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STATISTICAL ANALYSIS OF SKULLS OF TRIASSIC PROTEROSUCHIDS (REPTILIA, ARCHOSAUROMORPHA) FROM SOUTH AFRICA

by

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ABSTRACT

Size-related differences have previously been considered to be important in distinguishing the four proterosuchian archosauromorph species described from South Africa. Previous authors hypothesized that these differences were due to allometric growth. In this study, a statistical analysis of 85 parameters measured in 12 skulls, including all the type specimens, has been carried out. The results show that all the specimens can be fitted into a growth series, supporting a hypothesis expressed by Cruickshank (1972). Variation in the growth rate of parts of the proterosuchid skull and the possible functional significance of such allometric growth patterns are investigated. On the basis of specimens measured in this study and assuming that they all belong to a single species, it would appear that the South African proterosuchids did not display a strong degree of sexual dimorphism.

KEYWORDS: Archosauromorpha, allometry, function.

INTRODUCTION

A substantial number of proterosuchid specimens, including 12 reasonably complete skulls, has been collected from the *Lystrosaurus-Procolophon* Assemblage-zone (Early Triassic) in the northeastern Cape and Orange Free State, South Africa (Kitching 1977). These finds led to the description of four different species belonging to three genera of South African proterosuchids, namely *Proterosuchus fergusi* Broom 1903, *Chasmatosaurus vanhoepeni* Haughton 1924, *Elaphrosuchus rubidgei* Broom 1946 and *Chasmatosaurus alexandri* Hoffmann 1965.

A number of size-unrelated as well as size-related characters have been discussed previously in the literature (Broom 1903, 1906b, 1932, 1946; Huene Von 1908, 1926; Haughton 1924; Broili and Schröder 1934; Brink 1955; Hughes 1963; Hoffman 1965; Charig and Reig 1970; Charig and Sues 1976; Cruickshank 1972) to distinguish between the four species, or to dispute their validity. With the aid of a few simplified comparative drawings, Cruickshank (1972, Figure 1, p.90) hypothesized that the South African proterosuchid specimens represent a growth series and that many of the supposed differences between species are size-related.

An aim of this paper is to test Cruickshank's (1972) hypothesis. An attempt is also made to quantify growth patterns in the proterosuchid skull and to interpret the functional significance of such allometric growth patterns. The existence of possible cranial dimorphism is also investigated.

MATERIAL AND METHODS

Specimens studied and selection of parameters for analysis

The series of proterosuchid skulls studied is presented in Table 1. The skulls show significant variation in size, ranging in overall length from about 154mm to 363mm. The specimens all suffered varying degrees of taphonomic damage (Table 1).

Dodson (1975a) warned that the number and nature of characters selected in an allometric growth study are very important, since improper selection could result in an apparently flawless growth series really consisting of members of more than one species. In a study of *Diademodon*, Grine *et al.* (1978, p.52), selected characters which they thought best expressed "diademodontidness" in a similar way of reasoning to that used by Dodson (1975a) for lambeosaurine hadrosaurs.

In order to test Cruickshank's (1972) hypothesis of allometry in the proterosuchids and to study the functional significance of allometric growth patterns, characters reflecting ontogeny of the braincase, sensory organ capsules and structures related to the jaw mechanism, as well as those reflecting the general shape of the skull, were selected. In addition, the size-related taxonomic differences between the South African proterosuchids mentioned in the literature were quantified. The parameters measured are listed in Table 2 and most are illustrated in Figure 1.

Measuring procedure

Data from only undamaged, clearly discernable skull elements were recorded. A total number of 562 measurements was taken for 85 parameters which

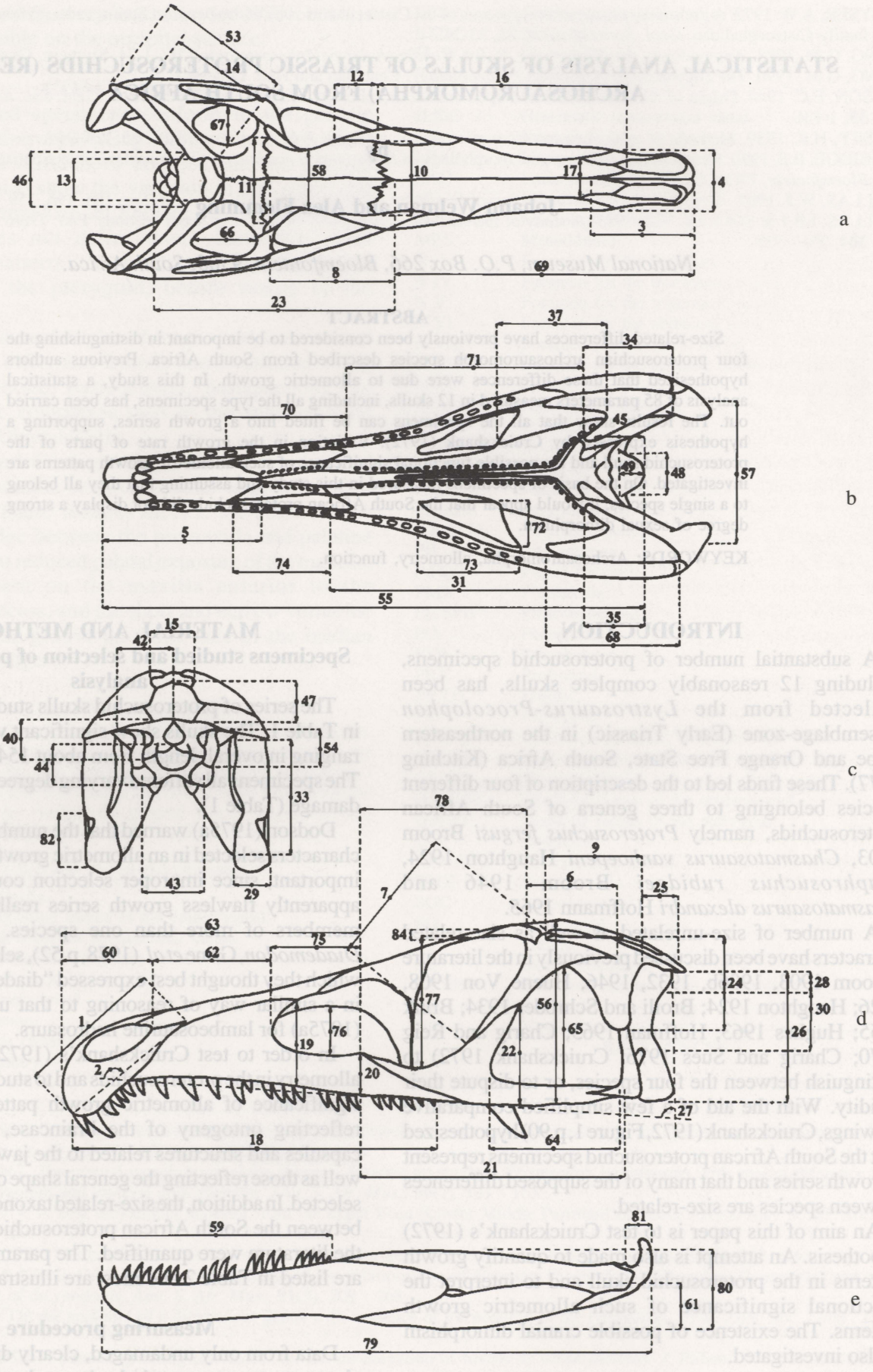

Figure 1. Proterosuchid skull measurements. Slightly modified reconstructions after Cruickshank (1972). a) Dorsal view, b) ventral view, c) occipital view, d) lateral view, e) lower jaw, lateral view.

represent 55.1% of the possible number of measurements if the skulls were all complete. The measurements were taken with a sliding vernier caliper, correct to the nearest 0.1mm. Each measurement was repeated three times. The Munich specimen was measured from published photographs and reconstructions.

Statistical analyses

To test quantatively Cruickshank's (1972) hypothesis that the proterosuchid specimens form a growth series, skull measurements were converted to logarithms and fitted to the equation of simple allometry, $y = ax^b$, similar to the bivariate procedure used by Grine *et al.* (1978), Dodson (1975 a,b, 1976), Gould (1966) and Tschanz (1988). This bivariate analysis of allometry was preferred instead of the readily used multivariate methods of factor analysis or principal component analysis (Shea 1985), due to the small sample size and incompleteness of the skulls used (Tabachnick and Fidell 1989, p.603). Shea (1985) illustrated that allometric coefficients computed using the bivariate and multivariate methods closely correspond.

In the present bivariate analysis two easily measurable, well represented standard comparative measurements (SCM's) were selected to indicate skull size, namely the width of the parietal between the temporal fenestrae and the length of the antorbital fenestra. According to Tschanz (1988) it is important that in bivariate analyses of allometry, standard measurements should reflect isometry. The SCM's were tested for isometry by calculating their allometric coefficient relative to total skull length. The allometric coefficients obtained were 0.913 and 0.990 for the width of the parietal between the temporal fenestrae and the length of the antorbital fenestra respectively. As these coefficients approach 1.0, isometry relative to total skull length is assumed for the selected SCM's.

The associations between the SCM and other measurements were studied through a correlation analysis, using the slope of the principal axis as the fitting procedure (Sokal and Rohlf 1981). The fitting procedure used is appropriate as it does not assume dependence of one variable on the other and as both the variables are allowed to be subject to measurement error (Gould 1966, p.599; Sokal and Rohlf 1981). The Pearson's correlation coefficient as a measure of linear association was also calculated, as were 95% confidence intervals on the slope of the principal axis and on the correlation coefficient itself (Sokal and Rohlf 1981).

Dodson's (1976) bivariate method was followed to establish whether cranial dimorphism is present in the skulls studied. It was assumed that if a large enough number of characters was measured, cranial dimorphism, if present, could be indicated. Seventy one bivariate scattergrams (similar to, and including the graphs in Figure 2 and 3) of 66 parameters were examined. The principal axis of the corresponding correlation analysis was drawn on each scattergram. Each skull received a score of +1 when the point representing the skull on a specific scattergram was lying above the principal axis, a score of -1 when the point was lying below the axis and 0 when equivocal. For each skull, the scores from all scattergrams were added and evaluated according to the method of Grine *et al.* (1978). The "rejection level" set for cranial dimorphism to be accepted was high - *i.e.*, it had to be indicated in 75% of the graphs. Therefore, a specific individual had to lie constantly above or below the axis before it was assigned to one of the morphotypes.

In order to assess allometry (relative growth) of specific skull elements relative to the SCM, the allometric/growth coefficients and their confidence intervals (b, L1 and L2 in Table 3) were interpreted following a procedure similar to that of Grine *et al.* (1978).

TABLE 1

List of proterosuchid specimens measured

Specimen number	State of preservation
SAM 591 Type *Proterosuchus fergusi*	Remains of palate, teeth and imprints of maxilla, antorbital fenestra, lower jaw, Quadrate *etc.*
T/M 201 Type *Chasmatosaurus vanhoepeni*	Lower jaw, left side of the skull, isolated skull table, distorting pressure from the top on middle of skull.
RC 59 Type *Elaphrosuchus rubidgei*	Skull without braincase, distorting pressure from the right dorso-lateral edge of skull.
QR 1484/C.3016 Type *Chasmatosaurus alexandri*	Well preserved except tip of snout, distorting pressure on the postero-ventral end of the skull.
SAM K140	Fairly complete skull, distorting pressure on the left dorso-lateral edge of the skull.
RC 96	Well preserved skull, laterally compressed.
BPI/1/4016	Complete skull, snout damaged, distorting pressure from the right dorso-lateral edge.
BPI/1/3993	Complete skull, snout damaged, distorting pressure from the right dorso-lateral edge.
QR 880/C/500	Snout damaged, without lower jaw, Temporal elements "wandered" during taphonomy.
GHG 72	Fragmentary temporal region without lower jaw. Distorting pressure on the right dorso-lateral edge of the skull.
GHG 231	Very big, well preserved skull, distorting pressure from the right dorso-lateral edge.
Broili and Schröder specimen	Big, fairly well preserved skull, laterally flattened.

TABLE 2

Proterosuchid skull variables measured

1 length of the premaxilla including the postero-lateral process of the premaxilla
2 angle between the maxilla and the premaxilla
3 length of the antero-dorsal process of the premaxilla
4 width of the snout at posterior ends of the nostrils
5 length of the palatal process of the premaxilla
6 length of the posterior process of the postorbital
7 length of the antero-ventral process of the postorbital
8 length of the frontal at the midline of the skull
9 length of the anterior process of the squamosal
10 width of the frontals at the sutures with the nasals
11 width of the frontals at the sutures with the parietals
12 length of the suture between the frontal and the prefrontal
13 the width of the parietals between the temporal fenestrae
14 length of the postero-lateral process of the parietal
15 width of the interparietal
16 length of the nasal
17 width of the nasals across the posterior ends of the posterior processes of the premaxillae
18 length of the upper toothrow.
19 height of the maxilla dorsal to the antorbital fenestra.
20 height of the maxilla ventral to the ventral process of the prefrontal
21 length of the jugal including anterior and posterior processes
22 height of the dorsal process of the jugal
23 length of the temporal region (occipital condyle to the mesokinetic bending line)
24 height of the ventral process of the squamosal
25 length of the posterior process of the squamosal
26 height of the quadrate
27 angle between the long axis of the quadrate and the tooth row
28 height of the quadrate dorsal to the dorsal end of the otic notch
29 width of the glenoid (ventral end of the quadrate)
30 height of the otic notch
31 length of the palatal process of the pterygoid
32* maximum height of the dorsal plates on the dorsal surface of the palate
33 maximum height of the quadrate process of the pterygoid
34 length of the quadrate process of the pterygoid
35 distance between the posterior edge of the transverse process of the pterygoid and the posterior margin of the occiptal condyle
36* height of the epipterygoid
37 length of the ectopterygoid
38* maximum height of the parasphenoid
39* length of the prearticular
40 vertical height of the exoccipital
41* width of the foramen magnum
42 length of the lateral process of the exoccipital that forms the ventral edge of the paroccipital process
43 distance between the centres of the basisphenoidal tubers
44 height of the basioccipital tuber
45 length of the groove-like depression in the postero-ventral surface of the basisphenoid
46 width of the supraoccipital
47 height of the supraocciptal
48 width of the occipital condyle
49 length of the occipital condyle
50* height of the prootic
51* length of the anterior half of the laterosphenoid
52* width of the laterosphenoid between the lateral ends of the capitate processes of the laterosphenoid
53 length of the paroccipital process
54 height of the ventral process of the opishtotic
55 lenth of the skull from the tip of the snout to the posterior margin of the occipital condyle
56 height of the temporal region of the skull
57 width of the skull: distance between the middle of glenoids
58 interorbital width
59 length of the toothrow in the lower jaw
60 length of the snout to the posterior margins of the nostril
61 height of the angular
62 distance between the nostril and the fenestra antorbitalis
63 length of the snout anterior to the orbit
64 length of the lateral temporal fenestra
65 height of the lateral temporal fenestra.
66 length of the upper temporal fenestra
67 width of the upper temporal fenestra

68 length of the subtemporal vacuity
69 length of the snout along its midline (mesokinetic line to tip of the snout)
70 length of the internal naris
71 distance from the internal naris to the posterior edge of the transverse process of the pterygoid
72 width of the suborbital vacuity
73 length of the suborbital vacuity
74 length of the vomers
75 length of the antorbital fenestra
76 height of the antorbital fenestra
77 height of the orbit
78 length of the orbit
79 length of the lower jaw
80 height of the lower jaw at the middle of the lateral mandibular fenestra
81 length of the retroarticular process
82 height of the dorsal process of the quadratojugal
83* tooth length; average estimate
84 frontal thickness above the orbit
85* tooth count
* not indicated in Figure1

Probability values (p) smaller than 0.05 were recognized as significant in all statistical decisions.

RESULTS

Allometric growth pattern

The results of the bivariate analysis are presented in Table 3 (intertemporal width as SCM) and Table 4 (length of the antorbital fenestra as SCM). Results included in Table 3 pertain to all skulls except SAM 591. In Table 4 the results refer to all skulls including SAM 591, but excluding BPI\1\3993 and GHG 72.

Results of an analysis of only 66 of the 85 possible parameters are included in Table 3 due to insufficient data for statistical analysis in the excluded cases. In only 8 of the remaining 66 instances (Table 3), a linear association between the variable analysed and the SCM was rejected, indicating the absence of allometric growth (Table 3, RL=y). However, very small sample sizes (Table 3, $n < 5$) in half these cases and the possibility of a high degree of measurement error in the rest ruled out a total lack of association for these characters. Considering the values of the correlation coefficients (Table 3, r) and the low incidence of rejection of linearity (Table 3, RL=y), it is apparent that the specimens included in these analyses do represent a morphologically homogeneous group of animals in various stages of ontogenetic development.

Results in Table 4 are restricted to those parameters which include the SAM 591 specimen. From Table 4 it is evident that a significant linear association is present in all cases, indicating that SAM 591 fits well into the growth series.

Bivariate scattergrams of SCM versus size-related parameters previously used to distinguish between species are presented in Figures 2 and 3.

Relative growth in different regions of the skull

The allometric coefficients (Table 3, b) indicate relative growth rate, ranging from 0.26 (for the length of occipital condyle [Y49]) to 2.86 (for the length of the orbit [Y78]). In most cases the allometric coefficients approximate 1.0 which indicates isometric or near isometric growth relative to the SCM (Figure 4).

Clear positive allometry is demonstrated (confidence interval entirely above 1) for the increase in the number of teeth (Table 3, Y85). Tooth size (Y83) also showed positive allometry (allometric coefficient well above 1), although it was less pronounced than the increase in the number of teeth. Apart from this, a general strengthening of the orbital region of the skull occurs by a broadening of the frontals anteriorly and posteriorly, as well as in their middle parts where they form the interorbital region. The length of the frontal also showed positive allometry.

In most instances where allometric coefficients are negative, the confidence limits ranged from below to above isometry. Definite negative allometry (where confidence limits of the growth coefficient are both less than one) occurred in the length of the middle part of the palate as indicated by growth coefficients of the length of the palatal process of pterygoid (Table 3, Y31), length of the ectopterygoid (Table 3, Y37), and by the relative shortening of the distance between the internal naris and the posterior edge of the transverse process of the pterygoid (Table 3, Y71). Another negative allometric trend is associated with a general dorso-ventral flattening of the skull with increase in size, reflected by the negative growth coefficients of the heights of the maxilla (Table 3, Y19, 20), the orbit (Table 3, Y77), the dorsal process of the jugal (Table 3, Y22), the temporal region (Table 3, Y56), the antorbital fenestra (Table 3, Y76) and the basioccipital tubers (Table 3, Y44). Negative allometric growth also occurred in the length of the postero-lateral process of the parietal (Table 3, Y14), as well as in the length of the upper temporal fenestra (Table 3, Y66). The only other variables in which definite negative allometry is evident are frontal thickness above the orbit (Table 3, Y84) and interparietal width (Table 3, Y15).

Cranial dimorphism

Results obtained for this part of the study (Table 5) are inconclusive. The total number of times that a point representing each individual lay either above or below the principal axis, did not exceed 75% except in three

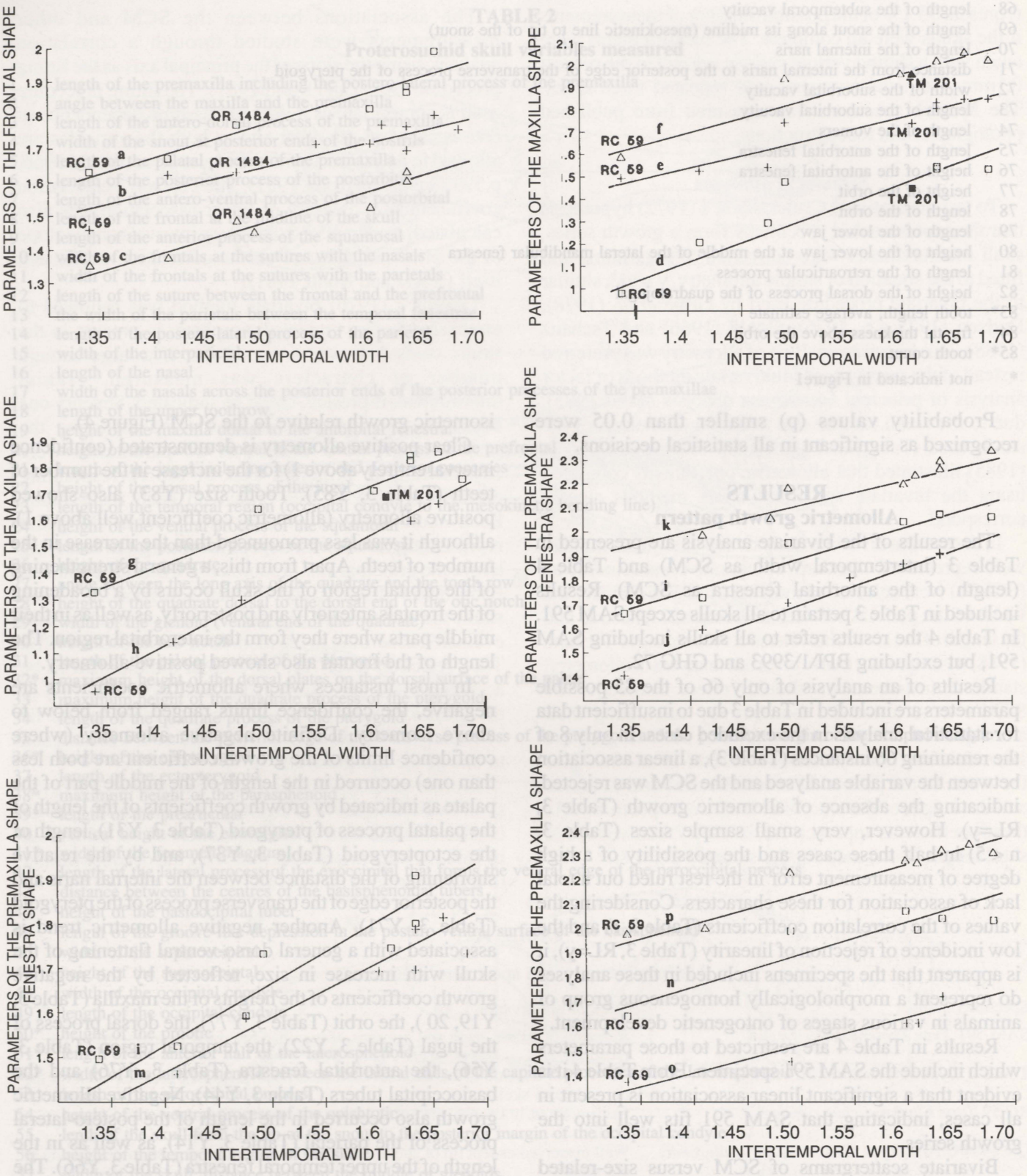

Figure 2. Bivariate scattergrams of allometry of taxonomically important skull elements of the South African proterosuchids. The scale on both axes is logarithmic and the measurements are in mm. In all the graphs, intertemporal width is used on the x-axis as Standard Comparative Measurement (SCM). The solid line represents the principal axis of the correlation analysis for the following variables. a) The length of the frontals, b) Width of the frontals at their suture with the parietals, c) Width of the frontals at their sutures with the nasals, d) Height of the maxilla ventral to the ventral process of the prefrontal, e) Length of the antorbital fenestra, f) Distance between the nostril and the antorbital fenestra, g) Height of the maxilla anterior to the antorbital fenestra, h) Height of the antorbital fenestra, i) Length of the lateral temporal fenestra, j) Height of the dorsal process of the jugal, k) Length of the jugal including anterior and posterior processes, l) Height of the ventral process of the squamosal, m) Length of the posterior process of the postorbital, n) Length of the premaxilla including the postero-lateral process of the premaxilla, o) Height of the angular and p) Length of the snout anterior to the orbit.

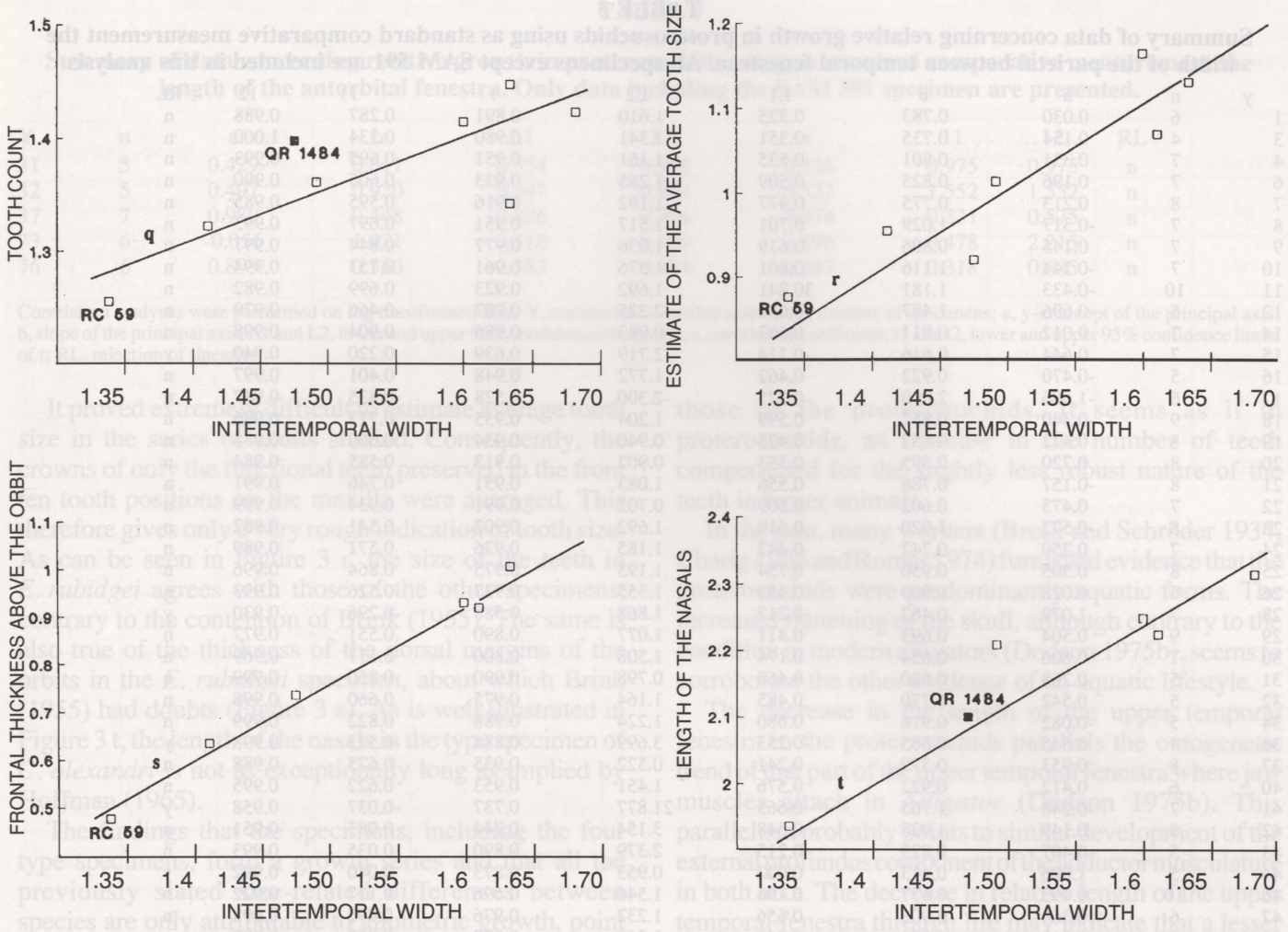

Figure 3. Bivariate scattergrams of allometry of taxonomically important skull elements of the South African proterosuchids. The scale on both axes is logarithmic and the measurements are in mm. In all the graphs intertemporal width is used on the x-axis as Standard Comparative Measurement (SCM). The solid line represents the principal axis of the correlation analysis for the following variables. q) Tooth count, r) Estimate of the average tooth size, s) Frontal thickness above the orbit and t) Length of the nasals.

cases (Table 5). In these cases, however, conflicting results were obtained by using scattergrams based on the two different SCM's (Table 5 a and b). This indicates that, with more than one SCM taken into account, and with the data available at present, dimorphism in the skulls cannot be demonstrated.

DISCUSSION

Cruickshank (1972) hypothesized that size-related characters previously used to distinguish species of the South African proterosuchids could be attributable to allometric growth. The high degree of linear association between the SCM's and other skull measurements indicates that specimens utilized in the present analysis do indeed represent a growth series of a morphologically homogeneous group of animals, thus supporting Cruickshank's (1972) hypothesis. In particular, we found that the shape of the frontals (Figure 2 a,b,c) of *E. rubidgei* and *C. alexandri* that Broom (1946) and Hoffman (1965) respectively thought were different from those of the two forms described earlier, actually conform in shape with those of the other skulls. The measurements of the maxilla (Figure 2 d, e, f, g, h) illustrate that, contrary to the opinions of Haughton (1924) when he described *C. vanhoepeni* and Broom (1946) when he described *E. rubidgei*, the shape of the maxillae in these forms fit in with the other specimens of the growth series. As far as shape of the lateral temporal fenestra is concerned, the separate elements surrounding the fenestra were measured to avoid subjective interpretation of the often distorted shape of the fenestra (Figure 2 i, j, k, l, m). Measurement of the separate elements unambiguously shows that the shape of the lower temporal fossa in *E. rubidgei* corresponds with its shape in other specimens, contrary to the contention of Broom (1946). Although Broom (1946) thought otherwise, the shape of the premaxilla (Figure 2 o, n, p) in *E. rubidgei* agrees in shape with all the other specimens where this element is preserved, allometry taken into account.

The tooth counts of the maxilla in the *E. rubidgei* specimen (Charig and Reig 1970) as well as in *C. alexandri* (Hoffman 1965) conforms to the allometric pattern of increase in the number of teeth with size (Figure 3 q).

TABLE 3

Summary of data concerning relative growth in proterosuchids using as standard comparative measurement the width of the parietal between temporal fenestrae. All specimens except SAM 591 are included in this analysis.

y	n	a	b	L1	L2	r	l1	l2	RL
1	6	0.030	0.783	0.325	1.610	0.891	0.287	0.988	n
3	4	0.154	0.735	0.351	1.341	0.980	0.334	1.000	n
4	7	0.331	0.801	0.535	1.161	0.951	0.695	0.993	n
6	7	0.196	0.825	0.509	1.285	0.933	0.605	0.990	n
7	8	0.213	0.775	0.477	1.192	0.916	0.595	0.985	n
8	7	-0.317	1.029	0.701	1.517	0.951	0.697	0.993	n
9	7	0.145	0.806	0.619	1.036	0.977	0.844	0.997	n
10	7	-0.144	1.116	0.801	1.576	0.961	0.753	0.994	n
11	10	-0.433	1.181	30.841	1.692	0.923	0.699	0.982	n
12	5	-0.696	1.487	-0.036	-2.225	0.707	-0.466	0.979	n
14	7	0.012	0.811	0.663	0.983	0.986	0.904	0.998	n
15	7	0.644	0.616	-0.114	2.719	0.639	0.220	0.940	y
16	5	-0.470	0.922	0.462	1.772	0.948	0.401	0.997	n
17	6	-1.606	2.090	-0.275	-2.300	0.528	-0.435	0.947	n
18	9	-0.340	0.857	0.599	1.204	0.935	0.713	0.986	n
19	8	0.472	0.652	0.425	0.940	0.934	0.669	0.988	n
20	8	0.720	0.595	0.353	0.902	0.913	0.585	0.984	n
21	8	-0.157	0.786	0.556	1.083	0.951	0.746	0.991	n
22	7	0.473	0.602	0.509	0.702	0.991	0.934	0.999	n
23	8	-0.572	1.020	0.619	1.692	0.902	0.541	0.982	n
24	7	0.250	0.742	0.442	1.185	0.926	0.571	0.989	n
25	8	0.505	0.950	0.754	1.193	0.975	0.864	0.996	n
26	6	0.028	0.809	0.453	1.355	0.937	0.526	0.993	n
28	7	1.079	0.462	-0.217	1.868	0.588	-0.296	0.930	y
29	9	0.504	0.693	0.411	1.077	0.890	0.551	0.977	n
30	7	0.606	0.654	0.174	1.508	0.800	0.117	0.969	n
31	5	0.268	0.620	0.468	0.798	0.990	0.850	0.999	n
32	5	0.542	0.770	0.485	1.164	0.975	0.660	0.998	n
34	5	-0.082	0.916	0.680	1.224	0.988	0.822	0.999	n
36	4	0.645	0.585	-0.253	3.699	0.884	-0.513	0.998	y
37	8	0.953	0.379	0.241	0.522	0.935	0.675	0.988	n
40	6	0.412	0.922	0.576	1.451	0.953	0.622	0.995	n
41	7	-0.248	1.765	0.663	21.877	0.737	-0.037	0.958	y
42	8	0.149	1.028	0.348	3.154	0.744	0.083	0.951	n
43	5	0.407	0.829	0.215	2.379	0.890	0.035	0.993	n
44	5	1.006	0.413	0.022	0.953	0.873	0.040	0.992	y
46	10	0.493	0.677	0.196	1.546	0.696	0.117	0.922	n
47	6	0.364	0.903	0.656	1.232	0.976	0.792	0.998	n
48	7	0.212	1.074	0.846	1.369	0.979	0.862	0.997	n
49	5	1.309	0.260	0.109	0.424	0.951	0.425	0.997	n
50	5	0.605	0.705	0.178	1.753	0.898	0.074	0.993	n
52	4	-0.511	1.258	0.459	4.866	0.956	-0.057	0.999	n
53	7	0.577	0.593	0.401	0.823	0.957	0.729	0.994	n
54	4	0.034	1.467	undefined	undefined	0.765	-0.741	0.995	y
55	8	-0.670	0.913	0.649	1.272	0.950	0.741	0.991	n
56	6	0.402	0.598	0.353	0.909	0.951	0.614	0.995	n
57	6	0.243	0.680	0.347	1.163	0.928	0.469	0.992	n
58	9	0.068	1.033	0.911	1.172	0.990	0.953	0.998	n
60	5	0.137	0.903	0.439	1.766	0.945	0.378	0.997	n
61	8	0.315	0.917	0.574	1.437	0.915	0.593	0.985	n
62	7	0.115	0.758	0.473	1.151	0.938	0.627	0.991	n
63	8	-0.385	0.878	0.627	1.213	0.952	0.749	0.991	n
64	7	0.106	0.740	0.524	1.010	0.963	0.766	0.995	n
65	4	0.004	0.931	0.153	4.406	0.938	-0.238	0.000	y
66	10	0.457	0.736	0.575	0.925	0.961	0.839	0.991	n
67	7	0.206	0.941	0.681	1.291	0.965	0.774	0.995	n
68	6	0.154	0.739	0.427	1.185	0.944	0.569	0.994	n
69	7	-0.213	0.795	0.526	1.159	0.949	0.686	0.993	n
71	6	0.162	0.702	0.584	0.836	0.992	0.925	0.999	n
72	5	0.220	0.995	0.340	2.894	0.902	0.095	0.994	n
73	7	-0.091	1.024	0.618	1.669	0.925	0.566	0.989	n
75	9	0.102	0.851	0.595	1.193	0.935	0.714	0.987	n
76	5	0.879	0.471	0.413	0.531	0.998	0.964	1.000	n
77	6	0.449	0.652	0.451	0.898	0.972	0.760	0.997	n
78	7	-3.510	2.862	0.941	-6.908	0.613	-0.261	0.935	y
79	7	-0.648	0.880	0.649	1.178	0.969	0.800	0.996	n
80	7	0.284	0.777	0.415	1.335	0.904	0.471	0.986	n
81	6	-0.550	1.801	0.957	4.771	0.894	0.299	0.988	n
82	5	-0.228	1.078	0.282	4.946	0.869	-0.058	0.991	n
83	7	0.466	1.024	0.603	0.752	0.916	0.525	0.988	n
84	7	1.047	0.594	0.530	0.662	0.995	0.967	0.999	n
85	8	-1.529	2.234	1.161	7.609	0.793	0.200	0.960	n

Correlation analyses were performed on log transformed data; Y, comparative variable number; n, number of specimens; a, y-intercept of the principal axis; b, slope of the principal axis; L1 and L2, lower and upper 95% confidence limits of b; r, correlation coefficient; l1 and l2, lower and upper 95% confidence limits of r; RL, rejection of linearity.

TABLE 4

Summary of data concerning relative growth in proterosuchids using as standard comparative measurement the length of the antorbital fenestra. Only data including the SAM 591 specimen are presented.

Y	n	a	b	L1	L2	r	11	12	RL
31	5	0.429	0.611	0.554	0.998	0.336	0.975	0.975	n
32	5	0.497	0.920	0.547	0.964	0.532	1.552	1.552	n
37	7	0.980	0.448	0.826	0.996	0.974	0.331	0.575	n
73	6	-0.056	1.021	0.310	0.989	0.896	0.478	2.215	n
76	6	0.899	0.560	0.583	0.994	0.947	0.318	0.685	n

Correlation analyses were performed on log transformed data; Y, comparative variable number; n, number of specimens; a, y-intercept of the principal axis; b, slope of the principal axis; L1 and L2, lower and upper 95% confidence limits of b; r, correlation coefficient; l1 and l2, lower and upper 95% confidence limits of r; RL, rejection of linearity.

It proved extremely difficult to estimate average tooth size in the series of skulls studied. Consequently, the crowns of only the functional teeth preserved in the front ten tooth positions on the maxilla were averaged. This therefore gives only a very rough indication of tooth size. As can be seen in Figure 3 r, the size of the teeth in *E. rubidgei* agrees with those of the other specimens, contrary to the contention of Brink (1955). The same is also true of the thickness of the dorsal margins of the orbits in the *E. rubidgei* specimen, about which Brink (1955) had doubts (Figure 3 s). As is well illustrated in Figure 3 t, the length of the nasals in the type specimen of *C. alexandri* is not as exceptionally long as implied by Hoffman (1965).

The findings that the specimens, including the four type specimens, form a growth series and that all the previously stated size-related differences between species are only attributable to allometric growth, point to the need for a revision of the taxonomy of the South African proterosuchids. Such a study is in progress by the first author of this paper.

The results obtained for cranial dimorphism support the contention that the skulls may represent a single species. Assuming the presence of only one species, the results indicate that such a species would be sexually indeterminate. This apparently weak expression of dimorphism in the proterosuchids, could be similar to the absence of sexual dimorphism in some dinosaurs (Rozhdestvensky 1965) and the therapsid *Diademodon* (Grine *et al.* 1978). In the present study, however, the sample size was very small (12 skulls) and well substantiated conclusions must await study of a larger series of fossils.

Inspection of those features of the skull that show positive and negative allometry suggests definite functional associations. The dramatic increase in the number of teeth and, to a lesser extent, in the tooth size, perhaps suggest a dietary switching during ontogeny. Nile crocodiles undergo a similar switching where individuals that are longer than 3-4m, turn from a diet of fish to a diet of land vertebrates (Cott 1961). The adult Nile crocodile tooth count is generally half that of the larger proterosuchid skulls included in this study. The teeth of modern crocodiles are also more robust than those of the proterosuchids. It seems as if in proterosuchids, an increase in the number of teeth compensated for the slightly less robust nature of the teeth in larger animals.

In the past, many workers (Broili and Schröder 1934, Charig 1965 and Romer 1974) furnished evidence that the proterosuchids were predominantly aquatic forms. The increased flattening of the skull, although contrary to the condition in modern alligators (Dodson 1975b), seems to corroborate the other evidence of an aquatic lifestyle.

The decrease in the length of the upper temporal fenestra in the proterosuchids parallels the ontogenetic trend of that part of the upper temporal fenestra where jaw muscles attach in *Alligator* (Dodson 1975b). This parallelism probably points to similar development of the external profundus component of the adductor musculature in both taxa. The decrease in relative length of the upper temporal fenestra through life may indicate that a lesser premium was placed on the speed of the jaw closing mechanism in the larger proterosuchids, since it is especially in the piscivorous modern crocodiles, where speed is very important for prey capture, that large upper temporal fenestrae associated with elongated snouts are found (Langston 1973).

It has long been noted that the skull of *Proterosuchus* was kinetic (Broom 1903, Versluys 1912 p.629,

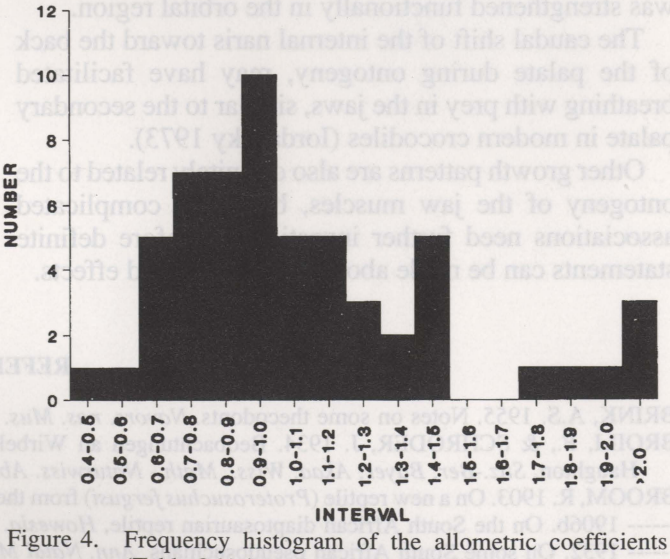

Figure 4. Frequency histogram of the allometric coefficients (Table 3 b) in proterosuchid skulls.

TABLE 5
Results of the analysis of cranial dimorphism in the proterosuchids

a) Parameter 75

	RC 59	BPI/1/4016	QR 1484	SAM 591	TM 201	SAM K140	BPI/1/339	GHG 72	QR 880	Broili spec.	RC 96	GHG 231
+1	5	27	42	3	24	6			15	11	25	14
0	1	1	-	1	-	-			1	2	2	1
-1	36	18	1	2	7	25			20	33	23	10
Sum	-31	+9	+41	+1	+17	-19			-5	-22	+2	+4
Total	42	46	43	6	31	31			36	46	50	25
%	74	20	95	16	55	61			14	48	4	16

b) Parameter 13

	RC 59	BPI/1/4016	QR 1484	SAM 591	TM 201	SAM K140	BPI/1/339	GHG 72	QR 880	Broili spec.	RC 96	GHG 231
+1	22	25	25		9	32	14	18	1	12	44	15
0	2	-	-		-	-	2	1	3	-	1	3
-1	22	22	25		24	3	36	2	37	42	11	10
Sum	0	+3	0		-15	+29	-22	+16	-16	-30	+33	+5
Total	46	47	50		33	35	55	21	41	54	56	28
%	0	6	0		45	82	40	76	39	55	59	18

Cruickshank 1972). It seems as if the abnormal strengthening of the orbital region in larger skulls could be related to strengthening of the skull roof, preventing bending other than in the mesokinetic hinge (Cruickshank 1972) between the frontals and the nasals, during kinetic movement. The presence of a well ossified laterospenoid attached to the ventral surface of the frontals in proterosuchids (Clark, *et al.* 1993), seems to give supportive evidence to the idea that the skull roof was strengthened functionally in the orbital region.

The caudal shift of the internal naris toward the back of the palate during ontogeny, may have facilitated breathing with prey in the jaws, similar to the secondary palate in modern crocodiles (Iordansky 1973).

Other growth patterns are also definitely related to the ontogeny of the jaw muscles, but these complicated associations need further investigation before definite statements can be made about their causes and effects.

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LIST OF ABBREVIATIONS

BPI	Bernard Price Institute, for Palaeontology, University of the Witwatersrand, Johannesburg, South Africa
GHG	Geological Survey, Pretoria, South Africa
QR/C	National Museum, Bloemfontein, South Africa
RC	Rubidge Collection, Wellwood, Graaff-Reinet, South Africa
SAM/SAMK	South African Museum, Cape Town, South Africa
TM	Transvaal Museum, Pretoria, South Africa.

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