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ALLOMETRIC RELATIONSHIPS OF THE SIAMESE CROCODILE, *CROCDODYLUS SIAMENSIS*.

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Abstract

Relationships of length and/or weight of the brain head, gut, kidneys, heart and the body of Siamese crocodiles, Crocodylus siamensis, 1 month to 4 years old including both males and females were studied.

In young crocodiles the rate of increase in body length relative to body weight was faster than in older animals. The body weight to body length ratio increased linearly with the body weight between 3-25 kg. In small animals less than 1 kg, the ratio was relatively smaller. Head weight was linearly proportional to the body weight. Head length was linearly proportional to total body length. The depth and the width of the head were both linearly proportional to the length of the head, but the head length was increasing more rapidly than either of the other two dimensions and head width increased more rapidly than the head depth. The brain weight increased with increase in head and body weight but a much slower relative rate. Brain, weight was linearly proportional to the body length.

As the brain and body of the crocodile grow they do not preserve the same proportions. There was exponential increase in the gut length with respect to increase in the body length. There was linear increase in kidney weight with respect to body weight and sigmoidal increase in heart weight with respect to the body weight of the crocodile.

Data were discussed based on genetic control, relative material distribution and anatomy and physiology of the animal during growth.

Introduction

Growth data for *Crocodylus siamensis* are rare although this species is raised in captivity in great numbers at the Samut Prakan Crocodile Farm, Samut Prakan, Thailand. This species of crocodile is near extinction in the natural habitat which makes it difficult to obtain wild specimens for study. This report concerns the allometric relationships of the body and several organs of the Siamese crocodile raised on the farm. Similar studies have been reported for the elephant seal¹, dolphins² and the cebus monkey³. The study of relative growth of body parts can include many things, such as organ weight/body weight, the body weight/length or the condition index which is maximum girth \times 100/total body length as was used for the elephant seals. This latter indicates the degree of "fatness" of the animal¹. The brain weight/body weight ratio indicates the degree of encephalization during development and growth of the animal². The ratio between the olfactory bulb size and the cerebrum size in the birds for example, has been used to correlate the olfactory functions of the animal⁴. Differential growth of organs of the body indicates how the body is programmed to distribute its resources to build up different parts of the body at different stages. Changes in allometric relationships of organs during growth and development may be explained directly or indirectly by the theories of biological pattern formation summarized by Summerbell⁵ which stated that, morphogenesis (change of the geometrical form), is determined directly by genes or indirectly by influencing gene expression via differences in regional environments in different anatomical regions as created by genes. A study of the relative growth of organs such as that reported here, may be one of the approaches to analysing differential growth and seeing the actions of genes in terms of growth in different anatomical locations. The analysis of data obtained here may be unique for this species or may be common to other species of vertebrates.

Materials and Methods

Siamese crocodiles, *Crocodylus siamensis*, were obtained from Samut Prakan Crocodile Farm, Samut Prakan, Thailand. All animals were bred and raised in captivity at this farm. Three groups of animals were used, namely, small (1-2 month old), medium (2 year old) and large (3-4 year old).

Crocodiles of the large and medium size were killed by experienced workers. The spinal cord was severed immediately posterior to the foramen magnum (See Fig. 1). In this procedure some blood was lost before weighing; this amount was estimated to be

less than 2 % of the body weight. Animals were then tagged, weighed, measured, and identified as to sex. About 1-2 hours after severing the spinal cords, the heads were removed and placed in dry ice for transportation to the laboratory and they were stored in a deep freeze compartment at -15°C .

The brain was exposed (See Fig. 1) by using bone saw, chisel, bone scissors and a small spatula. A few crystals of ice were removed from the surface, the meninges were then stripped away carefully and the brain was blotted and weighed. Brains to be used for regional measurements were weighed whole and then divided into eight parts according to Romer⁶ and as indicated in Fig. 2: olfactory bulb and stalk, cerebral hemispheres, dienephalon, mesencephalic tectum, cerebellum, and medulla. A small segment of cervical cord probably remained with the medullary section. Brain sections were blotted, and weighed.

The small crocodiles (1 month old) were transported alive from the farm to the laboratory, weighed on a triple beam balance, measured, and decapitated using a guillotine. The head was then weighed and kept on ice while the brain was being removed.

Data collected for crocodiles included: length-nose tip to tail tip in centimeters, body weight in kilograms, head weight in kilograms, whole brain weight in grams, weights of brain regions in grams and calculation of regional weights as percentages of whole brain weight. For some animals these additional data were collected (see Fig. 1 and 2): head length, head width, head depth, length of the brain from obex to olfactory bulb tip, olfactory bulb width, olfactory stalk width, optic lobe width, pons width, cervical cord width, cerebrum width. Brain weight to head weight ratio, brain weight to body weight ratio and body weight to body length ratio were calculated for some animals. In addition gut length (stretched length of gastrointestinal tract from throat to cloaca), kidney (2 kidneys) and heart weight were also measured. Allometric plots between pairs of parameters were made.

Results

Fig. 3 shows the allometric relationship between body weight and body length. In young crocodiles the rate of increase in length relative to body weight was faster than in older animals. Fig. 4 shows the relationship between the body weight and the body weight to body length ratio. The increase in this ratio was linear with respect to the increase in body weight between 3-25 kg. In small animals less than 1 kg, the ratio is relatively smaller. Fig. 5 shows that the head weight was linearly proportional to the body weight between 5-25 kg, however, in animals less than 5 kg the relationship was not quite clear, due to the small number of animals. The correlation coefficient for the males was 0.935 and for the females 0.950. During the same period the head length was linearly proportional to the total body length (Fig. 6). The depth and the width of the head were both linearly proportional to the length of the head (Fig. 7), but the head length

was increasing more rapidly than either of the other dimensions and head width increased more rapidly than the head depth.

The brain weight in this species of crocodile increased with increase in weight of the head (Fig. 8), but at a much slower rate. There was some indication that the relative rate of growth of the brain decreased slightly between "medium" and "large" sizes. Fig. 9 shows that in the young crocodiles (low head weight) the brain weight to head weight ratio was high, but as the head weight increased this ratio decreased. Fig. 10 shows the allometric relationship between brain weight and body weight. The relationship is very similar to that of brain weight and head weight. Fig. 11 is similar to Fig. 9 and emphasizes the much lower brain weight relative to body weight in older animals. Fig. 12 shows that the brain weight increased in direct proportion to the increase in body length throughout the size range of animals studied.

Table 1 was designed to show the proportions of body parts in large and small crocodiles and the change of these proportions in large vs small individuals. It was based on the measurements of a "composite" from each group, large and small. The greatest change was in body weight, 214.06 times; next was the head weight which increased 111 times; the brain weight increased 6.9 times; the head length increased 5.4 times and the length of the brain from obex to olfactory bulb tip increased 2.7 times.

As the brain of the crocodile grows it did not preserve the same proportions as can be seen from the dimensions in this table (Table 1) and from drawings in Fig. 13. Among the dimensions of the brain the relative length of the olfactory apparatus from optic chiasma to olfactory bulb tip increased markedly. The relative diameters of olfactory bulb tip increased markedly. The relative increase in diameters of olfactory bulb, pons, and cord were greater, and those of the olfactory stalk and optic lobes were less. Cerebral proportions were relatively constant over this size range.

The body weight to brain weight ratio of the large crocodile (body wt. 13.7 kg) is 2072.0 and of the small one (body wt. 0.064 kg) was 66.6. In the adult rat (body wt. 86-310 g) the range of this ratio was 55.13-153.3 (unpublished data). The percentage of the weight of brain regions as percent of whole brain weight of the large crocodiles (17.6 ± 2.9 kg and 163.1 ± 8.7 cm long) are shown in Table 2. As the brain was divided here, the largest part was the cerebrum representing 37.8 % of the total weight and the smallest part was the diencephalon constituting only 4.75 % of the total weight. The ranking of various brain region weight from greatest to the smallest was as follows; cerebrum, medulla, pons, olfactory bulb and stalk, cerebellum, tectum, tegmentum, and diencephalon.

There was exponential increase in the gut length with respect to the increase in the body length (Fig. 14) of the Siamese crocodile. This indicates faster increase in the gut length than increase in the body length during growth.

Fig. 15 shows that kidney (2 kidneys) weight was linearly proportional to the body weight at least for the size range studied.

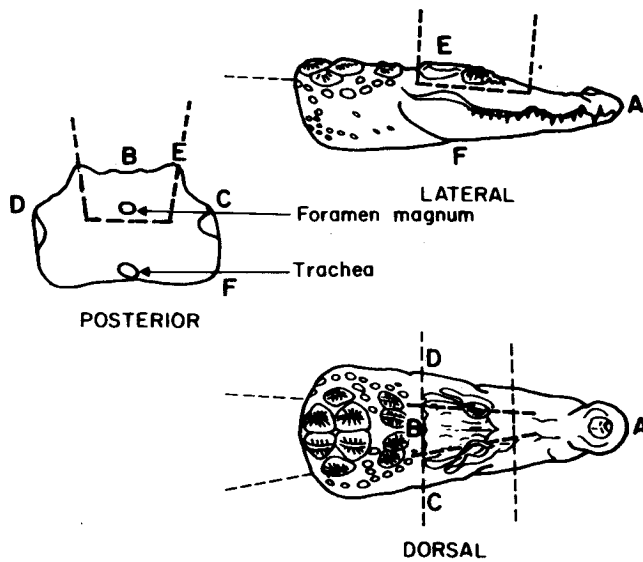


Fig. 1. Diagrams show the cuts made on the head of crocodile to expose the brain for removal (-----lines). They also show the land marks used for measuring the dimensions of the head. AB, head length (posterior margin of parietal bone to anterior margin of premaxilla); CD, head width (widest point, lateral projection of quadratojugal); EF, head depth (deepest point dorsal surface of squamosal bone to ventral surface of angular). DC was the level at which the farm worker severed the spinal cord. (The lateral and dorsal views of the head were modified from Lekagul *et al.*,⁷)

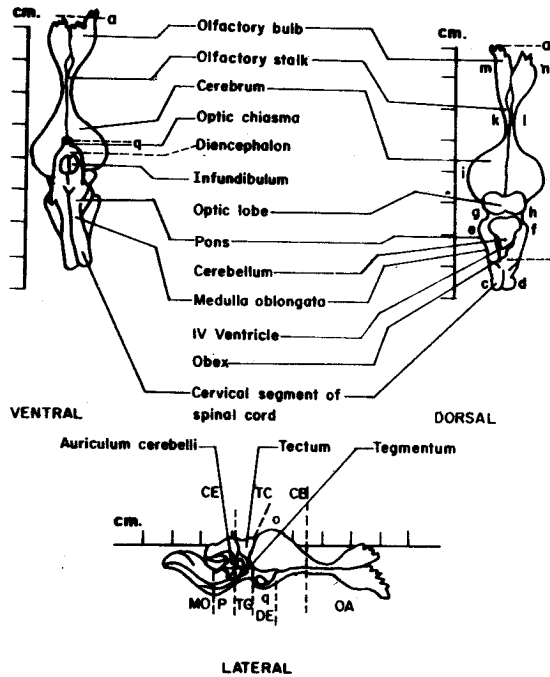


Fig. 2. Diagrams of the brain of large *C. siamensis*, to show the divisions of the brain used for the regional analysis and also the landmarks used in measuring dimensions of the brain. Parts dissected (bottom): OA, olfactory bulb + stalk; CB, cerebrum; DE, diencephalon; TC, tectum; TG, tegmentum; CE, cerebellum; P, pons; and MO, medulla oblongata. Landmarks use in measuring: cd, cervical cord lateral diameter; ef greatest width of pons; gh greatest width at level of optic lobes; ij greatest width of cerebrum; kl/2 diameter of olfactory stalk; mn/2 diameter of olfactory bulb; op cerebral depth (dorsal surface to optic chiasma); ba length of the brain (obex to tip of olfactory bulb); qa length of the olfactory apparatus; and ab-aq, length rest of the brain.

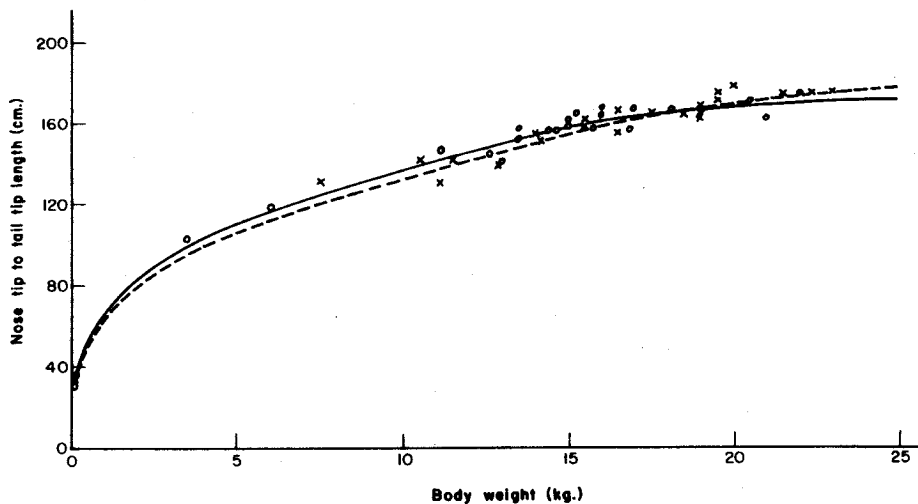


Fig. 3. The relationship between the body weight (kg) and the body length (cm) of male (x-----x) and female (o-----o) *C. siamensis*

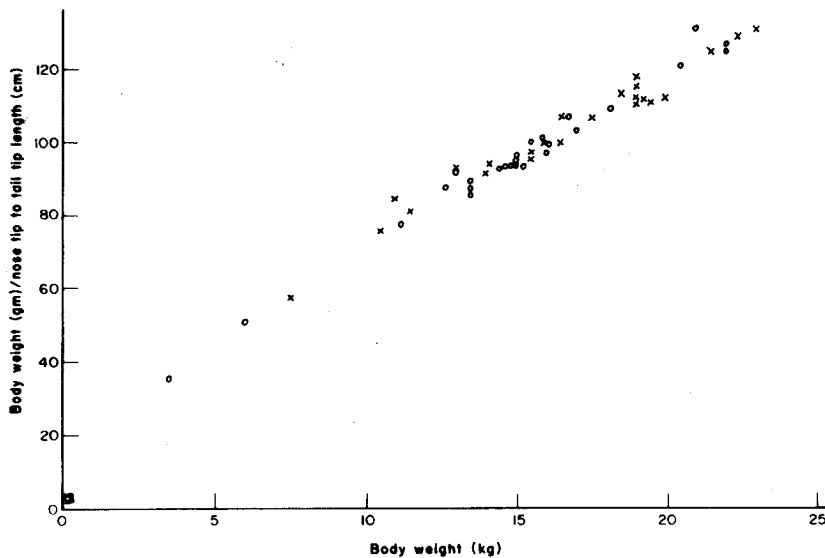


Fig. 4. The relationship between the body weight (kg) and the body weight (g) to body length (cm) ratio of the male (x) and female (o) *C. siamensis*

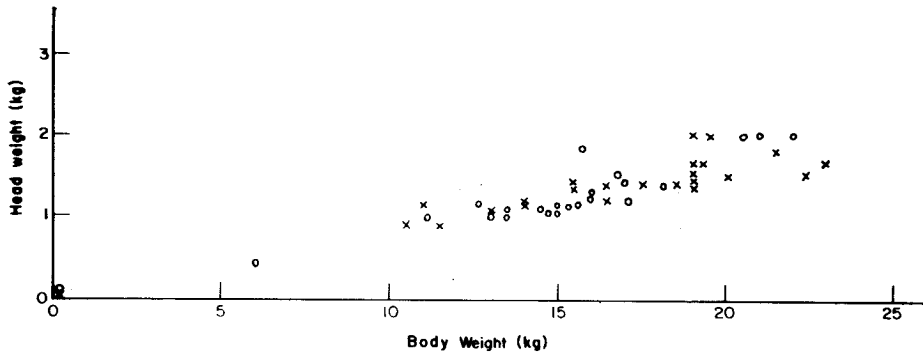


Fig. 5. The relationship between the body weight (kg) and the head weight (kg) of male (x) and female (o) *C. siamensis*. Male: Head weight (kg) = $0.089 - 0.077$ (Body weight, kg) $r = 0.935$, S.E.E. = 0.164. Female: Head weight (kg) = 0.088 (Body weight kg) $- 0.049$, $r = 0.950$ S.E.E. = 0.160. r = correlation coefficient, S.E.E. = Standard error of estimate

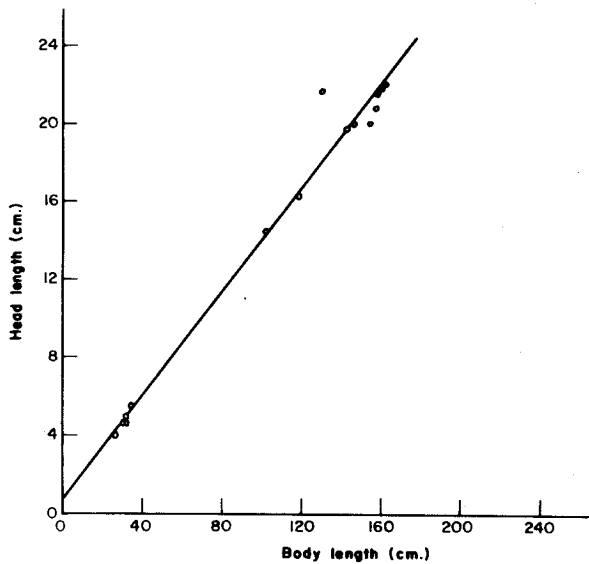


Fig. 6. The relationship between the body length (cm) and the head length (cm) of the *C. siamensis* The sexes are not separated. Head length (cm) = $0.737 + 0.133$ (Body length, cm), $r = 0.991$, S.E.E. = 0.985

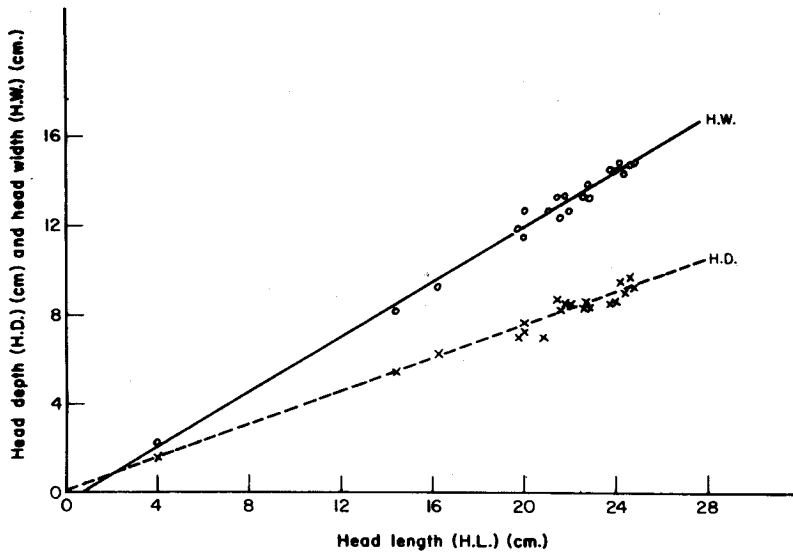


Fig. 7. The relationship between the head length (HL) and the head depth (HD); the head length (HL) and the head width (HW). of the *C. siamensis*. The data are not separated by sexes. Head depth (cm) = $0.001 + 0.372$ (Head length, cm), $r = 0.980$, S.E.E. = 0.350
 Head width (cm) = 0.0614 (Head length, cm) - 0.455, $r = 0.993$, S.E. = 0.335.

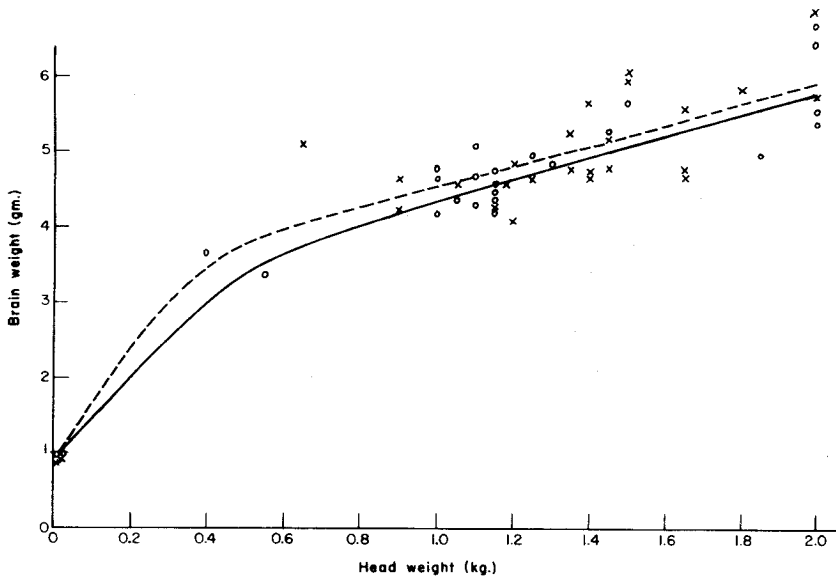


Fig. 8. The relationship between head weight (kg) and brain weight (g) of male (x-----x) and female (o-----o) *C. siamensis*

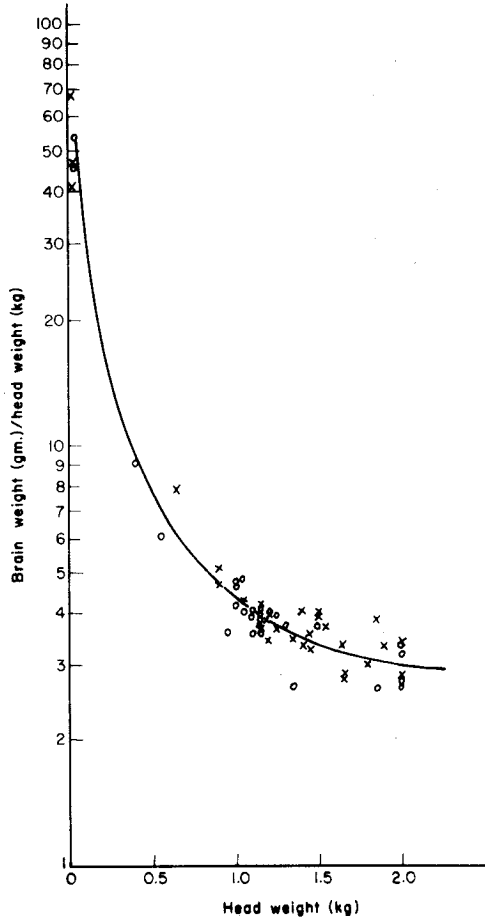


Fig. 9. The relationship between head weight (kg) and the brain weight (g) to head weight (kg) ratio of male (x) and female (o) *C. siamensis*. The x-axis is linear scale and the y-axis is logarithmic scale.

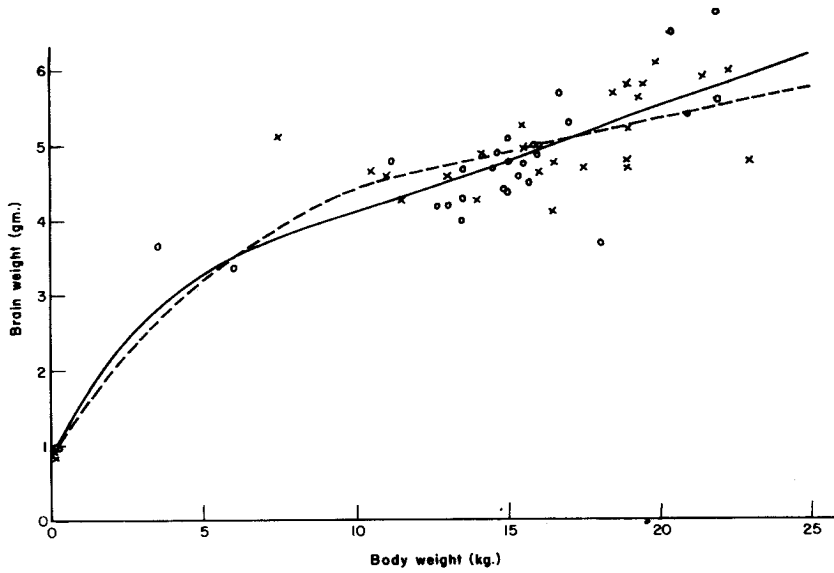


Fig. 10. The relationship between the body weight (kg) and the brain weight (g) of male (x-----x) and female (o-----o) *C. siamensis*.

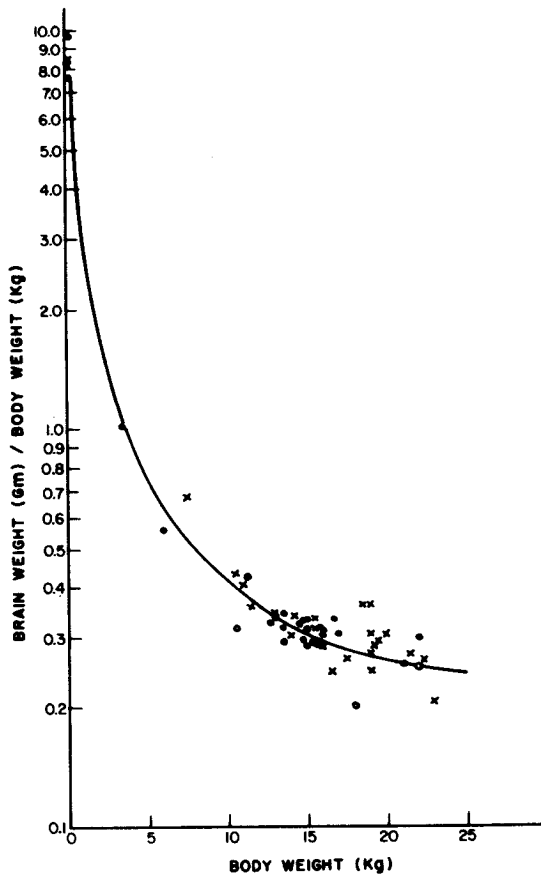


Fig. 11. The relationship between the body weight (kg) and the brain weight (g) to body weight (kg) ratio of the male (\times) and female (o) *C. siamensis*. The x-axis is linear scale and the y-axis is logarithmic scale.

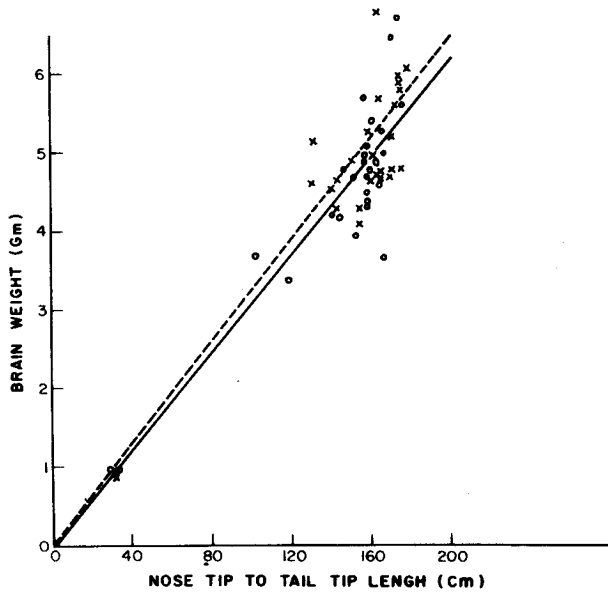


Fig. 12. The relationship between the body length (cm) and the brain weight (g) of male (x) and female (o) *C. siamensis*

Male: Brain weight (g) = 0.032 (Body length, cm) - 0.023 r = 0.899, S.E. = 0.548

Female: Brain weight (g) = 0.031 (Body length, cm) - 0.065. r = 0.885, S.E.E. = 0.571.

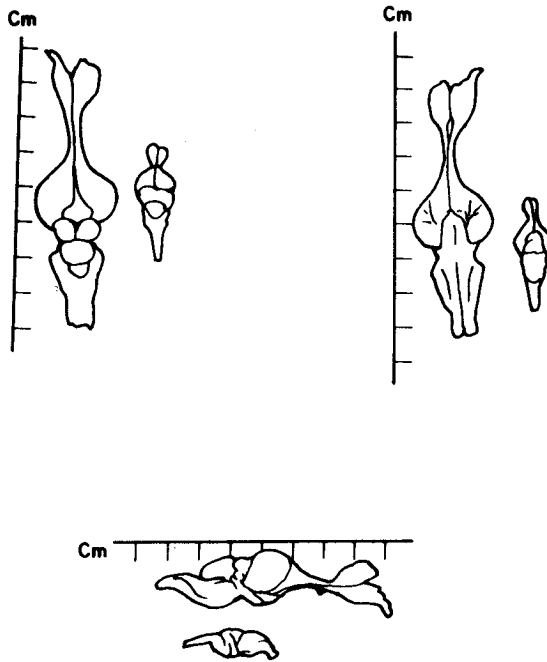


Fig. 13. Views of the brains of *C. siamensis* large and small. Larger animal: age 3-4 yrs, body length 157.0 cm, body weight 13.7 kg and brain weight 6.612 g. Small animal: age about 1 month, body length 29.0 cm, body weight 0.064 kg and brain weight 0.961 g.

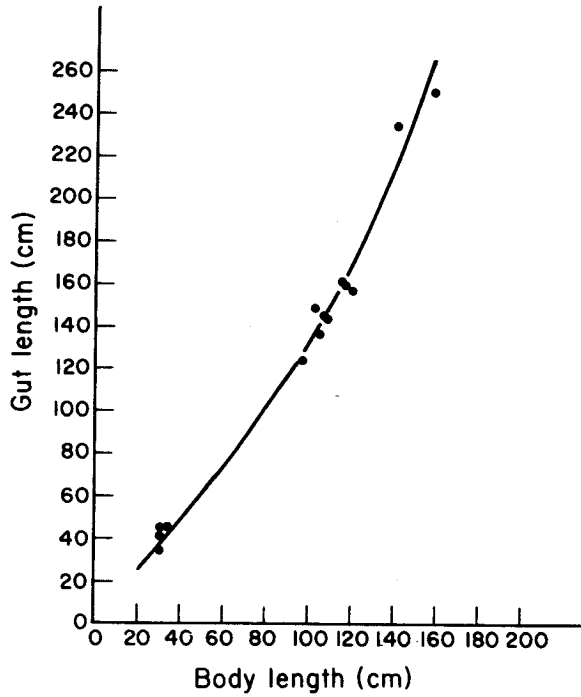


Fig. 14. The relationships between the gut length (cm) and the body length (cm). The gut length was taken from the stretched gastrointestinal tract from the throat to the cloaca. The body length was the nose-tip to tail-tip length of the Siamese crocodile.

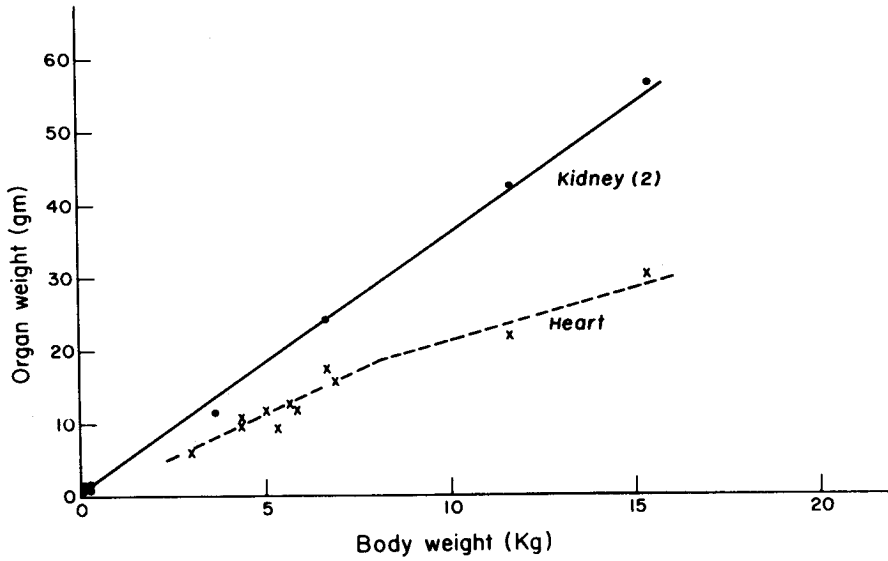


Fig. 15. The relationships between kidney and heart weight and the body weight of the Siamese crocodile. Kidney weight was the weight of two kidneys.

TABLE 1. DIMENSIONS OF TWO (COMPOSITE) CROCODILES: TYPICAL MEASUREMENTS FROM THE "LARGE" AND "SMALL" GROUPS INCLUDING RATIOS CALCULATED TO SHOW CHANGES IN BODY PROPORTIONS BETWEEN SMALL AND LARGE ANIMALS

Parameter	Small crocodile	Large crocodile	Parameter of large crocodile /parameter of small crocodile
Body length (cm)	29.0	157.0	5.41
Body weight (kg)	0.064	13.70	214.06
Brain weight (g)	0.961	6.612	6.88
Head weight (kg)	0.018	2.0	111.11
Head length (cm)	3.4	23.3	6.85
Head width (cm)	2.3	15.0	6.52
Head depth (cm)	1.5	12.0	8.0
Brain length obex to tip of olfactory bulb (cm)	2.4	6.5	2.71
Olfactory apparatus length (optic chiasm to olfactory bulb tip) (cm)	1.1	8.9	3.55
Length rest of the brain (cm)	1.3	2.6	2.0
Olfactory bulb width (cm)	0.2	0.7	3.5
Olfactory stalk width (cm)	0.1	0.15	1.5
Cerebrum width (cm)	1.3	2.5	1.92
Optic lobe width (cm)	1.2	1.4	1.17
Pons width (cm)	0.7	1.7	2.43
Cervical cord width (cm)	0.3	0.8	2.67
Cerebrum depth (cm)	0.9	1.85	2.06

TABLE 2. BRAIN WEIGHT, WEIGHT OF EACH BRAIN REGION AND CALCULATED REGIONAL BRAIN WEIGHT AS PERCENTAGE OF TOTAL BRAIN WEIGHT OF LARGE SIAMESE CROCODILES.

The crocodiles were 163.1 ± 8.7 cm long and 17.6 ± 2.9 kg body weight. Data were obtained from 9 male and 8 female crocodiles. Data of both sexes were not separated since there was no significant different in each parameter between male and female the size indicated.

	N	Weight (g) \pm SD	% of the whole brain weight \pm SD
Brain weight	17	5.046 ± 0.700	100.0
Olfactory bulb and stalk	17	0.451 ± 0.134	8.93 ± 2.66
Cerebrum	17	1.907 ± 0.388	37.80 ± 7.70
Diencephalon	17	0.240 ± 0.069	4.75 ± 1.36
Tectum	17	0.280 ± 0.060	5.55 ± 1.18
Tegmentum	17	0.271 ± 0.059	5.36 ± 0.12
Cerebellum	17	0.345 ± 0.110	6.83 ± 2.19
Pons	17	0.537 ± 0.147	10.63 ± 2.91
Medulla	17	0.685 ± 0.096	13.57 ± 1.89

N = number of individuals, SD = standard deviation.

There was linear increase in heart weight with respect to body weight between 3-7 kg Siamese crocodile, but the increase was relatively slower between 7-15 kg body weight.

Discussion

The data obtained concern the allometric relationships of parts of the body of *C. siamensis*, most of which have not been reported in the literature. Some comparisons of the data with those of other species of vertebrates will be made here. Implications of the data for explaining certain morphology of the species are also pointed out.

Fig. 3 gives the allometric relationship between the body weight and the body length. This relationship is very similar to that of the elephant seal¹ even though they are very different animals. The body weight to body length ratios as the function of the body weight is shown in Fig. 4. This shows changes in the degree of "fatness" and is similar to what Bryden¹ called the "condition index" in the elephant seal, that is maximum girth \times 100/total body length. Data obtained here indicate gradual increase in the body weight to body length ratio relative to the body weight in the crocodile between 3-25 kg. However, the ratio is relatively smaller for animals less than 1 kg. This indicates that small crocodiles are relatively thinner than are the larger crocodiles. This ratio for the small crocodiles was low and may be due to the fact that the newly hatched animals may obtain food qualitatively and quantitatively different from the consumed by larger crocodiles⁷. It is also possible that the greater body weight to body length ratio may be the result of greater bone density and/or muscular development.

The head weight is linearly proportional to the body weight in all sizes of the crocodile studied. This indicates relatively constant head weight to body weight proportion during growth. The head length increases proportional by to the body length, however the head itself showed different relative rates of growth in different dimensions as can be seen in Fig. 7. The relative growth rate is greater for length (L) than for width (W) and for width (W) than for depth (D). This results in the relatively longer snout of larger crocodiles.

Data in Figs. 8, 9, 10 and 11 indicates that in the smaller animal, the brain is better developed than to the head and the body; later other parts grow faster. This may be due to differences in physiological processes between small and large animals which could be explained partly by theories on biological pattern formation proposed by several investigators^{5,8}. The fact that the brain weight/body weight ratio is higher in the smaller animals than that of larger animals, is similar to data obtained in marine and costal dolphins², bat⁹, and dog¹⁰. Pirlot and Kamiya² proposed that the brain weight to the body weight ratio indicates degree of encephalization of different animal species. To compare the data presented here, brain weight (g)/body weight (kg), with those of Pirlot and Kamiya² which are the brain weight (g) \times 100/body weight (g), the data were recalculated to be the same ratios by dividing the recent data with 10. The equivalent

ratios for the *C. siamensis* are 1.0 - 0.76 for the 1 month old, and 0.03 for the 3-4 year old crocodiles. The marine dolphin (Pontoporia) has the ratio of 1.28 soon after birth to 0.48 in the adult (84.5 - 171 cm body length). The costal dolphin (Stenella) has the ratios of 9.37 - 4.88 in embryonic life, 4.1 soon after birth, and decrease to 2.87 in the 120 cm long juvenile specimen, whereas the ratio of the adult is 0.8-1.0. The ratio for the 196 g rat is about 0.93 (unpublished data). For the fruit-bat (*Artibeus jamaicensis*) it decreases from 15 to 6 over the entire fetal period (9) and in fetal dogs from 6.5 to 2.2¹⁰. It can be seen that even though the ratio is large in small crocodiles it is materially less than that in young mammals. The ratio in the adult crocodiles is less than that of adult mammals. This indicates less encephalization in the crocodiles compared to the mammals.

Table 1 shows changes in body parameters in small to large crocodiles, with the body weight increasing 214 times. In the elephant seal¹ the increase in weight of the adult is 80-90 times and in many mammals are 10-50 times¹¹. These differences may be due to differences in genetics control of the growth rate and maximal growth of those animals. The head weight increases 63.9 times and the brain weight increases 6.9 times between the 1 month old and 3-4 year old crocodiles. Differences in the relative growth of each part of the body may be due to regional differences in physiological and biochemical manifestation of gene expressions according to theories summarized by Summerbell⁵. That is, the growth rate and maximal growth of each organ can be determined by firstly, genetic potentials and secondly, such genetic potentials are limited by environmental conditions (such as, growth rates of surrounding organs, space availability for the expansion of the organ, rate of increase in the blood supply to the organ etc.) which are created directly or/indirectly by that set of gene or other sets of genes the govern growth rates and developments of other organs or conditions concerned.

Different parts of the crocodile brain itself do not grow in the same relative rate as can be seen in Table 1. Among dimensions of the brain the length of the olfactory apparatus from optic chiasm to the olfactory bulb tip and diameter of olfactory bulb increased the most as can be seen in Fig. 13. This is of course, related to the more rapid increase in length of the rostral portion of the head. Other parts also show differential growth rates and, therefore, some changes in brain shape can be seen. (See Fig. 13.)

The body weight to brain weight ratio of the large crocodile is 2072.0, while that of the adult rat is 153.3; this indicates a class difference.

Data on brain region weight as percentage of the whole brain weight tells the relative growth rate of each brain region with respect to the whole brain. It could also be an index for comparison between animal species. Similar data were obtained by Cobb⁴ but on diameter of brain regions relative to one another and on the relative size of each brain region related to its functional significance in the animal.

The fact that gut length is exponentially increased with respect to increase in the body length (nose-to-tail tip length) (Fig. 14) indicates higher in the gut length relative growth rate compared to the body length in the crocodile. This may be partly due to differences in factors that control their growth. Similar relationship on this in other species along with explanation on this are not yet located in the literature.

It can be seen in Fig. 15 that kidney weight increases linearly with the body weight. This indicate certain coordination between the growth of the kidney and the body by some yet to be determined mechanism.

The allometric plot between the heart and the body weight shows curving down of the heart weight in large crocodile. This indicates slow down of relative growth rate of the heart with respect to the body by some mechanism. It is also interesting for future investigation on physiological bases and effects of such changes.

In conclusion, allometric relationships of body parts of Siamese crocodile have been analyzed. Relative growth between the brain, head gut, heart, kidney and body parameters were emphasized. A few new ratios have been proposed to give greater insight into developmental changes in body proportions, which include body weight/nose tip to tail tip ratio, brain weight/head weight ratio and brain weight/body weight ratio.

Allometric relationships of body parameters of the Siamese crocodile reported here were compared with the same parameters in other species of vertebrates, some similarity and differences were discussed. Relationships among body parameters of the Siamese crocodile during growth may give specific meaning on certain anatomical, biochemical and physiological changes in the process of growth of the animal and can be used to compare with relationships of similar parameters of all other vertebrate species to give insight on certain genetic control on the processes of growth and development.

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บทคัดย่อ

ได้ทำการศึกษาอัตราการเจริญเติบโตสัมพันธ์ของร่างกาย, ทางเดินอาหาร, ไต, หัวใจ, หู และสมองของจระเข้ *Crocodylus siamensis* อายุระหว่าง 1 เดือนถึง 4 ปี

ในจระเข้ขนาดเล็กอัตราการเพิ่มความยาวสัมพันธ์กับน้ำหนักตัวจะมากกว่าในจระเข้ขนาดใหญ่ อัตราส่วนระหว่างน้ำหนักตัวต่อความยาวเพิ่มโดยตรงกับน้ำหนักตัวระหว่าง 3 - 25 กก. ในจระเข้ขนาดเล็กกว่า 1 กก. อัตราส่วนนี้จะค่อนข้างน้อย น้ำหนักหัวแปรโดยตรงกับน้ำหนักตัว ความยาวของหัวแปรโดยตรงกับความยาวตัว ความสูง และความกว้างของหัวแปรโดยตรงกับความยาวหัวแต่ความยาวหัวเพิ่มขึ้นเร็วกว่า 2 ทิศทางดังกล่าว และความกว้างของหัวเพิ่มขึ้นเร็วกว่าความสูงของหัว น้ำหนักสมองเพิ่มขึ้นเมื่อน้ำหนักตัวและหัวเพิ่มขึ้น แต่อัตราการเพิ่มสัมพันธ์ของสมองช้ากว่าการเพิ่มน้ำหนักตัวและหัว น้ำหนักสมองเพิ่มขึ้นเป็นสัดส่วนโดยตรงกับการเพิ่มความยาวตัว ส่วนต่าง ๆ ของสมองจระเข้เจริญด้วยอัตราไม่เท่ากัน ความยาวของทางเดินอาหารเพิ่มขึ้นแบบเอ็กซโพเนนเชียลเมื่อเทียบกับการเพิ่มความยาวตัว

น้ำหนักของไต แปรตรงกับน้ำหนักตัว แต่น้ำหนักหัวใจเมื่อเพิ่มถึงขนาดหนึ่งจะเพิ่มขึ้นช้าลงเล็กน้อยเมื่อเทียบกับน้ำหนักของตัวจระเข้

ได้วิจารณ์ข้อมูลในแง่การแสดงออกของยีนส์, การกระจายของสารไปยังส่วนต่าง ๆ ของร่างกาย, ภายวิภาค และสรีระวิทยาของสัตว์ ระหว่างการเจริญเติบโต