The Leatherback or Leathery Turtle

Dermochelys coriacea

P. C. H. PRITCHARD

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Dermochelys coriacea

compiled by

PETER C. H. PRITCHARD

from available literature, from his own unpublished data and from unpublished data supplied by Peter R. Bacon, H. Robert Bustard, Archie F. Carr, Tom Harrisson, Russell Hill, Harold F. Hirth, George Hughes, Reinhard Kaufmann, Antonio E. Montoya C. and Johan P. Schulz

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Foreword

This volume is the first in a new series of publications by the International Union for Conservation of Nature and Natural Resources entitled 'IUCN Monographs', which will present scientific treatises on subjects of special concern to the conservation of the world's natural resources. It is also the first in a projected series of papers on sea turtles, which are being prepared by the Marine Turtle Group of the IUCN's Survival Service Commission.

The Survival Service Commission is concerned with the conservation of threatened species. In March, 1969, it organized a small working meeting on marine turtles, all species of which are currently regarded as being in some danger of extinction. The immediate objectives of this meeting were to review existing information on marine turtles, to determine the national and international research and conservation priorities, and to examine the scope for future cooperation in this field. The long term aim was to provide a basis for a coordinated world plan for sea turtle conservation.

The delegates agreed to form themselves into a Specialist Group under the aegis of the S.S.C., and Dr P. C. H. Pritchard was appointed as the coordinator of the Group. Attention was drawn to the paucity of the data on the natural history of sea turtles, and one of the Group's proposals was that a series of monographs should be prepared on the seven species involved. The proposal is now being implemented. The data for these publications are obtained from published sources and from unpublished material provided by Group members, each compilation is the responsibility of an individual member, and the coordination of the series as a whole is being undertaken by Dr Pritchard.

The present monograph deals with the leatherback or leathery turtle *(Dermochelys coriacea)* and has been compiled by Dr Pritchard. Monographs presently in preparation, include 'The Green Turtle' *(Chelonia mydas)* by Dr Harold F. Hirth, and 'The Flatback Turtle' *(Chelonia depressa)* by Dr H. Robert Bustard.

The IUCN is confident that the dissemination of this information will do much to stimulate further research into the biology of the sea turtles and to promote more effective management of this hitherto largely neglected renewable resource.

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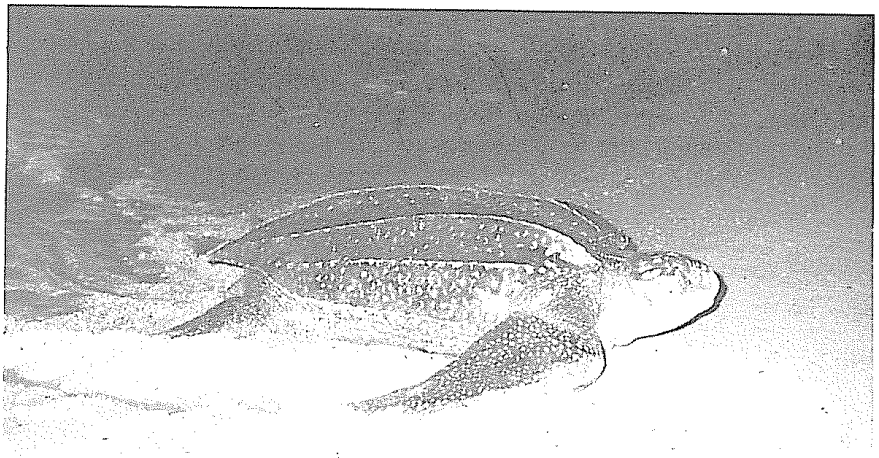
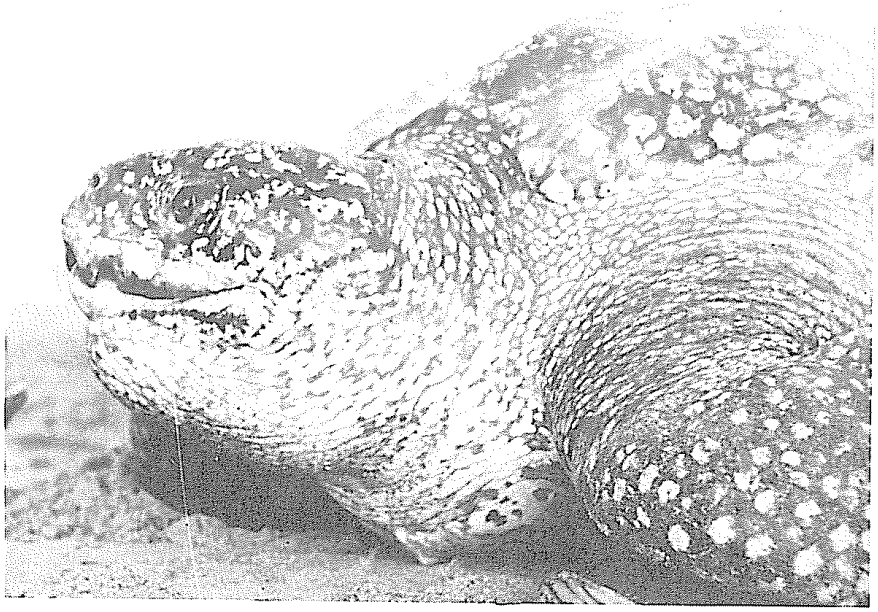


Dermochelys coriacea — Leatherback turtle, adult female, French Guiana.



Dermochelys coriacea—Leatherback turtle, adult female, Surinam.

SYNONYMY

1766 *Testudo coriacea* LINNAEUS, Syst. Nat., Ed. 12, 1: 350; Palermo, Sicily (Smith and Taylor 1950)

1771 *Testudo arcuata* CATESBY, Nat. Hist. Carolina, 2: 40; Fig. 40; coasts of Carolina and Florida (Mertens and Wermuth 1955)

1788 *Testudo lyra* LACÉPÈDE, Hist. nat. Quadrup. Ovip., 1: Synops., method., 111, Fig. 3: Mediterranean

1792 *Testudo tuberculata* SCHOEPFF, Hist. Testud., p. 144; no locality cited.

1814 *Chelonias lutaria* RAFINESQUE, Specchio Sci. (Palermo), 2, 9: 66; Sicily (fide Lindholm 1929)

1816 *Dermochelys (coriacea)* BLAINVILLE, Bull. Soc. Philom. Paris, p. 119

1820 *Sphargis mercurialis* MERREM, Vers. Syst. Amphib., p. 19; Mediterranean Sea and Atlantic Ocean

1822 *Coriudo (coriacea)* FLEMING, Phil. Zool. 2, p. 271

1828 *Seytina (coriacea)* WAGLER, Isis von Oken, p. 861

1829 *Dermochelis atlantica* LESUEUR (nomen nudum), in Cuvier, Regn. Anim. Ed. 2, 2: p. 14

1830 *Dermatochelys porcata* WAGLER, Nat. Syst. Amph.: p. 133

1832 *Chelyra (coriacea)* RAFINESQUE, Atlantic Journal, 1, p. 64

1884 *Sphargis coriacea* var. *schlegelii* GARMAN, Bull. US Nat. Mus. Washington, 25: 303; Guaymas, Sonora, Mexico (Smith and Taylor 1950)

1889 *Dermochelys coriacea* BOULENGER, Cat. Chelon. Rhynchoceph. Crocod. Brit. Mus.: 10, fig. 1

1899 *Sphargis angusta* PHILIPPI, An. Univ. Santiago de Chile, 104: 728; Tocopilla, Chile

SUBSPECIES

Garman (1884) proposed the subspecific name *schlegelii* for leatherbacks of the Indian and Pacific Oceans, and this has been followed by some authors ever since (e.g. Carr 1952; Schmidt 1953), even though Garman did not publish a description but merely referred to figures in Temminck's and Schlegel's *Fauna Japonica*. Smith and Taylor (1950) write that 'a common arrangement restricts *coriacea* to the Atlantic, *schlegelii* to the Pacific, either as species or subspecies. We are unable to find that anything more than geographic probability has led to such arrangement.' Even though these authors dismiss subspecies of *Chelonia mydas* with the same words (where they are certainly wrong), they are probably correct in this case. Carr (1952), while certainly not regarding subspeciation of *Dermochelys* as a proven fact, advanced the possibility of *coriacea* being darker and less spotted than *schlegelii* and of *schlegelii* having a somewhat greater skull length. However, until recent years no one has had adequate samples for valid comparison; we now know that leatherbacks from Tongaland and Trengganu may be more, less, or equally spotted as compared with leatherbacks from Costa Rica or French Guiana; and the head-length difference is based on a single illustration of one specimen of '*schlegelii*' from Japan. The best policy at present is probably simply to call all leatherbacks *Dermochelys coriacea* until reliable subspecific characters are described.

COMMON NAMES

Leatherback turtle; leathery turtle; trunkback turtle; luth; leatherneck turtle; Lederschildkröte (German); Lederschildpad (Dutch); laerskilpadde (Norwegian); trunk turtle; coriaceous turtle; tortue cuivrée (French); ait-kenti (Surinam); matamata (Guyana); laud (Mexico); canal (Mexico); siete filos (Mexico); chalupa (Mexico); tortuga de cuero (Mexico); tinglado (Mexico); siete quillas (Mexico); tortuga de altura (Mexico); garapacho (Mexico); galápago (Mexico); Orinook turtle (Trinidad); caldon (Trinidad); coffin-back turtle (Trinidad); caouana (Carib); tukutubuking (Carib); Tibisibisching (Carib); Dhāra käsbäva (Sinhalese); Thun Dhāra Käsbäva (Sinhalese); Vavul Käsbäva (Sinhalese); Thel Käsbäva (Sinhalese); Navu Käsbäva (Sinhalese); Māvalla (Sinhalese); Dhoni āmai (Tamil); Yelu vari āmai (Tamil); Bosange (Ghana); Kasa ya Noa (Swahili); Ibu (or Penyu) Kamba (Malaya); Ibu (or Penyu) Belimbing (Malaya); Ivundu (Thonga); Inhaca (Makua).

DESCRIPTION

The leatherback is one of the least mistakable of all turtles (see Plate I). Apart from the huge adult size, this species lacks the horny carapace scutes found in other sea turtles, the shell, instead, being covered with a continuous layer of tough, rubbery skin. The shell as a whole is deep and somewhat barrel-shaped, is raised into a series of longitudinal ridges (seven on the carapace and five on the plastron), and tapers posteriorly to a blunt point. The fore flippers are proportionately very long, while the neck is thick and grades smoothly into the shell. The soft parts are devoid of scales and claws, and the skin is velvety and so soft that, when nesting, the animal often rubs itself raw and bleeding in numerous places. The leatherback has peculiar jaw margins, the upper jaw bearing two tooth-like projections, flanked by deep cusps, at the premaxillary-maxillary sutures. The jaw surfaces themselves are simple cutting edges, and are devoid of the crushing or chewing plates found in other sea turtles. The eyelids are arranged in an almost vertical plane, so that the closed eye has the appearance of a vertical slit. When the animal closes its eyes the eyeballs appear to retreat a long way into their sockets.

Anatomically, the leatherback is so strikingly divergent that it is sometimes placed in a sub-order separate from all other turtles (the Athecae). The carapace derives its mechanical strength, not from a series of interlocking bones as in other turtles, but from a two-inch thick layer of oily cartilaginous material. Many of the usual shell bones have in fact been eliminated entirely; thus there are no neurals, pleurals or peripherals. The nuchal bone, however, is well developed, and is important as the origin of numerous muscles in the neck and shoulders. The plastron contains a narrow ring of flimsy bones that appear homologous to the epiplastra, hyoplastra, hypoplastra and xiphiplastra of other turtles; no indication of an entoplastron is present, except in occasional embryos. Since there are no pleural bones, the ribs are free of rigid bony connections, but, being buried in the cartilage layer, they have practically no free movement.

Just under the skin of the adult leatherback there is a continuous layer of mosaic bones, a few millimetres thick, extending as far as the marginal ridges, but absent on the plastron except for a few remnants on the ridges. These mosaic bones are enlarged and thickened along the ridges of the carapace. The ridges themselves are not smooth but are tuberculate, so that half or more of the enlarged mosaic bones are knobbed.

The skull is completely roofed over, and the supraoccipital process hardly protrudes beyond the parietals. The dermal bones of the skull are exceedingly thick, especially anteriorly, while the bones of the palate are very thin. Even in large adults the bones of the skull remain loosely sutured and fall apart completely when the flesh is removed.

In colour the leatherback is basically black on all dorsal surfaces and whitish below. However, the upper surfaces are usually heavily spotted with white, the spots being randomly placed except on the back of the neck and tail, where they form linear continuations of the dorsal ridges. The spots on the head are usually larger than those on the shell, and tend to coalesce on the jaws. Frequently the spots on the soft parts have a pink tinge, and sometimes they appear bluish (especially in Tongaland), but never yellow as some authors have stated. On the throat, plastron, and ventral surfaces of the limbs, the basic colour is pinkish-white, with variable amounts of black vermiculation.

The structure and colour of the leatherback are described in greater detail by Deraniyagala (1939).

SIZE

The leatherback is the largest living turtle species. While the smallest breeding adults from areas may be no longer than the largest green turtles, loggerheads, Galapagos or Aldabra tortoises, or giant soft-shells *(Pelochelys, Chitra,* etc.), leatherbacks do consistently reach a size and weight unequalled by any other turtle. It has even been suggested that the leatherback is the largest living reptile, but there is little doubt that several species of crocodile reach substantially greater weights than the biggest leatherbacks.

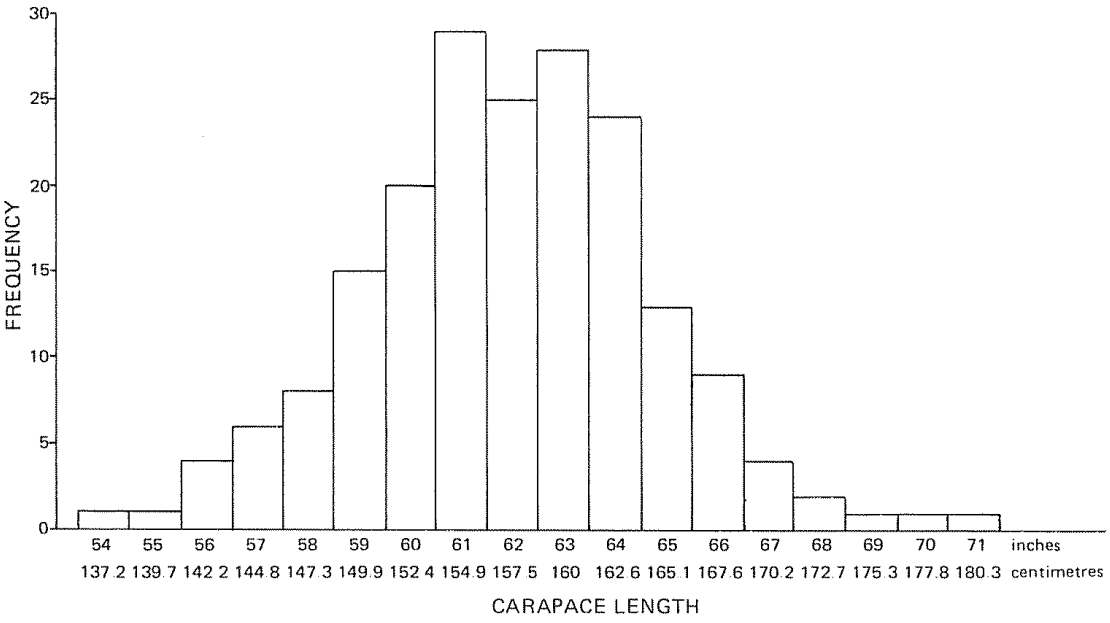
The actual size reached by the leatherback has been confused by variations in the methods of measurement (the actual method used frequently not being stated), and by guessed weights being given as actual weights. Although leatherbacks may be found predictably in relatively few places, they turn up occasionally almost everywhere, where they are reported by local newspapers which for journalistic reasons prefer to quote the more impressive-sounding total length instead of the carapace length.

The only large series of measurements of adults available was taken by Pritchard, who measured the carapace lengths of 192 mature female leatherbacks from French Guiana. The method used was to stretch a flexible tape as tightly as possible from the deepest part of the nuchal notch to the posterior tip of the shell, following a course along one of the two paramedian troughs in the shell (not along the median ridge). This gives a reproduceable measurement, and a close approximation to the straight-line length, which is difficult to measure accurately without special equipment. The lengths obtained are given in histogram form below (page 10).

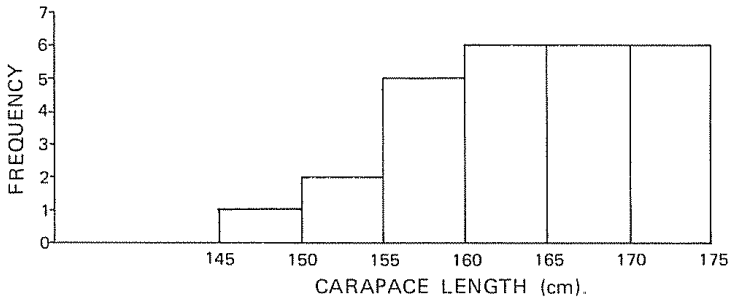
It is doubtful if a breeding leatherback could be much more than six feet (1.83 m) in carapace length, since the largest French Guiana specimens, 70 and 71 inches (c.1.8 m) in length, were so heavy that they could hardly move on land.

Hughes *et al.*(1967) measured the carapace lengths of 26 mature female leatherbacks from Tongaland, Natal, and plotted the histogram shown below.

Carapace length frequencies for mature female leatherback turtles *(Dermochelys coriacea)* from Silébâche Beach, French Guiana



Carapace length frequencies for mature female leatherback turtles *(Dermochelys coriacea)* from Tongaland, Natal



The Tongaland turtles were measured by passing a flexible tape over the median ridge of the carapace. Taking into account this difference in method, there would appear to be no significant difference in average length of mature females in the French Guiana and Tongaland populations.

Hughes also obtained detailed measurements of seven adult female leatherbacks set out below (page 11: all measurements in cm).

Bacon (1969) gives measurements of 20 adult females from Trinidad, as set out in the second of the two tables below (page 11).

Although it is not stated, it seems likely that some of Bacon's width measurements were taken over-the-curve, and others between perpendiculars.

Curved carapace length	Perpendicular length	Curved width	Perp. width	Head length	Head width
156.5	148.0	107.0	83.5	26.0	20.3
168.0	157.5	118.0	95.3	27.5	25.2
164.0	157.0	109.0	85.8	26.2	22.1
168.5	159.8	122.0	93.2	26.8	23.1
163.0	154.4	117.0	84.5	25.6	20.5
157.0	149.0	117.0	84.1	26.0	20.8
155.5	146.5	112.0	84.0	26.5	22.4

Curved carapace length (cm)	Carapace width (cm). Trinidad specimens.
178	—
165	—
150	75
150	110
153	113
185	95
180	90
125	—
150	—
165	114
150	110
135	113
157	112
137	117
150	75
170	110
175	110
158	117
146	111
150	109

Caldwell (1959) quoted the carapace length of a Florida leatherback as 6 feet 7 inches (200 cm), and the width as 3 feet 1 inch (94 cm). However, he gave the dimensions of another turtle as 5 feet 3 inch (160 cm) by 3 feet 1 inch (94 cm). Although leatherbacks do vary somewhat in shape, it is probable that in the first case the informant was quoting the total length, not the carapace length.

There would appear to be no factual basis for the statement of Noel-Hume and Noel-Hume (1954), that leatherbacks eleven feet (3. 35 m) in length had been found nesting on 'an uninhabited Caribbean island'.

Few leatherbacks have been weighed accurately. An unusually small mature female from Surinam, with carapace length 58½ inches (148.6 cm), weighed 651 lbs. (295.3 kg) after oviposition (Pritchard 1969). A 71″ (180 cm) leatherback with the same proportions would weigh about 1160 lbs.(526 kg), and the estimated weight could probably be raised to at least 1300 lbs.(590 kg) for a turtle in pre-breeding condition. Hirth (pers.comm.) reports a female leatherback captured near Aden on 9 July 1968, which had a carapace length of

63 inches (160 cm) and a weight of 672 lbs. (305 kg). Brongersma (1969) gives the following dimensions for a large dead male leatherback from the island of Ameland, Holland: total length (between perpendiculars): 8 feet (244 cm); carapace length: 5 feet 2 inch (158 cm) (fractured posteriorly; probably about 5 feet 7 inch (170 cm) originally); weight 1069 lbs. (485 kg).

Even though the head can hardly be retracted at all, the ratio total length: carapace length appears to be very variable. Deraniyagala (1939) gives the dimensions of two Ceylon leatherbacks as follows:

Total length	Curved carapace length	Curved carapace width	Arm Spread	Weight
82.7 inch (210.1 cm)	65 inch (165 cm)	32.3 inch (82 cm)	—	988 lbs. (448 kg)
90.3 inch (229.4 cm)	61.5 inch (156.2 cm)	34.2 inch (86.9 cm)	97.4 inch (247.4 cm)	—

Most published records of weights of leatherbacks for which there is some evidence that the weight was actually measured and not just estimated, fall within this range of values (i.e. 650 to 1300 lbs. or 295-590 kg). Carr (1952) quoted the following weights of leatherbacks caught on the Atlantic coast of the United States (mostly from newspaper accounts): 800 lbs. (363 kg); 1000 lbs. (454 kg); 1087 lbs. (493 kg); 1130 lbs. (513 kg); 1200 lbs. (544 kg); 1280 lbs. (581 kg); 'between 1200 and 1500 lbs.' (544-657 kg); 1600 lbs. (726 kg). The following weights have been recorded for leatherbacks from the Pacific coast of the United States (again culled from newspaper and other accounts by Carr): 800 lbs. (363 kg); 1000 lbs. (454 kg); 1100 lbs. (499 kg); 1200 lbs. (544 kg); 1286 lbs. (583 kg); 1575 lbs. (714 kg); 1902½ lbs. (863 kg). The last figure is suspect in that the carapace length was given as only 5 feet 2 inches (157 cm); Deraniyagala found that a turtle three inches longer than this (= 165 cm) weighed only 988 lbs. (448 kg). According to Hughes (pers. comm.), a leatherback caught near Laaiplek in western South Africa weighed 1420 lbs. (644 kg) one of the heaviest reliably recorded.

It is possible that leatherbacks mature at a much smaller size in the East Pacific than in the Atlantic. In September 1969 Pritchard found a number of leatherback remains on the beach at Piedra de Tlacoyunque, Guerrero, Mexico; one almost intact carapace measured only 44½″ × 28″ or 119.6 × 71 cm (straight-line, internal measurements), and an intact skull of another individual was only 7½ inches or 19 cm wide (the usual width of Atlantic leatherback skulls is about ten inches or 25.4 cm). There is no absolute assurance that these were nesting individuals, but the area is a known nesting-ground, and it seems unlikely that fisherman would catch several individuals of a legally protected animal at sea and transport them beyond the high tide mark of an open beach for slaughter.

Leatherbacks intermediate in size between hatchlings and adults are very rarely found. However, the Leiden Museum has a leatherback from Bonaire that, as a frozen, complete specimen, weighed 121 lbs. (55 kg), and had a carapace length of 3 feet 4 inches (101.5 cm). Another specimen from the same locality, in a shrunken and mummified state, has a carapace length of 11.2 cm (RMNH 13952 and 13942 respectively). Also, Caldwell (1959) illustrates a specimen from Indian River County, Florida, with a carapace length of between three and four feet (90-120 cm). A male weighing 419 lbs. (193 kg) was caught

at Nosy-Bé, Madagascar, in 1960 (Fitter 1961). A 471 lb. (214 kg) specimen was speared on July 7 1959 a few miles east of Santa Catarina Island, California (Norris, in litt, to A. F. Carr, 8 July 1959). Dunlap (1955) found that two female leatherbacks from the Gulf of Mexico, off southeastern Louisiana, weighing 478 (207 kg) and 600 lbs. (272 kg) respectively, were both sexually immature, or at least had never laid eggs, since the ovaries were unscarred, and the 'hymenal' membranes closing off the oviducts where they enter the cloaca were imperforate.

George Hughes has reported the stranding of baby *Dermochelys,* up to about 4 inches (10 cm) in length, on the east coast of South Africa during south-easterly gales.

Not only the great size, but many other peculiarities of the leatherback may be correlated with the skeleton remaining in an immature state (and thus presumably maintaining a potential for growth) throughout the life of the animal. At the hatchling stage, the leatherback skeleton is very similar to that of other hatchling sea turtles, the differences mainly being the absence of the minute centres of ossification of what later become the neural, peripheral and entoplastral bones. However, as growth proceeds, each shell bone remains the same shape; the bones send out none of the flanges and interdigitating rami that, in other turtles, eventually coalesce to form a coherent bony shell. The moveable part of the skeleton too remains immature, the vertebrae, limb bones and girdles having extensive cartilaginous extremities even in large adults. Also, as mentioned earlier, the skull bones do not fuse with age.

The dermal shell mosaic of *Dermochelys* is absent at hatching and gradually forms as the turtle matures. Although some have suggested that these bones are homologous with the dermal ossifications of crocodilians, it is equally likely that they are neomorphs.

SEXUAL DIMORPHISM

There appears to be no obvious difference in adult size between the sexes of Dermochelys. Deraniyagala (1939) described the sexual differences as follows: 'The male is readily recognizable by its elongate tail which is so long that the adpressed hind limbs only reach level with the cloaca whereas in the female the tail barely reaches half way down these limbs. The profile of the adult male is rather depressed, its plastron concave, the hips narrow and the corselet less deep than in the female. The dark interspaces of the plastron are also more persistent in the male and the terminal osterderm of each ventral ridge forms a strong prominence and probably assists it to retain its position upon the female during copulation. It also retains more traces of scale divisions.'

Photographs of adult male leatherbacks can be found in the papers by Villiers (1958) and Brongersma (1969).

COPULATION

Very few observations of copulation have been reported, but it is likely that it occurs during the early part of the nesting season. Schulz saw several copulating pairs off the coast of French Guiana in May 1969. The duration and the exact position of copulation have not been recorded. Whether or not eggs are fertilized in the same season that they are laid is not definitely known.

DIET

Brongersma (1969) gives an exhaustive account of the literature pertaining to the diet of the leatherback. He concludes that the diet consists mainly of Scyphomedusidae (jellyfish) and Tunicates (sea squirts), together with those animals which habitually live associated with these (amphipods and juvenile fishes — *Trachurus and Urophycis* — have been definitely identified). In Trinidad there is evidence that leatherbacks eat jellyfish of the genera *Physalia* and *Stomolophus* (Bacon 1969). Algae and sea-grass have also been found in several stomachs, but it is most likely that these were ingested accidentally when the turtle was feeding on something else. Indigestible material such as pieces of tree bark and plastic is also found in leatherback intestines from time to time; whether these can kill the turtle by blocking the alimentary tract is uncertain. Montoya (pers. comm.) reports fish remains and large numbers of hatchling ridleys in leatherback stomachs from Pacific Mexico.

Bleakney (1965) found that six Newfoundland leatherbacks had stomachs full of jellyfish (*Cyanea capillata artica*). Pritchard found nothing in the stomach or intestine of a leatherback killed just off the nesting beach in French Guiana. Whether or not these turtles normally feed during the nesting season is unknown. Pritchard and Mrosovsky found nothing but green slime (bile?) in the digestive tract of a leatherback that died of unknown causes after nesting in French Guiana. Fluid of a similar colour was also seen around the vent of a hatchling leatherback that had been kept dry and not fed since emergence.

The deeply-notched, sharp-edged jaws of the leatherback certainly appear adapted for holding and cutting up soft-bodied prey; they completely lack the massive construction and crushing plates found in jaws of *Caretta caretta* and *Lepidochelys*, which are known to feed on hard-shelled crustaceans and molluscs. It has been reasoned that the numerous, backwardly-directed, flexible papillae that line the entire throat and oesophagus of a leatherback are a special device to prevent jellyfish from slipping back up. However, these projections are present to a lesser extent in the throats of other sea turtles, including the herbivorous green turtle.

BREEDING RANGE

(a) North America (Atlantic coasts)

The leatherback breeds very rarely in the United States. Hildebrand (1963) was informed by a long-time inhabitant of Padre Island that a few nesting individuals had been seen on the island in the 1930's, but none had been seen there in recent years. In Florida a few individuals nest each year on the Atlantic coast; the northernmost record is from Flagler Beach, Flagler County (nesting witnessed 6 June 1947 by Ross Allen; recorded by Carr 1952); the southernmost record is from Miami, Dade County, where hatchlings were seen on the beach in July 1955 (Allen and Neill 1957). Another nested on South Beach, Fort Lauderdale, on 5 May 1969. All other Florida records are from Martin County, St. Lucie County and northern Palm Beach County (Caldwell 1959), except that Yerger (1965) recorded hatchling leatherbacks on the beach between Philips Inlet (Walton County) and Destin (Okaloosa County) around 1 September 1962; also an adult leatherback which emerged from the sea by broad daylight near Panama City, Bay County, on the Gulf Coast, in summer 1968, and walked around a little before returning to the sea, may have been looking for a nest site. Recorded nesting dates in Florida range from 15 April to 26 July.

(b) Central America (Atlantic coasts)

Very little leatherback nesting takes place on the east coast of Arrecife Alacranes, near Progreso, Yucatan, with somewhat greater numbers on Isla Pérez and Isla Pájaros. There are also vague word-of-mouth records of occasional individuals nesting on the Tamaulipas coast. Hildebrand (1963) mentions the coast of Veracruz as a nesting area for *Dermochelys*.

The leatherback has not yet been recorded from British Honduras (Neill and Allen 1959). There are also no definite records for Honduras, or for Nicaragua except in the extreme south (near Greytown). In Costa Rica, however, there is an important leatherback nesting beach at Matina, where Carr and Ogren found 18 nests two days old or less within a distance of $1\frac{1}{2}$ miles (2.4 km) in May; the breeding area extends about four or five miles (6 to 8 km) north from the mouth of the Matina River, but different parts of the beach appear to be preferred in different years. The nesting season in Costa Rica begins in April and continues abundantly through June, the latest recorded nesting being on 27 July.

(c) Caribbean and South America (Atlantic coast)

Nesting is sparse in Panama. In Colombia nesting has been recorded between the Rio Pedras and Cabo San Agustin (Quintana), and a beach near Acandí (Choco), Medem in 1962. The season extends from the end of April to the end of July. Very few data are available for leatherbacks in Venezuela, but N.O. Poonoi reports a good nesting beach at Punta Playa, on the Guyana border, and Trinidad fishermen familiar with the Venezuelan coast reported abundant nesting there to Peter Bacon. In Trinidad quite good nesting beaches exist on the north and east coasts; the season extends from March or April to July or early August. It is usually possible to see at least one or two nesting turtles each night at Matura Beach, on the east coast, during May and June. Nesting also occurs in Tobago; at least 18 nesting females were killed on a single beach there during the period 1967-1969 (Bacon 1969).

In Guyana leatherbacks are known to nest on Shell Beach, in the North-West District, at least from early May to early July; the numbers are unknown, but are probably small. In Surinam nesting is mainly concentrated on Bigi Santi Beach, in the Wia-Wia Nature Reserve. The numbers appear to have been increasing over the last few years — in 1964 it was rare to find more than two in a night, while in 1968 and 1969 it was not rare to find seven or eight in a night. In recent years a few leatherbacks have also been seen nesting on Baboon Santi, on the Surinam side of the mouth of the Marowijne River. However, the headquarters for leatherbacks in the hemisphere is a stretch of beach 10-15 miles (16-24 km) long on the French Guiana side of the Marowijne; in June and early July 1969 Pritchard and Greenhood estimated that up to 300 leatherbacks were nesting on a good night; the greatest number actually tagged on one night in 1969 was 74, while on 5 July 1970, 110 were tagged and 30 previously tagged individuals were found re-nesting. A small amount of nesting also occurs on beaches on the Ile du Cayenne, actually within the Cayenne City Limits. Several old writers mention leatherback nesting on the coast of Brazil, and it is almost certain that nesting still occurs there; but we do not know where or how much.

The leatherback appears to show a strong perference for mainland nesting, and records for nesting in the West Indies, apart from Trinidad and Tobago, are scarce. Definite records do exist for Jamaica, Puerto Rico, St. Thomas, St. Croix, St. Kitts, Nevis and Grenada, but on none of these islands do more than a few individuals nest each year.

(d) West Africa

No accurate data are available for leatherback nesting on the coast of West Africa; however, several museums have hatchlings from this area, and it seems almost certain that at least a moderate amount of nesting takes place. Villiers (1958) reported nesting taking place in June and July on the north-west coast of former French West Africa, but somewhat earlier south of there, judging by the capture of a hatchling off the Ivory Coast in May. Loveridge and Williams (1957) report two leatherbacks nesting on November 24 and 27 respectively, at the mouth of the Mahfa River, Liberia. In general, leatherbacks in the Atlantic and Indian Oceans nest in April-July in the Northern Hemisphere, and in October to February in the Southern; however, in some areas near the Equator there are two nesting seasons (e.g. in Ceylon, May-June and October-December), with a few turtles nesting in other months of the year; possibly such a situation obtains in tropical West Africa.

(e) Indian Ocean

On the East Coast of Africa there is a leatherback beach of moderate importance on the Tongaland coast of Natal. The season extends from mid-October to mid-February, with between 0 and 5 individuals nesting nightly on about 60 miles (100 km) of beach. Small numbers also nest on the coast of Moçambique south of Lourenço Marques.

Elsewhere in the Indian Ocean, the most famous nesting-ground is the coast of Ceylon. The season here reaches a peak in May and June, and another in October-December (Deraniyagala 1939). Deraniyagala reports that in the 1920's and 1930's at least seven could be found on one night, on the six kilometres of beach between Paiyagala and Maggona. Nesting records for India are scarce, but according to Deraniyagala egg-bearing females have been taken at Travancore, Tenasserim and at Calangute Beach, Goa; also in the Addu atoll at the southern end of the Maldive Archipelago. J. C. Daniel of the Bombay Natural History Society reports nesting, at least formerly, near Quilon, Kerala.

(f) South-east Asia and Australasia

In Malaysia, leatherbacks nest in very good numbers (up to about 80 per night) on 7½ miles (12 km) of beach in Central Trengganu; the season extends from May to about mid-September. Other nesting grounds, as yet unstudied, exist on the coast of New Guinea and on the west coast of Thailand, near and on the island of Pukhet. No nesting grounds are yet known to exist on the coast of Australasia, but Bustard (pers. comm.) has definite knowledge of two leatherbacks nesting in Fiji in 1969.

(g) Central and South America (Pacific coasts)

In the East Pacific, the northernmost nesting record is from Jalisco, Mexico, where 10-15 leatherbacks nest nightly during the season (October to March) on the 5 kilometre black sand beach at Ipala, and similar numbers nest on the 20 kilometre beach at Mismaloya. In Michoacan perhaps 10-12 nest each night spread over 50 kilometres of beach (Playa Manzanillo; Playa Cuyutlan; Boca de Pascuales); and further south nesting has been reported at Petatlán, Guerrero; Copalá, Guerrero; Chacahua; Playa Tomatal (near Puerto Escondido); Escobilla; Playa Larga (all in Oaxaca). Nesting probably occurs sporadically along the entire Pacific coast of Central America, but areas of high concentration are not known. Definite records are lacking for the Pacific coast of Colombia and

Ecuador, but extensive nesting in Peru is suggested (though not proven) by Carl Koford's discovery of the remains of at least 28 individuals within one kilometre of beach at Lagunillas on the Paracas Peninsula in September 1967 (report by letter to Archie Carr, 13 October 1969).

TYPES OF BEACH USED FOR NESTING

Hendrickson and Balasingam (1966) found that in Malaya the important leatherback beach in Trengganu had a coarser grain of sand than the green turtle beaches to the north and south. In Malaya sand grain size correlates with steepness of slope of the beach, and it seems reasonable that the very heavy-bodied leatherback would 'prefer' a beach with sufficient slope so that the climb to dry sand above the high tide mark would not involve a long overland trek. Leatherback nesting beaches in the Guianas are also steeply shelving.

Another characteristics of the Trengganu nesting beach is the unusual proximity of deep water (more than ten fathoms), which may assist the approach to shore of this presumably deep-water species.

The leatherback beach in Tongaland, South Africa, is about 60 miles (100 km) long. The slope of the beach is variable, being steeper where deep water approaches are present. Generally there is a short slope from the water's edge, then a platform 30-150 feet (9-30 m) wide, then another short slope to the dune vegetation. The total width of sand available to nesting turtles varies from 30-900 feet (9-275 m). All parts of the beach are backed by fairly dense coastal bush; there are no lagoons or marshes. The water off the beach is always clear; the beach is almost entirely silica sand, with very localized patches of coarse shell; no mud is present. The beach is stable except during occasional violent storms. The sea is usually fairly rough, with almost continuous surf. Rainfall is restricted to the summer months.

The nesting beach in French Guiana is 10-15 miles (16-24 km) long, being delimited to the west by the mouth of the Marowijne River, while to the east the beach eventually degenerates into mud. The beach is interrupted in a few places where mud and mangrove come right down to the sea; a great deal of hard clayey mud is exposed by low tide in certain parts of the beach used by nesting turtles. The beach itself has a steep shelf at the high tide mark, with a flat area of very variable width (up to 300 feet or 90 metres or more) on which turtles nest, though most nesting is done quite close to the sea. The beach is composed mostly of silica sand, with broken shell deposits in some areas. Rocks are absent, though they are numerous further to the east, near Cayenne. The water off the beach is always turbid. The sea is usually rough — only occasionally can a small boat make a landing. The beach is highly unstable, sand being eroded from some areas and accreted at others at a rapid rate; the overall movement of the beach is towards the west. Behind much of the beach is swamp forest, in many areas of which the trees are dead for a mile or two inland. Some parts are backed up by open salt-water lagoons.

Bigi Santi Beach, Surinam, is only 60-70 miles (100-115 km) away from the French Guiana nesting beach, and shares almost all of its physical characteristics. Shell Beach, Guyana, differs in that the beach material is predominantly or entirely broken shell, and the trees behind the beach are living. This beach is backed up by a mud-bottomed lagoon. The beach is moving westwards at a rapid rate.

Leatherbacks almost never nest on beaches protected by reefs; contact with a reef at low tide, especially in a rough sea, would probably be disastrous for this soft-skinned species.

NESTING PROCESS

The following account describes the nesting of a leatherback at Silebache Beach, French Guiana, on 11 July 1969.

The turtle was first seen, as a dark mound at the edge of the sea, at 11.23½ p.m. It spent several minutes at the edge of the water, remaining stationary most of the time, but was apparently stimulated to move up the beach by the wash of each wave, when the animal made about three heaving-forward movements, with all four limbs moving simultaneously, before resting again. The animal's breathing was distinctly audible from a distance of several yards. As the turtle gradually moved up the beach, it heaved forward two to five times before resting for 4 to 10 seconds. The track up the slope of the beach was sinuous — perhaps this represents an attempt to lessen the effective slope of the ascent, although it is also seen on occasion on the downhill slope from the crest of the beach to the nest site. At this stage not only heavy breathing but also periodic grunts were audible.

The turtle reached the high tide mark at 11.32, and two minutes later stopped moving forward and began to throw sand backwards with powerful simultaneous movements of the front flippers. In between the burst of sand-sweeping thrusts, the hind flippers and tail, working as a unit, would swing sand to left and right several times; when the front flippers stopped moving after each burst of activity, the hind part of the shell would be moved sharply to one side, and the hind flipper movement would commence. When the body of the turtle was not actually moving, the tail was thrust into the sand, as if appraising its texture.

At 11.45 the front flippers moved for the last time, and one minute later the hind flippers began to push sand outwards alternately with the leading edges. At 11.47 the turtle was still pushing rather than excavating sand with the hind flippers, and the tail was still 'appraising' the sand beneath it. However, by 11.48 the movement was gradually becoming a scoop as the mound of sand below the tail was removed, though the tail itself continued to thrust sand aside. By 11.50 the digging movement was established, the distal part of the flipper being curled into a palm as the entire flipper was thrust into the growing cavity; sand was picked up by two scraping thrusts with the leading edge, then was lifted out of the hole and deposited at one side. At this moment the opposite flipper kicks outwards and upward, ridding the site of sand from the previous stroke. The eyes were closed at the moment of the forward 'kick'; 'tears' were flowing copiously at this stage. As the hole became deeper, it became enlarged anteriorly by the scraping action of the flippers, and the lower part of the hole became slightly heart-shaped. The hind flippers carried out identical movements alternately in digging the nest, the body pivoting on its forward end to bring the working flipper directly over the hole. The movement continued until virtually no more sand was being brought out, then became slower and stopped. The flippers were spread out behind the body, partially overlapping and with one of them partly within the cavity. The tail and slightly everted cloaca were lowered into the cavity.

Oviposition commenced at 12.10 a.m. The first two eggs were of normal size but distinctly oval. Eggs were extruded in bunches at intervals of 10 to 20

seconds; the numbers in each bunch were as follows: 3; 4; 2; 3; 4; 2; 5; 3; 3; 1; 4; 2; 2; 2; 2; 2; 2; 2; 2; 2; 2; 3; 3; 2; 2; 2; 2; 2; 3; 3; 2; 2; 2; 3; 1; 2; 4; 1; 3; 1; 1 plus 4 yolkless; 1 plus 3; 2 plus 4; 2 plus 2; 1 plus 5; 1 plus 2; 3 yolkless. During each deposition the carapace was tilted very slightly just before the eggs were actually dropped. The turtle raised its head sharply from time to time. Some contraction of the muscular surface of the hind limbs was noticed during deposition, but no actual movement of the limbs.

The turtle started filling in the nest cavity at 12.20. The hind flippers kicked forward alternately and then pulled sand into the cavity, patting it down with up to seven or eight slaps. As the cavity filled, much weight was brought to bear on the impacted sand, and the forward kicking stopped. During this pressing-down movement the tail was stuck down into the sand. At 12.33 the turtle was still bringing in sand and pressing it down, but the hind flippers were now reaching out sideways as far as they could stretch to bring in more sand.

At 12.35 the front flippers moved for the first time in 50 minutes; they moved forward in a symmetrical 'breast-stroke' movement, chopped away at the sand in front of the turtle, and then threw it vigorously backward. Bursts of several such movements were interposed with a side-to-side swinging of the hind limbs and tail, acting as a unit. During this time 'tears' were hanging and swinging from the eyes in long, sandy dangles. The sand-chopping movement continued for a long time, throwing sand back and gradually moving the turtle forward. Initially this movement was in the direction of the sea, but then the turtle turned through more than 180° and started heading inland. However at 1.03 the turtle turned and headed directly for the sea, without pausing. It reached the sea at 1.05, and seemed to gain in vigour with contact with the waves; at this point the turtle rapidly moved out of sight.

The total time spent ashore in the above case was 101½ minutes. Three Costa Rica nesting leatherbacks were on shore for 80, 93 and 95 minutes (Carr and Ogren 1957). Hughes et al. (1967) found that Tongaland leatherbacks were generally on the beach for 90 to 120 minutes. Bacon (1969) found that in Trinidad the turtles are usually ashore for about 90 minutes.

The nesting sequence described above seems to be typical of the species in all respects, and no significant deviations from this have been reported for leatherbacks from other areas. However, some minor variations have been observed. Although leatherbacks ascending the beach in French Guiana usually leave a sinuous track, this has not been reported from other areas. Also the turtle may rest repeatedly on the return journey to the sea (Deraniyagala 1939), though even when this happens the animal seems to gain in energy from proximity to, and then contact with, the sea. In Surinam and French Guiana the track beside and across a completed leatherback nest often shows tight 'orientation circles', and sometimes the turtle may wander dozens of yards down the beach, turning in tight circles part or all of the way.

When leaving the sea and ascending the beach, the leatherback is probably less easily disturbed than any other sea turtle species, expect perhaps a ridley during an *arribada*. Flashlights shone on the face of the animal usually have no effect (though if the light is sustained the turtle will attempt to follow it), and the animal can even be gently touched. However, if tagged at this stage, the turtle will usually return to the sea. Perhaps correlated with the relative imperturbability of an emerging leatherback is the infrequency of 'half-moons' (non-nesting emergences), commonly seen with green turtles and other species. 'Trial nesting' is also rare — and is difficult to demonstrate,

since the presence of an observer could conceivably have disturbed the animal, and if the observer arrives at a later stage, his inability to find the eggs is no proof that none were laid.

As with all sea turtles, it is very difficult to disturb a leatherback that is actually laying its eggs, except sometimes whilst the first few eggs are being laid.

It is not rare to find individual leatherbacks one of whose hind flippers is ineffective in removing sand from the nest cavity, even though there may be no external sign of injury. Since all the actual digging work has to be done with the other flipper, the final hole is asymmetrical in such cases, and takes much longer than usual to complete.

In Surinam and French Guiana it sometimes happens that the nesting turtle starts to fill in the egg cavity before all of the undersized eggs have been laid; the animal pauses in its filling-in process to lay these or, occasionally, drops them on the sand as it returns to the sea.

NESTING FREQUENCY

Hughes *et al.* (1967) found the following intervals between recorded nesting emergences of leatherbacks in Tongaland: 9 days (3 cases); 10 days; 18 days; 27 days; 28 days; 30 days; 32 days; 36 days; 37 days; 48 days. All these records are consistent with the assumption that leatherbacks nest at intervals of either 9 or 10 (or, in one case, 11) days.

The Surinam leatherback tagging project, initiated by Pritchard and later continued by Schulz, Hill and personnel of the Surinam Forest Service, has yielded more abundant data on inter-nesting intervals. No turtles were found back on the beach between 4 and 6 days after tagging, or between 14 and 16 days; we may therefore assume that those turtles which were seen nesting again between 7 and 13 days after tagging were renesting for the first time. Out of 36 instances, intervals recorded were as follows: 7 days (1); 8 days (3); 9 days (5); 10 days (10); 11 days (12); 12 days (1); 13 days (4). The average inter-nesting interval was 10.33 days.

No turtles re-nested 14-16 days after tagging, or 26 days after tagging; recordings after 17-25 days may therefore be attributed to the second re-nesting. Recorded intervals in this bracket were 17 days (1); 18 days (4); 19 days (5); 20 days (9); 21 days (10); 22 days (1); 23 days (9); 24 days (6); 25 days (2). The average of the 47 cases was 21.44 days, or 2×10.72.

When one applies this average inter-nesting interval of about 10.5 days to the first and last recorded nestings of individual turtles during a season, it would appear that leatherbacks commonly nest six times during a season, sometimes seven times, and rarely eight or even nine times (two turtles were seen nesting 80 and 84 days respectively after tagging). Changes in complements of eggs deposited through the season have not been documented, but Hill (pers. comm.) found that the proportion of yolkless eggs is higher in the last clutch of the season.

A more massive leatherback tagging project by Pritchard in French Guiana in 1970 was so structured that only second returns to the beach could be recorded; tagging was carried out for one week, and was resumed for a further week after a break of thirteen days. Sixty-seven re-nestings were recorded, after the following intervals: 16 days (1); 17 days (5); 18 days (12); 19 days (18); 20

days (18); 21 days (8); 22 days (4); 24 days (1); the mean interval was 19.40 days, or 2 × 9.7 days. The discrepancy from the Surinam mean of about 10.3 to 10.7 days is puzzling, but may be attributable to the possibility that in many cases Surinam-nesting turtles were disturbed by over-enthusiastic taggers, and were obliged to postpone their nesting to the following night. It is also conceivable that the average inter-nesting intervals becomes slightly shorter as the season progresses, since the Surinam intervals recorded above were all early-season, while those from French Guiana are late-season.

LOCALIZATION OF NESTING ACTIVITY

Hughes et al. (1967) have found that in Tongaland leatherbacks at least sometimes return to the same areas to breed. The table below shows the actual distances between nests made by the same individual.

Time Interval and Distance between Observed Successive Crawls of Leatherback Turtles

Interval I			Interval II			Interval III		
Time (days)	Distance (miles)	(km)	Time (days)	Distance (miles)	(km)	Time (days)	Distance (miles)	(km)
10	3/4	1.2	18	9 1/4	14.9	9	6 3/4	10.9
1	1	1.6	48	6	9.7			
1	1/4	0.4						
9	1/4	0.4						
9	4 1/4	6.84						
30	4	6.4						

Also, two turtles found back on the beach two years after tagging had emerged 1/4 mile (0.4km) and 7 1/4 miles (11.7 km), respectively, from the sites of their earlier emergences. These, incidentally, are the only available data on the frequency of nesting seasons for the leatherback, apart from a single Surinam individual that nested in both 1966 and 1969.

The fact that if turtles are found back on the beach at all, they will usually be found quite near the earlier emergence site, is an unavoidable result of the fact that most tagging programs are conducted over relatively few miles of beach. In 1969 and 1970, when tagging personnel were working simultaneously on Bigi Santi and Krofija Passie, Surinam, and on Silébâche Beach, French Guiana, several cases were encountered of turtles moving more than sixty miles (100 km) and across large river mouths between nestings. In all cases the turtles moved eastward, from Bigi Santi/Krofija Passie to French Guiana. Details are given in the table set out overleaf (page 22).

Taking several factors into consideration — the relatively small number of leatherbacks that nest in Surinam, the relatively high number that have been recovered in French Guiana on the nesting beach later the same season, despite the very incomplete coverage of the beach in French Guiana by tagging personnel, the fact that perhaps a hundred times as many leatherbacks nest on a mid-season night in French Guiana as in Surinam, and the fact that only on one

Records of leatherback turtles found nesting in both Surinam and French Guiana

Tag.no.	Date of last recorded nesting in Surinam	Date seen nesting in French Guiana	Interval (days)
E1621	4 June 1969	25 June 1969	21
E1642	13 May 1969	9 July 1969	57
E1741	10 April 1969	3 July 1969	84
E1779	13 May 1969	9 July 1969	57
E1822	8 June 1969	28 June 1969	20
E2898	8 May 1969	1 July 1969	54
E3392	20 June 1970	7 July 1970	17
E3524	24 April 1970	15 June 1970	52
E3533	26 April 1970	5 July 1970	70
E3646	23 May 1970	3 July 1970	41

occasion has a leatherback been recorded nesting in Surinam in different years — it appears quite possible that Surinam does not 'have' a discrete nesting population of leatherbacks. Turtles found nesting there may be merely stragglers from the big French Guiana rookery, which manage to find their way back to 'headquarters' either later in the same season or in the next nesting season. However, it is also true that the majority of leatherbacks tagged early in a season in Surinam return to the same beach many times during the season; and the absence of any records in later years may be caused by the failure of the soft-skinned leatherback to hold a tag from year to year.

In Costa Rica, Carr (pers.comm.) has shown that leatherbacks may show a preference for different parts of the coast in different years. Fresh tracks were counted from a low-flying aircraft on 21 March 1965; 33 were seen north of Matina, but none to the south. On 20 March 1967, 43 were seen north of Matina and 13 to the south. On 3 April 1968, 4 were seen north of Matina and 21 south.

CLUTCH SIZE

Although markedly undersized, yolkless, dumb-bell-shaped or otherwise malformed eggs are only found in a small minority of nests of Cheloniid sea turtles, they are invariably present in leatherback nests, even at the beginning of the season, though the ratio of normal to undersized eggs is very variable. The undersized eggs tend to be laid towards the end of oviposition; frequently none appear until thirty or forty eggs of normal size have been laid, while the last few extrusions are often composed entirely of minute, yolkless eggs. However, Pritchard in French Guiana and Hughes in South Africa have both observed that the first couple of eggs to be laid are frequently ovate, rather than spherical, though of normal size.

The leatherback, despite its size, lays fewer eggs, on average, than any other sea turtle except *Chelonia depressa*. Pritchard (1969) records the following egg complements from a series of Surinam nests: 58 normal plus 40 undersized; 69 plus 11; 70 plus 1; 83 plus 23; 100 plus 35; 101 plus 39; 120 plus 12; 126 plus 40. Some other nests, in which only normal eggs were counted, contained the following numbers of eggs: 57; 65; 66; 70; 72; 72; 72; 75; 76; 79; 81; 83; 84; 86; 87; 90; 92; 98; 100; 102; 106; 113 (M = 86.0). Data provided by Schulz (1968) show substantial aggreement with these figures; 48 nests gave the same average (86 eggs), the distribution being as follows: 50-59: 2%; 60-69: 10%; 70-79: 23%; 80-89: 25%; 90-99: 23%; 100-109: 12%; 110-119: 4%. Schulz also noticed that mid-season clutches tended to be larger than early and late-season clutches; average clutches in April and June contained around 80 eggs, while those laid in May 1967 averaged 90, and in May 1968, 98. Sample sizes in each case, however, were only between 8 and 14; and twenty nests made by what is probably the same population in the first half of July (i.e. late season) at Silébâche Beach, French Guiana, contained the following numbers of eggs: 51 plus 15; 61 plus 41; 70 plus 27; 77 plus 29; 77 plus 43; 78 plus 23; 78 plus 44; 84 plus 27; 89 plus 22; 89 plus 50; 92 plus 25; 93 plus 48; 95 plus 17; 96 plus 57; 104 plus 12; 105 plus 9; 106 plus 10; 110 plus 19; 112 plus 35: (M = 88.1 normal, 29.1 undersized). Hill (pers. comm.) found that in Surinam the percentage of yolkless eggs in twenty nests ranged from 12.1 to 39.6, the mean being 25.3%. The average nest contained 87.0 normal eggs and 29.6 yolkless.

In Tongaland, South Africa, the mean clutch size is greater; Hughes *et al.* (1967) found the mean number of normal eggs in 24 nests to be 106 (S.D. ± 22); the mean number of undersized eggs was 30 (S.D. ± 27). The fewest normal eggs found in a nest was 58; the most was 160, which appears to be a record for the species. In Trinidad the clutch size ranges from 65 to 130 (Bacon 1969).

According to Balasingam (1967), the average clutch size of leatherbacks at Trengganu, Malaya, is 85-90, though his figure of 51, 582 eggs from 627 clutches gives a slightly lower average (82.3). The smallest number found in a nest was 33; the greatest was 140. In either case the mean clutch size is more similar to that in the Guianas than to that of the geographically closer Tongaland population.

Deraniyagala (1939) does not quote an exact mean for leatherback clutches in Ceylon, merely stating that 90-130 eggs are laid at a time, ten to fifteen of which are abnormally small or otherwise malformed.

Six leatherback nests from the Caribbean coast of Costa Rica, according to Carr and Ogren, contained 45 plus 7, 66 plus 38, 66 plus ?, 73 plus 34, 74 plus ?, and 80 plus 41 eggs (M = 67.3 normal eggs).

No series of egg counts from the East Pacific is available; however, according to Montoya, the mean clutch size on the Mexican Pacific is only around 50.

INCUBATION PERIOD

Seven natural nests on Bigi Santi, Surinam, hatched after 60, 60, 60, 61, 63, 65 and 68 days respectively. Deraniyagala (1939) found that transplanted nests in Ceylon hatched, on average, after 67 days, the extremes being 58 and 72 days. Hughes found that Tongaland nests hatched after 56 to 72 days. Balasingam (1967) found that transplanted clutches of Malayan leatherback eggs hatched after 53-60 days. Carr and Ogren (1957) found that two transplanted nests at Tortuguero and Matina, Costa Rica, hatched after 66 and 74 days respectively,

while hatchlings had already emerged from a natural nest after 58 days. A natural nest at Fort Lauderdale, Florida, hatched after 62 days (Frair, pers. comm.). Montoya (pers, comm.) reports that the incubation period in Mexico is 61 to 70 days.

Schulz (1968) perceived an interesting tendency for eggs laid later in the season to hatch after a shorter interval than early-season eggs, even though the actual hatching percentages were extremely low throughout the season. Actual data obtained were: ten clutches laid during the period 27 April to 31 May 1967, yielded 142 hatchlings, 6 of which emerged after 64 days, 9 after 65 days, 62 after 67 days, 21 after 68 days, 41 after 71 days, and 3 after 73 days. Eleven clutches laid during the period 1 June to 4 July yielded 138 hatchlings — 35 after 59 days, 2 after 60 days, 4 after 61 days, 42 after 62 days, 4 after 63 days, 37 after 64 days, 9 after 65 days and 4 after 66 days. The simplest explanation of the shorter average incubation time for the later clutches is that they were incubating after the rainy season had passed, and ground temperatures were higher. Similar trends were observed for green turtle and ridley nests.

In all cases these incubation periods refer to the interval between deposition of the eggs and emergence of the young at the surface; actual hatching probably precedes emergence by two or three days.

FERTILITY OF EGGS

Hughes *et al.* (1967) gave the following data for hatching success in four leatherback nests (not transplanted):

Total no. yolked eggs	69	84	106	139
No. of hatchlings	55	65	102	88
Infertile eggs	6	18	4	49
Hatchlings dead in nest	0	0	5	0
Hatchlings alive in nest	0	4	3	0
Hatchlings successfully out	55	61	94	88
Unhatched fertile eggs	8	1	0	2
Hatching success, percentage	79.7	72.6	88.7	63.3

Data on eleven Tongaland nests are now available; mean percentage hatch was 75.6%, S.D. ± 10.6.

Four non-transplanted nests containing an average of 86 eggs each produced 46, 71, 74 and 81 hatchlings (i.e. mean percentage hatch 76%) at Bigi Santi, Surinam, in 1964 (Schulz 1968). Montoya (pers. comm.) found that in Mexico the hatching rate in leatherback nests is about 70%, the remainder corresponding to about equal numbers of infertile eggs and retarded developers. Hill (pers. comm.) records that 16 natural leatherback nests on Bigi Santi yielded an average hatching percentage of only 19.9, while a total of eight transplanted nests yielded only five hatchlings altogether. He attributes this failure to the presence of yolk from eggs which had been broken when the nest was located by probing with a stick.

Balasingam (1967), working at Trengganu, Malaya, experimented with a total of 627 transplanted leatherback nests over a five year period. He found that hatching percentage was best when nests contained around 50 eggs, and was able to obtain an overall percentage hatch of 73.8 in artificial nests containing 46-50 eggs, while transplantation of whole nests, containing up to 140 eggs, yielded only a 34.4 to 58.9% hatch. He reasoned that a clutch of 46-50 eggs generated the optimum amount of heat throughout the egg mass; larger clutches became overheated in the middle, while smaller ones were a little too cool throughout. However, it is also possible that in large artificial nests the upper eggs are too close to the hot dry surface sand to have a good chance of hatching.

SIZE AND COLOUR OF EGGS

Hughes *et al.* (1967) found the mean diameter of 165 leatherback eggs from Tongaland, taken in groups of ten from 16 clutches, to be 53.07 mm, with a standard deviation of 1.49 mm. Eggs in one clutch ranged from 50 to 56 mm in diameter; there was no tendency for larger eggs to be laid earlier or later in the clutch than others, though, as mentioned earlier, markedly undersized and yolkless eggs, not counted here, are produced for the most part towards the end of oviposition.

Carr and Ogren (1959) found that 66 eggs from a clutch at Tortuguero, Costa Rica, ranged in diameter from 50.3 to 59 mm, the mean being 55.4 mm. Forty-five eggs from a clutch at Matina, a few miles down the coast, ranged in diameter from 50.1 to 53.6 mm, the mean being 51.8 mm.

Deraniyagala (1939) found that Ceylon leatherback eggs ranged in diameter from 50 to 54 mm, and weighed between 61 and 85 grams (usually between 70 and 80 grams). The actual mean of eighteen eggs from three different clutches was 52.5 mm, the range being 51 to 54 mm.

Montoya (pers. comm.) found that leatherback eggs in Mexico ranged from 51 to 56 mm in diameter. In Trinidad Bacon records extreme diameters of 52 and 65 mm. A distinctly oversized egg from French Guiana also had a diameter of 65 mm. The size of the yolkless eggs is very variable, ranging from a few millimetres to about 35 mm.

The eggs are almost always white. However a few with irregular green spots and blotches have been found in both Ceylon and Surinam. The green coloration is presumably bile.

TWIN EMBRYOS

Deraniyagala (1939) recorded five cases of two embryos within a single egg; in each, one embryo was distinctly smaller than the other Hughes *et al.* (1967) report a single similar case in Tongaland.

INJURIES

Among French Guiana nesting female leatherbacks, deep gashes in the shoulder region were seen quite often, while gashes in the back of the neck were less frequent but still quite common. The hind margins of both fore and hind flippers were often tattered and perforated, and sometimes the distal third of

half of either a fore or a hind flipper was missing. The skin in the thigh region is very soft, and twice turtles nested so that this part rubbed against a piece of wood with each stroke, with profuse bleeding resulting.

Every one of over a thousand nesting female leatherbacks seen in French Guiana and Surinam had a pinkish area on the crown of the head, in the area corresponding to the junction of the frontal and parietal bones, and this is apparently present in leatherbacks from other areas also. Possibly this is part of the normal colour pattern of the animal; however it has the appearance of an injury which has healed but to which pigment has not returned, and it may be the site of friction with the chin of the male during copulation. However, as Schulz has pointed out, it is strange that the wound never seems to be raw, but it always well healed.

Several individuals seen in French Guiana had a series of very deep, parallel, longitudinal scratch marks along the entire length of the head — possibly the result of being pawed by a jaguar while ashore. Occasional individuals in French Guiana and Surinam have the posterior projection of the carapace broken off, and in one case not only the rear part of the shell, but also the tail and a substantial volume of flesh from the thighs was missing, so that the vent appeared as a small opening in a postero-dorsal position. Unfortunately oviposition of this turtle was not witnessed, as it was already covering its nest when found.

Hughes *et al.* (1967) report that in Tongaland most injuries were restricted to the flippers, and in only one case (in which both hind flippers were completely lost) did the animal appear permanently inconvenienced by the injury. However, as in Surinam, occasional individuals lack the posterior tip of the carapace.

Brongersma (1969) mentions several records of leatherback turtles in northern waters having been injured or killed by ship's propellers. Bullet holes in the head and shell are not infrequently found in leatherbacks washed ashore in northern Europe.

TIMING OF NESTING

Leatherbacks almost always nest by night, although there are one or two cases on record of diurnal (late afternoon) emergences in Surinam. Hughes *et al.* (1967) report that in Tongaland encounters with nesting animals begin at around 7.30 p.m., with most encounters taking place around 11 p.m. In Trinidad emergences tend to coincide with a rising tide, and have only been recorded before midnight (Bacon 1969). In French Guiana nesting rarely takes place when the tide is extremely low, when the animal would be presented with a long, arduous climb to the nest site. On some nights (e.g. 27 June 1969) nesting was restricted to the hours when the tide was fairly high (12.30-3.30 a.m.), although the following night turtles were nesting at both high and fairly low tide. On 29 June most nested at rising tide, and a few at high and falling tide. However, on 7 July, none nested at rising tide, a few at high tide but most nested when the tide had gone about half way down. Those few which made an appearance at rising tide turned straight round in a 'half-moon' and returned to the sea. It seems that the bulk of nesting takes place in the middle hours of the night. Pritchard and Greenhood patrolled a 450-yard (400 m) stretch

of beach in French Guiana every hour of the night of 9-10 July 1969, and encountered the following numbers of turtles on the beach:

8-8.15 p.m.:	1 (plus 1 fresh, completed nest)
9-9.15:	4
10-10.15:	8
11-11.15:	11
12-12.15 a.m.:	10
1-1.15:	10
2-2.15:	11
3-3.15:	9
4-4.15:	3
5-5.15:	3

Two turtles were still on the beach at dawn.

Hill (pers. comm.) gives the following times of tagging for 52 leatherbacks nesting on Bigi Santi, Surinam, in 1969:

2-3 p.m.	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-1
1	0	0	0	0	3	1	4	15	11	6

1-2	2-3	3-4	4-5	5-6	6-7
4	4	3	0	0	1

Deraniyagala (1939) states that in Ceylon the leatherback usually emerges to nest between 9 and 11 p.m. Carr and Ogren (1959) describe the nesting of three individuals at Matina, Costa Rica, which emerged at 9.50 p.m., 9.55 p.m. (June 11), and 9.55 p.m. (June 12) respectively.

Leatherbacks are less put off by bad weather conditions than other species of sea turtle, and one finds just as many nesting on nights of pouring rain and high wind as on calm, clear nights.

There appears to be no lunar correlation of nesting; the motivation to nest is apparently governed entirely by internal factors.

An unexplained phenomenon is that, in French Guiana, at least, pre-nesting and nesting leatherbacks are much more easily disturbed on some nights than on others. No correlation of such behaviour with lunar conditions was discernible.

HATCHLINGS

Carr and Ogren (1959) give the following average measurements for 30 one-day-old sibling leatherbacks from Tortuguero, Costa Rica:

Carapace length:	62.8 mm.
Carapace width:	41.8 mm.
Plastral length:	53.6 mm.
Head width:	18.04 mm.
Depth:	26.3 mm.

Hughes *et al.* (1967) found Tongaland hatchlings to be slightly smaller - averaging 59.82 mm (± 1.98 mm) in length and 39.41 mm (± 1.47 mm) in width (N = 22).

Pritchard (1969) found that 25 random hatchlings from one nest ranged in length from 56 to 60 mm (mean 58.3 mm), and in width from 39 to 44 mm (mean 41.2 mm); plastral length ranged from 49 to 56 mm (mean 52.2 mm). Twelve from another nest ranged from 59.1 to 63.9 mm in carapace length, and 27 from a third nest from 54.6 to 60.6 mm.

Deraniyagala (1939) found that hatchlings in Ceylon ranged in length from 58 to 60 mm.

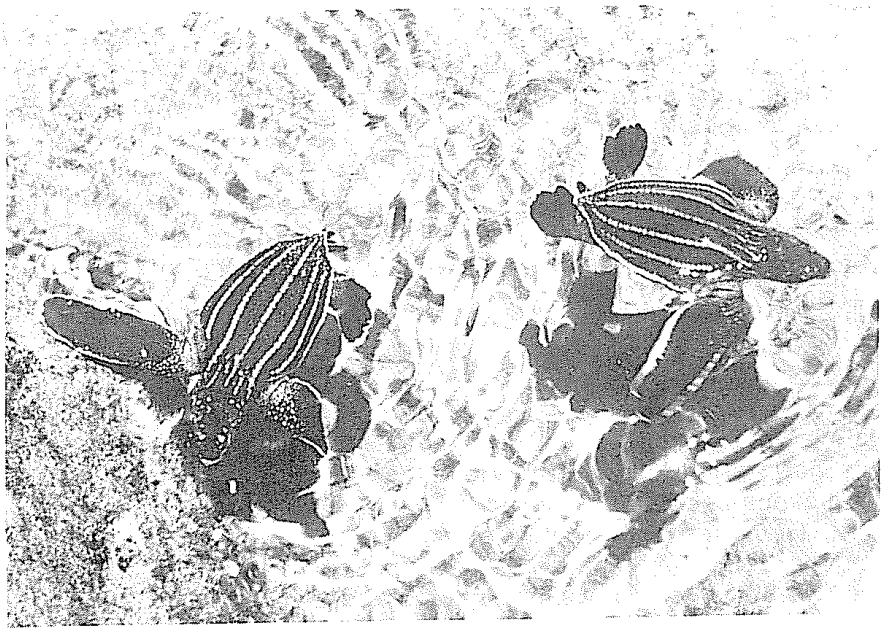
The hatchlings are similar to the adults in appearance (see Plate II), but the fore flippers are proportionately even longer, and both shell and skin are covered with small scales. These flake off after a few weeks. No trace of the epidermal layer of mosaic bones is present at hatching; this develops during the first year or two of life. The hatchling also possess striking white lines along each of the carapace ridges. These disappear well before maturity is reached, although their continuations along the skin of the neck remain.

As with all sea turtles, the hatchlings emerge from the nest 'explosively' - all appear at the surface with a period of about a minute, except for stragglers and slow developers. Emergence almost always takes place at night, usually shortly after dusk. Hatchlings fresh from a nest head seaward accurately and with great vigour even when placed well back on the beach, out of sight of the sea. However, those that have been kept for some hours are sometimes relatively inactive when released on the beach, orient poorly if at all, and tend to trip over their own front flippers. The normal gait of the hatchling is basically similar to that of the adult – that is, the front flippers make a 'breast-stroke' movement, thrusting the animal forward, while the hind flippers push back through an arc that brings them together behind the after point of the carapace. However, because of the relative lightness of the hatchling, the body raises high off the ground with each stroke. A typical, alternating, reptilian gait is also sometimes used (Hughes *et al.* 1967). While moving down towards the sea, the hatchlings quite frequently turn in small, tight, complete circles, called 'orientation circles' by Carr and Ogren (1959). Tracks of nesting adults also show such circles quite frequently; their extent and possible function are at present the subjects of a study by Nicholas Mrosovsky.

Almost all those who have tried to raise hatchling leatherbacks in captivity have found that they died within forty days or less, even though they may feed well. Until recently the only exceptions to this were Deraniyagala's successes in raising one to an age of 169 days, and another for 662 days (at which point it had a carapace length of 420 mm and a weight of about 16 lbs.), when it died from accidental pollution of its water. However, a hatchling from Fort Lauderdale reached an age of 79 days and a carapace length of 13.2 cm in the Ocean World Aquarium (Frair, pers. comm.), and Hendrickson now claims quantitative success in raising baby leatherbacks to weights in excess of twenty pounds, listing the following essential rules: (1) The animals should be kept in a soft-walled tank, since they continually swim into the walls, and all sores should be treated with Gentian Violet; (2) the temperature should not be allowed to vary from 80°F, and the animals should be fed entirely on chopped squid, not on fish. If they are kept too cool, or fed fish, they are likely to become fatally packed with undigested food.

PLATE II

Leatherback turtle hatchlings,
French Guiana.
Copyright Peter Pritchard; by courtesy of World Wildlife Fund.



Leatherback turtle hatchlings, Tongaland,
South Africa.
Copyright George Hughes; by courtesy of World Wildlife Fund.

NATURAL WASTAGE OF EGGS, HATCHLINGS AND ADULTS

In Surinam and French Guiana, a variable but fairly high percentage of nests is made below the high tide mark, and the eggs are killed by inundation with salt water. It is also common for nests to be made above the high tide mark, but for erosion forces to wash away the eggs before they hatch. Some eggs are lost to ghost crabs (*Ocypoda* sp.), but the nests being much deeper than those of *Chelonia* and *Lepidochelys* suffer a much smaller percentage loss. Crabs also kill hatchlings on their journey to the sea; Pritchard picked up several dozen hatchlings that had been killed by crabs in French Guiana in June and July 1969. Only a few from any one emergence had been killed; in all cases the crab had attacked the anterior part of the animal, so that the head and/or one or both front flippers had been severed and the contents of the shell cleaned out. In the Guianas birds are never seen eating baby turtles in the sea, but black vultures *Coragyps atratus* eat eggs that are accidentally left exposed by erosional or human forces, and also hatchlings that emerge from their nests by day (as they do sometimes after heavy rain). Large numbers of sharks may be seen just off the beach in French Guiana, and smaller numbers in Guyana and Surinam; these almost certainly constitute a menace to the hatchling turtles, but it is not known to what extent.

In Tongaland, Hughes reports that ghost crabs and ants may destroy some eggs, and occasionally monitor lizards *Varanus* sp. will dig out a nest. Hatchlings are killed by ghost crabs, genet cats *Genetta* sp. and water mongooses *Ictonyx* sp. Feral dogs constitute a serious menace to both eggs and hatchlings. According to Deraniyagala (1939), monitor lizards also dig for leatherback eggs in Ceylon, though they are not always able to find them.

Adults on the nesting beach in French Guiana occasionally become wedged under or behind the log jams and uprooted trees which litter the beach; in 1969 two turtles which had died in this way were found, and two more in 1970. Also, in 1970, three turtles were found dead in the middle of open areas of beach, with no external injury or other apparent cause of death. In Surinam, and probably French Guiana too, a few adults fall prey to jaguars, and Fitter (1961) reckons that in Trengganu it is only the high human population that prevents loss of nesting leatherbacks to tigers.

At sea the adult leatherback probably faces relatively few predators. Sharks may bite pices off them from time to time, but it is not known if they ever kill adults. Leatherback remains have been found in the stomachs of three killer whales caught off St. Vincent, West Indies (Caldwell 1969).

MIGRATIONS

Although over 4,000 nesting leatherbacks have been tagged during the last few years, not a single tagged individual has ever been recovered at sea (although numerous returns to the beaches where tagging took place have been recorded). There is no single place outside the breeding grounds where leatherbacks may be caught predictably in any numbers, and consequently there is no commercial fishery based on this species; the locality records which do exist for the most part represent scattered sightings at sea, accidental catches in fishing nets, and strandings of dead or weakened animals in shallow water or on beaches. It is nevertheless a virtual certainty that the leatherback is a highly migratory — or at least vagrant — animal; the numbers nesting on restricted beaches in several parts of the world could not possibly be sustained

by the productivity of the immediate vicinity, and healthy specimens of adult size frequently appear thousands of miles from the nearest nesting beaches. The impressive swimming equipment of the leatherback also suggests a long-distance migrant.

It is not known whether leatherbacks normally migrate — or wander — singly or in groups. Leary (1957) reported a school of about one hundred leatherbacks off the Texas coast, and Hendrickson, quoted by Fitter (1961), writes that 'over eighty visited the beach (in Trengganu) the night before I was there in August, and the pilot of an aircraft at the same time saw six flocks at sea, about forty strong.' Sometimes the distribution of nesting leatherbacks on a beach gives the appearance of the animals showing some tendency to form small aggregations. Deraniyagala (1939) wrote that '*Dermochelys* at times comes ashore to lay in small troops and as many as seven were taken on one night in May, 1929, on the beach between Paiyagala and Maggona (W.P.), a distance of about six kilometres.' In French Guiana, where two or three hundred turtles may nest during a night, one often finds a group of up to a dozen or so turtles nesting in less than a hundred yards of beach, yet practically no turtles will be found on the apparently identical stretch of beach on each side of this area. On a slack night late in the season (7 July 1969), two clumps each containing three nesting turtles practically touching each other were found, but there were only two other turtles on the entire $^3/_4$ mile (1. 2 km) stretch of beach patrolled.

Although the nesting range of the leatherback only just extends outside the tropics (in Florida and Natal), individuals are caught at sea in cold, northern waters more frequently than any other species of sea turtle. Eight records exist for Chesapeake Bay (Hardy 1969), all sightings being between June 3 and September 15; the northernmost record from within the Bay was from Dares Beach, Calvert Country, Maryland, where the salinity is approximately half that of pure sea water. Mitchill (1912) and Ford (1879) give records for New Jersey and Delaware, and McCauley (1945) and Jones (1968) give records for Virginia. Bleakney (1965) compiled no fewer than 88 records of leatherbacks from the coastal waters of New England and Canada — 4 from Connecticut, 5 from Rhode Island, 16 from Massachusetts, 1 from New Hampshire, 33 from Maine, 2 from New Brunswick, 25 from Nova Scotia, and 2 from Newfoundland. Fishermen from all major ports in Nova Scotia spoke of 'the turtle season' as extending from June to October; leatherbacks captured in these northern areas were active, apparently in full control of their movements, and had stomachs full of jellyfish (*Cyanea capillata arctica*).

It is interesting that the onset of the 'turtle season' in Nova Scotia coincides with the final weeks of nesting at points two thousand miles to the south. Whether the northern turtles have just completed a marathon swim at high speed from breeding grounds in the tropics is a fascinating question that will only be answered when large numbers of leatherbacks are tagged on the nesting beaches, and special trips made by scientific personnel in Nova Scotia to search for tagged turtles.

The leatherback is not known to breed in the Mediterranean, but specimens are known from Gabes Gulf, Hafacha near Tarf-el-Mâ, Monastir, Sidi Daoud and Cap Bon in Tunisia (Loveridge and Williams 1957); from Ḱelibia, Tunisia (Chakroun 1966); from the Golfe d'Arzeu, Algeria (Loveridge and Williams 1957); from Morocco (Pasteur and Bons 1960); from Yugoslavia (Pozzi 1966); from Palermo, Sicily (Smith and Taylor 1950); from the North and South Adriatic, Italy (Riedl 1963; Labate 1964); off Punta della Chiappa, east of Genoa, Italy (Capra 1949); about six miles from Maguelonne, Hérault, France (Harant 1949);

off La Nouvelle, Aude, France (Petit 1951); and just north of Alicante, Spain. Loveridge and Williams (1957) also record the species from the market in Alexandria, Egypt. It is interesting that the leatherback should be firmly associated in people's minds with the Mediterranean, even though it is only found there occasionally; this is probably because Linnaeus's type locality is in the Mediterranean. Pennant, quoted by Bell (1849), records the following anecdote: 'The late Bishop of Carlisle informs me that a tortoise was taken off the coast of Scarborough in 1748 or 1749. It was purchased by a family there, and several persons were invited to partake of it. A gentleman, who was one of the guests, told them it was a Mediterranean turtle, and not wholesome; only one of the guests ate of it, who suffered severely, being seized with dreadful vomiting and purging.' Also, in the Los Angeles Herald of 25 August 1901, one reads in an account of a leatherback caught near Santa Barbara, California, that 'it must have come from the Mediterranean'!

There are a number of records of leatherbacks from European Atlantic shores. Navaz and de Llarena (1947) report a specimen seen at a distance from San Sebastián, Spain, corresponding to about six hours' sailing. Ferreira (1911) quotes an old record from Perriche, Portugal, and there are at least three records from Finistère Department, France (off Trévignon, Bay of Concarneau, Vaillant 1896; between the Îles Glénans and the Île aux Moutons, Legendre 1925; and between Beg-Meil and the Île aux Moutons, Bouxin and Legendre 1947). Other records exist for Pertuis d'Antioche (between the islands of Ré and Oléron, Charente-Maritime, France, Valmont de Bomare 1771), and the island of Bruc (a dead specimen off Port-Blanc-en-Penvénan, Côtes du Nord, France; 'Le Temps', 20 Sept. 1925), Tranchet Beach, les Sables-d'Olonne, Vendée France ('Presse-Océan', 29 Oct. 1965), Damgan, Morbihan, France (P. Caron, in letter to L. D. Brongersma), and near Biarritz, Basse Pyrénées (Angel 1923). In the Netherlands a dead specimen was recently washed ashore at Ameland, Friesland (Brongersma 1969), and two earlier sightings from the Dutch coast include a record from off the village of Domburg, island of Walcheren, 17 July 1777 (van Iperen 1778), and a dead specimen observed on 29 May 1961, as it drifted past the lightship 'Texel' (53°1. 5'N. 4°22'E., 12 nautical miles due west of the island of Texel; L. Otto, in letter to L. D. Brongersma).

There is a record from Germany (a dead specimen at Friederikensiel, Jever District, August 1930; Greve 1931), while from Norway the earliest record is from Sundmöre (Pontoppidan 1753), and no fewer than nine have been observed since 1956, extending up to 69° 18' N. (Brongersma 1968a; Willgohs 1956, 1957).

There is a record from the south coast of Madeira, on 19 July 1955 (Brongersma 1968b), and a dead specimen was found on the north coast of Iceland in 1964 (Brongersma 1968a).

Taylor (1963) gives nineteen records of leatherbacks from the British Isles, spread fairly evenly over all coasts of England, Ireland, Scotland and Wales. Brongersma (1967) traced 42 records, extending from the Shetlands to the Channel Islands. Stephen (1953, 1961) gives records of a total of 18 Scottish leatherbacks, all but three of which were alive. All the live specimens captured or seen were encountered from June to November; in the winter months (December to March) only dead specimens have been recorded. It is possible that the leatherback is a voluntary, though occasional, visitor to British waters in the summer months, but that those specimens which do not leave the area by November are killed or incapacitated by the increasingly cold water.

The leatherback is a regular visitor to Japanese waters; Nishimura (1964) reports that in winter almost all Japanese records are from the Japan Sea

coast of Honshu, while occurrences on the Pacific side of Honshu and Hokkaido are concentrated in the warm season (May to September). In the north-east Pacific McAskie and Forrester (1962) report leatherbacks from British Columbia; one of these turtles, found on 23 September 1961, was so active that it could not be restrained for accurate measurement, even though the water temperature was only 53°F (11.7°C). Leatherbacks are known from all along the coast of California, even though most newspaper accounts of such records describe the animal as a 'new to science'. Hubbs (1961) gives records for north-western Baja California.

Leatherbacks are also found well south of their known breeding range; from Australia, specimens have frequently been recorded from Queensland (Fischer 1966; Bustard, pers. comm., who reports that leatherbacks are regularly caught in government shark nets in the south of the State), from New South Wales (Gray 1857), from the region of Sydney (Cogger 1960), and from Tasmania. Harrisson (pers. comm.) mentions purchasing in Sydney an aboriginal bark painting from Arnhem Land showing three men in a boat spearing an unmistakable leatherback. Leatherbacks are known from New Zealand (Graham 1964), and from the Cape of Good Hope (Hughes 1969). From the south-east Pacific, leatherbacks are known from Chile as far south as Chiloé Island (Philippi 1899). Goeldi (1906) in his 'Chelonios do Brazil', only mentions three sea turtle species (the green, loggerhead and hawksbill). However, Vaz-Ferreira and Blanca Sierra de Soriano (1960) record that the leatherback is frequently taken on the coast of Uruguay, both on the open Atlantic and in the mouth of the Rio de la Plata. It is not known how much further south the species may be found.

PARASITES AND EPIZOOPHYTIC ORGANISMS

Barnacles are rare on leatherbacks, probably because the smooth, soft skin makes attachment difficult. However, Hughes *et al.* (1967) found small ones on the carapace and neck region of Tongaland leatherbacks, and Bacon (1969) found that 'many' females in Trinidad carried barnacles of the genus *Platylepas*.

The Trematode *Astrorchis renicapite* (Leidy) has been found in leatherbacks from France (Heldt 1933), and Trematodes of undetermined species are quite commonly found in leatherback intestines. Dunlap (1955) found several flat parasitic worms, $1\frac{1}{2}$ inches (3.8 cm) long, in a leatherback from the Gulf of Mexico. Nematodes as well as Trematodes were found in a Norwegian leatherback, captured eight miles (13 km) west of Skarwy.

Dunlap (1955) found numerous amoebae resembling *Entamoeba histolytica* among the intestinal contents of the Gulf of Mexico specimen.

Remora or sucking fish (*Echeneis naucrates*), are sometimes found attached to leatherbacks (Yerger 1965); one specimen had four large remoras attached to the carapace and lateral edges of the plastron; another was accompanied by an estimated 1000 or more small remoras, which were apparently not attached to the turtle, though several attached to the body of the investigator when he entered the water near the turtle.

WORLD POPULATION ESTIMATES

The only meaningful and practicable estimate that can be made of world leatherback population numbers will be based on breeding females only; males are

rarely seen and impossible to count, while if we include immatures we would have a huge but very temporary peak in late summer, when hatchlings are being produced in great numbers from all the northern hemisphere breeding grounds.

As has been shown elsewhere in this paper, leatherbacks re-nest at intervals of about ten days; Hughes *et al.* (1967) found that leatherbacks may nest at least four times in a season, and Pritchard's Surinam data suggest that seven nestings in a season may not be rare. On the assumption, then, that an individual turtle nests at ten-day intervals for two months, and that a season lasts about four months, we may estimate the nesting population for a season as twenty times the number nesting on an average night. We have very little data on the interval between nesting seasons; however Hughes has found individuals nesting either two or three years after tagging, and there is one record of a Surinam turtle nesting in 1966 and 1969. We might therefore multiply one season's nesting population by 2.5 to estimate the total nesting population — that is, multiply the number nesting on an average night by 50.

On this basis, about 4,000 leatherbacks nest in Trengganu, Malaya, and about 15,000 in French Guiana. No other single nesting ground is of comparable importance, but at least 1,000 leatherbacks (possibly many more) nest at Matine Beach, Costa Rica, and perhaps 200-400 each in Trinidad, Surinam, Tongaland and Celyon (and South India). We can only guess at the size of the population that nests on eastern Pacific shores from Jalisco, Mexico to northern Peru; but it may be at least 8,000. Also odd individuals may nest in many other places, as outlined in the section on breeding range. Nevertheless the above populations would give a total of perhaps 29,000, and taking into account unknown or uninvestigated beaches, we may therefore estimate that there are between 29,000 and 40,000 breeding female leatherbacks in the world.

SURVIVAL SITUATION AND PROSPECTS

A total of less than 40,000 breeding females for a world-ranging species is not great — certainly world populations of leatherbacks are very much smaller than those of Pacific ridleys or green turtles, even though concern has been expressed over the future of both of those species. Nevertheless it is a much larger figure than Fitter's (1961) figure of perhaps 1,000 pairs — and before the discovery of the Trengganu rookery many people believed that the species was on the point of extinction. What is more important, there is no evidence that present numbers are yet substantially reduced from primordial, equilibrium population levels. The French Guiana beach, though between ten and fifteen miles long and with a wide nesting area, seems to be used practically to capacity — towards the end of the season the beach is a continuous expanse of old and new nests, and about one turtle out of five destroys an earlier nest while constructing its own egg cavity.

Future prospects for the various breeding populations of leatherbacks are variable. Egg collectors are probably still a serious problem in Costa Rica, as they were when Carr and Ogren visited the nesting grounds there in 1958; although conservation laws do cover leatherbacks, enforcement is concentrated on the green turtle, which nests further to the north and later in the year. In Trinidad the present situation is very serious; nesting turtles are frequently killed for their meat, although voluntary patrols organized by the Trinidad Field-Naturalists Club are achieving some success in lessening this. Bacon (1970) estimated that between 20 and 30% of the breeding population in Matura Bay is killed annually. The main hope is for parties of sightseers and tourists

to gather round each nesting turtle in such numbers that no poacher would dare attempt to kill the turtle. In Guyana the situation is probably hopeless. Although the Arawak and Portuguese green turtle hunters on Shell Beach, Guyana, do not usually eat leatherback meat, they regularly kill nesting leatherbacks on some strange logic that this is a worthless turtle and ought to be killed. However, the nesting populations there are small compared to those of Surinam and French Guiana, where few if any are killed. In Surinam the leatherback enjoys complete protection — and since the conservation personnel there move back nests made too close to the sea, the human presence actually benefits the turtles. In French Guiana sea turtles and their eggs are now protected by law; there are no enforcement personnel, but the beach where most of the leatherbacks nest is so remote that egg collectors are rare and sporadic, and killing of the adults apparently no longer takes place. However, eggs laid on beaches near the Carib villages in the mouth of the Marowijne River, separating Surinam from French Guiana, are almost all taken.

Nothing is known of the survival situation or prospects of the eastern Atlantic leatherback colonies, though it is very likely that human predation is intensive. Leatherbacks are probably safe on the Tongaland (Natal) nesting ground, as proclamation of the area as a complete sanctuary is imminent, and patrolling of the area will continue. However, leatherbacks found to the north in Moçambique are frequently killed.

Turtles nesting in Trengganu, Malaya, are never killed; however it seems certain that the number of eggs taken is excessive. The situation is such that no nest goes unnoticed, and only those bought from the licence-holders by conservation personnel have a chance to hatch. A total of 26, 581 hatchlings was released in the five-year period 1961-1965, and about 48, 000 released in the three-year period 1966-68. However, even an annual total of 16, 000 hatchlings represents the production of only two or three peak nesting nights, and it is to be hoped that funds will soon be available to increase greatly the annual purchase of eggs.

In Mexico the leatherback enjoys legal protection at all times, and the eggs, like those of all other sea turtles, may be be collected. It is probable that relatively few leatherbacks are killed illegally, although Pritchard found remains of at least four slaughtered individuals on the beach near Piedra de Tlacoyunque, on the Pacific coast.

Koford's discovery in September 1969 of remains of at least 28 slaughtered leatherbacks on one kilometre of beach at Lagunillas on the Paracas Peninsula in Peru may indicate that a nesting colony there is being decimated.

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