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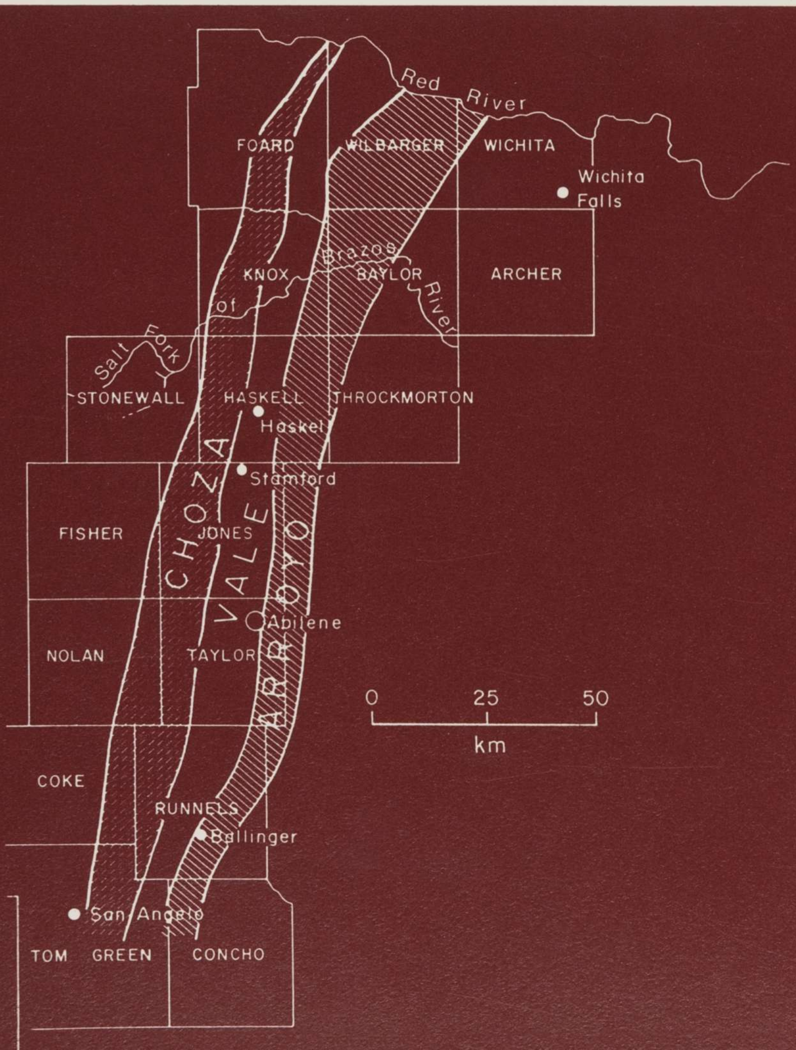
Everett C. Olson

July 1989



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The Arroyo Formation (Leonardian: Lower Permian) and Its Vertebrate Fossils

Everett C. Olson
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ABSTRACT

Studies of the Arroyo formation from northern Haskell County south to Runnels County, Texas trace the changes in organisms and environments from the "classic" terrestrial beds of Baylor and Wilbarger Counties to the fully marine sections to the south. Terrestrial deposits that contain vertebrate remains have been found only as far south as Haskell, Texas. Limestones, sampled and treated by acetic acid, have produced tetrapods to the level of Abilene, Texas. Among these are the commonest genera of the Arroyo, including several types of microsaurs. Notably absent is the highly terrestrial genus *Captorhinus*. Above the Lueders Limestone, the Arroyo section in the southern area consists of four marine limestones alternating with varied thicknesses of red mudstones, with small increments of sandstones and fine conglomerates. The distributions of the limestones and the clastics indicate four major transgressions of the sea, with a very irregular coastline during the peaks of transgression. The limestones have yielded a wide variety of fish, including xenacanthid sharks, various other Chondrichthyes, and dipnoan and palaeoniscoid Osteichthyes. Special attention is paid to the systematics, distributions, and habitats of the fish, with special emphasis upon the use of scale histology in taxonomic studies.

ACKNOWLEDGEMENTS

Field work over the 10 year span of this study was immensely enhanced by my wife, Lila Olson, by her ability to find obscure fossils in the field and to drive back-country in our Jeep as I plotted positions and ways of access to sites. Drs. Ernest Lundelius and Wann Langston, Jr., of the Vertebrate Paleontology Laboratory, The University of Texas at Austin, were of great help as consultants and in making available the facilities and services of the research laboratories on many occasions. The comments, criticisms, and suggestions of two anonymous referees contributed materially to the final content and form of the paper. Members of the Texas Bureau of Economic Geology at The University of Texas at Austin provided assistance in locating and determining the identity of the various limestones used in the study, activities that depended heavily upon the appropriate sheets of the Geological Atlas of Texas.

Drs. Ellis Yochelson and John Pojeta studied and analysed the invertebrates of samples from Sites 2 and 13. Specimens of palaeoniscids were supplied by the USNM for studies of thin sections. Benjamin Crabtree of UCLA was an assistant in the program and performed extensive studies on the variety of shape-patterns of the scales etched from the limestones with particular attention to their utility in taxonomy. Specimens of *Polypterus* that were used for studies of histological characters of scales and their distribution over the body came from the fish collections of UCLA.

The art work for the line drawings was done by Dr. Kathryn Bolles, as was the difficult photomicrography of whole specimens and transparencies used in the figures. Appropriate equipment for photomicrography was made available by Dr. William J. Schopf of the Department of Earth and Space Sciences, UCLA, and by Drs. C. C. Coney and J. H. McLean of the County Museum of Natural History, Los Angeles, California. Research support was provided by Grants 1638 and 3330 from the Research Committee, The University of

Figure 1. General distribution of beds of Leonardian age (Clyde, Leuders, and Arroyo) in Texas and Oklahoma.

California at Los Angeles, and in early phases of the work by National Science Foundation grant DEB 78998754.

INTRODUCTION

The Arroyo Formation is the lowest of the three formations that make up the Permian Clear Fork Group (Figures 1 and 2) of north central Texas. The area north of the Salt Fork of the Brazos River has been extensively studied by vertebrate paleontologists (Figure 2), and is the principal source of information about the terrestrial vertebrates that existed during the time of its deposition, augmented by data from Oklahoma and Germany. Emphasized in this paper are the Arroyo deposits that lie south of the Salt Fork of the Brazos, here termed the "southern area" in contrast to the better known northern area, here termed the "classic area." A summary of the vertebrate taxa now known from the classic area, together with those which this study has added from the southern area, is given in Table 1.

The type section of the Arroyo Formation lies about 240 kilometers south of the classic area, at Los Arroyos, near Ballinger, Runnels County, Texas (Figure 2). Outcrops of the Arroyo extend in a northeasterly direction from somewhat to the south of the type locality to the vicinity of the Red River, which lies between Texas and Oklahoma, and bounds Wilbarger and Wichita Counties, Texas on the north. At the type locality, the formation consists of 66 meters of marine limestone, shale, and lenticular gypsum. In the classic area, the section is composed of approximately 130 m of red mudstones, shales, sandstones and fine to coarse conglomerate.

Throughout most of its length, the lowest beds of the Arroyo Formation rest on the marine limestone of the Lueders Formation, the uppermost subdivision of the Albany Group. Overlying the Arroyo beds are the red, clastic, predominantly mudstone deposits of the Vale Formation. The Arroyo was named by Beede and Waite (1918). The contact between the Arroyo and Vale, as defined by Wrather (1917), lies at the top of the Standpipe Limestone. Because this limestone extends only as far north as the northern edge of Abilene, Texas, precise differentiation of the Arroyo and Vale formations is very difficult to the north of that city. Compounding the difficulties of study of the fauna and stratigraphy north of the Standpipe Limestone are the generally flat or rolling topography and an extensive cover of Cretaceous rocks and alluvium.

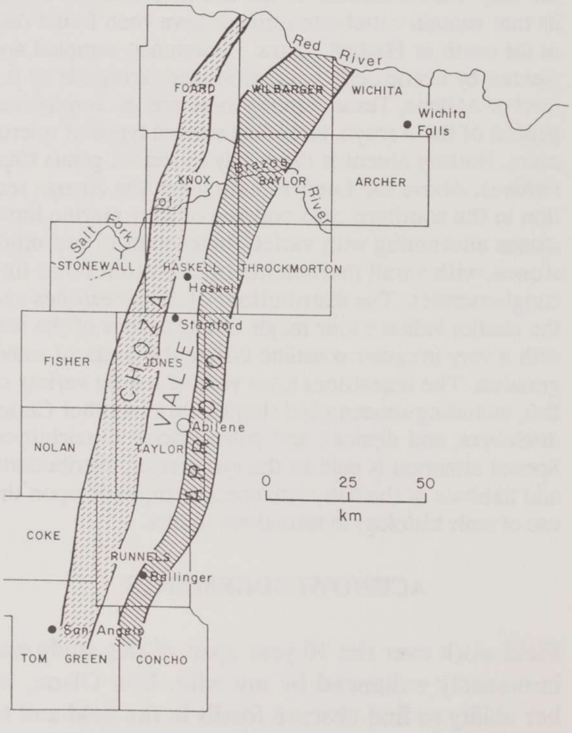

Figure 2. General distribution of outcrops of the Clear Fork group and its formations in North Central Texas (modified from Olson and Mead, 1982). In this paper, the area north of the Salt Fork of the Brazos River is termed the "classic area", that to the south, which is the particular focus of this paper, the "southern area".

Table 1. Faunal list of vertebrates known from the Arroyo Formation of north central Texas. The family Dissorophidae is considered by some to exclude *Trematops*, which is then assigned to the family Trematopsidae. The other listed genera then form the family Dissorophidae and the two families are grouped under suborder (or superfamily) Dissorophoidea. I have not followed this scheme here. The list is conservative, with questionable genera and species omitted. A question mark (?) before a taxon indicates either uncertain identification or, in the case of *Cacops*, *Varanops*, and *Casea*, uncertainty as to whether they are from Arroyo or Vale deposits. An asterisk (*) before a taxon indicates that it was first found in the course of the present study.

- CLASS CHONDRICHTHYES
  - Subclass Elasmobranchii
    - Order Pleuracanthodii
      - Family Xenacanthidae
        - *Orthacanthus platypternus* (Cope)
        - *Orthacanthus texensis* (Cope)
        - *Xenacanthus luederensis* Berman
    - Order Selachii
      - Suborder Hybodontoidea
        - *Polyacrodus* Jaekel
        - *?Hybodus* Agassiz
        - *?Acrodus* Agassiz

- CLASS UNCERTAIN
  - Subclass Acanthodii
    - Acanthodian spines

- CLASS OSTEICHTHYES
  - Subclass Actinopterygii
    - Order Palaeonisciformes
      - Suborder Palaeoniscoidea
        - *Brachydegma caelatum* Dunkle
        - **Amblypterus* Agassiz
        - **Acrolepis* Agassiz
        - **Elonichthys* Giebel
        - **Lawnia* Wilson
      - Suborder Platysomoidea
        - *Schaefferichthys* Dalquest
  - Subclass Sarcopterygii
    - Order Dipnoi
      - *Gnathorhiza serrata* Cope

- CLASS AMPHIBIA
  - "Subclass Lepospondyli"
    - Order Lysorophia
      - *Lysorophus tricarinatus* Cope
    - Order Microsauria
      - *Cardiocephalus sternbergi* Broili
      - *Euryodus primus* Olson
      - *Ostodolepis brevispinatus* Williston
      - *Pelodostis elongatum* Carroll and Gaskill
    - Order Nectridea
      - *Diplocaulus magnicornis* Cope
      - *Diplocaulus brevirostris* Olson
      - *Peronedon* Olson
  - Subclass Labyrinthodontia
    - Order Temnospondyli
      - Family Eryopidae
        - *Eryops megacephalus* Cope
      - Family Trimerorhachidae
        - *Trimerorhachis insignis* Cope
        - *Trimerorhachis mesops* Cope
      - Family Dissorophidae
        - *Trematops milleri* Williston
        - *Trematops willistoni* Olson
        - *Broiliellus arroyoensis* DeMar
        - *Dissorophus multicinctus* Cope
        - *Longiscutula houghae* DeMar
        - *Agelinosaurus aphthites* Williston
        - *Aspidosaurus chiton* Broili
        - *?Cacops aspidophorous* Williston
  - Subclass Batrachosauria
    - Family Seymouridae
      - *Seymouria baylorensis* Broili
    - Family Diadectidae
      - *Diadectes tenuitectis* Cope (Syn. *D. sideropelicus* Cope)

- CLASS REPTILIA
  - Subclass Anapsida
    - Order Captorhinomorpha
      - Family Captorhinidae
        - *Captorhinus aguti* (Cope)
        - *Labidosaurus hamatus* Cope
  - Subclass Synapsida
    - Order Pelycosauria
      - Family Ophiacodontidae
        - *Varanosaurus acutirostris* Broili
        - *?Varanops brevirostris* (Williston)
        - *Tetraceratops insignis* Matthew
      - Family Sphenacodontidae
        - *Dimetrodon giganhomogenes* Case
        - *Dimetrodon grandis* (Case)
        - *Secodontosaurus willistoni* Romer
      - Family Edaphosauridae
        - *Edaphosaurus pogonius* Cope
        - *Trichosaurus texensis* Williston
        - *?Casea broilii* Williston
  - Subclass Uncertain
    - Family Araeosceliidae
      - *Araeoscelis gracilis* Williston

Outcrops of Arroyo beds are relatively few and of limited areal extent. Fossils are of limited stratigraphic use, primarily because only five non-marine sites south of the classic area have yielded terrestrial vertebrates.

The southernmost of these five sites lies about 9.3 kilometers southeast of Haskell, Texas. Beds considered to be of Vale age are better exposed and more fossiliferous in this area, with some sites yielding post-Arroyo tetrapods such as *Labidosaurikos* (Olson and Mead, 1982). Near the Arroyo-Vale transition, however, fossils are rare and widely scattered. The practice of considering the beds in this region to be undifferentiated Clear Fork has been followed in recent years (see Barnes, 1972 and 1987).

Differentiation of the formations has proven less difficult in the classic area, where the Arroyo and Vale Formations carry distinctive vertebrate genera and species (Olson and Mead, 1982). Even there, however, fossils are rare and widely scattered near the boundary. Partly on the basis of fos-

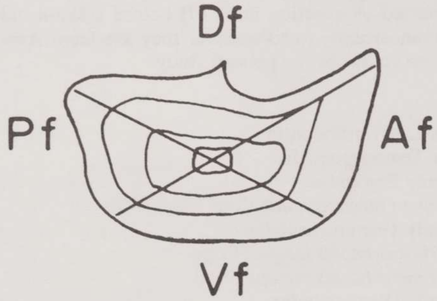

Figure 3. Sketch of a typical scale of a palaeoniscoid fish showing the positions of the four quadrants used in descriptions in text. Af, anterior quadrant; Df, dorsal quadrant; Pf, posterior quadrant; Vf, ventral quadrant.

sils and partly on sedimentological grounds, the top of the Arroyo in the classic area has been placed at the base of persistent, coarse conglomerates and sandstones which supersede evenly bedded red shales and mudstones considered to be uppermost Arroyo (Olson, 1958). The contact has been traced as far south as the south bank of the Salt Fork of the Brazos River in Baylor County.

The current study, initially undertaken as part of a study of the Vale Formation, was at first confined to efforts to extend the knowledge of vertebrate animals south of the classic area. As concepts of distributions of the fossils and the environments of deposition matured during the course of field work, and extensive deposits of vertebrates remained elusive, emphasis gradually shifted toward determination of the nature and positions of the marine and non-marine deposits, and how, if at all, the terrestrial vertebrate fauna of the Arroyo altered as one passed from the strictly terrestrial beds of the north to the fully marine deposits of the south. As this study was in progress, Schultze (1985) and Schultze and Chorn (1986) produced pertinent information about the marginal marine complexes in the Lower Permian of Kansas.

MATERIALS AND METHODS

The materials used in this study consist of terrestrial and marine organisms and sediments of the Arroyo Formation exposed in outcrops over the area between northern Runnels County to southern Baylor County, Texas (Figure 2), supplemented by materials from the Clyde and Lueders Formations which lie to the east of the Arroyo outcrops.

Terrestrial vertebrates were collected and prepared by standard techniques. Searches were made at some 60 sites of clastic outcrops ranging from roadcuts to areas that covered several acres. Red mudstones predominate in these sites, with small amounts of coarser clastics in the northern part of the area. Grab samples of mudstones, formed under a variety of depositional circumstances, were taken at 10 sites, washed, screened, and examined for organic remains.

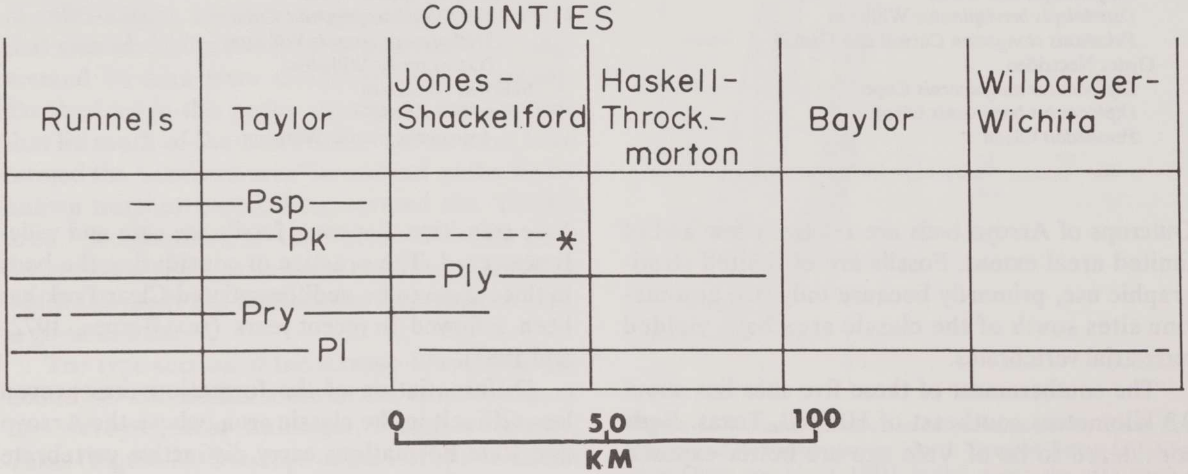

Figure 4. Distribution by counties (see Figure 2) of the Lueders and Arroyo Limestones: Pl, Lueders; Pry, Rainey; Ply, Lytle; Pk, Kirby Lake; Psp, Standpipe. The extent of Pk (*) is based on the Abilene Sheet of the Geological Atlas of Texas (Barnes, 1972); its northernmost outcrops were not visited in our field work.

Table 2. Locations, sediments, and faunas of the five terrestrial vertebrate sites of the southern area of the Arroyo Formation. For map locations see Figure 5. Catalogue numbers in the right-hand column are UCLA VP —.

Loc.	Sediments, conditions of deposition, location	Condition of fossils	Taxa
A	Coarse, gray-green conglomerate in stream cut. Stream laid by rapidly running water - point bar channel fill. 3 miles east of Heffner, Baylor County, Texas, near bridge over Lake Creek	Fragmentary bones and isolated teeth	*Orthacanthus platypternus*, 3641 Indet. vertebra of dissorophoid 3643 *Diplocaulus*, vert. and skull fragments, 3640 *Dimetrodon*, teeth, part. limb bone, vert. frags., coprolite 3642.
B	Conglomeratic channel fill incised in gray-red shale. West of FM 266, just east of tertiary road, about 10 miles NE of Haskell, Haskell County, Texas.	Well preserved, partial skull	*Diplocaulus* no number
C	Fine, lenticular conglomerate incised in red mudstone. Probably lateral flood plain deposit. East of FM 266, about 10.5 miles NE of Haskell, Haskell County, Texas.	Fragments of bone and teeth	*Orthacanthus, Dimetrodon*. Not collected.
D	Thin, fine conglomerate interbedded with red mudstone. Probably outwash on stream flood plain. East of FM 218, about 6 miles ESE of Haskell, Haskell County, Texas	Mostly fragmentary, but partial skeleton of *Dimetrodon.*	*Orthacanthus & Diplocaulus*, not collected *Dimetrodon*, 453, 477, 479 (1 individ.), 697, 699, Coprolites, 698.
E	Brown mudstone, close to stream channel conglomerate, 200 yds. long and 30 yds. wide. Broad bed of macerated coprolite, sandy mudstone, formed in pool at east end, with skulls of *Diplocaulus* and vertebra of *Dimetrodon*. To north of main site a clayball conglomerate with *Diplocaulus* and *Orthacanthus* 6 mi. SSE of Haskell, Haskell County, Texas.	Fragmentary to partial skull and jaws of *Diplocaulus*, part skulls, jaws, postcranial parts of *Dimetrodon*. Multiple elements of single individuals. *Lysorophus* in nodules, *Eryops,* fragmentary *Diadectes.*	*Orthacanthus platypternus*, 3647. *Lysorophus,* 3572. *Diplocaulus*, 478, 3501, 3506, 3516, 3523, 3525, 3527, 3528, 3562, 3565, 3568, 3569, 3570, 3574, 3576, 3577, 3780, 3632, 3633, 3634, 3635, 3636, 3639. *Eryops*, 3583. *Diadectes*, 3524. *Dimetrodon*, 3511, 3513, 3517, 3526, 3561, 3563, 3564, 3566, 3571, 3573, 3578, 3579, 3581, 3582, 3637, 3638.

Samples of limestone averaging about 4 kilograms in weight were obtained from about 50 sites, distributed from Runnels County to near the Salt Fork of the Brazos River. Stratigraphically, they came from six limestones, from lowest to highest: Clyde, Lueders (Albany Group), Rainey, Lytle, Kirby Lake, and Standpipe (Leonardian). The samples were treated with 10 percent acetic acid and residues were searched for organic remains under a binocular microscope.

Scales of palaeoniscoid fishes occur in all of the limestone samples and are the most abundant organic remains in most of them. Analyses of shapes, surface structures, and scale histology were used as bases for taxonomic assignments. With the exception of *Acrolepis*, analyses of the gross features proved to be of limited taxonomic value due to the extensive variation of shapes and surface texture over the body of any single fish.

Scale histology was studied by analysis of thin sections and scale transparencies. Horizontal and transverse thin sections were prepared by the usual means. Many scales proved to be translucent, and among them many preserved internal histological structures. Such scales, several hundred in all, were mounted on glass slides with gum arabic and rendered transparent by applications of xylenes. Camera lucida sketches of the histological structures were augmented by photomicrographs of the best preserved scales (see Figures 12, 13).

A serious question in the use of histological patterns of fish scales for detailed taxonomic analyses has been the extent to which histological features vary, both in their make-up and in their intensity, over the bodies of individual fish (e.g. see Aldinger, 1937; Cavender, 1963). To get an idea of the amount of variation to be expected within a single individual, scales of the extant fish *Polypterus* were sampled by taking five rows of scales from three tiers along the body length. Analysis of these samples showed that although shape varies strongly, along with intensity of the expression of some

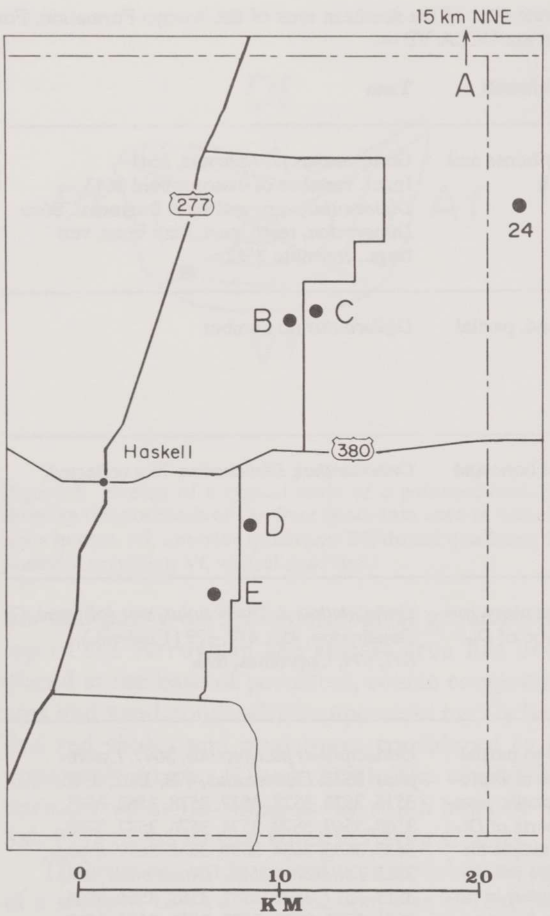

Figure 5. Sites B, C, D, E in Haskell County, Texas (see Figure 2). These, plus Site A to the north, are those that have produced tetrapods from terrestrial deposits. Also shown is Site 24, the nothernmost outcrop of marine Arroyo Limestone (Lytle Limestone) in western Throckmorton County, Texas.

histological features, the characteristic pattern (Figure 13G) remains recognizable throughout. The principal visible structures are the vascular plexus and the canals of Williamson. The vascular plexus lies in the dentine immediately internal to the surficial ganoine layer and consists of strong radial canals, bifurcated distally, and weaker concentric canals. The canals of Williamson appear as dark oval structures which penetrate the basal bone to the level of the canal plexus.

For individual scale analysis the four quadrant approach of Lagler (1947), as applied to palaeoniscids by Cavender (1963), was adopted (Figure 3). For terminological simplicity throughout our descriptions the characteristic palaeoniscoid dental tissues are designated as bone, dentine, and ganoine.

GENERAL CONDITIONS OF DEPOSITION OF THE ARROYO FORMATION

The terrestrial nature of the Arroyo deposits in the classic area has been documented repeatedly, from well before the time of Case's classic ecological studies (1915) to the present. This terrestrial condition persists northward to the vicinity of the Wichita Mountains in Oklahoma, where it is displayed in isolated outcrops of the lower part of Hennessey Formation and in fissure-fills in Ordovician limestones north of Fort Sill, Oklahoma. When the current study was initiated in conjunction with an intensive study of the Vale Formation of Haskell, Jones, and Taylor Counties, Texas, it was more or less assumed that, much as in the Vale as then known, the major portion of the Arroyo clastics of the southern area had been deposited under non-marine conditions. This assumption proved to be false. I had suggested earlier (Olson, 1958) that an alternation of marine transgressions and regressions provided a utilitarian model for studies in the area. This was in connection with an effort to determine the Arroyo-Vale boundary in the classic area. That this boundary was marked by a strong transgression, recorded in the Standpipe Limestone, is not true, as was supposed. Field work over the last decade, enhanced by the use of the Abilene and Wichita-Lawton Sheets of the Geological Atlas of Texas (Barnes 1972, 1987) has led back to the concept of repeated marine transgressions over the southern area during the time of Arroyo deposition, but equally has shown that they are not directly related to the Arroyo-Vale boundary in the classic area.

Four limestones, successively Rainey, Lytle, Kirby Lake, and Standpipe (Figure 4), interrupt the deposits of mudstones characteristic of that part of the southern area which lies north of Runnels County. The uppermost, the Standpipe, is succeeded stratigraphically by a few meters of mixed marine and terrestrial deposits (Wilson 1953), followed by the typically terrestrial beds of the Vale. In many Arroyo sections the exposures of limestones include several layers of calcareous sediment separated by gray and red mudstones, with the gray beds adjacent to the limestones. In other outcrops only one or two limestone layers are present. The composition and texture of the individual layers in a single section vary considerably, as is also the case in outcrops of each of the limestones along its strike. All limestones are composed principally of calcareous matter, but the

Table 3. Sediments and faunas of limestone samples from the southern area of the Arroyo Formation. N: site numbers, as plotted in Figures 5 and 6. FN: UCLA VP collection field numbers. FM: formations (Pcl=Clyde, Pl=Lueders) and members of the Arroyo Formation (Pry=Rainey, Ply=Lytle, Pk=Kirby Lake, and Psp=Standpipe). Some of the taxonomic designations are composite: hybodonts include both *?Acrodus* and *Polyacrodus*; palaeoniscids and microsaurs include a variety of genera.

Taxa that were found at one or more sites, but not included in the table are: phyllodont platysomid teeth and tooth plates (the former were present in all samples); rhipidistians, 1 scale from Site 2; labyrinthine teeth and possibly assignable jaw fragments, from Sites 13 and 24; *Gnathorhiza*, 2 teeth from Site 13; one specimen of *Archimedes* from Site 3; one nautiloid from Site 31.

N	FN	FMA	SEDIMENT	Linguloids	Ostracods	Worms	Gastropods	Pelecypods	Pelycosaurs	*Diplocaulus*	Trimerorhachids	Eryopids	Microsaurs	*Lysorophus*	Palaeonisc. vertebrae	Palaeonisc. teeth, jaws	Denticles	Hybodonts	*Orthacanthus*
1	12-6-2	Pcl	Marine, crystalline limestone, limonitic in places, fine sand residue.			X	X	X							X		X		
2	8-80	Pl	Sandy limestone, small concretions, bits of charcoal, small pebbles, rounded.	X	X	X	X	X	X	X	?	?			X	X	X	X	X
3	2-85		Sandy, gray granular limestone	X	X		X	X						?	X	X	X	X	
4	3-83A		Limestone, much clay, black debris	X	X	X	X								X	X	X	X	X
5	9-83		Dark, shaley limestone, recrystallized. Angular quartz in residue.		X	X	X	X		X		?			X	X	X	X	
6	6-8-2		Sandy, yellow limestone, fine inclusions.				X								X				
7	6-20-2	(Pry)	2 limestones, lower fucoidal, dark with lime fragments in matrix, much organic matter. Upper punky, no organisms.	X	X	X									X		X	X	X
8	6-12-2		Hard, gray limestone. Similar to lower bed, 6-10-2.		X		X								X			X	X
9	14-4-2		Yellowish limestone, dense, massive, uniform. Limonite, manganite, quartz in residue.		X	X	X								X	X	X		
10	10-83		2 limestone beds, upper thin, lower massive. Sand and clay in residue. Rich in fossils.	X		X								X			X		
11	9-80 5-83A		Varied limestone, hard, massive, finely conglomeratic. Appears to be all detrital.				X			X	X			X	X	X	X		
12	3-85		Thin bedded, sandy, gray limestone. Sand and clay in residue.		X	X	X	X		X	X			X	X			X	
13	6-80	(Ply)	Limestone, conglomeratic in places. Complete pelecypod shells. Angular quartz and clay in residue.	X		X	X	X	X	X	X	X	X	X	X		X		X
14	6-11-2		Varied limestone conglomerate.			X	X						X		X				
15	6-83A		Conglomeratic limestone, with limestone fragments, angular quartz in residue.			X	X								X			X	
16	1-84		Crystalline limestone, sandy residue.	X		X	X											X	
17	12-83		Sandy limestone, angular quartz residue.												X			X	X
18	6-3-2		Dense, sandy limestone, manganite in residue.												X			X	X
19	6-2-2		Rotten, recrystallized limestone.																
20	6-4-2		Gray, sandy limestone, recrystallized.				X								X				
21	2-83A		Same as 6-4-2.												X				
22	6-1-2		Rotten, crystalline limestone.												X			X	X
23	16-81 6-5-2 1-83A		10 ft. section of layers and lenses of conglomeratic limestone, calcareous sandstone, gray shale. Pisolitic in places. Marginal marine.	X	X	X	X		X	X	X		X	X	X		X	X	
24	87-1		6 ft. section of granular limestone, fine conglomerate (unfossiliferous). Interbedded red and gray mudstones.	X	X	X	X	X	?	X	?			?	X	X	X		
25	12-1-2	(Pk)	Crystalline limestone, massive, pebbly in places. Sand in residue.			X	X								X			X	
26	12-2-2		Massive, thick limestone, partly crystalline, punky in places.			X	X								X			X	
27	12-3-2		Thick limestone, mostly crystalline.				Xs								X		X		X
28	7-0-2	(Pap)	Thick layer of crystalline limestone. Coarse near base. Angular quartz in residue.				Xs								X		X	X	
29	7-2-3		Thin limestone layer in gray shale, sandy.			X	X											X	
30	7-2-2		Brown, sandy limestone, thin bedded.			X	X								X		X	X	
31	14-1-2		Fine grained, dense limestone			X	X	X							X		X	X	
32	14-2-2		Gray to brown limestone, high clay content. Few fossils.				X	X									X	X	

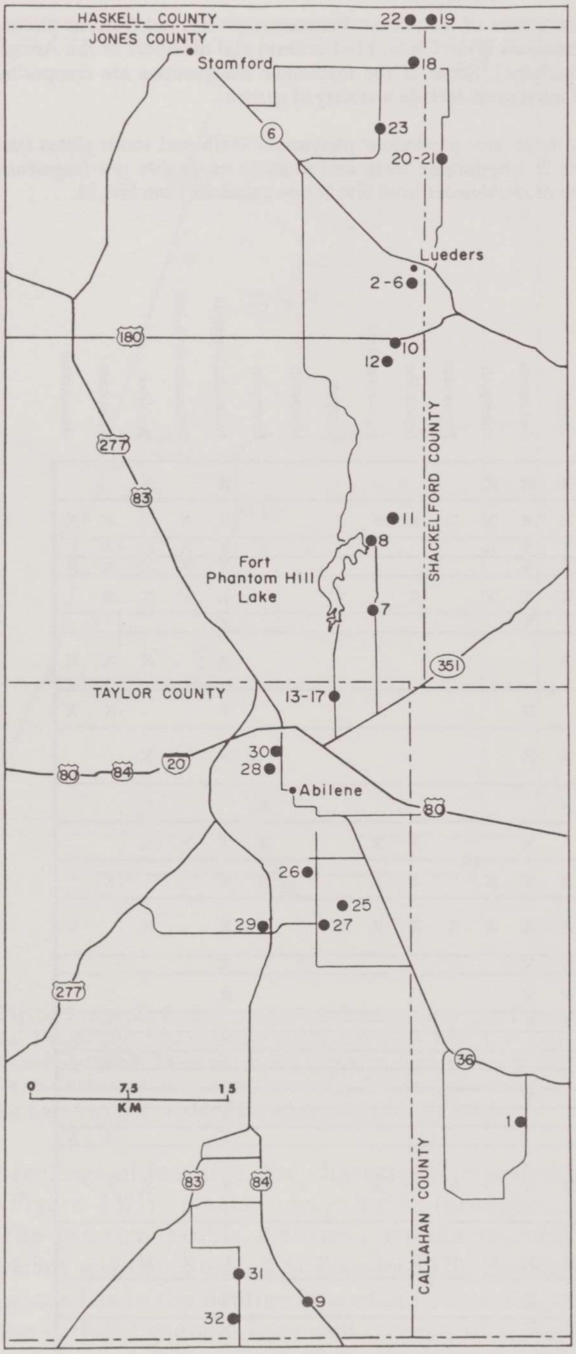

Figure 6. Sites of marine limestone samples over Callahan, Taylor, Shackelford, and Jones Counties, Texas (see Figure 2). Site 24, in Throckmorton County, is shown on Figure 5.

percentage of clay, silt, and sand varies and many of the limestones are partially or fully conglomeratic.

All of the limestone samples contained scales of palaeoniscoid fishes and reworked remains of pelecypods. In several samples the pelecypods are moderately well preserved, while in others they are fragmentary and widely scattered. Samples from two sites were examined by Drs. Ellis Yochelson and John Pojeta of the National Museum of Natural History. Yochelson sent me the following informal evaluation of the specimens:

> "As a general statement may I say that these [the pelecypods] are fairly poor specimens. On the other hand this sort of matrix always seems to yield rather poor specimens. Many have been moved and this may not be a life assemblage; on the other side of the coin I doubt that there has been much widespread transportation. Based on other studies, primarily in Kansas, I would guess that these are marine fossils, or at least ones that lived in nearly marine conditions. They are not open water marine in the sense of brachiopod-bryozoan assemblages, but likewise they are definitely not fresh water. Perhaps a lagoon with some fluctuation in salinity would satisfy my ecological speculations. (Present) *?Permophorus* (abundant) and *Myalina* or *Septimyalina*."

This analysis pertains to several other samples as well, but still others clearly were deposited under somewhat different conditions. Some were formed under the influence of fairly active currents. Most of the samples from sites south of Abilene, Texas, lack concentrations of pelecypods and tetrapod remains, tend to be moderately fine grained, and appear to have been formed under conditions more nearly approaching open-water marine, though not meeting all of the criteria set down above by Yochelson.

Discontinuities of outcrops along the strike are characteristic. Some clearly are the result of cover by later sediments and removal by erosion, but others seem to represent actual gaps in deposition, suggesting that the limestone deposits were formed in discrete estuaries, lagoons, or basins. To the extent that our samples can be considered reliable indicators of the organisms living at the time of their deposition, the distributions of tetrapods may have some bearing on this matter. Eight of the limestone samples from the Lueders and Arroyo Formations have produced remains of terrestrial vertebrates. These samples are distributed from

Figure 7. Photomicrographs of amphibian specimens from limestone samples. A. *Diplocaulus*, dermal skull surface; B. *Lysorophus*, vertebral centra and rib; C. *Eryops*, dermal skull surface; D. *Trimerorhachis*, dermal skull surface; E. Labyrinthine tooth, labyrinthodont amphibian or possibly crossopterygian; F. Labyrinthine teeth, ?*Eryops*; G. Caudal intercentrum, labyrinthodont amphibian. Bars for scale = 1 mm.

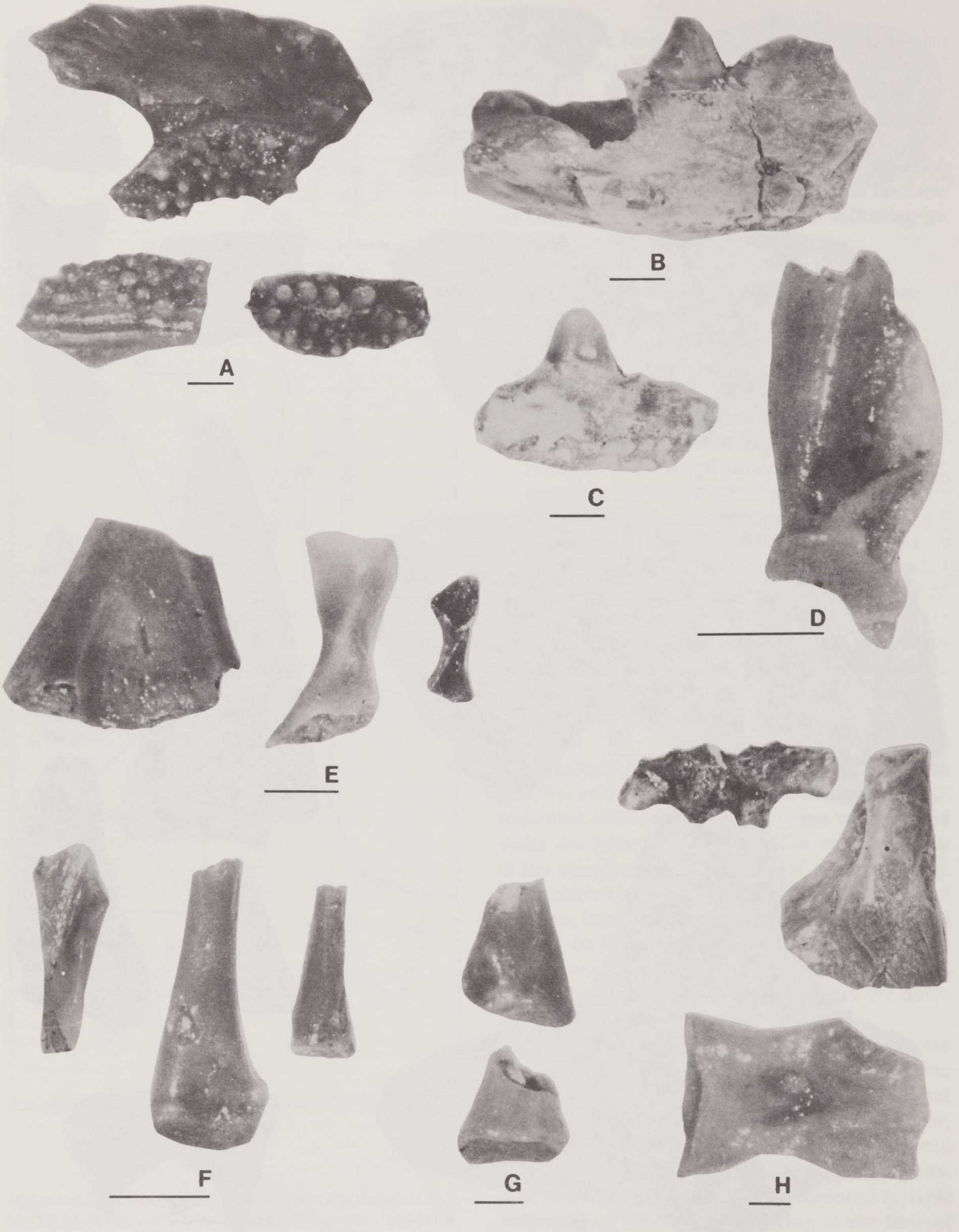

Figure 8. Photomicrographs of specimens of microsaur specimens from limestone samples. A. Skull fragments of *Pantylus*-like microsaur; B. Jaw of *Pantylus*-like microsaur; C. Tooth and jaw fragment of *Pantylus*-like microsaur; D. Quadrate of microsaur; E. Limb elements of microsaurs, cf. *Pedolopsis* and *Microbrachis*; F. Parts of slender microsaurian limb elements; G. Parts of stout microsaurian limb elements; H. Parts of vertebrate of microsaurs. Bar for scale = 1 mm.

the northernmost limestone outcrops (Figure 4) south to about the level of Abilene, Texas. Lueders beds with terrestrial tetrapods have been recorded as far north as the southern boundary of Wilbarger County, Texas (Berman, 1970). However, no remains of tetrapods have been found in any of the limestone samples or clastics south of Abilene, and it is reasonable to assume that these deposits were formed under marine conditions. The tetrapod-bearing limestones north of Abilene indicate that their deposition took place close to land, suggesting the existence of a complex pattern of marine and non-marine deposition along an irregular, rapidly fluctuating coastline. More specific delineations of the changing water-land relationships cannot be worked out from the sedimentary and fossil data now available.

TERRESTRIAL SITES AND FOSSILS

Only five sites that contain vertebrate fossils have been found in the terrestrial beds of the Arroyo Formation of the southern area (Figure 5, Table 2). All five lie in the upper part of the Arroyo section, above the level of the Lytle Limestone and, based on elevation, likely between the levels of the Kirby Lake and Standpipe Limestones.

Fossil-rich beds of the classic area occur in a direct line only about 15 km to the north of the northernmost of the five sites, but over the intervening area the strike of the beds swings northeastward so that the distance along the strike is somewhat greater. The area in between is largely covered by beds of the Quaternary Seymour Formation and Recent alluvium. Except at Site E, all fossils have come from channel and off-channel conglomerates. At Site E fragments have come from a small exposure of clayball conglomerate and fairly well preserved specimens from a 2 meter section of fine grained red-brown mudstone. Only at this site is the taxonomic diversity sufficient to give some idea of the variety of terrestrial vertebrates that existed in the southern area.

At Site E, an east-west ridge of mudstone about 200 meters long, 30 meters wide and 2 meters high yielded most of the fossils. At its eastern end, near the base, a small standing water deposit made up of silt and macerated coprolitic material produced *Dimetrodon* and *Diplocaulus*. This represents the only standing water deposit found in the southern area. *Diplocaulus* and *Orthacanthus* are present as well in the adjacent clayball deposit. At a slightly higher level, about 1/3 meter above the top of the mudstone ridge, is a coarse conglomerate channel fill deposit which contains no fossils. In the immediate vicinity of the fossiliferous beds, mudstones are exposed in a section approximately 25 meters thick and covering approximately 3 acres. Thorough searches of the mudstones revealed no organic remains beyond the areas of the fossils described. At this site a grab sample was taken from red mudstone about 10 meters from the fossiliferous ridge and at approximately the same stratigraphic level. It yielded no organic remains upon screening and washing. At Site E, as at the other four terrestrial sites, vertebrate remains occur either in stream deposits or close to them, suggesting that a riparian environment may have provided the principal habitat for terrestrial vertebrates of the area.

MARINE SITES AND FOSSILS

The Sites.- A total of 50 samples of marine limestone were collected, of which 35 samples representing 32 sites (Figures 5 and 6, Table 3) contained significant numbers of specimens. The remaining 15 samples were poor in organic content and contained only fish remains (predominantly scales) and scattered pelecypod fragments. In addition to the 26 Arroyo sites, one site from the Clyde and five sites from the Lueders were included for comparison. The richness of vertebrate remains in the limestones differed markedly in different samples. No significant taxonomic differences could be detected in samples from the same general area but from different stratigraphic levels *across* the strike of the Arroyo Formation. However, significant differences do occur *along* the strike of the individual limestones, probably related to geographic distribution and to the composition of the limestone, two not fully independent variables. From the latitude of Abilene southward the limestones tend to be low in clastic content, and tetrapods are absent but remains of fish and small invertebrates are present. To the north, some of the samples contain tetrapods along with remains of fish and invertebrates, and the limestones range from moderate to rich in clastic content. The differences along strike appear to relate directly to the environments of deposition, predominantly near-shore in the northern area and in more open marine waters to the south.

In texture and composition the limestones range from fine grained crystalline rocks with

Figure 9. Photomicrographs of fish specimens from limestone samples. A. Tooth of *Gnathorhiza*; B. Hybodont teeth; C. Phyllodont tooth plates of *Schaefferichthys*. D. Indeterminate teeth, ?hybodont. E. Three types of palaeoniscoid teeth, see text p. 20; F. Tooth of *Orthacanthus platypternus*; G. Jaws, some with teeth, of palaeoniscids. H. Ossified vertebrae of palaeoniscoid fishes. Bar for scale = 1 mm.

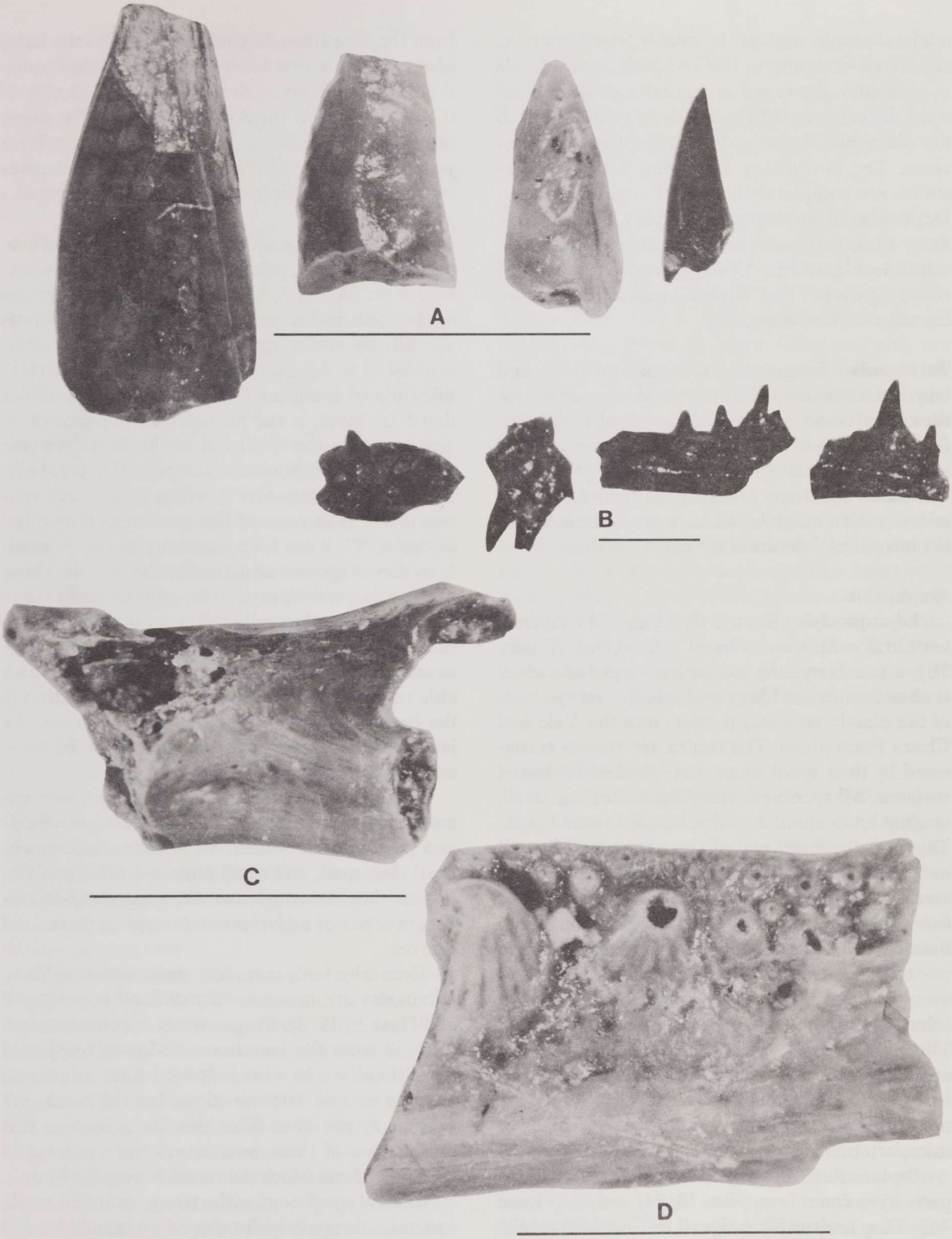

Figure 10. Photomicrographs of amphibian and reptile specimens from the limestone samples. A. Four pelycosaur teeth, three *Dimetrodon*, smallest to right, and an undetermined pelycosaur: B. Very small jaws and teeth, probably of microsaurs; C. Sphenacodont caudal vertebra; D. Labyrinthine teeth in fragment of palate, labyrinthodont amphibian or crossopterygian. Bars for scale, A, C, D = 6 mm; B = 1 mm.

minimal clastic content, to muddy, conglomeratic, calcareous deposits. In sections with several levels of limestone the range of compositional and textural differences between beds is comparable to the differences between limestones from different areas. The mudstones associated with the limestones are completely barren of organic remains. Depositional environments changed rapidly at many sites, partly as a result of changes in marine water levels and partly, it appears, because of changing events that altered erosion patterns on the adjacent land mass.

Tetrapods.- Fragments of lepospondylous and labyrinthodont amphibians and sphenacodont reptiles have come from one or more of eight sites (Table 3). Two of the eight sites are in the Lueders and the remainder in the Rainey and Lytle Limestones. Of the array of tetrapods recovered, only microsaurian amphibians have not been found in the terrestrial deposits of the southern area.

Amphibians

Lepospondyls.- Sites 2, 13, 23, and 24 contained vertebral centra and ribs of *Lysorophus* (Figure 7B), a small, aquatic, aestivating amphibian which is abundant in the lower and middle Arroyo beds of the classic area and persists into the Vale and Choza Formations. The centra are readily recognized by their spool shape and "pinched in" lateral surfaces. All specimens from these sites are small, ranging up to about 2 millimeters in central length. This is at the lower end of the size range of specimens of *Lysorophus* known from elsewhere and in marked contrast to the vertebrae of *Lysorophus* from terrestrial Site E, which average about 10 millimeters in central length. As for most tetrapod materials from these marine sites, the agents of transportation and deposition appear to have been selective, strongly biased towards small specimens. This might suggest habitat segregation of juveniles and adults, but inasmuch as small size is characteristic of all vertebrates from these sites, it appears more likely that it is the result of the processes of transportation and deposition.

Diplocaulus.- Fragments of skull and mandible parts have come from Sites 13, 14, and 23 (Figure 7A). They are readily assigned to Nectridea on the basis of the sculpture pattern on the dermal surfaces of the skull. The pattern is consistently found in *Diplocaulus*, but is also similar to that found in the diminutive nectridean genus *Peronedon*. In view of the small size of the known specimens from the limestone, they might pertain to the latter genus, which is best known from the Vale Formation. However, given the relative abundances of the two genera in the Arroyo deposits, the specimens from the limestones are more likely from young individuals of *Diplocaulus*. Representatives of *Diplocaulus* occur in all southern terrestrial sites except Site C.

Microsaurs.- Remains of microsaurs include partial mandibles, palates, teeth, limbs, and vertebrae from Sites 2, 5, 11, 12, 13, 23, and 24 (Figure 8). In some instances, incomplete teeth and jaws are difficult to distinguish from those of palaeoniscoid fish. The criterion that has been used for identification of teeth, and of palates and mandibles that bear teeth, is the presence or absence of an acrodin tip on the crowns of teeth, an apomorphic character of palaeoniscids (Ørvig 1973, Gardiner, 1984). In those instances in which jaws do not contain teeth, as in some of the specimens illustrated in Figure 8G, it has been necessary to rely primarily on the shape and structure of the alveoli. Those of the palaeoniscids tend to be symmetrically circular to ovoid, and usually contain the hollow roots of the simple teeth, whereas those of the microsaurs are ovoid to irregular, and generally contain either no roots or bony remnants of the teeth. On the basis of this somewhat suspect criterion, the jaws in the cited figure are considered to be palaeoniscoid.

Sediments at each of the sites from which microsaurs have come contain reworked pelecypods and palaeoniscoid scales. All include clastic materials, clay, sand, and small lime and silica pebbles. In part they are conglomeratic, suggesting deposition in areas of active currents near to terrestrial sources.

Even with fairly complete skulls and mandibles, microsaurs are taxonomically difficult (see Carroll and Gaskill, 1978). Fragmentary specimens, such as those from the limestones, seriously compound the difficulties. In what follows, I have attempted to make generic determinations, but the results are necessarily tentative. What they do indicate is that a minimum of three microsaurs were present in the faunas from which the remains were derived.

Several specimens with strong, rounded teeth, somewhat irregularly distributed on mandibles and and palates (Figure 8A-C), resemble the mandibles and palates of *Pantylus* and *Leiocephalikon* (Carroll and Gaskill 1978, Figures 25 and 46, respectively). Inasmuch as *Pantylus* is Permian and *Leiocephalikon* is Westphalian, tentative assignment is made to *Pantylus*. However, it is important to note that the specimens from the limestones are much smaller than other known specimens of *Pantylus*.

The quadrate (Figure 8D) is almost certainly microsaurian and may pertain to *Pantylus*. Partial vertebrae (Figure 8H), although likely microsaurian, are not assignable to family.

The extremely small toothed jaws from Sites 18 and 24 (Figure 10B), could have come from a microsaur or a diminutive reptile. The presence of irregularly placed, small accessory teeth indicates probable microsaurian affinities. Closest resemblances are to *Microbrachis* (Carroll and Gaskill, 1978, Figure 114a), and tentative assignment is made to this genus.

Limb elements (Figure 8E-G) are of three general types. Those illustrated in Figure 8E resemble comparable elements of *Pedolopsis* and *Microbrachis* (Carroll and Gaskill, 1978, Figure 125), both known from the Arroyo Formation. The "large" specimen in Figure 8E may be merely from a larger individual of the same genus. The specimens illustrated in Figure 8G may be from *Pantylus*. Those in Figure 8F appear to belong to a slender limbed microsaur, but no more definite assignment is practicable. Such slender limb bones are fairly common in samples in which other microsaurs occur. The vertebral parts illustrated in Figure 8H presumably belong to microsaurs, but they are not otherwise assignable.

A minimum of three types of microsaurs are present. All remains are from extremely small representatives of the taxa to which they have been tentatively assigned. They represent an otherwise unrecorded element of the Arroyo terrestrial fauna of the southern area.

Labyrinthodonts.- Eryopids are represented by fragments of the dermal surfaces of skulls, teeth, and intercentra. Fragments such as the one illustrated in Figure 7C occur in samples from Sites ?2, 11, 12, 13, 23, and ?24. Small caudal intercentra (Figure 7G), one from Site 13 and a second from Site 24, are probably eryopid. In addition, large labyrinthine teeth which occur in samples from Site 13 (Figure 7F) probably pertain to *Eryops*. Figure 7E illustrates a moderately large labyrinthine tooth that probably came from a crossopterygian, although its labyrinthodont affinities cannot be ruled out. Much the same applies to the partial jaw illustrated in Figure 10D. *Eryops* has been identified from Site E of the southern terrestrial Arroyo.

Trimerorhachis (Figure 7D) is represented by a few skull fragments from Sites 2, 5, and 13. Identification has been based on the surface sculpture of the dermal bones. Otherwise this genus has not been found over the southern area, either in nonmarine or marine deposits.

Reptiles.- Reptilian remains are rare in the limestone samples, being represented mainly by teeth (Figure 10A, B). They have been found in samples from Sites ?4, 11, 12, 13, 23, and ?24. Most of the teeth are elliptical in cross-section with serrated anterior and posterior edges. They probably are from small individuals of the sphenacodont *Dimetrodon*. The smallest tooth in Figure 10A is nearly circular in cross-section and appears to have come from some other pelycosaur. A few small vertebrae and partial vertebrae occur at Site 13. The best preserved (Figure 10C) is a small sphenacodont caudal vertebra that could pertain to *Dimetrodon*, but is not definitely assignable to the genus. On the whole, the near absence of reptilian remains is striking, likely a result of the aquatic conditions. In the case of pelycosaurs, it may be a matter of sampling related to size. However, size clearly has not been a factor in the absence of *Captorhinus*, which is a common constituent of the classic Arroyo beds.

Aquatic Vertebrates.

Class Chondrichthyes.- Teeth of *Orthacanthus platypternus* (Figure 9F) occur in samples from Sites 2, 3, 4, 7, 13, 16, 23, and 24. Deposition appears to have taken place in estuaries or lagoons and open waters, based on the sedimentary characteristics of the limestones. This species of *Orthacanthus* is abundant in fresh water Arroyo deposits of the classic area and is present in terrestrial deposits of the southern area as well. Its occurrence in "open-water" limestones as well suggests that it was euryhalic. No trace of *Xenacanthus*, also common in terrestrial Arroyo beds, has been found.

A wide variety of dermal denticles has been recovered, many of which came either from elasmobranchs or hybodonts (Figure 11B). These represent various types common in the Permo-Carboniferous. The denticles from the Carboniferous have been organized into a nontaxonomic, utilitarian system by Tway and Zidek (1982, 1983). All of the denticles recovered from the limestone samples can be fitted into one or another of their categories and no further effort to treat them systemat-

Figure 11. Photomicrographs of fish and invertebrate specimens from limestone samples. A. Palaeoniscoid palates, with teeth; B. Chondrichthyan dermal denticles; C. Gastropods, D. Annelid worms E. Ostracods. Bar scale = 1 mm.

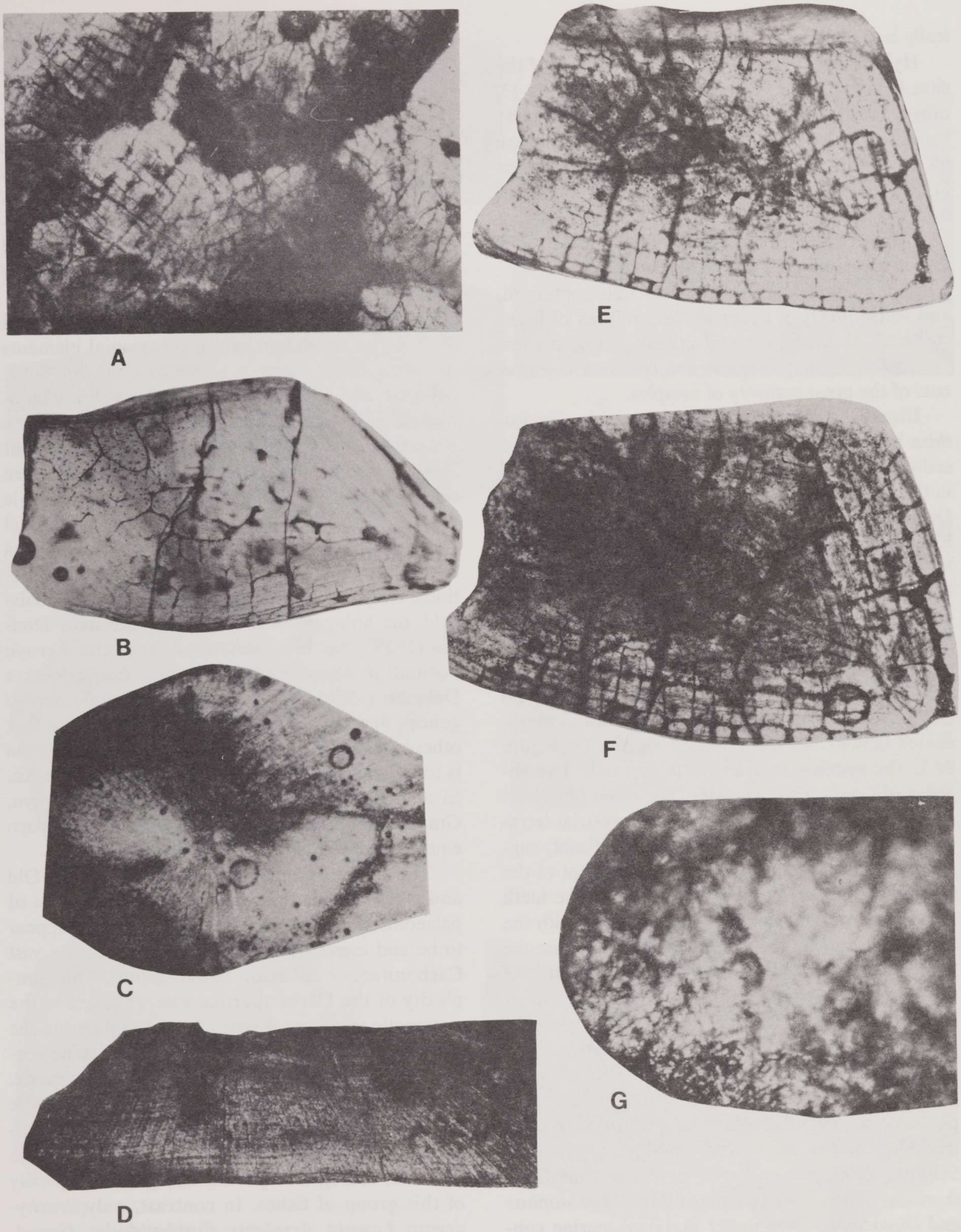

Figure 12. Photomicrographs of scales of palaeoniscoid fishes. A. *Elonichthys browni* (USNM UF440), parts of several scales. B. Transparency of immature scale of elonichthyid; C. Horizontal section of subcircular platysomid scale; D. Transverse section of platysomid scale; E, F. Transparencies of scale of *Lawnia*, different exposure times to bring out different features - note central sinuses in E; G. Transparency of indeterminate scale, Type 6 in the text, showing complex pattern of dentinal canals in ventral-posterior areas. Detail obscure because of depth of canal layer. Not to scale. Enlargements, A, C, D about x 25, B, E-G about x 50 to 60.

ically is made here.

Hybodonts (Figure 9B) occur in eleven of the sites (Table 3). They are oddly absent from Site 13, otherwise the most prolific source of vertebrate remains. *Polyacrodus* and *?Acrodus* have been identified based on the determinations of Johnson (1979, 1981). The problematic nature of *?Acrodus*, as Johnson has explained, is due to the somewhat indefinite root structure, coupled with a histology that is very similar to that of *Acrodus*.

Class Osteichthyes.- Dipnoi, Crossopterygii, and Actinopterygii occur in the samples of limestone. Both dipnoans and crossopterygians are rare, while actinopterygians are common constituents of the great majority of samples.

Dipnoi.- Although the dipnoan genus *Gnathorhiza* is a standard constituent of terrestrial Arroyo sediments of the classic area, it has not been found in the terrestrial samples from the southern area. On the basis of work in Kansas, Schultze (1985) has indicated that this genus may have inhabited both fresh and brackish waters, although the occurrences in the classic Arroyo all appear to be in freshwater deposits. In view of Schultze's determinations, it was anticipated that the genus might appear as a common member of the samples that indicated origin in estuaries and lagoons. This did not prove to be the case, for *Gnathorhiza* is represented only by two teeth, both from Site 13 (Figure 9A). The specimens are extremely small. The absence of *Gnathoriza* from all of the other limestone samples, including those that have terrestrial tetrapods, is probably environmentally significant, suggesting that this genus was not an inhabitant of the marine or brackish water environments. The teeth likely were washed in from the land along with the terrestrial tetrapods. Alternatively, the absence from other limestone samples may be a matter of sampling. *Gnathorhiza* does occur in the Lueders Formation in what Berman (1980) has interpreted as a bed deposited in a near-shore marine environment at his Site 1, and in a clay-pebble conglomerate of uncertain origin at his Site 2. Transportation appears to have been a factor in the distribution of the preserved Lueders organisms. Schultze (1985) has offered evidence that *Gnathorhiza* and associated amphibians *Lysorophus* and *Diplocaulus* lived under marginal marine conditions, based on samples from the Lower Permian Speiser Shale.

Crossopterygii.- Few traces of crossopterygians are present in the marine samples, and none is known from the terrestrial samples of the southern area. One scale, a few labyrinthine teeth, and a jaw fragment (Figures 7E, 10D) may represent crossopterygians. The specimens are relatively large compared to those of most of the tetrapods from the limestones, and absence of more recognizable remains of crossopterygians may be a function of the selectivity of transporting agents (see p. 14). Some of the samples contain relatively large, indeterminant fragments of cranial and postcranial bones, some of which may belong to members of this group.

Actinopterygii.- Scales, teeth, mandible and skull parts, and fragments of postcranial elements including ossified vertebral centra (Vaughn, 1967; Schultze and Chorn, 1986) represent the palaeoniscoid fishes in the limestone samples. They are characteristically abundant, and scales are present in all of the samples, including the 15 which are not listed in Table 3 because of their low organic content. Similar scales occur in many terrestrial Arroyo deposits of the classic area, although less commonly than in the underlying Wichita Formations. Only one well preserved skull of a palaeoniscoid, the holotype of *Brachydegma caelatum* Dunkle (1939), has been described from the Arroyo Formation. It and tooth plates of *Schaefferichthys* Dalquest (1966), a platysomid, are the only Arroyo genera described to date. This is not to say that others are not present, but rather that preservation is usually insufficient for description and diagnosis. In addition to the two genera from the Arroyo, *Grandfieldia* has been described from an Arroyo equivalent in Oklahoma (Daly, 1973).

The Lower Permian as a whole, both in the Old and New Worlds, has yielded a limited suite of palaeonisciform fishes. The various genera appear to be end members of persistent lines from a vast Carboniferous radiation of the group. The complexity of the Carboniferous assemblage and the systematic problems it poses are exemplified in the classification of Gardiner (1967) in which he recognized 38 families, of which 17 are monogeneric. Gardiner (1984) presented a detailed cladistic analysis of the palaeoniscids, with various modifications of relationships and consolidation of the taxa. His cladograms portray the great complexity of this group of fishes. In contrast, only *Brachydegma*, *Lawnia*, *Acrolepis*, *Eurylepidodes*, *Grandfieldia*, and *Schaefferichthys* have been identified throughout the full north American Lower Permian. Because remains are rare and tend to be fragmentary, mostly scales, these genera certainly represent only a portion of the taxa actually in exist-

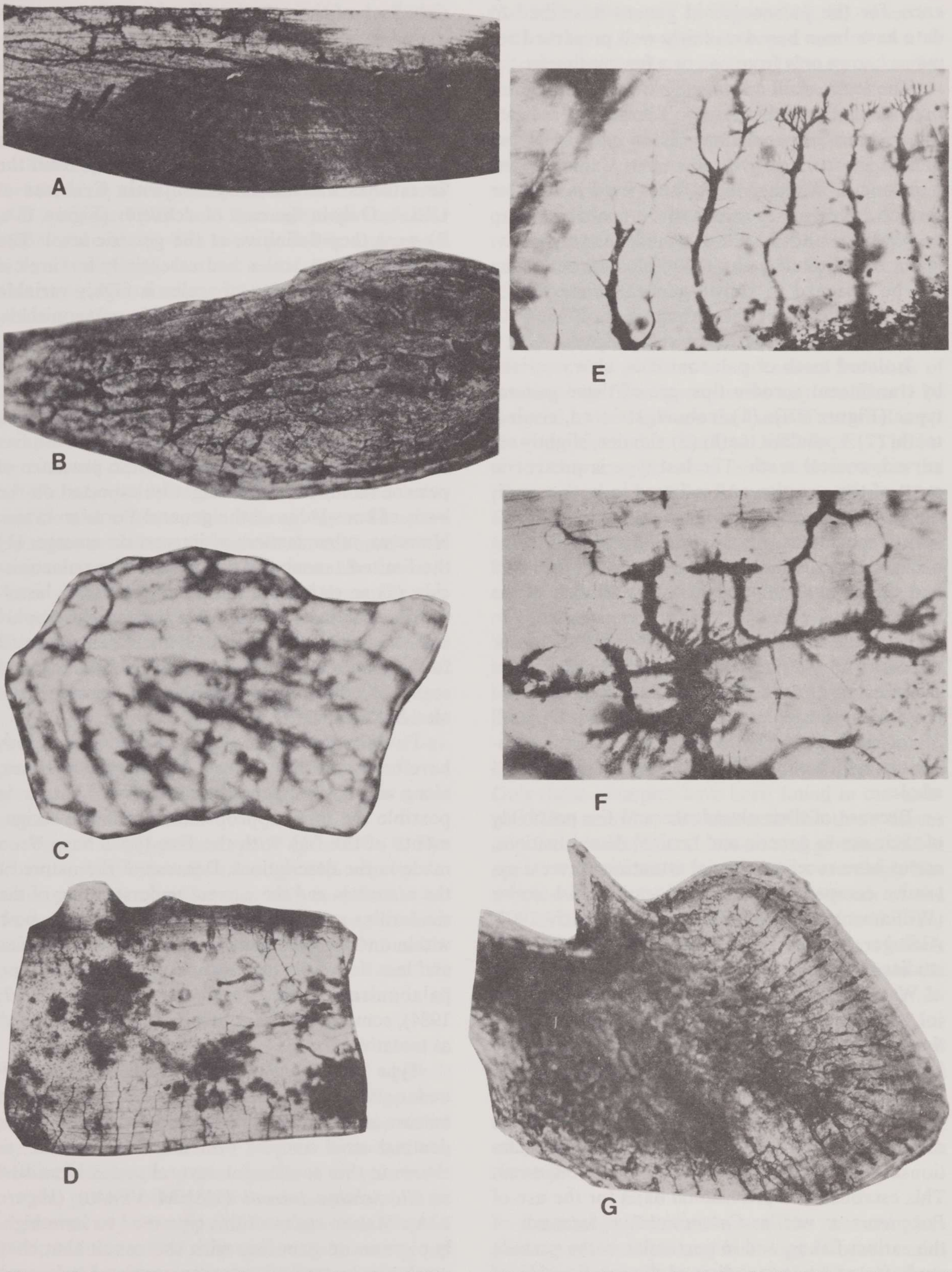

Figure 13. Photomicrographs of scales of palaeoniscoid fishes and *Polypterus*. A-C *Acrolepis*: A. longitudinal thin section, x18, B. horizontal thin section, x18, C. transparency of submature scale, x40. D-F transparencies of scale of *Amblypterus* at several different magnifications to show detail: D, x50; E, x150; F, x200. G. Typical midbody scale of *Polypterus* in transmitted light, showing resemblances to palaeoniscoid scales, especially to those of *Amblypterus*, x25.

ence, for the palaeoniscoid genera described to date have been based on fairly well preserved remains known only from one or a few specimens.

The teeth, skull and mandible parts, and vertebrae from the marine Arroyo Limestones indicate the existence of populations rich in individuals, but limited taxonomically compared to Carboniferous populations. Whether these fishes lived in fresh or marine water or, as seems more probable, were euryhalic cannot be determined unequivocally. None of the skull parts, mandibles, or vertebrae can be assigned to known genera, primarily because knowledge of the genera is insufficient to form a basis for the necessary comparisons.

Isolated teeth of palaeoniscids, characterized by translucent acrodin tips, are of three general types (Figure 9E): (1). robust, striated, conical teeth; (2). spatulate teeth; (3) slender, slightly recurved, conical teeth. The last type is present in most of the samples and is found in both mandibles and palates of a large number of the preserved specimens. Alveoli in jaws assigned to the palaeoniscids (Figure 9G) are of appropriate sizes and shapes to accommodate one or another of the three types of teeth.

The phyllodont tooth plates (Figure 9C) appear to pertain to the platysomid genus *Schaefferichthys* Dalquest (Johnson and Zidek, 1981). Isolated teeth from these plates occur in samples from all 35 recorded sites. The teeth do not have the acrodin tips which characterize the palaeoniscids as a whole.

Because of their abundance and the possibility of their use in generic and familial determinations, scales have received special attention. Several extensive comparative studies of "ganoid" fish scales (Williamson, 1849, Scupin, 1896, Goodrich, 1907, Aldinger, 1937, and Cavender, 1963), along with studies of scales of particular genera such as those of Watson (1925, 1928), have been used as a basis for the study of the Arroyo materials. In each of these studies greatest attention was paid to scale histology, augmented by analyses of surface and shape characteristics.

A significant systematic determination was the recognition by Goodrich (1928) of a probable relationship of palaeoniscoid fishes and *Polypterus*. This established a provisional basis for the use of *Polypterus*, as well as *Calamoichthys*, for study of the extinct fishes, and in particular in the present study for an understanding of the relationship of body position of the scales to their shape and histology (see p. 5). Beyond this suggestion by Goodrich, each of the other studies identified and discussed at some length the many problems that attend the use of scales in systematic studies of palaeonisciform fishes, particularly emphasized by Aldinger (1937) and Cavender (1963).

An extensive analysis of the shape and surface features of the scales in our collections from the limestones was made by Benjamin Crabtree of UCLA. Only in the case of *Acrolepis* (Figure 13A, B) were they definitive at the generic level. The majority of our scales had essentially featureless outer surfaces. Shape of scales is highly variable from place to place on the body in palaeoniscids, as in actinopterygians in general, and sorting by shape proved to be a better index of body position than of taxonomic relationships.

Histological studies have been of greater value. The taxonomic results of the histological studies for the most part merely indicate the presence of palaeoniscoid fishes that might be expected on the basis of knowledge of the general Permian fauna. However, other matters of interest do emerge: (1) the limited taxonomic diversity of the palaeoniscids; (2) an estimation of the utility of scale histology in analyses of fauna of a limited geographic and stratigraphic unit; and (3) the extent of detail that can be seen in three dimensions by the use of scales as transparencies without sectioning (see also Aldinger, 1937).

Five common scale types, as described below, have been determined from histological analyses, along with a rare pattern listed as Type 6. As far as possible the most appropriate taxonomic assignments of the fish with the five types have been made in the descriptions. Because of the nature of the materials and the current understanding of the similarities and differences of scale histology, both within and between genera, as well as the complex and less than fully understood systematics among palaeoniscoid fish as a whole (Gardiner, 1967, 1984), some of the assignments must be considered as tentative.

Type 1: *Elonichthys* type (Aldinger, 1937; Cavender, 1963) (Figure 12A, B).- Characterized in mature scales by a nearly complete rectangular dentinal canal complex over much of the scale, as shown in thin section for several scales identified as *Elonichthys browni* (USNM VF440) (Figure 12A). Mature scales of this type tend to have highly pigmented ganoine, with the result that they rarely can be treated as transparencies. Under very strong transmitted light, after extended application of xylenes, the typical dentinal canal pattern is visible in some mature scales but not reproducible in photomicrographs. The pattern in an immature scale is illustrated in Figure 12B. Note in particular the incipient development of dentinal canals, central sinuses, and the visible presence of bone cells in the anterior quadrant.

This type of scale pertains to the family Elonichthyidae, *sensu lato*, based on comparisons with Aldinger (1937: text figure 53) and Cavender (1963: plate IIIA). The most probable assignment is to *Elonichthys*, but scales of *Rhadinichthys*, *Ganolepis*, *Gonatodus*, and others show some resemblances in patterns of the dentinal canals.

Type 2: Platysomid type (Figure 12C, D).- Scales lacking enamel and dentine, based both on horizontal and transverse thin sections and transparencies. This type is abundant in many of the samples. Scales range in shape from circular to narrow and elongate. The bone tissue is somewhat indefinitely divided into a thin, laminated inner portion and a denser, thin external layer. Sharpey's fibers are prominent throughout. In the subcircular scales strong canals penetrate from the inner to outer surfaces, converging toward the outer surfaces. Scales of this type are assigned to the family Platysomidae, but the absence of canals in the outer layer differs from scales of this family described by Williamson (1849) and refigured by Aldinger (1937: text figure 49, plate 44, figure 3). The abundance of this scale type throughout the full stratigraphic section and similar abundance of the platysomid *Schaefferichthys* suggest that the scales pertain to this genus.

Type 3: *Amblypterus* type (Figure 13D, E, F).- Characterized by more or less parallel, slightly sinuous, radial dentinal canals, with very fine interconnecting cross-canals. Under high magnification the sinuous radial canals show intricately branching termini. The characteristic pattern is most fully developed in the ventral quadrant but occurs in all quadrants in fully matured scales.

Like the scales of *Lawnia*, described below as Type 4, scales of this type have ganoine which is not strongly pigmented in the mature stage, and patterns are readily apparent under transmitted light after the scales are treated with xylenes, which eliminate the partial opacity of the ganoine.

The pattern of dentinal canals of this scale type is consistently developed in *Amblypterus* (Scupin 1896; Aldinger, 1937; Cavender 1963), and is not found in any other scales in the literature utilized in this study.

Type 4: *Lawnia*, reduced amblypterid type of Cavender (1963, p. 77) (Figure 12E, F).- Characterized by a strongly developed set of closely spaced radial dentinal canals and strong concentric canals with well developed nodes at the intersections of the two sets. The pattern is most fully developed in the peripheral areas of the posterior and ventral quadrants but is present throughout in mature scales. It is visible around the ventral margins in immature scales. This pattern is characteristic of *Lawnia* Wilson (1953), and is fully illustrated by Cavender (1963: plate VI, figure O, plate XVI, figure A-O).

Type 5: Acrolepid type (Figure 13A, B, C).- Because fully mature scales are not translucent in this type, thin sections are necessary for study of the histology. This type of scale may confidently be assigned to *Acrolepis* on the basis of external morphology (Cavender, 1963, pl. XIV fig. F). The internal characteristics are fairly well shown in the photomicrographs of the thin sections (Figure 13A, B) and less clearly in Figure 13C, a photomicrograph of a partially translucent, immature scale. These scales conform closely to the patterns of *Acrolepis* described by Aldinger (1937) in the pattern of the dentinal canals, the strongly developed Sharpey's fibers, and the robust, ascending canals in the posterior portion of the scales. Structures of immature scales are similar but less fully expressed.

Type 6 (Figure 12G): This scale pattern is unlike that of any scale in the literature known to me. Only three examples have been found in our samples. The scale has the characteristic three tissues of palaeoniscids, bone, dentine and ganoine. What appear to be dentinal canals form a seemingly disordered array of small canals over much of the area of the scale, and are best exhibited in the ventral and posterior quadrants. Because of their small size and extended vertical distribution in the dentine layer, photomicrographs of the key structure have proven difficult and are shown only for the ventro-posterior quadrant. Because of the lack of additional clearly identifiable specimens it has not been possible to make either horizontal or transverse thin sections. This type of scale is not assignable to any family of palaeoniscids for which the scale histology is known.

Summary.- Examinations of the external morphology of *Acrolepis* and histology of other scales from the Arroyo (also Lueders and Clyde) Limestones have produced the following tentative identifications:

Platysomid (probably *Schaefferichthys*)
Elonichthys
Amblypterus
Lawnia
Acrolepis

Acrolepis occurs primarily in the highly argillaceous calcareous deposits of Sites 17 and 23. It is rare in other samples. The other types are widely distributed in the samples without any discernible taxonomic differences between samples. They are especially abundant in deposits with a high level of clastics and, except for the platysomids, relatively less abundant in samples of the purer limestones, particularly those from the area south of Abilene, Texas. In this range of abundance they exhibit an inverse relationship to that of the ossified palaeoniscoid vertebrae which, while fairly widely distributed, form a prominent part of samples of organisms from the crystalline limestones such as those of the Standpipe Limestone at and south of Abilene, Texas.

INVERTEBRATES

Pelecypods are present in all of the samples, and remains of annelid worms and ostracods are present in most (Figure 11D, E). Gastropods (Figure 11C) have been found in six samples and fragments of linguloid brachiopods in four. A poorly preserved specimen of a nautiloid cephalopod was present in a sample from the lower limestone of Site 18.

The pelecypods from Site 13 were identified by Yochelson and Pojeta (see p. 8) as the abundant *?Permophorus* and as *Myalina* or *Septimyalina*. The latter appears to dominate in samples in which moderately complete shells occur. At most sites specimens are fragmentary, damaged by transportation and reworking of the sediments. In the crystalline limestones with low clastic content, fragments of shells are relatively few and scattered.

Annelids (Figure 11D) are of two types, represented by tubes and burrows. Tubes with diameters ranging from less than 1 to about 3 millimeters are from *Spirorbis*-like serpulid worms. They range from partially coiled tubes to those that are complexly contorted. Small masses of burrows are preserved in globular encasements, which range from less than 0.5 to about 1.5 millimeters in diameter and are irregularly shaped.

Ostracods (Figure 11E) are all of a single type and probably belong to the genus *Bairdia*. All are diminutive for the genus. The gastropods (Figure 11C) are preserved largely as internal casts and do not show sufficient detail for generic assessment. They are all very small and most are low spired. Two high spired forms have been found in samples from Site 24.

The full array of invertebrates, including pelecypods and linguloid brachiopods, consists of organisms to be expected in the brackish waters of estuaries and in shallow marine waters. The only exception is the nautiloid, which presumably floated to the site of deposition. Some accumulations, such as those at Sites 2 and 13, as evaluated by Yochelson and Pojeta (see p. 8), were formed under moderately dynamic circumstances whereas others, such as those from the Standpipe Limestone, which are crystalline and low in percentage of clastics, presumably were deposited under low energy circumstances. None show any evidence of having been accumulated in the marine circumstances characteristic of more typical Permo-Carboniferous Limestones.

DISCUSSION AND SUMMARY

At the beginning of this paper two primary questions were posed, which were developed during the course of study:

1. To what extent are the vertebrates known from the classic area also present in the southern area?

2. What are the nature and extent of changes (if any) in the vertebrate fauna as one nears the sea margin away from the classic area?

In this discussion I will attempt to answer these questions as far as possible and to address subsidiary questions that the work has posed.

In all of the studies, as for all analyses of fossil organisms and environments, interpretations depend ultimately on the reliability of the samples. The Arroyo beds of the classic area have been repeatedly collected over a period of 100 years, and during the later part of that time have been subjected to systematic sampling. Comparisons of samples from many sites at approximately the same stratigraphic levels indicate that sample content varies taxonomically with the type of subenvironment. Well collected samples from each subenvironment show a strong consistency in taxa present and in the relative numbers of specimens in the various taxa. There is, thus, a basis for confidence that the part of the biota that was preserved has been adequately sampled.

The first question can be answered succinctly on the basis of extensive field work. Few productive nonmarine sites that contain vertebrate remains are currently exposed in the Arroyo beds south of the Salt Fork of the Brazos River. Additional exposures resulting from subsequent erosion are unlikely to materially alter this conclusion. Five non-marine sites have been found, all of which lie in the upper part of the Arroyo Formation.

The second question is much more complex, involving the geographic and stratigraphic distribution of tetrapods in the classic area, the environments of deposition of the five nonmarine tetrapod sites in the southern area, the stratigraphic relationships of the two areas, and the incorporation of information on the tetrapods of the marine limestones. The fish and invertebrate content of the limestones makes further contributions to a broader understanding of the Arroyo Formation.

During the time of deposition of the terrestrial Arroyo, the sea lay to the southwest of the land area. The strike of the Arroyo beds (Figure 2) runs slightly east of north, with the eastern component becoming more pronounced in the northern portion. The dip averages about 8 meters to the kilometer. As a result of the position of the sea and the strike and gentle dip of the beds, the transgressions of the sea are recorded first in the southern part of the area and then successively to the north. Thus this north-south orientation can be used in assessing the marine-nonmarine relationships, with the slight time lag in deposition of the individual beds considered insufficient to be a substantial factor in the faunal analyses.

The following general scenario applies to events in the classic area. After deposition of the Lueders Limestone, about the first 1.5 meters of the basal Arroyo beds consist of mixed marine-nonmarine deposits. Above this level, deposition was strictly nonmarine, including sedimentation in standing water, running water, and flood plain subenvironments (Olson, 1952a). In the classic area this pattern persisted, with irregular diminution in areas of standing water, to the upper part of the Vale Formation. Thereafter, evaporite deposits became prevalent, marking the onset of deposition of the Choza Formation (Olson, 1958). In the southern area the Bullwagon dolomite marked the resumption of marine conditions at the end of the Vale.

Within the classic area the vertebrates reveal no determinable differences from south to north at any given stratigraphic horizon, when samples from comparable subenvironments are compared. Temporally, as revealed through 130 meters of Arroyo sediments, changes in samples of the fauna do occur, as outlined by Olson and Mead (1982). Two reptiles, *Labidosaurus* and *Edaphosaurus*, have not been found in the upper part of the Arroyo. *Eryops* and *Seymouria* are sharply reduced in frequency. Each of these genera is most common in pond and pond-margin environments. Dissorophoids, which are irregular in their occurrences and were predominantly dry-land inhabitants, are reduced in number. *Diplocaulus* and *Dimetrodon* dominate numerically. *Dimetrodon*, as top predator of the system, has been shown to be highly adaptable to various circumstances. *Diplocaulus*, as discussed by Olson (1952b, 1958), was undergoing an environmental transition in which speciation took place. Thus the upper part of the Arroyo seems to have been marked by increasingly restrictive environments reflected both in the vertebrate faunas and sediments, with channel and flood plain deposition dominant and standing water deposition nearly absent.

All five of the terrestrial sites in the area south of the Salt Fork of the Brazos River lie in the upper part of the Arroyo. The fauna, primarily from Site E, compares favorably with that from the upper part of the Arroyo of the classic area. *Diplocaulus* and *Dimetrodon* dominate numerically, *Edaphosaurus* and *Seymouria* have not been found, and *Eryops* and *Diadectes* are known only from scraps. Within the limits of sampling, the faunas show no evidence of major changes as the sea margin is approached.

Although remains of tetrapods are consistently fragmentary and represent very small individuals of their taxa, all, with the possible exception of microsaurs, are from genera common in the terrestrial Arroyo faunas. Furthermore, most are from genera characteristically associated with river deposits. In view of their small size and sporadic occurrences throughout the Permo-Carboniferous, the absence of microsaurs from the terrestrial sites probably has little significance. As a group, they appear to have ranged over a wide variety of environments, in part due to their widely different morphologies. Some clearly were riparian.

The absence of the common Arroyo reptile *Captorhinus*, although possibly due to sampling, may have more significance. This genus first appears in the Arroyo beds, and is abundantly present in Arroyo equivalents at Grandfield and Ft. Sill, Oklahoma. It appears to have thrived under the developing dry-land terrestrial environments during the Arroyo and to have persisted into the Vale, being found as far south as the southern part of Taylor County, Texas (Olson and Mead, 1982). Its absence from both the terrestrial and marine deposits of the southern Arroyo likely indicates its failure to penetrate the marginal stream environments in which the terrestrial vertebrates lived.

Studies of fish were not an important part of the initial studies. Only *Orthacanthus*, *Xenacanthus*, and *Gnathorhiza* are well known from the classic area. However, the limestone samples yielded abundant fish remains, which have some bearing on general relationships of the classic and southern areas and upon the distributions of various taxa of fish.

Orthacanthus platypternus occurs mostly in stream deposits, but in the Arroyo beds it also is found in deposits formed in standing water. It is present in terrestrial deposits and several limestone samples in the southern area, including both those with tetrapods and those that have produced only fish and invertebrates. The latter occurrences are in moderately pure, crystalline limestones which have been interpreted to have formed in strictly marine areas of deposition. From this it would appear that this genus and species may have been euryhalic. *Xenacanthus*, a fairly common constituent of the nonmarine Arroyo, has not been found in the Arroyo Limestones, suggesting that at this time it may have been primarily a fresh water inhabitant. It does, however, occur in the Lueders Limestone in the classic area (Berman 1970).

Palaeoniscoid fish are abundant in the marine limestones, represented by trunk, skull, and jaw parts, teeth, and scales. Although such remains are abundant, the number of taxa is small compared to the extensive array observed during the adaptive radiation of the Carboniferous. Of the several tentatively identified genera, only *Acrolepis* appears to have lived solely in fresh or possibly brackish waters, occurring as it does only in fairly coarse, partly conglomeratic sediments with large amounts of clastics relative to the calcareous content. The other genera occur in all types of sediments and appear to have been euryhalic, inhabiting both fresh and salt water. The ossified vertebrae (Figure 9H) occur predominantly in limestones with small amounts of clastic materials which may well have been strictly marine. On the basis of the limited evidence from the terrestrial beds of the Arroyo and the more extensive data from the underlying Wichita beds, the palaeoniscids from the marine Arroyo Limestones appear to be representative of actinopterygian faunas of the terrestrial and near shore environments of the Lower Permian as a whole.

Gnathorhiza is known from only two specimens, both from Site 13, where it is associated with terrestrial genera and various fish. This association, together with its absence in all other samples of Arroyo Limestones, suggests that the genus was confined to fresh waters in the areas of Arroyo deposition. However, *Gnathorhiza* does occur in the underlying Lueders Limestone (Berman, 1970), and in the Speiser Shale in Kansas (Schultze, 1985).

Studies of the histology of palaeoniscoid scales of the Arroyo indicates that analyses of thin sections and transparencies of scales can produce reasonably profitable taxonomic results if applied over a fairly local area and limited stratigraphic section.

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