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ALLOMETRIC GROWTH IN THE DIADEMODONTINAE (REPTILIA; THERAPSIDA): A PRELIMINARY REPORT

by

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ABSTRACT

The hypothesis that many, if not all, of the South African and Zambian specimens, which have been regarded as different diademodontine genera and species, actually consitute a taxonomically homogeneous, ontogenetic growth series is tested. The principles of allometric growth were applied to this sample of fossils, which varied considerably in size and shape. The approach which was followed was exclusively morphometric. The results indicate that these specimens do represent various ontogenetic stages of a growth series of only a single species of *Diademodon* Seeley.

INTRODUCTION

An assemblage of moderately advanced, omnivorous-herbivorous, gomphodont cynodonts is well known from the *Cynognathus* Zone sediments of the Orange Free State and Cape Province, South Africa (Kitching, 1972). The most commonly occurring forms in these deposits are represented by a rather homogeneous assemblage of animals which have been grouped collectively in the subfamily Diademodontinae by Hopson and Kitching (1972). The fossil remains of these reptiles have been recovered also from the Ntawere Formation, Upper Luangwa Valley, Zambia (Kitching, 1963; Brink, 1963a), the Omingonde Mudstone Formation (Lower Etjo Beds) of South West Africa (Keyser, 1973), and also from the Lincheyu locality, Shansi Province, China (Young, 1961). The Diademodontinae appear to have been late Early Triassic to early Middle Triassic in age (Du Toit, 1954; Cox, 1967; Keyser, 1973).

A plethora of genera and species of diademodontines have been named (table 1); but only a few have been based on more than fragmented or distorted specimens, and still fewer have been adequately characterized such that any one genus or species can be readily distinguished from all others. Hopson and Kitching (1972) have proposed that the vast majority of these names are junior synonyms of *Diademodon tetragonus* Seeley. A detailed study of the dentitions of a number of diademodontine specimens (Grine, 1976a, 1976b and 1977), which included the types of *Diademodon tetragonus* and *D. brachytiara* as well as remains which had been regarded as specimens of *D. browni*, *D. mastacus*, *D. entomophonus* and *Gomphognathus* sp., revealed that these fossils represented a dentally homogeneous group. Grine (1977) noted that the number of postcanine molariform teeth in various diademodontine specimens may vary from five to 11, dependent upon the size of the skull; and that the smaller usually possess fewer teeth than do the larger specimens. He suggested that rather than the smaller fossils being regarded (on the basis of tooth number) as specifically distinct from the larger, the smaller specimens should be considered as representing ontogenetically younger stages of development than the larger ones.

TABLE 1

List of genera and species presently included in the subfamily Diademodontinae.

Diademodon tetragonus	Seeley 1894
brachytiara	Seeley 1894
mastacus	Seeley 1894
browni	Seeley 1894
entomophonus	Seeley 1908
platyrhinus	Broom 1913
parringtoni	Brink 1955
laticeps	Brink 1955
rhodesiensis	Brink 1963
Cynochampsa laniaria	Owen 1859
Gomphognathus kannemeyeri	Seeley 1895
polyphagus	Seeley 1895
minor	Broom 1911
haughtoni	Broili and Schröder 1935
grossarthi	Broili and Schröder 1935
broomi	Broili and Schröder 1935
(Diastemodon) dimorphodon	Seeley 1908
Octagomphus woodi	Broom 1919
Cyclogomphodon platyrhinus	Broom 1919
Protacmon brachyrhinus	Watson 1920
reubsameni	Broom 1950
Sysphinctostoma smithi	Broili and Schröder 1936
gracilis	Broom 1950
Cragievarus kitchingi	Brink 1965
Titanogomphodon crassus	Keyser 1973
Ordosiodon lincheyüensis	Young 1961
Trirachodon browni	Broom 1915

Brink (1963b) recorded and illustrated four specimens which had been recovered from a single "fossil pocket" on the farm Cragievar, near Burghersdorp, Cape Province. He regarded these as immature individuals of *Diademodon browni*, and noted that there "is some individual variation which could partly be accounted for in terms of growth" (1963b, p. 109).

The hypothesis entertained in this study is that many, if not all, of the 12 genera and 26 species which have been recognized for the Diademodontinae (table 1) may possibly constitute an ontogenetic, sexually dimorphic series of but a single species, *Diademodon tetragonus* Seeley. This paper constitutes a preliminary report of a much more detailed study (see Grine, Hahn and Gow, 1978).

MATERIAL AND METHODS

A series of 55 specimens (table 2) was examined. The material ranged from relatively undistorted, complete skulls (i.e. BPI. FN. 4669) to fragmented dentaries. The principles of relative (allometric) growth were applied to this sample of fossils, which varied considerably in size and shape. The approach which was followed was exclusively morphometric. A large number of variables of both the cranium and dentary were designated for measurement (fig. 1); but, due to the oftentimes fragmentary nature of the available material, there was no single specimen on which all 52 metrical characters could be recorded (see table 2). All measurements were taken with either a sliding Vernier caliper (in the cases of smaller dimensions) or the top segment of an anthropometer, and recorded to the nearest millimetre. The variables which were selected for measurement generally reflected the overall shape of the skull and its various parts rather than the configuration of individal bones or parts of bone developed from specific ossification centres.

In order to assess and describe quantitatively the processes of skull growth, the measurements were fitted to the bi-parametric power function (the equation of simple allometry):

$$y = ax^{\beta} \qquad (1)$$

where y is the variable whose increase relative to that of another variable is considered, x is a different dimension of the same skeletal complex, a is a numerical constant and β is the slope of the rectilinear plot (or simply the ratio of the specific growth rates of

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Figure 1. Diademodontid skull measurements (see opposite page)
A, norma verticalis; B, norma basalis; C, norma lateralis; D, norma occipitalis; E, norma verticalis of dentary; F, norma lateralis of lower jaw.

Variable	Description
1	Basal skull length
2	Total skull length
3	Pre-orbital length
4	Pre-orbital basal length
5	Pre-orbital total length
6	Cranial masticatory length
7	Cranial postcanine masticatory length
8	Hard palate length
9	Temporal fossa length
10	Cranial length to back of jugal flange
11	Cranial length to posterolateral edge of jugal
12	Total dentary length
13	Dentary length of coronoid process
14	Dentary length to angle
15	Mandibular masticatory length
16	Mandibular postcanine masticatory length
17	Symphyseal length
18	Total cranial width
19	Cranial width across jugal flanges
20	Interorbital width
21	Least snout width
22	Greatest snout width
23	Parietal width coincident with pineal foramen
24	Temporal fossa width
25	Bicondylar breadth
26	Post-temporal breadth
27	Width between post-temporal foramina
28	Greatest breadth of maxillary tooth rows
29	Least breadth of maxillary tooth rows
30	Maxillary bicanine breadth
31	Dentary thickness
32	Minimum intercorporal breadth
33	Minimum symphysial breadth
34	Maximum symphysial breadth
35	Mandibular bicanine breadth
36	Maximum post-temporal height
37	Maximum height of mid-temporal crest above maxillary base
38	Maximum height of postorbital above maxillary base
39	Maximum height of maxilla
40	Maximum height of corpus of dentary
41	Projected rameal breadth
42	Orbital breadth
43	Orbital height
44	Nasal aperture length
45	Foramen magnum height
46	Foramen magnum breadth
47	Mesiodistal diameter of maxillary canine (or socket)
48	Buccolingual diameter of maxillary canine (or socket)
49	Mesiodistal diameter of mandibular canine (or socket)
50	Buccolingual diameter of mandibular canine (or socket)
51	Maximum height of jugal
52	Pterygoid width

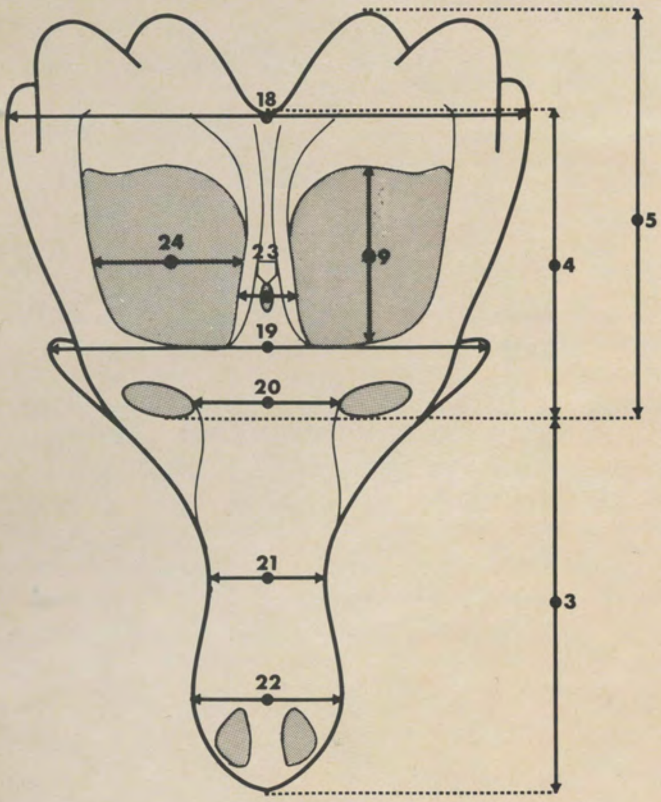

Fig. 1A

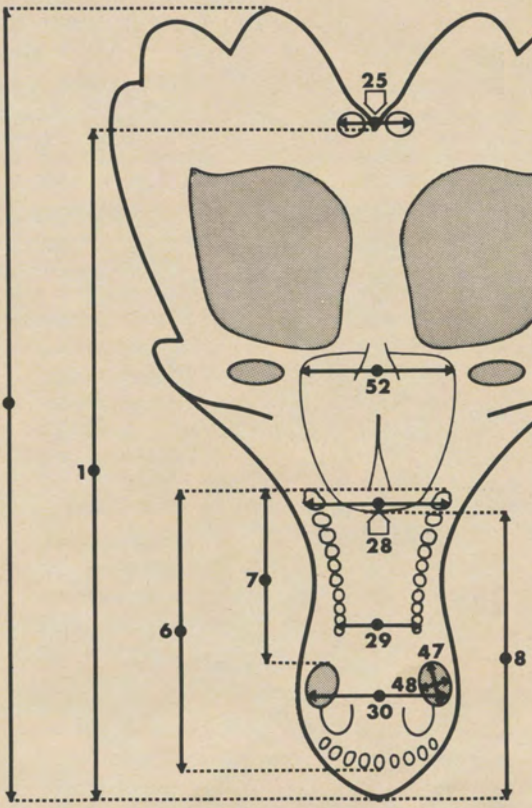

Fig. 1B

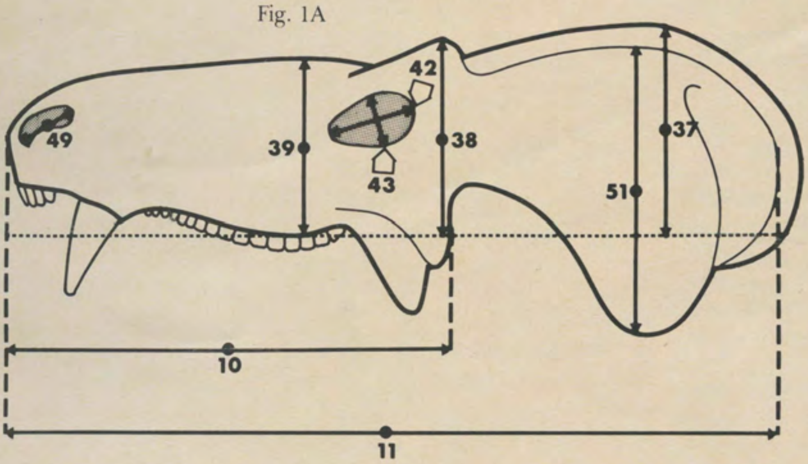

Fig. 1C

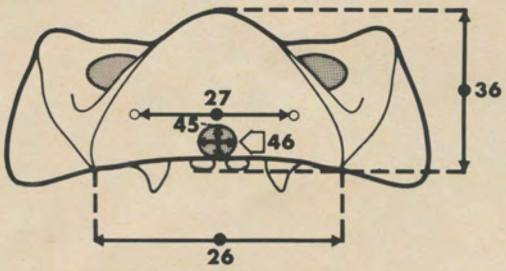

Fig. 1D

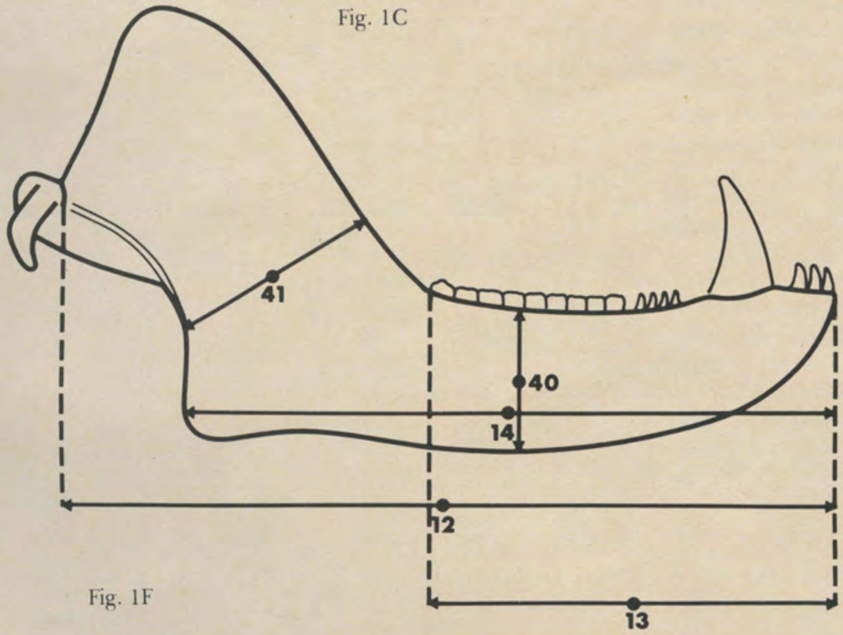

Fig. 1F

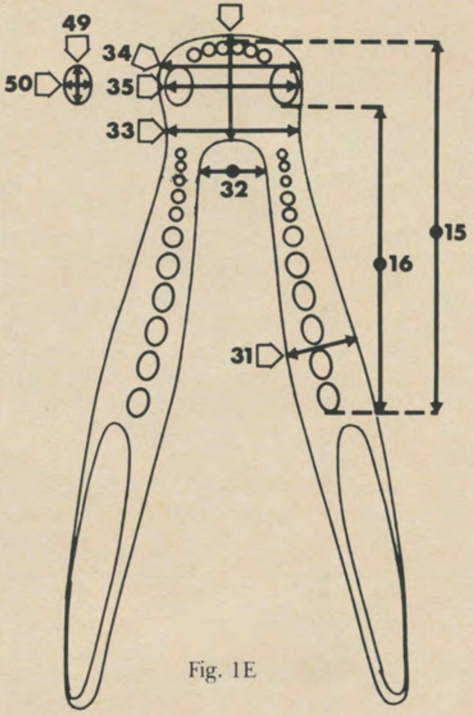

Fig. 1E

TABLE 2

List of specimens measured.

V, number of mensurable parameters recorded; BPI.FN., Bernard Price Institute for Palaeontological Research Field Number; G.S., Geological Survey, Pretoria; N.M., National Museum, Bloemfontein.

Specimen	Museum No.	Previous taxonomic designation	Specimen description	V
1	BPI.FN.3754	*Diademodon grossarthi*	Cranium	36
2	BPI.FN.3639	*Diademodon rhodesiensis* (type)	Skull	42
3	BPI.FN.2522	*Diademodon mastacus*	Cranium	29
4	BPI.FN.3757	*Diademodon haughtoni*	Snout	14
5	BPI.FN.4669	*Diademodon* sp.	Skull	46
6	G.S. R.322	*Titanogomphodon crassus* (type)	Cranium	7
7	BPI.FN.1695	*Diademodon* sp.	Snout	13
8	BPI.FN.1195	*Diademodon broomi*	Cranium	18
9	G.S. R.530		Cranium	17
10	BPI.FN.3758	*Diademodon browni*	Skull	40
11	BPI.FN.1177	*Diademodon* sp.	Skull	14
12	BPI.FN.3756	*Diademodon mastacus*	Skull	40
13	BPI.FN.3769	*Diademodon browni*	Skull	39
14	BPI.FN.3773	*Diademodon browni*	Cranium	34
15	BPI.FN.3772	*Diademodon browni*	Cranium	33
16	BPI.FN.4528	*Diademodon* sp.	Snout, dentary	13
17	BPI.FN.2519	*Cyclogomphodon platyrhinus*	Snout, dentary	21
18	G.S. R.531		Cranium	17
19	BPI.FN.4647	*Diademodon* sp.	Cranium, dentary	25
20	BPI.FN.3771	*Diademodon* sp.	Skull	25
21	BPI.FN.3776a	*Cragievarus kitchingi* (type)	Skull	25
22	BPI.FN.4658	*Diademodon browni*	Skull	40
23	BPI.FN.3511	*Diademodon browni*	Skull	36
24	BPI.FN.4529	*Diademodon* sp.	Snout, dentary	9
25	BPI.Fn.1169		Skull	8
26	G.S. R.483		Skull	19
27	G.S. R.327	*Diademodon tetragonus*	Dentary	13
28	G.S. R.321	*Diademodon tetragonus*	Dentary	7
29	G.S. R.321a	*Diademodon tetragonus*	Dentary	11
30	G.S. R.321b	*Diademodon tetragonus*	Dentary	11
31	G.S. R.321c	*Diademodon tetragonus*	Dentary	15
32	G.S. R.321d	*Diademodon tetragonus*	Dentary	3
33	G.S. R.319	*Titanogomphodon* cf *crassus*	Symphysis	7
34	BPI.FN.2666	*Diademodon* sp.	Dentary	10
35	N.M. C2707–30	*Diademodon entomophonus*	Dentary	12
36	N.M. C2707–31	*Diademodon entomophonus*	Dentary	12
37	N.M. C2707–32	*Diademodon entomophonus*	Dentary	7
38	N.M. C2705–33	*Diademodon entomophonus*	Dentary	15
39	N.M. C2705–34	*Diademodon entomophonus*	Dentary	3
40	N.M. C2706–35	*Diademodon entomophonus*	Dentary	10
41	N.M. C2705–36	*Diademodon entomophonus*	Dentary	15
42	N.M. C2707–37	*Diademodon entomophonus*	Dentary	3
43	N.M. C2707a	*Diademodon entomophonus*	Dentary	9
44	N.M. C2707b	*Diademodon entomophonus*	Dentary	10
45	N.M. C2707f	*Diademodon entomophonus*	Dentary	9
46	N.M. C2707h	*Diademodon entomophonus*	Dentary	14
47	N.M. C2706–50	*Diademodon entomophonus*	Dentary	8
48	N.M. C2706–51	*Diademodon entomophonus*	Dentary	13
49	N.M. C2707–1	*Diademodon entomophonus*	Dentary	13
50	N.M. C2707–2	*Diademodon entomophonus*	Dentary	12
51	N.M. C2707	*Diademodon entomophonus*	Dentary	6
52	N.M. C2705–8	*Diademodon entomophonus*	Dentary	9
53	N.M. C2705–12	*Diademodon entomophonus*	Dentary	15
54	N.M. C2709	*Diademodon entomophonus*	Dentary	14
55	N.M. C2709a	*Diademodon entomophonus*	Dentary	14

variables x and y). If equation (1) is converted to logarithms, then curvilinear growth relationships become linear, and the problem is reduced to the fitting of a straight line, thus:

$$\log y = \log a + \beta \log x \qquad (2)$$

Equation (2) may be rewritten as

$$Y = \alpha + \beta X \qquad (3)$$

where $Y = \log y$, $X = \log x$ and $\alpha = \log a$. With the establishment of linear relationships any line-fitting technique may be used to determine the slope. The slope of the "best straight line" through the data is regarded as the allometric coefficient.

Kermack and Haldane (1950) and Kermack (1954) have cautioned against the use of regression models which assume error to be related to only a single variable. The fitting procedure utilized here was that of Bartlett's best fit (Bartlett, 1949). This method has been recommended for analysis of allometric growth by Simpson, Roe and Lewontin (1960) and has been so used by Kidwell and Chase (1967) and by Dodson (1976).

If the estimates of α and β are to be of any value, confidence intervals must be calculated. Formulae for the calculation of these, and of the values of α and β, have been presented by Simpson *et al.* (1960) and will not be repeated here. In all results presented below, the upper and lower 95 per cent confidence limits for α and β have been calculated. Further analysis of our data will be approached through the utilization of multivariate techniques (see Grine, Hahn and Gow, 1978).

RESULTS

As most of the fossil specimens consisted of less than complete skulls, more than one mensurable character was used as the comparative base value x. The following parameters were used as x values:

(1) Basal skull length
(3) Pre-orbital length
(4) Pre-orbital basal length
(14) Dentary length to angle
(17) Symphysial length
(21) Least snout width

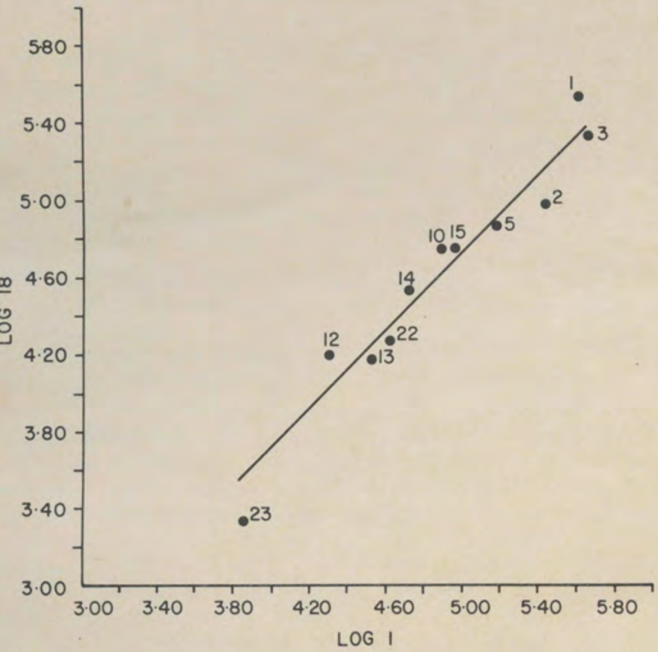

Figure 2

Specimen No.	Log X	Log Y	X	Y
23	3,85	3,33	47	28
12	4,30	4,19	74	66
13	4,52	4,17	92	65
22	4,62	4,62	101	71
14	4,72	4,53	112	93
10	4,90	4,74	134	115
15	4,96	4,74	142	115
5	5,18	4,87	177	130
2	5,44	4,97	230	144
1	5,62	5,53	275	253
3	5,66	5,33	287	207

β = 1,005 ±0,21
α = −0,303 ±0,10

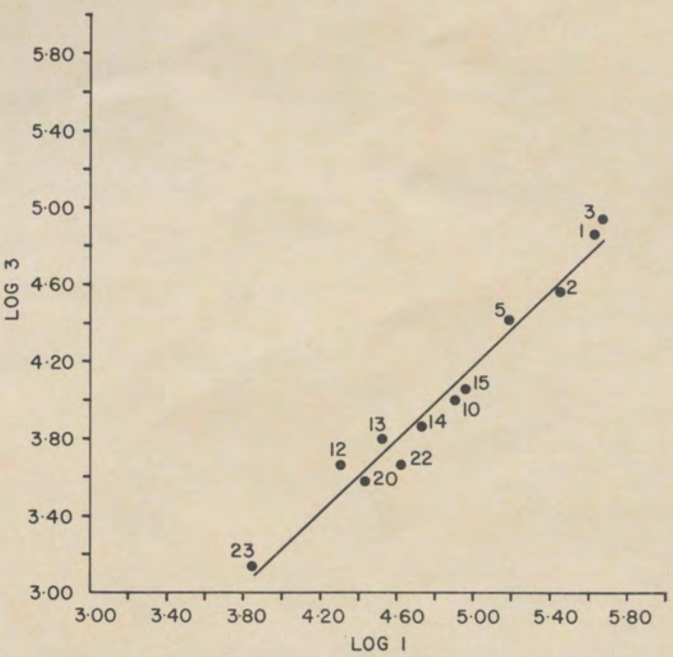

Figure 3

Specimen No.	Log X	Log Y	X	Y
23	3,85	3,14	47	23
12	4,30	3,66	74	39
20	4,43	3,58	84	36
13	4,52	3,81	92	45
22	4,62	3,66	101	39
14	4,72	3,87	112	48
10	4,90	4,01	134	55
15	4,96	4,06	142	58
5	5,18	4,42	177	83
2	5,44	4,58	230	98
1	5,62	4,87	275	130
3	5,66	4,95	287	141

β = 0,964 ±0,09
α = −0,625 ±0,04

All of the available measurements for each specimen were compared and plotted in a bivariate manner with each of the above base values.

Due to limitations of space, only two bivariate plots are presented here (figs. 2 and 3). Comparisons of variables 18 (Total cranial width) and 3 (Pre-orbital length) with variable 1 (Basal length) for some 11 and 12 crania respectively, indicate isometric or near isometric growth (allometric coefficients of 1,0 and 0,96 respectively). The logarithmic values of x and y, and the α and β values for each plot are presented. The amount of variability appears to be somewhat higher for cranial width than for pre-orbital length. Although the allometric coefficient for pre-orbital/basal length (0,96) appears to indicate isometric growth, Dodson (1975) found that for *Alligator mississipiensis* coefficients as close to isometry as 0,98 were significantly different from 1,0 at $p = 0,05$. For convenience, the specimen numbers (see table 2) have been placed next to their respective points on the plots. Both comparisons indicate a growth series extending from the smallest *Diademodon* specimen known (No. 23, BPI.FN. 3511) to the third largest fossil in the present sample (No. 3, BPI.FN. 2522). This series includes crania which have been regarded as specimens of *D. browni, D. Mastacus* and *D. (Gomphognathus) rhodesiensis* (the type specimen). Clearly, all of these crania can be accommodated in a single growth series according to these two (and at least some 25 other) bivariate cranial plots.

DISCUSSION

The preliminary results of this investigation lend support to the contention that many, if not all, of the South African and Zambian specimens which have been regarded as different diademodontine genera and species may constitute a taxonomically homogeneous growth series. The fossils from South Africa and Zambia probably represent various ontogenetic stages of a growth series of only a single species, *Diademodon tetragonus*. The possibility that this animal evinced sexual dimorphism will be examined fully in a later study (Grine, Hahn and Gow, 1978). Perhaps those specimens from South West Africa and China may be part of a phylogenetic growth series. The confirmation or refutation of these hypotheses, however, must await study of a larger series (including the type specimens) of these animals. This quantitative approach, combined with detailed morphological observations, may help to alleviate the taxonomic confusion which currently prevails in the literature on this group of Triassic mammal-like reptiles.

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