

NEW VERTEBRATE EVIDENCE FOR A SOUTHERN TRANSATLANTIC CONNEXION DURING THE LOWER OR MIDDLE TRIASSIC

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ABSTRACT. Two species of therapsid reptile found in rocks of probable Lower Anisian age, in the Province of Mendoza, Argentina, are compared with similar forms from the Cynognathus Zone of South Africa. One of them is a dicynodont, *Kannemeyeria argentinensis*, which differs from the African form *Kannemeyeria erithrea* in only minor details. The other is a cynodont, *Pascualgnathus polanskii*, which shows very clear similarities to the African genera *Trirachodon* and *Diademodon*. The striking affinities of these Argentine species with African forms are interpreted by the author as evidence that Africa and South America were connected in some way during the Lower Triassic time.

THE concept of continental drift, first popularized by Wegener and du Toit, has been revived in recent years. However, it is now based upon a considerable variety of new types of observation. The analysis of submarine geology, palaeomagnetic data, geophysical measurements of heat flow in continental and oceanic regions, interpretation of earthquake zones, computer matching of continental shelf outlines, and other investigations, have all contributed to the revival of the idea that the present arrangement of the continents is the result of the break-up of an original supercontinent. These different geological investigations are in agreement with new palaeontological work on Triassic tetrapods from Argentina (Bonaparte 1966a), which seem to indicate that South America and Africa were directly connected with one another during the early Triassic.

Two therapsids have been collected in the central region of the Province of Mendoza, Argentina, south of the city of San Rafael, and were found in the upper part of the Puesto Viejo formation. This formation has been studied recently by Gonzalez Diaz (1964) and is exposed in a geomorphological district which he calls the Piedmont Elevation of Mendoza. One therapsid is a kannemeyeriid dicynodont, *Kannemeyeria argentinensis* Bonaparte (1966b); it is represented by a complete and well-preserved specimen. The other is a diademodontid cynodont, *Pascualgnathus polanskii* Bonaparte (1966b); this is also represented by excellent specimens.

Though this Puesto Viejo fauna is as yet known by these two species alone, it is clearly different from, and older than, the previously known Argentinian Triassic fauna of Ischigualasto (Romer 1962). The Puesto Viejo fauna instead appears to be contemporary with the cynodont *Colbertosaurus muralis* Minoprio (1954) from the Potrerillos formation of Mendoza. However, like other terrestrial faunas of the southern hemisphere, the Puesto Viejo fauna cannot be assigned to a precise period of the Triassic. As far as its age relative to the other faunas is concerned, it may be significant that the cynodont *Pascualgnathus* appears to be more advanced than the diademodontids of the Cynognathus Zone of South Africa in several features, i.e. in having a slightly longer secondary palate, larger canines, and sub-parallel tooth rows. If the Cynognathus Zone is provisionally regarded as Scythian in age, it would appear reasonable to regard the Puesto Viejo as of Lower Anisian age. This would imply that some elements of the

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Scythian fauna survived into a later horizon in South America, just as they did into the later Ntawere and Manda formations of Africa (Attridge *et al.* 1964; Brink 1963).

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THE PUESTO VIEJO FAUNA

Kannemeyeria argentinensis

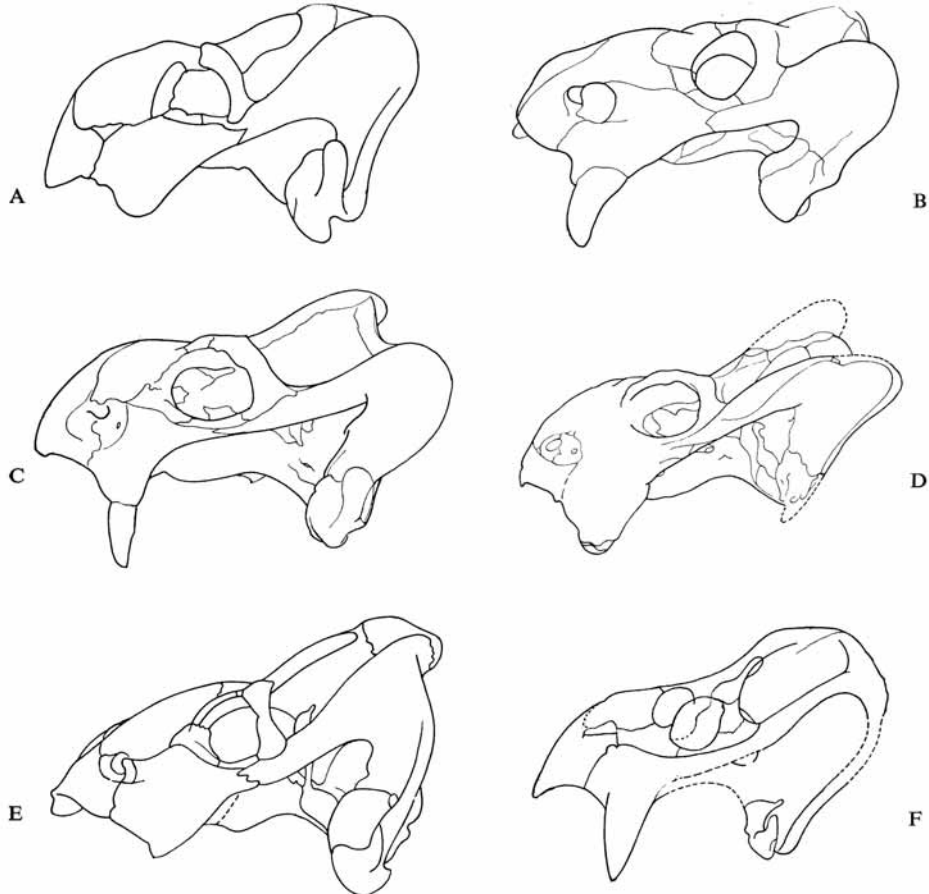
As can be seen from text-fig. 1, the new Puesto Viejo dicynodont is extremely similar to the South African genus *Kannemeyeria*, and is quite unlike the other known Triassic genera. In fact, no reason for separating it from the genus *Kannemeyeria* can be found, and its taxonomic status must therefore be established at the species level. The African species of *Kannemeyeria* are difficult to distinguish from one another; Cox (1966, pers. comm.) writes as follows: 'Unfortunately, as noted by Cruickshank (1965), the taxonomy of the South African species of *Kannemeyeria* is extremely obscure. However, the Argentinian form does appear to differ from *K. simocephalus* in lacking a fronto-nasal boss, and from *K. latifrons* in having ventrally (rather than antero-ventrally) directed canine tusks. In this last feature it is similar to the only other valid South African species, *K. erithrea*, and the skulls of these two forms are extremely similar. In the present state of our knowledge of the South African species, it is not possible to establish with certainty whether the Argentinian form is identical with *K. erithrea*, or whether it is specifically different.' The second, and somewhat more conservative course, of recognizing the Puesto Viejo form as a new species closely allied to *K. erithrea*, has provisionally been taken (Bonaparte, 1966a, 1966b). Some of the characters shared by *K. erithrea* and *K. argentinensis* are as follows:

1. The preorbital length is 30% and 31%, respectively, of the total length of the skull.
2. The structure of the 'narial depression', formed by maxilla, premaxilla, and septomaxilla.
3. The characters of the circumorbital bones, with similar rugosities on the prefrontal, frontal, and postorbital bones.
4. The characters of the 'lacrymal depression' that apparently communicates superficially with the 'narial depression'.
5. The exposure of the jugal in lateral view, behind the postorbital and above the squamosal.
6. The morphology of the maxilla and of its alveolar canine process.
7. The relation between jugal and maxilla below the orbit.
8. The characters of the median projection of the squamosal.
9. The pattern of ossification of the septosphenoid.
10. The topography of the parietal, and its relations with the squamosal.
11. The narrow parietal crest.
12. The projection of premaxilla posteriorly, separating the anterior ends of the nasals.

The differences between the two species are basically of a lesser degree, among which are a different extension of the epipterygoid ventrally, the presence of a ventral keel formed by both pterygoids, and the posterior projections of both squamosals, slightly more pronounced in *K. argentinensis*.

Affinities in the postcranial skeleton are evident between *K. argentinensis* and *Kannemeyeria sp.* illustrated by Pearson (1924), in the following aspects: the characters of the

pelvic girdle in the form of the ilium, the acetabulum and its borders, the proportions and the form of the ischia, and what can be seen of the pubis (incomplete in *K. argentinensis*).

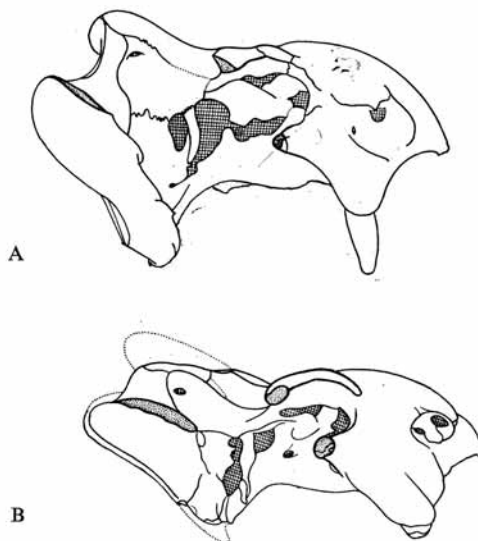


TEXT-FIG. 1. Skulls of some Triassic kannemeyeriids reduced to similar length, to compare with *Kannemeyeria argentinensis*. A, *Stahleckeria potens*, Brazil, after von Huene; B, *Dinodontosaurus turpior*, Brazil, after Cox; C, *Kannemeyeria argentinensis*, Argentina; D, *Kannemeyeria erithrea*, South Africa, after Watson; E, *Ischigualastia jenseni*, Argentina, after Cox; F, *Placerias gigas*, North America, after Cox.

Common characters of the hind limb are clear in the femur in nearly all its morphology, as for example in its flattened shape and in the relation between the femoral head and the trochanter major. The proportions of the femur differ in the two species; this may be due to their different size.

In the pectoral girdle there are affinities in the acromion process, the position of the coracoid foramen, and the depression which runs from this up the lower portion of the inner surface of the scapula.

In the humerus some affinities are noticeable and, bearing in mind the different size of the specimens compared, they are of interest. The well developed deltoid crest, the strong wide ectepicondyle, the well defined shaft in the middle of the humerus, are all characters common to both forms.



TEXT-FIG. 2. Lateral view of the skull, without the temporal and postorbital arches, of A, *Kannemeyeria argentinensis*, $\times \frac{1}{3}$; and B, *Kannemeyeria erithrea* (after Watson), $\times \frac{1}{2}$ approx.

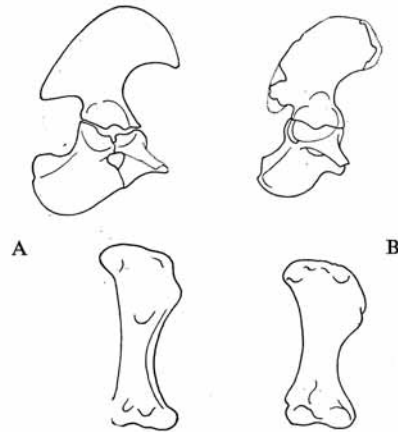
The ulnae of the two species are of different proportions: that of *K. argentinensis* is longer and thinner, but its proximal characters are very similar to those illustrated by Pearson. The few presacral vertebrae at our disposal and the few illustrated by Pearson show some common characters, such as the relative position of the zygapophysis and neural spine. The length of the vertebral centrum differs in the two species.

The skull of *K. argentinensis* is 26 cm. long, and that of South African species of *Kannemeyeria* ranges from 36 to 50 cm. long approximately. The difference of size is thus clear, and may well be the reason for the different proportions of some postcranial bones.

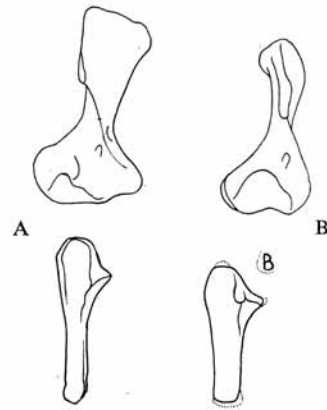
Pascualgnathus polanskii

This Puesto Viejo cynodont is of gomphodont type, but appears to be generically distinct from any previously known form. Though in some cranial characters it is

similar to *Exaeretodon*, the lumbar region is quite different. Furthermore, its dentition is different from that of *Exaeretodon*, *Ischignathus*, and *Proexaeretodon* (which are all traversodontid cynodonts from the Ischigualasto formation of Argentina), and from that of *Traversodon* and *Gomphodontosuchus* (from the Santa María formation of Brazil). *Colbertosaurus muralis* from the Potrerillos formation of Mendoza (Minoprio 1954) appears to be a related form, but the only specimen known is an incomplete mandible with broken teeth. Finally, the cranial characters of *Pascualgnathus* differ from those of the Brazilian form *Belesodon*. Though it is thus quite unlike the South



TEXT-FIG. 3. Lateral view of the right pelvis, and ventral view of the right femur, of A, *Kannemeyeria argentinensis*, $\times \frac{1}{4}$; and B, *Kannemeyeria* sp. (after Pearson), $\times \frac{1}{2}$ approx.

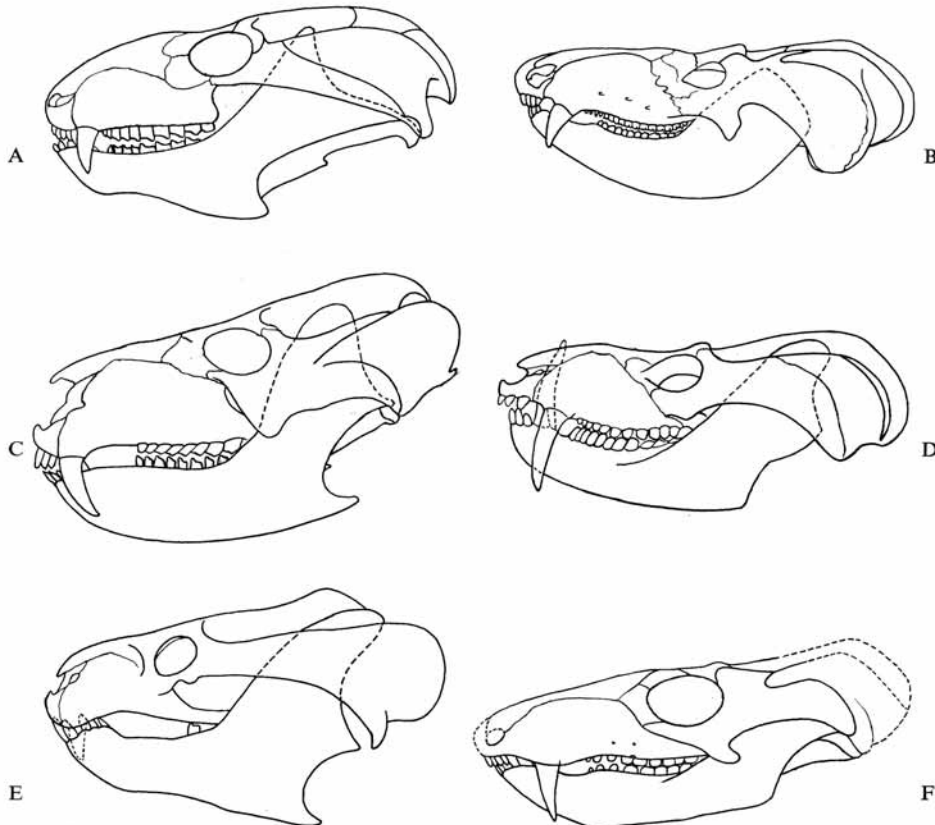


TEXT-FIG. 4. Ventral view of the humerus and median view of the ulna of A, *Kannemeyeria argentinensis*, $\times \frac{1}{4}$ and B, *Kannemeyeria* sp. (after Pearson), $\times \frac{1}{2}$ approx.

American genera, *Pascualgnathus* shows close similarities to the African genera *Trirachodon* and *Diademodon*, and it is thus considered as a diademodontid. The more obvious similarities between *Pascualgnathus* and *Trirachodon* are as follows:

1. The position of both postcanine rows is subparallel, with a minor outward divergence posteriorly.
2. Both have the same number of maxillary postcanine teeth.
3. More or less straight contact between each one of these teeth.
4. The first maxillary postcanines are small, and the others are progressively larger as far as the 7th-8th teeth, and then decrease posteriorly.
5. There are three teeth behind the level of the posterior border of the secondary palate.
6. There is a noticeable maxillary bulge from the row of teeth to the border of the maxilla.
7. There is a short diastema between the canine and the postcanine teeth (more pronounced in *T. berryi*).
8. The morphology of the choana roof (primary palate), up to the level where the pterygoids meet.
9. The position of the paracanine fossae.
10. The presence of a diastema between the incisor and canine teeth.
11. Both have the same number of incisor teeth, the third being the largest.
12. The characters of the area for the Jacobson's organ.
13. The apparent absence of the parietal foramen.

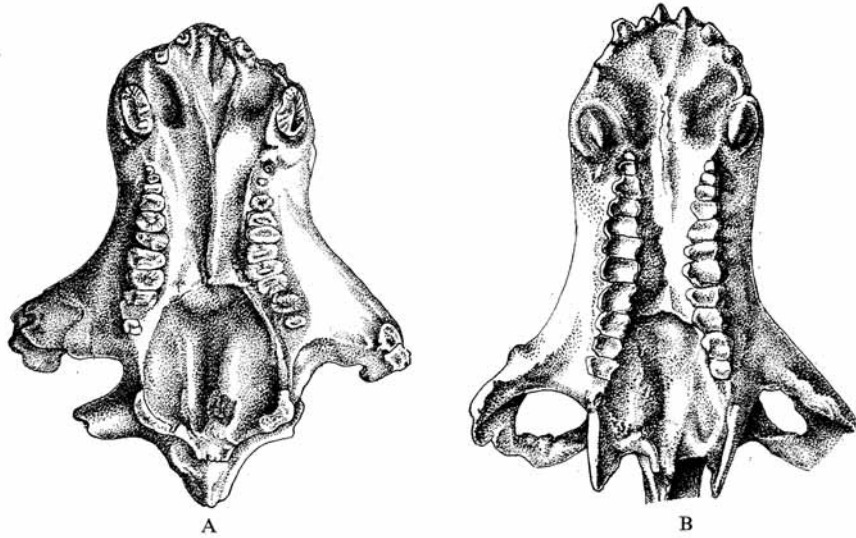
14. The parietal crest is thin and long.
15. There is an occipital crest which diverges slightly posteriorly.
16. The temporal fossae are lengthened and the temporal arch is subparallel to the axial plane.
17. The orbits are placed a little forward of the middle of the skull length.
18. The premaxilla extends anteriorly for a considerable distance beyond the canines.
19. There is a high coronoid process in the lower jaw.



TEXT-FIG. 5. Skulls and jaws of some Triassic gomphodont cynodonts, reduced to similar length, to compare with *Pascualgnathus polanskii*. A, *Traversodon stahleckeri*, Brazil, after von Huene; B, *Diademodon mastacus*, South Africa, after Brink; C, *Exaeretodon frenguelli*, Argentina, after Bonaparte; D, *Pascualgnathus polanskii*, Argentina; E, *Ischignathus sudamericanus*, Argentina, after Bonaparte; F, *Trirachodon kannemeyeri*, South Africa, after Broom.

The principal affinities with *Diademodon*, besides some of general terms, are particularly striking in the braincase region: the topography of the parietal bone, the venous foramen between parietal, prootic, and alisphenoid, the characters of the 'foramen lacerum anterius', and the parasphenoid rostrum.

In the postcranial skeleton, many axial elements of good diagnostic value show great similarities between *Pascualgnathus* and *Diademodon*. A succession of 17 articulated vertebrae have been preserved in *Pascualgnathus*, including 9–10 presacral, 3–4 sacral, and 3–4 caudal, all with the ribs. The vertebral centra, as well as the ribs, are very much like those of '*Microgomphodon*' Seeley (1895), which is possibly a juvenile *Diademodon* (*vide* Brink 1955, p. 31); the relative size of the ribs, their relation to each other, and their form (especially of the sacral ribs) are very similar. Even though these axial elements



TEXT-FIG. 6. Palatal view of the skull of A, *Trirachodon berryi* (from Seeley), $\times 1$; B, *Pascualgnathus polanskii*, $\times 1$.

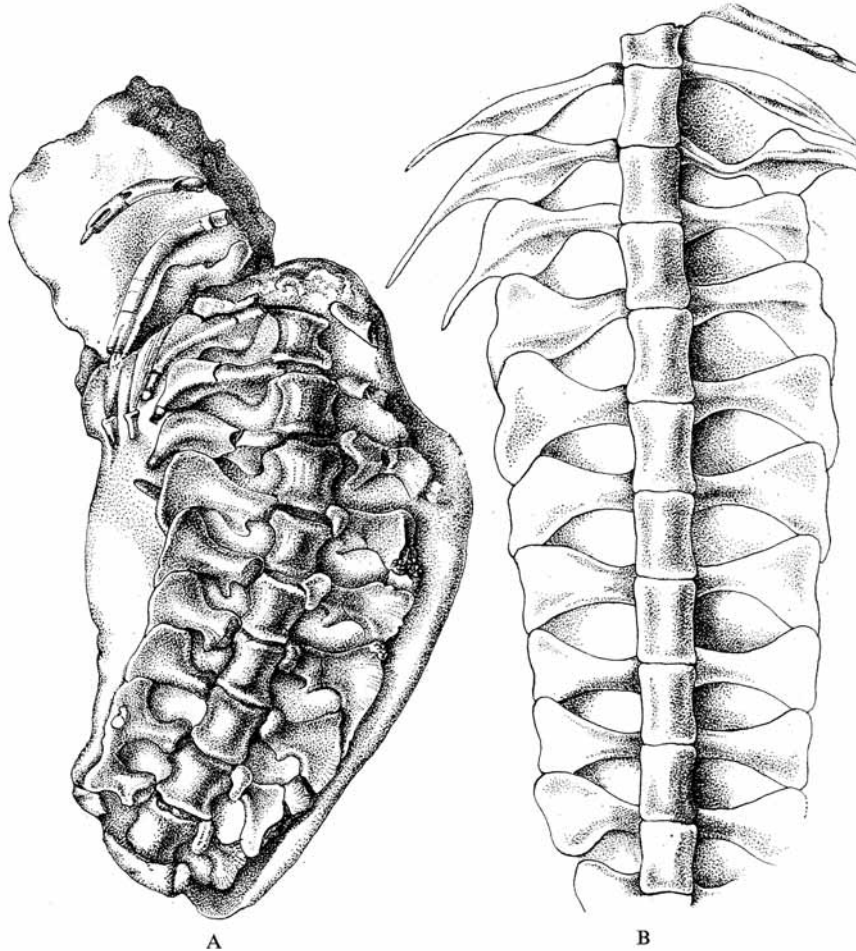
have been compared with those of a young specimen of *Diademodon*, the similarities observed seem highly significant.

It is possible to find resemblances in the other postcranial bones also. For the purposes of this paper the above points are adequate to establish that *Pascualgnathus polanskii* is a gomphodont cynodont related to the African diademodontids. Such characters as the hypertrophy of the canines, the absence of the internarial septum, the greater proportional extension of the secondary palate, and the smaller distance between the post-canine teeth rows, are anatomical features which suggest that *Pascualgnathus* may be more recent than the diademodontids from the Cynognathus Zone.

CONCLUSIONS

The significance of the similarity between these Argentinian species and the African forms must now be considered. Firstly, the characters of *K. argentinensis* appear to be more significant than those of *Pascualgnathus*. The kannemeyeriids, known from the

major part of Triassic times, are composed of a heterogeneous group of forms, and Cox (1965) has proposed their separation into three families. First Camp (1956) and later Cox (1965) have explained that adaptations to distinct herbivorous diets may be



TEXT-FIG. 7. Ventral view of presacral and two sacral vertebrae and ribs of A, '*Microgomphodon*' *oligocynus* (from Seeley), $\times 1$ (considered by Brink as a possible tiny *Diademodon*); B, *Pascualgnathus polanskii*. $\times 1$.

the cause of the noticeable strong variation in the skull morphology of these anomodonts. With this in mind, it is necessary to accept a great plasticity in the kannemeyeriids to react to different conditions, a fact which is in agreement with what is known of this

group. From this point of view, the affinities of *K. argentinensis* with the other species of the genus (especially *K. erithrea*) acquire great significance. Although the affinities of the cynodont *Pascualgnathus* with *Trirachodon* and *Diademodon* are somewhat less close, they are still of great interest. The cynodonts as a whole are apparently more conservative than the kannemeyeriids. Their evolutionary history is continuous, but is restricted to a single trend; as a result the South American, African, and the other cynodonts are comparable and their inter-relationships are more easily understood. However, this relative constancy and uniformity of the group within the cynodonts still seems inadequate to account for the extremely close affinity between *Pascualgnathus* and the African genera.

K. argentinensis and *P. polanskii* are thus very closely related to almost contemporaneous African forms. It is clear in the light of present knowledge that only a direct immigration from Africa to South America (or a common African-South American evolution), could explain such remarkable likeness between the therapsids from San Rafael, Argentina, and those from the Cynognathus Zone of Africa.

Among the works published in the symposium on *The Problem of land connection across the South Atlantic*, two papers on tetrapods (Romer 1952; Colbert 1952) discuss, from a different point of view, the probability of direct faunal interchanges between South America and Africa during Permo-Triassic times. Romer's conclusions were particularly liberal, recognizing the strong similarities between the Brazilian fauna (at that time the Ischigualasto and San Rafael faunas were unknown) and those of Africa, and accepting the direct interchange between the two southern continents as a possibility.

Among other authors that discuss the problem with analysis of Triassic tetrapods, Camp thought that, as far as the evidence from the Kannemeyeriidae was concerned, it seemed unnecessary to invoke theoretical southern connexions to explain the Triassic Dicynodont distribution: 'yet, the Dicynodont relationships do not entirely disprove such connections' (Camp 1956, p. 329). Reig (1962) accepted as a fact the immigration to South America of numerous Triassic tetrapods of 'Gondwana lineage', in our opinion without the necessary requirements of comparative analysis of the anatomy of the different groups involved.

Cox (1965) gives a list of the Triassic reptilian faunas of East Africa and South America, and considers different aspects of the relative ages of the faunas concerned. He suggests that the differences between the Argentine (i.e. Ischigualasto), Brazilian, and East African faunas could be explained either as resulting from their being of somewhat different ages or, alternatively, that the differences could be because they were on different continents. Cox mentions some conclusions on continental connexions by Creer (1964), but did not feel that there was sufficient evidence to permit a choice between these alternatives. We support, however, Cox's first alternative, that the Triassic fauna from Brazil and Argentina (only Ischigualasto), may be placed in the uppermost Middle Triassic or at least that of Ischigualasto more reasonably in the lowermost Upper Triassic and that, on the other hand, the East African Triassic faunas would be of Anisian age. The differences between these faunas are then due to their different ages.

As pointed out by Romer (1952, p. 250), to come to completely valid conclusions in relation to faunal connexions, the analysis must be based on comparisons of contemporary faunas. In this paper we have considered two species from Argentina of probable

Anisian age, with African genera of Scythian age. Nevertheless, the faunal elements known from Africa in recent years (Crompton 1955; von Huene 1942; Brink 1963; and others cited by Cox 1965) assigned to the lower Middle Triassic, show that such genera as *Kannemeyeria* and *Diademodon* survived beyond the Scythian Cynognathus Zone, into Anisian times. It does seem permissible, under these circumstances, to compare the Anisian San Rafael fauna with that of the Cynognathus Zone and, to some extent, with that of the Manda Beds.

The above affinities between the Argentine and African forms give good evidence of a type of direct faunal connexion which can only be interpreted as a solid continental union. The evidence for this conclusion meets the two fundamental requirements: (a) anatomical similarities of great significance, (b) very similar faunal ages.

REFERENCES

- ATTRIDGE, J., BALL, H. W., CHARIG, A. J., and COX, C. B. 1964. The British Museum (N.H.)—University of London joint palaeontological expedition to Northern Rhodesia and Tanganyika, 1963. *Nature, Lond.* **201**, 445–9.
- BONAPARTE, J. F. 1966a. Sobre Nuevos Terápsidos Triásicos hallados en el Centro de la Provincia de Mendoza, Argentina. (Nota previa.) *Acta geol. lilloana*, **8**, 91–100.
- 1966b. Una Nueva Fauna Triásica de Argentina. *Ameghiniana* **4**, 243–96.
- BRINK, A. S. 1955. A study on the skeleton of *Diademodon*. *Palaeont. afr.* **3**, 3–39.
- 1963. Two cynodonts from the Ntawere Formation in the Luangwa Valley of Northern Rhodesia. *Palaeont. afr.* **8**, 77–96.
- CAMP, C. L. 1956. Triassic dicynodont reptiles. Part 2. Triassic dicynodonts compared. *Mem. Univ. Calif.* **13**, 305–48.
- COLBERT, E. H. 1952. The Mesozoic tetrapods of South America. In 'Land connections across the South Atlantic, etc.' *Bull. Am. Mus. nat. Hist.* **99**, 237–49.
- COX, C. B. 1965. New Triassic dicynodonts from South America, their origins and relationships. *Phil. Trans. R. Soc. (B)*, **248**, 457–516.
- CREER, K. M. 1964. A reconstruction of the continents for the Upper Palaeozoic from palaeomagnetic data. *Nature, Lond.* **203**, 1115–20.
- CROMPTON, A. W. 1955. On some Triassic cynodonts from Tanganyika. *Proc. zool. Soc. Lond.* **125**, 617–69.
- CRUICKSHANK, A. R. I. 1965. On a specimen of the anomodont reptile *Kannemeyeria latifrons* from the Manda Formation of Tanganyika, Tanzania. *Proc. Linn. Soc. Lond.* **176**, 149–57.
- GONZALEZ DIAZ, E. P. 1964. Rasgos Geológicos y Evolución Geomorfológica de la Hoja 27d (San Rafael) y Zona Occidental Vecina (Provincia de Mendoza). *Rev. Asoc. Geol. Argentina*, **19**, 151–88.
- HUENE, F. VON. 1942. Die Anomodontier des Ruhuhu-Gebietes in der Tübinger Sammlung. *Palaeontographica*, **94**, 154–84.
- MINOPRIO, J. L. 1954. Theriodonte en el Triásico de Mendoza. *An. Soc. Cient. Argent.* **157**, 31–37.
- PEARSON, H. S. 1924. A dicynodont reptile reconstructed. *Proc. zool. Soc. Lond.* 1924, 827–55.
- REIG, O. A. 1962. Las Integraciones Cenogénicas en el Desarrollo de la Fauna de Vertebrados . . . etc. *Ameghiniana*, **2**, 131–40.
- ROMER, A. S. 1952. Discussion. In 'Land connections across the South Atlantic, etc.' *Bull. Am. Mus. nat. Hist.* **99**, 250–4.
- 1962. The fossiliferous Triassic deposits of Ischigualasto, Argentina. *Breviora*, **156**, 1–7.
- SEELEY, H. G. 1895. Researches on the structure, organization and classification of the fossil Reptilia. Part 9, Section 4. On the Gomphodontia. *Phil. Trans. R. Soc. (B)*, **186**, 1–162.

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