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Keyser, A. W.

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EVOLUTIONARY TRENDS IN TRIASSIC DICYNODONTIA

(Reptilia Therapsida)

by

A. W. Keyser

Geological Survey, P.B. X112, Pretoria.

ABSTRACT

Triassic Dicynodontia differ from most of their Permian ancestors in a number of specialisations that reach extremes in the Upper Triassic. These are (1) increase in total body size, (2) increase in the relative length of the snout and secondary palate by backward growth of the premaxilla, (3) reduction in the length of the fenestra medio-palatinalis combined with posterior migration out of the choanal depression, (4) shortening and dorsal expansion of the intertemporal region, (5) fusion of elements in the front part of the brain-case, (6) posterior migration of the reflected lamina of the mandible, (7) disappearance of the quadrate foramen and the development of a process of the quadrate that extends along the quadrate ramus of the pterygoid. It is thought that the occurrence of the last feature in *Dinodontosaurus platygnathus* Cox and *Jacheleria colorata* Bonaparte warrants the transfer of the species *platygnathus* to the genus *Jacheleria* and the erection of a new subfamily, Jachelerinae nov.

It is concluded that the specialisations of the Triassic forms can be attributed to adaptation to a *Dicroidium*-dominated flora.

INTRODUCTION

The Anomodontia were the numerically dominant terrestrial herbivores during the transition between Palaeozoic and Mesozoic time. They achieved their greatest diversity during the Upper Permian as is clear from the abundance of forms that are encountered in the Lower stage of the Beaufort Series of the Karroo System of South Africa and other Upper Permian strata in Africa including the Madumabisa Mudstone of Zambia and those in the Ruhuhu area of Tanzania.

Most of the Permian species of Dicynodontia were relatively small, but giant forms developed at times. Upper Permian reptilian faunas are uncommon on most of the continents and are only known from areas in Africa, India, U.S.S.R., Scotland and possibly China. As far as is known most of the Indian species are relatively small (Kutty, 1972). During the Triassic most of the Dicynodontia were large and show a number of peculiar specialisations not commonly encountered in Permian forms. These specialisations form the subject matter of this paper.

Evolutionary trends in Dicynodontia were first described by Toerien (1953 and 1955). He pointed out that the most significant trend along which Anomodontia developed was the tendency to increase the extent of the secondary palate with concomitant increase in the relative size of the palatine bones and a reduction in the size of the ectopterygoid and of the inter-pterygoid vacuity.

Cox (1965) pointed out that there is a tendency for an increase in size in the Triassic Dicynodontia which he divided into three families. He drew particular attention to shortening of the intertemporal region in the Triassic forms.

Cruickshank (1967) elaborated on many of the advanced features mentioned by Cox (1965) and added several new features to the list of known distinguishing features between Permian and Triassic Dicynodontia. In 1968 he also wrote a short paper in which the quantitative aspects of the increase in the relative size of the interpterygoid vacuity with the passage of geological time is discussed.

The evolutionary trends envisaged by these authors and a few other trends that can be noticed will be briefly discussed in the following pages.

(a) *Increase in total Body Size.*

Although most of the Permian forms are relatively small, giant forms occasionally developed in Lower Beaufort time. Most of the species known from the *Tapinocephalus* Zone of the Lower Beaufort Stage are relatively small with skull lengths very seldom more than 10 cm. During the following *Cistecephalus* Zone time numerous giant forms developed e.g. *Endothiodon, Aulacephalodon* and *Rhachiocephalus*. Skulls of the latter often reached a length of 50 cm and more (Keyser 1969, 1971).

During *Daptocephalus* Zone times several large Dicynodonts such as *Daptocephalus* and *Dinanomodon* replaced the large *Cistecephalus* Zone forms.

Most of the known Triassic dicynodont genera had skulls that were longer than 20 cm in adult specimens, the only exceptions being:

1. *Myosaurus gracilis* from the (Lower Triassic) *Lystrosaurus* Zone of South Africa.
2. A small dicynodont with a narrow intertemporal region discovered in the *Cynognathus* Zone (Lower Triassic) near Burgersdorp in the Republic of South Africa. The specimen is being described by Dr. N. Hotton III of the Smithsonian Institution.
3. Two species of smaller dicynodonts from the Puesto Viejo Formation of Argentina are currently being described by Dr. J. Bonaparte of the Instituto Miguel Lillo of Tucuman, Argentina. One of these, *Vinceria andina,* has been briefly described and figured (Bonaparte, 1971).
4. *Jimusaria* is a small dicynodont that does not appear to be a juvenile of one of the larger Chinese species. The age of this form is possibly Permian.

Some of the largest known species of dicynodonts lived during the Triassic. *Ischigualastia* from the Ischigualasto Formation of Argentina, *Placerias* from the Chinle Formation of Arizona and *Stahleckeria* from the Santa Maria Beds of Brazil are the largest forms in the group. All these genera are Upper Triassic in age. The youngest known dicynodont from the Carnian (uppermost Triassic) Los Colorados Formation of Argentina *Jacheleria colorata* Bonaparte 1971, though large, is smaller than these three genera.

(b) *Increase in the relative length of the Snout and Secondary Palate.*

When illustrations of Triassic dicynodonts are compared with similar illustrations of Permian forms one is immediately struck by the long snouts displayed by the Triassic genera (see Fig. 1). The degree of importance of long snouts is intensified by the relative shortness of the intertemporal regions of the Triassic species.

In the Middle Beaufort genus *Lystrosaurus* the snout is lengthened in a ventral direction (Cluver, 1971). The tendency to develop a long snout is only shown by *Kannemeyeria* among the lower Triassic genera. *Myosaurus* and the new form being described by Hotton from South Africa, the Chinese *Shansiodon,* and *Vinceria andina* from South America exhibit more or less the proportions of Permian dicynodonts.

During the Anisian the trend towards very long snouts is apparent. *Tetragonias njalilus* and *Rhopalorhinus etionensis* do not have very long snouts. *Kannemeyeria* was still in existence. The species of *Rechnisaurus* from India and the N'tawere Formation of Zambia are apparently very similar to *Kannemeyeria.* This genus has been placed in the family Stahlekeridae of Cox (1965) by both Chowdury (1970) and Crozier (1970). The specimens do, however, have a prominent ridge on the dorsal surface of the premaxilla and are both deformed so that there can be no certainty about the crested nature of the intertemporal region. In the author's opinion this genus had best be placed in the family Kannemeyeridae and is probably a descendant of the genus *Kannemeyeria.* It is even doubtful that a generic distinction can be upheld.

The members of the genus *Dolichuranus* from South West Africa and the N'tawere formation of Zambia (Keyser, 1973 b) have longer snouts than are found in *Tetragonias* and in this as well as in other respects approach the Upper Triassic *Dinodontosaurus* from South America.

All the known Upper Triassic dicynodont genera have exceedingly long snouts when compared with Permian, Lower and Middle Triassic forms. Examination of Fig. 29 of the paper by Cox (1965) emphasizes this statement (see also Fig. 1 in this paper). Extremes in this trend are the Chinese *Sinokannemeyeria* and *Parakannemeyeria* as well as the South American *Ischigualastia* and *Dinodontosaurus.*

Concomitant with the elongation of the snout there is an increase in the length of the secondary palate. A trend towards the increase of the length of the secondary palate was first described by Toerien (1953). At the time when Toerien wrote his paper most of the Triassic dicynodonts were still unknown. The later Triassic forms with extremely long snouts like *Dinodontosaurus* and *Ischigualastia* show this increase in the length of the secondary palate to an extreme and can therefore be regarded as the most advanced dicynodonts (Fig. 2).

Toerien demonstrated the existence of a trend to increase the extent of the secondary palate by an increase in size and forward growth of the palatine bones. This mainly applies to Permian genera. The most advanced forms, showing the most extensive palatine participation in the secondary palate, are *Tropidostoma,* an endothiodont, *Aulacephalodon, Pelanomodon, Oudenodon* and *Rhachiocephalus.* These are all advanced Permian forms.

In many of the Triassic genera the palatines are insignificant in the secondary palate, most of which is made up by the premaxillae, e.g. *Dinodontosaurus.* In these forms the very extensive secondary palate is due to backward growth of the premaxilla.

This is in part achieved by the exclusion of much of the maxilla from the roof of the mouth. This type of palatal structure is already found in the Upper Permian genus *Daptocephalus* (Ewer, 1961). In this genus the premaxilla has a posterior outgrowth that meets the palatines. The posterior outgrowth is much broader in the Lower Triassic genus *Kannemeyeria.* In many of the Upper Triassic forms e.g. *Dinodontosaurus* the palatine bones are no longer very extensive. (Fig. 2.)

(c) *Trend towards reduction of the interpterygoid vacuity.*

The relationships of the secondary palate and the interpterygoid vacuity have also been discussed by Cruickshank (1968). He showed quantitatively that

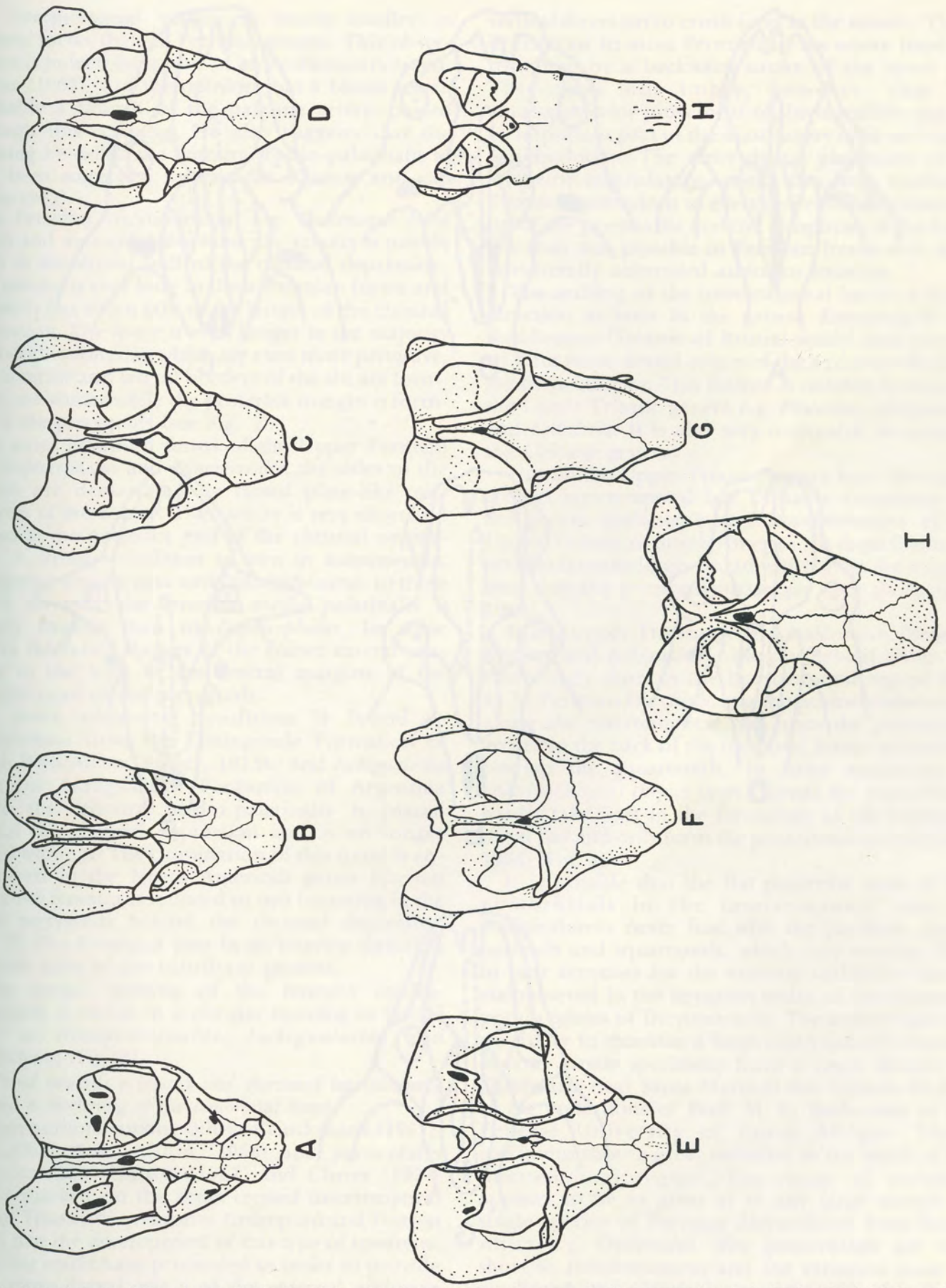


Fig. 1. Dorsal views of Permian and Triassic Dicynodontia (reduced to the same size for comparison). A, *Oudenodon baini* Owen (Permian); B, *Daptocephalus leoniceps* (Owen) (Permian); C, *Tetragonias njalilus* (Von Huene) (Triassic); D, *Ischigualastia jenseni* Cox (Triassic); E, *Aulacephalodon baini* (Owen) (Permian); F, *Kannemeyeria simocephala* (Weithofer) (Triassic); G, *Dolichuranus primaevus* Keyser (Triassic); H, *Parakannemeyeria dolichocephala* Sun Ai Lin (Triassic); I, *Dinodontosaurus platyceps* (Cox) (Triassic). Modified after various authors.

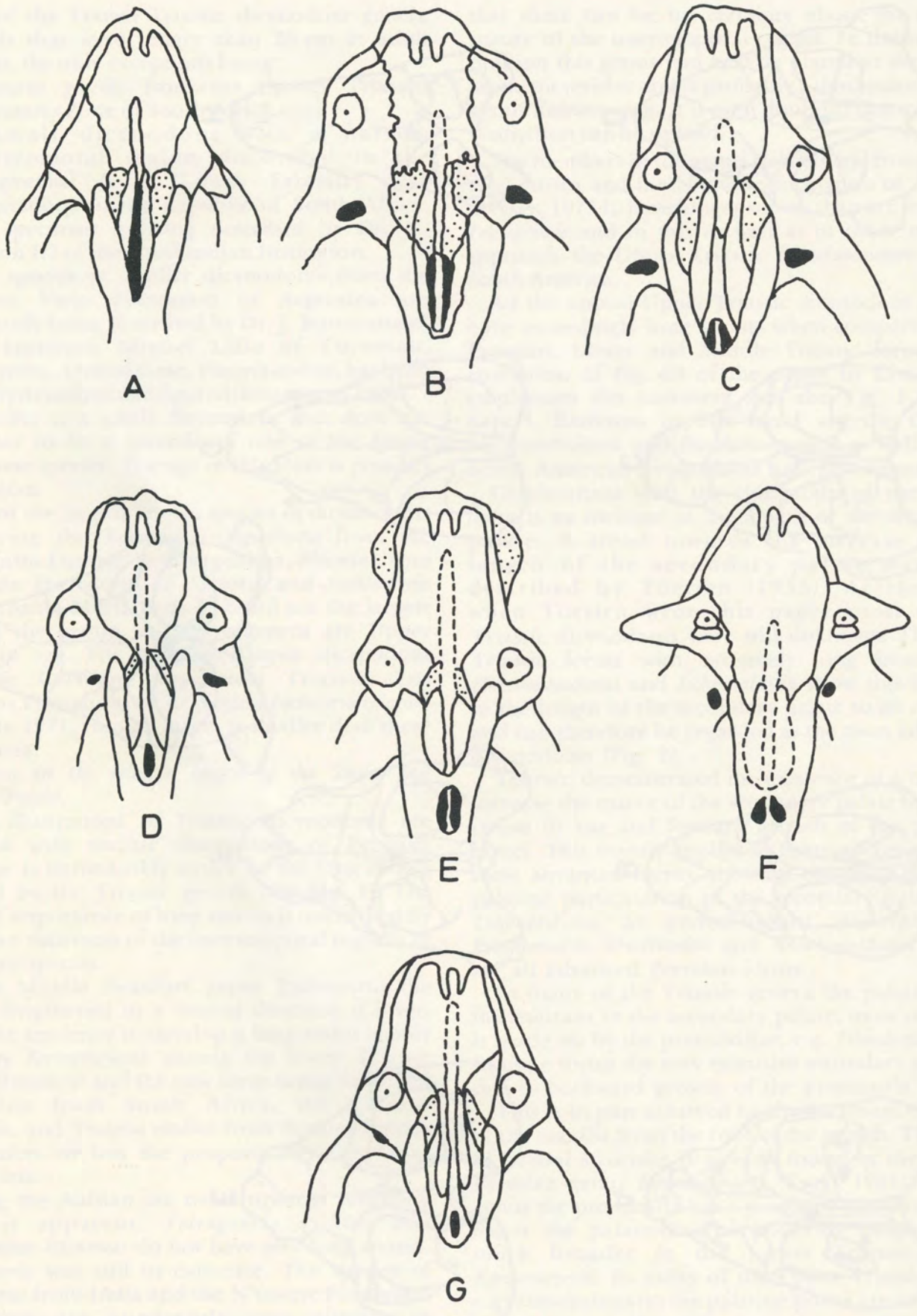


Fig. 2. Palatal view of Permian and Triassic Dicynodontia to show the development of the secondary palate and the interpterygoid vacuity. (all reduced to the same size). Palatine bones are indicated by dotting. A, *Oudenodon baini* Owen (Permian); B, *Aulacephalodon baini* (Owen) (Permian); C, *Daptocephalus leoniceps* (Owen) (Permian; D, *Kannemeyeria simocephla* (Weithofer) (Triassic); E, *Rhopalorhinus etionensis* Keyser (Triassic); F, *Placerias gigas* Camp and Wells (Triassic); G, *Dinodontosaurus platyceps* (Cox).

the interpterygoid vacuity is much smaller in Triassic forms than in Permian genera. This observation is indeed indicative of an evolutionary trend.

Cox (1968) is of the opinion that a blood vessel, probably a branch of the palatine artery, passed through this opening. He also suggests that the opening be called the fenestra medio-palatinalis as had been suggested by van der Klaauw and van Roon(1942).

In Permian Dicynodontia, e.g. *Oudenodon baini* Owen and *Aulacephalodon baini,* the vacuity is merely a slit in the dorsal wall of the choanal depression. The vacuity is very long in these Permian forms and normally has about 60% of the length of the choanal depression. The space is even longer in the majority of Endothiodontidae which are even more primitive. The anterior and lateral borders of the slit are formed by the vomer while the posterior margin is formed by the pterygoids (see Fig. 2).

In more advanced forms of the Upper Permian e.g. *Daptocephalus* and *Dinanomodon* the sides of the vacuity are demarcated by raised plate-like outgrowths of the vomer. The vacuity is very short and placed at the posterior end of the choanal depression. A similar condition is seen in *Kannemeyeria, Tetragonias, Dolichuranus* and *Dinodontosaurus.* In these forms however the fenestra medio-palatinalis is slightly smaller than in *Daptocephalus.* In these genera the raised flanges of the vomer extend ventrally to the level of the ventral margins of the palatine rami of the pterygoids.

A more advanced condition is found in *Rhopalorhinus* from the Omingonde Formation of South West Africa (Keyser, 1973b) and *Ischigualastia* from the Ischigualasto Formation of Argentina where the fenestra medio-palatinalis is placed behind the choanal depression and is no longer placed within it. The culmination of this trend is encountered in the North American genus *Placerias* where the fenestra is reduced to two foramina in the fused pterygoids behind the choanal depression (Fig. 2). The foramina pass in an interior direction on both sides of the cultriform process.

The dorsal opening of the fenestra medio-palatinalis is visible as a circular opening in lateral view in *Dinodontosaurus, Ischigualastia* and *Dolichuranus* (Fig. 3).

(d) *Trend towards a crested and shortened intertemporal bar and a shortening of the postorbital bones.*

Many authors, among others Cruickshank (1967), Cox (1965), Sun, Ai-Lin (1963) and particularly Crompton and Hotton (1967) and Cluver (1971) have remarked on the short crested intertemporal bars of Triassic dicynodonts. Crompton and Hotton noted that the development of this type of intertemporal bar could have proceeded in order to provide for a more dorsal origin of the external adductor musculature.

This more dorsal placement of the main muscles associated with the masticatory mechanism would have enabled the animals to exert more force in a vertical direction to crush food in the mouth. This is in contrast to most Permian forms where food was triturated by a backward stroke of the lower jaw. This does not imply, however, that the anteroposterior movement of the mandible was not an important part of the masticatory cycle of Triassic Anomodontia. The more dorsal placement of the adductor musculature would also have enabled a Triassic anomodont to exert more force between the tip of the premaxilla and the symphysis of the lower jaw than was possible in Permian forms with more horizontally orientated adductor muscles.

The arching of the intertemporal bar in a dorsal direction as seen in the genera *Kannemeyeria* and *Rabidosaurus* (Triassic of Russia) would have provided for a more dorsal origin of the adductor externus medialis muscles. This feature is notable in many of the Upper Triassic genera e.g. *Placerias, Ischigualastia* and *Jacheleria.* It is also very noticeable in many of the Chinese genera.

Not all the Upper Triassic genera have the raised crested intertemporal bar. Notable exceptions are the genera *Stahleckeria* and *Dinodontosaurus* of the Upper Triassic of South America. In these forms the occiput is exceedingly broad which gives the impression that the temporal fossae are very short (Cox, 1965).

In the Upper Triassic genera *Stahleckeria, Dinodontosaurus* and *Ischigualastia* the postorbital bones are exceedingly short in the intertemporal region (Fig. 4). In Permian Dicynodontia the postorbitals extend along the intertemporal bar from the postorbital arches to the back of the temporal fossae where they overlap the squamosals. In some specimens of *Dinodontosaurus turpior* (von Huene) the postorbitals hardly take part in the formation of the intertemporal bar and only form the postorbital arches (Cox, 1968) (Fig. 4).

It is notable that the flat posterior rami of the postorbitals in the intertemporal bars of Anomodontia never fuse with the parietals, interparietals and squamosals, which they overlap. This in part accounts for the extreme variability that is encountered in the apparent width of the intertemporal regions of Dicynodontia. The author had opportunity to examine a large collection of *Dinodontosaurus turpior* specimens from a single locality at Candelaria near Santa Maria in Rio Grande do Sul, in the collections of Prof. M. C. Barbarena of the Federal University of Porto Allegre. These specimens show a great variation in the width of the intertemporal region. The range of variation appears to be as great as in any large sample of single species of Permian dicynodonts from South Africa e.g. *Oudenodon.* The postorbitals are very short in *Dinodontosaurus* and the variation must be attributed to ontogenic variation in the living animals.

In the Indian genus *Wadiasaurus* Roy Chowdury from the Yerapalli Formation and in *Sangusaurus* Cox from the N'tawere Formation of Zambia,

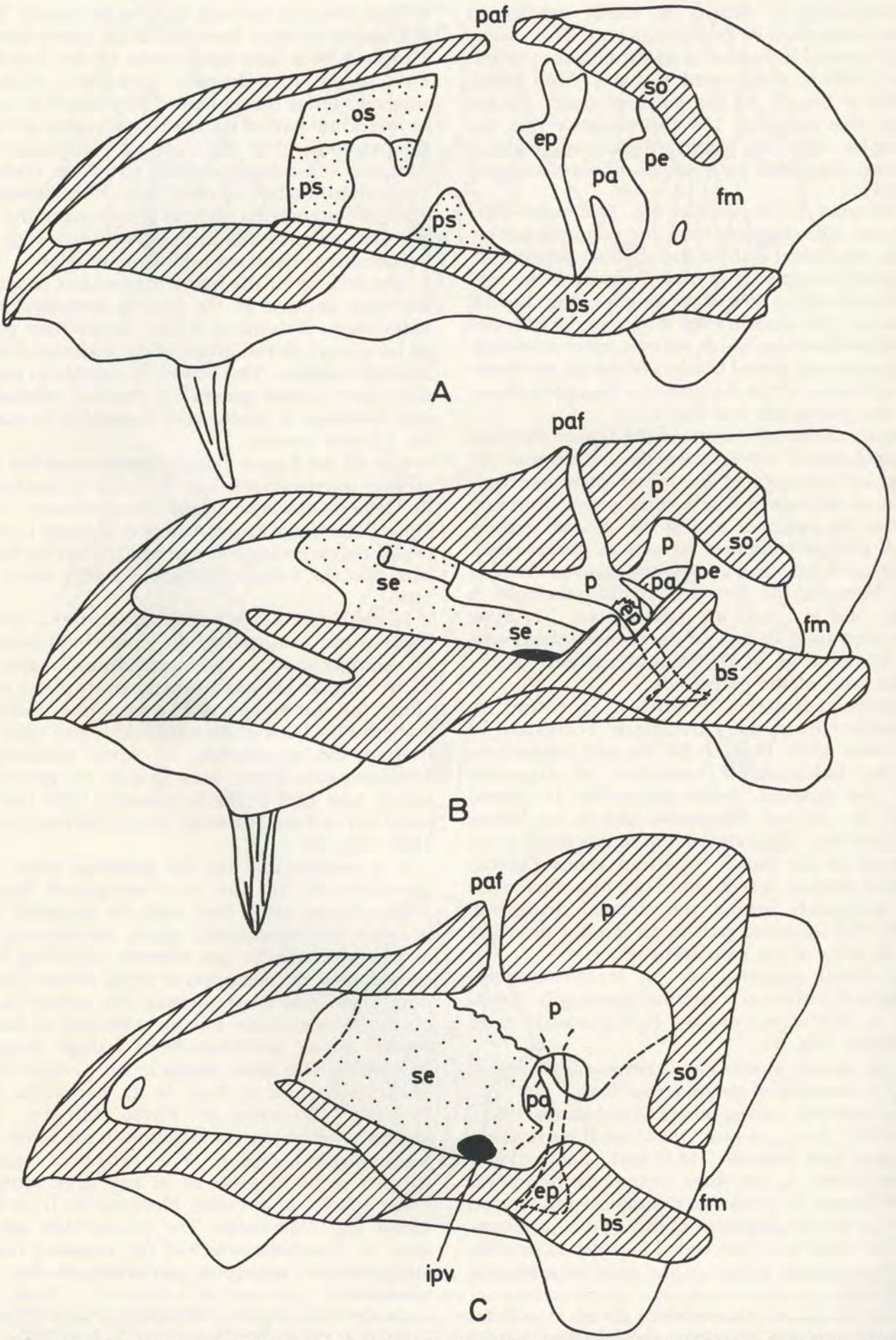


Fig. 3. Schematic reconstruction of saggital views to show the evolution of the sphenethmoid region in Dicynodontia (all reduced to the same size). A, *Dicynodon grimbeeki* Broom (after Agnew) (Permian); B, *Aulacephalodon baini* (Owen) (Permian); C, *Ischigualastia jenoseni* Cox (Triassic). The sphenethmoid is indicated by dotting. Cross hatching indicates the plane of section. Abbreviations: bs, basisphenoid, ep, epipterygoid, fm, foramen magnum, ipv, interpterygoid vacuity, os, orbitosphenoid, p. parietal, pa, pila antotica, paf, parietal foramen, pe, periotic, ps, presphenoid, se, sphenethmoid (undifferentiated,) so, supraoccipital.

peculiar boss-like thickenings of the postorbitals occur on the intertemporal region behind the level of the parietal foramen. There can be no certainty about the function of these bosses but it is conceivable that they could have related to sexual dimorphism as is found in living African Suidae where bosses occur on the maxillae of both sexes but are very large in sexually active males.

(e) *Fusion of elements in the Brain-case.*

In Permian Dicynodontia the back part of the brain-case is enclosed by the various occipital elements and the basis cranii. Farther forward the sides of the brain-case are formed by the periotics. The prootic and opisthotic are indistinguishably fused in most Dicynodontia. In anomodonts the sides of the front part of the brain are normally quite open and have no bony covering. In this open area the sides of the brain received some limited support from the finger-like processes of the prootic commonly referred to as the pila antotica and also the epipterygoids. Anterior to this the optical and olfactory lobes of the brain were probably housed in the orbitosphenoid wings of the sphenethmoid complex.

In most Permian Dicynodontia the sphenethmoid region consists of an anterior orbitosphenoid ossification formed of a vertical plate that stands in a groove on the dorsal surface of the cultriform process. This plate divides dorsally into two wing-like plates that probably contained the olfactory and optical lobes. A more posterior element normally referred to as the presphenoid also stands in the groove on the dorsal surface of the cultriform process. This condition is found in *Dicynodon grimbeeki* Broom (Agnew, 1958), *Pristerodon buffaloensis* Toerien (Barry, 1967) and *Cistecephalus microrhinus* Owen (Keyser, 1973a).

In more advanced Permian genera like *Oudenodon, Rachiocephalus* and *Aulacephalodon* (Keyser, in press) the anterior sphenethmoid ossification fuses with the posterior presphenoid element to form a single sphenethmoid ossification.

In many Triassic species the sphenethmoid fuses with the two ventral plates that the parietals send down to meet the epipterygoids and possibly even with the prootic. The only part of the brain that is laterally exposed in these forms is a small fenestra formed lateral to the sella turcica in the region of the prootic incisures for the passage of the nervus trigeminus.

This condition can be clearly seen in *Kannemeyeria* and in a specimen of *Ischigualastia* that belongs to the Instituto Lillo in Tucuman (Fig. 3).

It is interesting to note that fusion between the sphenethmoid and the parietals and prootics also occurred in moschopid Dinocephalia of the very much earlier *Tapinocephalus* zone of probably Middle Permian age (Boonstra, 1968).

(f) *Specialization of the Suspensorium and Lower Jaw.*

In Permian Dicynodontia as well as in most Triassic genera of Anomodontia the quadrate consists of a main condylar part, the lateral side of which is fused to the quadratojugal which in turn fuses with the squamosal and a median dorsal process. The dorsal process of the quadrate is firmly clamped between the paroccipital process of the periotic and the squamosal. Because of the fusion with quadratojugal very little or no movement of the quadrate relative to the rest of the skull was possible.

In the genera *Daptocephalus, Kannemeyeria, Dolichuranus, Tetragonias, Vinceria* and *Dinodontosaurus* the arrangement of the quadrate and quadratojugal is exactly as is found in the Permian genera.

The holotype of *Dinodontosaurus platygnathus* Cox 1968 from the Ischichuca Formation of Argentina exhibits an odd specialization of the quadrate not encountered in other anomodonts. (Figs. 5 and 6).* The anterior face of the dorsal process of the quadrate has a long tapered anterior process that lies along the outside of the quadrate process of the pterygoid for nearly its whole length. The dorsal process of the quadrate is reduced and is much smaller than that of Permian Dicynodontia. Examination of a large number of specimens of *Dinodontosaurus turpior* and *Dinodontosaurus platyceps* in South American collections have clearly shown that no pterygoid process is ever developed in these two species. It is therefore necessary to remove the species *platygnathus* from the genus *Dinodontosaurus.*

The quadrate foramen which is normally a slit-like opening between the quadrate and the quadratojugal is circular in *Dinodontosaurus platygnathus* and is placed close to and nearly above the condylar part of the quadrate.

The only dicynodont in which the quadrate foramen is absent is the South American genus *Ischigualastia* (Fig. 7). Concomitant with the disappearance of the quadrate foramen the reflected lamina of the lower jaw is placed very far back on the ramus and forms a posterior process on the ventral side of the ramus that touches the anteroventrally directed tip of the retroarticular process of the articular (Fig. 7).

The quadratojugal is a vertically placed plate of bone that extends from the lateral condyle of the quadrate to the lateral occipital flange of the squamosal in all other known dicynodonts. This plate is always nearly parallel to the long axis of the skull. In *Ischigualastia* the flat quadratojugal is not orientated parallel to the long axis of the skull but is swung out laterally to be orientated at nearly 90° to the long axis of the skull. This results in the disappearance of the quadrate foramen. It can be said that the foramen opens up to such an extent that it disappears.

As a generalisation it can be said that the quadrate foramen is generally wider and shorter in Triassic Dicynodontia than in Permian forms.

In Permian Dicynodontia the posterior edge of the reflected lamina of the angular is placed at about

* The type specimen of *Platycyclops crassus* Broom 1948 also displays this feature.

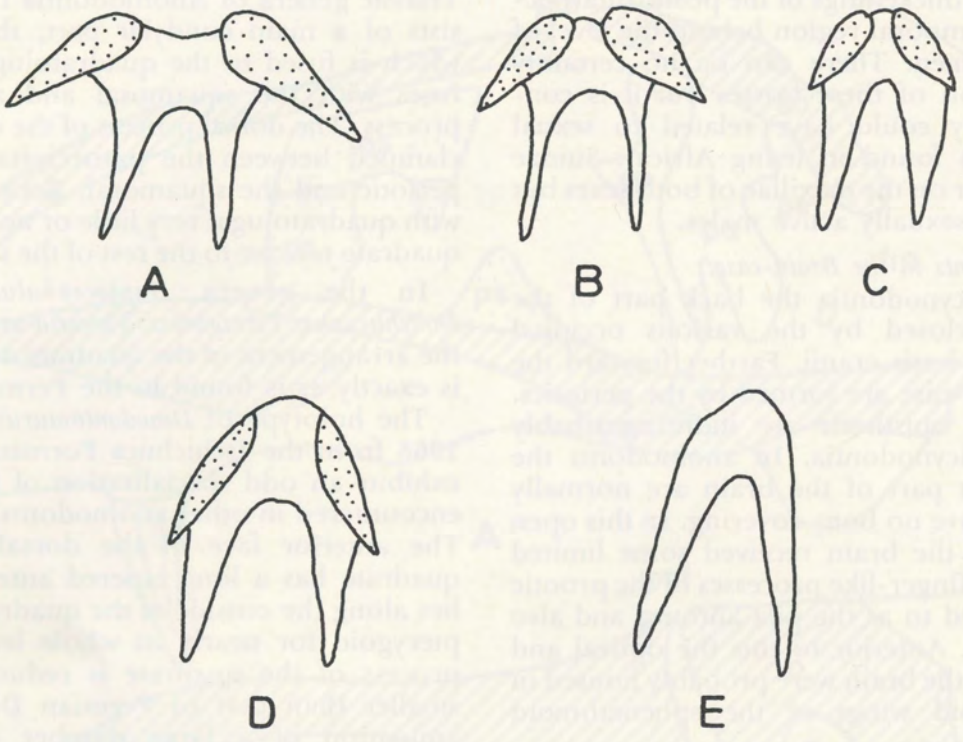


Fig. 4. Sections through the intertemporal regions of various Permian and Triassic Dicynodontia, immediately posterior to the parietal foramen. All reduced to the same size. Postorbital bones are indicated by dotting. A, *Rhachiocephalus,* B, *Daptocephalus,* C, *Dolichuranus,* D, *Kannemeyeria,* E, *Dinodontosaurus.*

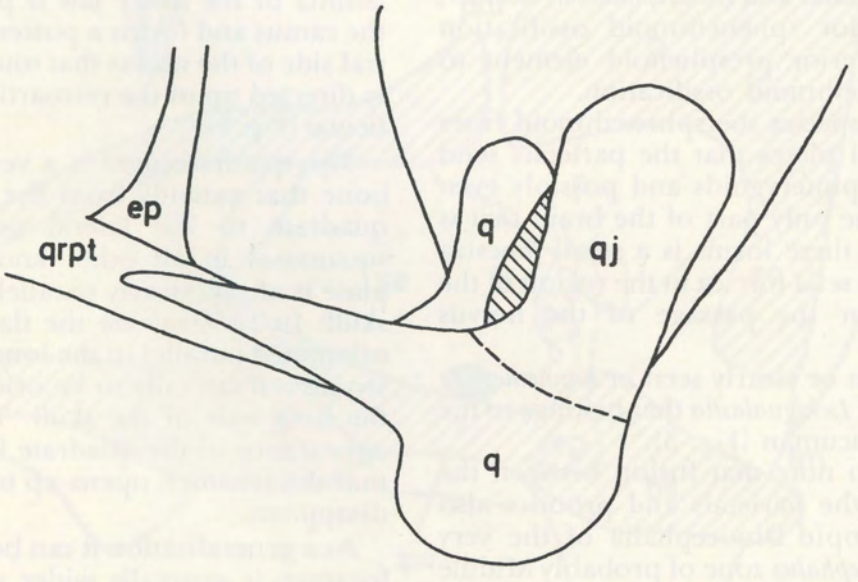


Fig. 5. Lateral view of the quadrate region of *Jacheleria platyceps* (about $\frac{1}{3}$ natural size). Abbreviations: ep, epipterygoid, q, quadrate, qj, quadratojugal, qrpt, quadrate ramus of pterygoid.

the level of the posterior third of the length of the ramus of the lower jaw.

In most Triassic Dicynodontia the reflected lamina is placed farther back and nearer to the articular. This is particularly noticeable in the *Rechnisaurus* lower jaw described by Crozier (1970) and in the jaw of *Jacheleria platygnathus* (Cox). In all Triassic Dicynodontia the reflected lamina is nearer to the articular than is the case in *Oudenodon, Rhachiocephalus, Aulacephalodon, Pristerodon, Emydops* or *Cistecephalus*. The culmination of this trend is seen in *Ischigualastia* where the reflected lamina is in contact with the retroarticular process of the articular (Fig. 7).

It is clear that a broadening of the quadrate foramen is associated with posterior migration of the reflected lamina. The culmination of this trend is found in *Ischigualastia* where the reflected lamina meets the articular and where the quadrate foramen disappears. This indicates that there was a functional association between these two structures in Anomodontia.

DISCUSSION

The following trends and their culmination in various Triassic Dicynodontia are discussed:

a. Increase in total body size.
b. Increase in the relative length of the snout and secondary palate by backward growth of the premaxilla.
c. Reduction in the length of the fenestra mediopalatinalis and its posterior migration out of the choanal depression.
d. Shortening and dorsal expansion of the intertemporal bar with concomitant shortening of the temporal fossae.
e. Fusion of elements in the front part of the brain-case.
f. Posterior migration of the lamina reflecta of the mandible.
g. Development of an anterior process on the quadrate which lies along the quadrate ramus of the pterygoid.
h. Disappearance of the quadrate foramen.

The South American genus *Ischigualastia* from the Ischigualasto Formation of Argentina is morphologically the most advanced form of the Suborder Anomodontia and displays all the advanced features mentioned in this discussion except the pterygoid process of the quadrate.

All these specializations can be attributed to adaptation of the masticatory mechanism to changes in environment including the food supply that was available to the animals. It is well known that a total change of the flora of the Southern Hemisphere occurred at the base of the Triassic when the *Glossopteris* flora was replaced by a *Dicroidium* flora dominated by pteridosperms and Bennettitales on all the Gondwana continents. The diet of Permian Dicynodontia probably consisted mainly of equisetalians and *Glossopteris* (Keyser, 1971) while the Triassic forms had to rely on the very different *Dicroidium* flora. It is therefore possible to relate the specializations of the masticatory apparatus to adaptation to the *Dicroidium* flora.

The genus *Daptocephalus* from the Uppermost Permian of the Beaufort Series of South Africa shows many of the advanced features of the later Triassic genera. Among these the long snout and secondary palate formed largely by backward growth of the premaxilla, the tiny posteriorly placed interpterygoid vacuity, the narrow intertemporal crest and short temporal fossae may be mentioned. These specializations indicate that *Daptocephalus* could be ancestral to many of the Triassic genera. It is also notable that *Daptocephalus* lived at a time when the *Glossopteris* flora was about to be superseded by a different flora. The evolutionary position of *Daptocephalus* will be discussed in a subsequent paper.

The evaluation of the advanced features encountered in the Triassic Dicynodontia leads to the consideration of their taxonomic significance.

The types of both *Jacheleria colorata* Bonaparte and *Dinodontosaurus platygnathus* Cox are very poor and fragmentary specimens. The type of *Jacheleria colorata* consists of a lower jaw and a very weathered posterior two-thirds of a skull. The type of *platygnathus* consists of a palate, an occiput and a lower jaw. The lower jaws of both species have a very flat profile along the dorsal surface and very long symphysial parts. Both species also have pterygoid processes on their quadrates. Although very little is known about these two species and though they are not of the same age it is best to refer the species *platygnathus* Cox to the genus *Jacheleria* Bonaparte. The development of a pterygoid process of the quadrate in both these species and the fact that such a process is not found in any other group suggests their removal from the Subfamily Stahleckeroinae (Lehman) and the erection of a new Subfamily *Jachelerinae* (nov.).

Cox (1968) described a new genus and species *Chanaria platyceps* from the Chanares Formation (now Ischishuca Bonaparte 1971) of Argentina which also contains specimens of *Dinodontosaurus brevirostris* Cox 1968. The former genus and species differs from the latter mainly in the extreme width of the intertemporal region of *Chanaria platyceps*.

In the light of the variation encountered in the Candelaria series of skulls the generic name *Chanaria* Cox must be regarded as a junior synonym of *Dinodontosaurus* Romer. As the species *platyceps* has page priority over *Dinodontosaurus brevirostris* the species found in the Ischichuca Formation has to be referred to as *Dinodontosaurus platyceps* (Cox).

Although there is not as wide a range of variation in the Triassic Anomodontia as is encountered in Permian forms (e.g. the difference between the giant *Rhachiocephalus* and smaller forms like *Cistecephalus* and *Emydops)* there is still enough variation to separate

the Triassic forms into several Subfamilies. The extreme forms of the Upper Triassic in which the various evolutionary lineages culminated are very different from one another but appear to be linked together by many intermediate genera and species. The large number of new discoveries that have been made in Africa, U.S.S.R., China and South America since 1965 when C. B. Cox proposed a classification of the Triassic dicynodonts into three families now indicate that major rethinking on the taxonomy of the group has become necessary.

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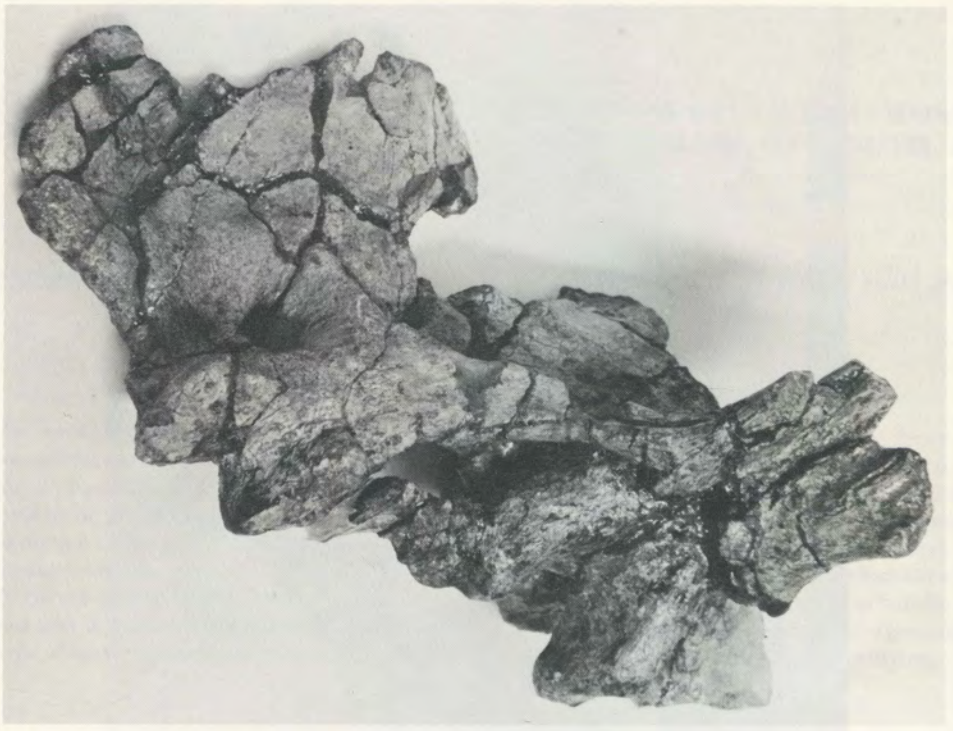
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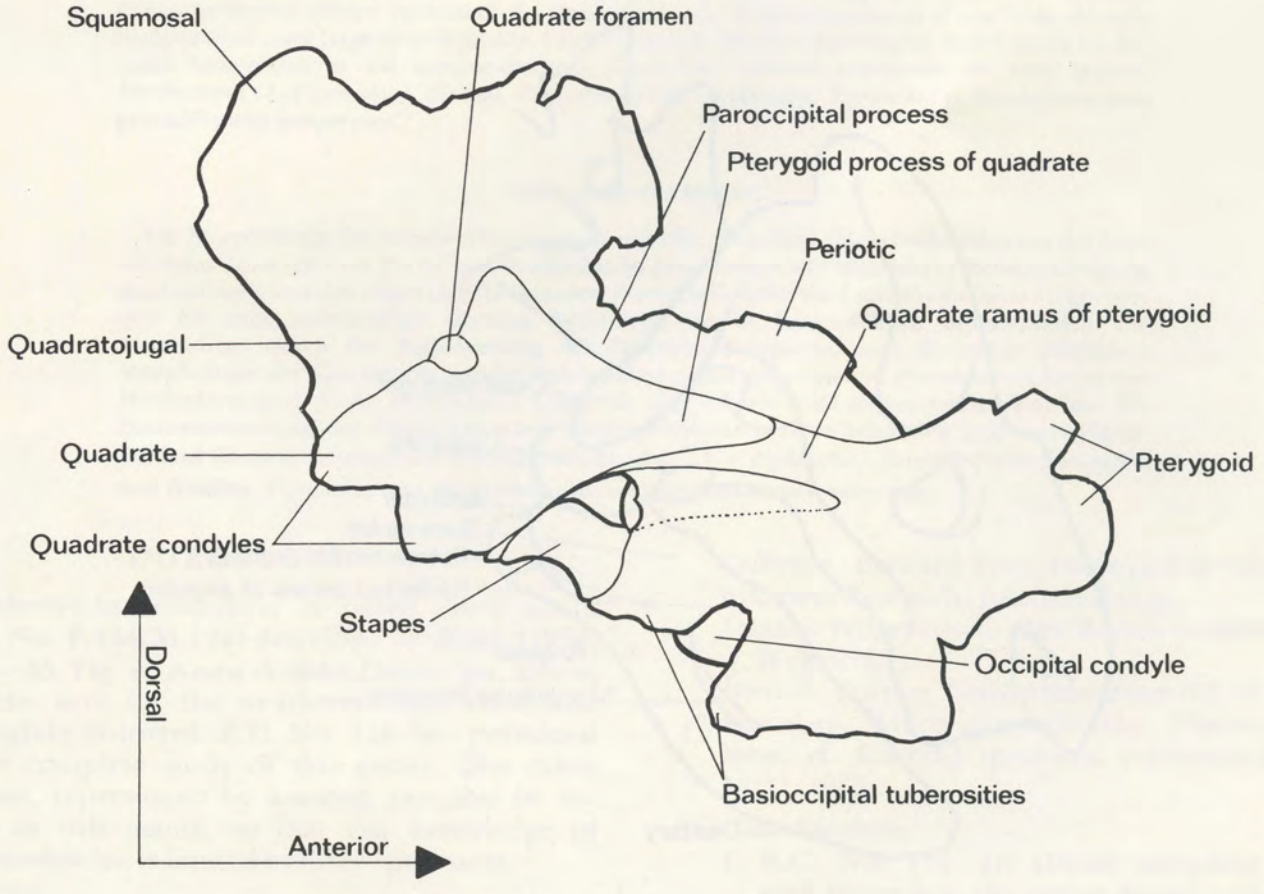


Fig. 6 *Upper*
Ventro-lateral view of the occipital part of the skull of *Jacheleria platyceps* showing the pterygoid process of the quadrate.
Lower
Tracing of photograph with the various elements annotated.



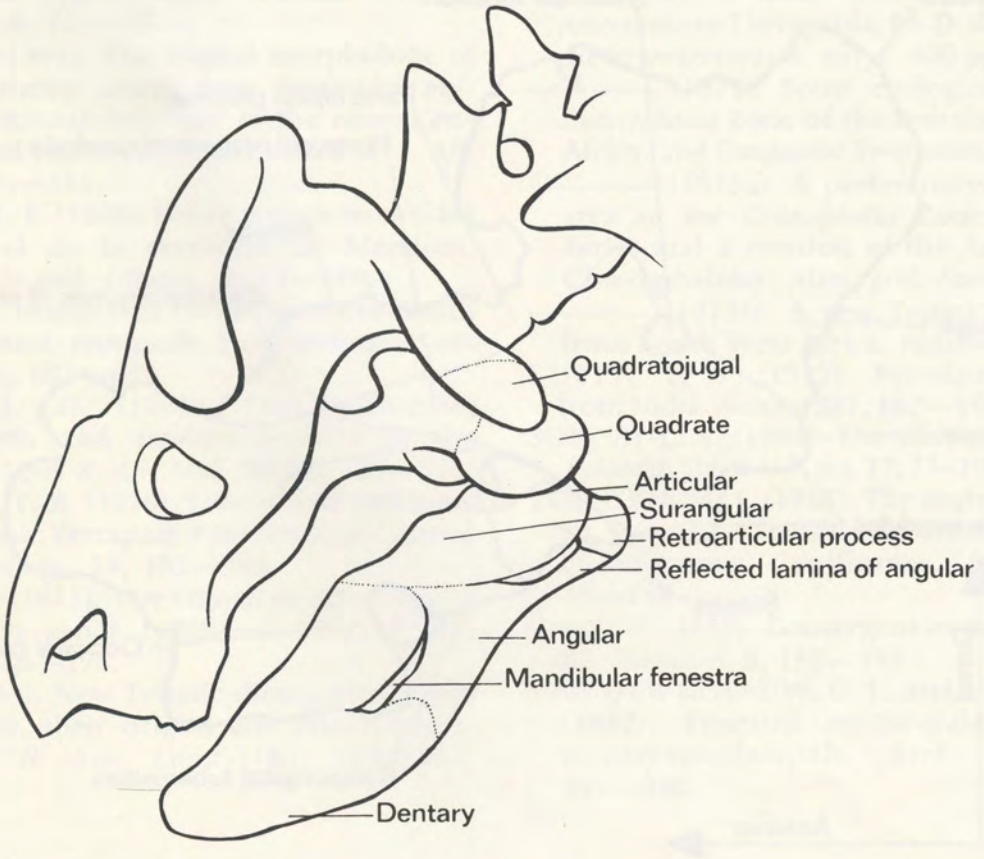


Fig. 7 *Upper*
Lateral view of the skull of a specimen of *Ischigualastia jenseni* in the museum of the Instituts Lillo, Tucumán, showing the joined reflected lamina and retroarticular process of the lower jaw and the absence of the quadrate foramen.
Lower
Tracing of photograph with the various elements annotated.