

ingestion. Unfortunately there is little in the crocodilian literature to assist in evaluating the relative importance of primary versus secondary ingestion of terrestrial arthropods. In the most detailed study of any crocodilian's stomach contents, Cott (1961) found a strong correlation between prey type and the size of individual *Crocodylus niloticus*. Below one meter in length, *C. niloticus* contain largely insects, a sizable proportion of these being terrestrial species. Spiders, including semiaquatic and terrestrial species, and anurans account for most of the remainder. There is a noteworthy simultaneous reduction in the percentages of arthropods and anurans in stomachs of larger *C. niloticus*. Some insects, however, continue to be encountered as size increases well beyond that at which anurans are apparently no longer utilized. The strong correspondence between utilization of arthropods and anurans is compatible with the secondary acquisition of arthropods by smaller crocodiles, but the continued presence of such prey in larger crocodiles suggests primary ingestion.

The stomach contents of our *Paleosuchus* are more suggestive of primary ingestion than of secondary. The vertebrate remains were all of fish but the arthropods were primarily terrestrial. Puncture wounds in some prey items suggest these had been grasped by the *Paleosuchus*, and the size of some arthropods suggests that they were not eaten first by an anuran, for an anuran large enough to have eaten the mole crickets probably would have been above the upper limit of prey size for crocodilians the size of ours (153-181 mm snout-vent).

Laboratory observations on *Caiman crocodylus* demonstrate that terrestrial insects constitute suitable prey for this species. Mole crickets, beetles, moths, millipede, and spiders were readily eaten by captive individuals when care was exerted to minimize conditioned, situational cues for the feeding response. These data will constitute a future paper on crocodilian feeding behavior and pertinent sensory cues (HWC), but it can be noted here that with a randomized feeding schedule and prey offered from a hidden position, juvenile *C. crocodylus* of 250 mm total length accept almost any insect at least 6 mm in the largest dimension. Insects less than 4 mm in their largest dimension were generally ignored. That the *C. crocodylus* would leave the water and crawl onto their basking platform to seize insects suggests insects active along the land-water interface could serve as prey for young crocodilians. Similar feeding behavior has been observed at night in wild juvenile *Alligator mississippiensis* in Florida; they have been seen taking moths that fall on the water surface, mole crickets thrown upon the water, and insects resting on lily pads and stems of emergent vegetation. On one occasion, in an artificially illuminated area, a group of 6 young alligators were observed to catch and eat 17 arthropods of undetermined species, but including beetles and moths, in an hour; four other attacks of indeterminate success were also recorded.

The foraging has not resolved the issue of the relative importance of primary versus secondary ingestion as the source of terrestrial arthropods in crocodilian stomachs. It is obvious, however, that no arbitrary position at either pole is defensible. Juvenile crocodilians do directly prey on terrestrial arthropods on the water surface and on the shoreline, but because of differential digestion of vertebrate and arthropod prey items, stomach analyses will always overestimate the utilization of such prey.

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JAMES F. JACKSON,¹ HOWARD W. CAMPBELL,² Department of Zoology, University of Florida, Gainesville, Florida and KENNETH E. CAMPBELL, Jr., Florida State Museum, University of Florida, Gainesville, Florida 32601, USA. Present addresses: 1) Museu de Zoologia de Universidade de São Paulo, Caixa Postal 7172, São Paulo, Brazil and 2) Office of Endangered Species, U.S. Dept. Interior, Wash., D.C. 20240, USA.

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ON THE MAXIMUM TOTAL LENGTH OF THE SALT-WATER CROCODILE (*CROCODYLUS POROSUS*)

It was once thought that the largest living crocodilian species was the Salt-water Crocodile (*Crocodylus porosus*). Boulenger (1889) and Barbour (1924) uncritically associated secondhand reports of maximum total lengths of 33 and 29 feet respectively with actual museum skulls, and on the basis of these authors' authority and the existence of actual if partial specimens, the maximum total lengths were widely regarded as established.

Schmidt (1944) noted, however, that head length comprised about one-seventh of the total length in a variety of crocodiles, and on the basis of this proportionality, he questioned the validity of both the 29 and 33 foot records and finally placed the maximum known total length of *C. porosus* at 20 feet.

Wermuth (1964) showed that the average ratio of head to total length for 70 museum specimens of *C. porosus* was 1:7.48, and although he recognized the significance of his measurements for estimating total length from skull length, he did not apply these estimates to the largest known skulls of *C. porosus*.

Bellairs (1969) calculated the ratio between head length and total length for 87 Nile Crocodiles (*C. niloticus*) ranging in size from 16 in. to 15 ft 5 in. and found the ratio to be a fairly constant 1:7.5. This ratio is virtually identical to that based on Wermuth's data for *C. porosus*, and a spot check of museum specimens by Bellairs showed a similar ratio for other species. Bellairs applied this ratio to the large skull on display in the British Museum (BM) gallery, thinking it belonged to Boulenger's alleged 33 foot animal, and calculated that the skull probably came from an animal no more than about 17.5 ft in total length. In fact, although the gallery skull is the largest skull in the BM, it does not belong to Boulenger's alleged 33 foot animal (letter from A. F. Stimson, 19 May 1972)—the skull of which is also in the BM—and thus on the basis of Bellairs' ratio, Boulenger's crocodile skull would have come from an animal even smaller than 17.5 ft.

Thus 3 authors have calculated ratios of head length to total length for *C. porosus* or its close relatives that make it clear that the largest *C. porosus* skulls reported could not have come from animals with the total lengths previously attributed to them.

In view of the great attention devoted to this topic it is interesting that a previously published set of measurements of head length and total length for a relatively large sample of *C. porosus* from a restricted geographical area has been completely overlooked. These data were part of an extremely valuable series of measurements made by Banks (1931) on 41 *C. porosus* from western Sarawak which ranged in size from 1.75 ft to 16.5 ft in total length. These data provide the basis for the most precise study yet available of the relationship between head length and total length for a geographically limited population of *C. porosus*, and they also provide the basis for yet another estimation of the relationship between head length and total length for this species.

In this paper I present the results of a regression analysis of Banks' data to predict total length from head length and then apply the results to an analysis of the 4 largest existing skulls of *C. porosus*—the largest of which has been overlooked by most zoologists.

The head measurement which Banks made on the intact animals was from the tip of the snout to the posterior edge of the parietal scute. Since the posterior edge of the parietal scute conforms almost exactly to the posterior edge of the supraoccipital bone on the medial posterior edge of the cranial shelf, Banks' head length measurements are essentially identical to the skull length as measured from the tip of the snout to the medial posterior edge of the cranial shelf.

Banks measured head length and total length for 39 of his 41 specimens and a graphic plot of these data (Fig. 1) reveals a nearly colinear relationships ($r = .993$) between the two variables despite the fact that the animals ranged widely in size and included both sexes. The least squares regression line of total length (y) to head length (x) for Banks' data has the formula $y = -4.39 + 7.49x$. This equation allows us to estimate the total length of any *C. porosus* for which the skull length (measured from the tip of the snout to the medial posterior edge of the supraoccipital bone) is known.

In Table 1 I have listed the 4 largest existing skulls of *C. porosus* along with the estimated total lengths of the whole animals based on the regression equation given above. The estimated total length of the animal with the largest skull in Table 1 is 18.04 ft. The 95 per cent confidence interval for this estimate is 17.06-19.02 ft. Thus, if the regression equation based on the Sarawak sample holds for the population from which this large specimen was taken, and if

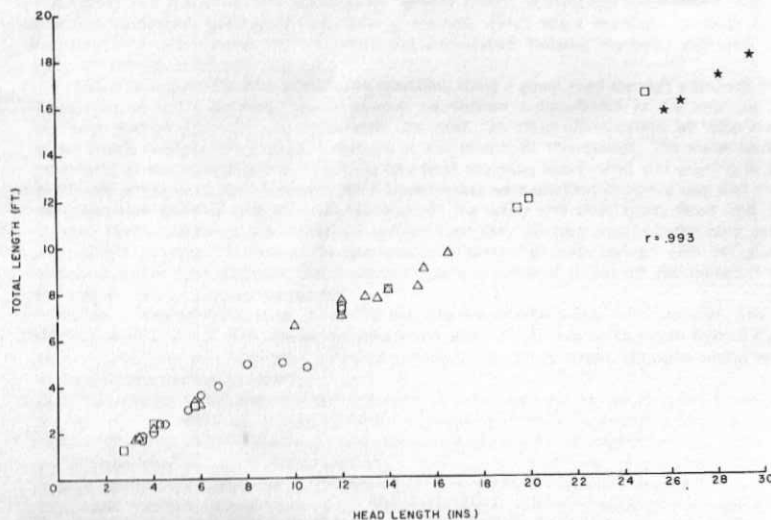


FIGURE 1. Scatter diagram of total length against head length for 39 Salt-water Crocodiles (*Crocodylus porosus*) measured by Banks (1931) in western Sarawak (open symbols) and the points (closed stars) for the 4 largest existing skulls of *C. porosus* as estimated from the regression equation ($y = -4.39 + 7.49x$) derived from Banks' data. Symbols for Banks' data: open circles: males; open triangles: females; open boxes: unsexed individuals.

TABLE 1. The 4 largest existing skulls of the Salt-water Crocodile (*Crocodylus porosus*) and the estimated total length of the specimens from which they came as based on the regression equation $y = -4.39 + 7.49x$. Abbreviations: BMNH—British Museum (Natural History); MCZ—Museum of Comparative Zoology.

Skull	Skull Length (cm)	Skull Length (in)	Estimated Total Length (ft)	95 Per Cent Confidence Interval for Estimated Total Length (ft)	Comments
Indian Museum	75	29.5	18.04	17.06 - 19.02	Noted but once in the literature by Prashad (1930)
Gallery Skull (BMNH)	71.5	28.15	17.20	16.24 - 18.16	Long mistaken for Boulenger's alleged 33 foot specimen
Barbour's alleged 29 foot specimen (MCZ)	67.4	26.5	16.17	15.22 - 17.12	"... said to have been 29 feet long... the largest crocodile skull in existence" (Barbour, 1924).
Boulenger's alleged 33 foot specimen (BMNH)	65.5	25.8	15.73	14.79 - 26.67	"Stated by the donor to have pertained to a specimen 33 feet long..." (Boulenger, 1889).

the regression equation holds for head lengths slightly larger than those from which it was derived, i.e., if there are no allometric changes occurring at larger head lengths, and if a one in 20 sampling error has not occurred, then the largest known skull of *C. porosus* could not have come from an animal over 19 ft in total length. And under the same set of assumptions, it is possible to say that the skulls of the alleged 29 and 33 ft crocodiles could not have come from animals much larger than 17.12 and 16.67 ft in total length respectively.

I should emphasize that there are larger figures for skull lengths of *C. porosus* available in the literature, but these are all based on other, generally unspecified, measures of skull length than the one used here, i.e., the distance from the tip of the snout to the medial posterior edge of the supraoccipital bone. The largest skull in the Indian Museum, for example, has been reported to measure 38 in. in total length (Prashad, 1930); the largest skull in the BM has been measured at 36.5 in. (Parker, in Brander, 1930), and the skull of the famous 29 foot crocodile has been measured at 34.5 in. (Barbour, 1924). Brander (1930) found a skull in the Elgin Museum which he said measured 27 in. in total length, but he did not state the method of measurement and the skull cannot now be located (letter from Ian Keillar, 12 May 1973). This was undoubtedly a large skull, perhaps second only to the Indian Museum specimen, but I see no reason to believe that its stated length bore any closer relationship to the length from the tip of the snout to the posterior edge of the supraoccipital bone than figures of similar magnitude given in the past for the other large skulls in Table 1.

If 19 ft is the largest plausible total length for *C. porosus* as estimated from skull length, what is the largest total length for the species as determined from the actual measurement of an intact animal?

In an attempt to answer this question, I reviewed all of the literature claims for large *C. porosus* I could find, and Banks' 16.5 ft animal is the largest that can be shown unequivocally to have been actually measured. Thus on the basis of an analysis of Banks' data and a review of published total lengths for *C. porosus*, I believe that there is no good evidence that the maximum total length of this species exceeds 18 or 19 feet.

As far as the largest most reliably measured crocodylian of any species is concerned, I agree with Schmidt (1944) that this record belongs to a 22 ft 3 in. male Orinoco Crocodile (*C. intermedius*) measured by Alexander von Humboldt's assistant Bonpland in 1800 (von Humboldt, 1852).

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ALLEN E. GREER, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, USA.

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NOTES ON THE FISHING BEHAVIOR OF WATER SNAKES

Very little is known about the foraging methods used by water snakes, as evidenced by the scarcity of published field observations. Brown (1958) summarized water snake foraging methods as follows: groping or exploratory method, direct attack method, and deep water hunting. The water snakes seem to show no stereotyped foraging methods, but vary this behavior with their habitat.

At 6:30 pm on 17 June 1973 while travelling along a gravel road through a flooded field 4 km west of Willis, Marshall Co., Oklahoma, we noticed a disturbance in the water at the discharge end of a culvert running beneath the road. On closer investigation we observed 4 water snakes feeding in an unusual manner (the water due to rising lake level following heavy rains) was draining to the south side of the road via the culvert. All 4 water snakes were oriented in such a way that their tails anchored them to the rocks at the edge of the water and their heads faced into the current. Before capturing the snakes we noticed that they all held their mouths open while their bodies remained motionless. On one occasion a small fish made contact with the gaping mouth of one of the snakes and that snake instantly snapped at it. It was not determined if the fish was actually caught and consumed.

Three *Natrix erythrogaster transversa* and one *Natrix rhombifera* were captured. The *N. rhombifera* was immediately forced to regurgitate and 13 fish ranging in length from 2-8 cm were counted. These were all later identified as the carp, *Cyprinus carpio*. No other snakes were observed in the immediate vicinity.

To determine whether this peculiar behavior was restricted to the daylight hours, we returned to the observation site at 10:30 pm and observed 3 more water snakes foraging in the manner described. These snakes were captured and all identified as *N. rhombifera*. At 11:00 pm on 19 June two *N. erythrogaster transversa* and two *N. rhombifera* were captured. Before capture these snakes were observed to be oriented in the fashion previously described.

Large numbers of small carp, *C. carpio*, were observed on both the north and south sides of the road, and since the water was draining from north to south through the culvert, many of these fish were being swept through this discharge. Once the water fully receded and the flow through the culvert ceased, the snakes would no longer be able to use the current to their advantage. They would have to resort to other foraging methods.

This "mouth-open" foraging behavior was described by Brown (1958) in *N. s. sipedon* and by Evans (1942) in *N. s. confluens*, *N. c. cyclopius*, *N. e. erythrogaster*, and *N. r. rhombifera*. In all cases, however, these snakes were swimming through the water, creating their own current while holding their mouths open.

Not only was it evident that the snakes were taking advantage of a unique feeding opportunity, but other snakes were apparently able to locate this culvert discharge with ease. After removing all the snakes from the discharge, others had taken their place within 4 hours. Burghardt (1968) demonstrated that watersnakes can show a preference for a particular food item by means of olfaction. It would be of interest to know how efficiently these snakes can locate food items underwater.

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JAMES C. GILLINGHAM, Department of Zoology, University of Oklahoma, Norman, Oklahoma 73069, USA and THEODORE RUSH, Box 334, Groom, Texas 79039, USA.

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PATHOLOGICAL LITHOPHAGY IN *TESTUDO HORSFIELDI*

The existence of lithophagy among tortoises and land-dwelling turtles is becoming an established fact. Observations by Kramer (1973), Skorepa (1966), and Sokol (1971) indicate that turtles do at various times ingest sand and pebbles along with their regular diet. The present note establishes the same habit as occurring pathologically in *Testudo horsfieldi* as well.

A captive female *T. horsfieldi* had been feeding well on lettuce, tomatoes and other greens for a period of 3 months after arrival in the collection. Subsequently, over a period of a month she stopped eating and became lethargic. During this time she was kept in a container with aquarium-type gravel. She continually refused food and water and lost weight rapidly. Then suddenly over a two week period she regained her lost weight but was never observed eating. One week later she died. Upon autopsy major portions of her intestines as well as her whole stomach were packed tightly with a large volume of gravel, the approximate weight of which was 30 grams (corresponding to about 7 per cent of her total body weight), and contained only insignificant amounts of ingested greens. Whether or not this mass of gravel was the cause of death was indeterminable.

This latest record of lithophagy does not seem to support the theory that sand and pebbles are only ingested as an aid in maceration of food. Instead, it suggests a pathological etiology heretofore undescribed. The tempting speculation is raised that this gravel was ingested as a pressure-compensatory device similar to the water-ingestion behavior of some aquatic turtles (Belkin, 1965; Jackson, 1969). When starvation leads to the mobilization of stored fats and subsequent reduction in weight and volume, internal pressure drops due to the rigid box the turtle is enclosed in. The compensatory mechanism is then the ingestion of water until