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MORPHOLOGY, INJURY AND GROWTH ANALYSIS OF *CROCODYLUS NOVAEGUINEAE* FROM THE FLY RIVER DRAINAGE, PAPUA NEW GUINEA

presented by

J. Jerome Montague

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MORPHOLOGY, INJURY AND GROWTH ANALYSIS OF *CROCODYLUS NOVAEGUINEAE* FROM THE FLY RIVER DRAINAGE, PAPUA NEW GUINEA

By

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ABSTRACT

MORPHOLOGY, INJURY AND GROWTH ANALYSIS OF *CROCODULUS NOVAEGUINEAE* FROM THE FLY RIVER DRAINAGE, PAPUA NEW GUINEA

BY

J. Jerome Montague

Formulae for predicting snout-vent length from 17 other body measurements and vice versa were derived from data collected on 1,073 wild New Guinea crocodiles (*C. novaeguineae*). Equations for predicting live body attributes from dried skulls also are presented. Relative growth and general growth form is described. A 1:1 sex ratio was found for animals between 50-167 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 fore and 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.

Abnormalities and injuries in 1,073 wild _C. novaeguineae_ are described and their frequency in various size, sex and geographic classes are presented. The most common abnormality was ventral parasite tracks from _Paratrichosoma crocodilus_. Except for leech and _Paratrichosoma_ infestations, anomalies were not correlated with capture location. The incidence of abnormalities and injuries tended to increase with increasing SVL.

Three hundred and twenty-three crocodiles, ranging in size from 28-84 cm SVL, were reared under rural farm conditions. They grew in total length at an average rate of 17 and 15.7 cm/yr for males and females, respectively. Growth rates decreased with increasing SVL in both sexes. Farmed crocodiles were heavier and had larger belly-widths than wild animals of equal SVL. Optimum commercial harvest size is, on a benefit-cost basis, about 30.5 cm (12 in) belly-width. Annual farm mortality was 9%, of which 30.6% could be eliminated by better management.

An evaluation of crocodile management plans for the Fly River drainage of Papua New Guinea was made and recommendations summarized.

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INTRODUCTION

Prior to 1966 there were no restrictions on crocodile exploitation in Papua New Guinea (PNG). By then, however, wild crocodile stocks and the mean size of marketed skins had declined drastically (Lever 1975a). The Crocodile Trade Protection Act of 1966 provided for a governmental agency to manage crocodile resources. This Wildlife Division, as it was named, hoped to regulate the crocodile harvest on a sustained yield basis and to increase the average size of skins sold (deVos 1979).

In the mid 1970's, the sale of crocodile skins above 50.8 cm belly-width, which was believed to be the minimum breeding size of both New Guinea (*Crocodylus novaeguineae*) and saltwater (*C. porosus*) crocodiles, was banned, thus eliminating the incentive for hunting adults (Tago 1977). In addition, the PNG government began a crocodile farming scheme as part of their conservation and management program (Bolton 1978).

Farmed crocodilians generally have lower mortality rates and faster growth rates than wild ones (Coulson et al. 1973, Joanen and McNease 1976a, Nichols et al. 1976). Assuming that similar results could be obtained with PNG's crocodiles, it was expected that the farming program would increase both the number and the average size of the skins exported without increasing the wild crocodile harvest.

Two types of farms were instituted: large commercial farms near urban centers holding 5,000 or more crocodiles, and village farms holding up to 500 animals (I.U.C.N. 1978). Since hatchling and smaller juvenile crocodiles comprised the largest segment of the wild crocodile population (Montague 1982a), and are replaced at regular intervals, crocodile farmers were encouraged to stock their farms with these size groups. Protection of the wild breeding stock would probably insure a continual supply of young crocodiles.

In 1977, the Food and Agriculture Organization of the United Nations (FAO) was invited by the PNG government to assist in the crocodile management program. The next year the two began a country-wide live crocodile buying scheme to supply commercial farms and provide an income for those villagers in crocodile areas that could not or would not farm. From 1978 to 1980, the Baboa Crocodile Station, in the Western Province, purchased 2,695 live New Guinea crocodiles which were air freighted to other farms (Montague 1980). It was from these animals and large crocodiles purchased for captive breeding that a sample of 1,073 was chosen for the morphometric study reported herein. A series of measurements and observations of abnormalities and injuries were taken from each animal. In addition, measurements were taken on 163 captive New Guinea crocodiles from the Baboa Station's farm stock.

The external morphology of crocodilians has been studied in detail only in the Australian saltwater crocodile (Webb and Messel 1978a). The only work on New Guinea crocodile morphology is composed of measurements from 16 skulls (Schmidt 1932).

Snout-vent length (SVL) has been established as the most accurate representation of crocodile size (Webb and Messel 1978a). Thus, the morphometric portion of this study was largely directed toward deriving equations to predict snout-vent length from seventeen other attributes and vice versa. The equations allow for an estimate of body size from isolated skulls, heads, tracks, belly slides, 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 if 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 and growth studies could thus provide this information for New Guinea crocodiles. The morphometric models also allow for a description of relative growth and growth form.

Geographic variation in body form was investigated. The body size at which mandibular teeth protrude through the premaxilla was compared with C. porosus (Webb and Messel 1978a). A cause for such tooth protrusion in crocodilians is hypothesized.

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. It sought differences in the 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. Morphometric models of C. novaeguineae were compared to similar models for C. porosus from Northern Australia (Webb and Messel 1978a). This comparison might help to identify ecological niche characteristics that may separate sympatric populations of C. novaeguineae and C. porosus in PNG.

Descriptions of anomalies in skulls and skeletons have been presented for a number of crocodilian species (Kalin 1936), but abnormalities and injuries afflicting New Guinea crocodiles and their frequency in natural populations were not known. Such frequency data are not available in crocodilians excepting C. niloticus (Cott 1961) and C. porosus (Webb and Messel 1977a). Such information is important in understanding the ecology of crocodile species.

Abnormalities and injuries in the sample of wild C. novaeguineae are described. A thorough tabulation of the frequency of injuries between sexes, size classes and geographic areas in the Western Province is presented. Knowledge of abnormalities and injuries afflicting crocodiles is important in order to minimize their occurrence on crocodile farms. Injuries common to New Guinea crocodiles were compared to those presented for C. porosus from Northern Australia (Webb and Messel 1977a).

New Guinea crocodile growth rates and size/age relations are a fundamental aspect of the species' natural history. This information is of considerable ecologic and economic importance in PNG where this animal is raised in captivity for both commercial and restocking purposes (Bolton 1981a). The high monetary value of crocodilian skins coupled with the serious world-wide decline in numbers (Gore 1978) have prompted numerous studies into the growth rate of this reptile family.

Due to the comparative ease of researching captive crocodilians as opposed to wild ones, growth has been better documented for farmed animals. In the past few decades, captive growth has been shown for Alligator mississippiensis

(Joanen and McNease 1972, 1976a, 1977, Coulson et al. 1973), *Caiman crocodilus* (Rivero Blanco 1974), *C. palustris* (D'abreu 1935, Deraniyagala 1939, Whitaker and Whitaker 1977), *C. simensis* (Yangprapakorn et al. 1971) and *C. niloticus* (Cott 1961, Blake 1974, Pooley and Gans 1976). To date, growth rates have at least been determined for wild *A. mississippiensis* (McIlhenny 1934, Chabreck and Joanen 1979), *C. porosus* (Webb et al. 1978), *C. niloticus* (Graham 1968) and *C. crocodilus* (Gorzula 1978).

For those species on which both wild and captive data are available, it is apparent that crocodilians grow faster under favorable captive conditions. These studies have also shown that captive growth rates vary intraspecifically and are directly dependent on the quality of care.

Growth trials were conducted to determine the optimum possible growth rates of *C. novaeguineae* under village conditions. This information will provide a basis for determining the time necessary to rear crocodiles to harvest size on PNG's bush farms (Montague 1981) and establishing size/age relationships.

METHODS AND STUDY AREA

Capture 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. To capture young crocodiles, generally a villager would either lie down in the front of a 5-14 m dugout canoe with a flashlight or he would have another man stand behind him with a light while one or more paddlers propelled the canoe at night along a route 3-5 m out from the lakeshore or river bank. When the hunter saw the red reflection of the tapetum in a crocodile's eye, he would vibrate the light beam on the water at that point. If the animal was no larger than 40 cm SVL and was in the water, the hunter moved his body forward so that most of his torso extended beyond the long prow of the boat. He would then grab the animal at the back of its neck with a swift lunge of his hand. If the animal was larger and was in the water, the paddlers directed the canoe so as to drive the crocodile onto the shore where several men would jump out with wet copra sacks so as to be between the crocodile and the water. A sack would be thrown over the animal's head while a man placed his weight with both hands behind the animal's neck. Crocodiles spotted on shore would be treated similarly.

Once the animal was captured, a bush string was tied around its snout and it was placed into bush material "bilum" or "sago" bags. The animals were then either brought to the Baboa Crocodile Station where we purchased them or were picked up by us on "buying patrols" to their villages (Montague 1980). The purchase price in the bush ranged from K.77 (US $1.16) to K3.77 (US $5.66)/in (2.54 cm) belly-width in the smallest and largest crocodiles respectively (Bates 1979). On buying patrols, crocodiles with jaws secured by rubber bands were placed into damp copra sacks; the copra sacks were placed onto special wire trays stacked in 5.7 m deHavilland river trucks (Figure 1) or 7 m wooden barges according to procedures of Whitaker (1979). The animals were then brought to the Baboa Crocodile Station at Lake Murray and placed into holding pens along with those animals purchased at the station. When 250-350 crocodiles had accumulated, they were packed six to a carton (Figure 2) (Whitaker 1979) and loaded aboard a Britten Normal "Islander" aircraft and flown 850 km to Ilimo Farms Inc. crocodile division in Port Moresby.

Crocodiles were purchased year round but most (77.1%) were purchased during the dry season, June - November, when crocodiles were concentrated in more accessible areas (Table 1) (Montague 1982a). Some 1,642 crocodiles were rejected for use in this study because hunters could not recall the exact location of capture or because more than 48 hours had elapsed between the time of capture and the time of measurement. If more than two days had passed, the crocodiles may have become starved, which would adversely affect the results.

Figure 1. The 5.7 m deHavilland river truck used to transport live crocodiles on buying patrols.

Figure 2. Cardboard cartons used to air-freight live juvenile crocodiles.


ilima farm
LIVE PUK PUKS

Table 1. Seasonal distribution of live crocodile purchases in the Fly River drainage, Western Province, PNG, June 1979 - May 1980.

Month	J	F	M	A	M	J	J	A	S	O	N	D
Number of Crocodiles	104	40	25	121	83	169	252	430	283	197	219	89
%	5.2	2.0	1.2	6.0	4.1	8.4	12.5	21.4	14.1	9.8	10.9	4.4

dry season (77.1%)

Fifty-four percent of the 1,073 wild crocodiles used in this study came from Lake Murray, while the remainder came from eight rivers in the Fly River drainage (Figure 3, Table 2). A complete description of the study area was presented by Montague (1982a).

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 Webb and Messel (1977b), and shipped to the Moitaka Government Crocodile Farm near Port Moresby. Although they had been in captivity from a few months to two years, they were used in this study because large New Guinea crocodiles were scarce and were needed to complete the morphometric model of this species in the wild. Since most of the developmental period of these animals' lives was spent in the wild and they were not overfed, it was felt that their contribution would add rather than subtract from the realism of the model.

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 1982a). 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 (Figure 4). Crocodiles

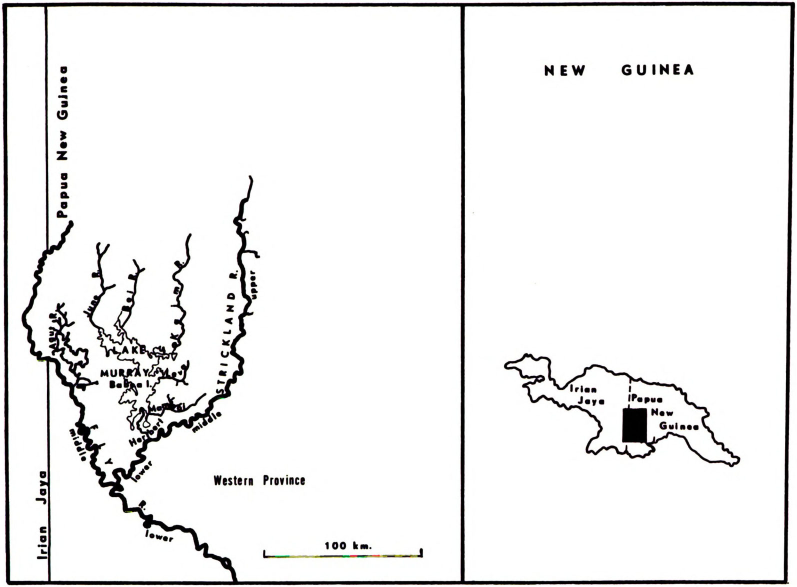


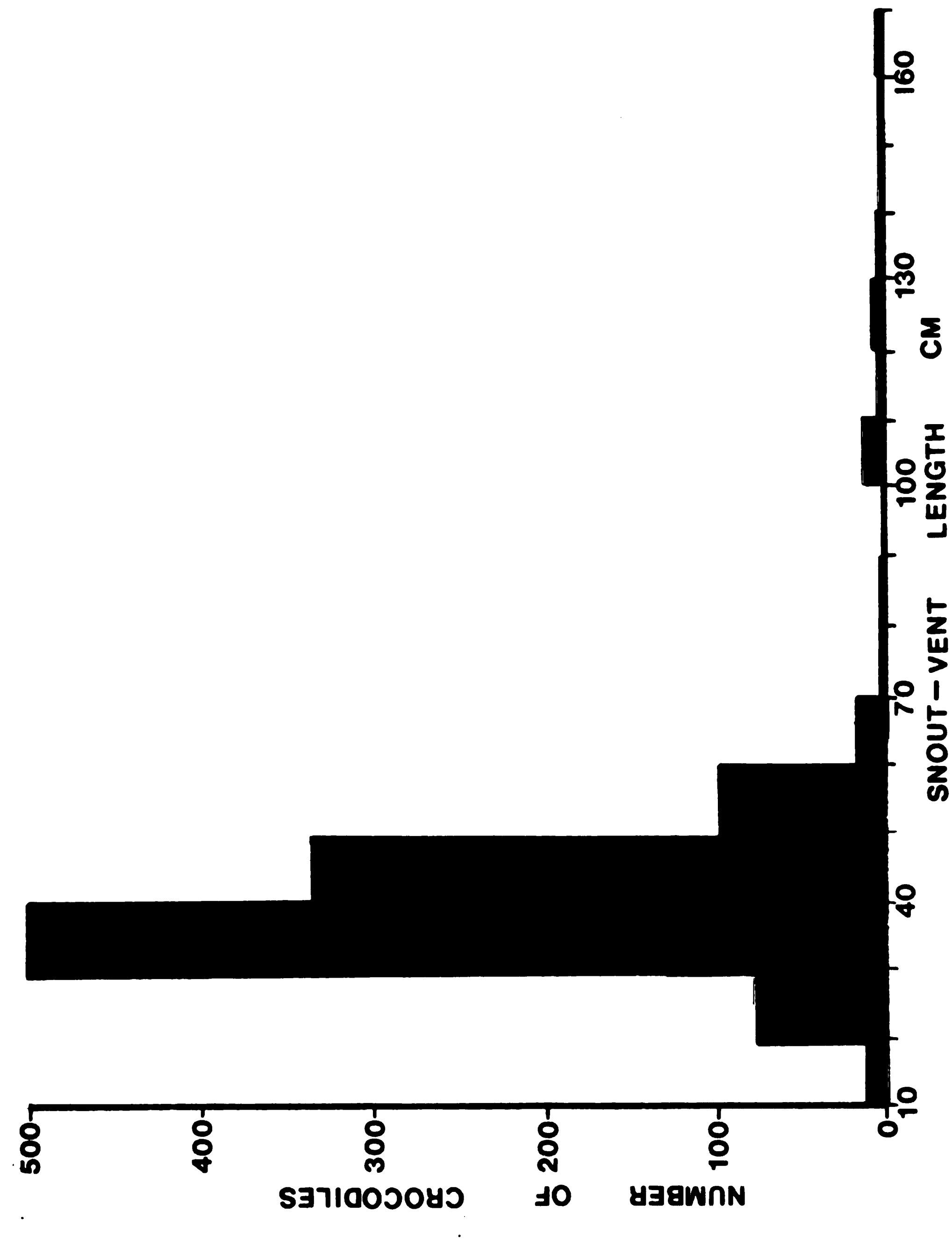
Figure 3. Waterways of the study area Western Province, PNG.

Table 2. Numbers of wild *C. novaeguineae* measured and examined from each area with locations described, Western Province, PNG.

Area	Location*	Description	Number of Crocodiles
Lake Murray	141°30'E, 7°S**	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***	Savanna	91
Strickland River	141°34'E, 7°20'S to 141°23'E, 7°35'S***	Gallery rainforest	84
Kaim River	141°32'E, 6°54'S	Savanna, rainforest	60
Leva River	141°36'E, 7°S	Swamp forest	59
June River	141°21'E, 6°20'S	Savanna, rainforest	31
Boi River	141°25'E, 6°50'S	Rainforest	20
Agu River	141°7'E, 7°5'S	Savanna, swamp forest	10
		Total	1,073

*Coordinates of river mouths unless otherwise indicated
**Lake center
***River section

Figure 4. Size frequency histogram of 1,073 wild *C. novaeguineae* from the Fly River drainage, PNG, used in the morphometric study, 1978 - 1980.


NUMBER OF CROCODILES
0
100
200
300
400
500
10
40
70
100
130
160
SNOUT-VENT LENGTH CM

in the 20-60 cm SVL classes were abundant in the sample, both because they were most common in the wild (Montague 1982a) and because they were a convenient size to catch and transport. There were few crocodiles in the 70-100 cm SVL size class in the sample (Figure 4) 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 was purchased as breeders.

Sex Identification

Crocodiles were sexed by placing the crocodile on its back, stroking its venter to calm it, inserting the little finger into the cloaca and feeling for the clitoris or penis (Chabreck 1963). If the cloaca was too small for inserting the finger, gentle pressure was applied around the cloaca to expose the genitals. These methods were found to be nearly 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 wild sex ratios in New Guinea crocodiles, 633 wild caught animals at Baboa Crocodile Station and 1,398 wild crocodiles purchased for resale were sexed.

Morphometry

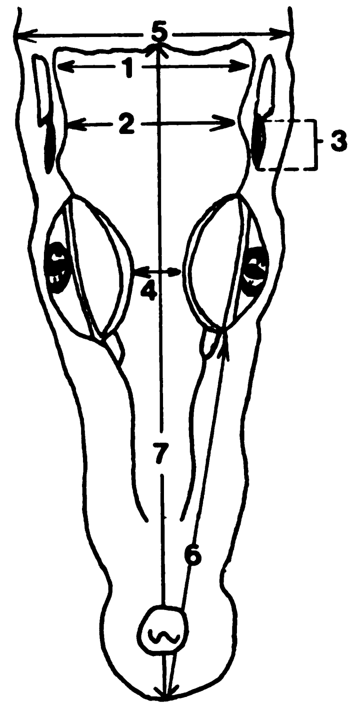
Snout-vent length and total lengths of *C. novaeguineae* were measured along the venter with a steel tape. Girth measurements were also taken with a steel tape pulled snug but not tight against the animal. Hand and foot widths, as well as some head and skull measurements from larger animals, were made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

The measurements, their description and abbreviation, modified from Webb and Messel (1978a), 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 extremeties of the cranial platform (Figures 5 and 6).

Figure 5. Vernier calipers used for taking head measurements such as cranial platform width (pictured).

Figure 6. *C. novaeguineae* head showing measurements.
1) Width of cranial platform (HPP).
2) Cranial platform mid-point 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).


5
1
2
3
4
7
6

8) Cranial platform mid-point width (HMP). Width of cranial platform where it is usually concave (Figure 6).

9) Interocular width (HIO). Shortest distance between the eyes (Figure 6).

10) Ear length (EL). Length of ear slit (Figure 6).

11) Maximum head width (HMW). Distance between the extremities of the surangular bones at the level of jaw articulation (Figure 6).

12) Snout-eye length (HSE). Tip of snout to anterior edge of orbit (Figure 6).

13) Total head length (HTL). Tip of snout to median posterior edge of platform (supraoccipital bone) (Figure 6).

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) = SVL - HTL.

18) Tail length (TAL) = TL - SVL.

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 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 1970-1978. New Guinea crocodile skulls were differentiated from *C. porosus* skulls using methods described by Schmidt (1928, 1932). All skulls had been dried for over one year and lacked all soft tissue.

Morphometric Analysis

The SPSS (Statistical Package for Social Sciences) sub-program 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:

$$Y = A + BX \pm E,$$

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 using 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) (Figure 8d), a logarithmic transformation was used for all equations involving BWT since these yielded a linear relationship. The SPSS sub-program 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 from 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 sub-adults and some adult females while the ≥ 100 cm SVL class was comprised entirely by adults. Slopes and intercepts of the various sample subsets designated above were compared using 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 4 and 5).

All of the above regression equations were also compared to similar equations presented for Australian C. porosus by Webb and Messel (1978a) to investigate morphological differences between the two species that may indicate niche separation in PNG. 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.

Data from 35 crocodiles representing all size classes were selected from the total sample using a stratified random sampling technique to undergo logarithmic transformation. Randomization was achieved by grouping the data into 10 cm units ranging from 10-110 cm SVL and a last group from 111-167 cm SVL. Crocodile identification numbers in each group were renumbered and four were selected from a random numbers table to be used in the sample (Lapin 1975). In those three groups that had less than 4 crocodiles (Figure 4), all were used. 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 to identify which parameters have a constant growth rate and which do not. The SPSS sub-program FACTOR was employed to run factor analyses on all variables to show which factor has the greatest contribution to variation.

Following Webb and Messel (1978a), all wild crocodiles used in the morphometric portion of the study were examined for evidence of mandibular teeth protruding through the premaxilla.

Abnormalities and Injuries

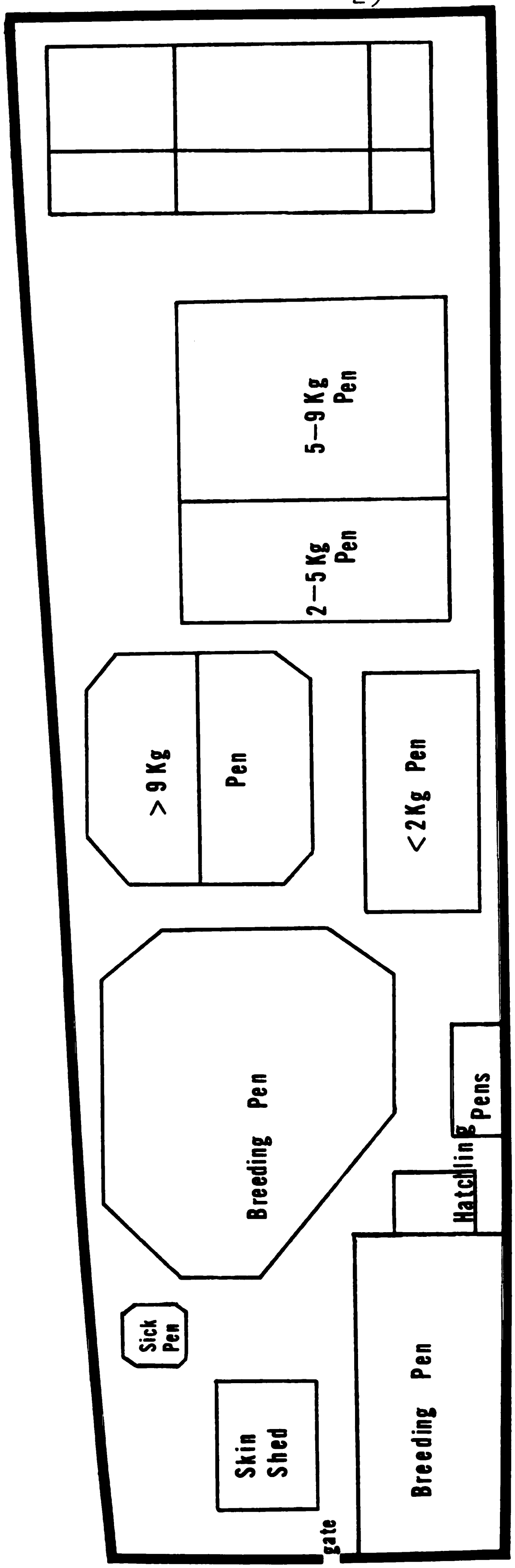
All live, wild New Guinea crocodiles used in the morphometric portion of the study were carefully examined for external abnormalities and injuries. Characteristic anomalies were photographed and described. The animals, however, were not closely examined for small scars, nor was the buccal cavity examined. Differences in abnormalities and injuries between sexes, area of origin and body size were analyzed and tested using contingency tables generated by the SPSS sub-program CROSSTABS (Nie et al. 1975).

Growth Trials

Captive growth trials were conducted between August 1978 and August 1980 at the Baboa Crocodile Station at Lake Murray in the Western Province, Papua New Guinea (PNG). The climate was mild tropical (Paijmans et al. 1971) with a mean annual temperature of 26.7°C, and a mean monthly variation of 2.2°C. Daily maximum temperatures of 31°-35°C occurred in the early afternoon. Sunshine fell on an average of 342 days/yr for an average of 4.5 hrs/day. Rainfall during the study averaged 325 cm/yr with the majority falling during the warmer, less humid January - June period (mean monthly relative humidity = 80%).

The crocodile farm (Figure 7) was designed as a demonstration facility for the development of 27 village

Figure 7. Site of the captive growth trials, Baboa Government Crocodile Farm, Lake Murray, Western Province, PNG. scale = 1:600.


5—9 Kg Pen
2—5 Kg Pen
> 9 Kg Pen
< 2 Kg Pen
Breeding Pen
Hatchling Pens
Sick Pen
Skin Shed
Breeding Pen
gate

crocodile projects on the Fly River drainage. The pens were constructed (Lever 1974, 1975b, Fresco 1978) of hardwood posts c. 15 cm X 170 cm buried into the ground c. 25 cm. Pools occupying c. ½ the enclosed area were dug to a depth of c. 80 cm and were irregularly shaped with sloping sides. Pen vegetation was primarily crows foot grass (Elusine indica), banana (Musa spp.), cassava (Manihot manihot) and bamboo (Bambusa spp.) (Paijmans 1976). The perimeter of the farm was enclosed by a 4 m cyclone fence to reduce chances of escape and theft. Bush materials were used throughout except for a diesel water pump, outboard motors for fishing and the cyclone fence.

Crocodiles used in the growth trials were purchased as part of the live crocodile buying scheme. At the beginning of the study, 390 New Guinea crocodiles from 28-58 cm SVL and 13 female and 3 male saltwater crocodiles from 38-64 cm SVL were individually numbered by clipping dorsal tail scutes following a modification of Messel et al. (1977) (Bolton 1981b). The growth trials were begun immediately without the settling in period advised by Joanen and McNease (1976a,b) which would bias the estimated time required to raise crocodiles on village farms. At one stage growth trials were begun on 48 crocodiles housed individually but were discontinued after two months as most animals refused to eat. Apparently pen mates were essential for normal appetites.

Biomass densities of penned crocodiles ranged from 1.7 to 3.9 kg of crocodile/m^2. These conditions were sometimes crowded but were not believed to negatively influence growth rates (Yangprapakorn et al. 1971, Coulson et al. 1973, Blake 1974). Crocodiles were divided into the following categories: $<$ 2 kg, 2-5 kg 5.1-9 kg, and $>$ 9 kg, in addition to a sick category (Figure 7). New Guinea and saltwater crocodiles were penned together. Bolton (1981b) found that this practice does not affect growth rates in either species.

Fresh lake water was pumped into each pond 2-3x/wk, as suggested by Coulson et al. (1973). All pens were equipped with several ponds so that once a month each could be drained and dried out while the animals used the undisturbed ponds. This allowed cleaning of the pond without disrupting crocodile feeding patterns (Blake 1974).

Fishing nets in Lake Murray were checked every morning (7 days/wk) and whole fish (Table 3) were chopped into sizes designated as appropriate for each pen by Fresco (1978). The animals were fed every day at c. 1400 hrs following the practices of Yangprapakorn et al. (1971). This was after the hottest time of the day but still warm enough for a crocodile to have a high ability to assimilate food for growth (Brattstrom 1965, Diefenbach 1975, Pooley and Gans 1976, Lang 1979). Since refrigeration facilities were not available, all food was fresh fish of the day. The amount

Table 3. Species composition, by weight, of fish fed to crocodiles at the Baboa Station, Lake Murray, April 1979 - March 1980. Identification from Munro (1967) and Roberts (1978).

Species	Common Name	Kg/Yr	Percent of Total
Lates calcarifer	barramundi	19,213	62.1
Pristis microdon	sawfish	5,295	17.1
Cochlefelis spatula	catfish	3,907	12.6
Fluvialosa papuensis	Strickland herring	922	3.0
Neosilurus aterater	catfish eel	731	2.4
Thryssa scratchleyi	oxeye herring	232	0.75
Kurtus gulliveri	nursery fish	184	0.60
Scleropages jardini	Jardines barramundi	113	0.37
Oxyeleotris lineolatus	mud fish	106	0.34
Strongylura kreffti	freshwater longtom	99	0.32
(unidentified)	blackfin	77	0.25
Cestragus goldiei	Goldie River mullet	53	0.17
	Total	30,932	100.00

of food each day depended on the quantity of that day's catch and was therefore irregular, but crocodiles were fed some fish every day. Leftover food implied ad libidum feeding on 64% of the days. These fish remains were cleaned out of the pens c. 18 hrs after feeding and weighed following Blake (1974) and Joanen and McNease (1976b, 1977). Crocodile feed was distributed in proportion to the crocodile biomass in each pen. Sick crocodile inspections were conducted every two weeks as recommended by Joanen and McNease (1977).

Growth was assessed every six months by measuring SVL, TL, belly-width (BW) and body weight (BWT). To determine a single mean growth rate for use by village crocodile farmers, individual growth rates were determined using $M_2 - M_1/t$, where M_1 and M_2 were the previous and current measure, respectively, and t = time in months. These were averaged for all 323 crocodiles. Growth rate differences were established for the size classes ($\pm$ 2 cm): 30, 40, 50, 60 and 70 cm SVL. One year's growth for all crocodiles in each size class was averaged. In both growth analyses, a "Z" test was used to see if male and female growth rates differed significantly. Also during these inventories, crocodiles that had grown into the next pen size were placed accordingly.

Size/age relationships were constructed using the growth curve formula (Fabens 1965, Crowe and Crowe 1969):

$$x = a - be^{-kt},$$

where x is size expressed as SVL; t = age in years; a = an upper bound of x; b = natural antilog of the Y-intercept of the slope in a regression equation relating the natural logarithm of x - a (y-axis) with time (x-axis); k = slope of the regression equation; and e = base of the natural logarithms.

One hundred and sixty-three *C. novaeguineae* divided nearly equally between 48 and 84 cm SVL were selected at the end of the growth trials for morphometric analysis. Following methods outlined earlier for wild crocodiles, regression equations were developed relating SVL with TL, BW and BWT for these farmed animals. Regression equations were compared between farmed and wild crocodiles by an "F" test.

Of the crocodiles used in these captive studies, some have been released into the wild (Wild Kingdom 1981), some kept as breeding stock or for demonstrations, while many were killed and skinned (Lever 1977).

Throughout the paper, statistical significance was set at the P = .05 rejection level.

RESULTS

Morphology

Predicting SVL from Body Dimensions

Scattergrams of snout-vent length (SVL) plotted against TL, TAL, TRL, HW, FW, HTL, HSE, HPP, HMP and EL seemed to approximate straight line relationships for these parameters throughout all but the very smallest size classes (Figures 8a, b, c, j, k, l, m, n, o and r respectively). All girth (Figures 8f - i), HMW, and HIO (Figures 8p and q) scattergrams showed slight allometry (curvilinearity) below 50 cm SVL, but except for BW (Figure 8g) they seemed to demonstrate a linear relationship in the larger size classes. Belly-width (BW) showed scattergram curvature throughout all size classes and was second only to body weight (BWT) in this regard (Figure 8d).

Webb and Messel (1978a) 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 transformation for the prediction portion of this analysis (Figure 8e). But logarithmic transformations were performed on all morphometrics for subsequent relative growth analysis (see beyond).

Based on correlation coefficients and standard errors (Tables 4 and 5), it seemed possible to predict SVL from a number of body measurements. To keep prediction error to a

Figures 8 a-r. Scattergrams for predicting snout-vent length (Y axis in mm) from other attributes (X axis) from 1,073 wild _C. novaeguineae_ of both sexes from the Fly River drainage, PNG, 1978 - 1980.

Each digit represents the number of crocodiles having nearly the same measurement while * = 1 crocodile.

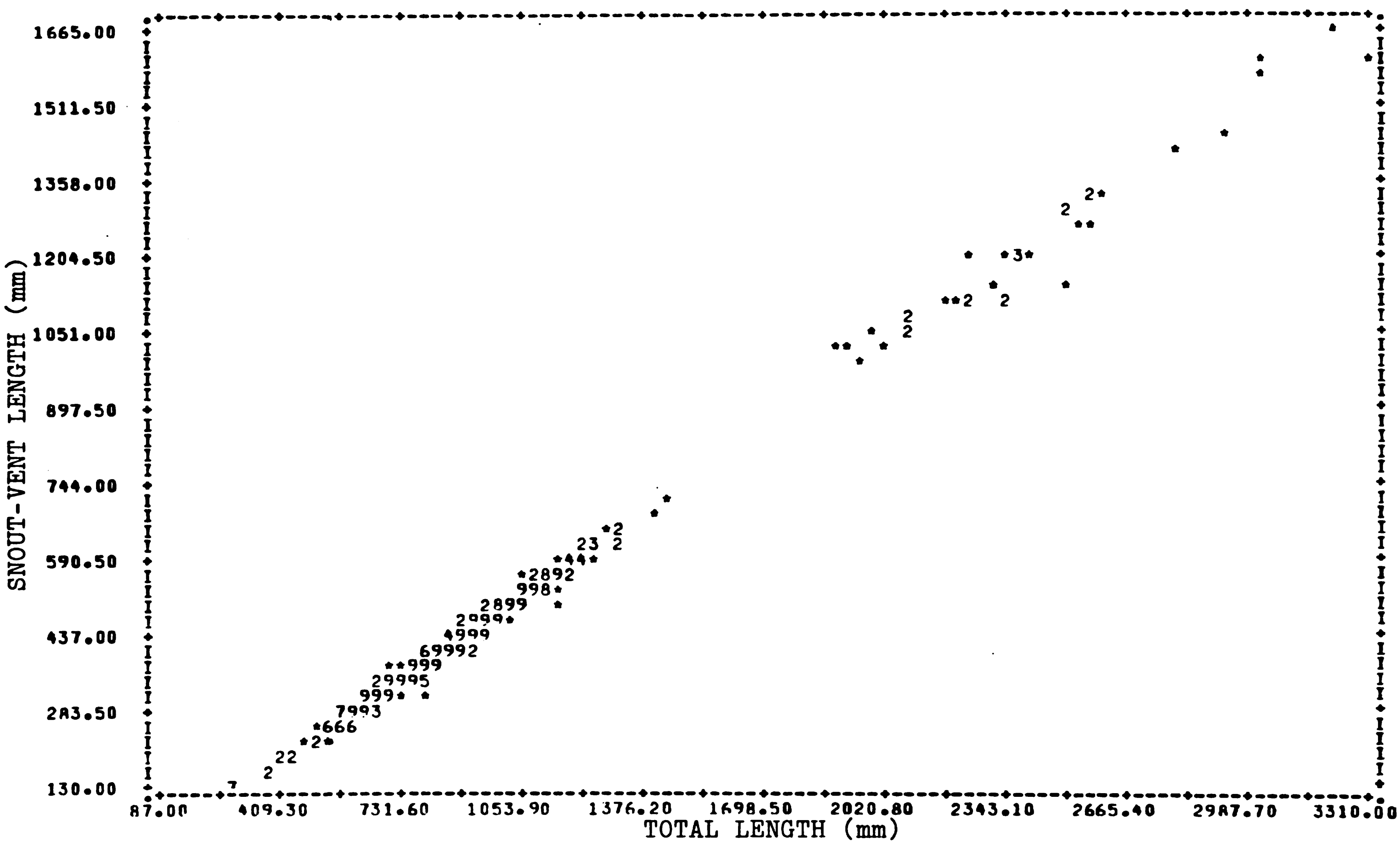


Figure 8a. Total length (TL).

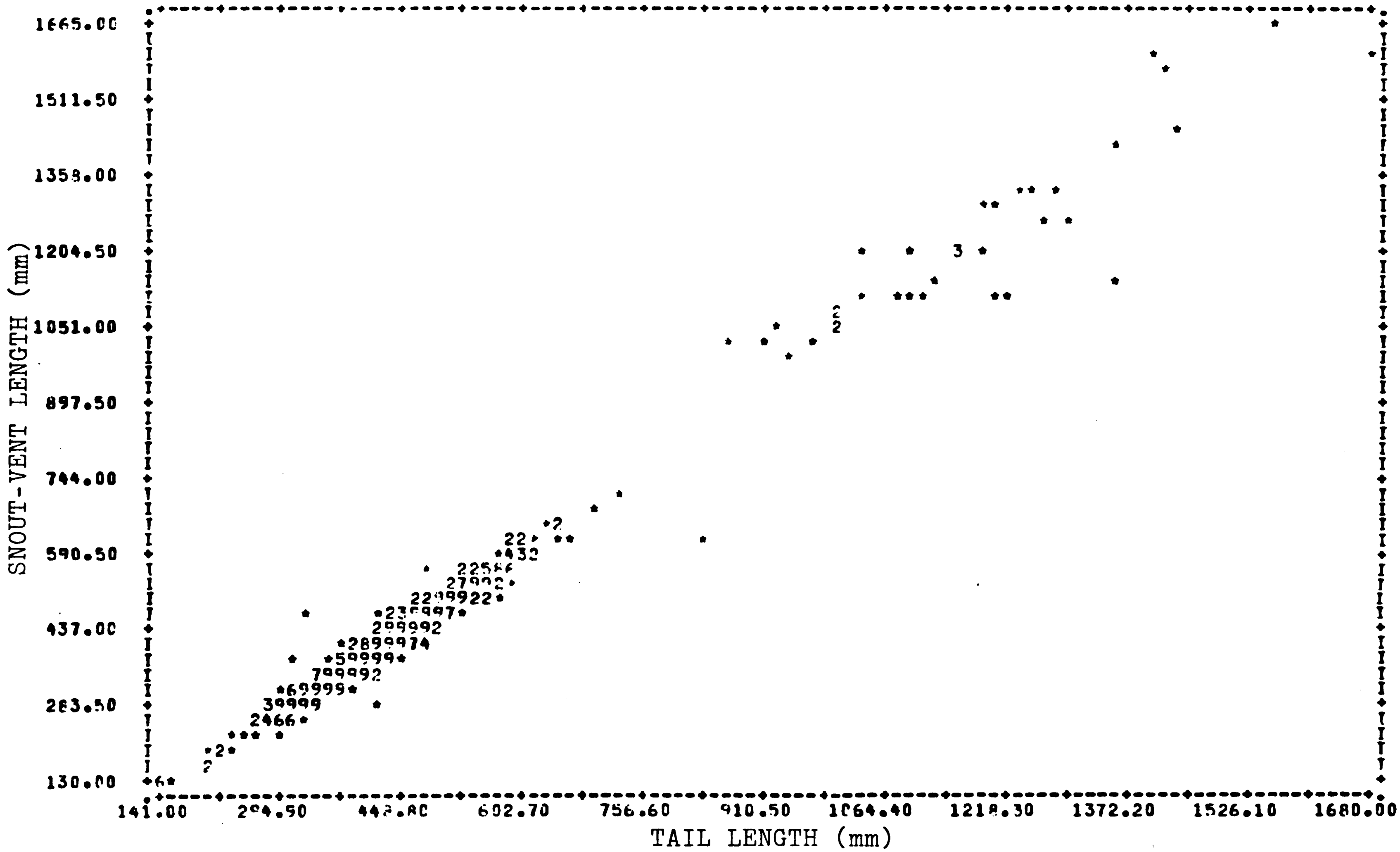


Figure 8b. Tail length (TAL).

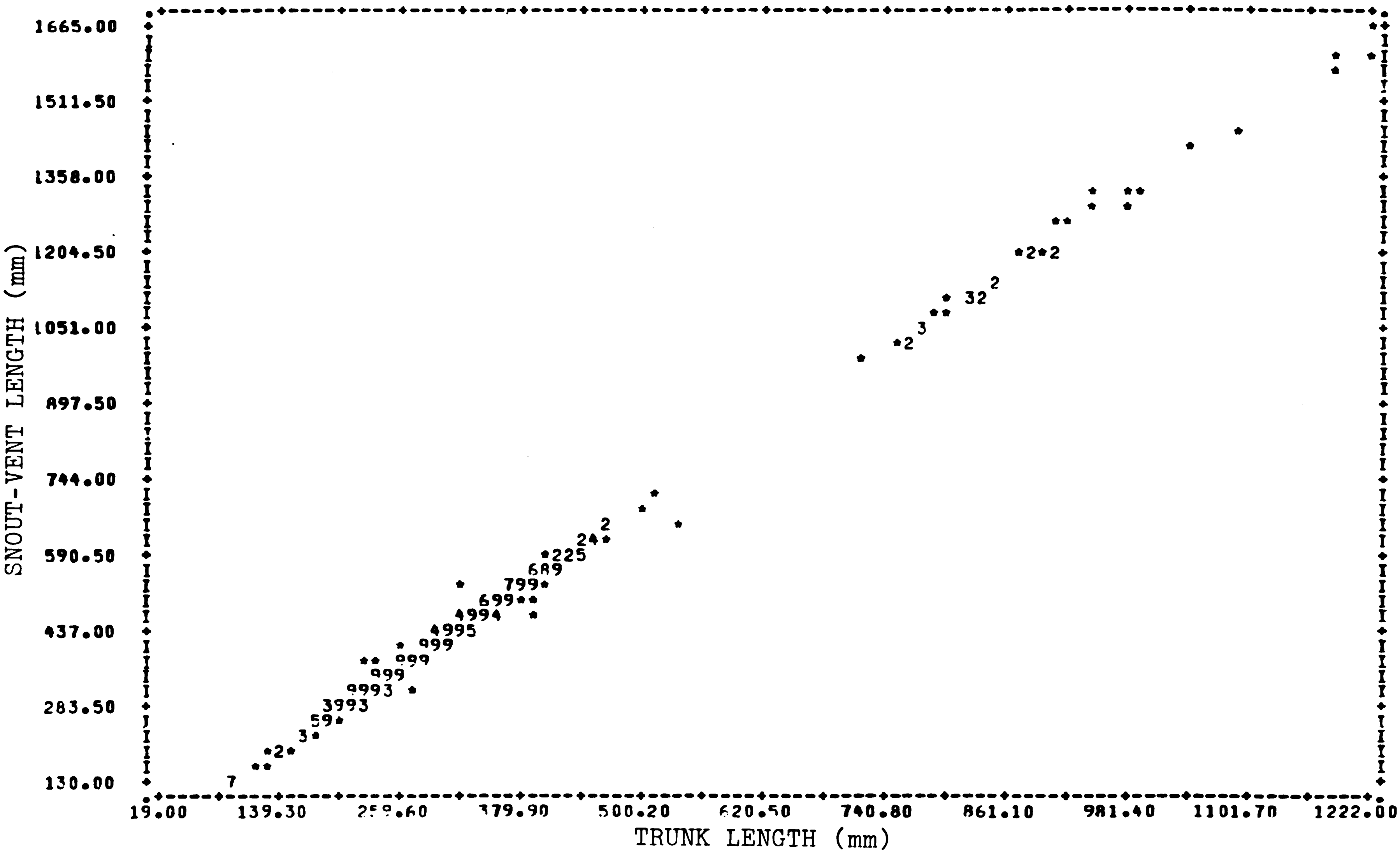


Figure 8c. Trunk length (TRL).

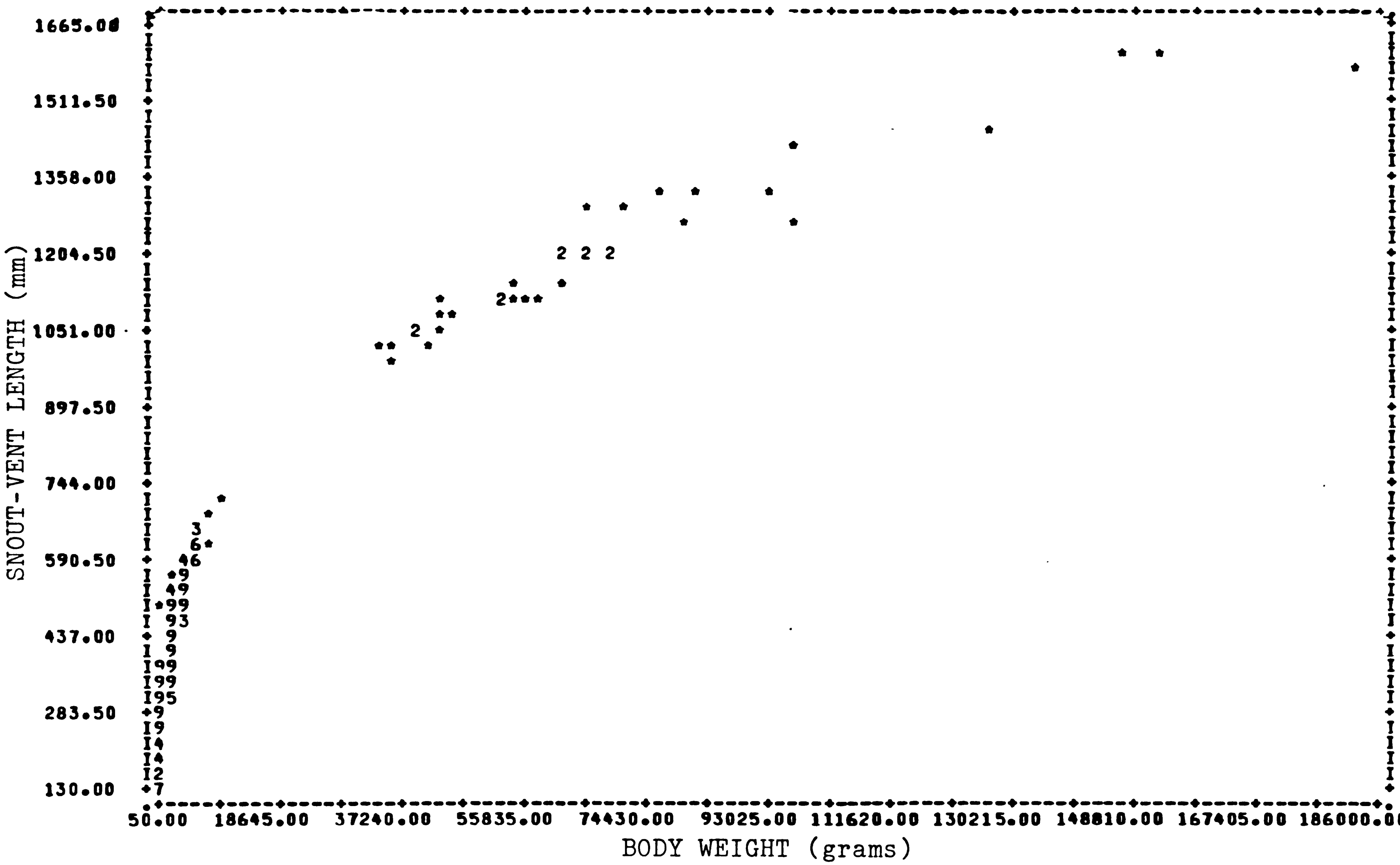


Figure 8d. Body weight (BWT).

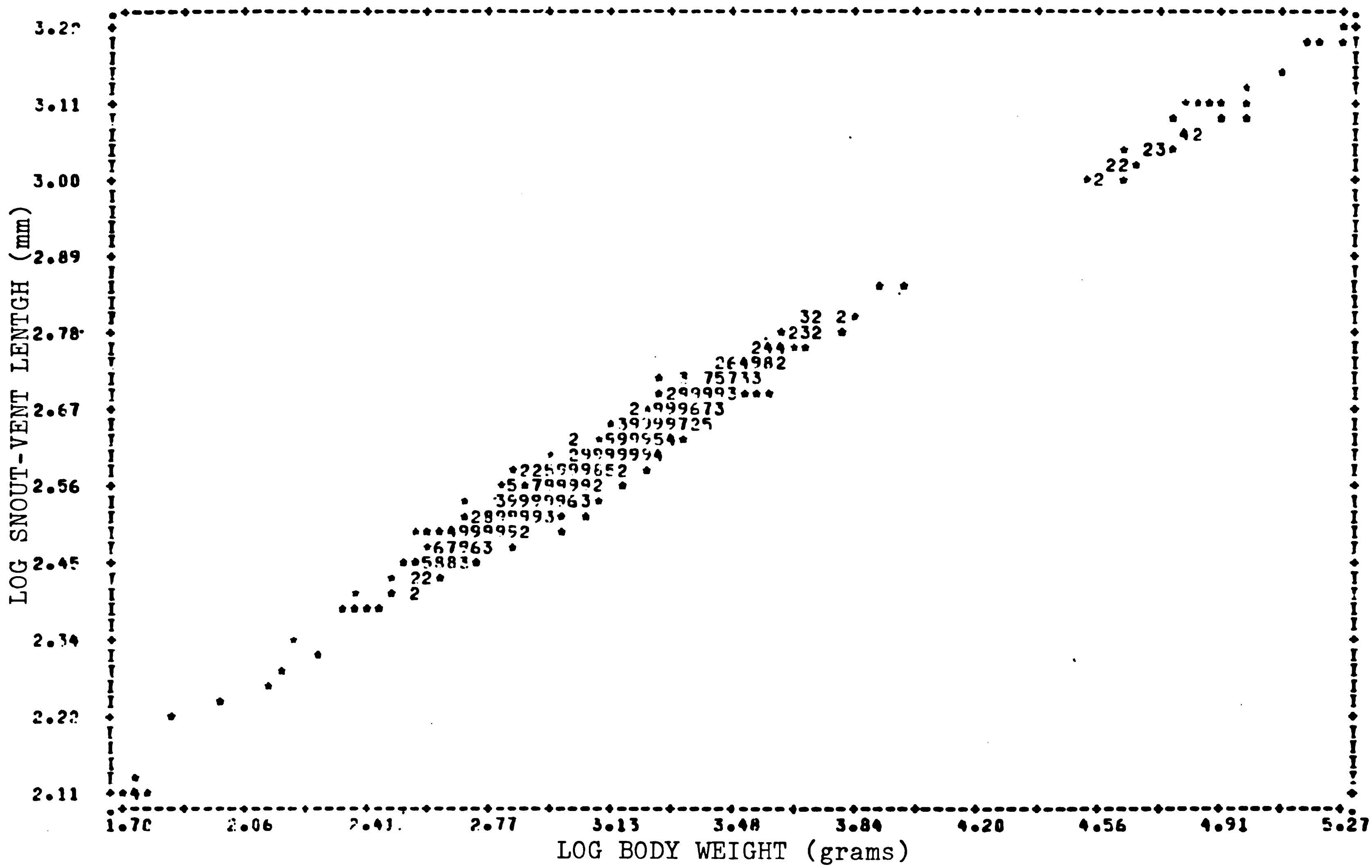


Figure 8e. Log body weight (LBWT).

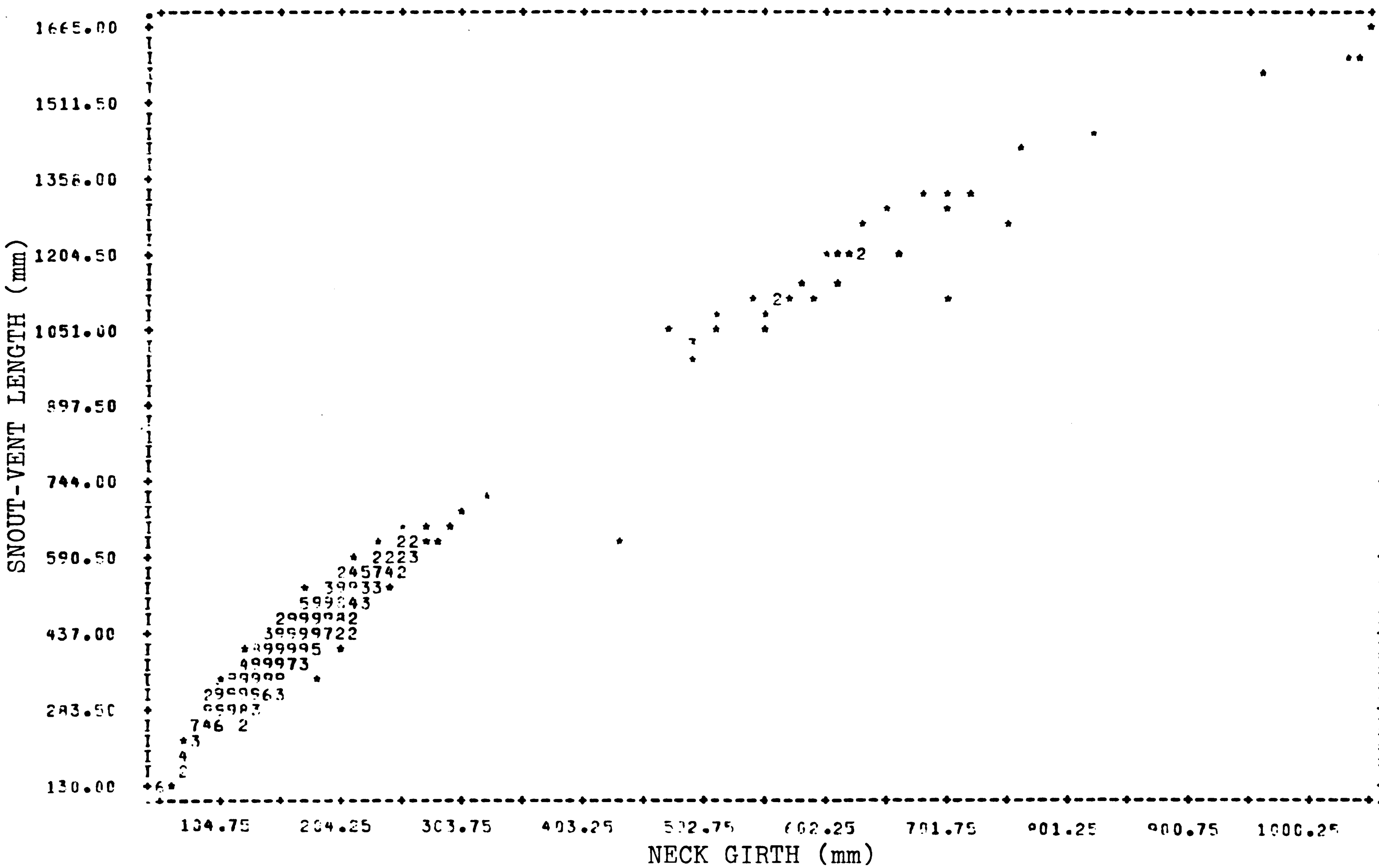


Figure 8f. Neck girth (NG).

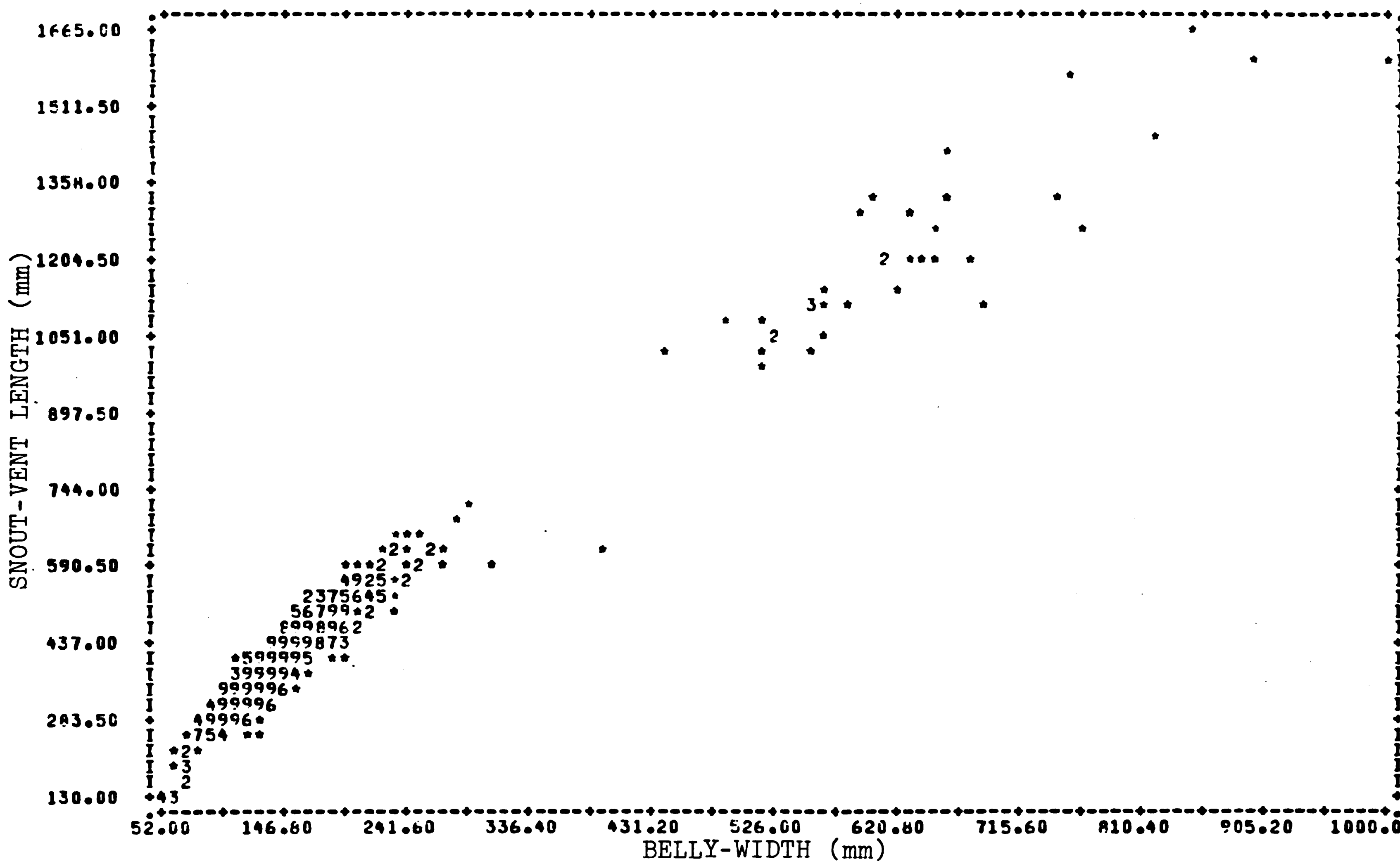


Figure 8g. Commercial belly-width (BW).

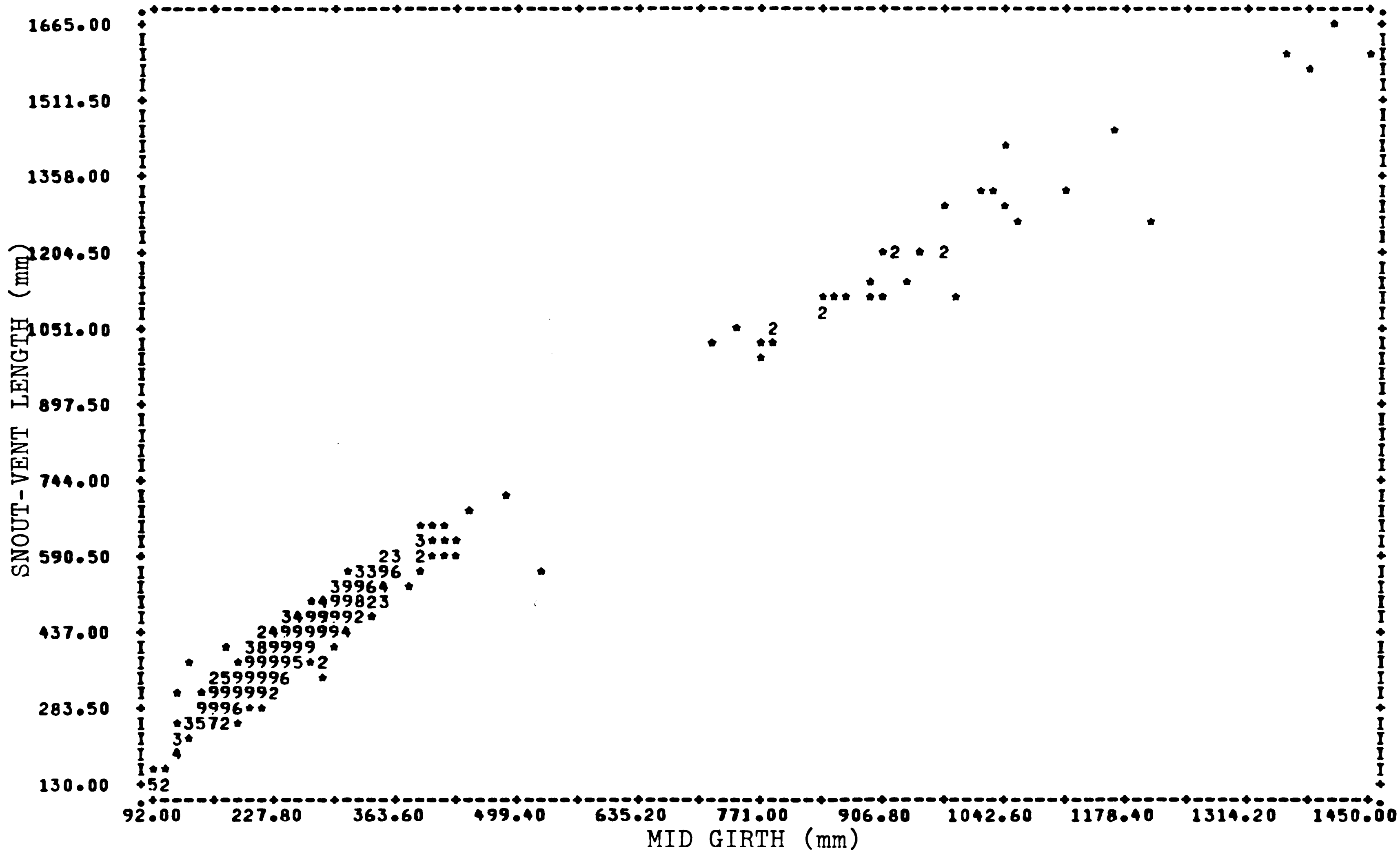


Figure 8h. Mid girth (MG)

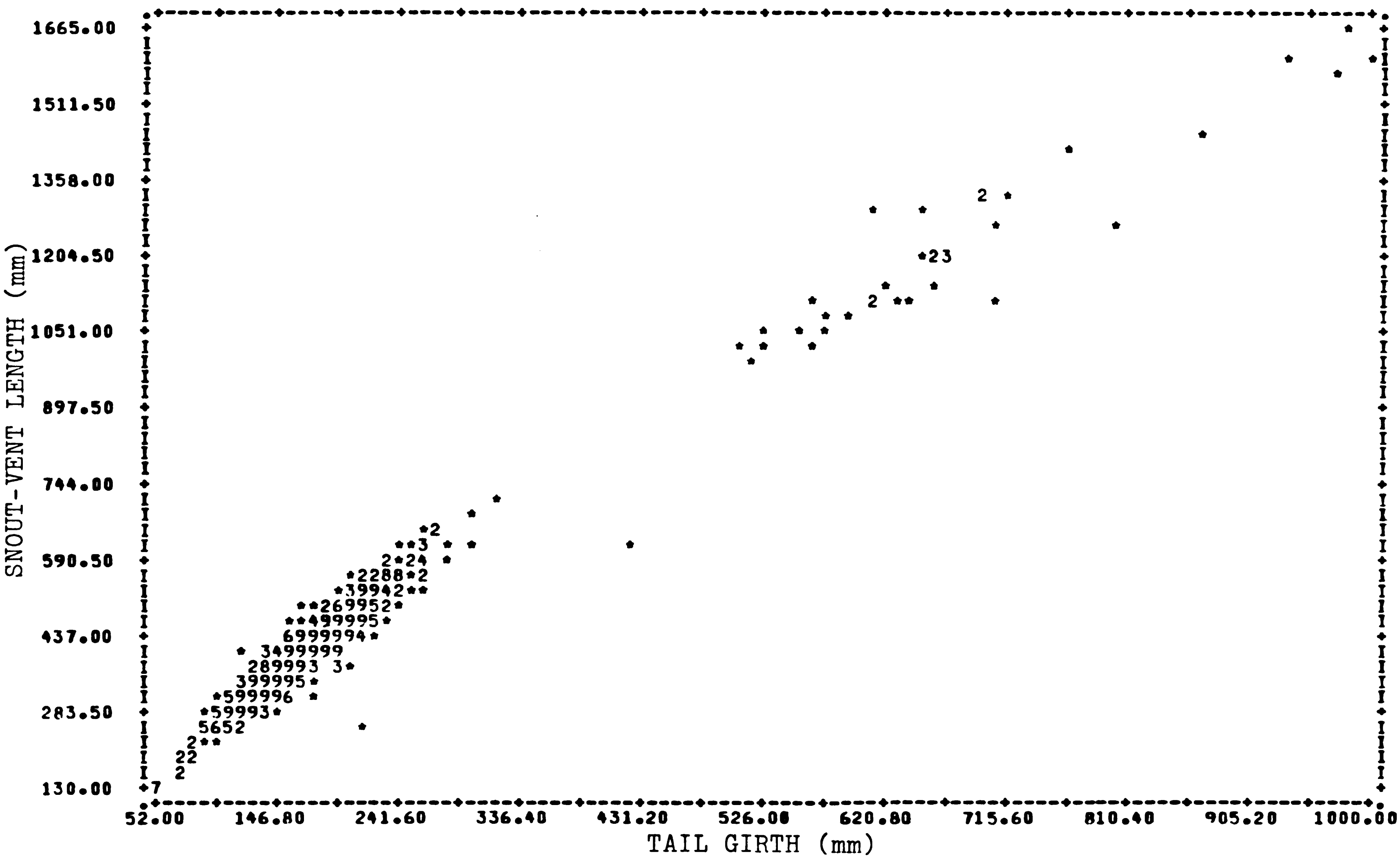


Figure 8i. Tail girth (TG).

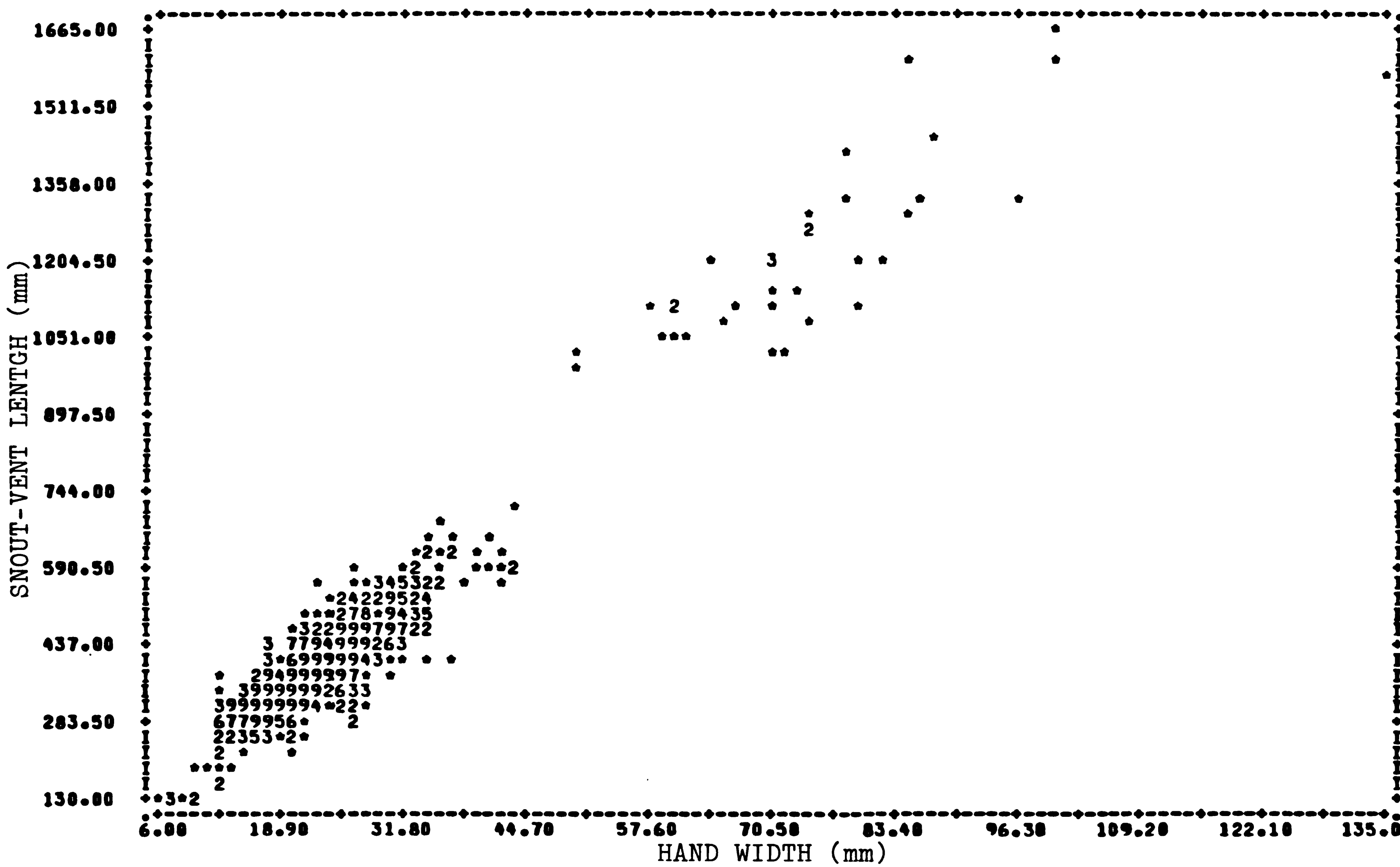


Figure 8j. Hand width (HW).

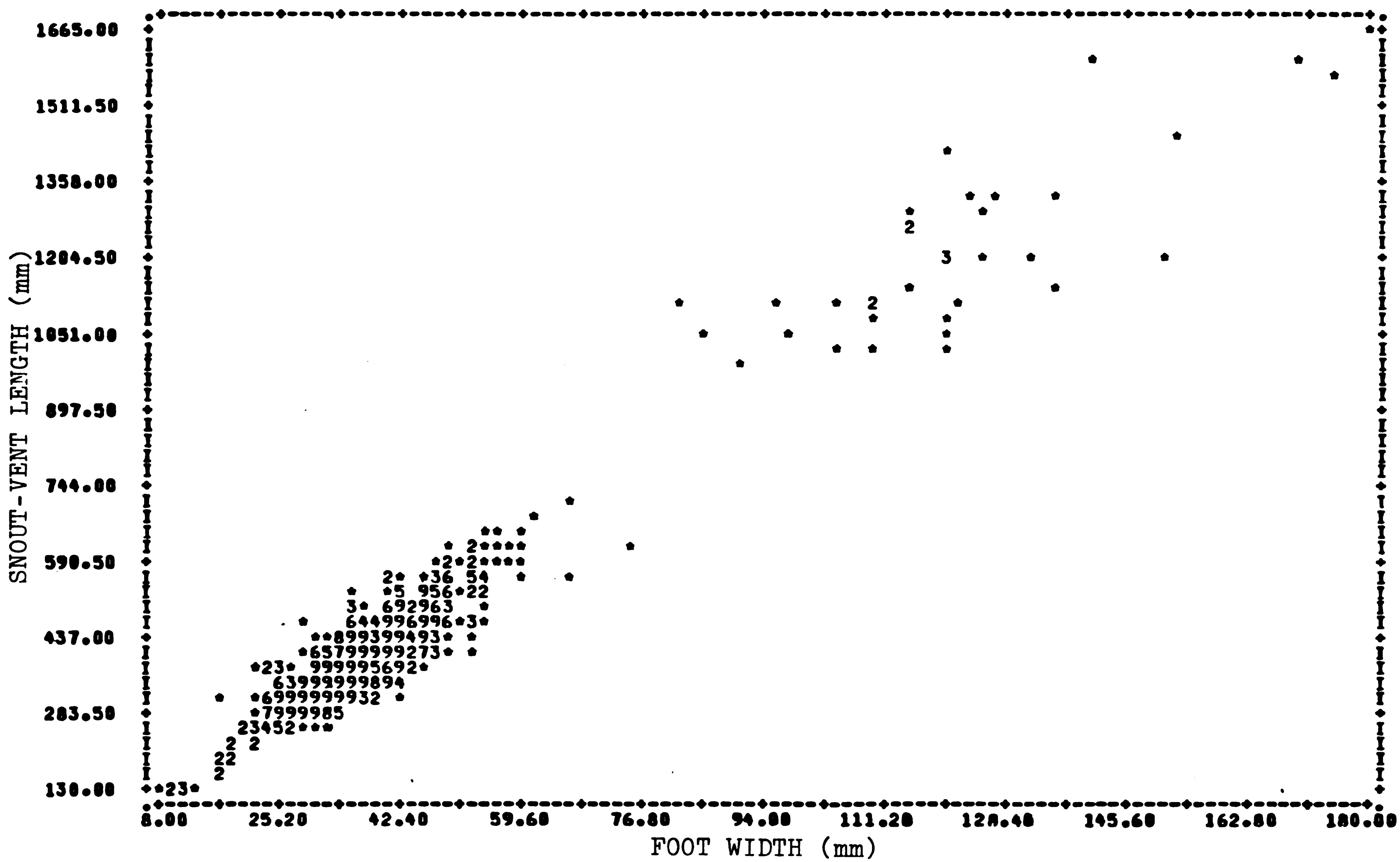


Figure 8k. Foot width (FW).

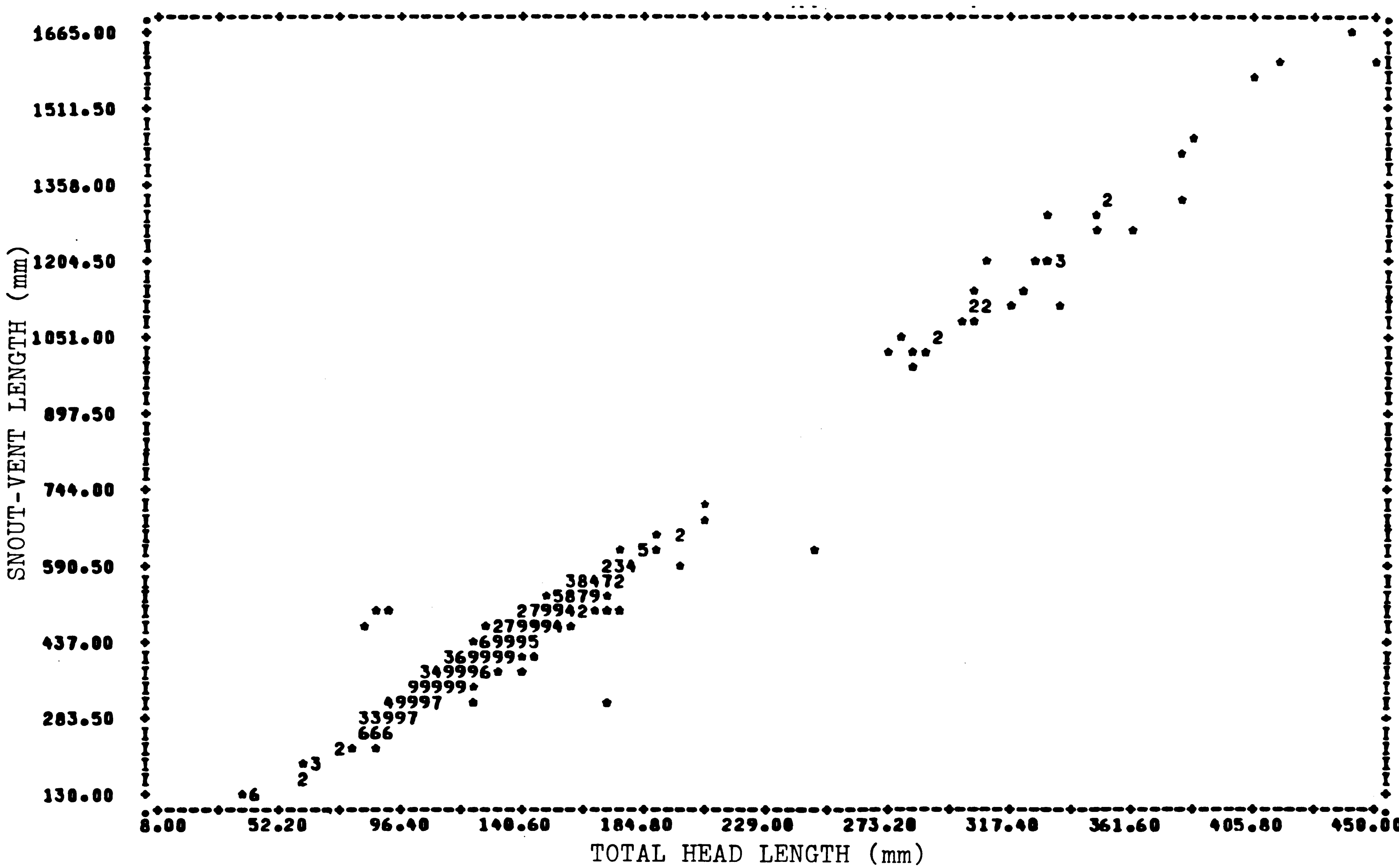


Figure 81. Total head length (HTL).

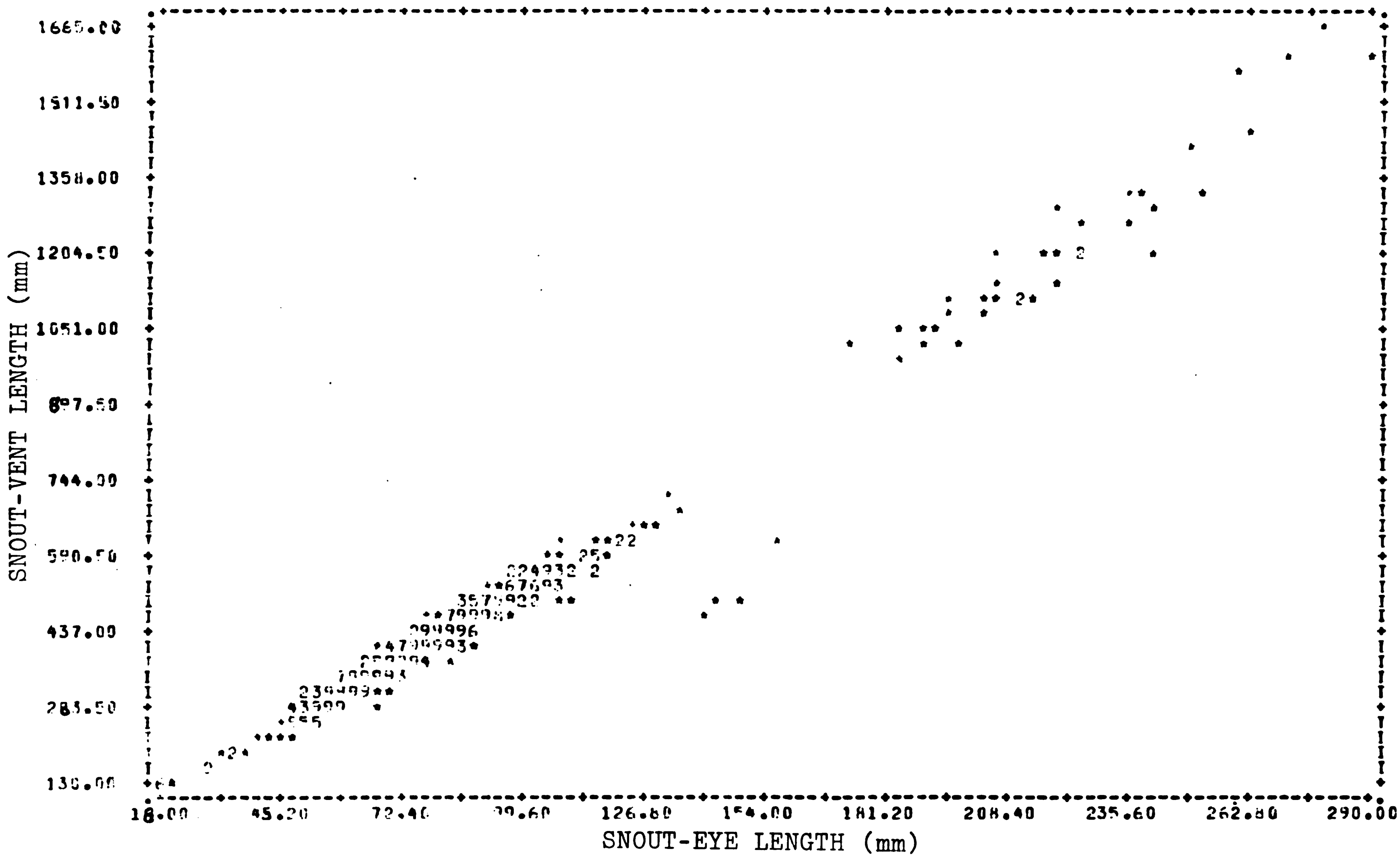


Figure 8m. Snout-eye length (HSE).

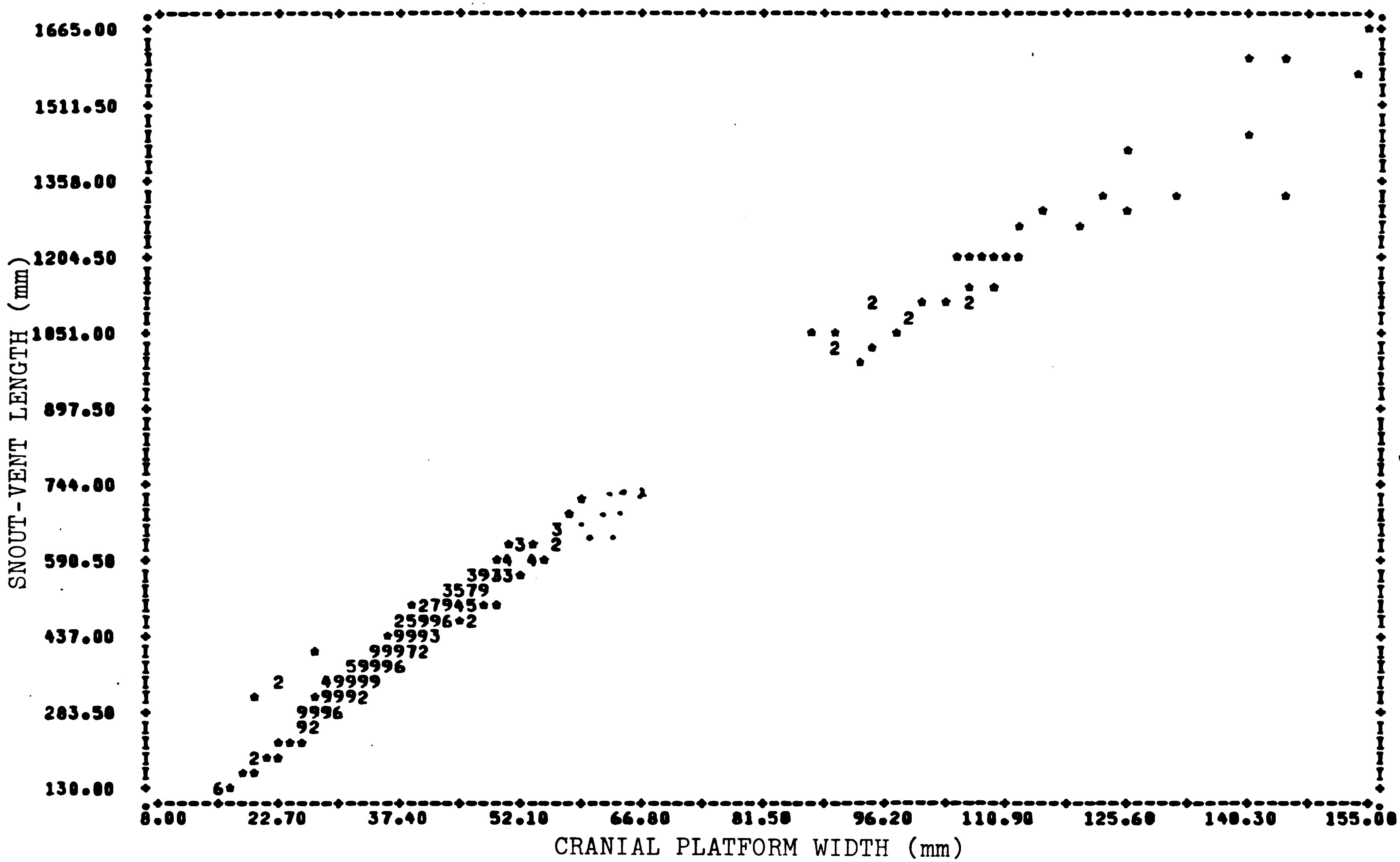


Figure 8n. Cranial platform width (HPP).

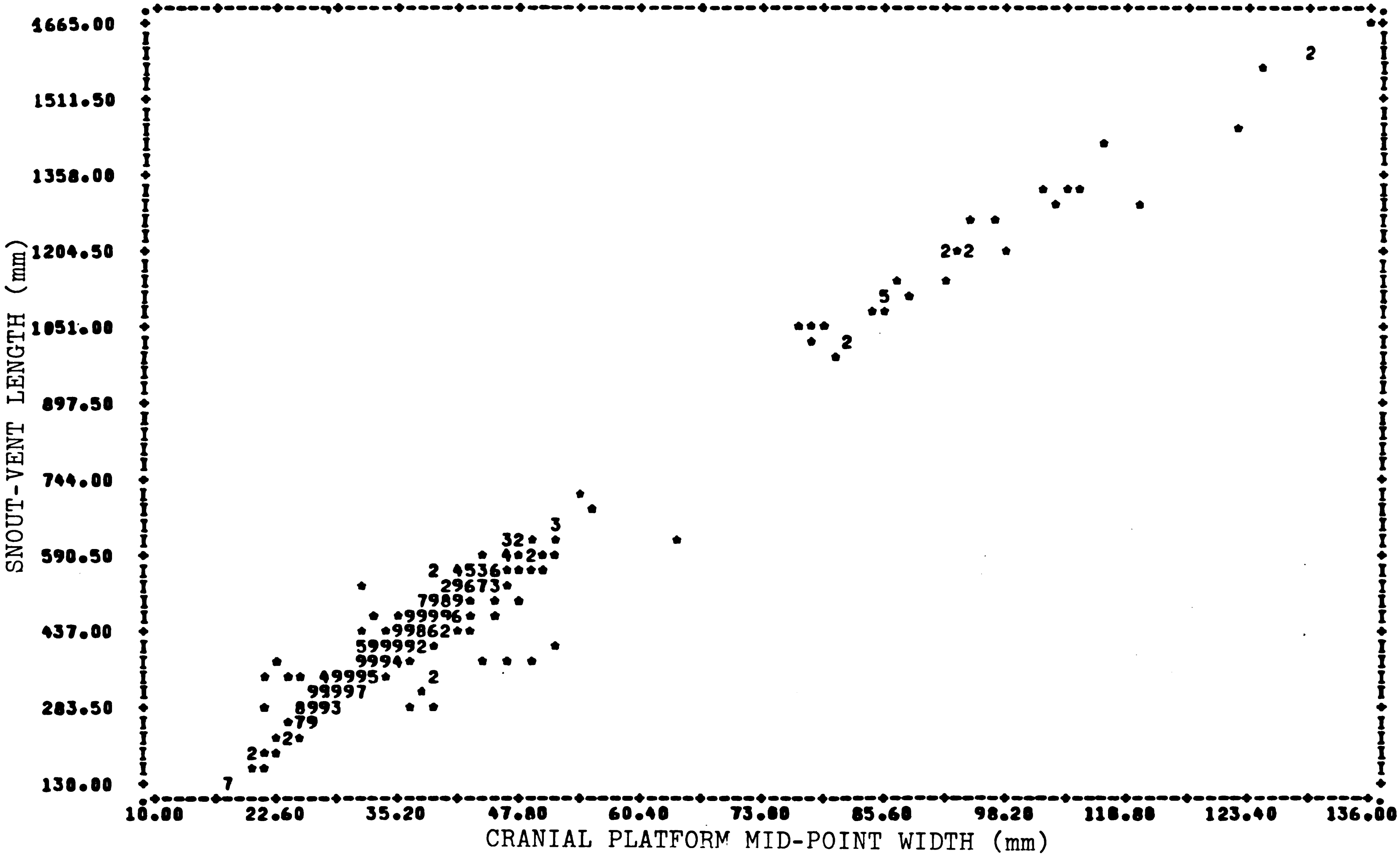


Figure 8o. Cranial platform mid-point width (HMP).

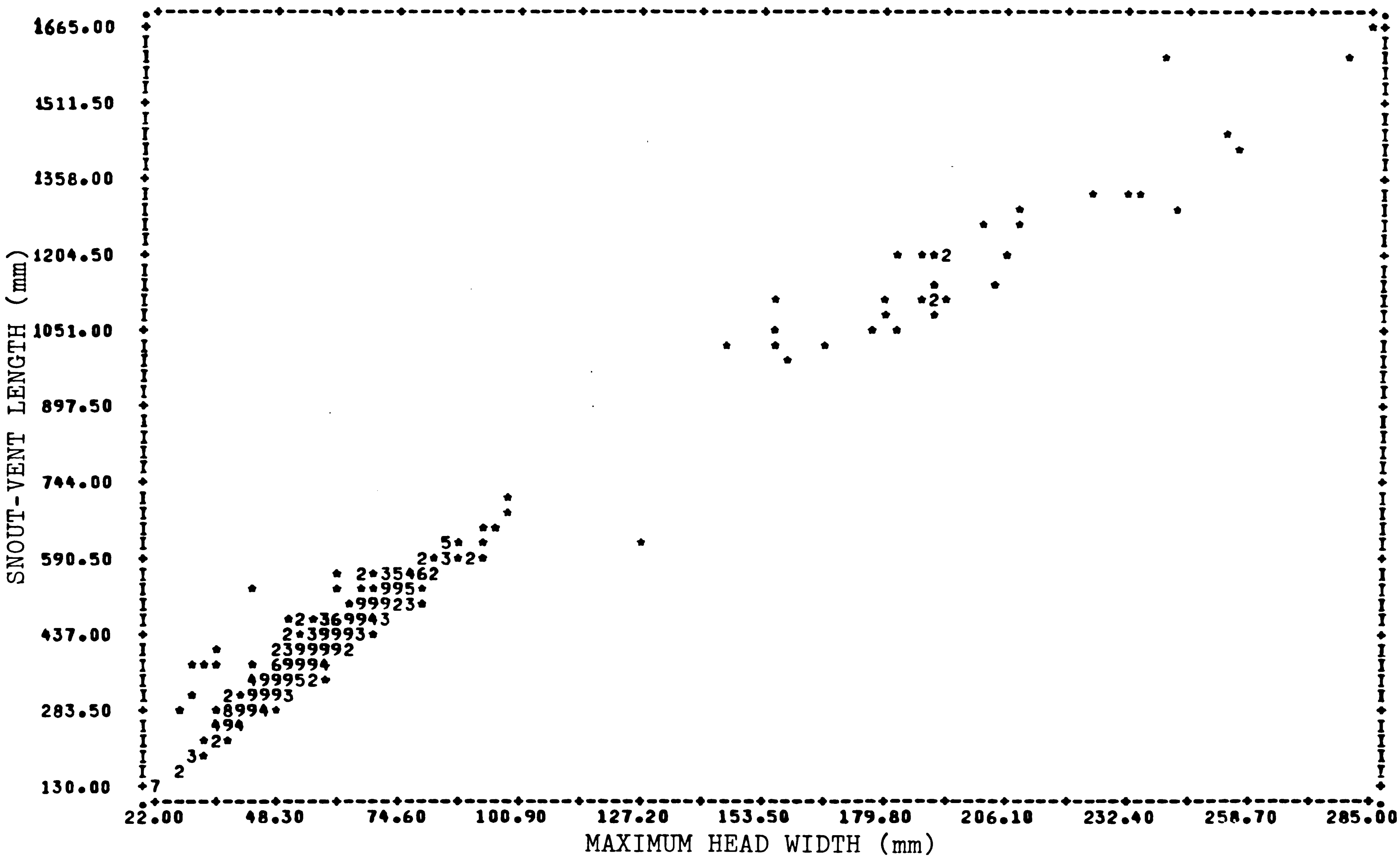


Figure 8p. Maximum head width (HMW).

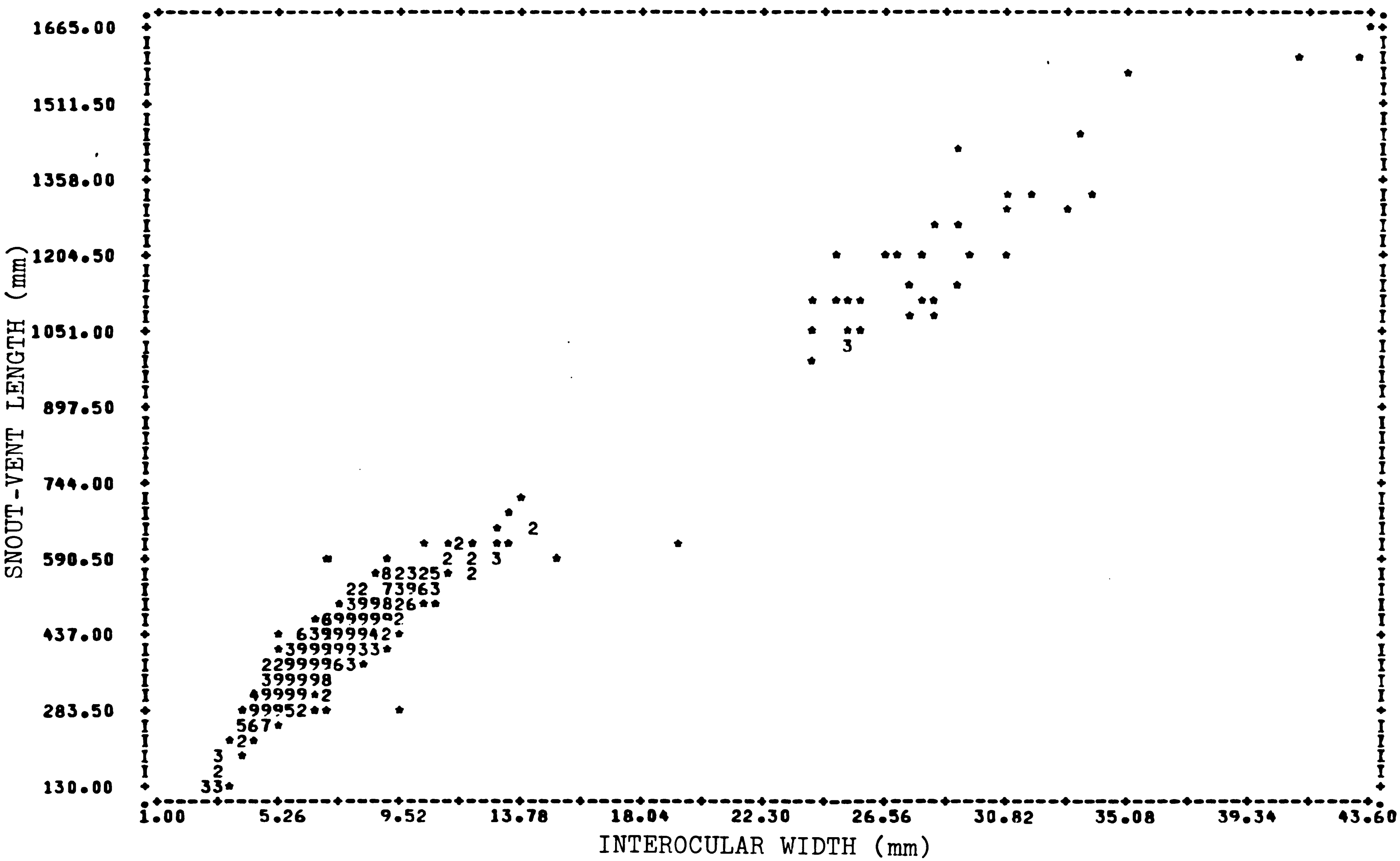


Figure 8q. Interocular width (HIO).

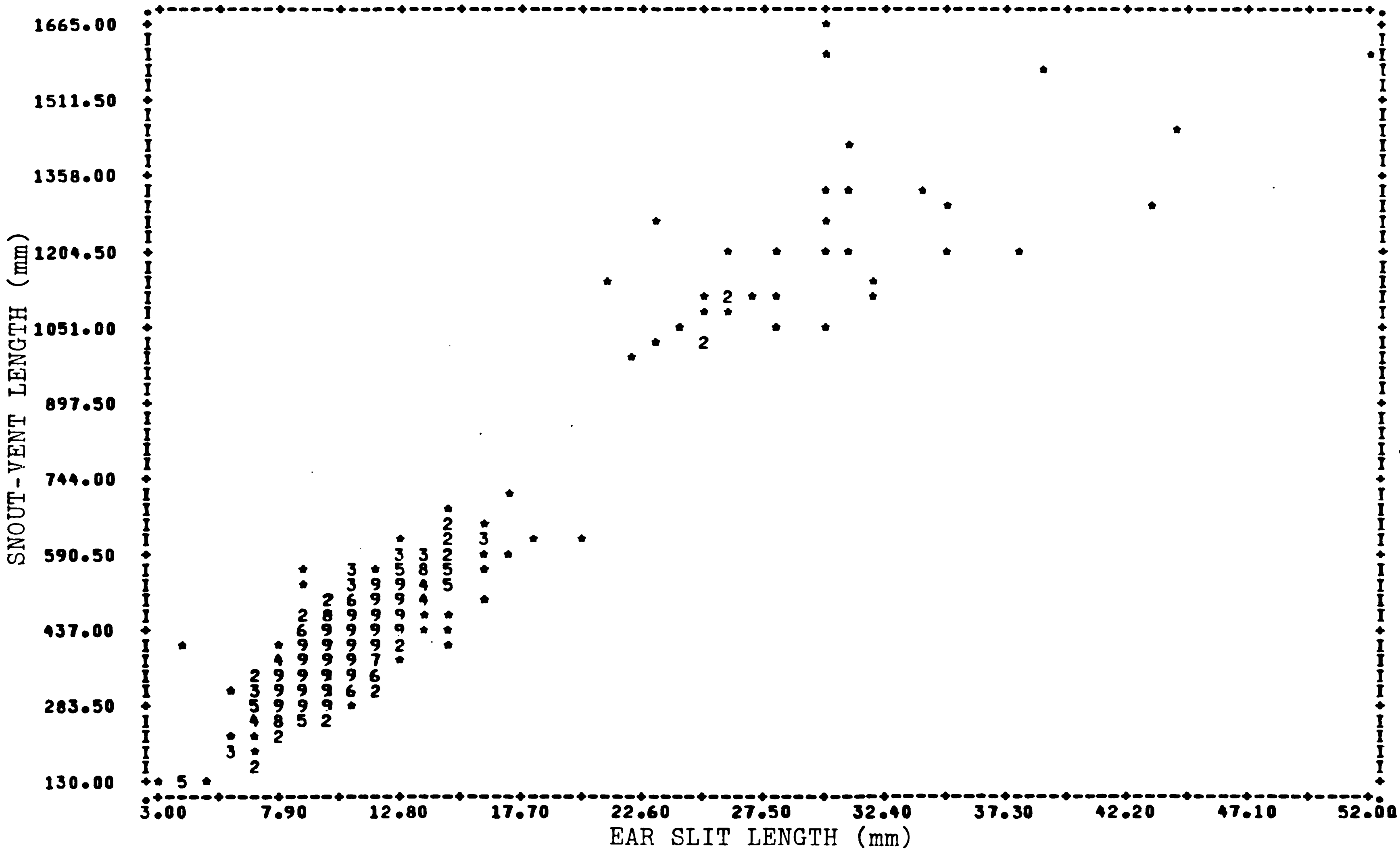


Figure 8r. Ear slit length (EL).

Table 4. Coefficients for predicting snout-vent length from other parameters in wild (unless designated "farmed") C. novaeguineae by linear regression analysis,* Western Province, PNG, 1978 - 1980.

A = Y-intercept; B = slope; E = standard error of the estimate; R^2 = correlation coefficient; N = number of crocodiles.

Eqn No.	Predictor X	Ranges (cm)	Sex**	A	B	E (cm)	R^2	N
1	Total length (TL)	29-100		-1.46	0.51	0.72	.988	923
2		101-335		5.73	0.49	4.15	.946	150
3	Tail length (TAL)	16-50		-0.13	0.97	2.14	.893	923
4		51-168.5		22.31	0.87	8.02	.809	150
5	Trunk length (TRL)	8-35		2.05	1.36	0.90	.981	923
6		36-122		4.90	1.32	1.48	.993	150
7	Neck girth (NG)	4-19		8.41	2.12	2.45	.859	923
8		20-48		33.06	1.72	2.86	.618	114
9		49-105		51.69	1.10	4.64	.935	36
10	Belly-width (BW)	4-17		9.87	2.18	2.79	.818	923
11	(farmed)	15.7-40		22.73	1.47	6.62	.891	163
12		18-100		40.28	1.32	8.30	.797	150
13	Mid girth (MG)	6-30		7.58	1.39	2.31	.875	923
14		31-145		36.62	0.89	5.45	.910	150
15	Tail girth (TG)	4-20		7.38	2.02	2.40	.865	923
16		21-98		36.12	1.30	5.79	.891	150
17	Hand width (HW)	0.6-2.9		13.32	11.46	3.76	.669	923
18		3-7.5	F	7.04	15.38	6.13	.940	74
19		3-13.5	M	10.48	13.96	6.63	.919	76
20	Foot width (FW)	0.8-4.5		11.00	7.78	3.74	.672	923
21		4.6-18		45.04	6.46	10.63	.657	150
22	Platform width (HPP)	1.5-4.5		-1.07	10.87	3.26	.956	923
23		4.6-15.5		7.30	10.26	4.28	.961	147

24	Platform mid point (HMP)	1.7-4 and 4.1-9.5 F	-5.72	13.69	2.46	.858	997
25		4.1-13.6 M	2.25	12.06	2.94	.984	76
26	Interocular width (HIO)	0.3-1.7	8.48	46.70	2.88	.806	1037
27		1.8-4.3	28.91	32.46	7.46	.831	36
28	Ear length (EL)	0.3-1.2	4.59	33.52	4.13	.601	923
29		1.3-5.2	71.61	17.31	13.92	.411	150
30	Maximum head width (HMW)	2-13	1.34	7.07	1.93	.913	1037
31		13.1-29.0	39.91	4.20	10.64	.656	36
32	Snout-eye length (HSE)	1.7-19	4.81	4.78	2.55	.929	1037
33		19.1-28	-6.99	5.91	5.71	.901	36
34	Total head length (HTL)	4-29.2	3.84	2.98	2.55	.848	1037
35		29.3-45.0	-4.54	3.85	4.38	.942	36
36	Log body weight (LBWT)***	53-21000	1.659	0.3077	0.018	.953	1037
37	(farmed)	1200-20700	1.760	0.272	0.062	.987	163
38		22000-186000	1.683	0.2920	0.013	.951	36

*Of the form Y = A + BX $\pm$ E.
**Formulae are for both sexes unless otherwise indicated by F or M.
***Body weight in grams, snout-vent length in mm.

Table 5. Coefficients for predicting body measurements from snout-vent length in wild (unless designated "farmed") C. novaeguineae by linear regression analysis,* Western Province, PNG, 1978 - 1980.

A = Y-intercept; B = slope; E = standard error of the estimate; R^2 = correlation coefficient; N = number of crocodiles.

Eqn No.	Predictor X	Ranges SVL (cm)	Sex**	A	B	E	R^2	N
39	Total length (TL)	13-50		3.75	1.93	1.40	.988	923
40		100-167		1.54	1.93	8.25	.947	150
41	Tail length (TAL)	13-50		4.29	0.919	2.08	.893	923
42		51-167		1.60	0.934	8.25	.809	150
43	Trunk length (TRL)	13-50		-0.98	0.722	0.66	.981	923
44		51-167		-3.22	0.757	0.85	.994	150
45	Neck girth (NG)	13-50		-1.45	0.405	1.07	.860	923
46		51-99		-11.30	0.596	2.17	.618	114
47		100-167		-39.45	0.846	4.07	.935	36
48	Belly-width (BW)	13-50		-1.37	0.376	1.16	.818	923
49		51-99		-9.63	0.540	2.32	.537	114
50	(farmed)	40-84		-10.64	0.595	5.24	.898	163
51		100-167		-10.87	0.598	5.58	.791	36
52	Mid girth (MG)	13-50		-2.05	0.631	1.56	.875	923
53		51-99		-11.73	0.816	3.38	.554	114
54		100-167		-28.44	1.017	5.82	.910	36
55	Tail girth (TG)	13-50		-1.13	0.429	1.11	.866	923
56		51-99		-7.22	0.540	2.08	.590	114
57		100-167		-18.19	0.694	4.24	.898	36
58	Hand width (HW)	13-50		-0.07	0.058	2.69	.669	923
59		51-127	F	-0.47	0.065	0.37	.934	74
60		51-167	M	-0.75	0.072	0.96	.919	76

61	Foot width (FW)	13-50		0.19	0.086	0.39	.672	923
62		51-99		-0.53	0.096	0.42	.523	114
63		100-167		-0.39	0.102	1.33	.657	36
64	Platform width (HPP)	13-50		0.11	0.092	0.72	.956	923
65		51-167		-0.68	0.097	0.64	.961	150
66	Platform mid-point (HMP)	13-50		0.81	0.063	0.17	.838	923
67		51-127	F	0.34	0.073	0.21	.988	74
68		51-167	M	-0.16	0.083	0.20	.981	76
69	Maximum head width (HMW)	13-50		0.28	0.129	0.26	.913	923
70		51-99		-0.66	0.149	0.57	.594	114
71		100-167		0.65	0.156	2.05	.656	36
72	Snout-eye length (HSE)	13-99		-0.44	0.194	0.35	.929	1037
73		100-167		3.25	0.152	0.92	.901	36
74	Total head length (HTL)	13-99		0.64	0.286	0.79	.848	1073
75		100-167		3.06	0.245	1.11	.942	36
76	Interocular width (HIO)	13-50		-0.03	0.017	0.06	.806	923
77		51-99		-0.60	0.029	0.14	.445	114
78		100-167		-0.25	0.025	0.21	.830	36
79	Ear slit length (EL)	13-50		0.31	0.018	0.10	.602	923
80		51-167		0.08	0.024	0.52	.362	150
81	Log body weight (LBWT)***	130-500		-4.900	3.097	0.056	.953	923
82	(farmed)	400-840		-6.188	3.574	0.063	.987	163
83		501-1670		-5.240	3.255	0.068	.951	150

*Of the form Y = A + BX ± E.

**Formulæ are for both sexes unless otherwise indicated by F or M.

***Body weight in grams, snout-vent length in millimeters.

minimum, it was necessary to perform linear regression analysis on data grouped into homogeneous classes of size, sex and captive status. Thus, equations are presented (Tables 4 and 5) for: ≤ 50 cm, 51-99 cm, and ≥ 100 cm SVL classes; male or female; and wild or farmed, when such groupings significantly improved prediction accuracy over equations derived from data including all subclasses.

As an example of how to use these tables, a wild crocodile with a belly-width (X) of 20 cm can be calculated from Table 4 to possess a SVL (Y) of:

$$Y = A + BX + E$$

$$\text{eqn. no. 12} \quad = + 40.28 + 1.32(20) \pm 8.3$$

$$= 66.7 \pm 8.3 \text{ cm}$$

The best estimators of SVL which were not composed primarily of SVL and would also be the most useful in the field were HSE, HPP and HMP, with correlation coefficients of above .97. Not surprisingly, the best predictors of SVL were TL (= SVL + TAL) and TRL (= SVL - HTL), which were largely composed of SVL. Tail length (TAL) would also be in this class of good predictors if tail tips were not sometimes missing. Girth measurements were intermediate in variability with commercial belly-width (BW) (essentially a girth measure) being the worst of the girth estimators. Hand (HW) and foot width (FW) were even worse predictors of SVL than girth parameters. The variation in these two measurements is deemed due primarily to difficulties in securing measurements in the field and not to variation within the population. The worst predictor of SVL was ear slit length (EL) with a correlation coefficient, with all data pooled, of .89.

Predicting Body Dimensions from SVL

In order to predict other body dimensions when SVL is known, another set of linear regression equations was determined using SVL as the independent variable (Table 5). When using Table 5 to predict a body dimension from a SVL that was derived from Table 4, however, it must be understood that the standard error of the estimate is determined by:

$$E_3 = \sqrt{((b_2 E_1)^2 + E_2^2)},$$

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).

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 c. 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 6). 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 6 is used in an equation from Table 4 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 5 to predict other body attributes, then the resulting standard error of the estimate (E_4) is calculated by:

$$E_4 = \sqrt{((b_3\ E_2)^2 + E_3^2)},$$

where b_3 is the slope of the third equation, E_2 is the error of the second equation and E_3 is the error from the third equation.

Sexual Dimorphism

Female crocodile morphometrics, on the average, displayed less variability than males. Other than the maximum adult size of males (Table 7), the only measurements in which males and females seemed to differ were hand width and platform mid-point width. Male hands were c. 6% wider than females' (Table 4, equations 18 and 19; Table 5, equations 59 and 60). But regression equations for these two parameters were not significantly different ("F" test, $P > .10$) between sexes.

Table 6. Coefficients for predicting live (fresh) head length (HTL) from other head attributes in *C. novaeguineae* skulls by linear regression analysis*, Western Province, PNG, 1978 - 1980.

A = Y-intercept; B = slope; E = standard error of the estimate; R^2 = correlation coefficient; N = number of crocodiles.

Eqn No.	Predictor X	Ranges (cm)	A	B	E (cm)	R^2	N
84	Snout-eye length (HSE)	14-31	0.68	1.48	1.0	.988	21
85	Platform width mid-point (HMP)	6-13.5	3.08	3.45	1.1	.945	20
86	Platform width (HPP)	6.4-17.5	9.55	2.40	1.2	.937	20
87	Maximum head width (HMW)	11-28.5	11.35	1.25	1.2	.936	19
88	Interocular width (HIO)	1.9-4.8	9.65	8.34	1.4	.915	21

*Of the form $Y = A + BX \pm E$.

Table 7. Morphometric ranges in centimeters and kilograms for 1,073 wild *C. novaeguineae*, Western Province, PNG, 1978 - 1980.

Parameter	Minimum (hatchling)	Maximum Female	Maximum 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 (HPP)	1.55	12.0	15.5
Cranial platform midpoint (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

Sex Ratio

A male/female sex ratio of 51.3% males and 48.7% females, or approximately 1:1 ("Z" test, α.10) was found for 2,031 wild C. novaeguineae which measured between 50-167 cm SVL (Table 8) when captured in the Fly River drainage, PNG.

Geographic Variation

The separate scattergrams, regression slopes, and intercepts generated using SVL as the dependent variable and other head attributes as the independent variable showed that, in these characteristics, populations from each of the nine geographic locations (Table 2) were not significantly different from each other. Geographic variation in external body structural dimensions evidently does not occur among New Guinea crocodiles within PNG's Fly River drainage.

Relative Growth and Growth Form

Principle component analysis conducted using SPSS program FACTOR showed the first axis to be size. The first eigen value was 95.6%, so only 4.4% of the variance resulted from factors other than size. 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 9).

Table 8. Sex ratio of wild - hatched C. novaeguineae when examined at sizes between 50 - 167 cm SVL, Fly River drainage, Western Province, PNG, 1978 - 1980.

Group Identity		% males		total #
Baboa Farm*		49.8		633
Buying Scheme**		52.0		1398
	Average	51.3	Sum	2031

*Wild caught but reared in captivity.
**Freshly caught.

Table 9. Allometric coefficients (after logarithmic transformations) for predicting snout-vent length from other New Guinea crocodile attributes, Western Province, PNG, 1978 - 1980. N = 35 animals, 26 - 167 cm SVL.

A = Y-intercept; B = slope; E = standard error of the estimate; R^2 = correlation coefficient.

Eqn No.[a]	Predictor Log X	A	B	Significance[b]	R^2
89	Belly-width (BW)	0.676	0.800	***	.989
90	Neck girth (NG)	0.645	0.804	***	.991
91	Tail girth (TG)	0.594	0.826	***	.996
92	Mid girth (MG)	0.438	0.840	***	.989
93	Interocular width (HIO)	1.719	0.850	***	.987
94	Maximum head width (HMW)	0.912	0.910	***	.994
95	Hand width (HW)	1.287	0.924	*	.981
96	Foot width (FW)	1.080	0.943	*	.989
97	Trunk length (TRL)	0.233	0.947	No	.998
98	Snout-eye length (HSE)	0.786	0.963	No	.995
99	Platform width (HPP)	1.021	1.023	No	.993
100	Total length (TL)	-0.380	1.038	**	.999
101	Tail length (TAL)	-0.139	1.079	***	.997
102	Total head length (HTL)	0.429	1.087	***	.999
103	Ear slit length (EL)	1.570	1.116	***	.991
104	Platform mid-point width (HMP)	0.980	1.149	***	.991

[a] Groupings indicate that allometric coefficients (B) were not significantly different from each other at p = .05 (p = .02 for TAL and HTL).

[b] Designates if B is significantly different from 1.0 at p = .05(*), p = .02(**) and p = .01(***).

Only three parameters, platform point-to-point width (HPP), snout eye length (HSE) and trunk length (TRL), were truly isometric (slopes = 1.0) (Table 9), changing in direct proportion to body size. Hand and foot width were very near isometry while total length (TL), which significantly differed from 1.0 at $p = .02$ but not at $p = .01$, showed slight positive allometry (slope > 1.0). Positive allometry, which indicates an increasing growth rate with increasing size, was pronounced for HMP, HTL, EL and tail length (TAL). Strong negative allometry (slope < 1.0) (significant at $p = .01$), 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 dimensions, belly-width and HIO had allometric coefficients that were not significantly different from each other (Table 9). 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 only related 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 7) have convex sides, making the HPP/HMP ratio < 1. As crocodiles approach

28-32 cm SVL this ratio = 1. Larger crocodiles have concave cranial platforms where HPP exceeds HMP and the HPP/HMP ratio is $>$ 1. The growth rate of interocular width (HIO) decreased markedly in relation to increasing SVL to c. 28 cm SVL. But at larger SVLs, HIO growth decreased at a steadily slower rate. All girth growth rates decreased quite rapidly up to c. 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 c. 55 cm SVL. Above that size, weight increased at a steadily increasing rate (allometric slope $>$ 3.0, Table 5), until at the largest size class, tiny changes in SVL represented gross increases in body weight (Figure 8d). For instance, a 25% increase in the length of a 100 cm SVL crocodile would result in a weight increase of well over 100%.

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, using equation 12 (Table 4), have a SVL of 106 $\pm$ 8.3 cm or a total length, using equation 40 (Table 5), of 205 $\pm$ 19.7 cm. Females of this species begin to lay eggs at a total length (TL) of c. 180 cm (Neill 1946, Jelden 1981, Callis pers. comm., pers. obs.). At that length they would have an estimated belly-width, using equation 2 (Table 4) and equation 51

(Table 5), of 41 ± 3.3 cm (c. 16 in). This is a figure far below the 50.8 cm BW (Lawrence 1977) or 205 cm TL currently set as the minimun size limit in an effort to protect breeders. Most captive males begin breeding at c. 200 cm TL (Whitaker 1979, Bolton 1981b, Callis pers. comm.), 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 mortality for 4-6 years (based on growth rates presented below) before they grow to the legal size. Montague (1982a) has shown that approximately 36% of the crocodiles ≥41 cm (16 in) BW in the Fly River drainage were less than 50.8 cm (20 in) belly-width. Utilizing 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 favor 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 (see below).

Differences Between Wild and Farmed Crocodiles

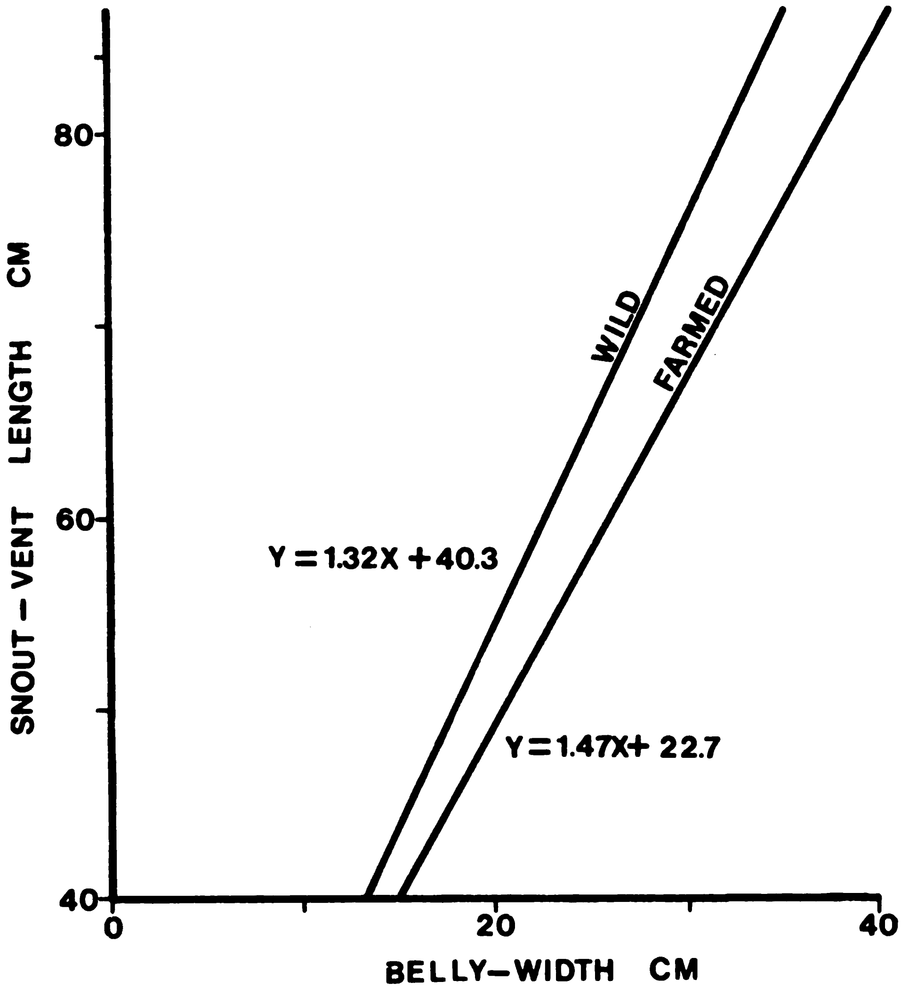
The regression equations relating SVL to TL in 163 farmed C. novaeguineae were not significantly different from those of wild crocodiles. But those equations relating SVL to belly-width (BW) (Table 4, equations 11 and 12; Table 5, equations 49 and 50) showed that farmed crocodiles had greater girth than wild crocodiles of the same SVL ("F" test; $P < .001$). 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 (Figure 9). For a wild 40.6 cm (16 in) BW crocodile, the proposed maximum legal skin size, this differential had increased to 16 cm (19.6%) in SVL (Figure 9).

The gap between wild and farmed crocodiles was not as great when relating SVL to BWT (Table 4, equations 37 and 38; Table 5, equations 82 and 83) but was still significant ("F" test; $P < .01$). Both farmed and wild crocodiles of 50 cm SVL weighed about the same, but at 84 cm SVL, farmed crocodiles were c. 12.5% heavier than wild ones. This differential may be even greater in larger, overfed crocodiles but data were not collected for any such farmed animals.

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 short-

Figure 9. Relation of belly-width (BW) to snout-vent length (SVL) in wild (N = 150) and captive (N = 163) *C. novaeguineae* from the Fly River drainage, PNG.


SNOUT - VENT LENGTH CM
80
60
40
WILD
FARMED
Y = 1.32X + 40.3
Y = 1.47X + 22.7
0
20
40
BELLY-WIDTH CM

change the crocodile skin buyer or seller due to 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 seems a single measure system will remain.

Belly-width has the largest standard error of the four girth measures, when used to predict SVL (Tables 4 and 5). 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 4 and 5), showed the least variability of the girth parameters. 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 that is not necessarily representative of girth over all parts of the animal. Since SVL cannot be measured on skins alone, it therefore might well be advocated to replace belly-width with neck girth as the standard crocodile trade measurement.

Mandibular Tooth Protrusion through the Premaxilla

The smallest _C. novaeguineae_ exhibiting mandibular tooth protrusion was a 28 cm SVL female with one tooth visible through the premaxilla, the most anterior bone of the upper jaw. 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 10), both mandibular teeth (54.3%) tended to protrude. All of the crocodiles examined between 71 cm and 100 cm SVL had protruding mandibular teeth (Table 10) and all over 71 cm SVL with protruding teeth had both teeth protruding.

Three of the 9 C. novaeguineae over 100 cm SVL with protruding mandibular teeth had indentations in the premaxilla rather than holes for the protruding teeth (Figure 10). Of the crocodiles over 100 cm SVL, 74% had tissue formed over the 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 predominant in females in the 21-70 cm SVL classes, but was statistically significant ("Z" test; $P < .05$) 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.

Table 10. Number of wild New Guinea crocodiles with one or two mandibular teeth protruding through the premaxilla, Fly River drainage, PNG, 1978 - 1980.

Size range in cm SVL	Number of crocodiles: Sex: Male	Female	Unknown	Total	% of total with protruding teeth	Crocodiles 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	1,073			

Figure 10. Types of mandibular tooth protrusion through the premaxilla in *C. novaeguineae*. (A) teeth protrude through holes (B) teeth protrude through indentations.

Differences Between New Guinea and Saltwater Crocodiles

Linear regression equations (Tables 4 and 5) for *C. novaeguineae* were compared to such equations describing identical parameters at similar size intervals in Australian *C. porosus* specimens (Webb and Messel 1978a). 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.

C. novaeguineae 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 c. 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. novaeguineae* (Table 7), saltwater crocodile TALs were c. 12% longer. Total length in relation to SVL also began to increase more quickly in *C. porosus* over 23 cm SVL and at 167 cm SVL, was c. 5.5% longer than *C. novaeguineae*.

Since TAL was roughly ½ 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 saltwater crocodile tail. The remainder of the difference in TL between the two was explained by the shorter C. porosus trunk.

Trunk length in the two species showed both a different Y-intercept and slope. The point at which morphological divergence between the two species began was also at 23 cm SVL for TRL. At that size, C. noveaguineae TRL began to be proportionately longer than C. porosus, and at 167 cm SVL, 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 (26% wider at 167 cm SVL) than C. porosus. None of the linear regression comparisons had different intercepts and similar slopes.

Comparisons of the scattergrams relating to body dimensions to SVL between the two species showed that all of the parameters except EL had similar degrees of spread. 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 of *C. porosus* showed slight negative allometry (curvature) for narrower hands and feet above 130 cm SVL. To the contrary, *C. novaeguineae* scattergrams indicated slight positive allometry for a wider foot above 100 cm SVL. Hand width in this latter species was linear throughout the larger size classes of both sexes.

Abnormalities and Injuries

Abnormalities and injuries are presented in their order of frequency in the New Guinea crocodiles sampled.

Parasite tracks: The most common abnormality, affecting 12.8% of the population (Table 11), was tracks on the ventral surface, resulting from the activities of the nematode parasite *Paratrichosoma crocodilus* (Ashford and Muller 1978) (Figure 11). The smallest size at which parasite tracks occurred was 27 cm SVL and the largest a 127 cm SVL female. The incidence of parasite tracks increased steadily from a low of 1.3% in the 21-30 cm SVL class to a high of 50% in the 71-80 cm SVL class (Table 11). There was a strong positive correlation between SVL and incidence of ventral parasite tracks when neglecting the largest size class. That size class reflected a reduction in the incidence of this phenomenon.

The occurrence of parasite tracks was significantly dependent on the animals' capture location ("X^2" test;

Table 11. Frequency of abnormalities and injuries in 1,073 wild <u>C. novaeguineae</u> from the Fly River drainage, PNG, 1978 - 1980.

Size in cm SVL	13-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100	101-110	111-167	total	% total
# Examined	11	77	498	338	96	15	2	1	0	11	24	1073	
# Injured	7	11	92	158	55	8	2	1	0	2	7	343	
% Injured	63.6	14.3	18.5	46.7	57.3	53.3	100	100	-	18.2	29.2	-	32.0
Category													
Parasite tracks	0	1	29	65	31	6	1	0	0	0	4	137	12.8
Leeches	0	3	30	30	13	1	1	1	0	0	0	79	7.4
Blue abdomen	0	1	14	22	4	0	0	0	0	0	0	41	3.8
Deformed trunk	0	0	7	14	1	0	0	0	0	0	0	22	2.1
Tail amputated	0	3	3	8	3	0	0	0	0	2	3	22	2.1
Digits amputated	0	3	1	9	0	0	0	0	0	0	0	13	1.2
Eye injuries	0	0	3	2	2	1	0	0	0	0	0	8	.75

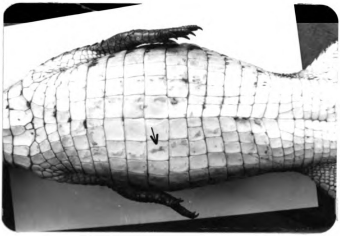
Yolk scars	7	0	0	0	0	0	0	0	0	0	0	7	.65
Humpbacked	0	0	0	5	0	0	0	0	0	0	0	5	.47
Crushed platform	0	0	3	1	0	0	0	0	0	0	0	4	.37
Misaligned jaw	0	0	2	0	0	0	0	0	0	0	0	2	.19
Toenails missing	0	0	0	1	0	0	0	0	0	0	0	1	.09
Growths (snout)	0	0	0	0	1	0	0	0	0	0	0	1	.09
Deformed tail	0	0	0	1	0	0	0	0	0	0	0	1	.09

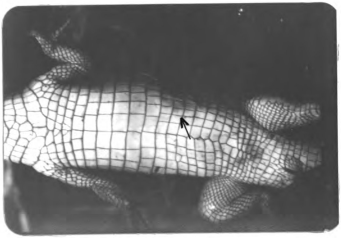
Figures 11 - 18. Abnormalities and injuries identified for 1,073 wild C. novaeguineae from the Fly River drainage, PNG, 1978 - 1980.

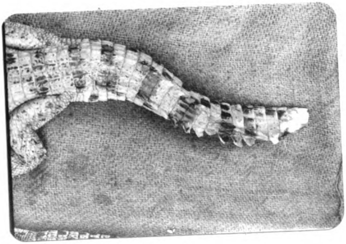
Figure 11. Tracks of the nematode parasite Paratrichosoma crocodilus on venter.

Figure 12. Bluish blotches on venter.

Figure 13. Severe tail amputation.







$P < .05$). Of the animals taken from the June and Strickland Rivers, 19% had tracks. The Mamboi, Leva and Kaim Rivers and Lake Murray localities were similarly high with values from 10-15% of the population. Few such parasite tracks were found on crocodiles from the other rivers and none were found on animals from the Agu.

This parasite significantly reduced the mean body weight of affected animals ("F" test; $P < .001$) and probably similarly lowers growth rates. In severe cases, it also reduces the market value of the belly skin (King and Brazaitis 1971). These nematode parasites were the most abundant abnormality afflicting these crocodiles and were indeed deleterious to the animals themselves.

Leeches: Unidentified leeches were found on 79 (7.4%) of the New Guinea crocodiles examined. Leeches were attached to the crocodiles either singly or in groups primarily at the junction of the two rows of raised anterior scutes and the single median row of scutes on the tail, between the digits, and around the eyes. The leeches were black in color and ranged from 4-12 mm in length. The single exception was the presence of white leeches on one of the animals from the Mamboi River.

Although no leeches were found in the smallest and largest size classes (Table 11), there was no correlation between body size and leech occurrence. Neither was there a significant difference in the mean body weight between crocodiles with leeches and those without them ("F" test; $P > .001$). Few of the attached leeches were engorged with blood.

Leeches, like nematode parasite infestations, were strongly dependent on capture location ("X^2" test; $P < .005$). Twenty percent of the crocodiles from the Mamboi River had leeches, while the percentage from Lake Murray, Strickland, Kaim and Leva Rivers ranged from 6-12%. The other four rivers produced crocodiles that seldom had leeches.

Blue blotches: Bluish blotches of unknown cause were found on the venter of 41 (3.8%) of the crocodiles examined. Although local Kune tribesmen felt that the discoloration (Figure 12) resulted from staining by extracts of the sago palm (*Sago* spp.), this explanation was never verified. The phenomenon occurred only on crocodiles between 21-60 cm SVL, and did not seem to affect the animals' health or reduce their market value. These blotches were slightly correlated with the location of capture ("X^2" test; $P < .10$). The highest incidence of blotches (8.8% and 9.7%, respectively) was from the Fly and June Rivers, two very different habitats.

Deformed trunk: On 2.1% of the crocodiles, the rib cage or lower back was malformed. The phenomenon, appearing as an indentation, was only found in crocodiles between 31-60 cm SVL, which indicates that the injury probably did not occur in hatchlings or adults.

Tail amputations: Tail amputations, presumably due to biting by other crocodiles or fish, were found in 2.1% of the population. In the 21-60 cm SVL size classes (Table 11), tail amputations ranged from 0.6-3.9% of the category sampled, but in animals over 100 cm SVL the frequency of injury was from 12.5-18.2%. Severe tail amputations doubtless affected the animals' swimming abilities (Figure 13), but in most cases only the tail tip was gone, probably having little effect on the animal. Small tail injuries were not recorded (Figure 14).

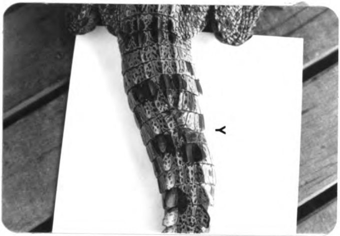
Digit amputations: Thirteen crocodiles (1.2%) had one or more amputated digits. These injuries were most prevalent in the 21-50 cm SVL size classes. Tail and digit amputations were the two most common evidences of violent injury.

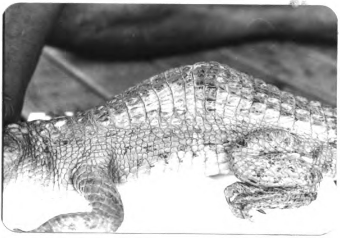
Eye injuries: Eight *C. novaeguineae* (0.75%) had injuries to one eye. None had both eyes damaged. One had a cataract, another's eye was swollen and bulging and six were totally blind in one eye as a result of massive injury or total removal. The incidence of injury increased from 0.6% of

Figure 14. Healed scar on the side of tail.

Figure 15. Hatchling with yolk scar.

Figure 16. Humpbacked crocodile.





the 31-40 cm SVL size class to 6.7% of the 61-70 cm SVL class. Evidently, blindness in one eye did not always severly affect the animals' survival.

<u>Yolk scars</u>: Although yolk scars are not really an abnormality or injury, since all hatchlings have them, they are mentioned here only because live crocodile buyers should be aware of them. Hatchlings with large yolk scars (Figure 15) require special captive care.

<u>Humpback</u>: Five crocodiles (0.5%) had humpbacks (Figure 16). All were in the 41-50 cm SVL class, corresponding roughly to an age of 2-3 years. Humpbacked crocodiles were otherwise in good physical condition.

<u>Broken cranial platform</u>: Four New Guinea crocodiles (0.4% of those examined) had wounds that crushed or removed portions of the cranial platform. In all four, the wounds healed well and did not seem to trouble the afflicted animals.

<u>Jaw misalignment</u>: Two <u>C. novaeguineae</u> (0.1% of all animals examined), both in the 31-40 cm SVL class, had misaligned jaws (Table 11). Afflicted animals had a poor bite. A farmed animal had a truncated mandible (Figure 17).

<u>Missing toenails</u>: One New Guinea crocodile was without claws on any digit. This was a rare (0.09% of the sample),

Figure 17. Truncated mandible in captive animal.

Figure 18. A 49 cm SVL female crocodile with a congenital tail deformity.

presumably congenital, abnormality that has not been recorded for any other crocodilian.

Growths: One *C. novaeguineae*, a 56 cm SVL female, had a round bump on its snout that was 18 mm in diameter and 6 mm high. A similar growth was described by Webb and Messel (1977a) on Australian *C. porosus*. Since the New Guinea crocodile was sold to a crocodile farm, the histological nature of the growth was not determined.

Deformed tail: One 49 cm SVL female New Guinea crocodile (0.09% of the 1,073 crocodiles examined) had kinks in its tail (Figure 18).

Of 26 *C. porosus* held at the Baboa Crocodile Station on Lake Murray, two died when clay formed permanent bowel obstructions (Figure 19). The clay, probably ingested while tunnelling or biting at food on a clay substrate, caused their abdomens to swell grotesquely from intestinal gases. This condition has also been reported in other salt-water crocodiles in PNG (Callis pers. comm.) and probably also occurs in *C. novaeguineae*.

Also at the Baboa Station, a 45 cm SVL female New Guinea crocodile was cannibalized when it tunnelled into a pen of the same species containing specimens 60-80 cm SVL (Figure 20). It is not known if cannibalism occurs in wild New Guinea crocodiles.

Figure 19. A captive C. porosus with a fatal bowel obstruction that probably also occur in C. novaeguineae.

Figure 20. A 45 cm SVL female C. novaeguineae which was cannibalized in captivity by 60 - 80 cm SVL crocodiles of the same species.

The only abnormality or injury whose incidence varied significantly between sexes were deformed trunks, which were more frequent in females.

Captive Juvenile Growth Rates

The 323 juvenile New Guinea crocodiles reared at the Baboa Crocodile Station, under conditions simulating the best village crocodile farm, grew at an average rate of 17 cm and 15.7 cm/yr total length for males and females, respectively (all size classes pooled). The corresponding rate of SVL increase was 8.7 cm and 8.1 cm/yr, respectively. Averaged over the 28-84 cm SVL range, males grew lengthwise faster than females "Z" test; $P < .10$). The range in total length growth rates between individuals was 7.0-34.1 cm/yr (3.4-17.4 cm SVL) for males and 5.4-26.8 cm/yr (2.5-16.7 cm SVL) for females, indicating wide variation. The largest crocodile on which data was collected was on 84 cm SVL male.

Monthly growth rates of male and female crocodiles of all size classes encountered on rural farms, except for hatchling and near breeding size animals, were compared. Since all animals were eventually sexed at a size above 50 cm SVL, sexing errors due to small size were corrected and do not bias the results. No significant difference in growth rates were noted in the 30 cm and 40 cm SVL classes (Table 12). However, all classes of ≥ 50 cm SVL showed that females grew progressively slower than equal-sized

Table 12. Comparison of monthly SVL growth rates of captive male and female New Guinea crocodiles by size class. The symbol $\bar{d}$ denotes the differences in the mean growth rates (male - female) within each size class.

Size Class* (cm SVL ± 2)	Mean monthly growth in cm SVL(± SD) **				$\bar{d}$	%***	P****
	Male	N	Female	N			
30	1.16 ± 0.51	11	1.06 ± 0.43	9	0.10	9.4	>.10
40	0.95 ± 0.36	26	0.86 ± 0.32	46	0.09	10.5	>.10
50	0.86 ± 0.29	47	0.67 ± 0.27	39	0.19	28.4	<.01
60	0.58 ± 0.19	54	0.52 ± 0.19	49	0.06	11.5	<.05
70	0.58 ± 0.24	32	0.47 ± 0.20	10	0.11	23.4	<.05
		170		153			

*Size at year's beginning.
**Mean growth rate at end of 12 months.
***Shows the extent to which males grow faster than equal size females.
****Significance of sexual differences in growth rates using a "Z" statistic to compare sample means.

males. The relatively low growth rate of males in the 60 cm SVL class (Table 12) may have resulted from experimental error.

This "Z" test indicated that growth rates of captive New Guinea crocodiles decline as length increases and that both sexes grow at similar rates until they are about 50 cm SVL. Beyond that size, the growth rate of females declines faster than that of males.

Size/age relationships are depicted using growth curves derived from growth records and morphometric data for both male and female crocodiles (Figure 21). Growth curves are described by the equations:

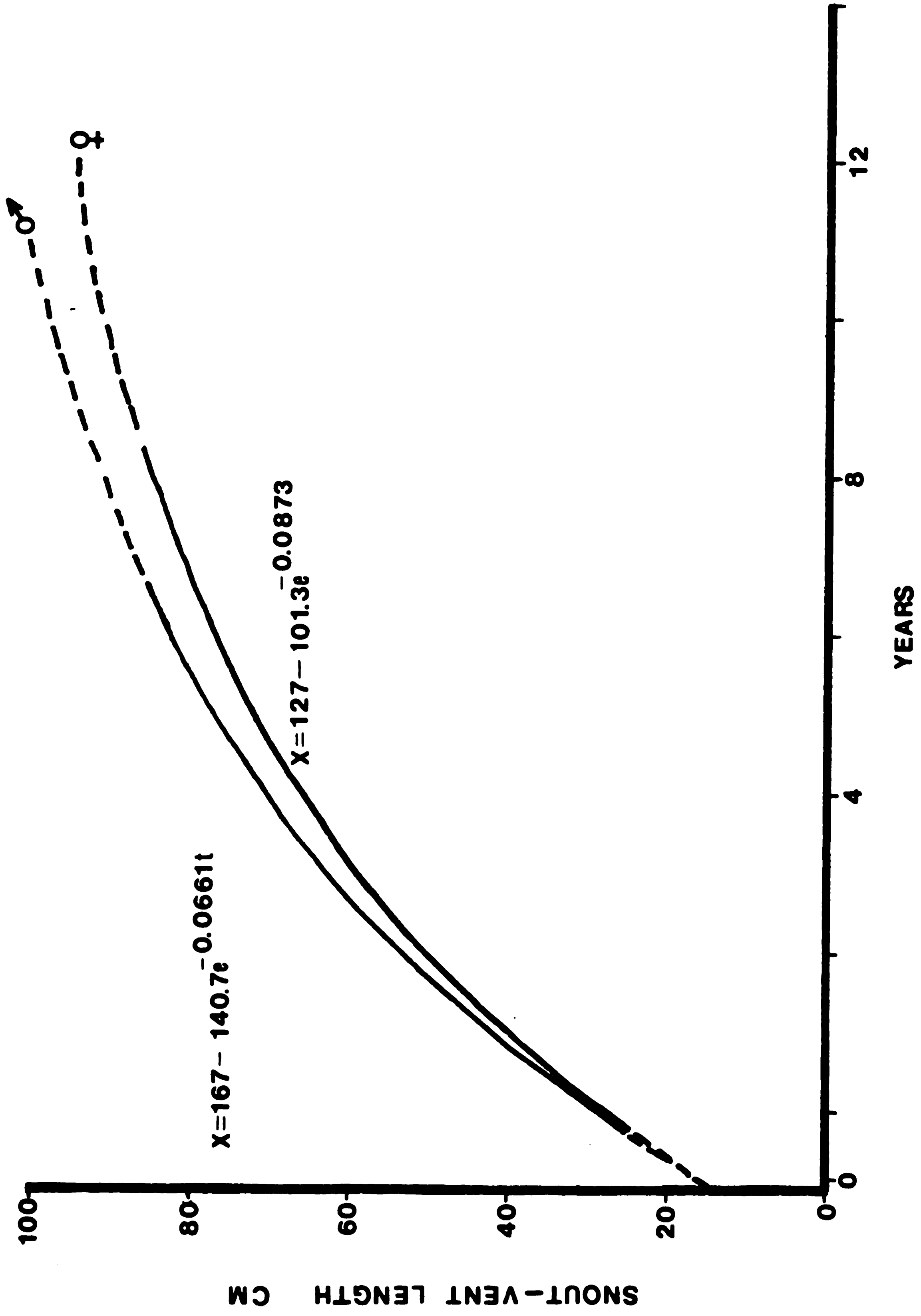
eqn. 105 males $X = 167 - 140.7e^{-0.0661t}$

eqn. 106 females $X = 127 - 101.3e^{-0.0873t}$

where X = SVL (cm), the constants 167 and 127 represent the maximum known SVL (cm) of male and female *C. novaeguineae*, respectively (Table 7); the constants -0.0661 and -0.0873 are the slopes of the allometric equations for males and females, respectively; 140.7 and 101.1 are the natural antilogs of the Y-intercepts in the above equations; and t is time in years. Equations 105 and 106 slightly overestimate SVL in young animals with the calculated curve crossing the actual curve at 2.0 and 3.0 years, respectively for males and females.

Sexual maturity is reached in C. novaeguineae at 1.8 and 2.0 m TL, at an approximate age of 10.5 and 12.5 years

Figure 21. New Guinea crocodile size/age relationship derived from captive growth data (males: N = 170; females: N = 153). Solid lines indicate size classes included in the data, while broken lines designate projections beyond the data. Equations approximate the plotted lines.


SNOUT-VENT LENGTH CM
0
20
40
60
80
100
YEARS
0
4
8
12
X=167− 140.7e−0.0661t
X=127− 101.3e−0.0873
♂
♀

for females and males, respectively, under the conditions of this study. Growth was not projected beyond the average age of sexual maturity (Figure 21) because crocodilian growth slows considerably at this point (McIlheny 1934, Webb et al. 1978).

Crocodiles consumed 5.67 kg feed/kg crocodile starting weight/yr. Of the food made available to the crocodiles, 8.2% was not eaten and was removed the next day.

Optimum Harvest Size

At 73 cm and 68.5 cm SVL for wild and farmed crocodiles respectively, the maximum price per unit BW was reached (Bates 1979) and the increase in SVL with increasing body weight (BWT) began to diminish (Figure 8d). Farmed crocodiles reach this BW in an average of 4.6 and 5.5 years for males and females, respectively. These lengths correspond to a belly-width (BW) of about 30.5 cm (12 in). A crocodile of 50.8 cm (20 in) BW produces 65% more income but weighs 450% more and requires proportionately more feed than a 30.5 cm BW animal. Although it may vary with changes in input cost, optimum harvest size seems to be c. 30.5 cm BW.

Captive Mortality Rates

Sixty-seven of 390 New Guinea crocodiles used in this two-year study died, indicating an average annual farm mortality of 9%. Some 30.6% of the mortality was a direct result of disturbances caused by the six-month inventories. Animals suffocated when piling in corners seeking security (Figure 22), or when several animals would become packed in tunnels trying to avoid capture. Another 14.5% of the dead were in poor condition at the start and never recovered. Six percent were killed in intraspecific fights, while 48.9% died of unknown causes.

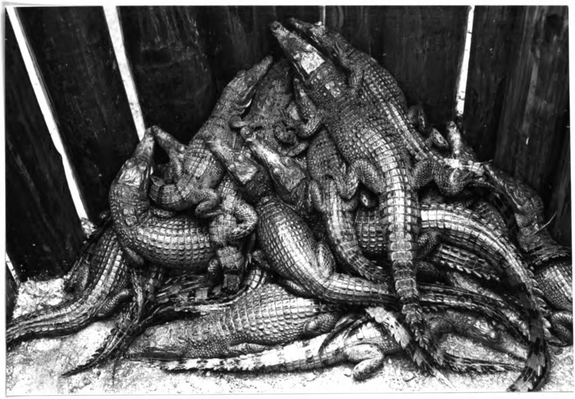
CONCLUSIONS

Sexual Dimorphism and Ratios

Kramer and Medem (1955) found that no *C. sclerops* 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 New Guinea crocodiles over 100 cm SVL was small (10 males and 26 females), sex differences in body proportion other than maximum size were not seen even in large adults.

A 1:1 sex ratio, as found for *C. novaeguineae*, has also been reported for *C. porosus* (Banks 1930, Webb and Messel 1978b) and *Caiman crocodilus* (Staton and Dixon 1977). Studies of the American alligator, however, have shown a

Figure 22. Disturbed juvenile *C. novaeguineae* often pile on one another when in captivity.



preponderance of males that ranged from 60.8% (Chabreck 1966) to 70.4% (Palmissano et al. 1973). Nichols and Chabreck (1980) hypothesized that alligator sex was determined after hatching by environmental factors, and that these factors cause more males to develop under favorable environmental conditions.

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 near identical raw data variation (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). In contrast, negative skull allometry (slope $<$ 1.0), due to large brain size at birth, is characteristic of most other vertebrates (Rensch 1960). A food-gathering function may be the predominant design factor influencing the shape of crocodilian skulls (Dodson 1975). In other crocodilians, prey sizes tend to increase with body size (McIlhenny 1935, Cott 1961, Graham 1968, Taylor 1979). A strengthening of the skull to handle large prey seems characteristic of New Guinea crocodiles also.

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 5, eqns. 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 that girth parameters do.

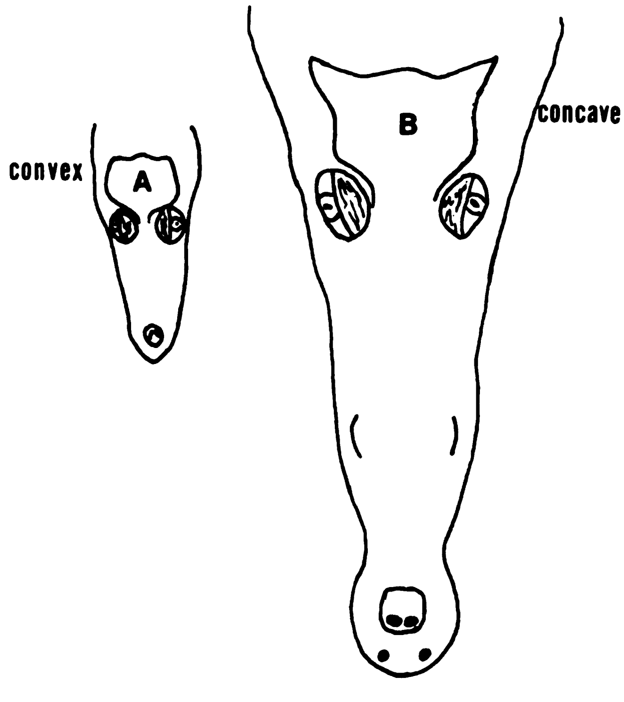
The close relation between hand and foot width, and head width and trunk length indicate that hands and feet become larger in direct proportion to increasing body length and width probably in order to support the body. That cranial platform mid-point width and ear slit length increase in the same growth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

The convex shape of the cranial platform, in hatchling New Guinea crocodiles (Figure 23), has also been noted in hatchling American alligators (Dodson 1975) and saltwater crocodiles (Webb and Messel 1978a). This characteristic convex shape of cranial platforms in young *C. novaeguineae* results 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. In *C. porosus* a HPP/HMP ratio of 1.0 was found in specimens up to 70 cm SVL while 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 1982b), the HPP/HMP value equals 1.0 at about the same fraction of the species' maximum size in both forms.

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

Figure 23. Convex shape of cranial platforms in hatchling (A) compared to concave shape in adult (B) *C. novaeguineae*.


convex
A
B
concave

study quantified this difference. Since a wild New Guinea crocodile is longer than a farmed crocodile of equal belly-width (Figure 9) and since inches of belly-width (BW) is used in PNG to determine purchase price, farmed crocodiles are worth more than wild ones. This information will be an additional incentive to farm crocodiles because crocodile farmers get the same price for a smaller skin than they would get for a skin from a wild crocodile.

Protrusion of Mandublar 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 protrusion occurs 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 1978a).

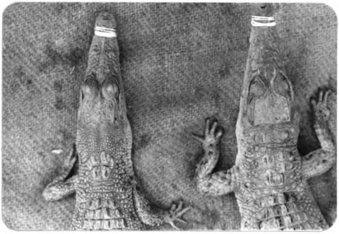
There was no evidence of any behavioral or ecological significance for protrusion of mandibular teeth through the premaxilla in juveniles, or the absence of this phenomenon in some large adults (Table 10; Figure 10). It seems probable that teeth grow proportionately faster than bone in young C. novaeguineae and push through the slowly growing premaxilla (Edwards pers. comm.). 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 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 larger prey, as suggested for C. porosus (Webb and Messel 1978a).

Habitat and Niche Separation

The primary reason for undertaking the morphological comparison between New Guinea and saltwater crocodiles (Figure 24) was to reveal factors that might clarify the ecological niche and habitat-separation between the two species in PNG hypothesized by Bustard (1968), Lever (1975a) and Whitaker (1980). Wermuth (1964) suggested that relative tail length was indicative of crocodile mobility and swimming efficiency. A TAL/SVL ratio > 1 in larger C. porosus may give this species greater propulsive force than the TAL/SVL ratio < 1 in C. novaeguineae (Edwards pers. comm.) and may indicate a different effect of the tail in the two species. C. porosus juveniles under 24 cm SVL have no apparent propulsive advantage over C. novaeguineae. As they become larger, however, the longer tails of the former might indicate an advantage. At sizes above 60 cm SVL trunk growth begins to slow in

Figure 24. Differences in outward appearance of (A) saltwater crocodile (C. porosus) and (B) New Guinea crocodile (C. novaeguineae), which include sharper scute crests, smaller scutes between the nuchal rosette and the cranial platform and sleeker appearance in the former.



A B

C. porosus, but not in New Guinea crocodiles, and this difference may become particularly pronounced. This proposed difference in swimming efficiency must 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 behavioral 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 or larger vertebrate prey (Taylor 1979).

Food and habitat requirements are probably similar in young of the two species. Larger C. porosus, however, probably seek and catch swift prey. In the case of very large C. porosus, which can be six times heavier and twice as long as C. novaeguineae (Montague 1982b), the former are certainly capable of overpowering larger prey than the latter. The greater propulsive force 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 1,174 km of open sea (Neill 1971), 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, fast-swimming fish such as barramundi 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, slower fish and other smaller vertebrates.

The fact that adult C. novaeguineae have foot widths and, to a lesser degree, hand widths proportionately wider than equal-sized C. porosus may 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 slippery mud banks. In short, New Guinea crocodiles should be more terrestrial than C. porosus. The narrow hands and feet of saltwater crocodiles would inhibit their travel through similar 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 in the area of limb morphology and may find that C. novaeguineae have longer, sturdier limbs than do saltwater crocodiles. A food preference study of the New Guinea crocodile should be conducted as defined by Petrides (1975) to complement those done for C. porosus (Allen 1974, Taylor 1979).

Abnormalities and Injuries

Parasite skin-tracks are not rare in crocodiles, having been recorded in C. johnstoni, C. intermedius, C. morletti, and C. niloticus (King and Brazaitis 1971). Webb and Messel (1977a) found ventral parasite tracks on only 0.9% of C. porosus examined from Northern Australia. The present study found such tracks, however, to be over 14 times as common in New Guinea crocodiles.

The smallest saltwater crocodile with parasite tracks found by Webb and Messel (1977a) was 60 cm SVL. This was over twice the size of the smallest C. novaeguineae with such tracks. These great differences in the degree of occurrence may well be due to differences in habitat salinity. Parasite skin-tracks are common on crocodiles of both species when they are caught from freshwater areas of PNG (Ashford and Muller 1978, pers. obs.). They are rare, however, in C. porosus from PNG estuarine areas where C. novaeguineae do not occur (Webb and Messel 1977a, Ashford and Muller 1978).

This study of C. novaeguineae found an increasing incidence of parasite tracks with increasing body length up to 80 cm SVL. Webb and Messel (1977a) found a similar increase in C. pososus up to 90 cm SVL. In both studies, the incidence of parasite tracks was reduced in the largest size classes. Perhaps in large crocodiles, the cornified layers of the skin become too thick or tough for *P. crocodilus* to penetrate.

Leeches were most abundant in PNG rivers like the Mamboi, where there were adjacent shallow marshes that abutted with swamp forest. Smith (1976) found leeches on the bodies of 26% of 35 American alligators in Texas. This figure would be high for New Guinea crocodiles in general but resembles the 20% recorded for the Mamboi River population. Leeches were not found on saltwater crocodiles in the tidal waters of Northern Australia (Webb and Messel 1977a). They were present, though, on both this species and *C. novaeguineae* from freshwater areas of PNG. Apparently, leeches that plague crocodiles do not survive in saline waters.

Since many attached leeches in PNG were not engorged with host blood and were often located on the crocodile where perpheral blood vessels were minimal, it seems probable that leeches use crocodiles primarily as dispersal aids and only secondarily as hosts (Hensley pers. comm.).

Webb and Messel (1977a) did not describe a deformed-trunk condition in Australian *C. porosus*, but did list scars and injuries to the trunk which might have included this anomaly. Trunk injuries were present in only 1.3% of their sample but deformed trunks alone were visible in 2.1% of crocodiles during the present study. It is not known why this difference exists. The absence of deformed trunks in the smaller size classes indicates that this anomaly did not result from nest-related injuries. Marcus (1981) stated that many rib cage deformities in herpetofauna result from dietary calcium or vitamin D deficiencies. Such deficiencies may also cause trunk deformities in C. novaeguineae.

This study of C. novaeguineae and that of Webb and Messel (1977a) for C. porosus both found an increase in the incidence of tail amputations with increasing SVL and may indicate that aggressive behavior is more common in larger crocodiles since adult crocodiles have no natural predators. This injury was only slightly more frequent in saltwater crocodiles than in New Guinea crocodiles (2.1% and 1.8% respectively).

Since only small crocodiles had obvious digit amputations, it would seem that predators were responsible for most of these injuries. Digits might have been bitten off either by predators, such as barramundi, which abound in the waters around Lake Murray, or by other crocodiles. As with tail amputations, lost digits occurred with the same frequency in both C. novaeguineae of New Guinea and C. porosus of Australia (Webb and Messel 1977a) possibly indicating that the causes were similar in the two populations.

Webb and Messel (1977a) also found a low incidence of head injury in Australian C. porosus (0.67% of 1,345 crocodiles), as was noted in C. novaeguineae. Crocodiles evidently are seldom injuried on the head. Jaw misalignment shown to reduce growth in C. porosus, may affect C. novaeguineae similarly. Humpbacks, eye injuries and missing toenails were not reported for wild saltwater crocodiles by Webb and Messel (1977a) but eye injuries were noted in captive C. porosus in New Guinea. The absence of the humpback condition in smaller size classes indicated that this was not a hatchling defect. Perhaps they become so afflicted due to a dietary deficiency similar to that which causes high-domed carapaces (kyphosis) in some turtles (Frye 1973). Misaligned toenails and amputated limbs reported for C. porosus by Webb and Messel (1977a) were not noted in C. novaeguineae.

Body injuries other than parasite tracks in the $\geq$100 cm SVL class were less common in C. novaeguineae (this study), and C. niloticus (Cott 1961) than in C. porosus (Webb and Messel 1977a). This could indicate a more aggressive behavior pattern in adult saltwater crocodiles and support for the long-held belief of their ferocity (Neill 1946, 1971).

Brachycephalia, a gross widening and shortening of the head, has been described in C. porosus (Kalin 1936) and C. niloticus (Pooley 1971). This condition has been attributed to a combination of captivity and poor diet.

It was not found in live wild C. novaeguineae, but the skull of a large New Guinea crocodile that had been reared at the Moitaka Government Farm (Appendix 1, #9) did show brachycephalia.

Truncated jaw(s), as found in captive C. novaeguineae (Figure 17) has also been reported in farmed C. niloticus (Blake 1974). It has not been observed in the wild and may only result from feeding injuries in captivity.

Growth and Farming

Growth rates of the captive Baboa crocodiles, reared under village conditions but with biologist supervision, were low when compared to those of other farmed crocodilians. At the Moitaka Government Crocodile Farm, a model commercial facility, C. novaeguineae grew nearly twice as fast (Bolton 1981b) as at Baboa. Wild juvenile C. crocodilus grew about 10 cm/yr TL, while captive specimens averaged 33 cm/yr TL (Gorzula 1978). Juvenile American alligators grew an average of 25.2 cm/yr TL in the wild (Chabreck and Joanen 1979), but have averaged 67 cm/yr under good captive conditions (Coulson et al. 1973).

The quality of captive care had a great effect on the growth rate of C. palustris captives. These ranged from 10.2 cm/yr TL (D'abreu 1935) to 51 cm/yr TL (Whitaker and Whitaker 1977). Although low, the 15.7-17 cm/yr TL growth rates for New Guinea crocodiles at the Baboa Farm undoubtedly were higher than at unsupervised village farms where food and fresh water supplies often seemed inadequate.

High growth rates were not achieved at Baboa because of fluctuations in the quantity of fish available to the crocodiles and because they refused to eat for up to six weeks after being handled during semi-annual inventories. At least one New Guinea crocodile at Baboa grew 34 cm/yr TL, indicating that the species is capable of rapid growth, though perhaps not when reared on a large scale under crowded and inefficient village conditions.

In Australia, wild _C. porosus_ under 80 cm SVL grew approximately 33 cm/yr TL (Webb et al. 1978). Surprisingly, this rate was equalled by Baboa's 16 captive saltwater crocodiles and was nearly twice as fast as Baboa's _C. novaeguineae_ captives. Since wild saltwater crocodiles grew at the same rate as Baboa's captives, perhaps wild _C. novaeguineae_ normally grow at the rate of their Baboa Farm counterparts. Capture-recapture studies should be conducted on wild _C. novaeguineae_ in the future to test this supposition.

Faster growth rates seem characteristic of male crocodilians. This was true in New Guinea crocodiles and in _C. niloticus_ (Graham 1968), _C. porosus_ (Webb et al. 1978) and _A. mississippiensis_ (Chabreck and Joanen 1979).

And 50 cm SVL, the size at which sexual differences in growth rates were first observable in *C. novaeguineae*, was the same as that reported for American alligators (Chabreck and Joanen 1979).

That New Guinea crocodiles reached sexual maturity at about 10 and 12 years of age for females and males respectively, (Figure 21), also is in some agreement with the average maturation of *C. niloticus* (Cott 1961, Graham 1968), and *C. porosus* (Webb et al. 1978), but is much older than the maturation of ages of *A. mississippiensis* (Nichols et al. 1976) and *C. crocodilus* (Staton and Dixon 1977).

A decreasing growth rate with increasing length, as found for *C. novaeguineae* in PNG, is characteristic of all crocodilians that have been studied (Chabreck and Joanen 1979, Webb et al. 1978, Bolton 1981b). The size/age curves described by equations 105 and 106 are not suitable for crocodiles above 100 cm SVL and are only marginally suitable for animals below 20 cm SVL; therefore, it is recommended that appropriate data be collected to complete this growth curve for all size classes.

The annual 9% mortality rate of captives from 28-84 cm SVL at Baboa compared reasonably with 20% hatchling and 5% juvenile deaths/yr for captive *C. simensis* (Yangprapakorn et al. 1971). The rate is high, however, when compared with the 0.6%/yr reported for captive American alligators (Joanen and McNease 1976a).

A 45% reduction in mortality on crocodile farms at Baboa and elsewhere in PNG could be achieved if: (a) animals were not captured and measured during inventories; (b) the sides of ponds were sloped to discourage tunnelling; and (c) debilitated animals were not purchased.

On even the best village crocodile farms in PNG, mortality was high and growth rates were about as low as wild crocodiles. It is recommended, therefore, that the village crocodile small farming program be eliminated in favor of larger commercial opperations that utilize fish and/or mammal offal with improved cost efficiency. At Baboa, captive crocodiles were fed 19,213 kg of barramundi/yr (Table 3), a very desirable table fish with a wholesale value of about K20,000 (US$30,000). A barramundi fishery established in conjunction with a crocodile farm to utilize both the high-quality meat and the waste products would be economically more efficient. Even if village crocodile farms were eliminated, an enhanced live-crocodile buying scheme would continue to provide a helpful income to rural crocodile hunters. It is suggested, also, that the price of live male _C. novaeguineae_ should be 9% higher than for females of the same size, since they grow an average of 9% faster.

SUMMARY OF RECOMMENDATIONS

Research

A key assumption of the PNG crocodile management scheme is that sufficient small crocodiles escape capture and natural mortality to replace wild breeding stocks which die of natural causes. This assumption seems valid for *C. novaeguineae*, but verification is critical. It is recommended that:

1) The annual replacement rate for wild breeding crocodiles be monitored and that juvenile survival rates be studied to confirm that they vary inversely with population density.

Before New Guinea and saltwater crocodiles can be effectively managed in the wild, it is essential that food and habitat requirements peculiar to each species in PNG be identified. It is therefore recommended further that:

2) Those differences in food and habitat preferences between the two species that were indicated by morphological adaptations be verified in the field.

Management

3) The maximum legal crocodile harvest size should be reduced to 40.6 cm (16 in) belly-width so that all breeding crocodiles, including females, are protected.

4) To maximize profits, farmed crocodiles should be harvested at 30.5-33 cm (12-13 in) belly-width.

5) Neck girth, being a more accurate estimator of skin area than belly-width, should become the standard commercial skin measurement.

6) Saltwater crocodiles should be kept on farms with slightly saline water to reduce the deleterious effects of nematode parasites.

7) Males grow faster than females, hence live male crocodiles should be purchased at a 9% premium.

8) Rural crocodile farms should be phased out in favor of efficient commercial farms which utilize waste meat products as feed.

9) To replace rural crocodile farms, the live crocodile buying scheme should be established on a more widespread basis.

10) No crocodile farms should be licensed unless there is a proven reliable annual feed supply equal to 6 times the total crocodile weight at the year's beginning.

11) Available technology for captive breeding and post-hatchling culture of crocodiles should be utilized to provide a successful means of supplimenting harvests of small crocodiles from the wild.

APPENDIX

Appendix 1. Dimensions in centimeters for some large C. novaeguineae skulls from the Papuan Region, PNG, 1978 - 1980.

Head No.	PNG Location	HTL Skull	HTL Appx. 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

*Approximated live measure allowing for 4% tissue loss (Webb and Messel 1978a).
+Heads that were actually measured when live as well as when dried skulls.

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