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The Ecology and Migrations of Sea Turtles, 3
Dermochelys in Costa Rica

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Since the beginning of a study of a breeding colony of the green turtle now being carried on with the help of National Science Foundation support (grants G 1684 and G 5479), it has been evident that the trunkback turtle (*Dermochelys coriacea coriacea*) is a regular nesting visitant along the Caribbean coast of Costa Rica. While no tagging of trunkbacks has been done, and while quantitative data are still lacking, the rudimentary state of recorded knowledge of the species makes it seem appropriate to set down the information that a few case histories and our casual observations have furnished.

COLONIAL NESTING IN THE TRUNKBACK

When Carr first went to Tortuguero in May, 1954, he saw trunkbacks just outside the surf line; and the only turtle tracks on the beach were those of trunkback and hawksbill, both of which are now known to begin laying before the arrival of the schools of *Chelonia*. Some 10 miles of the beach were surveyed on foot at that time, and the distribution of trails laid down since the last preceding obliterating rain, three days before, was plotted. There was no indication of colonial nesting, or of anything other than random stranding by single individuals.

Deraniyagala's account of the Pacific trunkback on the Ceylon coast (1939, p. 57) reveals that the females come onto the beach in small

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bands at nesting time. More recent observations, also, including Leary's surprising encounter (1957) with a flotilla of trunkbacks off the Texas coast, suggest that these turtles, while not massing in schools as large as those of the migrating green turtle, very likely travel in groups to selected nesting beaches. It is of interest that evidence of long-distance or mass breeding movements has now been found in all the five genera of sea turtles.

Tortuguero is a stretch of dark sand beach, closely backed by longshore lagoons and extending, unbroken by passes for 22 miles, from the mouth of the Parismina River, about 40 miles northwest of Puerto Limon, to the mouth of the Tortuguero River. To get to our research camp there, located towards the far end of the beach (near the mouth of Rio Tortuguero) we hire a small airplane at Limon. Since the outset, advantage has been taken of the trips up the beach to make track tallies of nesting turtles.

On a trip made in early June, 1955, no tracks were seen until the mouth of the Matina River, about 10 miles along the way, had been reached. Beginning there, however, and extending for 4 or 5 miles, there was a heavy accumulation of tracks of various degrees of recency, some trial "halfmoons," some clearly tracks going to and from completed nests. These were taken for green-turtle tracks at the time, and the observation was noted and dismissed from mind, in spite of the fact that when Tortuguero was reached it proved to be wholly devoid of green-turtle sign.

Interest was not refocused on this incident until 1957 when Carr, then on leave of absence at the University of Costa Rica, visited Tortuguero on May 4. This was the earliest date for any trip that up to then had been made to the camp. Again, when the mouth of the Matina River was reached, turtle tracks began to appear on the sand, this time in even greater concentration than on the previous occasion. Since by this time it had been established that July is the month when aggregate nesting by green turtles begins in Costa Rica, the return of the Matina colony could be viewed from a more educated viewpoint. The pilot was asked to circle the area for a while, and the tracks were examined with binoculars. This time it was clearly evident that they were too broad for green-turtle tracks and were almost surely those of *Dermochelys*, the largest of the sea turtles.

The concentration of tracks indicated mass use of the place by nesting turtles. If it was really sign of *Dermochelys*, the observation could be taken as evidence that the Atlantic trunkback is migratory and not just a wanderer as had been supposed. The "resident" trunkback popu-

lation of Costa Rican waters (if the term "resident" can anywhere be applicable to *Dermochelys*) is certainly not heavy enough to account for the indicated nesting aggregation. Moreover, the mere fact of there being strikingly more abundant nesting tracks in a 4-mile stretch of beach than anywhere else implies some sort of concerted reaction by the animals involved. It now seems probable that the mass arrivals were not due to chance convergence of individuals but were the result of mass travel to the area. The realization of this made it desirable that we return to Matina and establish the fact that trunkbacks really had made the nesting trails. It was not possible to land the airplane near Matina beach, and duties in San José made it impracticable to return for two weeks. On May 19 Carr took the train from the capital, got off at Matina station and by mule car followed the old Goshen Line towards the mouth of the river. Beacuse this line has no side tracks, it is necessary for one of two cars that meet to derail. During two such encounters, occupants of the car met proved to be turtle-egg hunters on the way to market with sacks of eggs. Examination showed these to be eggs of *Dermochelys*, as the people they belonged to said they were.

At the end of the "Down Matina" branch of the Goshen Line, it was a half-hour walk through the woods to a landing on the lagoon shore, and here a dugout was used to cross to the point on the beach where the heaviest concentration of tracks had been seen from the air. It was immediately evident from the tumbled topography of the higher parts of the beach here, and from the great width of the nesting trails, that the place was in fact a trunkback "rookery."

Within a distance of 1½ miles, 18 recent nests two days old or less were seen. All had been robbed by egg hunters. By each nest were a few discarded, malformed, or undersized, yolkless eggs such as trunkbacks seem always to include in a clutch (see below). An egg hunter bivouacked in the coco fringe had about 300 eggs, and all were eggs of the trunkback. As final proof that the breeding activity had been exclusively that of *Dermochelys*, the range in greatest width of the 18 recent tracks was found to be from 5½ to 7¾ feet. The lesser of these extremes is at least a foot greater than the broadest green-turtle track we have measured.

With the fact of heavy use of Matina beach by trunkbacks established, and with the indications that the use might be a regular annual event, it was decided to revisit the place with the idea of: (1) learning whether the assemblages there might be big enough to justify a tagging program; (2) documenting the apparent depredations of the egg industry and the apparent 100 per cent drain it seemed to impose; and

(3) getting information on nesting, incubation, and hatching in American *Dermochelys*.

The local word was that the nesting season began in April and was continued at least through June (our latest record is a nesting at Tortuguero on the night of July 27, 1957). Work at Matina was accordingly planned for early June, at the end of the school year at the University of Florida. Ogren reached the beach on June 9, and, although it was immediately apparent that the height of the season had passed and that competition with egg hunters from all the nearby inland towns was going to be severe, he set up a camp in the coconut fringe 4 miles north of the mouth of the river. On that evening, five trunkbacks nested between the camp and the mouth of the Matina River, and the eggs were in each case immediately taken by egg hunters. At this season, when eggs of other species are scarce, trunkback eggs are sold in the towns inland, along the railroad, for 75 centimos a dozen. In spite of this competition, and of the fact that the crest of aggregate emergence had passed, by outrunning, browbeating, and bribing the egg collectors Ogren was able to accumulate data and observations that extend our knowledge of trunkback reproduction on American shores.

NESTING PROCESS

Dermochelys is one of the most highly modified of all secondarily aquatic vertebrates, if indeed it is secondarily aquatic. Its activities during the short terrestrial nesting venture thus hold great interest for the student of behavioral phylogeny. As divergence of the trunkback from other turtle stems must have occurred very early in the history of the group, one might expect its nesting mannerisms to show fundamental departures from the pattern characteristic of other sea turtles. A reading of the only published account of nesting (that of Deraniyagala, for the Pacific trunkback) shows that this is not the case. The series of nesting maneuvers either is stubbornly conservative or has to a surprising degree been molded by convergence.

Deraniyagala's notes, while illuminating and for years wholly unique, were not made with the special aim of providing a basis for behavioral comparison among the genera, and, because the only other information in print comprises miscellaneous notes on dates and localities, it seemed possible that a careful comparative appraisal might reveal differences in points not mentioned by Deraniyagala. This has not proved to be the case. During June, 1958, at Matina detailed notes were made on nesting behavior of three trunkbacks, from the time of their emergence to their return to the water. The account below is a composite of those observations.

Stranding and Trip to Nest Site

No overt signs, such as the odd "smelling" of the sand that a green turtle sometimes engages in, of sensory appraisal of the stranding site were noted. During the process of coming ashore, and throughout the trip up the beach, the female trunkback seems far less skittish and easily frightened by lights and moving shapes than either the green turtle or the hawksbill. The play of several flashlight beams directed towards the Matina individuals caused no loss of the stranding drive.

Gait and Pace

The gait is similar to that of the female green turtle—a labored hauling-forward of the body by simultaneous movements of all four legs. It also resembles locomotion in the sea-seeking young, except that the latter lifts itself off the sand at the beginning of each forward push, while the adult drags herself along.

Selection of the Nest Site

Here again no specific orientation or assessment procedures are detectable. The female simply stops, after having moved for a certain distance over dry sand, and the stopping place becomes the nest site. Other species often show fastidiousness and appraisal behavior at this point, and several false stops and tentative swipes at the sand are made before finally the digging routine is begun. That our small sample of females actually observed was typical in this respect seems to be supported by the fact that the 40-odd trunkback nests that we have seen on widely scattered beaches have shown no clumping in any zone of the beach but have been distributed from the high-water mark to points well within the marginal vegetation. Each of the three Matina females stopped about midway up the beach, on level sand where no obstructions or changes in topography could be identified as stopping signs.

Excavation of the Body Pit

The concealing pit in which the turtle lies while digging the nest, laying, and covering the eggs is made by slow, bulldozer-like strokes of the fore limbs, working mostly together, while the hind legs scrape and push sand independently of the front fins and of each other. At the beginning of the operation, the most effective digging is that of the fore limbs, and, as this deepens the cavity more rapidly anteriorly, the body after a time comes to slope downward under the fore end of the turtle. Eventually, the work of the arms slows down and the kicking and

FIG. 1. The thrashing out of the basin ("body pit") in which the turtle lies while digging the nest cavity and laying. Up to this point the fore flippers have been used exclusively. The blur at the lower right is flying sand.

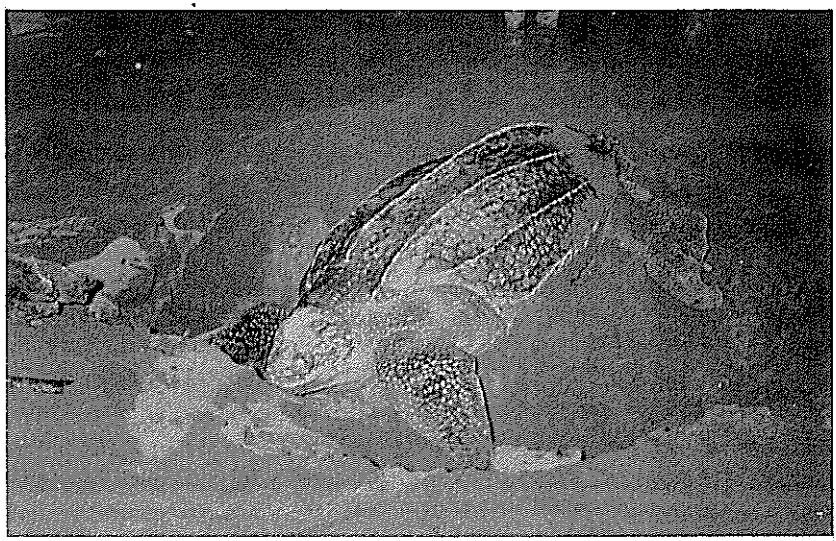

FIG. 2. Body pit completed anteriorly. It will now be deepened and enlarged behind by the scraping action of the hind feet.

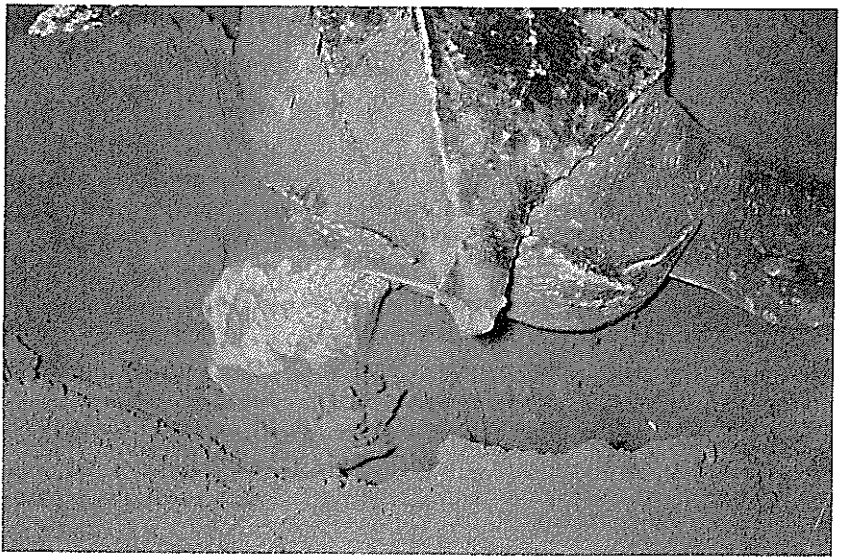

FIG. 3. Digging the egg cavity. Here the left hind flipper is bringing up sand, and the right hind flipper is about to kick forward to get rid of sand spilled near the nest by the previous digging stroke.

FIG. 4. Extreme positions in the reciprocal movements of back legs while digging the nest. The right flipper here is far forward, at the end of a kicking stroke, and the left has just dropped its load of sand.

scraping by the back flippers are accelerated, until eventually the latter are working alone.

Excavation of the Egg Cavity

When the dwindling mound under the back end of the body has been reduced to the general level of the bottom of the body pit, the hind feet continue to work away at this point, and the cavity that grows there becomes the nest. After a short period of scraping, the space under the after end of the body is sufficient to allow the tip of the working flipper to curl slightly, and from that point on it not only scrapes but scoops up and carries out handfuls of sand from the growing nest hole. This is a stage at which the observer expects to see some bizarre maneuver, because the broad crurocaudal fold into which the hind flipper extends seems about as well adapted to digging the bottom of a narrow hole as the wing of a bat would be. But there turns out to be nothing odd about the process. The tip simply curls into a palm, picks up the sand, lifts it slowly out of the hole, and drops it at one side. As this occurs, the opposite flipper kicks outward and upward, ridding the site of sand from the previous stroke, thereby completing a set of reciprocal bilateral motions that seem identical with those of the green turtle at this stage. The hind feet work alternately in digging the nest, the body pivoting on its forward end to swing the working flipper directly over the hole. Other sea turtles do this, too, but it is much more marked in *Dermochelys*, which, perhaps because of the shape of its back fin, must move the back of its carapace through as much as 2 feet of arc in changing over from one flipper to the other. While down in the hole, the tip and edge of the fin usually make four or five short scraping strokes at the walls and bottom before collecting the sand for removal. The flipper works most efficiently when brought to bear on the fore wall of the nest, and the cavity thus acquires an oblong cross section as it grows (cf. *Lepidochelys*, Carr, 1948).

Laying

When the nest is as deep as the fin will easily reach, the digging reflex wanes. The flippers are spread out flat behind the body, over and partly within the opening of the nest, into which the tail and cloaca are lowered. Almost immediately laying starts. Throughout the process part of one of the hind flippers remains in the nest, its distal sections pressed against the back edge of the nest. The eggs come out one, two, or three at a time. There is no curling of the flipper edges when the eggs are extruded, as is characteristic of hawksbill females, although a

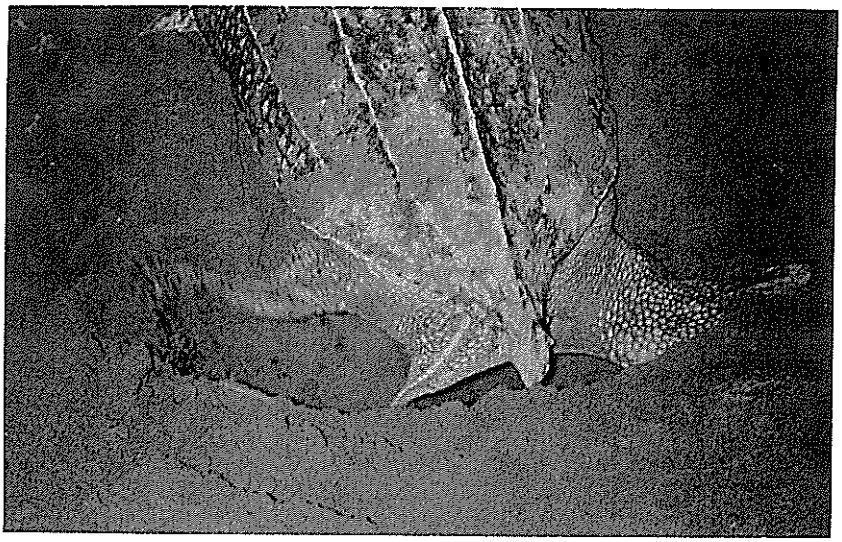

FIG. 5. Reversal of the reciprocal action of the two back flippers. The left is kicking forward and will immediately be returned to make the next digging stroke in the deepening nest; the right is dropping sand just scooped from the nest.

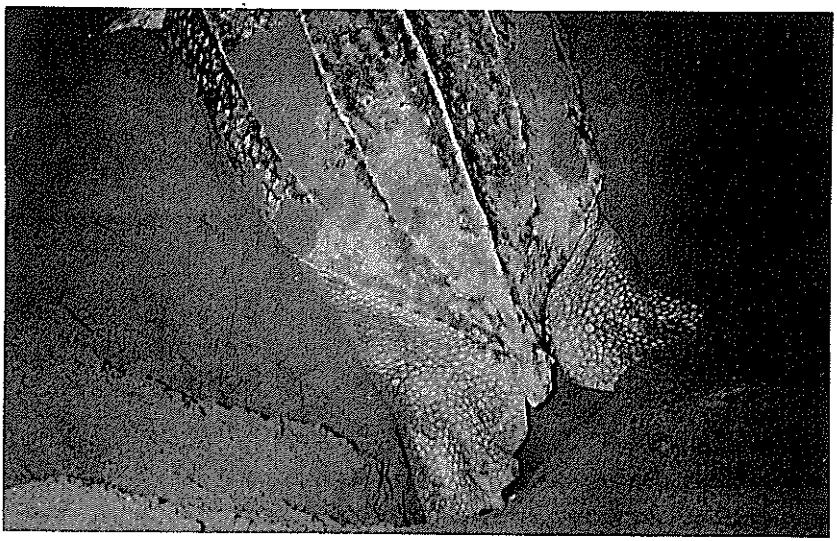

FIG. 6. Side wall of nest removed to show left hind flipper being lowered to scrape out and remove a flipperful of sand.

FIG. 7. Position of flippers during oviposition. The nest opening is directly below the right flipper.

slight contracting of the spread surface can be seen to accompany the cloacal contractions. Throughout the process the eyes are bathed by copious secretion. Schmidt-Nielsen and Ragnär (1958) have assembled direct and circumstantial evidence that marine reptiles of all four

TABLE 1

STAGE SCHEDULE OF THE NESTING PROCESS AS SHOWN BY AN INDIVIDUAL THAT EMERGED AT MATINA, COSTA RICA, JUNE 11, 1958, AT 9.50 P.M.
(Two other females that emerged at the same place during the same week took, respectively, 80 and 95 minutes to complete nesting.)

Stage of Nesting Venture	Time in Minutes
Going from surf to nest site	3
Digging body pit	17
Digging nest	5
Laying	15
Filling nest	5
Concealing site	40
Returning from site	8
Total	93

orders have a salt gland such as that found earlier in marine birds (Schmidt-Nielsen, Jörgensen, and Osaki, 1958; Schmidt-Nielsen and Schladen, 1958). *Dermochelys* can presumably be added to their list of sea turtles with such a gland.

Filling of the Nest

A few seconds after the last egg has dropped, and while the forelimbs are still anchored, motionless, the turtle starts filling the nest with her hind feet. Again they work alternately, each pulling and pushing in sand from the accumulation on its side of the opening. When the fill, rising in the nest, is high enough to be felt by the working flippers, the

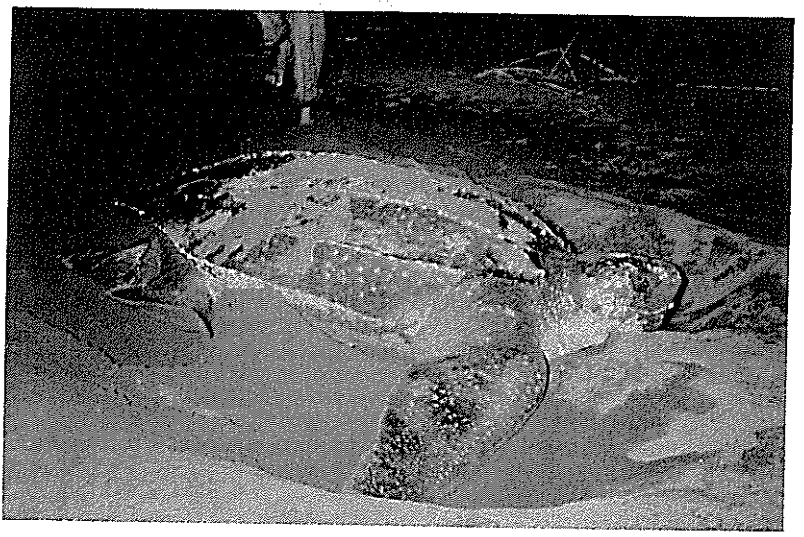

Fig. 8. Covering the nest. Front fins anchored while back fins scrape in sand.

edges of these tilt downward anteriorly in such a way as to press the fore margin into the sand over the nest. This is the beginning of a packing operation which increases as the filling nears completion. For several minutes the flippers keep up the packing work, sometimes pressing downward so hard that the plastron is raised from the sand.

Covering and Concealing the Pit

When packing has gone on for a while, the forelegs join in the work of filling. They work mostly together, making swiping, lateral strokes that begin far forward and throw sand back over the sides of the body

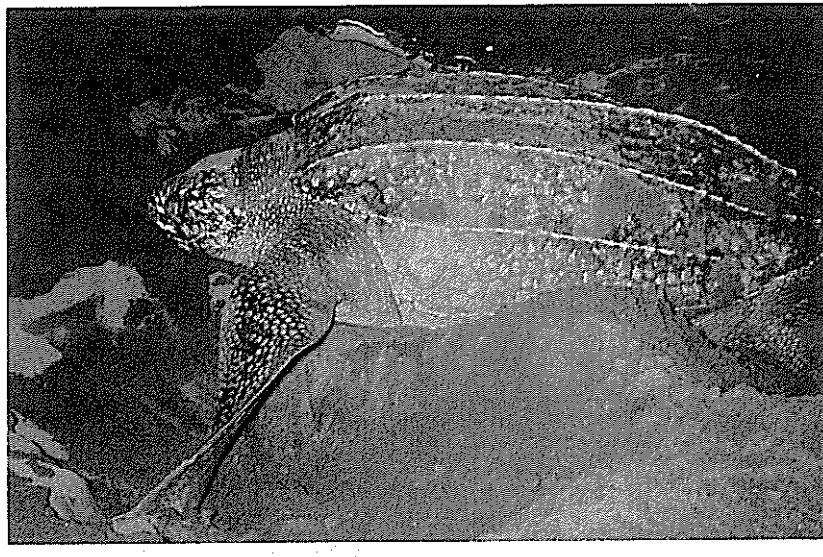

FIG. 9. Concealment of nest and body pit. The front flippers are here throwing sand backward.

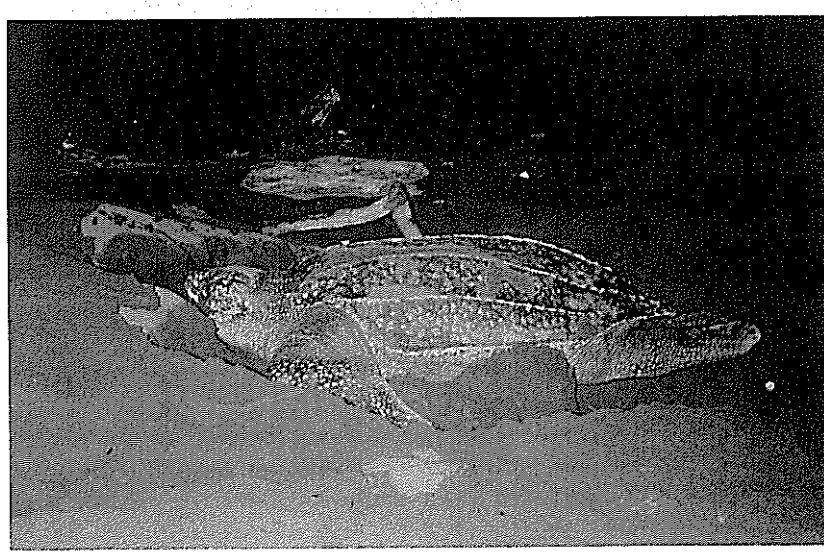

FIG. 10. Final stage of concealment, with the turtle in a depression at the end of a ploughed and furrowed strip leading away from the now thoroughly hidden nest site. Shortly after this picture was made, the turtle started to move away to the sea.

and into the pit. This operation, which is perhaps less violent than the work of a green turtle at the same stage, is accompanied by a steady slow dragging in of sand by the hind feet, which results in the building of a growing mound under the back end of the body. The strong strokes of the forelimbs drag the body a few inches forward each time, and as the original site is slowly left behind, the trail is marked by an irregular ridge, representing the mounding work of the hind feet, and two deep crescentic cavities show where the fore flippers did their last scooping. After the turtle has moved off thus for some feet, the concealment effort suddenly stops. Without discernible cues, the sand-throwing strokes of the fore flippers are supplanted by crawling strokes, and the turtle drags herself out of the cavity from which she was last throwing sand and without hesitation turns and moves in the general direction of the surf. As in her coming up to the nest site, her course appears to be determined by simple inspection of the landscape (which is of course a meaningless thing to say, and at best is only analogous to the human situation it suggests. Some field experimentation with green turtles to determine factors in terrestrial orientation has been done by us, and results of these will be summarized elsewhere [Carr and Ogren, MS]).

TABLE 2

DETAILS OF TWO EGG COMPLEMENTS OF *Dermochelys* FROM NESTS ON THE CARIBBEAN SHORE OF COSTA RICA (MEASUREMENTS IN MILLIMETERS)

	Tortuguero July 5, 1957	Matina June 12, 1958
Full-sized eggs		
Total number	66	45
Diameter, range	50.3–59.0	50.1–53.6
Diameter, mean	55.4	51.8
Yolkless eggs		
Total number	38	7
Diameter, range	15.8–45.4	19.7–41.7
Diameter, mean	32.6	34.3

The three turtles that furnished information for the above account came out of the water, respectively, at 9.50 P.M., 9.55 P.M. (June 11), and 9.55 P.M. (June 12). Detailed scheduling of the nesting activity of one of these is shown in table 1. Some of the steps are illustrated in figures 1–10.

EGGS

As might be expected, the egg of the trunkback is larger than that of any other sea turtle, being approached most closely in size by the egg of *Chelonia*. A feature of the trunkback egg complement, mentioned in all the published accounts and found by us to be apparently invariable, is the inclusion of a number of undersized, often misshapen, yolkless eggs. In the one case in which the position in the nest of these yolkless eggs was noticed they were at the top of the heap in the nest. It seems likely that they are usually laid last.

Details of egg complements in two nests are given in table 2. Numbers of eggs in four other nests at Matina and Tortuguero were as follows (the first number of the two in each set of parentheses indicates eggs with yolk; the second, yolkless eggs): 107 (73, 34); 121 (80, 41); 74, plus "numerous yolkless eggs"; 66, plus "numerous yolkless eggs."

INCUBATION AND EMERGENCE OF HATCHLINGS FROM THE NEST

The incubation periods for three nests observed were 74, 66, and between 51 and 58 days. The first two periods were those of two clutches that had been removed from the original nest and reburied where they could be watched. The other clutch hatched where laid. If the incubation period indicated by this small sample actually approximates the natural average for the species, the close agreement in this respect with the "thecophoran" sea turtles seems surprising.

The periods indicated above refer to the time between oviposition and the actual leaving of the nest by the young. Within recent years herpetologists have come to realize that in turtle nests the time of hatching of the individual eggs and the date the young leave the nest rarely coincide very closely. In fact, in some fresh-water species the interval may involve a whole winter, or a prolonged dry spell, passed by the hatched-out young in the nest. This would seem to be an adaptive reaction. In temperate regions the eruption of young from a clutch of eggs laid late (in October, say) would leave the young to face the winter before acquiring the responses needed for coping with the problems of hibernation. In a nest roofed over by dry clay, it may take a good rain to release the occupants, and a drastically prolonged drought presumably makes a tomb of the nest. Sea-turtle hatchlings face neither cold winter nor adobe nest roofs, but the depth of the nest alone imposes a considerable obstacle to their reaching the surface. Hendrickson (1958) has shown that in the Pacific green turtle the movement of hatchlings to the surface is not an independent upward digging venture by each

individual, but a group effort through which the ceiling of the nest is scratched down and the floor raised correspondingly until finally the thinning roof collapses and the turtles are able to come out all together in the "explosion" so often remarked on by observers.

Observations made at Tortuguero suggested that nestling trunkbacks behaved the same way. Accordingly, a pane of glass was fixed in one side of an excavated nest (reburied eggs), and hatching and emer-

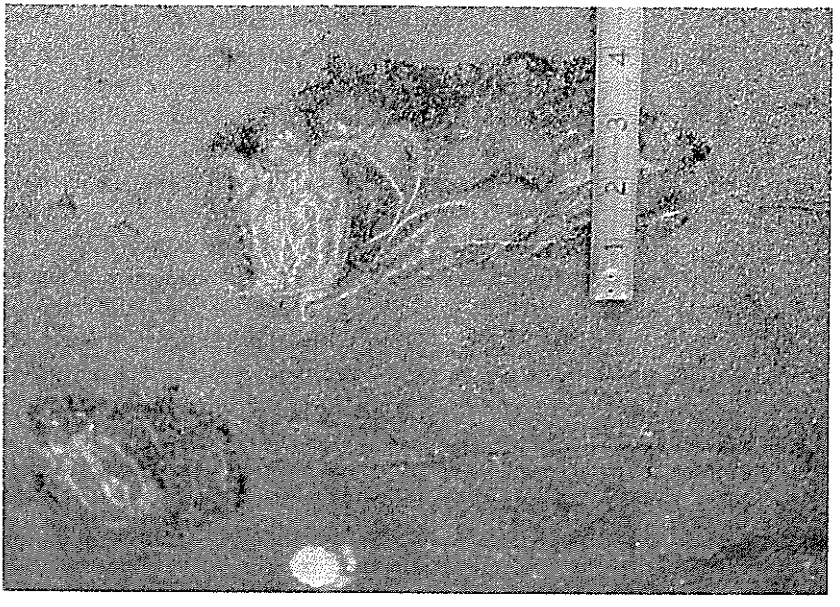

FIG. 11. Hatchling trunkbacks making their vertical climb to the surface through the sand over their nest (as seen through a glass pane in side of nest). Differences in time of hatching produced the two separate emergence groups shown. The white spot at the bottom of the picture is an unhatched egg marking the upper level of the original pile of eggs in the nest.

gence were watched. A lag in the hatching time of a part of the group split the brood into two emergence groups which remained separated, throughout the upward climb, by the amount of sand that the early hatchers clawed down on top of the eggs that hatched later (see fig. 11). It seems likely that the cases in which we have seen young of other species emerge in two or more groups have involved similar schisms in the original unit. In green turtles and hawksbills, there may be intervals of two or three hours, or sometimes even of a day or two, between such separate spurts of emergence of young from the nest. It

should be emphasized that within each group of the trunkback hatchlings most of the work was done in concert, any resumption of scratching by one member usually stimulating a period of energetic group effort.

It seems worth while to call attention to the adaptive value of group effort (of protocooperative hatching and emergence responses) in turtles. In the case of the sea turtle it appears unlikely that a single hatchling could ever, on its own (that is, deprived of the roof-sapping, floor-raising collaboration of a good-sized group of its fellows), make the long vertical trip from the bottom of the nest to the surface of the beach. Additional survival value surely accrues from the shortening of eruption time for the group as a whole, as the appearance of the first hatchling at the mouth of the opened nest is the signal to predators, and the signal probably rarely goes unnoticed for long.

Although little can be said about the real nature of the predation obstacle confronting emerging sea turtles, we know some of its aspects. When eggs have weathered the first few hours after deposition, they seem to acquire an immunity that lasts throughout the incubation period. Few creatures, other than man, are able to locate old turtle nests, although, when emergence is imminent, dogs stometimes are able to locate the site, perhaps because of the strengthening of the scent as the hatchlings' near the surface. But, when the first hatchling comes out, the ball is really in play. The first attention comes usually from sand crabs, which begin a silly fencing with the hatchlings which only occasionally brings any direct harm to them but which surely attracts the notice of buzzards and gulls. These in turn not only eat hatchlings themselves but bring on dogs and wild mammalian predators. Although it seems irresponsible to say so, we have seen persuasive evidence that the astonishingly prompt appearance, abreast of an erupting green turtle nest, of cub and shovel-nose sharks may sometimes be evoked by the sight of a convergence of vultures on the upper beach.

It thus seems clear that in sea turtles the emergence group of hatchlings is a survival unit in which undercrowding can result in entombment, and which by its explosive group emergence avoids the dangers attending a protracted, one-by-one leaving of the nest site.

EMERGENCE AND SEA-FINDING ORIENTATION IN HATCHLINGS

Besides some field manipulation of baby trunkbacks, with the aim of testing orientation capacity, we have observed behavior of naturally emerging young from two nests.

On July 28, Ogren found a single hatchling pushing its way out of the sand over a nest located in front of the northern end of the Tortuguero settlement. According to our assistant, Mr. Leo Martinez, the nest had been made during the first week of June, indicating an incubation period (or a time between laying and emergence of the young, which is not the same thing) of between 51 and 58 days.

After the first turtle had broken through the sand roof of the nest, others began appearing at the same spot, coming out several at a time and collecting in windrows about the foot of the board wall that had been raised around the nest. When a board on the ocean side was taken out, there was a fairly concerted rush for the opening by most of the turtles. Once outside, however, hatchlings at the edges of the group from time to time abandoned the correct course and for no apparent reason detached themselves, reversed direction, and for a time moved more or less directly away from the water. The majority maintained a generally correct seaward course, interrupted only by short periods of scrambling and turmoil when footprints or other small obstacles were encountered. Up to this point it was evident that the behavior of the hatchlings was diverging from the normal because of two extraneous factors, both stemming from the fact that the nest had been boarded about for safe keeping. These were the sudden onset of the "open-door" stimulus (the sudden influx of light on the side beyond which the goal lay) when the board was removed, and the mutually distracting and exciting effects of the initial crowding imposed by the wall.

The attention of the observer was at first monopolized by the movements of the group as a whole. As the group began to spread and break up, and the activities of individuals to be noted, several were seen to interrupt the straight limbs of their seaward course by making small, quickly executed circles. Since this original observation, this "orientation-circle" has proved to be a regular and perhaps unique part of the sea-finding travel of young trunkbacks—both of those leaving the nest and of experimental animals released on the upper beach after various sorts of post-hatching experience.

Another natural emergence from an undisturbed nest was witnessed at Tortuguero on July, 1957. As the nest was not fenced and the young turtles came out a few at a time, during two daylight hours, their individual behavior could be studied at leisure.

At 1.30 P.M. Stephen Carr came back from a walk on the beach, bringing a newly hatched trunkback that he had picked up a few hundred yards north of the camp. It was easy to find the place and to back-

track the hatchling to the nest site, where another individual was found just pushing up through the sand. The nest was located at the upper edge of a steep, 3½-foot ramp from the upper beach down to a perfectly flat terrace that spread for some 90 feet before dropping to water level in a newly eroded low bluff. Turtles emerging from the nest thus had only a foot or so between them and a quick drop in the appropriate direction for their water approach. From there on, however, for the whole distance across the broad, flat, rain-firmed terrace, geotaxis could clearly be ruled out as an orienting factor.

Between 1.30 and 3.00 P.M., the remaining turtles in the nest emerged, not from any one established aperture but in at least five separate

TABLE 3

MEASUREMENTS (IN MILLIMETERS) MADE JULY 29, 1956, OF 30 HATCHLING TRUNKBACKS THAT EMERGED JULY 28, 1956, AT TORTUGUERO, COSTA RICA

	Mean	Mode
Carapace length	62.8	64
Carapace width	41.8	42
Plastral length	53.6	53
Head width	18.04	18
Depth	26.3	27

places over a distance of 14 inches. Most of them appeared singly, but several pairs emerged, and twice three, and once four came out together.

On appearing at the surface of the sand, each turtle stayed there blinking for a while, then pulled free and without hesitation raced down the ramp. It was not possible to tell what stimuli motivated this first descending segment of the journey, but there was no hatchling in the lot that showed any hesitation in making the quick descent.

The first uncertainty was evident in each case in a zone extending from the foot of the ramp out for a distance of 18 feet. Somewhere in this region every turtle showed the most highly standardized orientation maneuver that we have seen in any of our work with sea-turtle hatchlings—the orientation circle mentioned above. Without exception, each turtle ended its first run towards the sea by stopping, raising its head, and then describing a tight little circle of no more than 4 inches in diameter. One of these circles in almost every case seemed

sufficient to reëstablish bearings, and when it had been completed the direction taken up was the correct seaward heading. Preliminary orientation, in the area about the nest, of all the turtles we saw emerge (and of all those that had come out prior to our arrival) was accomplished with a lateral spread of only 12 feet. Where the grouped trails entered the water the maximum distance across them was 38 feet. This actually included the trail of every turtle emerging. There were none that wasted time going up or down the beach and none that failed to take the seaward ramp as the correct first move.

One individual that had difficulty emerging, and that we finally helped out, went down the ramp, made 14 of the little orientation circles, and then took the proper course heading and followed it to the surf without further interruption. One of the last hatchlings to emerge made a normal trip to a point some 20 feet from the ramp, made two circles and then died, apparently from the extreme heat.

It is the general belief among people who live where trunkbacks nest that most emergences of young occur at night, as is also said to be the case with other sea turtles. It may be that this piecemeal emergence that we observed in the daytime was abnormal. Certainly it is hard to see why selection would not soon weed out any tendency towards sloppy scheduling of this sort. The heat of the sun alone appears to be a real hazard, and, besides the casualty mentioned above, we have frequently seen young green turtles succumb when exposed to direct sunlight during field experiments. The vulnerability to predators likewise must be much greater in the daytime.

Gait

The gait of the trunkback is not markedly different from that of the green turtle. Moreover, although there is a strong difference in rate of leg movement in the sea-seeking hatchling and the nesting female (the adult seeming labored and lumbering in its pace and the young frisky and for its size relatively rapid), when the movements of the legs are analyzed, they turn out to be the same in both cases. All the walking that we have seen baby trunkbacks do has been a rocking movement, with the four limbs working together. The long front paddles are used in a breast stroke like that of the adult green turtle, and while this stroke is being executed the hind flippers push back through an arc that brings them together behind the after point of the carapace. As this four-legged push begins, the body rises high off the sand, dropping back as the stroke is completed and being carried forward in a series of plunges. The newly emerged young often pause,

bend the still flexible body upward anteriorly, stretch the fore flippers upward and outward, and then resume their movement towards the water. Another occasional variation in the gait comes when, after one of the flops that end the little lunges, the turtle is left perched on some small irregularity in the surface of the sand—a ripple mark, twig, or shell, for instance. The feel of the new position evidently suggests water, and the swimming reflex is prematurely set up. The turtle begins furious flying movements with the fore paddles, and these continue for several seconds or until the hatchling has shifted off of the prop. The same reaction can sometimes be seen in an individual held lightly by the edges of its shell between thumb and forefinger.

FIELD TESTS OF ORIENTATION IN HATCHLINGS

Some simple tests were carried out on the beach at Tortuguero, with the aim of determining the flexibility of orientation capacity in the newly emerged hatchling and of extending the basis for behavioral comparison among the genera of sea turtles.

Some time ago we found (Carr and Ogren, MS) that green-turtle hatchlings taken from the erupting nest, placed directly in water (without being allowed to develop the usual patterns of sea-oriented locomotion), left there for periods of as much as a year, and then moved back to an artificial "nest" in the sand may start walking without difficulty and show no diminution of the capacity to find the sea. Although trunkbacks have not been available in numbers adequate for conclusive experiments of even this elementary sort, we soon noted a similar retention of sea-sense in them and set about testing their orientation adjustments under varied conditions, as described below.

Trial 1

Forty-eight young from a brood that hatched July 10 were caught before they reached the surf and were placed in a tank of water, where they immediately started swimming and soon began to feed. During the daytime they swam almost constantly. At night they floated motionless at the surface.

On the afternoon of July 14 they were removed and placed on the beach in a group, on a high, wave-cut bench that sloped slightly away from the sea, which was 30 yards away.

Of the 48, 12 failed to react. Of the remaining 36, all had established headings, not later abandoned, that kept within about 15 degrees of the perpendicular to the surf line, with the following timing:

After 3 minutes, 5 correct headings
After 5 minutes, 12 correct headings
After 10 minutes, 36 correct headings

Besides an initial period, which varied in duration, of what appeared to be aimless wandering about the point of release, the only marked deviation from course shown by these turtles was the "orientation circle" described in the foregoing account of natural emergence of young. This was usually a well-formed circle of from 4 to 6 inches in diameter, but sometimes involved a simple, 360-degree rotation of the body and, rarely, just a quick reversal of direction, a short walk directly away from the surf, then a sudden resumption of the proper course.

Throughout this test, as in their locomotion after natural emergence from the nest, turtles were seen to stop, apparently when their lunging gait landed them on top of small obstructions, and go through a period of rapid, slapping, swimming strokes before continuing down the beach.

Trial 2

Seven hatchlings from a nest that began erupting about dark on July 17 were gathered up as they emerged, moved some distance along the beach, and at 8.00 P.M. released in a group on wet, hard-packed sand that sloped sharply down to the water 35 feet away. The night was dark, with overcast sky and no moon.

After a short time of scrambling, all got their bearings and moved towards the sea on headings which, if the turtles had not been picked up just before they reached the water, would have diverged at the surf line by only about 5 yards. No circles were made by these individuals.

Our experiments with green-turtle hatchlings had shown that the sea-seeking young, caught just before reaching the water, then carried back to the nest and released there, show no evidence of disruption of orientation instincts. Hatchlings with this background were used in a test to determine reaction, while crawling to the sea in the dark, to a strong extraneous light source. The turtles used in the preceding test were gathered up just before entering the surf and released in a group in the uppermost wash of the waves. Preliminary trials had shown that the usual result of such a procedure was a rapid and uninterrupted movement of all individuals into the surf.

When a kerosene mantle (Tilley) lamp was set on the upper beach 35 feet from the site of release, the turtles immediately turned inland

and with only small deviations crawled rapidly to the lamp and tried to climb its base. They were thus literally tolled in from the sea by a phototaxis that completely overrode whatever cues guided the normal seaward movement.

The test was repeated with hatchlings released at three other points 35 feet from the lamp. In every case all individuals went to the lamp instead of to the water. It was noted that when a flashlight was played on hatchlings moving towards the water, they quickly changed course and headed for the light source (cf. reaction of adult female under similar circumstances).

Trial 3

The seven specimens used in the preceding tests were kept dry in a box overnight. On August 18 at 4.00 P.M. they were released on the beach in a group.

The sun was low over the woods on the other side of the lagoon behind the beach. The coco fringe rose some 30 yards from the point of release, which was on open sand 25 yards above the reach of the highest waves. Halfway between the point of release and the surf there was a low ridge, parallel to the surf line and high enough to hide the sea and to constitute the horizon for a turtle within a few yards of it (although not for one back at the site of release). Beyond the ridge there was no obstruction of any kind, and the sand sloped steadily to water level. There was no debris lying about the site of release or between it and the ridge.

Within one minute after release the first turtle was moving in the right direction. Within eight minutes the last to react had found a proper course. One individual failed to react and stayed where released. The leading hatchling reached the water 11 minutes after release. The spread of wandering by all the hatchlings about the point of release was 7 yards. The spread of crawl tracks at the surf line was 14 yards.

Throughout the trial all turtles made repeated small orientation circles as described above, even after reaching wave-wet sand.

On reaching the water the turtles were gathered up, placed in a tank of sea water, and kept there for two weeks. Taken out from time to time and placed on the beach, they showed gradual loss of capacity to appraise and react to the beach situation. On the fifteenth day, although released at a point only 10 feet from the surf, none reacted or did anything more than raise its flippers in the air and make irresolute efforts to rotate its body. It seemed evident that this development was

not due to general physical decline but to a loss of specific receptivity to orientation cues.

Trial 4

Thirty-four newly hatched trunkbacks were placed in water in a wooden trough 4 feet long, 1 foot wide, and 6 inches high. The tank was set on a stand under a lean-to roof that sloped seaward from the wall of a shed and opened towards the sea. The long axis of the tank was perpendicular to the eaves. All that was visible to the confined turtles, besides the walls of the tank itself, were the wall of the shed at the inland end of their tank, the overhang of the roof and tree-broken sky at either side, and a patch of unobstructed sky under the eaves at the seaward end of the tank. Within an hour all turtles but one had moved to and remained at the seaward end.

The trough was then rotated 180 degrees. After a half hour, all but three of the turtles had again moved to the seaward end. One of those not there was the one that had behaved similarly on the first trial and that later turned out to be ailing.

While these informal tests do not warrant any definite conclusions regarding the nature of orientation stimuli and responses in *Dermochelys*, they suggest that this sea turtle may react to horizon effects (e.g., clear versus obstructed, illuminated versus dull, horizons, among other things, as work with other turtles has also suggested; see Hooker, 1908; Parker, 1922; Noble and Breslau, 1938; Anderson, 1958). The most practical result is the indication that the seaward drive is retained for some days and through various kinds of post-emergence experiences, including periods spent constantly swimming in water. This suggests the feasibility of more searching manipulatory study. More extensive tests of these and other sorts have been carried out with hatchlings of *Chelonia*. Results and some implications of these will be discussed in another paper (Carr and Ogren, MS).

THE HATCHLING IN CAPTIVITY

Young trunkback hatchlings taken from the nest and placed in salt-water tanks show the same frenzied swimming urge that is so striking in newly hatched green turtles. They spend all illuminated hours aimlessly cruising their container, or simply pushing frantically for hours on end against the walls. This behavior, shared by *Dermochelys* and *Chelonia*, contrasts strongly with that of captive young *Eretmochelys*, which accepts confinement placidly and swims about only in a purposeful search for food. The difference suggests possible contrast in behavior

after leaving the nest under natural conditions. It seems likely that green turtles and trunkbacks spend the first hours or days following emergence from the nest in steady travel away from the place where they enter the surf. This is a point which clearly bears upon the troublesome question of what young sea turtles do, and where they go, in nature.

When young *Dermochelys* swim rapidly, the stroke is a synchronous "flying" movement of the two front fins, with the back legs trailing behind. In its wild dashing about, the turtle sometimes works its flippers so violently that its body bobs up and down at the surface with a plopping sound. Deliberate exploratory swimming is rare, during the first week or so, but when engaged in it usually involves a dog-paddle stroke such as is used by fresh-water turtles. When the young rest or cruise slowly at the surface, only the upper part of the back is exposed,

TABLE 4

DIMENSIONS (IN MILLIMETERS) OF 44 TRUNKBACK TURTLES NINE DAYS OLD THAT EMERGED JULY 10, 1957, AT TORTUGUERO, COSTA RICA

	Mean	Mode
Carapace length	67.2	69
Carapace width	47.9	48, 49

the head being held submerged and slanting downward. Unlike young green turtles, loggerheads, and hawksbills, which lay their front flippers flat along the carapace when sleeping, trunkbacks at rest fold their fore fins across the plastron or, more rarely, let them hang slanting backward, with the leading edge forward.

In breathing, the hatchling *Dermochelys* raises its head and simultaneously arches its shell-less, flexible body downward in the middle until it acquires a decidedly concave profile. This is a maneuver that probably has no counterpart among other turtles.

The young trunkback is even more bouyant than hatchling green turtles and finds difficulty in going to the bottom after sunken food, usually succeeding in doing this only through flurries of furious flipper work. Floating food is taken readily, once the feeding reactions have been set up, and it was found most practicable to exclude the denser articles from the diet as far as possible. The young trunkback will

take both animal and vegetable food but appears to be mainly carnivorous, taking fish or invertebrates impartially. In spite of the seeming hysteria with which their swimming is carried out during the first week after hatching, trunkbacks readily start feeding and soon learn to interrupt their ceaseless cruising long enough to come to the hand that holds food. Once within the range of strong stimuli from a bit of food the young turtle often becomes greatly excited, and the rate and strength of the breast stroke increase to the point that the fore part of the body may be lifted from the water at each upward stroke. Sometimes the turtle may even flip itself over backward.

Within a period of from two weeks to a month after hatching, all the trunkbacks that we have kept alive (some 60 individuals in six different tanks, from four different broods) have developed yellowish spots on the carapace. Scales soon begin falling from these places, which appeared to be sites of fungus or bacterial infection, and the eyes become discolored. Deraniyagala (1939) described similar infirmities in captive Pacific trunkbacks, but was able to rear at least one individual in captivity. We have been unable to keep trunkbacks alive for more than 41 days.

SYSTEMATIC NOTES

While some herpetologists regard *Dermochelys* as a monotypic genus, others have accepted Garman's (1884) nominal separation of the Pacific trunkback from that of the Atlantic. No real grounds for this separation have been shown. It seems likely that a study of adequate material will reveal that all characters so far used are merely the features that distinguish the sexes. As was suspected by Yañez (1951) and by Carr (1952), this is surely the case in the instance of *Sparghis angusta* described from the coast of Chile by Philippi (1899), who also recognized the occurrence of *coriacea* there. With the aim of looking up Philippi's specimens of these and other sea turtles, Carr visited the Museo de Historia Natural at Santiago in 1957. Two old, well-mounted, and well-preserved trunkbacks were found, one a broad-backed female and the other a long, narrow, long-tailed male. These seems little doubt that the female was Philippi's specimen of *coriacea* and the male the type of his *S. angusta*.

If world stocks of *Dermochelys* actually have undergone speciation, it seems clear that differences are trivial and that the characters will require statistical demonstration. Because adult trunkbacks are hard to get in abundance and awkward to store, it is likely that whatever decent taxonomic treatment the genus receives must involve hatchling

specimens. As a contribution towards a body of data on which an evaluation of world populations may eventually be based, we give below some characters of hatchlings from the Caribbean coast of Costa Rica.

Coloration

While nothing in the coloration of the few young specimens from Pacific localities that we have seen suggests any points of divergence in this respect, it may be that more adequate Pacific material will reveal color differences. At any rate, the black and white pattern of Costa Rican material seems quite constant. The typical pattern is shown in figure 12.

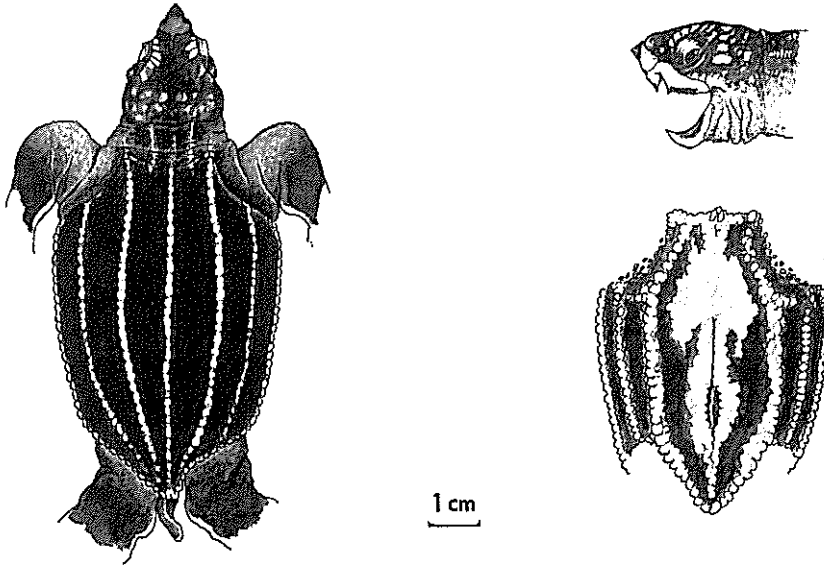

Fig. 12. Five-day old trunkback from Tortuguero, Costa Rica, showing typical pattern.

Dimensions

Measurements of young Costa Rican trunkbacks are given above in tables 3 and 4.

Scalation

Although the numerous small scales that cover the carapace and head of young *Dermochelys* are somewhat variable and are lost a few weeks after hatching, they are clearly delimited in most cases, and

series of them tend to be fairly homogeneous in size through some of the dimensions of the body. Some of these series may prove to be useful criteria for the study of speciation in the genus. Results of some counts that have seemed to us to be promising are shown in figure 13. Methods of counting the scales involved are indicated below. Incompletely separated scales are counted as two if they are separated across more than half of their width.

SCALES OF THE NEURAL RIDGE: These are the enlarged, usually pigmentless scales that cover the narrow middorsal ridge of the carapace.

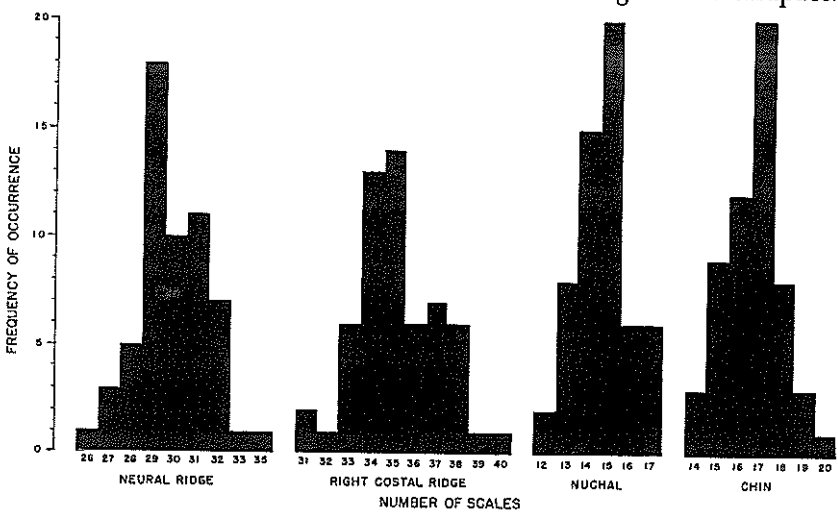

FIG. 13. Histogram showing frequency of four different scale counts in two broods of trunkbacks from Tortuguero, Costa Rica. One brood, comprising 21 turtles, emerged July 28, 1956; the other included 36 that emerged July 10, 1957.

The count begins with the first enlarged scale at the anteriormost edge of the carapace, which usually can be distinguished by its size from other scales of the nuchal region. Counting is continued posteriorly along the ridge to, and including, the large, usually unpigmented, elongated scale at the caudal end of the carapace, the small asymmetrical terminal scales being disregarded.

SCALES OF THE RIGHT COSTAL RIDGE: These are the enlarged, unpigmented scales of the row covering the ridge to the right of, and parallel with, the neural ridge. The series begins with the first big scale behind the small scales of the neck skin and continues posteriorly to the enlarged caudal scale of the neural ridge. If the series loses itself posteriorly among the undifferentiated scales of the carapace, as is often the

case, the count is continued along a line projected to the big caudal scale.

NUCHAL SCALES: Each of the anterior projections of the costal ridges of the carapace ends in a big, button-like scale. What appears to be a useful scale count includes the series along the curved fore margin of the carapace between these button-like anterior ends of the costal ridges. The scales to be counted lie behind a fold marking the zone where the small neck scales come up to the anterior edge of the carapace.

CHIN SCALES

The series counted here includes all scales, large and small, in contact with the single mandibular scale, beginning at one jaw angle and continuing to the other.

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