

lean beef, bone meal, cod-liver oil and vitamin concentrate (100:20:5:2 by weight). Sex was tentatively determined from plastron concavity and later confirmed at the end of the study on the basis of tail configuration.

After 650 days, this turtle and one control turtle were tested for visual ability and photographed. Criteria for visual function was rapid withdrawal from rapidly approaching objects. Discs (15 mm) in addition to lights were used in order to eliminate heat as a factor. Red, in addition to white test objects, were used because it is well known that turtles have a keen sense of color vision. Photographs taken at that time (Fig. 1) show the dorsal (A) and lateral (B) views of the control as well as dorsal (C) and lateral (D) views of the anophthalmic animal.

Termination for histological study of these two turtles followed immediately after the vision testing. Heads were fixed in buffered formalin for serial sectioning and hematoxylin-eosin staining. Every tenth section, including ophthalmic regions from both heads, was examined.

Fig. 2 shows this turtle's periodic carapace length (open, circular points) and body mass (crosses) measurements. Average control lengths (solid circular points  $\pm$  S.E.) and masses ( $X \pm$  S.E.) are also shown. Although the anophthalmic turtle was smaller than the average control turtle throughout the first 250 days, the differences were statistically insignificant (i.e. within two standard deviations of the control averages). At termination, sizes were almost identical.

This turtle, unlike the control animal, displayed no visual ability. Although it possessed vestigial eye-slits, there was no evidence of globes (Fig. 1). Histological examination showed total absence of formed ocular tissue. Some pigment, present in the orbit, however, may have been remnants of ocular tissues.

These results demonstrate growth without vision to be possible for this species. The smaller early size may have reflected initial feeding difficulties. A quantitative food intake record would have been useful. Field conditions may not permit comparable survival and growth. This turtle was secure from predators. Food presentation was such as to permit reliance on touch and chemical sensations.

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#### CROCODILIAN GALLOPING: AN UNIQUE GAIT FOR REPTILES.—

Three distinct terrestrial gaits have been reported for crocodilians: the high walk, the belly run and the gallop (Cott, 1961). The high walk is a symmetrical walking gait used during most terrestrial activity. The belly run is an escape reaction producing a rapid retreat into the water by sliding down a bank. The crocodile remains on its belly and, with posterolateral thrusts of its legs, slides itself down an incline. The gallop is an asymmetrical running gait of apparently infrequent occurrence and is rarely observed. The crocodilian gallop has been described as the fore- and hindlegs working in serial pairs similar to that of a bounding squirrel. Serendipitously, I filmed at 48 frames per second three sequences of galloping in juvenile *Crocodylus porosus*, total length of approximately 45 cm, and am able to describe and illustrate the crocodilian gallop for the first time.

The seven cine-tracings (Fig. 1) illustrate the range of body and leg movements during a single galloping stride and eliminate the necessity of a detailed description. Nonetheless, several points should be emphasized. Each contralateral pair of legs moves synchronously or nearly so. The back is extended during the unsupported stage of the gallop and is flexed when the body is supported by the forelegs. Maximum flexure occurs as the hindfeet touch down lateral to the foot prints of their ipsilateral forefeet. These facets of the crocodilian gallop were observed no matter how variable a stride appeared, and the strides were variable.

Of the 25 galloping strides examined only three possessed the synchrony of the gait diagram in Fig. 1. Five additional strides showed synchrony of contralateral pairs of legs, but each contained a quadrupodal support stage following hindfoot footfall. Many variable footfall patterns were observed: transverse gallop patterns in which the footfall pattern of hindfeet was identical to that of the forefeet; rotary or lateral gallop patterns in which the footfall pattern of the hindfeet was the reverse of that of the forefeet; patterns in which the hindfeet but not the forefeet were synchronized, as well as the converse. The variation is best demonstrated by examining the frequency of occurrence of the ten possible support postures (Dagg and de Vos, 1968) during the twelve strides of one galloping sequence. Six (50%) of the strides possessed a quadrupodal support stage, two (17%) a tripodal stage with one forefoot elevated, four (33%) a tripodal stage with one hindfoot elevated, all (100%) each of the two bipodal stages with either both forefeet or both hindfeet on the ground, none a bipodal stage with diagonal or ipsilateral pair of fore- and hindfoot support, five (42%) with support by single forefoot, two (17%) with support by single hindfoot, and eleven (92%) with a no support stage. If the contralateral pairs are completely synchronized, only four support postures are possible: quadrupodal, bipodal with either both forefeet or both hindfeet, and no support.

The timing and sequence of footfalls seem to be much less variable in mammals (Gray, 1968; Howell, 1965; Sukhanov, 1968). The lead foot may switch from one side to the other or the gait change from a transverse to a rotary gallop, but once changed, the

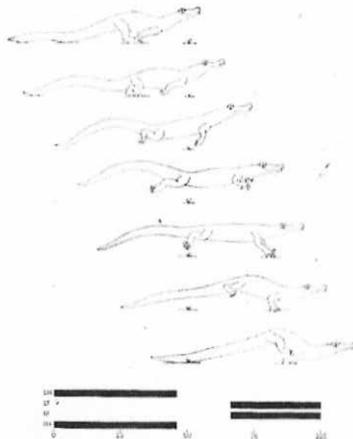


Fig. 1. Gait diagram and cine-tracings of the gallop of a *Crocodylus porosus*. Gait diagram depicts a single stride, and numbers refer to % of stride completed. There is no reference to time. Solid black lines show which foot (L.H., left hind; L.F., left fore; R.F., right fore; R.H., right hind) is on ground. Tracings illustrate principal body postures during gallop.

pattern is maintained. This low variability apparently reflects the fact that the mammalian gallop has been largely studied in large animals, such as horses and other ungulates. The gait sequences of small animals tend to be more variable than in larger ones (Hildebrand, 1966). Even if small mammals have as variable a gallop as crocodiles, the crocodilian gallop is still easily distinguishable. Comparison of the galloping crocodile's gait diagram with mammalian ones of Gray and Sukhanov shows that the synchronization of contralateral pairs of legs is much closer in the crocodile. The footfalls of a contralateral pair may not coincide, but liftoff is synchronized, e.g., in 76% and 72% of the galloping strides for the forefeet and hindfeet, respectively. The crocodilian gallop has the form of a rotary gallop, particularly since the main period of no support follows hindleg liftoff and extension of the body occurs during this no support stage.

The gallop developed from the high walk when the increasing speed of the latter re-

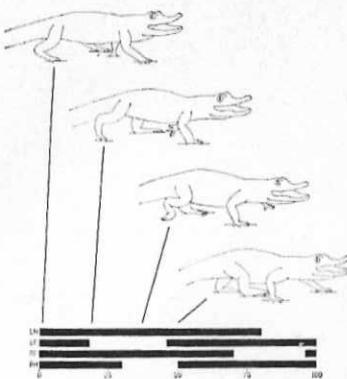


Fig. 2. A gait diagram and cine-tracings of high walk of a *Crocodylus siamensis*. Tracings are associated with gait diagram to illustrate support postures during first half of stride. Support postures in last half of stride would be mirror images of those of first half. Gait formula (Hildebrand, 1966) for diagram is 80, 40% with forefoot contact 90% that of hind.

sulted in periods of unipodal support, with the concomitant loss of balance. According to gait formula analysis (Hildebrand, 1966), the gait sequence of the high walk is a trot (Fig. 2) at a normal walking speed and marginally a lateral sequence, diagonal couplet gait at a very slow walking speed. The body maintains a tripodal or quadrupodal support posture for nearly 70% of the stride, and, there is no period of unipodal or no support. As the walking speed increases, a leg supports the body for a smaller proportion of each stride, thus reducing the amount of quadrupodal and tripodal support. Theoretically, if the no support period for each leg is doubled, there will be no periods of quadrupodal support, tripodal support for only 20% of the stride, unipodal support for 12%, and bipodal support for the remainder. During unipodal support, the crocodile falls on its belly and changes its gait sequence to a gallop with the contralateral pair of legs synchronized or nearly so. The above description is basically the sequence of transition observed in the cine-film, although instability was increased by leg movements becoming asymmetrical, i.e., irregularly spaced in time in relation to one another. This asymmetry

further enhances the loss of balance and the change to a galloping gait.

The gallop has been observed only in immature crocodylians less than two m in total length. Perhaps the massiveness of larger individuals prevents them from galloping, or their size eliminates the need for a means of rapid escape. Certainly, the ability to gallop in small crocodylians would seem to be highly selective. The difference in speed between the high walk and the gallop is significant and indicates the importance of galloping for escape. The *C. porosus* and *C. siamensis* walk an average of 3.3 km/hr (2.0–4.6, N = 6) and 3.4 km/hr (3.0–4.0, N = 4), respectively. The *C. porosus* galloped at an average of 48.9 km/hr (28.8–64.8, N = 9); speed was determined by the amount of time it took the specimen to travel one body length. These speeds appear to be the fastest yet reported for reptiles and are well within the range of mammalian galloping speeds. Although this high speed occurs only over short distances, the probability of escape is increased, particularly when a juvenile is galloping down a bank to the safety of water.

The *Crocodylus porosus* (total length of ca. 45 cm) was filmed at the D. A. S. F. Wildlife Laboratory, Moitaka, Papua-New Guinea through the courtesies of E. Lindgren and R. Lawson. The *Crocodylus siamensis* (total length of ca. 60 cm) was lent to me by C. A. Ross. To these individuals, I am grateful. My work in New Guinea was sponsored by Smithsonian Research Foundation Grant.

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THE MARINE CROCODILE, *CROCODYLUS POROSUS*, FROM PONAPE, EASTERN CAROLINE ISLANDS, WITH NOTES ON FOOD HABITS OF CROCODILES FROM THE PALAU ARCHIPELAGO.—A marine crocodile was captured on 28 March 1971 in a crude trap constructed of mangrove poles by residents of the Kitti Municipality on the south side of Ponape Island (7° N, 158° 20' E). The trap was built after three domestic pigs, which had been tied near the shoreline, had mysteriously disappeared over a six-month period. It was set in a mangrove area and baited with a live pig tethered at one end of the enclosure.

This record is particularly noteworthy because crocodiles are unknown from Ponape and the Eastern Caroline Islands in general. The specimen was identified as *Crocodylus porosus* Schneider by Peter T. Wilson, Director of the Marine Resources Division of the Trust Territory Islands. Wermuth (1953) recorded this species, which frequents mangrove swamps and brackish coastal areas, from the southeast Asian coast, extending from southern China to India; Ceylon; Sunda Islands (including Sumatra, Java, Borneo, Celebes, and Timor); Philippine Islands; Moluccas; Kei and Aru Islands; New Guinea; Bismarck Archipelago; Solomon Islands; New Hebrides; Fiji Islands and northern Australia. It also occurs in the Palau Archipelago, Western Caroline Islands, which is located approximately 800 km east of the Philippines. It is doubtful that this species has become established at Ponape. The captured specimen probably represents a migrant from an area within the normal distributional range. Ditmars (1957) reported that large and half grown individuals are frequently sighted from vessels far out to sea. The nearest known populations of this species are from the Bismarck Archipelago, some 1360 km to the south. Wilson (1964) reported this species common at Palau, in the western extremity of the Caroline Islands, but Palau lies nearly 2400 km west of Ponape.

Dispersal of this individual may have been achieved via the Bismarck Archipelago-Solomon Islands region. The South Equatorial Current which flows in a westerly direction is the dominant surface current in these latitudes (Sverdrup, Johnson and Fleming, 1942). However, a northerly gyre is created when this current system contacts the eastern boundary of the aforementioned island groups. Conceivably a crocodile swept out to sea in this system could be transported

across the equator in a northeasterly direction and would then be further aided on the course to Ponape by the North Equatorial Countercurrent. Another possible avenue of current-aided dispersal would be the longer route from Palau, Eastern Indonesia, or the Philippines via the easterly flowing North Equatorial Countercurrent.

The Ponape crocodile was a male measuring 380 cm total length. The specimen was not preserved, but several photos of it appeared in a publication of the Pacific Islands (Saipan) Trust Territory entitled *Highlights* (1 May 1971). The stomach contained a piece of mangrove wood, several unidentified crabs, an unidentified eel and fragments of a small green turtle. Crabs appear to be a common item in the diet of *C. porosus*, at least in smaller individuals. In specimens collected at Palau by Mr. Robert Owen during September–October, 1969, crabs were found in 15 of 16 specimens, ranging in total length from 118 cm to 300 cm. The stomachs also contained seaweed, fishes, bird feathers and sea snakes. Humans are occasionally attacked at Palau. The most recent fatality occurred in December 1965. A man was attacked and killed by a crocodile while spearfishing at night (0300). Local officials stated the victim was badly maimed with loss of one arm, a portion of the other, a lung and the liver. The attack was witnessed by a fellow spearfisherman. Wilson (1964) described a non-fatal attack at Palau which also occurred while the victim was spearfishing at night.

I thank Ronald Powell who provided the stomach content data for the Ponape crocodile. Thanks are also due Robert Owen, Palau District Entomologist, for providing stomach content data of Palau specimens and details on the fatal attack of 1965.

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