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DIPLOCAULUS

A STUDY IN GROWTH AND VARIATION

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INTRODUCTION

Recent years have seen a marked increase in efforts to treat paleontological materials quantitatively. Impetus to this trend was provided by the publication of *Quantitative Zoology*, by Simpson and Roe (1939). Although many paleontologists have been slow to follow the trend, it has become clear that a quantitative approach, if properly handled, can yield results of great significance in at least some phases of both invertebrate and vertebrate paleontology. I have been inclined to the opinion that such studies could have but limited application in my field of principal interest, the study of late Paleozoic tetrapods, since samples are commonly small, distortion extensive, and preservation poor in many instances. The present study was undertaken primarily to test the utility of quantitative work in analyses of a sample of early tetrapods.

Diplocaulus, a rather highly specialized early Permian amphibian, was selected for this study for several reasons. It is one of the most common genera in the Early Permian beds of Clear Fork age, and both large and small skulls have been obtained. This has made possible a study of growth within the species of the genus. Secondly, members of the genus have been reputed to exhibit high variability, a feature that seems to be expressed, perhaps less strikingly, in a number of Permian genera, such as *Captorhinus* and *Diadectes*. The taxonomy of the genus *Diplocaulus* appears to be in an unsatisfactory state as a result of this supposed variability, and an opportunity to test quantitative methods in the solution of taxonomic problems as well as in the interrelated problems of growth seemed to be at hand. *Diplocaulus* has certain disadvantages. Very little has been known of the genus from other horizons, so that comparison of samples from different stratigraphic levels is not practical. Recently, a collection of several skulls has been obtained from the Vale, which overlies the Arroyo, the source of the sample studied. These skulls will form a basis for comparison once they have been prepared, but they are not considered in the present paper. The habits of *Diplocaulus* are poorly understood, and the functions of certain parts of the skull have not been explained adequately.

More complete interpretation is desirable for analyses of the relationships of function and variation. Nevertheless, *Diplocaulus* is one of the best Permian genera now available for quantitative studies.

MATERIALS

Forty-seven skulls and partial skulls compose the sample treated in this report. Pertinent data concerning numbers, localities, and ownership are presented in Table 1. The skulls are figured in plates 1 to 7. Normally, such a complete pictorial record would not be required, but the complete series has been figured in order that the reader may fully understand the state of preservation of materials—an item of considerable importance in evaluating results. In the drawings, particular attention has been paid to accuracy of outline and osseous patterns. The pitted surface pattern has been omitted from the figures since it adds to the difficulty of interpretation of the dermal patterns.

All specimens of the sample have come from the Arroyo Formation of the Clear Fork. Precise data on localities are not available for many of the specimens, although it is possible to locate all but a few to within about one-half mile of the place in which they were collected. There is likewise little direct evidence concerning the nature of occurrence. This may, however, be reconstructed in part from the matrix, which has not been completely removed in most instances. In the present study it has been assumed that the specimens of the sample have been drawn from a fauna with lateral and limited vertical continuity. The lateral distribution over the restricted area from which the collections were made appears to have been continuous, and vertical continuity is suggested by the limited section from which the specimens have been drawn and by the fact that there are few evidences of change in other groups within the confines of the Arroyo beds. Analyses of *Diplocaulus* give no evidence of differentiation on the basis of localities.

The amount of preparation of different specimens varies widely. Those prepared solely for the present study, about half of the sample, have only their dorsal and lateral surfaces cleared of matrix. A few of the others are fully prepared. Extensive plaster reconstruction has been done on some specimens that were mounted for exhibition, and certain restorations are clearly faulty. Distortion is evident in a number of specimens. Specimens in which either reconstruction or distortion was excessive were eliminated from the sample. In addition to those that form the sample, about fifty specimens were

TABLE 1.—CONSTITUTION OF THE SAMPLE OF DIPLOCAULUS

Specimen number	Locality	Specimen number	Locality
C.N.H.M.—U.C. ¹		A.M.	
206	Craddock Ranch	4466	?Coffee Creek
221	Craddock Ranch	4467	Coffee Creek
222	Craddock Ranch	4469	East Coffee Creek
223	Craddock Ranch	4470	East Coffee Creek
229	Coffee Creek ²	4472	Hog Creek
410	Craddock Ranch	4473	Uncertain
564	Craddock Ranch	4484	Coffee Creek
636	Coffee Creek	4485	Hog Creek
637	Coffee Creek	4491	East Coffee Creek
1013	Beaver Creek	4494	?Coffee Creek
1015	?Beaver Creek	4498	Coffee Creek
1317	Pony Creek	4501	Hog Creek
1648	Craddock Ranch	4504	West Coffee Creek
1650	Middle Coffee Creek	4511	Clear Fork ³
1652	West Banks Brushy Creek	4512	Clear Fork
1654	Coffee Creek	4514	?Coffee Creek
1655	East Coffee Creek	4523A	Baylor County ⁴
1656	Middle Coffee Creek	4523B	Baylor County
1657	Coffee Creek	4530	Uncertain ⁵
1658	Coffee Creek	4537	Grey Creek
1660	Middle Coffee Creek	4589	Clear Fork
1661	Middle Coffee Creek	4597	Clear Fork
1663	Middle Coffee Creek	4752	Uncertain
P12689	Coffee Creek		

¹ C.N.H.M.—U.C.: The collection thus designated was recently presented to Chicago Natural History Museum. The numbers, with U.C. as collection designation, are not to be changed. P=paleontological collections at Chicago Natural History Museum. A.M.=American Museum of Natural History.

² The locality markings on a number of specimens do not give an adequate idea of their precise position. The general designation of Coffee Creek places the locality north of the Wichita River in the area drained by Coffee Creek. In some instances it refers to the principal valley that lay just north of the river prior to the development of Lake Kemp. In others, it refers to a locality that lay north of this on one of the three main branches of Coffee Creek, respectively noted as East, Middle and West Coffee Creek in other designations. All specimens so labeled come from approximately the same horizon over an area about five miles on a side.

³ Several specimens are merely labeled Clear Fork. Since there was no collecting in the Vale or Chozas during the time that they were gathered, this designation refers either to the Clyde or the Arroyo. It is clear from the matrix of the specimens so listed that they are from the Arroyo and most of them appear to have come from south of the Wichita River, from the broad area occupied by the breaks of Brushy Creek.

⁴ This listing gives almost no information of stratigraphic value. The two specimens so listed appear to have come from north of Seymour. On the basis of the matrix the most probable locality is the Craddock Ranch.

⁵ This specimen is listed as from the Wichita Basin. The matrix places it almost certainly in the Arroyo. No. 4752, also listed as uncertain, merely has the label "Texas." It also is quite surely from the Arroyo, but its locality is most uncertain.

available, but all were eliminated from consideration for these reasons or because of incompleteness, which made certain key measurements impossible.

ACKNOWLEDGMENTS

Many of my colleagues have given much time and effort to aid in the preparation of this paper and several institutions have made their collections available for study. Dr. Rainer Zangerl of Chicago Natural History Museum has been a consultant and with Mr. Robert F. Inger has taken X-ray photographs of the sample of *Bufo marinus* from the collections of the Museum. Dr. Edwin H. Colbert of the American Museum of Natural History, Dr. Claude W. Hibbard of the University of Michigan and Dr. Alfred S. Romer of Harvard University have supplied measurements of the amphibian *Trimerorhachis* for comparative purposes. I am deeply indebted to Mr. Robert Miller of the University of Chicago for his aid in many phases of the work. Dr. Sewall Wright and Dr. W. Allen Wallis, also of the University of Chicago, have been helpful in suggesting procedures in the statistical work.

Both Mr. Robert Miller and Mrs. Phyllis Hull have rendered valuable assistance to me in doing the calculation. The drawings for the illustrations were made by Mr. Melvin Douglas of Chicago, except figures 18 and 19, which are the work of Mr. John Conrad Hansen, Staff Artist, Chicago Natural History Museum.

Specimens were made available by the American Museum of Natural History, the University of Michigan, Harvard University and the United States National Museum. The remainder of the sample was drawn from collections recently transferred to Chicago Natural History Museum from the University of Chicago.

To each of the individuals who has participated in the work and to the institutions that graciously supplied specimens, I express my deep and sincere appreciation for their co-operation in helping me to bring this project to completion.

I. PROBLEMS AND METHODS

GENERAL PROBLEMS

It is well understood that the amount of variability in different genera and species differs widely—that some groups are notably stable and others highly varied. The scope of variability and tests of homogeneity and heterogeneity of populations can best be expressed by standard statistical parameters based upon analyses of samples drawn from natural populations. It has appeared to many students of Permian vertebrates that extensive variation at the species level is a common phenomenon in animals from that Late Paleozoic period, but how much of the variation is real and how much is merely apparent has not been demonstrated. I, among others, have adopted a conservative policy of referring closely similar variates, within reasonable limits, to a single species, on the assumption that real differences, if present, cannot be demonstrated. Recent work on *Diadectes* (Olson, 1947) is a case in point. *Diplocaulus* appears to provide a sample adequate for checking this taxonomic procedure, and there is reason to suppose that the methods developed and the conclusions reached during the work will aid in the study of less adequately known genera.

The several interrelated problems involved in this analysis consist of the determination of the taxonomic relationships of the specimens involved, the determination of differences that have been variously interpreted as specific and individual, the analysis of the development of these differences, and investigation of the reasons for their existence. Inasmuch as this study was undertaken as a test case and much of the work proceeded by trial and error, the methods and results are recorded somewhat in the form of a case history of the investigation. Preliminary steps are outlined in the present section. The second section consists of a summary of pertinent earlier studies on *Diplocaulus*, with comments on homologies of cranial elements and on taxonomy. The third section includes an analysis of the taxonomy, based in part on numerical data, with discussions of the characteristics of the genus and its species. Although such an analysis was not the primary objective of the

investigation, it is obviously impossible to study the growth of a species without an understanding of taxonomy. The fourth section comprises a study of growth of the skulls of one species of *Diplocaulus* and the bearing of the changes upon the supposed high variability of the species. Separation of the third and fourth sections is somewhat artificial, for taxonomy cannot be studied in most fossil amphibians and reptiles without taking growth into consideration. It has become increasingly evident, as the study has developed, that analyses of growth are of prime importance in studies of extinct amphibians and reptiles. There are, of course, no osseous structures that do not change as growth proceeds, no convenient organs, such as the enamel-covered teeth of mammals, which are unchanged except by wear after eruption. There is, furthermore, no definable terminal growth in members of these classes and no characters specifically definitive of skeletal maturity. Analyses which do not take growth factors into consideration will, in many instances, reach faulty conclusions.

Growth in fossils is, however, extremely difficult to study. Obviously, no time scale is available. It is, perhaps, possible to obtain some measure of relative time series, but the methods present serious difficulties in materials such as those considered in the present paper. Thus it is necessary to use the changes of one or more structures as a substitute scale. Characters selected in this capacity assume the role of independent variables, although there may be little justification for their selection in this capacity. A further problem in growth studies arises from the difficulty of adequate sampling—sampling that will include a wide series of growth stages. One gains the impression that the great majority of fossil amphibians and reptiles fall near the upper limits of growth for their particular species. While this is less true than descriptions would suggest, it does appear that most specimens fall within the upper 30 per cent of the probable size range of their group based on such linear features as over-all length, skull length, etc. Much may be done even within such limits but, as will be shown below, many significant features have their origins well below such a limit. This problem was not critical in the case of *Diplocaulus*, since the available specimens range from 14 to 147 mm. in skull length, with fair distribution throughout the size range. This unusual distribution makes the genus especially advantageous for study.

With these more general considerations in mind we may turn to problems more specifically concerned with the study of *Diplocaulus*.

TABLE 2.—MEASUREMENTS OF DIPLOCAULUS

Specimen number	<i>Sk_t</i>	<i>Sk_w</i>	<i>Pi-Fr</i>	<i>Ip_t</i>	<i>Pal</i>	<i>Fr_t</i>	<i>O-S_t</i>	<i>I_{0w}</i>	<i>L</i>	<i>O_w</i>	<i>R</i>
A.M. 4523A	14.0	12.7	...	2.5	4.4	5.9	2.8	1.7	1.9
U.C. 1660	19.0	18.5	3.8	3.0	3.0*
U.C. 206	23.0	22.0	...	3.6	7.3	10.3	4.0	2.8	4.6	4.6
A.M. 4523B	24.0*	22.6	...	5.2	7.0	9.0	5.3
A.M. 4752	31.0	40.0	2.8	6.4	9.2	13.7	8.0	3.4	6.2	6.2
U.C. 229	46.0	57.0*	...	9.5	9.9	21.7	7.0
A.M. 4485	50.0	54.0*	...	10.5*	15.6*	20.0*	14.0	6.0	6.0	5.8
A.M. 4589	63.0	14.0	15.0	29.0	16.5	9.5	9.5	10.0
U.C. 222	65.0	95.0*	...	16.0	16.0*	29.5	17.0	9.8	10.2	11.0
U.C. 1663	65.0	92.0*	4.0	17.0	17.2	8.5
U.C. 1658	68.0	108.0	4.5	16.2	17.0	27.6	17.0	11.0
U.C. 223	70.0	5.9	16.5	20.0	27.0	18.0	11.2	13.0	14.0
A.M. 4597	73.0	94.0	...	17.0
U.C. 1656	75.0	6.0	16.0	21.0	29.0	19.0	9.5	14.0	13.9
U.C. 1657	75.0	23.0
U.C. 1652	80.0	13.0
A.M. 4511	81.0	4.5	20.0	20.5	11.5	15.0	15.0
A.M. 4491	82.0	175.0*	5.5	18.0	19.0	34.2	22.0	11.0	12.8
U.C. 410	85.0	143.0	8.0	21.5	24.5	30.0	23.0	14.6	12.0
U.C. 1650	89.0	159.0*	...	20.4	21.0*	38.0*	23.0	13.0	13.5
P12689	89.0	118.0*	6.0	19.0	23.3	41.0	19.2	14.0	16.0	16.0
A.M. 4537	90.0	200.0*
A.M. 4512	90.0	3.9	21.0	21.0	39.0	13.0	16.0	15.0
A.M. 4530	95.0	28.5	13.6	11.5

TABLE 2.—MEASUREMENTS OF DIPLOCAULUS—continued

Specimen number	Sk_1	Sk_w	$Pi-Fr$	Ipl	Pal	Fr_1	$O-St$	Io_w	L	O_w	R
U.C. 1013	97.0	310.0*
A.M. 4504	97.0	7.1	21.2	25.5	41.0	25.2	15.0	14.2	14.2	14.2
U.C. 221	98.0	5.5	26.8*	25.9*	42.8	26.2	15.7	15.6	13.6	13.6
A.M. 4469	101.0	9.3	25.4	30.2	38.3	25.0	17.0	16.2
U.C. 1015	101.0*	260.0	...	28.0*	29.0*	37.0*	16.5	14.0	14.0	14.0
A.M. 4473	105.0*	6.0	25.0*	24.0	46.0*	17.5	15.2
A.M. 4494	105.0*	245.0*	...	31.0*
U.C. 1661	107.0	328.0	...	30.0	28.0*	42.0*	15.0	19.1	15.5	16.0	16.0
A.M. 4514	110.0	193.0	8.0	24.2	24.3	45.4	27.5	16.0	17.0	17.0
U.C. 564	114.0	340.0*	29.0
A.M. 4498	114.0	7.1	27.0	30.0	44.0	26.0	18.0	15.0	15.0	15.0
A.M. 4466	115.0	350.0*	7.8	25.5	28.0*	47.2	28.0	20.0	17.0	16.5	16.5
U.C. 1654	116.0*	8.0	46.0	20.4
A.M. 4467	118.0	370.0*	...	26.5	27.8	48.0	29.0	19.9	17.5	17.2	17.2
U.C. 636	119.0	360.0	9.2	27.8	29.2	49.0	27.0	17.1	18.2	19.0	19.0
A.M. 4470	119.0	298.0	...	25.0*	35.0	42.0	13.0	22.0	22.0	18.0	18.0
U.C. 1655	120.0*	29.5
A.M. 4472	127.0	398.0	9.1	34.0	30.5	50.0	31.0	22.0	19.5	18.5	18.5
U.C. 1317	129.0	320.0	28.0	18.2
A.M. 4501	130.0*	7.0	32.2	32.0	14.0	19.5	19.5
U.C. 637	135.0	325.0
U.C. 1648	136.0	335.0*	...	31.8	18.0	24.0	19.9	19.9
A.M. 4484	147.0	330.0

TABLE 2.—MEASUREMENTS OF DIPLOCAULUS—continued

Specimen number	Ot		Pmxl	Narw		Pofa		Poa		Paw		Paa		Ipw		Stl	
	L	R		L	R	L	R	L	R	L	R	L	R	L	R		
A.M. 4523A	2.6	Less than 1 mm.	4.4	4.4	3.8	3.7
U.C. 1660	3.3	3.4
U.C. 206	4.2	5.6	1.0	4.4	6.7	3.2	6.8	6.7	50	7.0*	7.2	7.9
A.M. 4523B	6.0	10.0	7.0	50.0	8.6
A.M. 4752	6.9	6.8	2.1	7.8	15	17	9.1	8.9	9.0	10.0	9.8
U.C. 229	8.8	55	45	16.1	180	16.1
A.M. 4485	6.5	6.5	4.8	40	50	16.0*	16.0*	230	18.5
A.M. 4589	9.5	11.0	4.5	20.0	20.0
U.C. 222	11.8	12.2	4.0	13.0	27.8	24.5	22.0	25.0	52	52
U.C. 1663	6.0*	25.0*	26.0	48*
U.C. 1658	6.2	18.0	75	110	25.4	26.5	489	455	25.0	24.0	58
U.C. 223	12.2	11.8	5.5	16.0	31.0	24.0
A.M. 4597	29.5	42
U.C. 1656	14.2	14.0	7.0	18.5	100	135
U.C. 1657
U.C. 1652	12.0	9.0	32.0*	67*
A.M. 4511	42.0*	61
A.M. 4491	14.1	17.0	8.3	26.0*	155	184	37.0*	38.0	48.0	41.0
U.C. 410	13.0	8.1	51.0	45.0
U.C. 1650	12.0	13.0	8.2	26.5	120	160	35.0
P12689	19.5	18.5	4.0	21.0	35.0	35.0	3055	38.0	37.0	53
A.M. 4537
A.M. 4512	19.3	19.6	38.2	39.0	50.0	48.0
A.M. 4530	13.8	12.0	16.0*	28.0

TABLE 2.—MEASUREMENTS OF DIPLOCAULUS—continued

Specimen number	Ot		Pmxl		Narw		Pofa		Poa		Paw		Paa		Ipw		Stl	
	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R
U.C. 1013	13.8	12.0	28.0	27.0
A.M. 4504
U.C. 221	15.8	15.4	9.7	23.8	246	375	40.0	50.0
A.M. 4469	16.5	16.5	7.8	25.3	200	115	190	405	29.5	31.0	750	78.0
U.C. 1015	15.4	9.0*	152	54.0	441	61.0	65.0
A.M. 4473	16.8	45.0*	58.0
A.M. 4494	67.0
U.C. 1661	15.2	3.6	25.0	77.8	68.0	1825	1840	96.0	93.0	168
A.M. 4514	16.0	18.0*	10.0*	44.8	45.4	1320	1165	45.5	98*
U.C. 564	12.2	61.0	63.0	74.0*	68.0
A.M. 4498	17.2	16.3	8.5	59.0*	35.0
A.M. 4466	18.5	18.3	11.8	28.0	255	270	580	565	67.0	1770	84.0
U.C. 1654
A.M. 4467	17.0	17.2	8.0	29.0	280	234	470	420	71.8	72.0	1995	1840	80.5	78.5
U.C. 636	20.2	20.3	10.0	27.0	285	190	455	72.0*	72.0	1930	86.0	86.0	137
A.M. 4470	16.8	5.2	31.0	92.0	88.5	91.0	130*	130
U.C. 1655	90.0	99.0
A.M. 4472	19.5	13.5	3.3	72.0	92.0	150
U.C. 1317
A.M. 4501	24.0	77.0	97.0
U.C. 637
U.C. 1648	21.0	8.0	88.0	82.0
A.M. 4484

TABLE 2.—MEASUREMENTS OF DIPLOCAULUS—continued

Specimen number	∠1		∠2		∠3		∠4		∠5		∠6		∠7		∠8		∠9	
	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R
A.M. 4523A	19°	16°	22°	86°	..	90°	67°	..	45°
U.C. 1660	18°
U.C. 206	..	17°	..	35°	20°	73°	70°	64°	34°	61°	58°	40°	40°
A.M. 4523B	24°	22°	..	29°	..	26°	..	79°	26°	..	50°	..	80°
A.M. 4752	19°	18°	16°	..	24°*	..	72°	73°	59°	58°	58°	47°	44°
U.C. 229	23°	..	18°	..	31°	..	71°	58°	..	66°	..
A.M. 4485	16°	..	15°	..	23°	..	79°	39°	..	59°	..
A.M. 4589	30°	49°
U.C. 222	22°	20°	16°	..	33°	31°	..	66°	40°	40°	43°	41°
U.C. 1663	..	25°	26°	..	61°	59°
U.C. 1658	22°	23°	15°	..	34°	32°	24°	25°	69°	66°*	49°	56°	..	27°	54°	52°	48°	48°
U.C. 223	31°	68°	51°*	56°*
A.M. 4597
U.C. 1656	31°	41°*	60°*	55°*
U.C. 1657
U.C. 1652
A.M. 4511	26°	27°	26°	..	35°	70°	78°	42°	..	59°	65°	67°	58°
A.M. 4491	..	29°	21°	32°	..	69°	60°	58°	..	63°	..
U.C. 410	28°	75°	63°
U.C. 1650	25°	18°	68°	63°	59°*	53°*
P12689	..	23°	22°	31°	..	24°	37°	51°
A.M. 4537
A.M. 4512	26°	28°	40°	72°	60°	58°
A.M. 4530

TABLE 2.—MEASUREMENTS OF DIPLOCAULUS—concluded

Specimen number	∠1		∠2		∠3		∠4		∠5		∠6		∠7		∠8		∠9	
	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R
U.C. 1013
A.M. 4504
U.C. 221	26°	..	26°	..	33°	80°	38°	..	61°	..	66°	..
A.M. 4469	19°	20°	..	16°	32°	28°	19°	72°	43°	..	43°	39°	..	52°	45°	..
U.C. 1015	30°	36°	76°	78°	47°	..	64°	..	59°	..
A.M. 4473	41°
A.M. 4494	23°	56°
U.C. 1661	..	45°	32°	31°	35°	..	67°	64°	52°	60°	57°	60°	55°
A.M. 4514	26°	25°	..	21°	32°	..	76°	59°	50°	63°	48°	51°	..
U.C. 564	27°	34°	..	32°	80°	53°	70°
A.M. 4498	33°	30°	74°	70°	48°	..	66°	..	59°	..
A.M. 4466	33°	..	29°	32°	40°	40°	45°	..	76°	76°	68°	..	54°	55°	65°	67°	58°	..
U.C. 1654	..	29°	..	24°	70°	60°*	54°	..
A.M. 4467	33°	33°	29°	29°	39°	39°	42°	..	73°	73°	65°	..	47°	48°	64°	64°	57°	58°
U.C. 636	..	33°	..	32°	40°	42°	..	73°	66°	62°	..	65°	..	58°
A.M. 4470	36°	33°	30°	31°	47°	51°	56°
U.C. 1655	40°	..	33°*	33°*	..	70°*	..	49°*	62°	..	59°	..
A.M. 4472	..	31°	..	28°	36°	47°	37°	69°	71°	62°	..	45°	..	57°	..	55°
U.C. 1317	42°	74°
A.M. 4501	..	35°	..	39°*	75°	69°	..	63°
U.C. 637	29°	45°
U.C. 1648	28°	28°	29°	..	65°	65°	49°	55°	56°
A.M. 4484

EXPLANATION OF SYMBOLS AND MEASUREMENTS

Explanation of symbols.—Subscripts: l =length; w =width; p =posterior; a =area; x =axis. Others: * = measurement approximate; L =left; R =right; for Sk_l , Sk_w , $Pi-Fr$, etc. see descriptions of measurements below.

Procedures in measurement.—All measurements are in millimeters and areal measurements in square millimeters. Linear measurements have been made with sliding calipers, angular measurements with a standard protractor, and areal measurements with a planimeter. Measurements represent the mean of a minimum of three trials. All measurements were made on a plane tangent to the dorsal platform of the skull, as if the skull were projected onto this plane by orthogonic projection.

Sk_l =Skull length. The distance from the tip of the snout at the intersection of the suture between the premaxillaries to the posterior margin at the intersection of the suture between the interparietals.

Sk_w =Skull width. The distance between the horn tips.

$Pi-Fr$ =Pineal-frontal length. The distance from the anterior margin of the pineal opening to the frontal-parietal suture at the junction of the suture between the parietals.

Ipl =Interparietal length. The distance from the anterior termination of the suture between the interparietals, at the point of intersection of the more posterior interparietal-parietal suture, and the posterior termination of the suture between the interparietals.

Pal =Parietal length. The distance from the intersection of the suture between the parietals and the parietal-frontal suture and the junction of the suture between the parietals and the more anterior parietal-interparietal suture.

Fl =Frontal length. The length of the frontal bone along the midline of the skull.

$O-S_l$ =Orbito-snout length. The distance along the midline of the skull from a plane tangent to the anterior margins of the two orbits to the tip of the snout.

Iow =Interorbital width. The minimum distance between the inner margins of the orbits normal to the axial plane of the skull.

O_w =Orbital width. The greatest width of the orbit along a line normal to the axial plane of the skull.

O_l =Orbital length. The greatest length of the orbit along a line parallel to the axial plane of the skull.

Pmx_l =Premaxillary length. The distance between the posterior termination of the suture between the premaxillaries and the intersection of this suture with the tip of the snout.

Nar_w =Narial width. The least distance between the inner margins of the nares.

2of_a =Postfrontal area. The area of the postfrontal to the nearest square millimeter as measured by planimeter.

- Po_l =*Postorbital length*. The distance from the midpoint of the postfrontal-postorbital suture to the termination of the posterior spur of the postorbital.
- Po_a =*Postorbital area*. Measured as in the case of the postfrontal.
- Pa_w =*Parietal width*. The distance from the suture between the parietals normal to the midline of the skull to the point of junction of the parietal, the squamosal, and the supratemporal.
- Pa_a =*Parietal area*. Measured as in the case of the postfrontal.
- Ip_w =*Interparietal width*. The distance from the level, on the midline of the skull, of the posterior termination of the suture between the interparietals normal to the midline of the skull to the greatest lateral extremity of the interparietal.
- St_l =*Supratemporal length*. Distance from the junction of the parietal, the interparietal and the supratemporal to the tip of the horn.
- $\angle 1$ =*Parietal angle*. The acute angle between the midline of the skull and a line from the tip of the snout, at the midline, to the junction of the parietal, the supratemporal and the squamosal.
- $\angle 2$ =*Interparietal angle*. The acute angle between the midline of the skull and a line from the tip of the snout, at midline, to the lateral extremity of the interparietal.
- $\angle 3$ =*Postorbital angle*. The acute angle between the midline of the skull and a line from the tip of the snout, at midline, to the posterior termination of the postorbital.
- $\angle 4$ =*Supratemporal angle*. The acute angle between the midline of the skull and a line from the tip of the snout, at midline, to the horn tip.
- $\angle 5$ =*Interparietal posterior angle*. The acute angle between the midline of the skull and a line between the posterior termination of the suture between the interparietals and the lateral extremity of the interparietal.
- $\angle 6$ =*Supratemporal posterior angle*. The acute angle between the midline of the skull at the level of the posterior termination of the suture between the interparietals and the horn tip.
- $\angle 7$ =*Postorbital axial angle*. The acute angle between the midline of the skull and a line through the midpoint of the postfrontal-postorbital suture and the posterior termination of the postorbital as marked by the postorbital spur.
- $\angle 8$ =*Interparietal axial angle*. The acute angle between the midline of the skull and a line through the midpoint of the suture between the interparietals and the lateral extremity of the interparietal.
- $\angle 9$ =*Parietal axial angle*. The acute angle between the midline of the skull and a line through the center of the pineal opening and the point of junction of the parietal, the squamosal and the supratemporal.

Members of this genus show undeniably striking differences in various characters, even when specimens of approximately the same size are compared. A cursory study seemed to indicate the alternatives in taxonomic procedure of recognizing a large number of species, ten or more, or of lumping all specimens into a single species. The presence of a large number of species of a single genus in a limited area and from beds of restricted vertical extent seemed improbable, so that the second alternative was adopted as a working hypothesis. Early studies tended to support the hypothesis but later work proved it, as well as its alternative, to be false. The specimens appear to represent two species, one including the majority of the specimens and the other a very few.

Initial problems in any study involving numerical data derived from measurements concern the unit or units of measurement and what to measure. Linear measurements throughout the paper are expressed in millimeters, a unit suitable to the range of sizes encountered. The problem of what to measure is particularly acute in animals such as *Diplocaulus*, in which there is little or no directive evidence to show what measurements and what comparisons might prove valid and useful. No real progress could be made until this problem had been settled, and considerable time was spent in random testing before it was solved. Certain possibilities were at once apparent: midline characters appeared to be stable; the length of the pre-orbital region, the skull width, the posterior curvature and certain others showed possibilities of discontinuous differences. A number of these were tested without definitive results, strengthening the working hypothesis that there was a single species. Eventually the early efforts of rigid analysis were temporarily abandoned and a series of twenty-seven measurements was made on each skull, in so far as this was possible. Since no skull showed all twenty-seven features, the size of the sample was somewhat reduced for any one series of measurements. The twenty-seven measurements were selected primarily on the basis of ease and accuracy of measurement. Linear, areal and angular measurements were used. Skull length, measured along the midline, was taken as the base measurement for comparison and was, in most cases, used as the independent variable. Measurements were then co-ordinated in a series of twenty-four tests that consisted in each case of the regression of the measurement in question on skull length. Each test was plotted as a scatter diagram on arithmetic, metric graph paper to give a basis for visual evaluation of the nature of the regression and the general correlation of changes in each series of measurements with changes in skull

length (see figs. 9-15). In some instances coefficients of correlation (r) were determined, as well as such items as regression coefficients (b_{YX} and b_{XY}) and standard deviation (σ), but for the most part these were not necessary in preliminary analysis. Curves were fitted to the scatter diagrams by the crudest methods. From the scatter diagrams a table of twenty-four tests was prepared by entering an estimate of the deviation of each specimen from the roughly plotted curves. O was used to indicate little deviation and the letters S , M , and L to indicate small, medium, and large deviations respectively. A plus (+) or minus (-) sign was used to indicate whether the deviation fell above or below the line of regression respectively. Each test was then studied in terms of its deviations in individual tests. From this work it became apparent that certain specimens might be different from the majority but that only a few of the twenty-four tests could be of value in a possible separation of the sample into two or more groups. Four tests were selected as possessing potentialities for this use. Each was then analyzed carefully and two of the four were discarded as indecisive. The remaining two suggested other tests; new measurements were made and new tests conducted. The crude analyses and their results are shown in Table 2; the measurements that were used are shown in Table 3.

At this point in the study the outlines of the taxonomy were apparent and the groundwork had been laid for quantitative studies of growth within a single species. The detailed work involved in the preliminary studies and in development of the suggestions obtained from these studies is given in the section on taxonomy and needs no further consideration at this point.

THE PROBLEM OF MEASUREMENTS

Only the dorsal dermal surface of the skull has been used in this study, for several reasons. Differences in skull shape, in position of the fossae of the sense organs, and in dermal patterns are all apparent in this aspect. The dorsal surface is usually well preserved and sutures are present in most skulls. In contrast, the occipital and palatal surfaces are poorly preserved in most specimens and, in many instances, do not permit easy differentiation of the component elements. Certainly, many more characteristics could be studied, but mere number becomes unimportant in view of the variety available on the dorsal surface and the fact that certain of these are of critical importance.

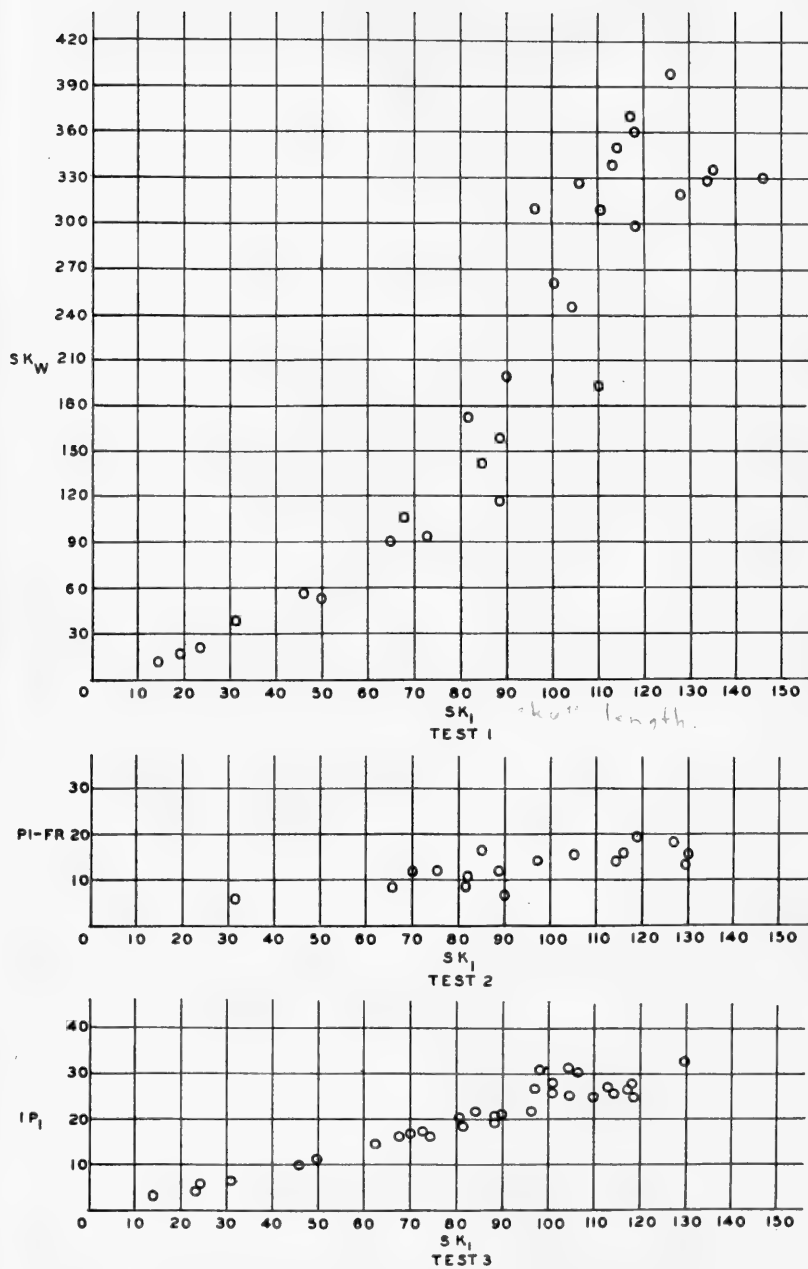


FIG. 9. Scatter diagrams of Tests 1 to 3.

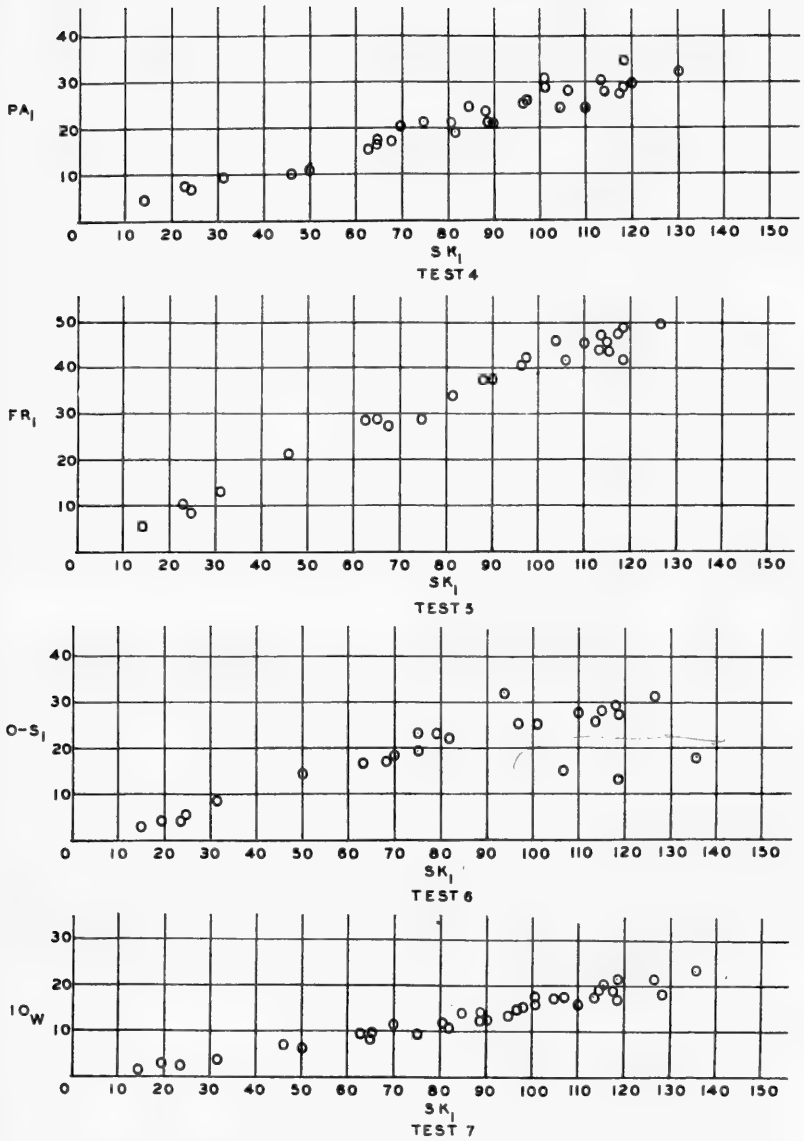


FIG. 10. Scatter diagrams of Tests 4 to 7.

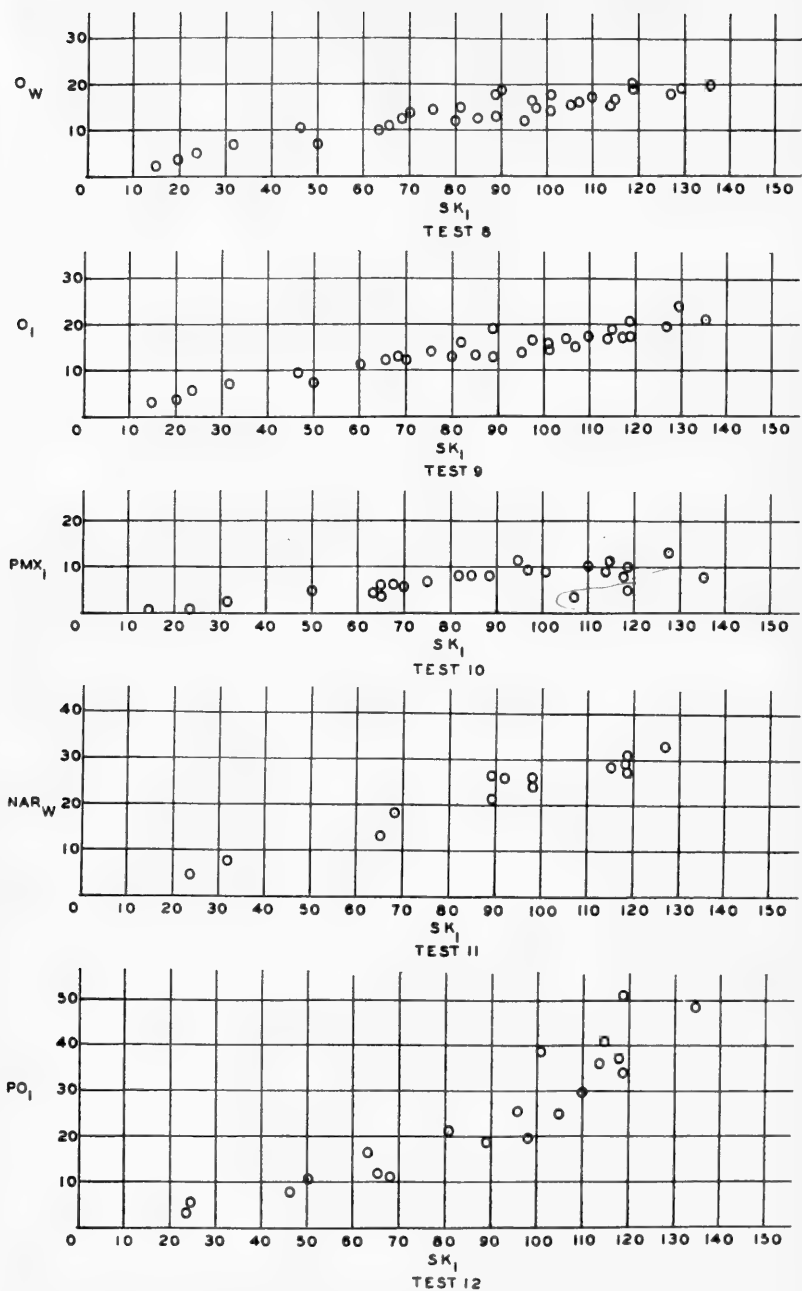


FIG. 11. Scatter diagrams of Tests 8 to 12.

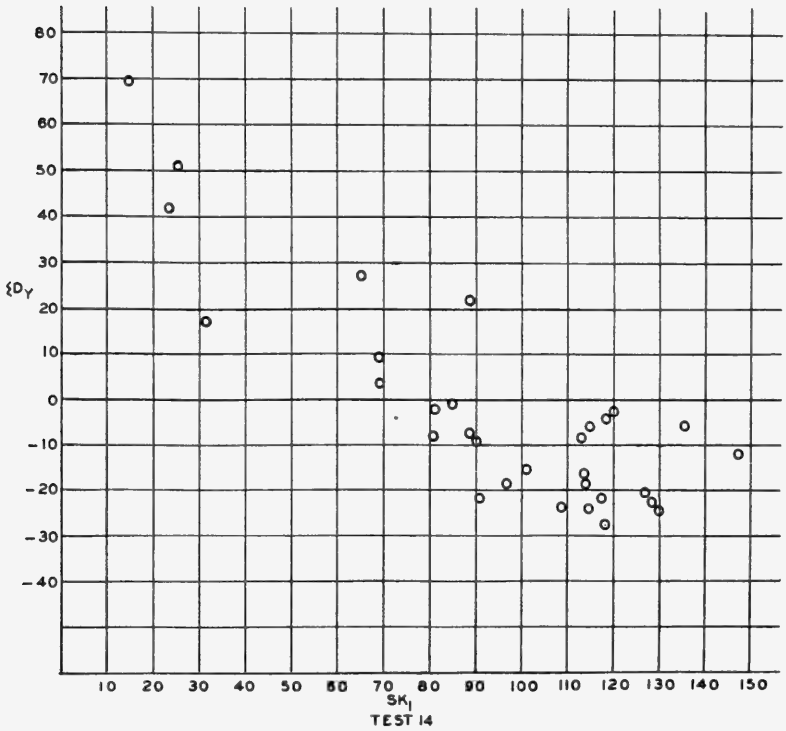
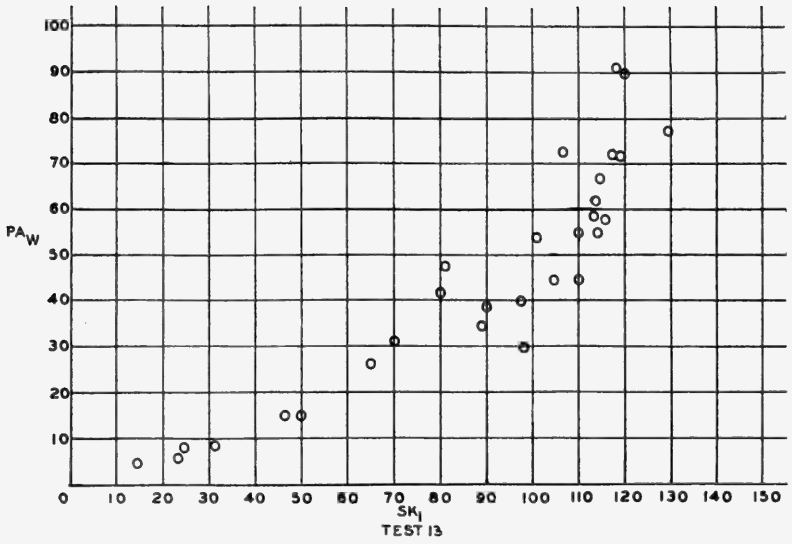


FIG. 12. Scatter diagrams of Tests 13 and 14.

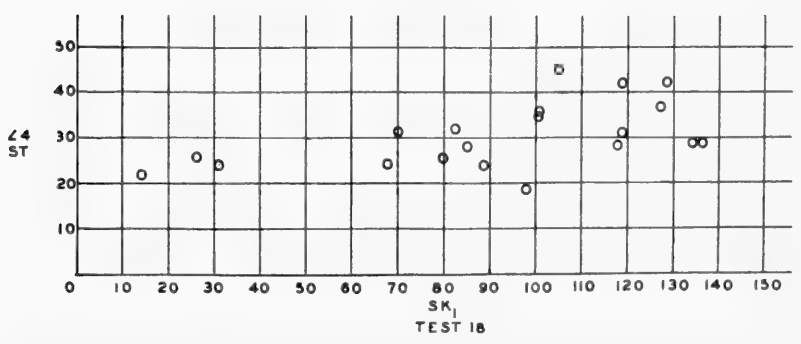
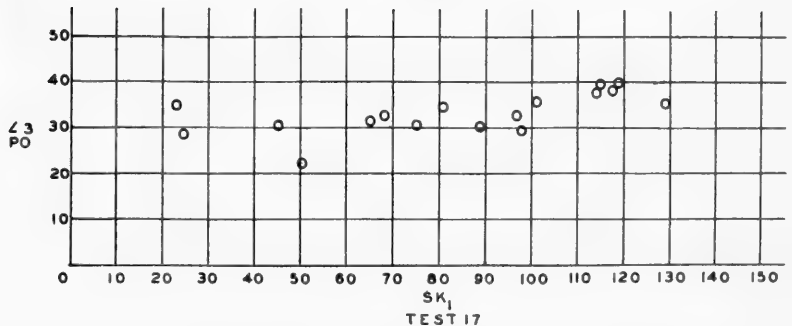
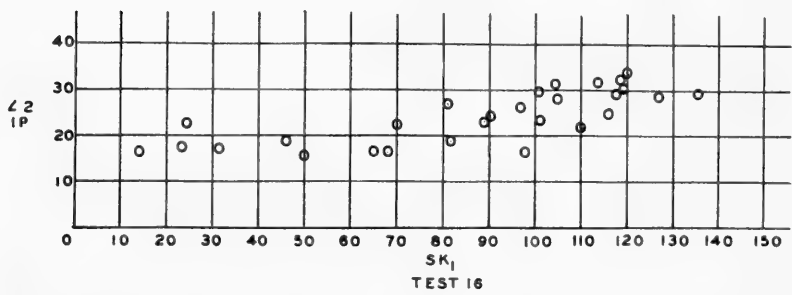
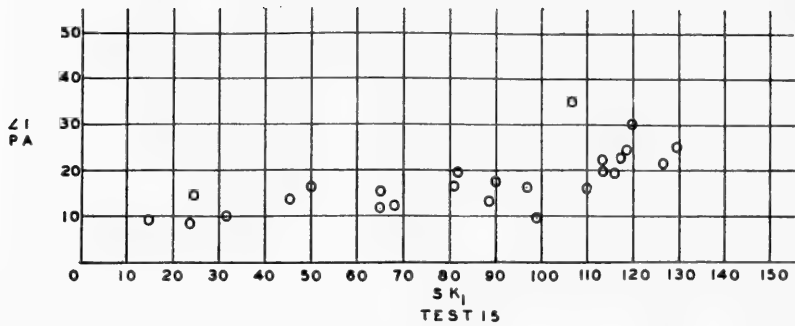


FIG. 13. Scatter diagrams of Tests 15 to 18.

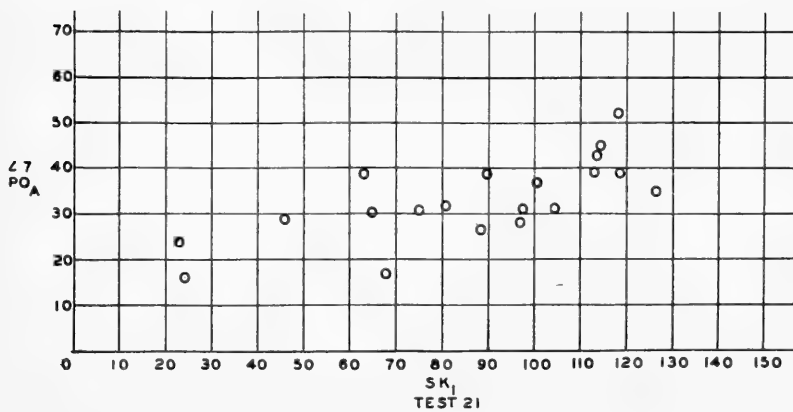
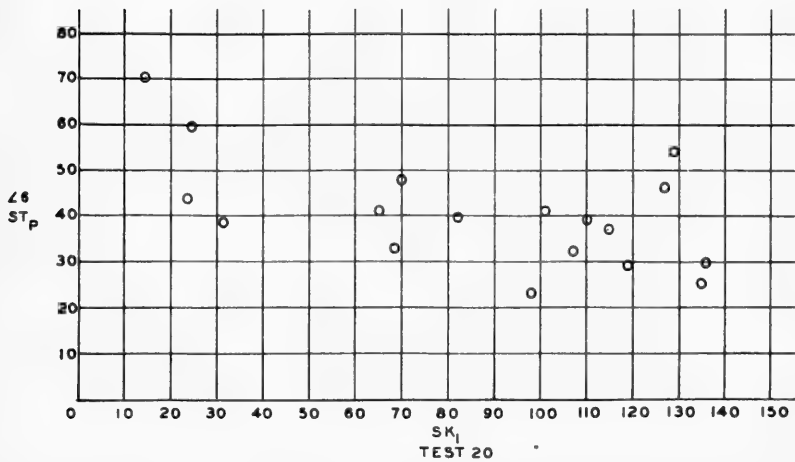
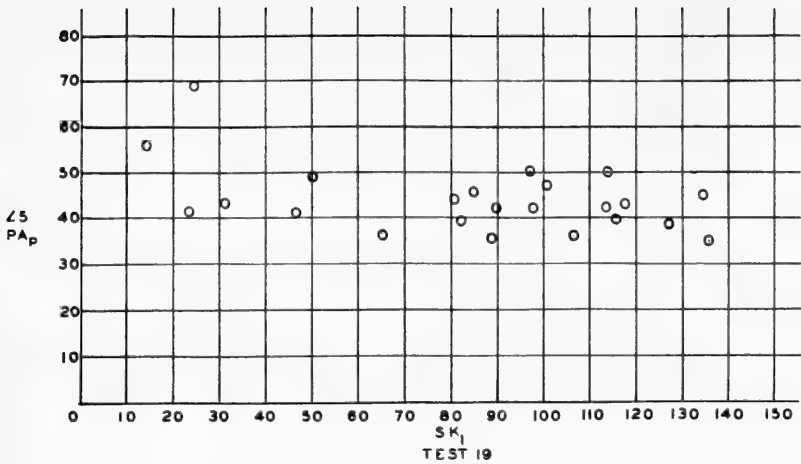


FIG. 14. Scatter diagrams of Tests 19 to 21.

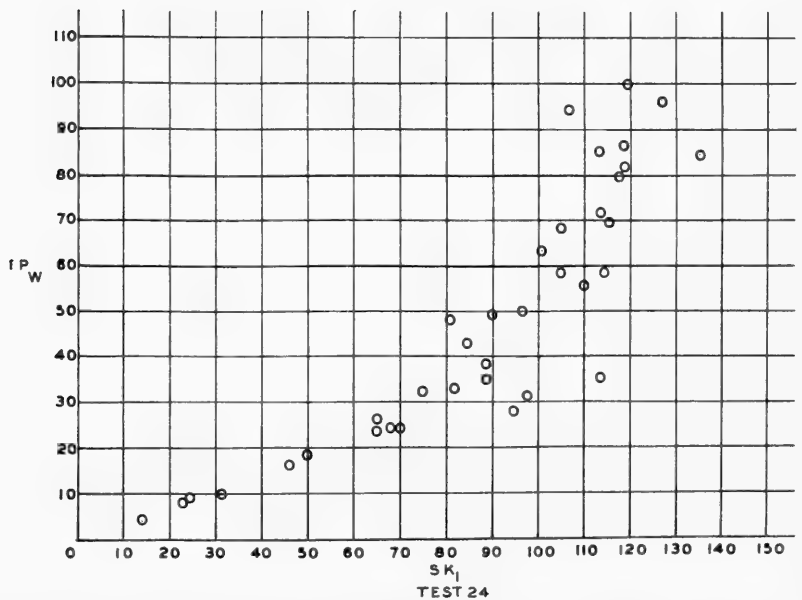
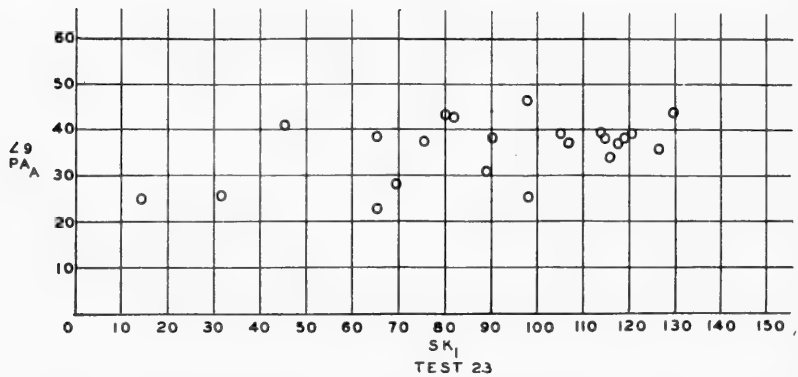
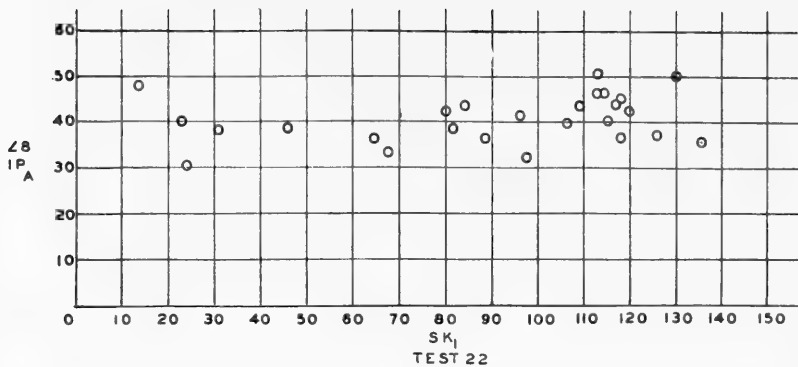


FIG. 15. Scatter diagrams of Tests 22 to 24.

SPECIMEN NUMBER	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	NO. DEVIATIONS IN DEV TESTS	
AM 4523A	0	-	0	S ⁺	0	0	0	0	0	0	-	-	0	0	0	0	0	0	M ⁺	0	-	S ⁺	0	0	3	4,19,22
UC 1660	0	-	-	-	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	
UC 206	0	-	0	S ⁺	0	0	0	0	0	0	0	0	0	0	0	0	M ⁺	0	0	0	0	0	0	0	2	4,17
AM 4523B	0	-	0	0	0	0	-	-	-	-	-	0	0	0	S ⁺	0	0	0	L ⁺	0	0	L	-	0	3	15,19,22
AM 4752	0	0	0	S ⁺	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4
UC 229	0	-	0	S ⁻	S ⁺	-	0	0	0	-	-	0	0	-	0	0	0	0	0	0	0	0	0	0	2	4,5
AM 4485	0	-	0	0	0	0	0	0	0	0	-	0	0	-	0	0	L ⁻	0	0	0	-	L ⁻	0	0	2	17,22
AM 4489	-	-	-	S ⁻	S ⁺	0	0	0	0	0	-	0	-	-	-	-	-	-	-	-	L ⁺	-	-	0	3	4,5,21
UC 222	0	-	0	0	0	0	0	0	0	S ⁻	0	0	0	L ⁻	0	0	0	0	M ⁺	0	0	0	0	0	3	10,14,19
UC 1663	0	0	0	0	-	0	0	0	0	0	-	0	0	0	0	0	-	-	0	0	0	0	0	0	0	
UC 1658	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	L ⁻	0	0	0	1	21
UC 223	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
AM 4597	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	
UC 1656	-	0	0	0	0	0	0	0	0	0	-	-	-	-	-	0	0	0	-	0	0	0	0	0	0	
UC 1657	-	-	-	-	-	S ⁺	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	1	6
UC 1652	-	-	-	-	-	-	-	0	0	0	-	0	-	-	-	-	-	0	-	-	-	-	-	-	0	
AM 4511	-	S	0	0	-	-	0	0	-	-	0	M ⁺	0	0	0	0	0	0	0	0	0	0	0	M ⁺	3	2,13,24
AM 4491	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
UC 410	0	S	0	0	S ⁻	0	0	0	0	0	-	-	0	-	-	-	-	0	0	-	0	0	0	0	2	2,5
UC 1650	0	-	0	0	0	0	0	0	0	0	0	0	-	-	-	0	0	-	S ⁻	-	0	0	0	1	19	
PI2689	0	0	0	0	0	S ⁻	0	0	0	S ⁻	0	0	0	L ⁻	S ⁻	0	0	0	0	0	0	0	0	0	5	6,10,14,15,20
AM 4537	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	

Even when measurements are restricted to the dorsal surface of the skull a number of problems remain. Distortion is recorded, of course, in any direct measurement. No attempt has been made to eliminate this effect, since any such effort would result in a subjective bias. Thus, the effects of distortion appear in the tabulations and calculations. For the most part the effects in the sample are relatively unimportant. More difficult problems are posed by the lack

TESTS

SPEC. NO.	3	5	6	10	12	13	14	15	17	18	19	20	21	24
CMPI 2689	0	0	S ⁻	S ⁻	0	0	L ⁻	S ⁻	0	0	0	-	S ⁻	0
UC 221	0	0	0	0	0	0	M ⁻	0	S ⁻	L ⁻	0	L ⁻	0	M ⁻
UC 1661	0	0	L ⁻	L ⁻	-	M ⁻	S ⁻	L ⁻	-	0	S ⁻	0	-	L ⁻
AM 4514	0	0	0	0	0	0	S ⁻	S ⁻	S ⁻	-	0	0	0	M ⁻
UC 636	0	0	0	0	0	M ⁻	S ⁻	0	0	S ⁻	0	-	M ⁻	0
AM 4470	S	M ⁻	L ⁻	M ⁻	L	M ⁻	S ⁻	S ⁻	-	-	-	0	-	0
UC 1648	0	0	L ⁻	M ⁻	-	-	M ⁻	-	0	S ⁻	S ⁻	0	-	L ⁻

TABLE 3b.—CRUDE ANALYSES OF TWENTY-FOUR REGRESSIONS OF DIPLOCAULUS

of complete specimens. The midline length is extremely important, since it is one of the two variables in most of the regressions, but it cannot be obtained, because of breakage, for many skulls in collections and for this reason a number of specimens that would otherwise have proved of some value have not been included in the sample. In some instances it has been possible to make a close estimate of this value. These estimates have been checked in so far as possible by introduction of the specimens in regressions calculated without use of the estimated value. Estimates of other values, particularly skull width, have been used where they have been considered essential. All estimated values are specified in the table of measurements, Table 2.

Measurements of dimensions of individual bones pose several problems, since there are differences not only in size, but in proportion and shape as well. The technique has been to use a point or points that can be identified on homologous bones in all specimens in which the character is shown; for example, in the case of the anterior margin of the postorbital, a point midway between the

junction of the limiting suture with the postfrontal has been selected. For the postero-lateral termination of the parietal, the junction of the sutures separating the parietal, squamosal and supratemporal (tabular) was used. The most difficult measurements are those concerned with the outline of the skull. Special techniques, as discussed on page 133, were used. The problem of measurement is complicated by the fact that the dermal bones of the skull make contact with pronounced overlap, and any wear of the skull, prior to collecting or in preparation, tends to shift the position of sutures from that occupied when the surface was intact. No attempt to estimate the amount of shift has been made, so that any errors introduced by the factor of wear enter into the recorded measurements.

In spite of all these difficulties of measurement, typical of many paleontological samples, the results obtained appear to have validity. They provide an answer to the question that was uppermost in my mind at the time the work was undertaken, the question as to whether or not the nature of the materials would be such that significant results could be obtained.

EFFECT OF ASYMMETRY OF THE SKULL

Bilateral asymmetry must be taken into consideration in the measurements. Such asymmetry appears in the skulls of *Diplocaulus* as the result of three major effects: (1) the natural asymmetry apparent in the sutural patterns; (2) injuries during growth; (3) differential distortion after death. In making measurements the effects of asymmetry have been handled in various ways. If one side of the skull has been badly distorted while the other has suffered less, measurements have been based on the well-preserved side only. This obviously introduces a subjective analysis of the nature of distortion, but this is preferable to the drastic effects of entering measurements profoundly affected by damage. In cases in which there has been some distortion of both sides, but the distortion appears to have been somewhat compensatory, total raw measurements have been used without modification. In instances in which homologous elements on the two sides of such a skull were measured, mean values have been used. Skulls evidently highly distorted in any particular measurement have not been used for that measurement, but only extreme cases have been eliminated. In cases in which injuries have introduced an abnormality on one side, measurements have been based on the side not affected.

The case of normal asymmetry introduces other problems. These are well shown in the pattern of the midline sutures; for example, the anterior end of the suture between interparietals lies to the right of the midline in some specimens and to the left of the line in others. I have referred to individuals with the interparietal suture to the left as sinistral and to those with the suture to the right as dextral. It is possible to divide the skulls of *Diplocaulus* into three groups on this basis (see Table 4). It appears unlikely that asymmetry has resulted from any profound genetic difference, since the grouping that it suggests does not correspond with the one inferred from studies of several other features of the skull.

TABLE 4.—NATURAL ASYMMETRY OF THE INTERPARIETAL IN DIPLOCAULUS

Approaching symmetry	Dextral	Sinistral	Not determinable
A.M. 4589	P12689	U.C. 410	U.C. 222
U.C. 221	U.C. 229	A.M. 4467	U.C. 637
A.M. 4491	A.M. 4472	A.M. 4523A	A.M. 4494
	U.C. 1663	A.M. 4523B	A.M. 4589
	A.M. 4512	A.M. 4501	U.C. 1013
	U.C. 1650	U.C. 1648	A.M. 4484
	A.M. 4470	U.C. 564	A.M. 4485
	U.C. 1661	U.C. 1015	U.C. 1654
	A.M. 4752	U.C. 1655	U.C. 1660
	U.C. 206	U.C. 636	U.C. 1652
	A.M. 4473	U.C. 1658	U.C. 1317
	A.M. 4514	U.C. 223	A.M. 4530
		A.M. 4511	
		U.C. 1656	
		A.M. 4504	
		A.M. 4469	
		A.M. 4498	
		A.M. 4466	

Linear and angular measurements are, however, affected by this asymmetry and in most instances differ somewhat on the two sides of a single individual. It is possible, of course, to base all studies of the skulls on measurements of comparable sides, but it has been found that little is gained by such a procedure and that the results do not have a value that compensates for the new problems introduced. My practice has been to use the mean of the two values in all cases in which measurements of the same feature on two sides of the skull show differences.

II. REVIEW OF DIPLOCAULUS

HOMOLOGIES OF THE DERMAL ELEMENTS

Much has been written on the homologies of the skull elements of *Diplocaulus* and few of the bones of the dorsal dermal surface pose any problems. The figures of Williston (1909) and Douthitt (1917), based principally on U.C. 636, show elements in typical relationships, although they do not, of course, show variations in proportionate size and shape. The principal differences in the figures of various writers, so far as the limits of bones are concerned, occur in the analyses of the snout. Case (1911) shows a suture limiting the anterior margins of the median elements lying immediately anterior to the frontal, while Douthitt does not show this suture. As a consequence of the difference in interpretation, Case designates this pair of bones as nasals, while Douthitt, following Williston, recognizes but a single pair of bones—premaxillaries—that include the nasals and premaxillaries of Case. A study of the skulls now available, a series much more extensive than any available to Case, Williston, or Douthitt, confirms the determination that no suture is present and that the nasals are missing.

Another point of controversy concerns the two bones that lie posteriorly and postero-laterally to the orbits on each side of the skull. The bone that lies just behind the orbit gives the appearance of being a postorbital; if so, the element behind it would then have to be called supratemporal (see Romer, 1933, for example). The alternative explanation advanced by Watson (1913) and adopted by Douthitt (1917) appears to be more sound. The element behind the orbit appears to be the postfrontal and the bone postero-lateral to it the postorbital, which has been excluded from the circum-orbital series. The relationships of the two elements to each other and to surrounding bones suggest these identities. The postfrontal, according to this interpretation, is in contact with the frontal medially, the parietal postero-laterally and posteriorly, the jugal laterally and the bone identified as postorbital postero-laterally. The postorbital of this interpretation is in contact with the parietal medially, the squamosal postero-laterally, the jugal antero-laterally,

and the postfrontal antero-medially. All of these relationships are normal for these two bones in the amphibians, except for the jugal contact of the postfrontal and the parietal contact of the postorbital. Loss of the supratemporal has resulted in the latter contact in various genera. Interpretation of the more posterior element as supratemporal implies changes in which the contact with a tabular and an interparietal was lost. While this is possible—by elongation of the parietals, interparietals and tabulars—the conditions in related genera suggest that it is not what occurred. The most probable explanation is that given by Watson on the basis of *Batrachiderpeton*. This genus lacks the supratemporal (as identified by Watson) but has undoubted postfrontals and postorbitals. The orbits are lateral. As Watson has pointed out, migration of the orbits to a dorsal position separating the prefrontals and postfrontals and isolating the postorbital from the orbital margin would produce a condition like that of *Diplocaulus*. On these bases it appears that the element variously identified as supratemporal and postorbital is in reality postorbital. This terminology is followed in the present paper.

If the identity of the so-called supratemporal is in error, there remains in the temporal region of *Diplocaulus* but one element of the intertemporal, supratemporal, and tabular series characteristic of many amphibians. In this respect the genus agrees with the gymnarthrids.¹ The bone that forms the "horn" has commonly been called tabular, but in the gymnarthrids it is tentatively identified as supratemporal. If the second of the small elements behind the orbit were supratemporal there would be no choice but to call the more posterior bone tabular, but this does not appear to be the case. It is not unreasonable to assume that this single element of the temporal series is actually homologous in the various groups of lepospondyls. There is, however, little real basis for determination of the homologies of the bone. If it be assumed that the gymnarthrids and diplocaulids arose from a group in which intertemporal, supratemporal, and tabular were present, as is suggested by the almost certain origin of the tetrapods from rhipidistians, it must follow that two of the three bones were lost. Since there is no bone with the

¹ In a recent paper, Gregory (1948) has referred the Microsauria, including the Gymnarthridae, to the class Reptilia. His evidence strongly supports the assignment so far as at least some of the groups called microsaurians are concerned. The gymnarthrids, however, have certain features of the occiput, palate and dermal skull surface that suggest amphibian affinities. It may be that the gymnarthrids and the other families, usually considered as microsaurians, are not closely related. Detailed investigation of the skulls and vertebrae of the gymnarthrids must be made before this matter can be resolved.

relationships of the intertemporal, we may safely assume that this was one of the two. The tabular persistently makes contact with the interparietal medially, the supratemporal anteriorly, and the squamosal laterally in forms in which both supratemporal and tabular are present. The supratemporal lies between the interparietal and squamosal and meets the intertemporal anteriorly. If either the tabular or supratemporal were lost, and the other in part occupied its position, the condition in the gymnarthrids and *Diplocaulus* would obtain. In amphibians in which two of the three elements are present, the tabular tends to be restricted to the posterolateral corner of the dorsal platform. Rarely does it make contact with the parietal in spite of the progressive restriction of the posterior part of the skull. The supratemporal, on the other hand, maintains contact with the parietal and squamosal. It is this general tendency that had led to the tentative identification of the single bone in the gymnarthrids as supratemporal. The difference between the conditions of the gymnarthrids and *Diplocaulus* is primarily that, in the latter, the element is isolated from the postorbital and postfrontal. This could have resulted from the extensive lateral growth of the parietal. The case for calling the element in question supratemporal is as strong as that for calling it tabular. In view of the probable identification of the comparable bones in the gymnarthrids as supratemporals and of the evidence of relationships between the gymnarthrids and diplocaulids, the balance seems to favor homology with the supratemporal. This identification is used throughout the present paper.

REVIEW OF NAMED SPECIES OF DIPLOCAULUS

The genus *Diplocaulus* was proposed by Cope (1877) for *D. salamandroides*, a species based on a few vertebrae and part of a lower jaw from the Late Pennsylvanian beds of Vermilion County, Illinois. Subsequently, he described two species from the Permian of Texas, *D. magnicornis* Cope (1882) and *D. limbatus* Cope (1896). Broili (1904) added two more species from Texas, *D. copei* and *D. pusillus*. Case (1911) summarized and revised the work on the genus up to 1911; he pointed out that *D. copei* was indeterminate, since the three specimens described could not be distinguished from *D. magnicornis* and *D. limbatus*, and suggested that *D. pusillus* was of very uncertain assignment and might even be referable to the Family Trimerorhachidae. He recognized both of Cope's Permian species, contrasting them as follows:

D. limbatus Cope

1. Horns terminating in a point and curved inward at ends. The posterior edge of the skull more sharply concave.
2. Anterior edge of the frontal bone but little anterior to the orbit.
3. Vomerine teeth arranged in segment of a broad curve.
4. Anterior end of skull a segment of a broad curve.
5. Sculpture of the facial region distinctly radial from a point between the orbits.
6. Orbits larger.

D. magnicornis Cope

1. Horns terminating more bluntly or with spatulate ends. Not curved at ends. The posterior edge of the skull with a wide concavity.
2. Anterior edge of the frontal nearly midway between the orbits and the nares.
3. Vomerine teeth arranged as wide V with apex forward.
4. Anterior edge of skull sharper.
5. Sculpture of facial region not distinctly radial.
6. Orbits smaller.

Most of these supposed differences appear to be valid when viewed on skulls as distinctly different as those that Case was studying. Additional specimens have shown that there is actually a much greater degree of intergradation in most of the characters.

The most recent comprehensive review of the genus *Diplocaulus* was published by Douthitt (1917). He stated that the only valid character cited in Case's differentiation of *D. limbatus* and *D. magnicornis* is the nature of the postero-lateral horns of the skulls and that even this character will not invariably serve to differentiate skulls. He concluded, however, that there was no reason to question the distinctness of the two species. Douthitt accepted *D. pusillus* as distinct but agreed with Case in questioning the generic reference.

Relatively little taxonomic work on *Diplocaulus* has been done since the publication of Douthitt's paper. In 1918 Williston described two small skulls, U.C. 206 and 207, and assigned them to a new genus and species, *Platyops parvus* Williston. Case (1946) called attention to the fact that *Platyops* was preoccupied and proposed the generic name *Permoplatyops* to replace *Platyops* Williston. As will be shown, *Permoplatyops* seems to be an immature representative of the genus *Diplocaulus* and specifically the same as many of the larger skulls.

Mehl (1921) described a new species, *D. primigenius* Mehl, naming U.C. 564 as the type. The characters of the neural spines and the size and proportions of the vertebrae were considered definitive. The skull of this specimen is used in the present study and is

shown to be a normal member of the more common species. The vertebrae, it is true, pose some interesting problems. Their bearing on taxonomy is discussed below (p. 102). There is no basis for separation of Mehl's species from *D. magnicornis* on the basis of the skull, and analysis of the vertebrae will show that the supposedly definitive characters are subject to another interpretation.

The type of *D. limbatus* Cope, A.M. 4471, consists of a rather poorly preserved skull and lower jaws with vertebrae and part of the shoulder girdle. Few measurements could be taken on the specimen; only the length, orbito-snout length, approximate width of the skull at the termination of the horns, and interorbital width are sufficiently well shown to provide a basis for measurement. Much of Case's revised description was based on referred specimens A.M. 4470 and 4542.

The type of *D. magnicornis* Cope is listed by Case as A.M. 4472. This is an excellent skull (see pl. 5). The specimen labeled as the type in the American Museum of Natural History, however, is A.M. 4539. The species was described in 1882 and A.M. 4472 was not collected until 1896. This has been confirmed by examination of the field notes of C. Sternberg, the collector. The type consists of skull parts, vertebrae and other fragments. Efforts have been made to reconstruct the skull, which is large, perhaps 115 to 120 mm. in length, but it is so poor that few reliable measurements can be made.

The type of neither *D. magnicornis* nor *D. limbatus* is adequate for accurate description, although Cope was able to report in considerable detail on the latter. No skull is known for *D. salamandroides*, so that it cannot enter into the present discussion. My attempts to find additional material at the type locality have met with no success. The type of *D. pusillus* Broili, a very small skull, was in the Munich collections. A small referred skull, A.M. 4523A, figured by Case, has been available for study. There is every indication that this specimen at least is referable to *Diplocaulus*, although Case and others have questioned this assignment, and that it is an extremely immature specimen whose specific affinities are difficult to determine.

This short account summarizes the principal contributions to the taxonomy of the genus. Two species, *D. limbatus* Cope and *D. magnicornis* Cope, have received rather widespread recognition. *D. copei* Broili may be considered invalid, since the specimens upon which the description was based cannot be distinguished from the

other Permian species. *D. pusillus* Broili has been held to be distinct and questionably assigned to the genus *Diplocaulus*. *D. primigenius* Mehl has received little attention since it was named. *D. salamandroides*, the type of the genus, is from an earlier (Late Pennsylvanian) horizon than the Texas specimens. The material representing it is unfortunately so incomplete that it cannot positively be stated on the one hand that any Texas specimen differs from it specifically or, on the other, that the Texas specimens are congeneric with it. The most that can be said is that specific distinctions are likely on stratigraphic grounds and that generic identity is not opposed by the evidence available.

III. SPECIES AND GENUS

Various questions concerning the identity of several specimens here included in the genus *Diplocaulus* have arisen in the past. Williston (1918), for example, assigned U.C. 206 to a new genus, an assignment supported by Case (1946) and others. Case (1911) suggested that the smallest specimen, A.M. 4523A, might belong to the Family Trimerorhachidae, and Douthitt (1917) likewise believed that the specimen did not belong to the genus *Diplocaulus*. Other specimens have been assigned to the genus only tentatively. None of these investigators had access to a series including well-distributed intermediate stages from the smallest to the largest specimens. Now that such a series has been assembled it is possible to make generic assignments with considerable confidence. There are several pertinent items. Throughout the series the dermal bones have similar mutual relationships and a common pattern not found in any other recognized genus. The occiputs, palates and vertebrae, so far as these have been observed, argue strongly for close relationship. In all specimens the articulation of the skull and lower jaw lies well forward on the lateral margin of the skull. In addition to these general morphological similarities, the size distribution, based on the midline length of the skull, shows no marked breaks in continuity from the smallest to the largest specimen. There is continuous and regular change in various characters throughout the series. This will become more evident as regressions and ratios of certain structures are considered. All these factors strongly suggest a close relationship of all specimens included in the sample, a relationship that cannot be thought to transcend the generic level.

The problems of specific differentiation are treated first by appropriate quantitative methods, followed by an analysis of generic characters and comparisons of comparable characters of other genera of amphibians.

SPECIES

Initial examination of the sample, as noted in the introductory remarks, led me to believe that specific differentiation by inspection

was impossible, and thence I adopted as a working basis the hypothesis that there was but a single species with a wide range in shape. From a study of the initial twenty-four regressions, however, two important concepts developed: one, that there were certain relationships of skull parts that were constant throughout all specimens; the other, that there were certain relationships that showed marked deviations, with a tendency toward grouping, and that might serve to differentiate the sample into two or more groups. Two of the initial twenty-four tests gave particular promise in this direction, Test 6, involving orbito-snout length, and Test 10, involving premaxillary length. To these were added others not considered in the preliminary analysis. The results of these studies are summarized in the following paragraphs.

Analysis of Characters

ORBITO-SNOUT LENGTH: The suggestion that this might be a significant measurement came from the regression of orbito-snout length on skull length. The analysis, however, is based on ratios of skull length to orbito-snout length (Table 5), since the figures so obtained are more amenable to the types of study that must be used.

TABLE 5.—RATIOS OF $Sk_l/O-S_l$ IN DIPLOCAULUS

Sk_l	Ratio	Sk_l	Ratio	Sk_l	Ratio	Sk_l	Ratio
14	5.00	65	3.82	89	3.87	114	4.38
19	5.00	68	4.00	89	4.64	114	4.22
23	5.75	70	3.89	95	2.92	115	4.11
24	4.52	75	3.95	97	3.88	118	4.07
31	3.88	75	3.26	101	4.02	119	4.41
50	3.57	82	3.73	107	7.13	119	9.15
63	3.81	85	3.70	110	4.00	127	4.10
						136	7.56

TABLE 6.—FREQUENCY DISTRIBUTION OF $Sk_l/O-S_l$ IN DIPLOCAULUS

Class	No.	Class	No.	Class	No.
2.50-2.99	1	5.00-5.49	2	7.50-7.99	1
3.00-3.49	1	5.50-5.99	1	8.00-8.49	0
3.50-3.99	10	6.00-6.49	0	8.50-8.99	0
4.00-4.49	9	6.50-6.99	0	9.00-9.49	1
4.50-4.99	2	7.00-7.49	1		

Table 6 suggests two groups with discontinuous distribution, one containing twenty-six specimens and the other but three. The three with high ratios are U.C. 1661 and 1648 and A.M. 4470. It should be noted that there is a negative correlation of the ratio of skull length and orbito-snout length on skull length and that values in

excess of 5.00, except for the three specimens cited, occur in skulls less than 24 mm. in length.

A second approach, which is suggestive but not definitive, is through use of the coefficient of variability (V). This must be based, of course, on the ratios and not on direct linear measurements and so is not commensurate with values derived from linear measurements and cannot be compared with such values in estimating real variability. The symbol V_R is used for the coefficient based on ratios. The value thus derived may have meaning, however, if compared with results obtained by similar treatment of data from other sources. In this instance the coefficient of variability derived from ratios is 29.2 from the equation

$$V_R = 1.325 \times 100 / 4.5593$$

The value of V_R from a sample of 104 specimens of *Bufo marinus*, a species that shows a coefficient of variability of 10.0 in orbito-snout length based on linear measurements of adults, has a value of 18.8 for V_R , determined on the basis of the whole sample, using the ratio of skull length to orbito-snout length as in *Diplocaulus*. The sample of *Bufo marinus* is comparable in essentially all respects to that of *Diplocaulus*, consisting of immature and mature individuals and having been collected over a relatively wide area. The value 18.8 is decidedly lower than the 29.2 of *Diplocaulus* in spite of the fact that the coefficient of variability ($V=10$) is moderately high. There is some indication from this comparison that the sample of *Diplocaulus* may not be pure. An alternative explanation might be that *Diplocaulus*, assuming a single species, is excessively variable in the relationship tested; variability to the extent implied, however, is sufficiently rare to be improbable.

LENGTH OF THE PREMAXILLARY: The premaxillary enters into the formation of the preorbital region of the skull along with the frontal bone. Since it has been shown in the initial tests that the frontal length in relationship to skull length is moderately constant in the genus, it might be expected that the shortness of the snout in the three specimens separated from the rest in the preceding paragraph would result primarily from shortness of the premaxillary. Were this the case, the relationships of this bone should provide a particularly sensitive test. Part of the shortness of the snout, however, involves the relative position of the orbits and the frontals so that the premaxillary is not as effective a basis for differentiation as might be thought. Ratios for this relationship are given in Table 7.

TABLE 7.—RATIOS OF Sk_l/Pmx_l IN DIPLOCAULUS

Sk_l	Ratio	Sk_l	Ratio	Sk_l	Ratio	Sk_l	Ratio
14	28.0	70	12.7	98	12.5	119	11.9
23	23.0	75	10.7	101	11.2	119	22.5
31	14.7	80	8.9	107	29.7	136	22.7
50	10.4	82	9.9	110	11.0		
63	15.7	85	10.5	114	9.3		
65	10.0	89	10.9	114	13.4		
65	10.8	95	7.9	115	9.7		
68	11.0	97	10.0	118	14.7		

TABLE 8.—FREQUENCY DISTRIBUTION OF Sk_l/Pmx_l IN DIPLOCAULUS

Class	No.	Class	No.	Class	No.
7.0-8.9	2	15.0-16.9	1	23.0-24.9	1
9.0-10.9	10	17.0-18.9	0	25.0-26.9	0
11.0-12.9	6	19.0-20.9	0	27.0-28.9	1
13.0-14.9	3	21.0-22.9	2	29.0-30.9	1

The frequency distribution based on ratios of skull length to premaxillary length (Table 8) suggests the presence of two groups, using a class interval of 2, but the meaning is somewhat clouded, for the group of five specimens in classes 21.0-22.9 to 29.0-30.9 includes specimens U.C. 1661, U.C. 1648, A.M. 4470, A.M. 4523A and U.C. 206. The first three are large, 107 mm. or more in length, and the last two are very small, 14 and 23 mm., respectively. The two small skulls were included in the large suite of specimens differentiated by the orbito-snout length, while the three large skulls composed the small group. Placement of the small skulls on the basis of the premaxillary is less certain. There are two possibilities: that the small skulls actually belong to the group with which the ratios associate them, or that they pertain to the other group but are separated from it on the basis of ratios that result from differences between adults and juveniles. The scatter diagram (fig. 16) points the way to the most logical explanation.

On the basis of the distribution, the two small skulls could have been modified to give rise to either pattern in the large skulls. If they gave rise to the three large skulls with very high ratios, little change in ratio with increase in skull size occurred. But if this was the case, it must be assumed that the sampling, which was random, produced two very small and three large members of this group but failed to produce any intermediate-sized specimens. This is possible but seems improbable on ecological grounds, as discussed on pages 104-110. There can be little doubt that the three large skulls, U.C. 1661 and 1648 and A.M. 4470, differ significantly in this character from other large skulls. The contention that the two small skulls

actually pertain to the larger suite of specimens and that there was a very rapid change in proportion with increase in skull length is supported by the distribution on the scatter diagram and by distributions based on other characters. Results based on the premaxillary cannot be considered definitive when applied to the smallest skulls but the character is of great significance among large specimens.

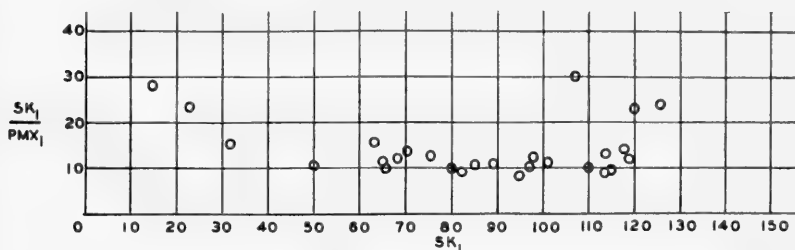


FIG. 16. Scatter diagram of ratios of Sk_1/Pmx_1 on Sk_1 .

Blind adherence to a single quantitative test in this instance would appear to lead to an improper conclusion.

POSTERIOR CURVATURE OF THE SKULL: It was believed, as preliminary analyses were being carried out, that the nature of the posterior curvature would prove to be useful. It is evident that there is considerable difference in the curvature in large skulls (cf. pls. 4-7). It is possible to devise various measurements that will express these differences quantitatively, and several have been used. For Test 14 the following system was used to give a single value that expressed the nature of the curve as desired for our purposes. A line, designated as the X-axis, was projected posteriorly from the midline termination of the skull as a continuation of the midline for the distance of one-half the skull length. A second line, the Y-axis, was constructed normal to X and projected to the level of the horn on either side. This line was then divided into ten equal parts between the midline and the level of intersection with the horn. Using all specimens, $N=32$, a mean value for X, the distance from the posterior margin of the skull to the line Y, was determined for each value of Y; that is, $Y=0$ at intersection of lines X and Y, $Y=1$, $Y=2$, etc. Deviations of X for each specimen at levels of $Y=0$ to 9 were determined and these were totaled and divided to give a mean deviation of X, M_{dx} , for each specimen. Various other methods were used as well, but the results in all

lacked definition and for the most part failed to express conditions as well as the one outlined above.

The results in Test 14 were not clearly definitive, so that the details of the test are not included. If skulls measuring more than 100 mm. only are used, two groups are clearly defined, one consisting of U.C. 1661, 1655 and 1648 and A.M. 4470, and the other including the remainder of the skulls over 100 mm. Posterior curvature will not, however, isolate partially grown skulls from the adults of either group, for the partially grown specimens are somewhat intermediate between the two groups in this character.

HORN LENGTH: Horn length as used in this paper refers to the distance from the level of the posterior termination of the midline of the skull to the tip of the horn, measured parallel to the midline. This measurement is strongly modified with change in skull size and relative growth is distinctly heterogonic. This poses some difficulties in differentiation of species. This characteristic is, of course, reflected in the ratios of Sk_l to horn length (H_l), Table 9.

TABLE 9.—RATIOS OF Sk_l/H_l IN DIPLOCAULUS

Sk_l	Ratio	Sk_l	Ratio	Sk_l	Ratio
23	5.71	89	2.22	118	1.31
31	2.82	98	1.88	119	0.88
65	1.71	101	1.58	119	1.59
65	2.50	105	2.19	120	0.86
68	2.06	107	0.82	127	1.55
70	1.94	110	1.62	136	0.97
85	2.12	114	1.52		

The frequency distribution of the ratios (Table 10) shows a decidedly skewed pattern, since there is a strong positive heterogony in relative growth of horn length in relationship to skull length that is evident in the ratios. In spite of this fact, three specimens, which have been separated on other bases, U.C. 1661 and 1648 and A.M. 4470, appear to be definitely distinct from the remainder, except for U.C. 1655, a specimen that has not entered into any of the previous determinations. If only skulls measuring over 100 mm. are used, and a smaller class interval than is practical for the whole

TABLE 10.—FREQUENCY DISTRIBUTION OF Sk_l/H_l IN DIPLOCAULUS

Class ¹	No.	Class	No.	Class	No.
0.75-0.99	4	1.50-1.74	6	2.25-2.49	1
1.00-1.24	0	1.75-1.99	2	2.50-2.74	1
1.25-1.49	1	2.00-2.24	3	2.75-2.99	1

¹ Value for skull of 23 mm. length, 5.71, falls in class 5.50-5.74. This is not entered in the table since it extends tabulation unnecessarily.

sample is used, separation into two groups is clear. Evidence for the sample as a whole is apparent from study of the relationships shown when the ratios are entered against skull length on double logarithmic paper (fig. 17). The isolation of the four specimens is evident and there are no specimens clearly intermediate between them and the smallest skulls. The remainder, on the contrary, appear to form an integrated pattern that would be expected in

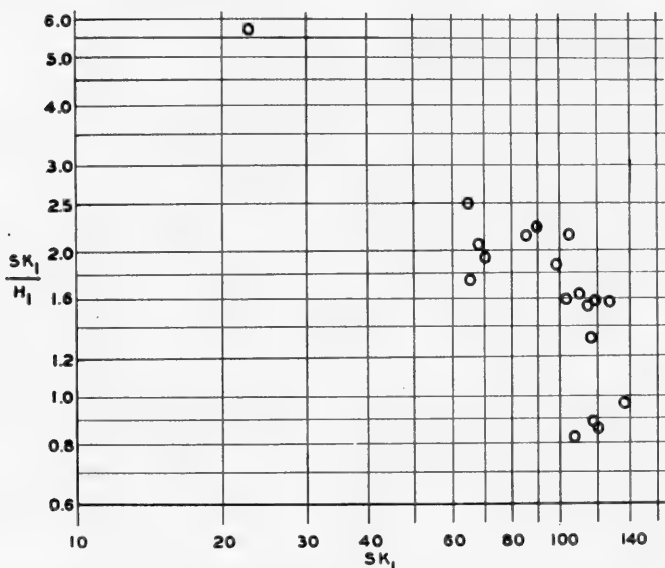


FIG. 17. Scatter diagram of ratios of SK_1/H_1 on SK_1 .

view of the nature of skull changes. This by no means precludes the possibility that the smallest skulls could represent growth stages of the group represented by the four large skulls, but it suggests that this was not the case. As was pointed out in the instance of premaxillary length, the ecological situation has an important bearing on this matter.

NATURE OF THE PARIETAL: The parietal bones seem to show considerable variation in a number of features within the genus, but linear measurements or ratios do not differentiate groups. There is, however, one feature, not readily amenable to measurement, that is important. The dorsal surface of the parietal, particularly of the distal end, assumes two distinct patterns. It is either essentially flat, or it is convex dorsally. Convexity appears in four skulls,

U.C. 1648, 1655, and 1661 and A.M. 4470. This character may be one that does not occur in immature specimens and, although it separates mature skulls into two groups, it may be valueless for very small skulls. From the nature of development of the parietal it appears most probable that the convexity would be evident, in the group in which it appears, by the time the 60 mm. stage of skull length was reached. There is no evidence of it in any skulls over this length except in the four cited.

THE BEARING OF POSTCRANIAL FEATURES: It is reasonable to suppose that differences of sufficient magnitude to allow separation of groups might be present in the postcranial skeleton of *Diplocaulus*, but the generally fragmentary nature of the postcranium in the majority of specimens has made studies of most elements difficult. With the known material, only the vertebrae appear to offer any possibility of fruitful study. The vertebrae of only twelve of the 100 specimens available can be used for comparisons. This results from incompleteness of the columns associated with the skulls, disarticulation of the vertebrae, which makes it impossible to determine their position in the column, and the fact that, although vertebrae are abundant in deposits in which skulls are known, associations of skulls and vertebrae are not common. Only crude quantitative methods can be used. Major differences between vertebrae associated with skulls that are very similar render the available data inadequate for the formulation of reliable conclusions.

The real problem in consideration of the vertebrae is whether or not observed differences have any real taxonomic significance. One species, *D. primigenius* Mehl, has been described on the basis of vertebral structure. The vertebrae in the type, U.C. 564, are certainly atypical in size and in development of the neural spine, but they are almost identical in both respects with the vertebrae associated with the skull of A.M. 4470. U.C. 564 and A.M. 4470 are very different in skull structure and consistently fall into different groups on the basis of skull features. The vertebrae are unknown in other specimens of the group to which A.M. 4470 belongs. Thus the question of the relative value of vertebral and skull patterns arises.

Measurements of the centra along the ventral midline of the sixth vertebra posterior to the occipital condyle are given in Table 11. This particular vertebra was selected, since it could be identified in the largest number of specimens. In the table, skull lengths are grouped on the basis of 10 mm. class intervals and the midpoint of

each class is used for determining ratios. Grouping was used because estimates of skull lengths were necessary for some specimens.

TABLE 11.—LINEAR MEASUREMENTS AND RATIO V_1/Sk_1 IN DIPLOCAULUS

Specimen Number	Sk_1	V_1^1	Ratio V_1/Sk_1
A.M. 4468.....	60-69	15	0.23
U.C. 1658.....	60-69	11	0.17
U.C. 1650.....	80-89	17	0.20
U.C. 1013.....	90-99	18	0.19
U.C. 221.....	90-99	16	0.17
U.C. 1015.....	100-109	25	0.17
A.M. 4478.....	110-119	30	0.22
U.C. 564.....	110-119	33	0.26
A.M. 4470.....	110-119	23	0.29
A.M. 4472.....	120-129	25	0.18
A.M. 4484.....	140-149	25	0.17

¹ V_1 =length of sixth vertebra.

The mean value of the ratios is 0.204. Distribution around the mean shows no significant relationship to skull size. There is, of course, some correlation of skull length and vertebral length. It is possible that distribution determined from an adequate sample would show some integrated pattern of relationship of the vertebral and skull characters. There is, however, no indication of the sort of separation that would be expected were the proportional differences significant as group characters. Additional support of this concept is afforded by the lack of correlation of vertebral and skull differences as shown in the similarities of the vertebrae and the major differences in the skulls of A.M. 4470 and U.C. 564.

Evidence bearing on the causes of differences in vertebrae is slight. As will be shown later, in discussions of the growth of the skulls, certain patterns may be interpreted as resulting from the retention of youthful features of form in large skulls, a possible indication that some factor or factors tending to retard attainment of complete maturity were active. If we assume that the vertebrae of U.C. 564 and A.M. 4470 have fully attained the adult condition, it is apparent that the vertebrae of the other large specimens have failed to attain this status in either size or form. The degree of maturity, if this be the explanation, varies widely in different individuals of approximately the same skull length. A most interesting implication, borne out by specimens with almost complete series of vertebrae, is that there was a marked difference in total body length in specimens with approximately the same skull length. Were a large series of specimens with well-preserved skulls and vertebral columns available, it might be possible to recognize concurrent im-

maturity of vertebrae and skulls in individuals. The material at hand gives no suggestion of such a correlation.

In summary, the following may be said: There is no positive evidence that vertebral characters can be used for specific differentiation. Vertebral variation in length and shape may be due to some factor or factors that acted to retard maturation of the skeleton, but as yet the evidence is merely suggestive.

The Bearing of Ecological Considerations on Group Differentiation

The use of the term species has been carefully avoided to this point in the discussion. We have been able to differentiate structurally two groups of *Diplocaulus*, one composed of a large number of specimens and one of very few. As yet the nature of this difference has not been discussed, since this would have clouded the issue of its mere existence. The two groups might represent two species or might represent the two sexes of one species. In the present section, until this matter has been considered fully, we will designate the group with the majority of individuals as *A* and that with the smaller number, including U.C. 1661, 1655 and 1648 and A.M. 4470, as *B*. The mode of occurrence of the specimens in the deposits and the interpretation of their former environment have an important bearing upon the interpretation of the two groups and upon reference of the smallest skulls in the sample to one or the other. Evidence of this sort, being in part conjectural and in part dependent upon negative evidence, cannot be conclusive in itself. Taken in conjunction with the morphological indications outlined in the preceding paragraphs, however, it does assume real meaning.

All specimens have come from the Arroyo Formation of the Clear Fork Group. Vertebrates occur under a wide variety of circumstances in these beds. A brief review of the nature of occurrences and assemblages is necessary to an understanding of the place of *Diplocaulus* in the fauna.

The Arroyo deposits in Baylor and Wilbarger Counties, Texas, from which the sample was drawn, overlie the marine Lueders limestone but are themselves entirely non-marine in origin. Red clays and sandstones predominate in the exposures in the valley of the Wichita River. In a few places, particularly in the easternmost exposures of the formation, gray and greenish-gray clays occur. Local transitions from red to green are characteristic of both the clays and the sandstones throughout the area. The sandstones occur in broad sheets and as linear deposits with widths seldom exceeding

fifty feet. At various places the linear sandstones grade into fine conglomerates. Over very limited areas, the crossbedding of the sandstones suggests aeolian origin. There is a gentle regional dip to the west in the area, but locally dips, up to about 10 degrees, are random in their orientation. The varied nature of the sediments and irregularities of local structure make it virtually impossible to do detailed stratigraphic studies.

Many specimens of vertebrates occur in the widespread, relatively homogeneous red clays. These clays appear to have been deposited for the most part on flood plains marginal to the streams. Wide expanses of the clays are barren of fossils, some carry scattered, usually disarticulated specimens, and in a few places there are concentrations of well-preserved skeletons, which, under particularly favorable circumstances, may form bone beds. It appears that these concentrations, which have yielded most of the good Arroyo specimens, represent deposits in ponds and ox-bows that lay marginal to the channels of the streams. The "*Labidosaurus* Pocket" in Baylor County, Texas, located by aerial photographs on CUM 3B 65, 7.3-1.1,¹ is one such case. The assemblage, as I have observed it, consists of *Dimetrodon*, *Edaphosaurus*, *Captorhinus*, *Seymouria*, unidentified small forms, and *Diplocaulus*. Another example of such an occurrence is the "*Broiliellus* Pocket," CUM 3B 6, 4.4-7.4, which has yielded *Dimetrodon*, *Edaphosaurus*, *Captorhinus*, *Seymouria*, *Eryops*, *Trematops*, *Broiliellus*, an undetermined genus of Dissorophidae, *Diplocaulus*, and *Xenacanthus*. A notable point concerning such localized assemblages is that the adjacent clays, very similar in appearance, are for the most part barren. Specimens that do occur in adjacent deposits usually consist of isolated bones or badly scattered partial skeletons. Presumably, they were buried some time after death occurred, perhaps during flood stages of the streams, after considerable disarticulation by carnivore action, decomposition, and water action.

An assemblage rather different from these concentrations in the red clays is present in the "*Lysorophus* Pockets" (Olson, 1939), which also occur in the clays but contain nodular masses with *Lysorophus*, small gymnarthrids, *Diplocaulus*, and occasional scraps of large tetrapods. Probably these also represent ponds, possibly drying ponds, in which small amphibians sought refuge by burrowing.

Another type of clay deposit consists of light-colored, homogeneous, gray clay. This type, which is commonly limited in extent,

¹ See E. C. Olson (1948) for use of this index system.

is more abundant in the Upper Clyde than in the Arroyo, but it does occur near the base of the Arroyo in the vicinity of Grey and Pony creeks. In such deposits occur fragmentary remains of carbonized plants, some gypsum crystals, and small concentrations of copper-bearing minerals. From the Upper Clyde, CUM 2B 150, around 3.4–2.6, the following vertebrate assemblage has been observed: *Dimetrodon*, *Ophiacodon*, *Captorhinus*, *Diadectes*, *Trimerorhachis*, *Eryops*, *Archeria*, and *Xenacanthus*. *Diplocaulus* has not been noted here but it does occur in the Grey Creek and Pony Creek localities in the Arroyo, under somewhat similar circumstances. The highly leached, reduced, underclay-like beds in these localities suggest deposition under swamp conditions.

The sandstone deposits appear to have been formed under a variety of circumstances, the majority as moderately widespread sheets on flood plains. They are moderately even-bedded, continuous laterally, little varied in dip, and nearly unfossiliferous. The very few vertebrates found in them are usually fragmentary; in only one instance have I encountered complete skeletons, these being a "nest" of three specimens of *Seymouria* in an extensive, ridge-forming sandstone along the western margin of Brushy Creek, Baylor County, Texas. Argillaceous sandstones, apparently also of flood plain origin, are usually mud-cracked and carry tracks of vertebrates and invertebrates. A few instances of windblown sands have been observed, but they are uncommon and completely barren of fossils.

In some places, for example in an area about one-half mile north of the "*Labidosaurus* Pocket," CUM 3B 64, 7.8–5.8, the sandstones are linear in outcrop and highly varied in dip over very short distances. In the area cited, linear deposits of sandstone with strikes of about N. 60° W. crop out over a considerable area. They show rapid changes in dip, and the sands grade into fine conglomerates at various places. The pattern and the distribution of particles suggest that the deposits were made in stream channels during times of vigorous water flow. It seems probable that the streams were intermittent, dry during part of the year and actively flowing over moderately extended periods. Fossil vertebrates occur sporadically in such sandstones and are usually fragmentary. *Dimetrodon*, *Edaphosaurus*, *Captorhinus*, *Diplocaulus*, and *Xenacanthus* have been recorded from the locality cited.

Certain of the fine conglomerates found in the Arroyo are also presumably of channel origin. There are widespread sheet con-

glomerates, which appear to be of flood plain origin, but they are rare and seldom fossiliferous. Many of the dark brown, fine conglomerates exhibit linear patterns suggestive of channel origin, and occasional junctions of two such deposits, plus a random orientation over limited areas, are interpreted as evidence that the small channels formed part of anastomosing or braided streams. As in the case of the channel sandstone deposits, the conglomerates appear to have been deposited under conditions of alternating wet and dry seasons. A wide variety of vertebrates, mostly fragmentary, have been obtained from the conglomerates: *Dimetrodon*, *Edaphosaurus*, *Diadectes*, *Captorhinus*, *Seymouria*, *Trematops*, *Trimerorhachis*, *Dissorophus*, *Diplocaulus*, and *Xenacanthus*. By far the most abundant are teeth of *Xenacanthus* and scraps of skulls, vertebrae, and girdles of *Diplocaulus*.

This survey of types of occurrences, assemblages, and the general life environment of Arroyo vertebrates is important for an evaluation of the conditions under which *Diplocaulus* lived, and this, in turn, is important in an evaluation of the nature of the differences between the two groups of *Diplocaulus*. It can hardly be denied that *Diplocaulus* was totally aquatic. Although it is recorded from all types of deposits, it is rarely found in those that can be interpreted as originating on flood plains. It is usually considered to have been a somewhat sluggish swimmer, a bottom-living animal that fed on soft foodstuffs, perhaps plants and small invertebrates. The function of the postero-lateral projections of the skull—the horns—is conjectural. It has been supposed that they supported lateral flaps of skin used for swimming in a skate-like fashion. The tail, which is poorly known, was believed by Douthitt (1917) to have been long and tapering, a view based on inconclusive evidence, although a whiplash tail and paired lateral flaps do occur together in a number of aquatic vertebrates. It is interesting to note, however, that it is not until the 100 mm. stage in skull length is reached that excessive breadth of skull is attained; any lateral fin-like structures could hardly have had an important function prior to this stage. No traces of them have ever been found, even in very fine sediments, and the posterior margin of the skull shows no markings that might be associated with such structures. Evidence concerning the presence of lateral flaps is therefore inconclusive, to say the least. The broad skull may well have served some entirely different function than a flap support, even, perhaps, one of aiding in working into sand or mud for protection from predators or during periods of dry weather.

The distribution of Groups *A* and *B* relative to the types of sediments in the area is of importance. Members of Group *A* have been found preserved under a wide variety of conditions, in pond deposits and swamp deposits and also in the sandstones and gravels of channel origin. On the other hand, the specimens that can definitely be referred to Group *B* all came from channel deposits. U.C. 1661 and 1648 were found in coarse sandstone deposited in stream channels. On the basis of the matrix U.C. 1655 and A.M. 4470 appear to have come from conglomeratic channel deposits. Extensive field work and studies of museum collections have revealed no evidence of occurrence of specimens with the characteristics of Group *B* outside of channel deposits. There is an association of specimens of Groups *A* and *B* in only one instance. No specimen with a skull length under 60 mm. has been found in the channel deposits, but this is probably a matter of poor preservation under turbulent conditions, for fragments of small plates and vertebrae have been found.

The conclusions that can be drawn from these ecological considerations, while inevitably based in part on negative evidence, nevertheless appear to be significant in their bearing upon the related questions of the assignment of small specimens to Group *A* or *B* and the meaning of the differentiation of the two groups.

It has been seen that the relationships of the orbito-snout length and skull length point strongly toward an association of the very small skulls with the larger specimens that may definitely be assigned to Group *A*. The other characters based on linear measurements are less definite in this respect, although in each instance reference of the small skulls to Group *A* seems the more logical deduction. The same applies to the nature of the dorsal surface of the parietal. The parietal and the premaxillary show, with little doubt, that all specimens with skull length 60 mm. or greater, except for the four that compose Group *B*, must be referred to Group *A*. It is, thus, only for skulls under 60 mm. in length that any doubt exists. All of these have come from clay deposits.

If it be assumed that any or all of these pertain to Group *B*, it follows that the immature stages of this group were spent in ponds and swamps. This is not impossible, but in order to bring it about the adults would have had to penetrate these breeding grounds. The death of many and the subsequent preservation of some would surely have been inevitable, yet no trace of an adult resembling the members of Group *B* has been found in the clays. We might assume, however, that only the females penetrated the still waters and that

Group *A* represents the females and Group *B* the males. This assumption presupposes that internal fertilization occurred within the group, in contrast to the mode of fertilization in extant amphibians. Even if the possibility of internal fertilization is granted, there remains the serious difficulty that the males, but not the females, must have left the environment in which the eggs were laid prior to reaching the 60 mm. stage, at which time the males would have been little differentiated functionally from the females if the pattern suggested by the small skulls be taken as a criterion for interpretation of the growth pattern. It also becomes necessary to explain the absence of 60 to 100 mm. males in deposits laid down in stream channels in which skulls of not much more than 60 mm. in length are preserved.

The continuity of sizes and form of skulls in the clay deposits and the absence in the clay and in deposits formed in stream channels of any skulls of Group *B* between 60 and 100 mm. in length, strongly imply that all specimens in the clay belong to Group *A*. The difficulty of assuming the two groups to represent males and females of the same species is accentuated by the disparity in numbers. Of perhaps thirty-five specimens that have come from sediments deposited in channels, only four can be assigned to Group *B*.

The total effect of differences in single skull characters upon skull shape and the dynamics of the skull as a leading structure in swimming also contribute something to the interpretation. Adult skulls in Group *A* are broad, flat, and relatively thin-boned, and hence poorly adapted, it would seem, to life in turbulent running water. The orbito-snout region is moderately long, and the eyes, which are thus well back on the skull, are directed dorsally, as in many bottom-living animals. The adult skulls in Group *B*, however, are moderately stream-lined, being narrower posteriorly, with long, posteriorly directed, tapering horns. The bone is thicker and the skulls appear to be somewhat deeper. The orbito-snout length is short, compared to that in Group *A*, and the eyes, lying closer to the tip of the snout, appear to have been directed somewhat forward. This would be expected in a more actively swimming animal. We seem to see, then, a contrast in adaptation, one to life in ponds and swamps and the other to life in rivers and streams. The occurrence of representatives of the first type in channel deposits may well be attributed to floods that swept them from their normal environments into streams, together with large reptiles and more strictly terrestrial amphibians, remains of which also occur in channel

deposits. There is in these observations evidence of a real ecological separation that supports a view that the two groups differ specifically.

In summary we may draw the following conclusions: Groups A and B represent different species. Group A inhabited ponds and swamps, while Group B lived in running water. Group A bred in the area from which the collections have been made, but Group B penetrated the area only during time of high water, following active streams, and presumably bred elsewhere.

Taxonomy

There appear, therefore, to be two recognizable species of the genus *Diplocaulus* in the Arroyo Formation, differing in morphological characters and, apparently, in habitat and adaptations as well. One comprises four individuals in the sample studied and the other the remainder.

The only question remaining is the relation that the various named species bear to these two groups. *D. magnicornis* Cope is the first described Permian species. The skull of the specimen, A.M. 4539, upon which the type description was based,¹ although poor, is clearly a member of the larger series, Series A of the foregoing discussion. This name clearly applies, therefore, to this suite of specimens. The types of *D. primigenius* Mehl and of *Permoplatyops parvus* (Williston) and the referred specimen of *D. pusillus* Broili (the type of which was lost long ago) are, as shown above, members of the same series and accordingly fall into the synonymy of *D. magnicornis*. This is also true of *D. limbatus* Cope. *D. copei* Broili may be rejected as indeterminate, as shown by Case (1911).

Diplocaulus magnicornis Cope

Diplocaulus magnicornis Cope, Proc. Amer. Phil. Soc., 20, p. 453, 1882.

Diplocaulus limbatus Cope, Proc. Amer. Phil. Soc., 34, p. 456, 1895.

Diplocaulus pusillus Broili, Paleontographica, 51, p. 24, 1904.

Diplocaulus primigenius Mehl, Jour. Geol., 29, pp. 48-56, 1921.

Permoplatyops parvus Williston, Contr. Walker Mus., 2, p. 110, 1918.

¹ In addition to the skull, A.M. 4539 formerly included scraps of other, specifically indeterminable skulls, two atlases, two axes, sixteen other complete vertebrae, interclavicle and clavicles and fragments of ribs. The association of these various parts is open to question. An atlas and axis and the third and fourth vertebrae, which are clearly associated with the skull, were described in detail by Cope. The remainder of the specimen, except for the skull, were, strictly speaking, cotypes. To stabilize matters, the skull, atlas and axis and third and fourth vertebrae are here formally designated as the lectotype. The remaining material has been recatalogued as A.M. 4539A.

Type (lectotype): A.M. No. 4539. Skull and four anterior vertebrae from Coffee Creek, Baylor County, Texas.

Hypodigm: Type and A.M. 4466, 4467, 4468, 4469, 4471 (type of *D. limbatus*),¹ 4472, 4473, 4478, 4494, 4498, 4501, 4504, 4509, 4511, 4514, 4523A, 4523B, 4527, 4528, 4530, 4538, 4543, 4589, 4597, 4742. C.N.H.M.-U.C. 206 (type of *P. parvus*), 207, 221, 222, 223, 229, 410, 564 (type of *D. primigenius*), 636, 637, 1013, 1317, 1650, 1652, 1653, 1654, 1656, 1657, 1658, 1660, 1663, P12689. U.S.N.M. 17884.

Horizon: Arroyo Formation, Clear Fork Group, Early Permian.

Diagnosis: Skull length less than five times orbito-snout length and less than sixteen times premaxillary length. Skull length greater than horn length. Surface of parietal bone flat, not convex dorsally.

Remarks: The characters cited in the diagnosis will separate skulls of adult members of this species from those of the other. It is impossible to know whether each would distinguish very small skulls, for no comparable specimens of Series *B* are available to make the necessary tests. It seems highly probable that the relationship of skull length and orbito-snout length would prove definitive. Were it possible to obtain a large representation of the two species in the very small size groups, separation might be made by quantitative studies, but it is improbable that adequate collections will ever be available. The character of the parietal surface almost certainly would not be definitive below a skull length of 50 or 60 mm. The small specimens, those under 60 mm., have been referred to *D. magnicornis* in the present paper on the bases of the relationship of the skull and orbito-snout length, of their apparent association with the adults of the species in various regression patterns, and of ecology.

The regression lines for characters analyzed in the two species would almost certainly prove to be significantly different could comparisons be made, but no regression lines for the second species can be determined.

The other species of *Diplocaulus*, Series *B*, present a less simple case. A specimen referred to *D. limbatus* Cope by Case and used as the basis for the revised description, A.M. 4470, is a member of this species. The type of *D. limbatus*, A.M. 4471, must be referred, as noted, to *D. magnicornis* on the basis of the orbito-snout length,

¹ This specimen does not appear in the tables. It is poorly preserved, but the orbito-snout length is measurable and indicates clearly that it belongs to this series.

one of the few observable characters. A new species must, therefore, be erected for the four specimens in Series *B*. This may be defined as:

***Diplocaulus brevirostris* sp. nov.**

Type: A.M. 4470, skull, vertebrae, and parts of appendicular skeleton. Coffee Creek, Baylor County, Texas. Collected by C. Sternberg, 1896.

Hypodigm: The type and A.M. 4544,¹ C.N.H.M.-U.C. 1648, 1655, 1661.

Horizon: Arroyo Formation, Clear Fork Group, Early Permian.

Diagnosis: Skull length at least seven times preorbital length. Skull length more than twenty-one times length of premaxillary. Horn length greater than skull length. Dorsal surface of parietal strongly convex dorsally.

Remarks: The listed characters apply to adults only, for the young stages of this species are unknown. The smallest known individual has a skull length of 107 mm. The nature of the posterior curvature of the skull will differentiate adults of this species from those of *D. magnicornis*, but it may be noted in plates 1-5 that the pattern of curvature in specimens of *D. magnicornis* of less than 100 mm. skull length, as well as that in A.M. 4514, approaches more closely the curvature in *D. brevirostris* than that in the larger skulls of the species to which they belong. If, however, the regression of horn length and a coefficient of curvature are studied on the basis of the whole sample, a separation of the two species is apparent. The skulls referred to *D. brevirostris* are distinctly mature, the bones are heavy, and the pitting of the dermal surface is highly developed. A basis for specific differentiation may lie in the degree of maturity attained and in the stage at which it is attained, but the sample of *D. brevirostris* is not large enough to more than suggest the possibility. Only one specimen of *D. brevirostris*, A.M. 4470, has associated vertebrae. These are large, mature, and very similar to those of C.N.H.M.-U.C. 564. At present there is no basis for separating the two species on vertebral characters.

¹ This specimen has not figured in the calculations and discussions. It was but recently identified as a member of the species in re-examination of fragmentary materials. Skull length is not available, but the short orbito-snout length is clear indication of its taxonomic position. This specimen, like the other four, was found in conglomerate. It, therefore, adds some strength to the arguments on ecology presented in earlier pages of the paper.

GENUS

Introduction and Methods

In the preliminary crude analyses it was apparent that certain regressions showed a close grouping of points around the regression lines, that is, correlation appeared to be very high, and offered no evidence to suggest that the sample was not homogeneous. These relationships involved the regressions of interorbital width, frontal length, parietal length and interparietal length on skull length. Other regressions, as noted, suggested that two groups might be present; still others showed such a wide scattering of points that their value in taxonomic work, in view of the size of the sample, was questionable.

In the present section attention will be focused on the four measurements that appear to be common to the genus as it is now understood and do not reflect species differences. The mere fact that these relationships are common to the genus in no way implies that they may not be common to other genera as well. They do, however, seem to offer possibilities for generic differentiation and one of the principal functions of this section is to study these relationships and their utility in taxonomic work.

Throughout the remainder of this section the genus will be considered as a unit and comparisons will be made with other genera treated in like manner. This practice affords an approach to the practical matter of differentiation of genera by applications of methods essentially the same as those usually applied to species. It does not imply that genera and species are considered as commensurate units. The samples of genera that have been used have not, of course, been drawn from populations in the strict biological sense of the word but are representative of populations in the statistical sense. It is necessary to analyze patterns of relative growth in various phases of the work. In such instances reference is made to growth patterns of the genus in question. Such patterns represent an estimate based on stages of growth of individuals of the included species of a genus just as the relative growth patterns determined for a single species represent an estimate based on a sample of individuals of that species.

The practical effect of using the genus rather than the species as a unit is, in most cases, to increase the dispersal of values, around a mean or a regression line, as the case may be, over that which obtains within a single species of the genus. In the case of the four measurements used in this study, however, dispersal has not been increased over that determined for *D. magnicornis* alone by inclusion

of specimens of *D. brevirostris* in the sample. It is possible, although improbable, that addition of smaller specimens of *D. brevirostris* would result in a significant modification. The effect of the presence of more than one species in the sample of *Trimerorhachis*, which is used for comparison, cannot be evaluated from the material available, but this is unimportant for present considerations, since our purpose is to treat the genus as a whole.

There is no difficulty in differentiating moderately well-preserved mature skulls of the genus *Diplocaulus* from those of any other known genus. The characters listed in Case's redefinition of the genus (1911) are sufficient for this purpose. That this sort of evaluation is not entirely satisfactory, however, is shown by the confusion that has arisen a number of times in generic assignment of small skulls and poorly preserved or unprepared larger skulls. Small skulls, now known to belong to the genus, have been referred variously to the families Trimerorhachidae and Gymnarthridae. It is to such cases particularly that quantitative methods, especially those involving the most commonly preserved part of the skulls, the central portion, can apply. Thus, if it can be shown that the four features that have been mentioned as being stable within the genus, differ from the same features in those genera that may be confused with *Diplocaulus*, an important step in taxonomic work will have been made.

To test the utility of the four relationships for this purpose, a series of samples of definitely identified specimens of Late Paleozoic amphibians has been studied and compared with *Diplocaulus*. A moderately large sample of *Trimerorhachis*, comprising twenty-four specimens, two specimens of *Trematops*, one of *Batrachiderpeton* (from Watson, 1913) and one of *Euryodus* have been used. The results, of course, are definitive for these genera only, but they suggest that certain of the characters and certain methods may have real value for more extended comparisons. It is possible to demonstrate only that a particular specimen or suite of specimens probably does not pertain to *Diplocaulus*, for lack of significant differences does not show that single specimens or suites of specimens are *Diplocaulus*. Furthermore, it is apparent, as would be anticipated, that not all of the four features are definitive in any one series of comparisons. Each case must be tested individually.

In the course of study of *Diplocaulus* it was found that two series of values, derived by different methods, were useful in expressing the nature of the relationships of the four linear measurements to

skull length, and in comparisons of the genus with other genera. Certain features of the regressions of each measurement on skull length, based on raw data, are of importance for comparison of the nature and patterns of relative growth. Only *Trimerorhachis*, among the Paleozoic amphibians, is represented by a sample adequate for such comparisons. To increase the scope of this approach a sample of *Bufo marinus*, studied by means of X-rays, has also been used for comparison. Ratios of skull length to each of the measurements in question have proven useful in more instances. These facilitate generic comparisons in those cases in which other genera are represented by only a few specimens and in comparisons of individuals with the sample of *Diplocaulus*. The regressions and ratios are, of course, intimately related, but each has its own particular characteristics and utility.

Three of the regressions, those of interorbital width, frontal length, and parietal length on skull length, may be expressed by an equation of the form $Y=a+bX$.¹ The pattern of relative growth is essentially isogonic. The fourth, the regression of interparietal length on skull length, is best expressed by an equation of the form $Y=bX^k$,² the growth pattern being heterogonic. Best fit has been determined by comparison of the coefficients of correlation, r and ρ respectively. This comparison cannot be made directly. The choice

¹ The symbolism throughout the paper has been adopted from *Quantitative Zoology*, by Simpson and Roe (1939), in the belief that this book is more familiar to the majority of North American vertebrate paleontologists than any other standard work. Only in cases in which items not considered in that book are treated in the present paper will the symbols used fail to appear in the appendix of *Quantitative Zoology* (pp. 380-382).

² As pointed out by Huxley (1932) and Simpson and Roe (1939) an equation of the form $Y=bX^k$ is commonly preferable when dealing with relative growth. In many instances, however, the formula for isogonic growth gives equally good approximations, and results obtained using one or the other equation do not differ materially. The advantage of the form $Y=a+bX$, when there is little or no choice of form, lies in the fact that it does not necessitate the use of logarithms and is easier to manipulate. In the present paper I have used $Y=a+bX$ where no choice exists or where better results are obtained from such usage. It should be recognized that use of this equation does not imply that there is no possibility that growth was actually heterogonic.

In studies of the midline for reconstructions of skull outlines in section IV, three of the relationships of bone lengths to skull lengths have been expressed by equations of the form $Y=a+bX$ while a fourth has been given as $Y=bX^k$. The heterogonic relationship is decidedly to be preferred for the last, but the others are better or equally well represented by an isogonic expression. The heterogonic equations for these three relationships, the regressions of Iow , FrI , and Pal on SkI , treated as isogonic throughout the paper are:

$$\begin{aligned} Iow \dots \dots \dots Y &= 0.086X^{1.124} \\ FrI \dots \dots \dots Y &= 0.980X^{0.924} \\ Pal \dots \dots \dots Y &= 0.369X^{0.917} \end{aligned}$$

of function (in this case linear or log) depended upon which was greater, r^2 or ρ^2 , since these values are estimates of how much of the total variance is explained by the equation. The ratios in each instance show a correlated regression on skull length but the value of the constant b is low in all cases under consideration, and, since the patterns of regression are not directly pertinent to growth, the fact that they exist has been neglected in the comparative work. The effect of the existence of regular change in ratios with change in skull length is to increase the spread of the values of the ratios in frequency distributions. They become somewhat less definitive than would be the case were, for example, only adults compared. The purpose of our work, however, is to make comparisons regardless of size, so that the full array of values must be used.

Analyses of *Diplocaulus*

TABLE 12.—PARAMETERS OF ISOGONIC REGRESSIONS OF DIPLOCAULUS

	N	M_X	M_Y	σ_X
I_{ow} on Sk_l	34	86.5±14.8	13.5±2.3	33.0±4.0
F_{rl} on Sk_l	29	82.0±15.2	33.5±6.2	31.2±4.1
Pa_l on Sk_l	32	83.0±14.4	21.0±3.7	31.4±3.8
	σ_Y	b_{XY}	b_{YX}	r
I_{ow} on Sk_l	6.0±0.7	5.20±0.26	0.171±0.009	+0.95
F_{rl} on Sk_l	12.3±1.8	2.53±0.0097	0.392±0.0014	+0.99
Pa_l on Sk_l	7.8±0.9	3.83±0.175	0.248±0.011	+0.97

RELATIONSHIPS OF INTERORBITAL WIDTH AND SKULL LENGTH: The orbits of *Diplocaulus* are circular and closely spaced, being directed dorsally or nearly so. Measurements of interorbital width were made across the frontal normal to the midline of the skull at the level of least interorbital distance. The regression of interorbital width on skull length is treated as isogonic in character. The estimating equation for this regression is $Y=0.171X-2.49$. Parameters for the regression are given in Table 12. Values of the ratios, Table 13, in this instance as in all others, have been obtained by dividing skull length by the values of the measurement in question, in the present case skull length by interorbital width (Sk_l/I_{ow}^1). In determination of the desired parameters, the mean (M) and standard deviation (σ),² the short method, as outlined by Simpson

¹ For abbreviations of linear measurements throughout the paper see explanations following Table 2.

² In cases of very small samples, those under $N=25$, σ has been determined by the formula $\sigma = \sqrt{\frac{\sum(f d^2)}{N-1}}$ and is noted as σ' .

TABLE 13.—RATIOS OF SKULL LENGTHS TO FOUR SERIES OF MEASUREMENTS
IN DIPLOCAULUS

Sk_i	Sk_i/Io_w	Sk_i/Fr_l	Sk_i/Pa_l	Sk_i/Ipl
14	8.24	2.37	3.18	5.60
19	6.33
23	8.21	2.23	3.15	5.75
24	2.67	3.43	4.62
31	9.11	2.26	3.37	4.84
46	6.57	2.12	4.65	4.84
50	8.33	2.50	4.76	4.76
63	6.63	2.17	4.20	4.50
65	6.63	2.20	4.06
65	7.64	3.78
68	2.46	4.00	4.20
70	6.25	2.59	3.50	4.24
73	4.29
75	7.89	2.59	3.57	4.69
81	7.09	3.95	4.05
82	7.45	2.40	4.31	4.56
85	5.82	2.83	3.47	3.95
89	6.84	2.34	4.24	4.36
89	6.36	2.17	3.81	4.68
90	6.93	2.31	4.29	4.29
95	6.99
97	6.47	2.37	3.80	4.58
98	6.24	2.29	3.78	3.66
101	6.12	2.64	3.34	3.97
101	5.94	2.73	3.48	3.74
105	2.28	4.38	4.20
105	3.39
107	5.94	2.55	3.82	3.57
110	6.88	2.42	4.35	4.54
114	6.33	2.59	3.80	4.22
115	5.75	2.44	4.42	4.51
116	2.52
118	5.96	2.46	4.24	4.45
119	6.96	2.43	4.10	4.28
119	5.40	2.83	3.40	4.76
120	4.07
127	5.77	2.54
129
130	4.06	4.40
136	5.66

TABLE 14.—PARAMETERS OF FREQUENCY DISTRIBUTIONS OF RATIOS
IN DIPLOCAULUS

	N	M	σ
Sk_i/Io_w	34	6.745±0.159	0.927±0.112
Sk_i/Fr_l	29	2.442±0.036	0.197±0.026
Sk_i/Pa_l	32	3.914±0.077	0.437±0.055
Sk_i/Ipl	31	4.442±0.087	0.485±0.062

and Roe (1939), has been used. In determination of the parameters of the frequency distribution of Sk_l/Io_w , listed in Table 14, a class interval of 0.5 was used.

RELATIONSHIPS OF FRONTAL LENGTH AND SKULL LENGTH: The relative growth of these dimensions, so far as can be determined from the sample, is isogonic. Pertinent parameters for the regression of frontal length on skull length are given in Table 12. The estimating equation for the regression is $Y=0.392X+1.0$. Values for the ratio of skull length to frontal length (Sk_l/Fr_l) are given in Table 13. Parameters of the frequency distribution of the ratios, determined using a class interval of 0.1, are listed in Table 14.

RELATIONSHIPS OF PARIETAL LENGTH AND SKULL LENGTH: The relative growth of the parietal and skull lengths, as determined from the sample, is isogonic. The estimating equation for the regression is $Y=0.248X+0.42$. Parameters for the regression are listed in Table 12. Values for the ratio of skull length to parietal length (Sk_l/Pa_l) are given in Table 13 and the parameters of the frequency distribution of the ratios, determined using a class interval of 0.2, are given in Table 14.

RELATIONSHIPS OF INTERPARIETAL LENGTH AND SKULL LENGTH: The pattern of relative growth of the interparietal with relationship to skull length is expressed as heterogonic. The estimating equation for the regression of interparietal length on skull length is $Y=0.117X^{1.155}$. Parameters of the regression are as follows:

<i>N</i>	$\log MX$	$\log MY$	<i>k</i>	<i>b</i>
30	1.86256	1.21933	1.155	0.117

Values of the ratios of skull length to interparietal length (Sk_l/Ip_l) are given in Table 13 and the parameters of the frequency distribution of the ratios, determined using a class interval of 0.3, are listed in Table 14.

The data listed in Tables 12-14 are analogous to verbal descriptions of skull characters and may be used in a somewhat similar but more precise fashion. They have an advantage of simplicity and may be used to express relationships of characters at desired growth stages. Their principal advantage, however, is that they are subject to rigid, objective treatment. The limitations of the data are those inherent in small samples. It is probable that, while use of larger samples would modify the values somewhat, addition of more specimens would not alter the results materially. Modifications of

the concept of the genus so far as the characters studied are concerned would be analogous to refinements introduced into verbal analyses by study of additional specimens. In the following paragraphs, the utility of the data will be tested in comparison of genera.

Comparison of Genera

The comparison of genera may be approached in various ways and at several levels. Generic assignments may be, and usually are, based upon characters that, in the opinion of the observer, are significant in the case or cases with which he is dealing. This was the method used in assembling the samples of *Diplocaulus* and *Trimerorhachis* for the present study. It is a necessary preliminary to the types of analyses carried out in the present section. Once the samples have been assembled, various comparisons may be carried out depending upon the objectives of the work and the nature of the comparative material available. The remaining part of section III is devoted to such comparisons.

The various specimens and samples that are here compared with *Diplocaulus* consist of carefully identified materials. At the outset we know that they are generically different from *Diplocaulus*. It has been pointed out that four relationships in the skull of *Diplocaulus* are moderately constant within the genus. Our object is to test these relationships in various ways in order to study their utility in differentiation of other genera from *Diplocaulus* and to determine, as far as possible, if the relationships are characteristic of *Diplocaulus*. To this end, three types of analyses have been made: (1) comparison of regression lines based on raw data; (2) comparison of sample means based on ratios; and (3) comparison of single specimens with the sample of *Diplocaulus* based on ratios.

(1) COMPARISON OF REGRESSION LINES: Regressions expressing relative growth appear to follow a pattern of heterogony in most cases, as brought out by Huxley (1932). In two of the four regressions to be considered in this work (Iow on Sk_l and Pal on Sk_l), the fit of the regression line to the data by the formula $Y=a+bX$ is better than that obtained by using the formula $Y=bX^k$. In the case of Fr_l on Sk_l an equally good fit is accomplished by both formulas. In these three instances the form $Y=a+bX$ has been used. Equations of the form $Y=bX^k$ for each of the regressions have been given in the footnote on page 115. Since only equations of these two forms are pertinent in the present studies, the number of types of differences between regression lines is limited. The most obvious difference is,

of course, that between the two types of formulas. Where it has been found that a certain relationship in one genus has one form and that the same relationship in another genus has the other, a real difference has been demonstrated. Where two or more samples show the form $Y=a+bX$ either a or b may differ or both may differ. Appropriate tests are available to determine the significance of such differences. Significant difference in b (b_{YX} in the regressions as used in this paper) denotes differences in the slopes of the lines. In instances in which significant differences in slope cannot be demonstrated, differences a (a_{YX} as used in this paper) may be important. In those cases where regression lines are parallel, differences of a indicate, in addition to lack of conformity of the point of intercept, lack of coincidence of the two lines. The approach to these problems involves testing the hypothesis that the two or more samples could have been drawn from the same population. In the case of $Y=bX^k$, analogous differences may be tested, k being an expression of slope on a logarithmic plot and b an expression of position. This is clear by comparison of $Y=a+bX$ and the logarithmic form of $Y=bX^k$, which is $\log Y = \log b + k \log X$.

TABLE 15.—MEASUREMENTS OF TRIMERORHACHIS

Specimen number	Sk_l	Io_w	Fr_l	Pa_l	Ip_l
A.M. 4569.....	37.6	11.6	7.0	16.2
A.M. 7116.....	54.4	13.0
A.M. 7116.....	58.5	8.3
A.M. 4895.....	62.3	10.0	18.5	21.5
A.M. 7116.....	65.4	10.3	19.3	23.7
A.M. 7116.....	67.9	10.5	20.7	26.0
A.M. 7116.....	70.6	11.8
U.M. 16009.....	78.7	12.3	22.0	23.5	10.0
U.C. 1104.....	80.0	14.0
A.M. 7116.....	80.7	13.9	23.2	31.2
A.M. 7116.....	81.1	13.2
U.M. 16009.....	81.5	16.6	10.8
A.M. 7116.....	87.5	16.1	26.5	30.5
U.M. 15994.....	89.0	17.3
A.M. 7116.....	102.4	18.1	39.4
U.M. 16009.....	106.0	15.2	27.0	28.1	10.0
U.M. 16009.....	107.1	18.6	36.7	34.8	11.5
U.C. 299.....	109.0	20.0	38.0	31.0	13.0
U.C. 689.....	115.0	21.0	38.5	39.0	13.0
U.C. uncat.....	118.0	20.0	41.0	34.0	12.5
A.M. 4570.....	122.5	23.5	31.3
M.C.Z. 1508.....	131.0	23.4	46.0	36.3	12.3
A.M. 4557.....	141.0	21.8	41.0	46.6
A.M. 4591.....	172.6	31.5

Our efforts in such tests are drastically limited by available materials. Among Paleozoic amphibians, only *Trimerorhachis* has

been available in sufficient numbers to allow comparisons of regression lines. Data for the sample of this genus are given in Table 15. *Bufo marinus* has been studied from a sample comprising 112 individuals. Results of these tests are not included, since they are not germane to the problem, but it should be noted that in all instances highly significant differences occurred. The tests involving *Diplocaulus* and *Trimerorhachis* fall into two categories, tests of differences of slope and tests of differences of position of the regression lines. The former includes analyses of relationships expressed by both the equations $Y=a+bX$ and $Y=bX^k$. These tests involve the general concepts of analysis of variance but, in the tests of slope, we have used the equation of Simpson and Roe (1939, p. 278) and an equation modified from it to be suitable for the use of logarithms. Tests for position have been based on analysis of variance, following the procedure of Tippett (1945).

Tests of Slope: The equation used for these tests so far as regressions conforming to $Y=a+bX$ has been taken from Simpson and Roe, but modified so that t , for evaluation of significance of difference, is attained directly from the equation by using b_{YX_1} (regression coefficient for *Diplocaulus*) minus b_{YX_2} (regression coefficient for *Trimerorhachis*) as the numerator and the Simpson and Roe equation as the denominator. The equation thus becomes as follows:

$$t = \frac{b_1 - b_2}{\sqrt{\frac{\Sigma(d_{Y_1}^2)(1-r_1^2) + \Sigma(d_{Y_2}^2)(1-r_2^2)}{N_1 + N_2 - 4} \left(\frac{1}{\Sigma(d_{X_1}^2)} + \frac{1}{\Sigma(d_{X_2}^2)} \right)}}$$

Entering a table of t , as in Simpson and Roe (1939, p. 206) or Snedecor (1946, p. 65), the significance of difference may be determined. Results for the three regressions tested, interorbital width, frontal length and parietal length on skull length are given in Table 17. N and r for the regressions are given in Table 16.

TABLE 16.—VALUES OF N AND r FOR DIPLOCAULUS AND TRIMERORHACHIS

<i>Diplocaulus</i>	I_{ow}	Fr_1	Pal
Est. Equation	$Y=0.171X-2.49$	$Y=0.329X+1.00$	$Y=0.248X+0.42$
N_1	34	29	32
r_1	+0.970	+0.992	+0.974
<i>Trimerorhachis</i>			
Est. Equation	$Y=0.16X+1.48$	$Y=0.37X-5.52$	$Y=0.241X+7.7$
N_2	24	14	16
r_2	+0.906	+0.995	+0.875

TABLE 17.—RESULTS OF TESTS OF SIGNIFICANCE OF DIFFERENCES OF bYX_1 AND bYX_2 IN *DIPLOCAULUS* AND *TRIMERORHACHIS*

Item	d.f.*	t	P*
<i>Io_w</i>	54	0.58	0.5
<i>F_{r1}</i>	39	1.52	0.1
<i>P_{a1}</i>	46	0.61	0.5

*d.f.=degrees of freedom; P=probability.

It is evident that in none of these three tests does the probability approach a value that allows the interpretation that the difference is significant. Throughout much of the paper a limit of 3σ has been used ($P=0.003$) but in comparisons of regression we will use $P=0.01$, the lowest value for P given in most tables, as the critical level. The results show that the slopes of the three regression lines under consideration cannot be thought characteristic of the genus *Diplocaulus*, since they are not significantly different from those in *Trimerorhachis*.

The relative growth of interparietal length and skull length, as expressed in the regression of interparietal length (Y) on skull length (X) in both *Diplocaulus* and *Trimerorhachis*, is heterogonic and may be expressed by an equation of the form $Y=bX^k$. In order to deal with a rectilinear regression line for comparison the figures must be treated logarithmically. An equation, equivalent to that on page 121, has been used for this purpose:

$$t = \frac{k_1 - k_2}{\sqrt{\left(\frac{\Sigma(d^2 \log Y_1) - \frac{\Sigma(d \log X_1 d \log Y_1)^2}{\Sigma(d^2 \log X_1)}}{N_1 + N_2 - 4} + \frac{\Sigma(d^2 \log Y_2) - \frac{\Sigma(d \log X_2 d \log Y_2)^2}{\Sigma(d^2 \log X_2)}}{N_1 + N_2 - 4} \right)} \times \frac{1}{\sqrt{\left(\frac{1}{\Sigma(d^2 \log X_1)} + \frac{1}{\Sigma(d^2 \log X_2)} \right)}}$$

N_1 is 29 and N_2 is 8 (*Diplocaulus* and *Trimerorhachis* respectively) and the estimating equations giving the value of k are $Y=0.117X^{1.155}$ for *Diplocaulus* and $Y=1.503X^{0.439}$ for *Trimerorhachis*. Using the equation the results in Table 18 are obtained.

TABLE 18.—RESULTS OF COMPARISON OF k (I_{pl} ON S_{kt}) IN *DIPLOCAULUS* AND *TRIMERORHACHIS*

I_{pl}	d.f.	t	P
	33	11.5	<0.01

At the 0.01 level of significance for 30 degrees of freedom, $t=2.750$. Thus it may be concluded that in this test *Trimerorhachis* and *Diplocaulus* are significantly different.

Tests of Coincidence of Lines: For comparable lines in the two genera in which slope does not differ significantly, it is of interest to test the coincidence of lines. This may be approached by the method given by Tippett (1945), an application of analysis of variance to position of regression lines. This proceeds on the hypothesis that two or more samples were drawn from a single population. The samples are combined to form a single sample and are also treated individually. Comparison is then made between the independent (between arrays) and residual (within arrays) sources of variance.¹ Results obtained by this method are given in Table 19.

TABLE 19.—RESULTS OF ANALYSIS OF VARIANCE TESTING COINCIDENCE OF REGRESSION LINES OF I_{0w} , F_{r1} , P_{a1} ON Sk_l IN DIPLOCAULUS AND TRIMERORHACHIS

	N_1^*	N_2^*	<i>d.f.</i>	<i>F</i>	<i>F</i> for $P=0.01$
I_{0w}	34	24	{ Between arrays, 2 Within arrays, 54 }	14.1	5.01*
F_{r1}	29	12	{ Between arrays, 2 Within arrays, 39 }	103.0	5.21*
P_{a1}	32	16	{ Between arrays, 2 Within arrays, 44 }	32.8	5.12

* N_1 applies to *Diplocaulus* and N_2 to *Trimerorhachis*. For I_{0w} based on degrees of freedom between arrays=55; for F_{r1} based on degrees of freedom between arrays=38.

¹Since I have found no instances of use of this method in paleontological literature, a few words of explanation may be in order. The sum of the squares of the residual source of variance are determined for the two samples—more may be used—by the equation:

$$s = \left(\Sigma d^2 Y_1 - \frac{(\Sigma dX_1 dY_1)^2}{\Sigma d^2 X_1} \right) + \left(\Sigma d^2 Y_2 - \frac{(\Sigma dX_2 dY_2)^2}{\Sigma d^2 X_2} \right)$$

where Y_1 and X_1 represent Sample 1 (*Diplocaulus*), and Y_2 and X_2 represent Sample 2 (*Trimerorhachis*). The sum of the squares for variance within arrays is obtained from the expression:

$$\left(\Sigma d^2 Y^1 - \frac{(\Sigma dX^1 dY^1)^2}{\Sigma d^2 X^1} \right) - s$$

where $\Sigma d^2 Y^1$ is the sum of the squares of the deviations of Y from the grand mean, $\Sigma d^2 X^1$ is the sum of the squares of the deviations of X from the grand mean, and $\Sigma dX^1 dY^1$ is the sum of (deviations of Y from the grand mean) \times (deviations of X from the grand mean). To obtain variance in each category the sums of the squares for the independent and residual sources of variance are divided by the degrees of freedom for each. The independent variance is then divided by the residual and the significance of the difference may be obtained from a table of F (variance ratio) as given on pages 222–225 of Snedecor (1946). This method is fully explained by Tippett. The symbols that he used have been converted to those followed in the present paper.

There is a high degree of significance in each of the F values and the hypothesis that the pairs of samples came from the same population is negated. We have found then that, although the pattern of relative growth between the length of the three bones considered and skull length is the same within observed limits of skull lengths, that there is a ratio difference in the relationships considered, that is, the relationship of the linear measurements of the three bones to skull length. This difference is reflected in studies of ratios in a later part of this section. In this aspect of the regression lines there is a real difference between the two genera.

If the various lines be extrapolated to $X=0$ it becomes apparent that a biologically impossible situation occurs. In cases in which Y is negative, a real situation may be expressed when $Y=0$, for the skull may have length prior to the appearance of dermal bones. Dermal bones do not commonly appear in a single, small area and grow by simple accretion or expansion but rather as osteoblasts over a wider area, so that even in a very early stage of development, at the time of first appearance of a bone as an entity, which must be somewhat arbitrarily defined, the bone has a finite and not inconsiderable length as compared with skull length. We cannot say how far back in ontogeny there originated the pattern of relative growth that we have determined for *Diplocaulus* and *Trimerorhachis*. It seems evident, however, that there were drastic changes in the nature of most of the curves in early stages of development. Since this is certainly true for those in which the value of Y is positive, it is almost certainly the case as well in instances where the value of Y is negative, although this is not clearly demonstrated. The pattern in *Diplocaulus* appears to have been established by the 14 mm. stage. If we extrapolate the line, for example, of the regression of parietal length on skull length so that $X=0$, then $Y=0.42$, an impossible situation. Therefore, between $X=0$ and $X=14$, changes not evident in the line of regression must have occurred. Huxley (1932) pointed out that in early embryonic periods, during histological differentiation, growth rates are different from those such as we have determined. In this stage occurred the development of the bones that we are studying. In *Diplocaulus*, since we know the pattern at a very small size, we may surmise that the stage of establishment of the pattern of relative growth that we have determined, followed very closely upon the stage of differentiation of the dermal bones. The evidence in *Trimerorhachis* is less conclusive.

A study of *Bufo marinus* has been made to accompany that of *Diplocaulus*, as noted above. It is apparent in this genus that the pattern in various relationships of skull bones, either isogonic or heterogonic as the case may be, is established at the time, in the metamorphosed individuals, when the limits of the bones can be distinguished in the X-rays. In cases where the bones have not as yet met, if one-half of the distance between bones is added to each, the relationships of the bones to skull length is that which would be predicted by extrapolation of the curve based on larger and more mature individuals. It thus appears that in this species the pattern of relative growth originated at a very early stage, prior to the complete roofing of the skull.

We may assume, on fairly sound evidence, that this was the case in *Diplocaulus* and, on less good evidence, that it was true for *Trimerorhachis* as well. If this is so, the lack of coincidence of regression lines, even though the slope is about the same, has real meaning for any stage that might be expected to occur in the fossil record. How generally the regressions of *Diplocaulus* would differ from those of other Paleozoic amphibians cannot be stated, because of the lack of adequate samples. Regression lines may be characteristic of the genus, but it would require analyses of samples of all amphibians now known plus all those which may be found to even approach a reasonable answer.

(2) COMPARISON OF MEANS: Of the Paleozoic amphibians available for comparative studies, only *Trimerorhachis* is represented by a sufficiently large number of specimens to allow a profitable comparison of means of samples. The procedure involves comparison of the means of the frequency distributions of the ratios.¹ We know that the two samples represent different genera. The problem, then, is whether the variates to be tested for the two samples differ significantly in their means. To make the comparisons the following formula has been used:

$$\sigma_d = \sqrt{\frac{\sigma_1^2}{N_1} + \frac{\sigma_2^2}{N_2}}$$

In no case does $N_1 + N_2$ equal less than 30. For these tests, however, σ' has been used for σ in the equation. In each instance, here as in the following pages, the subscript ₁ refers to *Diplocaulus* and the subscript ₂ to *Trimerorhachis*.

¹ The accurate use of frequency distributions of ratios for comparisons involves the assumption that $Y = a + bX$ expresses the relationships of the pairs of values and that the value of a is 0 or close to 0. To the extent that the data fail to conform to these conditions, inaccuracies are introduced.

TABLE 20.—RATIOS OF SKULL LENGTHS TO FOUR MEASUREMENTS
IN TRIMERORHACHIS

Sk_l	Sk_l/Iow	Sk_l/Fr_1	Sk_l/Pa_1	Sk_l/Ipl
37.6	3.4	2.27
54.4	4.2
58.5	7.1
62.3	6.2	3.37	2.90
65.4	6.3	3.16	2.76
67.9	6.5	3.28	2.61
70.6	6.0
78.7	6.4	3.58	3.35	7.87
80.0	5.8
80.7	6.1	3.48	2.59
81.1	6.1
81.5	4.9	7.54
87.5	5.5	3.30	2.87
89.0	5.1
102.4	5.7	2.60	10.60
106.0	6.9	3.93	3.77	9.30
107.1	5.8	2.85	3.07
109.0	5.5	2.87	3.52	8.38
115.0	5.5	2.99	2.95
118.0	5.9	2.88	3.47	9.44
122.5	5.3	3.91
131.0	6.5	2.85	3.61	10.65
141.0	6.5	3.03
172.6	5.4	3.44

TABLE 21.—PARAMETERS OF FREQUENCY DISTRIBUTIONS OF RATIOS
IN DIPLOCAULUS AND TRIMERORHACHIS

	<i>Diplocaulus</i>			<i>Trimerorhachis</i>		
	N	M	σ'	N	M	σ'
Sk_l/Iow	32	6.745±0.17	0.945±0.12	23	5.859±0.18	0.810±0.12
Sk_l/Fr_1	30	2.442±0.04	0.194±0.03	13	3.210±0.09	0.372±0.07
Sk_l/Pa_1	32	3.914±0.08	0.446±0.06	16	3.080±0.08	0.442±0.08
Sk_l/Ipl	31	4.442±0.11	0.494±0.06	8	8.983±0.32	1.090±0.27

Comparison of *Diplocaulus* and *Trimerorhachis*: Ratios for *Trimerorhachis* are given in Table 20 and the parameters for the frequency distributions in the two genera in Table 21. Results of calculations determined for d/σ_d , with σ_d determined from the equation cited in the preceding paragraph, are summarized in Table 22.

It is evident that the means of the two samples are significantly different for each of the comparable frequency distributions. Samples of *Diplocaulus* and *Trimerorhachis* can be separated by use of the means of the ratios of the skull length to the four linear measurements.

TABLE 22.—RESULTS OF COMPARISONS OF MEANS
IN DIPLOCAULUS AND TRIMERORHACHIS

	d/σ_d
Sk_l/Iow	3.7
Sk_l/Fr_1	-7.1
Sk_l/Pa_1	6.1
Sk_l/Ipl	-11.5

Materials to extend such tests to other Paleozoic genera are not available. It would be desirable to conduct such tests on *all* known genera of Late Paleozoic amphibians, for only by such a complete series of tests could it be determined whether or not the ratios of *Diplocaulus* are probably characteristic of the genus. Tests involving comparison of means, as used in such cases, can, of course, be made only on samples of known composition. Their function is not to differentiate samples, although such use may be made of means by slightly different methods, but to test the differences in one or more features between groups known to be different on other bases.

It must be emphasized that a significant difference in the means does not imply that all or even a large percentage of the specimens in one sample would show a significant difference from the other sample in the character tested. This is made clear in the next series of tests, which involve comparison of single specimens of *Trimerorhachis* with the sample of *Diplocaulus*. It is possible, however, in any large sample, to calculate the percentage of specimens that probably would be significantly different.

(3) COMPARISON OF SINGLE SPECIMENS WITH DIPLOCAULUS: Determination of the probability that a single specimen could have been drawn from a "population" from which a sample was derived, in this instance the sample of *Diplocaulus*, is by far the most useful of the methods discussed in this section in view of the difficulty of obtaining adequate samples of most genera. The procedure involves determining the absolute distance (expressed by d) of the appropriate value for the specimen being tested from the mean of the sample with which comparison is being made, and division of this value by the standard deviation of the sample (σ). The probability that it could have been drawn from the population is readily determined from the value of d/σ . As before, we will use 3σ as the critical level of significance.

The simplest approach to this problem is to determine 3σ for each of the desired frequency distributions of the sample and the value of d for the appropriate characters of each specimen. Whether or not the difference is significant can then be determined by inspection. Since, however, 3σ has been arbitrarily selected, more precise figures from which probabilities may be determined have been obtained in the present work from d/σ .

In each of the cases tested, the approach is designed to test the utility of the ratios when used in the manner outlined, for, of course,

it is already known that the specimens are not *Diplocaulus*. As in earlier tests, the results are definitive only for the genera tested and few generalizations can be made.

Trimerorhachis and *Diplocaulus*: In each of the four series of ratios all specimens of *Trimerorhachis* that have yielded a particular measurement are tested against the sample of *Diplocaulus* by the method outlined above. The results of the tests are shown below in Table 23. For rapid estimation the values of 3σ are also entered. For M and σ of *Diplocaulus* see Table 14.

TABLE 23.—COMPARISONS OF SINGLE SPECIMENS OF TRIMERORHACHIS WITH THE SAMPLE OF DIPLOCAULUS

Sk_l	Sk_l/I_{ow}		Sk_l/Fr_l		Sk_l/Pa_l		Sk_l/Ip_l	
	d	d/σ	d	d/σ	d	d/σ	d	d/σ
	Values of 3σ for <i>Diplocaulus</i>							
	Sk_l/I_{ow}		Sk_l/Fr_l		Sk_l/Pa_l		Sk_l/Ip_l	
	2.781		0.592		1.411		1.454	
37.6	3.325	3.6	1.63	3.7
54.4	2.545	2.6
58.5	0.350	0.4
62.3	0.545	0.7	-0.93	-4.8	1.01	2.3
65.4	0.305	0.3	-0.72	-3.7	1.25	2.8
67.9	0.254	0.3	-0.84	-5.3	1.30	2.9
70.6	0.745	0.8
78.7	0.345	0.4	-1.13	-5.7	0.56	1.3	-3.43	-7.1
80.0	0.945	1.0
80.7	0.645	0.7	-1.04	-5.3	1.42	3.2
81.1	0.645	0.7
81.5	1.845	2.0	-3.10	-6.4
87.5	1.245	1.3	-0.86	-4.4	1.04	2.4
89.0	1.645	1.8
102.4	1.045	1.1	1.31	3.0	-6.16	-12.9
106.0	0.155	0.2	-1.48	-7.5	0.24	0.6	-4.86	-10.1
107.1	0.945	1.2	-0.41	-2.1	0.84	1.9	-3.94	-8.1
109.0	1.245	1.3	-0.33	-1.7	0.39	0.9
115.0	1.245	1.3	-0.55	-2.8	0.96	2.2
118.0	0.845	0.9	-0.44	-2.3	0.44	1.0	-5.0	-10.3
122.5	1.445	1.1	0.00	0.0
131.0	1.145	1.2	-0.41	-2.1	0.30	0.7	-6.2	-12.2
141.0	0.245	0.3	0.87	1.9
172.6	1.345	1.4	-1.00	-5.1

Table 23 shows that the probability of differentiating a specimen of *Trimerorhachis* from the sample of *Diplocaulus* by this method is low, for Sk_l/I_{ow} and Sk_l/Pa_l . The ratio Sk_l/Fr_l accomplishes a separation in eight of thirteen cases tested. In only one case is $d/\sigma < 2$. The values of d/σ in the case of Sk_l/Ip_l are so high that differentiation probably will occur in all cases that may be encountered.

Trematops and *Diplocaulus*: Although these genera are only distantly related they have certain resemblances, particularly in midline characters, that could prove confusing in small specimens. The following tests serve to illustrate ready means of differentiation. Linear measurements, ratios and results of tests of significance are given in Table 24.

TABLE 24.—LINEAR MEASUREMENTS AND RATIOS OF TREMATOPS, AND SIGNIFICANCE OF DIFFERENCES FROM DIPLOCAULUS

Specimen number	Linear Measurements				
	Sk_1	Io_w	Fr_1	Pa_1	Ip_1
M.C. 1584	70	17	19	15	7.5
M.C.Z. 1414	74	16	23	17	8.5
A.M. 4205	145	30

Sk_1	Ratios			
	Sk_1/Io_w	Sk_1/Fr_1	Sk_1/Pa_1	Sk_1/Ip_1
70	4.1	3.7	4.7	8.7
74	4.6	3.2	4.3	9.3
145	4.8

Sk_1	Significance of Differences							
	Sk_1/Io_w		Sk_1/Fr_1		Sk_1/Pa_1		Sk_1/Ip_1	
	\bar{d}	d/σ	\bar{d}	d/σ	\bar{d}	d/σ	\bar{d}	d/σ
70	2.645	2.8	-1.258	-6.4	-0.786	-1.8	-4.858	-10.0
74	2.145	2.3	-0.758	-3.8	-0.386	-0.9	-4.258	-9.2
145	1.945	2.1						

Neither the ratio Sk_1/Io_w nor Sk_1/Pa_1 shows significant differences from the mean of the sample upon the basis of 3σ , but the values of Sk_1/Io_w do show probabilities of less than 0.04 in all cases and of 0.005 in the case of U.C. 1584. Both examples of the other two ratios show significant differences from the sample of *Diplocaulus*. The results in general agree with those obtained in comparisons of single specimens of *Trimerorhachis* with the sample of *Diplocaulus*.

Batrachiderpeton and *Diplocaulus*: The data on *Batrachiderpeton*, Table 25, have been taken from the illustrations given by Watson (1913). This genus is of particular interest in view of the fact that it is a Pennsylvanian relative of *Diplocaulus*. If it be assumed that it is near to the ancestral line of *Diplocaulus*—and there is some evidence to support such a conclusion—the comparisons give insight into certain changes that have occurred in the evolution of *Diplocaulus*. A single specimen is hardly adequate for reliable conclusions but the comparisons, at least, give some insight on the general direction if not the magnitude of changes. Tabulations for comparative purposes are included in Table 25.

TABLE 25.—LINEAR MEASUREMENTS AND RATIOS OF *BATRACHIDERPETON*, AND SIGNIFICANCE OF DIFFERENCES FROM *DIPLOCAULUS*

<i>Linear Measurements</i>									
<i>Sk_l</i>		<i>I_{ow}</i>		<i>Fr_l</i>		<i>Pa_l</i>		<i>I_{pl}</i>	
38		15		9		14		7	
<i>Ratios</i>									
<i>Sk_l/I_{ow}</i>		<i>Sk_l/Fr_l</i>		<i>Sk_l/Pa_l</i>		<i>Sk_l/I_{pl}</i>			
2.35		4.22		2.07		5.43			
<i>Significance of Differences</i>									
<i>Sk_l/I_{ow}</i>		<i>Sk_l/Fr_l</i>		<i>Sk_l/Pa_l</i>		<i>Sk_l/I_{pl}</i>			
<i>d</i>	<i>d/σ</i>	<i>d</i>	<i>d/σ</i>	<i>d</i>	<i>d/σ</i>	<i>d</i>	<i>d/σ</i>		
4.215	4.4	-1.778	-9.0	0.844	1.3	0.988	2.0		

If we may consider the differences of the single specimen of *Batrachiderpeton* from the sample of *Diplocaulus* as a general indication of generic differences between the two, certain interesting points may be made. The ratio of Sk_l/I_{ow} of *Batrachiderpeton* is significantly different from that of *Diplocaulus*. In Watson's discussion (1913) of bone homologies of the orbital region, he stressed the effect of lessening interorbital width in the morphological changes by which *Batrachiderpeton* might approach the condition of *Diplocaulus*. This, being written when relatively few specimens of *Diplocaulus* were known, particularly in the smaller sizes, might be open to question on the basis that comparison did not take into consideration the pattern of growth in *Diplocaulus*. But here we see that the difference is significant even when a large sample including a wide range of sizes is considered. Inasmuch as there is actually a negative regression of the ratios on skull length, it becomes apparent that the condition compared is more pronounced when specimens of *Diplocaulus* of about the same skull length as *Batrachiderpeton* are considered than when the latter is compared with large specimens of the former. Furthermore, it may be noted that the differences in the ratios is in contrast to the lack of significant differences in the comparison of the labyrinthodonts *Trimerorhachis* and *Trematops* with *Diplocaulus*. In all genera tested to this point, the ratio of Sk_l/Pa_l is similar. The ratio Sk_l/Fr_l of *Batrachiderpeton* is decidedly different from that of *Diplocaulus*, so different that it appears improbable that any of the values that might be obtained from a sample of *Batrachiderpeton* would fail to show significance. It is difficult, and probably incorrect, to apply to this case the methods of Simpson and Roe (1939) for determining the probable variability of a taxonomic unit represented by a single specimen,

since the method involves the coefficient of variability (V), which has questionable applicability in a group without definable terminal growth (see discussion, pp. 144-149). The ratio of Sk_l/Ipl is not clearly significantly different in *Batrachiderpeton* and the sample of *Diplocaulus* ($d/\sigma=2.0$). This is in striking contrast to the situation with respect to *Trimerorhachis* and *Trematops*, in which the difference shows a high level of significance.

Euryodus and *Diplocaulus*: *Euryodus* is a gymnarthrid and probably more closely related to *Diplocaulus* than *Trimerorhachis* or *Trematops*. The skulls of gymnarthrids are subject to confusion with small skulls of *Diplocaulus* unless certain critical structures are visible. If it is possible to show that there is a good chance of differentiation, using midline characters, which are commonly preserved, difficulties of differentiation will have been much reduced. Linear values, ratios, and the significance of comparisons with *Diplocaulus* are given in Table 26.

TABLE 26.—LINEAR MEASUREMENTS AND RATIOS OF EURYODUS AND SIGNIFICANCE OF DIFFERENCES FROM DIPLOCAULUS

Linear Measurements							
Sk_l	Io_w	Fr_l	Pa_l	Ipl			
32	10.0	7.2	11.8	5.5			
Ratios							
Sk_l/Io_w		Sk_l/Fr_l		Sk_l/Pa_l		Sk_l/Ipl	
3.2		4.4		2.7		5.8	
Significance of Differences							
Sk_l/Io_w		Sk_l/Fr_l		Sk_l/Pa_l		Sk_l/Ipl	
d	d/σ	d	d/σ	d	d/σ	d	d/σ
3.545	3.8	-1.958	-9.9	1.214	2.8	1.358	2.8

As in the case of *Batrachiderpeton*, Sk_l/Io_w and Sk_l/Fr_l differ significantly in *Euryodus* from the sample of *Diplocaulus*. The values of d/σ in these two sets of comparisons are quite comparable. Likewise Sk_l/Pa_l and Sk_l/Ipl are not certainly significant, although both, in which $d/\sigma=2.8$, are very near the selected level of 3σ .

The two lepospondyls tested against *Diplocaulus* show a common pattern of differences and the two labyrinthodonts another common pattern. That this is more than coincidental for the two groups cannot be demonstrated from the limited materials available for study. There is, however, a suggestion here of an area for additional study, for should some such pattern emerge from more extensive

investigation, the sample of *Diplocaulus* might prove of considerable value in determining the major affinities of specimens that are difficult to place.

IV. GROWTH AND VARIATION

METHODS

The data thus far presented have indicated that the most profitable approach to studies of problems of growth and variation in the skulls of *Diplocaulus* would be through analysis of changes of total shape. This could be supplemented by more detailed analyses of changes of individual bones but, for the present, studies have been limited to the broader problems of shape change.

The problems of changes of shape with changes in size are complex and special methods must be applied to various cases. It was found in the present studies that none of the more conventional methods was satisfactory. Deformed co-ordinates, for example, give a moderately satisfactory visual concept of changes but do not permit a comprehensive quantitative analysis, and various graphical and numerical methods were abandoned in favor of the ones discussed below, either because they did not give an adequate concept of change or because they could not be applied because of incompleteness of materials.

The change of shape with size, as used, is based upon change in size as expressed by increase in length of midline length of the skulls. Certain general conclusions may be reached by inspection of the specimens of the sample. Maximum width increases disproportionately with respect to skull length. There appear to be marked differences in skull width in skulls that do not differ markedly in length. These differences are sufficient to lead the observer to expect only moderate correlation between increase in skull length and increase in width. There is, further, a suggestion that increase in width will show a positive heterogonic relationship to increase in length.

To test the validity of these observations it has been necessary to apply quantitative methods. Since the skull as a whole is subject to changes in size, there is no point that can be considered as stable within the area defined by the outline of the skull. It would be possible, of course, to select any point that could be determined on all specimens, and use it as a basis for measurements, arbitrarily

assuming it to be fixed, but this could give no more than an approximation of true conditions. It has been found more practical and realistic to recognize total plasticity and base measurements on a series of points whose relationships to change in midline skull length, the base measurement, may be understood. Since we are dealing with changes of shape of the whole skull, and not of component bones and bone limits or junctions, or positions defined by other skull features, points may be used only if their relationships to the basic change in size are relatively simple. None of the definable points along the skull margin, except the anterior and posterior termination of the midline, bear simple relationships to change in skull length. Points defined by sutural junctions, such as that of the parietal, supratemporal, and squamosal, do not show uniform and simple changes as the skull length increases. It has been shown, however, that a series of points along the midline—(1) the level of the anterior orbital margin, (2) the junction of the parietal and frontal, and (3) the junction of the parietal and interparietal—do show a relatively simple and regular relationship to change in skull length in *D. magnicornis*. These points, plus the posterior termination of the midline and the horn tips, may be used as base points at which significant measurements of skull width may be made. The point of intersection of a line through these points, normal to the midline, and the skull margin is significant since it relates a point on the skull margin to a point that shows regular change in skull length.

Points of intersection, so derived, migrate laterally as skull length increases and the length of the lines between the points defined on the left and right sides of the skull may be taken as a measurement of skull width at homologous levels along the midline. Using the five levels specified in the preceding paragraph, we may derive the following measurements of width:

W_1 =Width at anterior margins of orbits.

W_2 =Width at junction of frontal and parietal.

W_3 =Width at junction of parietal and interparietal.

W_4 =Width at posterior termination of midline of skull.

W_5 =Width at posterior termination of horns.

Measurements of skull length pose difficulties much like those encountered in width measurement, for homologous points along the posterior margin of the skull cannot be used because of the difficulty of determining their location and because of their variability in position. Length measurements should show some dependency

TABLE 27.—MEASUREMENTS OF SKULL WIDTH (*W*) IN DIPLOCAULUS

Specimen number	<i>W</i> ₁	<i>W</i> ₂	<i>W</i> ₃	<i>W</i> ₄	<i>W</i> ₅
A.M.N.H. 4523A	7	11	12	14	13
U.C. 206	13	15	19	20	22
A.M.N.H. 4523B	12	16	24	25	23
A.M.N.H. 4752	20	30	39	40	40
U.C. 229	40	54	59	63	57
A.M.N.H. 4485	27	37	45	51	54
A.M.N.H. 4589	45	73	88	98	..
U.C. 222	45	77	90	101	95
U.C. 1663	52	78	87	98	92
U.C. 1658	47	72	84	98	108
X.U.C. 223	51	76	101	109	...
A.M.N.H. 4511	..	95	125	146	...
U.C. 410	60	88	106	123	143
P12689	56	97	115	123	118
U.C. 1650	62	..	133	156	159
A.M.N.H. 4512	66	118	147	180	...
U.C. 1013	77	186	...
A.M.N.H. 4504	80	126	164	186	...
U.C. 221	72	105	110	135	120
A.M.N.H. 4469	74	124	171	202	...
U.C. 1015	77	114	170	200	260
A.M.N.H. 4494	75	200	245
A.M.N.H. 4514	78	126	155	176	193
U.C. 564	98	135	205	238	340
A.M.N.H. 4498	85	128	201	248	...
A.M.N.H. 4466	100	157	212	265	350
A.M.N.H. 4467	80	127	193	248	370
U.C. 636	76	138	194	233	360
A.M.N.H. 4472	103	167	217	255	398
A.M.N.H. 4501	112	180	250	314	...

TABLE 28.—MEASUREMENTS OF SKULL LENGTH (*L*) IN DIPLOCAULUS

Specimen number	<i>L</i> ₁	<i>L</i> ₂	<i>L</i> ₃	<i>L</i> ₄	<i>L</i> ₅
A.M.N.H. 4523A	15	15	14	12	11
U.C. 1660	18
U.C. 200	23	25	26	27	27
A.M.N.H. 4523B	21	21	22	21	24
A.M.N.H. 4752	26	29	31	44	44
A.M.N.H. 4485	52	62	62
A.M.N.H. 4589	72	77	80
U.C. 222	70	77	100	113	113
U.C. 1663	70	78	87	93	88
U.C. 1658	71	80	94	99	99
U.C. 223	72	82	88	100	..
U.C. 410	83	90	100	107	115
P12689	93	98	118	122	107
U.C. 1560	98	107	..	140	..
A.M.N.H. 4512	99	105	115	125	135
U.C. 1013	95	102	131
A.M.N.H. 4504	103	112	114	121	..
U.C. 221	105	127	150	152	156
A.M.N.H. 4469	104	113	121	127	140
U.C. 1015	102	112	121	134	149
A.M.N.H. 4473	115	123	148
A.M.N.H. 4514	118	128	146	153	169
U.C. 564	114	121	134	146	155
A.M.N.H. 4498	116	127	137	153	157
A.M.N.H. 4466	120	130	140	147	162
A.M.N.H. 4467	119	131	142	157	165
J.C. 636	120	146	147	159	168
A.M.N.H. 4472	131	131	154	172	185

upon variations that appear in the width measurements. Series of points determined on equally spaced lines, as used for example in Test 14 (pp. 99-100), fail in this respect, since they do not take into consideration the changes in relative rates of width change with increase in skull length. The points along the posterior margin likewise should bear relationship to changes in midline skull length. To accomplish these two aims it was necessary to depend primarily upon the points established for width measurements along the lateral margins of the skulls. Through each of the points determined for width measurements lines parallel to the midline were drawn to intersect the posterior margin of the skull and to a line constructed normal to the midline at the level of the tip of the snout. The lengths of the various lines so constructed were designated as L . In addition, a more medial measurement was derived by constructing a line parallel to the midline of the skull through the center of the orbit. It can be shown that the distance from the midline to the level of this line changes in essentially isogonic relationship to skull length with increase in that length. This gives six possible measurements of length. Construction of the various lines, however, showed that the line through the point marking W_4 did not in all cases intersect the posterior margin of the skull and that some of its values were not commensurate with those of the other five measurements. This line was therefore discarded as a measure. The measurements used for length are thus as follows:

- L_1 =Length at level of center of orbit.
- L_2 =Length at level of termination of W_1 .
- L_3 =Length at level of termination of W_2 .
- L_4 =Length at level of termination of W_3 .
- L_5 =Length at level of termination of W_5 .

The combined use of width and length measurements determined by these methods made it possible to study related changes in lateral and longitudinal growth. The changes can be nicely evaluated along two axes to give a quantitative picture of skull changes. Measurements for values in the sample are given in Tables 27 and 28.

GROWTH OF SKULL

Analysis of Growth

Using values of skull widths, skull lengths, and appropriate values from the midline and orbital regions, we may obtain mean values of the skull dimensions at desired size levels based on skull

length. By plotting these values a series of reconstructions of mean skull patterns may be obtained. The series of stages shown in figure 18 (20, 40, 60, 80, 100, 120, and 140 mm. stages) has been developed in this way. Lines between plotted points have, of course, been sketched on the basis of knowledge of the marginal patterns of the species. These drawings, while merely graphical expressions of values calculated from the various equations, are most instructive in a study of the general patterns of growth in *D. magnicornis*.

In order that plotting might be undertaken it was necessary to determine equations for the regressions of each series of measurements involved in skull length. It will be noted that some of the equations are of the form $Y=bX+a$ and others of the form $Y=bX^k$. These indicate isogonic and heterogonic patterns of change, respectively. The best fit for each regression was determined by comparison of the squares of the coefficients of correlation, r^2 for the rectilinear equation and ρ^2 for the logarithmic equation. In cases where ρ^2 was appreciably greater than r^2 , the form $Y=bX^k$ was used, but where r^2 was greater than ρ^2 or the two were approximately equal, the form $Y=bX+a$ was used. The equations, in which X is skull length and Y the measurement in question, are as follows:

<i>Pmxl</i> ¹	$Y = 0.1076X - 1.06$
<i>Frri</i>	$Y = 0.329X + 1.00$
<i>Pal</i>	$Y = 0.248X + 0.42$
<i>Ipl</i>	$Y = 0.117X^{1.155}$
<i>O-Si</i>	$Y = 0.1183X^{1.172}$
<i>Iow</i>	$Y = 0.171X - 2.49$
<i>Ow</i>	$Y = 0.1442X + 0.976$
<i>W₁</i>	$Y = 0.82X - 6.06$
<i>W₂</i>	$Y = 1.35X - 15.53$
<i>W₃</i>	$Y = 0.5443X^{1.227}$
<i>W₄</i>	$Y = 0.2697X^{1.417}$
<i>W₅</i>	$Y = 0.2534X^{1.413}$
<i>W₅</i> (100 to 140 mm.).....	$Y = 0.0343X^{1.923}$
<i>L₁</i>	$Y = 1.04X - 0.24$
<i>L₂</i>	$Y = 1.14X - 6.2$
<i>L₃</i>	$Y = 0.7875X^{1.103}$
<i>L₄</i>	$Y = 0.5769X^{1.189}$
<i>L₅</i>	$Y = 0.5663X^{1.225}$

Each of the seventeen equations for the regression lines has been determined by the method of least squares. From them the value of Yc (calculated value of Y at the desired level of skull length) has been determined, using the appropriate relationship. The results of these determinations at 20 mm. intervals, beginning with $X=20$, are given in Table 29. The plotted mean skull shapes are

¹ For explanation of abbreviations see Table 2.

based on these figures. It should be noted that in the case of W_5 it was necessary to use two equations to take into account the rapid change in rate of relative growth that took place between the 80 and 100 mm. stages.

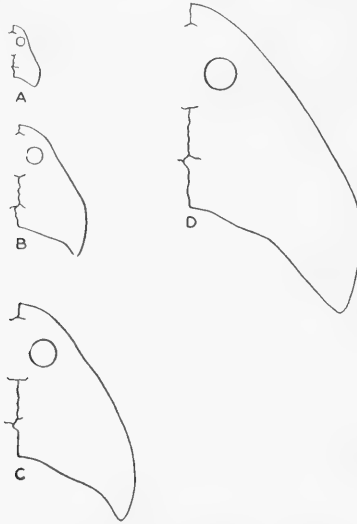


FIG. 18a. Mean growth stages of *Diplocaulus* reconstructed from estimating equations. $\times \frac{1}{3}$. A, 20 mm. stage; B, 40 mm. stage; C, 60 mm. stage; D, 80 mm. stage.

TABLE 29.—VALUES FOR PLOTTING MEAN SKULL STAGES OF DIPLOCAULUS

Skull width (X)	20	40	60	80	100	120	140
Pm _l	1.09	3.24	5.40	7.55	9.70	10.85	13.00
Fr _l	8.84	16.68	24.52	32.36	40.20	48.04	55.88
Pa _l	5.44	10.40	15.36	20.32	25.28	30.24	35.20
Ip _l	3.72	8.29	13.24	18.48	23.88	29.49	35.22
O-S _l	3.96	8.92	14.35	20.10	25.80	32.30	38.80
Io _w	0.93	4.35	7.77	11.19	14.63	18.07	21.49
O _w	3.86	6.74	9.63	12.88	15.40	18.28	21.16
W ₁	10.34	26.74	43.14	59.54	75.94	92.34	108.74
W ₂	11.65	38.65	65.65	92.65	119.65	146.65	173.65
W ₃	21.50	50.40	82.70	117.80	154.80	193.60	233.90
W ₄	18.81	50.22	89.21	134.10	184.00	238.20	296.40
W ₅	17.47	46.51	82.49	123.70 ¹	240.60	341.60	459.60
L ₁	20.80	41.36	62.16	89.96	103.76	124.56	145.86
L ₂	22.18	44.98	67.78	90.58	113.38	136.18	158.98
L ₃	21.40	46.10	72.00	98.90	126.60	154.70	183.40
L ₄	20.30	46.30	75.50	105.60	137.80	171.10	205.50
L ₅	22.20	52.00	85.40	121.50	159.60	199.60	241.00

¹Two values given. The lesser (used in plotting) calculated from $Y=0.2534X^{1.413}$ and the greater from $Y=0.0343X^{1.923}$.

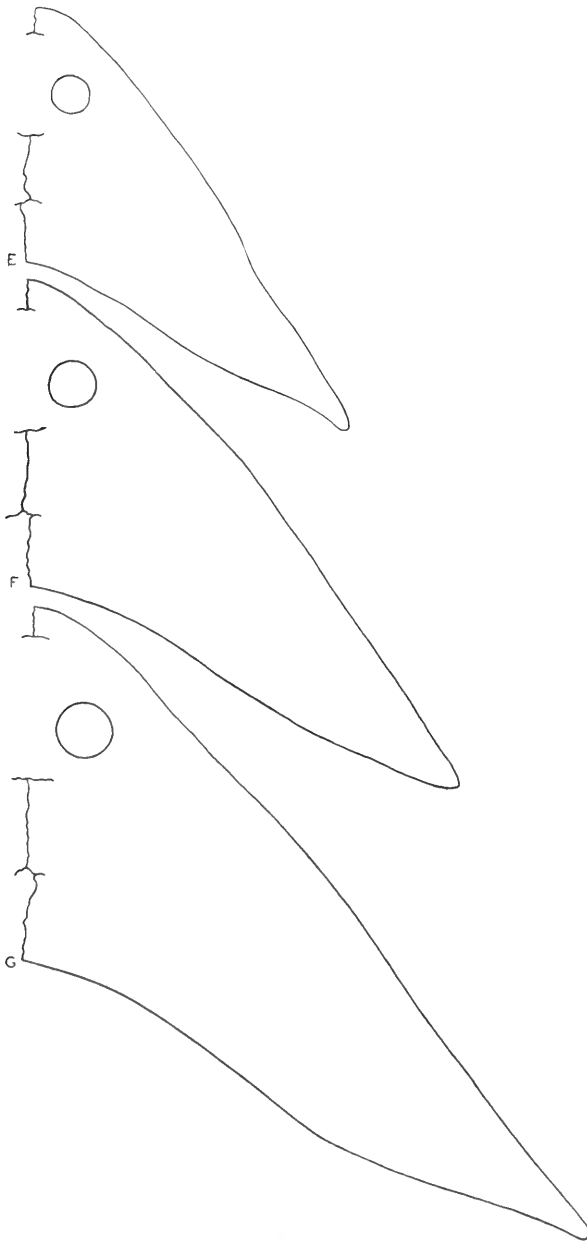


FIG. 18b. Mean growth stages of *Diplocaulus* reconstructed from estimating equations. $\times \frac{1}{3}$. E, 100 mm. stage; F, 120 mm. stage; G, 140 mm. stage.

Discussion of Changes in Skull Shape

It is apparent from the equations and from the plotted skull outlines that vast changes took place in skull shape with change in skull length in *D. magnicornis*. In dorsal aspect the skull at 20 mm. has a shape not unlike that of skulls of certain other genera of Late Paleozoic amphibians, notably *Trimerorhachis*. It is this fact that

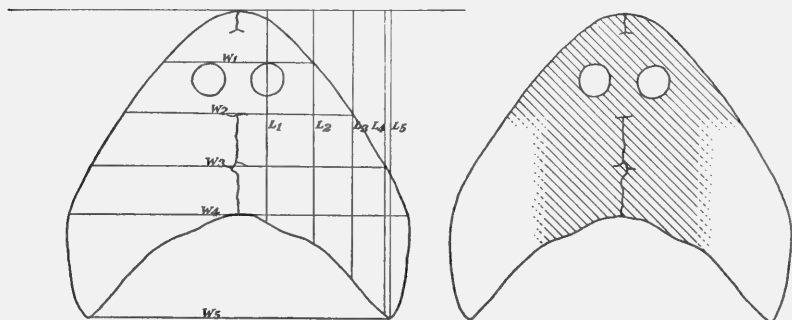


FIG. 19. "Stable" and "unstable" parts of growing skulls in *Diplocaulus* based on 80 mm. stage.

has resulted in the assignment of some of the smallest skulls of *Diplocaulus* to the Trimerorhachidae. At this stage the horns are poorly developed. The changes in the anterior part of the skull are for the most part isogonic, except for the relationship of the orbito-snout length to skull length. The shape changes proceed without acceleration of growth rates. Similarly, length relationships at levels L_1 and L_2 are best explained as isogonic. In essence this means that changes in the zones limited by a line somewhere between W_2 and W_3 , with respect to width, and L_2 and L_3 , with respect to length, maintain a stable growth pattern in which the trends and rates established very early do not modify materially throughout the growth series (fig. 19). The lateral migration of L_2 , controlled by the position of the posterior midline point of the frontal (involving Pmx_1 and Frl , both isogonic) is also essentially isogonic. The zones limited as noted above may be thought of as relatively stable parts of the skull, parts in which the changes are simple and steady. It is perhaps significant that the dermal surface of these zones overlies the brain, includes the openings of the sensory organs, pineal, orbits and external nares, and encompasses essentially the full extent of the upper and lower jaws.

The remainder of the skull is subject to positive heterogonic growth. The horns gradually appear between the 20 and 80 mm.

stages with their dominant direction of growth posterior, to produce a pattern shown in figure 18, D. The posterior curvature developed approaches that witnessed in adults of *D. brevirostris*, and were the rate of W_5 maintained and the rate of L_5 accelerated a pattern closely resembling that of these adults would result. The pattern in the orbito-snout region, however, would be very different, and no conceivable change from the 60 mm. stage or even the 40 mm. stage of *D. magnicornis* could produce the pattern of *D. brevirostris*.

Between 80 and 100 mm. there tends to be a rapid alteration of the direction of the axis of growth of the latero-posterior corners of the skull. This is seen in a comparison of the second equation for W_5 with that for L_5 . The result is that lateral growth, which increases rapidly, takes ascendancy over posterior growth, and the horns become directed postero-laterally rather than posteriorly. There is, in effect, a rotation of the horns. It occurs, of course, through differential additions and resorptions of bone. The main bone affected is the supratemporal, which expands rapidly postero-laterally. The changes result in a pattern at 100 mm. decidedly different from that at 80 mm.

It is not to be thought that this change occurred at precisely the same skull length in all individuals. There is no known instance in which any skull under 90 mm. shows marked effect of the acceleration of lateral growth, and some skulls, almost to the 100 mm. stage, show little evidence of rapid change. The usual stage of initiation thus appears to be after the 90 mm. stage has been passed. Two skulls at 101 mm. show pronounced effects, much like those shown in the mean 100 mm. skull outline (see pls. 3 and 4). Almost all skulls over 100 mm. have assumed a pattern in which lateral extension of the horns is pronounced. There is, however, one striking exception, A.M. 4514, which, at 110 mm., maintains a pattern not unlike that of the 80 mm. stage (compare fig. 18, D, and pl. 4, C). If the regression line of W_5 for 20 to 80 mm. be extrapolated, it is found that the value of W_5 of A.M. 4514 departs from it but little, whereas this value deviates markedly from the line plotted from the equation for W_5 from 100 to 140 mm. This skull appears to represent a case of extreme retardation of the onset of rapid lateral growth, retardation, of course, only in the relationship to skull size as measured along the midline and not necessarily in time. From the evidence available it seems that acceleration in relative lateral growth of the latero-posterior region of the skull may begin slightly before the 90 mm. stage and usually develops between 90 mm.

and 100 mm.; but it may in some instances be delayed until at least the 110 mm. stage is reached. Moderate attainment of what may be considered the adult pattern is commonly attained at about 100 mm.

The tendency toward increasingly rapid lateral growth in the latero-posterior zone is maintained until at least the 130 mm. stage. That it could have continued much beyond this stage seems improbable, since an unwieldy structure, foreshadowed in the reconstruction of the 140 mm. stage, would develop. There is only slight evidence of the course of events beyond the 130 mm. stage. One skull, U.C. 637, measures 135 mm. in length, but distortion and breakage make the measurement somewhat unreliable. As reconstructed, the long horns are directed posteriorly (pl. 6) but it is evident that the horns have been rotated medially a minimum of some 30 degrees. The pattern with the horns in more normal position would approximate that of the 140 mm. reconstruction moderately closely. A.M. 4484 measures 147 mm. in length. The specimen is badly crushed and this may have increased the length several millimeters. The horns are weathered and in part missing; they extend only a short distance beyond the otic notch. It may be that full knowledge of the horns would show a pattern not unlike that of the 140 mm. reconstruction. This, however, must be conjectural, for it is possible, on the basis of what is known of the skull, that the horn development was more nearly like that shown in the 120 mm. reconstruction. In any event, it is quite certain that the horns of A.M. 4484 did not assume the pattern indicated by extrapolation to a 145 mm. stage. There is vague evidence, then, of retardation of horn growth in very large skulls, but this is based on a single, badly preserved specimen and is at best only suggestive.

The zones in which the rapid changes take place may be thought of as decidedly plastic in contrast to the stable areas noted previously. The causes and effects of the changes in the plastic zones must remain somewhat obscure, but we may speculate on them briefly to good advantage. If the ancient amphibians followed the general patterns of development witnessed among anurans and urodeles, we should expect some evidence of a marked break in growth continuity at some stage in their development. The stage of metamorphism varies widely among modern groups; bufonids, for example, pass through metamorphism when relatively small, and ranids when relatively large. The relative amount of growth after metamorphism is thus very different in the two groups. There is no evidence of a break in rates of change in the plastic portions of the skulls of

D. magnicornis from the 14 mm. to about the 90 mm. stage. What occurred prior to the 14 mm. stage we do not know. There is, however, an abrupt change at about 90 mm. and it seems logical to suppose that this change indicates the initiation of the adult condition. It has been noted earlier (pp. 102-104) that there are some puzzling circumstances surrounding the condition of the vertebrae. Very large, fully matured vertebrae are developed in a few large specimens, U.C. 564 for example, among the specimens that compose the sample of *D. magnicornis*. Other specimens, with approximately the same skull lengths, however, have much smaller vertebrae. It may be that the large vertebrae, found in very few instances, represent a pattern that developed with complete maturity, and that the smaller vertebrae, which in various characteristics are like those of specimens with skulls under 90 mm. in length, represent vertebrae that have not undergone this change. If so, it would seem that in many instances maturation of the postcranial axial skeleton was retarded and perhaps never fully accomplished. We have noted at least one instance of retardation of change of rate in lateral growth of the skull and there is less clear evidence of other cases. What evidence there is suggests that neoteny may have played an important part in the development of *Diplocaulus*, particularly in the postcranium. The environment, entirely aquatic so far as can be determined, is one in which this phenomenon is commonly encountered.

It is evident that the rapid change in the skulls must have been correlated with important functional changes. Until such time as adequate evidence on the function of the lateral projections of the skull may come to light, it is impossible to make a critical analysis of the nature of the functional changes. It is clear that the areas housing the brain and sense organs and the regions of the jaws and dentition were not drastically modified. Changes must be related primarily to mobility of the animals. It would appear that smaller individuals had a capacity for more active swimming than the fully matured animals. If there was a membrane attached to the horns and used for locomotion, or any other purpose, it could hardly have been functionally important below the 90 mm. stage. It might have developed beyond this stage to an effective level for locomotion and have offset to some degree the effects that the change in skull-shape presumably had in retarding activity. This would suggest a rather marked change in the method of locomotion and, presumably, in the postcranial structures associated with locomotion. Although there is some evidence of decided change in the vertebrae

from one specimen, it is evident that most specimens did not undergo full development in this region. The development of such a membrane, which is purely hypothetical, or of a decided flattening of the body, which the ribs of some specimens suggest, could have been of but moderate use in locomotion. It might, however, have functioned in a very different way. As mobility decreased, protection from predators must have become a more difficult problem. Concealment rather than escape must have been important. In a number of flat animals—skates or flounders, for example—concealment is attained by covering the body with bottom sediment. It is possible that *Diplocaulus* adopted this method of concealment, using a mobile lateral portion of the flattened body as a mechanism for covering. The environment suggested by the sediments in which many specimens of *D. magnicornis* occur, sluggish or quiet waters, fits this interpretation. Indications of dry periods also suggest that burial would be of advantage to the animals. On the other hand, specimens of *D. brevirostris*, with a probable stream habitat, did not develop such large latero-posterior horns, the sedentary habits, or, presumably, the decidedly flattened bodies.

THE PROBLEM OF VARIABILITY

One of the most striking features of a series of skulls of *D. magnicornis* is the wide diversity of shapes. Even series containing only relatively large skulls, those over 100 mm. in length, show this phenomenon. The conclusion that the species is highly variable (see Douthitt, 1917, for example) has followed. The best statement of variability, in the biological sense, is made through use of the coefficient of variability of Pearson, determined from the formula $V=100\sigma/M$, in which M is the mean of the sample. It seems quite certain that statements to the effect that *Diplocaulus* is highly variable are based upon the concept of dispersal about a mean expressed by this coefficient. If this is not the case, they have no apparent meaning. The studies that have been made upon *Diplocaulus* in the preparation of the present paper and a consideration of the real meaning of V lead to serious doubts concerning the appropriateness of the application of V to a case such as that presented by this animal.

Relative variability can have meaning only in terms of some empirically determined or arbitrarily assigned standard. Simpson and Roe (1939) have pointed out that, for recent samples among the vertebrates, values of V between 4 and 7 represent coefficients

of variability most commonly encountered and this gives a reasonable basis for evaluation of samples to which the concept may be applied legitimately. If, therefore, values much higher than 7 are obtained we may be justified in believing that the sample analyzed is highly variable, and, assuming the sample to be homogeneous, that this is true biological variability. It is an easy step from this basis to the determination of the value of V for the various characters of *D. magnicornis* and comparisons with similar measurements from other species. In fact, it is quite simple to "prove" by this means that in a number of characteristics *D. magnicornis* is highly variable. Numerous characters have been analyzed in this way in the course of the study and values ranging from 15 to 30 have been obtained. The procedure has been outlined and carried out in this study only because it appears to be a quantitative application of the thought processes that have been followed to arrive at the conclusion that the species is highly variable. The conclusion reached is meaningless, for it involves a misapplication of the concept of V .

The coefficient of variability has been applied most commonly, among vertebrates, to teeth and skeletal elements in fossil mammals. Teeth, provided with an enamel covering, once fully formed, change only through wear. Mammalian bones, in most instances, cease to increase in size as the animal attains maturity. In these instances, determination of the dispersal of values about the sample mean expresses real biological variability and the coefficient of variability may properly be used. The bones of amphibians and reptiles, at least in the majority of cases, do not have a determinable terminal growth. Although the growth is clearly slower in late stages, it does not cease during the lifetime of an individual. Any determination of variability in terms of V must necessarily reflect the effects of changes in size and proportion continuing so long as growth continues, and is thus not commensurate with values determined from a sample, such as one of mammals, in which growth has ceased. Values obtained from a sample composed of individuals that have not reached a stage of cessation of growth do not express variability in its true biological sense. This applies not only to amphibians and reptiles but also to such features of mammals as the antlers of deer and, probably, skull shape in cases where cranial areas are underlaid by sinus systems (for example, in sloths, titanotheres, etc.) or where excrescences, such as the "horns" of titanotheres, continue to grow after maturity has been attained. It is recognized that continuing change of the antlers in deer gives no basis for calling the species highly variable, nor does it give a basis for calling the antlers highly

variable. This has been, perhaps, less clearly recognized in other groups of mammals, for certainly such forms as sloths and titanotheres, in which cranial sinuses are highly developed, have seemed to present a rather bewildering array of variability. The effects upon taxonomy of such misinterpretation may be disastrous.

The case of *D. magnicornis* appears to be one common to the amphibians and to many reptiles, but one in which certain growth characteristics impart particular emphasis to the factors involved. It cannot be denied, I believe, that there exists in *D. magnicornis* a theoretical or, better, a potential variability, but in view of the conditions of growth the problem of determination of this variability can have no satisfactory answer. Only were the animals to reach a stage at which growth definitely ceased would variability commensurate with that expressed by V exist. Tests of variability at any stage, either before or after cessation of growth, essentially measure the differing effects of relative growth between individuals, but only when growth has ceased is there a common basis among specimens for determination of biological variability. Until that stage is reached, and probably in *D. magnicornis* it never was, variability as expressed by V is potential only.

There are several approaches to the problem, but each contains a fallacy or poses an insurmountable sampling problem. The soundest approach, in theory, is to deal with a sample in which growth has slowed nearly to the point of cessation. Such a sample, rarely obtained and difficult to recognize among living lower vertebrates, is a virtual impossibility among fossils. An approach through measurement of variability at different growth stages measured by some dimension or by time may appear attractive. It is not uncommon practice in dealing with mammals, particularly with man, to measure variation of an age group in one character or another, but here, as in reptiles or amphibians, what is measured is not biological variability but factors pertaining to differential growth in time. Determinations for age groups of amphibians or reptiles can properly be compared to such data, provided that appropriate time relationships can be established, but this is not a comparison of variability as implied in the coefficient of variability.

It seems clear that the concept of V cannot be applied to any group during growth in the same way that it can be applied after the termination of growth. Various techniques may be used for study of the dispersal of values about regression lines and these may be applied to growth series. While they are valuable for com-

parative purposes, from none does a concept of variability comparable to that of V emerge, and we remain without a basis for comparison of variability in the sense desired. This follows simply from the fact that none can be based upon the physiological processes basic to the concept of variability, in the absence of those processes in the groups considered.

If we cannot then determine the scope of variability in *D. magnicornis*, what value can be derived from analyses of the patterns of growth? First, as discussed in the preceding section, the general nature of changes in skull pattern may be determined. Second, the extent of deviation from the mean pattern at appropriate levels may be determined. This may be taken directly from the regression diagrams or may be calculated. As has been pointed out above, this is not a measure of variability of the skulls nor does it provide a basis for determination of variability. It does, however, give a basis for analysis of the great differences in skulls of approximately the same size in terms of skull length.

There appear to be two principal factors entering into the development of the wide differences in skull shapes: (1) differential growth rates of various parts of the skull; (2) differences in the stages of onset of acceleration of growth in latero-posterior parts of the skulls.

Differential growth rates may be determined readily from the equations that are given on page 137 for any stage of skull development in terms of skull length. We may compare, for example, the rate of growth along the midline and that of the horn tip (W_5) as expressed above the 100 mm. level, by the equation $Y = 0.0343X^{1.923}$. We find that as the length of skull increases from 100 to 110 mm., skull width increases from 240 to 282 mm. Thus over this interval width is increasing at a mean rate of about 4:1 over length, with, of course, increased relative rate from 100 to 110 mm. The increase between the 110 and 120 mm. stages of skull length is 59 mm., from 282 to 341 mm., or a mean ratio of about 6:1. The case selected for illustration of method is the most extreme in the skull but the same principle applies to all cases of relative heterogonic growth. A 10 mm. change in skull length is relatively minor in large skulls and the difference occasioned by it is not particularly apparent under casual observation. Thus two skulls that appear to be about the same length may show striking differences when compared with respect to width. It is rather common practice to think of size in terms of an axial measurement, skull length in this instance, and hence it may appear that two skulls of the same "size" are very

different. Furthermore, the tendency to think of variability in terms of size is normal since the importance of deviations from the mean in linear dimensions is directly related to the magnitude of the mean. Thus may follow the conclusion—erroneous, as pointed out above—that the length-width relationships are indicative of high variability.

The second important factor is the stage of growth acceleration in the latero-posterior parts of the skull. This applies most strikingly in the case of W_5 , in which there is an abrupt change of considerable magnitude. It applies less, but in an equally real manner, in all cases of heterogony in which there is steady acceleration. This is a somewhat more subtle relationship and, on the basis of data available for *Diplocaulus*, not subject to critical analysis. It is evident, however, as noted in the preceding paragraphs, that skulls of nearly the same length have widely different values of W_5 , which again will be used as an example. It is also evident that there is a change of rate of growth of considerable magnitude for W_5 between the 80 and 100 mm. stages in skull length. There is, however, evidence that some skulls have participated less and some more in this change at particular levels than have others. Such a skull is that of A.M. 4514, an extreme case, showing a value of 193 mm. for W_5 at skull length of 110 mm., a deviation of -89 mm. from the mean, $Y_c=282$. Clearly it has followed a growth pattern different from that of other skulls of approximately the same length. So far as this one specimen is concerned there has been no appreciable change from the rates predicted for skull growth below 80 mm. of skull length. Other skulls show the effect of differences in change of rates either in excess of that determined, with positive deviations, or less than the determined mean change, with negative deviations.

This effect produces a wide dispersal of points around the regression line. But the dispersal is not a function of variability in the biological sense. We may conceive a stage in the growth of *Diplocaulus*, purely hypothetical so far as the evidence from the sample is concerned, at which growth has virtually ceased and from which an approximation of real variability could be determined. The dispersal about the regression line, that is, the mean value, Y_c , properly determined for any particular regression at a particular value of X , does not necessarily bear any direct relationship to the variability at that hypothetical stage. It is exceedingly important to recall in this instance that skull length does not necessarily represent even a relative time scale, although it may approximate it,

and that time does not necessarily bear a close relationship to the hypothetical stage of growth cessation.

The effects discussed above offer probable "explanations" of why the skulls of *D. magnicornis* give the appearance of high variability. In terms of them it is clear that the specimens of a single species may exhibit wide diversity of form without respect to actual variability. We have no evidence, nor does it appear probable that evidence can ever be obtained, of the nature of biological variability in this species. It was stated above that many genera of Permian amphibians and reptiles seem to exhibit a wide diversity of form and that this phenomenon was one of the problems to be attacked in this paper. It seems probable that the "explanations" offered in these closing pages may apply to at least some of the other cases. Differential growth rates of different parts of the skeleton probably have played a very important part in producing wide diversity in structures in specimens that are quite similar in one or more dimensions. Different stages of appearance of adult characteristics become important principally when some important change of growth rates occurs at this threshold, but apply in lesser degree in all cases of heterogonic growth. They may become of particular importance in instances in which various foramina and fossae are characteristic of one growth stage but not of another, as in changes of infantile to adult circulatory patterns, and in instances in which bone dimensions are in part a function of the degree of ossification.

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PLATES

PLATE 1

Diplocaulus magnicornis Cope

- | | |
|------------------------------|-----------------------------|
| A. A.M. 4523A, $Sk_l=14$ mm. | H. A.M. 4589, $Sk_l=63$ mm. |
| B. U.C. 206, $Sk_l=23$ mm. | I. U.C. 222, $Sk_l=65$ mm. |
| C. U.C. 1660, $Sk_l=19$ mm. | J. U.C. 1663, $Sk_l=65$ mm. |
| D. A.M. 4523B, $Sk_l=24$ mm. | K. U.C. 1658, $Sk_l=68$ mm. |
| E. A.M. 4752, $Sk_l=31$ mm. | L. U.C. 223, $Sk_l=70$ mm. |
| F. U.C. 224, $Sk_l=46$ mm. | M. A.M. 4597, $Sk_l=73$ mm. |
| G. A.M. 4485, $Sk_l=50$ mm. | |

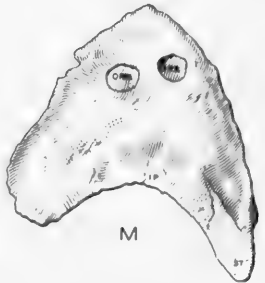
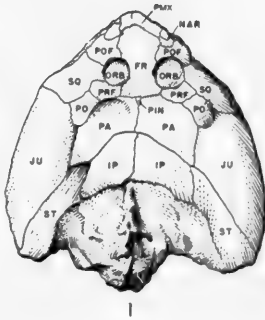
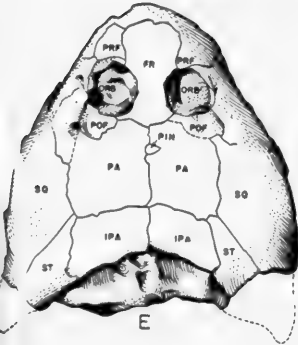
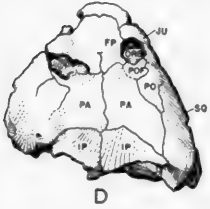
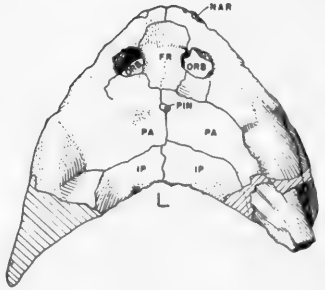
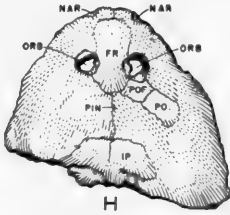
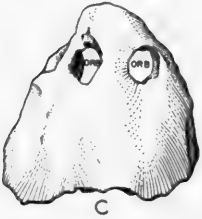
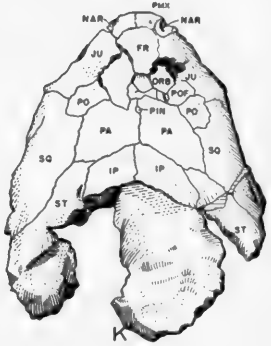
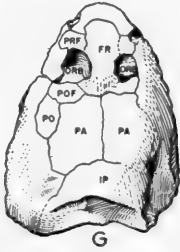
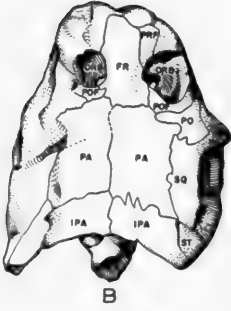
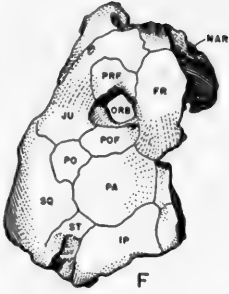
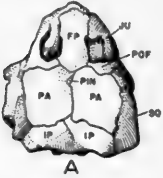


PLATE 2

Diplocaulus magnicornis Cope

- | | |
|-------------------------------|-----------------------------|
| A. U.C. 1656, $Sk_l=75$ mm. | E. A.M. 4491, $Sk_l=82$ mm. |
| B. U.C. 1657, $Sk_l=75$ mm. | F. U.C. 410, $Sk_l=85$ mm. |
| C. U.C. 1652, $Sk_l=80$ mm. | G. U.C. 1650, $Sk_l=89$ mm. |
| D. A.M. 4511, $Sk_l=81^1$ mm. | H. P12689, $Sk_l=89$ mm. |

¹ Approximate.

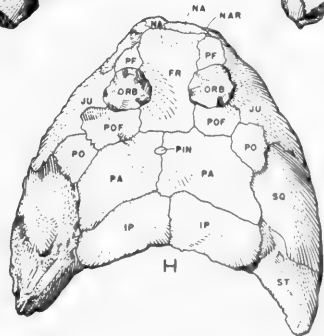
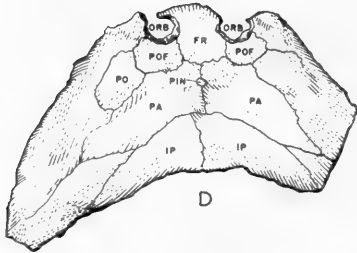
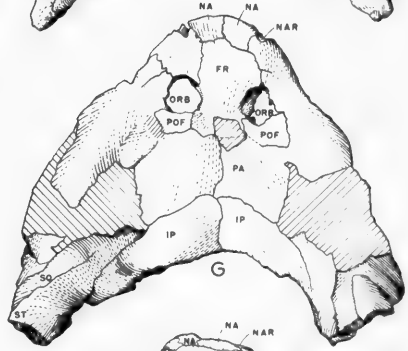
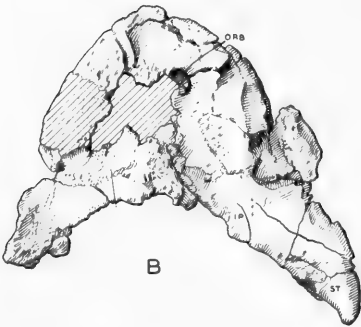
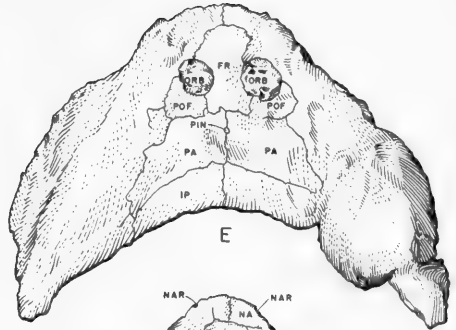
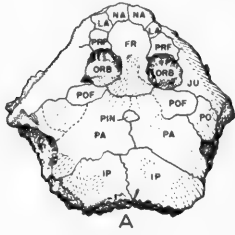


PLATE 4

Diplocaulus magnicornis Cope

- | | |
|--------------------------------|--------------------------------|
| A. A.M. 4473, $Sk_l=105^1$ mm. | E. A.M. 4498, $Sk_l=114$ mm. |
| B. A.M. 4494, $Sk_l=105^1$ mm. | F. A.M. 4466, $Sk_l=115$ mm. |
| C. A.M. 4514, $Sk_l=110$ mm. | G. A.M. 4467, $Sk_l=118$ mm. |
| D. U.C. 564, $Sk_l=114$ mm. | H. U.C. 1654, $Sk_l=116^1$ mm. |

¹ Approximate.

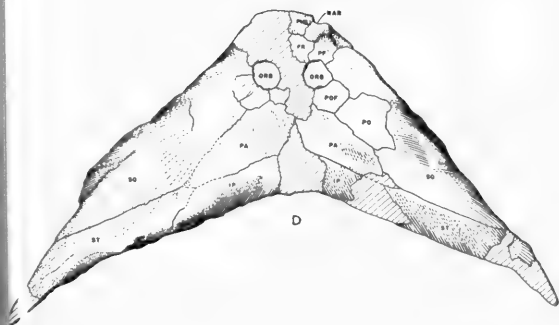
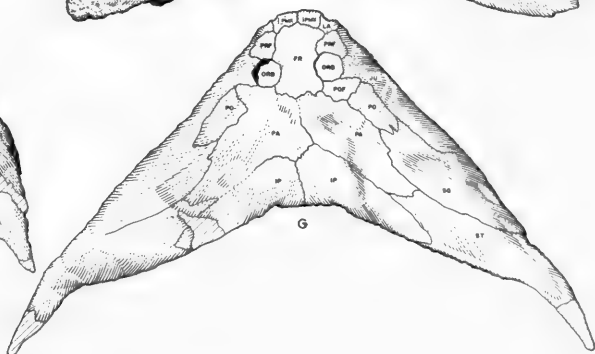
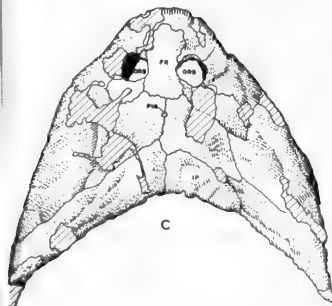
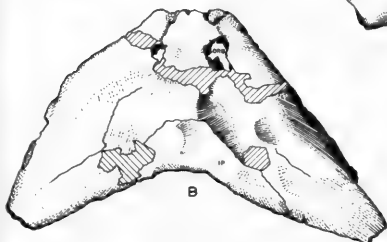


PLATE 5

Diplocaulus magnicornis Cope

A. U.C. 636, $Sk_l=119$ mm.

C. A.M. 4501, $Sk_l=130^1$ mm.

B. A.M. 4472, $Sk_l=127$ mm.

¹ Approximate.

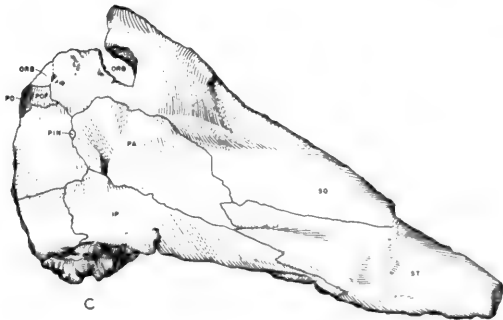
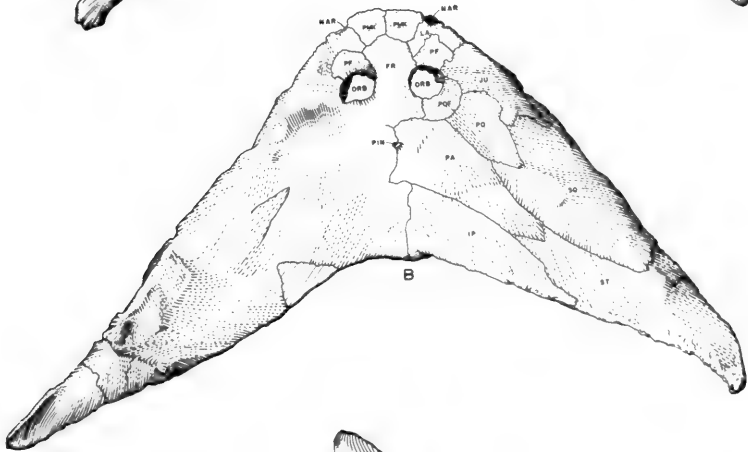
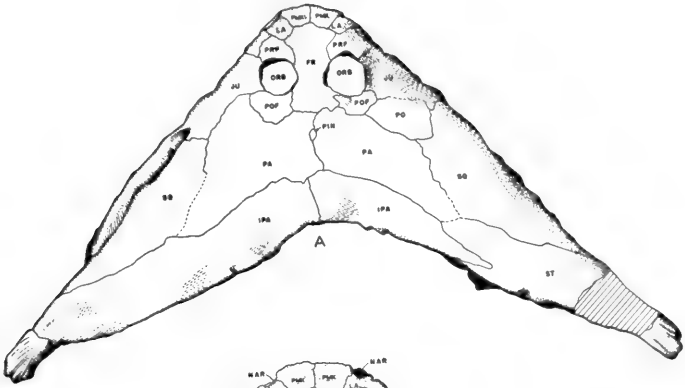


PLATE 6

Diplocaulus magnicornis Cope

A. U.C. 1317, $Sk_l=129$ mm.

C. A.M. 4484, $Sk_l=147$ mm.

B. U.C. 637, $Sk_l=135$ mm.

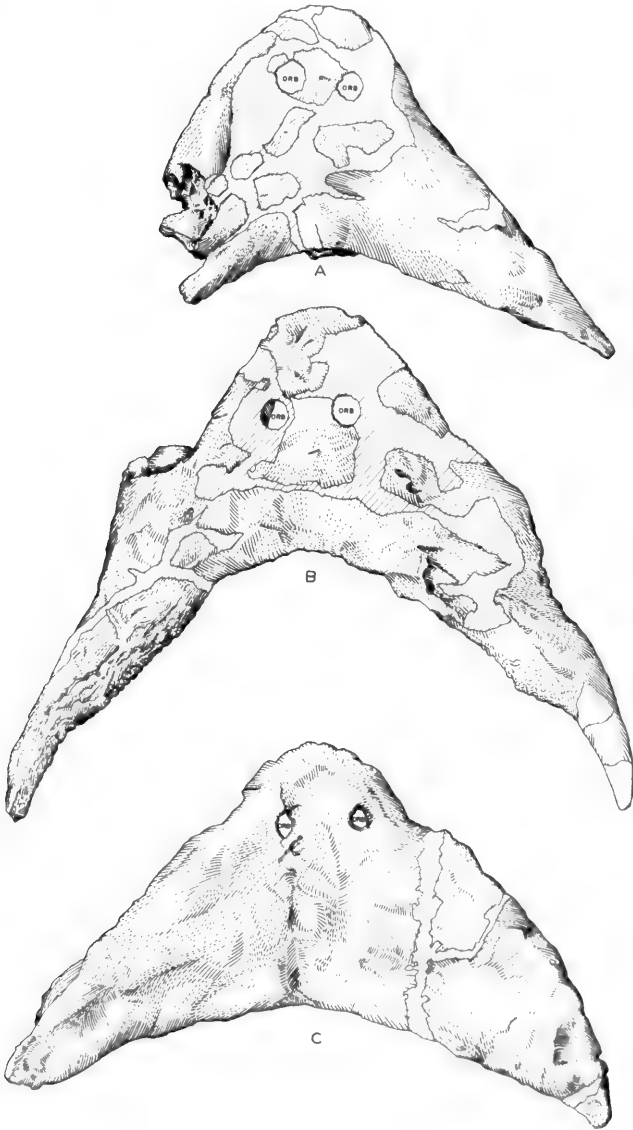


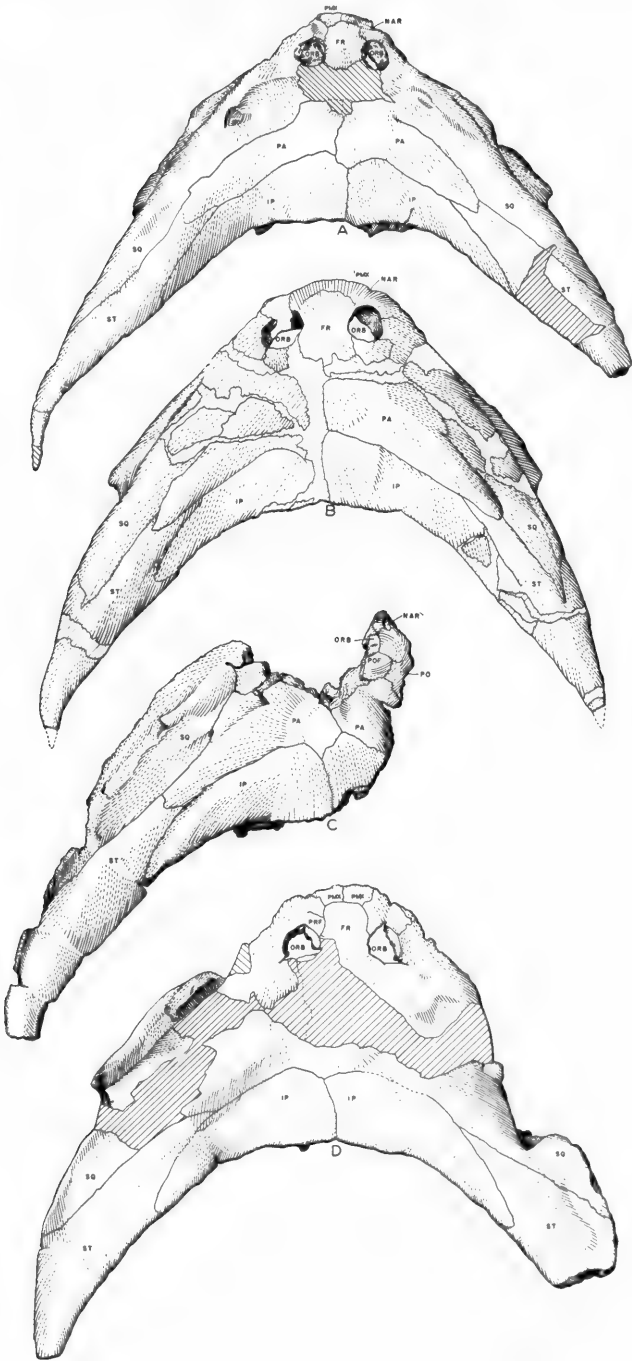
PLATE 7

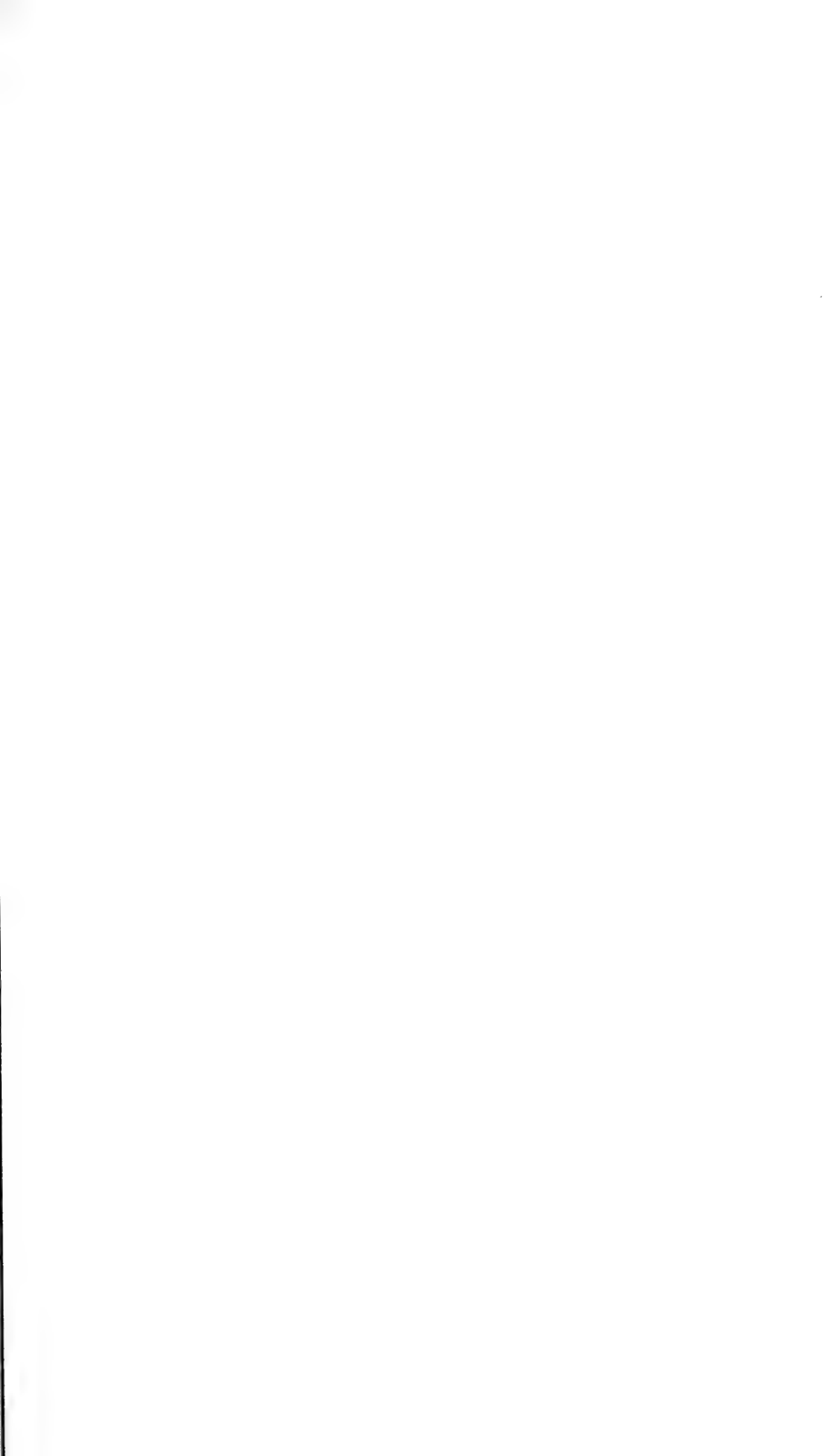
Diplocaulus brevirostris sp. nov.

- A. U.C. 1661, $Sk_l=107$ mm.
B. A.M. 4470, $Sk_l=119$ mm.
Holotype of species.

- C. U.C. 1655, $Sk_l=120^1$ mm.
D. U.C. 1648, $Sk_l=136$ mm.

¹ Approximate.







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