Handbook of

TURTLES

The Turtles of the United States, Canada, and Baja California

By Archie Carr

GRADUATE RESEARCH PROFESSOR, BIOLOGY,
UNIVERSITY OF FLORIDA, AND RESEARCH ASSOCIATE,
THE AMERICAN MUSEUM OF NATURAL HISTORY

Comstock Publishing Associates
A DIVISION OF
Cornell University Press
ITHACA, NEW YORK, 1952

PART I

INTRODUCTION

TWO hundred million years ago the reptiles, newly arisen from an uncommonly doughty set of amphibians, were on the verge of great adventures. They bore the mark of destiny in the shape of impervious scales and the new cunning to lay shelled eggs, and these devices insured them against the age-old disaster of drying out, both before birth and after, and let them gratify their growing curiosity about the vast and almost empty land. Along with the new equipment they had imagination and no end of notions for novel body designs. Today we call these old beasts cotylosaurs, or stem reptiles, because all the lines of vertebrate life above the amphibian level lead back to them as branches converge in the trunk of a tree.

The first of the innovations made by the stem reptiles was in a way the most extraordinary and ambitious of all—the most drastic departure from the basic reptile plan ever attempted before or since. By a cryptic series of changes, few of which are illustrated in the fossil record, there evolved a curious and improbable creature which, though it retained the old cotylosaur skull (with no opening in the temporal region), had a horny, toothless beak and a bent and twisted body encased in a bony box the like of which had never been seen. And more than this, within the box the girdles connecting the legs with the rest of the skeleton had by some legerdemain been uprooted and hauled down to an awkward position underneath the ribs.

The new animal was a turtle. Having once performed the spectacular feat of getting its girdles inside its ribs, it lapsed into a state of complacent conservatism that has been the chief mark of the breed ever since.

Of course, the turtle was not completed overnight. Just when he was finished is not clear. We know that there were no turtles in the Carboniferous, that in the Triassic there were very satisfactory ones, and that by Cretaceous times most of the modern trends had been established, and a lot besides that were later cut off. But no one knows with certainty what turtles looked like during the several million years between the Carboniferous and the early Mesozoic. Almost the only glimpse permitted us is the skeleton of a reptile from the Permian of South Africa, which has teeth in the jaws and a wide, flat body and conspicuously broadened ribs that seem to forecast the bony turtle carapace.

This animal, called *Eunotosaurus*, is intriguing to turtle genealogists because it appears to substantiate their postulated derivation of turtles from cotylosaurs. It comes from the proper time, it is evidently a modified cotylosaur, and it appears to be on the verge of developing a shell. It has, however, one serious drawback as a hypothetical turtle ancestor. The carapace of modern turtles does not, as is often claimed, develop just from wide ribs but from independent plates of dermal bone which expand markedly and fuse with one another and with the underlying ribs and vertebrae. There is no such carapace as this in *Eunotosaurus*, nor is there any bottom shell or plastron, which turtles seem to have pieced together from the abdominal ribs of the primitive reptiles, finished off in front by parts of the old dermal shoulder girdle (clavicle and interclavicle).

The unique chelonian armor and the contortions the skeleton had to undergo to fit into it, combined with the toothless beak, place the modern turtles in a position apart from all living reptiles. It has even been proposed (by Jaekel, 1910) to separate them entirely from other reptiles and place them, along with the duck-billed platypus, the echidna, and a few other misfits, in a new class of vertebrates (Paratheria). Most modern students, however, agree with Williston and Gregory in their belief that the turtles are direct descendants of the stem reptiles.

But what forces in the environment wheedled or coerced the plastic cotylosaurs along this particular line of specialization? To this question all sorts of explanations have been proposed. It has been suggested that the turtle ancestor learned to curl into a ball like an armadillo to conceal itself within a flexibly segmented armor now stiffened to form the shell. This idea was introduced as a possible explanation of the lack of coincidence between the laminae and the plates of the inner bony shell. One recent author envisioned the primitive turtle as a haunter of dense brush where a heavy shell permitted a bulldozerlike locomotion through the restraining vegetation, but most paleontologists will probably agree with Schmidt (1939) that this "seems to be sheer nonsense." Hay (1898) believed the extra scale rows on the shell of the alligator snapper to be all that was needed to establish the homology of the shell laminae of ordinary turtles and the twelve longitudinal keels of the widely divergent leatherback turtle, and accordingly concluded that *Macrochelys* is the most primitive living turtle and most like the ancestral form.

The consensus of opinion sees the first turtles as marsh reptiles like their cotylosaur forebears. They were almost certainly scaly and similar to lizards in form, and the series of changes that they underwent may have attended the development of a defense reaction by which the shoulders were hunched and the back bowed to draw the head back out of harm's way.

In many cases some inkling of the historical origin of an anatomical feature may be gained by studying its development in a growing embryo. The occurrence of lateral folds in turtle embryos, for instance, probably means that the ancestral form had these structures, which are today found only in lizards. It might accordingly have been hoped that the evolution of the relationship between the shell, ribs, and girdles during embryology would shed some light on the original history of these events, but such is not the case. Ruckes (1929a) presented the first adequate account of the embryonic changes that result in the unorthodox orientation of the girdles, but as one writer (Walker, 1947) puts it, "it is felt that phylogeny could not have followed the same course." In other words, the internal gymnastics required to shift the position of the girdles are so strenuous that it is hard to believe that the intermediate stages represent the design of ancestral forms.

Ruckes showed that the girdles do not, as formerly supposed, change their relative positions by migrating downward. They actually undergo no absolute motion, the whole change in the relative positions of skeletal parts being due to the manner of growth of the carapace and plastron. According to Ruckes, the shell rudiment, as seen in an embryo of the limb-bud stage, consists of a dermal band surrounding the embryo between the girdles, and readily evident on the middorsal line as a thickened strip. This middorsal area is the site of maximum growth, and since growth proceeds in all directions, the active, outer edges of the dermal area soon come to overlap the pectoral and pelvic regions. This radial spreading of the shell rudiment takes place while the ribs are still mere spurs projecting at right angles to the vertebrae. As the ribs begin their development, they become intimately associated with the spreading shell elements above them and these so influence the course of their growth that they begin to curve downward only after their ends have passed laterally beyond the girdles.

However this skeletal rearrangement may have come about historically, it satisfied the early turtles and allowed full expression of their philosophy of meditation and passive resistance. Down through the faraway Permian they sat in their shells and meditated as great events took shape. The coal forests withered, and with the coming of a new climate and flora the archaic animal types began to drop out. Winged insects arose and the reptiles grew in vigor and restlessness. The synapsidan clan moved aside to begin the experiments which, epochs later, produced the mammals.

The Permian ended, and the turtles watched as the main reptile stock found its evolutionary stride and through a hundred million years staged the most dramatic show the world has ever seen—the rise and spread and the incomprehensible decline of the incredible archosaurs. The turtles remained conservative through it all and though *some* of them took to the sea—sacrificing parts of the beloved shell for greater bouyancy and producing such multiton monsters as *Archelon*, with a twelve-foot flipper spread, and *Meiolania*, with a horned skull two feet wide—they always clung to their basic structural plan, as other lines tested and exploited and abandoned a thousand specious schemes.

They remained unimpressed as *Pteranodon* cruised the skies and another strain of slim and athletic archosaurs devised Archaeopteryx and the birds, and as the Squamata dabbled in mososaurs and snakes. They remained turtles; they even began to prosper as never before, while the dinosaurs bellowed and pounded down through the Jura toward their utter and senseless doom in the Cretaceous, when the last *Brachiosaurus* laid down his fifty tons to rest and the final tyrannosaur gasped out the anticlimax to nature's greatest venture in mayhem. (Among those present when Triceratops fell was a genus of turtles, now known as *Podocnemis*, which to this day populate in placid abundance the streams of Brazil and Madagascar!)

The Cenozoic came, and with it progressive drought, and the turtles joined the great hegira of swamp and forest animals to steppe and prairie, and watched again as the mammals rose to heights of evolutionary frenzy reminiscent of the dinosaurs in their day, and swept across the grasslands in an endless cavalcade of restless, warm-blooded types. Turtles went with them, as tortoises now, with high shells and columnar, elephantine feet, but always making as few compromises as possible with the new environment, for by now their architecture and their philosophy had been proved by the eons; and there is no wonder that they just kept on watching as *Eohippus* begat Man o' War and a mob of irresponsible and shifty-eyed little shrews swarmed down out of the trees to chip at stones, and fidget around fires, and build atom bombs.

Turtle Functions and Capacities

RESPIRATION

The respiratory apparatus of turtles includes a glottis, which opens to receive air that has entered the pharynx from the internal nares and to admit it into the larynx, supported by the hyoid apparatus and connected with the trachea or windpipe. The trachea divides within the thorax into two bronchi, one of which enters each lung. The lungs are complex sacs with a large number of interior folds and subdivisions.

It is evident that the breathing process of a turtle cannot be wholly similar to that of an animal with a distensible thorax. Just how air is drawn in and expelled from the lungs has been much debated. Despite the fact that several early writers suggested the real character of the breathing mechanism, it has been repeatedly stated that the movements of the throat of a turtle represent impulses by which the hyoid apparatus pumps air into the larynx, as in frogs. It now seems more probable, however, that the hyoid movements are involved only in the olfactory sense and that breathing is accomplished more as in mammals than as in amphibia. According to Hansen (1941) and McCutcheon (1941), inhalation is effected by muscles located at each leg pocket and beneath the viscera. These operate like the mammalian diaphragm, contracting, enlarging the coelom and reducing pressure within it, and thus drawing air into the lungs. During inspiration the shoulder girdle rotates forward, but this is thought to be merely a passive movement. Expiration is produced by the contraction of two pairs of ventral muscles which push the viscera against the lungs and compress and deflate them.

To augment their oxygen supply, many aquatic turtles use the highly vascular pharyngeal cavity as a sort of gill, sucking in and expelling water and obtaining by this means sufficient oxygen to increase materially their capacity for remaining submerged. In a similar way, additional underwater respiration is effected by some species that augment the work of the pharynx by filling and emptying, through the anus, two thin-walled sacs that communicate with the cloaca. The currents set up by these pumping movements may be easily demonstrated if a small amount of dye or suspended silt is placed near the anal or nasal openings of a live turtle.

The possibility that soft-shelled turtles may be more dependent upon their aquatic respiration than has been suspected may be indicated by the observations of Dr. O. Lloyd Meehean, who during his fisheries studies in Florida lakes used large amounts of derris in poisoning lakes for fish population analyses. Dr. Meehean found that in nearly all the lakes which he poisoned, *Amyda ferox ferox* was killed in numbers, while no other turtle was affected. Since rotenone, the active principle of derris, apparently works through the respiratory system to kill fishes, one is tempted to conclude that *Amyda* is susceptible because of its cloacal or pharyngeal respiration. Lumsden (1924) stated that the respiratory needs of turtles are so slight that one inspiration may suffice for as long as two hours. There is a record of a turtle surviving for twenty-four hours in an atmosphere of pure nitrogen, and the difficulty of drowning turtles at ordinary temperatures is well known to collectors. A writer reported that one of his turtles lived under water for eight days, presumably satisfying its respiratory needs by anal and pharyngeal breathing.

Shaw and Baldwin (1935) suggested that the ability of turtles to go for long periods without breathing when on land is due to an ability to ventilate the lungs thoroughly, combined with a low "unloading tension" of chelonian hemoglobin as well as to unusually low oxygen requirements.

CIRCULATION

The heart of the turtle is three-chambered, with two auricles and a single ventricle. Tendency toward the four-chambered condition is seen in a rudimentary partition that incompletely divides the ventricle. Venous blood returns to the heart from the body over a large postcaval and two precaval veins and passes into the right auricle by way of the *sinus venosus*. From here it enters the right side of the ventricle, and when this contracts the blood is pushed out either through the pulmonary artery to the lung or through the left aorta, whence it may go directly to the viscera or enter the dorsal aorta. The pulmonary circuit is completed when oxygenated blood from the lungs returns to the left auricle through the pulmonary veins. This blood passes into the left side of the ventricle and with the next contraction it is pumped out through the right aorta, which joins the dorsal aorta. Owing to the incomplete nature of the septum in the ventricle, the blood is partially mixed there, and that which enters the aorta includes oxygenated blood from the left auricle and venous blood from the right auricle.

There are a renal portal system and a well-developed hepatic portal system.

EXCRETION

The excretory organs are two kidneys, each of which communicates by way of a ureter with the cloaca. The excretory product is stored in a bladder which in some species may be markedly distensible. The nitrogenous part of the urine of some turtles, at least, is insoluble uric acid instead of soluble urea, and the importance of this as a device permitting water conservation is mentioned in the discussion of *Gopherus agassizii*. It is of interest that the urine of the wholly aquatic *Chelonia mydas*, which is obviously never faced with the problem of conserving water, was found by Khalil (1947) to contain ammonia as the principal nitrogen end product. The bladder communicates with the outside by way of the cloaca and the anus.

DIGESTION

The digestive system of the turtle shows no distinctive features. In the mouth there is a broad tongue, fixed immovably to the floor of the cavity. Dorsally the mouth receives the internal nostrils (choanae of the skull), and behind the tongue a longitudinal slit or valve, the glottis, marks the divergence of the respiratory tube from the alimentary canal. A thin-walled pharynx leads into the narrow, thick-walled esophagus, and this communicates with the stomach. The narrow passage from the stomach into the small intestine is controlled by the pyloric valve, and the ileocecal valve separates the small intestine from the large intestine. Bile secreted by the liver reaches the small intestine by way of the bile duct, and the pancreas contributes its enzymes to the intestine by way of several ducts.

REPRODUCTION

Turtles reproduce sexually and fertilization is internal. The male copulatory organ is a distensible, grooved, unforked penis, attached to the fore wall of the cloaca and receiving the ends of a pair of *vasa deferentia* that bring spermatozoa from the two testes. The female organs include a pair of ovaries, each of which communicates with the cloaca by an oviduct.

All female turtles lay eggs; these are spherical or elliptical, usually white, and with a shell that varies from soft and leathery to calcareous and brittle. In some cases the shell is soft when first laid but hardens during incubation. Soft-shelled eggs usually have a dent in one side which normally disappears after a variable period of time in the nest.

Burger (1937) found that the sexual cycle of *Pseudemys s. elegans* could be initiated by gradually lengthened periods of illumination and suggested that the sexual behavior of turtles might be largely controlled by light, as in birds.

Courtship varies from the simple pursuit and mounting of the female by the male to a fairly complicated program of prenuptial tilting during which the male may bite the neck and shell of the female or butt and push her about, in some cases accompanying his activities with vocal noises. The most divergent courtship behavior appears to be that of *Chrysemys* and the *scripta* section of *Pseudemys*, in both of which the male swims backward before the female as he strokes or taps her face with his greatly elongated fingernails. Copulation occurs in the water in aquatic forms and either in the water or on land in terrestrial species. In some cases, notably in the sea turtles, the male grasps the anterior rim of the carapace of the female during coitus, while in others contact is established only posteriorly, where the hind legs of the male usually hook under the posterior edge of the shell of the female. There are almost no data on duration of copulation in turtles. There is one printed mention of a five-minute coital period, but the average is certainly much longer and in some cases, at least, may possibly continue for hours. Among the many bizarre amatory feats that popular legend ascribes to sea turtles, I find one that I believe will escape editorial censorship. While it is of course apocryphal, it is entertainingly so, and it also serves to emphasize the remark that we really know almost nothing about the subject:

> All the turtles from the Charibbeas to the Bay of Mexico, repair in Summer to the Cayman Islands. . . . They coot for 14 days together, then lay in one Night three Hundred Eggs, with White and Yolk but no shells. Then they coot again, and lay in the Sand; and so thrice; when the Male is reduced to a kind of Gelly within, and blind; and is so carry'd home by the Female [Oldmixon, *The British Empire in America*, 1708, Vol. 11, p. 338; as quoted by Lewis, 1940].

Darwin long ago observed that Galápagos tortoises roar during coitus, and Evans and Quaranta (1949) and Evans (1949) stated that the roars are emitted throughout the duration of the act, by captive specimens, at intervals of about five seconds.

Spermatozoa may be stored in the genital tract of the female and continue to fertilize eggs there for periods of at least four years after copulation, although the percentage of fertile eggs in clutches produced after the first season decreases progressively.

Sexual dimorphism usually includes a longer, thicker tail in the male, since the penis is housed in the base of the tail and is extruded from the

anus near the tip. Besides being longer and with more terminally located vent, the tail of the male is more strongly prehensile than that of the female, being in some species markedly so, and is sometimes equipped with an enlarged conical terminal scale that serves as an instrument to use in grappling for copulatory contact. In some species the plastron of the male is concave, to accommodate the convex carapace of the female during coitus. As was mentioned above, in a few emydid turtles, and most strikingly in the *floridana* section of *Pseudemys*, the nails of the fore feet are markedly elongate. In the marine species, a single nail on each flipper of the male is enlarged and curved inward for grasping the shell of the female.

Sexual differences in coloration are most marked in the *scripta* section of *Pseudemys*. The development of a secondary melanistic coloration by some old males is described under the account of that group. In species in which the male is much smaller than the female, the former usually tends to retain the vivid juvenile color pattern, while this fades in the larger females.

The sexes may be of similar size, or either may be to varying degrees the larger. The most extraordinary disparity in size is found in *Graptemys* and *Malaclemys*. In *Graptemys barbouri*, for instance, males mature at less than 100 mm. (3.94 inches) in shell length, while most of the mature females have shells about 200 mm. (7.88 inches) long and some may exceed 250 mm. (9.85 inches).

In some turtles (*Graptemys, Malaclemys*, some *Pseudemys*) the heads of the older females may become astonishingly enlarged; in other forms (Kinosternidae) enlarged heads may be characteristic of old males.

It has been observed that the female box turtle is more timid than the male; in aquatic species the reverse is frequently true.

Sex is determined in turtles (in one form at least) by a difference in the egg cells, part of which have one more chromosome than the rest and produce males when fertilized, while those lacking the extra chromosome make females. In many species, at least, females outnumber males. Forbes (1940) pointed out that most reptiles deviate from the usual 1:1 ratio. Risely (1933) found 2.3 females for each male of *Sternotherus odoratus*, and for diamondback terrapins (*M. t. centrata*) Hildebrand (1933) derived a ratio of 5.9 females per male. Marchand (1942, MS) counted 3.6 females for every male of Tennessee *Chrysemys p. dorsalis*. Of 281 desert tortoises examined by Woodbury and Hardy (1949), 151 were females and 101 were males (sex not determined in 29).

The eggs of turtles are laid in holes in soil, sand, or decaying vegetation

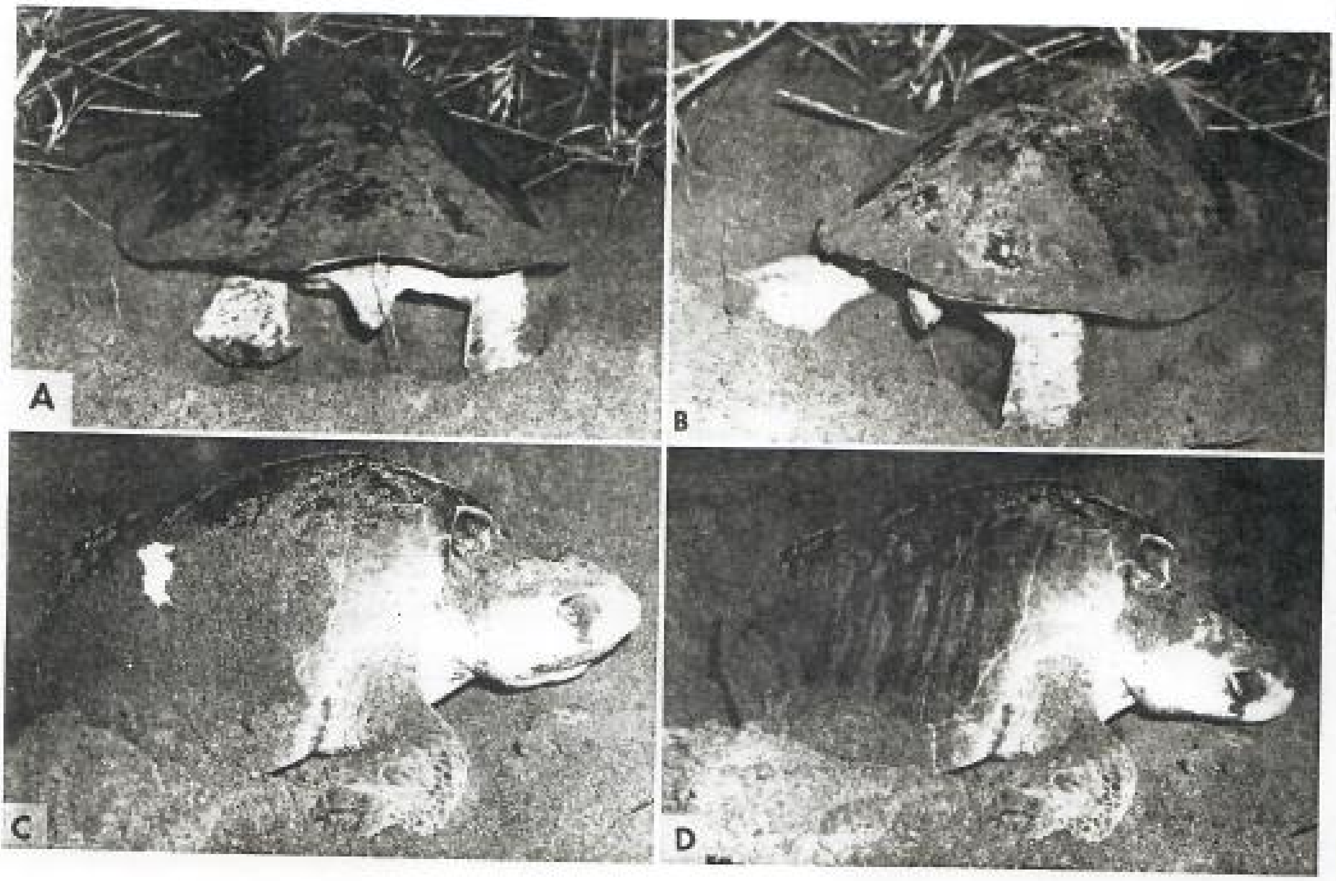


Plate 1. (*Facing page.*) A series of flashlight photographs of the nesting activities of a Pacific ridley (*Lepidochelys olivacea*) on Isla de Ratones, Honduras. *A:* Digging the nest. Rear view of a turtle with a flipperful of sand poised before being thrown to the side. This feat of delicately curling the edges of a highly modified swimming appendage and meticulously removing sand with it from a narrow-mouthed hole 18 inches deep never fails to astonish the observer. *B:* Sand from the deepening hole is thrown to one side. *C:* Head up. A bunch of eggs will fall into the nest momentarily. Note the closed and tearful eyes and the protruding hyoid apparatus. *D:* Head down. At this moment the eggs are falling into the nest.

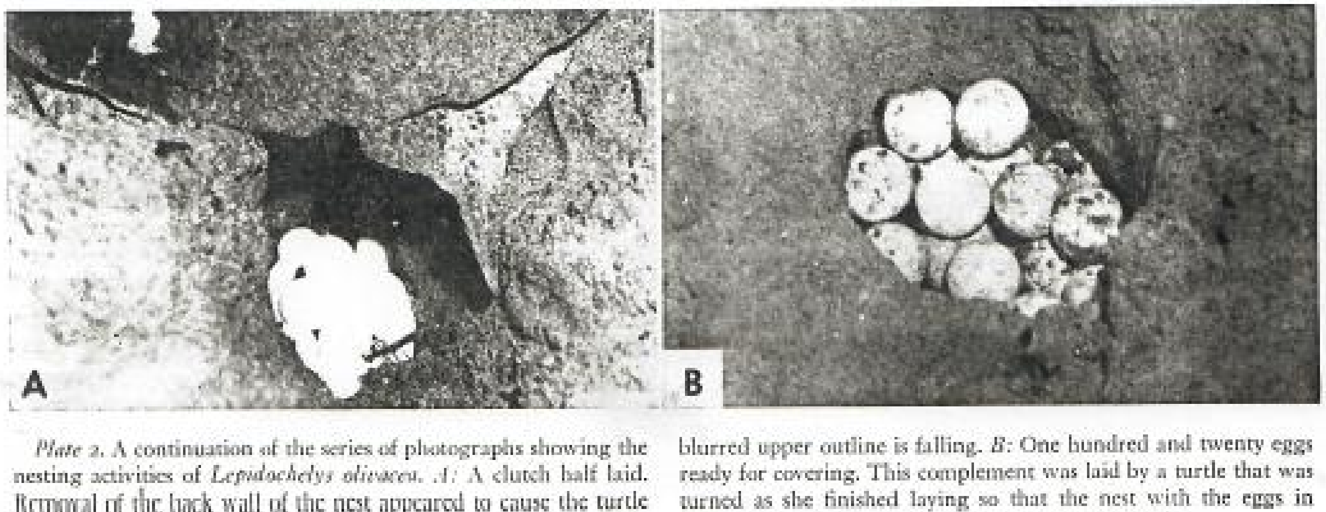
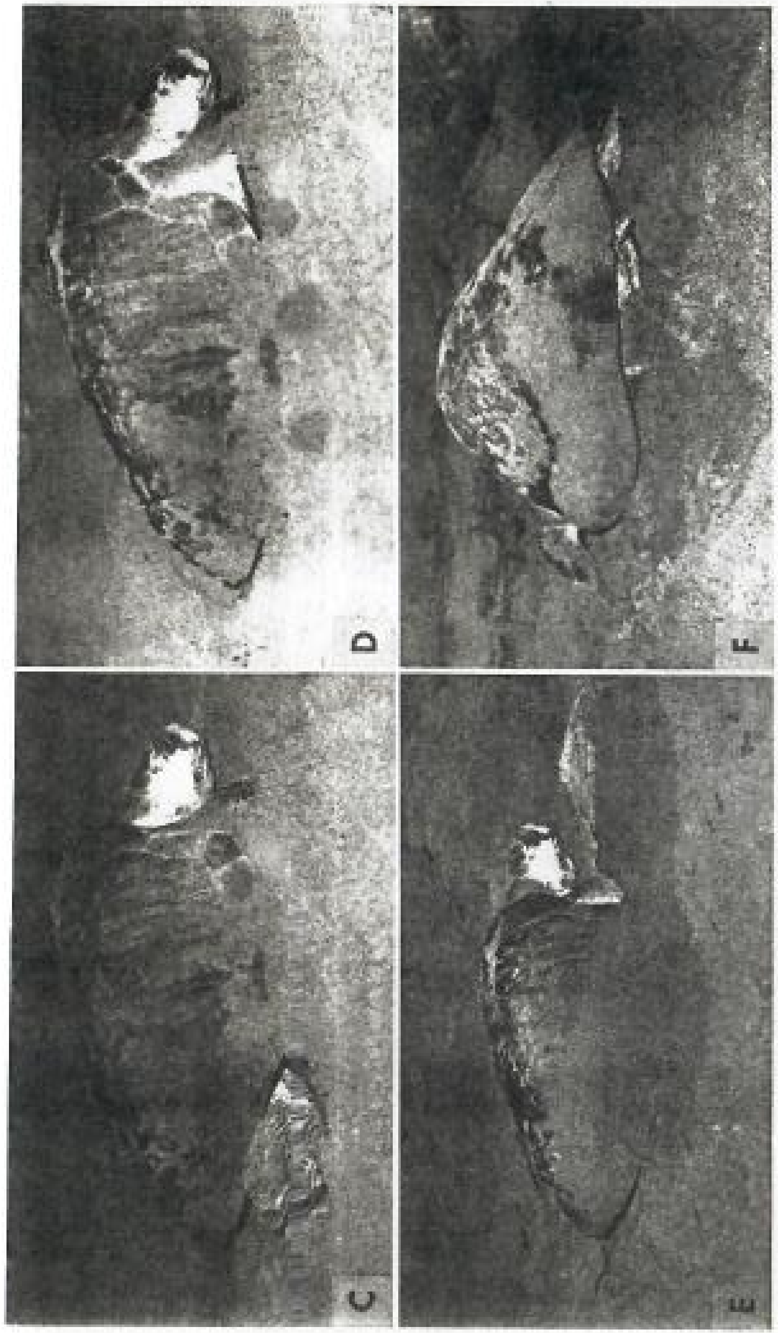


Plate 2. A continuation of the series of photographs showing the nesting activities of *Lepidochelys olivacea*. *A:* A clutch half laid. Removal of the back wall of the nest appeared to cause the turtle no anxiety. She merely pressed a flipper against the side of the cavity to prevent caving and continued to lay. The egg with the blurred upper outline is falling. *B:* One hundred and twenty eggs ready for covering. This complement was laid by a turtle that was turned as she finished laying so that the nest with the eggs in place but still uncovered might be photographed.



(*Plate 2, continued*) C. Filling in. The right hind flipper is pushing sand into the hole. Note that the eye is now open. *D:* Pounding the spot over the nest. The turtle has lifted herself on all four legs and will suddenly relax and fall abruptly on the sand, packing it tightly. This maneuver is repeated many times. *E:* Filling and packing done, the turtle flings sand over the area with her fore flippers to hide her handiwork. *F:* The nest has been covered and concealed to the mother's satisfaction. She has taken two steps back toward the water. Her maternal instincts have been satisfied and will probably trouble her no more until next year. She will never see her offspring to recognize them, and will not care. (Photographs by Margaret Hogaboom.)

such as leaf mold or rotten wood. The nests are dug by the female. She may excavate a preliminary basin by sweeping motions of the fore legs; the nest proper, however, is dug by the hind feet, which work alternately throughout the operation to form a narrow-mouthed, more or less flask-shaped hole of a depth determined by the length of the stretched hind leg. The process is sometimes, but not always, attended by the wetting of the soil by cloacal bladder water which softens it and makes digging easier. It is often stated that the chief purpose of this wetting down of the site of the cavity is to provide a moist environment for the eggs. Cunningham (1923), however, showed that the eggs do not take on water during the first few days after deposition, and it appears likely that the water from the cloaca is designed merely to improve the mechanical condition of the soil.

As the eggs are laid, the female usually makes some attempt to arrange them in the bottom of the nest with a hind foot. The covering process, likewise, is performed by the hind feet, which rake in soil from behind and from the sides. When the hole has been filled the site is pressed and trodden by the hind feet and may be pounded by the plastron. Some effort at concealment, such as the flinging about of sand with the fore feet or the kicking of sand by the hind feet, may be made. Females of some species crawl back and forth across the site to obliterate signs of their work.

Among the mud turtles of the genus *Kinosternon* the nesting instinct is poorly developed, some of them often making no nest at all, but planting their eggs singly in shallow holes and sometimes only half covering them.

The number of eggs in a clutch varies from one (the single large egg of the African *Testudo tornieri*) to a maximum obscured by the numerous unfounded guesses and estimates that have appeared in print, but which probably lies between 200 and 300. The largest complement recorded for any North American fresh-water turtle was one of eighty eggs deposited by a Canadian snapper. There is some correlation between the size of the species and the size of the clutch, and considerable correlation between the size of the individual and that of the egg complement. A large mature turtle may lay as many as twice the number of eggs deposited by a newly matured and smaller individual. Many turtles lay more than once a year, seven visits to the nesting beaches (by a green turtle) being the maximum number that has been definitely demonstrated. There is evidence that some fresh-water turtles may lay at least three times during a season, although others almost certainly lay all their eggs for the season

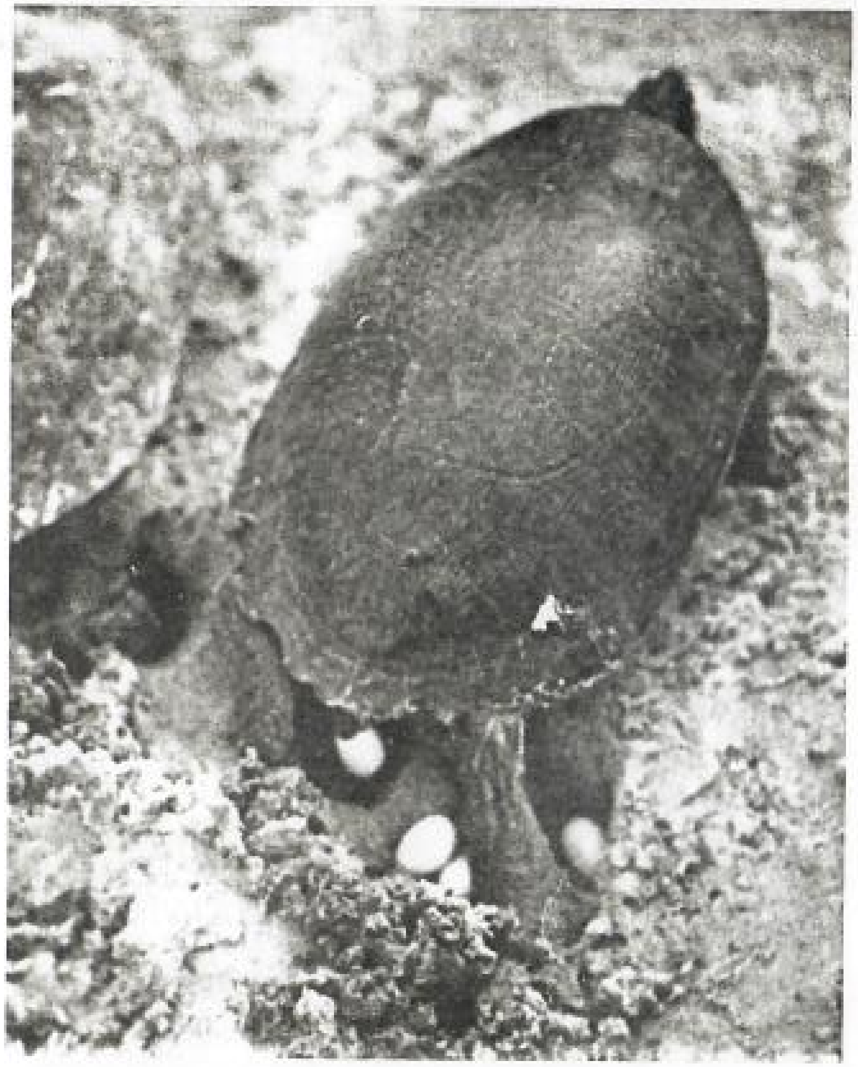


Plate 3. A captive peninsular turtle (*Pseudemys f. peninsularis*) laying its eggs. (Courtesy Ross Allen.)

at one time. There is a conspicuous need for further investigation of this subject.

Incubation periods normally range between two and three months, but are so strongly affected by humidity and temperature that no given species adheres very closely to a definite schedule. Overwintering is common, both by unhatched eggs and by hatchlings that may await either the more pro-

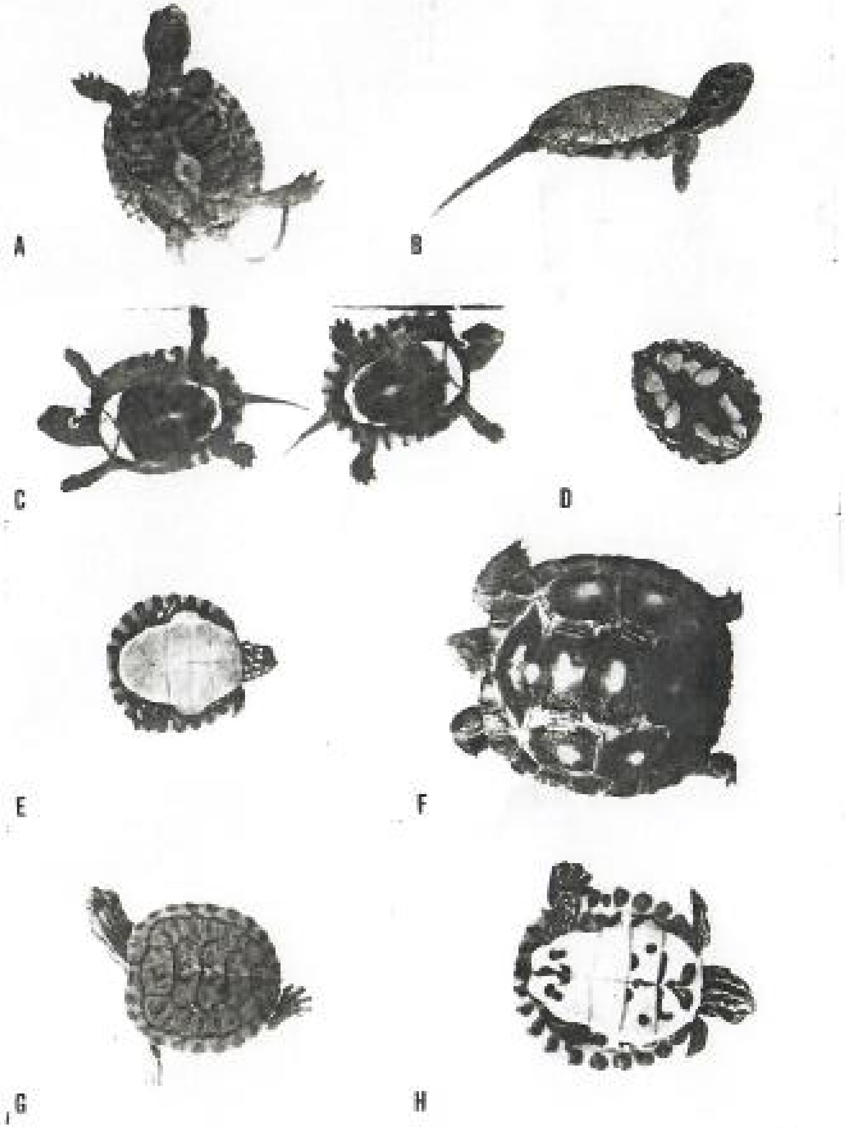


Plate 4. Young turtles. *A: Clemmys insculpta;* Ithaca, New York. *B: Clemmys marmorata pallida;* Perris, California. *C: Clemmys muhlenbergii;* New York. *D: Kinosternon subrubrum steindachneri;* Gainesville, Florida. *E: Chrysemys picta dorsalis;* Plaquemine, Louisiana. *F: Gopherus berlandieri;* Edinburg, Texas. *G: Pseudemys scripta elegans;* Plaquemine, Louisiana. *H: Pseudemys floridana mobilensis;* Plaquemine, Louisiana.

pitious temperatures of spring or the spring rains that soften the roof of the nest and free them. Thus the time actually required to hatch the eggs and that which elapses prior to the emergence of the young from the nest may be very different, and for this reason there is available little reliable information on natural incubation periods.

Interspecific hybridization among turtles apparently is not common. Hildebrand (1933) described reciprocal crosses between the Texas and northern diamondback terrapins, but these forms have subsequently proved to be intergrading races of one species. Shaw found an aberrant sea turtle that he suspected might be a hybrid between *Caretta caretta* and *Lepidochelys olivacea*, and in many places fishermen believe that the loggerhead crosses regularly with both the green turtle and the hawksbill, but this has never been demonstrated. There are indications that *Pseudemys floridana peninsularis* and *P. nelsoni* may sometimes interbreed in the extreme southern part of peninsular Florida. Risely (1941) suggested that the occurrence of hermaphroditic turtles may be the result of hybridization, but the cases which he cited involved intergrade specimens between subspecies and not the progeny of interspecific crosses.

SENSES, BEHAVIOR, AND INTELLIGENCE

The chelonian nervous system has no marked peculiarities. It is considerably in advance of that of amphibians, the cerebral hemispheres being much more prominent and a gray cerebral cortex being distinguishable from a white medulla. The cerebellum is also larger, indicating a greater capacity for co-ordination and correlation of movements. There are twelve pairs of cranial nerves. Some notes on senses and reactions are given below.

Hearing and voice: Anyone who has watched a dozen turtles slide off a log in concerted response to a slight noise a half mile down-river will be loath to accept the pronouncement that turtles do not hear well, but such appears to be the case. Although the auditory apparatus is complete, there being a tympanic membrane connected with a well-developed inner ear by a slender columellar bone and a Eustachian tube leading from the middle ear into the pharynx, atmospheric vibrations are apparently not picked up readily and what appears to be hearing is often actually the "feeling" of vibrations of the water or of the substratum. It is thus curious to note that a diverse scattering of species is able to emit sounds that have appeared to numerous writers to warrant the name "voice."

Some instances of turtle vocalization are surely illusory, like that of an early New England naturalist who wrote of *Chrysemys:* "The shrill, piping note of this species is frequently heard in May and June—especially during intervals between showers on hot, sultry days."

Cope (1865) quoted Berendt's assertion that the Mexican *Staurotypus* has "two very distinct voices" and that *Geomyda* makes "a soft, melancholy piping that is rather touching when killed." Both a mercy cry and a roar or grunt of anger are attributed to sea turtles, the leatherback and green turtle being most frequently mentioned in this respect. An old generic name of the leatherback (*Sphargis*) is derived from a Greek word signifying "to make a noise."

In many cases the "voice" credited to turtles is merely sound incidental to the exhalation of the breath or to frictional contact between parts of the body. I have several times heard from mud turtles squeaks or yelplike noises which I am sure were caused by the "gnashing" of their jaw surfaces, and similar sounds are occasionally made by *Terrapene* in closing its shell. On the other hand, there is no question but that some species bark or grunt as a regular and perhaps functional feature of their mating program, and in such cases the word "voice" is no misnomer even though the sounds are not made by orthodox vocal cords.

The enlarged scales on the inner surface of the hind leg of kinosternid turtles have often been called "stridulating organs," one writer even professing to have heard them in use. It is now believed, however, that the big scales merely help the male hold the shell of the female during copulation.

In the Florida backwoods there are still plenty of people who will tell you that the baby-chick cheep of oak toads in chorus is made by scorpions (by which they mean lizards of the genus *Eumeces*), and in the Nicaraguan rain forest I was repeatedly assured by otherwise astute machetemen that the baritone trill of the big marine toads was the voice of the *terciopelo* or fer-de-lance. When such intrenched misconceptions as these, and all instances of merely incidental mechanical noise, have been discounted in the case for the voice of the turtle, there still remain a few examples of genuine vocalization that would well repay further investigation.

Smell and taste: It has been repeatedly stated that the sense of smell is acute in turtles, and while this probably is true, there are few experimental data to support the assertion. The pulsating movements of the throat are thought to be connected in some way with the olfactory sense. Allard (1949) found no evidence that box turtles are capable of long-range smelling, and performed a simple experiment to determine whether odors emanating from nearby objects are perceived. He wrapped a fish in burlap, made a similar package containing only a stone, and placed both on the ground near a number of box turtles. The bundle containing the stone was not noticed, but one turtle made a considerable effort to open that containing the fish.

The presence in turtles of axillary and inguinal (and other) scent glands is common but the odors secreted by them may be purely protective, and the extent to which the animals may use them in keeping track of each other is not known.

The nature and relative acuity of the sense of taste in turtles has not been determined. Its existence is probably indicated by the fact that turtles often take into their mouths bites of substances that are subsequently spat out, presumably owing to their unpalatability. The distinction between taste and olfaction in aquatic forms is probably academic.

Touch: The sense of touch is well developed, although so intimately involved with the vibratory sense that the two are at times difficult to distinguish. Even a hulking horny-skinned tortoise is able to feel the contact of a straw tip dragged along its flank. A delicate tactile sense is demonstrated by a nesting female arranging her eggs with a hind foot, and the sensitivity of the partly everted cloaca of the nesting ridley to variations in the texture of the soil is extraordinary.

Behavior, intelligence, and visual perception: The magnetism of turtle personality stems more from good-humored quaintness and elfin drollery than from intellectuality. Turtles, it must be said, are not very intelligent. If this remark engenders in the bosom of the cheloniophile the urge to disprove my statement by citing the genius of a pet turtle that comes to the table to lift an appealing foot and gaze wistfully up at the diners, or even at some one especially beloved diner, my rebuttal is ready. I have seen a possum and a salamander do the very same thing, and surely these must represent the nadir of cerebral evolution.

Tinklepaugh (1932) averred that the wood turtle equaled the "expected accomplishment of a rat" in learning the intricacies of an experimental maze, but one must conclude that Tinklepaugh had known only feeble-minded rats.

Yerkes (1901) found that terrestrial turtles hesitated to walk off platforms a foot in height, and that when placed in positions six feet in elevation they were obviously apprehensive. Aquatic turtles, on the contrary, showed little concern at either elevation, an attitude that Yerkes charitably attributed to the impunity that attends their falling from logs into the water.

A hundred and twenty years before Yerkes made his inquiries into the subject of chelonian space perception, Gilbert White had written of a pet tortoise:

> Because we call this creature an abject reptile, we are too apt to undervalue his abilities and depreciate his powers of instinct. Yet he is, as Mr. Pope says of his lord,
>
> "—Much too wise to walk into a well:"
>
> and has so much discernment as not to fall down an haha, but to stop and withdraw from the brink with the readiest precaution.

The mental superiority of terrestrial turtles as compared with aquatic species has been mentioned by numerous writers.

The most penetrating investigations of turtle mentality were those of Casteel (1911), who tested discriminatory ability by decorating with different patterns of lines the walls of the tunnels leading to two boxes, in which, respectively, palatable food and an electric shock were administered. In this device, painted turtles learned to distinguish between black and white, between vertical and horizontal lines, and between lines of varying widths, in one case even recognizing the difference between lines two and three millimeters wide.

Quaranta and Evans (1949) found the principle of "reward training" to be effective in experiments with Galápagos tortoises, and Quaranta (1949) devised tests to measure color discrimination in these animals. He found that they readily learned to distinguish between orange and blue-green, between blue and green of the same intensity, and even between blue and gray.

A tendency toward elementary social organization has been noted in the order of precedence that is soon established when tortoises or box turtles are grouped in captivity.

Kitchin (1949) was convinced that the rather complex behavior of nesting diamondback terrapins is probably merely a series of mechanical and reflexive responses to contact stimuli. Allard, however, reached a somewhat different conclusion after observing the changes in the reactions of a female box turtle that he took from a nest she was in the process of covering and placed first on bare soil and then on an artificial nest:

> These versatile changes in behavior, involving a return to earlier phases of a train of reactions, would indicate something either remotely approaching reason, or a perceptive sensitivity that involves a very appropriate adaptiveness of behavior, step by step. The animal seemed to behave like an automatic machine so long as a normal course of action was allowed, but a change in conditions readily broke up the covering process at any point, and reestablished an

earlier phase wherever this was demanded. Would not most men follow a similar chain of reactions and behaviors under such conditions?

Disposition: In general, turtles are an inoffensive race. Having specialized in defense rather than in equipment for aggression, they usually retire into their shells when molested. It is interesting to note that those forms with the most inadequate shells are generally the most irascible; Eigenmann (1918) offered the following succinct comments in this connection:

> Correlated with the defective armature in the soft-shelled turtle we find the extreme of pugnacity. A soft-shelled turtle will snap and bite on suspicion from the time it is half way out of the shell. The disposition of the snapping turtle, with exposed ventral surface, is proverbial. The musk turtle will bite, as anyone who has collected their eggs can testify. On the other hand, the well-protected painted, geographic and Blanding's turtles, and above all the terrestrial and perfectly armored box turtle are the gentlest of creatures which no amount of provocation will induce to bite.

It should be pointed out that Eigenmann's remarks refer merely to the average temperament of a given species, since various writers have noted the marked variety of personality and disposition that is revealed when an observer becomes intimately acquainted with the individuals in a population. Allard showed that even the confirmedly meek and pacific box turtle may have periods of aggressive ill temper.

SIZE, GROWTH, AND AGE

If there is one thing that the casually interested person knows about turtles, it is that they live to be very old. Their enviable longevity has been extolled in classic mythology, in literature, and in folk belief, and so dominates man's thinking about turtles that when one is found the remark "I wonder how old *he* is" is automatic, whether the subject be a truly antique tortoise or a sprightly virgin cooter of two short summers. Unlike most animal myths, this one is so well grounded in fact that no real debunking is necessary, although the popular concept will bear some qualification.

The whole subject of turtle growth and longevity can be embraced by two generalizations, as follows: (1) turtles do attain great age in some cases, perhaps the greatest of any living vertebrate animals; and (2) they grow and reach maturity far more rapidly than has until recently been supposed. The box turtle engraved with the legend "G. Washington, 1751" beyond doubt came from the hands of charlatans, although even such

uncertain evidence as this permits gullible souls like me to daydream. Sadly, though, the authentic minority of these inscribed tortoises are indistinguishable from the fakes, and the dates can be accepted only in a very few exceptionally clear cases.

The only reliable means of gaining an idea of how long turtles live is to live with them, and this course can become monotonous in the extreme. Gilbert White kept his famous tortoise fifteen years after it had reached an age known to be at least forty years, and on numerous occasions captive tortoises have officially passed the century mark. A giant Aldabran tortoise was supposed to have lived on St. Helena for more than 120 years and to have been well known to the exiled Napoleon. However, my friend Arthur Loveridge has found evidence that this animal was actually a composite of two individuals whose periods of residence on the island overlapped. Another tortoise from the Seychelles was said to have lived for more than one hundred and fifty years in Mauritius.

That these huge tortoises mature much more rapidly than might be suspected is indicated by the fact that a specimen of *Testudo vicina*, taken in the Galápagos Islands when it weighed 29 pounds, attained a weight of 450 pounds by the time of its death fifteen years later. Ninety other young Galápagos tortoises brought to the United States at an average weight of 18.5 pounds weighed 44.3 pounds each at the end of two years. Six others taken to Hawaii in 1929, when they weighed 26.5 pounds each, reached average weights of 63 pounds by the end of the following year. Another individual, probably three years old and weighing 29 pounds, reached a weight of 360 pounds during seven years' residence in California. (What would it have done in Florida!) During the succeeding seven years, however, this tortoise gained only 65 pounds more.

A captive loggerhead grew from a hatchling to a weight of 80 pounds in four and one-half years. Hawksbills, which are smaller than loggerheads but still large as turtles go, may attain sexual maturity at the surprisingly early age of three years, at which time they may weigh 30 pounds.

Smaller turtles may require as much time to reach maturity as the most ponderous ones, and their expected life span is not by any means proportionately shorter. In the northern parts of their range, box turtles mature sexually in four or five years and at shell lengths of from 3½ to 5 inches. Nichols estimated that at least 20 years may be required for a New York box turtle to complete its growth, and that the life expectancy is about 40 or 50 years, with good evidence that individuals may attain ages of between 80 and 123 years.

Cagle's work with *Pseudemys scripta elegans* (1944b, 1948a) revealed that females of this form may become sexually mature when only about three years old and with shells about 6 inches long, while the males may reach their mature length of about 3½ inches within "slightly more than one growing season."

The very largest turtle is the leatherback (*Dermochelys*), and while considerable vagueness surrounds its upper weight limits, it probably reaches a weight of 1,500 pounds and possibly even a ton. The biggest green turtles and loggerheads weigh between 500 and 1,000 pounds, although here also the most imposing records are enshrouded in doubt. Runners-up to the marine turtles in point of size are the giant Testudos, which, pushed by the occult force that makes gigantism common among island animals of many sorts, have reached measured weights of as much as 560 pounds. If a recently published record of a 403-pound alligator snapper is accepted, then I suppose *Macrochelys* must be regarded as the largest fresh-water turtle in the world. That its longevity may match its size is indicated by the fact that Conant and Hudson referred to two individuals that had in 1948 resided in the Philadelphia Zoo for 57 and 47 years, respectively.

A limited amount of very interesting information concerning growth rates in turtles has been obtained from a study of rings in the scales of the carapace and plastron. The laminae of the turtle shell adjust to the growth of the bones beneath them by eccentric growth around the granular infantile scale or "areola." During periods of rapid growth the scale is enlarged by accretion of new scale substance, which is generally believed to be applied over the entire under surface of the previous scale, around the edges of which it projects as a marginal ring. During periods of inactivity growth slows down or stops and a peripheral wrinkle appears and often is impressed on the underlying bone. Thus, as in the case of tree rings, clay varves, and fish scales, a count of the accumulated rings should afford some idea of the number of good seasons and lean seasons that alternated throughout the period of ring formation. Moreover, since the normal annual winter-summer cycle in a temperate region produces alternating periods of high and low activity in turtles, it is reasonable to conclude that the striae on turtle scales are seasonal growth rings, or "annuli," which reflect, individually, the height of the sun and, in the aggregate, the age of the turtle in years.

Unfortunately, however, for the student of turtle age and growth, several factors tend to disrupt the sequence of annuli. The more important of these are as follows:

(1) The fact that the more infantile (older) parts of each lamina wear away, destroying all but the more recently formed annuli.

(2) The fact that many turtles shed the laminae sporadically or periodically, which eventually results in the smoothing out of the topography of the scale, as well as that of the bony plates.

(3) The fact that any marked fluctuation in the physiologic level of the animal may cause a break in the rate of scale deposition. Minor breaks tend to confuse the chronology of major ones. Either too few or too many rings for the elapsed years may result from such factors.

(4) The fact that in southern latitudes without marked annual temperature cycles, the growth of turtle scales, like that of the wood of rain-forest trees or of the scales of Florida bass, is often even and without major interruptions. In areas with a monsoon climate the alternation of a wet and dry season may substitute as an annulus builder, but in many places even this effect is lacking and laminal rings are merely reflections of small or sporadic physiologic changes.

In spite of the limitations imposed by these factors, growth rings are a useful tool for investigations of the natural history of turtles. Thus, though in *Pseudemys* the first annulus is rarely visible after three years, Cagle has used growth rings extensively in his valuable studies of this group. As he points out, even though loss of the earliest rings may make it impossible to determine the exact age of the specimen, the fact remains that "(a) in most individuals [in Illinois] not more than one is formed annually, (b) the zone between any two annuli represents one season of growth, (c) the approximate period of time represented by any area between rings is determinable."

The equation used by Cagle in computing rates of growth for periods covered by discernible annuli is one in wide use among ichthyologists, having been used first with turtles by Sergeev (1937). It is as follows: $\frac{L_1}{L_2} = \frac{C_1}{C_2}$, with C_1 representing the length of the annulus, C_2 the length of the whole plastral lamina, L_2 the length of the turtle in terms of the sums of the lengths of the plastral laminae, and L_1 the unknown, or length of the plastron of the turtle at the time the annulus was formed. This method was found to have high validity in furnishing data for previous seasons of growth.

The obliteration of laminae by such seasonal shedding as is undergone by *Chrysemys* and *Pseudemys* is not abrupt but is gradual and progressive. Nichols believed that in *Terrapene*, which apparently does not molt, growth rings give a reliable accounting of age through the first five years of life and a fair degree of accuracy for ages between seven and fifteen years. After fifteen years, however, they are of little value.

Woodbury and Hardy (1949) agreed with Miller (1932) that the age of the desert tortoise cannot be determined from growth rings.

Mattox showed a correlation between the number of rings in sections of the long bones of *Chrysemys picta marginata* and the size of the individual. His correlation could probably be extended to include age as well, although this has not been demonstrated.

TURTLE ADAPTATIONS

It seems a curious anomaly that the more noteworthy adaptations to be found in modern turtles are mostly reversals of the primary chelonian tendency toward skeletal hypertrophy. The heavy shell of the primitive turtle, though a valuable asset to a paludal or semiaquatic animal more concerned with turning the teeth of its rapacious contemporaries than with improving its own locomotor ability, has been repeatedly modified as one stock after another has spread into new environments. Three principal adaptational trends are discernible: one toward more effective aquatic locomotion, as seen in sea turtles; another along lines demanded by terrestrial life; and a third toward the type of bottom-lurking that has molded the soft-shelled trionychids in their extraordinary pattern. Each of these courses has, for different reasons, brought about a reduction of the bony shell.

The most highly aquatic of all reptiles, with the possible exception of the sea snakes, is *Dermochelys;* in it the most extensive loss of shell bones may be seen. In the other marine turtles the plastron is incomplete and embryonic gaps in the bony carapace persist toward the lower ends of the ribs for varying periods after hatching, and even into maturity.

Along with their jettisoning of shell bone, the sea turtles have abandoned the typical chelonian swimming stroke, in which diagonal fore and hind legs kick alternately, to adopt a new and much more effective method whereby the highly modified fore flippers are raised and lowered like the wings of a bird in flight. This system, which necessitates some remodeling of the pectoral girdle, enables the sea turtles to attain the greatest speeds of any modern reptiles. Deraniyagala (1939a) called *Dermochelys* "the swiftest living tetrapod," and mentioned 100 meters in 10 seconds as the maximum speed of some thecophorans. Anyone who has watched a green turtle (which I think is the best swimmer among Thecophora) in full flight, as, for instance, after being surprised by a glancing blow from an iron, will probably have little difficulty in accepting Deraniyagala's figures, even though they place leatherbacks on a par with the best human runners of the hundred-yard dash.

Land turtles also have reduced their shells, although for a somewhat different reason. An emydine turtle grown to the size and shape of an Aldabran tortoise, and with proportionately massive shell bones, would be so ponderous that locomotion would be out of the question. To avoid awkward increase in the weight-to-volume ratio, tortoises, and especially some of the giant island forms, have decreased the thickness of their shells to a striking degree. The carapace is often much elevated, apparently as a measure to increase total volume and thereby heighten resistance to desiccation, and perhaps also as an inconvenience to gnawing predators that might easily crack a flat shell. There may be extra spaces for water storage in such tortoises, and water conservation is also furthered by extended retention of urine, a course made possible by the insolubility of the excreted uric acid. Tortoises walk on the tips of their toes, and their feet are columnar and elephantine except in the case of the few burrowers, in which the fore feet may be vertically flattened, laterally sweeping shovels.

As an additional protective device some land turtles (as well as a few kinosternids) have in their shells transverse hinges that allow them to be closed, either partially or completely. The movable parts are usually sections of the plastron, but in the African genus *Cinixis* there is a hinge across the carapace.

Of all the terrestrial turtles the most drastically modified is another African form, the soft-shelled tortoise (*Testudo tornieri*). In this small species, which is an inhabitant of rocky terrain, reduction of the thickness and distribution of the bones of the carapace have rendered it so flexible that the animal can squeeze itself into narrow rock crevices or beneath or between boulders, inflate its body with air like a toad caught by a snake, and resist the most determined efforts to extricate it.

Although the soft-shelled turtles of the family Trionychidae appear at first glance to owe their unique features to the exigencies of aquatic locomotion, a closer perusal shows them to be more probably adaptations to bottom dwelling. That the ambushing of prey is an ancient turtle custom is probably indicated by the concealing conformation, adornment, and coloration of the primitive Chelydridae (in one of which a lure for the attraction of potential victims is added to the equipment for ambuscade) and of such luridly inanimate-looking creatures as the pleurodiran *Chelys fimbriata* of South America. While it has yet to be demonstrated that soft-shells hide themselves for the purpose of waylaying the animals that they eat, instead of merely to escape notice, there seems little doubt that the greater part of their time is spent in concealment. The thin, soft edges of the pancake shell conform readily to bottom contours and make it easy for the turtles to shuffle themselves into sand or silt. They usually lie in water so shallow that the long neck can carry the schnorkellike nostrils to the surface for air, from time to time, without the necessity of the turtle's dislodging itself. Between times, the head may be withdrawn beneath the mud with only the tip of the tubular snout protruding to prolong the period of submergence by admitting water for pharyngeal respiration.

This appears to be the world-wide trionychid way of life, and it seems likely that the flatness of the shell and the flexibility imparted to its margin by the loss of the peripheral bones may be primarily adaptations favoring concealment beneath bottom deposits, and that the elongate neck and proboscis, the capacity for effective pharyngeal respiration, and the fast strike and steel-trap grip of the jaws may likewise all be modifications toward this end.

Turtles and Men

ECONOMIC USES

The practical importance of turtles to man lies mostly in their contribution, actual and potential, to his diet. There can be little doubt that people have been eating turtles pretty steadily for as long as they have had the wits to get them out of their shells; and they probably had been eating turtle eggs long before that. While for some groups turtles have served merely as an occasional delicacy, other people, more fortunately located, have leaned heavily upon them as a dietary staple. In a few cases the role of the turtle as gastronomic accessory to man's machinations has been spectacular. For instance, the very reliable chelonioligist Georg Baur, who visited the Galápagos Islands in the 1880's, gathered data on which he based an estimate that early whaling ships had carried away from the teeming tortoise population of this tiny archipelago no fewer than ten million giant testudos. Exploitation of the giant tortoises of the Indian Ocean was probably little less extensive, and the part the sea turtles played in supporting early exploration and colonization, though hard to appraise accurately, was unquestionably a vital one.

Perhaps no reptile has attained the gastronomic glamour of the little diamondback terrapin, which during the gilded first quarter of this century brought prices as high as $120 a dozen. No less profound reverence, however, has been held by the English for the green turtle and by the Japanese for their succulent *Suppon* (soft-shell). These are the recognized aristocrats among table turtles, but the whole group is edible, and I suppose that all the species are eaten by someone, except, perhaps, for a few which are sporadically poisonous. I never heard of anyone in the United States eating a mud or musk turtle, but *Staurotypus* is relished in parts of Mexico and the Mosquito people of Nicaragua roast *Kinosternon* in its shell and eat it with gusto.

The recent development of improved refrigeration methods will almost certainly impose heavy drains on turtle populations. Markets have shifted because of disruptions brought by the two wars. The diamondback has declined in favor, and British aldermen eat fewer green turtles than formerly; but on the other hand I know a number of people who within the past few months have made their first enthusiastic acquaintance with green-turtle meat through a local establishment that features it on a popular carry-away lunch. The deep-fried steaks here are a far cry from Key West chicken turtle with chines and calipees, or from an authentic curry, or green-turtle soup in New Orleans; or for that matter from Carr's broiled ridley filets with lime butter; but people like them, and this bodes no good for the green turtle.

Of the fresh-water turtles of the United States, the snapper (*Chelydra*, and to a lesser extent *Macrochelys*) is easily the most important. Besides being a turtle, and accordingly good to eat, the snapper is big and widely distributed. It has made wide gains in popularity in recent times, although Philadelphia has of course been aware of its virtues for many decades. The soft-shells are just as savory as the snapper, although less well known; and it seems probable that these two could be made the basis for a much-expanded industry. Better than either of them (in my private judgment) are the gopher and the "Suwannee chicken," but like most of their near relatives these are too locally distributed to support a commercial market.

It seems to me that in any plan to extend human food resources by more intelligent exploitation of the sea, the green turtle should receive careful consideration. It not only furnishes meat of unsurpassed quality but, being herbivorous, it is able to utilize huge volumes of forage provided by the submarine pastures of turtle grass and manatee grass that cover immense circumtropical areas. While at the present time the green turtle is not abundant, we have good evidence that it once grazed these pastures in numbers incomparably greater than now, and that the depletion was a result of short-sighted exploitation by man. To me the fact that green turtles have survived at all indicates that they are an uncommonly tough breed.

These points suggest that in this animal important economic potentialities await only an intelligent plan of management. The chief obstacle would be our almost complete ignorance of the bionomics of the present populations. When painstaking investigations have furnished a sound basis for practical schemes of protection and control, and international agreements have implemented these, it seems highly probable that the green turtle hordes could be restored to their three-fathom meadows to harvest for us the almost inexhaustible stores of energy held there.

People do other things with turtles besides eat them. The tortoise-shell industry is as old as civilization. Oils extracted from turtle fat are used around the world for various purposes. There is no way of estimating the monetary value of the swarms of baby turtles sold as pets, but millions of hatchlings are caught annually for this market. Great numbers of turtles are bought by biological supply houses for laboratory dissection, and in parts of the Mississippi Valley large quantities of turtle eggs are sold as fish bait.

Certain species of fresh-water turtles are in slightly bad odor with one school of conservationists because of alleged predation on or competition with other useful aquatic organisms—mainly waterfowl and game fishes. On the whole, however, this aspect of their relation to man is probably of far less significance than their value as a source of food, and there would appear to be much need for conservation measures based on this concept. The work of Lagler in Michigan suggests that as more is learned of the detailed feeding activity of turtles the popular notion that they are implacable enemies of the fish culturist will be discarded.

METHODS OF COLLECTING TURTLES

Fresh-water turtles are most frequently taken in traps, and the variety of devices used for ensnaring them is imposing. Besides the conventional baited barrel net or fyke net rigs, which are of limited value for catching mature individuals of herbivorous species, various traps that exploit the

sunning habit of turtles are used. In some of these a trap door is sprung when the turtle crawls onto a platform just above water level; but a simpler variation is a wire basket nailed to the side of a favorite sunning station, with its open top flush with the surface of the water. The efficacy of this is much enhanced if the collector can make occasional abrupt appearances from the off side of the log and thus force the sunning turtles to dive into the basket. This is one of the favorite methods of catching the famous "Suwannee chickens," and as many as twenty or thirty are sometimes taken at one time in this way. Sunning stations are also sometimes strewn with steel traps or with treble fishhooks fastened by short lengths of line.

In some places turtles may be caught in a seine, but mature turtles are skillful at eluding this type of attack and it is useful mainly where large numbers of young are concentrated in suitable waters.

In northern regions, where turtles sometimes congregate to hibernate, large catches are occasionally made when a group is located by probing with a pole in holes under logs, in old muskrat houses, and in similar favored sites. Soft-shells lurking in the sand of river bars and diamondback terrapins in the mud of coastal marshes are also often located by the probing bar, although the latter are best taken in stop nets, where such are still legal.

In clear water up to twenty feet in depth, a bullen, or net rigged on a hoop at right angles to the end of a long shaft, is often useful. If the water is no more than three feet or so in depth and is choked with aquatic vegetation, no method surpasses the simple procedure of wading about at night with a flashlight. In the numerous Florida lakes and ponds that afford such conditions this technique has been found very effective, and as many as seventy-five turtles have been taken by three people in one evening in this way.

Another direct-approach method, more adaptable than the above, is that developed by Mr. E. Ross Allen and Dr. Louis Marchand whereby a swimmer equipped with diving mask is pushed along, face under water for reconnaissance, by a slowly moving boat equipped with an outboard motor. When a turtle is sighted it is chased down by the swimmer, seized, and dumped into the boat.

Most carnivorous turtles and young individuals of many species bite baited hooks with some enthusiasm. The horny jaws make them adroit bait stealers, but some species, notably soft-shells and kinosternids, are easily caught by hook-and-line fishing.

Soft-shelled turtles have been found susceptible to suffocation by the concentrations of rotenone in standard use in poisoning fishes.

All turtles wander more or less widely on land, either during laying season or during sporadic migrations, and at such times they are of course easily taken.

Sea turtles are nowadays caught commercially in large-meshed (six-to-twelve-inch) nets tied of twine about 33 threads, and usually from 100 to 200 feet long and from 20 to 40 feet deep. These are buoyed by floats and either anchored or left to drift. They are often used in conjunction with painted wooden decoys, which appear to increase their efficacy considerably.

Where sea turtles are still abundant, more direct methods may be used. A bullen or hoopnet can be used to drop over a cornered or surprised turtle, or where the catch is to be butchered for local consumption, grains or harpoons are often used, but the injuries caused by these almost preclude their use for taking green turtles for export or hawksbills from which carey is to be stripped. What to me seems an incomprehensibly refined skill is that sometimes attained by veteran turtle hunters—Carib, Mosquito, or "Conch," who with almost incredible timing are able to intercept the swift and erratic course of a fleeing green turtle with the long curving trajectory of a heavy grains pole thrown from a moving boat. In former days much use was made of the "peg," or spear with a loosely socketed, cylindrical, naillike point that caused much less damage than barbed points.

If sea turtles can be found while sleeping they often may be approached, caught, and held at the surface by a swimmer who prevents their sounding by tilting the fore edge of the shell upward. In this operation the possibility of a wound from the raking claw of a flipper is a real hazard.

Far and away the most colorful method by which men catch turtles is that which employs the remora or shark sucker (*Echeneis naucrates* and other species). Comparable to falconry in its appeal to the imagination, this ancient custom was apparently prevalent among all the sea Caribs, and it still persists among some of their descendants, as well as among various peoples in the Pacific and Indian oceans. Gudger (1919) wrote an exhaustive account of the practice, and DeSola (1932) told of witnessing the capture of a hawksbill in this way off the southern coast of Cuba in the Bight of Manzanillo, where Columbus had observed the same thing on his second voyage in 1494.

The following description of the use of the remora in catching turtles in Mozambique waters appeared in the *Histoire naturelle des poissons* (1829;

vol. III, p. 490) of Lacépède, who obtained his information from the naturalist Commerson:

> There is attached to the tail of the living Naucrates a ring of diameter sufficiently large not to incommode the fish, and small enough to be retained by the caudal fin. A very long cord is attached to this ring. When the Echeneis has been thus prepared, it is placed in a vessel full of salt water and the fishermen place this in their boats. They then sail toward those regions frequented by marine turtles. These animals have the habit of sleeping at the surface of the water on which they float and their sleep is so light that the least noise of an approaching fishing boat is sufficient to wake them and cause them to flee to great distances or to plunge to great depths. But behold the snare which is set from afar for the first turtle which the fishermen perceive asleep. They put into the sea the Naucrates, furnished with its long cord. The animal, delivered in part from its captivity, seeks to escape by swimming in all directions. There is paid out to it a length of cord equal to the distance which separates the sea turtle from the boat of the fishermen. The Naucrates, restrained by the line, makes at first new efforts to get away from the hand that masters it. Soon, however, perceiving that its efforts are in vain, and that it cannot free itself, it travels around a circle of which its line is in some fashion a radius, in order to meet with some point of adhesion, and consequently to find rest. It finds this asylum under the plastron of the fleeing turtle, to which it attaches itself easily by means of its sucker, and gives thus to the fishermen to whom it serves as a fulcrum, the means of drawing to them the turtle by pulling the cord.

Although I have never had the privilege of seeing a turtle taken by remora fishing, that the adhesive force which one might furnish would be more than adequate was demonstrated to me when the bow of my small boat was once pulled around through half a circle by a big remora that took my hook when attached to a good-sized shark. The pull on the hand line was sufficient to cause it to slip through my fingers.

THE INSCRUTABLE TURTLE

In the mystic philosophy of the ancient Hindus the earth was a hemisphere, resting flat side down on the backs of four elephants; and these mighty beasts stood on the back of a single ponderous tortoise. American Indians believed that before there was anything else there was a great turtle floating in a primal sea, and all the animals lived upon his carapace. The earth as man knows it was built on this foundation by the crayfish, which vanquished the beaver and the muskrat in a diving contest to bring up mud from the bottom of the sea and build the dry land.

Although no other folk system appears to have assigned to the turtle such a fundamental role as that on which Hindu and Amerind so strikingly agree, nearly all races that have inhabited turtle country have shown preoccupation with these engaging animals. Among many Asiatic peoples the turtle is still sacred. Burmese Buddhists adorn the shells of Batagurs with gold leaf and release them at the river's edge with propitiatory ceremony. Smith (1931) mentioned a temple in Bangkok in which *Hieremys* and *Geomyda* are placed in great numbers by people who hope to gain merit in the next world by thus saving a life. With the inconsistency that is so often a part of religious practice, those who leave the turtles there lose immediately all interest in them and allow them to starve.

In Chinese religious belief, too, the turtle has always held a high station, from time immemorial having been revered for its wisdom and benevolence. The ancient Chinese consulted the complex fissures traversing burned turtle shells to learn of the will of the Supreme Ruler. Pope identified fragments used in such rites as belonging to the now extinct Chinese turtle *Pseudocadia anyangensis.*

The Greeks believed that even the gods held the turtle to be sacred. The lute was said to have been invented in about the year of the World 2000 by Mercury, who made the first model from the shell of a turtle found on the bank of the Nile. On Mount Parthenon in Arcadia the gods killed the venerated trunkback (alleged to have been the original lute turtle from the seven longitudinal ridges on the back which suggested the strings of a lute) only when pressed by need of a new lute. Even then they probably had trouble wheedling a specimen out of the god Pan, who was custodian of turtles.

In his *Natural History*, Pliny the Elder attributed to turtles strongly developed medicinal properties and described sixty remedies derived from them. A sample nostrum from his list follows:

> The flesh of the sea tortoise, mixed with that of frogs, is an excellent remedy for injuries caused by the salamander; indeed there is nothing that is a better neutralizer of the secretions of the salamander than the sea tortoise [*Natural History of Pliny*, Bohn's Classic Library, London, 1885, vol. 6, p. 16].

Nearly all the tribes of North American Indians were much interested in turtles, and one species or another was regarded as sacred throughout most of the continent. According to Speck (1943), the tortoise was everywhere seen as "endlessly wise and shrewd and a kindly advisor"; and the occurrence of the charmed numbers 12 and 13 in the laminae of the shell demanded added veneration. Turtle shells were used as ceremonial rattles by many tribes, and the Seminoles sometimes tied them in clusters to the knees of dancers. The benign virtue of the Indian folk turtle was locally impugned by the Creeks, who thought box turtles caused droughts and floods and accordingly dashed them to pieces on sight.

In the rural United States today, turtle tales lack the character and imagination of those about snakes, falling short of them both in variety and in dramatic impact. In this country, other things being equal, the richness of a given folklore is in direct proportion to the violence or morbidity of the subject, and by these criteria snakes, of course, have it all over turtles. You can still hear it said that a turtle won't let go till it thunders, or that a beheaded turtle won't die until sundown, or that tortoises live five hundred years, or that snappers bite broomsticks in two. But on the whole, turtle stories are merely exaggerations of attributes that turtles to some degree actually possess, and they seem pale and anemic compared with snake stories.

This generalization is true except in the case of the sea turtles. There is nothing pale about sea-turtle stories. They make as virile and dynamic a body of legend as I know of; and they are alive today. I have heard the same gripping yarns in Spanish and in English of every Caribbean shade, and they are told every day in Carib, Mosquito, French, and Danish, and who knows in what other recondite tongues elsewhere. The stories are of all sorts, and I have referred to a few of them in the accounts of the species to follow. But the best of them scrupulously eschew all subjects except sex in bizarre forms and I have had to bow to convention and exclude them. As Audubon put it, "The loves of the [sea] turtle are conducted in a most extraordinary manner, but as the recital of them here must prove out of place I shall pass them over." I might add, "with real regret," and point to the relatively mild quotation on page 8 of this book as an innocuous sample from a robust branch of ethnozoology.

Terminology of Turtle Structures

In order to prepare adequate descriptions of turtles it is necessary to have for the taxonomically significant features a terminology that is as concise as it can be made. There must be available a set of anatomical terms each of which clearly applies to one single structure and to no other. While such a nomenclature has been devised for the skull and plastron of turtles, the loose ambiguity of the names in vogue for the epidermal and bony elements of the carapace is astonishing.

This confusion has existed since the time of the earliest writers on the classification of the turtles, and even in the works of such important turtle students as Gray, Bell, Agassiz, LeConte, and Baur we find the epidermal segments referred to more or less indiscriminately as "scales," "plates," "scutes," "scutella," and "shields," and in some cases most of these words are used synonymously in the description of a single specimen. Moreover, at one time or another most of these synonymous terms have been transferred temporarily to the corresponding section of the underlying bony shell. It is easy to see that the chances for confusion in such a situation would be great; and they have been fully realized in many cases.

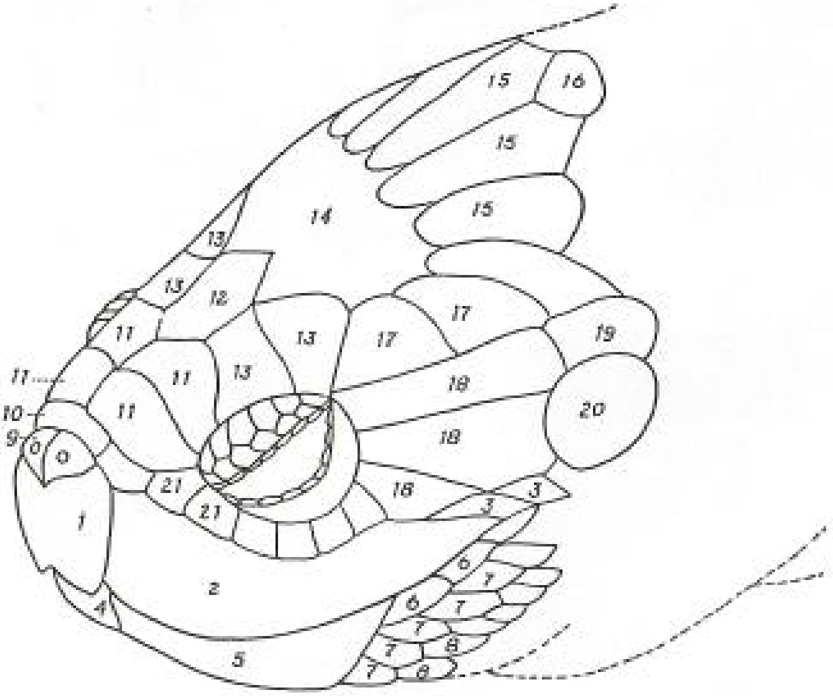


Figure 1. Generalized scalation of the head of a turtle. *1*, rostral; *2*, first supralabial; *3*, supralabials; *4*, mental; *5*, first infralabial; *6*, infralabials; *7–8*, postmandibulars; *9*, nasal; *10*, frontonasal; *11*, prefrontals; *12*, frontal; *13*, supraoculars; *14*, frontoparietal; *15*, parietals; *16*, interparietal; *17*, temporals; *18*, postoculars; *19*, supratympanic; *20*, tympanum; *21*, preoculars. (After Deraniyagala.)

Boulenger, to whom we owe a debt for stabilizing the descriptive terminology of reptiles, employed the words "nuchal" and "costal" for both horny segments and bones but was consistent in distinguishing the shell-scales from the bony elements by the respective terms "shield" and "plate." Thus, since Boulenger usually associated these dual-purpose terms nuchal and costal with the qualifying words plate or shield, it is nearly always possible to understand from his context how the term has been applied.

However, this course sometimes demands close attention if the association is to be kept in mind. Moreover, later turtle students have been less careful than Boulenger, often reverting to the older, indiscriminate designation of scales and bones alike as either plates or shields, as their moods have dictated. As one example among many possible, Freiberg in his "Catálogo sistemático y descriptivo de las tortugas argentinas" (1938) uses the words *nucal*, *costales*, and *marginales* for both bones and scales.

This is a melancholy situation, and there is no real reason for its existence. The late Dr. Leonhard Stejneger was well aware of this awkward weakness in terminology and many years ago adopted in his own writings a more rational scheme, by which the horny and bony parts of the carapace are designated by two wholly distinct sets of names. His system was a consistent adherence to the policy of some early writers to use Greek names for the bony pieces and Latin names for the scales of the carapace. Unfortunately, Dr. Stejneger published no full explanation of his revised nomenclature, and consequently it was not extensively adopted by other herpetologists.

Like all well-devised nomenclature, Dr. Stejneger's series of names offers the dual advantage of maximum clarity and brevity. I have adopted it with slight modifications in this book and commend it to the consideration of turtle students in general.

REVISED TERMINOLOGY

Because of the impracticability of salvaging any precision with the popular old terms such as plate, shield, and scute, they are abandoned and the scales of the carapace are referred to as "laminae," singular "lamina."

For the so-called "vertebral" laminae the term "centrals" is selected, while the corresponding bones retain the name "neurals."

Similarly, the bony plates covering the ribs become "pleurals" and the horny laminae above them, "laterals."

For the outer series of laminae the word "marginals" is retained, while the bones there are called "peripherals."

For the bone commonly known as "nuchal" the name "proneural" is proposed, and the corresponding lamina is designated "precentral."

The term "pygal" is restricted to the bony plate, and the last pair of marginal laminae are called "postcentrals" or, when fused, "postcentral."

The ambiguous word "supracaudals" refers more correctly to epidermal structures on the upper side of the tail itself, as for instance the supracaudal tubercles of the snapping turtles.

The terms indicating the boundaries between the bones of the shell and those between the laminae must also be revised. Thus, that between two laminae becomes a "seam" and the impression of the seam on the surface of the bone beneath a "sulcus," while the articulations between the bones retain the name "sutures."

There has been considerable confusion likewise from the indiscriminate use of the words "jaws" and "mandibles" for both the bony structures and their external bony coverings. It thus seems convenient to employ the terms "mandible" and "maxilla" for the bony jaws alone and to adopt the word "beak" for the horny sheath and "tomium" for its cutting edge.

The following brief accounts of some of the structural features commonly used in the classification of turtles have been largely abstracted from Hay's *Fossil Turtles of North America,* with a few abbreviations and modifications. The accounts refer primarily to the generalized *Pseudemys s. scripta,* and the modifications to be seen in such groups as the soft-shelled and marine turtles will be pointed out later under the appropriate headings. For more detailed discussions of turtle osteology the reader is referred to Boulenger's *Catalogue of the Turtles of the British Museum* and Smith's section on reptiles and amphibians in the *Fauna of British India.*

PARTS OF THE BONY SHELL

The shell of the turtle consists of two parts, an upper, the *carapace,* and a lower, the *plastron.* On each side between the fore and the hind leg, the two parts are joined by the *bridge.*

The carapace is composed of a large number of bones, each of which is articulated with the adjoining bones by jagged sutures. In front of and behind the bridge the outer ring of bones (the peripherals) projects freely like the eaves of a roof.

Along the mid-line twelve of the bones of the carapace are arranged in a row. In front is the *proneural* bone (usually known as the nuchal). Behind this comes a series of eight *neurals.* The last of these is followed by two *epipygals* and the hindermost of these is succeeded by the *pygal,* as the last of the median series. The neurals are connected with the neural arches of the dorsal vertebrae, of which they appear to be mere expansions. The proneural, the epipygals, and the pygal are not connected with the vertebrae.

On each side of the series of neurals, and articulating with them, are eight *pleurals.* Outside of the pleurals, extending around either side of the body from the proneural to the pygal is a series of bones (usually eleven in number), the *peripherals.*

The plastron comprises a median bone, the *entoplastron,* and four paired bones: the *epiplastra,* the *hyoplastra,* the *hypoplastra,* and the *xiphiplastra.* On each side, between the fore and hind legs, the hyoplastron and the hypoplastron articulate with peripherals three to seven inclusive to form the bridge. The notch from which the front leg protrudes is the *axillary notch* and that from which the hind leg emerges is the *inguinal notch.* The part of the plastron in front of the axillary notches is the *anterior lobe,* and that behind the inguinal notches is the *posterior lobe.*

Just behind the axillary notch the hyoplastron sends upward a strong process, the *axillary buttress,* which fuses immovably (ankyloses) with the inside of the lower end of the first pleural. In front of the inguinal notch the hypoplastron sends up a similar process, the *inguinal buttress,* which fuses with the inside of the lower end of the fifth pleural.

EPIDERMAL LAMINAE

The bones of the carapace and plastron are covered by a number of horny laminae. The meeting edges of these are called *seams* and the impression of a seam on the underlying bones appears as a furrow, or so-called *sulcus.* The laminae coincide neither in number nor position with the underlying bones, and it is seldom that the seams coincide with the sutures.

Carapace. At the fore end of the carapace, on the mid-line, there is a small lamina, the *precentral.* Then comes a row of five large laminae, the *centrals,* each extending laterally beyond the neural bones. The seams separating these laminae cross, respectively, the first, third, fifth, and eighth neurals. On each side of these centrals is a row of four large laminae, the *laterals.* The seams between these descend respectively on the second, fourth, sixth, and eighth pleural bones.

The borders of the carapace are invested by a series of marginal laminae, eleven on each side. The seams dividing these from the lateral laminae run along near the upper border of the peripheral bones. At the free borders of these peripherals the laminae turn downward and appear on the under side of the bony shelf. The last pair of marginals, often fused into one lamina, are called the *postcentrals,* or the *postcentral.*

A short series of small laminae is found in *Macrochelys* between the posterior laterals and the marginals; these are called *supramarginals.*

Plastron. A median longitudinal seam runs from the front to the rear

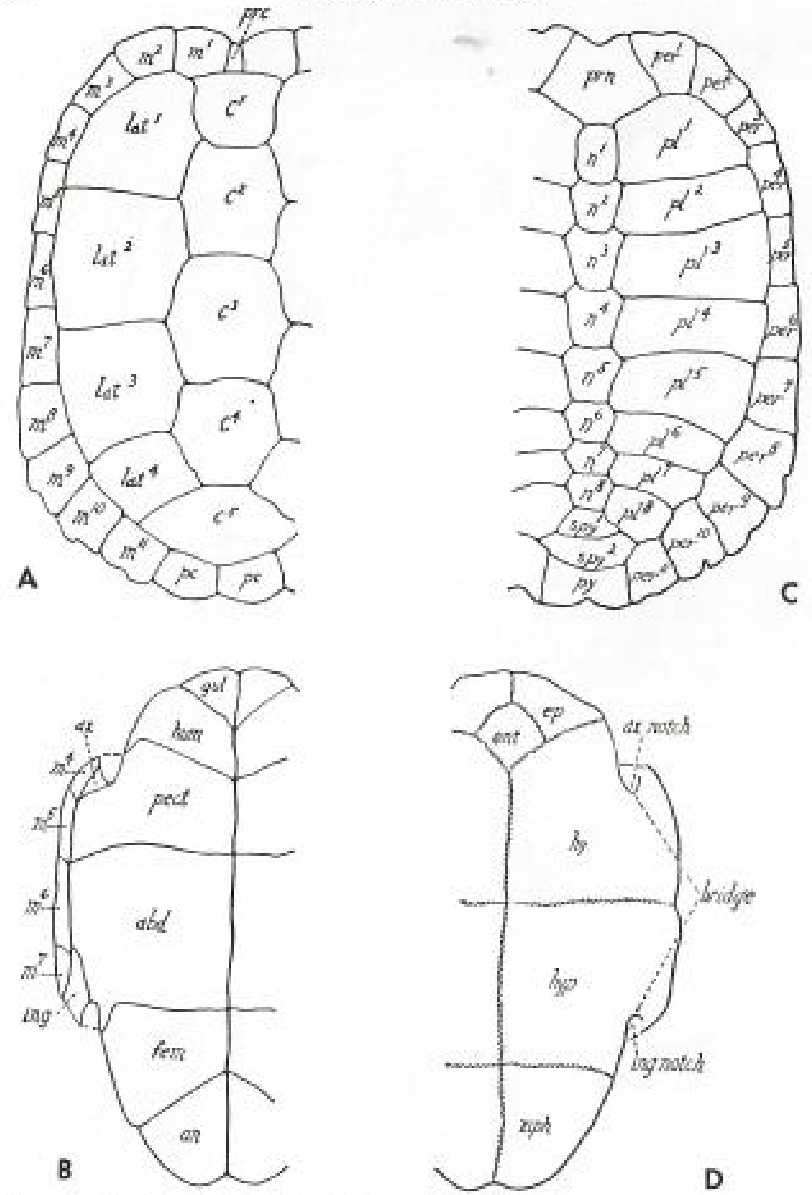


Figure 2. Epidermal shell (*A and B*) and bony shell (*C and D*) of an emydid turtle (*Pseudemys s. scripta*). Epidermal laminae: *prc*, precentral; *m*, marginals; *lat*, laterals; *c*, centrals; *pc*, postcentrals; *gul*, gular; *hum*, humeral; *pect*, pectoral; *abd*, abdominal; *fem*, femoral; *an*, anal; *ax*, axillary; *ing*, inguinal. Shell bones: *prn*, proneural; *per*, peripherals; *pl*, pleurals; *n*, neurals; *spy*, suprapygals; *py*, pygal; *ep*, epiplastron; *ent*, entoplastron; *hy*, hyoplastron; *hyp*, hypoplastron; *xiph*, xiphiplastron; *ax notch*, axillary notch; *ing notch*, inguinal notch.

of the plastron, separating the laminae of each pair. In front there is a pair of *gular* laminae; then a pair of *humerals*, followed by the *pectorals*, the *abdominals*, the *femorals*, and finally by the *anals*. At the back edge of each axillary notch there is an axillary lamina, while at the front edge of each inguinal notch is found an *inguinal* lamina.

In some turtles there is a single lamina between the gulars which is known as the *intergular*. Similarly in others (Cheloniidae) there is a lamina in the posterior angle between the anals, the so-called *interanal*.

The axillary and inguinal laminae belong to a series known as *inframarginals*, which form a complete row in the Cheloniidae and in others.

THE BONES OF THE SKULL

The skull [1] seen from above shows three pairs of bones which join at the median line. In front are the *prefrontals*, extending backward to the middle of the orbits and with their anterior ends forming the roof of the nasal cavity. A strong process descends from each to join the vomer and the palatine, and to form the front wall of the orbit. Behind the prefrontals are placed the larger *frontals*. The *parietals* form the roof and much of the lateral walls of the brain case, and the exterior end of each sends downward a strong process that joins the *pterygoid*. Besides the pterygoid, the lower border of the parietal articulates with the *pro-otic* (otosphenoid) and the *supraoccipital*. The latter bone is greatly prolonged backward and it forms a small part of the boundary of the *foramen magnum*.

The *maxilla* bounds the nasal cavity on the side and the orbit below, and its lower border forms an acute cutting edge. Posteriorly the maxilla articulates with the *jugal*. The hinder part of the rim of the orbit is formed of the jugal below and of the *postfrontal* above. These two bones form a postorbital bar of moderate width.

A large *tympanic cavity* is excavated in the *quadrate* and below this cavity the quadrate descends to form a movable articulation with the lower jaw. In the hinder border of the quadrate there is a small, deep notch for the passage of a long, rodlike bone, the *columella*. Interposed between the anterior border of the quadrate and the jugal bone is the *quadratojugal* (paraquadratum). The jugal and quadratojugal form the zygomatic arch. Above and behind the quadrate is the *squamosal*.

The sides of the hind part of the skull are each occupied by a long ex-

---

[1] For a detailed account of the bones of the skull, see Siebenrock, Das Kopfskelet der Schildkröten, Sitz. Ber. Akad. Wiss. Wien, Math.-Nat. C., vol. 106, pt. 1, July, 1897, 84 pp., 6 pls.

cavation, the *temporal fossa.* The floor of this is formed of the parietal on the inside, of the pro-otic and *paroccipital* in the middle, and of the quadrate and squamosal on the outside. The pro-otic and the quadrate enclose the *foramen carotico-temporale.*

As seen from below, the anteriormost bones of the skull are the *premaxillae,* bounding the nasal cavity below and forming part of the roof of the mouth. On each side and behind the premaxilla is the *maxilla.* It presents outwardly the cutting edge already mentioned. Its inner border joins, in front, the *vomer* and, posteriorly, the *palatine;* while the middle portion is mostly a free edge, forming the lateral boundary of the *choana.* Between the two borders is a broad *alveolar,* or *triturating,* surface.

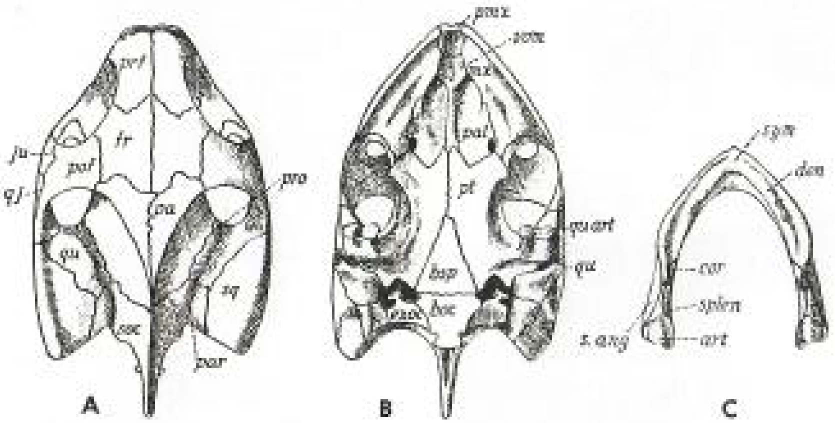


Figure 3. Skull bones of an emydid turtle. *A* (dorsal view): *prf,* prefrontal; *fr,* frontal; *pa,* parietal; *soc,* supraoccipital; *pof,* postfrontal; *ju,* jugal; *qj,* quadratojugal; *qu,* quadrate; *sq,* squamosal; *par,* paroccipital. *B* (ventral view): *pmx,* premaxillary; *mx,* maxillary; *vom,* vomer; *pal,* palatine; *pt,* pterygoid; *bsp,* basisphenoid; *boc,* basioccipital; *exoc,* exoccipital; *qu art,* articulating process of the quadrate. *C* (lower jaw, dorsal view): *sym,* symphysis; *den,* dentary; *cor,* coronoid; *splen,* splenial; *art,* articular; *s ang,* supra-angular.

The mid-line behind the premaxillae is occupied by the single *vomer.* Anteriorly it divides the nasal passages from each other; laterally it articulates with the *palatines,* and posteriorly, with the *pterygoids.* The free lateral projection of the latter is the *ectopterygoid* process. The palatines assist in roofing the nasal passages and in forming the alveolar surface already mentioned. Between each palatine and the maxilla of its side there is an opening, the *posterior palatine foramen.*

The pterygoids meet each other at the mid-line anteriorly, but posteriorly are separated by the *basisphenoid.* They extend backward so far as to exclude the latter bone from contact with the quadrates. The lateral border of each pterygoid is mostly a sharp free edge. Behind the basisphenoid comes the *basioccipital.* It is met on each side by the *exoccipital,* and all three of these bones join in forming the *occipital condyle.* From the ventral view is seen also a portion of the paroccipital and squamosal. On each side of the basicranial axis, foramina for the passage of various nerves and blood vessels are evident.

Each ramus of the lower jaw is composed of six bones. In front is the *dentary,* forming the alveolar surface of the jaw, and completely co-ossified with its fellow of the opposite side at the *symphysis.* On the lower border of the jaw this bone extends backward nearly to the articulation with the quadrate. The upper border of the jaw, behind the alveolar surface, is formed in front by the *coronoid* bone, posteriorly by the *supra-angular.* These two bones are to be seen both from the outside and from the inside of the jaw. Behind the supra-angular is a nodular bone, the *articular,* that articulates with the quadrate. On the inner surface of the jaw, near the posterior end, are two bones, the lower called the *angular* or splenial, the upper the *prearticular.*

Shell Abnormalities and Their Meaning

The horny laminae of the turtle shell are subject to extensive variation. Although some irregularities appear to be random changes, others may involve the consistent recurrence of a lamina in a particular position, either in one or in several species. Moreover, laminae that occur as supernumerary scales in one turtle may form an integral part of the shell in another. Although such regular or correlated variations are today not especially surprising, similar trends having been observed in most groups of animals that have received attention, they were avidly seized upon by the less genetically sophisticated students of the early 1900's as of possible significance in the vexing problem of the ancestry of turtles, and a voluminous literature on the subject has been built up.

One of the first students to make an inventory and suggest an explanation for laminal anomalies was the erudite naturalist Gadow, who, however, unwittingly based his analysis of 1899 on material that included at least two, and perhaps as many as four, different forms of sea turtles, which of course vitiates the significance of his data. Moreover, Gadow became hopelessly entangled in a mystical, orthogenetic interpretation of the apparent decrease in the adult laminal count from that of the juvenile. He

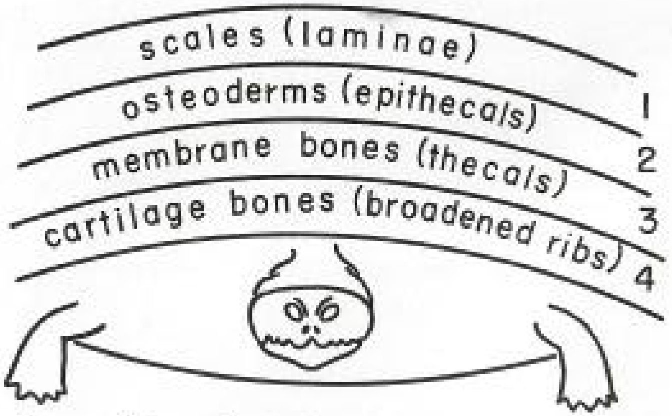


Figure 4. Diagram showing layers in the carapace of the theoretical turtle ancestor. Among living forms, *Dermochelys* has layers *2* and *4*, and ordinary turtles have *1*, *3*, and *4*.

saw in this a (presumably guided) progression of the individual toward a goal of perfection—the same goal, evidently, toward which the whole turtle line had been striving for millenniums! Although this vaporous interpretation of scale variations was in itself of little value, it at least served to focus the interest of other turtle students on the subject.

The most important descriptive papers in this field were those of Newman (1906b) and Coker (1910). The former gave the results of an examination of 476 specimens of *Graptemys* and 183 of *Chrysemys*, while Coker took his data from 243 specimens of *Malaclemys*, of which 45 per cent showed some laminal abnormality and 20 per cent had more or fewer than the normal number.

Besides an addition or loss of laminae, these writers found numerous cases of fusion or incomplete division of normal or abnormal scales, and variation in the size or form of a scale was common. Among the diamondback terrapins showing abnormalities, asymmetry was as frequent as symmetry, and the addition of laterals occurred with or without disturbance of the central series. No significant difference in the incidence of variations in young and old individuals could be shown, but females showed more disorder than males. The most frequent variation was the occurrence of an inguinal lamina in 21 per cent of all specimens. The plastron was much less variable than the carapace, but in it asymmetry or partial fusion was noted occasionally, as was the presence of extra laminae in the plastral series.

Various students have noticed that a reduction in the number of laminae is of much less frequent occurrence than an increase, and that variations tend to occur more often at the posterior end of the carapace than at the anterior end.

The most marked variation is found in the shells of sea turtles, in some of which it is difficult to determine what the characteristic scale number actually is on a basis of the limited series of specimens available. Asymmetry in *Lepidochelys olivacea* appears to be almost as common as symmetry. *Caretta* is also extremely unstable in this respect, and one specimen in which the entire carapace was covered by only three laminae has been noted. It is at least possible that the occasional hawksbills that turn up with the shell covered by a solid, unsegmented sheet of horn may be variants of this type, although they are more generally believed to be individuals from which the carey has been stripped by heat.

Coker suggested that supernumerary scales might in some cases be due to injuries to the embryo produced by crushing or pressure in the nest, since he found a relatively high incidence of irregularity in loggerhead hatchlings from transplanted eggs. Lynn (1937), however, was inclined to attribute them to chance "fusion or division" during embryology.

The majority of students have regarded variation in chelonian laminae as of some phylogenetic significance. An increase in number has been interpreted as reminiscent of the many-scaled armor from which the modern shell has been derived through reduction in laminal number.

Several writers have noted a coincident change in the number of laminae and the number of bones beneath them, and this has been taken as evidence for the origin of the bony shell in an old carapace of osteoderms, or dermal platelets of bone imbedded in the skin. However, both Newman and Coker called attention to the fact that while coincidence of variation in marginals and underlying peripherals was common, little or no correlation between centrals and neurals or between laterals and costals could be shown. Lynn suggested that the correspondence between marginals and peripherals might be the result of the establishment of a new center for laminal development when a new bone appeared; while he saw in the more infrequent coincidence of bones and scales elsewhere merely a mechanical necessity for the filling of gaps in the horny covering when extra bones lengthen the shell.

Interpretation of laminal instability, and especially of correlated changes in the scales and bones of the shell, is necessarily shaded by one's concept of the shell of the turtle ancestor and thus of the taxonomic position of

Dermochelys. Some earlier writers regarded the leatherback as directly ancestral to all modern turtles. Baur (1887b) commented as follows:

"That the carapace of the Thecophora has developed from the carapace of the Athecae has been proved by a specimen of *Eretmochelys imbricata* in which I found small, polygonal plates of the same shape as those of *Dermatochelys* suturally connected with the third, fourth, fifth and sixth costal plates."

If such a position for the leatherback were accepted, the variation in laminae might be interpreted as harking back to a time when each scale covered an ossicle of the primitive armor.

Today, however, few students regard *Dermochelys* as directly in the line of turtle descent. Newman suggested that the extra laminae recall a stage in which the evolving turtle was adorned with a series of scale rows similar to the seven principal and seven alternating rows of the "tail-trunk" of the clearly primitive *Chelydridae*; and Hay's views regarding the homology of the twelve rows of shell laminae in alligator snappers and the twelve longitudinal keels of *Dermochelys* were mentioned earlier.

It seems reasonable to suppose that the roof of the shell of the primitive turtle was four-layered (see Figure 5), with the ribs broadened and overlaid by independent membrane bones (thecals), which in turn were covered by scales (the laminae) with bony cores (epithecals) like those on the backs of crocodilians. If these strata are numbered from 1 to 4, beginning with the uppermost, then the leatherback can be supposed to have retained 2 and 4, and the thecophoran 1, 3, and 4. The normal occurrence in thecophorans of stratum number 2 is limited to such isolated cases as the bony osteoderms of the fore legs of tortoises and the caudal scales of snapping turtles.

Hay (1922, 1928) and Noble (1923) carried on a spirited debate over the significance of certain splinters of bone discovered beneath the laminae of the shell of *Chelys.* Hay regarded these as vestiges of the epithecal bones of fossil turtles, and thus of the dermal mosaic of *Dermochelys,* but Noble was convinced that they were merely the result of local ossification at the sites of old injuries. There is little question but that such bones do sometimes form after injury, but Noble's argument that this was the case in Hay's specimens of *Chelys* were by no means conclusive. Moreover, there appears to be little room for doubt that an epithecal layer occurred in the shells of ancient turtles, as well as in the highly specialized armor of *Dermochelys.* Hay believed that in primitive forms the laminae corresponded with these epithecal ossicles, and that since modern thecophorans have lost the epithecals there is no reason for any correspondence in their scales and bones (and we find laminae covering parts of from two to as many as ten of the thecal bones).

It was pointed out by D'Arcy Thompson that the present arrangement of the laminae of the carapace, with their trinodal and equiangular seam junctions, is merely an expression of a widely applicable principle of conservation of border. Examples of the same type of hexagonal symmetry are seen in as apparently unallied phenomena as mud cracks, the cells of the comb of the honeybee, and the shells of extinct Eurypterids.

Hay suggested that the areola of the lamina corresponds with the original position of the epithecal bone beneath the scale, and Newman, in a detailed account of the development of the chelonian color pattern, gave evidence that there is intimate association between pigmentation and dermal ossification, summarizing his section on this subject thus:

"All of the carapace markings have thus been accounted for as the growth centers of existing or lost scutes [laminae]. This has been done in a species with a highly intricate color pattern (*Graptemys*), and could be applied successfully, I believe, to any other species."

Plate 5. Humpbacked specimen of *Pseudemys scripta scripta.* Mature when taken, this kyphotic individual lived a year at the Ross Allen Reptile Institute before dying of unknown causes.

That this belief was justifiable seems to be corroborated by pattern development in late embryos of *Pseudemys.*

A different type of shell abnormality, of consistent occurrence among turtles but most frequent in *Amyda,* is a freakishly humped condition known as "kyphosis." Nixon and Smith reviewed the literature on this subject and listed occurrences of kyphosis in fourteen species of turtles belonging to five different families. The condition is presumably caused by irregularity in the scheduling of processes that amalgamate costal plates and ribs during embryology, thus thrusting the backbone into an abnormally strong curve.

PART II

ACCOUNTS OF SPECIES

KEY TO THE FAMILIES

1 Limbs modified to form paddles, the wrist and ankle joints rigid; species wholly marine 6

1′ Limbs not modified to form paddles, the wrist and ankle joints movable except where modified in *Gopherus* for digging; no wholly marine species included 2

2(1′) Shell covered with numerous horny plates; cutting edge of upper jaws not concealed by fleshy lips 3

2′ Shell covered with a leathery skin, its edges pliable; cutting edge of upper jaws concealed by fleshy lips .... *Trionychidae* (p. 411)

3(2) Plastron small and cross-shaped, not nearly covering soft underparts; tail more than half the length of shell ...... *Chelydridae* (p. 48)

3′ Plastron not small and cross-shaped, forming a more complete covering for soft underparts; tail less than half the length of shell 4

4(3′) Laminae of the plastron twelve, the pectorals in contact with the marginals 5

4′ Laminae of the plastron ten or eleven, the pectorals not in contact with the marginals .... *Kinosternidae* (p. 73)

5(4) Feet elephantine or shovellike; toes not webbed .. *Testudinidae* (p. 320)

5′ Feet not elephantine or shovellike; toes more or less webbed .... *Emydidae* (p. 111)

6(1) Shell covered with horny plates .... *Cheloniidae* (p. 341)

6′ Shell covered with a leathery skin .... *Dermochelidae* (p. 442)