CITES—APPENDIX I. Shall include all species threatened with extinction which are or may be affected by trade. Trade in specimens of Appendix I species must be made subject to particularly strict regulation in order not to endanger further their survival and must only be authorized in exceptional circumstances.

CITES—APPENDIX II. Shall include

(a) all species which, although not necessarily now threatened with extinction, may become so unless trade in specimens of such species is subject to strict regulation in order to avoid utilization incompatible with their survival and

(b) other species which must be subject to regulation in order that trade in specimens of certain species referred to in subparagraph (a) may be brought under effective control.

(Note: The concept embodied in subparagraph (b) involves protection of species that are not threatened by extinction but which, because of similarity of appearance to threatened species, make it difficult or impossible for government officials to determine which species are being commercially traded. These species are said to be threatened owing to their similarity to species which are not threatened. Unfortunately, to the untrained eye crocodilians appear superficially similar.)

Integumentary System

The skin of crocodilians serves as a barrier or armor protecting the inner tissues and organs from external elements. It plays an important role in defense and camouflage. It consists of an outer layer or epidermis made of a hard, horny material called keratin. The scales are thickenings of this keratin and are interconnected by hinges of a thinner layer of tissue. Some crocodilian scales may appear to overlap, but for the most part they are distinct structures that form part of a continuous epidermal sheet. They are not separate structures like fish scales.

The inner layer or dermis consists of connective tissue and is traversed by blood vessels and nerves. In crocodilians this layer contains small plates of bone called osteoderms which lie beneath and reinforce the horny epidermal scales.

Crocodilian scales are not periodically shed and replaced as in snakes and lizards. They grow slowly as the animal grows and are replaced gradually as they're worn.

The value of the hide or skin represents the primary reason crocodilians are so severely endangered. The hides of most species are in strong demand to make leather goods such as shoes, boots, handbags, and

wallets. The dorsal or back hide of crocodilians is heavily cornified and lies above bony plates and generally is not used for leather. The sides and abdomen, however, are much more supple, and it is these parts of the hide that are commonly used for leather goods. The exceptions are two species of *Caiman* and four species of the subfamily Crocodylinae that have bony plates lying beneath their bellies or ventral scales. These are impossible to remove without forming blemishes during the curing process—although recent technical advances have made this less of a problem than in the past.

The number of scales and their arrangement are used as distinguishing characteristics with the postoccipital and nuchal scales being of most importance. The postoccipital scales are on the dorsal surface at the base of the skull and the nuchal scales are located on the nape of the neck immediately after the postoccipital scales.

The last dorsal scale ends at the posterior margin of the upper thigh of the hind leg. The scales on the tail are similar to those on the back. The tail also has a comb or double-rowed crest of triangular scales vertically along the top, which merge about midway down to form a single fused row of crests. In most species there is a comb-like set of scales on the feet as well.

While the epidermis of most reptiles is devoid of any glands and pores, crocodilians possess a pair of glands on the underside of the jaw and a pair of glands in the cloaca, which emit a musky odor. It is believed, but it has not been definitely proven, that the glands under the jaw are somehow involved in the salt balance,[1] given the penchant for some species to occupy brackish and saltwater environments. The glands near the cloaca excrete a musky substance that is believed to be involved in either mating or defense or both. Johnson and Wellington (1982) say yearlings in the lab clearly respond to scent from adult male cloacal glands.

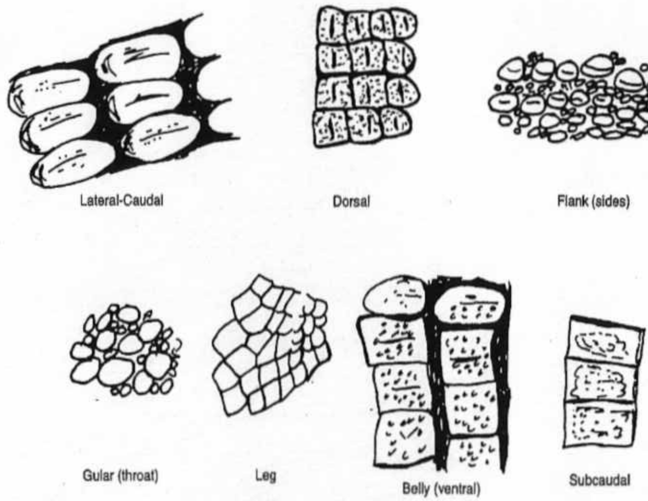
The armored skin on the head is stretched tight and fused firmly over the skull, which makes a sturdy head and protects it during battle with large prey.

The American alligator, which had become severely depleted by 1970 because of hunting for its hide, has weakly developed abdominal osteoderms which are not linked by joints so that it is especially easy to remove them during processing without leaving any blemishes.

Brazaitis (1987) indicates the following characteristic scale shapes which occur at different parts of the body:

1. Dorsal scales. These are square or rectangular and nearly always ossified. They usually have a well-defined ridge or keel.

[1]The glands involved in salt balance are located at the base of the tongue. All species including species living exclusively in fresh water have the jaw glands.

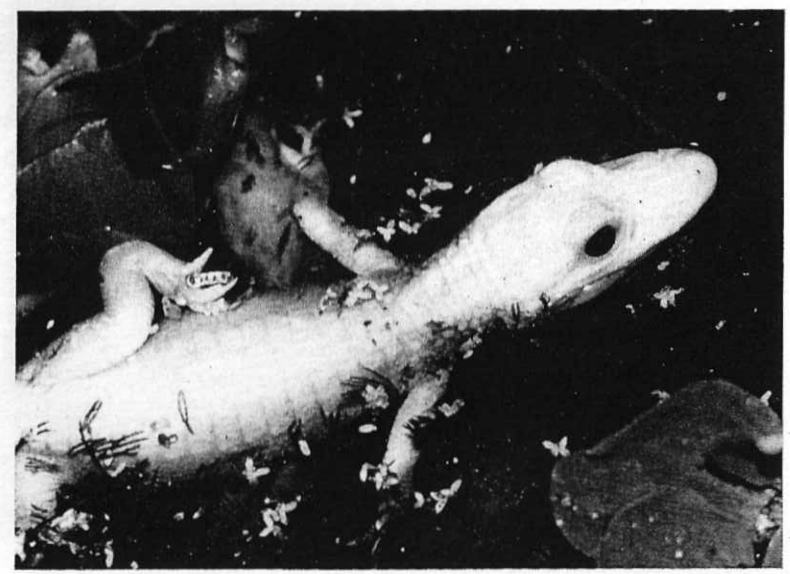


Crocodilian scale types (*after Brazaitis*).

2. Flank scales. The skin of the sides or flank is usually composed of finely creased, soft epidermis bearing a few randomly situated, ovate, or nearly rounded scales. This area may also consist of oval, round, or rectangular scales that may be either keeled or unkeeled. Flank scales may be arranged in either regular or irregular patterns or rows.
3. Gular scales. These are round or ovate scales found on the sides of the throat or under the chin (e.g., snout) extending to the collar region, where they become known as collar scales at the point of attachment to the front leg.
4. Leg scales. These are diamond-shaped scales usually arranged in oblique rows.
5. Lateral-Caudal scales. These scales are found along the sides of the tail and are rectilinear with rounded corners. They are keeled.
6. Sub-Caudal scales. These are the scales found on the ventral or belly-side of the tail. They are smooth (unkeeled) and rectangular.
7. Double-Caudal Verticils. These scales are found on the dorsal surface of the tail between the beginning of the tail at roughly the point of the thighs and extend about halfway down the length of the tail at which point they fuse and become known as single caudal verticils. These scales form the comb or crest of the tail described previously.

8. Ventral (belly) scales. The belly scales are usually square along the ventral mid-line and are arranged in transverse rows. The ventral scales together with the scales of the flank are the parts of the hide used in making leather goods provided they are not backed by structures known as bony osteoderms.
9. Nuchal scales. These scales, also known as "bucklers" or "plates," are large, almost square scales, the number and arrangement of which varies from one species to the next.
10. Postoccipital scales. These scales lie anteriorly to the nuchals at the base of the skull. They are ovate in shape and their number and arrangement also varies between species.

Crocodilian skin contains pigment cells or chromatophores which are responsible for coloration. While some reptiles such as the chameleons can change color rapidly (metachrosis), crocodilians may alter their

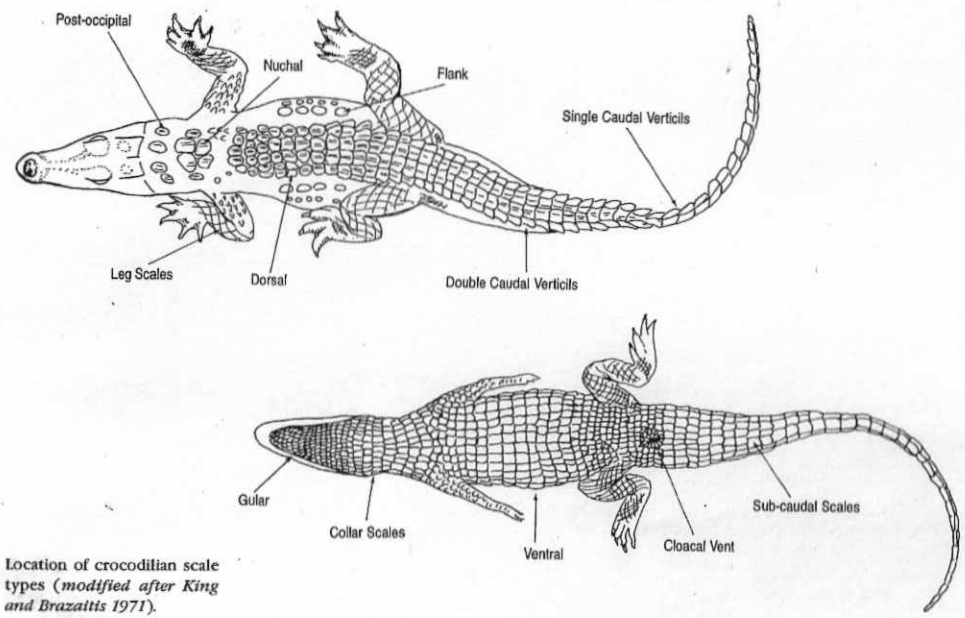


Albino American alligator juvenile (*Courtesy Audubon Zoological Gardens, New Orleans*).

skin coloration in a much less rapid and dramatic fashion. At least one species has been shown, over a period of years, to completely change its adult coloration. In addition the juveniles of several species have colors and patterns which differ markedly from their adult counterparts.

Skin pigmentation varies from light charcoal to brown to olive-green to almost completely black. Belly and lateral scales tend to be lighter, ranging from "off-white" to light brown to various shades of tan. Many species have transverse bands of coloration which are prominent in juveniles but tend to become indistinct in adults. Albinos are known to occur but are extremely rare.

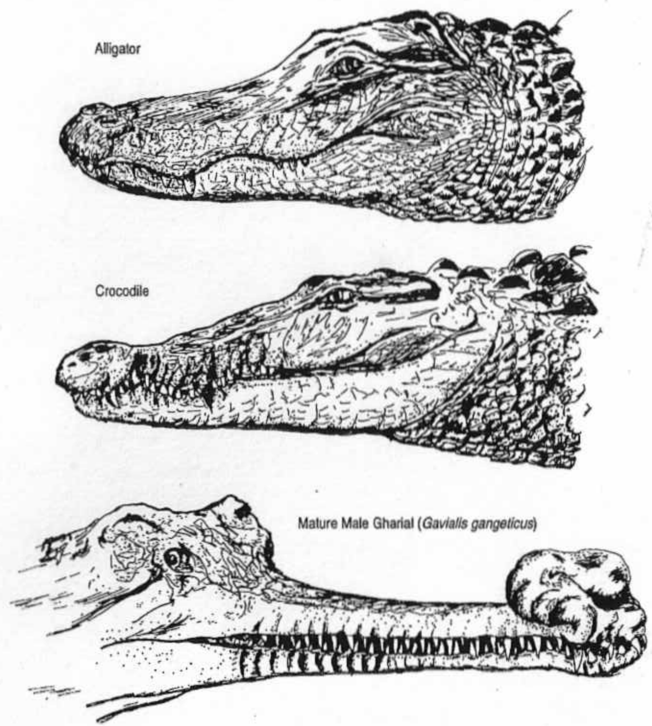
Brazaitis (1987) further indicates that the skin of species from Crocodylinae and Gavialinae can be separated from that of the Alligatorinae on the basis of structures called integumentary sense organs (ISOs). ISOs are absent from all members of the subfamily Alligatorinae (except on the head) whereas they are present among species in the subfamilies Crocodylinae and Gavialinae. ISOs are best seen from the posterior part of nearly



Location of crocodilian scale types (*modified after King and Brazaitis 1971*).

all body scales. However they are most easily visualized on the belly scales, all of which contain at least one ISO although some may contain two or three.

Brazaitis (pers. comm. 1989) says that the role of the ISO is not completely understood but because they contain nerve endings, it is apparent they serve some sensory purpose related to either the tactile senses or the perception of subsonic or underwater vibrations. Some crocodilians produce subsonic sounds by vibrating their sides in the water and ISOs may be the organs used by crocodilians to detect these vibrations.



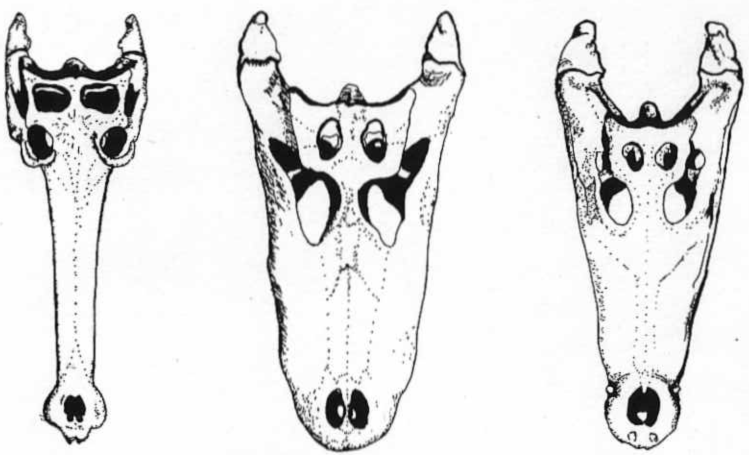
Crocodilian snout types. *Top:* Alligator. *Center:* Crocodile. *Bottom:* Mature male gharial (*Gavialis gangeticus*).

Musculo-Skeletal System

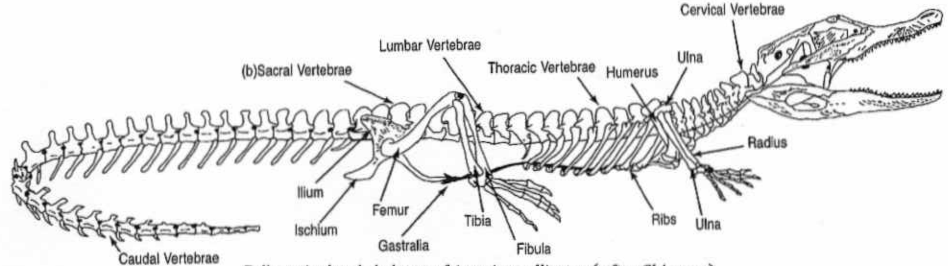
According to Romer (1976) the crocodilian skull is diapsid, meaning it has two openings in the temporal region. The upper opening is smaller and nearly fused whereas the lower opening is larger and forms a trough in which the auditory apparatus is sited. The nostrils lie on the front of the snout set within a bony orifice. These nares can be closed by folds of skin when the animal submerges. A long nasal passage follows the length of the snout from the nostrils to their posterior openings or choanae which open at the rear of the palate. These choanae can also be sealed by muscular flaps in the mouth which permit crocodilians to open their mouths underwater without flooding their respiratory tracts.

Crocodilians have a secondary palate framed by the premaxillary, palatine, and pterygoid bones of the skull. It forms a shelf the length of the snout. They are the first animals on the evolutionary scale to have a complete palate, separating nasal and oral cavities.

The vertebral column is divided into five sections: 9 cervical vertebrae, 12 dorsal (thoraco-abdominal) vertebrae, 3 sacral vertebrae, and some 32 to 42 caudal vertebrae. Each vertebra is convex on its posterior surface and articulates with another by what resembles a ball-and-socket joint. Neill (1971) says that this arrangement affords crocodilians maximum



Crocodilian skull shapes. *Left:* Gharial. *Center:* Alligator. *Right:* Crocodile.



Fully articulated skeleton of American alligator (*after Chiasson*).

flexibility, especially in the tail. It is the serpentine motion of the oar-like tail that enables crocodilians to propel themselves in the water.

Crocodilians have eight pairs of true ribs and an additional eight pairs of floating abdominal ribs or gastralia.

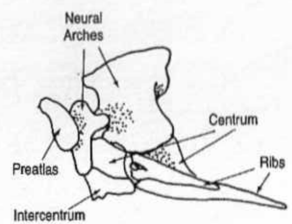
The pelvic girdle has a short ilium, a narrow pubis, and a short, wide ischium.

The front limbs attach to the pectoral girdle which is analogous to the shoulder and collar bones of man. The pectoral girdle consists of paired bones known as the coracoid, procoracoid, clavicle, and scapula. Attached to these are two single elements, the sternum and interclavicle. The bones of the limbs are also analogous to those of mammals. The front limbs consist of a long bone known as the humerus and two shorter bones that work in harmony but anatomically oppose each other—the radius and the ulna. The bones of the front feet include the carpals, metacarpals, and phalanges or toes. The rear limbs consist of the thigh bone or femur, plus tibia and fibula which also oppose each other. The bones of the rear feet are known as the tarsals, metatarsals, and phalanges.

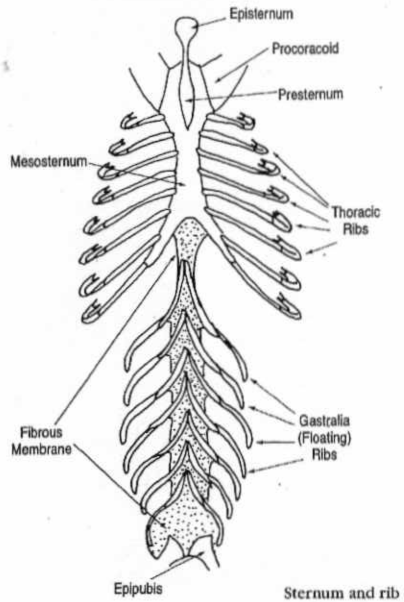
Young wild crocodilians contain very little adipose or fat tissue under their armored hides. Fat tissue is not widely distributed but occurs at specific sites such as at the base of the tail. It occurs on the thighs and bellies as the animal gets older. Crocodilians rank among the most muscular and powerful of the reptiles.

Crocodilians possess a number of tiny, specialized muscles which serve to retract the eyes deep into their orbital sockets—a protective mechanism that goes into action if anything touches the surface of the eyes. In close combat with other animals, the eyes represent a point of vulnerability, so they've evolved this unique way of taking the eyes out of action when appropriately stimulated to do so. Even when not touched directly, the eyes may recede as the animal snaps or bites.

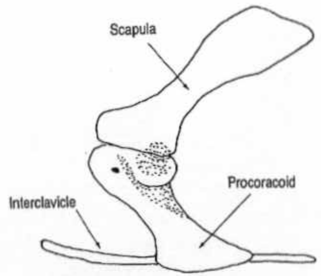
Other small specialized muscles help crocodilians lead their amphib-



Alligator vertebrae (*after Jollie*).



Sternum and rib cage of the alligator (*after Chiasson*).



Pectoral or shoulder girdle of the American alligator (*after Jollie*).

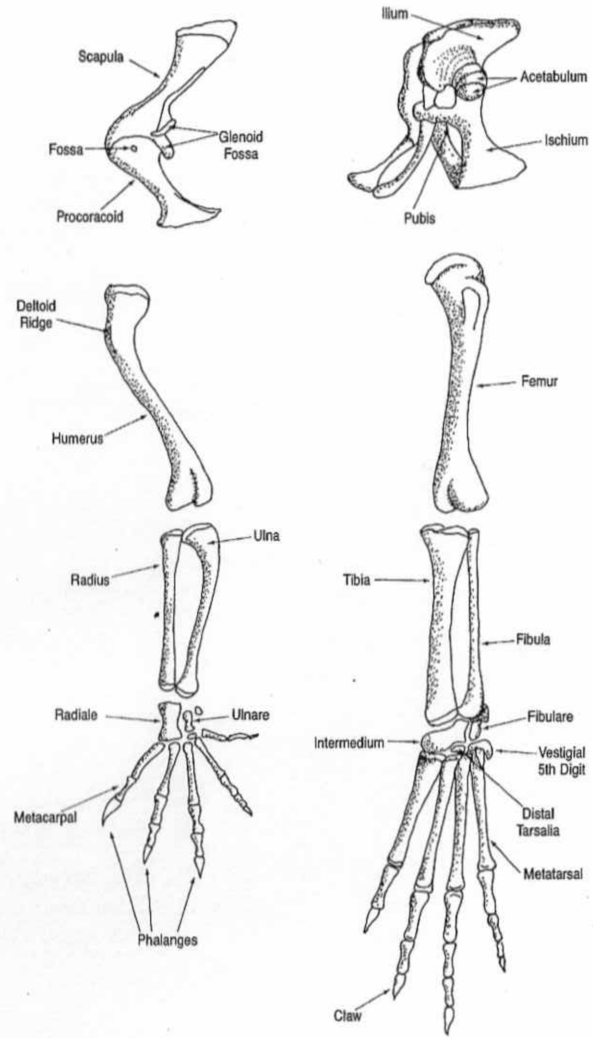
ious existence by closing the external nares or nostrils as well as the internal nares or nasal choanae. They can further prevent the trachea and respiratory tract from flooding while underwater by sealing the trachea with the gular fold or glottis.

Specialized muscles work their nictitating membranes or semitransparent eyelids, also put into action when submerged, and special muscles even close off their ear drums to prevent water from entering the auditory canal.

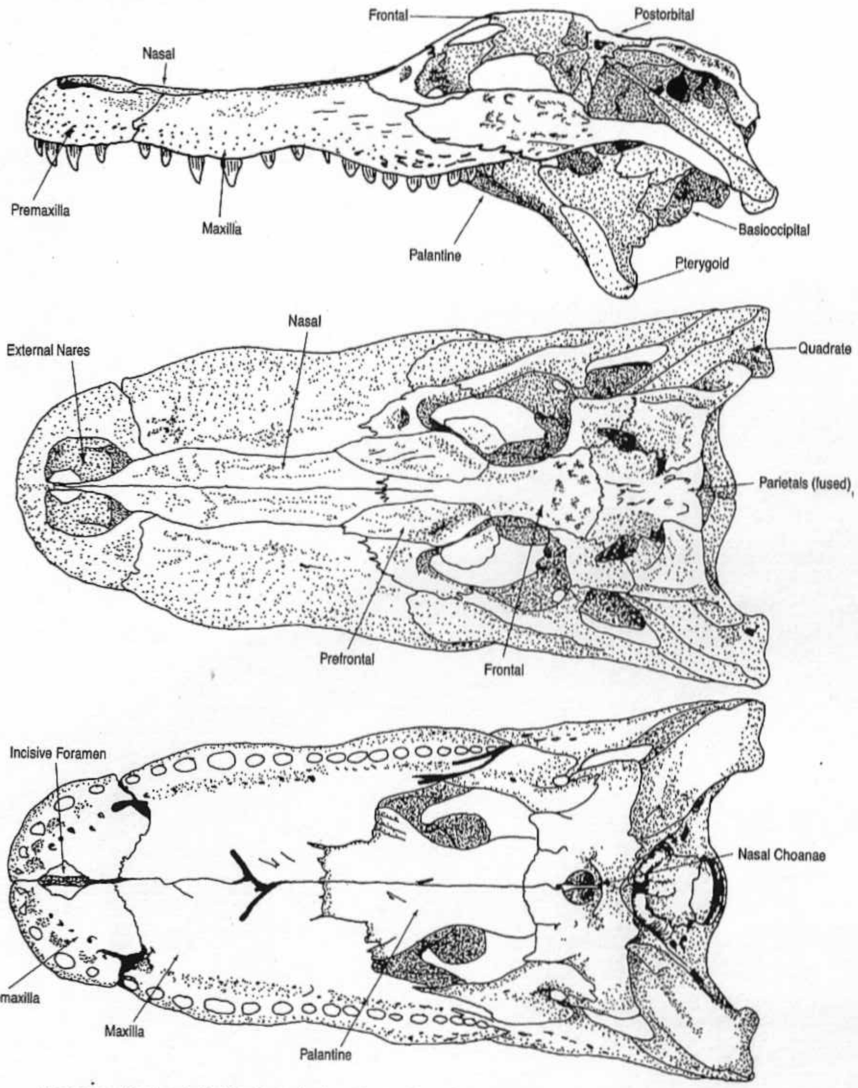
Muscles are described and named by their points of origin, insertion, and function. The nerves which operate the various muscles become a key part of their description.

Locomotion

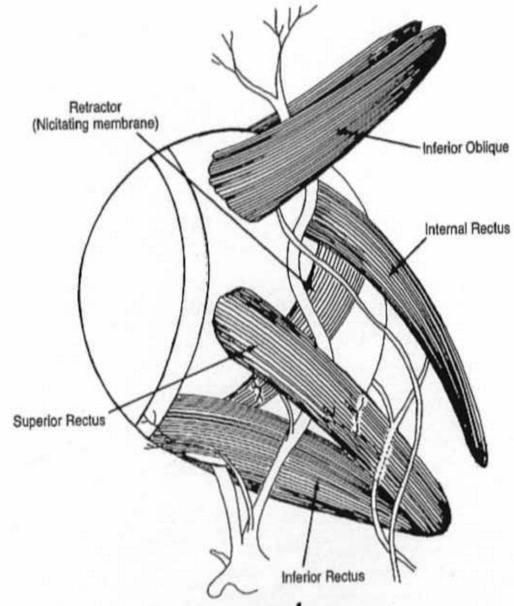
Given their heavy bodies, the limbs of crocodilians appear relatively small and seemingly useless. With the exception of the gharial, however, this is



Pectoral (*left*) and pelvic (*right*) girdles with front and hind limbs of the American alligator (*after Chiasson*).



American alligator skull. *Top:* Lateral view. *Center:* Dorsal view. *Bottom:* Ventral view (*after Jollie*).



Crocodilian eye muscles (*after Chiasson*)

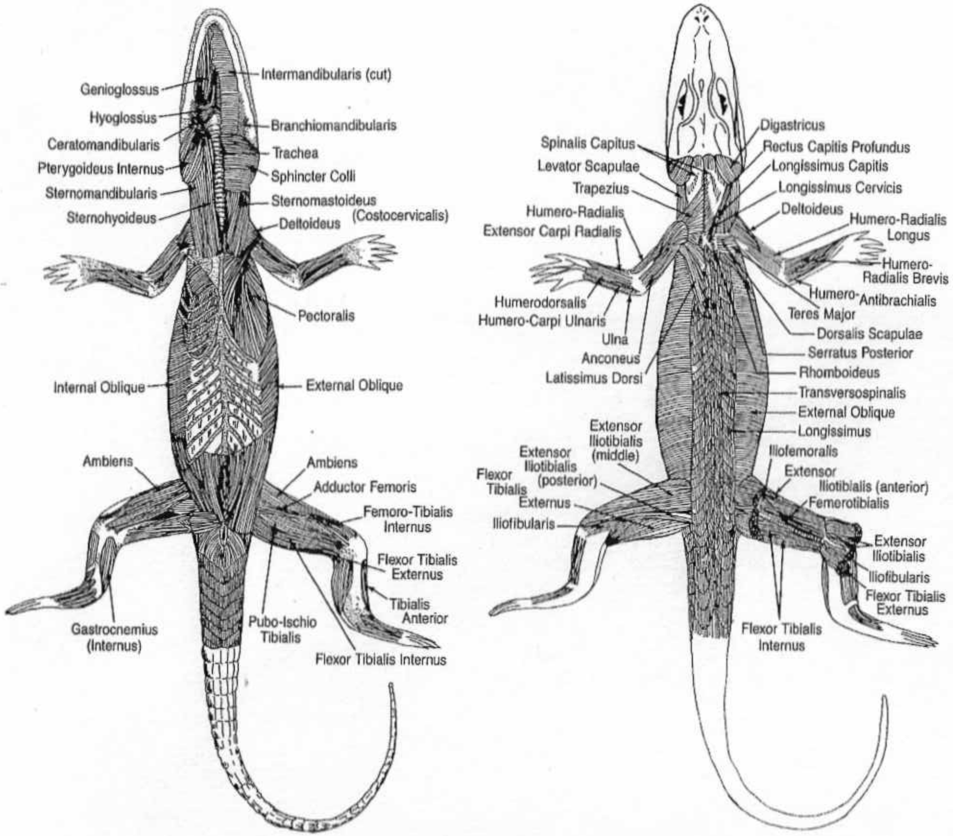
not the case. They not only can swim effortlessly in the water but are capable of a wide variety of effective gaits on land as well.

The hind feet have four toes that are webbed; the inner three toes of the hind foot are heavily clawed as well. The front feet have five toes and are smaller than the hind limbs.

Crocodilians have deep sockets in their thigh bones which serve to articulate the rear limbs. Bakker (1986) points out that crocodilian feet have a "bent-hinge" joint which not only allows a fair amount of forward flexing but enables rotational ability as well.

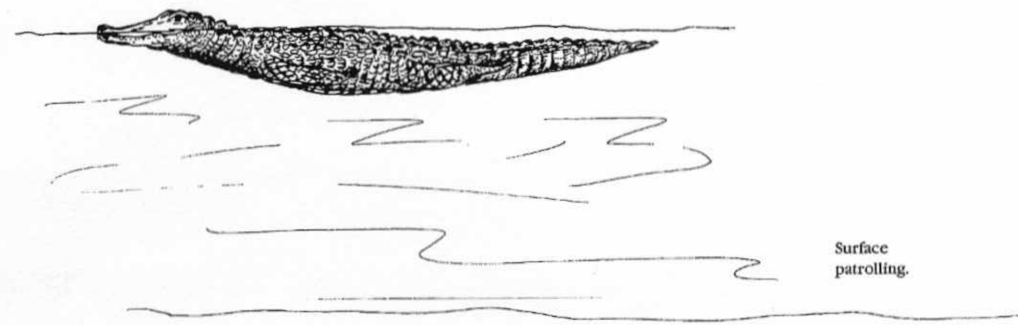
An extensive analysis of locomotion in crocodilians has been performed by Lewis (1985) while spending over a thousand hours observing three pair-sets of captive juvenile caimans. Lewis catalogued the following modes of locomotion:

1. Belly-run-dive
2. Belly-run-leap-dive
3. High-walk-run-dive

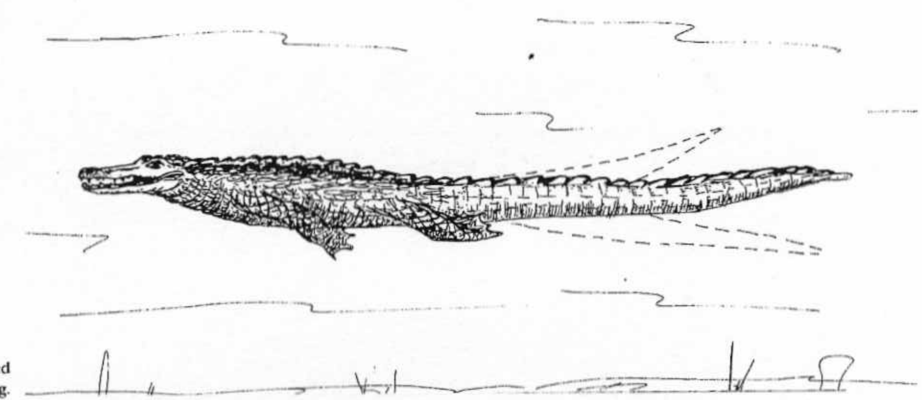


Surface musculature. *Left:* Ventral view. *Right:* Dorsal view (*after Chiasson*).

4. High-walk-jump-dive
5. Surface patrolling
6. Quadrupedal-bottom-walk with horizontal float and tail movements
7. Bipedal-bottom-walk-with horizontal float and tail movements
8. Sinking
9. Surface-dive, head-first
10. Aquatic-leap

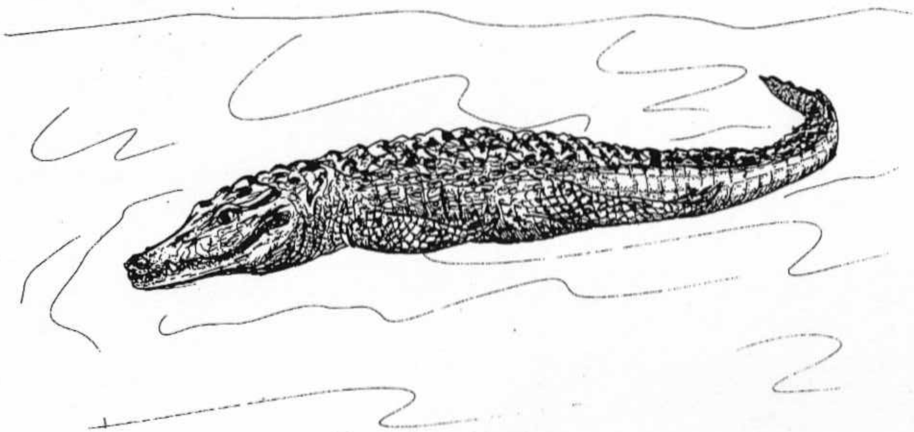


Surface patrolling.



Submerged patrolling.

11. Submerged patrolling
12. Surface-torpedo-swimming
13. Submerged-torpedo-swimming
14. Hauling-out
15. Bipedal-bottom-walking with horizontal float and limb paddling
16. Surface-over-the-shoulder-dive
17. Casual-high walk
18. Belly sprint with rapid serpentine tail movements
19. Terrestrial bipedal-stand without support

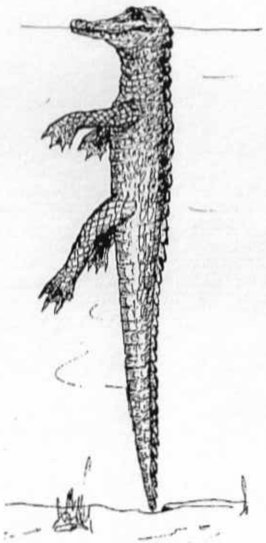


Submerged "torpedo" swimming.

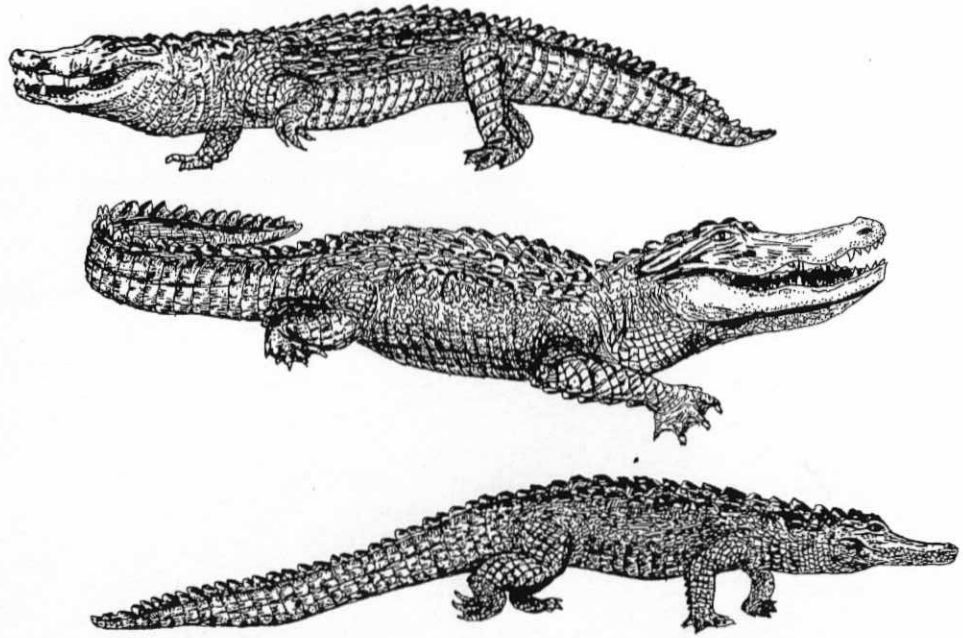
20. High-walk with lateral head movements
21. Bail-out with head thrown back
22. Obstacle climbing
23. High walk-freeze-high walk
24. Belly-slide with limbs tucked

Crocodilians are normally quadrupeds—that is, they walk on all fours, but unless you've seen it, it is hard to imagine any crocodilian leaping into the air and standing on the two hind legs. Yet they do engage in momentary bipedal stances primarily while leaping or jumping to capture prey either from the water or on land. In the water, they have been observed floating in a sort of semi-bipedal stance with the hind legs walking on the bottom and the front half of the body and limbs off the ground. The support provided by surrounding water enables crocodilians to engage in bipedal bottom walking for extended periods whereas such a gait on land is limited to a few seconds, using the tail and front legs to achieve balance.

When swimming rapidly, crocodilians hold their legs tucked in at their sides and move torpedo fashion using the serpentine movement of their tails to propel themselves. When stopped in water they use their feet to doggy paddle. Crocodilians also float in the water with their tails and part of their bodies angled downward, leaving the nostrils, eyes, and ears at just above surface level.



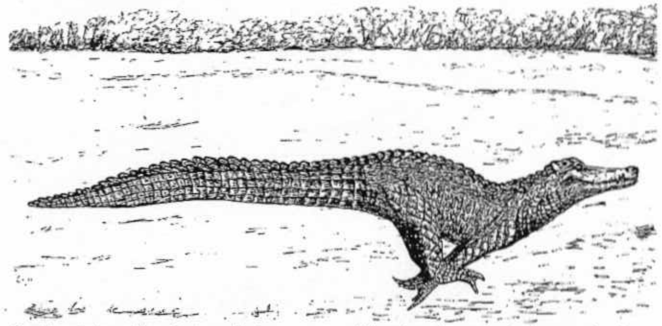
Vertical (bipedal) surface patrolling with limb paddling.



Top: High walk with lateral head movements. *Center:* Belly run. *Bottom:* High walk—Freeze.

While their home is clearly the water and they are most efficient there, most species of crocodilians can be surprisingly agile on land and almost as effective in prey capture as in the water, especially when the element of surprise is on their side. Crocodilians will literally jump or leap out of the water and grab prey on the embankment and then drag it back in. On land crocodilians can run or gallop quite fast but only in sprints or bursts of speed, so an animal or person capable of any endurance at all can usually outrun a hungry or angry crocodilian. But if one gets too close, too curious, or doesn't see the animal, then the crocodilian can inflict considerable damage.

Of all crocodilians, the gharial is least effective on land and hauls itself out of the water only to bask, build its nest, and lay its eggs. Its limbs are



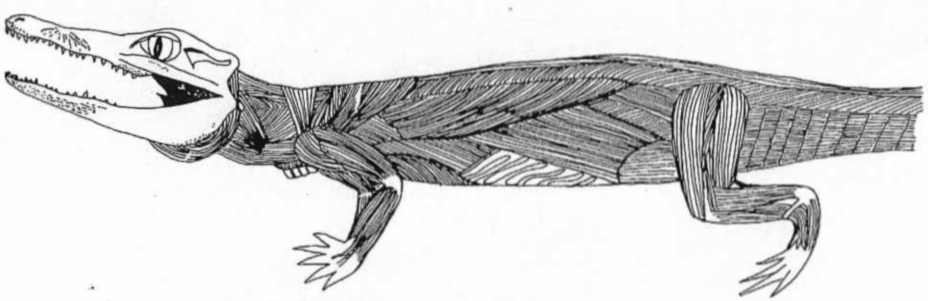
Rapid sprint or gallop during which some crocodilians have been clocked at speeds of up to 26 mph (42 km/h).

exceedingly weak, and on land it must resort to sliding around on its belly as high-walking and running are impossible.

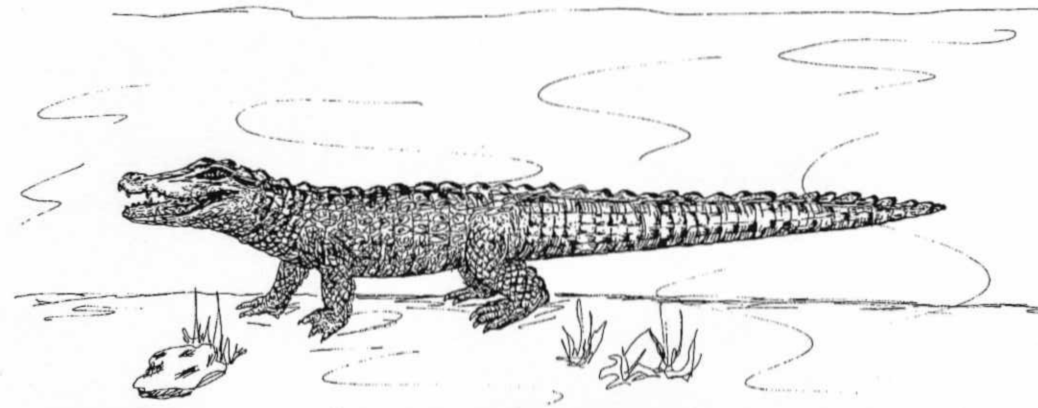
Urogenital System

As in other reptiles and birds, crocodilians possess a multipurpose structure called the cloaca which serves as the terminus for the intestinal, urinary, and genital systems. The cloacal vent is a vertical slit-like opening located on the ventral surface at about the level of the hind legs.

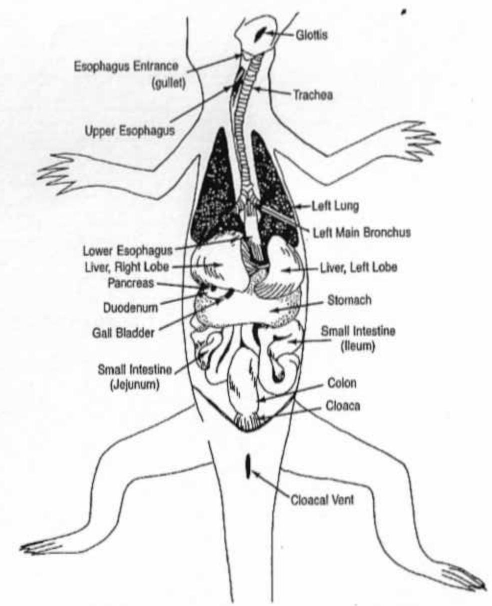
Crocodilians of both sexes excrete urine and feces through the cloaca. Females use it as a receptacle by which they engage in copulation with the males. Sperm is introduced into the female cloaca via an erectile penis. The



Surface musculature—lateral view (*after Chiasson*).



Quadripedal bottom walking with horizontal float and tail movements. Note: mouth open but no water enters respiratory tract due to nasal and glottic closures.



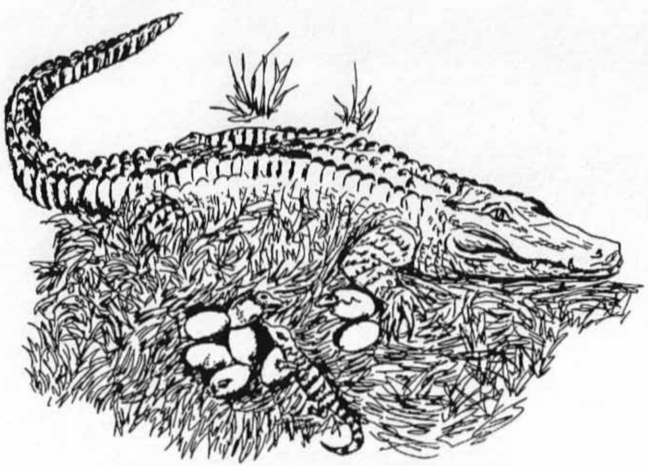
Visceral organs—ventral view (*after Chiasson*).

male is also able to retract the penis which is then housed within his cloaca. The male's sperm is carried from the testes into the penis through the Wolffian ducts or vas deferens. Once fertilized, the female's eggs are passed out of the body via oviducts through her cloacal vent as well.

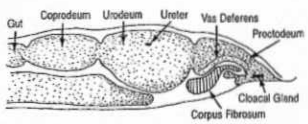
Crocodilians have no urinary bladder, so urine is excreted whenever it is formed. Urine is formed by a pair of advanced kidneys known as metanephros. These organs are remarkably adept at conserving water and producing a relatively small volume of urinary liquid for excretion. Nitrogen-based wastes are excreted primarily as uric acid rather than as urea and ammonia. Since uric acid is not very soluble and only small amounts of water are excreted, the urine of crocodilians often appears as a white, semisolid paste which consists largely of this substance. Crocodilian urine closely resembles the excrement passed by birds.

Reproduction

Male crocodilians have a single, undivided penis with which they engage in true sexual intercourse. The male reproductive organs also consist of a pair of testes which are suspended internally. In the female, paired ovaries



American alligator at nest opening.



Sagittal section of the crocodilian single, undivided penis (*after Ihle et al. in Jollie*).

produce anywhere from as few as 20 to as many as 90 eggs per season in some species. Fertilization occurs in the oviducts after which the eggs develop shells and are passed out of the female into the nest through the cloaca. As a rule female crocodilians mate only once per year. The female Mugger or Indian Marsh Crocodile may mate twice a year. Courtship goes on for hours and even days whereas mating and intercourse are usually completed in minutes. A single clutch of eggs depletes the female of calcium, lipids, and proteins and in most species recovery to normal levels can take as long as a year. However, males of many species are not monogamous and may mate with more than one female per season given the opportunity to do so.

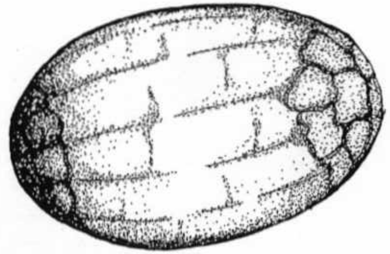
The mating and reproductive process commences with the onset of warmer weather in areas with seasonal temperature variations. In tropical climates mating may be timed to allow the eggs to hatch just before or after the onset of the rainy season so that the young arrive during times of high water. Specific reproductive patterns are considered under each species account and vary considerably.

Following courtship, mating, and copulation, the male usually departs and leaves the female alone to prepare her nest, lay her eggs, and tend her nest and young. In some cases males have been observed getting involved in the defense and care of the nest and young. Some species build elaborate mound nests whereas others simply deposit their clutch in hole nests excavated for the purpose.

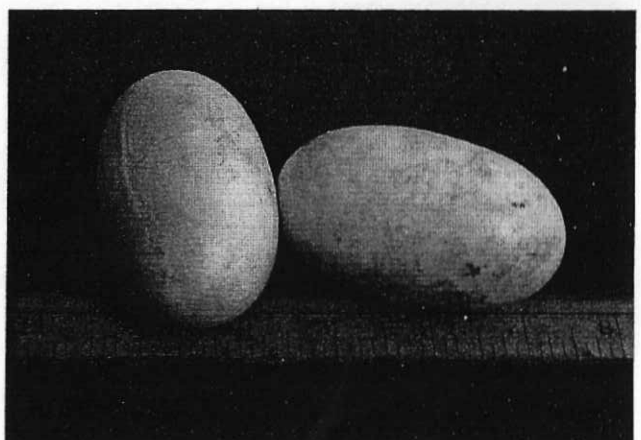
Crocodilians are oviparous, reproducing by means of amniotic eggs incubated outside the body. Unlike the aquatic eggs of fish and amphibians, reptile eggs are not jellylike, are fertilized internally, and are encased in shells composed of fibers laid out at right angles. In addition the shells of crocodilian eggs are reinforced by calcium which renders them especially tough. These sturdy containers serve to protect the eggs during their early development and prevent a host of insects, fungi, and bacteria from damaging them. They also provide at least temporary protection against short bouts of dehydration or flooding.

Crocodilian eggs initially contain albumen, yolk, and a small mass of embryonic tissue which is located toward the top of the egg. As development of the egg progresses within the oviduct, water is drawn from the albumen and is secreted below the embryo onto the internal surface of a structure called the vitelline membrane which surrounds the yolk and embryo. The developing crocodilian embryo is surrounded by a number of membranous structures. The amnion is a fluid filled shock absorber. The chorion acts as a lung enabling some gas exchange to occur, and closely allied to it is the allantois which serves as a receptacle for metabolic wastes. Yolk and the albumen provide nutrition to the embryo, an arrangement identical to that of the birds according to Astheimer et al. (1989).

According to Ferguson (1985), it is irrelevant which way crocodilian eggs are laid because the embryos within always wind up oriented atop the upper surface of the yolk which is where they should be to develop normally. If a crocodilian egg is turned after the embryo has attached itself to the yolk while still young (2nd to 10th day), the embryo remains attached to the yolk but now is beneath rather than atop it. It will drown in the yolk and die. Studies by Webb et al. (1987) indicate that rotation of crocodilian eggs occurring after the first 24 hours but before the respiratory and excretory functions of the chorion and allantois are adequately developed (about the 13th day) will result in embryonic death. Rotation of older eggs (15+ days) appears to be safe. The critical period when eggs should not be handled or rotated appears to be between days 1 and 15. The implications of these findings are obvious for field workers who collect crocodilian eggs for hatching in the laboratory. Each egg should be marked as to its top before being removed from its nest and maintained top-side-up.



Egg of the Nile crocodile showing distinctive webbing pattern prior to hatching.



Eggs of American alligator. *(Photo by Raymond L. Ditmars; courtesy of American Museum of Natural History)*

As incubation proceeds, acids produced by the bacteria inside the nest start a process of eating away the tough crocodilian egg shell. Pits begin to form in the outer calcium reinforced layer, making the eggs somewhat porous. Ultimately this process exposes the inner shell layer which appears almost honeycomb or web-like. Tiny channels form in this layer which permit respiration to take place between the now almost fully developed fetus and its outside environment. The almost totally eroded shell also facilitates unaided hatching which is otherwise impossible given the construction of the crocodilian egg when it is first laid. In fact, if shell erosion is incomplete, the juvenile will die in its shell unless it is helped to hatch by the female. Many species of female crocodilians have been observed assisting not only in the opening of the nest but in the cracking open of the shells as well. Since eggs incubated in the laboratory are not easily supplied with bacteria which erode the outer shell, such eggs must be opened by the lab staff attending the eggs. When the juvenile is ready to emerge, it loudly emits a "distress" call or vocalization from within the shell which can be clearly heard outside the nest.

Juveniles emerge from their eggs as fully formed versions of the adult except for size and obviously sexual development. In some species both color and color patterns differ between juveniles and adults. Hatching alligators are black and off-white but change to black and yellowish within several days.

The time it takes for eggs to incubate and hatch is indirectly related to environmental temperature and its direct effect on the egg chamber (incubation) temperature. In areas where average temperatures are higher, the eggs incubate more rapidly and hatch sooner than in cooler locales. Incubation times, in general, range from 40 to 90 days or more. Average incubation times for individual species are given in the species accounts.

It has been well established that the sex of newborn crocodilians is not dependent on inherited chromosomes but rather on incubation temperatures. Eggs incubated at higher temperatures are predominantly male; in fact, if the temperature inside the nest remains at least 93° F, more than 75% of the hatchlings are male, but more females are born over a greater range of average temperatures compared to males. It would appear that the sex of the developing crocodilian is determined sometime between the 7th and 35th day.

Ferguson and Joanen (1983) made an exhaustive study of this relationship in the American alligator. They concluded:

1. Alligator sex is determined by the time of hatching and is irreversible.
2. Alligators do not appear to produce sex chromosomes, a fact which precludes any genetic determination of offspring sex.

Captive baby alligators being assisted from shell at Gatorland Zoo, Kissimmee, Florida (*Courtesy Florida Department of Commerce, Division of Tourism*).

3. The sex of alligator offspring is determined by egg incubation temperature: 30°C (86°F) or below produces females and 34°C (93°F) or above produces males.
4. The temperature sensitive period for sex determination is between 7 and 21 days for eggs at 30°C and between 28 and 35 days for eggs at 34°C.
5. Nests constructed on levees tend to be hotter than those built on wet marsh. Levee-sited nests produce 100% males whereas wet marsh nests produce 100% females. Dry marsh nests have more intermediate average temperature profiles so that the hottest part

(top) of the nest produces all males and lower, cooler levels produce females.

Working at the Rockefeller Wildlife Refuge in Louisiana, Ferguson and Joanen also found that female hatchlings outnumbered males by a ratio of 5 to 1. They also determined that females hatching from eggs incubated at 30°C weigh more than males hatching from eggs incubated at 34°C, the reason being that the females incubated at the cooler temperatures tend to absorb more abdominal yolk just prior to hatching. These extra energy reserves enable such females to grow faster and become sexually mature ahead of animals with lighter birth weights. Ultimately, male crocodilians outgrow females, and mature males are longer and weigh more than females of the same age.

Recent research has confirmed that hormone controls prepare crocodilians for reproduction. Other cues that regulate reproductive cycles include day length, rainfall as well as physiological cycles which, over millenia, have improved the chances for reproductive success, and to some extent, the survival rate of hatchlings.

The evolution of seasonal reproductive controls include the timing of adequate food supplies, the availability of appropriate nest sites, ambient temperatures, rainfall and times of low predation risk. These factors coincide with hormonal cycles and become total reproductive control systems which over time tend to coincide with the optimal time and place for reproduction. These are called *ultimate factors*.

Proximate factors are external occurrences that actually induce the onset of reproductive behaviors. These include the correct habitat, ritualized displays such as touching, unusual movements, calling, aggressive displays toward intruders and social stimulation.

For crocodilians it is clearly rainfall that most often defines the breeding seasons in the tropical and neotropical regions. Tropical nesting seasons also may last longer than those in more temperate climates.

Growth and Development

Although it is difficult to generalize, many surveys reveal that up to 90% of newborn or juvenile crocodilians may not survive their first year. Of this number some 50% may not hatch, and of those that do, an additional 40% die as a result of predation by large birds, turtles, fish, carnivorous mammals as well as from pathogenic bacteria, viruses, and parasites. Juveniles occupy a "micro-habitat" or niche distinct from their adult counterparts, and this plus a number of other behaviors, including holing and the use of distress calls, helps some animals survive.

Note: Other effects of higher incubation temperatures

The size of the hatchling is smaller at higher temperatures but there is more abdominal yolk present (Lang *et al.* 1989).

Alligators incubated at intermediate temperatures (30.6°C/31.7°C) grow faster than those incubated at higher or lower temperature extremes.

The color pattern in the American alligator also differs at different incubation temperatures. Hatchlings incubated at 33°C are darker and have less surface area covered by whitish/yellowish crossbands compared to hatchlings incubated at 33°C (Deeming and Ferguson, 1989).

The thermal preferences of juvenile Siamese crocodiles studied by Lang (1987) seemed to be affected by incubation temperature. Males from eggs incubated at 32.5 to 33°C selected higher temperatures.

Alligator snout, dorsal view shows flattened duckbill configuration seen in longterm captives. (*Courtesy of Florida Department of Commerce, Division of Tourism*)

Growth continues throughout the life span of all crocodilians. The fastest rate of linear growth occurs during the first two years and declines with age thereafter. Averages for the first five years indicate that most species grow at a rate of between 12 and 18 inches per annum. And while weight increases with length, weight as a percentage of length goes up with age. While linear growth slows down, the crocodilian does not stop adding pounds; in other words, although they are not getting very much longer, they continue to add pounds and get fatter.

Bony epiphyses are secondary centers of ossification commonly found at the end of long bones and on the margins of flat bones. During periods of growth, epiphyses are separated from the main portion of bone by cartilage. They provide a structural boundary beyond which growth can no longer occur. Crocodilian bones do not have epiphyses, and it is believed this is one reason that linear growth continues, although quite slowly, until the animal dies.

Sexual maturity is dependent on size, and it is related to age only insofar as age accompanies growth. Therefore, it is possible for animals of the same size but of different ages to both be sexually mature, and it is possible for a smaller animal not to be sexually mature even though it is the same age as a larger animal.

Growth in captivity depends on an abundance of proper food, optimal ambient temperatures, and sufficient space. If any one of these factors is deficient, then growth in captivity will be retarded. Under ideal conditions captive growth may equal or even exceed noncaptive growth rates.

Arguments over the longest and heaviest crocodilians occur regularly. Tales of exceptionally long or heavy animals tend to be exaggerated like the well known "one that got away" fish story. The oldest known captive specimen was an American alligator that lived in captivity for 56 years. It is doubtful that any crocodilians in the wild could exceed this record given the perils they must face. In addition, crocodilians, even the largest species (*C. porosus*), rarely exceed 20 feet in length, so stories of animals 25 or 30 feet in length are rather doubtful and at best may be unintentional or excited exaggerations. Insofar as weight is concerned, even the largest animals rarely exceed 2,000 pounds, and specimens averaging around 10 to 12 feet usually weigh between 500 and 600 pounds. The maximum sizes given in the species accounts by no means represent the average maximum size, but rather represent all-time world records that have been set down in writing, and in some cases have been verified by the *Guinness Book of World Records*. These animals are exceptions rather than the rule.

Although females may grow faster than males or at the same rate as males during the first five years of life, eventually males outgrow them.

The accelerated growth and development of captive or farm born and raised crocodilians is of special concern to crocodilian farming enterprises for reasons related to financial return. The more quickly animals can be raised to market-ready size, the faster the turnover will be. The financial incentive is coupled with the need to make room for each year's hatch.

The state of Florida is home to a number of such operations and Foster Farms, Inc., in Okeechobee County is a prime example. It is a 165 acre alligator breeding and rearing facility. It has about 55 acres of breeding pens which contain 660 breeding *Alligator mississippiensis*.

Eggs are collected from the pens between May and July and incubated for 60 to 65 days. Hatchlings are nursery reared for the first 10 months, reaching a length of about 24 inches and are then moved to the main raising buildings for the next 10 to 22 months. Within 30 months the alligators reach a length of about 50–60 inches.

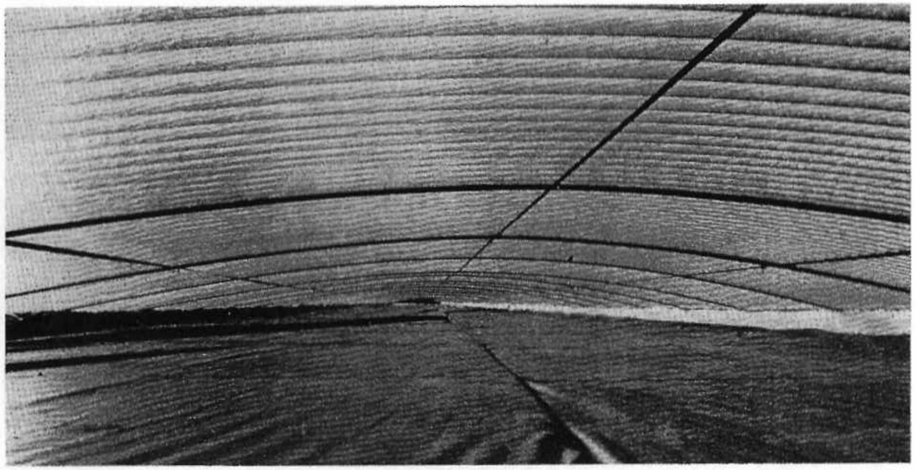
The nursery and rearing buildings consist of seven concrete block and prestressed structures with a total area of 32,000 square feet. At any one time they house about 8,000 animals in various stages of development. The buildings are maintained at 89°F year round. At the present time there are two systems used for controlling the temperature. The first is an in-slab heating system which consists of zoned hot water pipes connected to circulation pumps activated by heat sensors in the water. The hot water source is a propane fired boiler. The second system is the washdown and refill water. To insure against thermal shock, which may not only affect growth rate but actually kill some alligators, the buildings are cleaned and filled five days a week using 78,000 gallons of 89°F water each filling day. This system is also heated by a propane boiler.

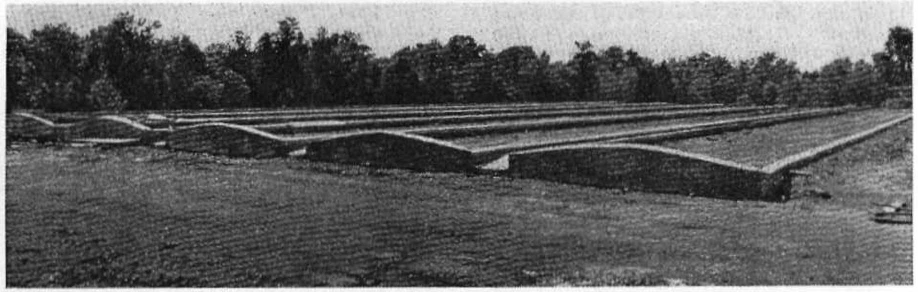
However, the expense of maintaining a fossil-fuel based temperature controlling system cuts deeply into the profitability of such operations. The cost of raising animals to market size is increased considerably and if market prices for hides and meat do not reflect these increased costs many such farms sustain losses or are marginally profitable at best.

The advantage of being in Florida is that there is considerable environmental heat, but it is not year round, and for three to four months each year even in the more southern parts of the state the temperature drops below optimal feeding levels needed by crocodilians as well as other ectotherms. This temperature imposed fasting period diminishes growth rate and delays the time it takes to bring animals to market. But by providing year round optimal temperatures and maintaining the animals in darkened enclosures, continued, uninterrupted growth can be achieved. The reason for keeping the animals in the dark is related to their feeding patterns in nature. Alligators are normally active at night and this is their usual feeding time although they will feed in daylight given the opportunity. During the day their preferred activity is to bask in the sun, raising their body temperatures which enhances the digestion and metabolism of the evening meal.

The key problem facing Foster Farms and similar operations is how to maintain the alligators at constant optimal temperatures irrespective of ambient temperatures and to do so with as little investment in fossil-fuel generated energy as possible. The answer has been provided by Solar Development, Inc. (SDI) of Riviera Beach, Florida which, based on technical applications developed by the TVA, has designed what is known as a "shallow solar pond" solar energy system to meet alligator temperature requirements.

A 20,000 square foot shallow solar pond system was installed at a textile plant in Georgia at a cost of $11 per square foot. The unit was capable of providing up to 241,000 BTUs per square foot per year and is capable of producing about 200,000 gallons of hot water daily. The plant's savings in coal amounted to an estimated $18,700 per annum as of 1986. This example





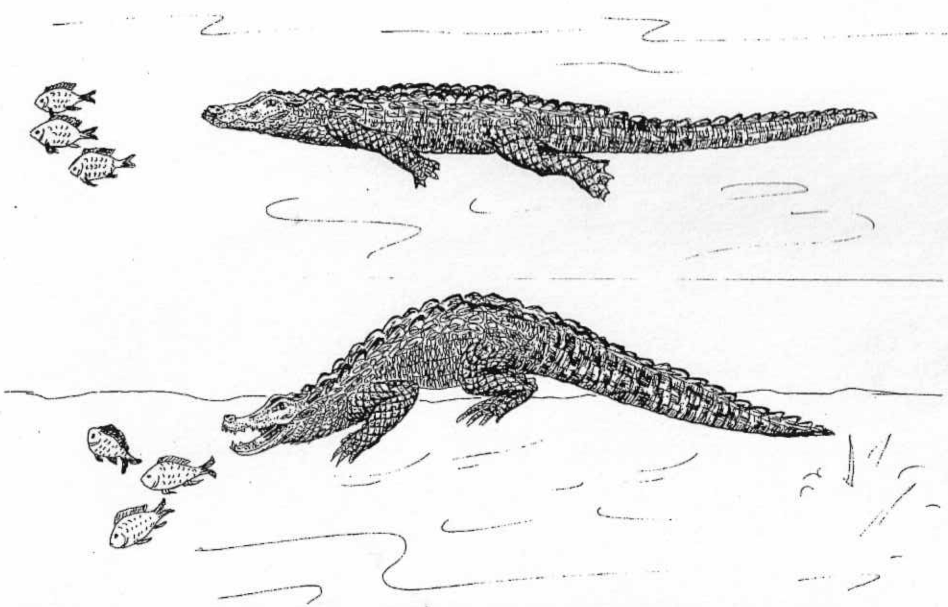
Above: **Shallow solar energy ponds as seen from within. Black rubber bags hold the water under a roof of corrugated fiberglass.** ***Below:*** **Solar-energy ponds as seen from the outside. (*Courtesy Tennessee Valley Authority*).**

would pay for itself in about 11 years but other variables including the amount of water needed, the temperature to which it must be heated and the cost of fossil fuel energy at other localities may improve substantially on the cost savings determined for this example. In Florida, fossil fuels and nuclear energy are particularly expensive but solar energy is plentiful. The use of solar energy for alligator farming should be especially profitable, even over the short term.

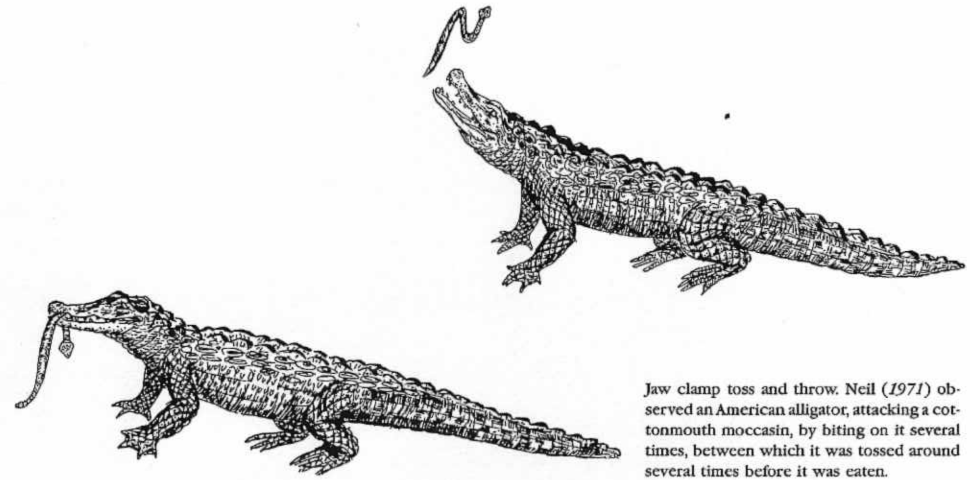
Digestive System and Feeding

Crocodilians are carnivorous or meat-eating predators that find their meals both by preying on live animals as well as by consuming dead organisms or carrion. As predators, they're most successful by using the element of surprise to their advantage. While appearing to be asleep or drifting aimlessly along in the water, crocodilians will suddenly lunge for a bird, fish, turtle, frog, or even a mammal drinking from the shore. This practice is known as opportunistic feeding. Crocodilians will also stalk their prey although most stalking is done underwater.

The diet of crocodilians is as varied as the parts of the world they inhabit. Crocodilians occasionally ingest vegetation but only accidentally when foraging among water plants for prey that may be hiding.



Aquatic leap and jaw clamp. Graham (*1973*), observing Nile crocodile, noted they would startle a school of fish, which would disperse. The crocodile gave a wriggle of its tail and thrust its body completely out of the water and then landed among the fish, confusing them further and then snapping them up in a frenzy.

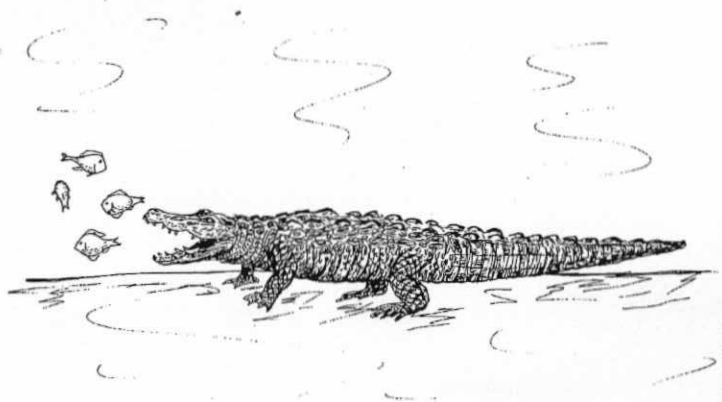


Jaw clamp toss and throw. Neil (*1971*) observed an American alligator, attacking a cottonmouth moccasin, by biting on it several times, between which it was tossed around several times before it was eaten.

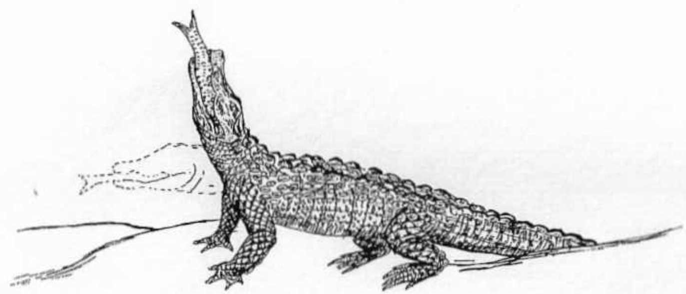
Crocodilians stop feeding at temperature extremes. Optimal feeding temperatures lie between 25°C and 35°C. As temperatures go below these optimal ranges, crocodilians become increasingly inactive and they become stressed as temperatures go above them. Consequently, crocodilians in some geographic locales may spend a considerable portion of each year without feeding at all. It has been estimated that crocodilians can go for as long as a year, if necessary, without food.

The digestive tract of crocodilians begins with their fearsome jaws—jaws which University of Florida experts have determined can snap shut exerting pressures of 1,300 pounds per square inch. This pressure is sufficient to break the limbs or even the neck of large prey, thus disabling or killing the intended victim. Crocodilian jaws can effortlessly crack open the hardest turtle shell in much the same way a human might bite open the tender shell of a peanut.

All crocodilians have what is called "thecodont" dentition and evolved from a group of prehistoric animals known as thecodonts. Theca in Latin means pouch. The teeth of crocodilians are set but not rooted, in pouches or sockets called alveoli. As they are worn, broken, or lost, new teeth grow in. Aged crocodilians may, however, permanently loose teeth. Crocodilian teeth are strong, cylindrical-conical structures angled both horizontally and vertically. They are suitable for grasping and tearing but are incapable of chewing or grinding down food.



Quadrupedal bottom-stand-lunge and open jaw clamp. Once the fish swim within range, the submerged crocodilian lunges forward, with jaws snapping (*Graham and Beard, 1973*).



Terrestrial swallowing.

After tearing a piece of flesh down to manageable bits, crocodilians swallow them whole. Crocodilians have been observed feeding by wedging killed prey or large carcasses of carrion between tree trunks, roots, or rocks along embankments and then tearing them apart—an intelligent and amazing behavior bordering on a primitive form of tool use. The rocks and roots are used as vise grips to hold the prey steady so chunks of meat can be torn off without the meal being thrashed about.

Appetite in crocodilians depends on the availability of heat. To maximize and improve digestion, an animal that has just fed will seek warmer temperatures to help speed up the digestion and metabolism of the meal.

Alligator, partially submerged with head in complete vertical thrust. This posture is used to obtain the benefit of gravity in order to swallow (*Courtesy of Florida Department of Commerce, Division of Tourism*).

Below 22°C, the American alligator will not eat, and some species will regurgitate a meal rather than digest it if heat does not become available.

Swallowing is accomplished by angling the food in the mouth and then lifting or raising the snout so that the head is almost in a vertical line with the esophagus. The tongue has no role in manipulating or pushing the food rearward since it is firmly fixed to the floor of the mouth and is capable of very little motion. It serves primarily as a taste sense organ and contains glands that in some species are involved in salt excretion.

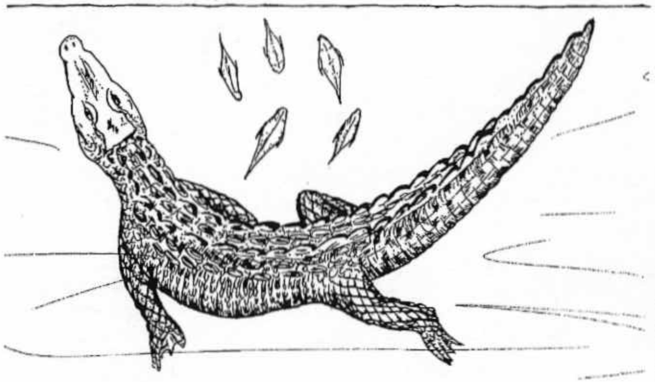
As the food is swallowed, it passes through the gullet or esophagus—a long, muscular tube that terminates in a two-compartmented stomach, which is discussed below.

Adult crocodilians can eat up to 20% of their body weight in a single meal which may take 3 to 7 days to consume and completely digest. If the stomach becomes full, crocodilians may continue to eat, storing food in the esophagus until room is available for it to pass on through the gastrointestinal tract. After the food has been thoroughly processed and digested, the fecal matter remaining is passed out of the body through the intestines and exits via the cloaca.

In his book *The Dinosaur Heresies* (1986), Robert T. Bakker gives the following intriguing account of the crocodilian gizzard which is formed out of the fundal portion of the crocodilian's compartmented stomach.

> A white mouse sacrificed to a hungering alligator posthumously provides a most important clue. The bones of the mouse show up quite clearly in the alligator's stomach on the laboratory's television X-ray monitor. But the mouse's bones are not alone. The alligator's after-stomach is lined with hard, dense objects—gizzard stones. The gizzard stones[1] are convulsed by sudden muscular contractions of the gizzard's walls. The monitor clearly show the mouse is being chewed, not by teeth in the mouth but by stones in the gizzard.
>
> Naturalists who study big 'gators and crocs in the wild find huge masses of gizzard stones when they cut open the animals to study their feeding habits. The stones are found only in one chamber of the stomach—the gizzard—and this one chamber has walls with grooves and folds to permit expansion and contraction. Even without X-ray monitoring, it is obvious that this stomach chamber is a churning compartment designed to crush and pulp the prey's body after the gastric juices begin their preliminary chemical treatment. Crocs usually select very hard stones—quartz and granite pebbles, for example—to line their gizzards. If such materials are lacking in their native streams, they may use angular bits of hard wood, pieces of glass bottles, or whatever else is available. I have also seen one or two near-perfect fossil alligator skeletons containing a neat bundle of hard

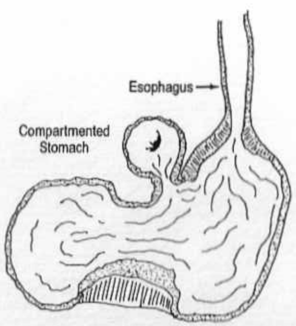
[1] Technically known as gastroliths.



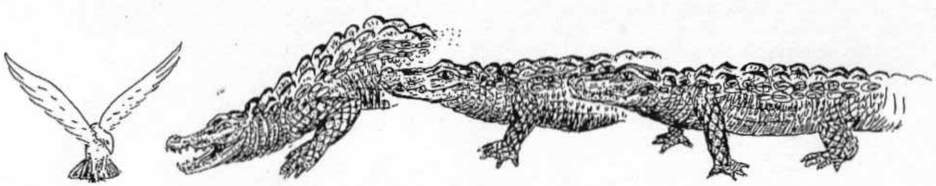
Semicircular body corral. Crocodilians may create a corral with their bodies to trap and consume fish (*Graham and Beard, 1973; Guggisberg, 1972*).

pebbles clustered between the ribs precisely where the gizzard was in life. These fossilized gastric mills demonstrate plainly that gizzard stones have been an essential functional component of crocodilian food processing for many millions of years. And the study of crocodilian gizzards leads to some intriguing conclusions about evolution both in birds and in the Dinosauria.

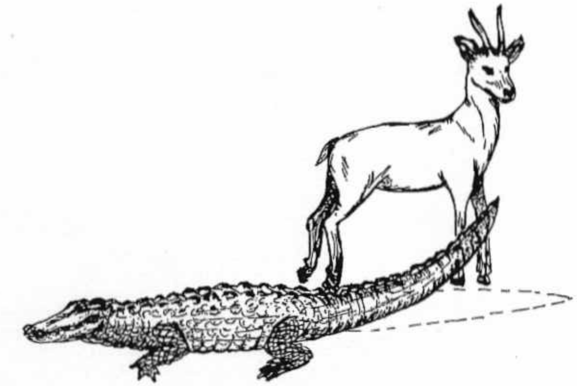
Zoos mislead their visitors by the way these species are housed. Birds are in the Bird House, of course, and crocodiles are always segregated to the Reptile House with the other naked-skinned, scale-covered brutes. So the average visitor leaves the zoo firmly persuaded that crocodilians are reptiles while birds are an entirely different group defined by "unreptilian" characteristics—feathers and flight. But a turkey's body and a croc's body laid out on a lab bench would present startling evidence of how wrong the zoos are once the two stomachs were cut into. The anatomy of their gizzards is strong evidence that crocodilians and birds are closely related and should be housed together in zoological classification, if not in zoo buildings.



Crocodilian stomach, frontal section (*after Chiasson*).



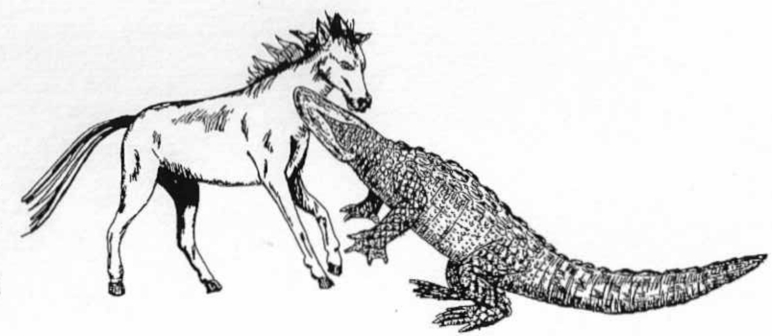
High walk, freeze and arched lunge. Crocodilians may seize prey such as birds fluttering close to the ground by arching their backs and lunging.



Prey capture: tail strike.

Both birds and crocs have the identical plan to their specialized gizzard apparatus, and this type of internal food processor is absent in the other reptiles—lizards, snakes, and turtles. In both birds and crocs, the gizzard is a thick-walled, muscular crushing compartment with two great tendons reinforcing the walls of muscle (these are shiny sheets of tough tissue you cut off the turkey gizzard before cooking it). In both birds and crocs, the muscular gizzard is just aft of the thin-walled glandular stomach where food is softened by gastric juices.

Since both birds and crocodiles swallow their food without chewing it, this digestive system arrangement makes a lot of sense. Whether this element of the anatomy justifies the grouping of crocodilians as a member

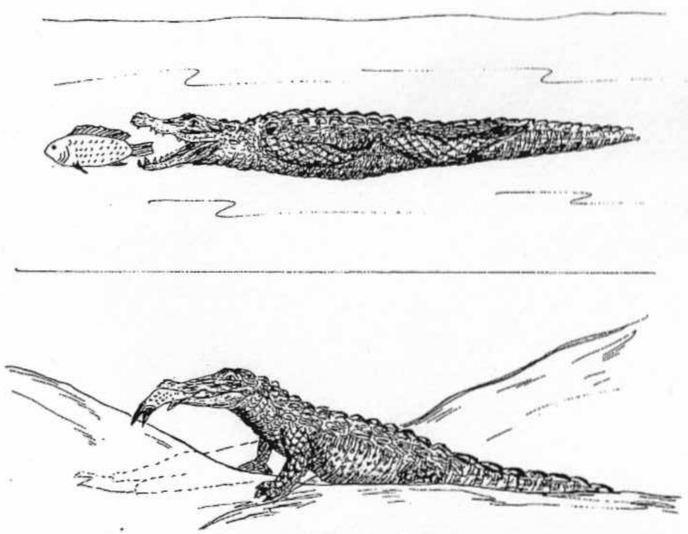


Incipient bipedal stance and jaw clamp to neck of prey. The Nile crocodile has been observed by Guggisberg (*1972*) engaging in this atypical terrestrial means of attack against a donkey.

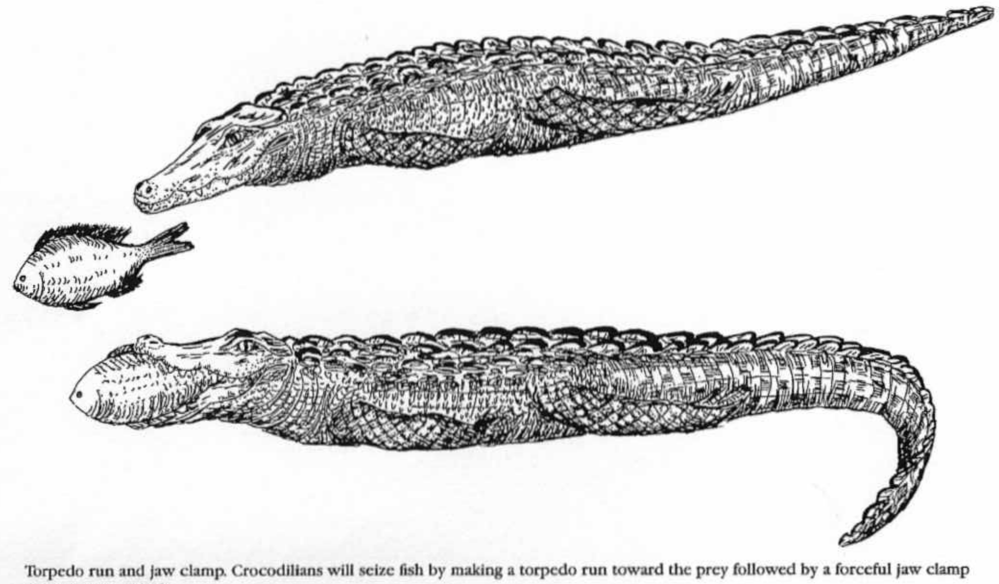
of the Class Aves or Birds is a matter for considerable conjecture. However, crocodilians share many characteristics with other reptiles as well as with the birds.

According to Coulson and Hernandez (1964) crocodilians experience extreme shifts in plasma pH levels on an almost daily basis. When excited or stressed, pH levels drop precipitously, often to levels incompatible with life in other species (e.g., below 7). However, the ingestion of food matter in crocodilians produces a profound alkalemia with pH levels reaching 7.8 to 8 but with no apparent ill effects. Predictably such high pH levels would cause involuntary wavelike muscular contractions called fasiculations, tetany, muscle spasms, irritability, and twitching. In humans, pH levels this high often result in convulsions and potentially fatal cardiac arrhythmias such as ventricular fibrillation.

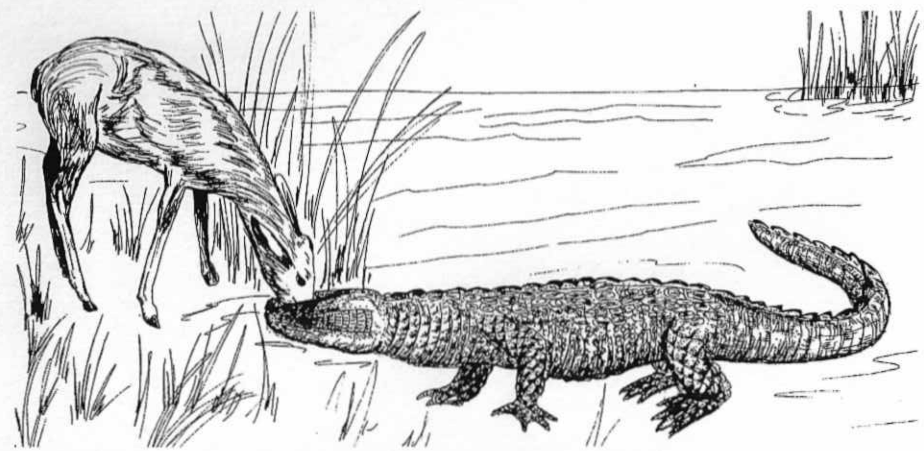
The alkalemia seen in crocodilians in association with food ingestion is attributed to the production of highly concentrated hydrochloric acid in the stomach. In order for the stomach to produce such large amounts of concentrated HCl, Cl shifts from the plasma NaCl, leaving a large store of



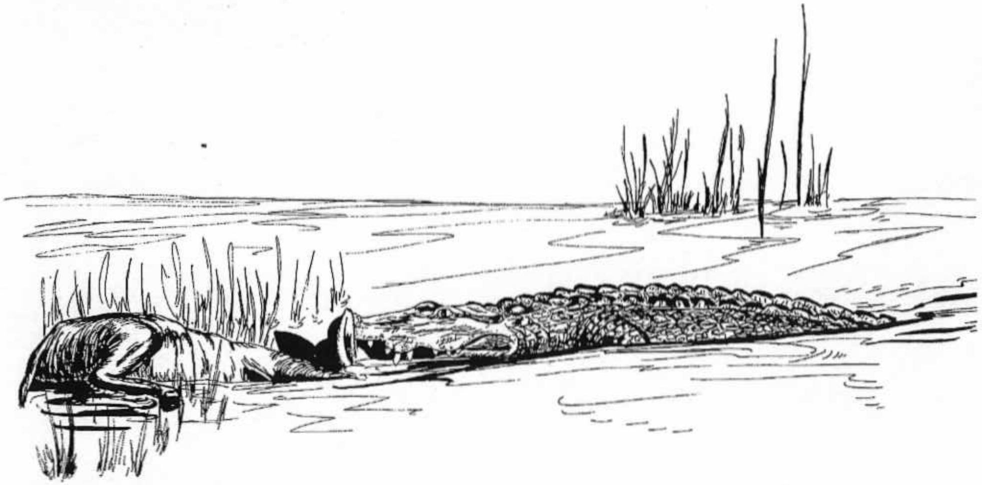
Jaw clamp and bashing. Graham (*1973*) reported a 9-foot Nile crocodile which seized a large fish in the water, came ashore with the animal still struggling in its mouth and then began to bash it on the ground until it was unconscious or dead.



Torpedo run and jaw clamp. Crocodilians will seize fish by making a torpedo run toward the prey followed by a forceful jaw clamp (*Guggisberg, 1972*).



Head jaw clamp and drowning. Prey drinking at water's edge are seized by the head and dragged underwater until it drowns or ceases to struggle (*Guggisberg, 1972*).

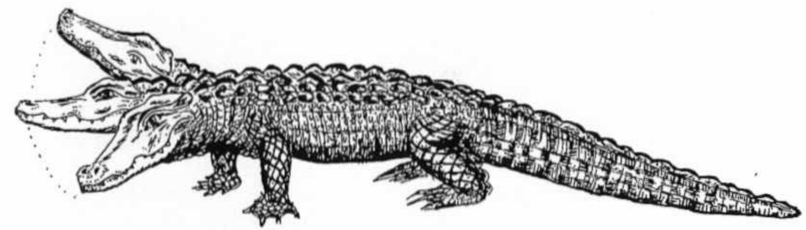


Jaw clamp, pull into water. Once the prey is down, crocodilians may clamp their jaws over the head of the animal to drag it into the water.

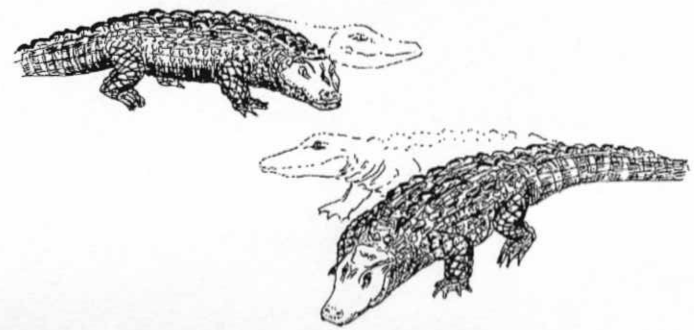
sodium (Na) to react with plasma carbonic acid (metabolically produced CO_2 in water or H_2CO_3). The sodium (Na) and H_2CO_3 react to form a base, sodium bicarbonate ($NaHCO_3$) in excessive amounts, thus producing what Coulson and Hernandez refer to as the "alkaline tide," and exaggerated to an exceptionally high degree.

Circulatory System

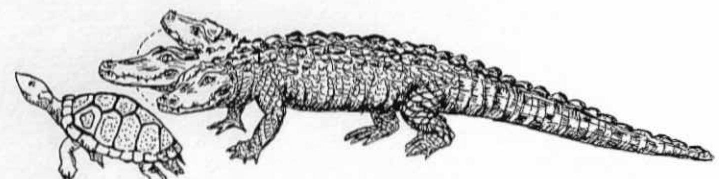
Crocodilians are the only reptiles with a four-chambered heart and separate pulmonary and systemic circulations. Deoxygenated blood is returned from the systemic venous circulation to the right side of the heart. It is received by the right atrium and flows into the right ventricle, which than propels it to the lungs where it releases excess carbon dioxide and absorbs oxygen from the inspired air. From the lungs the oxygenated blood is returned to the left atrium and flows into the left ventricle, which then pumps it into the systemic arterial circulation. Crocodilian heart rates are



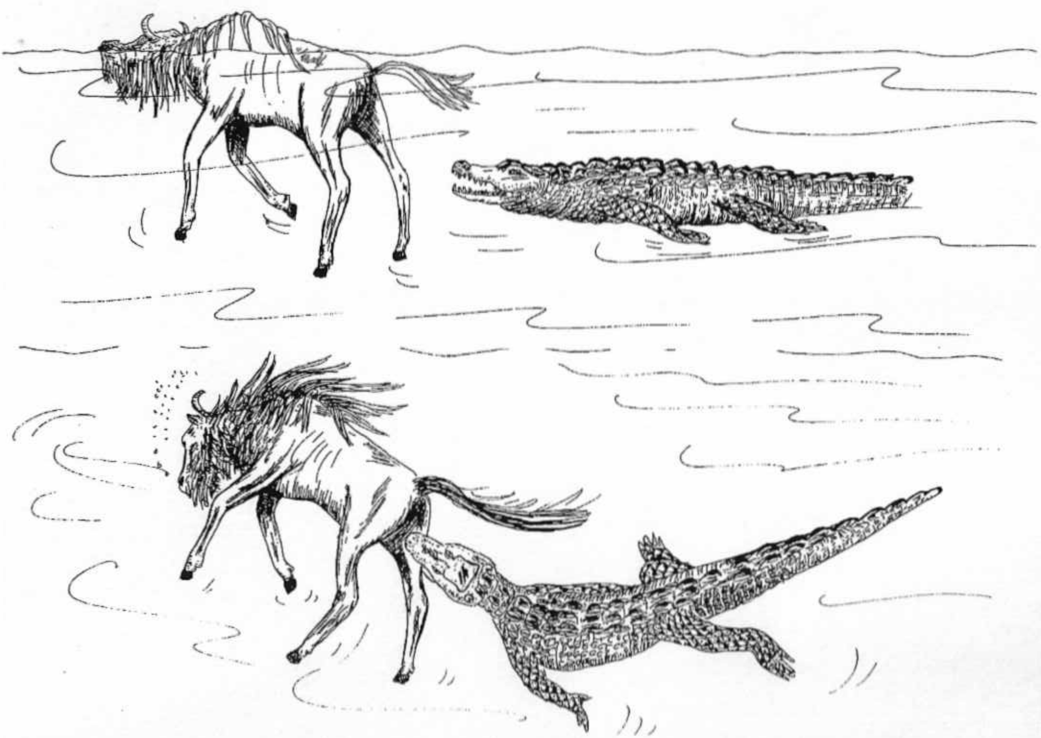
Crocodilians are able to swing their heads in a 60° arc.



Foraging behavior: lateral head turn and turn away.



Snout rub, speculative hunting. Neil (*1971*) says alligators may forage by approaching potential prey, swinging the head so that one side of the snout contacts the substratum. Neil believes sense organs on the sides of the snout help it identify prey. Florida American alligators usually forgo snapping at the Florida red-bellied turtle (*C. nelsoni*) because it is unable to crack its very tough shell.

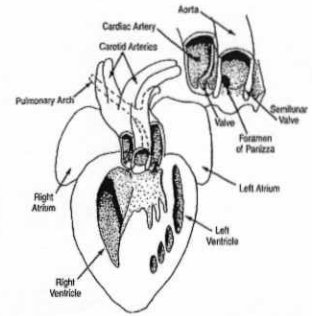


Underwater to surface, seize and drag under. A crocodilian observing prey from below, quickly ascends toward surface, seizes prey by limb and drags it under to drown (*Guggisberg, 1972*).

slow—beating 24–45 times per minute at 28°; 15–16 times per minute at 18°C and only 5 to 8 times per minute at 10°C.

When deoxygenated venous blood is allowed to mix with freshly oxygenated blood, this results in an event known as venous admixture. Venous blood, which is deoxygenated, still has oxygen left in it, but it is roughly 25% to 30% less saturated with oxygen compared to oxygenated arterial blood. When deoxygenated venous blood mixes with oxygenated arterial blood, the volume of oxygen in the oxygenated blood diminishes somewhat by virtue of its dilution with the deoxygenated blood.

In endothermic birds and mammals, including humans, small amounts



The crocodilian heart (*after Jollie*). There is a complete separation of right and left atria and ventricles. The only connection between the two sides of the heart is through the foramen of Panizza which connects the right and left aortic trunks. The most peculiar feature is that the left aortic and pulmonary trunks leave the right chamber of the heart, while the right aortic trunk, bearing the carotid arches, comes from the left chamber (*Jollie, 1972*).

of venous admixture can be tolerated, but increased amounts are disabling and ultimately fatal. In ectotherms, the metabolism can be more readily adjusted to the presence of deoxygenated blood, which is present in the systemic arterial circulation as a consequence of the three-chambered heart arrangement in amphibians and all reptiles except for crocodilians. The existence of a four-chambered heart in crocodilians, from an evolutionary standpoint, may be one of the predisposing conditions required for endothermy.

In the three-chambered hearts of amphibians, there are two atria and one ventricle. The right atrium receives blood from the venous circulation from where it then flows into the one and only ventricle where a fraction of the volume is then pumped to lungs, gills or epithelial mucosa and epidermis for gas exchange. The left atrium receives the reoxygenated blood from the gills, lungs, and skin from where it flows into the same ventricle where a fraction of the blood therein is pumped into the systemic arterial circulation. The blood in the ventricle at any one time may be considered a mixture of oxygenated and deoxygenated blood.

Crocodilians have four fully formed heart chambers, but there is a small window (foramen of Panizza) located between the aortic blood vessels or arterial outflow tracts. This opening may permit venous admixture, and its operation depends on the pressure in left ventricle. Blood will flow through the opening from the area of higher pressure to the area of lower pressure. While the animal is breathing then, the chamber is effectively open because the left ventricular pressure is higher than the right ventricular pressure. A small amount of oxygenated blood may leak from left to right, but this is of no consequence. However when the animal is submerged, the pressure in the lungs from the air trapped within retards the flow of blood through the pulmonary capillary bed, a condition called pulmonary hypertension. This pressure is transmitted back through the pulmonary circulation all the way to the right heart. When the animal is submerged, the right ventricular pressure is increased. Crocodilians can remain submerged by engaging in anaerobic metabolism, and by remaining very inactive they can tolerate this lack of oxygen for various lengths of time. In most adult crocodilians such times can last as long as six hours.[1] When they return to the surface, the pressure in the right ventricle goes down as normal pulmonary ventilation resumes.

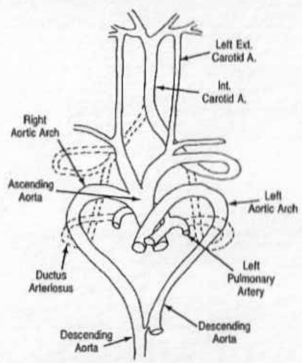
The hemodynamics of crocodilian circulation and the functional anatomy of the heart are extremely difficult to assess and are mostly based on dissections and physiological models rather than on in-vivo hemodynamic measurements which would require cardiac catheterization and the direct monitoring of pressures in various parts of the cardiopulmonary system.

[1] R. A. Coulson et al. (1989) reckon that alligators over 200 kgs. can stay submerged to 12 hrs at 28°C and for several days at 7 to 10°C.

Alligators submerge with a lung full of air which consists of four gases: oxygen, carbon dioxide, water vapor, and nitrogen. Nitrogen, which is inert and is not involved in gas exchange, represents the largest amount of gas present both by percentage and partial pressure. As the oxygen in the lungs of the submerged animal is used up, it is replaced by carbon dioxide until the lungs have no oxygen and can hold no more carbon dioxide. This ultimately results in declining oxygen levels in the blood accompanied by rising carbon dioxide levels. In addition, increased carbon dioxide levels and declining oxygen levels lower blood pH. Some of this acid is buffered by various systems in the blood, but eventually these too are overwhelmed. What happens next that permits the crocodilian's most prodigious ability to remain submerged is theoretical or based on empirical observations. It is difficult to perform baseline blood chemistries on restrained adult animals on the surface let alone under natural conditions while they are submerged. Also, it is theoretically impossible to perform cardiac catheterizations and the fluoroscopic dye and pressure studies necessary to confirm the exact means by which the animal shunts blood from now almost totally useless lungs to its peripheral circulation. Anatomical studies on the position of the foramen of Panizza indicate that it swings open or closed, depending on point of view, enabling blood from the right heart to enter the outflow tract leading to the descending or abdominal aorta. This diverts blood from the lungs, which are severely or almost totally devoid of oxygen, to the less oxygen sensitive organs such as the liver and stomach. On the other hand, blood returned from the lungs which may still have oxygen in them, is directed to the more oxygen-dependent organs such as the heart and brain. However, no one has quantified the amount of blood shunted away from the lungs, the amount of blood that remains in the pulmonary circulation and left side of the heart, or the means by which the foramen of Panizza becomes functional. In Ross and Garnett (1989), a simplified diagram and accompanying text indicates that while diving, the foramen of Panizza "closes" and by so doing isolates the outflow tract to the descending aorta away from the left side of the heart. This permits unoxygenated blood from the right side of the heart to pass into the lower portion of the systemic arterial circulation which supplies tissues that are more tolerant of decreased oxygen levels.

Respiratory System

Crocodilians are air-breathing animals and possess a pair of well-developed multichambered lungs located in the thoracic cavity. Ventilation of the lungs is accomplished by both voluntary and involuntary muscle



Crocodilian aortic arches (*after Goodrich in Jollie*).

action. The principal ventilatory muscles are the *intercostals* located between the ribs and a large, diaphragm-like muscle that separates the abdomen from the liver and the chest cavity. It is known as the *septum posthepaticum*. By alternately contracting and expanding, these muscles cause a drop in the pressure around the lungs, creating a pressure gradient or difference between the outside air pressure, the intrapulmonary, and the intrathoracic pressures causing air to flow into the lungs until equilibrium is reached. Air can be held in the lungs for prolonged periods by closure of a glottic valve or gular fold, and this is the principal mechanism by which crocodilians can remain submerged for periods of an hour or more. Larger animals are capable of longer breath holds than smaller ones. When the crocodilian returns to the surface, the glottic valve relaxes, and the air in the lungs is expelled as a result of the elastic recoil of the lung tissue. This process is known as passive exhalation.

Crocodilians are perfectly suited for their amphibious existence, and to this end one of their assets is a built-in "snorkel." They can lie in the water, hanging unseen just below the surface with only their slightly elevated nostrils and eyes protruding above the surface. They can close off the mouth, which is underwater, from the entrance to the airways thus preventing any water from entering the lungs. They can rest like this for hours, breathing through their nostrils, without being seen.

An elongated palate, which forms the entire roof of the mouth from the tip of the snout to the gullet, assures the animal that any water taken into the mouth will remain there or be swallowed, but never inhaled. This capability also enables them to swallow prey under water without aspirating water into the lungs. They cannot forcibly spit out water that enters the mouth; some drains by gravity, the rest is swallowed.

The inhaled air traverses a long nasal passage above the palate and exits into the pharynx through two rear openings known as the posterior nasal choanae. From here the air travels down a long windpipe or trachea which divides into the left and right lungs. The plan is similar to that of mammals and functions in the same way.

Blood enters the lungs via the branches of the pulmonary artery pumped by the right ventricle. It then flows into the pulmonary capillary network which carries it to the pulmonary units or alveoli where excess carbon dioxide is expelled and additional oxygen is absorbed. After leaving the alveoli, it is returned to the left side of the heart via the pulmonary veins, and it is then pumped into the systemic arterial circulation.

Seymour et al. (1987) studied the reasons why large crocodilians, on occasion, suddenly die of apparent cardiorespiratory arrest during or immediately after capture. The study measured blood pH and pCO_2 levels and found that during the struggle of capture the pH dropped to such precipitously low levels as to be normally incompatible with life. The normal blood pH of crocodilians falls within the same range as humans, between 7.35 and 7.45. Seymour's study revealed that crocodilians can tolerate remarkably high levels of acidemia or decreased blood pH (pH = 6.6 to 6.8). These levels would kill most vertebrates almost immediately. However, the study revealed that the animals could survive these levels if allowed to recuperate from their struggle. After capture the animals are often quickly tied and bound and dragged behind a boat underwater, and this represents the "straw that breaks the animal's back," pushing the pH to even lower and now certainly intolerable levels of around 6.4 to 6.6 causing the animals to become unconscious and drown.

Further confounding the study of cardiorespiratory dynamics in crocodilians is what is already known in mammals and humans about the effect of cyclic respiration itself on the return of blood to the heart and cardiac output. The late Andre Cournand and co-workers received a Nobel prize for their work on the effect of positive pressure on cardiac output in humans. A crocodilian that dives with its lungs full of air and holds it there against a closed glottis is engaging, in effect, in an event human physiologists call the Valsalva maneuver. It occurs in humans for short periods of time when bearing down during labor and childbirth or during a difficult bowel movement. It serves to raise the intrathoracic pressure (pressure inside the chest wall but outside the lungs) which impedes the blood flow returning to the heart from the systemic venous circulation. At the same time it increases central venous pressure and keeps a fraction of the returning blood away from the right side of the heart and subsequently out of the lungs. As a treatment, this positive pressure is administered (by retarding the exhalation of air from the lungs) to humans suffering from left heart failure and pulmonary edema. Pulmonary edema of cardiac origin occurs because of the failure of the left side of the heart to pump the blood returning from the lungs out to the arterial circulation fast enough. The blood backs up in the pulmonary capillaries and the liquid part spills out into the airspaces (alveoli) of the lungs. In effect this drowns the patient. It would appear that crocodilians expose themselves to their own continuous positive airway pressure whenever they dive. By holding a volume of gas in the lungs constantly while submerged, crocodilians also serve themselves by retarding the flow of blood through the pulmonary capillary bed in addition to preventing the entry of water into the airways and lungs.

If the above factors do not add enough confusion to this subject, then there is another mechanism which may also serve the submerged crocodilian which has been documented in humans. It involves response of the pulmonary capillaries to the presence of hypoxia or lowered oxygen

levels. In what is obviously a mechanism meant to also divert blood away from useless lungs, the pulmonary capillaries constrict in the presence of low oxygen levels.

Designing experiments to determine if human responses also occur in crocodilians is not an easy task, and finding the resources and facilities to enable such research may be even more difficult. This discussion is included here only to point out that much more work needs to be done before any thorough understanding of crocodilian underwater physiology can be made.

There is considerable disagreement among observers regarding how long crocodilians can stay submerged. The ability to remain underwater without breathing air depends on size, water and air temperature, the metabolic status of the animal and whether or not it has recently fed. Therefore, no one observation is representative in all situations. In personal communications from field workers in Florida, it has been stated that in particularly cold water some large animals are able to stay submerged, if they haven't eaten recently, as long as 4 to 6 hours. This should be a simple enough area to research, even under laboratory or captive conditions.

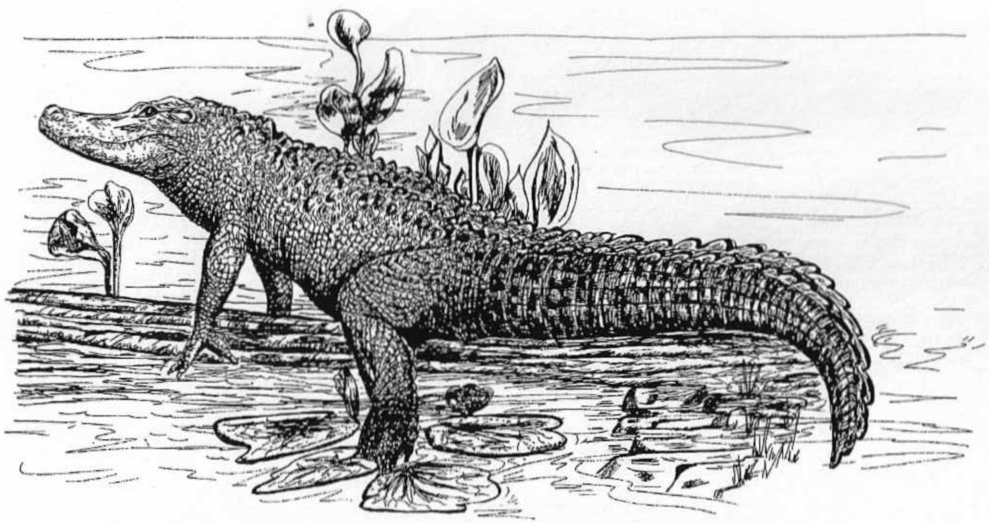
As in all vertebrates, the rate and depth of breathing in crocodilians increases with increased metabolism and activity levels and diminishes with lowered metabolic rates and inactivity. At 28°C, at rest, the American alligator breathes at a rate of only 2.5 to 3 breaths per minute.

Other factors concern the wide swings in blood pH of crocodilians which have a profound affect on the affinity of hemoglobin for oxygen, which, in turn, affects the unloading of oxygen to the tissues. A high pH or alklaemia increases the affinity between oxygen and hemoglobin and decreases unloading of oxygen to the tissues. As Coulson and Hernandez (1964) have pointed out, the chief occasion for crocodilian blood pH to increase is during the digestive processing of food matter in the stomach. On the other hand, during times of stress and energy expenditure, many researchers have demonstrated that blood pH decreases. This decreases the affinity between oxygen and hemoglobin and increases the unloading of oxygen to the tissues. The dissociation of oxygen from hemoglobin is also affected by other factors including blood PCO_2 levels, and body, or more accurately, blood temperature levels. A decreased PCO_2 increases hemoglobin-oxygen infinity and decreases dissociation or unloading to the tissues; an increased PCO_2 does the opposite. In the case of temperature, decreased temperatures act like decreased PCO_2 levels and increased temperatures act like increased PCO_2 levels. The implications of these biochemical responses, known as the Haldane and Bohr effects, in terms of crocodilian ability to endure stress or remain submerged, are not clearly understood.

Thermal Regulation

Crocodilians, unlike birds and mammals, are *ectotherms*, which means their temperature is regulated from "outside" the body; environmental conditions dictate crocodilian body temperature although crocodilians and other reptiles selectively engage in behaviors which give them some control over their body temperature. Birds and mammals, on the other hand, are *endotherms*. Their body temperature is regulated internally.

Although *ectothermic* and *endothermic* are the preferred terms, two other sets of terms have been used with respect to thermal regulation. Commonly, birds and mammals are referred to as warm blooded and reptiles, amphibians and fish are called cold-blooded. These common popular terms are not accurate. A crocodilian basking in the sun with a body temperature of 95°F can hardly be called cold blooded. Specialists also disdain the use of two other terms in this respect. Poikilothermic which means "of varying temperature" for reptiles and homeothermic for birds and mammals which means "of constant temperature." While somewhat more accurate than warm and cold-blooded, these terms may *not always be correct*. Crocodilians can maintain remarkably constant body temperatures, and birds and mammals can have their body temperatures vary because of fever or extreme environmental hypothermia or hyperthermia.



Crouched, bottom sitting. Crocodilians may lurk submerged in shallow water, ready to lunch, by squatting or crouching like a dog.

Crocodilians and other reptiles seek environmental conditions which enable them to have some control over their body temperature and which enable them to maintain favorable temperatures for their activity. Alligators and crocodiles emerge from the water to bask in the sunlight, and in extremely hot weather they can cool their brains and head, at least, by lying for hours with their jaws open. This causes evaporative cooling across their extremely long palate. They can also cool themselves by alternately entering and leaving the water which also produces evaporative cooling, this time to the entire body.

Even under unfavorable temperature conditions, crocodilians can adjust their metabolic rates to stay in tune with prevailing temperatures, so that the relative intensity of metabolism can remain basically unchanged even if temperatures are not ideal. This ability is called temperature compensation. Birds and mammals achieve metabolic homeostasis by internally regulating their body temperature within a narrow range. Reptiles accomplish the same thing by regulating their metabolism internally because they can't do it for their body temperature.

In cold weather, crocodilians will retreat to their subterranean "holes" and lower their basal metabolic rate considerably. If they are unable to deal with prolonged hot spells, they'll do the same thing—enter their holes and become as inactive as possible. While no one has measured the temperatures inside crocodile or alligator holes at various times of the year, it is reasonable to conclude that during cold weather they are warmer than surface conditions whereas in hot weather they're relatively cooler. They are ideal thermo-insulated sanctuaries for crocodilians when climatic conditions at the surface become too severe.

Captive crocodilians should have a range of temperatures available to them (25°–35°C) as they will select the temperature best suited to their needs at any particular time. Thermoregulatory behaviors are well developed almost from the moment hatching occurs. Newly hatched juveniles, those that are feeding, and juveniles with infections all seek higher temperatures (90°F to 93°F) whereas nonfeeding, older juveniles prefer somewhat cooler locales. Exposure to constant temperatures in the 90°'sF results in weight loss unless the animal is able to feed almost constantly. Thermal stress will ultimately kill crocodilians. On the other hand cooler temperatures inhibit feeding and decrease immunity to infectious disease.

Baby crocodilians are gregarious creatures that like to rest piled atop each other. By so doing they may create a somewhat amorphous mass that mimics the heat-conserving abilities of larger single individuals.

Nervous System and the Senses

The crocodilian nervous system, as in all vertebrates, relies primarily on specialized nerve cells or neurons which orchestrate a wide variety of activities including metabolism, senses, locomotion, heart and respiratory function, and complex biochemical reactions and interactions.

The nervous system is divided into two parts: the central nervous system consisting of the brain and spinal chord and the peripheral nervous system consisting of all nerve pathways leading to and from the central nervous system. The autonomic or peripheral nervous system is further divided into sympathetic and parasympathetic branches which serve to oppose each other. If one part causes specific muscles to contract, the other causes them to relax. If one speeds up heart rate, the other slows it down, and so forth.

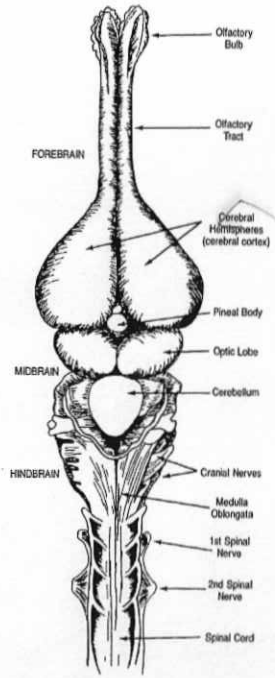
The main organ of the central nervous system is the brain. It is located within and is protected by a sturdy bony cranial cavity atop the head. In crocodilians the brain weighs not more than 0.8% of the total body weight which compared to higher mammals and man makes it a relatively small brain. The crocodilian brain is divided into five principal parts:

1. The **forebrain** which consists of the olfactory bulbs—centers for receiving stimuli involved in sensing smell.
2. The **cerebrum** or **cerebral cortex**. Crocodilians are the first animals on the evolutionary tree to have a true cerebral cortex, implying they are capable of conscious thought processes and learning.
3. The **midbrain** which is the site for receptors from the optic nerve responsible for conveying visual stimuli.

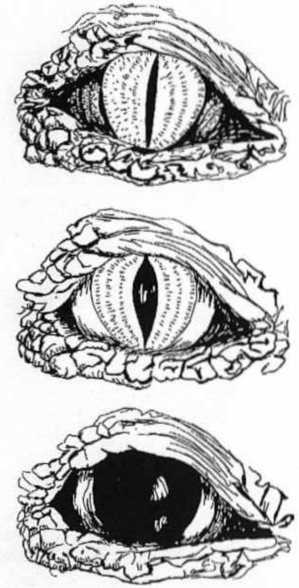
4 and 5. The **hindbrain** which consists of the **cerebellum** and **medulla oblongata**. These two areas control vital motor centers and contain nerve endings responsible for hearing senses and equilibrium or balance.

The brain stem leads to a spinal cord which, as in other terrestrial vertebrates, possesses twelve pairs of cranial nerves.

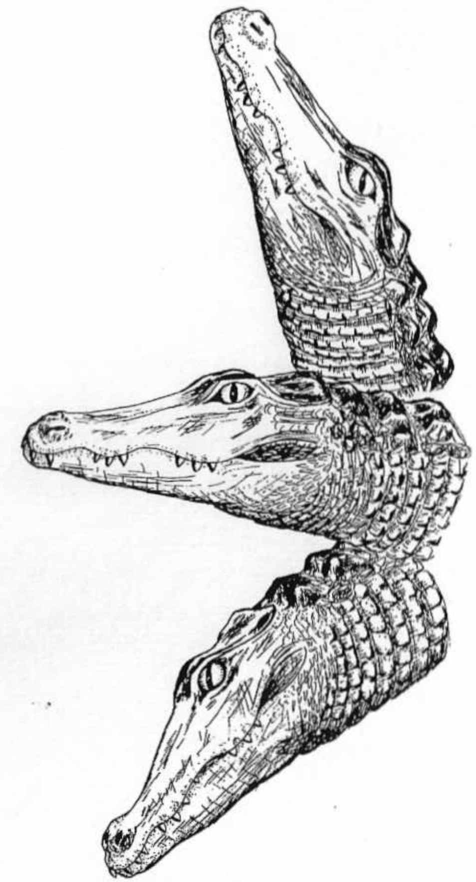
The eyes of crocodilians are suited for both day and night vision. At night they have a large dilated pupil capable of visual acuity in "available" light. In the daytime the pupil constricts to a narrow, vertical slit which modulates or restricts the entry of light. Crocodilians possess yellow, yellowish-green, and in several species, brown irises. Crocodilians demonstrate a sense of vision that enables them to recognize prey on land and in the water, their mates, their young, their nest, their environment, and their enemies. They can see both near and far, and have color vision, but they



Brain, American alligator, dorsal view.



Crocodilians have a vertical slit-like pupil that dilates laterally in darkness. *Top:* Bright light. *Middle:* Moderate light. *Bottom:* Low light.



Crocodilian eye pupils remain vertical with the horizon regardless of head tilt; vision is distorted only when the animal is upside down on its back.

have limited depth perception. In air their far vision is better than near; underwater their vision is limited.

At night crocodilian eyes reflect any bright light that is shone at them, including moonlight. This ability is due to presence of a reflective layer in the eye called the *tapetum lucidum*. It lies directly behind the retina and acts as a mirror, causing the eyes to light up at night. The same property can be observed in the eyes of other animals, including domestic dogs and cats. Unfortunately for the crocodilian, it enables poachers to spot them at night by "eye-shine," and in the United States, at least, this method of hunting is generally prohibited except during open seasons. By counting the pairs of eyes, however, wildlife specialists use "eye-shine" to make population counts.

The narrow, vertical pupil of crocodilians is always held at 90° to the horizon, even when the head is tilted. However, should the animal be turned over on its back, the pupil would "see" upside down, and would cause a momentary loss of orientation and confusion probably similar to the sensation known as vertigo.

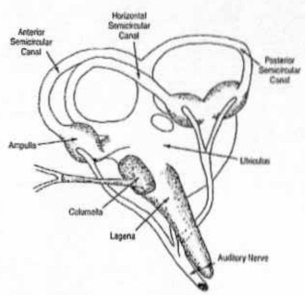
Thanks to a third transparent eyelid called the nictitating membrane, crocodilians can partially or fully cover their eyes when partially or fully submerged. This membrane acts like built-in diving goggles and enables them to have limited underwater vision.

Many crocodilians are not capable of complete binocular vision (viewing an object with both eyes focusing on it at the same time) because their eyes are set on opposite sides of the head but in some species such as the American alligator the eyes are oriented to permit a slight degree of binocular vision. According to Bellairs (1971), there is at least a 25° binocular overlap in alligators.

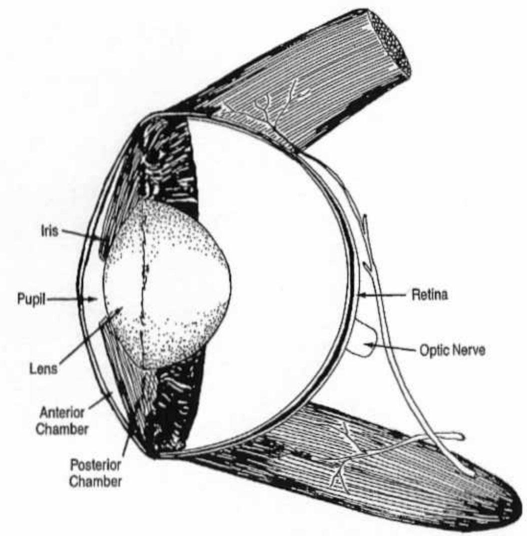
Crocodilians have inconspicuous external ears and ear drums which are located just posterior to the eyes on each side of the head. When submerged crocodilians close their ears with special muscles, thus preventing entry of water. Crocodilians do not rely on ear transmitted sound while under water but have the ability to detect sounds primarily in tones of low or even subsonic frequencies on the surface. Crocodilian vocalizations, which are deep, throaty sounds (bellows, roars, moans, grunts) are well within this range.

A single bone, the stapes, conducts sound waves received by the tympanum or ear drum to the inner ear. Underwater sounds and vibrations may be detected by integumentary sense organs located beneath the scales. Such sounds may also be transmitted, though muffled, via the ears.

Orientation toward home is a "sixth sense" that has been documented in a variety of amphibians, reptiles, and higher animals. Tales of dogs and cats that have traveled hundreds—even thousands—of miles from release



Internal and middle ear (*after Chiasson*)



Crocodilian eye (*after Chaisson*).

or loss sites to "back home" have been well documented. Sea turtles, fish and migratory birds travel thousands of miles, returning to the same nesting grounds every year with remarkable precision. Crocodilians also possess this ability although not for as long a distance as birds, fish or sea turtles. Homing has been studied in the American alligator, the Saltwater crocodile, the Spectacled caiman and in the Australian freshwater crocodile. Webb et al. (1983) documented that *C. johnstoni* was capable of homing after being translocated nearly 19 miles upstream. After 15 months, out of a group of 17 translocated animals, 7 were recaptured at the original capture site. One was halfway between the capture and release site. None was found at or near the release site.

Crocodilians may home using solar-compass orientation, navigating by gauging or analyzing the angle of the sun in the sky. Translocations that take place close to the winter dormancy period support this view. As the days grow shorter, animals trying to make their way home will stop and den until sunnier days return. A number of other factors have been documented by Murphy and Coker (1983) with respect to homing:

1. *Distance between capture and release sites.* Longer distances lessen the possibility of successful homing.

2. *Accessibility to capture site.* Open water routes back to capture sites increase the chance of homing success. If routes between the capture and release sites are either nonexistent or have physical or habitat barriers, then the chances of homing success decrease. However, even with such barriers, studies of American alligators show they continue to move toward home (capture site) even a year after being translocated.
3. *Sex.* Adult females return to their homes or capture sites more often and with greater speed and accuracy than males. Subadult males are least likely to return home after translocation.
4. *Size and/or age.* The smaller and younger the animals, the less likely they will try to home and the less likely they will home successfully if they do try.

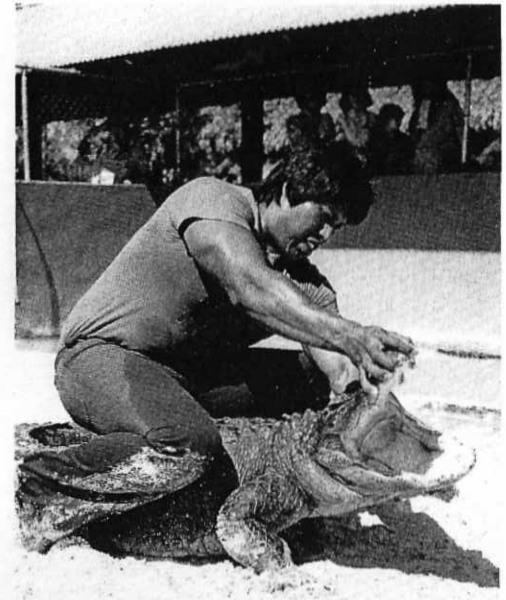
Human-Crocodilian Relationships

Humans and crocodilians have been interacting since the dawn of civilization. The arena for this early interaction was probably Africa, and Asia. It can be presumed that crocodilians preyed upon humans for food, but as man became a hunter, he stalked the crocodilians and was much more successful.

Descriptions of the Nile crocodile were recorded by the ancient Greeks, and the Romans captured live specimens 50 to 100 years B.C. to exhibit in their menageries in Rome. Nile crocodiles figure prominently in the Bible. Women and children washing clothes in the Nile have been attacked, killed, and eaten by crocodiles dating back thousands of years up to the present day. Wherever and whenever humans meet crocodilians, there is bound to be fear, revulsion, and on occasion injury or death for either the person or the animal. Strangely, there is rarely any "hatred."

Crocodilians, however, have recently been the losers in this interspecies battle. While surviving for tens of millions of years, it has just been within the last hundred years that the few species remaining on earth have been so severely threatened with extinction. The discovery that their hides make prized leather has been the chief cause of this demise. Secondary causes include hunting of the animal for sport and for food (including eggs) and loss of habitat due to human encroachment.

In this century government agencies began keeping records of crocodilian confrontations, attacks, and fatalities. As would be expected, the largest number of such reports involve confrontations which result in no injury, followed by attacks that caused injury including serious injuries such as the loss of a limb, and thirdly by attack which result in human



Miccosukee Indian alligator wrestler, shown here in the difficult job of holding open the jaws of an alligator at a popular Florida tourist attraction (*Courtesy of Florida Department of Commerce, Division of Tourism*).

deaths. Since 1948 there have been a total of 95 recorded unprovoked alligator attacks on people in Florida. Of these, there were only five fatalities. There have been tens of thousands of reported confrontations. In 1988, during a six-month period (January–June) there were three serious attacks by alligators on humans in Florida, one of which resulted in the death of a four-year-old girl in Englewood. According to Hughes (1989) in Northern Australia, Western Australia, and Queensland, between 1975 and 1987 there were 12 fatal attacks by crocodiles on humans.

There are measures people can take to prevent such gruesome confrontations and deaths. These measures have been collected from a variety of wildlife agencies and field experts and represent a consensus. Professional herpetologists called upon to counsel the general public may find the following advice useful.

Whether you reside in or are just visiting areas known to be inhabited by crocodilians, the following rules can help keep you safe:

1. Always stay alert, don't use intoxicants, think ahead, try to stay calm, and never panic.
2. If you see a crocodilian, never charge or bluff it.
3. If you're in the water and you see a crocodilian, swim as quietly as possible to shore. If that's not possible, keep calm and stay as motionless and as quiet as possible.
4. Know where small children are AT ALL TIMES; teach them to respect crocodilians. Use pictures or take them to the zoo if necessary to reinforce this teaching. It's reasonable to tell them that the animals they're looking at can hurt them.
5. Keep dogs and cats under close supervision and control. If necessary, leash or cage them on outings or when you reside in areas with crocodilian-occupied waters nearby.
6. Fisherman should keep their bait or strings of fish-catch in covered buckets or chests of ice. Never store fish on a string trailing from the side of your boat, or you may attract an unwanted crocodilian. In Florida most canal fishing occurs from shorelines or off bridges. This is the safest way to fish in such waters. Clean fish well away from the water and dispose of the remains in a covered receptacle.
7. NEVER swim in waters you even suspect may be occupied by crocodilians. Especially don't let children in or even near such waters.
8. If you're out to snap a picture of a crocodilian in the wild, do it from at least 20 feet away. Use a telephoto lens for best results and for close-ups.
9. Never throw anything at a crocodilian unless you're in imminent danger and are using projectiles as weapons. Never hit or prod an alligator with a stick. If you can do this, you're TOO CLOSE. Use a stick only as a weapon, if necessary, to fight off an attack. Don't go looking for a fight.
10. NEVER FEED wild crocodilians. They learn quickly to associate humans with food. They may also come to think of humans as food although this has never been proven. They have been trained to perform in stage acts using a food-based reward system.
11. If confronted by a crocodilian, yield the right of way with as wide a detour as possible. DON'T PROVOKE IT. Back away slowly if the animal is moving toward you. Always keep your eyes firmly fixed on it. Crocodilians are good sprinters and you may have difficulty outrunning one on land—so always keep a respectable distance.

12. If contact occurs, you can avoid injury or even save your life by holding the animal's jaw shut. Although they can snap their jaws shut with amazing force, crocodilians can't open them with the same degree of power. This is a trick that Florida's Indian tribes must have learned a long time ago and today enables them to wrestle with alligators to the delight of tourists. There are other tricks involved such as turning the animal over on its back to disorient it by distorting its vision—but this is difficult in the field—especially with larger animals (>3 feet).
13. Crocodilians may use their powerful tails as weapons and can knock large prey right off their feet with them, so stay away from this end of the animal. Always try to jump clear from any land confrontation.
14. Although this should be obvious, never chase a crocodilian that's retreating from you even if you feel you have the upper hand. The situation can turn around without warning. That especially includes the admonition NEVER to follow a crocodilian into the water. Your chance of surviving a contact confrontation in the water is far less than on land. Many crocodilians are shy and retiring, but animals develop different personalities under varying circumstances. A female alligator almost never attacks on land except if she perceives a threat to her nest. Exceptionally well-fed animals will never go out of their way to endanger themselves in a confrontation just to get a meal. If they're hungry, that is a different matter. Field workers netting juveniles for tagging experiments have learned that the distress calls emitted by the babies mobilize adults in the area toward their source. Often they have to quickly release the young in order to avoid the risk of attack.

There is no way to reliably predict the results of confrontations in the wild between humans and crocodilians, so the best thing to do is to avoid them.