



PERMIAN LAKE FAUNAS: A STUDY IN COMMUNITY EVOLUTION

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ABSTRACT

Samples of vertebrates from two Lower Permian Lakes in Oklahoma, one in a wet and one in a dry climate, are compared. Major differences in faunal compositions and trophic patterns distinguish the two types. The record of these two faunal types, traced through series of similar lakes of the Lower Permian, reveal changes in communities which correspond to modification in climates. Faunal changes of the primarily aquatic vertebrate complexes resulted primarily from accommodation of genera and species to new circumstances either by physiological modifications or by shifts to occupation of other environments. Very few new genera or species entered into the aquatic complexes during the duration of the two types of lakes.

INTRODUCTION

Throughout the Late Carboniferous and Early Permian extensive deposits of terrestrial sediments were formed in subsiding belts adjacent to open seas and evaporite basins. Such sediments are best known from the Early Permian of mid-continental North America and it is to this region that our study is directed. Similar deposits, both of red beds and coal measures, however, extended in a circum-equatorial zone across the eastern United States, western Europe and at least as far east as the Ural Mountains of the Soviet Union. The specific circumstances treated here in detail are broadly applicable to other areas both within and beyond the present continent of North America.

In North-Central Texas and Oklahoma, where the Permo-Carboniferous red beds are fully developed, a coherent ecosystem existed and evolved as a unit from the Late Carboniferous to near the end of the Early Permian. The vertebrates of this system constitute the Permo-Carboniferous Chronofauna (Olson 1952, 1971). Within the ecosystem four principal habitat subzones have been differentiated: rivers and streams; lakes and ponds; lake and stream margins; and "uplands, in large part made up of divides between streams. The present study concentrates on the ecology of one of the subzones, the lakes, with special attention to their aquatic and semi-aquatic faunas and the relationships of the aquatic constituents to members of the other life zones.

Within the study area, sediments indicate the existence of four types of standing water environments, as follows:

1. Permanent lakes
 - (1) Large bodies of water, with areas measurable in square miles.
 - (2) Small bodies of water, generally less than a square mile in area.
2. Semi-permanent lakes, subject to partial seasonal drying and limited in area, usually less than a square mile.
3. Temporary small ponds, subject to nearly total drying.
4. Swamps, either individual or formed along the margins of large lakes.

Gradation between these types occur, of course, but the categories are moderately distinct and definable on the basis of the sedimentation which took place from their waters.

We will be concerned primarily with small, permanent lakes [type 1 (2) above] and semi-permanent lakes (type 2 above). The other types will enter into the discussion, but in a less direct way.

Collections of vertebrate fossils from two ancient lakes have produced exceptionally large numbers of specimens and provide a basis for interpretations that can be extended to less favourable sites. One of these lake deposits is near Waurika, Oklahoma, in the Oscar Formation and the other is in the vicinity of Orlando, Oklahoma, in the Wellington Formation, Figure 1. The latter is the more recent of the two, Figure 2. Because no evident evolution of the common vertebrates occurred over the Permian area as a whole during the span of time encompassed by

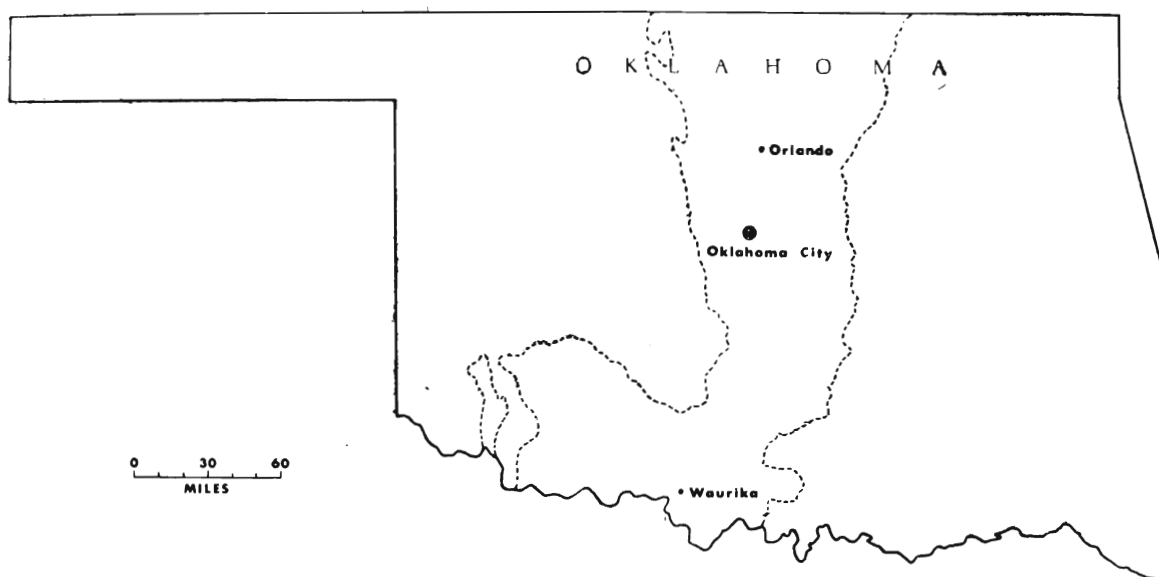


Figure 1. Oklahoma, showing the positions of the Waurika and Orlando sites. The area within the dashed line includes the outcrops of Lower Permian deposits.

these two lakes, it is assumed that the faunal differences between the two are environmental rather than temporal.

The Waurika sediments were formed in a small, permanent lake; those at Orlando were deposited in a semi-permanent lake which was subjected to considerable restriction during seasonal dry periods. These interpretations of the nature of the lakes based upon sediments of the lake beds, deposits formed in the vicinity of the lake beds, and the sedimentological evidence of the general climatic conditions over the full area of deposition of the terrestrial Permian sediments. Inevitably the nature of the vertebrate remains influences the interpretations as it confirm or denies the purely physical data.

The characteristics of the two samples of vertebrates, from Waurika and from Orlando, are discussed in appendices A and B respectively. The data used in interpretations in the text as the basis for ecological analyses are presented in these appendices and in the tables accompanying the text.

THE FAUNA AND THE CLIMATE

The vertebrates collected at the two localities are given in Table 1. Genera or genera and species are used along with higher categories as most appropriate. Table 2 lists the common Permo-Carboniferous vertebrates with data on their habits and their roles in the trophic structure of the ecosystem. For the most part only genera are given in this list, but where genera are not pertinent to the present study families, or higher categories, are entered. Species are difficult to use at this level in many instances and the named species are by no means commensurate in their coverage (see for example Olson, 1967). Specific differences, if any existed, are not determinable between

the genera common to the Waurika and Orlando sites. It appears probable that none existed. During the evolution of the system as a whole, however, species do assume some importance, and, where this is the case, species names are used.

Of the 21 categories listed in Table 2, 13 occur in the Waurika sample and 9 occur in the Orlando sample. The 5 that do not occur in either are all highly terrestrial. The samples from each of the lakes include a substantial number of genera and species of vertebrates characteristic of Early Permian times and some of these are known only from lakes and ponds. Two genera, *Cricotillus* and

Period	TEXAS			OKLAHOMA		
	Series	Group	Formation	Series	Group	Formation
PERMIAN	LEONARDIAN	Clear Fork	CHOZA	CIMMARONIAN	Hennessey	BISON
			VALE			SALT PLAINS
			ARROYO			KINGMAN SILTSTONE
			CLYDE			FAIRMONT SHALE
						GARBER
	WOLFCAMPIAN	Wichita	BELLE PLAINS	GEARYAN*	OSCAR	
			ADMIRAL			
			PUTNAM			
			MORAN			
			PUEBLO			
					WELLINGTON	
					VANOSS	

Figure 2. A stratigraphic chart for the Lower Permian of Texas and Oklahoma. The Gearyan is considered Upper Pennsylvanian by the Oklahoma Geological Survey.

Table 1—Number of individuals of the various vertebrate groups represented at Orlando and Waurika and percentages of each group in the total sample. Data for summation of Waurika specimens from Table 7. tr. less than 1%.

Vertebrate Group	Orlando		Waurika	
	Number	%	Number	%
<i>Xenacanthus</i> sp.	2	tr	1217	73
Ganoid scales	0	0	65	4
<i>Sagenodus</i> sp.	0	0	5	tr
<i>Gnathorhiza serrata</i>	36	2	0	0
<i>Lysorophus tricarinatus</i>	22	1	?1	tr
<i>Diplocaulus magnicornis</i>	1734	81	59	4
<i>Crossotelos annulatus</i>	159	7	0	0
<i>Pantylus</i> sp.	0	0	1	tr
<i>Eryops megacephalus</i>	1	tr	39	2
<i>Trimerorhachis insignis</i>	122	6	81	5
<i>Zatrachys</i> sp.	0	0	5	tr
<i>Cricotillus brachydens</i>	3	tr	0	0
<i>Archeria</i> sp.	0	0	60	4
<i>Diadectes</i> sp.	1	tr	12	1
Captorhinomorph	55	3	1	tr
<i>Ophiacodon retroversus</i>	0	0	33	2
<i>Edaphosaurus claviger</i>	2	tr	55	3
<i>Dimetrodon cf. limbatus</i>	7		40	2
	2144	100	1674	100

Pleuristion are unique to the Orlando site, but as discussed in appendix B, the taxonomy of these two genera is unclear.

A brief analysis of the general climatic conditions under which the Permo-Carboniferous Chronofauna lived will help to establish the physical context in which the study of the lake faunas is set. With the passage of time from the beginning of the Permian until the end of the Leonardian (see Figure 2) progressive changes in the terrestrial sediments in North-Central Texas and Oklahoma indicate climatic modifications from a wet, non-seasonal climate to one which was dryer and strongly seasonal with respect to rainfall. The general responses of the various types of Permian vertebrates to such climatic changes are shown in Table 3.

This trend accelerated during the middle portion of the Early Permian, especially during the initiation of the

Arroyo Formation. Furthermore, at any given time during the Early Permian, a cline from wetter to drier existed along a roughly north-south axis, extending from the transition from marine to terrestrial conditions at the south, through North-Central Texas and southern and

Table 2—The principal vertebrate groups that made up the Permo-Carboniferous chronofauna, their habitats and feeding habits, with the presence or absence in the faunal complexes at Orlando and Waurika indicated : X—present; O—absent.

Vertebrate Group	Principal habitat	Principal Feeding habit	Waurika	Orlando
PISCES				
<i>Xenacanthus</i>	.. aquatic	.. predator	.. ×	×
Paleoniscoids	.. aquatic	.. Carnivore-herbivore.	×	0
Ganoids	.. aquatic	.. predator	.. ×	0
<i>Sagenodus</i>	.. aquatic	.. invertebrate feeder.	×	0
<i>Gnathorhiza</i>	.. aquatic aestivator	carnivore-invertebrate feeder.	0	×
AMPHIBIA				
<i>Eryops</i>	.. Semi-aquatic	predator	.. ×	×
<i>Trimerorhachis</i>	.. aquatic-?facultative aestivator	predator	.. ×	×
<i>Zatrachys</i>	.. aquatic	.. carnivore	.. ×	0
Dissorophidae	.. terrestrial	.. various	.. 0	0
<i>Archeria</i>	.. aquatic	.. predator	.. ×	0
<i>Cricotillus</i>	.. aquatic	.. predator	.. 0	×
<i>Seymouria</i>	.. terrestrial (adults)	predator	.. 0	0
<i>Diadectes</i>	.. terrestrial	.. herbivore	.. ×	×
REPTILIA				
<i>Protocaptorhinus</i>	.. terrestrial	.. insectivore, etc.	×	0
<i>Pleuristion</i> *	.. terrestrial	.. insectivore, etc.	0	×
<i>Labidosaurus</i>	.. terrestrial	.. carnivore	.. 0	0
<i>Ophiacodon</i>	.. semi-aquatic	carnivore-piscivorous	×	0
Eothyrididae	.. terrestrial	.. carnivore-insectivore	0	0
<i>Edaphosaurus</i>	.. semi-aquatic	herbivore	.. ×	×
Nitiosauridae	.. terrestrial	.. omnivore	0	0
<i>Dimetrodon</i>	.. terrestrial	.. predator	.. ×	×

Table 3—Genera and groups of Permian vertebrates with indication of their reaction to changes in rainfall and seasonality. The reaction to decrease in total rainfall and accompanying increase in seasonality of rainfall is indicated by a X, under columns showing no change, decrease in numbers (strong or moderate) and increase in numbers (strong or moderate), and uncertain.

Genus or group	No Change	Decrease in numbers	Increase in numbers	Uncertain
		Mo-Strong	Mo-Strong	
FISHES				
<i>Xenacanthus</i>		X		
Paleoniscoids			X	
Ganoids.....			X	
<i>Sagenodus</i>		X		
<i>Gnathorhiza</i>			X	
LEPOSPONDYLOUS				
AMPHIBIANS				
<i>Lysorophus</i>			X	
<i>Diplocaulus</i>			X	
<i>Crossotelos</i>			X	
<i>Gymnarthrids</i>			X	
TEMNOSPONDYLOUS				
AMPHIBIANS				
<i>Eryops</i>		X		
<i>Trimerorhachis</i>	X			
Small trimerorhachids			X	
Dissorophids		X		
<i>Zatrachys</i>		X		
Trematopsids			X	
ANTHRACOSAUR				
AMPHIBIANS				
<i>Archeria</i>		X		
<i>Cricotillus</i>			X	
<i>Seymouria</i>			X	
<i>Diadectes</i>		X		
REPTILES				
Captorhinids			X	
<i>Araeoscelis</i>			X	
<i>Ophiacodon</i>		X		
Eothyrids			X	
<i>Edaphosaurus</i>		X		
<i>Dimetrodon</i>		X		

central Oklahoma. Early appearances of low rainfall and seasonality are also recorded in the Lower Permian beds of New Mexico (Olson and Vaughn, 1970), but the trend from wet to dry is not evident in the Permo-Carboniferous Dunkard deposits in the eastern part of the United States.

The two lakes at Waurika and Orlando lie along this north-south axis, about 150 miles apart, Figure. 1. The time difference between the two sites is not great with respect to the overall rate of climatic change, and the climatic differences between them relates to the geographical rather than to the temporal trend. The Waurika area was separated from central Oklahoma, at least partially, by the positive elements of the Wichita and Arbuckle mountains and this separation probably accentuated the climatic differences.

COMPARISONS OF THE TWO LAKE FAUNAS

The members of the aquatic vertebrate complexes from the two lakes are listed in Table 4, along with minimum

Table 4—Comparisons of the lake faunas at Waurika and Orlando, based on minimum numbers as derived in appendixes A and B. Ganoids, and paleoniscoids, both present at Waurika and absent at Orlando are not entered because no numbers could be obtained. *Zatrachys*, present at Waurika is not entered because it is rare.

Genus	Waurika (contemporary individuals)	
	Number	Percent
<i>Xenacanthus</i>	40	36
<i>Sagenodus</i>	20	18
<i>Trimerorhachis</i> ..	30	27
<i>Archeria</i>	10	10
<i>Diplocaulus</i>	10	10
Totals	110	99
Orlando (averaged over full time span of lake)		
Genus	Number	Percent
<i>Gnathorhiza</i>	20	19
<i>Diplocaulus</i>	38	35
<i>Crossotelos</i>	10	9
<i>Lysorophus</i>	22	20
<i>Trimerorhachis</i> ..	10	9
<i>Cricotillus</i> (+)* ..	8	8
Totals	110	100

*Added to the 3 specimens of *Cricotillus* are 5 of an unnamed predator which was long snouted and apparently rather close ecologically.

It is assumed that *Xenacanthus* was not present at Orlando, as discussed in Appendix B.

numbers of individuals and percentage of these in the minimum totals. Data from which these figures were derived are given in Tables 1 to 3 and in appendices A and B. Some of the most common aquatic genera are illustrated in reconstructions in Figure 3.

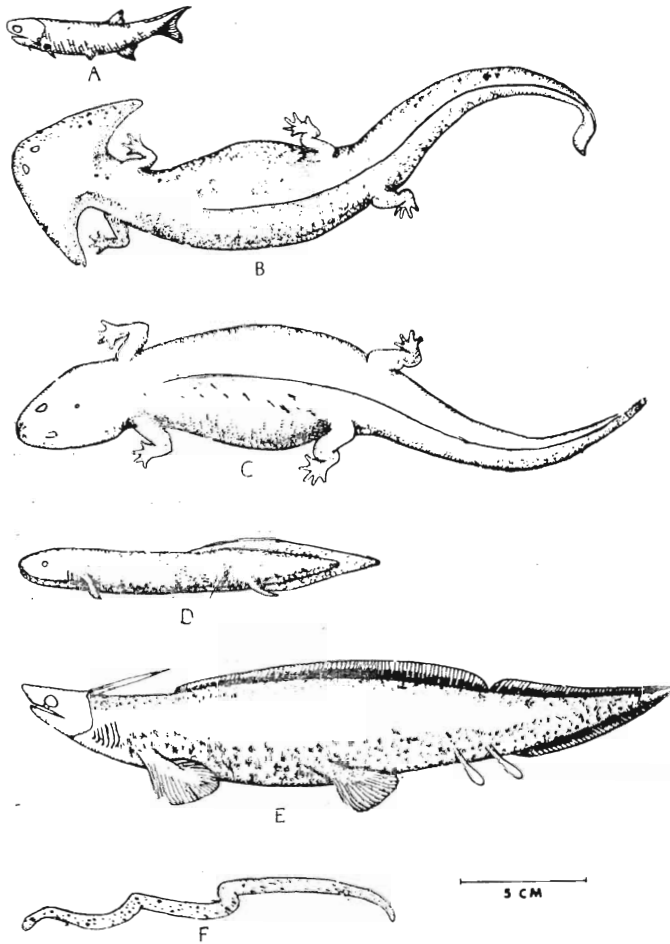


Figure 3. A reconstruction of the typical aquatic vertebrates of the faunas considered in this study. A—paleoniscoid; B.—*Diplocaulus marginicornis*; C.—*Trimerorhachis insignis*; D.—*Gnathorhiza serrata*; E.—*Xenacanthus* sp.; F. *Lysorophus tricarinatus*. Approximately to scale based on young adults.

The differences in composition of the two lakes faunas at the generic level is immediately apparent in Table 4. Only *Trimerorhachis* and *Diplocaulus* are common to both, although *Archeria* and *Cricotillus* are ecological equivalents and possibly congeneric (see appendix B).

The differences loom greater when the ecological roles and the numbers of both the common and distinctive genera are taken into account (see Table 2). The persistent lake at Waurika was dominated by two predators, *Xenacanthus* and *Trimerorhachis*, which together make up 63 percent of the minimum aquatic faunal assemblage. Added to this is the 10 percent contributed by the predator *Archeria*. In contrast, *Trimerorhachis* and *Cricotillus*,

the only highly predaceous aquatic genera at Orlando account for only 17 percent, whereas *Diplocaulus* and *Crossotelos* contribute 44 percent. Also very important at Orlando are *Gnathorhiza* and *Lysorophus*, which together form 39 percent of the total estimated numbers of individuals.

These percentages are, of course, crude estimates, but the scope of the differences is clearly far greater than the errors of estimate. The conservative ways in which the numbers of individuals were calculated from the numbers of specimens almost certainly minimizes the actual dominance of the most abundant species. The ecologies of the two lakes, based on these conservative figures, were widely different.

ECOLOGY OF THE WAURIKA LAKE

As estimated, over 70 percent of the aquatic fauna at Waurika was made up of rather large predators. *Sagenodus* and *Diplocaulus* were possible sources of adult prey, but obviously from the simple standpoint of biomass the adults alone were insufficient to form the animal base of the aquatic ecosystem. Neither *Sagenodus* nor *Diplocaulus* can be considered to have been strictly herbivorous and probably both were primarily carnivorous. This poses a major problem. Either the sampling and estimates of numbers produce a severely false picture of the faunal composition as far as these vertebrates are concerned, or else important elements are missing from the complex then only these genera, as adults, are considered. It seems highly unlikely that the repeated collections could have introduced severe biases or that the preservation was sufficiently selective to have drastically modified the taphocoenosis relative to the biocoenosis. Some answers to the apparent ecological imbalance are suggested in Figure 4 where, with the assumption that the sampling was adequate, an attempt to restore the food web is illustrated.

First, it is apparent that the semi-aquatic and terrestrial vertebrates, which are added to the picture, not only offer no solution, but if anything compound the problem. The three major food sources for the predators, beyond those shown in the sample, are indicated in the figure as the following :

1. Larvae and young. If *Sagenodus* and *Diplocaulus* produced large numbers of larvae and young and these were primarily herbivorous, which is probable, then a large unrecorded food source was available. Just what the relationships of larvae and young, as the case may have been, were to each other during the growth period must be uncertain. Larval predation by larvae may have entered in, as it does among some anurans, in particular *Scaphiophus* (Bragg, 1965). Both larval predation and cannibalism appear to have developed in relationship to xeric breeding habits, but may have spread to more mesic conditions in a genus such as *Diplocaulus*, which existed

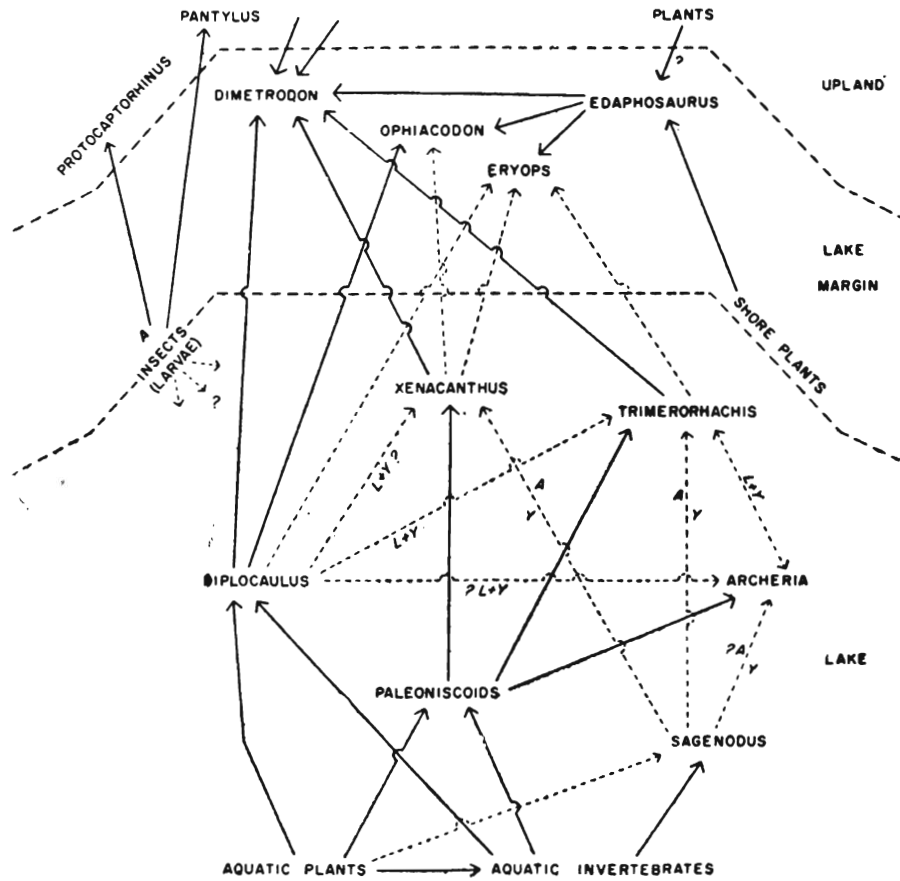


Figure 4. Reconstruction of the trophic web of the Waurika Lake. The arrows indicate the direction of food flow. Solid lines indicate the main flow lines; dashed lines, secondary flow lines. Area of Lake, Lake Margin and Upland indicated. Abbreviations: A, adult animals; L, larvae; Y, young animals.

under both conditions. If larval predation existed at all, it probably was more important in the Orlando type lake than in the Waurika type.

Without this aspect of breeding habits, the larvae and young may still have been an important factor in the food chain, serving as prey for partially matured predators and perhaps for full adults as well. Remains of very young stages, except for occasional specimens of *Diplocaulus* in aestivation burrows of *Lysorophus*, are almost never found. Their roles must, of course, remain speculative.

2. Paleoniscoid fishes. Remains are not common constituents of samples collected from the surface at Waurika. Nevertheless they certainly were abundant in the lake. Scales are common, although scattered, in the shales. Spiral "coprolites" of *Xenacanthus*, probably intestinal casts as indicated by Williams (1972) are abundant at Waurika. They contain concentrations of paleoniscoid scales along with small, indeterminate bones from various tetrapods. Clearly these small fish were an important element in the diet of the sharks (see also Williams 1972). They do not occur in other, rounded, non-spiral coprolites whose identity is uncertain.

3. Invertebrates. As is usual in the terrestrial Permian sediments of Texas and Oklahoma, invertebrates are rare in the beds at Waurika. Over the Permian area as a whole, during the time the lake existed, remains of small pelecypods, conchostracans and tracks and trails of invertebrates occur in some of the sandy and dolomitic sediments. Insect remains, sometime well preserved, are known in several places in Wellington dolomites known as the "insect beds". From these various bits of evidence it seems certain that a variety of pelecypods and arthropods, including insects, were abundant at this time and that many were inhabitants of the lake and its immediate vicinity. Undoubtedly many other kinds of invertebrates inhabited the lake. Among these were undeterminable types of "Worms" recorded by burrows in the sandier parts of the sediments. These invertebrates certainly included a wide range of plant feeders and probably were crucial in the energetics of the ecosystem.

The full vertebrate fauna of the lake, of course, included the semi-aquatic vertebrates that inhabited it part of the time and the terrestrial vertebrates which fed on both the semi-aquatic and aquatic animals and plants. Most of the semi-aquatic and terrestrial animals were predators and

remains in their coprolites from other areas in the Permian suggest that they fed both upon the lake predators and herbivores. The herbivores, *Edaphosaurus* and *Diadectes*, the latter perhaps a seed eater, lived in the vicinity of the lake, but, not, it appears, in large numbers. They probably were prey of the large, terrestrial predators, but as was discussed in an earlier paper (Olson 1961) could not have been a sufficient source of food for the abundant predaceous pelycosaurs, which found much of their food in the lakes and streams.

Vegetation, of course, lay at the base of the food web. The larger terrestrial and semi-aquatic flora is well known, but the small and micro-vegetation of the lakes and streams has left little record. In view of the low number of large herbivores, this little known vegetation probably was the principal source of food energy for the lake ecosystem.

ECOLOGY OF THE ORLANDO LAKE

Figure 5 portrays a reconstruction of the trophic relationships of the members of the fauna at Orlando where the lake was intermittently subject to partial drying. The figure shows that, as at Waurika, the base of the food chain probably lay in aquatic plants, introduced into the vertebrate pyramid mainly through the agency of invertebrates. Once again, however, invertebrates are essentially unknown at the site and their presence is deduced from other deposits in the general area. Unlike the Waurika samples, the one from Orlando shows no evidence whatsoever of paleoniscoids and it is presumed that they were absent. Perhaps these small fishes were unable to survive the dryer phase of the lake's cycle.

Trimerorhachis and *Cricotillus* are the relatively large predators. *Xenacanthus* is assumed to have been absent, being represented only by two fragmentary specimens which probably were washed in from adjacent sediments (see appendix B). Together the two large predators make up less than 20 percent of the total of the individuals derived from the minimum number estimates in Table 4. *Diplocaulus*, *Crossoctelos*, *Lysorophus* and *Gnathorhiza*, all possible prey of *Trimerorhachis* or *Cricotillus*, comprise about 80 percent of the vertebrate fauna. Even with this differential, the predators probably could not have survived had they fed on adults alone. In addition, of course, none of the four genera noted were strictly herbivorous. It appears that larvae and young must have played an important role in the food web, as suggested for the Waurika ecology. *Diplocaulus*, *Crossoctelos*, *Lysorophus* and *Gnathorhiza* likely fed on young, their own as well as others, and almost certainly found a major source of food among invertebrates. If this were in fact the case, then a reasonable trophic pattern could have existed without the presence of paleoniscoids, which appear to have been very important at Waurika.

Gnathorhiza and *Lysorophus* were aestivators, adding a life mode totally absent at Waurika. They did not, of course, feed throughout the whole year. *Diplocaulus* is not known to have been a strict aestivator and was an inhabitant of persistent lakes of the Waurika type. Very young individuals do occur in association with the remains of aestivating colonies of *Lysorophus*. It may be that the young of *Diplocaulus* followed this habit whereas the older individuals could survive severe conditions, when neces-

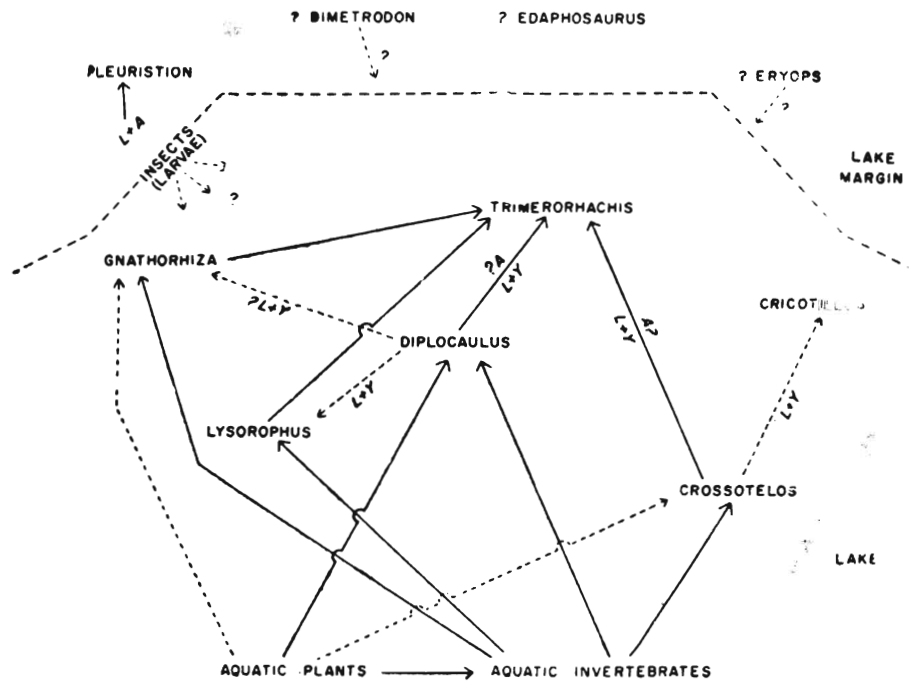


Figure 5. Reconstruction of the trophic web of the Orlando Lake. Symbols as in Figure 4.

sary perhaps with some degree of torpor, without requiring burrows or nests that were sufficiently developed to leave clear records.

The same may apply to *Trimerorhachis* and *Crossotelos*. The former clearly could survive the conditions of the Orlando lake during its maximum dessication. How severe the dessication may have been we do not know, but it was sufficient to induce aestivation in *Lystrophus* and *Gnathorhiza*. *Trimerorhachis* *Lysorophus* and *Gnathorhiza*. *Trimerorhachis* occurs in association with aestivation burrows of *Gnathorhiza* along the margins of very large lakes in the Lower Permian and seems to have thrived in a wide variety of circumstance, in large and small lakes, in rivers and in small streams. Apparently either by seeking residually wet places, perhaps in wet mud, or by partial aestivation, this genus was able to tolerate quite dry conditions for appreciable periods of time.

A striking feature of the Orlando lake is the presence of a relative abundance of the highly terrestrial captorhinomorph *Pleuristion*. Captorhinomorphs are known only from a single specimen at Waurika. As we will see in a subsequent section, captorhinomorphs are commonly present in sediments formed in lakes and ponds that have alternating wet and dry periods. Presumably as dry conditions set in, this terrestrial animal, which was probably an invertebrate feeder, gravitated to the concentration of food and water in the vicinity of drying lakes. Many of the specimens of *Pleuristion* are more or less intact. Apparently they were subject to little predation in the vicinity of the lakes where many died and were buried with little disturbance. It is likely that predators were largely inactive during the times that this small, terrestrial reptile was present in large numbers.

The near absence of semi-aquatic and terrestrial animals, except for *Pleuristion*, indicates that these genera were a little or no importance in the trophic scheme of the Orlando lake. As indicated in appendix B the scant remains were probably introduced from previously formed surrounding sediments. *Dimetrodon* did live in the vicinity of the lake, but its absence from the Orlando sample, except for worn scraps, indicates that its interaction with the aquatic fauna was inconsequential.

EVOLUTION OF THE LAKE FAUNAS

GENERAL

In the foregoing sections the ecological systems of two types of lakes have been analyzed in as much detail as possible. Other types of lakes existed, as indicated in the introduction, but they will be considered in this section only as they play subsidiary roles in the reconstruction of the evolution of the two types that are the center of interest.

During the very early Permian, when the climate was predominantly wet and without marked seasonality,

the majority of lake deposits were of the Waurika type and swamps were prevalent. Lowlands and warm to hot tropical climates were characteristic. In the Texas area such conditions, broken by successive marine incursions (Romer 1958, 1974) persisted throughout the deposition of the beds of the Wichita Group. They began to wane during the deposition of the final terrestrial formation of this group, the Clyde.

For this period, only broad generalizations on the ecology can be made, based largely on the genera of vertebrates present. Rough estimates of abundance, some information of floras and crude information on climates are available. Studies of the kind necessary for more specific analyses have not been made. It is clear, however, that faunas of the Waurika type, with an abundance of *Xenacanthus*, paleoniscoids, ganoids, *Sagenodus* and *Trimerorhachis*, associated with *Eryops*, *Ophiacodon*, *Dimetrodon* and *Edaphosaurus* predominated. *Diplocaulus* was not a common constituent of these faunas.

To the north, in central Oklahoma, during the deposition of the Wellington Formation, large, fresh water lakes, characterized by alternating beds of shale and thin dolomites, were present. Included among the dolomitic beds are the famous "insect beds" of Oklahoma. Marginal to these large lakes in places (for example at Perry site /1 and site /5, Olson 1967) were formed deposits which contained abundant remains of *Gnathorhiza* and *Trimerorhachis*. During this same time span, however, swamp deposits containing *Xenacanthus*, paleoniscoids, *Diplocaulus*, *Trimerorhachis*, *Eryops*, *Ophiacodon*, and *Dimetrodon* were also present within the general area (see Perry site /6, Olson 1967). This latter faunal complex is reminiscent of the Waurika type lakes and the faunas of the Texas Wichita as a whole. Considerable alternation of climatic conditions is suggested by the different depositional circumstances over this period of time.

With the beginning of the Clear Fork deposition in Texas and Oklahoma, dominance of the Waurika type lake waned and there after elements of the Orlando type lakes became increasingly prominent.

HISTORY AND EVOLUTION OF THE WAURIKA TYPE LAKES

The northernmost, fully developed Waurika type lake is that at Waurika itself, but as noted in the preceding section, swamps with similar faunas are known as far north as central Oklahoma. At the time that the lake at Waurika was in existence, dryer conditions were beginning to develop to the north of it. With the beginning of the Clear Fork in Texas, this condition had spread to the south, but persistent small lakes extend as high as the Middle Vale in the section. The best known lakes of this interval with their vertebrates are listed in Table 5. None of these lakes has been sampled in such a way that even a semi-quantitative analysis of its fauna is possible, but the

Table 5. The vertebrate composition of lakes of the Waurika type.

	<i>Xenacanthus</i>	<i>Paleoniscoids</i>	<i>Ganoids</i>	<i>Sagenodus</i>	<i>Gnathorhiza dikeloda</i>	<i>Lysorophius</i>	<i>Diplocaulus</i>	<i>Pantylus</i>	<i>Trimerorhachis</i>	<i>Eryops</i>	<i>Archamia</i>	<i>Zatrachys</i>	<i>Seymouria</i>	<i>Diadectes</i>	<i>Protocephalichthys</i>	<i>Captorhinus</i>	<i>Labidosaurus</i>	<i>Labidosaurikos</i>	<i>Edaphosaurus</i>	<i>Dimetrodon</i>
FORMATION AND SITE																				
Oscar Formation Waurika site	X	x	x	x	(x)	x	x	x	x	x	x	x	(x)	x	(x)				x	x
Arroyo Fm. (Mid) <i>Labidosaurus</i> pocket site		x					x	x					x			x	x		x	
Arroyo Fm. (Up.) Loc. BAA (Olson 1958)	(?)	x					X		x				x			x				x
Vale (Low.) Fm. Loc. B Z (Olson 1958)	X	x			x		x	x	x									x		x
Vale Fm. (Mid) Loc. KH (Olson 1958)	x								x	x										x

X—forming over 50% of the sample.

X—forming 10 to 20% of the sample.

x—forming less than 10% of the sample; or present but estimate impossible where only x entered for full row.

(x)—a single specimen, possibly not from lake sediments.

(?)—specimens probably washed in, genus not member of lake fauna.

generic content is of interest. During this time species of *Diplocaulus* and *Gnathorhiza* became important. The common lake species is *D. magnicornis*, but during the Arroyo *D. brevirostris* inhabited the streams (Olson, 1951). *Gnathorhiza serrata* is used to designate the aestivating lake dwelling lung fish, whereas *G. dikeloda*, not certainly known from the Arroyo, was basically a stream species, but one also found in lakes during the Vale. In the Fairmont shale of the Hennessey Group, *G. noblensis* was present, rather than *G. serrata*, but ecologically the two appear to have been essential equivalents.

From Table 5, it is evident that the faunal complexes of the permanent lakes of the Arroyo were notably different from the complex at Waurika, shown in Table 1. Reconstruction of the probable trophic web, Figure 6, indicates that the basic difference lies in the lack of a dominant aquatic predator in the Arroyo lakes. This role was taken over by semi-aquatic and terrestrial inhabitants of the marginal waters and shores of the lakes. *Diplocaulus* and paleoniscoids dominated the lake faunas and they presumably depended upon aquatic plants and invertebrates as their sources of food. As in other lakes, plants and invertebrates are rare and poorly preserved. High larval productivity of *Diplocaulus* and, perhaps, *Eryops*, was a basic aspect of the ecology, necessary to maintain a viable energy balance. Most young probably were consumed prior to reaching of a subadult condition and cannot be expected in usual samples.

The absence of *Xenacanthus* represents a basic change in the trophic structure. This shark thrived during the Arroyo in streams, some of which fed the lakes, in association with *Trimerorhachis* and *D. brevirostris*. The dryer climates presumably produced conditions in the lakes and ponds unfavourable to *Xenacanthus*, although there is no direct clue as to what factors were involved.

The river vertebrate assemblage that existed during the time of the Arroyo Formation was similar to that in the Waurika lake. With the beginning of the Lower Vale, this type of assemblage once again appeared in the lakes as seen for example at locality BZ, Table 5. *Xenacanthus* was abundant and in direct association with *D. magnicornis* and *Trimerorhachis*. *Sagenodus*, which had been extinct in the area since the end of the Clyde Formation, is absent, but the larger lung-fish, *Gnathorhiza dikeloda*, is present and possibly occupied a similar ecological niche. Semi-aquatic and terrestrial associations are similar, but *Ophiodon*, like *Sagenodus* had died out earlier and is absent.

The redevelopment of the Waurika type lake complex appears to have occurred as the faunal complex that had persisted in the streams during the Arroyo re-entered the lakes. Deposition of the Lower Vale was marked by a short-lived increase in precipitation and a reduction in seasonality. A lake habitat suitable to occupancy by the Waurika type aquatic vertebrate assemblage was re-established. Permanent rivers also were developed at this time. In one of the rare recorded instances of speciation, *D. recurvatus*

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FORMATION AND SITE	<i>Xenacanthus</i>	<i>Paleoniscoids</i>	<i>Ganoids</i>	<i>Sagenodus</i>	<i>Gnathorhiza dikeloda</i>	<i>Lysorophus</i>	<i>Diplocaulus</i>	<i>Pantylus</i>	<i>Trimerorhachis</i>	<i>Eryops</i>	<i>Archaria</i>	<i>Zatrachys</i>	<i>Seymouria</i>	<i>Diadectes</i>	<i>Protoptorinus</i>	<i>Captorhinus</i>	<i>Labidosaurus</i>	<i>Labidosaurikos</i>	<i>Edaphosaurus</i>	<i>Dimetrodon</i>
Oscar Formation Waurika site	X	x	x	x	(x)	x	x	x	x	x	x	x	(x)	x	(x)				x	x
Arroyo Fm. (Mid) <i>Labidosaurus</i> pocket site		x					x	x					x			x	x		x	
Arroyo Fm. (Up.) Loc. BAA (Olson 1958)		(?)	x				X			x			x			x				x
Vale (Low.) Fm. Loc. BZ (Olson 1958)	X	x			x		x		x	x								x		x
Vale Fm. (Mid) Loc. KH (Olson 1958)	x								x	x										x

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X—forming 10 to 20% of the sample.

x—forming less than 10% of the sample; or present but estimate impossible where only x entered for full row.

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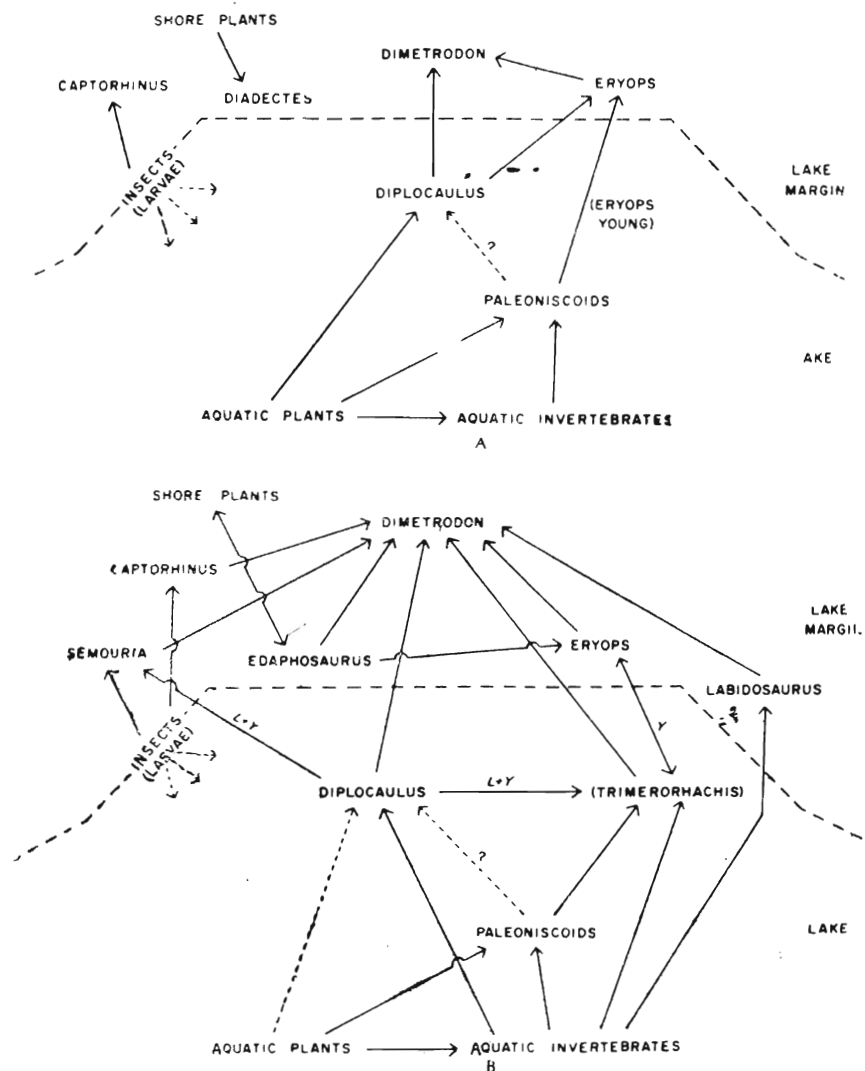


Figure 6. A. Reconstruction of the trophic web of a Waurika type Lake (site BAA, Olson, 1958); B. Reconstruction of the trophic web of a Waurika type lake (BA, Olson, 1958). See Table 5 and text pages. Symbols as in Figure 4.

arose from *D. magnicornis*, replacing the earlier river species *D. brevis*, which did not survive the end of the Arroyo, *D. magnicornis*, in turn, made its last appearance in the lakes of the Lower Vale.

The final recorded appearance of the Waurika type lake is in the Middle Vale, at site KH, Table 5. Here *Diplocaulus* is absent but the other principal elements are present. After this time *Xenacanthus* and *Trimerorhachis* continued to be present in the streams and the latter remained an important element in the Orlando type lakes.

HISTORY AND EVOLUTION OF THE ORLANDO TYPE LAKES

No fully developed faunas with an association of *Gnathorhiza*, *Lysorophus*, *Diplocaulus* and *Trimerorhachis* has been encountered in the interval between the Wellington and the base of the Vale Formation. Many sites, with hundreds if individuals of *Lysorophus*, occur through-

out the Arroyo Formation and associated with this amphibian are occasional remains of *G. serrata* and small, immature individuals of *D. magnicornis*. Such small sites, where *Lysorophus* aestivated, represent remnants of ponds which dried up completely during the dry season. In the Arroyo one aestivation site of *G. serrata* has been found (Romer and Olson, 1954). Neither in this nor in any of the well defined lake deposits, however, has an assemblage with the typical generic associations of the Orlando type been encountered.

With the beginning of the Lower Vale lake beds containing abundant remains of *Gnathorhiza*, *Lysorophus*, *D. magnicornis* and *Trimerorhachis* are once again present. Relative abundances suggest trophic relationships similar to those at Orlando. A reformation of the Orlando type aquatic complex took place, but in contrast to the redevelopment of the Waurika complex, the elements of the sys-

tem had not remained associated in another environment. Rather they were reassembled from genera that had been separate for a considerable period of time. *Gnathorhiza* and *Lysorophus* had existed, largely separately, in small, temporary ponds. *D. magnicornis* lived in permanent lakes and is found only occasionally as an aestivator, with very young individuals associated with *Lysorophus*. *Trimerorhachis* was present both in lakes and streams, but does not occur in association with either *Gnathorhiza* or *Lysorophus* during the Arroyo.

The Orlando type of ecology continues through the Vale into the Lower Choza and the equivalent Fairmont shale in Oklahoma, as shown in Table 6. Two well developed sites in the Upper Vale, plus some small, temporary pond sites are known. *D. magnicornis* is not present

in any of these and as far as known had become extinct over the study area. *D. recurvatus*, the derived stream species, lasted into the Choza. In samples from lakes in the Upper Vales and the site in the Fairmont shale, a small neotridean, *Peronedon*, is present in small numbers. It had long teeth and these, along with its small size, indicate that *Peronedon* and *Diplocaulus* occupied very different ecological niches.

The absence of *D. magnicornis* sharply altered the food web of the Orlando type ecology. Concurrent with the loss of *Diplocaulus*, *Lysorophus* increased in relative abundance, becoming the numerically dominant adult aquatic tetrapod. Both *Lysorophus* and *Gnathorhiza* in young and adult stages were suitable prey for *Trimerorhachis*. Sites in both the Choza and Fairmont shale have yielded a

Table 6. The vertebrate composition of lakes of the Orlando type.

	<i>Gnathorhiza</i>	<i>Diplocaulus magnicornis</i>	<i>Crossotelos</i>	<i>Peronedon</i>	<i>Coniorhynchus</i>	<i>Lysorophus</i>	<i>Eryops</i>	<i>Trimerorhachis insignis</i>	<i>Trimerorhachis rogersi</i>	<i>Tersomius</i>	<i>Cricotillos</i>	<i>Diadectes</i>	<i>Pleuristion</i>	<i>Captorhinikos valensis</i>	<i>Captorhinikos chozaensis</i>	<i>Captorhinikos parvus</i>	<i>Labidosaurikos</i>	<i>Edaphosaurus</i>	<i>Dimetrodon</i>
FORMATION AND SITE																			
Wellington Formation Orlando site	x	█	X			x	(x)	x			x	(x)	x					(x)	(x)
Arroyo Formation Reed Ranch (Romer-Olson 1954)	█																		
Small ponds (10+) (Olson 1939)	x	x				█													x
Vale Formation (lower) Small lakes (loc. Br, Bs, Bt, by Olson 1958)	x	x				x													
Vale Formation (upper) (Olson 1958)	█					x		x						x					
Loc. 1919 (Olson and Bolles, 1975)	█			x		X													
Small, temporary ponds (2) (Olson, 1958)						█													
Choze Formation (lower) Pipe site (Olson, 1958)	(x)					█		X						x		x			x
Nodule site (Olson, 1958)	█													x					
Fairmont Shale (Hennessey Gr.) Noble, Okla (Olson, 1967)	x			x	x	█			X					x	x				(?)

█—Over 50% of sample.

X—10 to 20% of sample.

x—less than 10% of sample; or present but estimate impossible where only x is entered for full row.

(x)—single specimen, probably not lake inhabitant.

(?)—questionable identification.

large number of small terrestrial animals reminiscent of the many specimens of *Pleuristion* at Orlando. The genera and species, of course, are different but the ecological positions of these small animals may have been similar. Probably all of them were primarily invertebrate feeders and tended to aggregate for food and water during dry periods.

Beds overlying the Lower Choza and Fairmont shale have not produced any evidence of vertebrate bearing lake sediments. Some small lakes were present during the Middle Choza, but only plant remains have been found in their sediments. It appears that in Texas and Oklahoma area this type of vertebrate ecology had come to an end.

SUMMARY AND CONCLUSIONS

Two lake faunas have been analyzed in as much detail as is possible by use of very extensive samples of their vertebrates. The generic composition and trophic structures of the two faunal complexes have been reconstructed revealing a striking contrast between them. One of the faunas existed in a permanent lake in an area of little seasonality; the other, in a lake subject to partial seasonal drying. These two lakes are taken as types and each has been followed through a rather long history which comprises much of the Lower Permian. This history extends through a time during which generally progressive climatic changes were taking place. The lake faunas, of course show responses to these changes.

The faunal changes for the most part were not of an evolutionary character, whereby the vertebrates of the lakes would have become adapted to new conditions. Genera and species of the aquatic environments tended to persist with little or no change. As disruptions of the physical aspects of the general ecology took place, species that lacked capacities to make physiological adjustments to new conditions disappeared from the lake environment, rarely showing detectable tendencies to respond by speciation. This may be due in part to the difficulty of detecting subtle changes in the fossil materials, but for the most part it appears to be a valid interpretation.

The vertebrate fauna of the permanent lake type, as found at Waurika and in many earlier sites, did not exist in permanent lakes during the relatively dry time when the Arroyo Formation was deposited. Many of its elements, however, remained associated in streams and rivers. One species, *Dimetrodon magnicornis*, which consistently gives evidence of high tolerance for desiccation, persisted in the lakes in the interval between the end of the Wichita (Oscar in Oklahoma) and the Lower Vale. With the Lower Vale, the Waurika type faunal complex re-entered the lake environment. During all of these changes little or no speciation took place.

The same sort of species persistence is characteristic of the vertebrates that inhabited the lakes that were subject

to partial drying, the Orlando type lake. Various genera that are characteristic of the Orlando faunal complex persisted through the Arroyo episode, but largely in isolation one from the other. During the formation of the Lower Vale, however, the Orlando type complex was reconstituted from isolated elements and, thereafter until near the end of the Lower Permian, continued and changed predominantly by loss of some of its constituents. Only near the end of this time did identifiable new species appear.

The primary conclusions to be drawn from this study of the evolution of two aquatic communities are as follows. The changes that each underwent during its history were strongly controlled by changing climatic conditions. The modifications came about not by evolutionary modifications among the constituents of the faunal complexes but by alterations in which already existing species and genera came into different ecological relationships, producing differently structured communities under different environmental circumstances. Some species, such as *Trimerorhachis insignis* were tolerant of a wide range of environments. Others such as *Xenacanthus* sp. prove to be much less so. *Diplocaulus magnicornis* could tolerate wide ranges of conditions in standing water, but was unable to exist in running water. It was the combined effects of these and similar differences in tolerances in other genera and species that determined the ecological structure of the lake communities through time as the controlling factors of the amount of rainfall and seasonality of rainfall varied.

ACKNOWLEDGEMENTS

Collections for this study were provided by the U. S. National Museum and the Field Museum of Natural History. I am particularly indebted to Dr. Nicholas Hotton III and Dr. John R. Bolt of these two institutions for allowing me the use of the collections and aiding in many ways in their study. Richard Lassen, of the University of California at Los Angeles, made one of the critical collections from Waurika, added to the Orlando sample and aided in the preparation of the samples. Lila Olson, my wife, aided in collecting over several years with remarkable patience in the dull process of picking up each scrap of bone under hot suns and humid winds.

The illustrations have been prepared by Sarah Wilkinson, Laboratory Scientist at The University of California at Los Angeles. Field work and laboratory study has been supported by National Science Foundation, Grant, GB 31283X.

APPENDIX A

THE WAURIKA SAMPLE

The specimens of the Waurika sample occurred in a gray-brown shale formed by deposition in a lake. The lake beds are enclosed laterally and above and below by

beds of sandstone in which are included lenses of red to brown sandy shale. The lake shales average about 1 meter in thickness. The full area extent of the lake cannot be determined accurately, but the beds occur over at least 10 acres and probably considerably more. Vertebrate remains, largely fragmentary are scattered more or less uniformly within the shale over the exposed areas. They show some tendency toward clumping but over the full area this effect is damped. Near the southern margin of the exposures, near the ancient lake shoreline, the beds are somewhat thicker and complete bones of large animals such as *Ophiacodon* and *Edaphosaurus* occur. Occasionally complete vertebrate of *Edaphosaurus* and *Dimetrodon* are encountered in other parts of the deposit.

Five samples, listed in Table 7, have yielded a total of 1682 specimens. The composition of each sample on the basis of the number of identifiable specimens of each genus is included in this table. Each of the samples was collected

in a different way and this is a matter of prime importance in interpretation.

Sample No. 1. United States National Museum (U.S.N.M.) collected by W. Dalquest. This is a selected sample in which well preserved and "unusual" genera have been included. Excellent representatives of the constituent genera are present, but there is a strong generic bias in the numbers of specimens.

Sample No. 2. Field Museum of Natural History (F.M.N.H.). A small selected sample which includes only well preserved materials.

Samples No. 3. University of California at Los Angeles (UCLA). A small, selected sample of well preserved specimens mainly obtained by quarrying the wall at the southern margin of the exposures (lake margin). Teeth of *Xenacanthus* were not included.

Sample No. 4. U.S.N.M., Nicholas Hotton III collector. The specimens came from a large block of matrix,

Table 7—The numbers of individual specimens in the vertebrate groups in each of the five samples from Waurika; the percentages of the sample for each group; the summation of the total sample and percentages of each group, tr, less than 1%.

Vertebrate Groups	USNM # ¹		FMNH # ²		UCLA # ³		USNM # ⁴		UCLA # ⁵		Total	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
<i>Xenacanthus</i> sp. ..	80	22	37	76	0	0	400	90	700	88	1217	72
Ganoid scales ..	38	11	0	0	0	0	20	5	7	tr	65	4
<i>Sagenodus</i> sp. ..	3	tr	0	0	0	0	0	0	2	tr	5	tr
<i>Gnathorhiza serrata</i> ..	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lysorophus tricarinatus</i> ..	?	0	0	0	0	0	0	0	0	0	0	0
<i>Diplocaulus magnicornis</i> ..	44	12	2	4	0	0	3	1	10	1	59	3
<i>Crossotelos annulatus</i> ..	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pantylus</i> sp. ..	0	0	0	0	1	5	0	0	0	0	1	tr
<i>Eryops megacephalus</i> ..	6	2	2	4	10	50	1	tr	20	3	39	2
<i>Trimerorhachis insignis</i> ..	24	7	2	4	5	25	10	2	40	6	81	5
<i>Zatrachys</i> sp. ..	2	tr	0	0	0	0	2	tr	1	tr	5	tr
<i>Cricotillus brachydens</i> ..	0	0	0	0	0	0	0	0	0	0	0	0
<i>Archeria</i> sp. ..	53	15	2	4	0	0	1	tr	4	tr	60	4
<i>Diadectes</i> sp. ..	9	3	0	0	2	10	0	0	1	tr	12	1
Captorhinomorph ..	1	tr	0	0	0	0	0	0	0	0	0	0
<i>Ophiacodon retroversus</i> ..	21	6	6	13	2	10	1	tr	3	tr	33	2
<i>Edaphosaurus claviger</i> ..	39	11	0	0	0	0	6	1	10	1	55	3
<i>Dimetrodon</i> cf. <i>limbatus</i> ..	37	10	0	0	0	0	0	0	3	tr	40	tr
TOTALS ..	358	99	51	101	20	100	444	99	801	99	1682	99

about $2 \times 1 \times 0.5$ m, removed from beds formed near the center of the lake. Bones and teeth occur in a zone about 1/4 meter thick. Fossils were removed and their genus and position tabulated. This is an unbiased sample for the area covered.

Sample No. 5. UCLA, Richard Lassen collector. This sample was collected from the surface over a relatively small area, about 1/10th of the total exposure. An effort was made to collect all the fragments that lay of the surface. This area had been "cleaned" the previous year so that most of the specimens came from a very thin layer of sediment, with specimens coming to the surface over a period of about 10 months. This represents as unbiased sample as can be obtained for an area of this size.

Together the samples provide an excellent representation of the genera and species preserved in the Waurika deposits. Only numbers 4 and 5 were collected without selection and these 2 only give some notion of the bias in numbers of individuals and taxa introduced by selective collecting of numbers 1 to 3. Sample number 4 covers much of the time interval over which accumulation of fossils took place. No major differences in genera or their relative numbers were found over this interval, so that the fauna in general seems to have been fairly constant over time.

Sample number 5 serves as a basis for estimation of the faunal composition of the lake over a short period of time. To arrive at such an estimate it is necessary to make a number of assumptions and to analyze each genus in an appropriate fashion. The following are the primary assumptions :

1. The area collected represents about 1/10th of the total area of the lake. This is a minimum estimation, and probably a considerable underestimation.
2. There was more or less uniform distribution of the aquatic genera over the area of the lake. This is borne out by general observations on distributions of surface materials, although concentrations vary somewhat.
3. The specimens in the sample were drawn from a contemporary assemblage. The way that sample number 5 was collected makes this a reasonable assumption.

Given these assumptions it is possible to arrive at a *minimum* number of individuals of each genus present in the lake at a given time. This, however, requires an additional step, an estimation of the number of individuals represented by fragmentary remains. This differs depending on morphology and mode of preservation for each genus.

THE AQUATIC GENERA

These are the genera which were full time, largely obligate, inhabitants of aquatic environments, near the lake (see Figure 3).

Xenacanthus. Only individual teeth of this fresh water

shark are preserved. The teeth occur throughout the area of the lake, but there is some clumping, which is lost in sampling. The number of teeth per cubic foot of sediment averages about 50, but is in excess of 100 in some places.

Teeth measure from about 2 to 20 mm along the long axis of the tooth base. The shape of the base varies somewhat with position of the tooth in the jaw but this could not be taken into account. The numerical distribution of tooth sizes grouped into three size classes is shown in Table 8.

Table 8

Size Group in mm	Number and % of teeth of <i>Xenacanthus</i> in 3 size groups. From sample 5		Number and % of teeth, in size groups in 1 jaw of an individual	
	No.	%	No.	%
2—8 (small) ..	210	34	8	33
8—14 (medium) ..	355	58	12	50
14—20 (large) ..	50	8	4	16
	615	100	24	99

Comparisons of the size distribution in the sample from Waurika and the number of teeth of comparable sizes in an individual shark estimated from illustrations in the literature (Table 8), show sufficient resemblances that the Waurika sample could have come totally from adult sharks. A greater size range with heavier concentration in smaller (younger) individuals might be expected, but is not realized. It is possible but not necessary, that the smaller teeth came from non-adults and the assumption is made that we are dealing with a sample of matured sharks. Deviation from this assumption would mean that our minimum estimate falls below the actual number present.

If it is judged that each shark contributed about 200 teeth to the sample, representing approximately 2 full generations of teeth, then it may be concluded that at least 3 to 4 sharks contributed to the sample and that over the full area 30 to 40 sharks were in existence at the time represented by the sample. It must be emphasized that this is a *minimum* estimate, based the most stringent restrictions. The number, 30 to 40, is probably sufficient to have maintained a population, but is almost certainly well below the actual number present.

Ganoids. Ganoid scales, probably from *Ectosteorhachis*, are the only known remains of moderate sized osteichthyans. Such scales are fairly common, occurring in patches, but rarely show up in surface samples, unless

special effort is made to locate them. No estimates of numbers of individuals is possible.

Paleoniscoids. Scales are scattered throughout the shales, but do not show up in surface-picked samples, being too small to be readily seen. They do not appear to occur in clusters. Scales of paleoniscoids of several types are abundant in the heteropolar coprolites from *Xenacanthus* (Williams, 1972). Clearly these small fish were abundant, but from the scattered scales alone there is no way to estimate numbers of individuals.

Sagenodus. Two tooth plates, clearly from different individuals, occur in sample number 5. With the assumptions made at the beginning of this section, this indicates a minimum number of 20 individuals over the lake as a whole. *Sagenodus*, however, is not evenly distributed and does not commonly appear in samples. The number estimate is thus somewhat questionable.

Trimerorhachis. This is the most abundant of the amphibians as far as specimens alone are concerned, making up about 6 percent of the total of sample number 5. Remains consist of skull parts, fragments of lower jaws, limb bones and vertebral intercentra. Six specimens of presacral intercentra are of sufficiently different sizes that they cannot have come from less than 3 individuals. Skull, jaw and other postcranial elements show a comparable size range, but are less definitive as to numbers. At least 30 individuals were present at one time in the lake by our methods of estimating minimum numbers. Distribution appears to have been fairly even, so that this minimum estimate is reasonable. As in the case of *Xenacanthus*, use of stringent constraints on estimation, indicate that the minimum estimate is low.

Diplocaulus. Vertebrae, skull and jaw parts, fragments of girdles and limb bones make up the sample. Although 10 specimens are present in the Lassen sample, number 5, all could have come from a single individual. The relatively high number in the Dalquest sample, number 1, probably results from ease of identification of the vertebrate while collecting. *Diplocaulus* is not evenly distributed so estimates are uncertain. It was not abundant and minimum estimates suggest that perhaps 10 were present as adults in the lake at a given time.

Archeria. Four small vertebrae are present in sample number 5. All could have come from a single individual. The relatively high number in the Dalquest sample, number 1, probably results from ease of identification in the field and the tendency of collectors to take those items which can be determined. A minimum number of 10 is indicated by the Lassen sample, number 5. Vertebrae of *Archeria* are encountered over the full area and appear to have been evenly distributed. The actual number probably was higher than that of *Diplocaulus*.

Zatrachys. Fragments of skulls, which are easily identified even from very small pieces are rare, but occur in 3

of the 5 samples. The data give no basis for estimating numbers, but certainly this amphibian was not abundant.

SEMI-AQUATIC GENERA

Semi-aquatic animals inhabited the margins of the lake and moved freely about in the lake waters. They were not necessarily confined to the lake but certainly interacted with the strictly aquatic animals.

Eryops. The 20 fragments in the Lassen sample may well have come from a single individual. They were close together and somewhat beyond the primary collection site. Small skull fragments and occasional intercentra are found throughout the deposit, but they give no basis for assessment of abundance.

Ophiacodon. Fragmentary specimens are found throughout the deposit. Near the shore, complete bones are present and parts of skulls have been found. Their epityle was well suited to an amphibious existence and probably preyed on both aquatic and terrestrial vertebrates. From the relatively low number found, it appears that *Ophiacodon* was not an important predator of strictly aquatic vertebrates.

Edaphosaurus. The remains usually found and recognized are the highly distinctive neural spines of the vertebrae. In several places, however, complete vertebrae have been found well away from the shoreline. Size differences and relative abundance indicate that a fairly large number of individuals lived in the vicinity of the lake. No more precise estimates of numbers are possible.

TERRESTRIAL ANIMALS

Dimetrodon, *Diadectes*, *Protocaptorhinus* and *Pantylus* are the primarily terrestrial animals that have been encountered. Only one specimen of each of the last two has been found and it is not at all clear that either genus interacted with members of the lake fauna. Both were in beds marginal to the lake. *Dimetrodon* is represented largely by readily recognized neural spines. Some fairly complete specimens of vertebrae have been found, but most are fragmentary. The genus clearly lived in the vicinity of the lake and probably preyed upon some of its larger inhabitants. Coprolites attributed to *Dimetrodon* from other sites have been found to contain fragments of both *Diplocaulus* and teeth of *Xenacanthus*. These two genera may well have been prey of this large carnivore in the Waurika lake.

Diadectes is known from a tooth fragment. Its role in the economy of the lake, if it had one, is uncertain. It may have fed on seed bearing plants along the shore, but there is no direct evidence to support this suggestion. It may not have been associated with the lake complex at all, for the tooth fragment may have been carried in by a stream from an adjacent area or from sediments deposited earlier. It is known to have existed in the area at approximately the time the lake existed.

APPENDIX B

ORLANDO SAMPLE

Exposures at this site occur over an area about 100 by 25 yards and in small outliers somewhat beyond this range. There is no way to determine, short of coring, the full extent of the lake, but it was not large, no more than 3 to 4 times the area of outcrop. The lake sediments consist of gray shale with interbedded lenses of sandstone. The total thickness is about one half meter on the average. The vertebrate sample consists of partial skeletons, skulls, jaws and postcranial elements preserved in nodules. Collections have all been made from the surface, with the exception of two fairly well preserved partial skulls and skeletons of *Diplocaulus*. Preservations of exposed material is good, but below the surface before interaction with the atmosphere the bone is soft and nodules are not well consolidated.

Collections have been made over a period of about 75 years, with parties from several institutions taking samples. Early collections at the Field Museum of Natural History, augmented by some made during 1950 and 1960, and collections at the University of California at Los Angeles are the sources of the sample used in this study. Collections present in other places have not been used because information on how they were collected is not available.

The total number of individual specimens in the composite sample is given in Table 1, with percentages and a comparative listing for the Waurika composite sample. The collections have been made by taking everything that was exposed at the surface at the times of collections so that the samples are non-selective. The composite sample was assembled from several collections and include specimens from the total section of the lake bed, thus representing deposition over the full span of existence of the lake. It indicates an average composition of the lake fauna, not the composition at a given time. It differs in this way from the Waurika sample number 5. The Orlando sample provides an excellent estimate of the genera and species present in the lake deposits. If it is assumed that there was little or no change in species and proportions over the period of deposition, the comparisons of percentages with those of sample number 5 from Waurika in Table 7 are not unreasonable.

Specimens of *Diplocaulus* dominate the sample numerically, outnumbering the next most abundant genus, *Crosso-telos*, by about 10 to 1, and *Trimerorhachis* by about 15 to 1. The numbers, as in the case of the Waurika sample, do not accurately reflect the relative abundance of genera and must be adjusted for each sample. The following paragraphs describe these adjustments and, where possible, include and estimate of minimum numbers of individuals contributing to the sample, but the minimum numbers are not adjusted to the lake dimension, as at Waurika.

AQUATIC VERTEBRATES

Xenacanthus. Two specimens, a partial tooth and a small piece of calcified certilage represent this genus. It seems probable, although not demonstrable, that *Xenacanthus*, was not a member of the aquatic lake assemblage. The remains probably were washed in from adjacent streamsediments in which they had been buried at an earlier time. This assumption is made in the text of the paper.

Gnathorhiza. Thirty six specimens have been recovered. All belong to *Gnathorhiza serrata*. Fifteen are skulls and jaws and are from different individuals. About half of the remainder consist of bundles of large numbers of ribs, sufficient to suggest that they too came from separate individuals. The sample thus contained at least 20 to 25 individuals. The skulls have considerable size range, indicating a spread in age groups within the sample.

Diplocaulus. Eighty one percent of the specimens belong to this genus and all appear to pertain to *Diplocaulus magnicornis*. The sample includes vertebrae, single and in short series, skull and jaw parts, fragments of girdles, limb bones, and two fairly complete individuals.

Of the vertebrae, 499 from the presacral region are well enough preserved and exposed that the length of the centrum can be measured. Measurements grouped into classes are listed in Table 9. Two size classes, 4.0-5.9 and

Table 9—Distribution of the sizes of presacral vertebrae of *Diplocaulus* in Orlando sample, based on maximum length of the centrum measured along the base.

Central Length in mm	Number	
4—5.9	2	} cervicals plus presacrals n=48
6—7.9	46	
8—9.9	121	} presacrals, except first 4, —cervicals n=401
10—11.9	174	
12—13.9	62	
14—15.9	39	
16—17.9	2	
18—19.9	2	
20—21.9	1	
Total	449	

6.0-7.9 include cervical vertebrae of larger animals and a few non-cervical vertebrae of small animals. They have been eliminated from the calculations upon which the estimates are based. The remaining 401 vertebrae are from the post-cervical, presacral region. Even within this region considerable variation in vertebral length occurs along the column. Thus, although individuals of different

sizes are included in the sample, it has not been possible to sort the vertebrae into size groups that would indicate age relationships. It is thus assumed that all representatives are adults.

The presacral column of *Diplocaulus* consists of about 20 vertebrae, so that the number in columns contributing to the sample of 401 is 16. Using this figure the minimum number of contributing specimens is 25. Undoubtedly this is well below the actual number of contributors, for it is based on the assumption that all vertebrae from each individual have been preserved and recovered. If the non-measurable specimens of vertebrae, 300 in all, are added on the same basis of 16 per individual, 19 or 20 more were present, but this figure must be reduced to accommodate the fact that some are caudals and some cervicals. About 1/4 seem to fall in these categories, so that 14 or 15 additional individuals seems a reasonable estimate. This brings to 40 the probable minimum number.

A sample of left "horns" indicates the presence of at least 37 individuals. Skull parts, jaws and limb elements show a wide size range, from adult to subadult sizes, but except for the horns' do not give a good basis for estimation of numbers. On the basis of the data available a minimum number of 40 is used in the text.

Crossotelos. The vertebrae of this nectridean resemble those of *Diplocaulus* but presacrals are readily differentiated by the structure of the transverse processes. Vertebrae have not been successfully associated with skull, jaw and limb elements. The illustrations of limbs in the literature are subject. Four specimens of partial skulls and jaws that may represent *Crossotelos* have not been entered into the overall sample. Although similar to skulls and jaws of *Diplocaulus* they have long, sharp teeth, beyond the range of variation of *Diplocaulus* as usually constituted. It is possible that they belong to *Crossotelos*, but this cannot be confirmed. It is likely, however, that some of the skull materials among the 1734 specimens entered as *Diplocaulus* in Table 1 do, in fact, pertain to *Crossotelos*.

Lysorophus. Twenty two specimens of the aestivating, lepospondylous amphibian have been found, each representing a single individual. Most of the specimens are coiled, in aestivating position, but a few appear to have been preserved from the free swimming phase of their existence.

Cricotillus. This genus is similar in most respects to *Archeria*, the well known Wichita embolomorous amphibian. It differs in some aspects of the teeth and skull (Olson, 1970). Three and possibly 4 specimens are in the sample. Whether or not this genus can be synonymized with *Archeria*, is not entirely clear, but there can be no question that it was ecologically very similar. Included with this genus in Table 4, but not entered in Table 1, are several specimens that appear to have been similar, long snouted predators, but with well developed, rounded palatal teeth and an opposing set on the lower jaw. They

represent an undescribed genus of labyrinthodont amphibian. Here they have been grouped with *Cricotillus* from an ecological point of view, pending full study and description. Together, *Cricotillus* and the undescribed genus represent an ecological element much like *Archeria* in the Waurika lake.

Trimerorhachis. Altogether 12 fragments of *Trimerorhachis* have been found. They consist of skull and jaw parts, girdles and limb bones. The fragments do not provide a sample suitable for determining a minimum number because there is little consistent duplication of parts. Size differences are extensive and from these alone 8 to 10 individuals contributed to the sample. Presumably this number is quite low, but no way of determining the extent of underestimation exists.

SEMI-AQUATIC GENERA

Eryops, *Diadectes* and *Edaphosaurus* belong in this group. None was a certain member of the lake faunal complex. One fragment of *Eryops* has been identified. *Diadectes* is known from single, worn tooth. Two fragments of neural spine of *Edaphosaurus* appear in the sample. All these specimens are badly worn, as if transported, and it seems probable that all were washed in from adjacent deposits as the lake sediments were forming. Probably none lived in the immediate vicinity of the lake.

TERRESTRIAL GENERA

Pleuristion. This captorhinomorph genus was named on the basis of a few vertebrae from the Orlando locality. It has not been identified elsewhere. In 1970 (Olson, 1970) a skull and other post-cranial material were added to the type and an amended description was made. Clearly all of the captorhinomorph material from Orlando belongs to a single genus and species. It is questionable, however, that *Pleuristion* is a valid genus. The vertebrae are possibly indeterminate. Many of the features of material now known suggest affinities with other genera of captorhinomorphs, particularly with *Protocaptorhinus*. Pending resolution of the taxonomic problems, the name *Pleuristion* is used in the text.

Many more specimens are available than were present in 1970. Ten of these occur in large nodules and appear to be individuals that were buried intact but suffered some damage during diagenesis. Other specimens are parts of skulls and jaws, limb bones, and miscellaneous postcranial assemblages and individual bones. The nodules and skulls indicate that at least 20 individuals are represented in the sample. This is a minimum number, probably low. In any event, the number is substantial relative to the number of any other terrestrial animal in this sample or in that from Waurika.

Dimetrodon. This genus is represented by spine fragments, 5 in number, and 2 worn teeth. The spine

fragments could have come from a single vertebrae. Probably these remains were washed into the lake deposit from adjacent beds. *Dimetrodon* did, however, live in the vicinity at the time the lake was in existence, for it has been found in contemporary beds a short distance away. The evidence that the genus interacted with the lake fauna is minimal, but interaction is not out of the question.

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