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## FAUNA OF THE UPPER VALE AND CHOZA: 6

### DIPLOCAULUS

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#### INTRODUCTION

A recent publication (Olson, 1951) contains an analysis of the genus *Diplocaulus* from the Arroyo Formation of the Permian Clear Fork group. In an earlier report, a preliminary account of the fauna of the Vale (Olson, 1948), it was stated that the study of *Diplocaulus* from the Vale would be deferred until the data on the Arroyo sample had been fully studied. Once that study had been completed, work on the Vale representatives of this genus was carried out with the results reported in the present paper. The quantitative data for the Arroyo sample, reported in full in the cited analysis, are included in this paper only in so far as they are essential to the comparative tables. Conclusions concerning the Arroyo specimens that are important in the present study may be summarized briefly as follows: There are two species of *Diplocaulus* in the Arroyo, *D. magnicornis* Cope and *D. brevirostris* Olson. *D. magnicornis*, by far the most abundant, was predominantly a pond dweller, whereas *D. brevirostris* inhabited streams. The two species may be differentiated by the following features:

1. The ratio of skull length to orbito-snout length.
2. The ratio of skull length to premaxillary length.
3. The nature of the posterior curvature of the skull.
4. The ratio of skull length to horn length.
5. The nature of the surface of the parietal bone.

The relationships of interorbital width and frontal, parietal and interparietal length to skull length were found to be no more variable for the genus than for *D. magnicornis* alone. The measurements were expressed both as regressions on skull length and as ratios with respect to skull length. It was, furthermore, shown that certain

other genera of Paleozoic amphibians, *Trimerorhachis*, *Trematops*, *Batrachiderpeton* and *Euryodus*, differed significantly from *Diplocaulus* in two or more of these features.

Study of patterns of relative growth in *D. magnicornis* indicated that mature skull shape was attained in this species when midline skull length had reached about 100 mm. and that the changes that resulted in the mature shape were initiated between the 80 and 100 mm. stages of skull length in most instances. There appeared, however, to be a rather wide range in the stage of initiation of the change, for in a few specimens the immature shape persisted well beyond the 100 mm. stage. With the development of maturity, lateral growth of the horn tips underwent rapid and continuing acceleration. These conclusions provide a basis for study of the Vale specimens of *Diplocaulus*.

Stratigraphic evidence suggests that there was not a great time interval between deposition of the Arroyo beds from which *Diplocaulus* has been obtained and the producing beds of late Vale age. The thickness of intervening beds, although not known, cannot be much in excess of 500 feet, and there is no evidence of a pronounced hiatus. Sedimentation probably was moderately rapid, as attested by the nature of the sediments and the inferred mechanics of deposition. It would not be expected that extensive changes would occur in a population of moderate size and considerable homogeneity, evolving in place with only moderate environmental change, but rather that changes would be slight, difficult to recognize, and perhaps not demonstrably significant, particularly if samples were small. Rarely has it been possible to study the pattern of such evolution among amphibians, since samples are usually very small and stratigraphic relationships uncertain. Even in the case of *Diplocaulus*, the aspects that can be evaluated are limited by the smallness of samples; certain items of considerable interest are, however, revealed. Some of the conclusions and interpretations in the closing pages of this paper are admittedly speculative, but I feel that their inclusion is justified by their relationship to progress in the study of the Vale fauna.

#### THE VALE SAMPLE

Thirteen specimens of *Diplocaulus* have been recovered from the Vale.<sup>1</sup> Twelve are partial skulls and one is a well-preserved vertebra.

<sup>1</sup> Since the preparation of this paper several more specimens have been found. They confirm the results of the present study.

Of the twelve partial skulls, nine display one or more characters that can be used for comparison with the Arroyo sample. Brief descriptions of the skulls and other pertinent data are given in Table 1.

TABLE 1.—COMPOSITION OF THE VALE SAMPLE OF *DIPLOCAULUS*

Specimen number	Locality	Description
C.N.H.M.-U.R. 17 . . . .	KH	Large skull with anterior part missing. Preserved part in excellent condition.
C.N.H.M.-U.C. 1666 . . .	KE	Well-preserved skull, somewhat shattered. Extremities of horns absent.
C.N.H.M.-U.C. 1664 . . .	KD	Partial skull with much of left horn missing. Right half well preserved.
C.N.H.M.-U.C. 1665 . . .	KA	Excellent skull, somewhat flattened, with extremities of horns missing. Right horn preserved by impression in clay in field and sketched for comparative purposes.
C.N.H.M.-U.R. 18 . . . .	KH	Part of mid-section of large skull. Horns and posterior part of dorsal platform absent. Posterior limit of central portion of skull preserved as impression in conglomerate.
C.N.H.M.-U.R. 19 . . . .	KD	Excellent skull with snout somewhat damaged and part of anterior margin of left horn missing.
C.N.H.M.-U.R. 20 . . . .	KC	Fragmentary skull. Much of left horn fairly well preserved.
C.N.H.M.-U.R. 21 . . . .	KD	Impression of much of right horn in conglomerate.
C.N.H.M.-U.R. 22 . . . .	KH	Impression of much of right horn in conglomerate.

Measurements used in the study are listed in Table 2. About fifty specimens identified as *Diplocaulus* have been encountered in three years of collecting. Most of these were left in the field because of their extremely fragmentary nature. All were found in red conglomerates and all but a few occurred in coarse conglomerates that are of stream channel origin. Of the sample of nine, seven were found in such conglomerates. C.N.H.M.-U.C. 1666 and -U.R. 20 were preserved in finer, sandy conglomerates that suggest less turbulent conditions but, nevertheless, conditions that must have involved running water. Essentially all other types of vertebrates known from the Vale have been noted, at least as scraps, in the conglomerates, and associations under these circumstances have little real meaning with respect to ecological relationships. It is important, however, that no traces of *Diplocaulus* have been found in fine-grained, vertebrate-producing clays.

#### TAXONOMIC RELATIONSHIPS

It is necessary to do no more than see the Vale specimens to know that they must be referred to the distinctive genus *Diplocaulus*.

TABLE 2.—MEASUREMENTS OF SKULLS OF VALE *DIPLOCAULUS*  
(In Millimeters)

Specimen number	Skel	Ipl	Ipw	Pal	Frl	Pmaxl	Iow	O-Sl	Ow	W4	W5	L5	Horn end
C.N.H.M.													
U.C. 1664	86.5	17.5	53.0	20.6	38.2	6.2	13.0	15.5	14.7	144	240	158	crook
U.R. 19	94.5	21.5	54.0	21.5	...	...	16.5	19.0	15.0	164	265	158	crook
U.C. 1666	105.0	21.2	58.0	26.2	40.0	...	19.3	23.0	17.0	174	...	...	...
U.C. 1665	107.5	20.3	58.0	23.6	44.2	9.3	16.4	28.7	18.4	160	...	...	crook
U.R. 18	125.0	...	...	...	50.0	11.5	24.8	29.0	15.4	...	...	...	...
U.R. 17	...	34.0	70.0	...	...	...	...	...	...	194	314	...	crook
U.R. 20	...	...	...	...	...	...	...	...	...	...	...	...	crook sl.
U.R. 21	...	...	...	...	...	...	...	...	...	...	...	...	crook
U.R. 22	...	...	...	...	...	...	...	...	...	...	...	...	crook

Abbreviations: *Skel*, dorsal midline skull length; *Ipl*, length of suture between parietals; *Ipw*, greatest width of interparietal measured normal to midline of skull; *Pal*, length of suture between parietals; *Frl*, length of frontal on midline of skull; *Pmaxl*, length of suture between premaxillaries; *O-Sl*, orbito-snout length measured on midline of skull from level of anterior margin of orbits to tip of snout; *Ow*, minimum orbital width measured normal to skull length; *W4*, skull width at level of posterior termination of suture between interparietals; *W5*, skull width between horn tips; *L5*, length of skull from tip of snout to extremity of horn on line parallel to midline of skull; *Iow*, interorbital width. *Crook sl.*, slight development of character designated as "crook" (see p. 152).



Likewise their close resemblance to *D. magnicornis* and their differences from *D. brevirostris* in relative snout length, posterior curvature, length of horn, and nature of the parietal are evident. To test these conclusions, however, quantitative studies of the ratios of the skull length to various skull dimensions were made and their results coordinated in Table 3;  $d/\sigma d$  was computed from the following formula in which the Vale and Arroyo samples are 1 and 2 respectively:

$$d/\sigma d = \frac{M_1 - M_2}{\sqrt{\frac{\sigma_1^2}{N_1} + \frac{\sigma_2^2}{N_2}}}$$

$\sigma_1$  and  $\sigma_2$  were determined from the expression  $\sigma = \sqrt{\frac{\sum(f d^2)}{N-1}}$ .

The first four comparisons involve characters which did not differ significantly in the two species of Arroyo *Diplocaulus* and two or more of which, in various cases, gave a basis for differentiating *Diplocaulus* from other genera of amphibians. The last two were

TABLE 3.—COMPARISONS OF MEANS OF RATIOS OF  
*D. MAGNICORNIS* AND *DIPLOCAULUS* FROM THE VALE

Ratio	$N_1$	$N_2$	$M_1$	$M_2$	$\sigma_1$	$\sigma_2$	$d/\sigma d$
<i>SkI: Iow</i>	5	34	5.88±0.32	6.74±0.159	0.712±0.23	0.927±0.112	2.4
<i>SkI: Frl</i>	4	29	2.45±0.08	2.44±0.036	0.168±0.06	0.197±0.26	0.0
<i>SkI: Pal</i>	4	32	4.48±0.19	3.91±0.077	0.381±0.13	0.437±0.055	1.8
<i>SkI: Ipl</i>	4	31	4.89±0.19	4.44±0.087	0.369±0.13	0.485±0.062	1.3
<i>SkI: O-Sl</i>	5	21	4.64±0.31	3.92±0.260	0.689±0.22	1.172±0.180	0.9
<i>SkI: Pmax</i>	3	19	12.10±0.96	11.20±0.450	1.670±0.56	1.950±0.310	1.0

See Table 2 for explanation of abbreviations.

shown to be different in the two species of Arroyo *Diplocaulus*. In no cases in Table 3 is there significant difference between the two samples. So far as these characters are concerned, the sample of *Diplocaulus* from the Vale modifies the generic parameters but slightly and could have been drawn from the same population as the sample of *D. magnicornis* from the Arroyo.

The characters used in differentiation of the species of Arroyo *Diplocaulus* but not listed in the table—posterior curvature of the skull, horn length, and the nature of the parietal—cannot be treated as concisely, either because of sample size or because the character is less readily subject to quantitative treatment. In the case of posterior curvature and horn length, it is apparent that the specimens from the Vale are much closer to *D. magnicornis* than to *brevirostris*. The parietal of the Vale *Diplocaulus* lacks the dorsal convexity characteristic of *D. brevirostris*. These facts, added

to the fact that the means of ratios of skull length to orbito-snout length and premaxillary length of the Vale *Diplocaulus* fall very close to the sample means of *D. magnicornis*, which is significantly different from that of *D. brevisrostris*, make it apparent that the Vale sample cannot be referred to *D. brevisrostris*.

The evidence advanced to this point, then, excludes the members of the Vale sample from *D. brevisrostris* but does not exclude them from *D. magnicornis*. It does not, of course, demonstrate that they do pertain to the latter species. The skulls of *D. magnicornis* and *Diplocaulus* from the Vale have been compared in detail in an effort to find other possible differences. Non-quantitative investigation suggests that three characters might be useful for differentiation:

1. The strong backward flexure of the horn tip. This inflection is evident in most of the Vale specimens and in only a few from the Arroyo.
2. The stage of attainment of the mature shape of the skull. It appears that full maturity might have been attained at a smaller stage in the Vale specimens than in those from the Arroyo.
3. The thickness of bone of the skull roof. The bone seems to be thinner in the specimens from the Vale.

Each of the differences is relatively slight and all other features that have been observed and tested have proven to lack significant differences. It seems quite certain that, whether the two samples belong to the same species or not, the Vale population was derived directly from that of *D. magnicornis* from the Arroyo.

It is my opinion that the three features listed above and the fact that the two samples come from different formations would be considered an adequate basis for specific differentiation were the usual methods of separation of Late Paleozoic tetrapods applied. Such a conclusion, so reached, whether correct or incorrect, is relatively sterile and gives little basis for further analysis since the processes operative in specific recognition can do no more than vaguely suggest the dynamics of origin and change of species. Each of the three points can, however, be treated more critically, provided sufficient material is available. Such treatment not only gives a test of validity but suggests, as well, something concerning the processes by which the Arroyo population may have given rise to that of the Vale and the amount of change that has taken place.

*Horn inflection, the character of "crook."*—It has been observed that the extremities of the horns in various specimens of *Diplocaulus*

are inflected posteriorly, making a more or less well-defined angle with the more medial curve of the posterior margin of the horn. For the sake of easy reference in the text and tables, this character has been called "crook." Among the specimens of *D. magnicornis*, the character is absent in some and appears in various degrees of

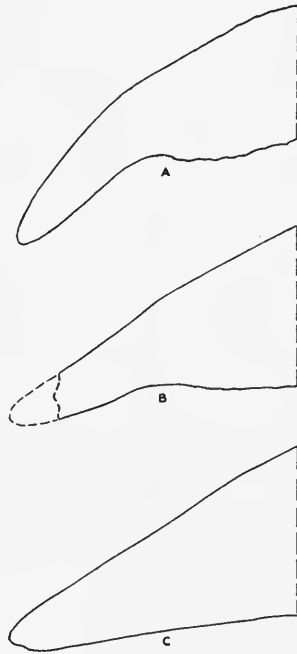


FIG. 57. The forms of horn termination in *D. magnicornis* of the Arroyo: A. C.N.H.M.-U.C. 1015, full development of crook. B. C.N.H.M.-U.C. 564, partial development of crook. C. C.N.H.M.-U.C. 1317, absence of crook.

intensity in others. The nature of the material precludes the possibility of a strictly quantitative evaluation of the degree of development of "crook" in individuals, although this would be possible by use of angular measurements were the specimens better preserved. It is possible, however, to recognize three general categories: one in which the character is absent, a second in which development is slight to moderate, and a third in which it is highly developed (fig. 57). In the third type there is normally a constriction of the horn at the level of the angle. The dominance of this type in the sample from the Vale is shown in figure 58.

The percentage relationships of the three categories based on a sample of twenty-five specimens from the Arroyo and one of seven from the Vale are listed in Table 4. The percentage which has attained full expression of the character is the most important for purposes of determining the probability that the samples could

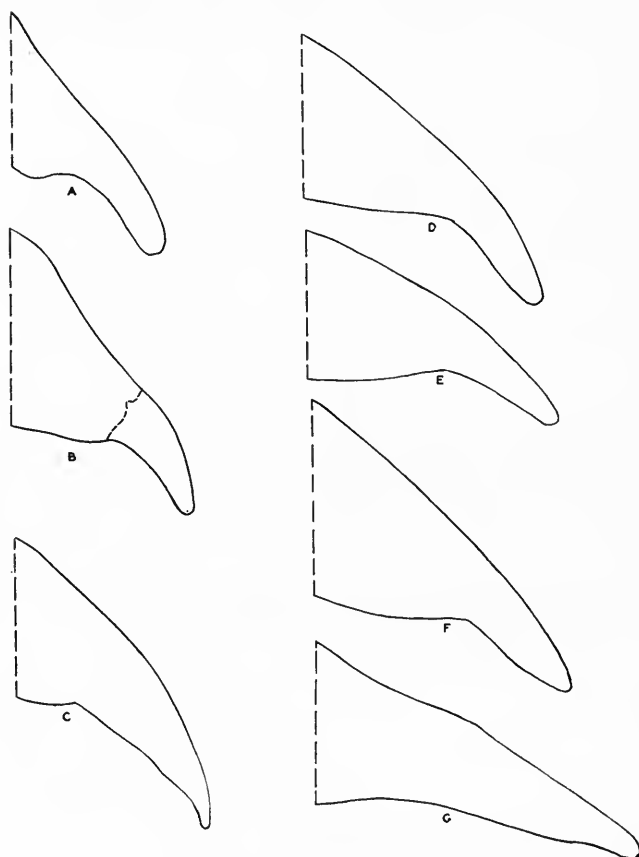


FIG. 58. The forms of horn termination in *Diplocaulus* from the Vale. A-F. C.N.H.M.-U.C. 1664, U.C. 1665, U.R. 19, U.R. 17, U.R. 21, U.R. 22, showing full expression of crook. G. C.N.H.M.-U.R. 20, showing partial expression of crook.

have been drawn from the same population, since full expression is characteristic of the sample from the Vale. Analysis of the sample from the Arroyo on this basis shows that for a sample of seven drawn from the Arroyo, based on the estimate from percentages in

TABLE 4.—DISTRIBUTION OF THE CHARACTER "CROOK"

Degree of expression	<i>D. magnicornis</i> Arroyo N=25		<i>Diplocaulus</i> of Vale N=7	
	Number	Per cent	Number	Per cent
Full.....	4	16	6	86
Partial.....	7	28	1	14
None.....	14	56	0	0

the sample of twenty-five, the probability limits of the occurrence of "crook" are 0-4. The probabilities that the Vale sample could have been drawn from the same population as the Arroyo sample are hence slight.

*Stage of maturity.*—Specimen C.N.H.M.-U.C. 1664 from the Vale has a midline skull length of 86.5 mm. and has attained a fully mature skull pattern (fig. 59). It was noted earlier that full maturity was, on the average, attained at about the 100 mm. stage in Arroyo specimens. Actually the smallest stage at which full maturity occurs in any known Arroyo specimens is 101 mm. In spite of the fact that there is considerable variability among the Arroyo specimens in the stage of development of maturity, the rather marked difference recorded between the minimum stages of the Vale and Arroyo specimens, a difference of 14.5 mm. in skull length, would seem to suggest that maturity was attained at a smaller stage in the former. A scatter diagram for  $W5^1$  against skull length, a measurement important in the development of maturity, including the distributions of both the Arroyo and Vale samples, however, shows the error of making any such assumption on the basis of the

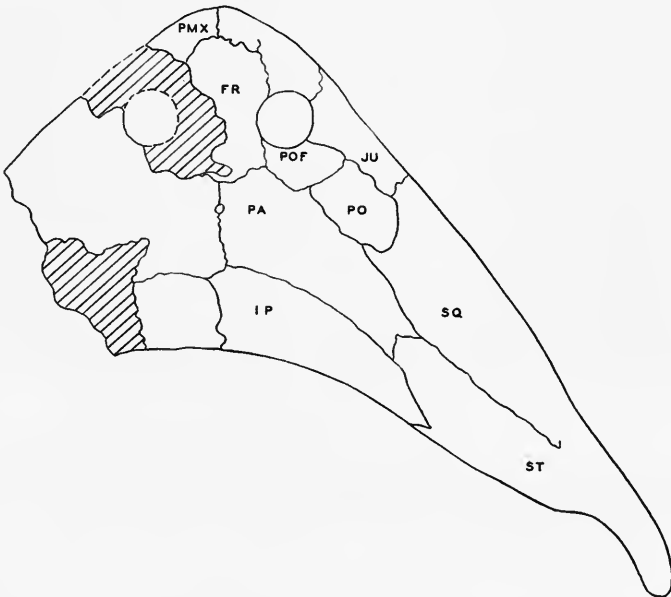


FIG. 59. C.N.H.M.-U.C. 1664, showing full development of mature skull shape and pattern of dermal bones at 86.5 mm. stage of skull development;  $\times \frac{1}{2}$ .

<sup>1</sup> For this and other abbreviations see Table 2.

few specimens from the Vale which show  $W5$  (fig. 60). A scatter diagram of  $W4$  (fig. 61) on skull length indicates that no difference exists in this character. It is not, of course, demonstrated that the regression patterns of  $W5$  on skull length for *D. magnicornis* and *Diplocaulus* from the Vale are the same, but it is evident that the Vale sample is not sufficiently large to give a basis for quantitative

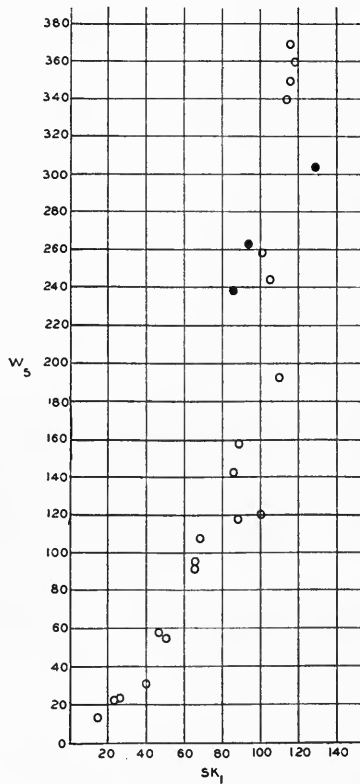


FIG. 60. Scatter diagram of skull width at horn tips ( $W5$ ) against midline skull length ( $SkL$ ) in *D. magnicornis* from the Arroyo (open circles) and *Diplocaulus* from the Vale (filled circles).

conclusions, in view of the marked similarities of the distributions. The best approach to this problem is by means of an analysis of variance of the slope and position of the regression lines of the two samples, assuming that it could not be demonstrated that the two curves were of different families, but data for the Vale sample are insufficient to make this procedure meaningful. It is possible that additional collecting may provide an adequate sample, but at

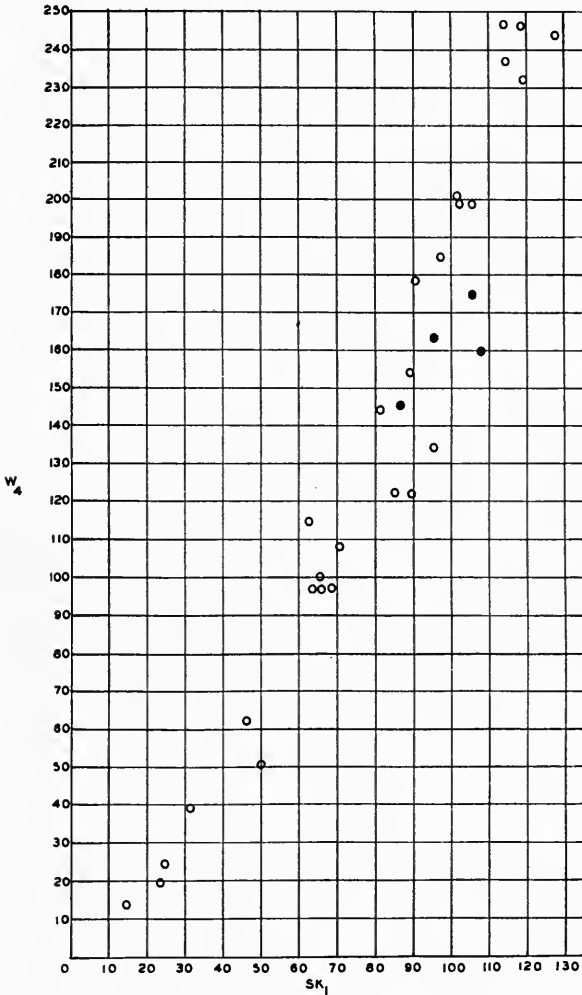


FIG. 61. Scatter diagram of skull width at level of posterior termination of suture between interparietals ( $W_4$ ) against midline skull length ( $SK_1$ ) of *D. magnicornis* of the Arroyo (open circles) and *Diplocaulus* of the Vale (filled circles).

present there is no real basis for considering the two samples different in the stage of development of maturity.

*The thickness of the skull roof.*—Testing the concept that the bones of the skull roof of the Vale *Diplocaulus* are thinner than those of *D. magnicornis* from the Arroyo poses certain technical problems. Roofing bones vary considerably in thickness over the area which they occupy and are especially subject to variation at their margins.

In addition, the dorsal surface of the roofing bones is deeply pitted in *Diplocaulus* so that a measurement taken at the base of a pit and another at the crest of a dividing ridge may be very different. To overcome these difficulties measurements were made on one of the large bones of the dorsal platform, the parietal, by sampling its thickness at four places (fig. 62) and by making all measurements from the crests between the pits. The measurements were made by drilling four 1/16th-inch holes through each parietal into the underlying matrix. These holes were etched with acid and dried; then liquid latex was injected. When the latex had hardened, it was removed, and the thickness of bone, which was recorded upon it, was measured. Nearly identical results were obtained on the same specimens for several trials, indicating that the measurements are reliable. These measurements sampled parietal thickness in four places and gave it a usable mean value. The measurements and their means, which were used in all studies, are shown in Table 5.

TABLE 5.—MEASUREMENTS OF THICKNESS OF  
THE PARIETAL BONE  
(In Millimeters)

Specimen number	Sk1	ARROYO SAMPLE				Mean
		1	2	3	4	
C.N.H.M.-U.C. 1658	68	1.1	1.4	1.9	2.0	1.3
C.N.H.M.-U.C. 1650	89	1.6	1.5	1.6	1.8	1.6
C.N.H.M.-U.C. 1031	97	1.6	1.6	...	2.4	1.8
C.N.H.M.-U.C. 1015	101	1.7	3.0	4.0	1.4	2.5
A.M.N.H. 4494	105	2.7	2.6	2.4	2.1	2.4
A.M.N.H. 4473	105	2.3	2.2	2.7	2.7	2.5
C.N.H.M.-U.C. 564	114	3.0	2.8	2.2	3.5	2.9
C.N.H.M.-U.C. 636	119	3.0	2.7	2.0	3.5	2.8
C.N.H.M.-U.C. 1654	120	2.6	3.0	3.3	3.1	3.0
A.M.N.H. 4501	130	3.2	6.2	....	4.9	4.7

Specimen number	Sk1	VALE SAMPLE				Mean
		1	2	3	4	
C.N.H.M.-U.C. 1664	86.5	1.5	1.6	1.5	1.9	1.6
C.N.H.M.-U.R. 19	94.5	2.0	2.2	1.2	1.5	1.7
C.N.H.M.-U.C. 1666	105.0	1.5	2.0	1.2	2.6	1.8
C.N.H.M.-U.C. 1665	107.5	1.9	1.6	2.6	1.5	1.9
C.N.H.M.-U.R. 18	125.0	1.2	1.4	3.5	3.0	2.3

Inspection of the mean values in the table and of a scatter diagram of the regressions of the two sets of mean values on skull length (fig. 63) suggests that a real difference in bone thickness, particularly in the rate of change of bone thickness with increase in skull length, might exist. It is, however, exceedingly important that sample size, which is small in both instances, should not be neglected in this estimate and that all safeguards necessary for working with



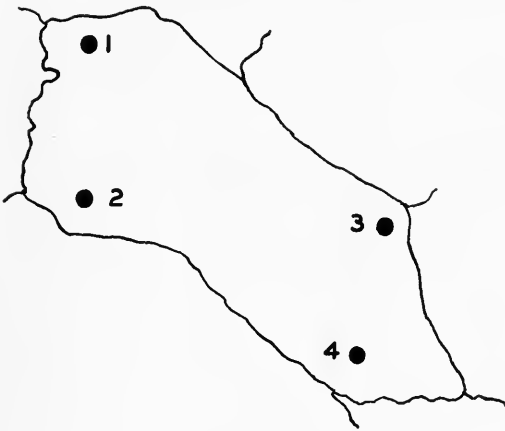
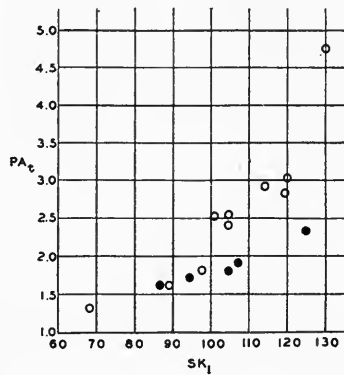


FIG. 62. Diagram of parietal bone showing position of four measurements used for sampling thickness of bone.

FIG. 63. Scatter diagram of mean thickness of parietal (*Pat*) against mid-line skull length (*Sk<sub>l</sub>*) in *D. magnicornis* of the Arroyo (open circles) and *Diplocaulus* of the Vale (filled circles).



small samples be observed. The danger signal is raised by the large standard errors recorded in Table 6. Nevertheless, the inspection of values seems to offer some support to the original concept that the two samples might differ with respect to bone thickness.

This concept was studied and tested from a number of points of view by the following procedures:

1. Both samples were studied as rectilinear regressions ( $Y = a + bX$ ) and curvilinear regressions ( $Y = bX^k$ ).
2. Tests for non-linearity were made for the Arroyo sample and for a combined sample. This test consists of a special case of analysis of variance following Tippet (1945, pp. 192-194).
3. Tests for differences in slope, involving *byx* of the equation  $Y = a + bX$  and *k* of the equation  $Y = bX^k$ , for rectilinear and

curvilinear regressions respectively, following Simpson and Roe (1939, p. 278) and Olson (1951, p. 119).

4. Tests were made for difference of position of lines in rectilinear regression. The test consists of a special case of analysis of variance, following Tippet (1945, pp. 186-188; also see Olson, 1951, pp. 119-123).
5. Tests of the differences of means of the samples were made. This was done by using ratios of skull length to bone thickness. Since both samples are very small and, at best, give somewhat uncertain estimates of parameters of the populations they represent, a somewhat different approach to this problem was used. The two samples were combined and  $\sigma$  for the universe that they represent was determined (using  $N-1$ ). This value of  $\sigma$  was then entered in the expression

$$t = \frac{M_1 - M_2}{\sqrt{\frac{\sigma^2}{N_1} + \frac{\sigma^2}{N_2}}}$$

to test the hypothesis that the two means could have been drawn from a universe with the same value of  $\sigma$ .

The parameters involved in these various studies and tests, based on the raw data (the means, of Table 5), are given in Table 6. The results are of special interest when compared to the inferences derived from the raw data and are, for that reason, briefly summarized below:

1. The values of  $r$  for the Arroyo and Vale samples treated as rectilinear regressions (Table 6, No. 1) are both significant in spite of the small size of the samples. The value of  $k$  in the curvilinear regression for the Arroyo sample (Table 6, No. 2) is rather high and suggests that the allometric pattern might best fit the data (the value of  $\rho$  is  $\pm 0.84$ ). These two types of regression were studied because of their possible bearing on other tests.

2. The test for non-linearity of the Arroyo sample—one for the Vale sample can be of little value because of the smallness of the sample—failed to show significant departure from linearity. This is based on the value of  $F$  (variance ratio). In this instance  $F=1.36$  ( $N_1=3$ ,  $N_2=6$ ) whereas  $F$  at the 0.05 level of significance is 9.78. Test of the combined samples for non-linearity likewise failed to indicate departure from linearity:  $F=1.89$  ( $N_1=6$ ,  $N_2=7$ ) while the 0.05 level of significance is 3.87. It cannot, then, be demonstrated that there is departure from linearity in either instance.

TABLE 6.—PARAMETERS IN STUDIES AND TESTS ON RELATIONSHIPS OF BONE THICKNESS TO SKULL LENGTH IN ARROYO AND VALE *DIPLOCAULUS*

1. SAMPLES TREATED AS RECTILINEAR REGRESSIONS ( $Y = a + bX$ )						
Sample	$N$	$Mx$	$My$	$\sigma_x$	$\sigma_y$	$r$
Arroyo	10	105.0 ± 5.44	2.55 ± 0.30	17.7 ± 3.96	0.975 ± 0.22	+0.88
Vale	5	103.7 ± 6.50	1.86 ± 0.12	14.6 ± 4.59	0.27 ± 0.08	+0.98

2. SAMPLES TREATED AS CURVILINEAR REGRESSIONS ( $Y = bX^k$ )							
Sample	$N$	$M\log x$	$M\log y$	$\log x$	$\log y$	$bYX$	$k$
Arroyo	10	2.01463 ± 0.0257	0.37497 ± 0.0521	0.08175 ± 0.0183	0.16580 ± 0.0371	0.0006	1.79
Vale	5	0.01467 ± 0.0274	0.01416 ± 0.0269	0.06075 ± 0.0191	0.05980 ± 0.0188	0.0011	0.96

3. COMBINED SAMPLES TREATED AS RECTILINEAR REGRESSION ( $Y = a + bX$ )			
$N$	$Mx$	$My$	$r$
15	104.4 ± 4.21	2.3 ± 0.22	+0.79

4. RATIOS ( <i>Skl: Pal</i> ) FOR COMBINED SAMPLES		
$N$	$M$	$\sigma$
15	47.75 ± 2.3	8.96 ± 1.6

3. Tests for difference of slope, in spite of the apparent difference in the scatter diagram (fig. 63), have negative results. If regressions are treated as rectilinear,  $t=1.28$  with a combined sample size of 15. At 0.02 level of significance with 13 degrees of freedom,  $t=1.35$ . If the regressions are treated as allometric,  $t=1.75$ . At the 0.1 level of significance with 13 degrees of freedom,  $t=1.77$ .

4. Since there is no demonstrable difference in slope, it is appropriate to test the position of lines. This was carried out for rectilinear regressions only.  $F=5.3$  ( $N_1=2$ ,  $N_2=11$ ). At the 0.01 level of significance  $F=7.20$ . There is thus no clear evidence of significant difference in position.

5. Comparison of means of ratios represents a somewhat different approach to the same relationships basic to item 4. Following the method outlined in item 5 (p. 160),  $t=2.46$ . At the 0.02 level of significance with 13 degrees of freedom,  $t=2.65$ . Once again there is no significant difference demonstrated.

The results of this rather lengthy series of tests have been included primarily to emphasize the caution that must be exercised in making non-quantitative judgments on the basis of small numbers of specimens. The differences that have been studied are no less than many which have been used in various studies of Permian vertebrates as indications of specific differences. Each test, in this case, however, has indicated that separation on the basis of the relationships studied is not justified by the evidence.

*The development of the Vale Diplocaulus.*—It has been shown in the preceding pages that, with respect to characters that seemed possibly different, the Vale sample can be shown to differ from that of the Arroyo only in the character of "crook." This one feature, however, provides evidence that the two samples could not have been drawn from the same population. The suggestion, then, is that the Vale sample may be considered specifically distinct from *D. magnicornis*. This seems hardly justifiable, however, unless there is a strong probability that it was reproductively isolated from *D. magnicornis* and was not merely a partially isolated segment of a population that, analyzed as a whole, would prove to be not different from *D. magnicornis*. A decision as to whether or not this was true must rest in part on negative evidence in this case and in all similar cases concerned with extinct groups. There are, however, several items that are pertinent to the problem and have a bearing upon the mode of change from the Arroyo *D. magnicornis* (assumed to be ancestral to the Vale population) to *Diplocaulus* of the Vale.

It is known that some members of the population of *D. magnicornis* possessed the character of "crook" fully expressed, that others had it partially developed, and that in a large percentage of the population the character was not expressed. The character was fully developed in a much higher percentage of the Vale population. This could have occurred either through complete isolation or through partial isolation that permitted continuing, although restricted, interbreeding. I have cited evidence (1951) indicating that *D. magnicornis* dwelled primarily in quiet waters, ponds and swamps. Every specimen that has been found in beds of Vale age, a number of them excellently preserved, has come from coarse to fine conglomerates deposited in actively running waters and, in at least a very high percentage of cases, in stream channels. This in itself, although suggestive, may constitute no real proof that they lived in the environment of deposition. It is also true, however, that no trace of *Diplocaulus* has been found in any of several vertebrate-producing clay deposits in the Vale in spite of the fact that vertebrates are abundant and include such genera as *Eryops*, *Trimerorhachis*, *Lysorophus*, *Waggoneria*, *Captorhinus*, *Dimetrodon*, and *Xenacanthus*. These genera, with the exception of *Waggoneria*, are normally associated with *D. magnicornis* in the clays of the Arroyo.

The stream environment in Arroyo times was occupied by *D. brevis*. No trace of this species, which is readily distinguished from *D. magnicornis*, has been encountered in the channels of the Vale. There appear to have been some modifications of environment between the time of deposition of the Arroyo and Upper Vale beds, at least between the environments in the areas from which *Diplocaulus* has been obtained. The frequency of stream channels is higher in the more recent beds, bedding is in general much more even except in the immediate vicinity of the channels, much of the coarse material of the conglomerates was derived from the beds immediately adjacent to the channels, and local concentrations of bone in the clays are rare. The beds of the Vale formation are penetrated by gypsum, derived from beds that once lay over it in all cases in which the evidence concerning the sources is clear. To the west, in only slightly later beds, layers of primary gypsum occur.

Although both the deposits of the Arroyo and those of the Vale appear to have had a deltaic origin, the coarse conglomerates of the Vale, their locally derived pebbles, the infrequent occurrence of pond deposits (and complete absence of swamps), and the fact that gypsum was deposited not long after the vertebrate-bearing beds

had been formed all suggest that there was a trend toward conditions in which there was greater effective dryness. Rainfall may not have been less in total amount but rather more concentrated seasonally. There is evidence of seasonal fluctuation in Arroyo times (Olson, 1951), but this seems to have been accentuated during the Vale.

These facts, inferences and assumptions make possible a not unreasonable reconstruction of the evolution of the Vale *Diplocaulus* from its predecessor in the Arroyo. During the Arroyo the population of *D. magnicornis* was probably moderately large, since specimens have been found in some abundance over a fairly wide area, diversified and somewhat segmented by its pond-dwelling habits. Low in frequency in the population was the type possessing full development of the character "crook." This type tended to approach *D. brevirostris* to a limited degree in horn character and was, perhaps, like *D. brevirostris*, somewhat better adapted to life in running waters than the more characteristic members of the species. It does not appear to have penetrated the stream environment during Arroyo times, perhaps because the environment was occupied by *D. brevirostris*. The frequency of the latter, however, appears to have been low. If for any reason *D. brevirostris* were to have been eliminated from the streams, the individuals of *D. magnicornis* with the character of "crook" would have had the opportunity to invade the stream environment. The fact that *D. brevirostris* has not been found in the Vale beds suggests that this elimination did take place, although there is no evidence of why it occurred. Furthermore, if, as the evidence suggests, climatic trends were tending to reduce the number of habitable ponds and swamps, pressure toward an environmental shift from ponds to streams would continually increase. This would tend to be accentuated still further by increase in the relative number of semi-terrestrial and aquatic predators, among the latter particularly those types that lived in both streams and ponds, including the omnipresent xenacanth sharks. Decimation and eventual extinction of the pond-dwelling *Diplocaulus* could have resulted, leaving as survivors only those parts of the population that had made the shift to stream life.

In early stages of the shift, members of the stream-living group presumably would have been only partially isolated from the pond dwellers and complete isolation would have come only when the pond dwellers were eliminated. The critical question in the evaluation of the taxonomic position of the Vale group hinges upon this matter of complete isolation. We are dealing with specimens col-

lected over a relatively restricted area and it certainly is not unreasonable to assume that in other areas, in which the sequence of climatic events might have been different, the population of *D. magnicornis* might have continued with little modification. The deposits are, however, deltaic and thus probably rather limited in areal extent. Climatic changes normally affect relatively wide areas and thus it would appear probable that the whole of the deltaic area would have been similarly affected. If this is the case, it is logical to assume that the changes described operated throughout the environment of the population and that what has been studied represents a reasonable sample of what was taking place over the whole breeding area of the population. The very high penetrance of the character "crook," contrasted with low penetrance in the Arroyo population, also suggests that isolation was complete.

It would be of great interest to know how much time was involved in this series of events. We only know that sedimentation was moderately rapid and that not much more than 500 feet of beds were deposited. From the geological standpoint, the time must have been short. The nature of the change in the skulls is such that it could have taken place in a very short time.

The reconstruction of the events in the evolution of *D. magnicornis* to *Diplocaulus* of the Vale seems to me to be in keeping with the facts as known. It is certainly possible that additional evidence may require modifications but the direct evidence and inferences suggest that the Vale sample represents a population that was isolated from the type of population encountered in the Arroyo. If this be correct, the Vale population meets the criteria of a species in so far as these may be determined from extinct groups: it is morphologically distinct (in a statistical sense) and reproductively isolated. For these reasons, it should be considered a new species, as follows:

#### ***Diplocaulus recurvatus* sp. nov.**

*Type*.—C.N.H.M.-U.R. 19 (fig. 64). Skull with part of left antero-lateral margin missing. From Knox County, Texas, approximately seven miles north of Vera, locality KD.

*Hypodigm*.—Type plus C.N.H.M.-U.R. 17, U.C. 1664, U.C. 1665, U.C. 1666, U.R. 18, U.R. 20, U.R. 21, U.R. 22.

*Horizon*.—Upper part of Vale Formation, Clear Fork group, Early Permian.

*Diagnosis.*—Terminal ends of horns characteristically strongly recurved with constriction at medio-posterior part of flexure.

*Remarks.*—This species differs from *D. magnicornis*, so far as the observed parts of the skull are concerned, only in the frequency of

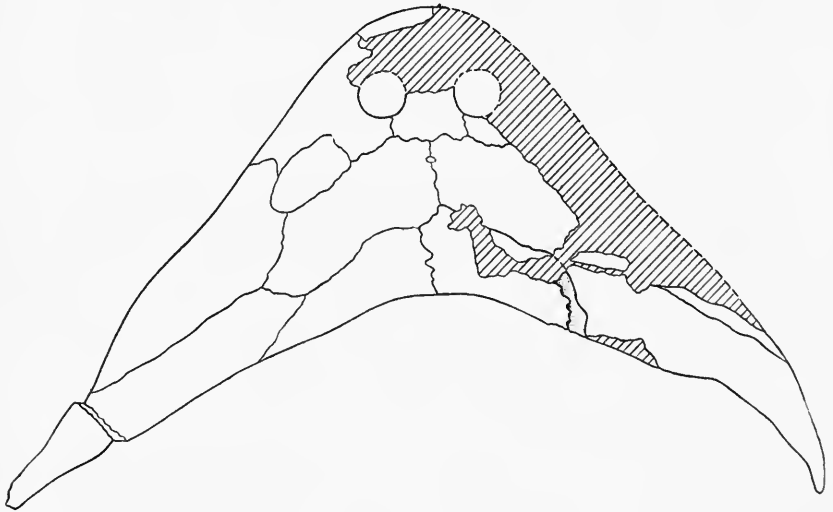


FIG. 64. The type of *D. recurvatus* from the Vale, C.N.H.M.-U.R. 19;  $\times 2/5$ .

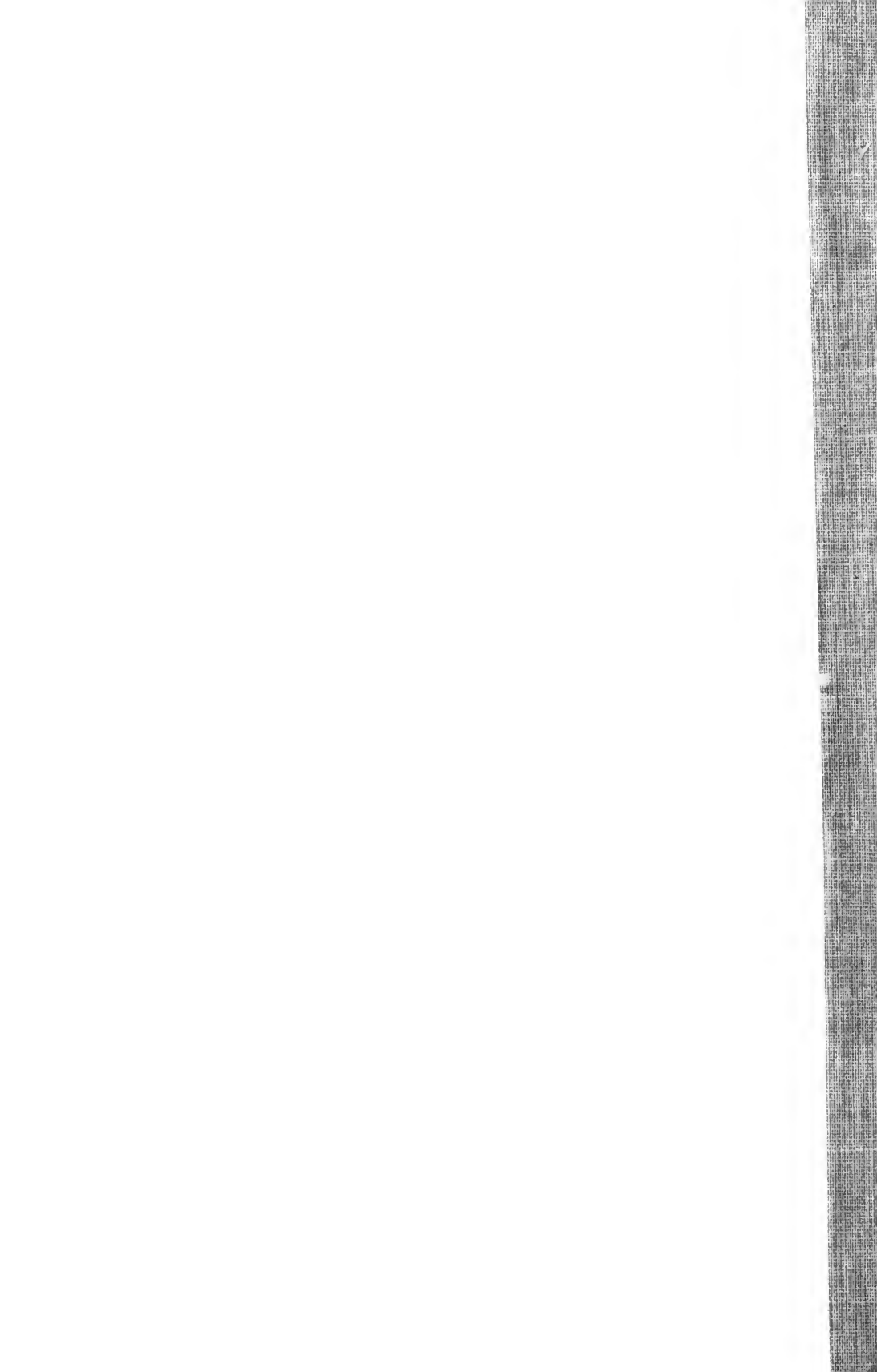
occurrence of the recurved horn. It differs from *D. brevirostris* in the relative length of the snout, in the lack of dorsal convexity of the parietal bone, in the relative width of the skull at the level of the horn tips (in adults) and in the pattern of posterior curvature of the skull (in adults).

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