estimated). He chased her into shallow water (7.5 cm) and repeatedly bit her hindquarters, especially her thighs. This continued for about 5 minutes and then he moved around her side so as to face her and continued biting at her forelegs and head. Eventually (about 3 minutes later) he pulled his head in slightly, extended his forelegs held closely together to the limit, palms outward, and began titillating the sides of her face and neck with his elongated, curved foreclaws. After several series of titillations (about 3 minutes later) he moved around her side to the rear and attempted to mount as she moved into deeper water (15-20 cm). He placed his hindfeet under the posterior edge of her carapace and locked them above her pulled-in hindfeet for support. His forelimbs rested on her carapace just posterior to the median. Several attempts were made to bring his tail under her's to affect coition, but he was finally dislodged. The male made several more unsuccessful attempts at copulation, but finally broke contact at 1:20 pm. The female remained passive through all, only occasionally moving about. A male *G. flavimaculata* and a male *G. geographica* in the same tank ignored the courtship activities. Male *Chrysemys picta* and *C. scripta* were also courting in both indoor and outdoor tanks.

The above description differs from courtship of male *G. barbouri* and *G. flavimaculata* as reported by Wahlquist (1970). In these turtles, the male approached the female with his neck extended, made nose contact, and then began titillation. Wahlquist did not report biting, and nose contact did not occur during the present observation. The titillation of the female's head closely resembles that of male *Chrysemys picta* (Ernst, 1971) and *C. scripta elegans* (Cagle, 1950). Biting behavior is unknown in these turtles, but does occur in the Mexican subspecies, *C. scripta taylori* (Davis and Jackson, 1973), which lacks long foreclaws; the biting response may be abnormal since Davis and Jackson did not use females of *C. s. taylori*. Since *Graptemys* and *Chrysemys* are closely related (Ernst and Barbour, 1972), the courtship patterns indicate that *G. pseudogeographica* may have evolved from *Chrysemys*.

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THE FEEDING HABITS OF CROCODILIANS: VALIDITY OF THE EVIDENCE FROM STOMACH CONTENTS

Prey selection by crocodilians has received limited attention. Although some information concerning food preferences, sensory cues utilized in prey selection, prey capture behavior, and changes in these parameters with age is based largely on anecdotal accounts, our understanding of crocodilian feeding habits is based largely on stomach analyses. However, their validity has been challenged on the grounds that secondary ingestion, i.e., the acquisition of prey items contained in the gut of the primary prey species, may make their interpretation difficult (Neill, 1971). Of particular concern in this regard are data suggesting differential utilization of invertebrate prey

by juveniles and vertebrate prey by adults (Cott, 1961; Fogarty and Albury, 1967; Giles and Childs, 1949; Kellogg, 1929; Valentine, et al., 1972). While this difference may appear reasonable when the change in size of the predator is considered, it is still difficult to account for the high proportion of terrestrial as opposed to aquatic invertebrates found in juvenile crocodilians (Cott, 1961; Kellogg, 1929). Neill (1971) believes juvenile crocodilians do not forage away from water and contends that the terrestrial invertebrates are secondarily obtained from the stomachs of anurans they consume. The chitin of the invertebrate exoskeleton would prove more resistant to digestion than vertebrate muscle and bone and would remain after evidence of the vertebrate prey had disappeared. We have tested this hypothesis of differential digestion.

Eleven juvenile *Caiman crocodilus*, 225-275 mm in total length, were obtained from commercial sources and housed together in a 100 X 45 cm tub until used. During the experiment the air temperature varied between 18-26 C, and the caiman had a dry basking platform and access to a 120V heat lamp at 60 cm for 12 of each 24 hours. This physical situation allowed the specimens to maintain body temperatures in excess of 30 C when the heat lamp was on or to seek cooler temperatures if necessary.

Prior to their use the caiman were not fed for 3 days. Each was then force-fed a dead *Hyla squirella* that had been fed a large mealworm (*Tenebrio molitor* larva) about one hour prior to its death (by freezing). Two individuals were each additionally force-fed a dead mealworm marked with India ink and a dead *Acris gryllus* that had just eaten a *Drosophila*. They were then returned to the tub and a 12 hour period of access to the heat lamp began.

The caiman that received only *Hyla squirella*, including a mealworm, were sacrificed by freezing at 12(2 specimens), 16(2 specimens), 19(3 specimens), 22(1 specimen), and 24(1 specimen) hours after feeding. The two other specimens were sacrificed 30 and 36 hours after feeding. Stomach contents of each specimen were removed and examined under a dissecting microscope to determine the relative condition of the anuran and insect remains. In addition, we examined the stomach contents of 3 juvenile *Paleosuchus trigonatus* collected near Iberia, Madre de Dios, Peru, and preserved 8 hr after collection.

The anuran and insect remains in our experimental series were digested at vastly different rates, but between specimens that carried on digestion for equal time periods there was no qualitative variation in these relative rates. After 12 hr the frog remains were strongly altered although still recognizable as *Hyla*. The mealworm was exposed but not free from the frog's coelom. After 16 hr the frog was identifiable only to order and the mealworm had separated from it, though surrounded by a remnant of frog muscle. After 19 hr the frog was recognizable only as vertebrate muscle and bone and the mealworm was softened but intact. Stomachs of the specimens which digested for 22 and 24 hr contained tiny fragments of muscle tissues and intact mealworms. Thus, 16 hr or more after secondary ingestion of an insect, distinction between primary and secondary ingestion of the insect would be impossible. The specimens sacrificed after 30 and 36 hr showed no evidence of the two anurans fed them, but the mealworms and *Drosophila* were still present in their stomachs. The mealworms that had been secondarily ingested were largely intact, and those fed directly were only slightly more disarticulated.

The stomachs of the *Paleosuchus* contained both vertebrate and invertebrate remains. Unidentified fish bones were present in all, and one also contained a strongly digested 45 mm specimen of an unidentified catfish. Beetle carapaces and beetles were found in two; several moths, some with antennae and legs still attached, in one; a millipede in one; a dipteran larve in one; lycosid spider fragments or whole individuals in two; and all contained mole crickets or fragments thereof. Two specimens contained gastroliths; one had 7, the other 5. Several of the beetle carapaces and the mole crickets had holes in the exoskeleton which were the same size as the *Paleosuchus* teeth.

These experimental results demonstrate a clear difference between the rates of disappearance of vertebrate and arthropod remains from caiman stomachs, as predicted by Neill (1971). Thus, arthropods found in crocodilian stomach analyses may often result from secondary

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 crocodilus* 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. crocodilus* 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. crocodilus* would leave the water and crawl onto their basking platform to seize insects active along the land-water interface could serve as prey for young crocodilians 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 lilypads 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 forgoing 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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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 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 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.

he results of a regression analysis of Banks' data to predict total
en apply the results to an analysis of the 4 largest existing skulls
ich has been overlooked by most zoologists.

hich Banks made on the intact animals was from the tip of the
the parietal scute. Since the posterior edge of the parietal scute
the posterior edge of the supraoccipital bone on the medial
helf, Banks' head length measurements are essentially identical to
from the tip of the snout to the medial posterior edge of the

ngth and total length for 39 of his 41 specimens and a graphic
veals a nearly colinear relationships (r = .993) between the two
the animals ranged widely in size and included both sexes. The
f total length (y) to head length (x) for Banks' data has the
This equation allows us to estimate the total length of any *C.*
ngth (measured from the tip of the snout to the medial posterior
) is known.

he 4 largest existing skulls of *C. porosus* along with the estimated
nals based on the regression equation given above. The estimated
ith the largest skull in Table 1 is 18.04 ft. The 95 per cent
mate is 17.06-19.02 ft. Thus, if the regression equation based on
the population from which this large specimen was taken, and if

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 crocodilian of any species is concerned, I agree with Schmidt (1944) that this record belongs to a 22 ft 3 in. male Orinoco Crocodile (*C.*

r = .993

10   12   14   16   18   20   22   24   26   28   30
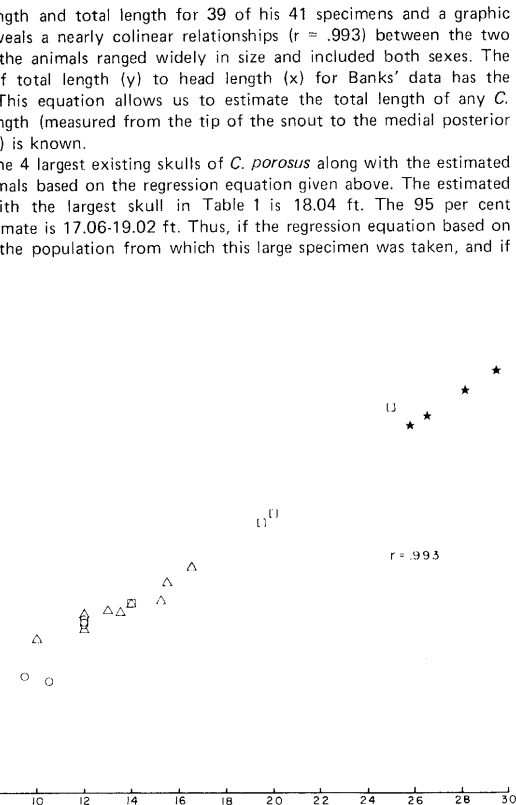
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NOTES ON THE FISHING BEHAVIOR OF WATER SNAKES

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 at the mouth of this culvert. The water on the north side of the road (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 one *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. cyclopian, 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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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