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Morphometric Analysis of *Crocodylus porosus* from the North Coast of Arnhem Land, Northern Australia*

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Abstract

Utilizing measurements from 1354 *C. porosus*, we have derived formulae for predicting snout–vent length from 17 other attributes. The specific problem of predicting body size from an isolated head or skull is treated separately and some data are presented on proportional tissue loss in skull preparation. Sexual dimorphism was examined, and is demonstrated in interocular width, the width at the midpoint of the cranial platform, and the length of the tail. Discriminant analysis has been used to distinguish males from females on the basis of external measurements of both the whole animal and the isolated head. Hatchling *C. porosus* from Arnhem Bay and the Blyth River have longer heads than those from the Liverpool River. *C. porosus* from Sarawak have longer tails and are heavier than those from northern Australia. Predicting the maximum size of *C. porosus* from large skulls in museums is difficult because of variations in basic skull shape. The body size at which mandibular teeth protrude through the premaxilla is quantified.

Introduction

To study growth and movement in *Crocodylus porosus*, a mark–recapture study was initiated on the north coast of Arnhem Land, northern Australia. Between June 1973 and January 1976, a total of 1354 individuals were caught, measured, marked and released. A series of measurements was taken from each animal and these form the basis of the present paper.

The morphometric study was undertaken mainly to fulfil practical needs arising from general research into the ecology of *C. porosus*. Much of the study is devoted to predicting snout–vent length from other measurements and vice versa. The derived equations allow body size to be predicted from isolated heads or segments of heads, and are the first step in the development of techniques by which body size can be estimated from calibrated photographs of heads, overcoming the need to catch crocodiles during surveys. In addition, they can be used to predict body size from track measurements and to construct models of *C. porosus* for comparison with other species or for theoretical studies in which size is a variable.

Quantitative assessments of relative growth (Dodson 1975) have not been attempted, though the general form of growth is described. A relationship between any two attributes is considered as either isometric or allometric, depending on whether it is linear or non-linear respectively.

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Sexual dimorphism and local geographic variation are examined and a comparison is made between *C. porosus* from Australia and those from Sarawak, as measured by Banks (1931). The question of the maximum size of *C. porosus* (Greer 1974) is re-evaluated in the light of additional data.

Snout–vent length was chosen as the basic index of body size because total length was dependent on tail length and the tail was sometimes damaged. In addition, tail length was also found to be slightly sex-dependent. Body weight was rejected because it could vary with the amount of food in the stomach and the reproductive condition, and be reduced by evaporative loss between capture and weighing.

The majority of specimens used were juvenile. Although unfortunate from the viewpoint of thorough representation of all size classes, this was unavoidable because *C. porosus* populations in northern Australia are recovering from overexploitation and contain mostly juveniles. Cott (1961) found a similar juvenile preponderance in recovering *C. niloticus* populations.

Our general studies of *C. porosus* are continuing; when further information on adults is available it may be necessary to re-examine some relationships described in this paper.

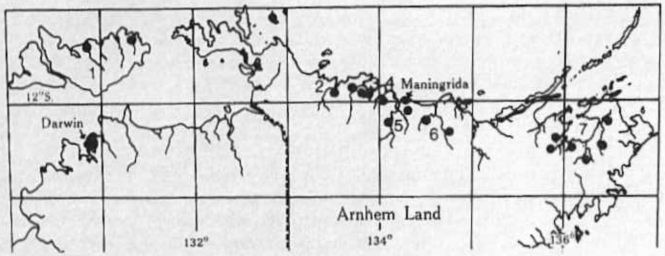


Fig. 1. Sites from which *C. porosus* were examined. *1*, Melville I. *2*, King River. *3*, Junction Bay. *4*, Rolling Bay. *5*, Liverpool and Tomkinson Rivers. *6*, Cadell and Blyth Rivers. *7*, Arnhem Bay.

Methods

The localities from which specimens have been examined are shown in Fig. 1. Catching methods and general habitat have been described elsewhere (Webb and Messel 1977; Webb *et al.* 1977). Most specimens were caught at night in tidal rivers and weighed, measured and released the following day.

Total and snout–vent lengths of *C. porosus* less than 2 m long were measured by laying the crocodile on a table beside an inlaid rule. The snout was butted against a vertical plate at zero, and a sliding caliper, mounted on the rule, was moved to either the cloaca or tail tip. Animals longer than 2 m were straightened on the ground and lines drawn at the required levels; the distance between the lines was then measured with a tape. Girth was measured with either a tape measure or a piece of cord subsequently laid against a rule. Hand and foot widths were measured with a tape; all head measurements were taken with large-gaped vernier calipers. Body weight was measured with either Salter spring balances (100 ± 5 g; 200 ± 10 g; 500 ± 10 g; 1 kg ± 25 g; 5 kg ± 50 g; 12 kg ± 100 g) or clock balances (130 ± 0·5 kg), or with a Martin-Decker Su5 crane scale (1360 ± 0·5 kg).

The measurements, the abbreviations used for some of them, and the nearest whole unit to which measurements were made, are listed below:

(1) Total length (TL). Tip of snout to tip of tail. 1 cm.
(2) Snout–vent length (SVL). Tip of snout to anterior extremity of the cloaca. 1 cm.
(3) Neck girth. Circumference of neck at level of nuchal rosette. 1 cm.
(4) Mid-body girth. Maximum girth of trunk. 1 cm.
(5) Tail girth. Maximum girth of tail butt, just posterior to cloaca. 1 cm.
(6) Width of horny layer. The width of the most anterior row of dorsal scutes with six individual scutes (usually the third row); similar to a measure used with commercial hides (see King and Brazaitis 1971). 1 cm.
(7) Cranial platform, point-to-point width (HPP). Straight-line distance between the posterior lateral extremities of the squamosal portion of the cranial platform. 1 mm. (Fig. 2).

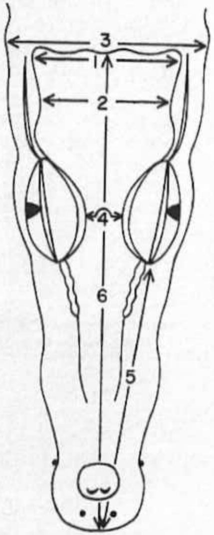


Fig. 2. Diagram of *C. porosus* head showing measurements. *1*, Width of cranial platform, HPP. *2*, Cranial platform midpoint width, HMP. *3*, Maximum head width, HMW. *4*, Interocular width, HIO. *5*, Snout–eye length, HSE. *6*, Total length of head, HTL.

(8) Cranial platform mid-point width (HMP). Width of the cranial platform, anterior to (7), where it is usually concave. 1 mm. (Fig. 2.)
(9) Head maximum width (HMW). Posterior to cranial platform, actually the distance between the extremities of the surangular bones at the level of articulation of the jaw. 1 mm. (Fig. 2.)
(10) Snout–eye length (HSE). Tip of snout to anterior edge of orbit, i.e. to the concavity of the lacrimal bone. 1 mm. (Fig. 2.)
(11) Total length of head (HTL). Tip of snout to median hind edge of platform, i.e. the supraoccipital bone. 1 mm. (Fig. 2.)
(12) Interocular width (HIO). Shortest distance between eyes, i.e. the interocular width of the frontal bone. 1 mm. (Fig. 2.)
(13) Ear length (HE). The length of the ear flap. 1 mm.
(14) Hand width. Maximum span of fingers when spread out but not stretched. 1 cm.
(15) Foot width. Maximum span of the three clawed toes, when spread out but not stretched; N.B. not the maximum width of the foot. 1 cm.

(16) Body weight (BWT). Accuracies as above.
(17) Trunk length. Derived from SVL − HTL.
(18) Tail length. Derived from TL − SVL.

Notes were taken on the extent of mandibular tooth protrusion through the premaxilla. In all animals, an attempt was made to determine sex by direct observation of the penis or clitoris. The cloaca was spread open with fine forceps or a haemostat (in specimens <2 m TL) or by hand (specimens >2 m). The shape of the male and female organs are distinctive in specimens over 40 cm SVL; experienced observers can correctly sex hatchlings of at least 20 cm SVL. Some errors in sexing of hatchlings were made in the initial phases of the study, and until confirmation of early results is obtained from recaptures we feel it safer to regard all animals under 40 cm SVL as unsexed. The sexing method will be described in detail elsewhere after the above checks have been made.

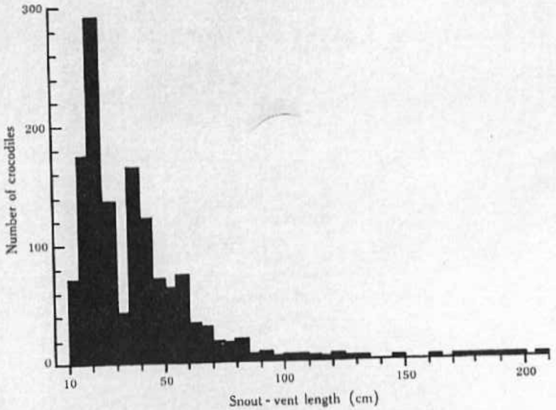


Fig. 3. Size–frequency histogram of *C. porosus* examined.

Body sizes at maturity are not known precisely. Unpublished data accumulated from a variety of sources indicates that females mature at approximately 110 cm SVL and males at approximately 160 cm SVL. For convenience in the text, specimens less than 100 cm SVL are referred to as juveniles. The term hatchlings is used to describe juveniles up to 30 cm SVL, which are within their first year of growth (unpublished data). Depending on sex, the terms adult and subadult are used to refer to *C. porosus* larger than juveniles which are respectively longer or shorter than the maturity estimates given above.

All data was analysed by computer using the SPSS Package of Statistical Programs (Nie *et al.* 1975). Statistical procedures generally follow those described by Bailey (1974), Nie *et al.* (1975) and Zar (1974).

Results

The size–frequency histogram (Fig. 3) demonstrates the relative abundance of juveniles in our sample. The lack of specimens between 30 and 35 cm SVL is a sampling error resulting from catching mainly in successive dry seasons (May–November), when hatchlings are a discrete size class.

In some 30 measurements, data appeared clearly erroneous (the measurements indicated *C. porosus* with markedly deformed heads, yet no such abnormality was noted on the data sheet). It was assumed that recording errors had been made, and as such measurements were at least four standard deviations from the mean, they were deleted from analyses aimed at predicting body dimensions.

For all statistical tests, the 5% rejection level was used as the criterion of significance.

Predicting SVL from Single-attribute Measurements

Most relationships between attributes and SVL were well described by straight lines, obvious regions of allometry being largely restricted to sizes of less than 40 cm SVL (Figs 4*a*–4*q*). Logarithmic transformation did not increase correlation coefficients significantly, except for the relationship between SVL and BWT ($P \ll 0\cdot001$; *t*-test), which is transformed in all subsequent analyses.

The method used to predict SVL from attribute measurements was to determine the regression equation describing the line of best fit with SVL as the dependent variable (Y) and the predictor as the independent variable (X). The equation is $Y = A + BX \pm E$, where Y and X are as above, A equals the Y-value when X is 0, and B is the regression line slope. E is the standard error of estimate, an overall indication of the dependence of Y on X (Zar 1974).

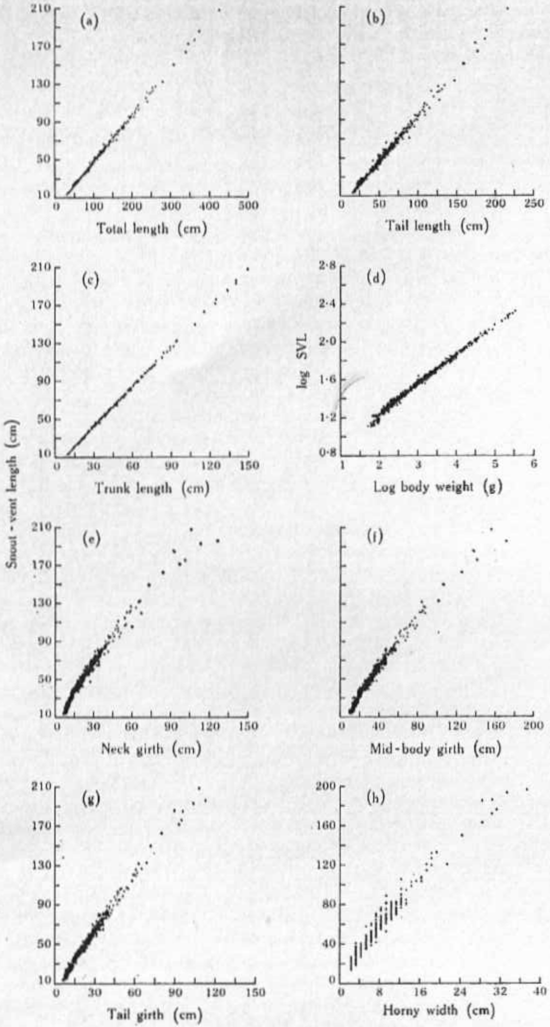
Sexual dimorphism and the allometric relationships referred to above could both affect prediction accuracy by incorporating inherent variability and non-linearity respectively. To overcome this problem the data were categorized into four groups on the basis of SVL: group I (13–20 cm), group II (21–40 cm), group III (41–126 cm) and group IV (127–207 cm).

Groups I and II contained individuals from the smallest caught (13 cm SVL) to the maximum size in which sex was not determined (40 cm SVL). They were divided into two groups so that the influence of non-linearity was reduced and, for practical purposes of predicting SVL, could be ignored. Group III was a sample of known males and females, the upper limit of 126 cm being determined by the largest female measured. An effect of sexual dimorphism on prediction accuracy could only be searched for in group III. Group IV consisted of subadult and adult males for which there were no equivalent-sized females; 207 cm SVL was the largest *C. porosus* measured. The general assumption was made that within each group the relationship between SVL and each other parameter was linear.

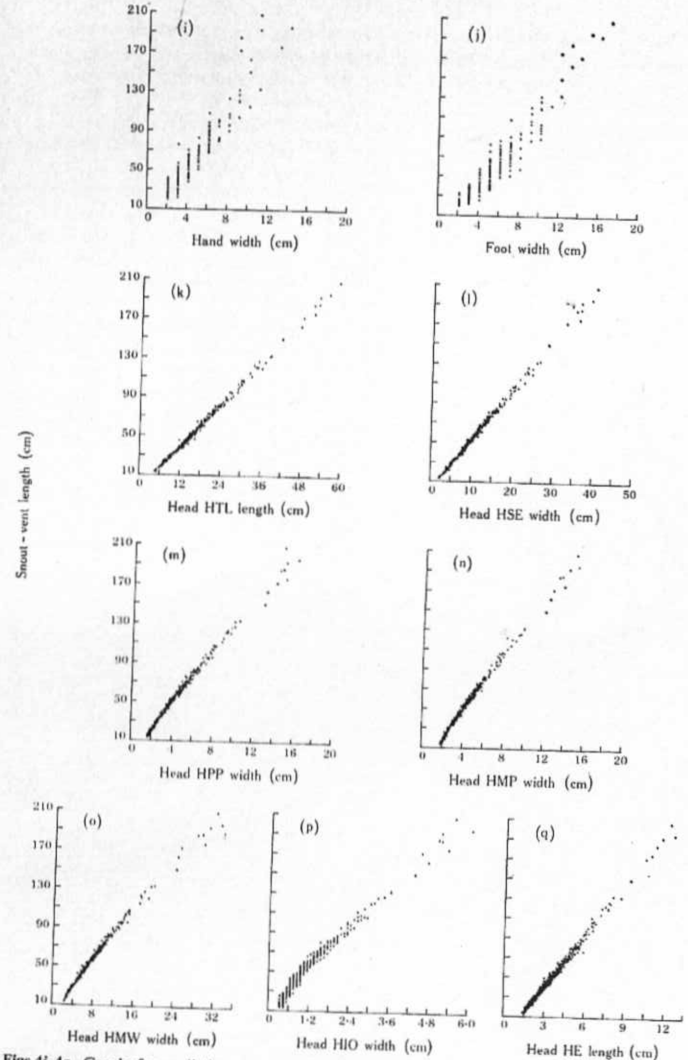
Regression lines relating SVL to each other attribute were calculated for each group, and in group III for males and females separately. The male and female lines (group III) were then tested for significant differences in either slope or elevation (*d* statistic; see below). A combined group III line was calculated if the male and female lines were considered coincidental, i.e. if slopes and elevations were not significantly different.

For each relationship between an attribute and SVL, the slopes of the separate lines for each group were then tested for significant differences (*d* statistic). If the slopes of adjacent groups were not significantly different, the data were lumped and a new line calculated. The minimum number of equations thus derived were included in Appendix 1.

A significant difference between males and females (discussed later) in group III was found in the slopes of the lines relating SVL to TL, HIO, HMP, and tail length; there were no significant differences in elevations. In the relationship with these



Figs. 4*a*–4*h*. Graphs for predicting snout–vent length from other attributes.



Figs 4*i*–4*q*. Graphs for predicting snout–vent length from other attributes. HTL, total length of head. HSE, snout–eye length. HPP, width of cranial platform. HMP, cranial platform midpoint width. HMW, maximum head width. HIO, interocular width. HE, ear length.

attributes, the male regression line was compared with the group IV line, and if no significant differences were found a combined line was calculated, applicable to males above 40 cm and up to 207 cm. If E was appreciably increased by combining two groups, the separate group equations were maintained.

Thus, in Appendix 1, the selection of the correct equation for predicting SVL is determined by the attribute to be used as a predictor, the attribute size range, and in some cases the sex of the animal under consideration.

For predicting SVL from hand and foot widths, two general equations were included to cover the size ranges, because the measurement limit (to nearest centimetre) was too large to allow meaningful comparisons of groups I, II and III.

When comparing the male and female regression lines in group III, it was found that the variances around the lines were significantly different (F test; $P < 0{\cdot}05$; Appendix 1). This invalidated the use of the t-test for comparing slopes and elevations (Zar 1974). The d statistic (Bailey 1974) was used to compare slopes, and a modification of it (after Brownlee 1965) to test elevations. The modification was: $d = (A_1 - A_2)/\sqrt{(\text{var. } a_1 + \text{var. } a_2)}$, where A_1 and A_2 are the Y values when $X = (\bar{X}_1 + \bar{X}_2)/2$, and var. a_1 and var. a_2 are the intercept variances.

As a check on the male–female differences in group III, multiple regression analysis with dummy variables was also used; the same results were achieved.

Predicting Body Dimensions from SVL

As the equations in Appendix 1 were only valid for predicting SVL from other attributes, a separate set, with SVL as the independent variable, were needed for accurately predicting other attributes from SVL (Appendix 2).

If a SVL to be used in an equation in Appendix 2 is itself derived from Appendix 1, the standard error of estimate of the resulting prediction is calculated by: $E_3 = \sqrt{[(b_2E_1)^2 + E_2^2]}$, where E_3 is the final standard error, E_1 is the error from the first equation, E_2 is the error from the second equation and b_2 is the slope of the second equation.

Predicting SVL from an Intact Head

For the specific problem of predicting SVL from an isolated, intact head, a more precise prediction was obtained for each group by using multiple regression analysis with a combination of head measurements. In groups III and IV, HIO and HMP were not included in the analyses, because they were partly sex-dependent. The results are in Appendix 3. The equation for predicting SVL is: $Y = a + b_1X_1 + b_2X_2 + b_3X_3 \pm E$, where Y is SVL, a is the regression intercept, b_1–b_3 the respective slopes for attributes X_1–X_3, listed in Appendix 3.

Predicting SVL from a Skull

The equations so far presented were derived from measurements of intact animals. Their use with measurements from skulls gives an underestimate of SVL proportional to the relative loss of tissue in skull preparation. Some data on tissue loss came from heads on which three comparable measurements had been made (Table 1). In these, the mean loss of HTL was 4·3% (of the original measurement), that of HIO was 8·1% and that of HMP was 11·1%.

Sexual Dimorphism

Male and female regression lines for predicting SVL had significantly different slopes when attributes TL, HIO, HMP and tail length were used as predictors (see p. 5).

The TL and tail length differences indicate that males have longer tails than females. The difference is not large and at the SVL of our largest female (126 cm) the predicted tail lengths would be 133·5±2·2 cm for males and 130·7±2·6 cm for females respectively (from equations 69 and 70).

The wider HIO and HMP measurements of females (relative to SVL) indicate expansion of the central portion of the skull. A male of 126 cm SVL could be expected to have a HIO of 3·1±0·1 cm and a HMP of 9·0±0·1 cm, whereas a female would have 3·2±0·11 cm and 9·2±0·1 cm respectively.

Table 1. Comparison of measurements of *C. porosus* heads before and after skull preparation

Attribute	Specimen TL (cm)	Intact head (cm)	Skull (cm)	Percentage loss Head	Percentage loss Skull
Head total length	335	48·3	46·4	3·9	4·1
	337	46·4	43·5	6·3	6·7
	226	30·0	29·2	2·7	2·7
Cranial platform midpoint width	398	14·9	12·6	15·4	18·3
	355	12·8	11·7	8·5	9·4
	337	12·2	10·8	11·4	13·0
	226	7·7	7·0	9·1	10·0
Interocular width	398	5·2	5·0	3·8	4·0
	335	4·9	4·5	8·2	8·9
	337	4·6	4·2	8·7	9·5
	226	2·6	2·3	11·5	13·0

These differences are slight; however, our largest female is quite small when compared to other known females. For example, the HIO's of a male (335 cm TL) and a female (337 cm TL) obtained before the present study were 4·6 and 4·9 cm respectively, even though the TLs were nearly identical. The 3-mm difference in HIO would account for approximately 20 cm of TL prediction, should the one formula be used for both predictions.

External Measurements as Sex Discriminators

Discriminant analysis (Klecka 1975) was used to determine whether sex could be predicted from attribute measurements. In this analysis, the classification of a *C. porosus* as either male or female depends on the position of its calculated discriminant score relative to known males and females. If discrimination is good, the discriminant scores of males and females will form normal distributions with minimal overlap; the score of an unsexed animal can be compared with these and assigned a sex on the probability that it came from one or the other of the distributions.

The analysis supplies standardized and unstandardized coefficients. The former show the relative contribution of each attribute to the discrimination, and the latter are needed for calculating the discriminant score by the formula:

$$D = C + C_1V_1 + C_2V_2 + \ldots C_iV_i,$$

where D is the discriminant score, C a given constant and C_1–C_i unstandardized discriminant function coefficients for each of the attributes V_1–V_i.

Initially, only head measurements were used in the analysis, both as raw numbers and as ratios of head length. Analyses of all individuals over 40 cm SVL showed poor sex discrimination, and using the best derived discriminant function (head measurements as ratios) sexed 59·9% of the *C. porosus* used in the analysis correctly (χ^2; $P < 0\cdot001$; $n = 426$). Because sexual dimorphism probably increases with body size, the measurements were separated into SVL categories of 40–60, 60–80, 80–100, 100–120 and 100–207 cm. Each category was then analysed separately using both ratios and raw measurements. In the three categories of <100 cm, discrimination remained poor, correct classification being 57·5% (40–60 cm; $P = 0\cdot01$), 62·8% (60–80 cm; $P = 0\cdot031$) and 56·0% (80–100 cm; $P = 0\cdot549$). In the 100–120 cm group, there were only 11 individuals, and correct classification was 81·8% ($P = 0\cdot035$). With the addition of the 12 individuals of >120 cm correct classification increased to 87% ($P < 0\cdot001$).

The discriminant coefficients and characteristics of the male and female score distributions for the latter two groups are given in Appendix 4. The standardized coefficients (st. in Appendix 4) show that HIO and HPP, as ratios of HTL, were major contributors to the discrimination in the 100–120 cm SVL category. The HMW:HTL ratio was three times as important as any other ratio in the 100–207 cm group. The spread of the male and female scores overlapped within one standard deviation in the 100–120 cm group, and within two standard deviations in the 120–207 cm group.

With the addition of SVL to the head measurements, discrimination improved, 62·4% of animals over 40 cm SVL being correctly classified ($P < 0\cdot001$). In the 40–60 cm group (run separately) 62·0% were correctly classified ($P < 0\cdot001$). The coefficients and score characteristics of groups above 60 cm are in Appendix 4.

The 60–80 cm group had 65·1% correct classification; however, there was considerable overlap of the distributions. SVL was the major contributor to the discrimination. In the 80–100 cm group, correct classification increased to 79·2% ($P = 0\cdot004$), SVL again being the major contributor. In the 100–120 cm group there was 100% discrimination ($P = 0\cdot001$) with HTL as the major contributor; there were only 11 *C. porosus* in this sample. With the addition of the measurements from animals above 120 cm SVL, classification decreased to 91·3% ($P < 0\cdot001$), one male and one female being incorrectly classified; HTL remained the major discriminator.

With the addition of TL and the deletion of HMP (whose contribution was not statistically significant), correct classification increased to 100% ($P < 0\cdot001$), in the 100–207 cm group; TL was the major contributor. The inclusion of total length meant that five *C. porosus* had to be deleted from the analysis, because they had the tips of their tails missing. These five did not include the two individuals wrongly sexed in the analysis of the same group with TL included, but rather four of the larger males and one female.

Thus, Appendix 4 contains coefficients and score distributions for seven discriminant functions. If the sex of a *C. porosus* is required and only the isolated head is available, the coefficients in Nos 129 and 130 can be used, if the animal is over 100 cm SVL as determined through Appendix 1 or 3. The probability of the derived score being either in the male or female distributions can be calculated, and this is the probability of the specimen being either a male or a female.

If measurements from the whole animal are available, equations 129–135 can be used.

Geographic Variation of C. porosus *on the North Coast of Arnhem Land*

Examination of geographic variation was limited to hatchlings between 20 and 35 cm SVL because: (1) It is probable that these animals come from nests in the rivers in which they were caught and are not immigrants into the system (Webb *et al.* 1977); (2) They are an abundant size class; (3) Geographically this size class is the most widespread in our data, i.e. in some rivers only hatchlings were caught and processed; (4) Most relationships between head measurements can be well approximated by straight lines in the 20–35 cm SVL size range.

The measurements from hatchlings caught in various rivers were combined into six groups corresponding to the following geographic regions (see Fig. 1): (1) Melville I., 131° E., 11°30′ S. ($n = 3$); (2) King River, 133°32′ E., 11°50′ S. ($n = 10$); (3) Junction Bay, 133°55′ E., 11°50′ S. ($n = 4$); (4) Liverpool River, 134°10′ E., 12°10′ S. ($n = 185$); (5) Blyth River, 134°35′ E., 12°10′ S. ($n = 123$); (6) Arnhem Bay, 136°10′ E., 12°20′ S. ($n = 123$).

The relationship between HMW (dependent variable) and each other head measurement was examined by means of multiple regression analysis (with a combination of dummy variables), to determine whether hatchlings from any of the rivers were different from each other, in terms of a contribution to the overall variance of the data.

Only in the regression relating HMW and HTL were there significant differences between the hatchlings from different rivers. Separate regression lines for the Arnhem Bay and Blyth River hatchlings were not significantly different from each other (in either slope or intercept), but both were significantly different (in slope) from the line of the hatchlings from the other rivers combined (d statistic; Arnhem Bay $0\cdot002 > P > 0\cdot001$; Blyth River $0\cdot01 > P > 0\cdot002$).

This indicated that the Liverpool River, and rivers to the west of it, contained hatchlings with longer heads (relative to HMW) than those in the rivers to the east. That no significant differences occurred when HSE was used as an independent variable suggests that the difference is in the part of the head posterior to the eyes.

Discriminant analysis (see p. 9) was used in an attempt to determine a discriminant function by which the hatchlings from the various systems could be identified. The hatchlings from the rivers with small samples could not be discriminated and were deleted from the analysis. A separate analysis included only hatchlings from the Liverpool River, Blyth River and Arnhem Bay.

There was almost equal distribution of Arnhem Bay hatchlings between Arnhem Bay and the Blyth River and vice versa; however, together, hatchlings from these two rivers were well distinguished from those of the Liverpool River.

Arnhem Bay and Blyth River Hatchlings were combined and an additional analysis carried out.

Of the 422 hatchlings, 70·6% were classified into their correct rivers, i.e. Liverpool or Arnhem Bay–Blyth River combined (χ^2 $P < 0\cdot001$). Each of the measurements used in the analysis made a significant contribution to the discrimination and the unstandardized coefficients for determining the discriminant score were: SVL, −0·022; TL, 0·04; HPP, 11·20; HMP, −2·02; HMW, 3·98; HSE, 1·46; HTL, −4·00; HE, −6·57; constant, 2·02 (equation No. 136). The mean of the Liverpool River hatchling scores was 0·52±0·95 (s.d.; $n = 183$). The mean from the combined Arnhem Bay and Blyth River hatchlings was −0·40±1·04 (s.d.; $n = 239$). There is thus considerable overlap of score distributions.

As the standardized discrimination coefficients indicate the relative contribution of each attribute to the discrimination, they are listed: HTL, 4·7; HPP, 2·9; HMW, 2·00; HE, 1·6; HSE, 1·1; SVL, 0·8; HMP, 0·5; TL, 0·3. HTL was clearly the single parameter with the greatest contribution to the discrimination.

Comparison of C. porosus *from Australia and Sarawak*

Banks (1931) presented measurements (TL, HTL, BWT and tail length) of 41 *C. porosus* from western Sarawak. He noted one individual (his No. 26) as having the tail tip missing. Another (his No. 33) was reported as having a tail length of 3 ft 1½ in. and a TL of 7 ft 10 in.; proportions markedly different from the remainder of his sample. Also, his No. 1 was recorded as having a tail length of 3½ in., which appears to be a printing error (8½ in. would seem more realistic). The above three specimens were deleted from the analyses described below.

Table 2. Comparison, between Sarawak and Australian *C. porosus*, of the regression line coefficients necessary to predict attributes from total length

P, probability that slopes of regression lines are from the same population. NS, not significant

Dependent variable		Australia	Sarawak	Significance slopes
Head total length	*b*	0·137	0·132	NS
	a	0·84	1·38	
Tail length	*b*	0·512	0·489	$P \ll 0{\cdot}001$
	a	0·47	0·69	
Log body weight	*b*	3·220	3·318	$0{\cdot}05 > P > 0{\cdot}02$
	a	−3·04	−3·33	

Individuals between 40 and 238 cm TL were chosen for comparison. The large females in Banks' (1931) sample were thereby deleted, leaving an equivalent size range of *C. porosus* from Australia and Sarawak.

The regression lines relating each of the attributes to TL (independent variable) were calculated for both groups, and the slopes and intercepts tested for significant differences using the *d* statistic (Table 2). There were significant differences in the slopes of the lines relating tail length and BWT to TL, which indicated that the tail length of Australian *C. porosus* increased at a greater rate than that of Sarawak *C. porosus*; however, the difference was slight and could reflect the fact that Banks measured tail length to the centre of the cloaca whereas we measured it to the anterior margin of the cloaca.

Body weight of Sarawak *C. porosus* increased at a greater rate than that of Australian *C. porosus*, which is consistent with the Sarawak form having a relatively short tail, or a greater portion of its TL as SVL.

In order to examine whether Sarawak males and females showed dimorphism in the relationships described above, separate regression lines for each sex were calculated and compared. No significant differences could be demonstrated.

Growth Form

Examination of the changes in morphometric ratios as a function of increasing body size allows an understanding of growth in *C. porosus*. Fig. 5*a* is a plot of the TL:SVL ratio; as tail length is derived from TL−SVL this ratio has the same distribution of points. A separate scale is on the right-hand axis of the figure. The tail is relatively long in juveniles, though the allometry with increasing size is only slight. Measurements from all individuals are included on these figures, and points well separated from the mean trend are those deleted from analyses aimed at predicting SVL (see p. 5).

Fig. 5*b* is a plot of the HTL: trunk ratio against SVL. Hatchlings have relatively long heads, and growth of the trunk is proportionally greater than the growth of HTL, allometry being distinct in animals under 70 cm SVL. In *C. porosus* over 70 cm SVL, growth rates of the head and trunk approach isometry, the ratio being approximately 0·4.

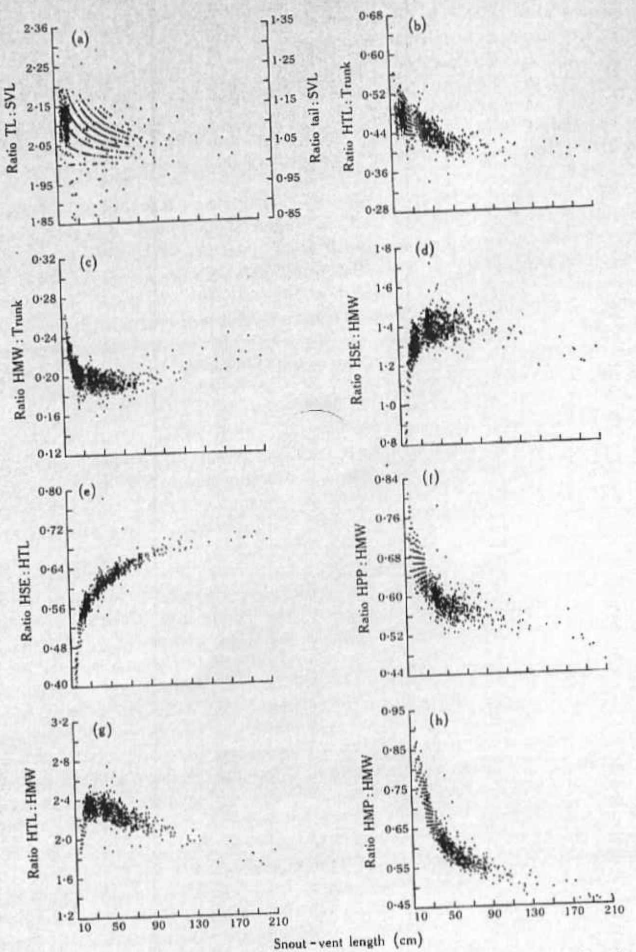
Fig. 5*c* shows the ratios of HMW to trunk; there is a pronounced allometry in the juveniles, trunk length increasing at a much greater rate than HMW; however, in animals between 25 and 70 cm SVL, HMW and trunk length grow in proportion. In animals of more than 70 cm SVL, HMW increases at a greater rate than does trunk length. The allometry in the HMW:trunk relationship in animals under 25 cm is pronounced when compared to the relatively slight allometry of the HTL:trunk ratio (Fig. 5*b*). This indicates that HTL itself is increasing at a proportionally greater rate than HMW. The latter relationship is demonstrated in Fig. 5*g*, a plot of the HTL:HMW ratio. Allometry in *C. porosus* up to 25 cm SVL is distinct, and HTL increases at a proportionally greater rate than HMW. In *C. porosus* of more than 40 cm SVL, HMW increases proportionally faster than HTL.

The initial growth in HTL results from a high growth rate in the region between the eye and the snout (HSE). In hatchlings the snout is relatively short compared with the rest of the head; however, it increases more rapidly than any of the other head regions up to an SVL of 25–30 cm (Figs 5*d*, 5*e*). The growth rate of HMW exceeds that of HSE in *C. porosus* over 70 cm SVL, though the allometry is not as great as that demonstrated for the HTL:HMW ratio (Fig. 5*g*). Thus, even though HSE is growing proportionally faster than the postorbital region of the head (Fig. 5*e*) in *C. porosus* over 70 cm SVL, the growth rate of HMW is still proportionally greater than that of HSE.

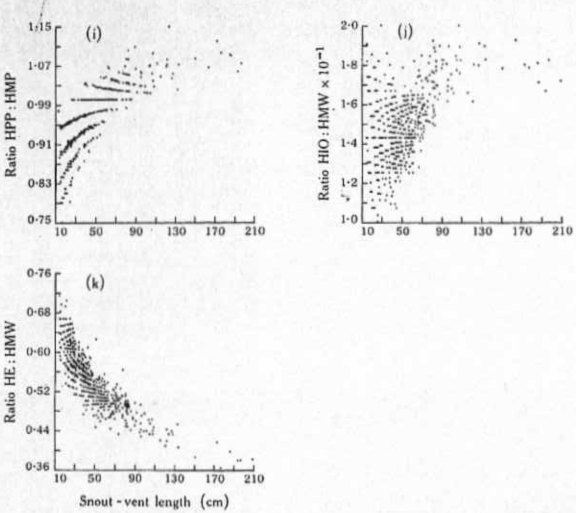
The cranial platform in hatchlings has convex sides (Fig. 5*i*). This convexity is reduced as growth occurs until the lateral surfaces are parallel, and the HPP:HMP ratio equals 1·0, i.e. when *C. porosus* are between 30 and 70 cm SVL. With continued growth, HPP exceeds HMP, the lateral surfaces becoming concave.

There is pronounced allometry between HPP and HMW (Fig. 5*f*), the former increasing more slowly than the latter. In animals over 50 cm SVL, the relationship approaches isometry; however, the largest *C. porosus* shows a reduction in the ratio. A similar relationship is found in the HMP:HMW ratio (Fig. 5*h*). Trends in the HIO:HMW ratio (Fig. 5*j*) in juveniles are masked by the relative inaccuracy of the HIO measurement. HIO clearly increases at a greater rate than does HMW up to approximately 70 cm SVL, after which the relationship seems isometric.

The HE:HMW ratio (Fig. 5*k*) is largest in hatchlings, and the steady decline indicates that juvenile HMW increases at a proportionally greater rate than HE.



Figs 5a–5h. Graphs demonstrating morphometric ratios as functions of snout–vent length. TL, total length. SVL, snout–vent length. HTL, total length of head. HMW, maximum head width. HSE, snout–eye length. HPP, width of cranial platform.



Figs 5i–5k. Graphs demonstrating morphometric ratios as functions of snout–vent length. HIO, interocular width. HE, ear length.

To summarize, in hatchlings head length is a large portion of SVL. In comparison with that in larger *C. porosus* the cranial platform is wide, its lateral surfaces are convex, the interocular width and distance between the snout and eye are small, and the ear flap is relatively long.

In the initial stages of growth (up to 25–30 cm SVL) there is extreme allometry. Increases in the HSE region are greater than those in head width, which is reflected in an overall lengthening of the head relative to its width. This occurs even though the posterior part of the cranium (indicated by the HE : HMW ratio) is increasing more slowly than head width. Interocular width increases faster than head width, whereas the width of the cranial platform does not. The lateral sides of the platform tend to become parallel.

In *C. porosus* between 25 and 70 cm SVL, head width, trunk length and snout–eye length increase isometrically and their growth rate appears to be surpassed only by interocular width. The growth rate of the above regions exceeds that of cranial platform width, total head length and ear flap length. That the increases in head width surpass those in head length, yet are in proportion to those in the snout–eye region, indicates a considerable reduction in the linear growth of the postorbital region.

In *C. porosus* over 70 cm SVL, head width increases at a proportionally greater rate than trunk length, though still in isometry with interocular width.

The posterior and midpoint widths of the cranial platform tend toward isometry; however, their rates of growth appear proportionally less than that of head width. Head total length increases in proportion to trunk length, though growth in head length appears to result from an allometry between the pre- and postorbital regions

Table 3. Dimensions of large *C. porosus* heads

Head No.	Locality	TL (cm)	Head or skull	HPP	HMP	HMW	HSE	HTL	HIO	Notes
S1	Aust., Mary R.	615	Skull	23·5	18·9	48·0	44·3	66·6	7·5	Wildlife Section, Dept. of Northern Territory
S2	Aust., Mary R.	560	Skull	19·5	17·2	48·5	48·0	68·7	7·8	Private coll., Mr C. Howells, Darwin
S3	—	—	Skull	18·0	15·4	38·9	46·7	64·5	6·8	AMNH No. 15179; Mook 1921*b*
S4	—	—	Skull	20·5	17·7	47·8	50·0	71·5	8·2	BMNH No. 47.3.5.33
S5	Bengal	(33?)^A	Skull	18·3	15·7	41·0	45·6	65·5	7·2	BMNH No. 43.8.18.4
S6	Manila(?)	(29?)^A	Skull	20·1	17·5	44·8	48·8	67·4	7·1	MCZ, on display; Barbour 1924
S7	—	—	Skull	—	—	47	—	75	—	Indian Museum; width Prashad 1930; length Greer 1974
S8	—	—	Skull	—	—	40·6	—	—	—	U.S. Club, India; Prashad 1930
S9	—	—	Skull	—	—	47	—	—	—	Brander 1930
S10	Sarawak	503	Head	—	—	—	—	63·5	—	Banks 1931
S11	Sarawak (?)	—	Skull	—	—	—	—	71	—	Banks 1931
S12	India	(23–24)^A	Skull	—	—	—	—	100	—	Private coll., Raja of Kanika, India; Daniel and Hussain 1973
S13	—	—	Skull	18·5	—	—	45·2	62·0	7·0	Zool. Inst. Leningrad; Iordansky 1973
S14	—	—	Skull	20·4	—	—	51·6	74·0	8·2	Zool. Inst. Leningrad; Iordansky 1973
S15	Aust., Tomkinson R.	422	Head	14·8	14·9	32·0	40·5	58·8	5·5	This study, No. 1299
S16	Aust., Tomkinson R.	399	Head	16·2	15·1	32·9	39·3	55·8	6·0	This study, No. 889
S17	Aust., Liverpool R.	394	Head	15·0	14·2	30·6	36·7	52·9	5·1	This study, No. 363
S18	Aust., Goomadeer R.	379	Head	14·7	13·5	29·2	36·6	52·7	5·0	This study, No. 887
S19	Aust., Tomkinson R.	371	Head	14·4	13·2	28·2	35·5	51·2	5·1	This study, No. 1300
S20	Aust., Dongau Creek	360	Head	15·0	13·7	29·7	36·3	51·5	5·3	This study, No. 1000
S21	Aust., Liverpool R.	344	Head	14·1	12·6	25·0	33·0	48·0	4·5	This study, No. 931

^A Length in feet.

in specimens up to 150 cm SVL, after which snout–eye length and head total length grow in proportion.

Large C. porosus *Skulls*

The largest *C. porosus* caught and measured in the present study, a male from the Tomkinson River, was 422 cm TL and 207 cm SVL.

Two skulls in Darwin are appreciably larger than the head of this specimen; their dimensions are given in Table 3.

Skull S1 is in Wildlife Section, Department of the Northern Territory, Darwin. It came from a *C. porosus* caught and killed by fish poachers on 1 July 1974. The specimen was entangled in a net set in the Mary River (131°40′ E., 13°S.). The skinned carcass, without the head (measured by a Wildlife Officer, Mr. V. Pederson) was 18 ft with an estimated ±3 in. (548±8 cm); the tail was complete. The skull has a total length of 66·6 cm, making the total length of the crocodile at least 615 cm (Fig. 6).

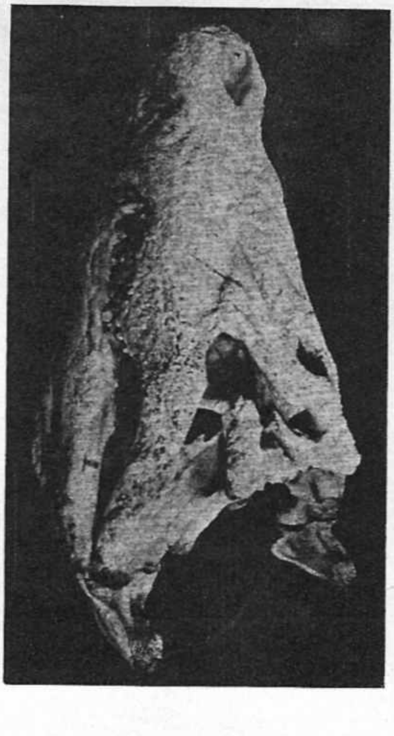


Fig. 6. Skull of a *C. porosus* (No. S1) whose total length was at least 615 cm. Measurements are given in Table 3.

The second skull, S2, is owned by Mr C. Howells, a resident of Darwin. It came from a *C. porosus* shot in a lagoon of the Mary River drainage in 1968. The TL of the crocodile was 18 ft 6 in. (564 cm) (measured by Mr Howells); the tail was complete. This second skull, although longer and broader than S1, came from a crocodile 51 cm shorter. Visual comparison of S1 and S2 indicates that S1 is more massive than S2, which is reflected in the width of the cranial platform (Table 3).

When S1 and S2 are compared with other large *C. porosus* skulls (Table 3), there are some striking differences, primarily in the relationship of HSE to HMW. In S1 and S2, HSE is less than HMW, whereas in the others (S3–S6), it is appreciably more. The longer snouts of S3–S6 are in turn reflected in HTL's which, relative to HMW, are longer than in S1 and S2. This basic difference in skull proportions invalidates the derivation from the Australian specimens of predictive formulae which would be applicable to the others. Until additional data on the measurements of large *C. porosus* from other parts of the world are available, or the differences in the skulls prove to be within the variability of Australian specimens, we cannot predict the total length of the crocodiles from which S3–S14 were obtained.

To derive a predictive equation for large Australian *C. porosus*, the measurements of S1 and S2 were corrected for tissue loss by adding estimates based on the limited data on tissue loss given previously (see p. 8). The measurements were corrected as follows: HTL, HSE, HMW and HIO by 4%; HPP and HMP by 10%. These new measurements were then combined with the measurements from the seven largest *C. porosus* caught in the present study (TL 360–422 cm), and a multiple regression analysis carried out with TL as the dependent variable. The resulting equation was: $\text{TL} = 82{\cdot}54 + 6{\cdot}51\,\text{HMP} + 21{\cdot}59\,\text{HTL} - 30{\cdot}15\,\text{HSE} + 8{\cdot}55\,\text{HMW} - 5{\cdot}25\,\text{HPP} \pm 3{\cdot}49$ cm (equation No. 137); all measurements being considered as coming from intact heads. This formula should be treated with caution because of the relatively small amount of data from which it was derived.

Table 4. Number of *C. porosus* with one or two mandibular teeth protruding through the premaxilla

Range SVL (cm)	No. of specimens M+F	M	F	No. with teeth M+F	M	F	With two protruding (%)	With one protruding (%)
31–40	192	71	121	12	2	10	6·3	66·7
41–50	171	86	85	35	13	22	20·5	45·7
51–60	120	66	54	56	28	28	46·7	46·4
61–70	67	34	23	30	19	14	44·8	36·6
71–80	32	17	16	16	11	9	50·0	12·5
81–90	18	9	9	17	8	9	94·4	17·6
91–100	8	4	4	8	4	4	100·0	12·5
101–110	7	2	5	6	2	4	85·7	0
111–207	20	16	4	20	16	4	100·0	5·0

The difference in the proportions between the Australian *C. porosus* and S3–S6 results in unrealistic predictions of TL if the formula is used with these skulls, e.g. S3 would have the same total length as S15, even though the skull is larger in all dimensions. The proportionally long snout makes a large negative contribution to the total.

Tooth Protrusion Through Premaxilla

Of the *C. porosus* over 110 cm SVL examined, all except one had either two of the anterior mandibular teeth protruding through the premaxilla, or holes indicating that protrusion had occurred (Table 4). The exception was a 775-cm male with a single protruding tooth and no other hole.

The smallest *C. porosus* exhibiting this phenomena was 34 cm SVL; it had a single tooth protruding. Of the 192 *C. porosus* between 31 and 40 cm SVL examined, only 12 (6·3%) had protruding teeth; 8 (66·7%) of these had a single tooth protruding.

As SVL increased, the percentage of *C. porosus* exhibiting tooth protrusion increased and the precentage with a single tooth decreased. In no group was the difference in the proportion of males and females with tooth protrusion significant at the 5% level (χ^2 test).

Discussion

Wermuth (1964) examined the relationships between head, trunk and tail length in 21 species of crocodilians. He found that *C. porosus* had a proportionally longer tail that the other species (relative to trunk length) and attributed this to its habits, i.e. long distances travelled at sea. He also found that the distribution of the ratio of tail length to trunk length in *C. porosus* was bimodal, whereas that in *C. niloticus* was unimodal. Although his animals were unsexed, he suggested the bimodal distribution could reflect sexual dimorphism.

In the present study, a significant male–female difference in tail length was found, which tends to confirm Wermuth's (1964) explanation of the bimodal distribution; however, we found no obvious bimodal distribution in the ratio of tail length to snout–vent length. If, as suggested by Wermuth (1964), tail length is indicative of mobility, the above difference could indicate that male *C. porosus* are more mobile than females. This has been definitely shown in *Alligator mississippiensis* (Joanen and McNease 1970, 1972), and appears to be so in *C. porosus* (Webb *et al.* 1977).

That such a small difference in tail length could affect swimming efficiency seems unlikely, though it is possible that the length difference is an indication of more basic differences in tail shape (e.g. effective lateral surface area). It is also possible that the difference represents a slight dimorphism in the location or size of the cloacal slit. However, if this were so one would expect sexual dimorphism in the relationship with snout–vent length and most of the other attributes, which was not found.

The relatively wider interocular and platform midpoint widths of female *C. porosus* may represent phenomena more widespread amongst the Reptilia. The functional significance of this difference is obscure, though it could be related to sex recognition; it would seem too minor to be related to a functionally significant strengthening of the skull.

Kramer and Medem (1955), in their study of caiman body proportions, found no external features, other than maximum total length, which could be used as sex discriminators. They did not examine the number of attributes looked at in the present study, nor did they have the benefit of the range of statistical methods now available for this type of problem; thus, it is possible that such differences do occur.

The discriminant analysis carried out in the present study can be used to classify individuals of certain sizes as males or females on the basis of external measurements. In specimens over 100 cm SVL the classification was 100% effective in the *C. porosus* used, if total length was included as a variable. In specimens under 100 cm SVL classification was less effective. When the equations are used to classify *C. porosus* of unknown sex, many individuals are in the region of overlap of the discriminant scores and cannot be sexed.

The significant classification ($P < 0{\cdot}001$) of crocodiles in the 40–60 cm SVL category (though there was also considerable overlap) indicates that even at this size sexual dimorphism of the attributes measured is present.

The examination of the form of *C. porosus* growth indicated a broadening of the head (relative to SVL and HTL) in specimens over 80 cm SVL. Kramer and Medem (1955) demonstrated this same trend in *C. porosus* with measurements of the width of the snout (a measurement not taken in the present study). Mook (1921*a*) showed that a broadening of the head was distinct in *Crocodylus acutus* and *Caimen sclerops*, much more so than in *A. mississippiensis*. Dodson (1975) found a strong positive allometry in snout length, but not snout width, in relation to head length in *A. mississippiensis*; he interpreted this as a strengthening of the head related to the progressive increase in the size of prey taken.

Juvenile *C. porosus* feed mainly on the small crustacea, insects and fish of the water's edge (Allen 1974; Taylor, MSc Thesis in preparation; personal observations), whereas adults appear to feed mainly on larger mammals, birds, larger crabs, fish and other reptiles (Allen 1974; personal observations). The development from juveniles to adults sees a change in hunting methods from a continual hunting and catching of small items, to less frequent and more specific attacks on larger items. The broadening and strengthening of the head could well be an adaptation to more efficient capture of large prey as suggested by Dodson (1975) for *A. mississippiensis*.

From the formulae given in Appendices 1–3, it is possible to reconstruct *C. porosus* up to 207 cm SVL. It is not valid to extrapolate relationships to animals longer than this and therefore not possible to use the formulae to predict SVL of the *C. porosus* belonging to the large skulls in museums (see Table 3). An attempt was made to formulate a satisfactory equation for this purpose by combining the measurements of the largest *C. porosus* from the present study with those from two large skulls of known-sized *C. porosus* from Australia. However, it was found that the basic proportions of the Australian skulls differed from the others, invalidating the use of the formulae for specimens outside Australia.

Greer (1974) extrapolated from Banks' (1931) data and concluded that the largest *C. porosus* known from skulls would be between 17 and 19 ft. The large Darwin skull (S1; Table 3) would, on the basis of his formula, have a total length of 488 cm (16 ft), yet the specimen was at least 615 cm (20 ft). The skulls purported to belong to 33-ft and 29-ft specimens (Table 3; Greer 1974) are neither excessively long nor broad, and, as Greer (1974) pointed out, the total length measurements would seem to be in error. However, until more data are available on the variation to be expected in large *C. porosus*, no firm predictions would seem valid. The problem created by the differences in proportions of the skulls of large *C. porosus* could possibly be avoided if the assumption was accepted that growth of the head *per se* is related to body length. It would then be possible to derive a relationship between volume of bone in the skull and total length which would be independent of skull proportions.

It appears that the longest *C. porosus* skull in existence (though not necessarily from the longest crocodile) is that reported by Daniel and Hussain (1973), i.e. 100 cm from the snout to the posterior edge of the cranial platform.

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Appendix 1. Coefficients for Predicting Snout–Vent Length from other Measurements by Linear Regression Analysis

A, regression line intercept. *B*, slope. *E*, standard error of estimate. 'Variances' gives the probability (*P*) of male and female variances (group II, see p. 8) being the same. 'Slopes' gives the probability that the slopes of male and female regression lines (group III) being the same.

Eqn No.	Predictor	Ranges (cm)	Sex	*A*	*B*	*E* (cm)	Variances	Slopes	*N*
1	Total length	260–425	M	−0·72	0·49	1·1	—	—	231
2		80–260	M	−0·34	0·49	1·1	$P < 0·002$	$0·01 > P > 0·002$	224
3		80–260	F	−1·36	0·50	1·3	—	—	192
4		85–260	M+F	−0·87	0·49	1·2	—	—	416
5		25–85	M+F	−0·28	0·48	0·6	—	—	874
6	Tail length	135–220	M	−1·16	0·95	2·2	—	—	231
7		45–135	M	−0·18	0·94	2·0	$P < 0·001$	$0·01 > P > 0·002$	224
8		45–135	F	−2·04	0·97	2·6	—	—	192
9		45–135	M+F	−1·12	0·96	2·3	—	—	416
10		22–45	M+F	0·28	0·91	1·2	—	—	612
11		13–22	M+F	0·43	0·88	0·6	—	—	263
12	Trunk length	28–150	M+F	1·81	1·38	0·7	$0·002 > P > 0·001$	—	445
13		14–28	M+F	0·83	1·42	0·3	—	—	617
14		9–14	M+F	−0·83	1·48	0·2	—	—	267
15	Neck girth	65–125	M	63·5	1·18	11·6	—	—	11
16		15–65	M+F	12·9	1·85	3·3	—	—	424
17		8–16	M+F	2·2	2·45	2·1	—	—	623
18		5–9	M+F	2·5	2·04	1·5	—	—	267
19	Mid-body girth	90–170	M	50·5	0·93	9·5	—	—	9
20		23–90	M+F	9·5	1·35	3·1	—	—	422
21		13–23	M+F	1·5	1·66	2·4	—	—	621
22		6–13	M+F	3·3	1·26	1·7	—	—	269
23	Tail butt girth	65–115	M	41·4	1·47	7·7	—	—	11
24		17–65	M+F	7·5	1·90	2·9	—	—	420
25		8–17	M+F	3·7	2·12	2·0	—	—	623
26		5–9	M+F	4·2	1·79	1·3	—	—	267
27	Horny layer width	18–40	M	84·0	3·18	18·3	—	—	11
28		3–18	M+F	6·9	6·49	4·2	—	—	1004
29		0·4–3·0	M+F	11·5	2·48	2·0	—	—	266
30	Foot width	3–15	M+F	−0·1	13·87	11·7	$0·05 > P > 0·02$	—	184
31		0·5–3·5	M+F	10·7	8·42	5·7	—	—	216
32	Hand width	5–18	M+F	−8·2	12·12	11·9	$P < 0·001$	—	184
33		0·6–5	M+F	8·4	6·66	5·1	—	—	225
34	Platform width (HPP)	3·2–17	M+F	1·29	12·58	2·5	—	—	444
35		1·8–3·2	M+F	−6·61	14·54	1·3	—	—	621
36		1·4–1·9	M+F	−11·33	16·28	1·4	—	—	269
37	Platform width (HMP)	9·5–16	M	−4·19	13·85	2·5	—	—	237
38		3·2–9·5	M	−7·73	14·67	1·9	—	—	226
39		3·2–9·5	F	−5·74	14·26	2·0	—	$0·02 > P > 0·01$	197
40		3·2–9·5	M+F	−6·68	14·45	2·0	—	—	423
41		1·6–3·3	M+F	−15·83	17·06	1·3	—	—	887
42	Maximum head width	18–35	M	32·98	5·16	7·2	—	—	11
43		5·2–18	M+F	3·86	6·87	1·9	—	—	420
44		2·9–5·2	M+F	−0·79	7·57	0·8	—	—	614
45		2·0–2·9	M+F	−7·86	9·91	0·6	—	—	268
46	Snout–eye length	7·5–41	M+F	2·89	5·04	2·7	—	—	445
47		3·6–7·5	M+F	3·27	4·87	0·9	$0·02 > P > 0·01$	—	619
48		1·8–3·6	M+F	6·10	3·93	0·5	—	—	268
49	Head total length	13–60	M+F	−4·30	3·60	1·8	—	—	445
50		7–13	M+F	−1·38	3·32	0·8	$0·002 > P > 0·001$	—	617
51		4–7	M+F	1·24	2·87	0·5	—	—	265
52	Interocular width	3·3–5·8	M	19·29	32·27	3·9	—	—	236
53		0·7–3·3	M	16·30	34·92	3·2	—	$0·01 > P > 0·002$	225
54		0·7–3·3	F	17·64	32·93	3·4	—	—	198
55		0·7–3·3	M+F	17·19	33·75	3·4	—	—	423
56		0·4–0·8	M+F	4·02	44·44	2·6	—	—	621
57		0·2–0·7	M+F	13·73	8·50	2·2	—	—	269
58	Ear length	3·0–13	M+F	−8·44	16·82	3·0	—	—	441
59		1·3–3·0	M+F	−9·20	16·83	1·4	—	—	879
60	Log. body weight[A]	1·3–300	M+F	0·6521	0·3035	0·0134	—	—	440
61		150–1300	M+F	0·6074	0·3175	0·0143	—	—	614
62		50–160	M+F	0·4047	0·4045	0·0253	—	—	269

[A] Weight in kilograms for equation 60, in grams for 61 and 62.

Appendix 2. Coefficients for predicting Attribute Measurements from Snout-Vent Length by Linear Regression Analysis

Headings as in Appendix 1. 'SVL ranges' refers to the range of snout–vent lengths applicable to each equation. Predicted values are in centimetres, with body weight in grams.

Eqn No.	To predict	SVL ranges (cm)	Sex	*A*	*B*	*E* (cm)	*N*
63	Total length	127–207	M	1·73	2·04	2·3	231
64		41–126	M	1·24	2·05	2·2	224
65		41–126	F	3·40	2·01	2·6	190
66		41–126	M+F	2·34	2·03	2·4	426
67		13–40	M+F	0·83	2·06	1·1	876
68	Tail length	127–207	M	1·73	1·04	2·3	231
69		41–126	M	1·24	1·05	2·2	226
70		41–126	F	3·40	1·01	2·6	192
71		41–126	M+F	2·34	1·03	2·4	426
72		21–40	M+F	0·60	1·06	1·3	613
73		13–20	M+F	0·80	1·06	0·6	261
74	Trunk length	41–207	M+F	−1·28	0·72	0·5	445
75		21–40	M+F	−0·52	0·70	0·2	620
76		13–20	M+F	0·18	0·67	0·2	267
77	Neck girth	127–207	M	−26·5	0·69	8·8	11
78		41–126	M+F	−5·7	0·52	1·8	434
79		21–40	M+F	0·3	0·37	0·8	623
80		13–20	M+F	2·4	0·28	0·5	268
81	Mid-body girth	127–207	M	−35·0	0·96	9·7	9
82		41–126	M+F	−5·6	0·71	2·3	432
83		21–40	M+F	1·3	0·52	1·3	623
84		13–20	M+F	5·0	0·35	0·9	269
85	Tail butt girth	127–207	M	−18·4	0·62	5·0	11
86		41–126	M+F	−3·0	0·51	1·5	430
87		21–40	M+F	−0·6	0·43	0·9	623
88		13–20	M+F	0·7	0·38	0·6	267

Appendix 3. Coefficients for Predicting Snout–Vent Length from Head Measurements, by Multiple Regression Analysis

'HTL ranges' and 'SVL ranges' indicate the head lengths and corresponding approximate snout–vent lengths for which each equation is applicable. a, regression constants. b_1–b_3, slopes for listed attributes X_1–X_3. E, standard error of estimate. For abbreviations of measurements, see p. 3. For formula, see p. 8.

Eqn No.	HTL ranges (cm)	SVL ranges (cm)	a	b_1 (X_1)	b_2 (X_2)	b_3 (X_3)	E (cm)	N
125	35·4–58·4	120–207	−26·00	10·27 (HTL)	−10·36 (HSE)	3·39 (HPP)	2·7	10
126	12·6–35·4	41–126	−1·44	1·67 (HTL)	3·71 (HPP)	1·77 (HMW)	1·3	426
127	6·7–12·5	21–40	1·20	1·75 (HTL)	3·41 (HMW)	1·40 (HIO)	0·7	610
128	4·0–6·6	13–20	0·48	1·39 (HTL)	2·44 (HPP)	1·86 (HSE)	0·4	260

Appendix 4. Coefficients for Determining the Discriminant Score of a *C. porosus*

'SVL range' indicates the snout–vent length for which the equation is applicable. st., standardized coefficients. unst., unstandardized coefficients. For equations 129 and 130 (head measurements only) attributes must be used in the form of ratios of total head length; for equations 131–135 (all measurements), as whole numbers.

Equation No.	129	130	131	132	133	134	135
SVL range (cm)	100–120	100–207	60–80	80–100	100–120	100–207[A]	100–207[B]
Percentage correct	81·8	87·0	65·1	79·2	100	91·3	100
Significance (P)	0·035	<0·001	0·005	0·004	0·004	<0·001	<0·001
Sample size ($M+F = N$)	$4+7 = 11$	$14+9 = 23$	$50+37 = 87$	$12+12 = 24$	$4+7 = 11$	$14+9 = 23$	$10+8 = 18$
Mean ± standard deviation	−1·05						
Males	−1·05±1·21	0·70±1·19	0·28±0·91	0·90±0·89	−2·41±0·92	−0·86±1·04	1·90±0·94
Females	0·60±0·88	−1·09±0·56	−0·39±1·10	−0·90±1·10	1·54±1·04	1·33±0·93	−2·38±1·07
Classification errors							
M to F (%)	25	21	18	17	0	7	0
F to M (%)	14	0	58	25	0	11	0
Coefficients							
Constant	66·67	−13·67	7·60	−7·14	32·63	5·74	−6·87
SVL (st., unst.)	—	—	−3·0; −0·50	3·1; 0·50	4·5; 0·62	7·7; 0·22	−21·1; −0·66
TL (st., unst.)	—	—	—	1·50; 0·12	—	—	27·6; 0·42
HPP (st., unst.)	−1·3; −236·85	0·3; 25·83	1·6; 3·42	−0·6; −1·22	−5·9; −8·82	−3·5; −1·17	4·8; 1·82
HMP (st., unst.)	0·2; 26·79	−0·6; −62·48	−1·7; −3·86	—	−4·3; −7·21	1·6; 0·58	—
HMW (st., unst.)	0·3; 21·55	1·6; 46·61	1·9; 2·18	−1·7; −1·53	8·1; 5·21	−3·7; −0·57	3·6; 0·63
HSE (st., unst.)	−0·8; −78·74	0·1; 7·63	1·8; 1·48	−1·8; −1·24	7·3; 4·19	12·8; 1·78	12·3; 1·90
HTL (st., unst.)	—	—	−0·6; −0·35	−1·0; −0·51	−12·3; −5·19	−18·3; −1·84	−13·9; −1·53
HIO (st., unst.)	1·3; 366·79	−0·4; −72·24	−0·5; −2·51	0·3; 1·63	1·7; 8·32	2·2; 1·93	−11·9; −12·03

[A] Excluding total length.

[B] Including total length.