Morphometric Analysis of *Crocodylus novaeguineae* from the Fly River Drainage, Papua New Guinea

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Abstract

Formulae for predicting snout–vent length from 17 other body measurements and vice versa were derived from data collected on 1073 wild *Crocodylus novaeguineae*. Equations for predicting live body attributes from dried skulls also are presented. Relative growth and general growth form are described. A 1:1 sex ratio was found for animals between 50 and 167 cm snout–vent length (SVL). Current laws in Papua New Guinea are based on size criteria and protect wild breeding males. However, the laws do not take into account the smaller breeding size of females and thus subject about 36% of adult females to legal hunting mortality. Of all girth-related measures, neck girth was found to be the best predictor of commercial value. New Guinea crocodiles have shorter tails, longer trunks and wider hind feet than saltwater crocodiles, *C. porosus*; these differences may be related to ecological niche and habitat separation in Papua New Guinea. The morphological characteristics of New Guinea crocodiles better adapt them for life in marshes and swamps, while those of *C. porosus* better suit them for life in large, open rivers and estuaries.

Introduction

The external morphology of crocodilians has been studied in detail only in the Australian saltwater crocodile, *Crocodylus porosus* (Webb and Messel 1978*a*). The only work on the morphology of the New Guinea crocodile, *C. novaeguineae*, is composed of measurements from 16 skulls (Schmidt 1932). The present study was largely directed toward deriving equations to predict snout-vent length (SVL) from 17 other attributes and vice versa in *C. novaeguineae* from the Fly River drainage, Papua New Guinea (PNG). The equations allow for an estimate of body size from isolated skulls, heads, tracks, belly slides and portions thereof, and from calibrated photographs of heads. The ability to determine the size and approximate age of crocodiles without catching them is a great advantage to wildlife managers when conducting surveys in which size and age are of interest.

The study sought to determine whether sexual dimorphism was sufficient to enable the sex of *C. novaeguineae* specimens to be ascertained from body measurements alone. Since the sex ratio in wild crocodilians is important for determining productivity (Chabreck 1966), data used for the morphometric study could thus provide this information for *C. novaeguineae*. The morphometric models also allow for a description of relative growth and growth form. Geographic variation in body form was investigated.

The study was also undertaken to answer matters of practical and immediate importance to crocodile management in PNG. It sought to determine whether the law prohibiting the sale of crocodile skins over 50·8 cm (20 in.) belly-width does indeed protect the wild *C. novaeguineae* adult breeding stock (Lawrence 1977). It sought differences in the skin surface area of wild and farmed crocodiles that should be reflected in the skin and live crocodile

pricing system. This study questioned whether belly-width was indeed the best single measure of commercial skin size.

The body size at which mandibular teeth protrude through the premaxilla was compared with that in *C. porosus* (Webb and Messel 1978*a*). A cause for such tooth protrusion in crocodilians is hypothesized. Morphometric models of *C. novaeguineae* were compared to similar models for *C. porosus* from northern Australia (Webb and Messel 1978*a*). The
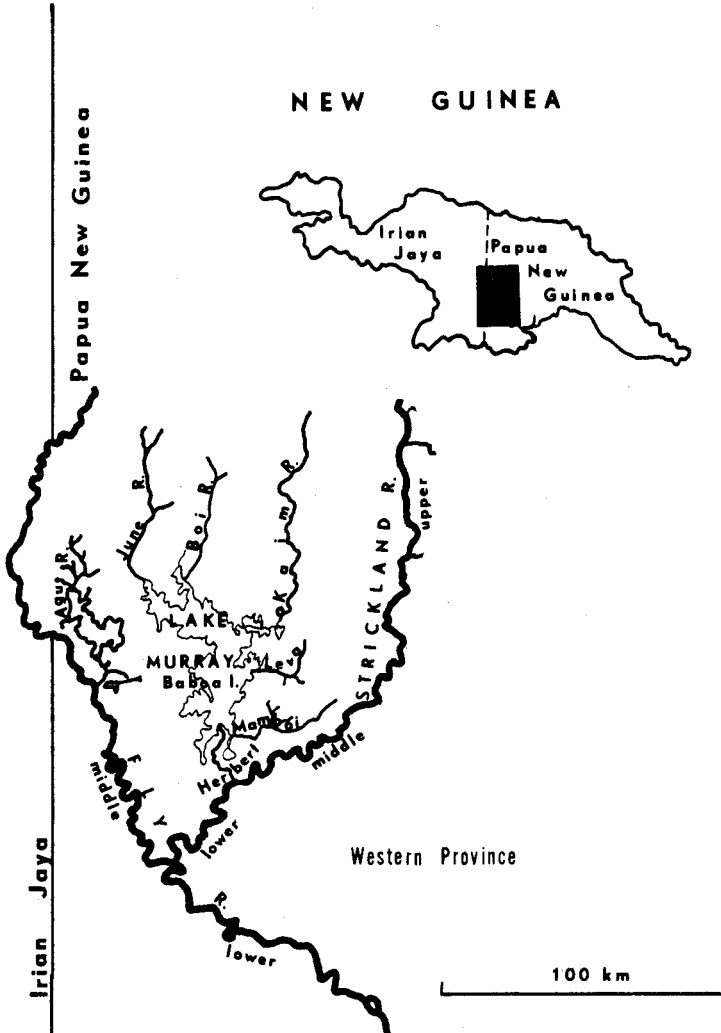

Fig. 1. Waterways of the study area, Western Province, Papua New Guinea.

primary reason for undertaking this comparison was to reveal factors that might clarify the ecological niche and habitat-separation between the two species in PNG hypothesized by Bustard (1968), Lever (1975) and Whitaker (1980).

Study Area and Methods

Most of the crocodiles used in this study were captured by village crocodile hunters from the Kuné, Youngum, Miwa, Zimikani and Zikagu tribes of the Fly River drainage, Western Province, and

purchased as part of a government-sponsored live crocodile buying scheme. From 1978 to 1980, 2695 *C. novaeguineae* were purchased at the Baboa Crocodile Station and later airfreighted to commercial farms (Montague 1981). Some 1642 of these were rejected for use in this study because hunters could not recall the exact location of capture or because more than 48 h had elapsed before the time of measurement. If more than 2 days had passed, the crocodiles may have become starved, which would adversely affect the results. Of the 1073 wild crocodiles used in this study, 54% came from Lake Murray, and the remainder came from eight rivers in the Fly River drainage (Fig. 1; Table 1). A complete description of the study area was presented by Montague (1983).

Table 1. Numbers of wild *C. novaeguineae* measured and examined from each area, and their locations in the Western Province of PNG

Coordinates are for the mouths of rivers unless otherwise stated; A, centre of lake; B, section of river

Area	Location	Description	No. of crocodiles
Lake Murray	141°30′E., 7°S. (A)	Swamp forest	582
Mamboi River	141°2′E., 7°10′S.	Swamp forest	136
Fly River	141°7′E., 7°5′S. to 141°23′E., 7°35′S. (B)	Savannah	91
Strickland River	141°34′E., 7°20′S. to 141°23′E., 7°35′S. (B)	Gallery rainforest	84
Kaim River	141°32′E., 6°54′S.	Savannah, rainforest	60
Leva River	141°36′E., 7°S.	Swamp forest	59
June River	141°21′E., 6°20′S.	Savannah, rainforest	31
Boi River	141°25′E., 6°50′S.	Rainforest	20
Agu River	141°7′E., 7°5′S.	Savannah, swamp forest	10
Total			1073

Thirty of those crocodiles over 100 cm SVL used in this study were adults captured in the wild from Lake Murray, using methods similar to those of Webb and Messel (1977), and shipped to the Moitaka Government Crocodile Farm near Port Moresby. And, in order to evaluate morphometric differences between farmed and wild animals, a sample of 163 farmed *C. novaeguineae* ranging from 40 to 84 cm SVL was taken from the Baboa Station's captive stock.
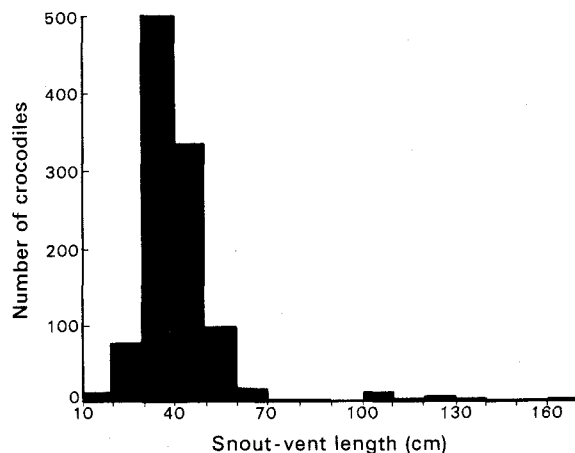
Fig. 2. Size frequency histogram of 1073 wild *C. novaeguineae* from the Fly River drainage, PNG, 1978–80.

Size Distribution

Although similar, the size distribution of New Guinea crocodiles captured for the present study was not identical to that reported for the actual wild crocodile population in the Fly River drainage

(Montague 1983). Hatchlings were not purchased at the beginning of the study, due to a lack of facilities to care for them; hence the small number of animals in the 10–20-cm SVL class (Fig. 2). Crocodiles in the 21–60-cm SVL classes were abundant in the sample, both because they were most common in the wild (Montague 1983) and because they were a convenient size to catch and transport. There were few crocodiles in the 71–100-cm SVL size class in the sample (Fig. 2) because they were too big to easily catch alive and were usually simply killed for their skins. But since crocodiles over 100 cm SVL were mostly over 50·8 cm belly-width and thus illegal to sell as skins, a small number were purchased as breeders.

Sex Identification

Crocodiles were sexed by placing each crocodile on its back, stroking its venter to calm it, and manually feeling for the clitoris or penis (Chabreck 1963). In crocodiles 50–60 cm SVL gentle pressure was applied around the cloaca to expose the genitals. These methods were found to be 100% effective for crocodiles ≥ 50 cm SVL. Sexual dimorphism was investigated only for those animals above 50 cm SVL where sex recognition was certain. In order to determine sex ratios in wild New Guinea crocodiles, 633 wild-caught animals at Baboa Crocodile Station and 1398 wild crocodiles purchased for resale were sexed.
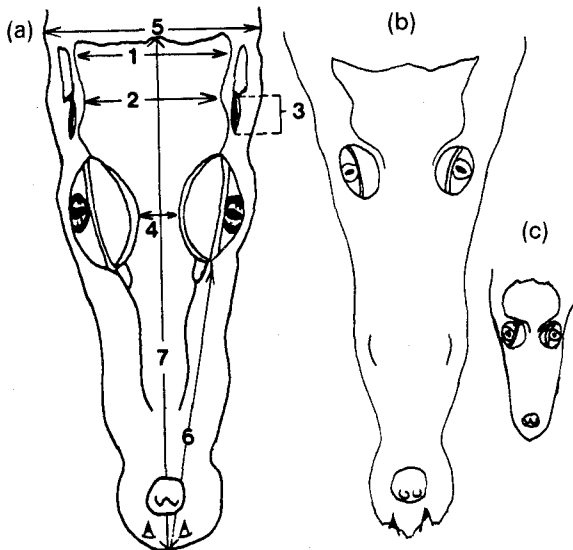

Fig. 3. Head of *C. novaeguineae*, dorsal view. Measurements, in (*a*): *1*, width of cranial platform, HPP; *2*, cranial platform midpoint width, HMP; *3*, ear slit length, EL; *4*, interocular width, HIO; *5*, maximum head width, HMW; *6*, snout–eye length, HSE; *7*, total head length, HTL. Mandibular teeth protrude through holes in the premaxilla (*a*) or through indentations (*b*). The cranial platform is concave in adults (*b*) in contrast to its convex shape in hatchlings (*c*).

Morphometry

Snout–vent length and total lengths of *C. novaeguineae* were measured along the venter with a steel tape. Girth measurements were also taken with a steel tape pulled snug but not tight against the animal. Hand and foot widths, as well as some head and skull measurements from larger animals, were made with a steel rule. Head measurements other than those above were made with vernier calipers. All head morphometrics were taken to the nearest millimetre, and all others to the nearest centimetre. Body weight was determined either with Salter spring scales (500 ± 5 g), clock scales (12 kg ± 50 g, $200 \pm 0·5$ kg) or a platform balance ($500 \pm 0·5$ kg).

The measurements, their description and their abbreviation, modified from Webb and Messel (1978*a*), are listed below in order of convenience of measurement on live crocodiles:

(1) Snout–vent length (SVL); tip of snout to anterior of cloaca.
(2) Total length (TL); tip of snout to tip of tail.
(3) Neck girth (NG); circumference of neck at nuchal rosette.
(4) Belly-width (BW); body circumference at the third most anterior horny dorsal scute minus the width of the horny layer; the measure currently used in PNG when purchasing live crocodiles or skins (Lawrence 1977).
(5) Mid girth (MG); maximum girth of trunk.
(6) Tail girth (TG); maximum girth of tail butt.

(7) Cranial platform, point-to-point width (HPP); straight-line distance between the lateral extremities of the cranial platform (Fig. 3).

(8) Cranial platform midpoint width (HMP); width of cranial platform where it is usually concave (Fig. 3).

(9) Interocular width (HIO); shortest distance between the eyes (Fig. 3).

(10) Ear length (EL); length of ear slit (Fig. 3).

(11) Maximum head width (HMW); distance between the extremities of the surangular bones at the level of jaw articulation (Fig. 3).

(12) Snout–eye length (HSE); tip of snout to anterior edge of orbit (Fig. 3).

(13) Total head length (HTL); tip of snout to median posterior edge of platform (supraoccipital bone) (Fig. 3).

(14) Hand width (HW); maximum span of the forefoot toes when spread but not stretched.

(15) Foot width (FW); maximum span of the three clawed toes on the hind feet when spread but not stretched.

(16) Body weight (BWT).

(17) Trunk length (TRL); snout–vent length minus total head length.

(18) Tail length (TAL); total length minus snout–vent length.

Twenty-one large *C. novaeguineae* skulls used in this study were measured in the same manner as those of live crocodile heads. Fifteen skulls were measured in the villages of the Fly River drainage while I was on live crocodile buying patrols. Three crocodiles were measured alive and later as dried skulls. Others were collected by the staff of the Baboa Crocodile Station from 1970 to 1978. New Guinea freshwater crocodile skulls were differentiated from *C. porosus* skulls by methods described by Schmidt (1928, 1932). All skulls had been dried for over 1 year and lacked all soft tissue.

Morphometric Analysis

The SPSS (Statistical Package for Social Sciences) subprogram REGRESSION (Nie *et al.* 1975) was used to determine the regression equation describing the line of best fit with SVL as the dependent variable (Y) and the other attribute as the independent variable (X). This equation was of the form: $Y = A + BX + E$, where Y and X are as above, and A is the Y-intercept, B is the slope of the line and E is the standard error of the estimate. Equations were also determined with SVL as the independent (predictor) variable and each of the other attributes as the dependent variable (Zar 1974). Due to the extreme allometric (curvilinear) nature of body weight (BWT) (Fig. 4*d*), a logarithmic transformation was used for all equations involving BWT, since these yielded a linear relationship. The SPSS subprogram SCATTERGRAM was used to create plots of points described by regression equations.

Separate regressions were derived for wild males and females, and for three size classes: ≤ 50, 51–99, and ≥ 100 cm SVL. For farmed crocodiles, only the major growth elements of SVL, TL, BW and BWT were considered (see below). Regression analysis of head characters with SVL was undertaken for crocodiles for each of the nine geographic areas, to test local variation.

The size classes were set as above because scattergrams of many morphometric parameters were curvilinear in crocodiles below 50 cm SVL. The 51–99-cm size class included subadults and some adult females, and the ≥ 100 cm SVL class was composed entirely of adults. Slopes and intercepts of the various sample subsets designated above were compared by means of an F-test (Neter and Wasserman 1978). If these varied significantly from the lines generated by the combined data, then the subset regressions were presented; otherwise, only equations derived from combined data were listed (Tables 2, 3).

To investigate morphological differences between the two species, all of the above regression equations were compared to similar equations presented for Australian *C. porosus* by Webb and Messel (1978*a*). Particular attention was paid to those parameters whose Y-intercepts were similar and slopes different, or which had similar Y-intercepts and different slopes, between the two species. The general form of growth was described for individual parameters by inspecting the scattergram for relative changes with increasing body size.

To examine relative growth, morphometric data underwent logarithmic transformation. Allometric equations (Simpson *et al.* 1960) were derived from the transformed data to identify growth fields (morphometrics which grow at the same proportional rate), and also which parameters have a constant growth rate and which do not. The SPSS subprogram FACTOR was employed to run factor analyses on all variables to show which factor has the greatest contribution to variation.

Following Webb and Messel (1978*a*), all wild crocodiles used in the morphometric portion of the study were examined for evidence of mandibular teeth protruding through the premaxilla.
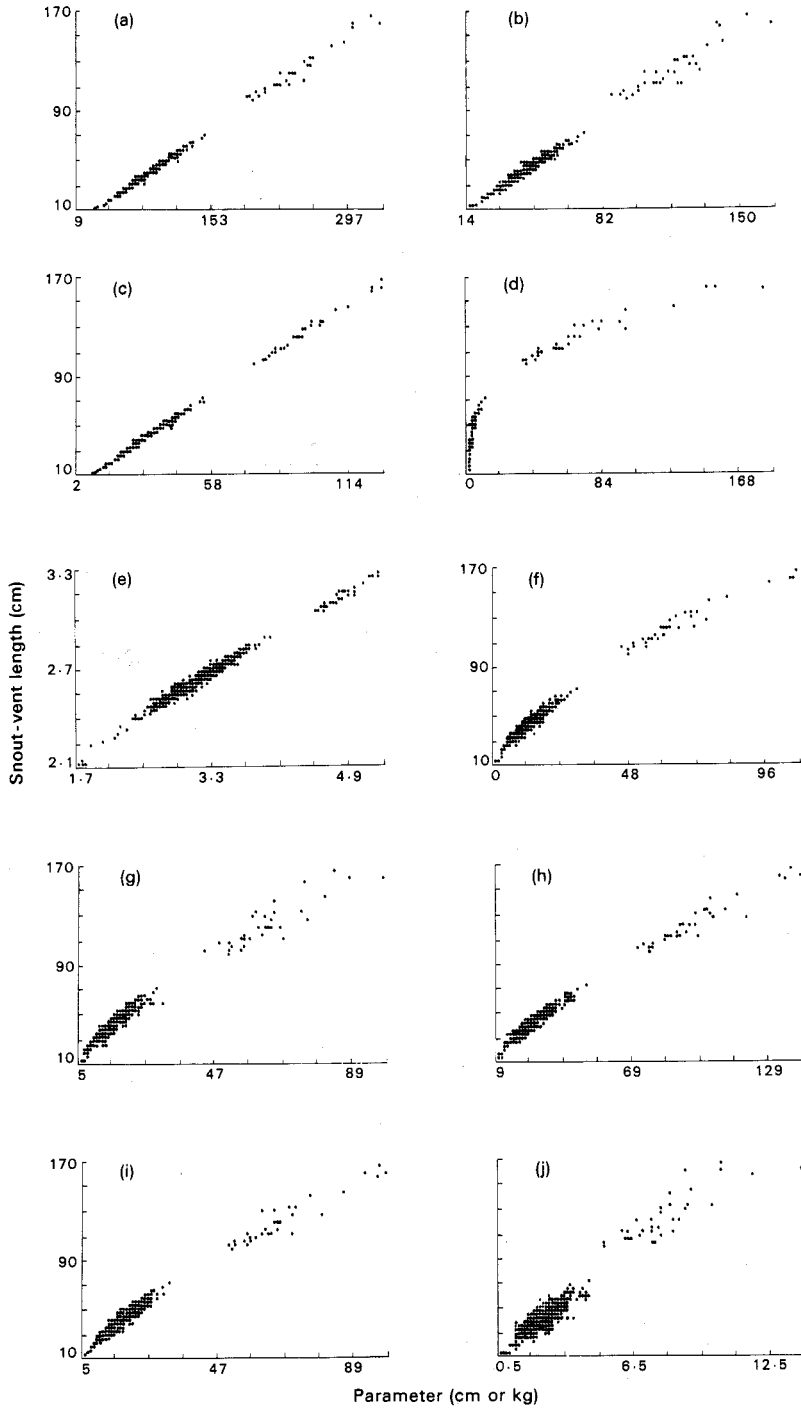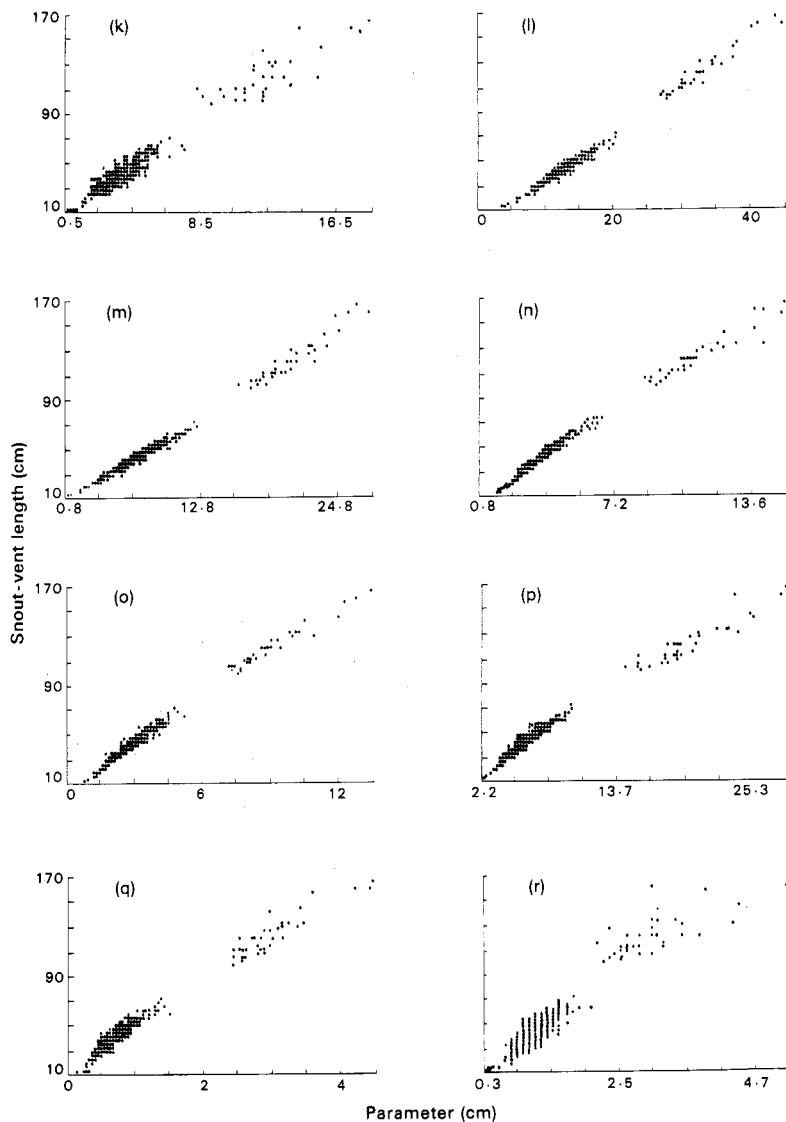
Fig. 4. Scattergrams for predicting snout–vent length (*Y*-axis) from other attributes (*X*-axis) from 1073 wild *C. novaeguineae* of both sexes from the Fly River drainage, 1978–80. Measurements are in centimetres unless otherwise stated: (*a*) total length TL; (*b*) tail length TAL; (*c*) trunk length TRL; (*d*) body weight BWT (kg); (*e*) log body weight in grams (note that the *Y*-axis shows log snout–vent length); (*f*) neck girth NG; (*g*) belly width BW; (*h*) mid girth MG; (*i*) tail girth TG; (*j*) hand width HW; (*k*) foot width FW; (*l*) head length HTL; (*m*) snout–eye length HSE; (*n*) platform width HPP; (*o*) platform midpoint width HMP; (*p*) head width HMW; (*q*) interocular width HIO; (*r*) ear slit length EL. Many crocodiles with nearly the same measurements appear as only one dot.

Table 2. Coefficients for predicting snout–vent length from other parameters in *C. novaeguineae* by linear regression analysis

Analysis is of the form: $Y = A + BX + E$, formulae are for both sexes unless indicated by 'F' or 'M'. A is the Y-intercept; B the slope; E the standard error of the estimate; R^2 the correlation coefficient; N the number of crocodiles. Animals are wild unless noted as farmed.

Eqn No. and predictor X	Range (cm) and sex	A	B	E (cm)	R^2	N
1. Total length (TL)	29–100	−1·46	0·51	0·72	0·988	923
2.	101–335	5·73	0·49	4·15	0·946	150
3. Tail length (TAL)	16–50	−0·13	0·97	2·14	0·893	923
4.	51–168·5	22·31	0·87	8·02	0·809	150
5. Trunk length (TRL)	8–35	2·05	1·36	0·90	0·981	923
6.	36–122	4·90	1·32	1·48	0·993	150
7. Neck girth (NG)	4–19	8·41	2·12	2·45	0·859	923
8.	20–48	33·06	1·72	2·86	0·618	114
9.	49–105	51·69	1·10	4·64	0·935	36
10. Belly-width (BW)	4–17	9·87	2·18	2·79	0·818	923
11.[A]	15·7–40	22·73	1·47	6·62	0·891	163
12.	18–100	40·28	1·32	8·30	0·797	150
13. Mid girth (MG)	6–30	7·58	1·39	2·31	0·875	923
14.	31–145	36·62	0·89	5·45	0·910	150
15. Tail girth (TG)	4–20	7·38	2·02	2·40	0·865	923
16.	21–98	36·12	1·30	5·79	0·891	150
17. Hand width (HW)	0·6–2·9	13·32	11·46	3·76	0·669	923
18.	3–7·5, F	7·04	15·38	6·13	0·940	74
19.	3–13·5, M	10·48	13·96	6·63	0·919	76
20. Foot width (FW)	0·8–4·5	11·00	7·78	3·74	0·672	923
21.	4·6–18	45·04	6·46	10·63	0·657	150
22. Platform width (HPP)	1·5–4·5	−1·07	10·87	3·26	0·956	923
23.	4·6–15·5	7·30	10·26	4·28	0·961	147
24. Platform midpoint (HMP)	1·7–4; 4·1–9·5, F	−5·72	13·69	2·46	0·858	997
25.	4·1–13·6, M	2·25	12·06	2·94	0·984	76
26. Interocular width (HIO)	0·3–1·7	8·48	46·70	2·88	0·806	1037
27.	1·8–4·3	28·91	32·46	7·46	0·831	36
28. Ear length (EL)	0·3–1·2	4·59	33·52	4·13	0·601	923
29.	1·3–5·2	71·61	17·31	13·92	0·411	150
30. Maximum head width (HMW)	2–13	1·34	7·07	1·93	0·913	1037
31.	13·1–29·0	39·91	4·20	10·64	0·656	36
32. Snout-eye length (HSE)	1·7–19	4·81	4·78	2·55	0·929	1037
33.	19·1–28	−6·99	5·91	5·71	0·901	36
34. Total head length (HTL)	4–29·2	3·84	2·98	2·55	0·848	1037
35.	29·3–45·0	−4·54	3·85	4·38	0·942	36
36. Log body weight (LBWT)[B]	53–21000	1·659	0·3077	0·018	0·953	1037
37.[A]	1200–20700	1·760	0·272	0·062	0·987	163
38.	22000–186000	1·683	0·2920	0·013	0·951	36

[A]Farmed.   [B]Body weight in grams, snout–vent length in millimetres.

Results

Morphology

(i) Predicting SVL from body dimensions

Scattergrams of SVL plotted against TL, TAL, TRL, HW, FW, HTL, HSE, HPP, HMP and EL showed linear relationships for these parameters throughout all but the very smallest size classes (Figs 4a–4c, 4j–4p, 4r). All girth (Figs 4f–4i), HMW, and HIO (Figs 4p, 4q) scattergrams showed slight allometry (curvilinearity) in animals of less than 50 cm SVL, but except for BW (Fig. 4g), they were reasonably well modelled by a linear relationship in the larger size classes. Belly-width (BW) and body weight (BWT) were curvilinear throughout the size range (Fig. 4d).

Webb and Messel (1978*a*) found that logarithmic transformation did not significantly improve the linearity of any morphometric parameter except body weight. Since their parameters were nearly identical to those here, only body weight underwent logarithmic

Table 3. Coefficients for predicting body measurements from snout–vent length in *C. novaeguineae* by linear regression analysis

Conventions, and location of the study, as in Table 2

Eqn No. and predictor X	Range SVL (cm) and sex	A	B	E	R^2	N
39. Total length (TL)	13–50	3·75	1·93	1·40	0·988	923
40.	100–167	1·54	1·93	8·25	0·947	150
41. Tail length (TAL)	13–50	4·29	0·919	2·08	0·893	923
42.	51–167	1·60	0·934	8·25	0·809	150
43. Trunk length (TRL)	13–50	−0·98	0·722	0·66	0·981	923
44.	51–167	−3·22	0·757	0·85	0·994	150
45. Neck girth (NG)	13–50	−1·45	0·405	1·07	0·860	923
46.	51–99	−11·30	0·596	2·17	0·618	114
47.	100–167	−39·45	0·846	4·07	0·935	36
48. Belly width (BW)	13–50	−1·37	0·376	1·16	0·818	923
49.	51–99	−9·63	0·540	2·32	0·537	114
50.[A]	40–84	−10·64	0·595	5·24	0·898	163
51.	100–167	−10·87	0·598	5·58	0·791	36
52. Mid girth (MG)	13–50	−2·05	0·631	1·56	0·875	923
53.	51–99	−11·73	0·816	3·38	0·554	114
54.	100–167	−28·44	1·017	5·82	0·910	36
55. Tail girth (TG)	13–50	−1·13	0·429	1·11	0·866	923
56.	51–99	−7·22	0·540	2·08	0·590	114
57.	100–167	−18·19	0·694	4·24	0·898	36
58. Hand width (HW)	13–50	−0·07	0·058	2·69	0·669	923
59.	51–127, F	−0·47	0·065	0·37	0·934	74
60.	51–167, M	−0·75	0·072	0·96	0·919	76
61. Foot width (FW)	13–50	0·19	0·086	0·39	0·672	923
62.	51–99	−0·53	0·096	0·42	0·523	114
63.	100–167	−0·39	0·102	1·33	0·657	36
64. Platform width (HPP)	13–50	0·11	0·092	0·72	0·956	923
65.	51–167	−0·68	0·097	0·64	0·961	150
66. Platform midpoint (HMP)	13–50	0·81	0·063	0·17	0·838	923
67.	51–127, F	0·34	0·073	0·21	0·988	74
68.	51–167, M	−0·16	0·083	0·20	0·981	76
69. Maximum head width (HMW)	13–50	0·28	0·129	0·26	0·913	923
70.	51–99	−0·66	0·149	0·57	0·594	114
71.	100–167	0·65	0·156	2·05	0·656	36
72. Snout-eye length (HSE)	13–99	−0·44	0·194	0·35	0·929	1037
73.	100–167	3·25	0·152	0·92	0·901	36
74. Total head length (HTL)	13–99	0·64	0·286	0·79	0·848	1073
75.	100–167	3·06	0·245	1·11	0·942	36
76. Interocular width (HIO)	13–50	−0·03	0·017	0·06	0·806	923
77.	51–99	−0·60	0·029	0·14	0·445	114
78.	100–167	−0·25	0·025	0·21	0·830	36
79. Eat slit length (EL)	13–50	0·31	0·018	0·10	0·602	923
80.	51–167	0·08	0·024	0·52	0·362	150
81. Log body weight (LBWT)[B]	130–500	−4·900	3·097	0·056	0·953	923
82.[A]	400–840	−6·188	3·574	0·063	0·987	163
83.	501–1670	−5·240	3·255	0·068	0·951	150

[A] Farmed.   [B] Body weight in grams, snout–vent length in millimetres.

transformation for the prediction portion of this analysis (Fig. 4*e*). Logarithmic transformations were performed on all morphometrics for the relative growth analysis (see p. 404).

On the basis of correlation coefficients and standard errors (Tables 2, 3), it seemed possible to predict SVL from a number of body measurements. For instance, a wild crocodile with a belly-width (X) of 20 cm can be calculated from Table 2 and the equation given on p. 399 to possess a SVL (Y) of: $+40\cdot28+1\cdot32\,(20)\pm8\cdot3$, i.e. $66\cdot7\pm8\cdot3$ cm.

The best estimators of SVL, which were not composed primarily of SVL, were HSE, HPP and HMP ($r^2=0\cdot97$). Not surprisingly, the best predictors of SVL were TL (i.e. SVL + TAL) and TRL (i.e. SVL − HTL), which were largely composed of SVL. As a predictor of SVL, tail length (TAL) was confounded by the occurrence of tail tip amputations, often not readily discernible in the field. Girth measurements ($r^2=0\cdot92$–$0\cdot95$) and commercial belly width (BW) ($r^2=0\cdot91$) (essentially a girth measure) were reasonably highly correlated with SVL, but hand (HW) and foot width (FW) were less correlated ($r^2=0\cdot90$). Variation in the latter measurements were partly due to difficulties in standardizing the measurement in the field, and does not necessarily imply variation within the population. The worst predictor of SVL was ear slit length (EL) with a correlation coefficient, with all data pooled, of $0\cdot89$.

(ii) *Predicting body dimensions from SVL*

To predict body dimensions from SVL, another set of linear regression equations was determined with SVL as the independent variable (Table 3). When Table 3 is used to predict a body dimension from a SVL that was derived from Table 2, the standard error of the estimate is determined 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 (Webb and Messel 1978a).

Table 4. **Coefficients for predicting live (fresh) head length (HTL) from other head attributes in *C. novaeguineae* skulls by linear regression analysis**

Conventions and locality of study as in Table 2

Eqn No. and predictor X	Range (cm)	A	B	E (cm)	R^2	N
84. Snout–eye length (HSE)	14–31	0·68	1·48	1·0	0·988	21
85. Platform midpoint (HMP)	6–13·5	3·08	3·45	1·1	0·945	20
86. Platform width (HPP)	6·4–17·5	9·55	2·40	1·2	0·937	20
87. Maximum head width (HMW)	11–28·5	11·35	1·25	1·2	0·936	19
88. Interocular width (HIO)	1·9–4·8	9·65	8·34	1·4	0·915	21

(iii) *Predicting live body attributes from a skull*

This study (Appendix 1) and that of Webb and Messel (1978a) both found that head length (HTL) is reduced by about 4% from live to skull measure, due to tissue loss. In order to increase the sample size for linear regression analysis, other HTLs based on cleaned skulls alone (Appendix 1) were expanded by 4%.

The best predictors of live HTL from cleaned skulls were HSE and HMP with standard errors of 1·0 and 1·1 cm, respectively (Table 4). Interocular width (HIO), with an error of 1·4 cm, was the least suitable predictor of live head length. It must be remembered that if an HTL derived from an equation in Table 4 is used in an equation from Table 2 to predict SVL, then the resulting standard error of the estimate is calculated as in the last section. If this SVL is in turn used in an equation from Table 3 to predict other body attributes, then the resulting standard error of the estimate (E_4) is calculated by: $E_4=\sqrt{[(b_2b_3E_1)^2+(b_3E_2)^2+E_3^2]}$. Variables are as previously defined. The general error equation is:
$E_n=\sqrt{[(E_{n-1})^2+(E_{n-2}b_{n-1})^2+(E_{n-3}b_{n-1}b_{n-2})^2+(E_{n-4}b_{n-1}b_{n-2}b_{n-3})^2+\ldots\;n-1=0]}$.

Sexual Dimorphism, Sex Ratio, and Geographic Variation

Other than the maximum adult size of males (Table 5), the only measurements in which

males and females seemed to differ were hand width and platform mid-point width. Male hands were about 6% wider than females' (Table 2, equations 18 and 19; Table 3, equations 59 and 60). But regression equations for these two parameters were not significantly different (*F*-test, $P > 0.10$) between sexes.

A male:female sex ratio of 51·3% males and 48·7% females, or approximately 1:1 (*Z*-test, > 0.10) was found for 2031 wild *C. novaeguineae* (50–167 cm SVL) examined from the Fly River drainage.

Regression slopes, and intercepts (SVL as the dependent variable and other head attributes as the independent variable) from the nine geographic locations (Table 1) were not significantly different from each other (*F*-tests, $P > 0.05$). Geographic variation in external body structural dimensions evidently does not occur among *C. novaeguineae* within the Fly River drainage in PNG.

Table 5. Morphometric ranges in centimetres and kilograms, for 1073 wild *C. novaeguineae*

Parameter	Minimum (hatchling)	Maximum	
		Female	Male
Snout–vent length (SVL)	13·0	127·0	167·0
Total length (TL)	28·0	257·0	335·0
Neck girth (NG)	5·5	75·0	105·0
Belly-width (BW)	5·2	76·0	100·0
Mid girth (MG)	9·2	120·0	145·0
Tail girth (TG)	5·2	80·0	98·0
Cranial platform width (HPP)	1·55	12·0	15·5
Cranial platform midpoint width (HMP)	1·68	9·52	13·6
Interocular width (HIO)	0·28	2·90	4·3
Ear length (EL)	0·30	3·00	5·20
Maximum head width (HMW)	2·15	20·00	28·00
Snout–eye length (HSE)	1·75	22·50	28·95
Total head length (HTL)	4·00	36·00	45·00
Hand width (HW)	0·60	7·50	13·50
Foot width (FW)	0·80	11·50	18·00
Body weight (BWT)	0·053	96·00	186·00
Trunk length (TRL)	8·70	91·00	122·2
Tail length (TAL)	14·10	130·00	168·5

Relative Growth and Growth Form

In order to better explain relative growth, the change of body proportions as organisms grow (Dodson 1975), Bartlett's best-fit allometric models were constructed from logarithmic transformed data (Simpson *et al.* 1960) (Table 6). Only three parameters, platform point-to-point width (HPP), snout–eye length (HSE) and trunk length (TRL), were truly isometric (slopes = 1·0) (Table 6), changing in direct proportion to body size. Hand and foot width were very near isometry, and total length (TL), which significantly differed from 1·0 ($0.02 > P > 0.01$), showed slight positive allometry (slope > 1.0), increasing growth rate with increasing size. Positive allometry was pronounced in HMP, HTL, EL and tail length (TAL). Strong negative allometry (slope < 1.0) ($P < 0.01$), indicating a decreasing growth rate with increasing SVL, was shown by all girth measurements, belly-width, interocular width (HIO) and maximum head width (HMW).

Comparison of the 95% confidence intervals (Lapin 1975) showed that all girth dimension, belly-width and HIO had allometric coefficients that were not significantly different from each other (Table 6). These body parts changed at the same rate. Likewise, spread digit width and HMW changed at the same rate. Other morphometrics that changed at the same rate were: HSE and TRL; TL and HPP; HMP and EL; and HW, FW and TRL. Tail length

was related only to HTL, and then only in the wider 98% confidence band. Spread digit width and TRL were the only body dimensions that were related to two growth fields.

Cranial platforms in hatchlings (Table 5) have convex sides, but they become steadily concave with age (size) (Fig. 3). The HPP:HMP ratio therefore changes from <1 to >1, shifting at 28–32 cm SVL. The growth rate of interocular width (HIO) decreased markedly in relation to increasing SVL to about 28 cm SVL. But in larger animals, HIO growth decreases at a steadily slower rate. All girth growth rates decreased quite rapidly up to about 40 cm SVL and, like HIO, decreased more slowly as crocodiles grew beyond this size. Weight had the slowest proportional change in relation to increasing SVLs of all parameters up to about 55 cm SVL. Above that size, weight increased at a steadily increasing rate (allometric slope $>3 \cdot 0$, Table 3), until in the largest size class tiny changes in SVL represented gross increases in body weight (Fig. 4d). For instance, a 25% increase in the length of a 100-cm-SVL crocodile would result in a weight increase of well over 100%.

Table 6. **Allometric coefficients (after logarithmic transformations) for predicting snout–vent length from other attributes of *C. novaeguineae***

$N = 1073$. Groupings indicate that allometric coefficients (B) were not significantly different from each other at $P = 0.05$ ($P = 0.02$ for TAL and HTL). Significance column designates if B is significantly different from 1.0 at $P = 0.05$ (*), $P = 0.02$ (**) and $P = 0.01$ (***). Other conventions as in Table 2

Equation number and predictor (log X)	A	B	Signif- icance	R^2
89. Belly-width (BW)	0·676	0·800	***	0·989
90. Neck girth (NG)	0·645	0·804	***	0·991
91. Tail girth (TG)	0·594	0·826	***	0·996
92. Mid girth (MG)	0·438	0·840	***	0·989
93. Interocular width (HIO)	1·719	0·850	***	0·987
94. Maximum head width (HMW)	0·912	0·910	***	0·994
95. Hand width (HW)	1·287	0·924	*	0·981
96. Foot width (FW)	1·080	0·943	*	0·989
97. Trunk length (TRL)	0·233	0·947	NS	0·998
98. Snout–eye length (HSE)	0·786	0·963	NS	0·995
99. Platform width (HPP)	1·021	1·023	NS	0·993
100. Total length (TL)	−0·380	1·038	**	0·999
101. Tail length (TAL)	−0·139	1·079	***	0·997
102. Total head length (HTL)	0·429	1·087	***	0·999
103. Ear slit length (EL)	1·570	1·116	***	0·991
104. Platform midpoint (HMP)	0·980	1·149	***	0·991

Differences between Wild and Farmed Crocodiles

The regression equations relating SVL to TL in 163 farmed *C. novaeguineae* were not significantly different from those for wild crocodiles. But those relating SVL to belly-width (BW) (Table 2, equations 11 and 12; Table 3, equations 49 and 50) showed that farmed crocodiles had greater girth than wild crocodiles of the same SVL (*F*-test; $P < 0.001$). A wild crocodile of 20·4 cm (8 in.) BW would have a SVL 1·5 cm (5·7%) longer than a farmed one of equal BW. For a wild crocodile of 40·6-cm (16-in.) BW, the proposed maximum legal skin size (see below), this differential had increased to 16 cm (19·6%) in SVL.

Differences between wild and farmed crocodiles were not as great when the relationships of SVL to BWT were compared (Table 2, equations 37 and 38; Table 3, equations 82 and 83) but were still significant (*F*-test; $P < 0.01$). Both farmed and wild crocodiles of 50 cm SVL

weighed about the same, but at 84 cm SVL farmed crocodiles were about 12·5% heavier than wild ones. This differential is probably even greater in larger, overfed crocodiles, but no data were collected from them.

Mandibular Tooth Protrusion through the Premaxilla

The smallest *C. novaeguineae* exhibiting mandibular tooth protrusion was a female, 28 cm SVL, with one tooth visible through the premaxilla. Only 3·9% of the 77 crocodiles examined in the 21–30-cm SVL class had protruding mandibular teeth. All were female and all had only one visible tooth. As SVL increased, the percentage of crocodiles with teeth which pierced the upper jaw increased, as did the proportion with two teeth protruding. Of the animals with protruding mandibular teeth, single tooth protrusion predominated in all size classes below 41 cm SVL, but in the 41–50-cm SVL class (Table 7) both mandibular teeth (54·3%) tended to protrude. All of the crocodiles examined between 71 and 100 cm SVL had protruding mandibular teeth (Table 7), and all over 71 cm SVL with protruding teeth had both teeth protruding.

Table 7. Numbers of wild New Guinea crocodiles with one or two mandibular teeth protruding through the premaxilla

Size range (cm SVL)	M	F	Number of crocodiles Unknown	Total	With protruding teeth (%)	Of those with protruding teeth With one protruding (%)	With two protruding (%)
13–20	1	—	10	11	—	—	—
21–30	27	36	14	77	3·9	100·0	0·0
31–40	197	215	86	498	18·1	70·0	30·0
41–50	167	148	23	338	58·9	45·7	54·3
51–60	49	44	3	96	78·1	16·0	84·0
61–70	12	3	—	15	93·3	28·6	71·4
71–80	1	1	—	2	100·0	0·0	100·0
81–90	1	—	—	1	100·0	0·0	100·0
91–100	—	—	—	—	—	—	—
101–110	—	11	—	11	9·1	—	100·0
111–167	10	14	—	24	33·3	—	100·0
Total	438	472	136	1073			

Three of the nine *C. novaeguineae* over 100 cm SVL with protruding mandibular teeth had indentations in the premaxilla rather than holes for the protruding teeth (Fig. 3). Of the crocodiles over 100 cm SVL, 74% had tissue formed over sites where teeth presumably once protruded through the premaxilla. This tissue either left a filled depression or closed the gap so completely as to be unnoticeable.

Mandibular tooth protrusion was more common in females than males in the 21–70-cm SVL classes, but the difference was statistically significant (Z-test; $P<0.05$) only in the 41–50-cm SVL class. Above 70 cm SVL there was no difference in the proportion of males and females with protruding mandibular teeth.

Discussion

Sexual Dimorphism and Ratios

Kramer and Medem (1955) found that no *Caiman crocodilus* body proportion could be used as a sex discriminator except maximum size, as did this study of *C. novaeguineae*. Dodson (1975) found that *Alligator* lack strong secondary sex characters. Webb and Messel (1978a) found it difficult to determine sex from external morphology in Australian *C. porosus* under 100 cm SVL. Although the sample of *C. novaeguineae* over 100 cm SVL was small

(10 males and 26 females), no sex differences in body proportion, other than maximum size, were apparent.

A 1:1 sex ratio, as found for *C. novaeguineae*, has also been reported for *C. porosus* (Banks 1930; Webb and Messel 1978*b*) and *Caiman crocodilus* (Staton and Dixon 1977). Studies of *A. mississippiensis*, however, have shown a preponderance of males that ranged from 60·8% (Chabreck 1966) to 70·4% (Palmisano *et al.* 1973). Webb *et al.* (unpublished) found 33·0% males in a population of *C. johnstoni*. Ferguson and Joanen (1982) have demonstrated unequivocally that in *A. mississippiensis* sex is determined by incubation temperature and is fixed by the time the eggs hatch. Incubation temperatures of 34°C or above created male hatchlings, whereas those of 30°C or below resulted in female hatchlings. Further, it is highly likely that all crocodilians have their sex determined by incubation temperatures. Therefore, sex ratios other than 1:1 probably result from use of nesting materials and or seasonal temperature fluctuations that consistently result in relatively higher or lower incubation temperatures.

Relative Growth and Growth Form

Principal component analysis of raw data for *Alligator* skeletons (Dodson 1975) indicated that 95·2% of the variation in body form resulted from size alone. A nearly identical variation in raw data (95·6%) was found for the present sample of *C. novaeguineae* morphometrics. Size masks all other variation factors in crocodilians when measurements are taken from animals representing a large size range such as from hatchlings to adults.

Confidence bands were necessary to verify true isometry (linearity, logarithmic slopes = 1·0) and, to a lesser degree, statistical likeness between allometric coefficients (slopes). Body dimensions in similar growth fields (morphometrics with equal logarithmic slopes) were more distinct than the relation of morphometrics to isometry.

It is interesting to note that most *C. novaeguineae* skull morphometrics were either isometric or positively allometric (slope > 1·0). Negative skull allometry (slope < 1·0), due to large brain size at birth, is characteristic of most other vertebrates (Rensch 1960). So, although *C. novaeguineae* also have large brains as hatchlings, their skulls still grow relatively faster than their body in general. This would support Dodson (1975) in his theory that a food-gathering function may be the predominant design factor influencing the relative growth of crocodilian skulls. In short, the skull is rapidly strengthened to handle larger prey. Prey sizes tend to increase with body and head size in other crocodilians (McIlhenny 1935; Cott 1961; Graham 1968; Taylor 1979).

Slight positive allometry of total length results from its components: isometric trunk length and positively allometric skull and tail length. All girth measurements show negative allometry and counteract the extreme positively allometric character of weight (slope > 3·0, Table 3, equations 81–83), so that large weight increases in adults reflect small changes in girth. Interocular width may simply be a component of a larger head girth measurement (not used in this study) since HIO seems to increase in the same growth field as girth parameters do. It may be of interest to note that HIO was one of the only measures which could be used to discriminate male from female *C. porosus* (Webb and Messel 1978*a*).

The close relation between hand and foot width, and these two with head width and trunk length, indicate that the hands and feet become larger in direct proportion to increasing body length and width, probably in order to support the body. That cranial platform midpoint width and ear slit length increase in the same growth field may convey an auditory function as the primary factor in their design. Similarly, that tail length and head length grow at the same rate could represent a counterbalancing function between the two.

The convex shape of the cranial platform in hatchling New Guinea crocodiles (Fig. 3), has also been noted in hatchling *A. mississippiensis* (Dodson 1975) and *C. porosus* (Webb and Messel 1978*a*). This characteristic convex shape of cranial platforms in young *C. novae-*

guineae could partially result from the fact that, as in *Alligator*, skulls grow at a greater rate than body length in general (Dodson 1975). Thus, crocodilian skulls that seem dwarfed at hatching can grow to adequate size by adulthood. But, more likely, the concave cranial platforms in larger animals have a functional significance (e.g. presenting a wider platform to the sun) not needed in the embryos, where the cranial platform is only used as protection for the brain. In *C. porosus* a HPP:HMP ratio of 1·0 was found in specimens up to 70 cm SVL, but the largest *C. novaeguineae* with a similar ratio was only 34 cm SVL. This difference in the maximum size of occurrence could result from the fact that, since *C. porosus* may grow to be nearly twice as long as *C. novaeguineae* (Montague 1984), the HPP:HMP ratio equals 1·0 at about the same fraction of the species' maximum size in both forms.

Implications of the 50·8-cm (20-in.) Belly-Width Law

A wild *C. novaeguineae* of either sex with a belly-width (BW) of 50·8 cm (20 in.) would, by equation 12 (Table 2), have an SVL of 106 ± 8·3 cm, or a total length, by equation 40 (Table 3), of 205 ± 19·7 cm. Females of this species begin to lay eggs at a total length (TL) of about 180 cm (Neill 1946; Jelden 1981; Callis, personal communication; author's observations), with an estimated belly-width (equations 2, 51) of 41 ± 3·3 cm (about 16 in.). This is a figure far below the 50·8 cm BW (Lawrence 1977) or 205 cm TL currently set as the minimum size limit in an effort to protect breeders. Most captive males begin breeding at about 200 cm TL (Whitaker 1979; Bolton 1981; Callis, personal communication), when given the opportunity in the absence of larger males (Lang 1980). This is a TL figure not far below the maximum legal skin size. Therefore, the current PNG law protecting breeders is effective for most wild breeding males but exposes young breeding females to legal hunting for 4–6 years before they grow to the illegal skin size of 50·8 cm BW (Montague 1982). Montague (1983) has shown that approximately 36% of the crocodiles of ≥ 41 cm (16 in.) BW in the Fly River drainage were less than 50·8 cm (20 in.) belly-width. Given the sex ratio of 1:1 presented above, then 36% of wild breeding New Guinea crocodile females can be legally killed for their skins.

Although this law is acceptable as it stands because it does protect most wild breeding males and 64% of breeding females, it seems that proper management should favour crocodile production and not the skin trade. A 41 cm (16 in.) BW maximum legal skin size would eliminate the incentive for killing any breeding crocodile and would be nearer the optimum harvest size of about 30·5 cm (12 in.) BW (Montague 1982).

Differences Between Wild and Farmed Crocodiles

Farmed crocodiles have long been considered to be relatively heavier and more stocky than their wild counterparts (Coulson *et al.* 1973; Blake 1974), and the present study confirms this difference for *C. novaeguineae*. Since a wild New Guinea freshwater crocodile is accordingly longer than a farmed one of the same belly-width, and since inches of belly-width (BW) is used in PNG to determine purchase price, farmed crocodiles of a given length are worth more than wild ones.

Best Commercial Skin Measure

Any true calculation of a crocodile's surface or commercial skin area should include both a length and girth measurement. Using only one of the two will often shortchange the crocodile skin buyer or seller, because of individual variation in the relation of the paired measures. But since a single measurement, belly-width (Lawrence 1977), has long been the convention for crocodile trade in PNG, and is simpler for villagers to use, it may well remain.

Belly-width has the largest standard error of the four girth measures, when used to predict SVL (Tables 2, 3). It therefore showed the greatest variation between individuals of equal SVL. Neck girth (NG), on the other hand, with a standard error nearly half that of the belly-width

equation (Tables 2, 3), showed the least variability of the girth paramaters. Belly-width and mid-girth measurements depend heavily on the amount of air in the crocodile's lungs and consequently result in disproportionate calculations. Tail butt girth is directly dependent on fat deposition and is not necessarily representative of girth over all parts of the animal. Since SVL cannot be measured on skins alone, neck girth may well be advocated to replace belly-width as the standard crocodile trade measurement.

Protrusion of Mandibular Teeth

Since the smallest *C. novaeguineae* with mandibular teeth protruding through the premaxilla were female, and since this phenomenon was predominant in females up to 70 cm SVL, it seems that teeth protrude at smaller sizes in females than males. This difference probably reflects the fact that females reach sexual maturity and maximum size at a shorter length than males. Sexual differences in mandibular tooth protrusion were not significant in Australian *C. porosus* (Webb and Messel 1978*a*).

There was no evidence of any behavioural or ecological significance for protrusion of mandibular teeth through the premaxilla in juveniles, or for the absence of this phenomenon in some large adults (Table 7; Fig. 3). It seems probable that teeth grow proportionately faster than bone in young *C. novaeguineae* and push through the slowly growing premaxilla (Edwards, personal communication). As crocodiles grow past 100 cm SVL, tooth growth may slow as the skull becomes thicker and wider. Eventually the thickness of the premaxilla exceeds the, now stabilized, mandibular tooth length and the premaxilla is pushed forward by increasing head length. In some very large animals the orifice in the premaxilla is replaced by bone. All this may be an adaptation to handle the stress of taking increasingly large prey, as suggested for *C. porosus* (Webb and Messel 1978*a*).

Differences Between C. novaeguineae *and* C. porosus

Linear regression equations (Tables 2, 3) for *C. novaeguineae* were compared to equations describing identical parameters at similar size intervals in Australian *C. porosus* (Webb and Messel 1978*a*). Equation components for the two species were compared and placed in categories: (1) similar *Y*-intercept and similar slope; (2) similar *Y*-intercept but different slope; (3) different *Y*-intercept but similar slope; or (4) different *Y*-intercept and different slope.

For *C. novaeguineae*, the morphometric regression equations were similar in both slope and intercept to those reported for *C. porosus* except for total length (TL), tail length (TAL), trunk length (TRL) and foot width (FW). TL and TAL had similar intercepts but different slopes. At about 23 cm SVL, TAL was about the same between the two species, but as SVL increased *C. porosus* had a proportionately longer tail. At 167 cm SVL, the maximum size of *C. novae-guineae* (Table 5), *C. porosus* TALs were about 12% longer. As expected, total length in relation to SVL also began to increase more quickly in *C. porosus* over 23 cm SVL, and at 167 cm SVL it was about 5·5% longer than in *C. novaeguineae*.

Since TAL was roughly half of TL in both species, and the 5·5% increases in *C. porosus* TL was almost half the 12% increase in *C. porosus* TAL alone, then most of the TL difference between the two species was accounted for by the longer tail of the saltwater crocodile. The remainder of the difference in TL between the two was explained by the shorter trunk of *C. porosus*.

Trunk length in the two species showed both a different *Y*-intercept and a different slope. The point at which morphological divergence between the two species began was also at 23 cm SVL for TRL. At that size, *C. novaeguineae* TRL began to be proportionately longer than that of *C. porosus*, and at 167 cm SVL it was 4% longer.

Foot width, the only other parameter on which the two species differed, also showed different *Y*-intercepts and slopes. Foot widths were similar between the two species up to

about 60 cm SVL but larger *C. novaeguineae* had a significantly wider foot (54% wider at 167 cm SVL) than did *C. porosus*. None of the linear regression comparisons had different intercepts and similar slopes, which suggests that the proportions at hatching are similar.

Comparisons of the scattergrams relating to body dimensions and SVL between the two species showed that all of the parameters except EL had similar variability. Possibly because of measuring difficulties, ear slit length (EL) had the greatest variation of all parameters in New Guinea crocodiles, whereas ear flap length (a similar but not identical measurement) was closely correlated with SVL in saltwater crocodiles.

Scattergrams for *C. porosus* showed slight negative allometry (curvature) for the hands and feet of animals > 130 cm SVL, whereas in *C. novaeguineae* there was slight positive allometry for foot width above 100 cm SVL. Hand width in this latter species was linear throughout the larger size classes of both sexes.

Habitat and Niche Separation

Wermuth (1964) suggested that relative tail length was indicative of crocodiles' mobility and swimming efficiency. A TAL:SVL ratio of > 1 was found in the larger *C. porosus* and may give this species greater propulsive force than the TAL:SVL ratio of < 1 in larger *C. novaeguineae* (Edwards, personal communication). Thus, *C. porosus* and *C. novaeguineae* under 24 cm SVL have equivalent propulsive abilities. As they become larger, however, the proportionally longer tails of the former might indicate advantage. At sizes above 60 cm SVL trunk growth begins to slow in *C. porosus*, but not in New Guinea crocodiles, and this difference may become particularly pronounced. This proposed difference in swimming efficiency could have an effect on feeding patterns and perhaps also on habitat preference in the two species. It is at about this same size (70 cm SVL) that Australian *C. porosus* begin to undergo some basic behavioural changes in life style, including dispersal (Webb and Messel 1978b), a change in growth rate (Webb *et al.* 1978) and an increase in the proportion of larger vertebrate prey (Taylor 1979).

Although little is known of the food habits of *C. novaeguineae*, food and habitat requirements are probably similar in the young of the two species. Large *C. porosus*, however, probably seek and catch larger prey. Very large *C. porosus*, which can be six times heavier and twice as long as *C. novaeguineae* (Montague 1984), are certainly capable of overpowering larger prey than the latter species. The greater propulsive force of the tail of *C. porosus* probably gives it the ability to range farther and to fight against stronger currents than New Guinea crocodiles. Saltwater crocodiles have been known to swim 1174 km of open sea, and have expanded their range over an area that extends from India to Fiji (Neill 1971). But New Guinea crocodiles have not extended their range beyond their main island (Whitaker 1980).

If these interpretations are correct, *C. porosus* in the Western Province should inhabit wide, swift-moving rivers such as the lower Fly and Strickland, and should feed primarily on large fish such as barramundi *Lates calcarifer*, and larger mammals and birds, as indicated by Taylor (1979) in Australia. New Guinea crocodiles, on the other hand, should avoid fast, open water by residing primarily in swamps, marshes, lakes and smaller rivers while feeding on smaller fish and other smaller vertebrates.

The fact that adult *C. novaeguineae* have foot widths proportionately wider than those of equal-sized *C. porosus* would seem to indicate that the former is better adapted for life in shallow, muddy, vegetation-clogged waters. Wider hands and feet would give New Guinea crocodiles a better grip when pushing through clumps of grass and climbing steep mud banks. In short, New Guinea crocodiles should be more terrestrial than *C. porosus*. The narrow feet of saltwater crocodiles may inhibit their travel through such terrain. But the reduced hydraulic drag resulting from narrow feet would complement the propulsive advantage of the more aquatic saltwater crocodile's longer tail.

Further research should perhaps be directed to the area of limb morphology, in that the wider feet of *C. novaeguineae* may be reflected in limb musculature and sizes. A food preference study of the New Guinea crocodile should be conducted, as defined by Petrides (1975), to complement those done for *C. porosus* by Allen (1974) and Taylor (1979).

Acknowledgments

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Appendix 1.   Dimensions in centimetres for some large *C. novaeguineae* skulls from the Papuan Region, PNG, 1978–80

Live measurements are approximated, allowing for a 4% tissue loss (Webb and Messel 1978*a*) except Nos 6, 8 and 15 which were measured both live and as dried skulls

Head No.	Locality	HTL Skull	HTL Live	HSE	HPP	HMP	HMW	HIO
1	South coast (Daru Wildlife Bldg)	45·0	46·8	31·0	14·4	12·2	28·0	4·8
2	South coast (Daru Wildlife Bldg)	44·5	46·3	30·5	14·8	12·9	28·2	4·3
3	Lake Murray (Magipopo)	42·8	44·5	29·5	13·5	11·6	24·0	4·2
4	Agu River (Mipan)	42·5	44·2	30·5	17·5	13·5	26·0	4·3
5	Kaim River	41·7	43·4	29·0	12·9	11·5	23·6	3·9
6	Baboa Farm (captive)	41·3	43·0	28·7	14·0	12·1	26·8	4·0
7	Kaim River	40·7	42·3	28·1	12·9	11·1	23·6	3·7
8	South coast (Daru Wildlife Bldg)	40·2	41·4	28·0	12·7	11·4	23·1	3·4
9	Moitaka Farm (captive) (wide skull)	38·9	40·5	26·5	14·0	11·7	28·5	3·8
10	Fly River (Komovai)	38·5	40·0	26·5	12·4	10·9	22·0	3·6
11	Lake Murray (Magipopo)	35·8	37·2	24·7	10·5	9·3	19·0	3·2
12	Agu River (Kuem)	35·0	36·4	24·0	11·0	10·1	—	3·2
13	Lake Murray (Magipopo)	34·0	35·4	23·2	10·0	8·9	17·5	3·2
14	Fly River (Komovai)	33·5	34·8	23·0	9·9	9·1	19·3	3·0
15	Baboa Farm (captive)	33·3	35·0	22·3	10·9	9·5	19·5	3·0
16	Lake Murray (Usokov)	32·0	33·3	21·6	—	—	14·4	2·8
17	Agu River (Mipan)	29·2	30·4	20·0	8·2	7·3	14·7	2·6
18	Kaim River (Kapikam)	28·7	29·8	19·2	8·8	7·8	15·1	2·2
19	Agu River (Kuem)	25·5	26·5	17·6	7·2	—	12·6	1·9
20	Agu River (Mipan)	22·7	23·6	14·8	6·4	5·9	11·3	1·7
21	Lake Murray (Egiza)	22·7	23·6	15·1	7·0	6·2	11·2	1·7