FIELDIANA · GEOLOGY

Published by

CHICAGO NATURAL HISTORY MUSEUM

Volume 10 | March 7, 1958 | No. 32

FAUNA OF THE VALE AND CHOZA: 14

Summary, Review, and Integration of the Geology and the Faunas

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INTRODUCTION

The first thirteen papers of this series have been devoted to descriptions of the vertebrates collected from the Permian Vale and Choza Formations of northern Texas during the years from 1946 to 1954 (Olson, 1951a, 1952a, 1954, 1955a, and 1956). In addition, preliminary reports on the fauna of these formations (Olson, 1948, 1951b) and a synthesis of the evolution of the faunas (Olson, 1952b) have been published. Short comments on stratigraphy, environments, and faunal associations were included in these papers. These observations were necessarily limited by incompleteness of the work, and by emphasis upon a particular suite of animals in each study. There is a vast amount of work still possible in the Vale and Choza Formations, both in the areas covered in the course of these studies and in areas which have not been prospected for vertebrate remains. For the time being, however, no additional collecting or study is contemplated, and it is thus appropriate to collate and summarize the results to date. This final paper of the Vale-Choza series is devoted to this end.

THE SECTION AND FORMATIONAL BOUNDARIES

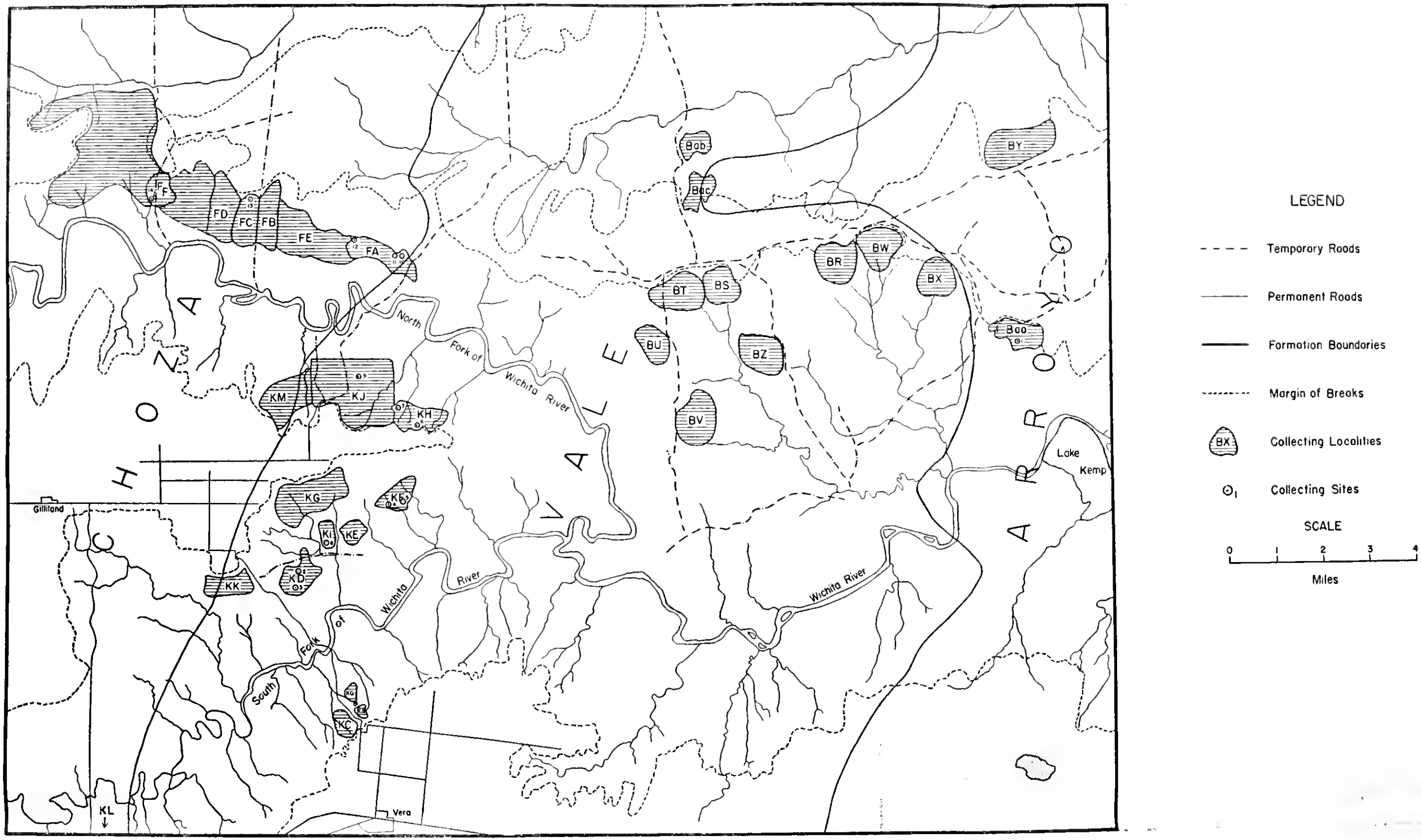
The Vale and Choza Formations are part of the Clear Fork group, which includes, as well, the Arroyo Formation, which underlies the Vale, and, according to various writers, the still older Lueders Formation and the underlying Clyde. Above the Lueders, which comprises marine limestone and shale, the beds of the Clear Fork, in the area studied, are in large part terrestrial and consist predominantly of red shales, sandstones and conglomerates. In the upper part of the Choza,

Library of Congress Catalog Card Number: 51-13674

No. 836

semi-marine conditions are encountered for the first time above the Lueders and very basal Arroyo. To the south of the area of our field work, the Arroyo, Vale, and Choza are predominantly marine (see fig. 176, B). A terrestrial deposit of early Vale age (Wilson, 1948), however, is known in Taylor County, about 100 miles to the south of the southernmost deposits in Knox County. It is clear that at this, and probably other times, the non-marine deposits extended far to the south of the area that has furnished the data for this report. In the marine section, the top of the Arroyo Formation is marked by the Standpipe Dolomite, one of several dolomites of this formation. The type section occurs in Taylor County, not far from the early non-marine Vale deposits mentioned above. The overlying Vale Formation in Taylor and adjacent counties consists largely of marine shales, sandy shales, and sandstones. The type section is at the old Vale post office in Runnels County. The top member of the Vale is the extensive Bullwagon Dolomite, which is thin, about 5 feet in Taylor County, but thickens to the south and southwest to about 40 feet of dolomite and shale in Tom Green County (Sellards, Adkin, and Plummer, 1932). The type section of the Choza Formation is at Choza Mountain, near Tennyson, in Coke County. In this area the formation consists of red shales and thin dolomites, with the Merkel Dolomite the most persistent member. To the north, from the type locality the beds of dolomite diminish in thickness and do not extend into the area with which this report is concerned.

Neither the Standpipe Dolomite nor the Bullwagon Dolomite, which mark the top of the Arroyo and the top of the Vale respectively, is present in the area that has been studied. The problem that this poses with respect to determination of formational boundaries is self-evident. It has been necessary to use indirect physical criteria to determine the limits of the formations, and the results are certainly open to some question. The reasoning that has been used is as follows: We may visualize the area of sedimentation with which we are concerned as the site of a major delta, on which sediments were deposited in part under marine and in part under non-marine conditions. Changes concomitant with transgressions and regressions of the sea can be expected to occur not only along the strand line, but also in more remote parts of the two phases of the delta. We are interested in particular in the changes on the terrestrial segment, at some distance from the sea. It is evident from modern deltas that there is a more or less regular and interpretable change in physiography and the nature of sedimentation as distance from the delta margins increases. This, of course, is specific to a particular suite of circumstances and is not



MAP OF AREA COVERED IN REPORT, INCLUDING PARTS OF BAYLOR, KNOX AND FOARD COUNTIES, TEXAS

The hachured and lettared areas have produced the preponderance of vertebrates from the Vale and Choza Formations. In addition, areas to the north and south of Lake Kemp and between the hachured localities have provided stratigraphic data. The exposures east of Vera, along the south wall of the South Fork of the Wichita River, have not been studied in detail.

the same for various deltas. The problem, in the case under discussion, is one of interpretation of the extent of the sea from the evidence of non-marine sedimentation and land forms.

The existence of dolomites in the marine section, as they replace clastics, would appear to represent conditions under which the sources of the clastic sediments were more remote, assuming no major changes in the source areas, than they were during times of deposition of clastics. The Standpipe Dolomite thus is taken to represent a time of moderate transgression of the sea over previously non-marine parts of the delta. The deposition of shales and sands that follows is interpreted as a reversal of the trend, to conditions of regression. These conditions persisted without a major transgression until the time of deposition of the Bullwagon Dolomite, which marks the end of the Vale. The northward extent of the dolomite and the fact that it thins to the north from Taylor and Runnels Counties, in the direction of Baylor and Knox Counties, offer some confirmation of this interpretation.

With this in mind, we may turn to the conditions on the non-marine parts of the delta. In western Baylor County there occurs a persistent series of even, red shales (fig. 176, A). This series appears to continue with general northwest-southeast strike across the area of concern. In places, broad, thin lenses of fine gray to green conglomerates are interbedded with the shales. These range up to about 50 feet in width and are only a few inches thick. Fine selenite crystals are present within these lenses. The lenticular cross sections and linear disposition of the long axes of the lenses suggest that they represent very broad channels of shallow, relatively sluggish streams. The maximum extent along the long axis that has been observed is about one-half mile. The included salts indicate that the waters under which deposition took place were saline during some phase of deposition. Similar salts do not occur in the enclosing shales. The deposits of fine conglomerate are interpreted as having been deposited by streams that drained the surface of the delta, which was very low and had little relief at this stage. The streams appear to have been subject to tidal invasion from adjacent, brackish or salt water. The even red shales were formed on the delta surface when this surface lay very close to sea level and when open water of the sea, or brackish water of lagoons, was not far distant. The beds, in keeping with this line of thought, are interpreted as correlatives of the Standpipe Dolomite. They are thus taken to be the uppermost deposits of the Arroyo Formation. Overlying beds are assigned to the base of the Vale

Formation. The general trace of the red shale may be seen on the map, as shown by the line indicating the Arroyo-Vale boundary.

A boundary so established is somewhat arbitrary and transitional rather than precise. The thickness of the series of even red shales is variable, ranging from about 25 to 50 feet, and the base and top are transitional, with beds below and above, respectively. The situation is further complicated by the gradual increase of elevation of the present land surface away from the channels of the valleys of the North and South forks of the Wichita River, and by the highly irregular local relief to the north and south of the valleys. This relief is generally between 20 and 50 feet but in places rises to over 100 feet, where an early Pleistocene cap rock of gravel, sand and shale has persisted (fig. 177, B). The transition between the Arroyo and the Vale thus traces a sinuous course on the map. This is in large part controlled by topography but results in part from the varied thickness of the red shale.

There is a faunal break at the stratigraphic level marked by the even red shales. The shales themselves are very poor in fossils. Only *Lysorophus* and fragments of spines of *Dimetrodon*, among the vertebrates, have been found. Occasionally, well-preserved plant impressions occur over restricted areas, with the red shale as the preserving matrix. Immediately above the red shales, in the coarser clastics, occur *Gnathorhiza dikeloda*, *Labidosaurikos barkeri*, *Trematopsis seltini*, and an undetermined species of *Captorhinikos*. Of these genera, only the first is known from the Arroyo, and it is represented by a different species, *G. serrata*. *Edaphosaurus*, *Seymouria*, *Trematops*, and *Broiliellus*, typical genera of the Arroyo, have not been found in beds younger than the even red shales. The physical evidence of a break is thus supported by faunal evidence, but the vertebrates, of course, provide no evidence of the time equivalence of the division to the boundary drawn between the Arroyo and Vale in the marine section to the south.

The boundary between the Vale and the Choza has been drawn on somewhat similar physical evidence. It again must be considered transitional. The line between these formations (see map) marks a zone of rapid shift from the highly channeled section, typical of the upper Vale, to the evenly bedded red and green shales, which have few channel deposits, called basal Choza. There is a rapid increase in the increment of primary anhydrite, which is abundant in the middle and later Choza but apparently absent in the Vale. The changes are considered to reflect the changes in the extent of the sea marked by the deposition of the Bullwagon Dolomite. The terrestrial deltaic area does not appear to have risen high above sea level at any time during the Choza, for channel deposits are few and beds have broad lateral extent. Anhydrite becomes increasingly abundant with time. The percentage of terrestrial beds in the section decreases steadily from basal to the middle Choza. Shortly after deposition of the initial beds of Choza, marginal deposits formed in evaporite basins; these deposits can be identified in southern Foard County (see fig. 184, A). After the mid-Choza, basin deposits predominate and no beds that can be certainly considered non-marine have been found.

There is no distinct faunal break at the Vale-Choza boundary. The number of genera known from the Choza is less than that from the Vale, but this may in large part be the result of the paucity of collecting localities in the Choza. *Captorhinikos chozaensis* replaces *C. valensis*, and *Casea halselli* replaces *C. nicholsi*. A new species of *Trimerorhachis, T. rogersi*, appears in the Choza, and a new but unnamed genus of eryopid has been found in the middle Choza. For the most part, however, differences are expressed merely by the absence of genera and species that are typical of the Vale.

The Choza Formation is overlaid by the San Angelo Formation of the Pease River group. A strong erosional unconformity marks the contact (fig. 183, B), and, in many places, the sandstones and conglomerates of the basal San Angelo have been deposited in channels cut in the Choza shales. Immediately below the disconformity is a thin, altered zone of green shale, from 3 to 12 inches thick. The zone is rarely absent and serves as a convenient and reliable marker of the contact. At many sites where the contact is exposed, a bed of sandstone, which ranges from about 6 inches to a foot in thickness, is present from 5 to 15 feet below the disconformity. This has been considered as the base of the San Angelo in reports on some of the sites. The red shales between the sandstone and the coarse clastics of the San Angelo are characteristically like the shales of the Choza in composition, color, and texture, and seem best associated with the Choza. Neither the basal coarse clastics of the San Angelo nor the shales that lie immediately under them carry vertebrate fossils.

The faunal break between the Clear Fork and the San Angelo Formation of the Pease River group is marked (Olson and Beerbower, 1953). Only one genus, *Xenacanthus,* is common to both. *Cotylorhynchus,* known from the Hennessey shale of Oklahoma, is present in the San Angelo, but this genus has not been found in the Texas Clear Fork.

Thickness of the formations.—Evidence on the thickness of the terrestrial beds in the areas covered in this report is insufficient for accurate statements. The figures cited in an earlier paper of the series—500 feet for the Vale and 1,000 feet for the Choza—are based on estimates that follow from an assumption of a northwesterly dip of 50 feet per mile. This gives a reasonable approximation. Subsurface data to check the figures are not available, and measured sections in surface exposures are of little help, since sections are incomplete and beds are subject to rapid lateral variation of lithological units. The problem is complicated further by the probable loss of anhydrite in the surface sections (see Roth, 1945, for examples). The estimates are thus at best rough, but they are sufficient for purposes of the studies of the vertebrates that have been undertaken.

SEDIMENTARY AND STRUCTURAL CHARACTERISTICS OF THE VALE

From base to top, the Vale Formation is characterized by the presence of channel deposits. It is this feature that distinguishes the Vale from the Arroyo below and the Choza above. The dominant sediment throughout the section, however, is red shale, and the total section has a strong red cast over the area of outcrop. Major sedimentary types may be grouped into shales, sandstones, grits and conglomerates on the basis of the sizes of particles of which they are composed. There are minor amounts of "siltstone" and anhydrite. The former occurs in small channel deposits, and the latter as dikes, injected from above, and as thin layers along bedding planes lateral to the dikes. No primary anhydrite has been found in the Vale over the area studied.

1. *Shales* (figs. 177-179).—Shales, which form the major sediments of the Vale, appear to have been laid down under two principal conditions of sedimentation: on flood plains away from the immediate vicinity of major channels, and in bodies of standing water. Flood plain shales are predominantly red in color, but occasional brown, green, and gray patches and lenses are present. The light color of some of the shale has resulted from reduction of original red sediment, as shown by transition zones. Reduction is charac-

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FIG. 176. Sedimentary types in Arroyo. A. Evenly bedded red shale of uppermost Arroyo Formation. Note light layer in foreground, composed of very fine, green conglomerate and apparently deposited in shallow channel. Locality BY, western Baylor County, Texas. B. Marine dolomite and shale of Arroyo Formation in Taylor County, Texas.

A

B

teristic where plant remains are abundant. Intricate imbrications of green and red shales in various localities, however, indicate a difference in chemical composition at the time of deposition and suggest that there existed an initial color differentiation. Only major bedding is generally evident in the shales of the flood plains, for internal structures have been largely obliterated by compaction after deposition.

Shales deposited in bodies of standing water commonly are lighter in color than the typical shales of the flood plains. The areas of single deposits are restricted, rarely exceeding one quarter square mile. The lighter colors appear to have been induced by reduction resulting from the action of the products of accumulated organic remains. A few instances of deep red pond or lake shales have been observed. These presumably accumulated in the absence of abundant plant remains. Several of the deposits that apparently were formed in bodies of standing water exhibit bedding, apparent in fine banding, but, for the most part, whatever bedding may have existed has been destroyed by compaction. The shapes of the pond or lake deposits vary from nearly circular to ovoid, with the long axis as much as three times the length of the short one. Ox-bow forms are not uncommon. Typically, the marginal beds of these deposits dip from 3 to 10 degrees toward the basins, and these beds form a convenient means of recognition of the extent of the deposits. Some of the dip may be due to differential compaction, for the marginal beds tend to be somewhat coarser than those deposited away from the shore line. There are, however, in the Choza, two instances in which small tree trunks have been preserved in upright position in these dipping beds. In each case the beds intersect the long axes of the trunks at the angle of dip. If, as seems probable, the trees were approximately vertical in life, the dip must be considered to be initial rather than secondarily induced by compaction.

In most cases deposits in the channels that lead into the ponds or lakes can be identified. The sediments formed in the channels tend to be coarse sandstones or conglomerates. No outlets have been identified in any instance, but only under ideal conditions would recognition be possible, since the sediments would tend to be fine-

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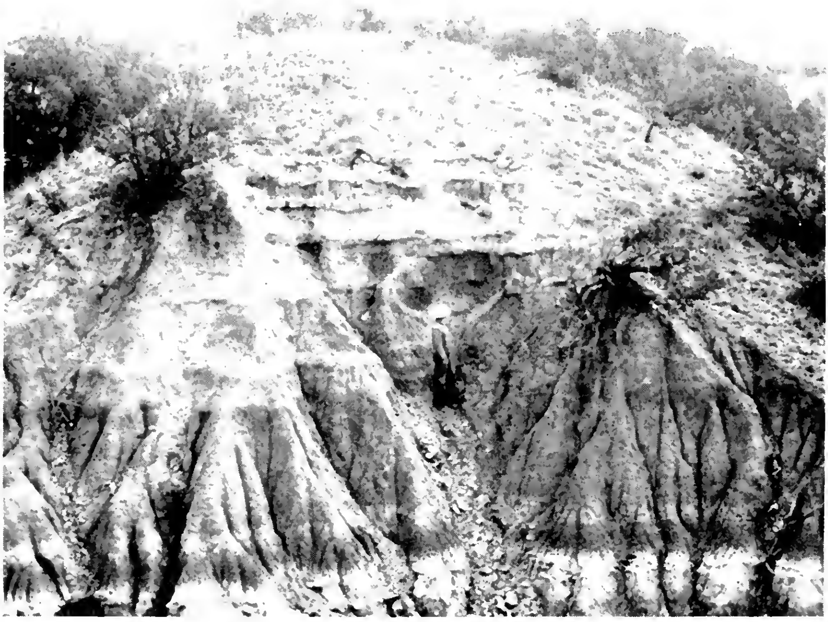
FIG. 177. Sedimentary types in Vale Formation. A. Evenly bedded pond deposits of mid-Vale age. Locality KH, Knox County, Texas. B. Contact of Permian transition zone between Vale and Choza Formations and early Pleistocene. Contact at level of feet of figure. Locality KK, Knox County, Texas.

A



B

grained. Since, however, the dipping beds continue around the basins with interruption only at the points of inlet, it has been assumed that regular and persistent outlets were seldom present, and the bodies of water have been considered as predominantly pond types. A typical situation is shown in figure 185, based on a pond in the late Arroyo in which it was possible to determine the approximate distribution of vertebrates in both the pond and the channel.

In addition to the typical ponds, described above, temporary bodies of standing water can be recognized throughout the Vale. One type is indicated by the presence of coiled skeletons of the aestivating amphibian, *Lysorophus*, which occurs in high concentration over areas no more than a few feet in diameter. The matrix is consistently a red, green, or red and green fine shale. The skeletons are preserved in nodules. It is assumed that these deposits were formed in temporary ponds, which supported *Lysorophus* during swimming phases of its existence and served as the site of aestivation during dry periods. Obviously, where remains are found, conditions suitable to active life failed to return. A second type of temporary pond is indicated by lungfish burrows, which also give evidence of aestivation (see Romer and Olson, 1954). One such pond in the middle Vale is known to have covered several acres. Two other smaller deposits of similar nature have been found in this formation. The sediments are fine-grained, red shales.

Deposits formed in bodies of standing water are generally from 3 to 5 feet in thickness, although exceptional cases of thickness up to 20 feet have been noted. Except for these extreme cases, it must be assumed that the ponds in which the deposits formed were of relatively short duration, perhaps from 10 to 50 years. These sediments, along with others, suggest a rather rapidly changing landscape. The temporary ponds, and the aestivating animals contained in their deposits, are indicative of seasonality in rainfall.

2. *Sandstones and grits* (figs. 178, B, 179, B).—Medium- to rather coarse-grained clastics occur in three general situations. Some fills of smaller channels, with widths no more than 10 feet, are formed of sandstone or grit. These occur in the early Vale but are rare above the middle part of the formation. Sandstones and grits are charac-

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FIG. 178. Sedimentary types in Vale Formation. A. Light-colored deposits of shale between deep red shales (dark in photograph). The light-colored shales were formed in a pond deposit of late Vale age. Locality KJ, Knox County, Texas. B. Coarse, irregularly dipping beds of clastics found close to major channel. Early Vale age, Locality BR, western Baylor County, Texas.

A

B

teristic of the areas immediately adjacent to major stream channels in the lower half of the Vale (fig. 178, B), and throughout this part of the section they are encountered as thin, rather persistent layers interbedded with red shales at some distance from the channels (fig. 178, A).

The sandstones formed marginal to the channels tend to be coarse and to merge into deposits composed of grit-sized particles. They are characteristically cross-bedded and dip, somewhat irregularly, from 5 to 10 degrees toward the axes of channels which they border. In some instances the top parts of the channel deposits, which are predominantly composed of conglomerate, grade laterally into this type of coarse clastic.

The more evenly bedded sandstones, away from channels, range from fine to coarse, and are variously cross-bedded and ripple-marked. They appear to have been deposited in early stages of flooding, when currents were active, in contrast to the shales, which appear to represent waning stages of flooding. These sandstones range from red to gray and green in color and show little evidence of color change by reduction after deposition. They persist, although in reduced numbers both vertically and laterally, to the top of the Vale.

3. *Conglomerates* (figs. 180, 181).—Conglomerates in the Vale may be classified into two major types on the basis of composition. One is composed of a shale or sandy shale matrix in which occur larger particles highly varied in composition (fig. 180, A). The other has a similar matrix, but the larger elements are exclusively "clay-balls" or "clay-pebbles" (figs. 180, B, 181, B). The large fragments in the second type are formed of the shales in which the channels are incised, but it is convenient to follow the usual terminology of "clay-pebble" conglomerate in references to them. This type of conglomerate occurs characteristically in channel fills but occasionally is present as thin sheets lateral to the channels. The first-mentioned type occurs in channel fills and in the dipping complexes of sands, shales, and grits marginal to major channels. Colors in both types range from deep brown through red to light red, gray and green. Reduction after deposition has clearly been responsible for light colors

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FIG. 179. Sedimentary types in Vale Formation. A. Shales and bedded sandstones formed about two miles from major channel. Early Vale age, Locality BT, western Baylor County, Texas. B. Small channel fill composed of siltstone and incised in red shale. Channel marked by pick. Early Vale age, Locality BX, western Baylor County, Texas.

A

B

in some cases. Large channel fills, for example, tend to be green to light gray at the margins and red in the center portions. Where cracks and joints penetrate the red deposits, reduction has produced local green bands along the fractures. It is possibly important, in this regard, that the green portions rarely carry vertebrate fossils.

Clay-pebble conglomerates are first encountered at the beginning of the upper half of the Vale. Below this, only the other type of conglomerate is present. In the middle Vale the ranges of the two types overlap, but in the upper Vale clay-pebble conglomerates are dominant and the other type is extremely rare. Clay-pebble conglomerates formed in channels show mud-cracking in several observed cases (see fig. 181, B). The cracks form four- and five-sided patterns. The conglomerates behaved as a homogeneous sediment as mud-cracks developed during drying, for the cracks are developed uniformly, without respect to components of the conglomerates.

4. *Other sediments.*—In addition to the principal sedimentary types just described, there occur moderately fine-grained, calcareous deposits, which may be termed "siltstones," and anhydrite, or derived gypsum. The siltstones occur characteristically in small channel deposits, with cross sections not exceeding two feet in horizontal dimension. The channels in which they occur have been seen to pass directly into the larger channels, with an abrupt change of sediment from siltstone to conglomerate. The fine-grained channel deposits are characteristically green to gray in color, although several instances of light red deposits have been observed. There is no evidence of secondary alteration, so it is assumed that the colors represent approximately the color at time of deposition. Occasionally concentrations of fragmentary vertebrates occur in the small channels, but about 90 per cent carry no organic remains whatsoever.

Anhydrite, or gypsum, occurs predominantly in dikes. These cut the more or less horizontal beds of shale and sandstone in which they occur at approximately a right angle to the bedding. In every case in which it has been possible to make a determination, the dikes were injected from above. Where bases are preserved, termination is generally at the bedding plane of some hard layer. The bases are very narrow, and the upper parts progressively wider, reaching

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FIG. 180. Sedimentary types in Vale Formation. A. Heavy conglomerate blocks derived from thick channel fill (maximum thickness about seven feet) of major stream. Early Vale age, Locality BR, western Baylor County, Texas. B. Clay-pebble conglomerate blocks from large channel fill. Late mid-Vale age, Locality KJ, Knox County, Texas.

A

B

a maximum of about 16 inches in observed cases. Normally there is a narrow band of bright green sediment at the contact of the dike and adjacent shales, presumably the result of very local reduction of the shales. At their bases, the dikes are commonly in contact with thin, horizontal beds of anhydrite, which pass laterally from the dike along bedding planes. Thicknesses range from one-fourth inch to about one inch. Crude re-crystallization has induced a roughly vertical structure in these thin beds. In addition to the gypsum dikes, there are fine networks of siliceous dikes composed of chalcedony, and sandstone dikes are not uncommon.

There is no regular sequence of beds from the base to the top of the Vale, but, as indicated in the discussion of the various types of sediment, broad trends are sufficiently persistent to make it possible to determine the approximate position of outcrops in the section by the proportions of types of sediment present. The general features, of course, also provide one basis for inferences concerning changing conditions of sedimentation and the general environment of the delta.

The lower third of the Vale is characterized by fine to coarse channel deposits, in which the matrix is shale and sandy shale and the coarser fragments are varied in composition. There are several large channels in this part of the section (see fig. 180, A) and, lateral to these, many smaller channels associated with the dipping sandstones and grits (fig. 178, B). Fragments in the conglomerates range up to about 2½ inches in maximum diameter and are subangular to well rounded. The predominant color is dark brown, but green deposits are not rare. Away from the channels, evenly bedded shales constitute the major element. There are few pond deposits. Those that are present appear to represent temporary ponds, for they contain remains of *Lysorophus* preserved from the aestivating phase of the existence of this amphibian. The shales of the lower part of the Vale tend to be lighter red than the typical maroon shales of the underlying Arroyo Formation, but they lack the orange-red cast of the shales of the middle and upper parts of the Vale.

This highly varied array of sandstones, shales and conglomerates persists without major change into the middle part of the Vale. At the top of the lower third of the section, however, the first evidence

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FIG. 181. Sedimentary types in Vale Formation. A. Evenly bedded red and light green shale (in bank) and small clay-pebble conglomerate channel fills (around figure in foreground). Late mid-Vale, Locality KJ, Knox County, Texas. B. Mud-cracks on surface of large (green) channel fill composed of clay-pebble conglomerate. Late Vale, Locality KB, Knox County, Texas.

A

B

of clay-pebble conglomerate is encountered. This type of channel fill is characteristic of the upper part of the Vale; in fact, only two large fills not of this type have been encountered in the upper 200 feet of the section. The small channel fills in the upper part of the Vale consist of fine, gray to green, calcareous mudstone. All of the channels above the middle Vale had sinuous courses and anastomosed to produce a braided stream pattern. In abundance, composition, and sinuosity of their courses, the channels of the upper Vale are in sharp contrast to those of the lower Vale and the underlying Arroyo.

Dipping, coarse clastics, so characteristic in the lower part of the Vale, are rarely encountered in the higher beds. Most of the channels are incised in red shales and lack dipping marginal beds. Sheets of sandstone and grits, however, are developed on the flood plains lateral to the bands of anastomosing channels. In some instances these can be traced directly to the sediments of the upper parts of the channel fills.

The shales of the upper half of the Vale are predominantly bright orange-red in color. Well away from the channel courses, the shales are evenly bedded, and occasional thin beds of white to green, sandy shale are interbedded with the more abundant red shales (see fig. 177, B). Pond deposits are irregularly scattered through the flood plain deposits and interrupt the regularity of the bedding. The number of ponds tends to increase in frequency from the middle to the upper Vale. Several of the pond deposits show a fine bedding of alternating fine and coarser material, with an average thickness of less than one half inch. It seems probable that seasonal changes were responsible for the banding, but the layering may have developed from introduction of sediments during individual floods, which were not necessarily seasonal.

SEDIMENTARY AND STRUCTURAL CHARACTERISTICS OF THE CHOZA

The transition from the Vale to the Choza, as discussed earlier, occurs over a vertical distance of about 50 feet. It is particularly

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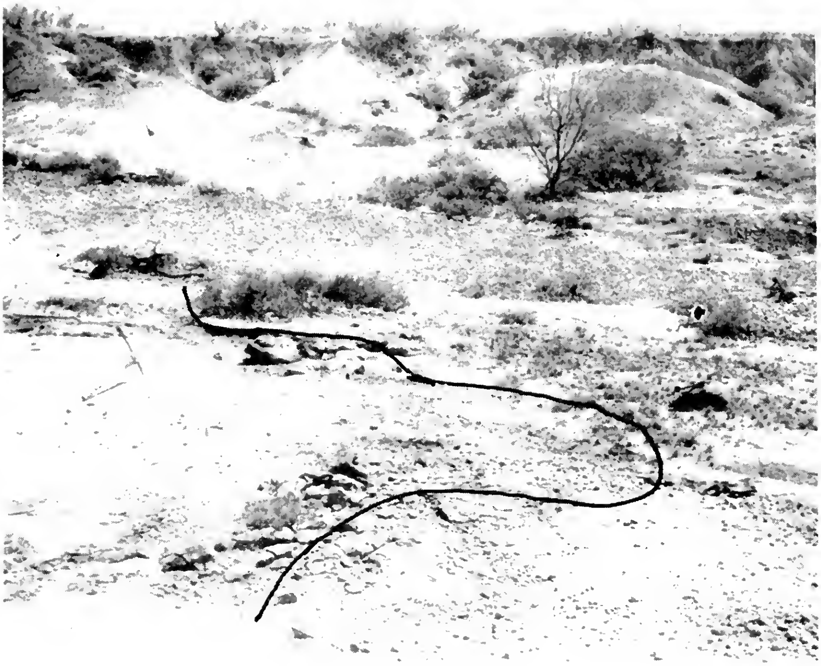
FIG. 182. Sedimentary types in Choza Formation. A. Pond deposit, shown by light-colored beds in background. Note marginal dip. Channel fill of clay-pebble conglomerate leading to pond (shown by line on photograph). Pond margin is at far end of line. Early mid-Choza, Locality FC, Foard County, Texas. B. Evenly bedded evaporite basin deposits. Light-colored layers are high in anhydrite. On west side of Benjamin Crowell Highway along north side of valley of South Fork of Wichita River, Knox County, Texas.



A

B

well shown in exposures on the north side of the South Fork of the Wichita River, along the abrupt valley wall about one mile north of the river along the road from Vera to Gilliland in Knox County (see fig. 177, B). Here there is a thick Pleistocene cap composed of light-colored sands and gravel and lenses of fresh-water limestone. The large channel deposits, characteristic of the upper Vale, decrease rapidly in frequency through this zone. Bedding becomes increasingly even, with individual beds more persistent, and there is a rapid increase in thin beds of primary anhydrite. It is impossible to draw a line that divides the sedimentary types of the Vale from those of the Choza within this zone, but the differences between the beds above and below the zone are striking and are persistent over the area studied.

Coarse clastics form a very small percentage of the total sedimentary deposits of the Choza. The percentage decreases steadily from the base of the Choza to the middle of the formation, and there are almost no coarse clastics in the upper half. Clay-pebble conglomerate, formed in channels, occurs in the lowest 200 feet, but higher in the section light green conglomerates and light-colored siltstones form the channel deposits. The shales of the Choza are light red, orange-red, light green, and white. The beds formed by the shales are usually very extensive laterally (fig. 182, B). In the upper half of the Choza, interbedded layers of anhydrite add a third type to the array of persistent beds. Gypsum biscuits, in the red shales, are found throughout the section. In collecting area FA (see map) there is a persistent, hard, fine shale or siltstone, which occurs throughout the site and forms a persistent cap of the low rounded hills of red shale (fig. 183, A).

Pond deposits occur in the lower half of the Choza but have not been found in the higher parts of the section. As a rule the pond deposits tend to be light-colored (fig. 182, A), as in the Vale, but the pond sediments at the pipe site (see map; also Olson, 1955a) are deep red in color. This deposit, unlike most others, shows no evidence of an abundance of plant material in the shales. It seems probable that the light color of other pond sediments is due to chemi-

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FIG. 183. Sedimentary types in Choza Formation. A. Fine conglomerate (light material in foreground) and siltstone, forming bench in mid-ground, in even red shales of early Choza age. Locality FA, Foard County, Texas. B. Contact of late Choza and basal San Angelo Formations, showing channeling of San Angelo into Choza, compositional differences of formations, and reduced zone represented by light-colored band immediately below San Angelo. Locality HA, just north of Pease River on Crowell-Quanah Highway, Hardeman County, Texas.

A

B

cal action of the products of vegetation, which is preserved in macerated form in great abundance, whereas an amount insufficient to result in reduction was deposited in the shales of the pipe site. The light-colored deposits are characteristically barren of vertebrates, although the channels leading to them carry fragments of bones and teeth. Sediments which incorporated large amounts of plant material during their formation apparently were unfavorable for preservation of vertebrates.

The upper half of the Choza is composed in large part of red and green shales and beds of anhydrite. There are, however, exceptions to this predominant pattern; for example, a persistent, brown, ripple-marked sandstone, from 6 to 8 inches thick, is found over a broad area in the upper part of the middle Choza (fig. 184, B). The ripple marks were formed by oscillating currents, and the sand presumably was deposited under the waters of the evaporite basin at a time of rather low concentration of salt. All of the upper half of the Choza Formation appears to have been formed under non-terrestrial conditions, presumably in the shallow waters of evaporite basins. At an earlier stage both terrestrial and basin facies can be recognized in contiguous areas of deposition. This is seen, for example, at locality FE (see map and fig. 184, A). Here the red shales of the terrestrial deposits are clearly differentiated from the gray and green sediments of the basin, and fine-grained channel deposits show the courses of channels that led from the margin of land into the basin. No remains of vertebrate or invertebrate fossils have been found in the basin deposits of the Choza, so that there is no record of life from the mid-Choza to the base of the San Angelo. It is by no means impossible that future studies may reveal terrestrial facies above the level from which the highest fossils are now known. Exploration to the north of the area which we have studied is indicated. Our studies, however, have failed to reveal the existence of such deposits.

ENVIRONMENT DURING THE VALE AND CHOZA

A brief account of the physical environment during the time of deposition of the Vale and Choza was presented in 1951 (Olson,

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FIG. 184. Sedimentary types in Choza Formation. A. Hard, fine-grained clastics formed near offshore margin of an evaporite basin deposit. Low hills in background (to north) are formed of non-marine Choza shales. Locality FE, early Choza, Foard County, Texas. B. Sediments formed in evaporite basin in early Late Choza. Cap rock formed by a series of cross-bedded, ripple-marked, brown sandstones. Located about one mile west of western margin of Locality FF, Foard County, Texas.

A

B

1951a), and environmental aspects of particular localities have been reviewed in preceding papers of this series. In the present section these earlier reports will be amplified and brought into as coherent a sequence of events as is possible in light of the present information.

Evidence on physical environment comes from three primary sources: (1) the sediments, (2) the fauna, and (3) the flora. The general aspects of the sedimentary evidence have been presented above. The sedimentary types, their distributions, and their structural characteristics all point to an origin of the sediments on the non-marine phase of a large delta. Thereafter, deposition took place under the waters of evaporite basins, on the non-terrestrial portion of the delta. There can be little question that the land form upon which the vertebrates lived was deltaic through the whole recorded vertebrate history of the Vale and Choza.

Early in the Vale, streams appear to have been perennial. Evidences in the sediments of repeated and marked changes in the capacity of the water of the streams to transport materials, suggest seasonality. There was relatively little ponding, but small, temporary ponds, probably rain pools, did exist. Their seasonal nature is suggested by the fact that they were inhabited by aestivating amphibians and lungfish. Topography appears to have been very low at the outset, when flood plains were broad and channel deposits were composed of shales, fine conglomerates, and sand. Rapid increase of local relief, however, took place during the early part of the Vale. Throughout the lower third of the Vale, drainage was reasonably well adjusted, following the low deltaic phase of the latest Arroyo.

By mid-Vale time, clay-pebble conglomerates appear as channel fills and by late Vale they form the predominant channel sediments. Braided streams have replaced the perennial, large streams of the early Vale. Each of the systems of anastomosing channels appears to represent a single phase of deposition. The clay-pebble conglomerates indicate periods of drying between major periods of water flow. Channels occur in closely spaced vertical intervals but are consistently separated by intervening layers of shale (see fig. 181, A). One hill, in locality KF, shows 9 levels of channels in a section of about 50 feet. Although the channel deposits that occur in particular areas have the same general direction of flow, the individual courses of one level show no correspondence, except in general trend, to those in the preceding or following level. It would appear that the major control of streams was persistent but that the local patterns were obliterated between periods of abundant water.

These facts suggest that the late middle and upper Vale deposits were formed in a climate characterized by intermittent rainfall, with extended periods of drying between the wet periods. Water action evidently was vigorous, for the clay-pebbles represent fragments derived locally, presumably torn from the banks and deposited not far from the source of the pebbles, as water lost its power to transport. Mudcracks, present in some of the channels, give additional evidence of drying after periods of intense water action (fig. 181, B).

Both permanent and temporary bodies of standing water were characteristic of the middle to late Vale. Drying, while not sufficient to obliterate the large, deep bodies of water, was effective in eliminating the majority of ponds formed during a wet period. Aestivating animals and, perhaps, banded bedding in some of the permanent ponds furnish additional evidence of seasonality.

There was sufficient moisture the year round to support a flora that included such plants as *Gigantopteris*, *Taeniopteris* and *Walchia*.[1] Strictly terrestrial herbivores and carnivores flourished, and semi-aquatic and aquatic vertebrates were present in abundance. True aridity is thus out of the question. The flora and fauna probably could have been supported by a rainfall as low as 25 inches per year, the approximate amount in the area today, for fish, amphibians, and reptiles thrive under present circumstances. The sediments, however, suggest greater periodicity than that which now exists, and indicate an approach to marked monsoonal conditions.

There is little specific evidence concerning the range of temperature. Clearly the faunal elements could have tolerated a considerable range. The large size of such forms as *Eryops*, *Casea*, and *Dimetrodon* argues for a moderately high mean temperature, with extremes somewhat limited. The same general interpretation seems to follow from what is known of the flora. The work now in progress on the latter should provide much more evidence than is now available.

With the onset of Choza times, the relief of the delta appears to have lowered rapidly from a maximum reached in the late part of the Vale. The margins of the evaporite basins moved steadily toward the area of the delta that has been studied. By the time that about 300 feet of the present section had been deposited, basin deposits were being formed along the southern margin of the area covered by this report. With the beginning of the Choza the climate appears to have entered a stage of increasing aridity. The trend in this

[1] Recently collected floras are being studied by Dr. Sergius Mamay of the United States Geological Survey.

direction continued at least to mid-Choza. The water supply was still intermittent, for there is continued evidence of flooding and drying, but it remained sufficient to preserve permanent ponds until the mid-Choza. The sediments formed in temporary ponds yield specimens of *Lysorophus* throughout the earliest Choza, but thereafter are devoid of any evidences of vertebrate life. Presumably the duration of these ponds was too short to provide a suitable habitat for the aestivating lungfish and amphibians.

Floral evidence on the physical environment of the Choza is not extensive. There is one important point, however. Remains of plants have been found only along the margins of watercourses and in the vicinity of permanent bodies of standing water. Some vegetation certainly existed elsewhere, but it seems reasonable to conclude that rich vegetation was in large part restricted to the vicinity of flowing water and ponds. A similar concentration has been noted for the remains of vertebrates.

After mid-Choza, deposits were formed largely, if not entirely, in evaporite basins, and thus there is no direct evidence of climatic conditions in emerged parts of the delta. If the deltaic biota persisted, it did so in some area that has not been covered in this study. Prior to the deposition of the basal beds of the San Angelo, there appears to have been an emergence of the land, to form the surface upon which the terrestrial beds of that formation were deposited.

AREAL LIMITATIONS OF INTERPRETATIONS

As shown on the map, the study that has provided the basis for the interpretations of the preceding sections was limited in areal extent. The fact that the exploration was not extensive along the strike of the exposed beds raises serious problems concerning the reliability of the generalizations. We have, in essence, a section in time so limited in geographical extent that spatial differences between exposures can be virtually ignored. A segment of the delta has been witnessed as it was modified during fluctuations that affected a much broader area of adjacent land and sea. The environmental changes thus, in part, reflect events that were not necessarily regional but rather may have been related to the position of the part of the delta observed relative to the position of the sea at a given time.

It is not possible, without a great deal of additional work, which is not contemplated at present, to weigh properly changes that are regional against those that are apparent only because different parts of the delta, relative to the sea and uplands, have been sampled at different times. Changes of the fauna, however, have a bearing on this point. Those that occurred between the Arroyo and the Vale provide a case in point. Over the area studied there is a pronounced sedimentary change. The deposition of even red shales in the late Arroyo was followed by formation of irregular and coarse beds early in the Vale. A marked faunal change occurred at this level. A number of genera disappeared, and soon afterwards genera and species, unknown before, formed an important part of the fauna. The problem is whether this apparently major change, both sedimentary and faunal, was a local phenomenon, or whether it was of broader significance and took place over a large part of the delta.

The sedimentary evidence cannot be extrapolated to provide an answer. The fauna, however, offers a key to the situation. If the changes were local, and the apparent extinctions and additions were unreal, a return to the physical conditions under which the Arroyo animals lived would be expected to have been accompanied by the return of a similar fauna, which, although temporarily excluded from the area, had existed in other areas of the delta where conditions were suitable. If, on the other hand, the restrictive conditions were so widespread that the fauna was disrupted throughout its range, there could be no return with the re-establishment of suitable conditions, and the fauna would show the effects of disruption and reorganization. There is no evidence of a recurrence of the Arroyo type fauna, even in somewhat modified form, at any level in the Vale, in spite of the fact that Arroyo conditions are approximated, so far as can be told from the sediments and flora, at various times during the Vale.

The evolution of the chronofauna of the delta, as shown in the area studied, proceeded in response to environmental modifications, which, although viewed only locally, must have been sufficiently widespread to have an effect over much of the range of the deltaic chronofauna. Observed faunal changes cannot be interpreted merely as reflections of different parts of an unchanging or slowly evolving fauna of which now one part and now another is found in the beds studied. Local changes, rather, are more realistically viewed as reflections of a major pattern of change that took place over the delta as a whole. Changes in different parts of the delta from one time to the next would not, of course, have been the same in physical expression, and the effect witnessed locally must be considered as the resultant not only of the ostensive physical changes, but of the sum total of modifications over the entire range of the chronofauna.

TABLE 1

Approximate Stratigraphic Levels of Vertebrate Collecting Localities

Formation	Level	Localities
CHOZA	Upper	
	Middle	FF
	Lower	FD, FC, FB, FA, FE, KM, KL
VALE	Upper	KK, KG, KJ, KD, KA, KB, KC
	Middle	KI, KE, KH, KF
	Lower	BT, BU, BV, BZ, BS, BR, BW, BX, BAB, BAC

COLLECTING LOCALITIES

The general area over which collections of vertebrate fossils have been made, outlines of collecting localities, and positions of specific sites are shown on the map. The system of indexing of localities is based on aerial photographs, in the absence of adequate maps and local datum points. This system was explained in an earlier report (Olson, 1948), and the photo-indices for the various localities have been published in earlier papers of this series. Localities have been defined for ease of reference, and their areas have been based upon topographic and stratigraphic criteria. The first letter of a locality designation refers to the county in which the locality occurs: B for Baylor County, K for Knox County, and so forth. The second letter, and subsequent letters, were given in alphabetical order as localities were studied, and thus the letter sequence has no special stratigraphic or geographic significance. The photographic indices are expressed in inches and tenths of inches from the picture margin, normal to this margin, from the left and lower margin in this order.

Sites are specific, restricted areas within localities and have been named on the basis of some appropriate feature such as an animal or geological characteristic. The named sites are, for the most part, the ones that have yielded an appreciable number of fossils. By no means all places that have produced fossils, however, are so specified.

The approximate stratigraphic positions of localities are shown in Table 1. For convenience, as in earlier discussions, the Vale and the Choza are divided into lower, middle, and upper parts. This division is based merely on position relative to the base and top of the formation, and not upon any recognized stratigraphic breaks within the section.

The localities and sites are presented in summary style in the following compilation. A brief statement on the general nature of the sediments is given. Under "Vertebrates" the genera and species are listed, followed by the number of individuals identified, designated by the number in parentheses. This is followed by a phrase describing the environment of sedimentation in which the specimen(s) was found.

LOWER VALE

Locality BR

Sediments: Irregularly distributed sandstone, silts, red shales, and fine conglomerates. A few poorly developed channel deposits. Deposition mainly on flood plains lateral to principal stream channels. Some pond deposits of red shale.

Vertebrates:

Diplocaulus magnicornis (2); in pond shales
Trimerorhachis insignis (?); in stream gravel
Eryops megacephalus (2); in flood plain
Labidosaurikos barkeri (1); in flood plain
Dimetrodon gigashomogenes (10); in flood plain, stream deposits

Locality BS

Sediments: Flood plain deposits of even red shales and sandstones with irregular dips. Several small pond deposits. Formed near main stream channel.

Vertebrates:

Diplocaulus sp. (1); in pond shale
Dimetrodon gigashomogenes (1); in pond shale

Locality BT

Sediments: Predominantly flood plain shales and sandstones with a few large channel deposits containing large fragments. A few small pond deposits.

Vertebrates:

Xenacanthus cf. *platypternus* (50); in channel conglomerate
Lysorophus tricarinatus (15); in pond shale

Eryops megacephalus (2); in channel conglomerate
Dimetrodon gigashomogenes (1); in flood plain shale

Locality BU

Sediments: Even red and green shales, interbedded sandstones. Many small channel deposits. Formed at some distance from major stream channel.

Vertebrates:

Eryops megacephalus (1); in channel conglomerate
Diplocaulus recurvatus (1); in channel conglomerate
Labidosaurikos barkeri (1); in flood plain shale
Dimetrodon gigashomogenes (5); in channel conglomerate

Locality BV

Sediments: Irregularly dipping sandstones, grits and fine conglomerates in sheets. Off-channel flood plain deposits.

Vertebrates:

Diplocaulus sp. (1); in flood plain gravel
Eryops megacephalus (1); in flood plain gravel
Labidosaurikos sp. (1); in flood plain gravel
Dimetrodon gigashomogenes (7); in flood plain gravel

Locality BW

Sediments: Dipping sandstones and fine conglomerates interbedded with red shales. Deposition close to major channel. Small channel deposits of fine conglomerates present.

Vertebrates:

Xenacanthus cf. *platypternus* (100); in channel conglomerate
Diplocaulus sp. (1); in red shale, uncertain origin
Eryops sp. (3); in flood plain shale
Diadectes sp. (1); in channel conglomerate
Dimetrodon gigashomogenes (7); in flood plain shale and channel conglomerate

Locality BX

Sediments: Even red shales with thin beds of sandstone and some green shales. Red shales in pond deposits. Formed well away from major stream channel.

Vertebrates:

Gnathorhiza dikeloda (3); in pond shale
Captorhinus cf. *aguti* (2); in flood plain shale
Labidosaurikos barkeri (2); in flood plain shale
Dimetrodon gigashomogenes (6); in pond shale

Locality BZ

Sediments: Dipping sandstones, sheets of red and green conglomerate. Pond shales.

Vertebrates:

Pond site (CUM 6B 62, 3, 30-1.48)

Xenacanthus cf. *platypternus* (100); in pond shale
Gnathorhiza dikeloda (3); in pond shale
Diplocaulus sp. (2); in pond shale
Trimerorhachis sp. (3); in pond shale
Eryops sp. (2); in pond shale
Labidosaurikos barkeri (1); in pond shale
Dimetrodon gigashomogenes (3); in pond shale

Scattered finds

Lysorophus tricarinatus (25); in pond shale
Gnathorhiza dikeloda (1); in pond shale
Labidosaurikos barkeri (1); in flood plain gravel
Dimetrodon gigashomogenes (2); in flood plain gravel

Locality Bab

Sediments: Evenly bedded red shales, passing to fine grits and sandstone in the western part of the area. Western part lower Vale, eastern part upper Arroyo. Western deposits formed near stream channels.

Vertebrates:

(from the Vale)

Trematopsis seltini (1); in flood plain shale
Gnathorhiza dikeloda (2); in channel grit
Labidosaurikos sp. (1); in flood plain shale

Locality Bac

Sediments: Evenly bedded red shales in eastern part, passing to coarser clastics at the western margin. Westernmost part lower Vale, central and eastern part upper Arroyo.

Vertebrates:

(from the Vale)

Dimetrodon gigashomogenes (1); in channel margin sandstone

MIDDLE VALE

Locality KF

Sediments: An area of isolated exposures. Producing beds predominantly channel fills, formed of fine siltstones or coarse, clay-pebble conglomerates. Some marginal sandstones, grits and conglomerates.

Vertebrates:

Fish site (CGV 5 24, 6.00-5.62)

Gnathorhiza dikeloda (100); in siltstone channel fills
Trimerorhachis cf. *insignis* (100); in siltstone channel fills
Waggoneria texensis (1); in siltstone channel fills

Captorhinikos valensis (3); in siltstone channel fills
Labidosaurikos sp. (1); in siltstone channel fills
Dimetrodon gigashomogenes (1); in siltstone channel fills

3 channel hill site (CGV 5 24, around 6.9-5.8)

Gnathorhiza dikeloda (3); in clay-pebble conglomerate
Gnathorhiza serrata (1); in clay-pebble conglomerate
Diplocaulus recurvatus (5); in clay-pebble conglomerate
Waggoneria texensis (type) (1); in clay-pebble conglomerate
Captorhinoides valensis (type) (1); in clay-pebble conglomerate
Dimetrodon gigashomogenes (3); in clay-pebble conglomerate

Scattered finds

Lysorophus tricarinatus (3); in clay-pebble conglomerate
Xenacanthus cf. *platypternus* (25); in clay-pebble conglomerate
Dimetrodon gigashomogenes (3); in flood plain shales

Locality KI

Sediments: Rocks exposed are varied in type and origin. Clay-pebble channel conglomerates, marginal sandstones and grits, pond shales, and flood plain shales and sandstones all well represented.

Vertebrates:

Pink nodule site (CGV 5 24, 1.5-3.72)

Gnathorhiza dikeloda (5); all specimens from nodules that form coarse clay-pebbles in conglomerates
Gnathorhiza serrata (2)
Lysorophus tricarinatus (50)
Captorhinikos sp. (2)
Labidosaurikos barkeri (10)

Scattered finds

Gnathorhiza dikeloda (100); in pond shales
Xenacanthus cf. *platypternus* (50); in clay-pebble conglomerate
Eryops megacephalus (2); in channel sandstone
Labidosaurikos barkeri (2); in flood plain sandstone
Dimetrodon gigashomogenes (3); in flood plain sandstone

Plants (tentatively identified):

Walchia
Gigantopteris
Taeniopteris

Locality KE

Sediments: Fine- to medium-grained conglomerate channel fills, incised in red and green flood plain shales.

Vertebrates:

Xenacanthus cf. *platypternus* (5); in channel conglomerate
Diplocaulus recurvatus (2); in channel conglomerate
Dimetrodon gigashomogenes (2); in channel conglomerate

Locality KH

Sediments: Exposures over an area with extensive east-west extent. Western part of upper Vale. Exposures in steep-sided arroyos along south side of North Fork of Wichita River. Clay-pebble conglomerate channel fills abundant. Flood plain shales and sandstones, several deposits of pond shales.

Vertebrates:

Clay hill site (CGV 5 26, 8.15-3.95)

Xenacanthus cf. *platypternus* (150); in pond shale and channel conglomerate
Trimerorhachis cf. *insignis* (7); in pond shale and grit
Eryops megacephalus (3); in pond shale
Diplocaulus recurvatus (2); in channel conglomerate
Dimetrodon gigashomogenes (4); in pond grit

Diplocaulus quarry site (CGV 5 26, 6.30-4.95)

Diplocaulus recurvatus (15); in channel conglomerate

Chocolate hill site (CGV 5 26, 6.30-4.95)

Trimerorhachis cf. *insignis* (15); in pond shale

Scattered finds

Xenacanthus cf. *platypternus* (100); in channel conglomerate
Trimerorhachis cf. *insignis* (5); in channel conglomerate
Diplocaulus recurvatus (2); in channel conglomerate
Captorhinikos valensis (1); in channel conglomerate
Labidosaurikos barkeri (3); in channel conglomerate
Dimetrodon gigashomogenes (6); in channel conglomerate

UPPER VALE

Locality KA

Sediments: A small area dominated by thick deposits of clay-pebble conglomerate channel fills incised in red shales.

Vertebrates:

Quarry site (CGV 2 20, 3.2-7.1)

Xenacanthus cf. *platypternus* (10); in channel conglomerate
Captorhinikos valensis (2); in channel conglomerate
Captorhinus aguti (1); in channel conglomerate
Labidosaurikos barkeri (2); in channel conglomerate
Dimetrodon gigashomogenes (1); in channel conglomerate

High channel site (CGV 5 20, 3.30-6.85)

Diplocaulus recurvatus (4); in channel conglomerate

Scattered finds

Lysorophus tricarinatus (5); uncertain (nodule)

Locality KB

Sediments: Grit and sandstone marginal to large channels to the south in KA.

Red and green shale and sandstone flood plain deposits. A few small clay-pebble channel fills.

Vertebrates:

Xenacanthus cf. *platypternus* (10); in channel conglomerate
Diplocaulus recurvatus (2); in channel conglomerate
Captorhinus aguti (1); in marginal grit
Dimetrodon gigashomogenes (2); in marginal grit
Edaphosaurid, n. gen., unnamed (1); in marginal grit

Locality KC

Sediments: Poor exposures in deep gorges along south wall of valley of South Fork of Wichita River. A few large channel deposits, clay-pebble conglomerate, marginal sandstones and grits, and evenly bedded flood plain red shales.

Vertebrates:

Xenacanthus cf. *platypternus* (5); in channel conglomerate
Diplocaulus recurvatus (2); in channel conglomerate
Trimerorhachis cf. *insignis* (1); in flood plain shale
Captorhinikos valensis (1); in flood plain shale
Dimetrodon gigashomogenes (2); in flood plain sandstone
Casea nicholsi (type) (2); in flood plain sandstone

Locality KD

Sediments: Open exposures showing a variety of types of sediments. Clay-pebble conglomerate fills abundant, flanked by marginal beds of dipping sandstone. Extensive flood plain sandstones and shales.

Vertebrates:

Quarry site (CGV 2 193, 6.4-5.2)

Gnathorhiza dikeloda (1); in channel conglomerate
Diplocaulus recurvatus (type) (5); in channel conglomerate
Dimetrodon gigashomogenes (2); in channel conglomerate

Weathered boulder site (CGV 3 193, 7.18-4.22)

Xenacanthus cf. *platypternus* (10); in channel conglomerate
Lysorophus tricarinatus (2); in channel conglomerate
Diplocaulus recurvatus (1); in channel conglomerate
Captorhinikos valensis (1); in channel conglomerate
Captorhinus? (1); in channel conglomerate

Scattered finds

Xenacanthus cf. *platypternus* (5); in channel conglomerate
Lysorophus tricarinatus (3); in channel conglomerate
Diplocaulus recurvatus (1); in channel conglomerate
Waggoneria texensis (1); in marginal grit
Labidosaurikos barkeri (2); in flood plain shale
Dimetrodon gigashomogenes (3); in flood plain sandstone
Rept., n. gen., affin. uncert. (1); in flood plain sandstone

Plants: A large collection of plants has been obtained from a green patch in red flood plain shales and from flood plain sandstones. This collection is being studied by Dr. Sergius Mamay of the U. S. Geological Survey. A relatively large number of genera and species is included.

Locality KG

Sediments: Exposures in steep slopes along north margin of valley of South Fork of Wichita River. Principal sediments are red and green flood plain shales, with thin, interbedded sandstones. Even bedding is characteristic. A few small channel deposits present in eastern part of area. Close to Vale-Choza boundary, and uppermost beds may be Choza in age.

Vertebrates:

Lysorophus tricarinatus (5); in shales, uncertain origin
Dimetrodon gigashomogenes (1); in flood plain shales

Locality KK

Sediments: Along steep slopes of north margin of valley of South Fork of Wichita River. Largely evenly bedded red and green flood plain shales. A few siltstone channels and one large channel with flat pebbles up to eight inches in length. Anhydrite beds increasing in number, continuity and thickness to west. Beds transitional between Vale and Choza.

Vertebrates:

Xenacanthus cf. *platypternus* (1); in siltstone channel fill
Lysorophus tricarinatus (100); in pond, red shale
Trimerorhachis cf. *insignis* (1); in fine channel conglomerate

Locality KJ

Sediments: Even red and green shales with interbedded thick layers of sandstones and thin sheets of conglomerate. All apparently flood plain in origin. One large channel deposit and a few fine-grained channel deposits. Occasional pond deposits of light red shale. Westernmost beds transitional between Vale and Choza Formations.

Vertebrates:

Lysorophus tricarinatus (200); in red shale of permanent pond
Diplocaulus recurvatus (15); in channel conglomerate
Trimerorhachis cf. *insignis* (1); in fine conglomerate, origin uncertain
Dimetrodon gigashomogenes (1); in flood plain shale

LOWER CHOZA

Locality FA

Sediments: Uniformly bedded, laterally extensive beds of red and green shale over most of area. Low hills capped by hard, siltstone layer. Small clay-pebble conglomerate channels in eastern part, apparently Vale age. Thin sheets of fine conglomerate, with marl pebbles, in central and western part of areas, apparently lag gravels formed on flood plain. A series of siltstone channels at western margin (*Diplocaulus* site). Widely scattered pond deposits. Thin green beds of shale rich in anhydrite.

Vertebrates:

Pipe site (CZW 1C 59, 3.9-2.2)

Lysorophus tricarinatus (300); all specimens from site from red shale pond deposit
Trimerorhachis rogersi (type) (25)
Cacops sp. (2)
Captorhinikos chozaensis (5)
Labidosaurikos barkeri (3)
Dimetrodon gigashomogenes (3)

Green nodule site (CZW 1C 59, 3.6-2.6)

Lysorophus tricarinatus (30); in pond shale
Captorhinikos chozaensis (type) (1); in pond shale

Diplocaulus site (CZW 1C 59, 2.49-3.79)

Xenacanthus cf. *platypternus* (3); all specimens from fine-grained, siltstone channel deposit
Diplocaulus recurvatus (22)
Captorhinikos chozaensis (1)
Dimetrodon gigashomogenes (2)

Scattered finds

Gnathorhiza dikeloda (3); in channel conglomerate
Lysorophus tricarinatus (15); in shales, temporary pond
Diplocaulus recurvatus (1); in channel conglomerate
Trimerorhachis cf. *rogersi* (2); in channel conglomerate

Locality FB

Sediments: Highly varied shales, sandstones, and conglomerates grading into hard, dark, fine-grained deposits of anhydrite basin to the south. Channels leading into basin. Bedding generally even, with some interbedded anhydrite. A few channel deposits and pond deposits of fresh-water origin in northern part of area.

Vertebrates:

None found.

Locality FC

Sediments: Evenly bedded alternating red and green shales and sandstone gypsum biscuits abundant in shales. Hills capped in western part of area by hard, brown, crossbedded and ripple-marked sandstone. Scattered pond deposits with channel leading to them.

Vertebrates:

Plant locality (CZW 2C 45, 5.37-7.35)

Xenacanthus cf. *platypternus* (5); in channel conglomerate
Eryopid, gen. indet. (1); in channel conglomerate
Dimetrodon gigashomogenes (2); in channel conglomerate

Single find:

Casea halselli (type) (1); in flood plain red shale (CZW 2C 45, 4.81-7.79)

Plants: At plant locality, stems, trunks, and branches of thickly spaced trees at pond margin. Macerated plant remains in pond shale. Preservation insufficient for determination in either type of occurrence.

Locality FD

Sediments: Evenly bedded red shales, rich in anhydrite, green sandstone layers and yellow, rippled-marked, hard sandstone. A few small channel deposits of fine conglomerate.

Vertebrates:

Captorhinus? (1); in red shale flood plain

Locality FE

Sediments: Evenly bedded red and green shales and sandstones, rich in anhydrite. Massive conglomerates adjacent to anhydrite basin.

Vertebrates:

None

Locality KL

Sediments: Evenly bedded red and green shales with thin layers of anhydrite. Anhydrite also in fine conglomerates with fine green matrix. Fine conglomeratic deposits apparently of flood plain origin, but some possibly developed in channels.

Vertebrates:

Lysorophus tricarinatus (10); in siltstone nodules, origin uncertain
Dimetrodon gigashomogenes (1); in conglomerate

Locality KM

Sediments: Varied red, green and yellow shales, with evenness of bedding increasing to west. Anhydrite abundant in western part. Pond shales in western half of area. A thin sheet of fine conglomerate, with lenses suggesting channels, is present over a wide area in the central and western parts of the locality. It occurs near the base of the exposed section.

Vertebrates:

Xenacanthus cf. *platypternus* (1); in fine conglomerate
Diplocaulus recurvatus (1); in fine conglomerate

MIDDLE CHOZA

Locality FF

Sediments: A large area marked by a hard, ripple-marked sandstone that caps the hills and produces an abrupt topography. Principal sediment is a red brown shale, rich in anhydrite. Pond and channel deposits, leading to the ponds, occur in the southwestern part of the area and contain the only fossils found (CZW 2C 84, 3.2-2.7).

Vertebrates:

Trimerorhachis? (2); in fine channel deposits leading to pond

Eryopid, gen. nov. (not named) (1); in fine channel deposits leading to pond

Plants: Large stems and trunks of trees in the vicinity of the channel ponds. Preservation is too poor to allow identification.

UPPER CHOZA

A moderately extensive area has been covered in reconnaissance fashion (see map). Evenly bedded red and green shales, with much anhydrite, and interbedded layers of sandstone and anhydrite predominate. No channel or pond deposits were observed. The beds appear to have been formed under water, presumably brackish water of evaporite basins, and the chances for discovery of plants or vertebrates are very poor. No fossils, other than possible worm burrows in sandstone, were observed. Coverage was not sufficient to show conclusively that there are no terrestrial deposits, but there was no sign of their existence.

THE FAUNA

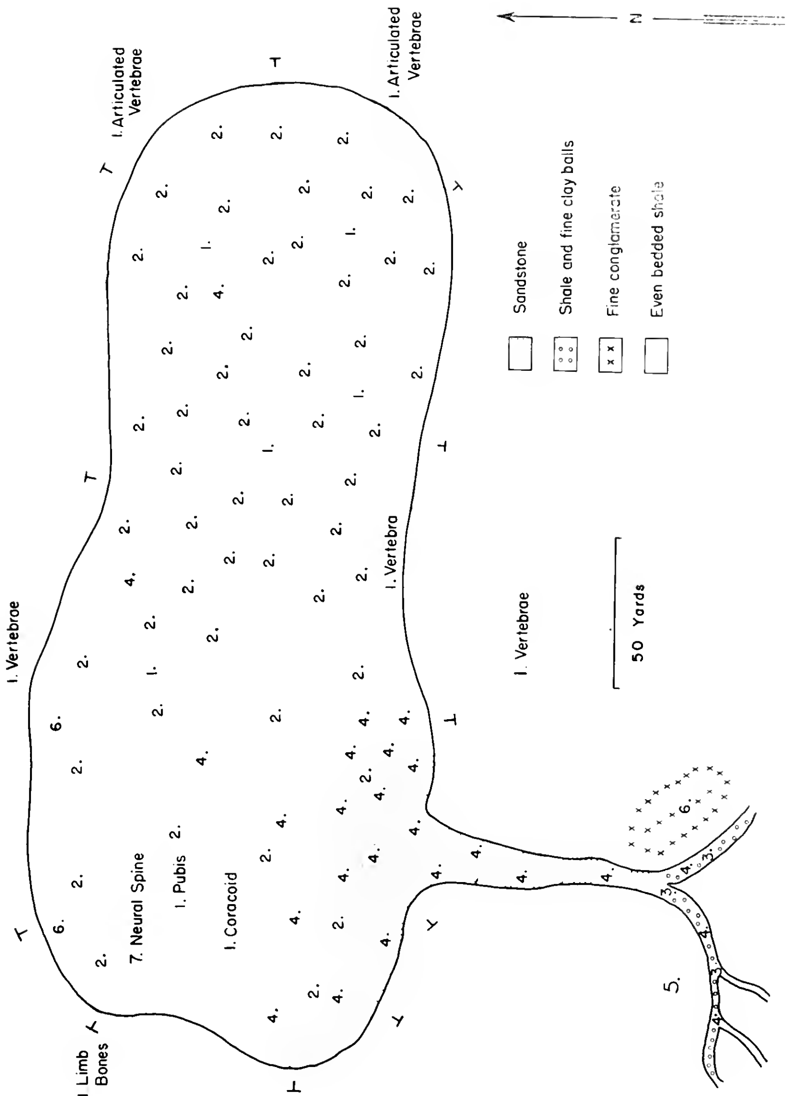
The known fauna of the Vale and Choza Formation, as given in Table 2, includes 17 genera and 23 species of fish, amphibians, and reptiles. In addition, there are 2 unnamed genera, one amphibian and one reptile, and undetermined palaeoniscoid fish. The list includes *Varanops brevirostris* and *Casea broilii*, which are only tentatively assigned to the Vale, since the stratigraphic position of the pocket from which they were taken is uncertain. *Cacops* also has come from this pocket. This genus has been found in the Choza as well, but the materials are such that it is impossible to determine whether the species from the two levels are the same or different. Eight of the 17 genera are not known from beds earlier than Vale in age, and the unnamed genera, similarly, have not been recognized in pre-Vale beds. Of the named species, 13 are not known prior to the Vale, if *Varanops brevirostris*, *Casea broilii*, and *Cacops aspiderphorus* are considered to be of Vale age.

The occurrences by localities (pp. 425-434) present much of the essential information on assemblages, modes of occurrence, and stratigraphic position. Remains, of course, are not necessarily preserved under the conditions in which the animals lived, for the animals that inhabited one of the habitat subzones can be preserved in sediments formed in any of the other subzones. In general, the greatest mixing is to be expected in deposits formed in channels and the least in flood plain deposits formed away from the major channels. Terrestrial animals found in considerable numbers in ponds may be considered to have spent at least part of their time on pond margins. The most reliable inferences on habitats can be drawn from the species that are known from deposits of the off-channel flood plains, and from those that have been found only in deposits that represent a single subzone.

The following genera and species are known from flood plain deposits: *Dimetrodon gigashomogenes*, *Casea nicholsi*, *C. halselli*, *Captorhinus aguti*, *Trematopsis seltini*. Specimens are consistently low in frequency at any one place, either a single individual or, at most, two or three individuals being found at a particular site. With the exception of *Dimetrodon gigashomogenes*, the species are relatively rare. The four genera were morphologically well adapted to active terrestrial life, and, with the confirming evidence of occurrence, may be considered to have inhabited the flood plains and the divides between river systems. Both *Dimetrodon* and *Captorhinus* have been found in channel deposits, presumably washed in during times of actively flowing water. *Dimetrodon* is a frequent member of pond assemblages, so characteristic that it can hardly be considered to have been included merely by accident. In the pond deposits, away from the margins, the bones of this genus are commonly disarticulated, scattered, and fragmentary. In marginal beds, on the contrary, complete bones and partially articulated skeletons are the rule. The distribution of specimens determined from a surface collection of a completely exposed pond deposit in the late Arroyo is shown (fig. 185). The marginal occurrence of *Dimetrodon* is typical for such deposits. It may be assumed that the inhabitants of the ponds provided a source of food for *Dimetrodon*. This is supported by the fact that large coprolites, evidently those of a carnivorous animal and lacking the typical markings of sharks, contain fragments of skull plates of *Diplocaulus*, an abundant form in pond deposits in the Arroyo and earliest Vale. There seems no other possible source of these coprolites than *Dimetrodon*.

Diplocaulus recurvatus has been found only in stream deposits, in contrast to its precursor, *D. magnicornis*, which is characteristic of pond deposits. Complete absence from the ponds, the other possible habitat, strongly suggests that the streams represent its true habitat. *Xenacanthus* similarly is abundant in the stream deposits;

FIG. 185. Map of a complete pond deposit in the late Arroyo Formation (Locality Baa). The long axis of the pond is about 300 yards. Sedimentary types, dip of beds, and distributions of vertebrates as shown by keys. Vertebrate types indicated by numbers as follows: 1, *Dimetrodon gigashomogenes;* 2, *Diplocaulus magnicornis;* 3, *D. brevirostris;* 4, teeth of *Xenacanthus;* 5, *Diadectes;* 6, *Captorhinus aguti;* 7, *Eryops.* To be noted especially are: (1) The separation of the two species of *Diplocaulus, D. magnicornis* in the pond and *D. brevirostris* in the stream. (2) The remains of *Dimetrodon,* which are partially articulated in the marginal deposits of the pond, but fragmentary and completely disarticulated in the pond. (3) The distribution of the teeth of *Xenacanthus* in the stream deposit and in the sediment carried into the pond by the stream, contrasted with the absence away from the mouth of the stream.


I. Articulated Vertebrae
I. Articulated Vertebrae
I. Vertebrae
I. Vertebra
I. Vertebrae
7. Neural Spine
I. Pubis
I. Coracoid
I. Limb Bones
N
Sandstone
Shale and fine clay balls
Fine conglomerate
Even bedded shale
50 Yards

however, it is associated with *Diplocaulus magnicornis* in late Arroyo and early Vale ponds and continues to occur in these deposits after *Diplocaulus* is no longer present. Again, from coprolites, it is clear that *Diplocaulus* was a source of food for this shark, both in standing and running water. Palaeoniscoid fish, similarly, appear to have formed an important part of the diet of *Xenacanthus*. In addition to *Diplocaulus* and *Xenacanthus*, all other common genera are present in deposits formed by the waters of streams. Remains are usually fragmentary. In two cases, however, articulated vertebral columns of *Dimetrodon* have been encountered in clay-pebble conglomerates formed in channels. Also, nodules that include a considerable portion of the skeletons of *Lysorophus* have been found in clay-pebble conglomerates.

Pond deposits, as noted earlier, appear to have formed under two circumstances: in perennial ponds and in temporary ponds. Two species are commonly encountered in the deposits of temporary ponds: *Lysorophus tricarinatus* and *Gnathorhiza dikeloda*. Both occur under conditions that suggest aestivation (Olson, 1956, and Romer and Olson, 1954). In a few instances, in the Arroyo, remains of very young individuals of *Diplocaulus magnicornis* have been found with assemblages of *Lysorophus*, suggesting that *D. magnicornis* may have been an aestivator, at least in early stages of its life. No association of *D. recurvatus* and *Lysorophus* has been found in pond deposits.

Lysorophus tricarinatus lived in permanent ponds both in the Vale and the Choza, as is indicated by occurrences in localities KJ and FA. Here there is no indication of aestivation either in coiling of individuals or in high incidence of individuals of a given size over a small area.[1]

A generalized illustration of the supposed distribution of major types of vertebrates is given (fig. 186). The principal habitats are

[1] The problems of the species of *Lysorophus* and of size distributions in temporary pond deposits have been discussed in an earlier paper (Olson, 1956). They may be briefly summarized as follows: If the species name used here, *L. tricarinatus*, is correct, it follows that this species ranged from late Pennsylvanian, for it was named from a Pennsylvanian deposit in Illinois, until near the end of the early Permian. While this is not impossible, it seems unlikely. There is, however, no detectable morphological difference in the vertebrae of the Pennsylvanian. Thus, if we take a morphological basis for species designation, as has been done in this work, reference of all the materials to *L. tricarinatus* is implicit. This should not, however, be taken in illustration of persistence of a species, or for other evolutionary speculation, since the assignment is based on materials that may not be definitive. It was also noted that the individuals of a sample from an aestivating colony tended to group closely about some mean based on vertebral length. These appear to represent one phase of the growth series. At least four "yearly" stages have been noted. This phenomenon is not observed in deposits formed in permanent ponds.

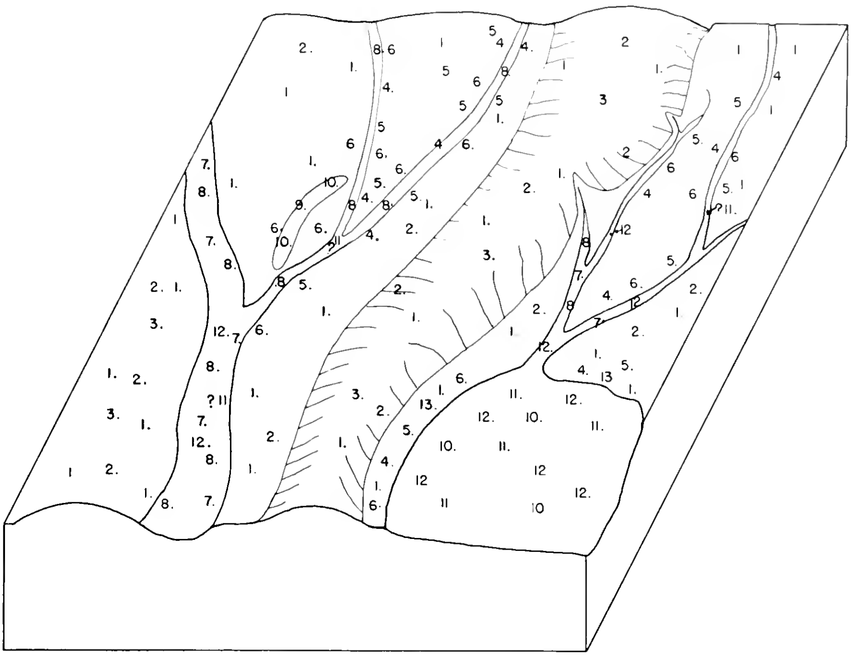


FIG. 186. A generalized, block diagram to show the subzonal distribution of principal genera of the Vale and Choza delta vertebrates. The proximity of zones and their limited extent are, of course, exaggerated to meet space requirements. The numbers indicate particular genera as follows: 1, *Dimetrodon;* 2, *Captorhinus;* 3, *Casea;* 4, *Captorhinikos;* 5, *Labidosaurikos;* 6, *Eryops;* 7, *Diplocaulus;* 8, *Xenacanthus;* 9, *Gnathorhiza;* 10, *Lysorophus;* 11, *Trimerorhachis;* 12, Palaeoniscoids; 13, *Waggoneria.*

indicated, but there is no implication that mobile terrestrial animals were restricted to the zones in which they have been found. In all probability such animals as *Dimetrodon* and *Casea* roamed widely over the surface of the delta.

FAUNAL EVOLUTION

The associations, types of occurrences, and inferred habitats and diets of the known genera of fish, amphibians, and reptiles from the Arroyo, Vale and Choza, have provided a basis for interpretation of the evolution of the vertebrate complex as it moved through time. Modifications of the physical environment have been inferred from the sediments and from the occurrences and associations of the organisms. The evolution of the vertebrate complex, termed a chronofauna, was considered rather thoroughly in an earlier paper (Olson, 1952b). New materials and additional studies of the sediments have not altered the picture presented at that time. This matter will thus be considered in summary form.

The basic structure of the faunal complex remained stable from the beginning of the Arroyo through the middle Choza. Some elements persisted unchanged, so far as the morphology of the skeleton is concerned, and preserved their basic role in the economy of the system. *Dimetrodon gigashomogenes* is the best example, for it was the dominant, large predator for the duration of the chronofauna. Some elements were lost, but they were replaced, roughly, by ecological counterparts. The caseids, for example, appear to have occupied, in the Vale, the position of such large herbivores as *Diadectes* and *Edaphosaurus* of the Arroyo. Many changes took place within the complex, in the form of various evolutionary phenomena, but fundamentally the deltaic environment was occupied in a coherent and consistent way, with niches similarly filled throughout the whole time. There was, in short, no major reorganization in the interactions of the vertebrates in the chronofauna. The stability depended, apparently, upon the persistence of a major habitat. Although there were sharp fluctuations over relatively short periods of time, as at the Arroyo-Vale boundary, and slow modifications, such as that which occurred during the Vale, these were not sufficient to disrupt the central core of the economy. The closest approach to disruption took place at the end of the Arroyo, but the early Vale assemblage shows the fauna to have had sufficient tolerance to environmental change to make adjustments below the level of major reorganization.

With the development of restrictive conditions in the Choza, the subzonal assemblages appear to have suffered isolation. Restricted communities, around concentrations of water, survived, but this appears to be all. It may be supposed that the reduction of numbers of individuals and lessening of intercommunication would have had drastic effects upon the chronofauna, which had survived through many millions of years with its elements in intimate contact. The final result would have been either a marked adjustment to meet the new conditions or a total disruption of the chronofauna. There is some evidence of adjustment in the presence of a new species of *Trimerorhachis* in one of the isolated ponds, in the changes of *Casea* on the flood plains, and in the presence of a new eryopid in mid-Choza. Beyond the mid-Choza, there is no further evidence of the history of the vertebrates on the Clear Fork delta. The one clue to the fate of the fauna comes from the overlying San Angelo Formation. At the time of deposition of the San Angelo, conditions which would appear to have been reasonably suitable for the existence of the Clear Fork chronofauna were re-established. A new complex, only very distantly related to the earlier one, is present. Very clearly this assemblage did not descend directly from the Clear Fork chronofauna. Evidently, in the area under consideration, the chronofauna suffered so much disruption that it did not persist as an entity.

In the San Angelo beds there are three genera whose antecedents may be inferred with some confidence. Specimens of a very large *Dimetrodon* have been found. The cross sections of the neural spines and the relatively elongated vertebrae suggest affinities with *Dimetrodon gigashomogenes*. *Caseoides* shows many resemblances to *Casea halselli* of the Choza. These two genera are, of course, elements of the Clear Fork chronofauna.

Cotylorhynchus is found both in the Hennessey Formation of Oklahoma and in the San Angelo. *Dimetrodon* was a widespread genus, for it is known in Oklahoma and from the Dunkard Formation of eastern United States, from deposits that had a fauna somewhat different from that recorded on the Texas delta. *Casea* appears to have been similarly wide-ranging, for, although there is no direct record, it must have lived away from the Texas delta prior to its introduction in the late Arroyo or early Vale. It was suggested in discussions in the initial analysis of the Clear Fork chronofauna (Olson, 1952b) that *Dimetrodon* probably crossed faunal boundaries and existed as a component of two or more chronofaunas. The same probably applies to *Casea*. *Cotylorhynchus* was not a component of the Clear Fork deltaic chronofauna. If these interpretations are correct, the three genera with descendants in the San Angelo may owe their persistence to the fact that they lived beyond the range of the disrupted chronofauna. Less strictly terrestrial and mobile forms, however, may well have been limited to the chronofauna, and thereby failed to persist to provide stocks from which the known San Angelo genera arose. Although *Cotylorhynchus* of the Hennessey occurs in the San Angelo, no other genera from this fauna can be considered ancestors of the San Angelo fauna, and, at present, the source of this assemblage is unknown.

EVOLUTIONARY PHENOMENA IN THE CLEAR FORK

As the Clear Fork chronofauna evolved, a wide variety of evolutionary phenomena transpired. Each has some importance in its own right, but the most intriguing aspect of the information revealed by studies of the materials relates to the way in which each of the separate events contributed to the total evolution of the vertebrate complex. The following phenomena have been recorded:

1. Persistence of species without evident change in a single subzone over a long span of time.
2. Persistence of species with change in size in a single subzone.
3. Persistence of species in spite of change of habitat.
4. Speciation with a shift in habitat, with the derived species resulting from selection of a pre-existing element of the parent species.
5. Adaptive radiation during a shift in habitat.
6. Speciation without evident change of habitat or isolation.
7. Speciation without change of habitat, but with geographic isolation.

Each of these phenomena may be viewed discretely, but they take on more significant meaning as they are studied with respect to one another. Each must be evaluated, of course, with recognition of the limitations of the fossil record, both with regard to categorical levels of the change, or lack of change, and to interpretation of habitat. An effort to interrelate the changes to evaluate the validity of interpretations was presented in the first report on the chronofauna (Olson, 1952b). All but the seventh point were considered at that time. Only a single, illustrative example of each point will be included here, as follows:

1. *Dimetrodon gigashomogenes* persisted without evident change from the base of the Arroyo through the middle Choza. During this time it was the dominant, large carnivore of the chronofauna. Its prey changed notably during the span of time, but the species remained constant in its occupancy of the flood plains, divides, and pond margins of the delta.

2. *Lysorophus tricarinatus* is found as an aestivator in temporary ponds from the base of the Arroyo into the Choza. During the Arroyo and most of the Vale, four presumably annual growth stages are recorded in the organisms preserved from their aestivating phase. In the upper Vale and in the Choza, an additional large stage came into existence. Since there is no morphological change, other than size, it has been supposed that this added stage did not represent a genetic change, but merely one related to conditions that were permissive of greater size, reflected in the addition of a new growth stage.

3. *Xenacanthus* cf. *platypternus* inhabited both streams and ponds during its history; for example, near the end of the Arroyo it abandoned its previously exclusive stream habitat (in the Arroyo) and invaded the ponds. Later it was excluded from the ponds and was exclusively a stream dweller. The problem in this case is not the modifications of habitat, for these are clear, but the problem of the taxonomy of the shark. For the most part only teeth are available for study, and these are far from the best materials for specific determination. Although there is a marked range in both size and shape, no consistent differences are observed either in the different habitats or through the time represented. Thus it is concluded that a single species persisted without change.

4. The development of *Diplocaulus recurvatus* from *D. magnicornis* early in the Vale illustrates the development of a new species with modification of habitat. The parent species was a pond dweller and the derived species a stream dweller. The form typical of *D. recurvatus* makes up 15 to 20 per cent of the Arroyo population of *D. magnicornis*. It is assumed that this part of the parent population was morphologically "pre-adapted" to the stream life that the form resembling *D. recurvatus* was selected for at the time of enforced habitat change.

5. The captorhinomorph reptiles of the Arroyo, *Captorhinus aguti* and *Labidosaurus hamatus*, suffered impoverishment at the end of the Arroyo. The latter appears to have become extinct. *Captorhinus*, perhaps because it existed beyond the limits of the chronofauna, reappeared on the delta immediately after the end of the Arroyo. It appears to have been the ancestor of *Captorhinoides*, *Captorhinikos*, and *Labidosaurikos*. *Captorhinus* lived predominantly on flood plains and divides. Two of the derived genera, *Captorhinikos* and *Labidosaurikos*, lived primarily in the vicinity of bodies of water and perhaps obtained their food along pond margins. This environment was in large part left vacant in the transition from the Arroyo to the Vale, and the origin of these two genera is thought to be the result of a rapid adaptive radiation into this subzone. Thereafter, the genera persisted through the early Choza. A new species of *Captorhinikos* arose, but the species of *Labidosaurikos*, *L. barkeri*, remained unaltered.

6. The caseids give evidence of the development of species in time without shift in habitat or isolation, in the usual sense of the term. Three species are known; *Casea broilii* in the latest Arroyo or earliest Vale, *C. nicholsi* from the late Vale, and *C. halselli* from the

Choza. There is no reason to believe that these do not represent a direct line of descent. They are, apparently, stages in a phylum in which there was increase in size, broadening of the body, and shortening of the limbs. It is probable that these changes took place progressively, and that, were the whole line known, clear demarcation of the successive stages would not be possible. The record is such that the species are readily told apart.

7. *Trimerorhachis* shows speciation at two times in the record. Both cases occur under restrictive conditions where geographic isolation appears to have been extensive. One case is witnessed near the end of the Arroyo, when a new and short-lived species arose. The other occurred in the early Choza, during the time that the chronofauna was becoming fragmented into subunits that lived in the vicinity of the ponds and streams. At this time a new species, *T. rogersi*, first came into being. Presumably its ancestor was the extremely persistent *T. insignis* (Olson, 1955a).

Not included in this list of evolutionary events are the appearances of new genera for which no antecedents occur in earlier beds. The appearance of *Casea* in the early Vale is a case in point. Probably this genus, like others in this category, was an immigrant from some other faunal complex, able to establish itself during a time of relative impoverishment of the indigenous fauna. *Varanops* also may fall in this category, since it is unknown in the typical Arroyo beds.

Both physical and biological factors, acting together, are related to the evolutionary processes that have been noted. In general, the initial impetus toward change appears to have been provided by some physical event. In some instances, this alone appears to have been the primary factor, although, of course, unknown biological events may well have been involved. Isolation of parts of the population of *Trimerorhachis* illustrates this type of event. As far as can be determined, there were no changes in the associated biota as *T. rogersi* developed in the early Choza.

A second pattern is one in which physical events were basic to the initiation of biological change, but subsequent change was primarily related to biological circumstances. *Casea* illustrates this situation, as it was introduced during the late Arroyo impoverishment, which was the direct result of physical change, and then, apparently, evolved as a principal herbivore, becoming progressively better adapted to the biota, both the predators and the flora. Somewhat different is a third situation, illustrated by the captorhinomorphs as they radiated into the marginal water zone, which was impoverished in the late Arroyo, and continued evolution in a subzone that resembled an earlier one physically but differed markedly in the animals that it supported.

A fourth type of interaction is one in which the initial impetus was physical, but in which the modifications resulted from newly established proximity and interaction of two organisms, both of which had existed earlier. The best example is found in the invasion of the ponds by *Xenacanthus*, apparently occasioned by restriction of the stream habitat in the late Arroyo, and the impact of this invasion on the pond dweller *Diplocaulus magnicornis*. After a short period in which these two types co-existed, in a predator-prey relationship, *D. magnicornis* disappeared from the ponds. *D. recurvatus*, derived from it, was present in the streams, somewhat modified for life in running water. In this environment, *Xenacanthus* and *Diplocaulus* existed together and maintained a balance that appears to have been favorable for persistence of each. A stream species of *Diplocaulus*, *D. brevirostris*, lived in similar association in the Arroyo but appears to have been unable to make the transition from the stream to the pond during the late Arroyo, perhaps because it was not adapted to pond life, or possibly because *D. magnicornis* was already well established in the ponds.

Evolution in the deltaic fauna of the Clear Fork appears to have been cast within the general framework described briefly above. Much of it we can never hope to know directly, but even under this restriction the interaction of the physical biological factors provides a sound basis for developing understanding of the persistent framework of the chronofauna, within which the ebb and flow of smaller changes can be followed as they modify but do not disrupt the broad, primary characteristics of the evolving complex.

Evolution during the Clear Fork, as seen in the area studied, was not progressive, for no feature characteristic of more advanced types from the later Permian are seen to come into existence. The pelycosaurs, for example, show no trend toward a therapsid condition, in either skull or skeleton. *Dimetrodon* shows no change whatsoever. Caseids, while undergoing adaptive modifications, retain the fundamental characteristics of the earlier representatives. Captorhinomorphs show no trends toward any groups that might conceivably be derived from them. The same applies to the amphibians and the fish.

We are not, then, dealing with the main flow of evolution through the early Permian—the flow through which more advanced reptiles and amphibians came into being. Earlier, in the Wichita, under conditions somewhat different from those of the Clear Fork, there is greater evidence of "advancement." By Clear Fork time, in this area, stabilization had occurred, and the fauna continued to exist with great success as long as the deltaic conditions persisted.

The site of deposition and evolution in the Clear Fork is one typical of many of the late Paleozoic sites in which vertebrates are found, as emphasized in a consideration of world-wide conditions by Efremov (1950). These sites were lowland deltas, deposited along the marginal band between the land and the sea. Other early Permian localities, in New Mexico (Abo), and in Pennsylvania, Ohio, and West Virginia (Dunkard), are to some extent similar. These are relatively stable environments and presumably owe their preservation in part to their proximity to sea level. Whatever progressive evolution was taking place in North America, outside of the moderate progress shown in Wichita beds, was occurring in areas with different characteristics, probably in the continental interior, in uplands where there is little chance for preservation.

It appears that we must be content to see this evolution primarily in terms of fringe members that pushed out into areas more suitable for preservation. So far, the only glimpse of the results of non-deltaic evolution in the Permian of North America is provided by the fossils preserved in the San Angelo and Flower Pot Formations of Texas (Olson and Beerbower, 1953). A moderately diverse fauna is known from these beds. It shows a very marked difference from the fauna of the Clear Fork. At present, some tendency toward the therapsid condition has been revealed by members of this fauna. It is possible, as was suggested in a summary paper on this matter (Olson, 1955b), that the patterns of evolution in North America and the Old World were very different with respect to "advancement," although similar in their general adaptive directions.

TABLE 2

Complete Faunal List of Genera and Species of Vertebrates from the Vale and Choza Formations of North Central Texas

FISH

Xenacanthus cf. *platypternus*, early Vale through mid-Choza.
Gnathorhiza serrata, Vale.
Gnathorhiza dikeloda, early Vale through early Choza.
Palaeoniscoids, early Vale through early Choza.

AMPHIBIANS

Lysorophus tricarinatus, early Vale through mid-Choza.

Diplocaulus magnicornis, very early Vale.
Diplocaulus recurvatus, middle of early Vale through early Choza.
Eryops megacephalus, early Vale through early Choza.
Eryopid, gen. nov., not described, middle Choza.
Trimerorhachis cf. *insignis*, Vale.
Trimerorhachis rogersi, early Choza.
Cacops aspiderphorus, age uncertain, either late Arroyo or very early Vale.
Cacops sp., early Choza.
Trematopsis seltini, early Vale.

REPTILES

Diadectes cf. *tenuitectis*, very early Vale.
Waggoneria knoxensis, middle and late Vale and ?early Choza.
Captorhinus aguti, Vale.
Captorhinus? sp., Choza.
Captorhinoides valensis, middle Vale.
Captorhinikos valensis, Vale.
Captorhinikos chozaensis, early Choza.
Labidosaurikos barkeri, early Vale through early Choza.
Varanops brevirostris, age uncertain, either late Arroyo or very early Vale.
Dimetrodon gigashomogenes, (Arroyo), early Vale through early Choza.
Edaphosaurid?, gen. nov., undescribed, late Vale.
Casea broilii, age uncertain, either late Arroyo or very early Vale.
Casea nicholsi, late Vale.
Casea halselli, late early or mid-Choza.

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