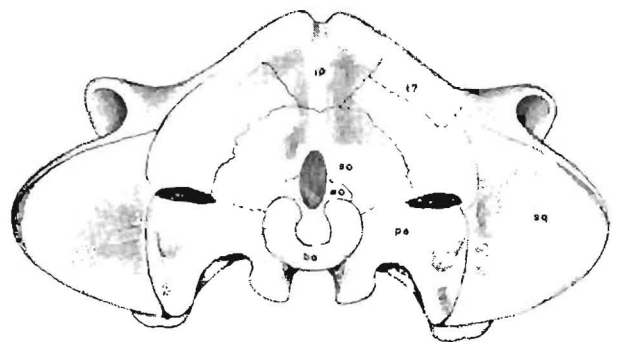
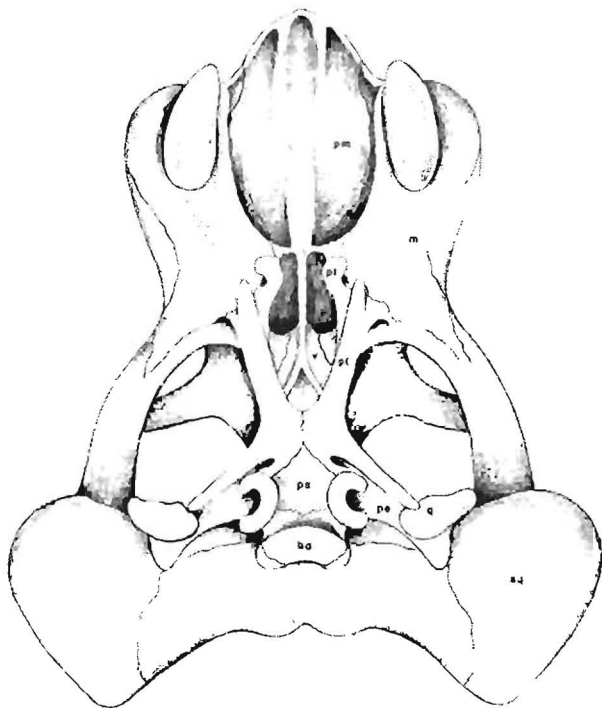
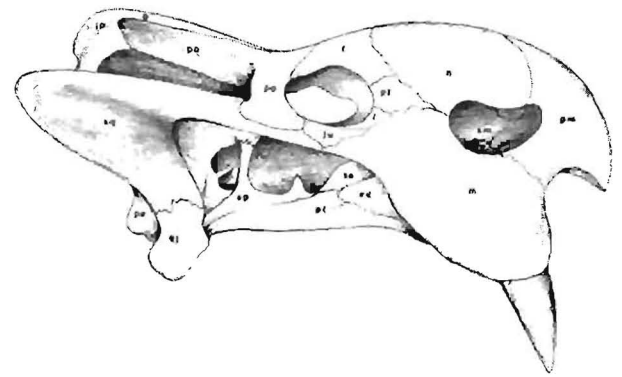
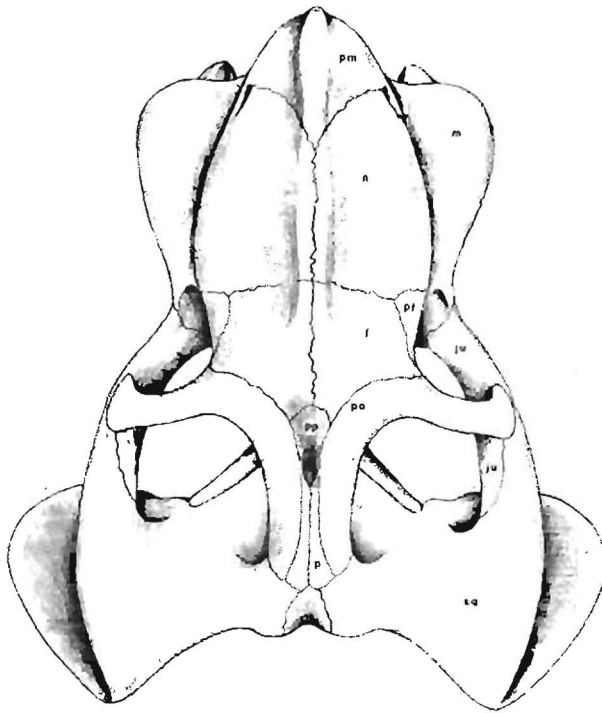
The bone on the surface of the snout has an irregularly pitted surface which could indicate that the horny covering of the upper jaws extended on to this part of the skull, and the caniniform processes are very large in this genus. This latter results in a very deep palate. The palatine bones are relatively small and the premaxilla extends far back, forming most of the secondary palate.

The external nares are placed high up in the snout, far above the alveolar margin. The septomaxilla is fused to the maxilla.

Discussion

The Triassic Dicynodontia, exclusive of the Lystrosauridae and other, minor, groups are a diverse group of specialised herbivores which have been divided into three broad categories to which Cox (1965) accorded familial status. These were:

(a) Kannemeyeriidae — genera with pointed snouts and high crested intertemporal regions and high, relatively



Figures 16-19

Kannemeyeria cristarhynchus (R.C.). Geol. Survey No. R313. Viewed in dorsal, lateral, palatal and occipital aspects respectively. (Scale 0.25 approximately)

narrow, occiputs, e.g. *Kannemeyeria*, *Sinokannemeyeria*, *Parakannemeyeria*, *Ischigualastia* and *Placerias*.

- (b) *Stahleckeridae* — genera with low, wide, occipital surfaces, short intertemporal regions and broad square-tipped snouts, e.g. *Dinodontosaurus* and *Stahleckeria*.
- (c) *Shansiodontidae* — more primitive Triassic dicynodonts which do not clearly belong in one of the two other families.

This was interpreted as two separate lineages descended from a primitive, more generalised, group (Cox, 1965).

In an earlier paper (Keyser, 1974) one of the authors pointed out eight evolutionary trends encountered in the Triassic dicynodonts, which have been reviewed on pp. 84 and 89 above. The evaluation of the features that are involved in these trends naturally leads to a search for some of the above advanced characters among the large variety of more primitive Permian dicynodonts.

As most Triassic dicynodonts are tusked, only tusked forms from the *Cistecephalus* zone can be considered as likely ancestors. As discussed above, *Odontocyclops* has several features that are found in Triassic dicynodonts; it has canine tusks, the fenestra medio-palatinalis is small and has raised margins within the choanal depression, the

septomaxilla is fused to the maxilla, the external nares are situated high in the snout far above the alveolar margin, and the anterior ramus of the footplate of the epipterygoid has characters indicative of an affinity with the Triassic Dicynodontia. *Odontocyclops* has more features in common with the genus *Daptocephalus* and *Dinanomodon* of the succeeding *Daptocephalus* zone than any other known dicynodont from the *Cistecephalus* zone. It is, therefore, likely that *Odontocyclops* must be closely related to the dicynodont stock that gave rise to the genera *Daptocephalus* and *Dinanomodon*. The large elongate nasal bosses that occur in *Odontocyclops* are not found in the two later genera where the bosses are small and only developed above the external nares. The occurrence of these large elongate bosses in *Odontocyclops* are indicative of specialisation and excludes it from direct ancestry to either *Daptocephalus* or *Dinanomodon*. However, substantial bosses occur in several broad-snouted Triassic genera, e.g. *Dolichuranus*, *Rhinodicynodon* and *Tetragonias*.

G. The Origin of *Kannemeyeria*

Dinanomodon has a sharply pointed snout, and a similar structure is encountered in *Kannemeyeria*. A prominent ridge is formed on the dorsal surface of the premaxilla to strengthen the pointed tip. The palate of *Dinanomodon* does not differ very much from that of *Odontocyclops* except that the premaxilla is very much longer because of the longer snout. The fenestra medio-palatinalis is even smaller in *Dinanomodon* than in *Daptocephalus* and is placed far back in the choanal depression, the floor of

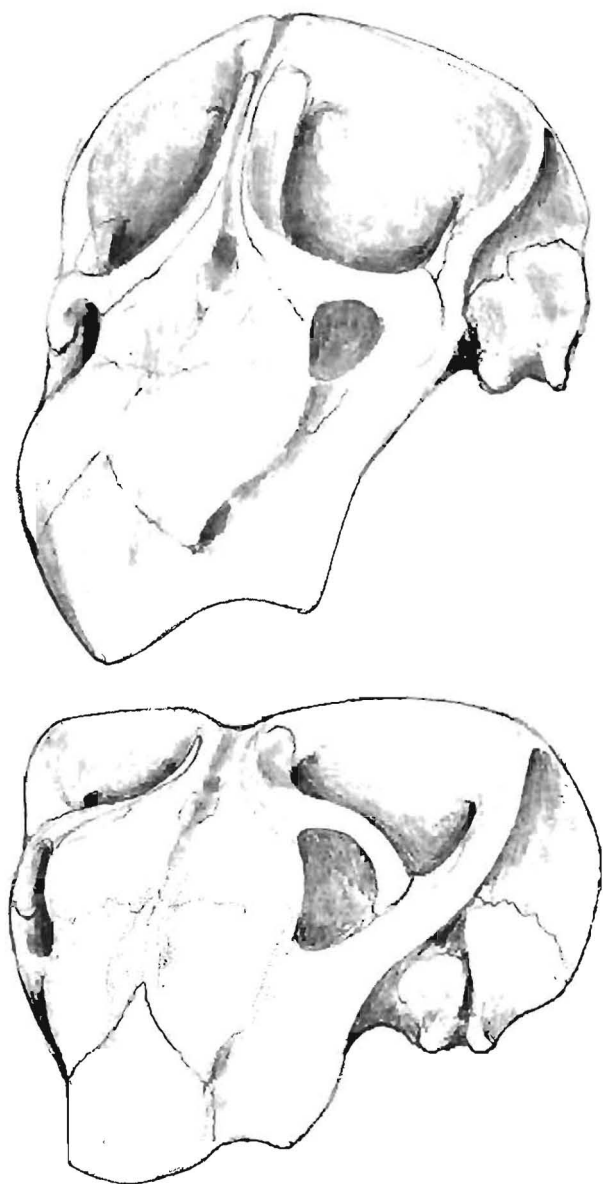


Figure 20

Antero-lateral views of skulls of *Ischigualastia* (a) and *Stahleckeria* (b) in the Instituto Lillo, Tucuman and the Paleozoologie Museum, Tübingen, respectively.

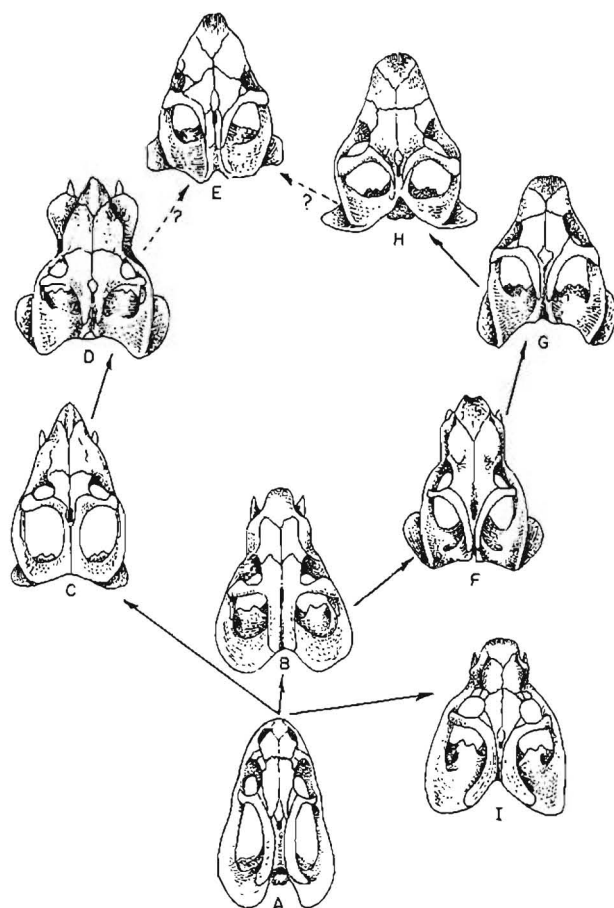


Figure 21

Family Tree of dicynodonts discussed in this paper. (A) *Dicynodon lacerticeps* Owen; (B) *Daptocephalus leoniceps* (Owen); (C) *Dinanomodon rubidgei* Broom; (D) *Kannemeyeria cristarhynchus* (R.C.); (E) *Ischigualastia jenseni* Cox; (F) *Dolichuranus primaevus* Keyser; (G) *Tetragonias njalilus* (Huene); (H) *Dinodontosaurus turpior* (Huene); (I) *Odontocyclops dubius* (Boonstra) gen. nov. See Table III for stratigraphic distribution of the larger Triassic genera.

which gradually becomes shallower in a posterior direction, thus bringing the opening of the fenestra medio-palatinalis to the level of the ventral surface of the pterygoid girder. *Dinanomodon* differs from *Kannemeyeria* mainly in the much longer temporal region of the former genus. The intertemporal bar of *Dinanomodon* forms a high dorsal crest as is the case in *Kannemeyeria*. *Kannemeyeria* can be derived from *Dinanomodon* by shortening the intertemporal region (Fig. 21).

Dinanomodon is separated from *Kannemeyeria* by a considerable gap in time. *Dinanomodon* occurs in the *Daptocephalus* zone, which is separated from the *Cynognathus* zone by the *Lystrosaurus* zone. No large Dicynodontia other than *Lystrosaurus* are known from this zone.

Kannemeyeria-like dicynodonts were extremely successful and achieved wide geographical distributions. The genus *Kannemeyeria* itself is known from the Beaufort Group of South Africa, the Omingonde Formation of South West Africa, the Ntawere Formation of Zambia, the Yerrapalli Formation of India, the Manda Beds of Tanzania and the Puesto Viejo Formation of Argentina. Dicynodonts that are very similar to *Kannemeyeria* are also known from China and Russia. Many of the genera that have been described from these countries are so similar to *Kannemeyeria* that it is likely that many of them will be included in the same genus (see below).

The highly specialised Upper Triassic genera *Ischigualastia* from the Ischigualasto and Santa Maria Beds of South America, and the genus *Placerias* from the Chinle Formation of the United States of America, resemble the kannemeyerids in having narrow and/or crested intertemporal regions and pointed snouts. No intermediate forms between them and *Kannemeyeria* have yet been found and their inclusion in a separate family is merely a matter of convenience (see below).

H. The Origin of *Dinodontosaurus*

The genus *Daptocephalus* can be derived from an *Odontocyclops*-like form by reduction of the intertemporal bar and concomitant elongation of the snout. *Daptocephalus* retains the square tip of the premaxilla as found in *Odontocyclops*.

Several authors have stated that *Daptocephalus* could be ancestral to many of the Triassic Dicynodontia, e.g. Camp (1956), Ewer (1961), Cruickshank (1967), Crompton and Hotton (1967) and Cluver (1971). These authors based this view on the relative proportions of the skull, which in many ways resembles the skull of *Kannemeyeria*.

It is here thought that *Daptocephalus* is already advanced on a line leading to the dinodontosaurid dicynodonts and is not on the lineage leading to *Kannemeyeria*, because of its broad square-tipped snout which contrasts sharply with the snout of the kannemeyerids where a pointed tip of the premaxilla with a prominent ridge on the dorsal surface of the bone is developed. No ridge is developed on the anterior and dorsal surfaces of the premaxilla in *Daptocephalus*.

A series of genera leading from *Daptocephalus* through the shansiodonts *Dolichuranus* and *Tetragonias* to *Dinodontosaurus* (Fig. 21) can be arranged as an evolutionary lineage. The relative ages of the strata from which the fossils were collected is in agreement with the serial arrangement. In Fig. 21 it can be seen that the main trend in this group is the shortening of the intertemporal region. During this development the posterior ramus of the postorbital in the intertemporal region becomes very short. In *Daptocephalus* the postorbital extends back to meet the occipital part of the squamosal. In *Dolichuranus* (Keyser, 1973) and *Tetragonias* (Cruickshank, 1967) the postorbital extends back to a level behind the parietal foramen while in *Dinodontosaurus* the postorbitals hardly take part in the formation of the intertemporal bar.

The relationships of the various bones in the palate and choanal region had already been established in *Daptocephalus* and underwent very little change during the evolution of the group. In this lineage the palatal portion of the skull increases with the increase in snout length. The size of the fenestra medio-palatinalis is progressively reduced.

There are a large number of other dinodontosaurid dicynodonts which could possibly have been included in this lineage but of which too little is known for certainty. The genus *Vinceria* (Bonaparte, 1971) which seems very similar to both *Shansiodon* and *Tetragonias*, lived contemporaneously with *Kannemeyeria* in the Puesto Viejo Formation of Argentina. It is morphologically intermediate between *Daptocephalus* and *Dolichuranus*. However, the available descriptions and drawings of the genus *Shansiodon* Yeh are adequate to place it within the lineage with certainty but it appears to occupy the same level of organisation as *Tetragonias*.

The various dinodontosaurid genera are very similar to one another and it would be very difficult to distinguish the anterior half of a skull of any one of them from another, had only these been preserved.

III. PREVIOUS CLASSIFICATIONS

A. General Review

Depending on the amount of information available and the predilections of individual palaeontologists, among other variables, the Triassic anomodonts have been assigned to anything from one to four families. The only family of these fossils which has not been subject to much doubt is the Lower Triassic Lystrosauridae (Cluver, 1971), anomodonts of a peculiar and distinct specialisation which can be regarded for these purposes as representing the most highly specialised lineage of dicynodonts. They must trace their ancestry into the Permian and do not give rise to any other group.

The most common way of treating the large Triassic anomodonts, in the days when but a few were known, was to include them all in one family. Thus Von Huene (1948, pp. 79–80), in his suborder Anomodontia, has six families (Endothiodontidae, Dicynodontidae, Cistecephalidae, Geikiidae, Lystrosauridae and Kannemeyeriidae). The distinction between the families Dicynodontidae and Kannemeyeriidae in this scheme would be seen to rest on the presence in the latter, of a high, narrow parietal region, nasals longer than frontals, up to eight sacral ribs and a high olecranon ulnae. The presence in most of strong tusks, weak hind legs and flat digging claws could not be considered distinctive for this family, as they occur in others, according to Von Huene (op. cit., p. 80). Furthermore, high, narrow parietal crests are almost solely the prerogative of *Kannemeyeria* itself, and on this basis several genera (e.g. *Stahleckeria* and *Dinodontosaurus*) would have had to be excluded.

Romer (1956), on the other hand, retained *Kannemeyeria*, *Dinodontosaurus*, *Placerias*, *Rhadiodromus*, *Sinokannemeyeria* and *Stahleckeria* as genera of equal standing, with Permian dicynodonts in the single family Dicynodontidae, which he noted (op. cit., p. 706) as being characterised in the following way:

“Molar teeth absent, post-frontal frequently absent.

Probably including several independent lines developed from a primitive endothiodont stock.”

In the same year, Camp (1956, pp. 305–341) compared most of the then known Triassic anomodonts in a diffuse and complicated analysis and in the abstract (p. 305) noted that:

“Detailed morphological evidence indicates that the large Middle and Upper Triassic dicynodonts of North and South America, as well as the genus *Kannemeyeria* . . . may belong to a single group: the family

Kannemeyeriidae ... the South American stahleckerians have diverged in one direction and the North American *Placerias* in another, although in some "conservative" features *Placerias* lies between the African and South American forms ..."

Camp makes two further statements which are worth recording. On page 325:

"If it can be granted that the genera of "kannemeyeriids" form a natural group, it remains to be shown to what degree they are related."

This is followed on page 327 by:

"The interrelationships of these three genera within the family are less certain than their unity."

But the implication throughout this work is that the Triassic anomodonts are all members of the family Kannemeyeriidae, but showing trends in two directions.

Lehman (*in* Piveteau, 1961, pp. 271–322) reviewed the Anomodontia and on pp. 321–322 deals specifically with the family Kannemeyeriidae. He clearly follows Camp's suggestions as to relationship, but goes one step further and formally erects two subfamilies to accommodate the trends noted by Camp.

1. The "Kannemeyeriinae" to accommodate those forms with ... "Antero-postero elongation of the squamosals with elevation of the parietal crest"
i.e. *Kannemeyeria* and *Placerias*
2. The "Stahleckeriinae" to accommodate those forms with ... "an apparent lateral expansion of the squamosals on the occipital surface"
i.e. *Stahleckeria*

However, the distinction of occipital proportions seems to be no longer valid (Table I).

TABLE I
Occipital Width : Height Indices for Triassic Dicynodonts

Category 1. Very wide occiput of width : height index $> 1.5 : 1$	
<i>Kannemeyeria simocephala</i>	1.6 : 1 Cruickshank, 1965
<i>Kannemeyeria simocephala</i>	1.64 : 1 Cruickshank, 1970
<i>Dinodontosaurus turpior</i>	1.64 : 1 Cox, 1965
<i>Dinodontosaurus turpior</i>	1.75 : 1 Cox, 1965
<i>Zambiasaurus submersus</i>	1.81 : 1 Cox, 1969
<i>Stahleckeria potens</i>	1.92 : 1 Cox, 1969
<i>Tetragonias njalilus</i>	1.82 : 1 Cruickshank, 1967
<i>Tetragonias njalilus</i>	1.61 : 1 Von Huene, 1942
<i>Sinokannemeyeria vingchiaoensis</i>	2.15 : 1 Sun, 1963
<i>Parakannemeyeria ningwuensis</i>	1.66 : 1 Sun, 1963
<i>Shansiodon wangi</i>	1.55 : 1 Sun, 1959
<i>Dinodontosaurus platyceps</i>	1.71 : 1 Cox, 1968
<i>Kannemeyeria cristarhynchus</i>	1.66 : 1 Crozier, 1970
<i>Dolichuranus latirostris</i>	1.51 : 1 Crozier, 1970
Category 2. Occiputs of width : height index $< 1.5 : 1$ but $> 1.2 : 1$	
<i>Ischigualastia jenseni</i>	1.22 : 1 Cox, 1965
<i>Parakannemeyeria youngi</i>	1.48 : 1 Sun, 1963
<i>Parakannemeyeria dolichocephala</i>	1.29 : 1 Sun, 1963
<i>Wadiasaurus indicus</i>	1.42 : 1 Roy Chowdhury, 1970
<i>Shansiodon wuhsiangensis</i>	1.45 : 1 Sun, 1959
<i>Dinodontosaurus brevirostris</i>	1.5 : 1 Cox, 1968
<i>Dinodontosaurus brevirostris</i>	1.46 : 1 Cox, 1968
Category 3. Very high occiputs of width : height index $< 1.2 : 1$	
<i>Placerias gigas</i>	1.18 : 1 Cox, 1965
<i>Dolichuranus primaevus</i>	1.08 : 1 Keyser, 1973
<i>Kannemeyeria argentinensis</i>	1.17 : 1 Bonaparte, 1966

These trends or adaptations were linked to masticatory processes, a thought that was elaborated by Cox (1965, pp. 502–506) who raised the status of Lehman's subfamilies to that of familial level, creating the Kannemeyeriidae and Stahleckeriidae to accommodate these forms. By this date the number and variety of described Triassic anomodonts had grown considerably beyond those known by Camp, and Cox was thus able to add another family, the Shansiodontidae, for those forms with neither of the specialisations recorded for the previous families.

Other reasons which Cox (1965, p. 502) used to link the Triassic Dicynodontia were:

"... the presence of a separately ossified olecranon process on the ulna ..." ("a notable feature") and "a well developed pubic tubercle ... [and] ... the inturning of the dorsal edge of the ischium."

Cox summarised his analysis of the postcranial features of these animals thus:

"As can be seen, this comparison ... does not provide any immediately apparent pattern of relationships between the genera except that *Sinokannemeyeria*, *Parakannemeyeria*, *Kannemeyeria* and *Placerias* all have similar scapulae ..."

For cranial features Cox noted:

"In *Kannemeyeria* the snout tapers anteriorly to a blunt point. The jaw muscles originate from the front face of an occipital plate which has been greatly heightened postero-dorsally. As a result, the temporal vacuity appears quite long in dorsal view and the intertemporal bar in lateral view projects above the level of the rest of the skull as a high median crest. The occiput is as high as it is broad.

"In *Stahleckeria* the snout is extremely wide and blunt. The jaw muscles originate from the front face of an occipital plate which has been greatly widened by the lateral extension of the squamosals. As a result the temporal opening appears comparatively short in dorsal view and the intertemporal bar in lateral view hardly projects above the level of the rest of the skull. The occiput is wide and low."

Using these summaries of characters, Cox nevertheless did not formally define the three families he proposed, only saying:

"Having recognised the divergent adaptations of *Kannemeyeria* and *Stahleckeria* ..." (p. 502) "these must surely be correlated with differences in their diet and mode of feeding" (p. 505).

In summary we accept that the presence of a separately ossified olecranon process of the ulna in most of the larger Triassic dicynodonts is an important character. We do not accept that the characters of the scapulae help in understanding relationships within the group as a whole and thus the one feature which can be applied universally within the larger Triassic dicynodonts is the contrast in snout shape between the *Kannemeyeria*-like genera and those with broad snouts, which seem to be in the majority.

Romer (1966) followed Cox's classification, noting within the Infra-order Dicynodontia the families Endothiodontidae, Dicynodontidae, Lystrosauridae, Kannemeyeriidae, Stahleckeriidae and Shansiodontidae. In this sense, the first two are Permian in age and the last four Triassic.

Much at the same time as Cox published his proposals, Cruickshank (1964, 1967 and 1968) suggested another approach to the problem, which tacitly assumed a close relationship of all the larger Triassic dicynodonts. In these papers it was proposed that the ancestral Triassic dicynodont was one of the less specialised members of the genus *Lystrosaurus*, and that the large Triassic dicynodonts evolved from a *Daptocephalus*-like form, through an aquatic stage represented by *Lystrosaurus*, to emerge eventually as fully terrestrial forms by the end of the Lower Triassic. It is clear that *Lystrosaurus* shows several of the features possessed by the more typical Triassic dicynodonts (e.g. very short fenestra medio-palatinales; "X"-shaped interclavicle; reduced ectopterygoids and postfrontals), but it is now equally clear that this genus represents the most specialised lineage of dicynodonts and that it is a sterile offshoot of some Late Permian relative of *Daptocephalus*.

Earlier than Cox, Sun (1963) summarised a set of views on the relationships among the kannemeyeriids following Camp's scheme. Some of her points are important (p. 107), e.g. *Placerias* is thought to represent a branch which was derived early from the kannemeyeriid ancestor and evolved along a different line from the others. In doing this, certain primitive characters were retained, e.g. small nasal, relatively large lacrimal, retention of postfrontal

and tabular. Specialisations included the reduction of the tusks, thickening of the posterior border of the squamosal and the upward extension of the ilium.

The Chinese genera described by Sun are thought, by Sun, to have a closer relationship to *Kannemeyeria* than does *Placerias*, a thought not out of keeping, considering their relative ages. Sun lists several characters which are held in common between *Kannemeyeria* and the Chinese kannemeyerids, viz. moderate expansion of the squamosal, without thickened rim; rather extended basicranial axis; postorbital and squamosals meet; developed maxillary process and tusk. It was also thought, by Sun, that *Kannemeyeria*, *Sinokannemeyeria* and *Parakannemeyeria* were at approximately the same level of evolution.

Sun's opinion was that *Sinokannemeyeria* was perhaps even less evolved than *Kannemeyeria*, though not significantly so. In her view (and she followed Camp in this) the low, broad skull with relatively broad temporal region and snout and the round maxillary process all indicated a more primitive stage of evolution than the condition in *Kannemeyeria*. To the above features were added notochordal pits in the vertebrae, a "cleithral groove" (Cruickshank, 1964, 1967) on the scapula and a shorter and more compact humerus. *Kannemeyeria* itself was considered specialised in its long, high parietal crest and *Parakannemeyeria* by a high curved skull with its unique parietal crest characters.

Stahleckeria was thought to be an early derivative of the *Kannemeyeria*-*Sinokannemeyeria* line, sharing with the latter a broad, low skull, laterally expanded squamosal and a low, broad occipital plate. The presence in *Stahleckeria* of a small maxillary process, without a tusk, was not thought significant enough to separate it from the line as envisaged by Sun. The broad, thick nasal with a thin, occipital rim of the squamosal was thought sufficient to separate *Stahleckeria* from *Placerias* and was used by Sun to indicate a closer relationship between *Stahleckeria* and *Kannemeyeria* than between *Placerias* and *Kannemeyeria*. In conclusion, *Dinodontosaurus* was recognised as being more closely related to the Chinese kannemeyerid genera than to *Stahleckeria*.

In retrospect, Sun's analysis of the relationships of the larger Triassic dicynodont genera suffered from her not apparently being aware of Lehman's work. The Chinese Triassic dicynodonts do not seem to have a "narrow, rounded snout" of the same type as *Kannemeyeria* itself, as is implied by Cox in his classification (op. cit., p. 508) and thus we prefer to link them to such broad-snouted forms as *Dinodontosaurus*, as Sun suggested in her original description. The similarities she recognised between the various Triassic dicynodont lineages, we regard as reinforcing the concept of a single, unified family, with two or three main co-evolving lines or subfamilies.

Cruickshank (1967) also recognised the great similarity of the Chinese genera and *Dinodontosaurus*. In a later paper this author summarised many of the points enumerated above in a "family tree" (Cruickshank, 1970, Fig. 4). This summary, following on a review of the genus *Kannemeyeria*, was the best available at the time, but was inadequate in several respects, particularly in the misinterpretation of the structure of the skull of the animal assigned to the genus *Proplaceras* nov. (Cruickshank, 1972).

This scheme distinguished four colateral branches of large Triassic dicynodonts, leading ultimately to (a) *Placerias*, (b) *Kannemeyeria*, (c) *Tetragonias* and (d) the *stahleckerids*. Without making a formal assessment on the status of *Kannemeyeria* and *Placerias*, Cruickshank (1972) was nevertheless able to say that "... although *Kannemeyeria* and *Placerias* are closely allied they represent two different evolutionary trends ..."

Notwithstanding Sun's statement (op. cit., p. 107), *Placerias* may well represent the end point of the *Kanne-*

meyeria evolutionary line, where the caniniform processes and reduced tusks could be undergoing a late reduction from the condition seen in forms such as *K. cristarhynchus* (Roy Chowdhury). We do not believe that *Sinokannemeyeria*, with many characters comparable to those of *Dinodontosaurus*, represents the basic stock from which the other larger Triassic genera could evolve. In fact this scepticism is inherent in the belief that the two main Triassic lineages can be traced to such genera as *Daptocephalus* and *Dinanomodon*. *Sinokannemeyeria* represents part of the broad-snouted evolutionary line, and is so treated in the classification which follows.

Finally, Keyser (1974) discussed the overall evolutionary trends to be seen in Triassic dicynodonts. These are (op. cit., p. 65):

1. Increase in total body size.
2. Increase in relative length of snout and secondary palate by backward growth of the premaxilla.
3. Reduction in the fenestra medio-palatinalis (interpterygoid space) and its posterior migration out of the choanal depression.
4. Shortening and dorsal expansion of the intertemporal bar with concomitant shortening of the temporal fossae.
5. Fusion of elements in the front part of the brain case.
6. Posterior migration of the lamina reflecta of the mandible.
7. Development of an anterior process on the quadrate, which lies along the quadrate ramus of the pterygoid.
8. Disappearance of the quadrate foramen.

The first trend was recognised by several of the early authors, and the second had been noted in part by Toerien (1953). The third trend was noted by Camp (1956) and elaborated on by Cruickshank (1967, 1968). One of the most important trends commented on by Keyser (op. cit.), is the fourth where the temporal fossae are noted as becoming shorter with time, in association with the shortening and dorsal expansion of the intertemporal bar. The fusion of the anterior elements in the brain case can be associated with the change in direction of the "temporalis" muscle stresses (Crompton and Hotton, 1967) and, Keyser remarked, the backward migration of the reflected lamina is associated with the elimination of the quadrate foramen. Of all these trends, that concerning the development of an anterior process on the quadrate (no. 7) seems to stand alone. Keyser used the last character to help define the subfamily Jachelerinae nov. within the Family Kannemeyeriidae Lehman, and concluded that because of the many discoveries made subsequent to 1965

"... major rethinking on the taxonomy of the group has become necessary." (Keyser, 1974, p. 66).

B. The Status of the Families *Kannemeyeriidae* and *Stahleckeridae* Cox

Before discussing the overall classification of the Triassic dicynodonts, the first necessity is to look at the two main families defined by Cox in 1965, as they seem to represent the clearest divergence of characters seen in the Triassic. This classification is basically sound but needs re-assessment. This has been done in part by Cruickshank (1978), who has discussed the palaeoecology of Triassic dicynodonts. However, several instances will be cited here of confusion which has arisen in referring specimens to the families *Stahleckeridae* and *Kannemeyeriidae* in particular, and to a lesser extent to the family *Shansiodontidae* Cox.

It is coincidental that in 1970, Roy Chowdhury and Crozier both described specimens, from India and Zambia respectively, which were placed into the taxon *Rechnisaurus cristarhynchus* Roy Chowdhury, a *stahleckeriid*, and which was originally described from the Yerrapalli Formation. This is of approximately Anisian age (Anderson and

Anderson, 1970) and, because another specimen was described later in the same year from the Zambian N'tawere Formation (Locality 16: Crozier, 1970), both these geological horizons are thought to be of equivalent age. It is thought that the N'tawere Formation in general is slightly younger than the (?Scythian) *Cynognathus* zone of South Africa, but older than the (?U. Anisian) Manda Formation of Tanzania (Anderson and Anderson, 1970).

The genus *Rechnisaurus* is defined from the type and only species, *R. cristarhynchus*, as being of moderately large size (about 380 mm skull overall length) with large canine teeth (244 mm in diameter), wide interorbital region and blunt snout with a strong median ridge on the anterior and dorsal surfaces of premaxilla which continues on to dorsal surfaces of nasal. This ridge is bounded by a pair of deep depressions. The maxillae are produced into powerful antero-ventrally directed caniniform processes bearing rugose rounded flanges postero-ventrally. The postorbital region is short, with short, wide temporal openings. The intertemporal bar is fairly narrow and dorsally concave in section. The parietal crest is described as not being high (but see below), with a low boss immediately behind the pineal foramen. The parietals form most of the intertemporal bar, and there is a sharp transition between dorsal and occipital surfaces.

In comparing the Zambian specimen with the type, Crozier (1970, p. 39) concluded that:

"This specimen agrees in all particulars with the type except for its size (465 mm) and the shape of the snout." (which is pointed as opposed to blunt in the type.)

Keyser (1973) described a fauna of approximately Anisian age from South West Africa and which contained a specimen (1973, Fig. 3, R313) assigned tentatively to *Kannemeyeria simocephala* (Weit). The genus *Kannemeyeria* Seeley is defined (Cruickshank, 1970) as follows:

"Medium to large sized skulls, tusked in both sexes. Zygomatic arches parallel or sub-parallel in dorsal view. Parietal crest high and narrow with no extensive exposure of interparietal on dorsal surface. A large orbit dominating the facial region and a relatively short precanine region of the snout.

$$\frac{\text{Interpterygoid space}}{\text{distance between nostrils}} \times 100 = 23\text{--}28 \text{ per cent.}$$

Labial fossae may be universally present." (The latter character is in fact the case.) Additionally *K. simocephala* (Weit) has the following characters:

"Large skull (about 450 mm overall length) with horizontal flanges on maxillae and a prominent mid-nasal ridge. Tusks run in line with jugal arch, though the tips on emerging may turn sharply downward. Lower jaw with normal up-turned tip. Prespinous fossa of scapula large and anterior blade of ilium small." (Cruickshank, 1970, pp. 50–51).

A close comparison of specimen R313 (Figs. 16–19) and the Zambian specimen of *R. cristarhynchus* is effected partly qualitatively and partly quantitatively in Table II. Bearing in mind the vastly different states of preservation and the necessity of having to rely on reconstruction to obtain some values from the Zambian specimen, it is clear that there is a great quantitative resemblance between R313 and B.P.I. 3638. This confirms Keyser's opinion (1974, p. 58) that:

"... this genus (*Rechnisaurus*) had best be placed in the family Kannemeyeriidae and is probably a descendant of the genus *Kannemeyeria*. It is even doubtful that a generic distinction can be upheld."

Qualitatively R313 and B.P.I. 3638 agree on the presence of the strong mid-nasal ridge flanked by depressions, the strong caniniform processes and in their temporal openings being shorter and their parietal crests not being as high as might be expected in a typical *K. simocephala*. The interpterygoid space : internal narial ratio for R313 is anomalously high in comparison with all other *Kannemeyeria* specimens which are described, with the sole exception of the juvenile B.P.I. 2092. That of B.P.I. 3638 is on the low side. In addition to the specific points enumerated above, it must be noted that they are both of approximately the same size in almost all dimensions, there only being minor points of difference.

Taking the comparisons further and investigating the relationship of R313 and B.P.I.3638, using *Kannemeyeria* specimens from the Beaufort series as a standard, it is seen

TABLE II
Some Characters of *Kannemeyeria* Specimens, in Millimetres

	Geol. Surv.		Univ. Calif.				Average adults (excl. BPI 2092)	
	BPI 3638	R313	BPI 4523	42916	BPI 1168	BPI 2092	SWA & Zambia	Beaufort
Length: a. palatal midline	365	355	359	371*	346*	230	360	358,6
b. dorsal midline	450*	409	436	413*	427	293	429,5	425,3
c. over squamosal wings	465*	444	477	452*	449	315*	454,5	459,3
Width over squamosals	454*	406	322	388	360*	—	430	356,6
Interorbital distance	150	140	147	170	155	100	145	157,3
Internasal distance	160	150	110	100	85*	50*	155	98,3
Width of parietal crest at level of pineal	53*	59	50	61	55	29*	56	55,3
Length behind postorbital or dorsal midline	140*	130	165	130*	175	113	135	156,6
Length in front of post- orbital or dorsal midline	310*	279	271	283*	252	180	194,5	268,6
Length of internal nares	105	82	96	77*	—	54	93,5	86,5
Length of fenestra medio- palatalis	18	29	16	19*	—	18	23,5	17,5
Diameter of tusks	36,5 × 31	40 × 29	29 × 27	22,5 × 18	29 × 26	18 × 16	38,25 × 30	26,8 × 23,6
Horizontal diameter: orbit	95	68	72	78	85	68*	81,5	78,3
Horizontal diameter: nares	55	55	63	46	48	37,5	55	52,3
Depth: caniniform process	145	150	72	104*	110	61	147,5	95,3
$\frac{\text{Ipt. space}}{\text{Int. nares}} \times 100$	17,6 %	35 %	16,7 %	24,5 %	—	33,5 ½	26,3 %	20,6 %
$\frac{\text{Preorbital length}}{\text{Total midline length}} \times 100$	69 %	69 %	62,5 %	68 %	59 %	61,3 %	69 %	63,2 %

* Estimate on damaged or distorted region

TABLE III
Stratigraphic Distribution of Triassic Dicynodonts

GENERA	SCYTHIAN	ANISIAN	LADINIAN	CARNIAN	NORIAN	RHAETIAN	Age Continent	
Kannemeyeria } Tetragonias }		Manda Fm					AFRICA	
Kannemeyeria } Dolichuranus }		Omingonde Fm						
Kannemeyeria } Dolichuranus }		N'tawere Fm						
Zambiasaurus } Sanguasaurus }								
Kannemeyeria		U. Beaufort						
Jacheleria					Los Colorados			
Stahleckeria } Dinodontosaurus }					Santa Maria			
Barysoma } Ischigualastia }					Ischigualasto		SOUTH AMERICA	
Dinodontosaurus			Ischichuca					
Kannemeyeria } Vinceria }		Puesto Viejo						
Kannemeyeria } Wadisasaurus }		Yerrapalli Fm.						
Sinokannemeyeria } Parakannemeyeria }	Er-ma-Ying Fm						CHINA	
Shansiodon								
Placerias					Chinle Fm.		N. AMERICA	
Uralokannemeyeria } Rabidosaurus }							RUSSIA	
Rhinodicynodon								
Rhadiodromus } Rhinocerocephalus }								
Elephantosaurus								

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that certain differences do, in fact, exist between the Zambian and South West African specimens on the one hand, and the Beaufort specimens on the other. This comparison allows several explanations. The most obvious is that the Beaufort Series specimens represent a true sample of *K. simocephalus* (Weit) and the Zambian and South West African specimens represent a sample of a population of an entirely separate species. Supporting this explanation is the markedly different pre-orbital proportions of the two groups (with the exception of Specimen 42916) viz. 60 per cent v. 69 per cent, allied with the markedly deeper caniniform processes in the later pair (average of 147 mm compared with 111 mm average). Likewise the interorbital distance of the Beaufort adults averages 158 mm and the same measurement averages 145 mm in the others. There is an inverse relationship with the internasal distance: the Zambian and South West African pair have broader nasal regions (average 155 mm) than the Beaufort (average 95 mm). The tusks of all the measured specimens have suffered damage of one kind or another, but it is clear that while the Beaufort specimens have fully cylindrical tusks of moderate diameter, the Zambian and South West African specimens have tusks oval in section and much heavier in structure. In the Zambian specimen, the reflected lamina of the angular touches the lateral condyle of the articular, a progressive character (Keyser, 1974), which is not preserved in the South West African specimen, because there is no lower jaw associated with it.

On the other hand, the heavy nose and tusks could indicate that these are male characters in very much the same way as Cox (1965, p. 494) distinguished his "Old Bull" *Dinodontosaurus turpior* from other specimens of that species, and as was done in a similar exercise by Cruickshank in 1967 for *Tetragonias*. However, in this study it is remarkable that the specimens fall into two groups, separable on sexual dimorphism and at the same time by some hundreds of kilometres! Therefore, we retain the two species *K. simocephalus* and *K. cristarhynchus* and have used this to reinforce our scepticism as to the usefulness of the Family *Stahleckeridae* Cox.

It is possible that the Upper Beaufort, N'tawere and Omigonde are, in fact, a group of horizons spanning the Scythian-Anisian boundary and the facts then could be interpreted thus: that the basal *Kannemeyeria* stock is represented by *K. simocephalus* which is a long ranging species, and that in the *Cynognathus* zone of the Beaufort it gave rise to a separate lineage of *Kannemeyeria*-like animals represented by the specimens from Zambia and South West Africa. *K. simocephalus* is also known from the Manda Formation (Cruickshank, 1965), the latest known true *Kannemeyeria*, later even than those specimens under discussion here.

Crompton and Hotton (MS.) have indicated that there is a general shift in the orientation of the jaw adductor muscles in Triassic anomodonts, leading from *Kannemeyeria simocephalus* (where the angle of insertion of these muscles is acute to horizontal) to the late-Middle and Upper Triassic anomodonts (*Dinodontosaurus*, *Ischigualastia*, *Stahleckeria* and *Placerias*), where the angle of insertion is much nearer the vertical. This trend is reflected in a shortening of the temporal openings, a deepening of the caniniform processes, where the tusks are retained, a broadening of the snout and reinforcing of the brain case (Keyser, 1974).

At this stage, therefore, and in context of the overview of the study as presented here, the following conclusions can be maintained:

1. The genus *Rechnisaurus* Roy Chowdhury is indistinguishable from the genus *Kannemeyeria* Seeley.
2. The characters of *R. cristarhynchus* R. C. are seen in a less elaborated fashion in *K. simocephalus* (Weit).
3. It is, therefore, possible that *R. cristarhynchus* R. C. represents

resents an offshoot lineage from the *K. simocephalus* (Weit) stock which evolved a shorter postorbital region, heavier snout and deeper caniniform processes.

4. If the above is true, then the two families, *Stahleckeridae* Cox and *Kannemeyeriidae* Cox, are not distinguishable and are hence no longer valid. All the large Triassic anomodonts are then likely to be members of the one family, viz. *Kannemeyeriidae* Huene, which, in turn, can be sub-divided into a number of subfamilies.

A similar exercise in discriminating between Cox's taxa can be done on the other dicynodonts from South West Africa, the genera *Dolichuranus* and *Rhopalorhinus*. The former has a snout of Shansiodont type, and was classified as such by Keyser (1973) in his original diagnosis of the material. The latter has a snout of very robust appearance, and the occiput was apparently very wide. From these characters, Keyser placed the genus in the *Stahleckeridae* Cox.

Subsequently a further collection of dicynodont material was made from the same localities which yielded the types of these two genera (Keyser and Cruickshank, in prep.). It is now clear that *Dolichuranus* and *Rhopalorhinus* represent the extremes of a morphological series and that the two genera are synonymous. The genus *Dolichuranus* has page priority. This serves to point out that the criteria defined by Cox for the Families *Shansiodontidae* and *Stahleckeridae* are not discriminative and that the status of these two families requires reassessment.

In the paper describing *Dolichuranus*, Keyser also pointed out that the specimen Crozier (1970) had called *Kannemeyeria latirostris* was in fact a member of the genus *Dolichuranus*. At the same time that *K. latirostris* was described, Crozier noted that it was not typical of the genus *Kannemeyeria* in several respects. However, the decision was taken to include it in that taxon, even though it was recognised as being slightly aberrant.

The reassessment of the genus *Dolichuranus* emphasises two points of Triassic dicynodont taxonomy. One is to reinforce the idea of the over-all great similarity of the family as represented in the Triassic and concomitantly, the extreme difficulty of applying Cox's criteria to effect objective taxonomic decisions.

A reassessment of *Stahleckeria* itself, based on the skull of the mounted skeleton in the Palaeozoology Museum in Tübingen, and a comparison of this specimen with skulls of *Ischigualastia* in the Museum of the Instituto Lillo, Tucuman, shows that these two genera are surprisingly similar (Figs. 20, 33, 34). The *Stahleckeria* skull has a much narrower snout than that normally illustrated (Camp, 1956, Fig. 45) and possesses a low dorsal ridge running on to the naso-frontal region.

The skull of *Stahleckeria* has much wider occipital flanges than does *Ischigualastia*, and in the latter genus there is no quadrate foramen and the reflected lamina of the angular contacts the lateral condyle of the lower jaw (Keyser, 1974). Apart from these facts, the differences between the two are hardly more than those used by Cox (1965) and Cruickshank (1967) to demonstrate possible sexual dimorphism in *Dinodontosaurus* and *Tetragonias* respectively. Both *Stahleckeria* and *Ischigualastia* are of course tuskless and "large". We therefore believe that there are insufficient grounds to separate them except at generic level, and will use this information to link all the large Late Triassic forms together as advanced *Kannemeyeria* descendants in a subfamily of their own (see below).

Ischigualastia occurs in the Santa Maria and Ischigualasto Formations (Barbarena, pers. comm.). *Stahleckeria* is unique to the Santa Maria and no material has been reported since Von Huene's discoveries.

Therefore, we recognise two main collateral lines of descent within the Triassic dicynodonts, to which we assign subfamilial status, viz. *Kannemeyeriinae* and *Dinodonto-*

osaurinae, and a third representing the very large specialised Upper Triassic end-forms which could be descended from either or both of the other subfamilies, to which we apply the name *Stahleckerinae*. A fourth subfamily is included to accommodate some poorly known specimens of the genus *Jacheleria* Bonaparte.

Thus the unifying characters of the larger Triassic dicynodonts are as follows:

1. Large body size, with skulls concomitantly rarely less than 25 cm overall. Typically they are 40 cm or more and tusked, but exceptions exist.
2. The snout is always as long or longer than the post-orbital region of the skull. The palatal region is elongated. The temporal fenestra may be very short (see 4 below).
3. The fenestra medio-palatinalis (interpterygoid space) is always less than 60 per cent of the length of the internal nares and less than 8 per cent of the total basal length of the skull. In late forms it lies outside the choanal depression and may at all stages of evolution have raised margins.
4. The interpterygoid bar becomes dorsally expanded in association with its shortening (see 2 above).
5. Elements in the front part of the brain case become fused.
6. The reflected lamina of the angular grows close to or contacts the lateral condyle of the articular.

7. The quadrate foramen disappears in those forms with firm contact of the reflected lamina and lateral condyle.
8. In some late specialised forms there is an anterior process of the quadrate which lies along the quadrate ramus of the pterygoid.
9. The epipterygoid develops an anterior ramus which has a dorsal process.
10. The intertemporal region is always narrower than the interorbital region.
11. The postfrontals are no longer seen on the dorsal surface of the skull.
12. The ectopterygoid is severely reduced or absent altogether.
13. The interclavicle is short and "X" shaped.
14. In all cases, except one, the ulna has a separately ossified olecranon process.

All the basic characters (i.e. 1–6, 9–13) are seen in the genus *Kannemeyeria*. The other characters we regard as derived. Hence as *Kannemeyeria* is the oldest known true Triassic dicynodont and the genus with which all other forms are compared, we propose to use it to derive the name for the principal family of Triassic dicynodonts in much the same sense as did Von Huene in 1948.

Table III summarises the occurrence of the genera in time and space.

IV. A REVISED CLASSIFICATION OF TRIASSIC DICYNODONTS

Order *Therapsida*

Suborder *Anomodontia*

Infraorder *Dicynodontia*

Family *Kannemeyeriidae*

1. Subfamily *Kannemeyeriinae*

Kannemeyeria simocephala

Kannemeyeria wilsoni

Kannemeyeria argentinensis

Kannemeyeria chrystarhynchus

Uralokannemeyeria vjuschkovi

Rabidosaurus cristatus

? *Rhadiodromus klimovi*

? *Rhinocerocephalus cisuralensis*

? *Sangaosaurus edentatus*

? *Wadisasaurus indicus*

2. Subfamily *Dinodontosaurinae*

Dinodontosaurus turpior

Dinodontosaurus tener

Dinodontosaurus platyceps

Dinodontosaurus brevirostris

Sinokannemeyeria pearsoni

Sinokannemeyeria yingchiaoensis

Parakannemeyeria dolichocephala

Parakannemeyeria youngi

Parakannemeyeria ningwuensis

Dolichuranus primaevus

Dolichuranus latirostris

Dolichuranus etionensis

Shansiodon wangi

Shansiodon wuhsiangensis

Tetragonias njalilus

Vinceria andina

Rhinodicynodon gracile

? *Zambiasaurus submersus*

Syn. *Dicynodon simocephalus*

Dicynodon latifrons

Kannemeyeria proboscoides

Kannemeyeria erithrea

Sagecephalus pachyrhynchus

Syn. *Kannemeyeria vanhoepeni*

Syn. *Lystrosaurus klimovi*

Syn. *Dicynodon turpior*

Dinodontosaurus oliveirai

Syn. *Dicynodon tener*

Syn. *Chanaria platyceps*

Syn. *Rhopalorhinus*

Syn. *Dicynodon njalilus*

3. Subfamily *Stahleckerinae**Stahleckeria potens**Ischigualastia jenseni**Placerias hesternus**Placerias gigas**Barysoma lenzii*Syn. *Stahleckeria lenzii*4. Subfamily *Jachelerinae**Jacheleria colorata**Jacheleria platygnathus*Syn. *Dinodontosaurus platygnathus*A. The Family *Kannemeyeriidae* Huene, 1948*Revised diagnosis*

Medium- to large-sized Triassic anomodonts with labial fossae and small fenestrae medio-palatinales; long snouts and pterygoid rami of epipterygoids with dorsal processes; tusked or tuskless; narrow intertemporal region; much reduced postfrontals and ectopterygoids; reflected lamina of angular approaches very close to, or contacts, lateral condyle of the articular; interclavicles short, "X"- or "V"-shaped, with ventral peg; ulna with separately ossified *olecranon ulnae* except in *Kannemeyeria*; descendants of *Dicynodontidae* s.s. through a form like *Odontocyclops* or some species of the genus *Dicynodon*.

1. Subfamily I *Kannemeyeriinae* Lehman, 1961 Emend*Diagnosis*

Large universally tusked forms with pronounced parietal crest; narrow pointed snout with well-developed single median ridge on the premaxilla and nasals; nasals have pronounced sculpture; no nasal bosses; postorbitals reach to, but do not overlap, the squamosals; perhaps descendants of a form like *Dinanomodon*.

(a) Genus *Kannemeyeria* Seeley, 1908 (Figs. 16–20).

Diagnosis: Skulls with zygomatic arches parallel or sub-parallel; orbit large and dominates facial region; precanine region short.

(i) *Kannemeyeria simocephala* (Weithofer) 1888 — Type species.

Synonyms — *Dicynodon simocephalus* Weit, 1888.

Dicynodon latifrons Broom, 1898.

Kannemeyeria proboscoides Seeley, 1908.

Sagecephalus pachyrhynchus Jaekel, 1911.

Kannemeyeria erithrea Haughton, 1915.

(ii) *Kannemeyeria wilsoni* Broom, 1937.

Synonym — ? *Kannemeyeria vanhoepeni* Camp 1956.

(iii) *Kannemeyeria argentinensis* Bonaparte, 1966.

(iv) *Kannemeyeria cristarhynchus* (Roy Chowdhury), 1970.

Synonym — *Rechnisaurus cristarhynchus* Roy Chowdhury, 1970.

Diagnoses: Species (i)–(iii) are discussed by Cruickshank (1970, pp. 50–51). Species (iv) is discussed above (pp. 93–96).

(b) Genus *Uralokannemeyeria* Danilov, 1971 (Fig. 22).

Diagnosis (after Danilov, 1971): A kannemeyeriine with broad, low parietal crest. (Otherwise indistinguishable from *Kannemeyeria* and is probably the same as *Kannemeyeria cristarhynchus*.)

(i) *Uralokannemeyeria vjushkovi* Danilov, 1971.

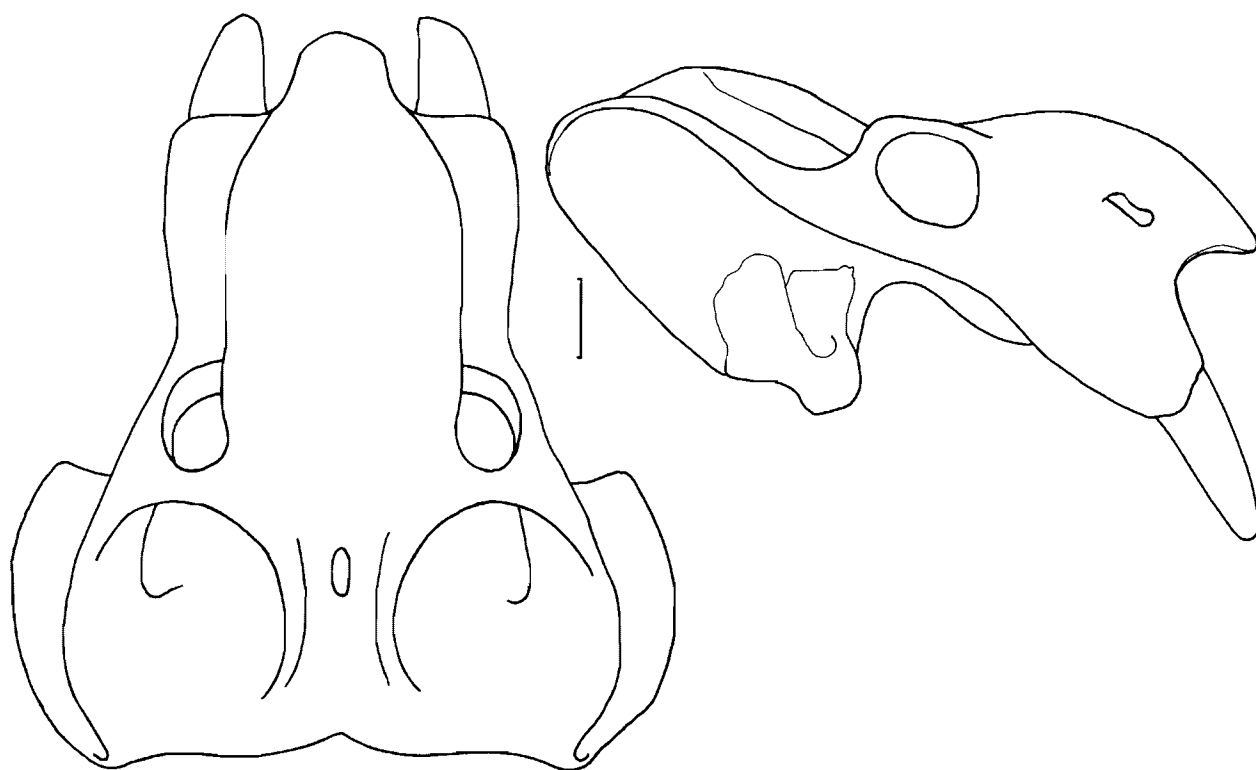


Figure 22

Uralokannemeyeria skull in two views. Scale is 5 cm.

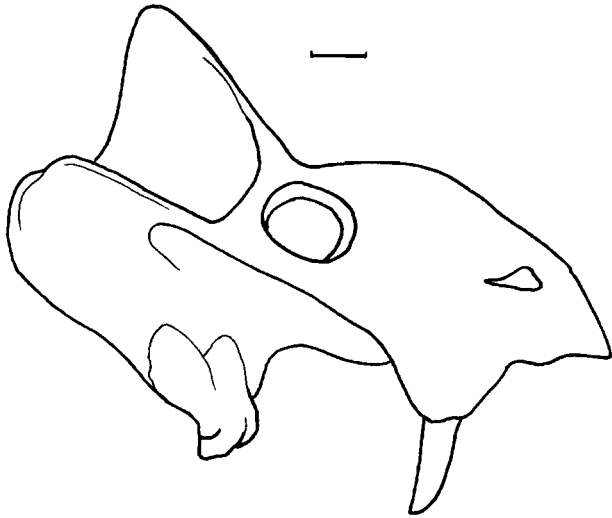


Figure 23
Rabidosaurus skull in lateral view. Scale is 5 cm.

- (c) Genus *Rabidosaurus* Kalandadze, 1970 (Fig. 23).
Diagnosis: A kannemeyeriine which differs from the type genus only in its excessively developed parietal crest. (It may be congeneric with *Kannemeyeria*.)
- (i) *Rabidosaurus cristatus* Kalandadze, 1970.
- (d) Kannemeyeriinae *incertae sedis*.
- (i) *Rhadiodromus klimovi* (Efremov), 1938.
Synonym — *Lystrosaurus klimovi* Efremov, 1938.
- (ii) *Rhinocerocephalus cisuralensis* Vjushkov, 1969 (Fig. 24).
- (iii) ? *Sanguasaurus edentatus* Cox, 1969.
- (iv) ? *Wadisasaurus indicus* Roy Chowdhury, 1970 (Fig. 25).

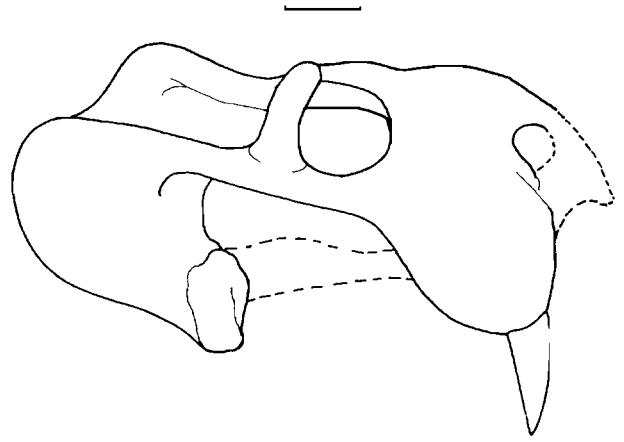


Figure 24
Rhinocerocephalus skull in lateral view. Scale is 5 cm.

Diagnoses: The last two forms — (iii) and (iv) — are tuskless, and although exhibiting other features in common with *Kannemeyeria*, may form the basis of a new subfamily. *Rhinocerocephalus* (ii) is also very probably closely related to *Kannemeyeria*, but the available figures and descriptions are inadequate for a definite conclusion.

2. Subfamily II *Dinodontosaurinae* Subfam. Nov.

Diagnosis

Small to large dicynodonts, all prominently tusked; parietal region never elevated; parietal processes of postorbitals short, or very short, rarely reaching the squamosals; nasal bosses present in some; wide square snout with one or more low ridges on the snout; perhaps descendants of *Daptocephalus*.

- (a) Genus *Dinodontosaurus* Romer, 1943 (Figs. 12–15).
Synonym — *Chanaria* Cox, 1968.

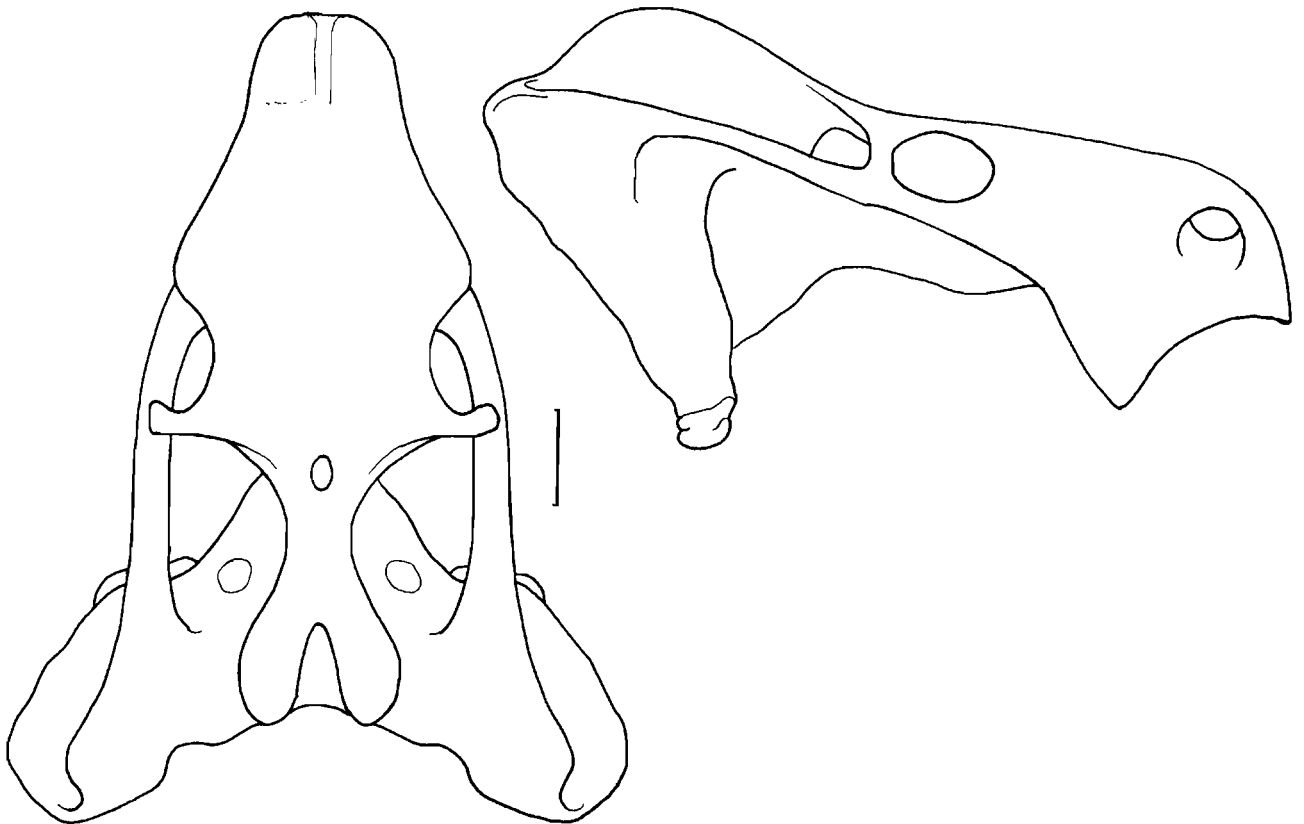


Figure 25
Wadisasaurus skull in two views. Scale is 5 cm.

Diagnosis: Moderately large form with short post-orbital region of the skull; snout rectangular in section with markedly blunt anterior margin; no nasal bosses; tabular absent; ectopterygoid much reduced, lying on dorso-lateral surface of pterygoid; parietal process of postorbital very short, extending barely to the level of the pineal foramen.

- (i) *Dinodontosaurus turpior* (Huene), 1935 — Type species.

Synonyms — *Dicynodon turpior* Huene, 1935.
Dinodontosaurus oliveirai Romer, 1943.

- (ii) *Dinodontosaurus tener* (Huene), 1935.

Synonym — *Dicynodon tener* Huene, 1935.

- (iii) *Dinodontosaurus platyceps* (Cox), 1968.

Synonym — *Chanaria platyceps* Cox, 1968.

- (iv) *Dinodontosaurus brevirostris* Cox, 1968.

Diagnoses: Differences between these species are pointed out in the main body of this contribution. The species *Dinodontosaurus platygnathus* is transferred to the genus *Jacheleria* (see below).

- (b) Genus *Sinokannemeyeria* Young, 1937 (Fig. 26).

Diagnosis: Moderately large skull with short post-orbital region; blunt snout with low mid-nasal ridge and small nasal bosses; anterior tip of premaxilla hollow; very prominent caniniform processes; roughened area on dorsal surface of skull; parietal crest wide, flat-topped or grooved; postorbitals run far round temporal openings towards squamosals; preparietal may be absent; very long dentary symphysis; humerus and femur broad and flat.

- (i) *Sinokannemeyeria pearsoni* Young, 1937 — Type species.

- (ii) *Sinokannemeyeria yingchiaoensis* Sun, 1963.

Diagnoses: Differences between these two species are pointed out in the main body of this contribution.

- (c) Genus *Parakannemeyeria* Sun, 1960 (Fig. 27)

Diagnosis: Large, narrow skull with arched nasal region and very short postorbital region; dorsal surface of skull less rugose than in *Sinokannemeyeria*,

and nasal ridges and bosses are absent; blunt snout with premaxillary excavation; caniniform processes prominent; parietal crest narrower than in *Sinokannemeyeria*; postorbitals shorter, preparietal may be absent; shorter dentary symphysis; longer forelimb and more slender propodials than in *Sinokannemeyeria*.

- (i) *Parakannemeyeria dolichocephala* Sun, 1960 — Type species.

- (ii) *Parakannemeyeria youngi* Sun, 1963.

- (iii) *Parakannemeyeria ningwuensis* Sun, 1963.

Diagnoses: *Sinokannemeyeria* and *Parakannemeyeria* are very similar and may prove to be congeneric when a larger range of morphological variations are known. The former genus is apparently from a lower horizon in the succession than the latter (Zones I and II, as opposed to Zones IV and V of the Er-ma-ying Formation).

- (d) Genus *Dolichuranus* Keyser, 1973 (Fig. 28)

Synonym — *Rhopalorhinus* Keyser, 1973.

Diagnosis: Medium-sized skull with moderately blunt snout and nasal bosses variably developed; indistinct mid-nasal ridge; preorbital and postorbital regions sub-equal in length; caniniform processes only moderately developed; premaxillary excavations variably developed; premaxilla reaches to level of orbits dorsally; postorbitals reach only to the back of the temporal openings; roughened area on skull extends only over nasal bosses; preparietal always present; very short mandibular symphysis.

- (i) *Dolichuranus primaevus* Keyser, 1973 — Type species.

- (ii) *Dolichuranus latirostris* (Crozier), 1970.

Synonym — *Kannemeyeria latirostris*.

- (iii) *Dolichuranus etionensis* (Keyser), 1973.

Synonym — *Rhopalorhinus etionensis* Keyser, 1973.

Diagnoses: Differences between these species are pointed out in the main body of this contribution.

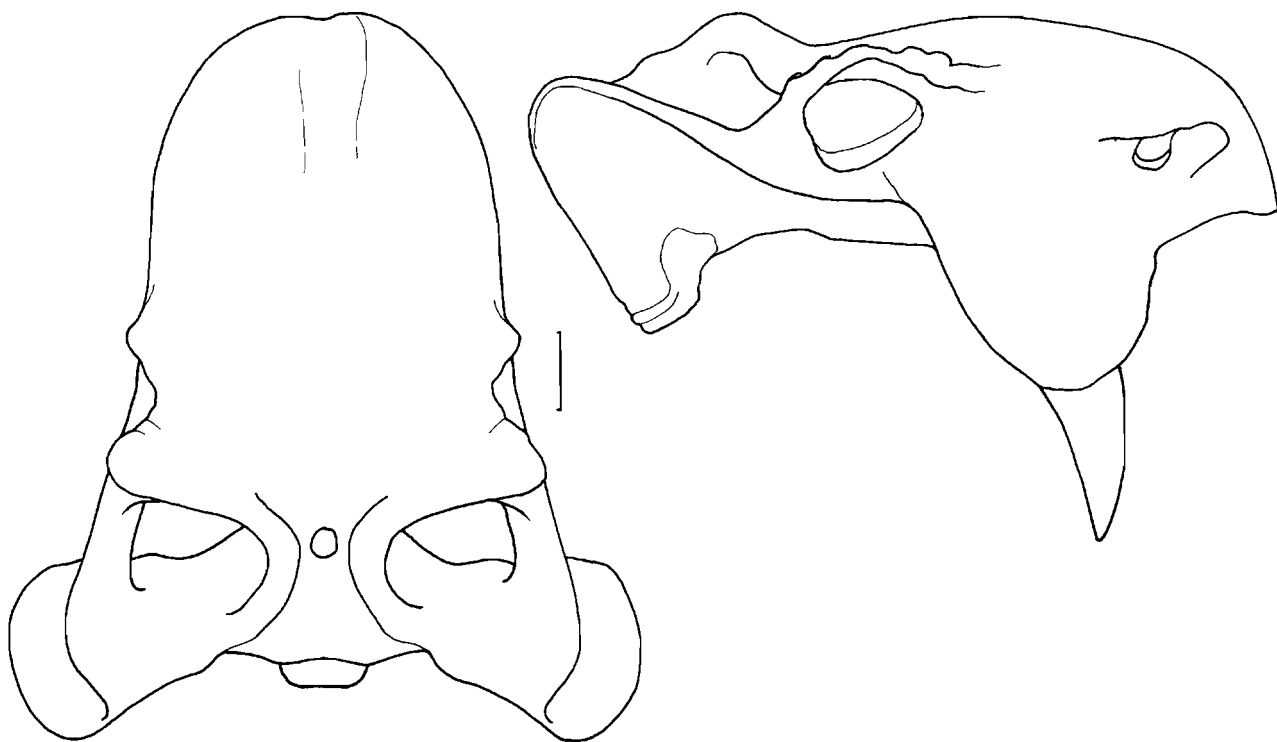


Figure 26
Sinokannemeyeria skull in two views. Scale is 5 cm.

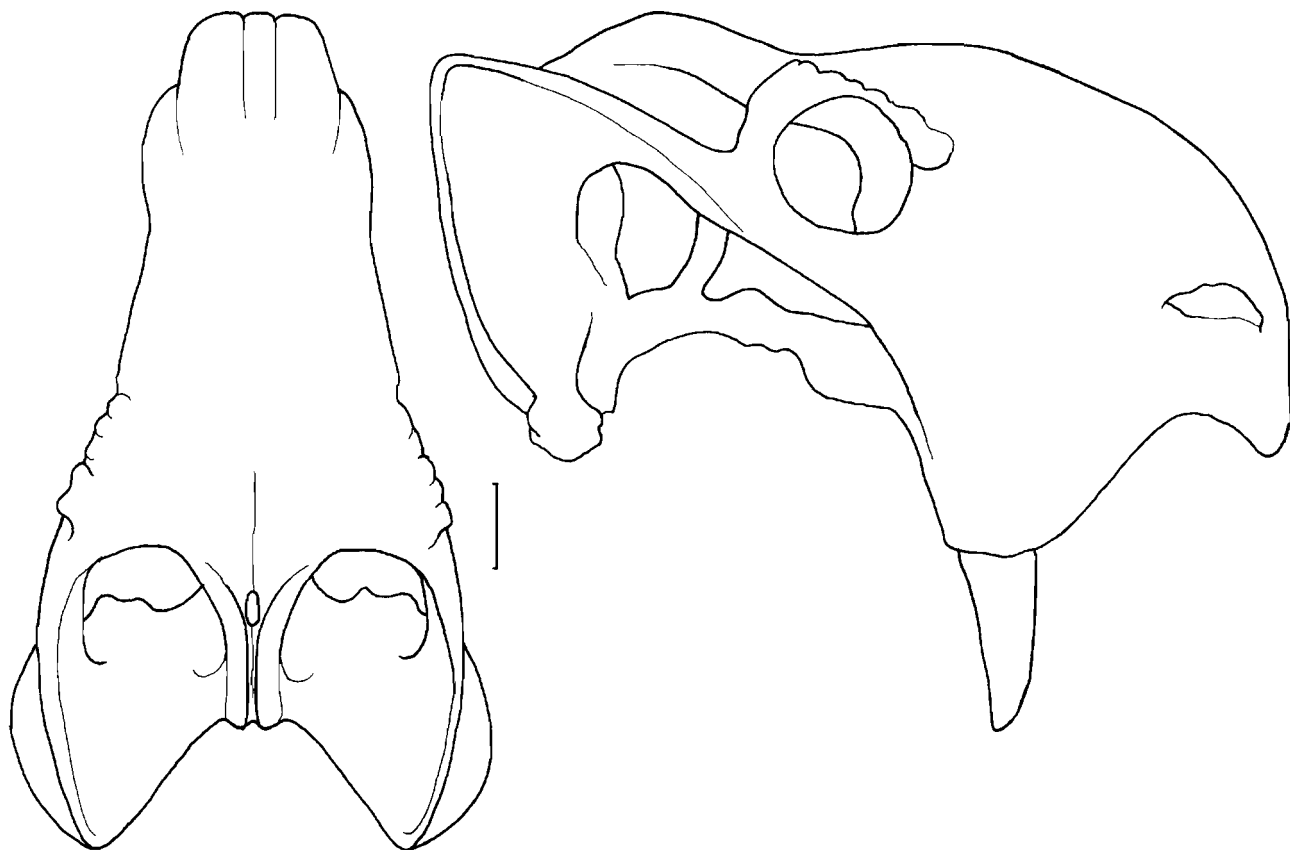


Figure 27
Parakannameyeria skull in two views. Scale is 5 cm.

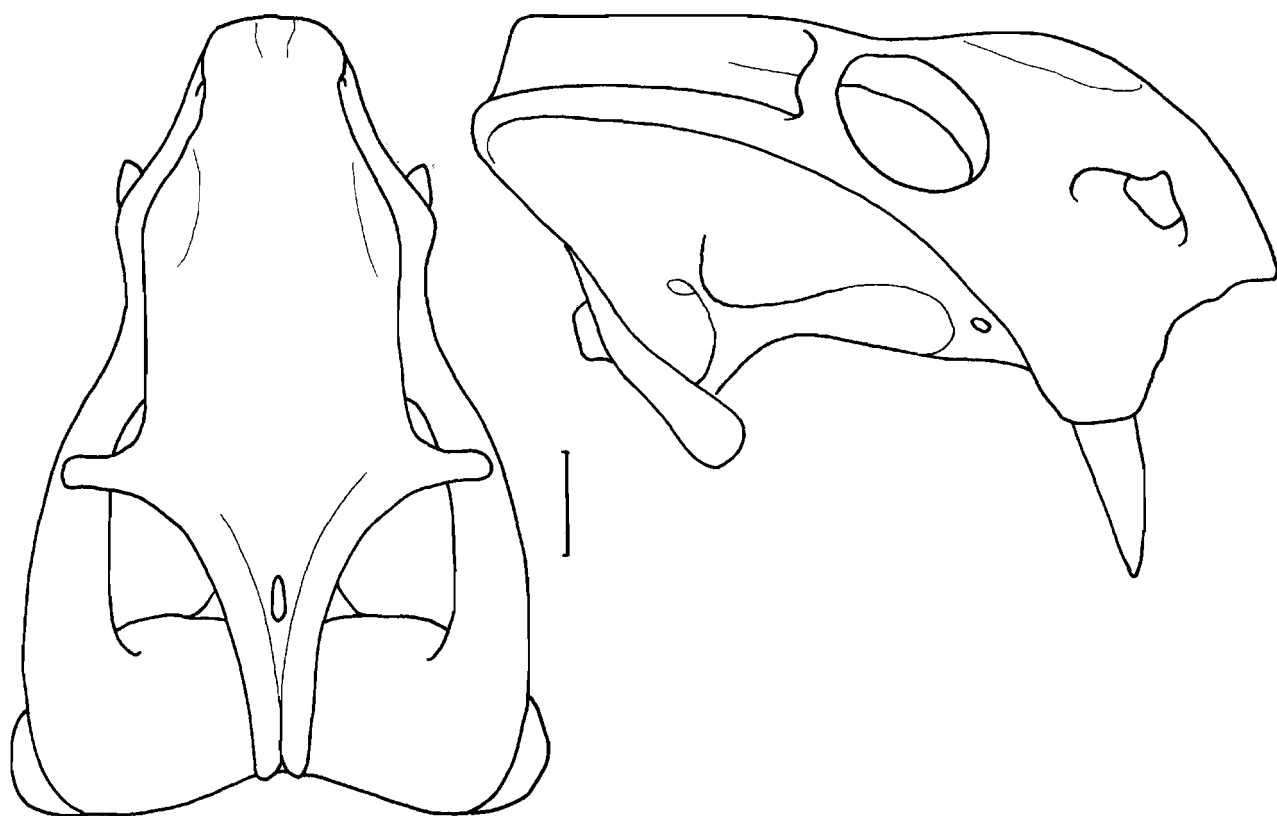


Figure 28
Dolichuranus skull in two views. Scale is 5 cm.

- (e) Genus *Shansiodon* Yeh, 1973 (Fig. 29).
Diagnosis: Skull small, preorbital and postorbital regions equal in length; snout blunt; nasal ridges and bosses present; caniniform processes moderately developed; femur with a very mammalian-like caput.

(i) *Shansiodon wangi* Yeh, 1959 — Type species.

(ii) *Shansiodon wuhsiangensis* Yeh, 1959.

Diagnoses: Differences between these two species are pointed out in the main body of this contribution.

- (f) Genus *Tetragonias* Cruickshank, 1967 (Fig. 30).

Diagnosis: Small, square skull; preorbital and postorbital regions equal in length; snout markedly square, mid-nasal ridge ends in frontal boss; nasal bosses end in nasal overhangs; postorbitals withdrawn from squamosals; males with cylindrical caniniform processes, more triangular in cross section in females.

(i) *Tetragonias njalilus* (Huene), 1942.

Synonym — *Dicynodon njalilus*.

- (g) Genus *Vinceria* Bonaparte, 1967 (Fig. 31).

Diagnosis: Small, square skull; snout not very blunt; preorbital and postorbital regions equal in length; maxillaries expanded around canines; postorbitals approach close to squamosals. (*Shansiodon*, *Tetragonias* and *Vinceria* are probably very closely related. The type specimens should be brought together for close comparison. We believe that they may prove to be congeneric.)

(i) *Vinceria andina* Bonaparte, 1967.

- (h) Genus *Rhinodicynodon* Kalandadze, 1970 (Fig. 32).

Diagnosis: (From illustrations only.) Very small skull, rectangular in dorsal aspect, with no mid-nasal ridge, but very prominent nasal bosses; postorbitals very short; caniniform processes enlarged and cylindrical.

(i) *Rhinodicynodon gracile* Kalandadze, 1970.

- (i) Dinodontosauridae *incertae sedis*.

(i) *Zambiasaurus submersus* Cox, 1969.

Diagnosis: This taxon was established on some immature skull fragments which show it to be tuskless, but with a blunt snout and low, broad parietal crest; short postorbitals and no preparietal or mid-nasal ridge. Its final placing will depend on the recovery of better material.

3. Subfamily III *Stahleckerinae non sensu* Lehman, 1961

Diagnosis

Large skulls of advanced morphology and of Upper Triassic age; tuskless, or with reduced tusks and small caniniform processes; usually a single low ridge on snout, which may be pointed, though less so than in *Kannemeyeria*; parietal crest variably developed; postorbital processes short; preparietal may be absent; as far as our knowledge stands at present, they could be either kannemeyerine or dinodontosaurine descendants.

- (a) Genus *Stahleckeria* Huene, 1935 (Figs. 20, 33).

Diagnosis: Very large square skull with very short temporal fenestrae; no preparietal; no tusks; small caniniform processes; snout not markedly blunt; low mid-nasal ridge; reflected lamina of angular approaches lateral articular condyle very closely; postorbital processes only moderately short.

(i) *Stahleckeria potens* Huene, 1935.

- (b) Genus *Ischigualastia* Cox, 1962 (Fig. 34).

Diagnosis: Large tuskless skull with slightly raised, broad parietal crest; substantial mid-nasal ridge, narrow rounded snout; postorbitals well separated from squamosals; occiput semi-circular in outline; tabulars probably absent; quadrate foramen absent; reflected lamina of angular contacts lateral condyle of articular; acromial process apparently absent from scapula; coracoid foramen on dorsal edge of precoracoid; femur with markedly offset caput.

(i) *Ischigualastia jenseni* Cox, 1962.

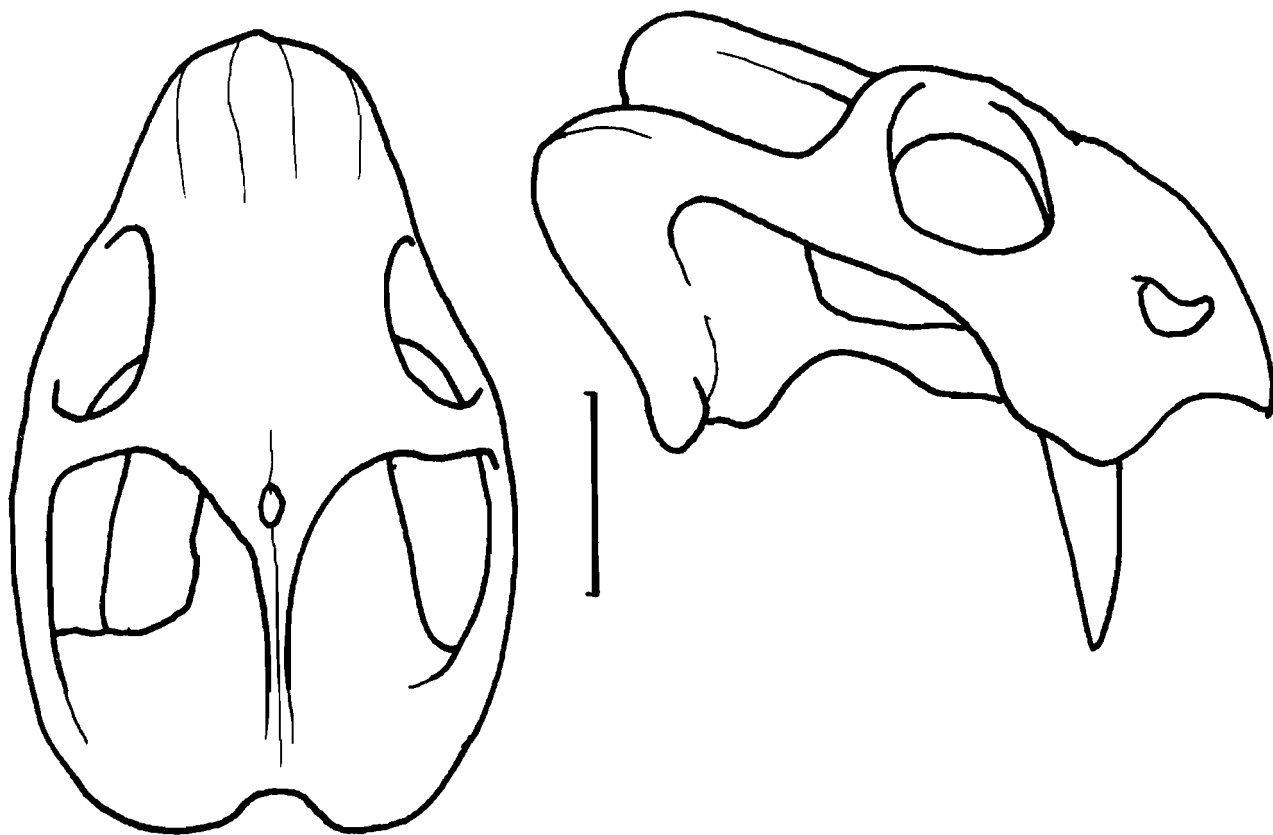


Figure 29
Shansiodon skull in two views. Scale is 5 cm.

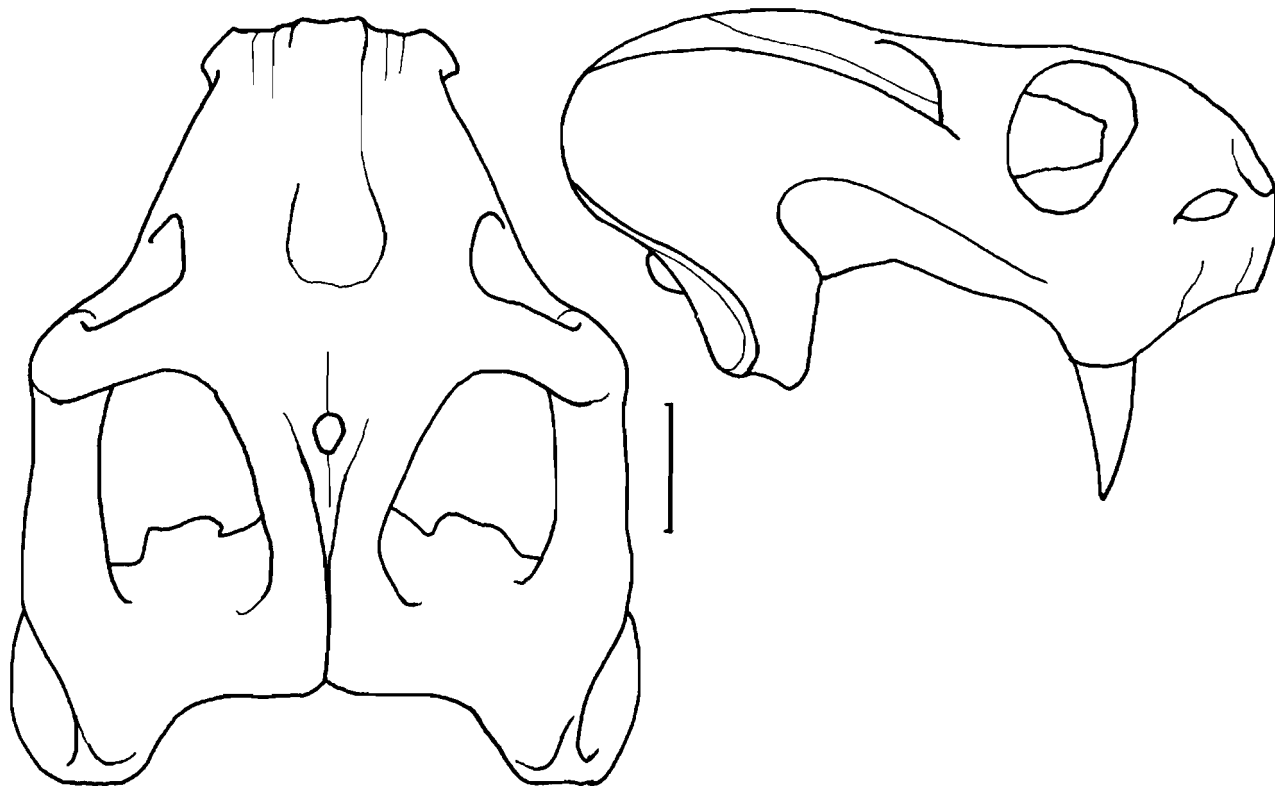


Figure 30
Tetragonias skull in two views. Scale is 5 cm.

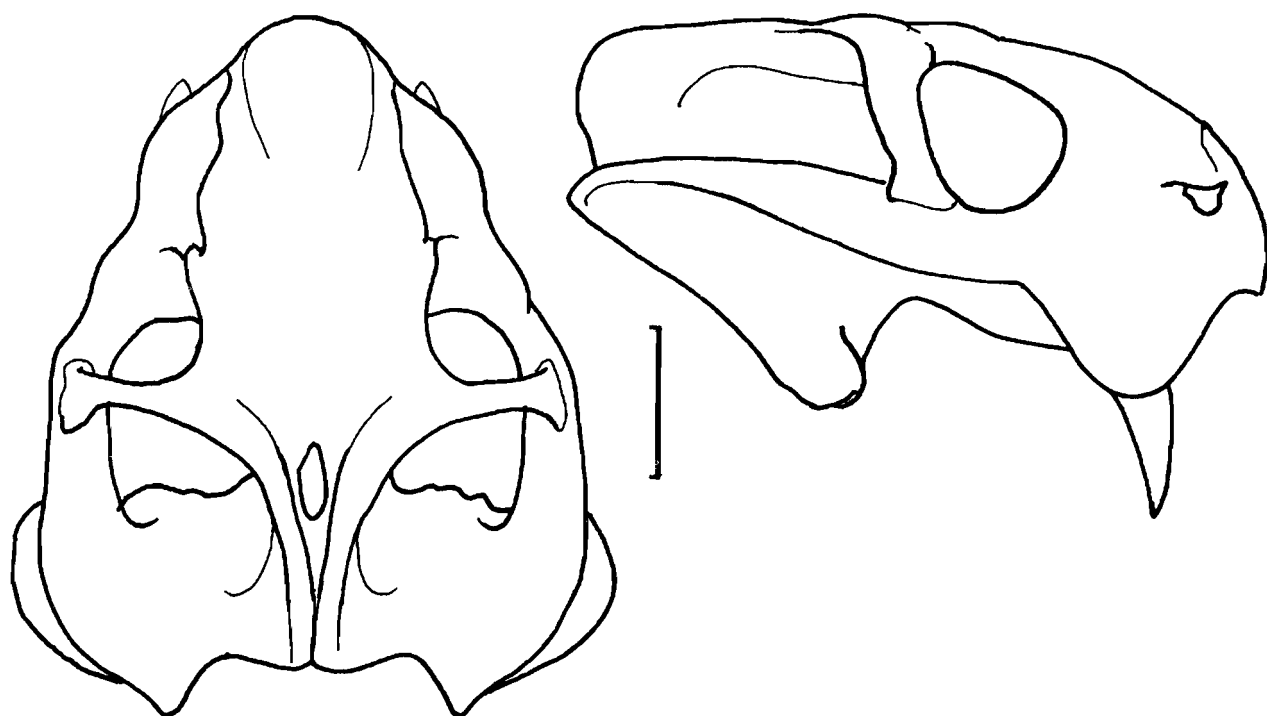


Figure 31
Vinceria skull in two views. Scale is 5 cm.



Figure 32
Rhinodicynodon skull in two views. Scale is 5 cm.

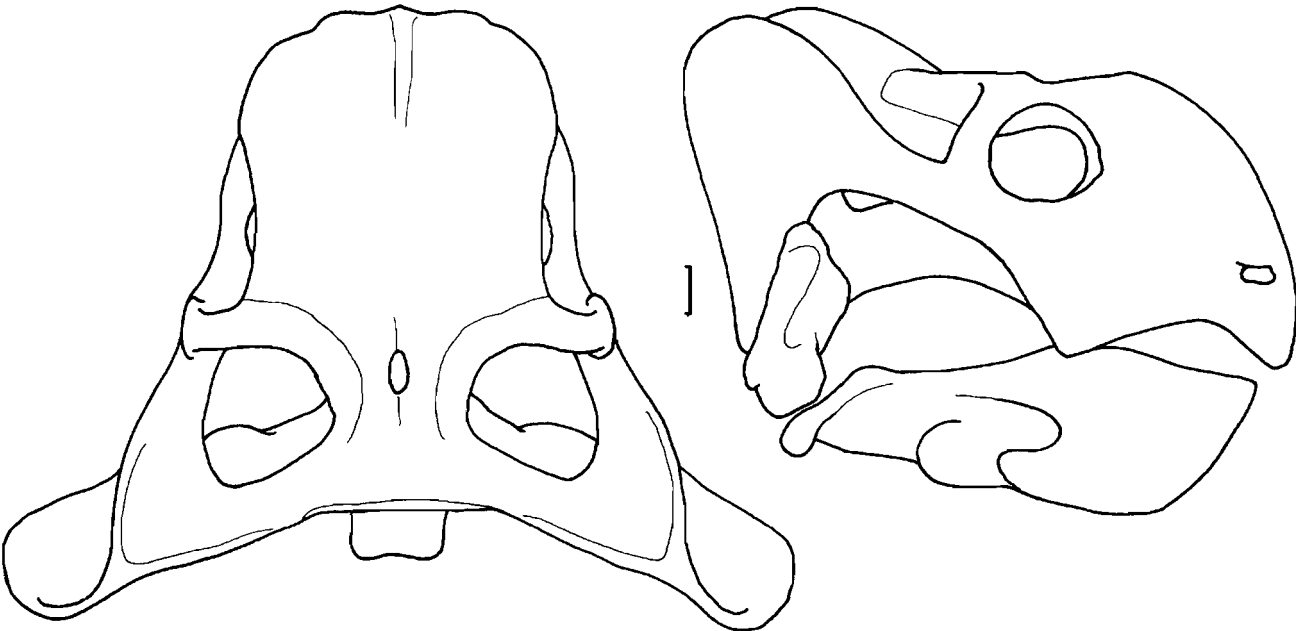


Figure 33
Stahleckeria skull in two views. Scale is 5 cm.

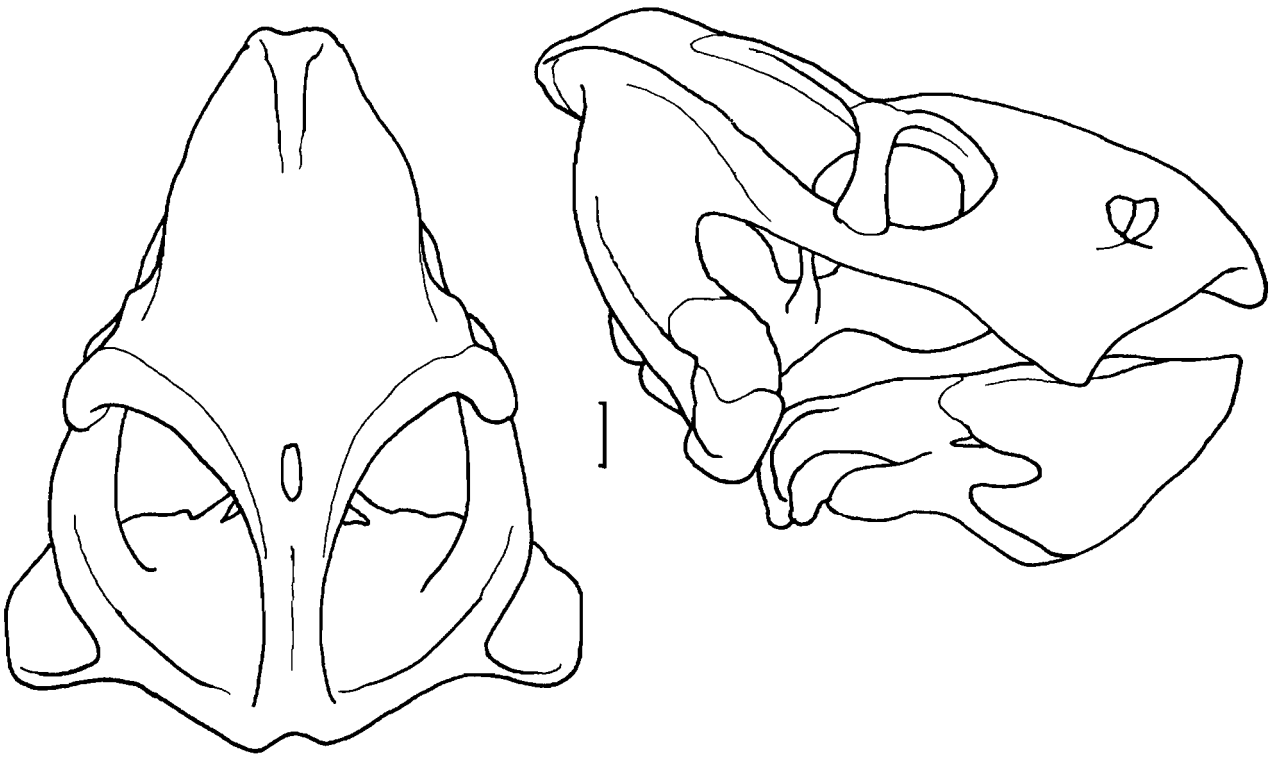


Figure 34
Ischigualastia skull in two views. Scale is 5 cm.

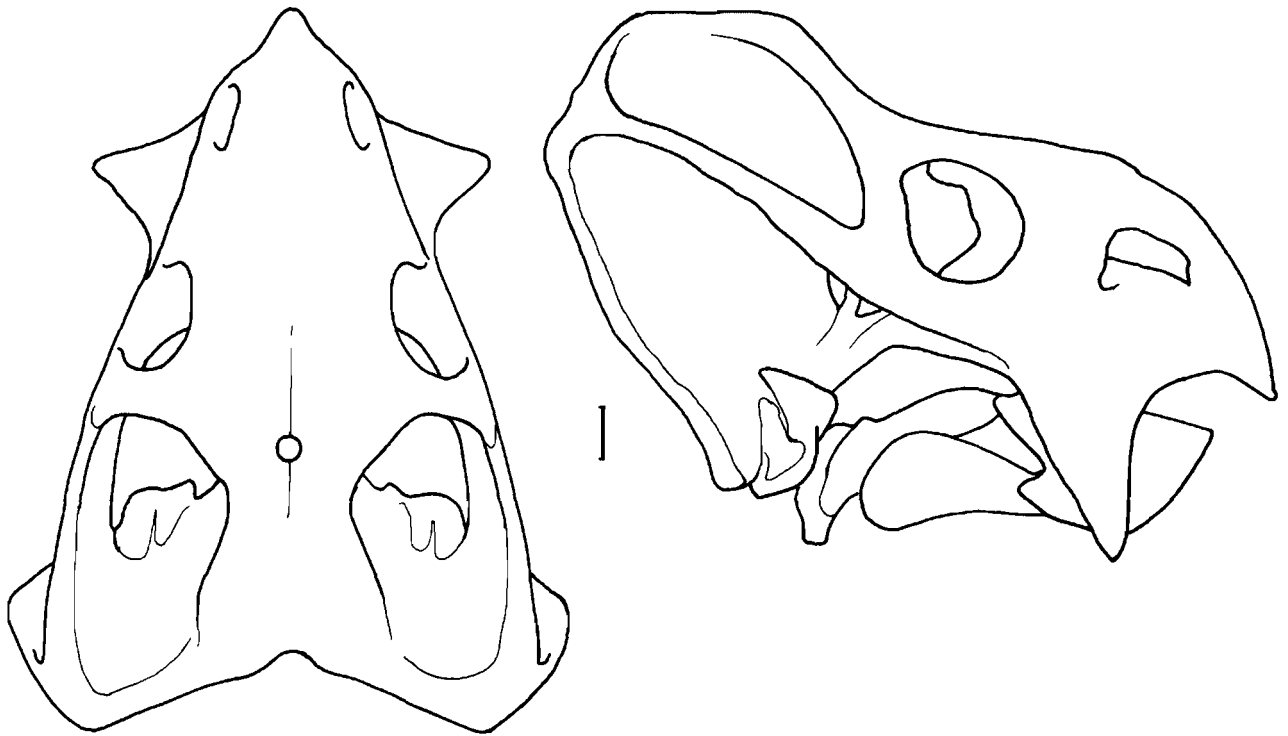


Figure 35
Placerias skull in two views. Scale is 5 cm.

(c) Genus *Placerias* Lucas, 1904 (Fig. 35).

Diagnosis: Large skull with sharp snout running into nasals of inverted "V" shape in cross section; prominent blade-like caniniform processes containing very reduced canines; parietal crest moderately high and convex dorsally; parietal processes of postorbitals short, reaching only to the level of the pineal foramen.

(i) *Placerias hesternus* Lucas, 1904 — Type species.

(ii) *Placerias gigas* Camp and Welles, 1956.

Diagnosis: Differences between these two species are pointed out in the main body of this contribution.

(d) Genus *Barysoma* Cox, 1965.

Diagnosis: Large skull, incompletely known, but believed to be closely related to *Ischigualastia*; occiput semi-circular in outline with similar parietal crest; acromial process present on scapula; limb bones much larger than in *Ischigualastia*.

(i) *Barysoma lenzii* (Romer and Price), 1944.

Synonym — *Stahleckeria lenzii* Romer and Price, 1944.

4. Subfamily IV *Jachelerinae* Keyser, 1974**Diagnosis**

Large forms with lower jaw symphysis having a very long flat profile; quadrate has a pterygoid process; not yet well enough known for any further diagnostic observations.

(a) Genus *Jacheleria* Bonaparte, 1971 (Fig. 36).

Diagnosis: Posterior region of temporal arches higher than the very long narrow parietal bar which does not form a high crest; temporal arches very slender.

(i) *Jacheleria colorata* Bonaparte, 1971.

(ii) *Jacheleria platygnathus* (Cox), 1968.

Synonym — *Dinodontosaurus platygnathus* Cox, 1968.

Diagnoses: Differences between these two species are pointed out in the main body of this contribution. This poorly known group is erected to accommodate Triassic dicynodonts with a pronounced pterygoid process of the quadrate. Such a process is also found in *Platycyclops* (*Rhachiocephalus*?) *crassus* Broom (Keyser, 1974), which could indicate that these rare forms may represent a separate lineage of familial status, descended from the Cryptodontia of the Beaufort Group.

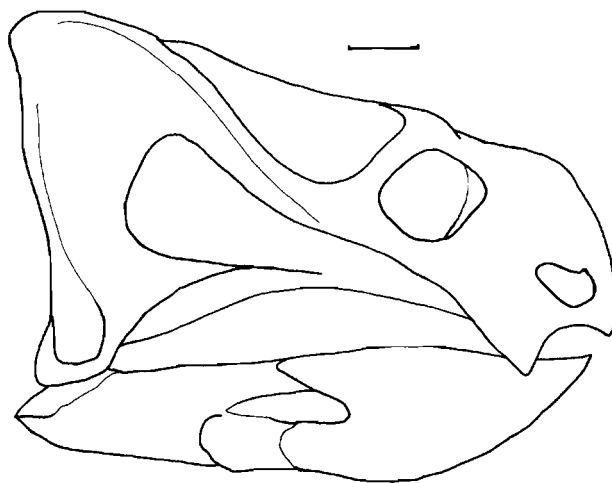


Figure 36

Jacheleria skull in lateral view. Scale is 5 cm.

B. Triassic *Dicynodontia Incertae Sedis*(a) Genus *Elephantosaurus* Vjushkov, 1969.

Diagnosis: Large skull represented by a fragment of the interorbital region, distinguishable from all Kannemeyeriids by the exceptional thickness of the skull bones; believed by Vjushkov to be closest to *Stahleckeria*.

(i) *Elephantosaurus jachimovitschi* Vjushkov, 1968.

C. Other *Dicynodontia* of Triassic Age(a) Genus *Lystrosaurus* Cope, 1870 (Fig. 37).

Diagnosis: Smaller, earlier, evidently amphibious form, highly specialised with a ventrally prolonged snout inclined virtually at right angles to the skull; terminal phalanges broadly flattened; ilia peculiarly notched. A total of 32 species had thus far been des-

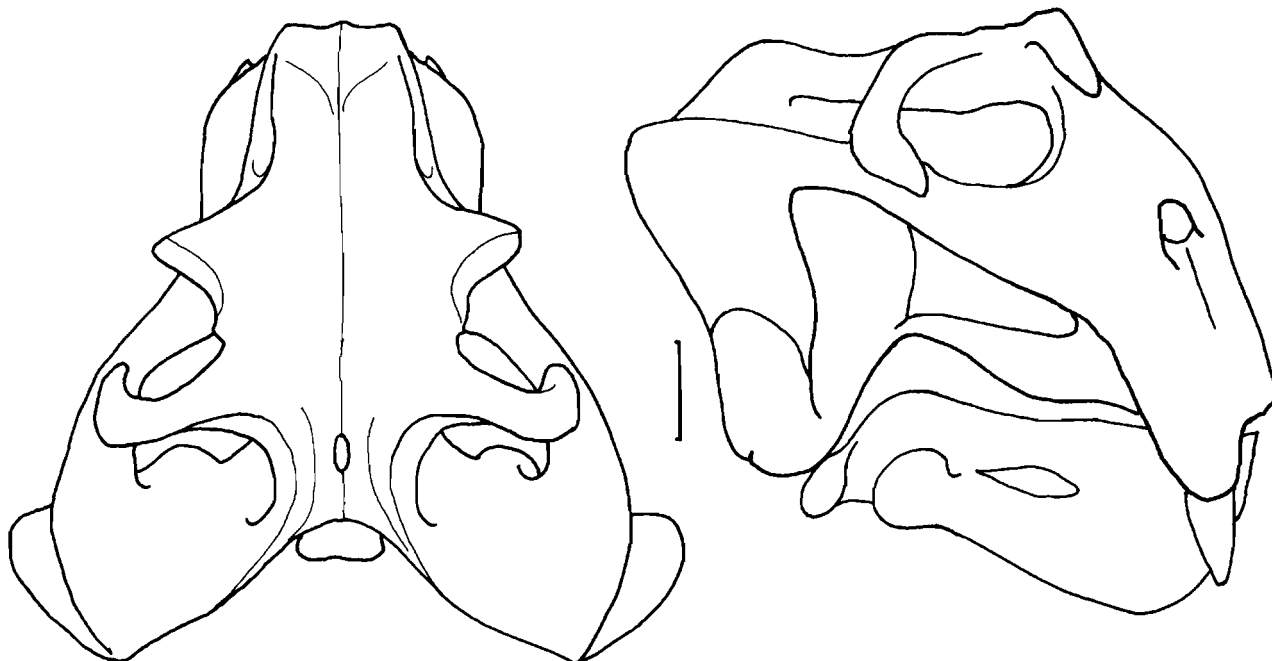


Figure 37

Lystrosaurus skull in two views. Scale is 5 cm.

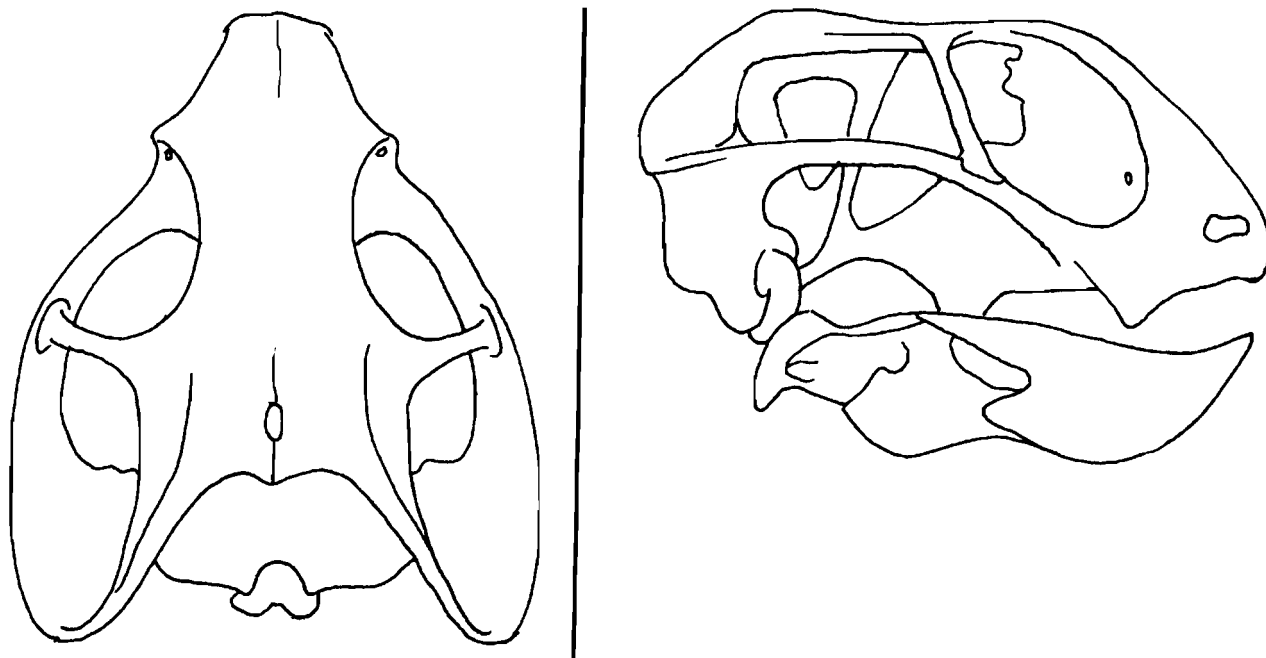


Figure 38
Myosaurus skull in two views. Scale is 5 cm.

cribed under this genus (two under the junior synonym *Prolystrosaurus*), some species having originally been introduced under preoccupied or superfluous generic names like *Ptychognathus*, *Ptychosiagum* and *Mochlorhinus*. Five of these 32 species occur outside the Karoo basin of South Africa in South and East Asia. After earlier attempts at synonymising some of the 27 South African species, Cluver (1971) succeeded in reducing them to nine. Possibly these nine species can be reduced even further to only four, bearing growth stages and sexual dimorphism in mind. The nine species recognised by Cluver could then possibly be synonymised as follows (A. S. Brink, pers. comm.):

- (i) *Lystrosaurus curvatus* (Owen), 1876.
Synonyms — *Lystrosaurus bothai* Broom, 1941.
Lystrosaurus oviceps Haughton, 1915.
Lystrosaurus rubidgei Broom, 1940.
- (ii) *Lystrosaurus declivis* (Owen), 1860.
- (iii) *Lystrosaurus murrayi* (Huxley), 1895.
- (iv) *Lystrosaurus platyceps* (Seeley), 1898.
Synonyms — *Lystrosaurus maccaigi* (Seeley), 1898.
Lystrosaurus putterilli (Van Hoepen), 1915.

To these can be added the Asian species:

- (v) *Lystrosaurus broomi* Young, 1939.
- (vi) *Lystrosaurus hedini* Young, 1935.
- (vii) *Lystrosaurus incicivum* (Repelin), 1932.
- (viii) *Lystrosaurus orientalis* (Huxley), 1865.
- (ix) *Lystrosaurus weidenreichi* Young, 1939.

Lystrosaurus and *Geikia* belong to the Family Lystrosauridae Romer, 1966.

- (b) Genus *Myosaurus* Haughton, 1917.
Diagnosis: Very small form known from one locality in the South African *Lystrosaurus* zone.
(i) *Myosaurus gracilis* Haughton, 1917 (Fig. 38).
Myosaurus (along with some other earlier forms) belongs to the Family Myosauridae Kitching, 1977.
- (c) Genus *Kombuisia* Hotton, 1974.
Diagnosis: A small form from the *Cynognathus* zone (uppermost Scythian) of South Africa.
(i) *Kombuisia frerensis* Hotton, 1974 (Fig. 39).
Kombuisia is a member of the family Dicynodontia Romer, 1966.

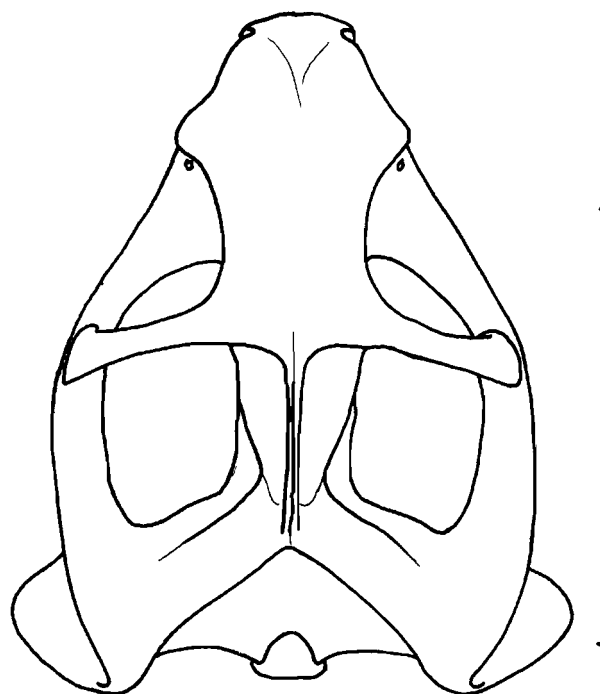


Figure 39
Kombuisia skull in two views. Scale is 5 cm.

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A. W. Keyser,
Geological Survey,
P.B. X112,
0001 Pretoria.

A. R. I. Cruickshank,
Bernard Price Institute for Palaeontological Research,
University of the Witwatersrand,
2001 Johannesburg.

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