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Parallelism in the Evolution of the Permian Reptilian Faunas of the Old and New Worlds

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INTRODUCTION

When vertebrate remains were first encountered in the San Angelo Formation of Texas, we could not avoid speculations about resemblances of the newly found reptiles to mid-Permian forms of Russia and South Africa. Doubtless part of the speculation was prompted by a subconscious feeling that the fossils from these areas should show resemblances. It soon became apparent, however, that in size, at least, some of the North American reptiles did rival the largest of the relatively gigantic forms of the Old World mid-Permian. A more thorough study has shown that there is a notable similarity of adaptive types and that evolution, which appears to have been independent in the Old and New Worlds during the Permian, has produced a number of interesting parallels. Furthermore, it would appear that there is a rough time equivalence of the rocks in which these adaptive counterparts appear in the Old and New Worlds.

By the time that deposition of the San Angelo beds of north central Texas was taking place, the old, familiar, earlier Permian deltaic fauna had disappeared, at least in the Texas area, and had been replaced by a strikingly different assemblage. At about the same time, in Russia and South Africa, there appeared assemblages unknown from any earlier deposits. The Old World faunas have been studied for many years and described and discussed in numerous publications. The San Angelo forms have been known but a short time. Their general structure and relationships to earlier reptiles were considered in some detail in an earlier paper (Olson

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and Beerbower, 1953). Field work in 1953 and 1954 has added greatly to the knowledge of the described genera but has increased the generic list of seven only by one or two possible additions. In 1953 a find was made in the Flower Pot Formation, which directly overlies the San Angelo Formation in Texas (Olson, 1954). The specimens from this formation, with one or two exceptions, appear to be congeneric with members of the San Angelo assemblage. Field work has now been sufficiently extensive that it appears unlikely that the list of genera will be materially increased by additional work in the Texas area. It is thus a rather small array of genera that provides a basis for comparisons with the more extensive assemblages of Russia and South Africa. Even so, the comparisons yield much that is of interest in the areas of evolution and zoogeography. It is the principal purpose of this paper to outline the evolutionary history that led to the development of these assemblages, to compare the assemblages, and to attempt to evaluate their meanings.

There are, of course, many problems in such a study, and the conclusions must be considered in light of the difficulties. There is the problem of correct evaluation of the role of each species in the economy of the ecological system, the problem posed by the lack of information about the totality of the systems, the problem of correlation between continents, and that posed by the incomplete nature of the record of ancestral stocks. An effort has been made throughout this paper to point out the specific nature of these difficulties and the ways in which they have affected interpretations.

THE GROUPS OF ANIMALS CONSIDERED

Since the San Angelo and Flower Pot assemblages are almost exclusively reptilian, comparative studies are restricted to this class of animals. The major groups and pertinent subgroups that play an important part in the study are given in the classification on page 387.

The Diadectomorpha and Captorhinomorpha are often grouped into a single order of primitive reptiles, order Cotylosauria, in spite of the fact that the association has been repeatedly questioned by prominent students in the field. In the present analysis, the two groups play very different roles, and for this reason, if no other, they must be considered separately. Early captorhinomorphs were small and were lizard-like in general proportions. They appear to have been fast-running, carnivorous to omnivorous, terrestrial animals

CLASS REPTILIA

- Subclass Parareptilia¹
 - Infraclass Diadecta
 - Order Diadectomorpha
 - Family Diadectidae
 - Family Pareiasauridae
 - Family Procolophonidae
- Subclass Eureptilia
 - Infraclass Captorhina
 - Order Captorhinomorpha
 - Suborder Captorhinomorpha
 - Infraclass Synapsida
 - Order Pelycosauria
 - Suborder Ophiacodonta
 - Suborder Sphenacodontia
 - Suborder Edaphosauria
 - Family Edaphosauridae
 - Family Caseidae
 - Order Therapsida
 - Suborder Titanosuchia
 - Suborder Tapinocephalia
 - Suborder Anomodontia
 - Suborder Theriodonta
 - Infraorder Gorgonopsia
 - Infraorder Therocephalia

and to have played an important role in the early faunas. Later in their history, large herbivores, up to five or six feet in length, developed. *Diadectes* and other closely related genera represent the Diadectomorpha in the late Pennsylvanian and early Permian. They were heavy-bodied, slow-moving herbivores. They were succeeded later in the Permian by the massive, herbivorous pareiasaurs, and the lightly built, small procolophonids. The latter appear to have been adaptively similar to some of the smaller and earlier herbivorous captorhinomorphs.

Pelycosaurs were primitive mammal-like reptiles. The earliest, the ophiacodonts, appear to have arisen directly from primitive captorhinomorphs and to have accentuated the carnivorous potentialities of the ancestral stock. From the ophiacodonts came the active, highly predaceous sphenacodonts, of which *Dimetrodon* is the best known representative. The source of the edaphosaurians is less certain. The genus *Edaphosauria*, genotype of the family Edaphosauridae, occurs very early, near the beginning of the pelycosaur record. The caseids appeared first in the early Permian and

¹ Classification after Olson (1947).

became prominent only in the upper beds of this time. Both families consisted in large part of rather ponderous, slow-moving, terrestrial to semi-aquatic herbivores.

The therapsids, which were advanced mammal-like reptiles, probably arose from the sphenacodonts. There seems to be no doubt that this was the origin of the titanosaurs and theriodonts. The source of the tapinocephalids and anomodonts is less certain, but a sphenacodont ancestry seems most probable. If this was the case, later sphenacodont history set the stage for radiation into herbivorous modes of life as well as for increased adaptive spread in the carnivorous realm. This concept is important in the interpretation of the early radiation of therapsids and in evaluation of the differences between Old and New World radiations in the mid-Permian.

The fact that only reptiles can be considered in our comparisons limits the interpretation of faunal evolution. Undoubtedly both fish and amphibians, among the vertebrates, invertebrates, and plants, played a role in the modifications of the reptiles. Xenacanth sharks, primitive actinopterygians, dipnoi, and crossopterygians, among the fish, and lepospondylous and apsidospondylous amphibians are components of the Permian vertebrate faunas. The roles, both minor and major, that they have played in a Permian chronofauna have been discussed for the Clear Fork of North America elsewhere (Olson, 1951). It may be assumed that they were equally effective in less well-studied faunas and that their impact was in large part a function of the adaptive types present in a given area. Fortunately for our purposes, the taxonomic groups were widely dispersed in the Pennsylvanian and early Permian, and similar adaptive types within the higher categories occur in the various areas that have been studied. Thus, the fish and the amphibians probably played rather similar roles in the economy of contemporary ecological structures in the areas with which we are concerned. There seems fair justification for an assumption that, in a broad sense, the effects of fish and amphibians were more or less constant in the various areas during the time considered and that differences in reptilian evolution were dependent largely on other factors. Knowledge of directly associated invertebrates during this time is very slight. Understanding of the plants is somewhat better, but no co-ordinated studies to evaluate the effects of botanical differences have been made. It is beyond the scope of this report to attempt an evaluation of the effects of differences in the plants, but it seems probable that they were of considerable importance.

GEOLOGICAL AND GEOGRAPHICAL DISTRIBUTION OF REPTILES

The pertinent data are summarized in Table 1. There are, however, certain problems of contemporaneity of faunas that need to be considered, and important points of spatial and temporal distribution that require special emphasis. These can be treated by a systematic summary of the temporal sequences:

1. Late Pennsylvanian (Stephanian): The striking resemblances between the North American and European middle to late Stephanian vertebrate faunas have been discussed in some detail by Romer (1945) in his comparison of the North American faunas with that from Kounova in Bohemia. The general aspects of these faunas show clearly that they can be considered ancestral to the early Permian faunas of both North America and Europe. The similarities between the two continents are so great that it seems highly probable, as Romer argued, that there was direct and intimate connection between the two areas. Whether or not this type of fauna spread beyond the limits of the two continents is not known.

2. Early Permian (Autunian): The most complete vertebrate-bearing early Permian section in North America is found in the red beds of north central Texas. An excellent fauna has also come from the Abo (Cutler) of New Mexico, and a small, but most interesting series of assemblages is known from the Dunkard Formation of Ohio, West Virginia, and Pennsylvania. The Texas section may be extended into Oklahoma, where sporadic finds indicate a vertebrate fauna similar, in many respects, to that of Texas, but different in some important details.

The Texas section and probable time equivalents of the Abo and Dunkard are shown below:

	<i>Texas</i>	<i>New Mexico</i>	<i>Ohio, West Virginia, Pennsylvania</i>
Clear Fork Group.....	{ Choza
	{ Vale
	{ Arroyo
	{ Clyde
Wichita Group.....	{ Belle Plains	?	...
	{ Admiral	Abo	Dunkard
	{ Putnam		
	{ Moran	?	?

The faunas of Wichita age in Texas, New Mexico, Ohio, West Virginia, and Pennsylvania, while similar in higher categories, show many detailed differences. They indicate a geographic variation

TABLE 1.—DISTRIBUTION OF REPTILES

		North America	Western Europe	Russia	Africa
Late Permian (Thuringian)			Therapsids Diadectomorphs Pareiasaurids	Therapsids Diadectomorphs Pareiasaurids	Therapsids Diadectomorphs Procolophonids Pareiasaurids
Middle Permian (Saxonian, Kazanian)	L			Therapsids Titanosuchids Tapinocephalids Anomodonts	Therapsids Titanosuchids Tapinocephalids Anomodonts
	M			Pelycosaur Ophiacodonts Diadectomorphs Procolophonids Pareiasaurids	Theriodonts Gorgonopsians Therocephalians
	E	Pelycosaur Sphenacodonts Edaphosaurians Caseids Captorhinomorphs ?Therapsids Anomodont-like			Pelycosaur Sphenacodonts Diadectomorphs Pareiasaurids ?Captorhinomorphs
Early Permian (Autunian)	C h o z e a	Pelycosaur Sphenacodonts Edaphosaurians Caseids Captorhinomorphs			
		Pelycosaur Sphenacodonts Edaphosaurians Caseids Captorhinomorphs Diadectomorphs (basal only) Diadectids			
	G A r r o o u y p	Pelycosaur Ophiacodonts Sphenacodonts Edaphosaurians Edaphosaurids Captorhinomorphs Diadectomorphs Diadectids			
		Pelycosaur Ophiacodonts Sphenacodonts Edaphosaurians Edaphosaurids ?Caseids Captorhinomorphs Diadectomorphs Diadectids	Pelycosaur Sphenacodonts Edaphosaurians Edaphosaurids Diadectomorphs Diadectids		
W i G c r h o i u t P a	Pelycosaur Ophiacodonts Sphenacodonts Edaphosaurians Edaphosaurids ?Caseids Captorhinomorphs Diadectomorphs Diadectids	Pelycosaur Sphenacodonts Edaphosaurians Edaphosaurids Diadectomorphs Diadectids			
Pennsylvanian (Stephanian)		Pelycosaur Ophiacodonts Edaphosaurians Edaphosaurids Captorhinomorphs	Pelycosaur Ophiacodonts Sphenacodonts Edaphosaurians Edaphosaurids Captorhinomorphs		

in North America, during the early Permian, as great as that between North America and Europe at the beginning of the period.

The only known continuous sequence of early Permian vertebrates is from Texas, and it is from this area that most of our knowledge of faunal evolution in the early Permian has come. There is a recognizable, reasonably coherent fauna throughout the early Permian, but there are important changes in composition and these have an important bearing on the constitution of the mid-Permian assemblage. The most important among the changes are as follows:

CAPTORHINOMORPHA: Very primitive, carnivorous to omnivorous genera occur in the lowest part of the section (*Proterothyris*, *Romeria*). These are replaced by the well-known genus *Captorhinus* in the middle Wichita. A larger genus, *Labidosaurus*, is present with *Captorhinus* during the Arroyo. With the inception of the Vale, the captorhinomorphs began a rather extensive adaptive radiation that produced herbivores found in the Vale and Choza. There are four genera known from the Vale: *Captorhinus*, *Captorhinikos*, *Captorhinoides*, and *Labidosaurikos*. All except *Captorhinoides* occur in the Choza. It is significant that after the very early Wichita all captorhinomorphs were either omnivores or herbivores and that the early carnivorous potential was not realized within the order.

No captorhinomorphs are known in post-Stephanian times in Europe. The record during the Autunian is poor, yet it seems probable that had the captorhinomorphs undergone a development comparable to that in the New World some record would have come to light. This absence, if real, may have had an important bearing on the evolution that produced the mid-Permian fauna of Europe.

DIADLECTOMORPHA: In the Texas beds there is but a single genus of this group, *Diadectes*. *Diasparactus*, *Diadectes*, and possibly a third genus are known from New Mexico, and *Desmatodon* is present in the Dunkard. So far as is now known, *Diadectes* did not persist beyond the lowest Vale time. At least two genera of diadectids are present in the Autunian of western Europe. Presumably this family formed an important element of the fauna.

PELYCOSAURIA: Ophiacodonts are prominent during the Wichita and persist in very reduced numbers into the early Clear Fork. Thereafter they are unknown. These primitive pelycosaurs probably came from the early captorhinomorphs and have emphasized the carnivorous potentials of that group. Sphenacodonts persist into the mid-Choza, into the youngest vertebrate-producing beds of the Clear Fork. There is considerable diversity of genera and species

in the Wichita and the Arroyo, but thereafter only a single species, *Dimetrodon gigashomogenes*, is present.

The two families of the edaphosaurians have very different histories and must be considered separately. There is diversity of the Edaphosauridae in Wichita times. One genus, *Edaphosaurus*, persists through the Arroyo. A single specimen of the family Caseidae is known from the Abo of New Mexico, but the family is not known from the Texas section until the beginning of the Vale. Three temporally successive species of *Casea* occur in the Vale and Choza. A second genus, *Cotylorhynchus*, is present in the Hennessey Formation of Oklahoma, a Vale or Choza equivalent.

Sphenacodonts and edaphosaurids are known from the western European Autunian. As in North America, the genus *Edaphosaurus* is present, but in Europe this genus alone represents the family. Three genera of sphenacodonts are recognized by Romer and Price (1940). *Haptodus*, which is at about the same level of development as *Sphenacodon* and *Dimetrodon*, is much the best known. Caseids have not been found in the Old World.

The fauna of the European Autunian resembles that of the very early Permian of North America in the presence of *Edaphosaurus* and sphenacodonts. The case for continuity of the continents, however, is not particularly strong, for the two faunas could have been derived independently from the common Stephanian fauna. Also, the degree of divergence of the mid-Permian faunas of the Old and New Worlds indicates that separation had occurred well down in the early Permian.

No other Autunian faunas have been described, although Price, in informal communication, has indicated that there may be an Arroyo equivalent in Brazil. The latest early Permian assemblage in North America includes sphenacodonts, caseids, and captorhinomorphs. Of these, only the first is known from the early Permian of Europe.

3. Mid-Permian. The mid-Permian faunas of Russia and South Africa differ markedly in constitution from the earlier Permian assemblages of either North America or western Europe. Therapsids and diadectomorphs are the principal reptiles. The diadectomorphs are pareiasaurs and procolophons, rather than diadectids. There are only remnants of pelycosaurs. No captorhinomorphs are known from Russia. One family, Milleretidae, has been reported from South Africa, but, as Broom (1938), who described the material, has noted, the assignment is open to doubt.

The North American assemblage.—The families of reptiles in the North American mid-Permian are the same as those in the late Clear Fork, except for the family of one genus, *Dimacrodon*, which has therapsid affinities. The change, at the generic level, is striking. It seems improbable that the mid-Permian fauna was derived directly from the known fauna of the Choza. Of the reptiles, only *Coty-lorhynchus*, which is present in the Hennessey of Oklahoma, has been found in earlier beds. Most striking is the strong tendency toward large size. There existed forms that approximate pareiasaurs, titanosuchids and tapinocephalids in general dimensions and bulk. There appear to be strong resemblances in the types of changes and adaptations in the New and Old Worlds, but changes that stemmed from very different immediate ancestors. The reptiles of Russia and South Africa have been thoroughly described in such general works as Romer (1945), Broom (1932), von Huene (1940), and Olson (1944). The North American materials have been but recently discovered and have only been described briefly (Olson and Beerbower, 1953). The salient features of this fauna are as follows:

Seven genera of reptiles have been identified from the San Angelo and Flower Pot Formations of Texas. In addition, xenacanth sharks and a problematic amphibian jaw have been found. The ranges and numbers of specimens are shown in Table 2. It has been noted that the mid-Permian reptiles were strikingly larger than the largest of their immediate predecessors. Table 3 gives examples of the differences, based on comparisons of available materials.

The identified genera and their principal characters are as follows:

Rothia: This is a large captorhinomorph which probably ran from five to six feet in length. The skull was heavy and the palate was set with long, irregularly spaced teeth. The animal was undoubtedly a herbivore and probably was somewhat like the edaphosaurids in habits. There is no certain ancestor among known captorhinomorphs.

Steppesaurus: This is a large sphenacodont, about one-fifth to one-fourth larger than the largest known specimens of *Dimetrodon*. Like *Dimetrodon*, it had greatly elongated neural spines. The spines and general structure suggest that it arose from *Dimetrodon*. *Dimetrodon* was widespread through Oklahoma and Texas during the Clear Fork and appears to have crossed boundaries between adjacent ecosystems.

TABLE 2.—GENERA OF VERTEBRATES KNOWN FROM SAN ANGELO
AND FLOWER POT FORMATIONS OF TEXAS

Genus	SAN ANGELO				FLOWER POT		Sediments	Habitat(s)
	Lower	Middle	Upper	Lower	Upper			
<i>Xenacanthus</i>	0	0	3	0	0	clay pebble conglomerate	stream channels	
" <i>Trimerorhachid</i> ".....	0	1	0	0	0	gray siltstone	pond margin	
<i>Rothia</i>	0	2	3	2	2	red shale, sandstone	flood plain, pond margin	
<i>Steppesaurus</i>	0	2	1	0	0	red shale, clay pebble conglomerate	flood plain, swamp margin	
<i>Tappenosaurus</i>	0	1	9	1	1	red shale, gray shale, sandstone	flood plain, swamp	
<i>Dimacrodon</i>	0	0	3	0	0	green sandstone	flood plain	
<i>Cotylorhynchus</i>	0	0	1	1	1	green sandstone, red shale	flood plain	
<i>Caseoides</i>	0	5*	0	2*	2*	red shale	flood plain	
<i>Angelosaurus</i>	0	1	0	2*	2*	red shale	flood plain	

* One specimen listed as *Caseoides* from mid-San Angelo may possibly belong to a closely related genus. Two specimens listed as *Caseoides* from Flower Pot are probably this genus but material is quite fragmentary. Two specimens listed as *Angelosaurus* are tentatively assigned. They are closely related but have not been studied in sufficient detail to make identification certain.

Tappenosaurus: This carnivorous reptile was the giant of the fauna. It probably stood about 5 feet at the shoulder and, assuming a sphenacodont type of tail, was at least 18 feet in length. What is known of the skull indicates sphenacodont affinities, but there is no known ancestor in the earlier Permian.

Cotylorhynchus: This genus occurs in the Hennessey Formation of Oklahoma. The San Angelo-Flower Pot representative is about one-fourth larger than the Hennessey species. *Cotylorhynchus* was a herbivore of caseid affinities.

Caseoides: This genus is somewhat larger than *Casea halselli* from the Choza but could well have been derived from the genus *Casea*. It is one of the commonest genera in the San Angelo-Choza and probably was an important element of the fauna. Its adaptive characters appear to be similar to those of the late Vale and Choza species of *Casea*, for it was evidently a slow-moving, herbivorous inhabitant of flood plains and margins of bodies of standing water.

Angelosaurus: This genus has been tentatively assigned to the Caseidae. It was a large, clumsy herbivore with short limbs and relatively enormous feet. The body structure tended to be massive throughout. There is no known ancestor of *Angelosaurus* in the earlier Permian.

Dimacrodon: This genus has been tentatively assigned to the Therapsida. Unfortunately it is known largely from jaws and skull fragments. It has a pair of enlarged "canine" teeth and small post-canine teeth. There were no "incisors" and the broad symphysis of the lower jaw probably was covered by a horny beak. There are no certain ancestors in the earlier Permian. It is quite possible that this "therapsid" was from a sphenacodont stock and that it evolved independently of the Old World therapsids.

There are uncertainties in the correlations between the three areas that are our chief concern and at present there is no way of resolving the difficulties. Presumably the greatest hope lies in the use of botanical remains, but the materials necessary have not as yet been obtained. The North American deposits have been placed in the mid-Permian on the basis of local stratigraphic and faunal evidence (see Olson and Beerbower, 1953). The same in general is true for the Russian and South African deposits. The North American deposits are certainly no younger than earliest mid-Permian, but they lie above typical terrestrial Leonard deposits. This assignment compares favorably with that made for Zone I (*Rhopalodon* Zone) and, perhaps, Zone II (*Titanophoneus* Zone) of

TABLE 3.—MEASUREMENTS OF GENERA OF SAN ANGELO REPTILES AND COMPARATIVE MEASUREMENTS OF VARIOUS GENERA FROM EARLIER PERMIAN

Based on largest known specimens from both San Angelo and earlier Permian; measurements in centimeters.

<i>Rothia</i>					
Genus		Probable total length	Skull length		
<i>Rothia</i>		165	26		
<i>Labidosaurus</i>		90	20		
<i>Labidosaurikos</i>		165	30		
<i>Captorhinus</i>		35	8		
<i>Captorhinikos</i>		50	10		

<i>Steppesaurus</i>		
Genus	Jaw length	Ulna length
<i>Steppesaurus</i>	59	27
<i>Dimetrodon</i>	39	20

<i>Tappenosaurus</i>					
Genus	Est. total length	Femur length	Humerus length	Pelvis height	Centrum length dors. vert.
<i>Tappenosaurus</i>	540	50	45	55	7.6
<i>Dimetrodon</i>	328	27	24	..	5.2

<i>Dimacrodon</i>	
Genus	Jaw length
<i>Dimacrodon</i>	20 (est.)
(no comparative material)	

<i>Cotylorhynchus</i>	
Genus and species	Humerus length
<i>Cotylorhynchus hancocki</i> (San Angelo)...	39.0
<i>Cotylorhynchus romeri</i> (Hennessey)....	31.5

<i>Caseoides</i>			
Genus and species	Humerus length	Femur length	Prox. width femur
<i>Caseoides</i>	15.7	14.5	7.3
<i>Casea broilii</i> (Lower Vale).....	7.2	8.5	2.5
<i>Casea nicholsi</i> (Upper Vale).....	10.0	8.5	3.9
<i>Casea halselli</i> (Middle Choza).....	6.3

<i>Angelosaurus</i>				
Genus and species	Humerus length	Femur length	Centrum length dors. vert.	Pubo-isch. symphysis length
<i>Angelosaurus</i>	18.9	21.6	3.9	19.5
<i>Casea nicholsi</i>	10.0	8.5	2.3	12.2
<i>Casea halselli</i>	2.9	19.2

Russia. The earliest Russian beds in which vertebrates are found are generally considered slightly older than the earliest producing beds of the African Beaufort Series (*Tapinocephalus* Zone). This relationship is based largely on local stratigraphic evidence and upon the contained faunas. More important than the precise time relationships between the areas, however, is the fact that more or less equivalent evolutionary levels have been reached in Russia and South Africa and that a somewhat similar adaptive stage is recorded in the San Angelo and Flower Pot Formations of North America. There is an event equivalence, even though some time differences may exist.

EVOLUTIONARY RESEMBLANCES AND DIFFERENCES BETWEEN THE MID-PERMIAN OF THE OLD AND NEW WORLDS

If the taxonomic differences between the mid-Permian reptiles of the Old and New Worlds are ignored, and adaptive types considered, striking resemblances become apparent. Most obvious is the comparable large size of a number of the animals in both areas. This relative gigantism is spectacular in North America, coming as it does shortly after the disappearance of the typical, deltaic fauna of the early Permian, where proportions are more modest. The giants of the earlier Permian were *Dimetrodon* and *Cotylorhynchus*. The marked increase of the mid-Permian *Steppesaurus* and *Cotylorhynchus* over their predecessors has been noted. More amazing is the great size of *Tappenosaurus*. Equal size is recorded in titanosuchids, tapinocephalids, some theriodonts, and the pareiasaurs in the mid-Permian of Russia and South Africa. Here the size seems less striking, in the lack of knowledge of earlier faunas.

Resemblances go far beyond the mere coincidence of size, and extend to more specific adaptations. The adaptive resemblance of *Tappenosaurus* to the titanosuchids is clear. It can hardly be denied that they represent parallel trends from a common, but somewhat remote sphenacodont ancestry. The analogy between *Steppesaurus* and such theriodonts as the gorgonopsians and early therocephalians is evident. *Steppesaurus* is an adaptive relict in the mid-Permian, for it changed little, in an adaptive sense, from *Dimetrodon* of earlier times, although it was involved in a very different ecological situation. The stability of *Dimetrodon* itself under changing conditions is well shown by the persistence of the genus for nearly the full span of the early Permian, and the persistence of a single species, *D. gigashomogenes*, through most of the Clear Fork. A similar genus,

Steppesaurus, appears to carry on this tolerance, as it occupies a theriodont-like place in the mid-Permian fauna. The two known carnivores of the San Angelo and Flower Pot find close parallels in the principal carnivores of the mid-Permian of Russia and South Africa, the titanosuchids and the theriodonts.

The situation with respect to herbivores is more difficult to visualize, for there is less actual resemblance in form, and evidence of the ecological positions in the economy of the fauna must be the principal basis for judgment. The closest morphological resemblance, so far as known structures are concerned, is between *Dimacrodon* and some of the early anomodonts. In the broad symphysis of the jaws, the presumed horny beak, the large "canines" and small post-canines, they are very similar. It seems highly improbable, from the differences in the rest of the faunal elements and geographic remoteness, that there was anything but a rather remote common ancestry, so that this would appear to be a valid case of parallelism, or, perhaps, convergence.

The remaining herbivores are captorhinomorphs or caseids in North America, in contrast to the anomodonts, tapinocephalids, pareiasaurs, and procolophonids in the Old World. *Angelosaurus* and *Cotylorhynchus* were large, slow-moving vegetarians that must have provided an important food supply for the large carnivores. In this sense they were associated with the vegetation on the one hand and the predators on the other in much the same way as were the tapinocephalids and pareiasaurs. Neither of the North American genera had a skeletal structure as massive as that of these two types, nor had they assumed as upright a pose. Nevertheless, they represent marked departures from the earlier herbivores of Texas and their differences appear to be directly related to their place in the changed ecological situation. The development of the pareiasaurs and tapinocephalids similarly can be presumed to have taken place during the evolution that led to the large Old World carnivores.

Rothia and *Caseoides*, both of which are more frequently encountered in the deposits than the larger herbivores, fill the position of the smaller plant-eaters, occupied in large part by the anomodonts in the South African and Russian mid-Permian.

Here the analogy ends, for we are faced with the puzzling fact that at present almost no traces of animals smaller than *Rothia* have been found in the San Angelo or the Flower Pot. This is true in spite of the fact that types of deposits, which, in earlier sequences, have yielded an abundance of small vertebrates, have been explored

thoroughly. During the last year, beds in swamps and swamp margins that were rich in large vertebrates and in plants have been combed, without the discovery of small reptiles, amphibians, or fish. These studies have led to the interpretation of the San Angelo and Flower Pot faunas as marginal phases of better-integrated faunal units that included all elements necessary to a balanced economy (Olson and Beerbower, 1953). There are no counterparts of procolophonids, small anomodonts, or small theriodonts in the San Angelo-Flower Pot fauna.

ORIGIN AND EVOLUTION OF THE NEW AND OLD WORLD MID-PERMIAN FAUNAS

A coherent interpretation of the origin and evolution of the faunas requires certain assumptions. It is assumed that the faunas in the Old and New Worlds arose from a common ancestral Pennsylvanian stock. This stock is considered to have been spread, with continuity, over both the Old and New Worlds. Such evidence as we have concerning the Pennsylvanian supports this hypothesis. It is assumed, further, that the common characteristics of the faunas of the Old and New Worlds appeared at more or less the same time, during the late part of the early Permian. We know that the elements had not appeared in North America prior to this time and such evidence as there is of the early Autunian of Europe gives no suggestion of their presence in Europe. A coincidence of conditions favoring increased size and other adaptive similarities and evolutionary thresholds that permitted exploitation of these conditions must have occurred in both areas. In other words, in both the Old and New Worlds there existed in the late part of the early Permian comparable opportunities and stocks able to take advantage of these opportunities. While the opportunities may well have been much the same, the stocks seem to have been very different.

What is known of the early Permian faunas in western Europe gives some indication that differences may have been initiated by that time. So far as we know there were no caseids and no captorhinomorphs present. These, however, are dominant elements of the late early Permian in North America, and captorhinomorphs were abundant during all of early Permian. Sphenacodonts, edaphosaurids, and diadectids were present in the early Permian of the Old World. In North America diadectids and edaphosaurids gave way to the caseids and captorhinomorphs during the late part of the early Permian. In the Old World the edaphosaurids failed,

but the procolophonids and pareiasaurs, presumably diadectid descendants, give indication that this group was successful.

The predominant reptilian types of the early Permian in western Europe were the sphenacodonts. It is from this stock that the therapsids appear to have stemmed. If this is the case, there must have been a rapid and pronounced adaptive radiation of this group late in the early Permian, to produce both herbivores and carnivores. In the absence of captorhinomorphs and caseids, which maintained a balance with carnivorous sphenacodonts in North America, such a radiation would be a most probable event. The only reptilian competition to the herbivore radiation would have been supplied by the relatively unprogressive diadectomorphs. The radiation would compare in part to the rapid adaptive changes in the captorhinomorph stock in North America, a radiation that appears to have filled the gap left by the disappearance of the diadectids and edaphosaurids. It would compare as well, once herbivores had been established, with the caseid radiation that began in North America during the Vale.

The difference in stocks of the herbivores may be supposed to have had an important impact on the carnivores. In the Old World, under the hypothesis advanced above, they stemmed from the advanced and highly active sphenacodonts, whereas in North America, except for *Dimacrodon*, herbivores developed from the relatively unprogressive captorhinomorphs and caseids. Selective pressure for activity in the Old World must have been far in excess of that in the New. The keynote to the origin and evolution of the therapsids and finally to evolution of the mammals, appears to have been continued emphasis on activity. Of course there were many bypaths, in which ponderous and slow therapsids developed, but fundamentally the level of activity in a therapsid-dominated fauna must have been higher than that in one where pelycosaurs played the primary role.

We do not as yet know, and may never know, the history of reptiles after the early mid-Permian in North America. There is little indication in what is known of the early mid-Permian fauna that it was likely to approach and pass the therapsid threshold necessary to the radiation seen in the Old World. As long as the isolation, which must have existed to preserve the pelycosaur-captorhinomorph lines in North America, persisted, adaptive modifications of this stock without "progressive" modifications of fundamental structures would appear to be the most probable course of events.

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