

THE PANGAEA DICYNODONT *RECHNISAUROS* AND THE COMPARATIVE BIOSTRATIGRAPHY OF TRIASSIC DICYNODONT FAUNAS

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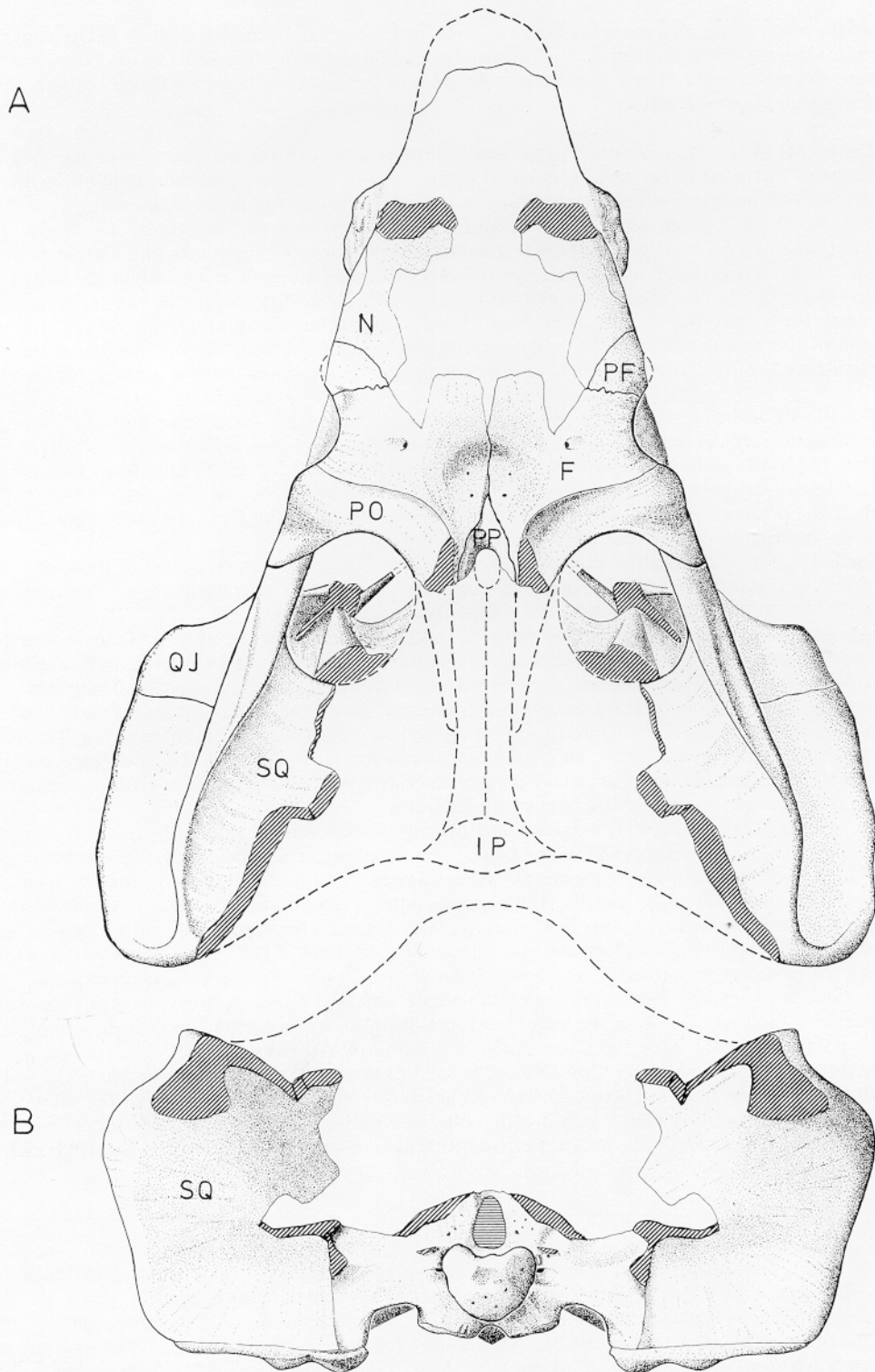
ABSTRACT. A dicynodont from the Triassic Manda Beds of East Africa is found to belong to the kannemeyeriid genus *Rechnisaurus*, first described from India, with which the genus *Shaanbeikannemeyeria* from China and Mongolia is congeneric. The divergent skull modifications of the Families Lystrosauridae and Kannemeyeriidae from the primitive Permian dicynodont skull morphology are explained in functional terms, both being adaptations to increase the length of the jaw adductor muscles. The kannemeyeriid pattern is similar to that of the ceratopsian dinosaurs, while that of the lystrosaurids seems also to be the result of feeding adaptations rather than suggesting semi-aquatic life. The relative ages of dicynodont-bearing Triassic faunas are reviewed in the light of recent changes in taxonomy and biostratigraphy.

THE Triassic Manda Beds of Tanzania were discovered by Stockley in 1930 (Stockley 1932), and his fossils were described by Haughton (1932). Further collections were made by both Parrington and Nowack in the 1930s. Study of this material showed that the fauna contained a large amphibian, the rhynchosaur *Stenaulorhynchus*, thecodontians, cynodonts, and dicynodonts (Haughton 1932; Huene 1938*a*, 1938*b*, 1942, 1950; Parrington 1946; Crompton 1955; Cruickshank 1965, 1967, 1986; Cox and Li 1983).

The British Museum (Natural History) and London University Joint Palaeontological Expedition to Northern Rhodesia and Tanganyika spent six weeks collecting in the Manda Formation in 1963 (Attridge *et al.* 1964), and 184 specimens of dicynodonts, cynodonts, rhynchosaurs, and thecodontians were collected from 27 localities. These localities are shown on the accompanying map (Text-fig. 1), which is based on a mosaic of aerial photographs and on survey work by the late Dr W. W. Bishop (then Curator of the Uganda Museum). Local villagers provided the names of the streams.

Bishop (1968) described the geology of the area. The Manda Formation is 2000 m thick, being a series of purple to chocolate-coloured mudstones interbedded with grey to whitish sandstones and grits of variable thickness and persistence. Though reptile bones were found from 150 m above the base of the Formation to 60 m below its top, 65% of the specimens collected were found in two levels, 1180 m and 1310 m above its base. Below the Manda Formation lies the 700 m thick Kingori Sandstone Formation, from which Cruickshank (1986) reports the dicynodont *Kannemeyeria*. Below the Kingori Sandstone lies the 275 m thick Kawinga Formation, and the base of the exposed sequence in the area is made up of the 535 m thick Ruhuhu Formation, in which the 1963 Expedition found a few specimens of endothiodont dicynodonts, some of which bore canine teeth lateral to the main maxillary tooth-row.

The dicynodont *Angonisaurus* from locality 12 in the Manda Formation has already been described (Cox and Li 1983). The present paper is concerned with a large dicynodont from this formation, and with its implications for the structure, classification, and comparative stratigraphy of Triassic dicynodonts.



TEXT-FIG. 2. *Rehnisaurus cristarhynchus*; BM(NH) R11955, $\times 0.2$. A, dorsal view, at right angles to interorbital area. B, occipital view. For abbreviations see Text-figure 3.

Tanzania, from the lower of the two main fossiliferous levels of the Manda Formation. Much of the skull was found lying on its ventral surface on the top of a low sandstone hillock. Many fragments of the dorsal surface had already been weathered off and had rolled down the sides of the hillock. They were found scattered over an area of a few hundred square metres.

Description. The whole of the snout anterior to the caniniform processes of the maxillae is missing, as is the dorso-median part of the snout as far back as the level of the front of the orbits, and the whole of the dorso-median part of the skull posterior to the pineal foramen and dorsal to the foramen magnum.

In dorsal view (Text-fig. 2A), the skull is 570 mm broad across the occiput, and tapers anteriorly. The preserved part of the skull is 590 mm long, but the original length was probably about 650 mm. The interorbital region is broad. There is a depression in the postero-median region of the frontals, behind which the bone rises steeply to form the beginning of a high intertemporal bar. The lateral walls of the depression are formed by ridges which mark the junction of the postorbital and frontal, and which curve antero-laterally, dying out towards the root of the post-orbital bar. There is no trace of a postfrontal bone. The preparietal forms the lateral and anterior walls of the pineal foramen, and tapers anteriorly to a sharp point projecting between the frontals.

The lateral walls of the pineal foramen diverge posteriorly, suggesting that these surfaces extended posteriorly as the inner surfaces of a pair of ridges along the intertemporal bar, which would then have had a median groove. The width of the posterior end of the postorbital bone, which extends laterally as a wing from the more median bones, suggests that the anterior part, at least, of the intertemporal bar, was quite wide. The ventral surface of the posterior ends of the postorbital bones are at a sharp angle to the interorbital region, indicating that the intertemporal bar rose abruptly postero-dorsally.

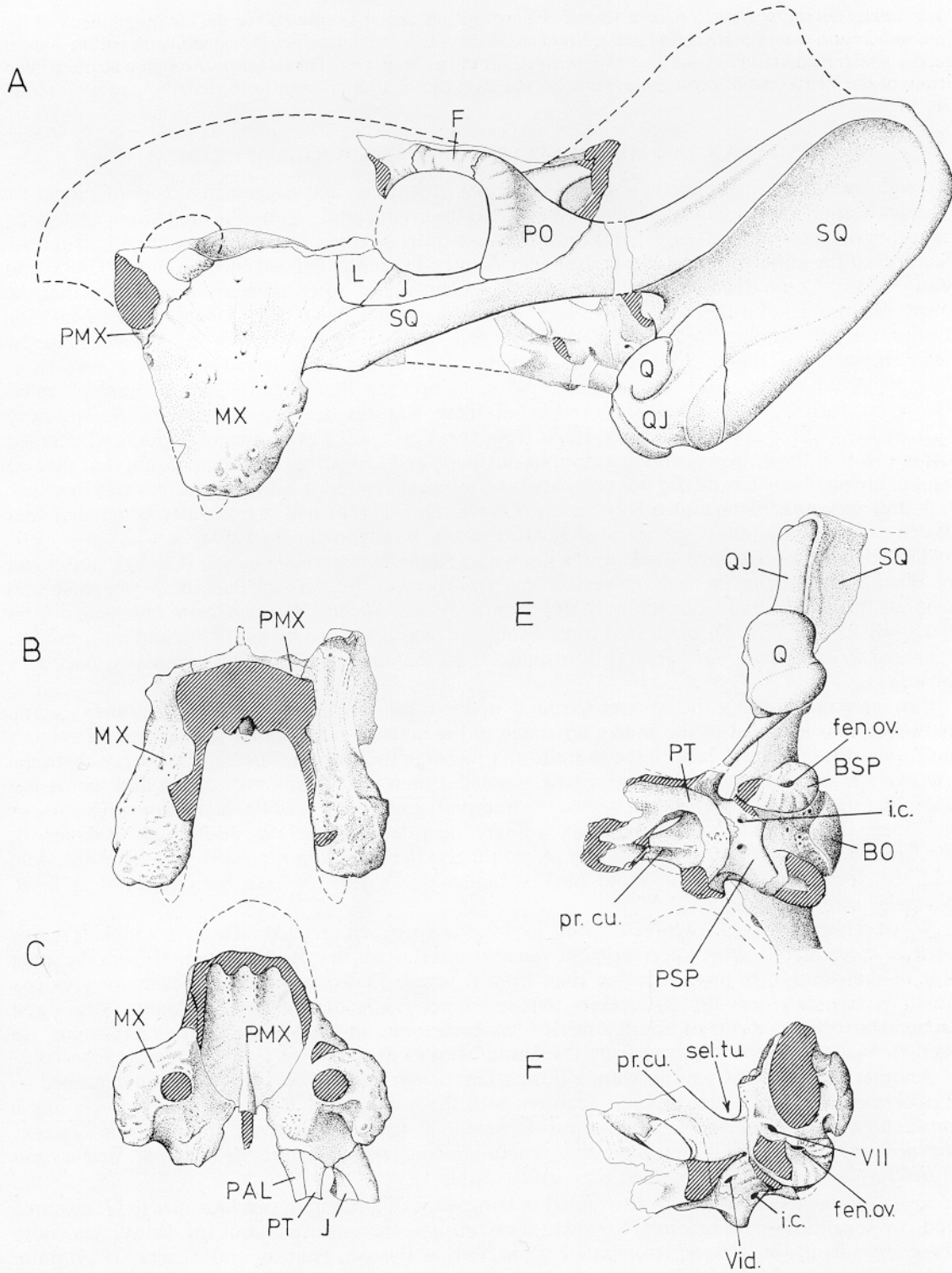
The dorso-medial region of the occiput is missing (Text-fig. 2B). The ventro-lateral corner of the squamosal extends a considerable distance lateral to the quadrate condyles. As is usually the case in large vertebrates, the foramen magnum is small in comparison with the size of the occipital condyle.

The nasal region of the snout has been crushed ventrally, and is not shown in lateral view (Text-fig. 3A). The suspensorium extends at a great angle antero-ventrally and runs smoothly into the zygomatic arch. The lower end of the post-orbital bar therefore lies not far antero-dorsally from the quadrate condyle. There is a deep pit between the main body of the quadrate and the quadratojugal, above the lateral quadrate condyle, which may have been the attachment area for a ligament restricting the anterior movement of the lower jaw. The outer surface of the posterior end of the zygomatic arch is concave dorso-ventrally. The ventral edge of the zygomatic arch below the orbit is quite sharp. The squamosal extends anteriorly to overlie the outer surface of the maxilla as far forwards as the posterior edge of the base of the caniniform process.

The secondary palate (Text-fig. 3B, C) is long and narrow, with almost vertical side walls. It is very deep, its surface lying 125 mm above the ventral end of the caniniform processes. The moderately-sized tusk emerges from the inner surface of the caniniform process, not from its apex. A rugose area extends dorsally from the root of the tusk on the inner side of the maxilla. The posterior edge of the caniniform process extends postero-laterally as a massive, rugose flange. Further posteriorly, a large foramen between the jugal, the maxilla, and the pterygoid runs dorsally into the maxillary antrum surrounding the base of the tusk. The mid-region of the palate, posterior to this point and anterior to the region around the interpterygoid vacuity, is missing.

The quadrate condyles (Text-fig. 3E) are orientated in an antero-medial direction; this area is not distorted, and this feature raises questions as to how the lower jaw functioned, since it is normally presumed to have had a simple antero-posterior sliding/rotating movement (e.g. Crompton and Hotton 1967). The interpterygoid vacuity (or fenestra medio-palatinalis, see Cox 1968, p. 13) and basicranial axis are well-preserved. The whole basicranial axis is greatly shortened. There is therefore only a very short median contact of the pterygoids behind the fenestra; this region is raised into a transverse, ventrally-projecting ridge, which lies only just anterior to the basisphenoid tubera. The internal carotid foramina can be seen piercing the parasphenoid. A

TEXT-FIG. 3. *Rechnisaurus cristarhynchus*; BM(NH) R11955, $\times 0.2$. A, lateral view. B, anterior view of snout. C, palatal view of snout. D, ventral view of basis cranii and quadrate region. E, lateral view of braincase. Abbreviations: BO, basioccipital; BSP, basisphenoid; F, frontal; IP, interparietal; J, jugal; L, lacrimal; MX, maxilla; PAL, palatine; PF, prefrontal; PMX, premaxilla; PO, postorbital; PSP, parasphenoid; PT, pterygoid; Q, quadrate; QJ, quadrato-jugal; SQ, squamosal; fen.ov., fenestra ovalis; i.c., internal carotid foramina; pr.cu., processus cultriformis of parasphenoid; sel.tu., sella turcica; Vid., Vidian canal; VII, foramen for facial nerve.



little antero-dorsal to these, a pair of foramina on either side are the openings for the anterior branch of the internal carotid artery and for the palatal branch of the VIIth cranial nerve; they open from within a short recess, which is therefore a truncated Vidian canal (Text-fig. 3E, F, i.c.). The foramen through which the main trunk of the VIIth cranial nerve exits from the braincase can be seen anterior to the fenestra ovalis (Text-fig. 3F, VII).

THE TAXONOMIC POSITION OF THE MANDA SPECIMEN

Though the skull is incomplete, it shows a number of features that suggest its taxonomic identity. The acute angle between the intertemporal bar and the interorbital region, the moderately elongated snout with a median nasal ridge, and the antero-ventrally directed suspensorium, are all diagnostic features of the kannemeyeriid dicynodonts, as slightly differently defined by Cox and Li (1983) and King (1988). Comparisons between the Manda specimen and other kannemeyeriids show that the most obvious similarities are with *Shaanbeikannemeyeria* Cheng, 1980, from the Er-Ma-Ying Formation of China. Both have wedge-shaped skulls, strong rugose maxillae, a narrow intertemporal bar that nevertheless has a slight median longitudinal groove, and a very short interpterygoid vacuity and median pterygoid neck between that vacuity and the parasphenoid. However, further comparison shows that all these features are present also in *Rechnisaurus* (Chowdhury 1970; Bandyopadhyay 1989) from the Yerrapalli Formation of India, and detailed comparison of the drawings and descriptions of Cheng and Chowdhury leave no doubt that the two genera are identical. Cheng did not compare his Chinese dicynodont with Chowdhury's 1970 genus, but that was possibly because Keyser and Cruickshank (1979) had erroneously concluded that *Rechnisaurus* was a junior synonym of *Kannemeyeria* (Bandyopadhyay 1989).

The Chinese species must therefore be known as *Rechnisaurus xilougouensis* (Cheng), and it can be distinguished from the Indian species, *R. cristarhynchus*, by the fact that the premaxillae and frontals project medially into the frontals. A third species, *Shaanbeikannemeyeria buerdongia* from the lower Er-Ma-Ying Formation of Inner Mongolia, was described by Li (1980), and must now be renamed *Rechnisaurus buerdongia* (Li); it differs from the other species in having smaller maxillary processes.

The incompleteness of the African specimen makes it difficult to compare with the other species. However, it is identical to the Indian specimen in the unusual feature that the squamosal extends far forwards to reach the base of the caniniform process of the maxilla. The only differences between the two specimens are that the canine tusk is smaller than in the Indian specimen and that it has a strong ridge around the posterior rim of the interpterygoid vacuity, while the Indian species shows no ridge. The Manda specimen is accordingly regarded only as an additional specimen of *Rechnisaurus cristarhynchus* Chowdhury. Accordingly, the missing postero-dorsal part of the skull and the dorsal outline of the snout in Text-figures 2A, B and 3A have been restored as in *R. cristarhynchus*.

When it was collected, two features of the Manda specimen recalled advanced kannemeyeriids such as *Placerias*: its short interpterygoid vacuity, and the fact that its tusk emerges from the inner side of the caniniform process rather than from its apex. This is probably the basis for Keyser's (1980, p. 62) statement that 'A species that resembles *Ischigualastia* from the Santa Maria and Ischigualasto Formations of South America has been found in the Manda Beds of Tanzania.' (In fact, *Ischigualastia* is not known from the Santa Maria Formation.)

Another dicynodont from the Manda Formation, *Sangusaurus* (Cox 1969) has been described by Cruickshank (1986). It shares many features with the holotype of *R. cristarhynchus*, including a small boss just posterior to the pineal foramen, a feature otherwise unknown in Triassic dicynodonts. It is possible that these two genera are congeneric, despite the fact that *Sangusaurus* is tuskless and has a more pointed premaxilla (Table 1).

Rechnisaurus was thus widely distributed in Pangaea, being found in two localities in Gondwana, and two localities in Asia, some 16,000 km away around the western end of the Tethys Sea. Both these areas lie in the Triassic temperate regions and, as Parrish, Parrish, and Ziegler (1986) point out, no Lower or Middle Triassic therapsids have been found between palaeolatitudes 35° N and

35° S, in the tropical regions. The absence of *Rechnisaurus* from this intermediate belt of latitudes is thus merely part of a more general pattern. The presence of species of that genus both north and south of this tropical band shows that this therapsid, at least, was able to traverse this area. The absence of fossils therefore suggests that conditions there were unsuitable for fossilization, rather than that therapsids did not inhabit these regions. A similar pattern of absence of Triassic tetrapod fossils in general from an equatorial band of latitudes has already been documented (Cox 1973a).

TABLE 1. Cranial features of kannemeyeriid dicynodonts.

	IT/IO at angle	Quadrate forwards	Strong maxilla	Tusks	Midnasal ridge	Blunt snout	Wedge- shaped skull
<i>Kannemeyeria</i>	+	-	+	+	+	+	+
<i>Rechnisaurus</i>	+	+	+	+	+	+	+
<i>Uralokannemeyeria</i>	+	+	+	+	+	+	+
<i>Rabidosaurus</i>	+	+	?	+	+	-	?
<i>Sangusaurus</i>	+	+	+	+	+	?	+
<i>Wadiazaurus</i>	+	+	±	±	+	+	-
<i>Ischigualastia</i>	+	+	-	-	-	-	+
<i>Jachaleria</i>	+	+*	-	-	-	-	+
<i>Placerias</i>	+	+	+	+	-	-	+
' <i>Moghreberia</i> '	+	+	+	+	?	-	+

+ = character present; - = character absent; ± = character present in some specimens, absent in others; ? = character unknown; * = see text; IT = intertemporal bar; IO = interorbital bar.

The relationships of Rechnisaurus. *Rechnisaurus* shows a number of features that appear to a greater or lesser extent in several other Triassic dicynodonts (Table 1): pronounced angulation between the intertemporal bar and the frontal region, pointed out by King (1988); an antero-ventrally directed suspensorium; a strong maxilla, usually bearing a tusk and with a rugose antero-ventral flange; a median nasal ridge; a skull that is wedge-shaped in dorsal view, and a bluntly pointed snout. The Family Kannemeyeriidae of Cox and Li (1983) begins with the Early Triassic *Kannemeyeria*, in which the suspensorium is directed ventrally. It continues with a number of Middle Triassic genera (*Rechnisaurus*, *Uralokannemeyeria*, *Rabidosaurus*, *Sangusaurus*, *Wadiazaurus*), in which the suspensorium is directed more antero-ventrally. In all these genera the snout is bluntly pointed and bears a median dorsal nasal ridge. In *Wadiazaurus* and in the Late Triassic genera (*Ischigualastia*, *Jachaleria*, *Placerias*, '*Moghreberia*'), the snout has become pointed and lacks this ridge. In the tuskless members of the group (*Jachaleria*, *Ischigualastia*) the maxilla is, not surprisingly, less well-developed than in the remaining genera - a correlation between these two features is strongly supported by the fact that, in *Wadiazaurus*, some specimens (presumably male) are tusked and have a strong maxilla, while others (presumably female) are tuskless and have a poorly developed maxilla (Bandyopadhyay 1988). (The poorly preserved skull of *Moghreberia* Dutuit, 1980 seems so similar to that of *Placerias* Camp and Welles, 1956 that these two genera may well prove to be identical, while the few fragments of *Azarifeneria* Dutuit, 1989 are very similar to the corresponding portions of *Ischigualastia* Cox 1965.)

King has recently (1988) provided a new classification of Triassic dicynodonts, which differs in several respects from that of Cox and Li (1983). As she rightly comments (King 1988, p. 69), 'Until a complete revision of the Middle and Late Triassic material, using first-hand information, is undertaken, no absolute consensus of opinion on their relationships can be expected.' A difference between the two classifications is that King separates *Ischigualastia* and *Placerias* from the kannemeyeriids, and links them more closely with the *Zambiasaurus-Stahleckeria* group. This is

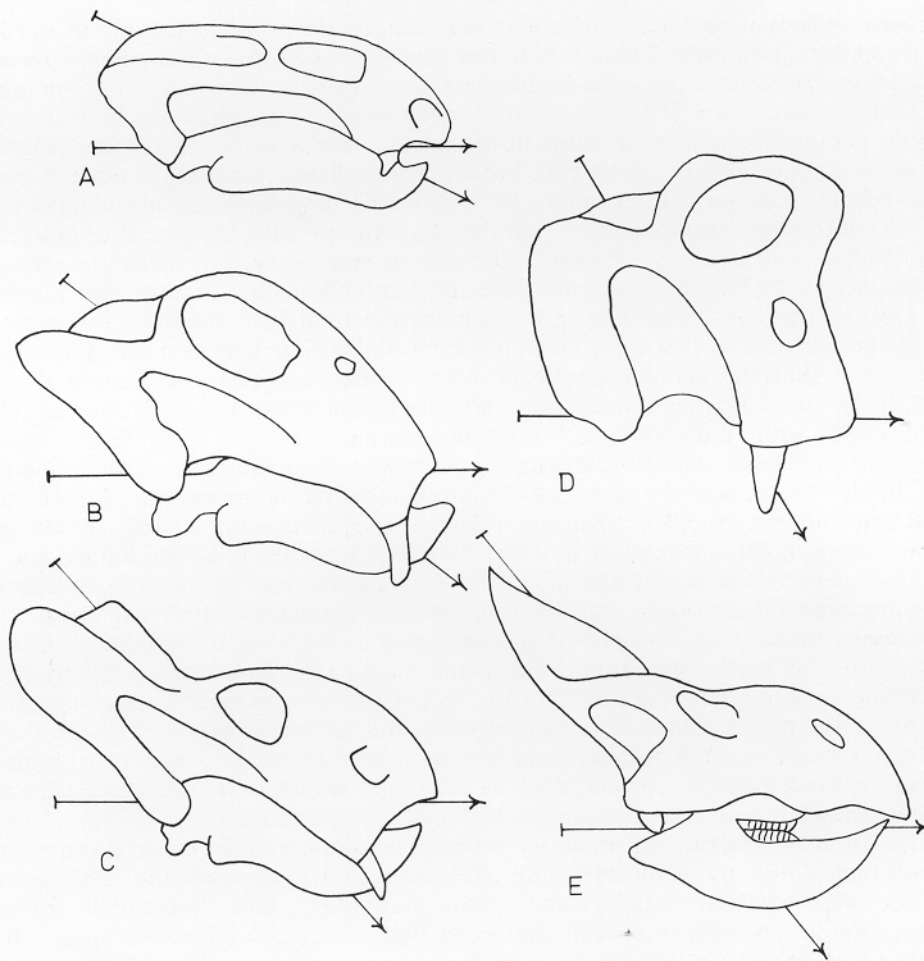
despite the great difference between the shapes of the occipital plates and snouts of these two groups (Cox 1965), and despite the fact that it is then necessary to suggest that a long, high intertemporal bar at an angle to the frontal region evolved independently in the *Kannemeyeria* group and in the *Placerias* group.

The feature that unites the *Placerias* group to the *Stahleckeria* group (and also to the *Sinokannemeyeria* group) in King's (1988) cladogram is that the parietals are covered incompletely by the postorbitals. She here refers to a condition in which the postorbital did not extend as far posteriorly as the parietal-interparietal suture, so that the posterior parts of the parietals are exposed in the skull roof. King (1990, p. 225) defines the character as merely 'Postorbitals do not extend far posteriorly'. This is indeed true of *Ischigualastia* and *Placerias*. But in *Stahleckeria* the posterior extent of the postorbital is uncertain: Huene reconstructs it as extending posteriorly to meet the squamosal in his skull no. 2 (Huene 1935, pl. 5), but Camp's (1956, fig. 45) drawings of a cast of the same specimen show a short postorbital. In her diagnosis of the genus *Stahleckeria* King (1988, pp. 107–108), makes no statement on this character. In the other stahleckeriid genus, *Zambiasaurus*, the postorbital appears to have extended back as far as the junction between the parietal and the interparietal (Cox 1969). The posterior parts of the parietal are indeed exposed in all of these genera, but this would be true irrespective of the posterior extent of the postorbital, because the latter bone is lateral to the wide parietal, rather than dorsal to it.

According to King (1988, 1990), the features of the postorbital and parietal mentioned above are found in the *Sinokannemeyeria* group (which includes also *Parakannemeyeria*, *Uralokannemeyeria*, *Dinodontosaurus*, and *Rhadiodromus*), as well as in the *Placerias* and *Stahleckeria* groups. However, though the postorbital does not extend far posteriorly in *Dinodontosaurus*, it does so in *Sinokannemeyeria* and *Parakannemeyeria* (Sun 1963) and *Uralokannemeyeria* (Danilov 1971); the situation in *Rhadiodromus* (Kalandadze 1970) is uncertain. The posterior part of the parietal is widely exposed in all these genera except *Parakannemeyeria*, but this 'genus' may merely consist of skulls of *Sinokannemeyeria* that have been compressed laterally, those of the latter genus having instead been compressed dorso-ventrally. *Sinokannemeyeria* has a wide snout, with canine teeth set wide apart and projecting backwards, a wide intertemporal bar between the postorbitals, and a low, wide occiput. *Parakannemeyeria* has a narrow snout, with canine teeth set close together, a narrow intertemporal bar covered by the postorbital bones, and a high, narrow occiput. These are exactly the differences that might be expected if the two sets of skulls had been affected by the two different types of plastic deformation that would have resulted from the different orientations of deposition. The two genera are both from the Er-Ma-Ying Formation of China (Sun 1963, 1989b).

The exposure of the parietal, which King does not mention in her (1990) list of taxonomic characters, thus appears in this case to be more reliable than the degree of posterior elongation of the postorbitals, which she retains as a character. But such an osteological detail has no obvious adaptive value in itself, and may arise from quite different skull shapes. For example, the parietal is likely to be exposed if the intertemporal bar is extended postero-dorsally into a crest, far away from the centres of ossification of the postorbitals. But it is also likely to be exposed if the intertemporal bar is very wide, as in *Lystrosaurus*. It is therefore preferable to try to identify the underlying adaptive changes that may in turn have led to the appearance of these features. In the case of the postero-dorsal extension of the intertemporal bar, one of the features that unites the *Placerias* group with the kannemeyeriid group, this change seems to involve a fundamental change in the jaw muscle system, to meet an adaptive need that *Lystrosaurus* achieved in a different way, as follows.

Most Permian dicynodont genera have a long, low skull, in which the intertemporal-interorbital bar, like the zygomatic arch and the palatal surface, are parallel with one another. The posterior edge of the maxilla and the suspensorium leading down to the palate are also parallel to one another, but run antero-ventrally. In the Permian dicynodont *Emydops* (Crompton and Hotton 1967), the adductor muscles run at a shallow angle (c. 35°) down to the lower jaw because of the long, low skull. The horizontal component of their action is therefore much stronger than the vertical component, and there is little vertical bite force (Text-fig. 4A). Extra attachment surface for



TEXT-FIG. 4. Lateral views of skulls of A, *Emydops*; B, *Lystrosaurus ?murrayi*; C, *Rechinisaurus cristarhynchus*; D, *Lystrosaurus mccaigi*; E, *Protoceratops*. Axes indicate direction of action of adductor internus jaw muscles from postero-lateral corner of temporal vacuity, and jaw axis from quadrate condyle along surface of palate. The distances between the anterior surfaces of the quadrate condyles and the anterior end of the snout are the same in drawings A-C and E. (A and B, after Crompton and Hotton 1967; C, skull after Cheng 1980, lower jaw from *Kannemeyeria* after Camp 1956; D, after Brink 1952; E, after Dodson 1976.)

the inner portion of the adductor muscles is provided by the postorbital bones extending as wings projecting laterally from the intertemporal bar.

In *Lystrosaurus* (Text-fig. 4B), a greater vertical component to the action of the adductor muscles has been achieved by shortening of the skull, as noted by Cluver (1971). In order not to reduce the length of these muscles, which would have reduced the gape, the whole palatal structure has been moved antero-ventrally, paralleled by a similar antero-ventral extension of the suspensorium. The whole muscle mass is now at a steeper angle to the palatal surface (*c.* 50°), and is therefore accommodated in a more vertically-orientated column, and the temporal vacuity is shorter. Because the palate has extended anteriorly, the snout in contrast is longer as well as deeper. Postorbital wings still project laterally from the intertemporal bar.

The resulting skull morphology, in which the orbit and nostril remain dorsally placed, has been likened to that of a hippopotamus, and it has therefore been suggested that *Lystrosaurus* was semi-

aquatic (Broom 1902; Watson 1912). Though, in the specimen described by Crompton and Hopson (1967), which appears from their illustrations to be a specimen of *Lystrosaurus murrayi*, the external nostril is at the level of the ventral edge of the orbit, that of *Lystrosaurus mccaigi* is placed below the orbit (Text-fig. 4D). Brink (1951) states that there was a groove running dorsally from the postero-dorsal margin of the external naris in this species, and suggests that fleshy nostrils were directed upwards to open in front of the eyes, but the morphology is certainly not clearly indicative of semi-aquatic life. The jaw muscles in *L. mccaigi* would have been the most dorso-ventrally directed (*c.* 60°) of those of any dicynodont. They would therefore have been the most powerful and, as Watson (1912) comments in the context of the massiveness of the jaws of *Lystrosaurus*, this is difficult to reconcile with the softness of most aquatic plants. Watson also notes that the powerful sacrum of *Lystrosaurus* is surprising in an aquatic animal (though it would not be as surprising in a semi-aquatic animal that had to support its weight on land for long periods). Earlier, Broom (1903) had stated that the shoulder-girdle of *Lystrosaurus* was different from that of other dicynodonts in having a smaller interclavicle and a larger sternum. He suggested that this was somehow correlated with an aquatic life, but did not explain this.

Nothing indicates that the earlier or later dicynodonts were semi-aquatic, so *Lystrosaurus* would represent a brief, unique aquatic excursion. It would also be surprising to find this unusual environment suddenly very widespread in the world at the time of *Lystrosaurus*, for the genus is known from deposits in Africa, Antarctica, India, European Russia, and China. King (pers. comm. 1989; 1991) has come to the same conclusion, that *Lystrosaurus* was not aquatic, independently. None of the arguments is conclusive, but they suggest that the matter requires re-evaluation.

Kannemeyeriids appear to have achieved an orientation of the adductor muscles similar to that of the lystrosaurids, but partly by an antero-ventral movement of the palate and partly by a postero-dorsal extension of the intertemporal bar (Text-fig. 4C). The adductor muscle mass now runs at an angle of *c.* 50° to the palate, and almost parallel to the intertemporal bar. As a result, the lateral postorbital wings to the intertemporal bar are lost, because they are no longer at an appropriate angle to provide attachment for the adductor muscles, and would have obstructed the access of these muscles to the more postero-dorsal part of the intertemporal bar.

Chrulaw (1976) noted the general similarity between the skull architecture of dicynodonts and that of ceratopsian dinosaurs, comparing only *Dicynodon* and *Lystrosaurus* with *Triceratops*, in which the parieto-squamosal 'frill' extends more posteriorly than horizontally. The skull architecture of kannemeyeriids is instead similar to that of the primitive ceratopsian dinosaur *Protoceratops* (Text-fig. 4E). In that genus, as in the kannemeyeriids, the skull is postero-dorsally extended to provide a greater length for the jaw muscles (Haas 1955; Ostrom 1966) which run at about 50° to the axis of the lower jaw, and there is a narrow, horny beak on the anterior end of both the upper and lower jaws. In the ceratopsians, however, there is a battery of cutting teeth posterior to the beak, and later ceratopsians developed a coronoid process and a greatly elongated posterior 'frill' to the skull to improve the mechanics of the use of this posterior dentition. Ostrom (1966) suggests that this system, in which only antero-posterior jaw movements were possible, was particularly adapted for chopping up fibrous food, and that the Late Cretaceous ceratopsians may have fed on the leaves of cycads and palms.

The kannemeyeriids thus appear to have an advanced feeding system, and it may be no coincidence that they survived (as the Late Carnian *Placerias* group) longer than any other dicynodont. These Late Triassic kannemeyeriids are also the only dicynodonts found in the Triassic tropics (cf. Parrish, Parrish and Ziegler 1986), and had a much more extremely pointed premaxilla than their earlier Triassic kannemeyeriid relatives. The stahleckeriids, by contrast, appear to have increased the area available for insertion of the jaw muscles mainly by lateral expansion of the squamosals, and had a very blunt anterior end to the premaxilla; it may also be no coincidence that this group became extinct during the Middle Triassic, perhaps because of competition from advanced rhynchosaurs and gomphodonts, or because of a diminution in their preferred plant food.

RELATIVE AGES OF THE TRIASSIC DICYNODONT-BEARING FAUNAS

Triassic dicynodonts, being large and common terrestrial herbivores, are useful in documenting Triassic biogeography and stratigraphy. Anderson and Anderson's (1970) review of Triassic stratigraphy was mainly a statement of opinion, it lacked systematic discussion of the data upon which it was based, and was confined to Gondwana biostratigraphy. Their views, as reflected in a later paper on Permo-Triassic tetrapod distribution (Anderson and Cruickshank 1978) have been followed in King's (1988) review of the Dicynodontia. The following review integrates work since 1970 on new faunas, reassigned genera, and redated faunas and their implications for dicynodont evolution and taxonomy.

The earliest Triassic dicynodont is *Lystrosaurus* from the *Lystrosaurus* Zone of South Africa, and the Fremouw Formation of Antarctica, the Panchet Formation of India, the Ryabinian horizon of European Russia, and the Chiu-T'sai-Yuan-Tze Formation of China (Colbert 1982). (An isolated dicynodont quadrate bone from Australia was identified as that of *Lystrosaurus* by Thulborn (1983) but, as pointed out by King (1983), it is impossible to identify it to generic level.)

The *Lystrosaurus* fauna contains rhytidosteid amphibians, found in several parts of the world, but only in formations of early Scythian (Griesbachian-Smithian) age (Cosgriff 1984). The most direct evidence of the age of these faunas is the rhytidosteid *Deltasaurus* in the marine Kockatea Shales of Western Australia, a close relative of *Rhytidosteus* of the *Cynognathus* Zone of South Africa. The Kockatea Shale contains ammonites and a microflora suggesting a Lower Scythian age – either Smithian (Anderson and Cruickshank 1978; Camp and Banks 1978) or, according to Banks (1978), Dienerian. Lozovskiy (1985) has also independently dated the *Lystrosaurus* beds of the Moscow basin as lowest Triassic, based on fresh-water conchostracans.

Above the *Lystrosaurus* Zone in South Africa lies the *Cynognathus* Zone, but it has long been recognized (Cosgriff 1984) that there is a sharp break between these two. The characteristic dicynodont is *Kannemeyeria*. An association between *Kannemeyeria* and other large dicynodonts has been reported from two faunas, but both these reports have since been shown to be erroneous. Crozier (1970) identified two dicynodonts from the lower fossiliferous horizon of the N'tawere Formation of Zambia, recognizing one as a new species of *Kannemeyeria*, and the other as *Rechnisaurus cristarhynchus*. However, Keyser and Cruickshank (1979) and Bandyopadhyay (1989) have shown that the latter specimen is quite different from *Rechnisaurus*, and appears to belong to *Kannemeyeria*, which is thus the only dicynodont from this horizon in the N'tawere Formation. The presence of the cynodont *Diademodon* in this horizon as well as in the *Cynognathus* Zone of South Africa further supports the view that these two formations are of similar age (Cox 1969).

Kannemeyeria was also described by Cruickshank (1965) from the Manda Formation of Tanzania, in which *Rechnisaurus* is also found, but he has since shown (1986) that the specimen instead came from the underlying Kingori Sandstone Formation.

Both *Kannemeyeria* and *Diademodon* are found in the Omingonde Formation of South West Africa (Keyser 1973), which therefore also appears to be of an age similar to that of the *Cynognathus* Zone. However, the presence of *Titanogomphodon*, which is more advanced than the other diademodonts in having a secondary basin on the crowns of the molariform teeth (Keyser 1973), suggests that the Formation may be of slightly later date.

Kannemeyeria is thus known from the *Cynognathus* Zone of South Africa and from deposits in other parts of Africa (Zambia, Tanzania, South-West Africa), that are therefore presumably of similar age. It is also known from the upper part of the Puesto Viejo Formation of Argentina (Bonaparte 1966), accompanied by the cynodont *Cynognathus* – the zone fossil of the *Cynognathus* Zone. *Kannemeyeria* is therefore known only from south-western Gondwana.

The *Cynognathus* Zone is commonly viewed as being of late Early Triassic age (e.g. Anderson and Anderson 1970), but there is no way in which its age can be determined in terms of the classic European non-marine German sequence or marine Alpine sequence. All that can be attempted for the succeeding Triassic faunas is to place them in relative order – and even this is complicated by ecological biases of some of the faunas, and by recent re-assignments of some synapsid genera.

The next-youngest diverse, well-documented Triassic fauna is that of the Manda Formation of Tanzania. This contains traversodontid cynodonts and rauisuchid thecodonts, which are absent from the *Cynognathus* Zone. It also contains the rhynchosaur *Stenaulorhynchus*, while the only rhynchosaurs in the *Cynognathus* Zone are *Howesia* and *Mesosuchus*, which are more primitive in lacking the interlocking blade and groove jaw apparatus of the later rhynchosaurs (Benton 1980, 1983). There is therefore little doubt that the Manda Formation is of later age than the *Cynognathus* Zone. Its exact age cannot be directly established, but the Manda rhynchosaur *Stenaulorhynchus* is closest to *Rhynchosaurus* (Benton 1983), which is found in England both in the Midlands and in the Otter Sandstone Formation of Devon (Benton 1990). The age of the Midlands species is difficult to establish, different elements in the faunal and floral assemblage being interpreted to indicate ages ranging from Late Scythian to Late Ladinian (Benton 1990). However, the age of the Otter Sandstone vertebrate fauna, which includes fishes, amphibians and reptiles, may be Anisian (Milner *et al.* 1990).

Manda dicynodont genera are found also in three other faunas, *Rechnisaurus* in the Yerrapalli Formation of India and in the Er-Ma-Ying Formation of China, and *Sangusaurus* in the upper fossiliferous horizon of the N'tawere Formation of Zambia (Cruickshank 1986). The Yerrapalli fauna contains the dicynodonts *Rechnisaurus* and *Wadiasaurus*, an erythrosuchid and a prestosuchid thecodontian, a trirachodont cynodont, and a labyrinthodont amphibian (Bandyopadhyay 1988). The age of the Er-Ma-Ying Formation is somewhat perplexing. It is now divided into upper and lower portions (Sun 1989). The faunas of each portion contain the thecodontian reptiles similar to genera in the *Cynognathus* Zone of South Africa: *Halazhaisuchus* of the lower portion and *Shansisuchus* of the upper portion are respectively similar to *Euparkeria* and to *Erythrosuchus* of the *Cynognathus* Zone (Sun 1989). This seems to suggest that both faunas are similar in age to the South African fauna, but the lower fauna also contains *Rechnisaurus* (*Shaanbeikannemeyeria*), which is found also in the Manda fauna. *Rechnisaurus* in the Er-Ma-Ying Formation suggests an age similar to the Manda Formation, while the other elements must be seen as anomalous, perhaps due to the considerable distance between the Chinese and African faunas. The upper fossiliferous horizon of the N'tawere Formation of Zambia contains the dicynodonts *Sangusaurus* (Cruickshank 1986) and *Zambiasaurus*, the traversodont cynodont *Luangwa*, and fragments of thecodontians.

Manda-like dicynodonts in the Donguz Formation of European Russia include *Rabidosaurus*, *Rhadiodromus* (= *Rhinocerocephalus*), and *Rhinodicynodon* (Kalandadze 1970), and *Uralokannemeyeria* (Danilov 1971). Apart from the shansiodont *Rhinodicynodon*, all of these are very similar to *Rechnisaurus* in skull proportions. Three other dicynodont genera from the Donguz Formation have been described more recently, but these (*Edaxosaurus*, *Elatosaurus*, and *Calleonasus*; Kalandadze and Sennikov 1986) are known only from respectively an 'upper jaw bone' and two nasal bones, and are effectively *nomina nuda*. The rest of the Donguz fauna comprises temnospondyl amphibians (the capitosaur *Eryosuchus*, Ochev 1966; plagiosaurs, Shishkin 1986), the procolophonid *Orenburgia* (Ochev 1968; Ivakhnenko 1977); thecodontians (*Dongusia*, 'Erythrosuchus' Ochev 1980; *Vyushkovisaurus* Ochev 1982; *Vytshegdosuchus*, *Dongosuchus* Sennikov 1988), and traversodont cynodonts (Tatarinov 1974, 1988). The thecodontians are fragmentary, and the other groups are from such long-lived lineages that they provide little information on the age of the Donguz Formation. Thus, unfortunately, one can only rely on the slender evidence of the similarities of the *Rechnisaurus*-like dicynodonts discussed above, and provisionally view it as if similar age.

As noted earlier, the Manda Formation cannot be dated more precisely than Anisian. The other four faunas just discussed offer such poor evidence on dating that they are all ascribed provisionally to the Anisian, this reflecting also the fact that they appear to be later than the Scythian *Cynognathus* Zone fauna, and earlier than the South American faunas to be discussed next.

The South American dicynodont faunas include those of the Chañares and Ischigualasto Formations of Argentina, and of the Santa Maria Formation of Brazil. Cox (1965, 1968, 1973b), and Bonaparte (1982) have discussed the relative ages of these South American Middle-Late Triassic faunas. An important new element has been the documentation by Barberena (1977) of the

consistent differences between two faunal assemblages in the Santa Maria Formation, which now makes it possible to resolve some apparent anomalies. The fact that the Santa Maria fauna included the rhynchosaur *Scaphonyx* (also known from the Ischigualasto fauna) and the early dinosaur *Staurikosaurus* gave the impression that the whole Santa Maria fauna must be considerably younger than the Manda fauna (Cox 1965, 1968, 1973). However, Barberena (1977) has since shown that these elements are found only in deposits near the town of Santa Maria. He names this the Rhynchocephalian Assemblage, but now that it has been realized that rhynchosaurs and sphenodontids are not closely related (Carroll 1977), a more appropriate name would be the Rhynchosaur Assemblage; its age is discussed below.

Barberena (1977) points out that the rhynchosaurs, abundant in this Rhynchosaur Assemblage, are wholly lacking in deposits from the Xiniquá and Pinheiros areas, respectively to the west and to the east of Santa Maria; these localities instead contain an abundance of stahleckeriid dicynodonts (*Stahleckeria* and *Dinodontosaurus*), as well as chiniquodont cynodonts. He names this fauna the Therapsid Assemblage. (Though he shows the kannemeyeriid dicynodont *Jachaleria* as found in this Assemblage, Bonaparte (1982) states that it is instead from the much later Caturritá Formation of Brazil.)

Dinodontosaurus and the traversodont cynodont *Massetognathus* (Hopson and Kitching 1972) are found also in the Chañares Formation of Argentina. In addition to these similarities at generic level, the two faunas are similar in containing chiniquodont cynodonts and in lacking rhynchosaurs. They therefore appear to be of very similar, if not identical, age and character. It is difficult to estimate that age precisely, since the chiniquodont cynodonts range widely in age, from the Early Triassic Manda fauna to the Late Triassic Argentinian faunas of Ischigualasto and Las Esquina (Hopson and Kitching 1972; Bonaparte 1982). However, the Chañares herbivorous cynodonts do appear to be somewhat more advanced than those of the Manda fauna (Romer 1967). This suggests that the Chañares/Santa Maria Therapsid Assemblage is later in age than the Manda fauna, and may therefore be provisionally placed in the Ladinian.

Barberena (1977) rightly points out that the discovery that the Rhynchosaur Assemblage is younger than the Therapsid Assemblage makes it unnecessary to postulate that merely ecological differences were the reason why rhynchosaurs and dicynodonts had not been found together. However, since rhynchosaurs were present in the Manda fauna, which is clearly older than the Therapsid Assemblage, a problem remains. The absence of rhynchosaurs from the Chañares/Santa Maria Therapsid fauna must have been caused by either geographical or ecological factors.

A geographical cause, in the sense of a geographical barrier between the South American and East African localities, seems unlikely. Apart from the general similarities in Triassic faunas throughout Pangaea (Cox 1973a), the dicynodont *Kannemeyeria* is found in both Africa and Argentina, the Brazilian dicynodont *Stahleckeria* is closely related to the Zambian genus *Zambiasaurus* (Cox 1969), and the rhynchosaur *Stenaulorhynchus* of the Manda Formation is related to *Rhynchosaurus* of Britain (Benton 1983).

An ecological explanation therefore remains more plausible, though its precise nature can only be guessed at. Rhynchosaurs were clearly herbivorous (Benton 1983), and therefore may well have competed with dicynodonts. Though the two groups co-exist in the Manda fauna, it may be that the climatic conditions of the South American areas, far closer to the periphery of a Gondwana continent that still lacked Andean mountains, may have been moister and may have encouraged a lush flora, which may have favoured the dicynodonts. The two groups again co-exist in the Late Triassic Ischigualasto fauna, but the stahleckeriid dicynodonts of the Chañares/Santa Maria Therapsid Assemblage had by then disappeared, and only the kannemeyeriids co-existed with the rhynchosaurs.

The next-youngest dicynodont-bearing faunas are those of the Ischigualasto Formation of Argentina, the Chinle Formation of North America, and the Argana Formation of Morocco. Only the kannemeyeriid type of dicynodont is found in these. Their ages have recently been re-evaluated by Olson and Sues (1986), on the basis of palynoflorule and plant megafossil evidence, and they are now considered to be of Late Carnian age (though this evidence is indirect, rather than direct

interfingering of terrestrial and marine deposits). The presence of the phytosaur *Paleorhinus* in the Moroccan fauna as well as in the Dockum Formation of Texas and in the Popo Agie Member of the Chugwater Formation of Wyoming also suggests an age no later than the Late Carnian (Ballew 1989), and Litwin (1986) similarly suggests a Late Carnian age for the Lower Unit of the Petrified Forest Member of the Chinle Formation (which contains *Placerias*) on the basis of its plant spores. Hunt and Lucas have also very recently (1991) suggested a Late Carnian age for these faunas on the basis of the presence in all of them of elements coeval with the phytosaur *Paleorhinus* of the German Blasensandstein.

If such a Late Carnian age is provisionally accepted for the Ischigualasto fauna, the question arises as to what age should be assigned for the Santa Maria Rhynchosaur Assemblage. The presence of the rhynchosaur *Scaphonyx* in both faunas suggests that there is no great difference in their ages. This is supported by Hopson's (1985) restudy of the traversodont cynodont *Gomphodontosuchus braziliensis* from the Rhynchosaur Assemblage, which shows that it is probably a juvenile specimen closely related to *Exaeretodon* of the Ischigualasto fauna. The Rhynchosaur Assemblage, also, is therefore given a Late Carnian age in Table 2.

However, the Ischigualasto fauna differs from the Chinle/Dockum fauna, as it is still dominated by mammal-like reptiles such as the dicynodonts and cynodonts, while the North American faunas are instead dominated by archosaurs such as the thecodontians and early dinosaurs. Though there may also be an ecological component to these differences, they suggest that the Ischigualasto fauna is rather more archaic and older than the North American faunas.

The last known dicynodont is *Jachaleria* from the Los Colorados Formation of Argentina (Bonaparte 1971) and from the Caturritá Formation of Brazil (Araújo and Gonzaga 1980). This genus is clearly very closely related to *Ischigualastia* (Table 1: Araújo and Gonzaga [1980] state that the posterior orientation of the suspensorium in *Jachaleria* and the curved shape of the zygomatic arches in *Ischigualastia* are probably the result of distortion), which suggests that these formations are not very much later in time than those mentioned in the preceding paragraph, and they too are given a Late Carnian date.

TABLE 2. Relative ages of Triassic dicynodont-bearing strata (figures indicate age in millions of years, from Cowie and Bassett 1989).

220	Late Carnian	Los Colorados; Caturritá; Chinle
	Late Carnian	Ischigualasto; Argana; Santa Maria Rhynchosaur Assemblage
230	Ladinian	Santa Maria Therapsid Assemblage; Chañares
235	Anisian	Manda; Upper N'tawere; Yerrapalli; Donguz; Omingonde; Er-Ma-Ying
240	Late Scythian	<i>Cynognathus</i> Zone; Lower N'tawere; upper Puesto Viejo
	Early Scythian	<i>Lystrosaurus</i> Zone; Panchet; Ryabinian horizon; Chiu-T'sai-Yuan-Tze; Fremouw; lower Puesto Viejo
250		

The sequence of Triassic dicynodont-bearing faunas that results from the above review is shown in Table 2. It cannot be too strongly emphasized that the relative ages of these faunas are considered to be much more reliable than their absolute ages in terms of the Scythian-Carnian classic sequence.

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