

ONTOGENY AND SEXUAL DIMORPHISM IN *AULACEPHALODON*
(REPTILIA, ANOMODONTIA)

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(With 10 figures and 6 tables)

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ABSTRACT

A large number of *Aulacephalodon* crania have been examined by means of biometrical (allometric) methods. The results of this investigation indicate that this sample represents a morphometrically homogeneous group, and that probably only a single species of *Aulacephalodon*, viz. *A. baini*, is represented in the Permian sediments of South Africa and Zambia. A qualitative analysis of nasal boss and temporal arch morphology indicates that these features are related to sexual dimorphism. Sexual dimorphism of the cranium appears to have been expressed in individuals with a basal skull length of between 190 and 245 mm. The geographical distribution of these fossils has been examined also.

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INTRODUCTION

Numerous anomodont fossils have been recovered from lower Beaufort Group sediments of South Africa. Well over 100 anomodont species have been described from *Cistecephalus* Zone strata alone. The *Cistecephalus* Zone, as defined by Kitching (1970, 1977), includes both Broom's (1906) *Endothiodon* Zone and the lower and middle portions of his *Cistecephalus* Zone. Kitching (1970, 1971) has classified the upper horizons of Broom's (1906) *Cistecephalus* Zone as the *Daptocephalus* Zone.

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One of the most commonly occurring forms in these sediments is a rather homogeneous group of anomodonts which have been referred to the genus *Aulacephalodon* by Haughton & Brink (1954) and Keyser (1969). The fossil remains of this reptile appear to have a rather limited stratigraphic range; in the *Cistecephalus* Zone, they occur in sediments with a vertical thickness of some 330 m, but they are concentrated in a relatively thin horizon (about 80 m) in which the zone fossil, *Cistecephalus*, occurs abundantly (Keyser 1969). *Aulacephalodon* has been recovered, albeit rarely, from within the first 3 m of the overlying *Daptocephalus* Zone (Kitching 1977), and fossils of *Aulacephalodon* have been found in comparatively large numbers at the northern (Chikonta) localities of the upper Member of the Upper Madumabisa Mudstone 'Formation', Luangwa Valley, Zambia (Drysdall & Kitching 1963).

A number of genera and species of aulacephalodonts have been described, but only a few have been based on more than fragmented fossils, and none has been diagnosed adequately. In very few instances has either ontogenetic growth or sexual dimorphism been considered in the description of a new taxon.

Owen (1844) described the first species of this group, on the basis of a single specimen, as *Dicynodon baini*. He later referred a second specimen to *D. baini* because it showed 'the same character of the tusk' as the type-species (Owen 1876). A second species, *D. tigriceps*, was described also by Owen (1855). Seeley (1898) divided *Dicynodon* into two subgenera. He proposed that those forms of *Dicynodon* which exhibit a short snout and a wide cranium be included in the subgenus *Aulacephalodon*. Broom described two further species of *Dicynodon*, viz. *D. laticeps* (Broom 1912) and *D. moschops* (Broom 1913). In 1921 he proposed a new genus, *Bainia*, for the 'tusked specimens of *Dicynodon*'; he included the species *D. baini*, *D. tigriceps* and *D. laticeps* in the genus *Bainia* and named two more species, *B. peavoti* and *B. haughtoni* (Broom 1921). Later, Broom (1932) recognized the validity of Seeley's (1898) subgeneric name *Aulacephalodon* but, as pointed out by Keyser (1969), he altered the spelling, probably as a mistake from the spelling of Seeley's (1898) other subgenus *Aulacocephalus*, to *Aulacocephalodon*. Broom considered that, '*Aulacocephalodon* . . . ought to be accepted for the group of broad skulled anomodonts typified by *Dicynodon baini* if we regard them as worthy of separate generic rank. . . . Certainly they must be placed in at least a subgenus, and I think we can quite safely regard *Aulacocephalodon* as a distinct genus. Some years ago I proposed the name *Bainia* for the large broad-headed types not fully recognising the claims of Seeley's name' (Broom 1932: 191-192).

He referred six species, namely *Dicynodon baini*, *D. tigriceps*, his own *D. laticeps*, *D. moschops*, *Bainia peavoti*, and *B. haughtoni* to the genus '*Aulacocephalodon*'; and he described a new species, *A. latissimus* (Broom 1932). In the same work Broom (1932, fig. 65A-B) figured the dorsal and lateral views of an apparently nearly complete cranium with the legend, 'view of skull of *Aulacocephalodon whaitsi*, Broom'; however, there is no accompanying description which serves to define or differentiate that taxon. Accordingly, the name

Aulacocephalodon whaitsi does not satisfy Article 13 of the International Code of Zoological Nomenclature (1964) and it must, therefore, be considered as a nomen nudum. The generic name '*Aulacocephalodon*' was used subsequently by Broom (1936, 1937, 1940, 1941, 1948), Broom & George (1950), Van Hoepen (1934), and Haughton & Brink (1954). However, Keyser (1969) has pointed out that the name '*Aulacocephalodon*' is probably an incorrect subsequent spelling of Seeley's name *Aulacephalodon* and thus '*Aulacocephalodon*' has no status in nomenclature; the correct generic name is *Aulacephalodon* Seeley.

Broom (1928) described the species *Dicynodon milletti*, and Van Hoepen (1934) placed this species in *Aulacephalodon*; Keyser (1969) has referred it to *Oudenodon*, as a junior synonym of *O. baini*, and he has noted that Broom's (1913) *Dicynodon moschops* (which Broom referred to *Aulacephalodon* as a valid species in 1932) probably represents a valid species of *Pelanomodon*.

To date some seventeen species which have been referred to *Aulacephalodon* have been described (Table 1). Keyser (1969) has examined the supposed features that have been used in the diagnosis of various *Aulacephalodon* species and has concluded that, for most of these characters, their variability and susceptibility to diagenetic distortion makes them highly questionable as taxonomic criteria. He made the important observation that, since many of the features used to distinguish the various species are to at least some extent size-dependent, the possibility that these species are all synonyms deserves consideration.

TABLE 1

List of suggested synonyms of *Aulacephalodon baini* (Owen).

<i>Dicynodon baini</i>	.	.	.	Owen, 1844
<i>Dicynodon tigriceps</i>	.	.	.	Owen, 1844
<i>Dicynodon laticeps</i>	.	.	.	Broom, 1912
<i>Bainia peavoti</i>	.	.	.	Broom, 1921
<i>Bainia haughtoni</i>	.	.	.	Broom, 1921
<i>Aulacephalodon latissimus</i>	.	.	.	Broom, 1932
<i>Aulacephalodon nesamanni</i>	.	.	.	Broom, 1936
<i>Aulacephalodon nodosus</i>	.	.	.	Van Hoepen, 1934
<i>Aulacephalodon luckhoffi</i>	.	.	.	Broom, 1937
<i>Aulacephalodon hartzenbergi</i>	.	.	.	Broom, 1937
<i>Aulacephalodon coatoni</i>	.	.	.	Broom, 1941
<i>Aulacephalodon brodiei</i>	.	.	.	Broom, 1941
<i>Aulacephalodon cadlei</i>	.	.	.	Broom, 1948
<i>Aulacephalodon pricei</i>	.	.	.	Broom & George, 1950
<i>Aulacephalodon vanderhorsti</i>	.	.	.	Broom & George, 1950

Consequent upon Keyser's suggestion, the hypothesis entertained in this study was that many, if not all, of the aulacephalodont specimens which have been described possibly constitute an ontogenetic series of a single species of *Aulacephalodon*. A number of aulocephalodont crania were biometrically analysed in an attempt to ascertain whether an ontogenetic growth series could be demonstrated for this anomodont, and also whether the phenomenon of allometric growth could explain the supposed morphological differences between

the various proposed taxa. The possibility that sexual dimorphism was expressed in the cranium of *Aulacephalodon* (as suggested by Broom 1937, 1948; Keyser 1969) has been examined.

MATERIAL AND METHODS

Thirty-three specimens were examined. The material ranged from relatively undistorted crania to portions of the skull. The principles of relative (allometric) growth were applied to 18 of the crania (Table 2, Nos. 1–18) whilst the remainder of the specimens received less rigorous biometric treatment. Some 31 different measurements were defined (Fig. 1), but, because of the often fragmentary and distorted nature of the fossils, there were only 4 specimens for which all 31

TABLE 2

List of all specimens of *Aulacephalodon* examined in this study.

Specimen	Number	Previous taxonomic designation	Description	V	Sex
1	SAM-3328	<i>A. haughtoni</i> (T)	cranium	12	indet.
2	SAM-8747	<i>A. latissimus</i> (T)	cranium	28	female
3	SAM-K1221	<i>A. luckhoffi</i> (T)	cranium	25	female
4	BPI.FN. 1207		cranium	31	indet.
5	BPI.FN. 806	<i>A. pricei</i> (T)	cranium	31	male
6	BPI.FN. 300	<i>A. baini</i>	cranium	31	? female
7	BPI.FN. 904		cranium	26	indet.
8	BPI.FN. 4087	<i>A. baini</i>	cranium	30	female
9	BPI.FN. 4124	<i>A. cf. baini</i>	cranium	29	female
10	BPI.FN. 642	<i>A. cf. baini</i>	cranium	7	male
11	BPI.FN. 2594	<i>A. sp.</i>	cranium	14	male
12	BPI.FN. 634	<i>A. vanderhorsti</i> (T)	cranium	28	male
13	BPI.FN. 2460	<i>A. sp.</i>	cranium	31	male
14	BPI.FN. 3950	<i>A. cf. baini</i>	cranium	20	female
15	BPI.FN. 2983	<i>A. baini</i>	cranium	29	male
16	BPI.FN. 4106	<i>A. baini</i>	cranium	12	female
17	BPI.FN. 493	<i>A. baini</i>	skull	23	male
18	BPI.FN. 304	<i>A. baini</i>	cranium	29	female
19	TM 287	<i>A. hartzenbergi</i> (T)	snout	*	indet.
20	TM 1494	<i>A. brodiei</i> (T)	skull	*	female
21	TM 4043	<i>Aulacephalodon</i>	cranium	*	female
22 +	TM 4118	<i>A. sp.</i>	cranium	*	female
23 +	TM 953	? <i>Aulacephalodon</i>	occiput	*	
24 +	TM 2043	<i>A. sp.</i>	snout	*	female
25 +	TM 4471	<i>A. sp.</i>	cranium	*	indet.
26 +	TM 1506	<i>A. sp.</i>	skull	*	indet.
27 +	TM 4468	<i>A. sp.</i>	snout	*	indet.
28 +	TM 4452	<i>A. sp.</i>	cranium	*	indet.
29 +	TM 4467	<i>A. sp.</i>	cranium	*	indet.
30 +	TM 4469	<i>A. sp.</i>	cranium	*	
31	GS K30	<i>A. baini</i>	snout	*	female
32	GS R550	<i>A. baini</i>	cranium	*	male
33	GS RS415	<i>A. baini</i>	cranium	*	male

V = number of mensurable parameters recorded; * = specimens not included in the allometric analysis; + = specimens for which no locality data are available (thus, not included in Table 6); (T) = holotype; SAM = South African Museum, Cape Town; BPI.FN. = Bernard Price Institute for Palaeontological Research, Johannesburg; TM = Transvaal Museum, Pretoria; GS = Geological Survey, Pretoria.

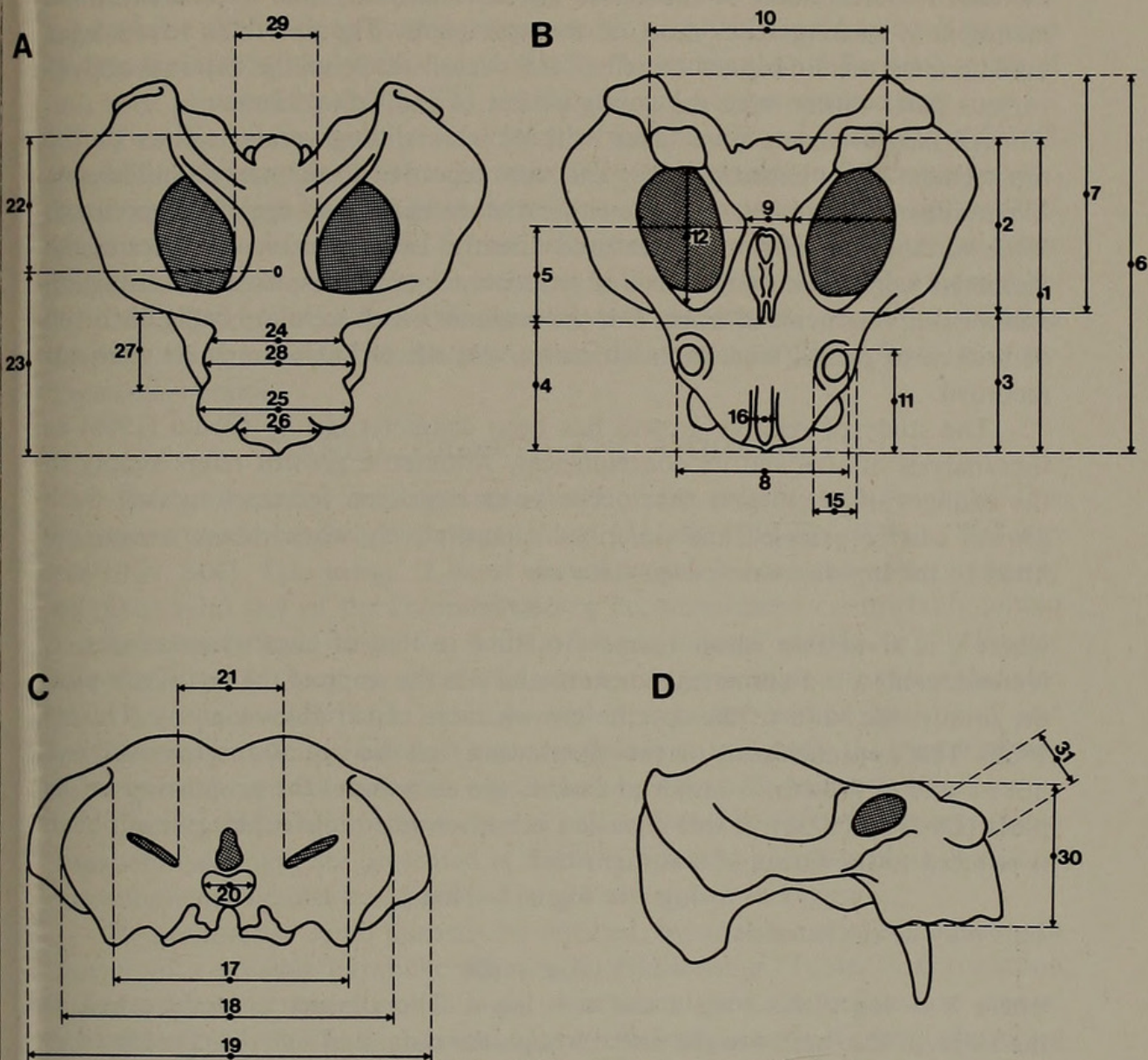


Fig 1. *Aulacephalodon* cranial measurements. A. Dorsal. B. Basal. C. Occipital. D. Lateral. 1. Basal cranial length. 2. Basal temporal length. 3. Basal snout length. 4. Palatal length. 5. Pterygoid fossa length. 6. Total cranial length. 7. Temporal cranial length. 8. Bicanine breadth. 9. Least presphenoid breadth. 10. Interquadrate distance. 11. Canine-snout length. 12. Temporal fossa length. 13. Temporal fossa breadth. 14. Buccolingual diameter of canine (or socket). 15. Breadth of caniniform process. 16. Width between premaxillary ridges. 17. Least squamosal breadth. 18. Intermediate temporal breadth. 19. Greatest cranial width. 20. Breadth of occipital condyle. 21. Least post-temporal fossa breadth. 22. Post-pineal length. 23. Pre-pineal length. 24. Least interorbital width. 25. Greatest width between nasal bosses. 26. Snout width. 27. Orbital length. 28. Greatest width between prefrontal bosses. 29. Intertemporal width across pineal foramen. 30. Greatest snout length. 31. Length of nasal bosses.

metrical features could be recorded. The cranium only was measured, as the mandible is missing from most of the specimens. The variables selected for measurement were designed to reflect the overall shape of the cranium and its various parts rather than the configuration of individual bones.

All measurements were taken with either a sliding vernier caliper or the top segment of an anthropometer and were recorded to the nearest millimetre. In a number of instances, owing to either distortion or breakage of the specimen, some variables could not be measured directly. In these cases estimates of the diameters were made on the basis of symmetry in order to correct for distortion and missing fragments of bone. For those crania which were too badly distorted or broken to permit reasonable estimates, the affected measurements were not recorded.

The study of relative growth has been characterized by Gould (1966) as the analysis of size and its consequences. Allometric growth refers simply to the changes in proportion that occur as an organism increases in size. Such growth can be assessed and described quantitatively when measurements are fitted to the biparametric power function

$$y = ax^{\beta}$$

where y is a variable whose increase relative to that of another parameter, x , is considered; a is a numerical constant and β is the slope of the rectilinear plot, or, simply, the ratio of the specific growth rates of variables x and y (Huxley 1932). This approach rests on the observation that the size of an organism, and not its rate of growth, is important when one determines the proportions of its parts (Dodson 1975a). If this equation is converted to logarithms, the problem is reduced to the fitting of a straight line:

$$\log y = \log a + \beta \log x.$$

This may be rewritten as

$$Y = \alpha + \beta X$$

where $Y = \log y$, $X = \log x$ and $\alpha = \log a$. The allometric coefficient, β , is the slope of the 'best straight line' through the data, and may be considered as the value of Y when $X = 0$. Thus, β is the ratio of the specific growth rates of Y and X ; it serves as an indication of the intensity of differential size increase. Values of β greater than 1 (positive allometry) imply a differential increase of Y relative to X ; when β is less than 1 (negative allometry) the Y/X ratio decreases with an increase of the absolute magnitude of X . Isometry, when $\beta = 1$, represents the maintenance of geometrical similarity with size increase.

In determining the slope of the 'best straight line' through the data, Kermack & Haldane (1950) and Kermack (1954) have cautioned against the use of regression models which assume error to be related to only a single variable. Consequently, the fitting procedure utilized here was that of Bartlett's (1949) 'best fit'. This method was found to be the preferred procedure in a computer simulation of ten different methods by Kidwell & Chase (1967), because it (i) is highly accurate, (ii) has a small variance, (iii) has a simple procedure for setting confidence limits on the estimates, and (iv) includes a

simple linearity test. Bartlett's (1949) method has been recommended for analysis of allometric growth by Simpson *et al.* (1960) and has been so used by Dodson (1976) and Grine *et al.* (1978). A description of Bartlett's method has been provided by Grine *et al.* (1978) and will not be repeated here.

Two diameters, basal cranial length (variable 1) and basal snout length (variable 3) were utilized as comparative (x) measurements in the present study. Basal snout length was found to have a nearly isometric relationship to basal cranial length, and use of the former permitted specimens, for which the latter length was not obtainable, to be included in the analysis of sexual dimorphism.

In addition to a bivariate quantitative assessment, several qualitative features were examined in an attempt to define sexual dimorphism in *Aulacephalodon* crania.

CRANIAL GROWTH AND VARIABILITY

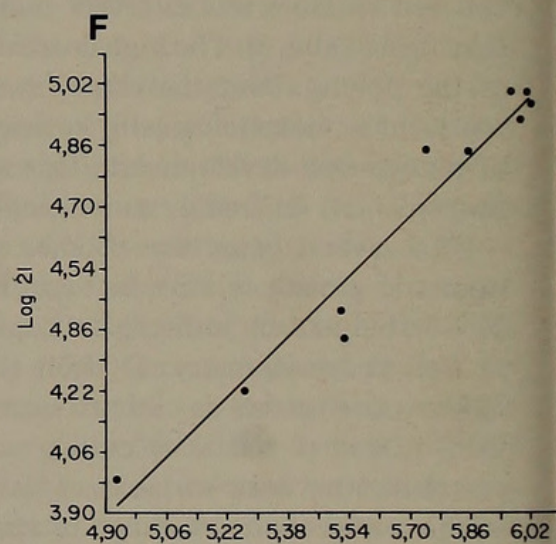
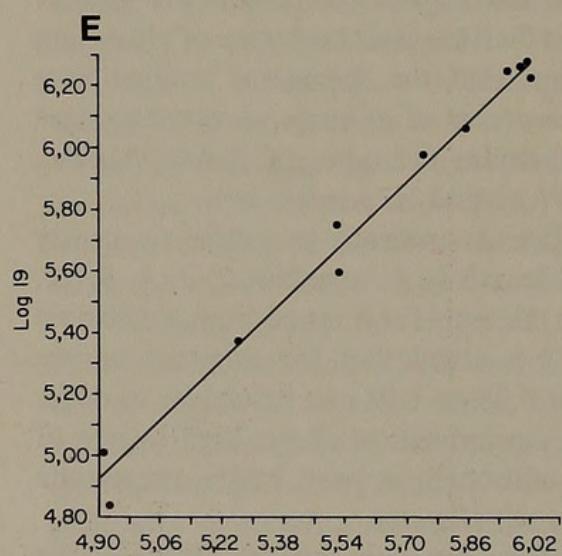
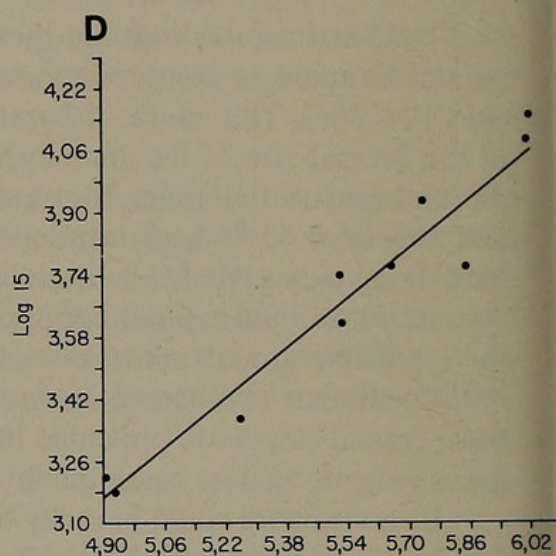
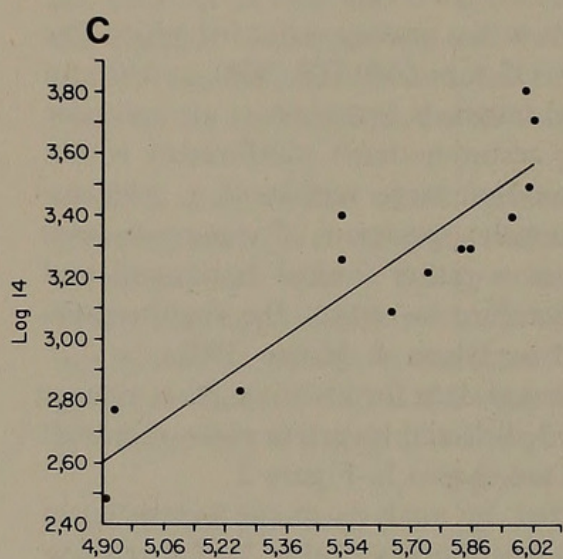
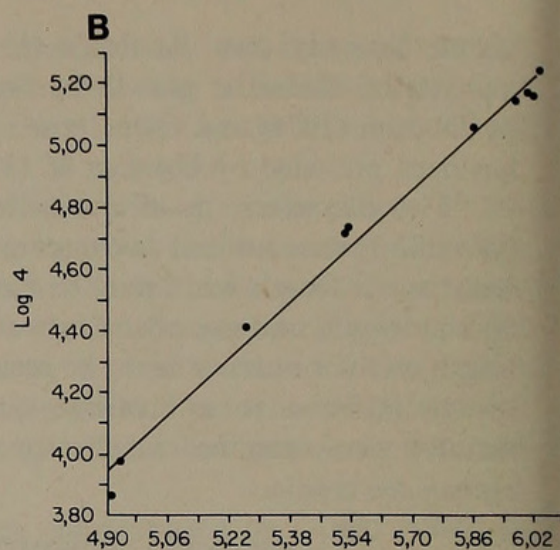
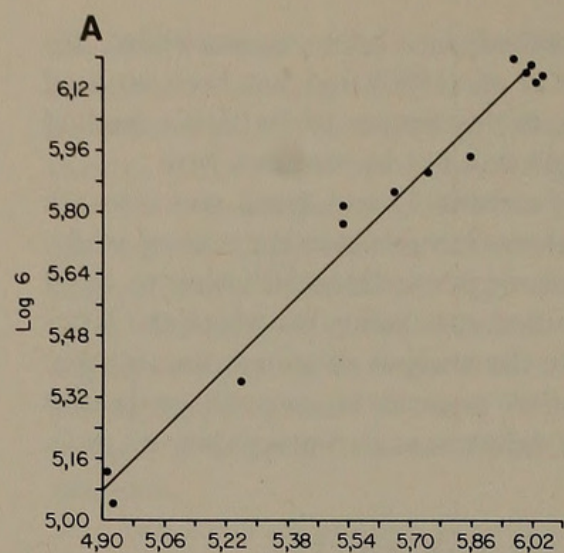
The basal cranial length of those fossils in the present series for which this parameter could be recorded ranged from 135 mm (BPI.FN. 904) to 410 mm (BPI.FN. 806). This range, if basal cranial length is accepted as an indicator of the general size of the cranium, can be accommodated comfortably within the ontogenetic size range for skulls of modern large reptiles (e.g. *Alligator* and *Crocodylus*). And, as mentioned previously, specimens of *Aulacephalodon* have been recovered from localities within a rather limited horizontal and vertical range. *Aulacephalodon* appears therefore to satisfy the requirements for a possible growth series as established by Olson & Miller (1951).

Coefficients of allometry and other relevant data for bivariate plots against basal cranial length are presented in Table 3. Selected bivariate plots of cranial measurements against basal cranial length are shown in Figure 2.

In no instance could linearity be rejected, by analysis of the *t* statistic, in favour of a possible parabolic (quadratic) relationship (Table 3). Correlation between variable sets is rather high; most correlation coefficients are greater than 0.95 (Table 3). The high correlation coefficients and the degree of clustering of the points about the slope lines suggest that the specimens studied here represent a morphologically homogeneous group of animals in various stages of ontogenetic development. This series includes the types of *Aulacephalodon haughtoni*, *A. latissimus*, *A. luckhoffi*, *A. pricei*, and *A. vanderhorsti*.

In several cases the allometric coefficients indicate isometric or nearly isometric growth relative to basal cranial length (e.g. variables 2, 3, 6, 8, 16, 21, 26), but in each instance the confidence intervals for β range from well below to well above isometry. Dodson (1975a) has noted that for *Alligator mississippiensis* coefficients as close to isometry as 0.98 or 1.02 can be shown to differ from 1.00 at $p = 0.02$ or even $p = 0.001$, an indication of the high degree of correlation between variables, which is conditioned, in part, by the magnitude of the ontogenetic size range of specimens of *Alligator*.

In three instances—palatal length (4), greatest cranial width (19), and the greatest width between the nasal bosses (25) (Fig. 1)—positive allometric



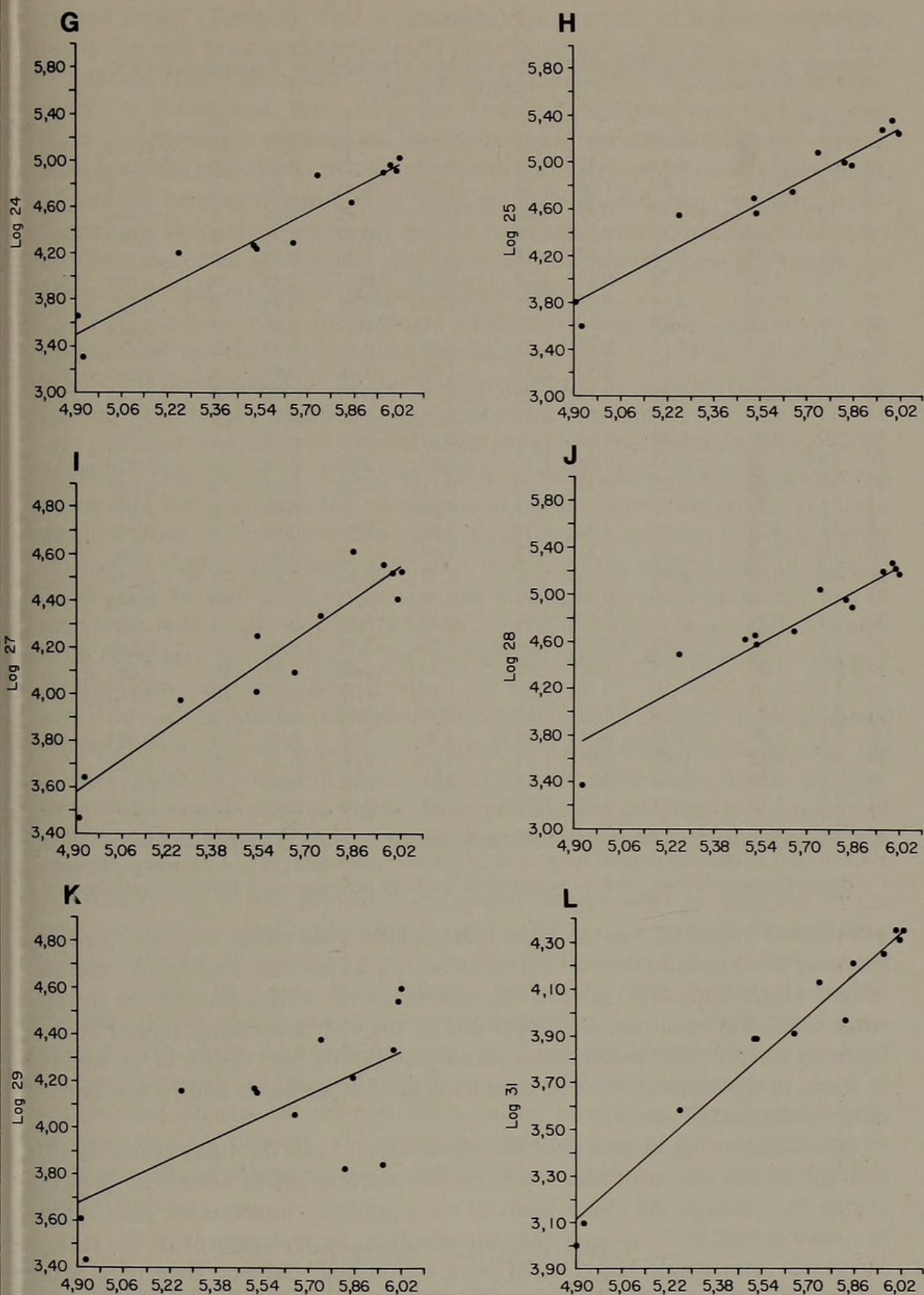


Fig. 2. A-L. Selected bivariate plots of *Aulacephalodon* crania. The scale on both axes is logarithmic. In each case the X-axis is basal skull length (variable 1). The solid line represents the calculated line of Bartlett's 'best fit'.

TABLE 3

Summary of data concerning relative growth and variability in *Aulacephalodon* (X = basal cranial length).

Y	N	β	α	β -CI	α -CI	r	df	t	RL
2	13	0,99	-0,46	0,87; 1,11	-0,50; -0,43	0,99	10	-0,713	No
3	13	0,99	-0,84	0,79; 1,19	-0,90; -0,78	0,97	10	0,444	No
4	10	1,15	-1,69	1,04; 1,26	-1,72; -1,65	1,00	7	-1,833	No
5	10	0,82	-0,52	0,63; 1,23	-0,62; -0,42	0,94	7	-1,036	No
6	12	1,00	0,18	0,85; 1,14	0,13; 0,22	0,99	9	0,069	No
7	12	0,91	0,19	0,63; 1,16	0,11; 0,28	0,95	9	-0,554	No
8	12	1,01	-0,78	0,59; 1,29	-0,89; -0,67	0,95	9	0,093	No
9	12	1,10	-2,64	0,78; 1,44	-2,74; -2,53	0,95	9	0,132	No
10	5	1,20	-1,49	—; 1,66	-1,80; -1,17	0,98	2	0,424	No
11	13	1,17	-2,13	0,86; 1,51	-2,23; -2,03	0,95	10	-0,886	No
12	11	1,12	-1,35	0,87; 1,53	-1,43; -1,26	0,96	8	-1,253	No
13	12	0,94	-0,67	0,59; 1,16	-0,76; -0,59	0,96	9	-1,192	No
14	13	0,87	-1,67	0,54; 1,17	-1,76; -1,57	0,91	10	1,756	No
15	10	0,81	-0,80	0,60; 1,01	-0,87; -0,73	0,97	7	-0,748	No
16	12	1,05	-2,95	0,64; 1,37	-3,07; -2,83	0,94	9	-0,470	No
17	12	0,91	-0,05	0,43; 1,39	-0,11; 0,20	0,86	9	0,063	No
18	11	1,14	-0,89	0,91; 1,45	-0,98; -0,81	0,96	8	2,070	No
19	11	1,21	-1,01	1,04; 1,33	-1,06; -0,96	0,99	8	0,754	No
20	10	0,89	-1,33	0,32; 1,13	-1,42; -1,24	0,96	7	-1,507	No
21	10	0,98	-0,91	0,71; 1,23	0,97; -0,84	0,98	7	-0,558	No
22	13	1,26	-2,60	0,80; 1,90	-2,77; -2,43	0,86	10	0,998	No
23	13	0,84	0,49	0,58; 1,04	0,42; 0,56	0,96	10	-1,205	No
24	12	1,31	-2,94	0,95; 1,64	-3,05; -2,83	0,96	9	0,580	No
25	13	1,33	-2,73	1,02; 1,57	-2,82; -2,65	0,97	10	0,669	No
26	13	1,01	-1,70	0,56; 1,34	-1,82; -1,59	0,93	10	0,163	No
27	12	0,87	-0,69	0,64; 1,10	-0,76; -0,61	0,96	9	-1,483	No
28	12	1,39	-3,08	0,81; 1,76	-3,20; -2,96	0,95	9	0,097	No
29	13	0,59	0,80	0,01; 1,07	0,63; 0,96	0,72	10	0,363	No
30	11	0,86	-0,76	0,31; 1,21	-0,91; -0,62	0,90	8	0,613	No
31	13	1,11	-2,33	0,91; 1,27	-2,39; -2,28	0,98	10	-0,139	No

Y = variable number; N = number of specimens; α -CI = 95% confidence interval for α ; β -CI = 95% confidence interval for β ; r = correlation coefficient; d.f. = degrees of freedom; t = Bartlett's test statistic; RL = rejection of linearity in favour of a parabolic relationship.

growth was indicated. On the other hand, whilst some eleven variables showed values of β less than 1,00, in all of these cases the 95 per cent confidence intervals ranged above isometry; variable 29, intertemporal width, showed the lowest value (0,59) but even here the upper end of the confidence limit ranged above isometry to 1,07. This parameter shows a particularly high degree of variability in terms of the magnitude of its allometric confidence limits and its low correlation coefficient (Table 3).

It is interesting to note that the diameters of both the tusks (variable 14) and the caniniform processes (variable 15) show negative allometric growth (Table 3), although the upper limits of the confidence intervals for each range to above isometry. It appears that the eruption, or replacement of the tusks, by which increasingly larger teeth were introduced, did not keep pace with cranial enlargement. Also, the size of the orbits, as judged by their length (variable 27), enlarged in a negative allometric manner compared to basal

cranial length (Table 3). This is generally characteristic of higher vertebrates, where the eyes are disproportionately large in young individuals.

Gould (1968) has noted that increase in size subjects organisms to different orders of forces and, thus, new morphological configurations to cope with these new forces are required. In his discussion of the allomorphism of species, Hennig (1966) maintained that knowledge of allometric correlation is important, because it permits recognition of linkages between different series of transformations that might otherwise not be recognized. New shapes produced by continuation of an ontogenetic allometric relationship into new size ranges are not independent taxonomic criteria (Gould 1966).

For the most part, the features which have been used variously in the diagnosis of new *aulacephalodont* species have been (i) the size of the nasal bosses, (ii) the shapes and sutural relationships of the individual bones of the cranium and (iii) the length-breadth ratio of the cranium.

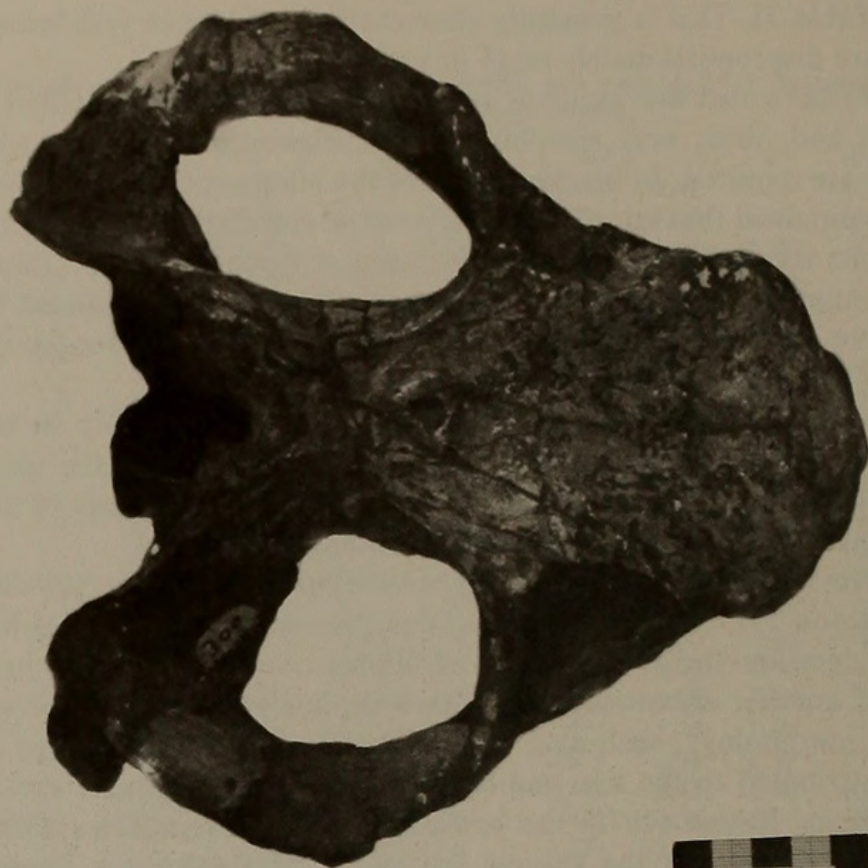
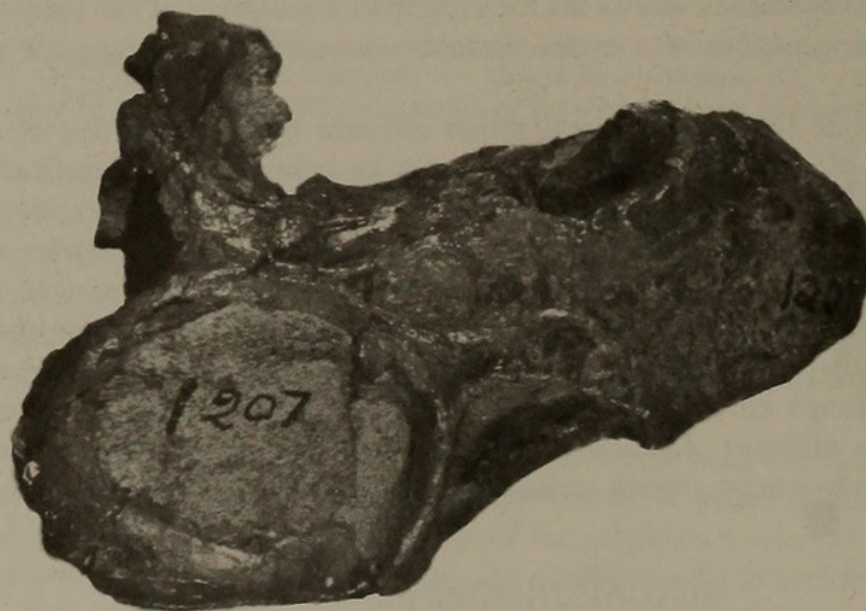
Although several *Aulacephalodon* specimens have been described as possible 'juveniles' (Haughton 1917; Broom 1921), no description of a new species has taken into consideration the phenomenon of allometry. Cluver (1971), in a detailed study of another anodont, *Lystrosaurus*, has recorded that minor changes in skull morphology, such as a change in the sutural relationships of bones, may be attributed to the size and consequently the ontogenetic age of individual specimens. Keyser (1972) has postulated that the characters which have been used to distinguish the various species of *Aulacephalodon* depend greatly upon the size of the individual.

It is evident that in *Aulacephalodon* rather marked changes in the shape of the cranium and its various parts occurred with increasing size. In general, the relative width of the skull across the zygomatic arches and across the prefrontal and nasal bosses, as well as the robusticity and sculpture of the temporal arches and other parts, show a rather dramatic increase with ontogenetic age (Fig. 3).

The results of the present investigation indicate that at least five of the type specimens of *Aulacephalodon* species could be interpreted as constituting a homogeneous ontogenetic growth series. Two other types—*A. hartzenbergi* and *A. brodei*—have been examined also, and whilst these specimens were not subjected to allometric analysis, it is evident that they, too, form part of the same growth series. Although not every type and available specimen has been studied, the results of this preliminary investigation appear to support the contention that perhaps all the specimens, which have been regarded previously as belonging to different *Aulacephalodon* species, constitute a taxonomically homogeneous ontogenetic growth series of but a single species, *Aulacephalodon baini* (Owen).

SEXUAL DIMORPHISM

Sexual differences of both living and fossil reptiles are generally poorly expressed in the skeleton, and, as such, they are difficult to identify (Olson

**B****A**

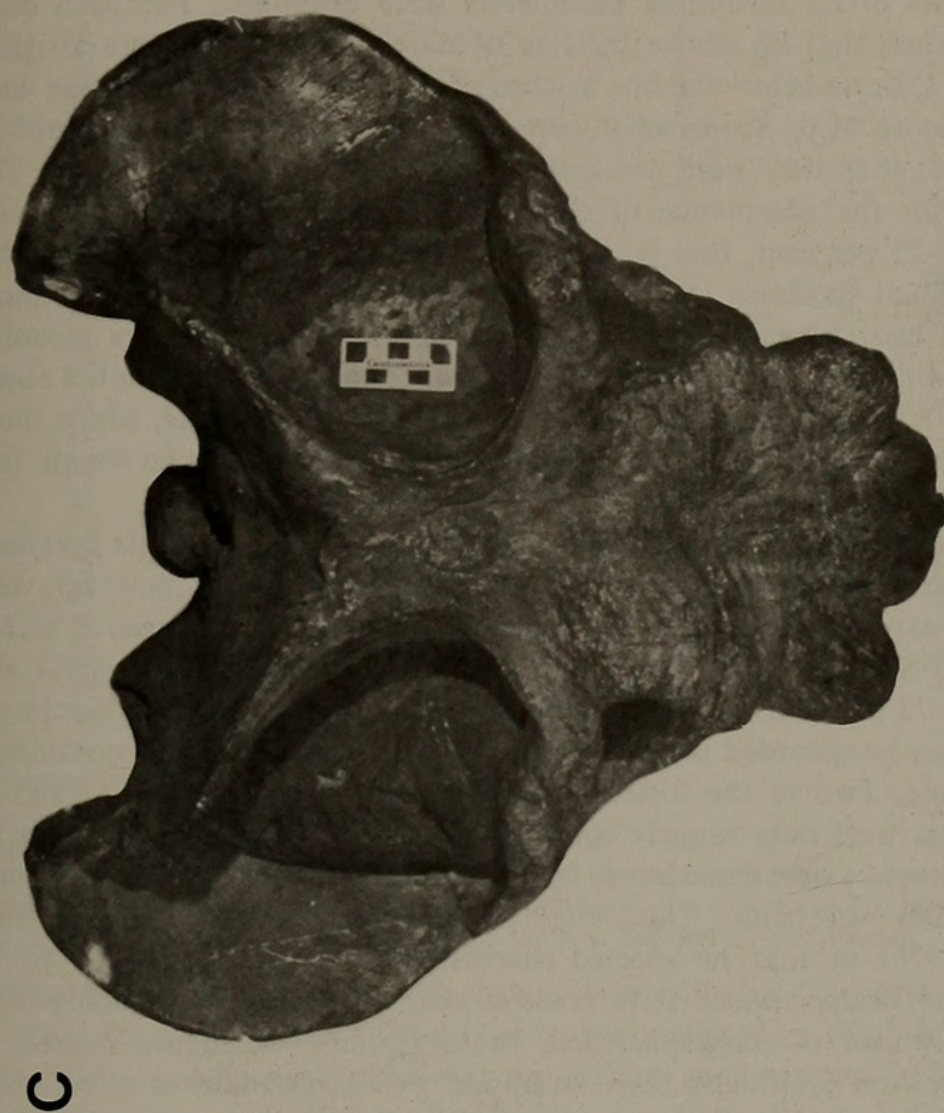


Fig. 3. Suggested ontogenetic series of *Aulacephalodon* crania. A. Small specimen, no. 4, BPI.FN. 1207; basal cranial length 138 mm. B. Specimen no. 6, BPI.FN. 300; basal cranial length 192 mm. C. Very large specimen, no. 5, BPI.FN. 806 (holotype of *A. pricei*); basal cranial length 410 mm. Scales in cm.

1969). Dodson (1976) has used successfully two complementary approaches to define quantitatively sexual dimorphism in skulls of a small ceratopsian dinosaur. His first approach made use of bivariate allometric plots, a use of ratios, whilst the second was based on multivariate statistical analysis.

In the present study an attempt was made to assess quantitatively sexual dimorphism in a growth series of *Aulacephalodon* crania. Dodson's (1976) bivariate technique was utilized but application of the multivariate approach was not attempted owing to the small sample size of relatively complete crania. Bivariate plots of all thirty-one parameters were examined. For each case, individual values that lay above the line of Bartlett's 'best fit' were assigned a score of -1 , those below the line a score of $+1$, and values on the line were accorded a score of 0 . Scores of 0 were very infrequent and were treated as indeterminate; thus they were not included in the final total of a score. The lower limit for the acceptance of either 'maleness' or 'femaleness' was set arbitrarily at 75 per cent, that is, at least three-quarters of the plotted points for an individual specimen lay to one side of the line. Only those specimens for which at least fifteen of the thirty possible variable plots were recorded were included in this part of the study (Table 4). Those fossils which fell above the line for 75 per cent of characters were considered to be male, whilst those that lay below the line for 75 per cent of traits were deemed to be female (see Dodson 1976).

Bivariate analysis of sexual dimorphism revealed that no single specimen exhibited a consistently male or female pattern. Two specimens, however, were consistent in expression in at least 74 per cent of the traits (specimens 2, SAM-8747, and 3, SAM-K1221), whilst a third (specimen 12, BPI.FN. 634) was consistent in 72 per cent of the characters. Accordingly, two of the specimens (2 and 12) may be accorded male status, whilst specimen 3 could be considered to be a female. Two of the fossils were completely indeterminate (7 and 8) and the others were only vaguely consistent in expression. In this analysis all available characters were considered; no selection of sexually distinctive features of the cranium was made. Thus, the technique utilized here differed from Dodson's (1976) in that he selected characters which were believed to be dimorphic for *Protoceratops*. It is possible that, in the bivariate analysis of sexual dimorphism in *Aulacephalodon*, those features which are related to sexual dimorphism could have been 'swamped' by a larger number of variables which are not dimorphic. Furthermore, as not all the specimens possessed all possible measurable features, it is possible that those traits which may be sexually related were not present in some of the fossils.

The principal cranial feature of *Aulacephalodon* which has been postulated to show sexual dimorphism is the relative size of the nasal bosses. Broom (1937) noted considerable variation in the size of the nasal bosses. He considered that the larger bosses were shown by male skulls, whilst females evinced more weakly developed bosses. He compared briefly two skulls which he considered represented a male and a female, and concluded also that the 'canine' tusks in

TABLE 4

 Bivariate sexual dimorphism scores for *Aulacephalodon* crania.
 Specimen

Variable no.	2	3	4	5	6	7	8	9	12	13	15	18
2	+	—	+	+	+	—	+	—	o	+	—	o
3	—	o	—	—	—	+	—	—	—	—	+	+
4			+	—	—	+	—	+	—	—	+	+
5			—	+	+	—	—	+	—	+	—	+
6	+	—	+	+	+	—	—	—	—	+	+	—
7	—	—	+	+	+	—	—	+	—	+	—	—
8	—	+	+	—	—	—	+	—	—	+	—	+
9	—		—	+	—	—	+	—	+	+	+	—
10			+	—	—		+			+		
11	+	+	+	—	—	—	—	+	+	—	—	+
12	—	—	—	+	+		+	—	+	+	+	—
13	—	+	+	+	—	+	+	+	—	—	—	—
14	+	+	—	—	+	+	—	+	—	+	—	+
15	—	+	+	—	+	—	+	—	—	+		—
16	—	+	+	+	—	+	o	+	o	+	—	+
17	—	+	—	—	+	+	+	—	—	+	—	+
18	+	+	—	o	+	—	—	—	—	—	—	
19	—		+	+	—	—	+	—	—	+	—	—
20	—	—	+	+	—			—		—	+	+
21	—		—	+	+		+		+	—	+	—
22	+	+	—	—	—	—	—	+	+	+	—	—
23	—	—	+	+	+	+	+	—	—	—	+	—
24	—	+	+	—	—	—	+	—	+	+	—	+
25	—	+	+	+	—	o	+	—	—	+	—	+
26	—	+	+	+	—	+	+	—	—	+	—	+
27	—	+	—	+	—	+	—	—	+	—	+	+
28	—	+	+	+	—		—	—	—	+	—	o
29	—	+	+	—	—	+	—	+	—	+	—	—
30	+	+	o	—	—	+	—	+		—	—	+
31	—	+	+	o	—	+	—	+	—	—	—	+
Dominant sign	—	+	+	+	—			—	—	+	—	+
Score	74	74	65	59	63	50	50	59	72	63	68	58

Score = percentage frequency of occurrence of the dominant sign. + = individual plot below the line of Bartlett's 'best fit'; — = individual plot above the line of Bartlett's 'best fit'; o = individual plot on the line. See text for explanation.

males are longer and further apart than in females. In his description of *A. cadlei* he noted the nasal bosses of the type to be smaller than those in the type of *A. rubidgei*, and he postulated that the former specimen was a female whilst the latter was a male (Broom 1948). The question of sexual dimorphism in dicynodont crania has been considered by several workers (Owen 1860, 1876; Broom 1912, 1932; Barry 1957; Tripathi & Satangi 1963). Cluver (1971) discussed the possibility that *Lystrosaurus* crania exhibited pronounced sexual dimorphism, but he concluded that the dimorphic skulls of that genus probably represent two groups of species. Keyser (1969) recorded that the nasal bosses of *Aulacephalodon* appear to increase in prominence concomitantly with an increase in skull size; he maintained also that the bosses were related to sexual dimorphism.

In light of the previous speculations which have related nasal boss size and shape variation to sexual dimorphism, these structures were examined both metrically and osteoscopically in the present series of crania.

As an indication of the relative size of the nasal bosses the length of the protuberances (variable 31), as well as the greatest width between them (variable 25), were considered. When these two parameters are compared to basal cranial length (Table 3), both are found to increase in a positive allometric fashion, although the confidence interval for nasal boss length ranges to below isometry. When these variables are considered against basal snout length (variable 3), the positive allometric nature of their growth rates is slightly more pronounced (Table 5) and the 95 per cent confidence limit for nasal boss length ranges as low as isometry only. The considerable degree of morphological variability which is evinced by the nasal bosses may be related to their rates of growth. Dodson (1975a, 1975b) found that in two living reptiles (*Alligator* and

TABLE 5

Summary of data concerning relative growth and variability in *Aulacephalodon* (X = basal snout length).

Y	N	β	α	β -CI	α -CI	r	df	t	RL
1	13	1,01	0,85	0,84; 1,27	0,79; 0,91	0,97	10	-0,444	No
2	13	1,00	0,38	0,73; 1,41	0,25; 0,48	0,93	10	-0,550	No
4	10	1,16	-0,71	1,09; 1,26	-0,74; -0,68	1,00	7	-0,912	No
5	10	0,83	0,18	0,60; 1,35	0,06; 0,30	0,93	7	-0,599	No
6	13	0,93	1,39	0,73; 1,16	1,32; 1,46	0,97	10	-0,548	No
7	13	0,93	0,93	0,67; 1,28	0,83; 1,03	0,93	10	0,480	No
8	14	1,01	0,07	0,69; 1,34	-0,04; 0,18	0,93	11	-0,113	No
9	12	1,11	-1,71	0,69; 1,77	-1,87; -1,54	0,88	9	-0,140	No
10	6	0,85	1,07	0,70; 2,18	0,61; 1,52	0,83	3	-0,747	No
11	15	1,13	-0,88	0,84; 1,51	-0,99; -0,77	0,92	12	-1,418	No
12	12	1,07	-0,13	0,81; 1,47	-0,22; -0,05	0,93	9	-2,404	Yes
13	13	0,99	-0,07	0,75; 1,22	-0,14; 0,01	0,97	10	0,353	No
14	15	0,88	-0,95	0,63; 1,16	-1,03; -0,86	0,92	12	1,186	No
15	10	0,80	-0,03	0,56; 1,09	-0,12; 0,06	0,95	7	-0,352	No
16	13	1,01	-1,88	0,70; 1,31	-1,98; -1,78	0,95	10	-0,220	No
17	13	0,86	1,09	0,43; 1,26	0,95; 1,22	0,88	10	-0,264	No
18	12	1,08	0,38	0,85; 1,42	0,29; 0,48	0,96	9	1,344	No
19	12	1,12	0,46	0,85; 1,42	0,36; 0,55	0,97	9	-0,082	No
20	10	0,92	-0,67	0,35; 1,18	-0,77; -0,58	0,95	7	-1,849	No
21	11	1,03	-0,32	0,86; 1,41	-0,39; -0,25	0,96	8	-2,142	No
22	13	1,27	-1,53	0,77; 2,09	-1,72; -1,34	0,83	10	0,687	No
23	15	0,82	1,32	0,60; 1,05	1,25; 1,40	0,94	12	-1,572	No
24	14	1,24	-1,45	0,94; 1,57	-1,56; -1,35	0,95	11	0,910	No
25	15	1,51	-2,44	1,02; 2,13	-2,63; -2,26	0,89	12	-0,705	No
26	15	0,97	-0,58	0,59; 1,34	0,70; -0,45	0,89	12	-0,114	No
27	14	0,89	-0,03	0,75; 1,06	-0,08; 0,03	0,97	11	-1,449	No
28	13	1,20	-0,98	0,44; 1,69	-1,13; -0,82	0,90	10	-0,076	No
29	15	0,68	0,86	0,25; 1,06	0,73; 1,00	0,80	12	-0,078	No
30	13	1,12	-1,36	0,75; 1,60	-1,46; -1,16	0,90	10	0,651	No
31	15	1,17	-1,62	1,00; 1,37	-1,69; -1,56	0,98	12	-1,507	No

Y = variable number; N = number of specimens; α -CI = 95% confidence interval for α ; β -CI = 95% confidence interval for β ; r = correlation coefficient; d.f. = degrees of freedom; t = Bartlett's test statistic; RL = rejection of linearity in favour of a parabolic relationship.

Sceloporus) the greatest variability is associated with the most strongly allometric variables. In *Aulacephalodon* the greatest width between the bosses (which includes the breadth of both these structures as well as the rest of the nasal bones) shows the strongest allometric growth compared to basal snout length (Table 5). The allometric nature of these protuberances is not quite so marked when basal skull length is used for comparison, but in the latter case (Table 3) fewer specimens were included. The width across the nasal bosses shows both stronger allometric growth and more variability than the length of these structures when the two are compared to either basal cranial (Table 3) or basal snout (Table 5) lengths.

Three rather distinct types of nasal boss morphology, as assessed qualitatively, were discerned in the present cranial series (Figs 4–5). In crania with 'Type 1' boss development (Figs 4A, 5A), the lateral margins of the nasal bones above the external nasal apertures show very little, if any, form of swelling; when viewed from above, the dorsal surface of the snout tapers anteriorly from the orbits. Nasal bosses of the second type (Figs 4B, 5B) project laterally to various degrees from the edges of the nasals above the external nares. The bosses project laterally and form a nearly flat (horizontal) surface with the nasal bones. Bosses of 'Type 3' (Figs 4C, 5C) also project laterally above the external nasal apertures, but are more swollen in appearance than those of the second type; they project dorsally as well as laterally. The third type of nasal protuberance projects above the dorsal surface of the nasal bones, and in several specimens a longitudinal 'gutter' is present between the midline of the nasal bones and the boss on each side.

The first type of nasal boss was found in small crania, whilst the second and third types appear in larger skulls. Nasal bosses of 'Type 1' are very slightly developed (Fig. 6). The second and third types of nasal bosses appear to increase in size with cranial length, but the two types can be distinguished in nearly all cases throughout a broadly overlapping range of individual size (Fig. 6).

In the present sample, skulls which show 'Type 3' nasal bosses achieve a larger size than those with bosses of 'Type 2' morphology. This apparent size difference, however, may be an artefact of sampling. Several specimens (e.g. 19, 25–29) show a nasal boss configuration that appears to be intermediate between the second and third types. Although the morphological configuration of the nasal bosses may be altered through burial deformation (e.g. a 'Type 3' could be changed to a 'Type 2' through vertical diagenetic pressures), in the vast majority of cases these structures seem to have suffered very little from such deformation. In one specimen (15, BPI.FN. 2983) the nasal bosses had been pushed ventrally so that they form a nearly horizontal transverse plane with the nasal bones, but the bilateral shallow longitudinal troughs are still discernible owing to the presence of the median sagittal nasal ridge.

Inasmuch as the present sample of *Aulacephalodon* crania exhibits a rather high degree of biometric homogeneity, it seems reasonable to suggest that the morphological differences shown by the nasal bosses may be sexual in nature.

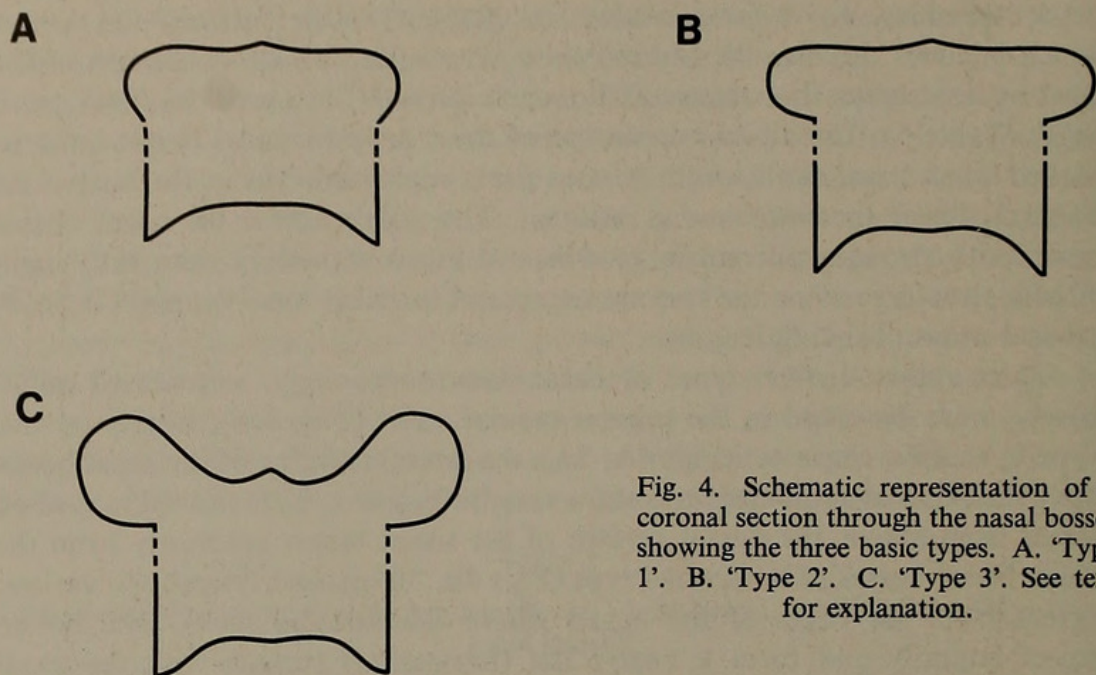


Fig. 4. Schematic representation of a coronal section through the nasal bosses showing the three basic types. A. 'Type 1'. B. 'Type 2'. C. 'Type 3'. See text for explanation.

Various cranial sizes, or inferred ontogenetic stages, are present for both the second and third types of nasal bosses, whilst the smallest, and presumably youngest, skulls in the present sample evince a 'Type 1' nasal boss. It is possible that the nasal bosses in *Aulacephalodon* could have served as a sexually selective feature for mate recognition and/or agonistic display mechanisms, or for both. Furthermore, the several relatively large crania (specimens 19, 25–26 and 29) which show nasal bosses intermediate in form between 'Types 2 and 3' may represent the antimodal overlap of the bimodal distribution of a discontinuous feature such as sexual dimorphism. However, a number of the crania in which the nasal bosses are indeterminate are broken and poorly preserved.

It is possible that those crania with the more robust, 'Type 3' nasal bosses represent the male condition. The same has been postulated obliquely by previous workers (Broom 1937, 1948; Keyser 1969).

In the present series, it appears that, once a certain cranial size had been reached, the nasal bosses assumed one of two rather distinct configurations (Fig. 7). It is suggested that the smaller crania, in which the nasal bosses are only slightly expressed ('Type 1'), represent relatively young, sexually immature individuals. Specimen 6 (BPI.FN. 300) possesses rather small nasal bosses of the 'Type 2' (female) configuration (Fig. 8). This fossil has been identified tentatively as female (Figs 6–7). It is possible that with growth the nasal bosses of both sexes were of a 'Type 2' configuration before sexual maturity (or dimorphism) had been achieved; the smallest positively identifiable male cranium is somewhat larger than the specimen in question. If this sample is at all representative of *Aulacephalodon*, then it seems that the expression of

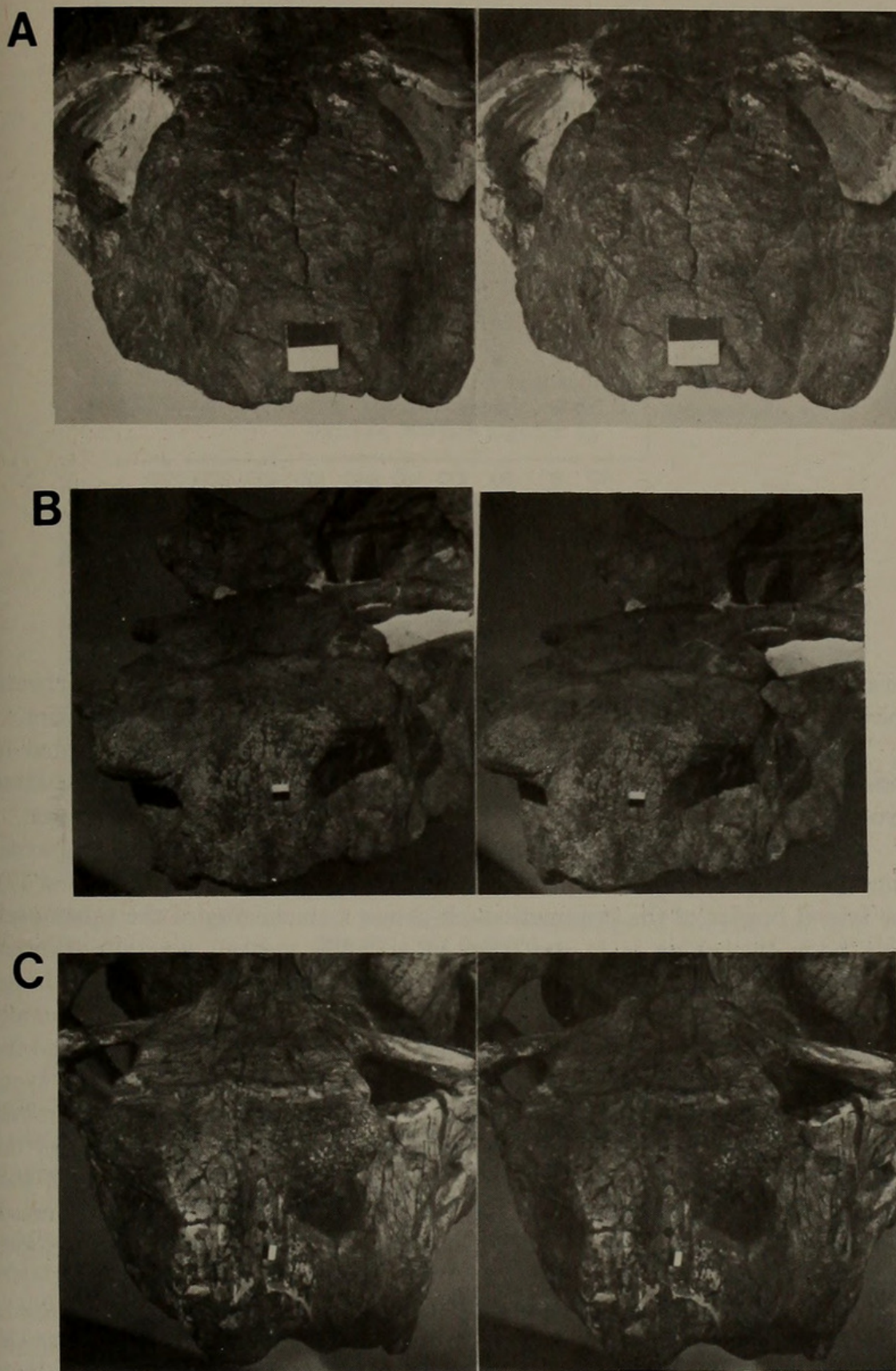


Fig. 5. Stereophotos of the three basic nasal boss configurations. A. 'Type 1', specimen no. 7, BPI.FN. 904. B. 'Type 2', specimen no. 18, BPI.FN. 304. C. 'Type 3', specimen no. 17, BPI.FN. 493. See text for explanation. Scales in cm.

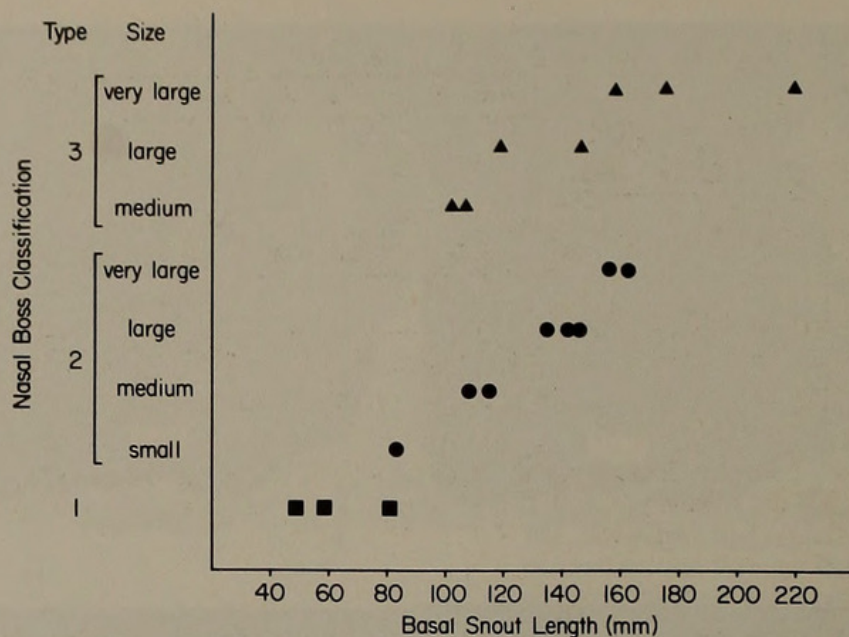


Fig. 6. Relationship of nasal boss size and morphotype to cranial (snout length) size.

sexual dimorphism was achieved by individuals when snout length was between about 80 and 95 mm and basal cranial length approximately 190 to 245 mm.

The nasal bosses enlarged in a positive allometric manner compared to snout and cranial lengths, but it appears that the general morphology of these structures remained relatively constant with an increase in individual size.

Another feature of the cranium also appears to be related to sexual dimorphism. In large presumptive male crania (e.g. specimens 5, 13, 15 and 17), the lateral border of the zygomatic arch shows a thickening of the squamosal. This body thickening is in the form of a gently curved, ventrally directed convexity, the lateral margin of which shows a rugose texture (Fig. 9). Large female crania, on the other hand, show no such thickening of the zygomatic arch; in these specimens the lateral margin of the squamosal is thinner and the arch has parallel dorsal and ventral surfaces. In smaller male crania the zygomatic arch is similar to those of females in that there is no sign of squamosal thickening. The significance of this thickening of the anterior portion of the zygomatic arch in larger male crania is enigmatic. Keyser (1969) noted that these squamosal 'bosses' may have been related to the jaw adductor musculature; but if this were the case it is puzzling why only the older males developed these structures.

Of the three crania sexed by bivariate analysis, the metrical diagnosis of two of them (specimens 3 and 12) agreed with the non-metrical assignment; however, whilst the third skull (specimen 2) was male according to the bivariate sexing technique, it shows a 'Type 2' nasal boss configuration, and although it is a fairly large specimen the zygomatic arches are not thickened.

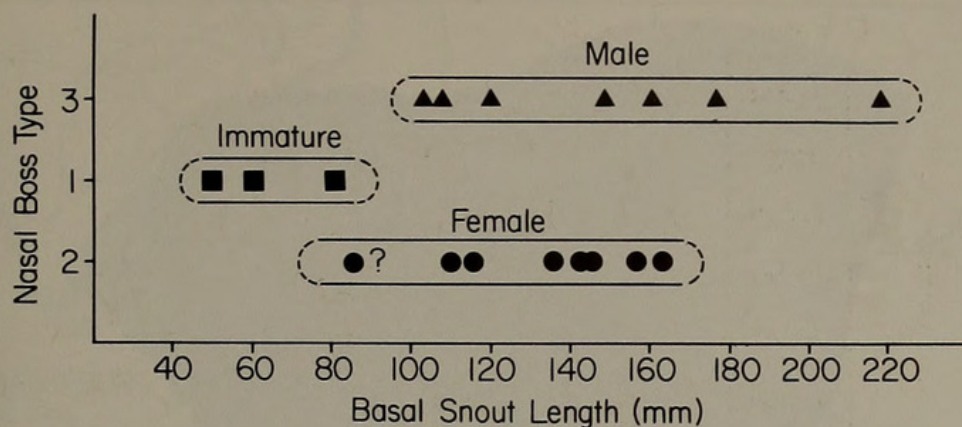


Fig. 7. Graphic representation of nasal boss morphotype compared to cranial (snout length) size. The questionable individual is specimen no. 6, BPI.FN. 300 (see Figs 3B, 8).

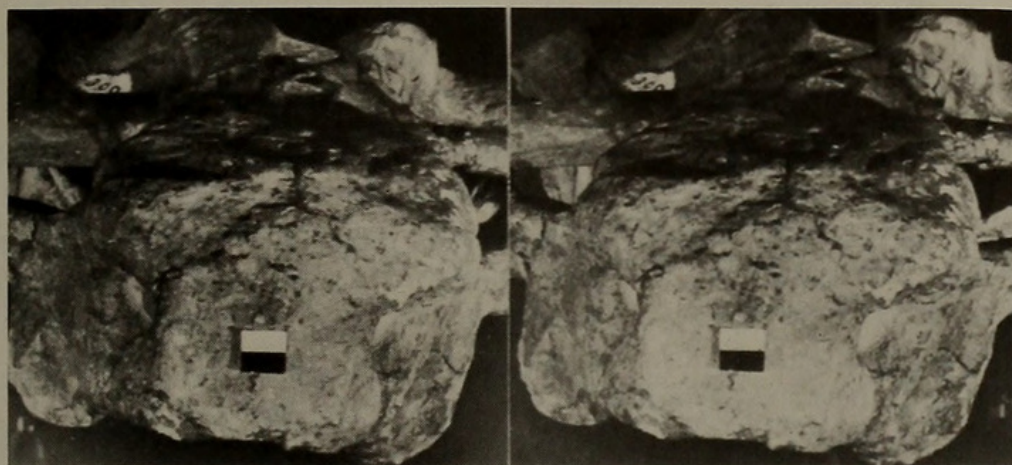


Fig. 8. Stereoview of nasal boss size and morphology of specimen no. 6, BPI.FN. 300. Scale in cm.

DISTRIBUTION

An important factor to be considered in an analysis of the biological implications of the Type 1, 2 and 3 nasal boss configurations of *Aulacephalodon* is the geographic and temporal distribution of these various types. The geographical distribution of the localities which have yielded the crania examined in this study is shown in Figure 10. Although the Madumabisa Mudstone 'Formation' is situated a considerable distance from the concentration of lower Beaufort localities in the Cape Province, the *Aulacephalodon* specimens found at the Zambian sites do not appear to be morphologically distinct from those recovered from the *Cistecephalus* and lower *Daptocephalus* zone sediments of South Africa (Drysdall & Kitching 1963).

The specimens examined in this study were recovered from localities over a rather limited geographical (Fig. 10) as well as vertical (Keyser 1969; Kitching

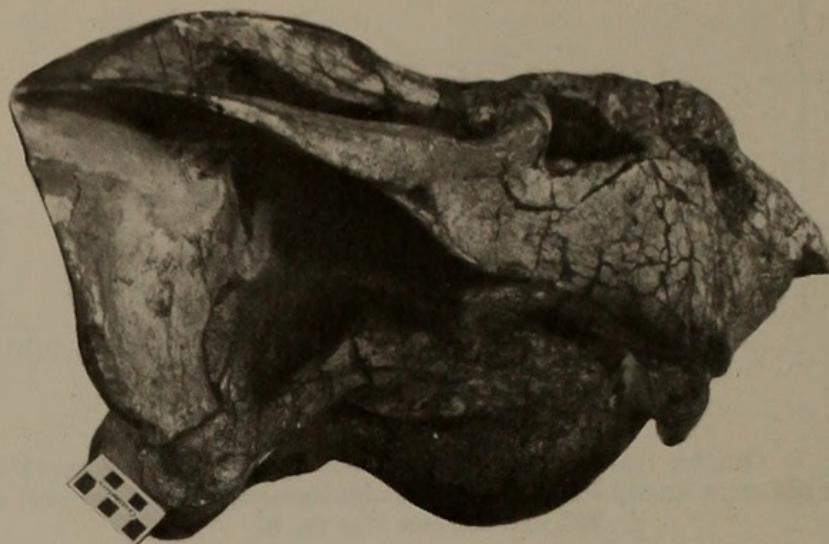


Fig. 9. Lateral view of a large *Aulacephalodon* skull showing the thickening of the squamosal at the anterior end of the zygomatic arch. Specimen no. 17, BPI.FN. 493. Scale in cm.

1977) range. There is no horizontal separation by either size or nasal boss morphology of the specimens; furthermore, two specimens (4 and 17) from the same site (Fig. 10R, Table 6) show considerable difference in both size and nasal boss configuration. One (BPI.FN. 1207) is a small individual with only minimal nasal boss development, whilst the other specimen (BPI.FN. 493) represents the largest skull in the sample and it possesses well-developed 'Type 3' nasal protuberances. Specimens which show variously Type 2 and 3 nasal bosses have been recovered from at least one other locality (Fig. 10I, Table 6).

The facts that specimens of various sizes with different nasal boss configurations have been recovered from single localities, and that there is no geographic or stratigraphic separation of specimens evincing different sizes and shapes, appear to support the hypothesis that the *Aulacephalodon* specimens studied here do, indeed, represent an ontogenetic growth series of a single species which evinced sexual dimorphism.

DISCUSSION

During the deposition of the *Cistecephalus* Zone sediments the terrain appears to have been characterized by broad, low gradient floodplains traversed by numerous, intermittent streams (Keyser 1970). The climate throughout this time, as inferred from the abundance of calcareous concretions and of 'desert roses', composed of pseudomorphs of calcite after gypsum (Keyser 1966), may have been sufficiently dry to warrant the term arid. The flora of the lower Beaufort seems to lack variety, the most commonly occurring plants being the equisetaleans, *Schizoneura* and *Phyllothea* (Keyser 1970). Both Keyser (1969, 1970) and Kitching (1977) have commented on the improbability

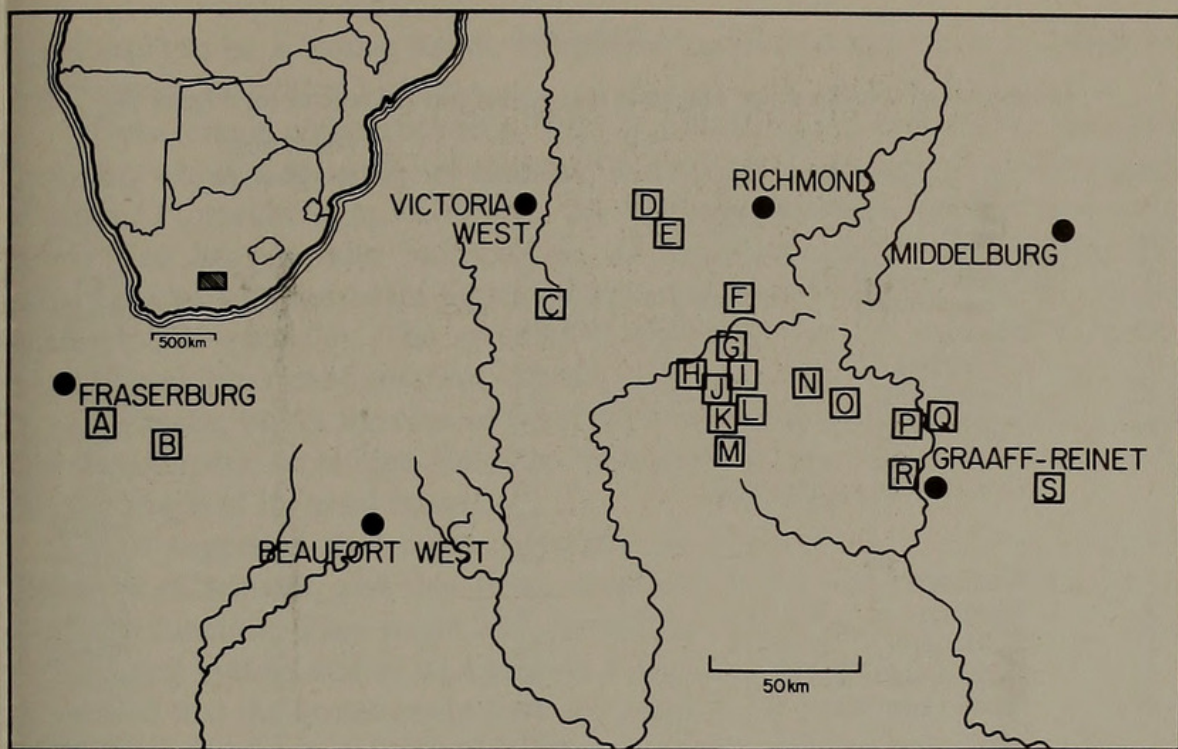


Fig. 10. Distribution of the localities from which the specimens examined in this study were recovered. A. Murraysburg commonage. B. Swaelkrans. C. Leeufontein. H. Ringsfontein. I. Graaff-Reinet commonage. J. Katbosch. K. Vleiplaats. L. Bultfontein. M. Leeuriviersberg. N. Houd Constant. O. Roodebloem. P. Matjiesfontein. Q. Petersburg. R. Hoekplaas. S. Ferndale.

of the synchronous and apparently sympatric coexistence of a large number of anomodont species under the ecological conditions envisaged for *Cistecephalus* Zone times. Keyser has noted the possibility that only a single species of *Aulacephalodon*, a large dicynodont, is represented in these strata.

Biometric (allometric) analysis of a fairly large sample of *Aulacephalodon* crania, which included seven of the seventeen type specimens, indicates that at least this group of crania constitutes a homogeneous and probably species-specific, ontogenetic growth series.

The ecological roles of at least two large extant reptiles, *Alligator* and *Crocodylus*, have been observed to change continuously throughout the life of the animal (Cott 1961; Dodson 1975a), the size and type of food obtained being a function of the size of the individual. Analogous food changes probably occurred with the Triassic cynodont *Diademodon* (Grine *et al.* 1978). Similar changes in the ecological role of *Aulacephalodon baini* might have taken place as a function of ontogenetically increasing body size, and thus increased the breadth of the niche occupied by this reptile; but this is by no means certain. Keyser (1972) has pointed out that *Aulacephalodon* possessed a relatively short, broad snout, reinforced by anterior longitudinal palatal ridges, and he concluded that biting was restricted to the tips of the jaws. *Aulacephalodon* probably had a horny beak at the tip of the snout, and it is possible that the changes in the

TABLE 6

Tabulation of locality data. The code corresponds to the legend for Figure 10.

Code	Locality	Specimen	Nasal boss morphotype	Sex
A	Murraysburg commonage	7	1	indet.
B	Swaelkrans	5	3	male
C	Leeurivierspoort	33	3	male
D	Modderfontein	9	2	female
E	Bloukop	8	2	female
F	Oudeplaas	13	3	male
G	Leeufontein	12	3	male
H	Ringsfontein	11	3	male
		15	3	male
I	Graaff-Reinet commonage	10	3	male
		18	2	female
		21	2	female
J	Katbosch	6	2	? female
K	Vleiplaats	3	2	female
L	Bultfontein	14	2	female
M	Leeuriviersberg	32	3	male
N	Houd Constant	20	2	female
		31	2	female
O	Roodebloem	1	1	indet.
P	Matjiesfontein	16	2	female
Q	Petersburg	19	? 3	? male
R	Hoeksplaas	4	1	indet.
		17	3	male
S	Ferndale	2	2	female

shape of the snout that occurred during growth may have been further accentuated by the beak.

Although sexual differences of both extant and fossil reptiles are generally poorly expressed in the skeleton, Dodson (1976) has provided convincing evidence of sexual dimorphism in skulls of the late Cretaceous dinosaur, *Protoceratops andrewsi*. He showed sexual dimorphism to be an important source of variability in this ceratopsian, and found that it was reflected in many characters of the skull apart from the obvious ones.

A preliminary and limited biometric (bivariate) analysis of *Aulacephalodon* skulls indicated that only three of the specimens in the sample could be assigned even possibly to a sex: two specimens were provisionally accorded male status whilst a third was regarded as possibly female. The nasal bosses of *Aulacephalodon* have been regarded by several workers as being related possibly to sexual dimorphism e.g. Broom 1937, 1948; Keyser 1969). A simple size and shape analysis of these structures throughout an ontogenetic growth series has revealed that they do, indeed, appear to be related to sexual differences (Figs 6-7).

The smallest crania exhibit only slightly developed nasal bosses ('Type 1'), whilst larger skulls evince either a somewhat flattened, laterally projecting boss ('Type 2') or a more bulbous, expanded structure ('Type 3'). The sex of the smaller crania could not be determined although Haughton (1917) considered SAM-3328 (specimen 1, described by Broom in 1921 as the type of *Bainia*

haughtoni) to be a 'young male'. It was not possible in this study to refute or substantiate Haughton's claim.

Those crania which showed a 'Type 2' nasal boss are believed to represent females, whilst it is suggested that males evinced a more strongly developed ('Type 3') protuberance. Although the bivariate sexing technique used here proved to be generally inconclusive, as discussed above, three specimens showed relatively consistent biplot patterns (SAM-8747, BPI.FN. 634—males; SAM-K1221—female). The qualitative determination of sex, based solely upon nasal boss configuration, agreed with the biometric determination in two instances; but in the case of SAM-8747, a relatively large specimen, whilst the biparametric technique indicated 'maleness', it was deemed to be a female on the shape of its nasal bosses.

It is suggested that males possessed relatively more strongly developed bosses than females, and that these structures might have served some sexual selective function. They might have served as important visual signs in a mate recognition system and/or as agonistic display mechanisms. Keyser (1969) has suggested that the bosses could have protected the eyes (from thorny vegetation or during fighting), supported horny growths, and possibly even served a thermoregulatory function.

While the size of the nasal bosses is related in an allometrically positive fashion to the growth of the cranium (as represented by either basal snout or basal cranial lengths), the morphotypic expression of their general configuration appears to have been established at the attainment of sexual dimorphism and to have remained recognizably distinct throughout continued ontogenetic development. Thus, the male and female configurations are discernible over a rather large size range, whilst the smaller specimens show only minimal boss development. If nasal boss morphology is sexually related, as indeed it appears to be, and if the present sample is representative of *Aulacephalodon*, then it seems that sexual dimorphism was first expressed when the base of the cranium attained a length of between 190 and 245 mm.

The locality data appear to support the hypothesis that the present sample represents a morphometrically homogeneous, ontogenetic growth series of a single species of *Aulacephalodon* and that with age this species exhibited sexual dimorphism of the nasal bosses and of the anterior portion of the temporal arch. The confirmation or refutation of these hypotheses must, however, await a more detailed biometrical and osteoscopic analysis of a larger series of specimens which includes all the type specimens of *Aulacephalodon*.

SUMMARY AND CONCLUSIONS

A biometrical (allometric) analysis of a number of *Aulacephalodon* crania was undertaken. The sample included representatives of various supposed species as well as the holotypes of a number of these. The results of this investigation indicate that this sample represents a morphometrically homogeneous,

species specific, ontogenetic growth series. The features utilized previously as taxonomic criteria can be understood as one result of allometric growth.

A qualitative analysis indicates that nasal boss morphology is related to sexual dimorphism. It is apparent that the smallest (ontogenetically youngest) individuals showed no or minimal nasal boss development, and that sexual maturity or at least the earliest expression of sexual dimorphism may have occurred in individuals with a basal cranial length of between 190 and 245 mm. The larger male crania show a thickening of the lateral margin of the temporal arches, and this is not present in small male or any female skulls. Large male crania show a thickening of the anterior portion of the temporal arches.

The locality data for the specimens in this sample support the inference that this group of fossils represents a species—specific ontogenetic growth series, and that sexual dimorphism was expressed in the cranium of *Aulacephalodon baini*.

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