

STUDIES OF THE SYSTEMATICS AND REPRODUCTIVE
CYCLES OF THE GENUS **Lepidochelys**

By

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INTRODUCTION

Lepidochelys is one of the five genera of living sea turtles, and is currently thought to include two forms (kempi and olivacea), which are given full specific status by most modern authorities, though only subspecific status (within the species olivacea) by others. Herpetologists commonly call both species 'ridleys', a vernacular name of unknown origin used by Florida turtle fishermen.

Lepidochelys kempi breeds only on the Gulf coast of Mexico, though non-breeding individuals are found throughout the Gulf of Mexico and on both sides of the North Atlantic Ocean. Lepidochelys olivacea is virtually circum-tropical in distribution, but there are odd areas of discontinuity in the range which are discussed in detail later.

Much of this thesis is taken up with an evaluation of the degree of difference both between L. olivacea and L. kempi and also between the olivacea populations at the extreme ends of the nearly circumglobal range - the populations in the East Pacific and in the Western South Atlantic. Many criteria - external, osteological, behavioral and physiological - were used, in an attempt to decide whether the separation of olivacea and kempi as full species was justifiable, and whether the extreme populations of olivacea showed sufficient divergence to justify subspecific or other

separation. If differences were found, an attempt would be made to rationalize them in terms of function; on the other hand, absence of even slight differences would constitute a remarkable testimonial either to the slowness with which sea turtles evolve, or to the uniformity of the marine environment in widely separated parts of the world.

When the writer started this study in 1965, there was no published record of any Lepidochelys having been tagged and later recovered, either at sea or on a nesting beach. Consequently the nesting cycles, both within a season (all other sea turtle genera are known to nest several times in a season) and from year to year were completely unknown. Nor were any data on migrations available, although it was presumed that these took place, since ridleys were known to form huge simultaneous nesting aggregations ('arribadas') in certain places, with many thousands of turtles being assumed to be drawn from considerable distances. The discovery of a small beach in Surinam where large numbers of ridleys nested enabled me to tag over 1000 female turtles and learn much about all these previously unknown aspects of ridley biology. These data are unfortunately not comparative, since for logistic reasons it was impossible to tag more than an insignificant fraction of the East Pacific turtles in the Honduras-nesting population that was studied; consequently recovery data for the latter population are exceedingly scant.

Since a formal taxonomic study of any animal group must be based on a sure knowledge of what names are 'available',

the comparative section of this thesis is preceded by a nomenclatorial history of the genus Lepidochelys, which takes careful note of all names in the literature which may appertain to members of this genus and attempts to evaluate their merits.

The possible significance of certain of the phenomena described (e.g. lamina variation, skull differences, arribada formation, interesting intervals) is discussed at the appropriate point in the text. Others (such as color) which I am unable to rationalize or discuss in a convincing fashion, I have still included for completeness' sake.

The discussion, which follows a literature survey of all fossil evidence which may bear on the problems in hand, is taken up with a 'value judgement' of the similarities and differences between different Lepidochelys populations and their bearing on the nomenclatorial situation, and also with a marshalling of all available evidence that applies to the problem of where and when the genus Lepidochelys originated and how the living forms reached their present distribution.

NOMENCLATORIAL HISTORY OF THE GENUS LEPIDOCHELYS

Despite the numerous well-defined points of difference which are now known to separate the genera Lepidochelys and Caretta, the ridley turtle of the Indian and Pacific Oceans, now known as Lepidochelys olivacea, was until comparatively recent years confused with the Pacific loggerhead turtle, Caretta caretta gigas, while both the South Atlantic enclave of the same species and the North Atlantic Lepidochelys kempi have been confused with the Atlantic loggerhead, Caretta caretta caretta. Consequently, in any discussion of the nomenclatorial history of Lepidochelys it is important to take note of all species described under the generic name Caretta, as well as others which are customarily synonymized with Caretta caretta.

Linnaeus (1758: 198) included two sea turtles in his *Systema Naturae*, calling them Testudo mydas and Testudo caretta. To these T. coriacea and T. imbricata were added later (Linnaeus 1766: 351). There is little doubt that the first of these names refers to the green turtle, the third to the leatherback and the fourth to the hawksbill, although in no case do types exist. Testudo caretta is usually thought to have been a composite of the loggerhead and the hawksbill, which Linnaeus realized in proposing the new name imbricata for the latter in 1766. It is unfortunate that the name caretta, based on the widespread vernacular name

carey for the hawksbill, was not reserved for that species, but the rules do not allow any further change to be made.

It was argued by Deraniyagala (1939b) that Linnaeus' description of Testudo caretta referred with equal accuracy to Caretta caretta and to Levidochelys kempi (then known as Thalassochelys (Colpochelys) kempi), and that the proper use of the name caretta must be based on the turtle illustrated by Schoepff (1792, pl. 16), which was labeled Testudo caretta and was accompanied by the first specific account of the species. Deraniyagala identified Schoepff's figure as kempi on the following grounds:

- 1) The presence of four inframarginals (on one side)
- 2) The presence of a single enlarged mandibular scale on each side
- 3) The subcircular shape of the carapace.

Parker (1939) challenged these conclusions, remarking that the 4-3 inframarginal count had been found in several specimens of the loggerhead but never in the ridley. He also pointed out that two accounts preceding Schoepff (those of Lacépède, 1788 and Bonnaterre, 1789) referred to the loggerhead, equating the name Testudo caretta with the more 'suitable' name Testudo caouana, a turtle described as yellow in color and therefore definitely not a ridley. Brongersma (1961) took Parker's side, citing further data to show that the inframarginal count of Schoepff's turtle suggested Caretta, that there were three mandibular scales in the drawing, not one, on each side (another fairly good Caretta character),

and finally that the carapace, although rather wide, was nevertheless within the known range of variation of Caretta. We need, therefore, concern ourselves no longer with the name caretta in our nomenclatorial history of the genus Lepidochelys.

The name Testudo viridi-squamosa Lacépède (1788) requires some comment. Some of the names used by Lacépède in this work are not binomial, and so there is some question as to whether any of the names are available nomenclatorially. Wermuth (1956: 405) identified Testudo viridi-squamosa with Lepidochelys kempi, and restricted the type locality to Bocas del Toro, Panama -- an unfortunate choice since this is well outside the range of kempi. Wermuth based his conclusions on Lacépède's description of the small, rounded head and greenish color of Testudo viridi-squamosa. It was later pointed out, correctly, by Brongersma (1961: 25) that the ridley has a large triangular head and is gray in color, and that, moreover, almost all of Lacépède's localities are well outside the range of kempi. It was concluded that Lacépède was probably referring to the green turtle, but that certainty was impossible and the name would best be suppressed. Testudo chloronotus Bechstein (1800) is a junior synonym of Testudo viridi-squamosa; Bechstein was apparently unaware that Lacépède's turtle had already received a specific name. Testudo mydas minor Suckow 1798 was considered by Wermuth (1956: 413) to be synonymous with Lepidochelys kempi. The type locality was given as Cape Blanco, Mexico. Brongersma

(1961: 26) equates this with Cape Blanco on the Pacific coast of Costa Rica, an impossible locality for kempi, though possible for olivacea. In view of the impossibility of making a certain designation, it seems best to suppress the name.

Chelonia multiscutata Kuhl (1820: 78) is the first name that can be associated with a species of Lepidochelys with reasonable assurance. The type, originally said to be in the collection of a Mr. Kuypers at Groningen, must now be considered lost; but according to the description, the type had eight costals on each side, and nine vertebrae. This scalation is moderately common for Lepidochelys olivacea, in which both costals and vertebrae may vary from five to nine or more. To the best of my knowledge, however, it is unknown for any other species - certainly it would be extremely rare. The carapace laminae were stated to be slightly imbricate, a condition present in hatchling Lepidochelys. Moreover the color was described as blackish-brown, a color frequently found in preserved hatchlings of Lepidochelys but not in those of other species of sea turtle. The action of Mertens and Wermuth (1961: 233) who followed Boulenger (1889: 185) in placing Chelonia multiscutata in the synonymy of Caretta caretta, must surely have been based on ignorance of the description of the animal on which the name is based. Nevertheless it would be wise to suppress this very appropriate name, since the name olivacea has become well established for the species, and in any case it would be necessary to select a neotype for multiscutata.

The name olivacea itself, then included in the genus Chelonia, was proposed by Eschscholtz (1829: 3) for two specimens - a 7-inch juvenile and a 28½-inch adult male - from Manila Bay, Philippines. The smaller individual was figured, the description was detailed, and there is no doubt that the description indeed refers to the Pacific ridley. In a footnote, Eschscholtz mentioned that olivacea differs from multiscutata in having fewer carapace laminae, 19 to 21 as opposed to 25 (not counting marginals); the variation between the two specimens failed to suggest to him that the number of laminae in the carapace was a highly polymorphic character in this species, and that the full range of variation in this number actually included that found in the type of multiscutata. Eschscholtz was, however, correct in differentiating olivacea from Chelonia cephalo (i.e. Caretta caretta) on the basis of the greater number of carapace laminae. The name Chelonia dussumierii was substituted for Chelonia olivacea by Duméril and Bibron (1835: 557), and must be considered a junior synonym of it.

The generic name Lepidochelys was first proposed by Fitzinger (1843: 30) to receive Eschscholtz' Chelonia olivacea. The combination Lepidochelys olivacea thus first appeared in 1843, and was used again by Girard (1858: 475), but did not gain general acceptance for about a century.

Gray (1844: 53) mentions Caouana ruppellii as a relative of the loggerhead, Caouana caretta, and the olive caouanne, Caouana olivacea. This name was listed by Wermuth and Mertens

(1961: 240) as a nomen nudum and a synonym of Lepidochelys olivacea. It is however not quite a nomen nudum - the description refers to the very large head (i.e. not a green turtle or a hawksbill), to the ridges on the upper jaw (i.e. Lepidochelys rather than Caretta), while the locality is given, with a query, as India, which would suggest L. olivacea and not L. kempi. On the same page the name Chelonia subcarinata, first used by Rüppell in a manuscript now in the Frankfurt Museum; is listed as a synonym of Caouana olivacea. This is a true nomen nudum, having never been published with a description. The name Chelonia subcarinata again appears in Gray (1873: 405) as a fossil from the London Clay, apparently allied to Caretta.

The names Chelonia polvaspis and Chelonia dubia are also nomina nuda. However the types of both are still in the British Museum (B.M. reg. nos. 63.12.4.119 and 63.12.4.122), and both are clearly recognizable as hatchlings of Lepidochelys olivacea. Both were included in a collection of reptiles from Java sent in by Bleeker - the former of the two names was included, though without description, in his list of species collected (Bleeker, 1857: 239).

Cephalochelys oceanica was a name proposed by Gray (1873a: 91; 1873b: 408) for a preserved specimen consisting of head, neck and forelimbs only, purchased from a dealer who said that it probably came from the Pacific coast of Mexico. According to Gray, "the size of the beak and the shields of the head leave no doubt that it is distinct." The specimen is now in

the British Museum, and is clearly a perfectly normal adult Lepidochelys olivacea, for which the origin 'Pacific coast of Mexico' seems very reasonable. Cephalochelys oceanica is thus a junior synonym of Lepidochelys olivacea; however if one were to designate the East Pacific population of olivacea as subspecifically distinct (which I do not think is justified for reasons given below), the subspecific name oceanica will become available.

The Atlantic ridley, Lepidochelys kempi, was first described by Garman (1880: 123), who included the species in the loggerhead genus, Thalassochelys. He based the species on two adult specimens received from Richard M. Kemp of Florida, and noted that the species was commonly considered a cross between the green and the loggerhead, being known as 'Bastard' in the Gulf of Mexico. Garman wrote that kempi was "distinguished from T. caouana [i.e. the loggerhead] by the short, round body, low humps, marginal plates, narrowness of head across occiput, and swollen jaws; from T. olivacea [i.e. the Pacific ridley] by shape of head, swollen jaws, and plates of the carapace. The compression of the anterior portion of the head of T. olivacea at once separates the species." In fact, the skulls of kempi and olivacea are not as different as Garman suggests, except perhaps in very old individuals. Garman tentatively suggested that kempi was of more than specific distinctness, and placed it in the new subgenus Colpochelys of the genus Thalassochelys. However, he also wrote "this will give to the species the name Colpochelys

kempi, Kemp's Gulf Turtle," i.e. as if Colpochelys were of full generic status, and this was repeated by some later writers (e.g. Schmidt and Dunn, 1917: 50). Nevertheless Garman showed uncanny insight in this paper, written almost 90 years ago, in recognizing (though not always by their present names) all the species of sea turtle recognized today, including Chelonia depressa, which has only recently been re-instated (Williams, Grandison and Carr, 1967: 1). However, the wisdom of this paper was largely ignored for many years afterwards; Chelonia depressa was relegated to the synonymy of Chelonia mydas, and the Pacific ridley and the Pacific loggerhead were amalgamated as one species. The latter custom destroyed the validity of much thoughtful work by Gadow (1899: 207), who studied orthogenetic variation in the shells of Chelonia, and attempted to rationalize the apparent reduction in lamina count as concurrent with the maturing of loggerheads (actually, his hatchlings were the multilaminate olivacea and his adults the pentecostal caretta).

Boulenger's 'Catalogue of the Chelonians' (1889: 186) acknowledged the existence of an Atlantic ridley, Thalassochelys kempfi, but otherwise included all loggerheads and ridleys in the world-wide species Thalassochelys caretta, on the following grounds: "The enormous amount of variation in the large series of Loggerhead Turtles in the Museum leave no alternative but to further multiply the number of species, or to admit only one. I have adopted the latter course." This ignoring of the perfectly good species Leidochelys olivacea

was to set a precedent for a widespread habit which lasted over forty years. Part of the confusion over the 'loggerheads' of the Indo-Pacific region may have been due to the fact that the true loggerhead, Caretta caretta (subspecies gigas) is a distinctly rare animal over most of the Indian and Pacific Oceans, while the ridley is widespread and, in many places, common. In addition, Gadow's misconception carried a lot of influence; he was a famous man, and he had seen a large number of specimens.

Boulenger's plan of only two genera (both the green turtle and the hawksbill were included in Chelone, and the loggerhead and Atlantic ridley in Thalassochelys) was quickly challenged by Baur (1890: 486), who proposed separate genera for the green turtle (Chelonia), the hawksbill (Caretta), the loggerhead (Thalassochelys) and the ridleys (Lepidochelys). Baur was the first to realize the close relationship between olivacea and kempi, and the first to include the latter in the genus Lepidochelys. Baur also recognized the Pacific green turtle as distinct from the Atlantic form (although not on grounds that now seem valid), correctly allocated Chelonia multiscutata to Lepidochelys olivacea (though he considered it an abnormal specimen, being unaware of the wide range in the number of costal laminae found normally in olivacea), and realized that Chelonia depressa was a frequently overlooked form meriting further study.

Philippi (1887, 1899) published two new names, Thalassochelys contraversa and Thalassochelys tarapacana, for two

Chilean sea turtles. Yañez (1951) has since shown that both were based on more or less normal specimens of Lepidochelys olivacea, but Wermuth and Mertens (1961: 233) erroneously include both forms in the synonymy of Caretta caretta gigas.

Hay (1908a) described a sea turtle from La Ventosa, Tehuantepec, Mexico, as representing a new species, Caretta remivaga. However, he limited his comparative material to Caretta caretta and to 'Caretta' kempi, and did not realize that his specimen was indistinguishable from Lepidochelys olivacea. (Even if the East Pacific ridley were to be considered subspecifically distinct from typical L. olivacea from the Philippines, the name olivacea (Gray, 1873) would have to be used, not remivaga.)

Schmidt (1953: 107) perpetuated both an unfortunate error and an unfortunate opinion in classifying the Atlantic and East Pacific ridleys as Lepidochelys olivacea kempi and Lepidochelys olivacea remivaga respectively.

Siebenrock (1909) considered Caretta remivaga to be to be merely a half-grown specimen of Caretta caretta. He admitted the validity of the Atlantic ridley (though only as a species of Caretta), but his confusion of Indo-Pacific Lepidochelys olivacea and Caretta was a serious error which persisted until Beraniyagala (1933) showed the two to be distinct. Stejneger (1907), showing somewhat more insight, called the Atlantic loggerhead Caretta caretta, overlooked the presence of this rare species in Asiatic waters, and called all Pacific 'Carettae' Caretta olivacea.

Much name-juggling between Caretta, Lepidochelys and Colpochelys occurred in the first half of the twentieth century. Ditmars (1910), although acknowledging the distinctness of caretta, olivacea and kempi, placed all in the same genus (Caretta). Pope (1939) and Deraniyagala (1939) used all three generic names. Deraniyagala, although having unrivalled knowledge of Lepidochelys olivacea, had little first-hand contact with kempi. Thus he distinguished Colpochelys and Lepidochelys on the following grounds:

1. Dorsally olive-green. Each inframarginal with a pore; costal scutes more than five pairs; limbs two or one clawed Lepidochelys olivacea

2. Dorsally dark grey. Inframarginals poreless; costal scutes in five pairs; limbs three clawed

Colpochelys kempi.

The first of these characters does not hold; Deraniyagala himself admits (1939a: 144) that half-grown olivacea are dark gray in color, while we now know that adult kempi are olive-green. The second character is also invalid; kempi has a pore in each inframarginal, and it is hard to see how this could have been overlooked. The third character is valid, though olivacea does occasionally have five pairs of costals, as Deraniyagala himself realized (1939a: 137). The fourth is invalid; both species have one large claw and one tiny claw, almost indistinguishable from an overlapping scale margin, on each flipper.

Later Deraniyagala (1943) swung to the other extreme and

lumped the two forms together as subspecies of Lepidochelys olivacea; the only difference between the two forms quoted was costal scutes usually in five pairs: kempi; costal scutes usually in more than five pairs: olivacea. This classification is followed even today by many writers, though for the most part by ones whose knowledge of the genus is second-hand or incomplete.

Carr (1942) was the first writer since Baur to recognize the close relationship between kempi and olivacea, and their distinctness from the loggerhead. In this and a later work (Carr, 1952) he lists the following characters separating the genera Caretta and Lepidochelys:

	<u>Caretta</u>	<u>Lepidochelys</u>
Frontal bones entering orbit	-	+
Maxillary bones in contact	+	-
Descending process of prefrontals in contact with palatines	+	-
Choanal fontanelles far forward, hidden	-	+
External orbital openings visible in ventral aspect	-	+
Posterior edge of nasal septum	sharp	rounded
Expanded ectopterygoid processes	-	+
Inframarginal count	typically 3	typically 4
Inframarginal pores	-	+
Enlarged mandibular scales	3	1

In addition Caretta can be distinguished from Lepido-
chelys in terms of shape, color, adult size, the pattern of
neural bones, frequency of nesting both within a season and
from year to year, and numerous features of nesting behavior.

The differences between the two species of Lepidochelys
are discussed at length in later sections of this paper.

DISTRIBUTION OF LEPIDOCHELYS KEMPI AND LEPIDOCHELYS
OLIVACEA

Lepidochelys kempi is known to form large breeding aggregations on the coast of Tamaulipas, Mexico, usually within a few miles of Rancho Nuevo, in the Municipio de Aldama (Carr, 1963: 298; Hildebrand, 1963; Chávez et al., 1967). Carr and Caldwell (1958: 246) report that fishermen throughout the central part of the coast of Veracruz, from Tuxpan to Alvarado, are familiar with kempi as a nesting animal. Carr (1961a:10) extended the known nesting range a little further south, to Montepio, Veracruz. Occasional nesting has also been recorded on the coast of Padre Island, Texas (Carr, 1961a: 11; Werler, 1951: 48).

The statement by Deraniyagala (1957: 110) that ridleys were known to nest in the vicinity of Miami, Florida, is apparently entirely without substance. In addition, his suspicion (Deraniyagala, 1943: 89) that the species breeds in the Azores is without real foundation, being based solely on the discovery of a single 10 cm juvenile in that area. De Sola and Abrams (1933: 12) mentioned finding eggs in two-foot-long Georgia specimens, but their statement that these individuals weighed only "about eight pounds" is confusing, to say the least, as Carr (1952: 402) points out. Caldwell et al. (1959) make no mention of any ridleys nesting with the numerous loggerheads in the Georgia coastal islands.

Kemp (quoted by Garman, 1880: 124) reports that "we know they come out on the beach to lay (in the Florida Keys) in the months of December, January and February, but cannot tell how often or how many eggs." Carr (1956: 18) queried this, as he could find no turtle fisherman in the Keys who had ever seen one nesting at any time. It becomes doubly unlikely when we consider that nesting in Mexico is now known to take place in May and June only.

Atlantic ridleys have been caught at sea throughout the Gulf of Mexico. Chávez (1968) found that females tagged at Rancho Nuevo while nesting were recovered both to the north and to the south; no less than eight were found near Ciudad del Carmen, Campeche, while others were found at San Pedro, Campeche; Dos Bocas, Tabasco; and Alvarado, Veracruz. To the north, tagged specimens were recovered from: 36 km SE of Vermilion Bay, Louisiana; 37 km E of Cameron, Louisiana; 11 km from Empire, Louisiana; 10 km and 15 km E of Les Isles Dernières, Louisiana; near Freeport, Texas; near Brownsville, Texas; and 41 km SE of Freeport, Texas. One specimen was found almost due east of the point of tagging, being caught between the Dry Tortugas and the Marquesas Keys.

Smith and Taylor (1950: 15) record the species from Isla de Mujeres, Quintana Roo, Mexico.

The ridley is found in sufficient numbers off the Gulf coast of Florida in the summer months (together with the green turtle) to support a small turtle fishing industry in the region between the mouths of the Withlacoochee and Crystal

Rivers (Carr and Caldwell, 1956). The species is found along the Gulf Coast right down to the Keys (records from Key West and Sand Key, Carr, 1942: 10). Ridleys from the Florida Gulf Coast are for the most part a few inches short of mature dimensions, but according to Carr and Caldwell (1958: 246), occasional larger individuals are found, usually further out to sea than the area patrolled by the turtle fleets.

Ridleys are unknown from the Bahamas. On the Atlantic coast of the United States they are very scarce south of Melbourne, Florida, though there is a sight record from Salerno, Martin County (Carr, 1942). The species has been recorded from Georgia, Southern Coast (De Sola and Abrams, 1933); North Carolina (U.S.Nat.Mus. 52015, 029244; Beaufort: USNM 55735 and Coker, 1906); Virginia, Northumberland County, near Reedville (USNM 86814); New Jersey, Atlantic City (Hay, 1908a); New York, Lower New York Bay (De Sola, 1931). There is no diminution in records as we proceed north. Dodge (1944) lists seven records of ridleys from the coast of Massachusetts, while Carr (1957) mentions an astonishing observation, passed on to him by William Schevill of the Woods Hole Oceanographic Institute, of several dozen yearling ridleys out of a "whole fleet of such turtles" being stranded on Woods Hole beaches while travelling out of Buzzard's Bay into Vineyard Sound. There is also a record from the coast of Maine, four from Nova Scotia, one from Cape Breton Island, and one from Cape Race, Newfoundland (Bleakney, 1955, 1965). There is also one record from Bermuda (Howbray and Caldwell, 1958), one from

the Azores (Deraniyagala, 1939b), two from Ireland (Galway Bay and Miltown Malbay, County Clare, Deraniyagala, 1938a and b), one from the Scilly Islands (Brit. Mus. Nat. Hist. 1925.12.23.1), one from the Channel Islands (Beaumont, Jersey, BM 1950.1.2.70), and several from Great Britain (Cape Wrath, Scotland; Ayr, Scotland; Tremadoc Bay, Wales; Milford Haven, Wales; Bristol Channel; Portreath, Cornwall; Pagham Beach, Sussex; Taylor, 1963). There is one record from the Netherlands, from Scharendijke, Schouwen Island (Brongersma, 1961: 11, 33), and one from St. Jean de Luz on the Basque coast of France (Brongersma, 1963: 439). There is also a record from Malta (Despott, 1930; identification corrected by Carr, 1957: 48).

There is no good record for the Caribbean; Dunn's (1918) record from Jamaica, although repeated by Pope (1939: 238), is refuted by Lewis (1940: 56), Grant, in Carr (1952: 397), and Caldwell (1961: 277). The Venezuelan records of Donoso-Barros (1964) and Flores (1966) clearly refer to Lepidochelys olivacea, and will be considered later. The record of a ridley from Gibara, Cuba (Aguayo, 1953) is thought by Carr (1957: 46), who examined the specimen, to refer to an olivacea, not a kempi. Loveridge and Williams (1957: 496) refer to "intergrades" between kempi and olivacea from the Cameroons. These were merely hatchlings of L. olivacea, some of which had five costals on each side of the carapace (the costal count character, normally the only way of distinguishing the juveniles of Lepidochelys, here clearly breaks down. However adults

may be separated by a number of characters, quite apart from the costal count).

It is very interesting that only adult ridleys have been found in the Gulf of Mexico, with the exception of near-adults on the Gulf coast of Florida, while all extra-Gulf (i.e. true Atlantic) records are based on juveniles, typically 20-30 cm in carapace length. The conclusion is inescapable that hatchling ridleys, after reaching the sea from their natal beach in Tamaulipas, Mexico, swim, or more likely are passively conveyed by the current, through the Straits of Florida and up the Atlantic coast of the United States, where they remain until they approach or reach maturity. Those individuals which are swept right out into the Atlantic and across to Europe are usually picked up in a dead or feeble condition, and probably all are lost forever from the breeding population, but those which remain in Atlantic waters of the United States, even as far north as Massachusetts, are usually quite healthy when caught and may well grow normally and migrate back southward into the Gulf of Mexico when they approach maturity. Once reproductive cycles are established, the mature turtles fan out throughout the Gulf between breeding seasons to avoid overcrowding of feeding grounds, but by this time they are sufficiently strong swimmers to avoid passive drifting out of the Gulf with the Gulf Stream.

Lepidochelys olivacea occurs in the Atlantic, Pacific and Indian Oceans. East Atlantic records are as follows: Mauretania: Port Etienne; Sénégal: Ham, M'Caparo, Joal and

Gorée Island; Liberia: north of Point Marshall; Ghana: Tensa; Ivory Coast: Tabou; Cameroons: Victoria; Gabon; Congo: Banana and Moanda (Carr, 1957: 49). Breeding is known to occur at least from Sénégal to the Congo.

West Atlantic records: nesting is known to occur in Guyana (Shell Beach and Dauntless Point, Leguan Island), and in Surinam at Bigi Santi, Eilanti and Babboon Santi (Pritchard, 1969). Nesting is very probable on the western shores of French Guiana, but has not yet been demonstrated; there is an adult shell from French Guiana in the Paris Museum (MNHN 03.226), but there is no information as to whether the turtle was caught on a nesting beach or at sea (Brongersma, 1968: 441).

Non-breeding records to the east and west of the breeding range are as follows: Cuba: Gibara (Aguayo, 1953, identification corrected by Carr, 1957: 46); Puerto Rico (Erdman and Caldwell, in press); Venezuela: Cumaná (Donoso-Barros, 1964); Trinidad (fishermen's reports mentioned by Carr, 1956, later confirmed by a head and shell sent to Carr by F. Assam). Returns of tags from females found nesting at Eilanti, Surinam in the course of the present study give the following additional localities: Brazil: Natal; open sea near 5°N, 45°W; between Amazon and Oyapoque Rivers (two records); Venezuela: 15 miles N of Punta Barima; Carúpano (where the tagged individual was one of a large group of turtles seen). Whether the Venezuelan records infringe the generalization that ridleys are absent from the Caribbean depends on whether we consider

Trinidad or Isla de Margarita to represent the eastern limit of the Caribbean on the South American coast.

East Pacific records: the northernmost record on the American Pacific coast is that of an adult specimen from Oregon (Carr, pers. comm.). There is also a record from northern California (Houck and Joseph, 1958: 219), and from central California (Monterey; G. Victor Morejohn, in letter to Carr, 1/31/68). Carr (1961a and b) gives definite records from the middle and southern waters of the Gulf of California, while a single skeleton from San Felipe, in the northern Gulf, is in the Los Angeles County Museum (Caldwell, 1962: 23). There are numerous records for the southern tip of Baja California, both near Cabo San Lucas itself and also from the southern part of the Pacific coast, at least up to Isla Margarita, and the extreme southern waters of the Gulf (Anon., 1967a and b). The northernmost nesting records for this species are from the vicinity of Topolobampo (Márquez, in press), and nesting probably occurs more or less abundantly along the entire Pacific coast of Mexico south of Mazatlan. Specific records are as follows: Bahia de Banderas, Nayarit/Jalisco border (pers. obs.); according to Montoya (pers. comm.) nesting in Jalisco just south of Bahia de Banderas sometimes takes the form of large arribadas; Colima: Manzanillo and Boca de Apiza; Michoacan: San Juan de Lima and Playa El Ticuis (Anon., 1966); Guerrero: San Luis de la Loma; Piedra de Tlacoyunque; Playa Encantada and Pie de la Cuesta (pers. obs. and Carr, 1961a: 9); Oaxaca: between Puerto Escondido and Puerto Angel

(Montoya, pers. comm.); the latter is also a known arribada site. Chiapas: the species is said to be very abundant in the Mar Muerto (Alvarez del Toro, 1960: 38), but no definite nesting record is available.

Little definite information is available for nesting in Guatemala, but people at the port of San José told Carr (1961a: 8) that ridley nesting was frequent there. Definite published records for El Salvador are also scarce, but I am told by Mr. Al Chable of Guatemala City that nesting occurs extensively along most of the coast. Extensive nesting also occurs in Honduras, in the Gulf of Fonseca (Carr, 1948 and pers. obs.), centered probably around Isla de Ratones. Some nesting also occurs in Nicaragua. Nesting has been recorded from near Punta Arenas, Costa Rica (Carr, 1961a: 8), and from the Nicoya Peninsula, Costa Rica (Caldwell and Casebeer, 1964). Definite records south of Costa Rica are hard to locate, but nesting almost certainly occurs in Panama and probably at least as far south as Guayaquil, Ecuador. At least three ridleys have been found in Chile, from near Arica, near Copiapo and near Coquimbo (Carr, pers. comm.).

Central and West Pacific records: ridleys are apparently unknown from the mid-Pacific islands. However in Oceania there are a few records of this species. McCann (1966a and b) makes the old mistake of confusing Lepidochelys with Caretta: thus he mentions the great variability in number of costals in New Zealand "loggerheads," and also says that some of his specimens were red-brown (i.e. true Caretta), and others were drab olive

(i.e. Lenidochelys). An illustrated specimen from Flat Point, Wellington District, New Zealand is clearly L. olivacea (see McCann, 1966b: pl. iv fig. 3; pl. v figs. 2 and 5).

Deraniyagala (1939a: 162) mentions young ridleys, possibly hatchlings, from Bundaberg, Queensland, Australia; there is also a record from Cape York (Boulenger, 1889: 186).

Cochran (1952: 682) figures a sea turtle from Arnhem Land, Australia, which, though labeled "green turtle," is clearly a ridley.

For the Philippines we have the type locality (Manila Bay); breeding is also known to occur in New Britain (Gadow, 1899); Celebes (three hatchlings in British Museum, nos. 71-9-1-48 to 50); Kuching, Sarawak (B.M. 1966.244-249); Talang Islands, Sarawak (Hendrickson, 1958: 495); Kelantan, Trangganu, Pahang, Tioman Island, Johore, Perak, Langkawi, and Penang, Malaya (Hendrickson, 1961: 215; Hendrickson and Alfred, 1961: 195); Bay of Bengal (Hatchlings in BM, nos. 68-4-3-144 to 149); Halmahera; Flores; Bonin Islands; southern Japan (Awa, Hondo, Toza and almost every suitable sandy beach in the area); Stejneger, 1907. Pope (1935: 24) writes that the ridley "abounds" off China and South Japan. Nesting has been reported on the coast of South Viet-Nam (Carr, pers. comm.).

Indian Ocean records: the species is known from Karachi; Seychelles; Ceylon (Dehivala, Karaduva, Modera, Aripu, Weligama, Calkissa, Bentota, Moratuva, Maggona, Colombo, Talavilo, Egoda, Talaimannar, Uyana, H'ndela, Machichechukate, Ilipandima,

Kelpitiya, Udappuva, Chilaw, Negombo, Matara, Hambantota) according to Deraniyagala, 1939a. The species is very rare along the coasts of East Africa and the Arabian Peninsula; there are no breeding records, and only four recorded cases of individuals having been caught at sea or found dead on shore, from the Gulf of Oman; Massaua, Eritrea; Lindi, Tanzania; Socotra (Loveridge and Williams, 1957). The record of Hughes et al., 1968, for Natal, was based on a misidentified kyphotic loggerhead. However, the species may possibly nest on the coast of Somaliland; Travis (1967) describes a turtle butchery he established on the coast of this country, most of the turtles used being nesting females. Although this concern was centered on the green turtle, the smaller shell in the picture of turtles being butchered opposite page 81 looks very like that of a ridley.

It is curious that, while our knowledge of the Atlantic ridleys was, until the last few years, based almost entirely on juvenile specimens, that of the Pacific ridley is based, apart from one of the types, almost without exception on adult specimens. Immature Pacific ridleys seem to be caught extremely rarely, and the few writers who have figured or described such specimens (e.g. Deraniyagala, 1939a; Márquez, in press) have used specimens raised in captivity from the hatchling stage. The reason for this may be, in part, that ridleys reach maturity in a very short time. Deraniyagala (1939a: 162) raised a specimen in captivity which weighed 42 pounds when 15 months old. This suggests (though of course

by no means proves) that ridleys might reach maturity, or at least mature size (about 65 pounds), after only two years. If their total life span is several decades, only a small fraction of the total population at any one time would be immature.

COMPARISON OF LEPIDOCHELYS KEMPI, L.OLIVACEA FROM
SURINAM AND L.OLIVACEA FROM PACIFIC HONDURAS AND
MEXICO

Shell Characteristics

The following parameters were analyzed in the three populations: absolute carapace length of mature females; relative carapace width; relative length of plastron; relative width of plastral bridge; absolute carapace length of hatchlings; relative carapace width of hatchlings; number of central laminae; number of costal laminae; number of marginal laminae; number of intergular laminae; number of inframarginal laminae; relative width of middle marginal laminae of adult females; shape of supracaudal and posterior marginal laminae; anterior carapace profile.

Absolute Carapace Length

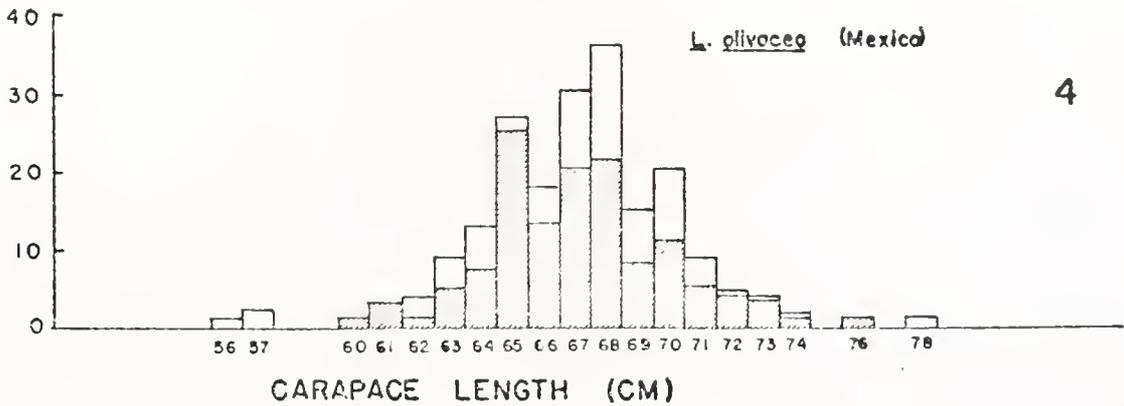
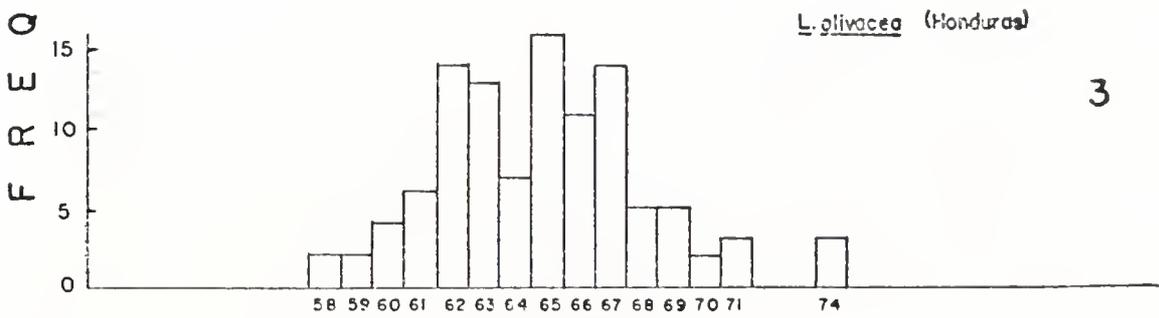
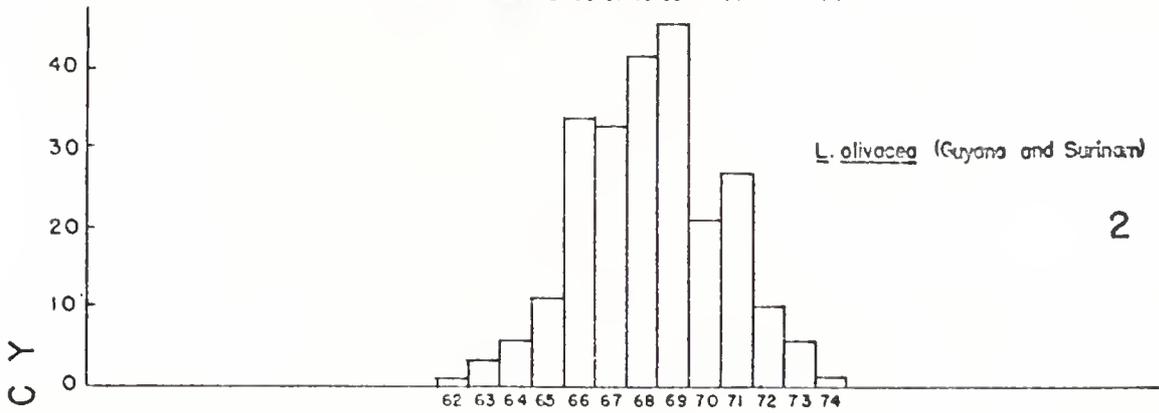
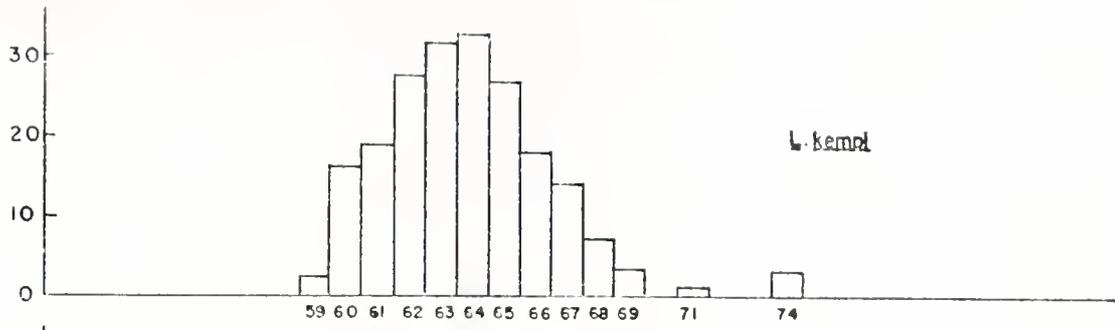
Figure 1 shows the straight-line carapace length for 203 mature female Lepidochelys kempi from Rancho Nuevo, Tamaulipas, Mexico (adapted from Chávez et al., 1967: graph 2, page 14). Figure 2 shows the same for 241 mature female Lepidochelys olivacea from Shell Beach, Guyana; Bigi Santi, Surinam and Eilanti Surinam. Figure 3 shows the same for 99 mature female Lepidochelys olivacea from the Pacific coast of Honduras. Figure 4 shows the carapace lengths of 201 Lepidochelys olivacea of both sexes (males shaded, females unshaded) caught at sea off the northern half of the Pacific

Figure 1. Distribution of straight-line carapace lengths for 203 mature female Lepidochelys kempi from Rancho Nuevo, Tamaulipas, Mexico (fide Chávez et al., 1967)

Figure 2. Distribution of straight-line carapace lengths for 241 mature female Lepidochelys olivacea from Shell Beach, Guyana, and Bigi Santi and Eilanti, Surinam

Figure 3. Distribution of straight-line carapace lengths for 99 mature female Lepidochelys olivacea from the Pacific coast of Honduras

Figure 4. Distribution of carapace lengths for 201 Lepidochelys olivacea caught at sea off north-western Mexico; shaded areas: males; unshaded areas: females (fide Anon., 1966a and b)



coast of Mexico (Jalisco, Colima, Baja California and Sinaloa); data from Anon., 1966, 1967a and b.

The first conclusion from the histograms in figures 1 to 4 is that the normal length of mature (i.e. nesting) female Lepidochelys kempi is less than that of mature female L. olivacea from Surinam; the respective modal length classes are around 63-63.9 and 68-68.9 cm respectively, while the minimum lengths are 59 and 62 cm respectively. The maximum lengths (74 cm) are the same, but the histograms suggest that 74 cm kempi are odd giant individuals, well separated from the normal range of carapace lengths, while the single 74 cm olivacea from Surinam is backed up by six 73 cm individuals and 10 of 72 cm.

The distribution curve for shell lengths of Honduras olivacea is amazingly similar to that for kempi; again we have a few giant 74 cm individuals, none of 73 or 72 cm, while the modal length class is 65-65.9 cm and the minimum 58 (excluding one deformed specimen, not plotted, only 52 cm long). The minimum breeding length in Honduras is thus 4 cm less than that in Surinam, while the modal length is also about 4 cm less.

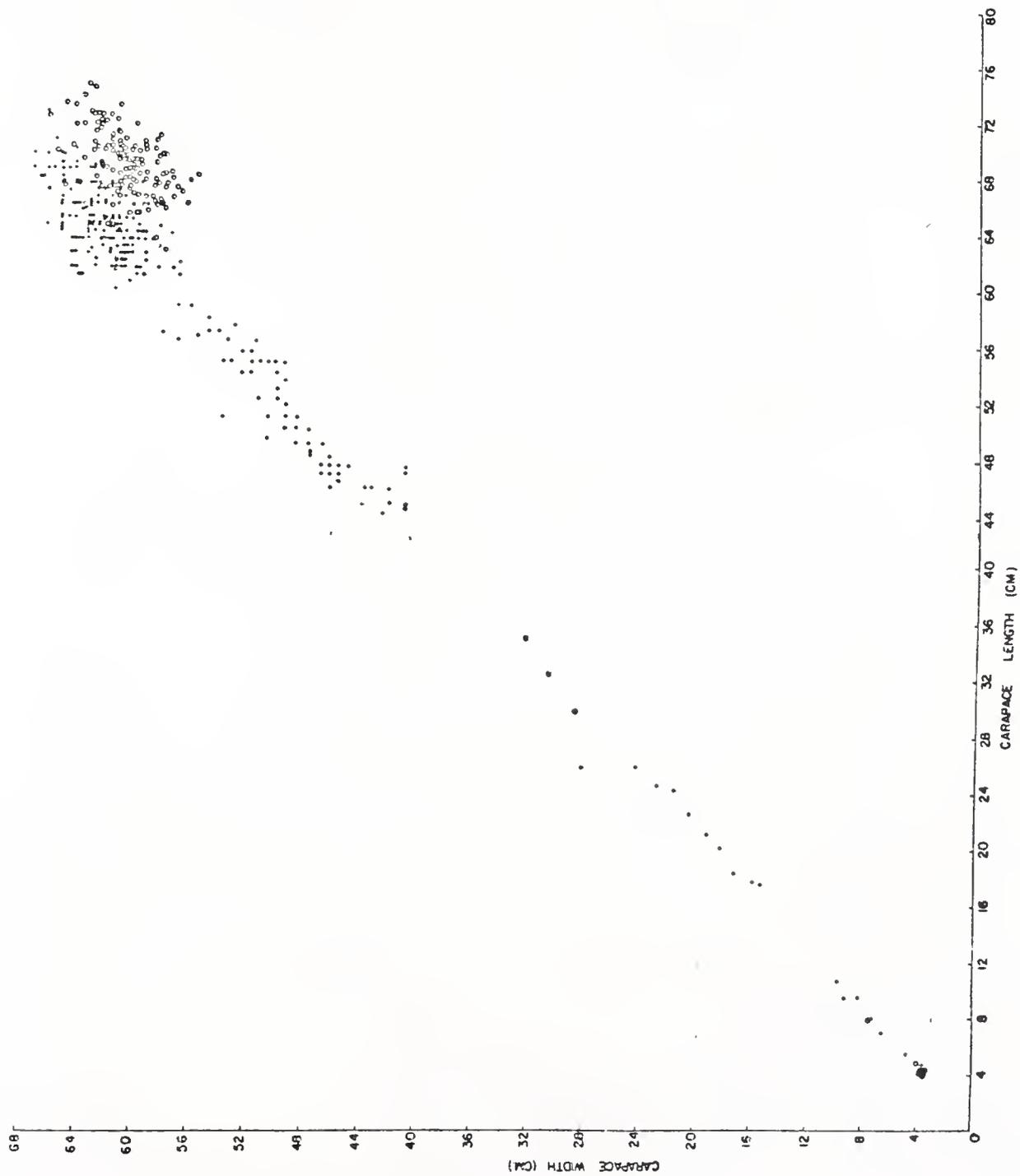
Because the Pacific Mexican turtles on which the fourth histogram was based were caught at sea, males were also included (shaded areas), and immature specimens may have been, although it is striking how large a proportion of the turtles are at least of mature size. The method of measurement was not stated, and it may well have been by means of a flexible

tape over the curve of the carapace. The discrepancy in such measurements is around 4 cm, which would bring the 78 cm individual down to a more reasonable 74 cm. (There are apparently only six reports of ridleys of carapace length more than 74 cm in the literature, and at least five of these records are suspect. Deraniyagala (1939a: 162) mentions a 79 cm Ceylon ridley. Hughes et al. (1967: 51) record an 80 cm shell, but Hughes and I have recently re-examined photos of the specimen and agree that it is in fact a kyphotic loggerhead. Caldwell et al. (1969: 23) mention a female Surinam ridley of carapace length 83 cm and weight 30 kg, and three males with respective carapace lengths of 100, 94 and 100 cm, and weights of 35, 34 and 35 kg. Since these weights are merely average for mature ridleys (Pritchard, 1969: 113), and since the males (which of course have longer tails) are so much longer, but little heavier, than the female, I feel sure that in all four cases overall length, and not carapace length, was measured.) Whatever the method of measurement used for the Mexican specimens, however, the figure does demonstrate that the males and the females are of closely comparable lengths.

Relative Carapace Width

Figure 5 shows a plot of carapace width against carapace length for Lepidochelys kempi and Lepidochelys olivacea. Hatchling and adult dimensions for Lepidochelys kempi, all from Rancho Nuevo, are taken from Chávez et al., 1967: 12, 13;

Figure 5. Carapace dimensions (width plotted against length) for Lepidochelys kempi (solid circles) and Lepidochelys olivacea (open circles)



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those of between hatchling length and 26 cm are taken from Márquez (in press); those between 26 and 63 cm, all from the west coast of Florida, are taken from Carr and Caldwell (1956: 21). All values for adult Lepidochelys olivacea are based on my own measurements of Surinam specimens; the three immature olivacea measurements are taken from Márquez (in press).

It may be seen that the carapace of kempi is on the average relatively wider than that of olivacea, and the overlap is so slight that no statistical test of significance is necessary. From the graph we may estimate the average carapace width of mature female kempi as 96.9 percent of the length, and that of mature female olivacea from Surinam as 88.2 percent of the length.

Figure 6 shows a plot of carapace width against carapace length for 107 mature female Lepidochelys olivacea from the Gulf of Fonseca, Honduras. The line on this graph represents the expected value of width/length for Surinam specimens, based on the scatter diagram shown in figure 5. It is clear that this line approximates closely to expected width/length values for Honduras ridleys also.

Relative Plastral Length

The scatter diagram in figure 7 was constructed by plotting values of plastral length against carapace length for 72 mature female Lepidochelys olivacea from the Gulf of Fonseca, Honduras. Assuming a linear relationship, the best

Figure 6. Carapace width plotted against carapace length for 107 mature female Lepidochelys olivacea from the Gulf of Fonseca, Honduras

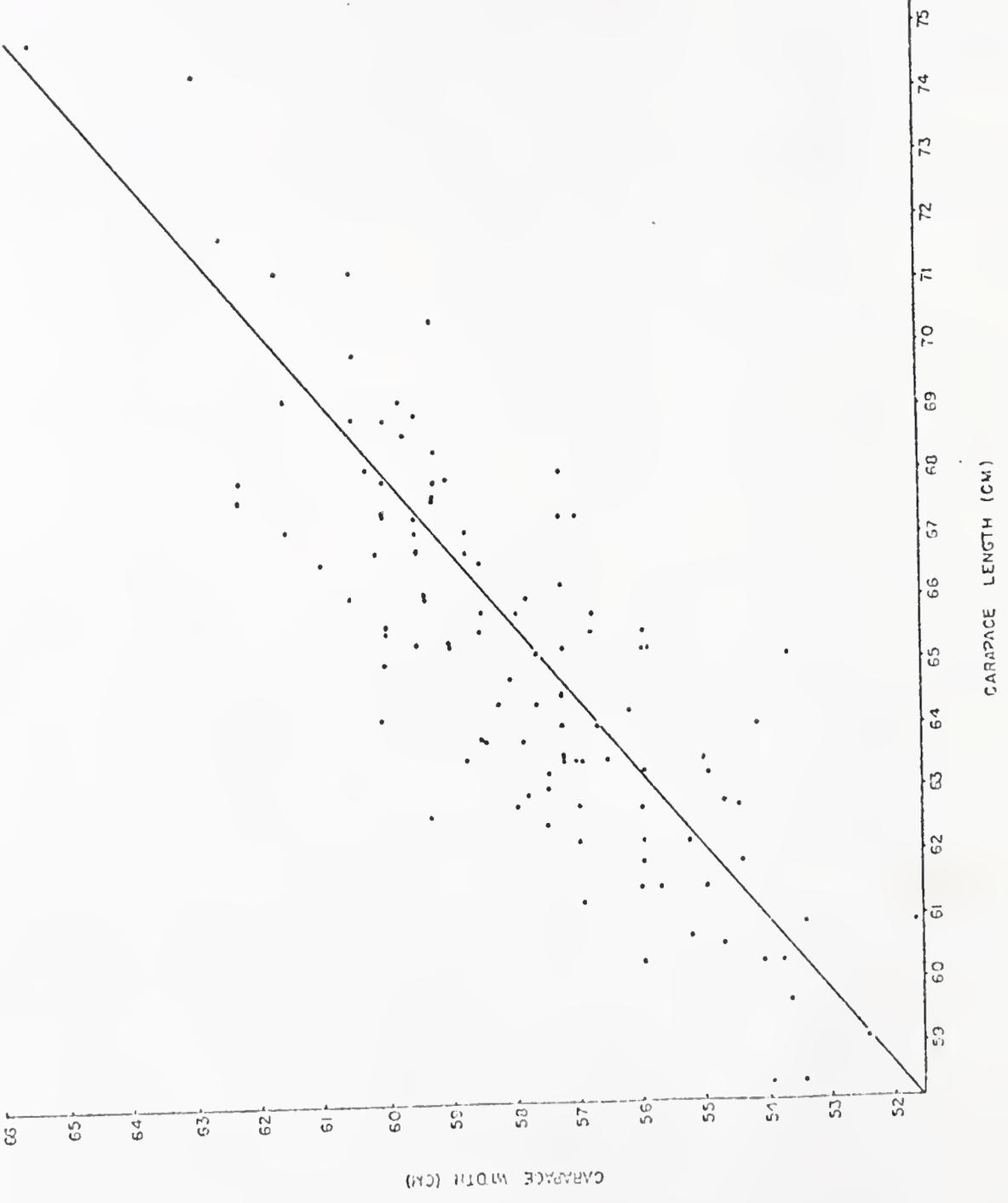
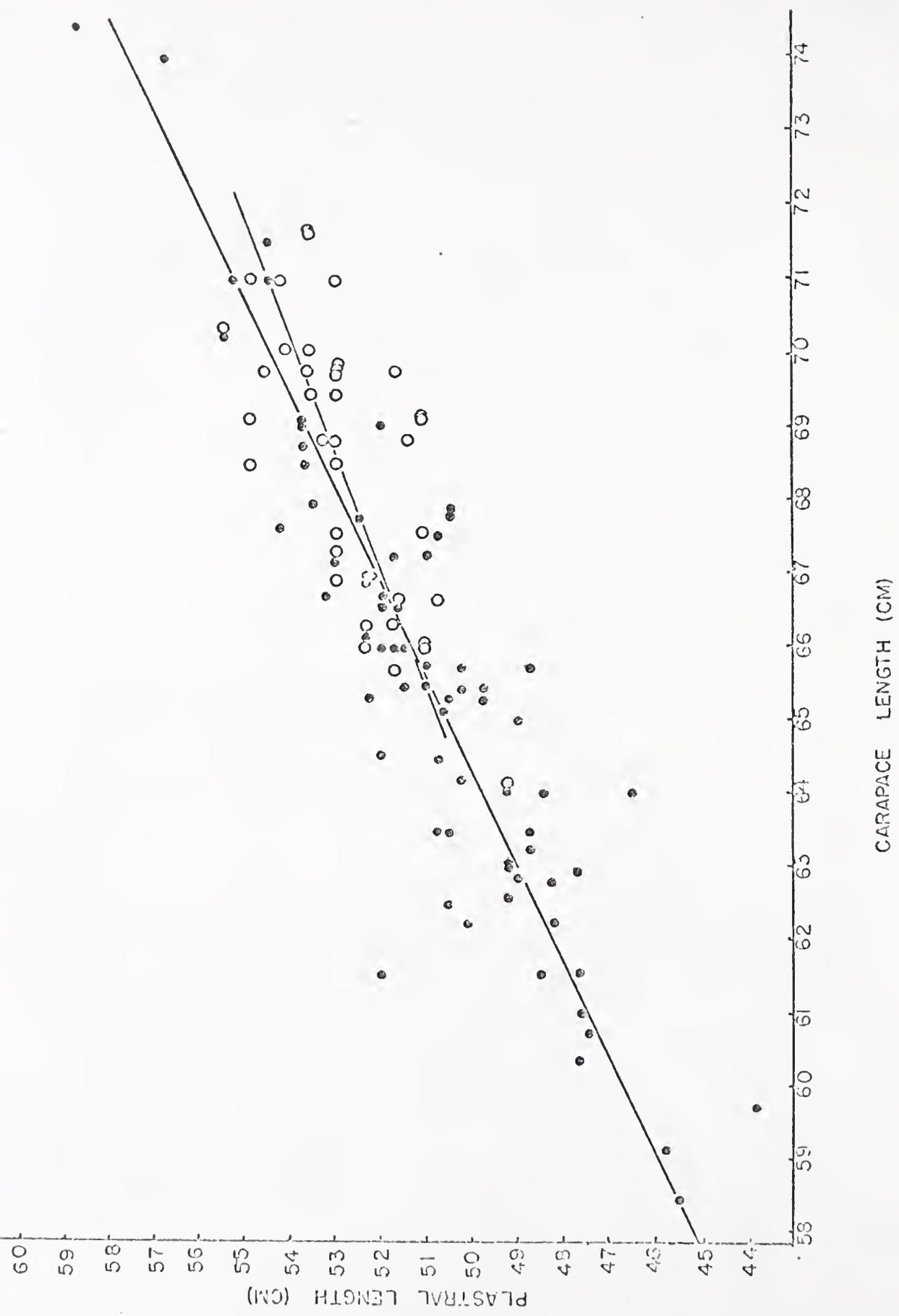


Figure 7. Plastral length relative to carapace length for 72 mature female Lepidochelys olivacea from the Gulf of Fonseca, Honduras (solid circles) and 36 from Eilanti, Surinam (open circles)



possible straight line was drawn through these points, giving the formula: expected plastral length = 0.783 X carapace length. Values of plastral length against carapace length for 36 mature female L.olivacea from Surinam were then plotted.

It can be seen from the figure that the smaller Surinam turtles (carapace length less than 69 cm) distribute themselves rather closely around the line of expected values for Honduras specimens; but for those longer than 69 cm, plastral lengths are in most cases distinctly less than the expected values, and the regression line for all the Surinam turtles thus has a shallower slope than that for the Honduras turtles. However, before interpreting this as a possible average difference between the populations, we should realize that Surinam turtles are on the average somewhat longer than those from Honduras, and that relatively few Honduras specimens over 69 cm in length are available for comparison. It may well be that the longest Surinam specimens are not larger in all parameters, but merely have a disproportionately long carapace not reflected in other parts of the body (e.g. the plastron); that is, that the relationship between carapace length and plastral length is not perfectly linear.

Relative Width of Bridge

The relative width of the plastral bridge is expressed in terms of the Bridge Index, a parameter defined as the shortest distance across the bridge, between the axillary and inguinal notches, divided by half the maximum breadth of the plastron

(Zangerl, 1958: 52). Since most of Zangerl's measurements were taken on skeletal or fossil material, it is presumed that the width across the bridge refers to the width across the hyo- and hypoplastral bones at the slight constriction adjacent to the anterior and posterior plastral lobes. In living or spirit specimens the anterior limit of measurement is a little difficult to fix, as the numerous axillary laminae tend to obscure the margin of the hyoplastron. Usually, however, the bones are just visible as a darker area beneath the laminae, and it was across this darker area that the measurements below were taken. The width of the plastron is easy to measure, especially in mature Lepidochelys in which the outer margin of the hyo- and hypoplastra is relatively smooth and not extensively indented as in many other sea turtles, particularly in juveniles.

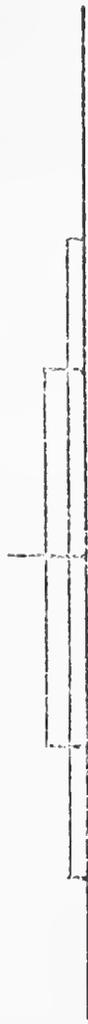
Samples of mature females from three populations of Lepidochelys had the following bridge indices:

L.kempi: 0.59; 0.61; 0.62; 0.63; 0.64; 0.65; 0.65; 0.67;
0.69; 0.70; 0.72 (mean = 0.65; n = 11; S.D. = ± 0.04 ;
95% confidence interval for mean = 0.65 ± 0.0235)

L.olivacea (Surinam): 0.61; 0.65; 0.65; 0.65; 0.67; 0.67;
0.69; 0.69; 0.70 (mean = 0.66; n = 9; S.D. = ± 0.026 ;
95% confidence interval for mean = 0.66 ± 0.0264)

L.olivacea (Honduras): 0.56; 0.58; 0.58; 0.64; 0.66; 0.68;
0.72 (mean = 0.63; n = 7; S.D. = ± 0.23 ; 95% confidence interval for mean = 0.63 ± 0.1593)

Figure 8. Mean value, 95 percent confidence interval for mean value, standard deviation and overall range of bridge indices for three Lepidochelys populations (mature females only)



L. kempfi



L. olivacea (Surinam)



L. olivacea (Honduras)

54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75

BRIDGE INDEX (%)

The mean values, 95 percent confidence intervals for the mean values, standard deviations and overall ranges for the three populations are plotted in figure 8. It may be seen that the confidence intervals for the mean values for each population overlap, and the differences between the mean values of our samples are therefore not statistically significant.

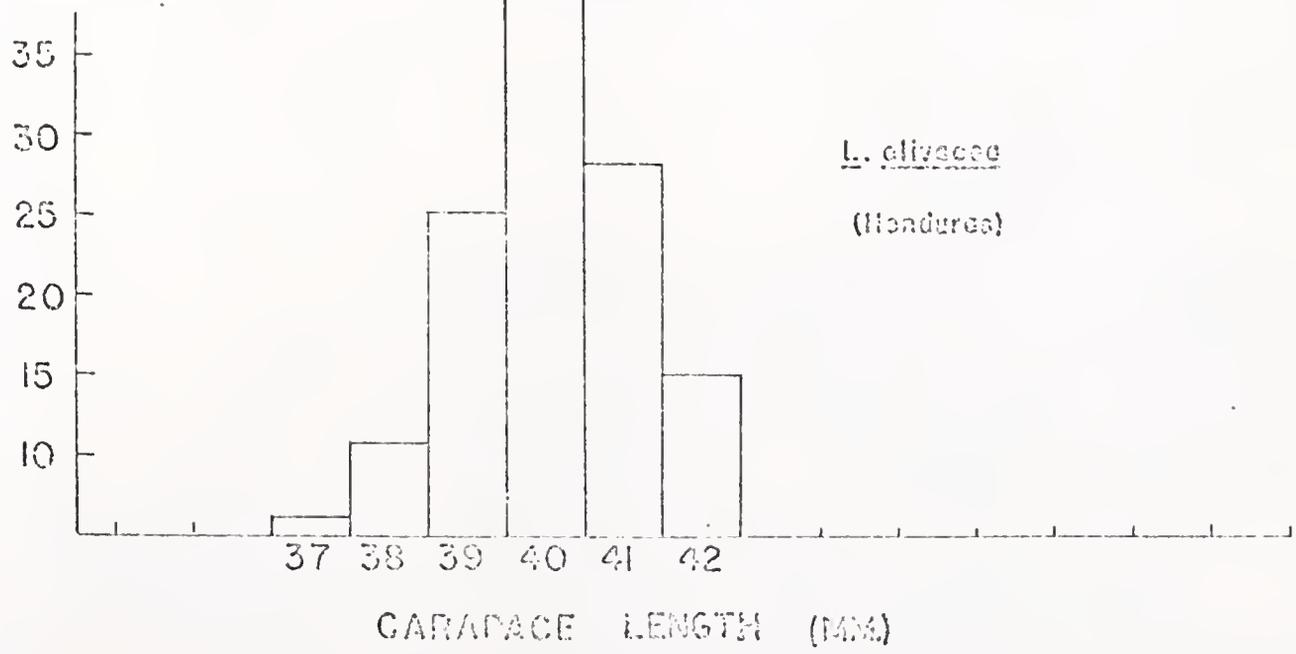
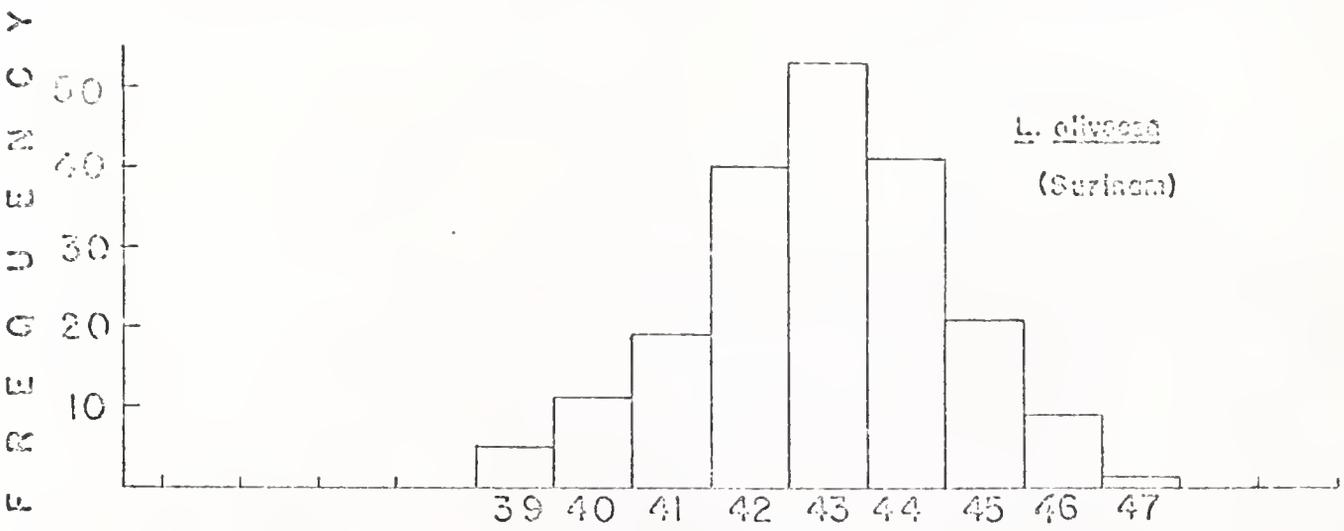
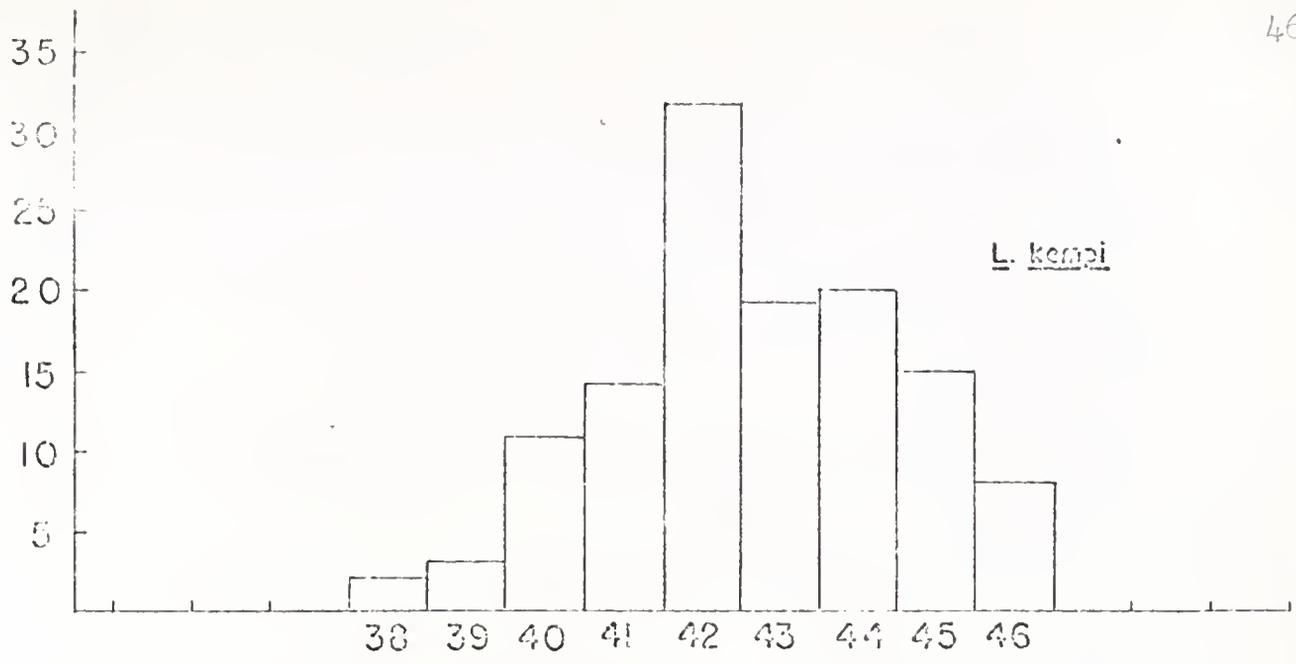
Zangerl (1958: 52) gave plastral indices for two specimens of each species of Lepidochelys, the two figures for kempi being distinctly lower than the two for olivacea. However since the specimens of kempi were both immature and the two olivacea mature, these data are not useful for comparative purposes.

Absolute Carapace Length of Hatchlings

Figure 9 shows carapace lengths for 124 hatchling Lepidochelys kempi from Tamaulipas, Mexico; 199 hatchling L. olivacea from Surinam; and 94 hatchling L. olivacea from Pacific Honduras.

The minimum length of the kempi hatchlings is between 38 and 38.9 mm. The maximum is between 46 and 46.9 mm. The modal length class is 42-42.9 mm. Surinam olivacea hatchlings are fractionally larger, the smallest being 39-39.9 mm and the largest 47-47.9 mm in length. The modal length class is 43-43.9 mm. The mean values are 43.15 and 43.3 mm respectively, and the difference between these, 0.15 mm, is so small relative to the limits of accuracy in measurement that it cannot be regarded as significant.

Figure 9. Distribution of straight-line carapace lengths for 124 hatchling Lepidochelys kempi (above); 199 hatchling L.olivacea from Surinam (middle); and 94 L.olivacea from Pacific Honduras (below)



CARAPACE LENGTH (MM)

Hatchling ridleys from Honduras, however, are substantially smaller, on the average, than those from Surinam, the smallest being 37-37.9 mm in length and the largest 42-42.9 mm. The modal length class is 40-40.9 mm; the largest Honduras hatchlings are thus smaller than those in the modal length class for Surinam hatchlings.

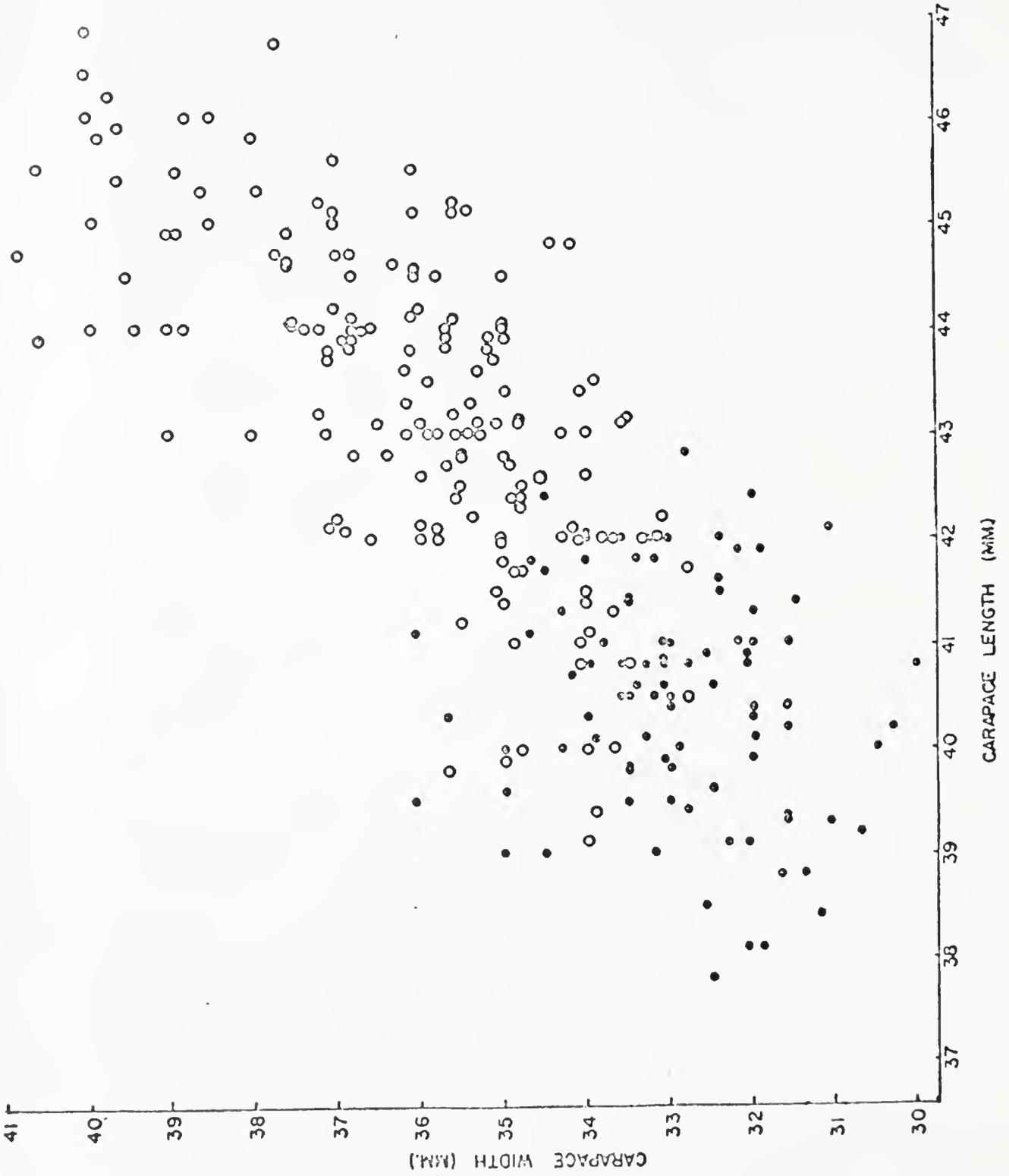
Relative Carapace Width of Hatchlings

Figure 10 is a plot of carapace width against carapace length for series of hatchling Lepidochelys olivacea from Honduras and Surinam. The difference in average dimensions between the two groups is striking and indeed there is rather little overlap. The average width/length ratio for the Honduras turtles is 0.813, while that for Surinam turtles is 0.833. This however must not be interpreted as a simple indication that Surinam ridleys are not only larger but are relatively wider on average. They may simply have hatched at a slightly more mature stage, which means they would not only be larger but would also have commenced the lateral expansion typical of half-grown and mature ridleys. Unfortunately no Honduras ridleys in the 43-47 mm bracket (i.e. a week or two old) were available for comparison with Surinam hatchlings in this size range.

Lamina Counts - General Discussion

With the obvious exception of the scuteless Trionychidae and Dermochelidae, lamina variation has been found in all

Figure 10. Carapace width plotted against carapace length for hatchling L. olivacea from Honduras (solid circles) and from Surinam (open circles)



turtle species for which series of reasonable size are available. Nevertheless, omitting sea turtles from discussion for the moment, it is possible in all cases to designate a certain lamina condition as the 'norm', deviations from which are not only relatively few in number but also are frequently asymmetrical and clearly abnormal. The commonest configuration for the majority of turtle species is as follows: the median dorsal series is composed of five laminae, the centrals or vertebrals, which are flanked by two series each comprising four costals or laterals, while the rim of the carapace consists of an anterior nuchal or proneural, two lateral series of eleven marginals, and posterior paired elements, the supra-caudals. The plastron consists of six pairs of laminae, called (from front to back) the gulars, humerals, pectorals, abdominals, femorals and anals, each being named after the organ or structure lying beneath. The plastron also contains a small lamina in each axillary notch, the axillary, and a corresponding lamina in each inguinal notch, the inguinal.

In certain turtle species or groups of species the normal condition is slightly different from this. Thus in the two species of Hydromedusa, the nuchal is expanded laterally and displaced posteriorly, so that the anterior marginals are in contact in front of it; while in several groups (e.g. many tortoises, genus Geochelone; certain sidenecks, family Pelomedusidae) the nuchal is absent. The central series normally numbers six in one genus (Notochelys), an extra small lamina being intercalated between the homologs of the fourth and

fifth centrals of other species - a not uncommon variation among many species for which the norm is five centrals. The marginal series is reduced to ten in mud turtles (*Kinosternidae*), and increased to twelve in one tortoise species (*Homopus boulengeri*). In many tortoise species the supracaudals are fused into a single lamina. A single gular only is present in *Kinosternon*, and both gulars and humerals are either absent or vestigial in *Staurotypus* and *Claudius*. The gulars are partially or completely separated by a median intergular in side-neck turtles (*Pleurodira*). The abdominals are widely separated in the *Chelydridae*. The axillary laminae are missing in certain forms (e.g. *Kinosternon abaxillare*), while both axillaries and inguinals are missing in *Cyclemys*, *Cuora*, *Terrapene*, *Geomyda spengleri* and many *Pleurodires*. In other forms (*Dematemys*, *Platysternum*) one or more inframarginals are intercalated between the axillary and inguinal on each side, separating the main plastral laminae from the marginals. *Macrochelymys* has a row of several subramarginals between the lateral marginals and the costals.

Lamina Counts of Sea Turtles

The four Cheloniid sea turtle genera (*Chelonia*, *Bretmochelys*, *Caretta* and *Lepidochelys*) also show several deviations from the typical chelonian lamina condition. Most conspicuous is a row of three or four inframarginals, which separate the main plastral elements from the marginals. Also the axillaries are fragmented into numerous laminae of different sizes, so

that there is no external demarcation of the point at which the integument of the axillary region becomes the anterior part of the plastral bridge.

The green turtles (Chelonia) have a triangular intergular lamina, while in the hawksbills (Eretmochelys) an interanal lamina is also present and the intergular may be longitudinally divided. In Caretta and Lepidochelys the intergular may be single, paired or absent, the interanal present or absent.

The Chelonine sea turtles (Chelonia and Eretmochelys) show no alterations in their typical carapace lamina conformations. However in Caretta and Lepidochelys an extra, small costal lamina is intercalated on each side in the area between the nuchal, the first two marginals, the first central and the first large costal. These extra costals are flanked by at least one extra marginal. Finally, a single species (Lepidochelys olivacea) has a marked tendency to subdivide the four large costal laminae, so that the actual costal count, in normal individuals, may range from five to about nine on each side. In fact a count of 5-5 is so rare that it is no longer possible to speak of this as the normal condition, and since no other particular costal configuration is predominant, Lepidochelys olivacea must be considered unique among turtles in having a truly polymorphic carapace. The central laminae of this species also show polymorphism, and may vary in number from five to eight or nine.

The costal laminae of L. olivacea are clearly divisible

into 'whole laminae' and 'half laminae', the whole laminae being homologous with the five costals of L.kempi, which, by contrast, is unusually stable in respect to the numbers of carapace laminae. Displacement of the homologs of the seams of L.kempi is usually slight in olivacea, though in cases of extreme splitting to eight or nine costals, the seams become displaced to lessen the size of the small first costal and the large last central. Division is typically by an almost perfectly straight, transverse break, but occasionally a split, though beginning in this fashion from the marginals, turns sharply aside before reaching the central series, and terminates at an intercostal seam. Incomplete division of laminae also occurs from time to time. In almost every case division takes place in the rearmost centrals; for example a 6-6 count is produced by division of the fifth costals on each side, or an 8-8 count by division of costals 3, 4 and 5. One exception was a Surinam shell with a 7-6 count in which only costal four on the right hand side was divided. Division of central laminae is concentrated in the region of the homologs of the third and fourth centrals of L.kempi. The last central, which is twice or three times the width of any of the others, is rarely divided, nor is the short first central.

Possible Significance of Multilamination

It seems impossible to rationalize the multilaminate condition in terms of function; the extra seams in no way alter the hydrodynamic form of the animal, and the laminae

are so thin that their precise arrangement could have no effect on the overall strength of the carapace. Nor could it cause any desirable alteration in the overall appearance of the animal, as one usually has to look very closely at adult ridleys to see the lamina boundaries at all. We can also presumably rule out atavism; as far as is known, even the earliest (Mesozoic) turtles had the typical pattern of five centrals and four costals, and apart from a few relatively recent Carettine fossils with five pairs of costals, and the single genus Clemmydopsis with only two pairs, no fossil species is known with other than four costals in the modal condition.

Carr (1957) suggests that the number of carapace laminae in Lepidochelys olivacea may be geographically correlated. Accordingly series of this species from the South Atlantic (Guyana and Surinam) and from the East Pacific (Honduras and Guerrero, Mexico) were studied and their carapace laminae counted. All available counts for Lepidochelys kempi were also obtained for comparative purposes. The following results were obtained.

Central Lamina Counts

The numbers of central laminae of 154 mature female Lepidochelys kempi found on the nesting beach at Rancho Nuevo, Mexico, by Chávez et al. (1967: 16) were distributed as follows: in 135 cases there were five centrals, in 15 there were six, and in four they were uncountable due to damage to the central

part of the carapace. To these we may add the counts for 59 hatchlings from several clutches from the same beach, sent to the writer by René Márquez. Of these, 47 had five centrals, 11 had six and one had eight. The somewhat greater frequency of six centrals in the hatchling series, as well as the presence of one specimen with eight, is probably attributable to slightly abnormal conditions in the artificial nests from which the turtles were hatched. Combining the two series (neither of which constitutes a true random sample of the species) we get: 182 turtles with five centrals; 26 with six; and one with eight. In all but two of the eleven cases of six centrals I examined personally, the extra central was a small square element intercalated between the fourth and fifth centrals, similar to that found in normal specimens of Notochelys platynota. In one of the other cases the extra lamina was an asymmetrical triangle between the somewhat distorted third and fourth centrals, and in the other the large last central was fragmented into four - two median elements classified as centrals and two lateral elements which were considered extra costals.

A series of 474 Lepidochelys olivacea from Surinam, composed in approximately equal part of adult females and random hatchlings from many clutches, gave the following central lamina counts: 72 individuals had five centrals, 200 had six, 185 had seven, 16 had eight and one had nine.

A series of 102 adult female olivacea from Honduras gave the following counts: 63 had five centrals, 37 had six and

two had seven. 126 hatchlings from Honduras (from several clutches) gave the following counts: 69 had five centrals, 39 had six, 17 had seven and one had eight.

For Surinam olivacea there is a clear Poisson-type distribution. A fair number of individuals have the minimum number of five centrals, but the typical counts are six and seven. Eight is rare, and more than eight almost unknown. The mean number of centrals is 6.31.

Combining the two Honduras series, we get the following totals: 132 had five centrals, 76 had six, 19 had seven and one had eight. This too gives a clear Poisson distribution. The minimum value is still five, but only half as many, not three times as many, have six, while seven is definitely rare, and more than seven almost unknown. The mean number of centrals is 5.51, 0.8 fewer than in Surinam. Since our samples number in the hundreds, while standard deviations are less than 1.5, standard errors of the means are so small that there is no need for further confirmation of the significance of this difference.

Deraniyagala (1939a: 137) supplies lamina counts for a series of 377 L.olivacea from Ceylon. Whether these were hatchlings, adults or both was not stated. Of these, one had only four centrals, 67 had five, 171 had six, 127 had seven, ten had eight and two had nine. This distribution is very similar to that for Surinam olivacea. The mean number of centrals is 6.24, only 0.07 different from the Surinam mean.

No large series of Lepidochelys from other areas are avail-

able in museums; nor have extensive tables of carapace lamina counts been published. However, a few hatchling specimens from other areas, now in the British Museum, were examined. Central counts are shown in Table 1.

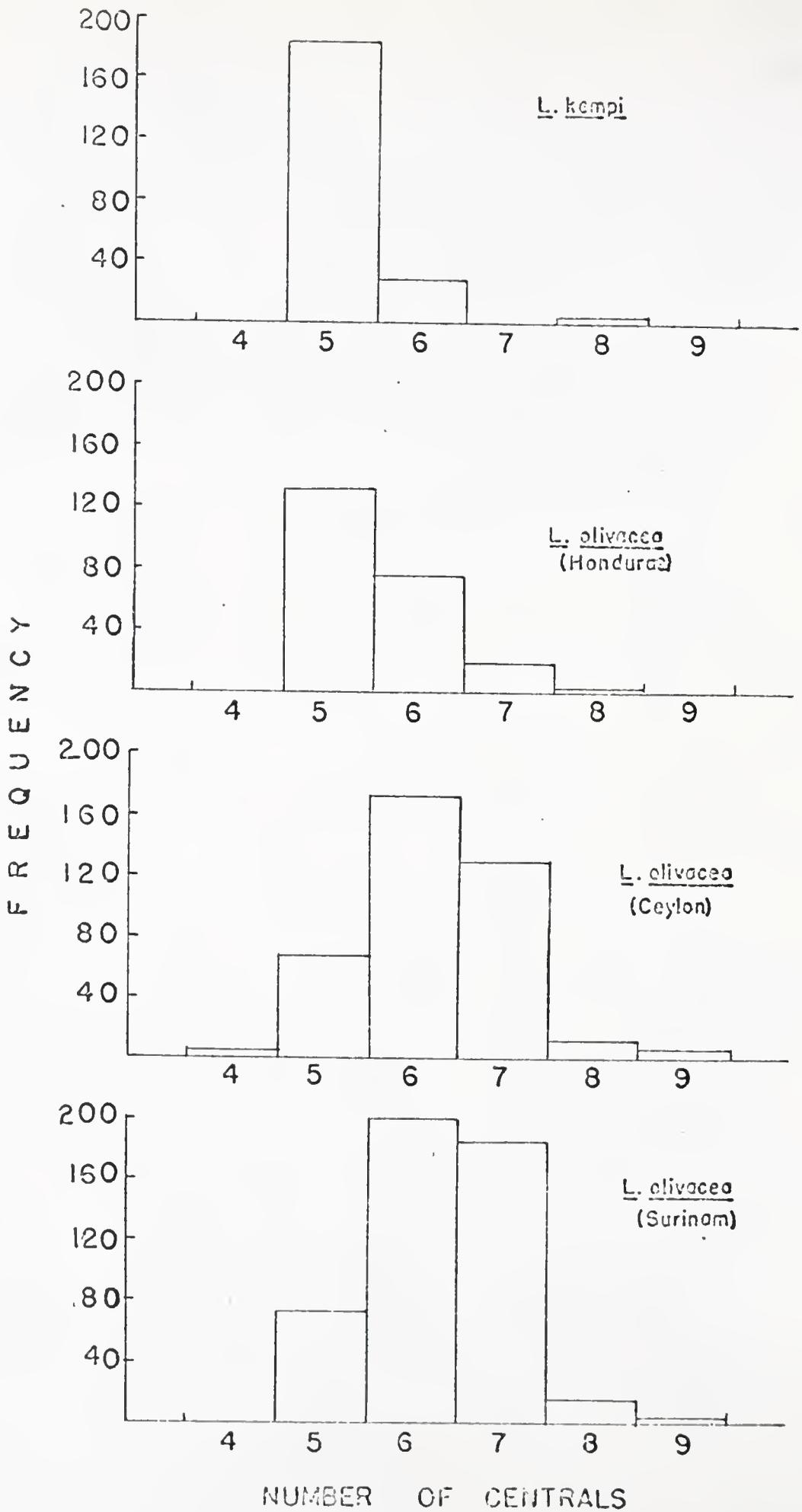
TABLE 1
RECORDED CENTRAL LAMINA COUNTS OF HATCHLING
LEPIDOCHELYS OLIVACEA FROM SEVERAL LOCALITIES

Locality	Central lamina counts
Banana, Congo	5; 5
Fort Marshall, Liberia	7; 5
Tensa, Ghana	6
Manado, Celebes	5; 5; 6
Karachi	5; 5; 6; 7; 7
Bay of Bengal	5; 5; 5; 6; 7; 7
Kuching, Sarawak	5; 6; 6; 6; 6; 7

These samples are, of course, much too small for comparative purposes. All we can say is that the only counts represented, 5, 6 and 7, are known to be common in specimens from all three oceans.

The counts for L.kempi and for L.olivacea from Honduras, Ceylon and Surinam are plotted in histogram form in figure 11. A progressive increase in average central count is apparent as we proceed westward from the Gulf of Mexico through the East Pacific, Indian and South Atlantic Oceans.

Figure 11. Relative frequency of different central lamina counts for four populations of Lepidochelys



Costal Lamina Counts

The relative stability of the typical 5-5 costal count of Lepidochelys kempi has already been mentioned. Carr and Caldwell (1956: 21) examined 96 specimens of immature kempi from the west coast of Florida. Of these only one deviant from a 5-5 costal count was encountered, an individual with a 6-5 count (in all cases the number of left costals is given first). Chávez et al. (1967: 16) counted costal laminae in 154 adult female kempi from the nesting beach at Rancho Nuevo; 5-5: 147; 5-6: 4; 6-5: 1; 6-6: 1; and one was uncountable because of indistinguishable seams. I counted the costals of 59 hatchlings from several clutches from Rancho Nuevo; 5-5: 54; 5-6: 1; 6-6: 4. The 6 count in the 5-6 individual and in two of the 6-6 individuals were caused by breaks across the lateral extensions of the large posterior central. In one of the other 6-6 counts the central series was fragmented into eight asymmetrical elements, and in the other the fifth costal on each side was split.

Combining these three series, we get: 296 5-5 counts; five 5-6's; two 6-5's and five 6-6's (n = 308).

A series of 743 Lepidochelys olivacea from Surinam was examined and their costal laminae counted (approximately 400 of these were mature females and the remainder hatchlings from several clutches.) Counts obtained are shown in Table 2, as are counts for 378 L. olivacea of unspecified age and sex from Ceylon (fide Deraniyagala, 1939a: 137) and for 102 mature females from the Gulf of Fonseca, Honduras.

TABLE 2

FREQUENCY OF DIFFERENT COSTAL LAMINA COUNTS FOR
THREE POPULATIONS OF LEPIDOCHELYS OLIVACEA

Costal lamina count	Surinam	Ceylon	Honduras
3-5	-	1	-
4-6	-	1	-
5-3	-	1	-
5-5	3	3	14
5-6	10	17	12
5-7	1	2	-
6-5	4	8	10
6-6	116	94	43
6-7	58	29	8
6-8	9	6	1
7-5	4	3	-
7-6	114	36	4
7-7	258	65	5
7-8	40	14	2
7-9	3	-	-
8-5	-	2	1
8-6	11	2	1
8-7	63	26	-
8-8	40	50	1
8-9	6	6	-
9-6	-	1	-
9-7	1	2	-
9-8	1	4	-
9-9	1	5	-
	n = 743	n = 378	n = 102
Mean left costals:	6.881	6.788	5.912
Mean right costals:	6.781	6.754	5.513

Large series of costal counts for Lepidochelys from other are not available at present. However Carr (1957: 49) tabulated all available counts for ridleys from the west coast of Africa (Mauretania, Sénégal, Liberia, Ghana, Ivory Coast, Comeroons,

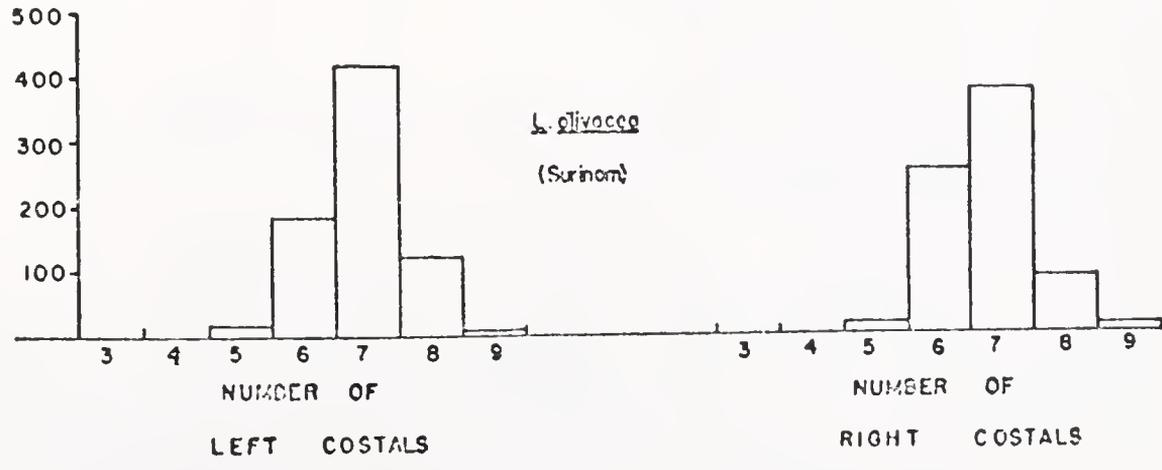
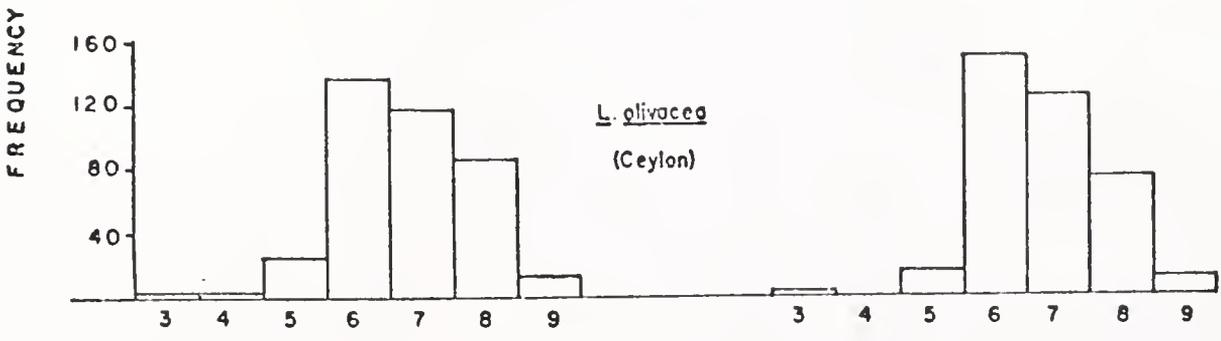
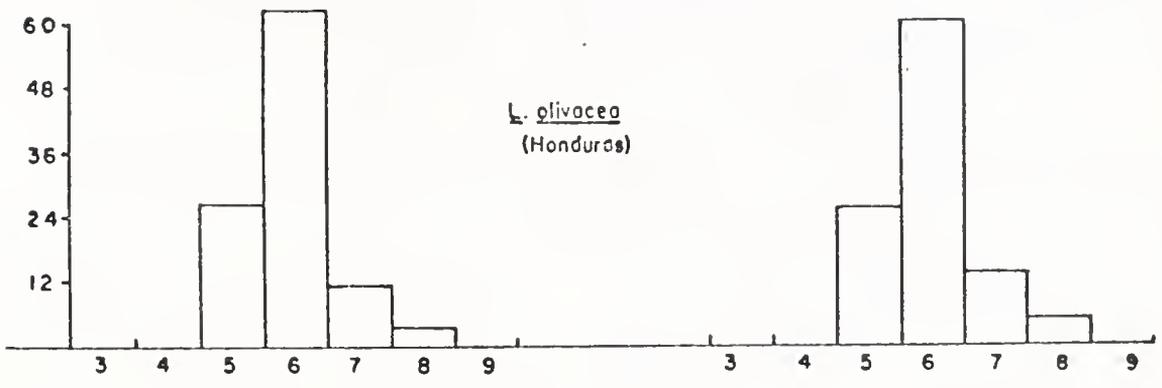
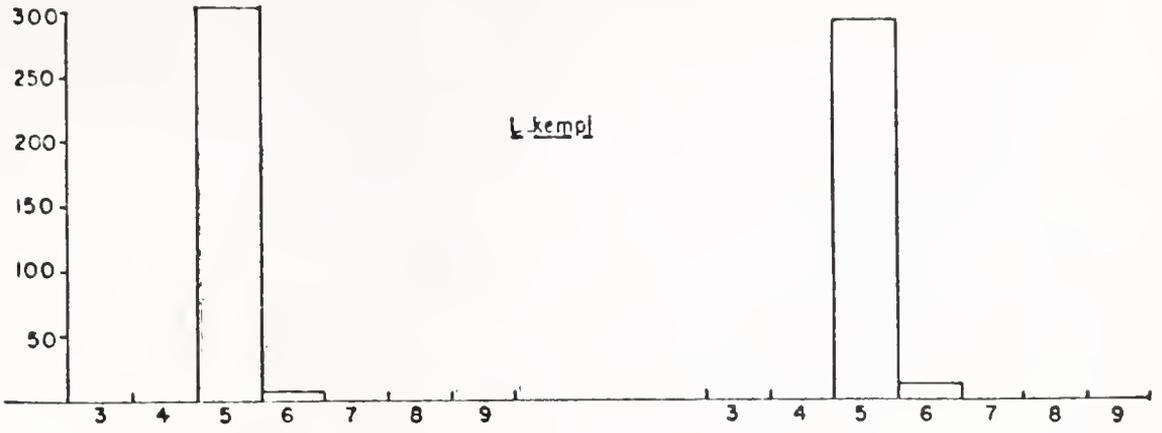
Gabon and Congo), as follows: two 5-5; two 6-5; ten 6-6; one 6-8; seven 7-6; seven 7-7; one 8-7. A series of six from Kuching, Sarawak included one 6-6; three 6-7; one 7-7; one 8-6. Six from the Bay of Bengal included four 6-6; one 7-6; one 7-7. Five from Karachi included one 5-6; two 6-6; one 6-7; one 8-8. Three from Manado, Celebes included two 6-6; one 7-7.

The histograms in figure 12 show the frequency of particular costal counts for the four Lepidochelys populations of which large series have been analyzed - those of the Gulf of Mexico, of Pacific Honduras, of Ceylon and of Surinam. A gradual increase in average costal count is apparent as we move west starting from the Gulf of Mexico. Thus, the kempi population of the Gulf of Mexico shows a massive preponderance of specimens with five costals, with a very small number with six. In Honduras we find the count of six is a little more than twice as common as five, while few specimens exceed six. In Ceylon the 5-count is rare, while 6 and 7 are of comparable frequency, and eight less common but still quite frequent. In Surinam the 7-count is the commonest by a large margin, while 6 and 8 are much fewer and 5 and 9 almost unknown.

Average values of costal and central counts for the four populations are plotted in figures 13 and 14.

It is evident from the tabulations of costal counts that individuals of L. olivacea bilaterally asymmetrical in this respect are nearly as common as symmetrical ones. The 743 Surinam specimens include 418 symmetrical individuals and 325 asymmetrical ones; of these 198 have the greater number of

Figure 12. Frequency of left and right
costal laminae for four populations of
Lepidochelys

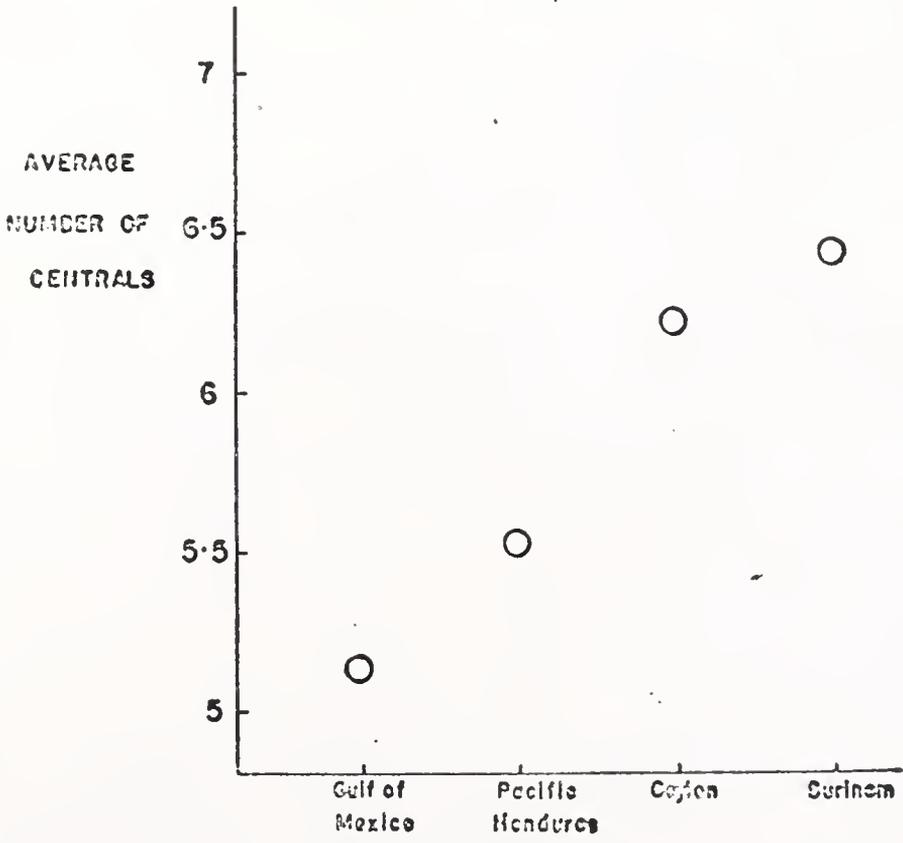
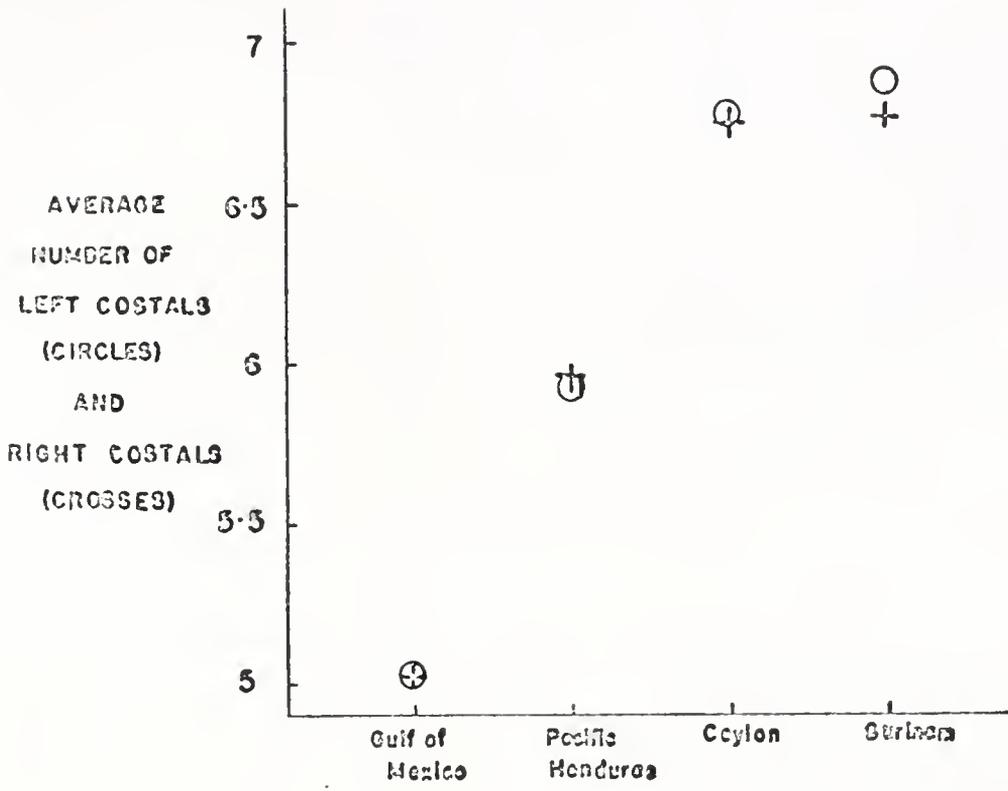


NUMBER OF
LEFT COSTALS

NUMBER OF
RIGHT COSTALS

Figure 13. Graph showing average number of left and right costal laminae for four populations of Lepidochelys

Figure 14. Graph showing average number of central laminae for four populations of Lepidochelys



laminae on the left, and 127 on the right. A similar breakdown of the 378 Ceylon specimens gives 217 symmetrical, 85 with more laminae on the left and 76 with more on the right. The 102 Honduras specimens include 63 symmetrical, 16 with more laminae on the left and 23 with more on the right. The respective percentages of symmetrical individuals in each sample are: 56.1; 57.4; 61.8. Asymmetry nearly always involves a difference of unity between the left and right costal counts; however two of the 36 asymmetrical Honduras individuals showed a difference of two, and one was asymmetrical by three. The 140 asymmetrical Ceylon individuals included 18 asymmetrical by two and three asymmetrical by three. The corresponding figures for the 294 asymmetrical Surinam turtles were: 29 differing by two; none differing by three.

Deraniyagala (1939a: 143) writes that a low average lamina count is a tendency of certain broods of hatchlings. That such may also be a result of different incubation conditions seems borne out by an analysis of three clutches of hatchlings from Isla de Ratonos, Honduras, shown in Table 3, two of which were not hatched under natural conditions. Brood 1 was hatched in Florida after the eggs had been brought back by car, while the eggs from which Brood 3 was hatched were taken 20 miles along a bumpy road before being re-buried. The Brood 2 eggs, however, were transferred immediately after laying to a nearby hatchery.

The extreme counts shown by Broods 1 and 3 could well have been produced by transporting the eggs. Lynn and Ullrich

TABLE 3

COSTAL LAMINA COUNTS FOR THREE BROODS OF
LEPIDOCHELYS OLIVACEA FROM ISLA DE RATONES,
 HONDURAS

Costal lamina count	Brood 1	Brood 2	Brood 3
2-3	1	-	-
4-4	8	-	-
5-4	3	-	-
5-5	5	26	-
5-6	3	11	-
6-5	4	8	-
6-6	2	43	5
7-5	-	4	-
6-7	-	4	-
7-6	-	6	2
7-7	-	1	7
6-8	-	5	-
7-8	-	4	4
8-7	-	-	10
8-8	-	4	32
7-9	-	-	1
9-7	-	-	5
8-9	-	-	8
9-8	-	-	9
10-7	-	-	1
9-9	-	-	10
9-10	-	-	1
10-9	-	1	1
10-10	-	-	4
10-12	-	-	1

	n = 26	n = 116	n = 101
Mean left costals:	4.808	5.921	8.238
Mean right costals:	4.846	6.039	7.973

(1950) experimentally produced hatchling Chrysemys and Chelydra with similar abnormalities by subjecting the eggs

to suboptimal moisture conditions.

In view of the plasticity of the costal lamina character it might be argued that little importance can be given to differences in average costal counts for turtles from different areas. However the average count for hatchlings from undisturbed nests is usually fairly close to the average for adult females from the same area. Thus, the respective left and right average costal counts for Brood 2 from Honduras (which was subjected to no embryonic trauma) were 5.921 and 6.039, which are very close to the average figures for mature females from that population (5.912 and 5.968). The averages for a brood of 88 hatchlings from Surinam were 6.659 and 6.648, and for a brood of 118 hatchlings, 7.070 and 6.965 (cf 6.881 and 6.781 for mature females from the same area).

Marginal Counts

The extreme variability of the central and costal laminae of Lepidochelys olivacea does not extend to the marginals. A marginal count of 12-12 is by far the commonest one for all known populations of both kempi and olivacea; deviations from 12-12 are probably no more frequent than they are in Caretta. Marginal count frequencies are given in Table 4.

The supracaudal laminae, although serially homologous to the true marginals, are not included in marginal counts.

Addition of extra marginals, to give counts of 13 and 14, takes place at the anterior part of the marginal row, in contrast to additional centrals and costals, which are almost

TABLE 4

MARGINAL LAMINA FREQUENCIES FOR THREE
POPULATIONS OF LEPIDOCHELYS

Marginal lamina count	<u>L.kempi</u>	<u>L.olivacea</u> (Honduras)	<u>L.olivacea</u> (Surinam)
10-11	-	-	1
11-11	-	1	2
11-12	-	7	5
12-12	40	304	208
12-13	7	17	20
13-12	7	33	12
12-14	-	2	-
13-11	-	1	2
13-13	4	19	6
13-14	-	3	-
14-13	-	1	-
14-15	-	1	-
15-15	-	1	-
	n = 58	n = 395	n = 258

invariably inserted towards the rear. However the rare specimens with fewer than twelve marginals on one or both sides usually showed missing seams in the rear marginal region, or between a posterior marginal and the adjacent supracaudal. Marginal counts of more than twelve were frequently associated with high costal counts.

Variation in Other Carapace Laminae

The nuchal lamina may be split in occasional individuals from all populations. Eradication of the seam between the nuchal and the first central may also occur, giving the

appearance of an absent nuchal. Both types of variation are rare and were not studied quantitatively.

No variation in the supracaudal laminae was observed, apart from the occasional missing seams mentioned above.

Variation in Plastral Laminae

The laminae of the plastron are strikingly stable in nearly all turtle species, including both species of Lepidochelys. No meristic variation was found in the main plastral laminae (gulars, humerals, pectorals, abdominals, femorals and anals) of either species. However the small intergular lamina may be present, absent or double. Table 5 shows the frequency of each condition for series of hatchlings of kempi and of olivacea from Honduras and Surinam.

TABLE 5
FREQUENCY OF DIFFERENT INTERGULAR
COUNTS FOR THREE POPULATIONS OF
LEPIDOCHELYS

Population	Number of intergulars			Mean number of intergulars for sample
	0	1	2	
<u>L.kempi</u>	22	23	15	0.88
<u>L.olivacea</u> (Honduras)	74	31	21	0.58
<u>L.olivacea</u> (Surinam)	120	66	73	0.82

No clear conclusion can be drawn from these data, since most of the Honduras specimens were drawn from only two or three clutches. However it is possible that the relatively frequent absence of the intergular relative to the single intergular condition in L.olivacea would be substantiated by larger samples.

Inframarginal Counts and Significance of Inframarginal Pores

The presence of three inframarginals in the genus Caretta and of four in Lepidochelys has been considered one of the better 'key' characters for separating the genera by many authors. Deraniyagala (1934: 208-209), in listing characters to separate Caretta, Lepidochelys, and Colpochelys, writes that Lepidochelys is characterized by four inframarginals on each bridge, Colpochelys by three or four, and Caretta by three, without any qualifying phrase on the possibility of exceptions. In later works (Deraniyagala, 1939a: 122; 1943: 87; 1945: 95), in which he includes Colpochelys under Lepidochelys, he states categorically in the keys that Lepidochelys has four inframarginals on each bridge, and Caretta three. Pope (1939: 278, 287, 288), Loveridge and Williams (1957: 492, 495) and Carr (1952: 343) likewise quote these meristics without qualification. Fraser and Parker (1953: 36) use the same character, but in each case add the word 'normally'. Conant (1958: 68-69), using the inframarginal count to differentiate between the Atlantic loggerhead and the Atlantic ridley, makes no mention that

the count is variable in the loggerhead, but states that the ridley 'usually' has four enlarged laminae on the bridge. Brongersma (1967: 9) again uses inframarginal counts in his key to sea turtle species, but adds in parentheses that Lepidochelys kempi rarely has three inframarginals, and in a footnote that some Caretta caretta have four or five inframarginals, but that, when this is so, the number is usually different on each side.

Authors who have discussed inframarginal counts have usually characterized them either as "enlarged scutes on the bridge" or have illustrated the plastron of a typical Caretta or Lepidochelys, in which the distinction between the inframarginals and the axillaries is admittedly obvious. Nevertheless specimens exist in which one (or more) of the enlarged axillary laminae is almost the same size as the anteriormost inframarginal, and we need a definition which will make clear the difference. Most authors seem to have assumed (and Brongersma, 1968: 441, has now quoted) the definition that an inframarginal is a lamina on the bridge which is in contact laterally with one or more marginal laminae and also mesially with one or more of the main series of plastral laminae (pectorals, abdominals and femorals). This will be the criterion which I shall use.

The variability of the inframarginal count of Atlantic loggerheads is clear from the counts of 154 hatchlings from Cape Romain, North Carolina, quoted by Baldwin and Loftin, in Caldwell et al., 1959: 343, shown in Table 6. Counts for 187

Indian Ocean loggerheads from Natal (from Hughes et al., 1967: 36) and for ten Pacific loggerheads from the Solomon Islands (from Carr, 1952: 394) are also given in the table.

TABLE 6
INFRAMARGINAL COUNTS FOR LOGGERHEAD TURTLES (CARETTA CARETTA) FROM THREE AREAS

Inframarginal count	North Carolina	Natal	Solomon Islands
3-3	57	145	7
3-4	21	20	-
4-3	14	10	-
4-4	56	10	2
4-5	1	-	1
5-4	2	-	-
5-5	2	-	-
6-4	1	-	-
5-3	-	1	-
3-2	-	1	-
	n = 154	n = 187	n = 10

These figures suggest that the 3-3 inframarginal count is useless for characterizing Atlantic loggerheads, but that it may be somewhat more reliable in the Indian and Pacific Oceans. However, full statistical treatment of the data in Table 6 is not warranted since we do not know how many clutches these series were drawn from.

The inframarginal count of Lepidochelys is more stable than that of Caretta. Chávez et al. (1967) examined a series of 154 adult female L. kempi found on the nesting beach at

Rancho Nuevo; 149 had four inframarginals on each side; one had 5-4; three had 5-5 and in the remaining specimen the seams could not be discerned so the count could not be taken. In a series of 59 hatchlings from the same locality, all had the 4-4 inframarginal count except one, in which the posterior inframarginal on the right, being small and triangular and thus failing to make contact with any of the main plastral laminae, was not counted. These data, together with the inframarginal counts for a series of hatchling Lepidochelys olivacea from the Pacific coast of Honduras and a series from Eilanti, Surinam, are shown in Table 7.

TABLE 7
INFRAMARGINAL COUNTS FOR THREE POPULATIONS
OF LEPIDOCHELYS

Inframarginal count	<u>L. kempi</u>	<u>L. olivacea</u> (Honduras)	<u>L. olivacea</u> (Surinam)
3-3	-	2	-
3-4	-	5	3
4-3	1	1	-
4-4	212	87	91
4-5	-	-	4
5-4	-	1	2
5-5	3	1	-
5-3	-	1	-
	n = 216	n = 98	n = 100

Approximately 95 percent of the kempi sample, and 89 and 91 percent respectively of the two olivacea samples had

four inframarginals on each side; however the 4-4 count is also sufficiently common in Caretta to render this character of little application for distinguishing the forms. But there is another inframarginal character which appears to be of 100 percent validity, and that is the presence in both species of Lepidochelys of a small pore located near the posterior margin of each inframarginal lamina, and another on the seam between the anterior inframarginal and the adjacent axillary lamina. Almost all authors who have discussed Lepidochelys have mentioned these pores; however only Carr (1963: 302) has discussed their possible significance. He writes:

If the exceptionally active nosing of the sand mentioned earlier is, as it seems, a smelling manoeuvre, it suggests that the ridley is more dependent on this sense than any of the other sea turtles. Moreover, the ridleys are the only sea turtles which have conspicuous secretory pores at each seam between the inframarginal scales. The function of the secretion from these pores is not known, but the most reasonable assumption is that it is an olfactory aid to sex - or species - recognition. If so, then it may be a signal for the final massing off the nesting beach, and possibly even a scent beacon that marks the sand of the shore for arribadas of later years.

It has not been demonstrated that the pores are secretory in function, though this does seem their most likely purpose. There is also no published account of the cytological morphology of the pore structure.

Fig. 15 shows transverse and frontal sections through the bone underlying an inframarginal pore of a mature female Lepidochelys kempi. The sun-dried plastron was found separate from the animal, and no further preservation was carried out.

Figure 15. Transverse and frontal sections through plastron of mature female L.kempi in region immediately underlying an infra-marginal pore



In may be seen that the plastron in this region is about 12 mm in thickness, the outermost 2-3 mm being hard, compact bone and the rest spongy and presumably vascular in life. The sections reveal cavities of capacity about 1 cc beneath each pore, reaching almost through to the visceral surface of the plastron, and with a lining about 1 mm thick of compact bone similar to that on the outer surface. This layer of bone is perforated in several places, by channels which may have carried blood vessels in life. The cavities have a thick inner lining of soft tissue, which was not studied microscopically.

Pending a proper biochemical and cytological examination of the cavities underlying the inframarginal pores of Lepidochelys, Carr's suggestion that they are secretory glands which aid in sex or species recognition seems most likely, and they may well aid in arribada formation - a behavioral characteristic peculiar to the genus. However, since it is now known that ridley arribadas at Rancho Nuevo, Mexico, do not always come ashore on the same exact stretch of beach, it seems unlikely that the sand is permanently marked by a secretion from these pores. However, the secretion may be discharged into the sea by ovigerous females and attendant males migrating from all parts of the Gulf of Mexico towards Rancho Nuevo, and may aid in the gradual formation and also the stability of large flotillas of turtles.

Possible Significance of Differences in Shell Shape

As we have already demonstrated, the carapace of adult Lepidochelys kempfi is, on the average, wider relative to its length than that of L.olivacea, as well as being distinctly lower. I have rationalized elsewhere that the expanded sides of the carapace of adult kempfi may be a device to compress the sand over the nesting site more compactly after nesting, and thus make it less likely that the odor of the new-laid eggs will attract terrestrial predators such as coyotes. When watching an Atlantic ridley stamp down the sand over the nest with vigorous rocking movements of the shell, one is indeed struck by how well the sides of the shell seem adapted to this function, and it is certainly important that the eggs be hidden as thoroughly as possible, considering the number of coyotes in the area.

The extra width of the shell of kempfi reflects itself in an increased width of the marginal laminae in the mid part of the series. Figure 16 shows the 7th, 8th and 9th marginals (or their homologs in cases of abnormalities in the anterior parts of the marginal series) for mature female L.kempfi from Rancho Nuevo, and also for mature female L.olivacea from Shell Beach, Guyana. It may be seen that, while the 8th marginal lamina of kempfi is often about as wide as long, in olivacea this lamina is usually at least 50 percent longer than wide.

Other, slight, differences between L.kempfi and L.olivacea are present in the region of the last marginals and

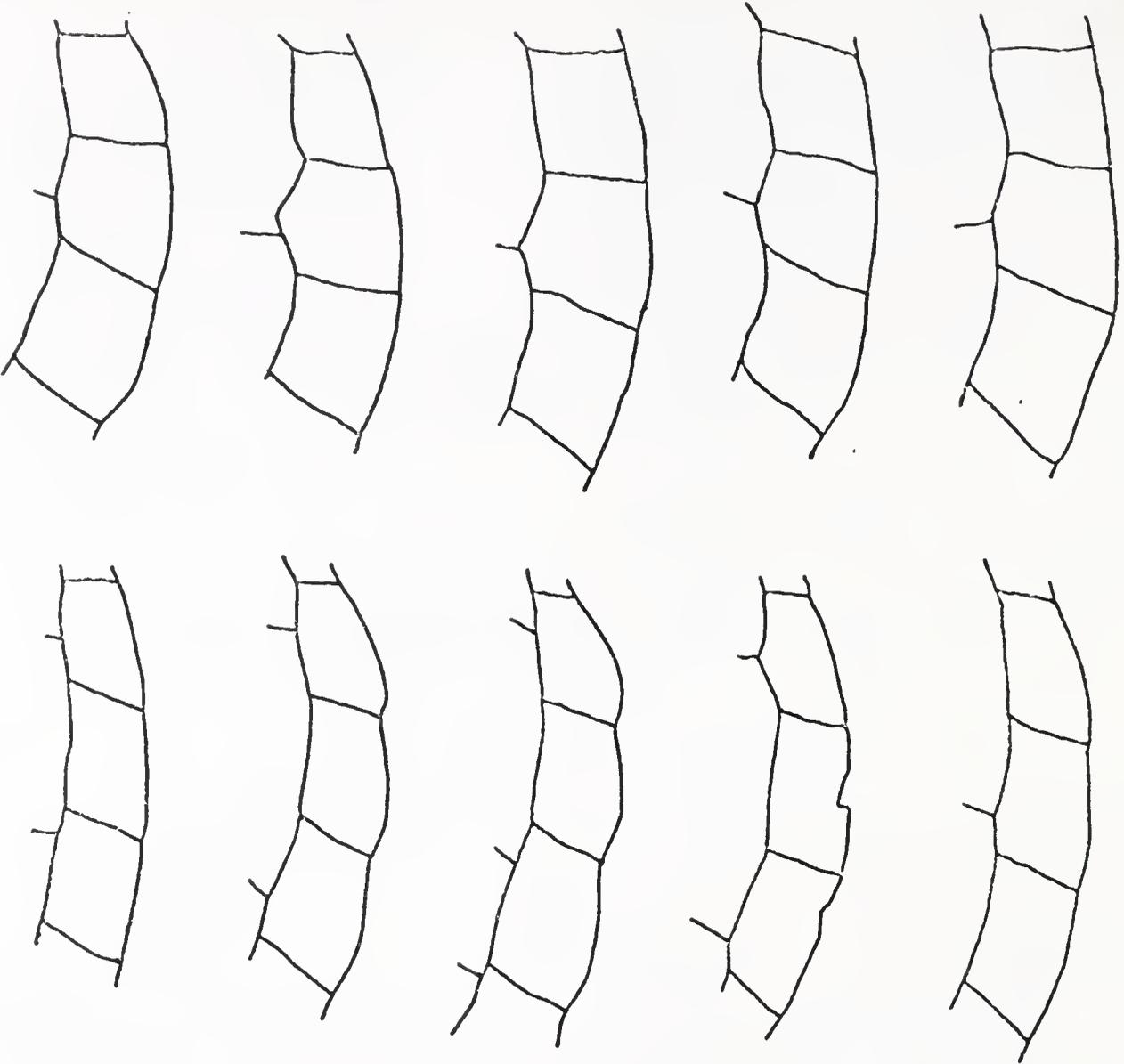


Figure 16. (above) mid-marginal laminae of *L. kempi* from Rancho Nuevo

(below) mid-marginal laminae of *L. olivacea* from Shell Beach, Guyana

the supracaudals. Figure 17 shows these laminae for specimens of L.kempi (mature females from Rancho Nuevo), and also for specimens of L.olivacea from Pacific Mexico, Shell Beach, Guyana, and Eilanti, Surinam. It may be seen that the seams separating the supracaudals from the posterior central tend to meet in a straight line in kempi, and at an obtuse angle in olivacea. Also the posterior corners of the marginals and supracaudals of kempi tend to be relatively smooth, so that the carapace margin is merely slightly wavy, while in olivacea these laminae have projecting corners, so that the hind margin of the carapace is frequently somewhat serrated.

The greater elevation of the carapace of olivacea relative to that of kempi was noticed by Carr (1961: 9). The actual height of the shell is hard to measure in the field, and the character was therefore studied by means of anterior-view, ground-level photographs. The carapace profiles shown in figure 18 corroborate Carr's observation; the carapace of L.kempi is low and gently rounded, while in most cases that of olivacea has a strikingly elevated, flat-topped central section.

The possible significance of the differences in carapace profile between the two species can, at present, only be guessed at. Possibly the lateral expansion of the shell of kempi is caused by a re-direction of growth vectors which in olivacea contribute to the progressive deepening of the carapace.

Figure 17. (left) posterior marginal
and supracaudal laminae for L.kempi
from Rancho Nuevo

(right) same for L.olivacea
from Guyana and Surinam

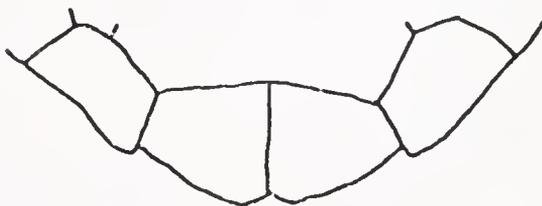
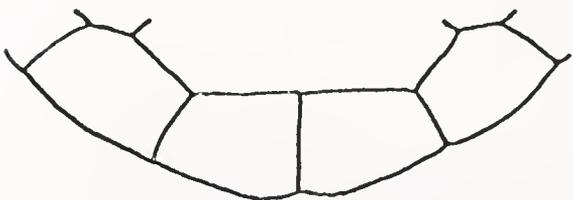
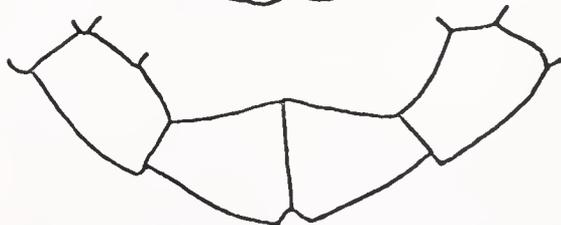
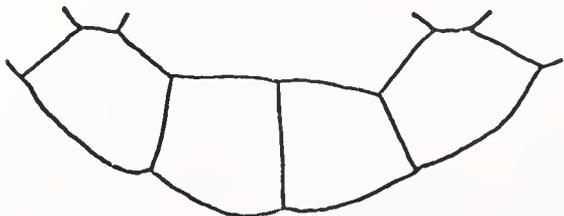
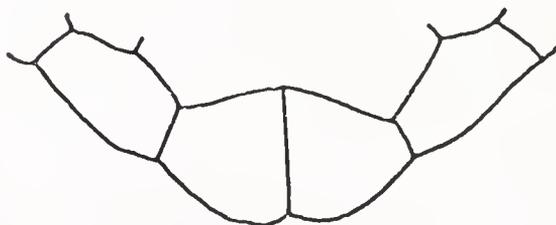
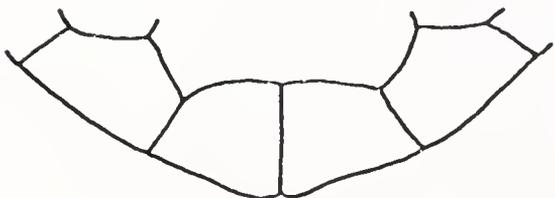
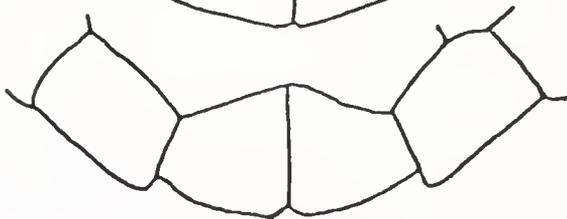
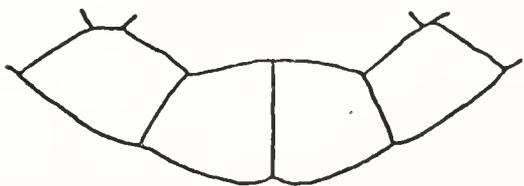
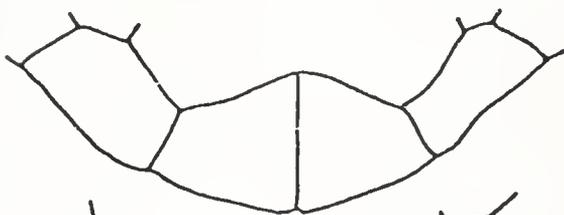
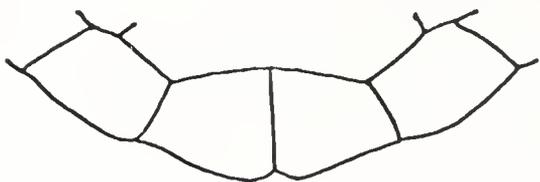
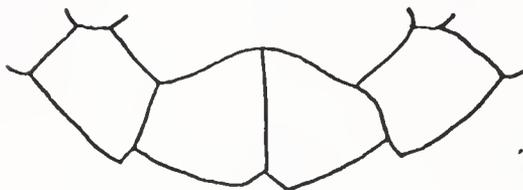
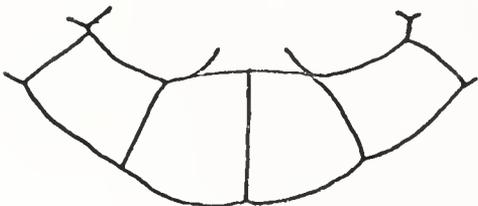
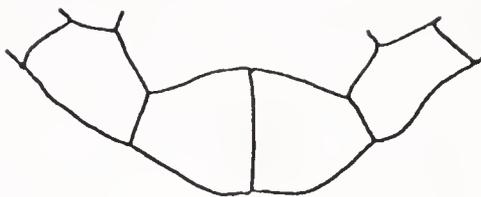
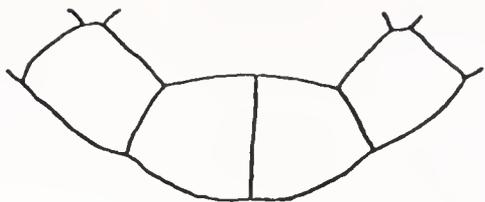
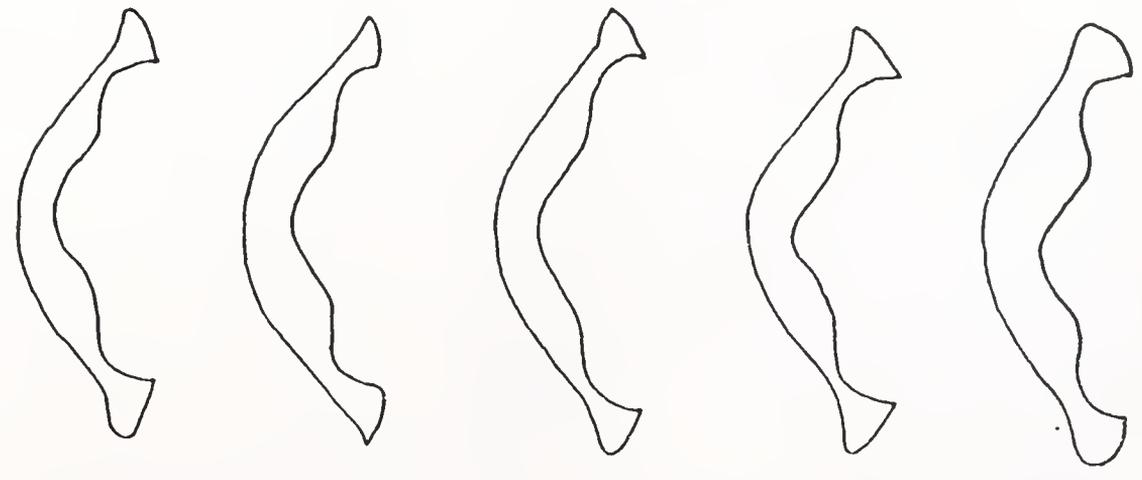
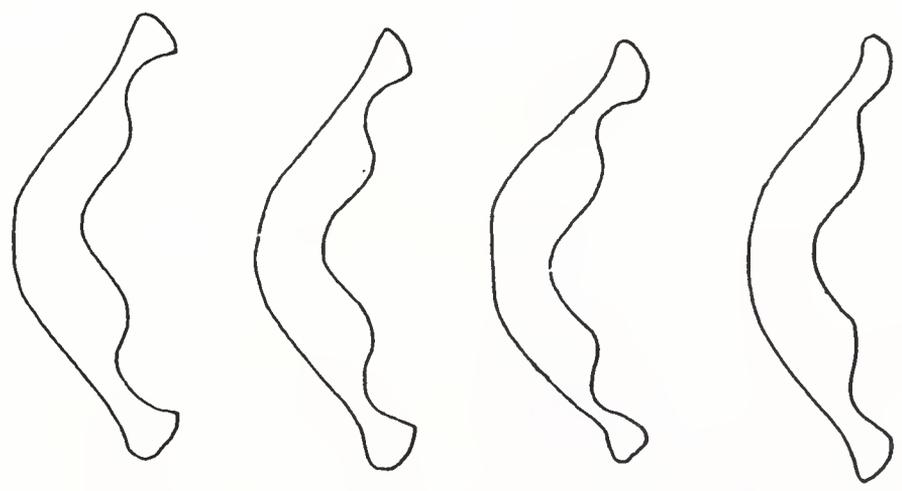
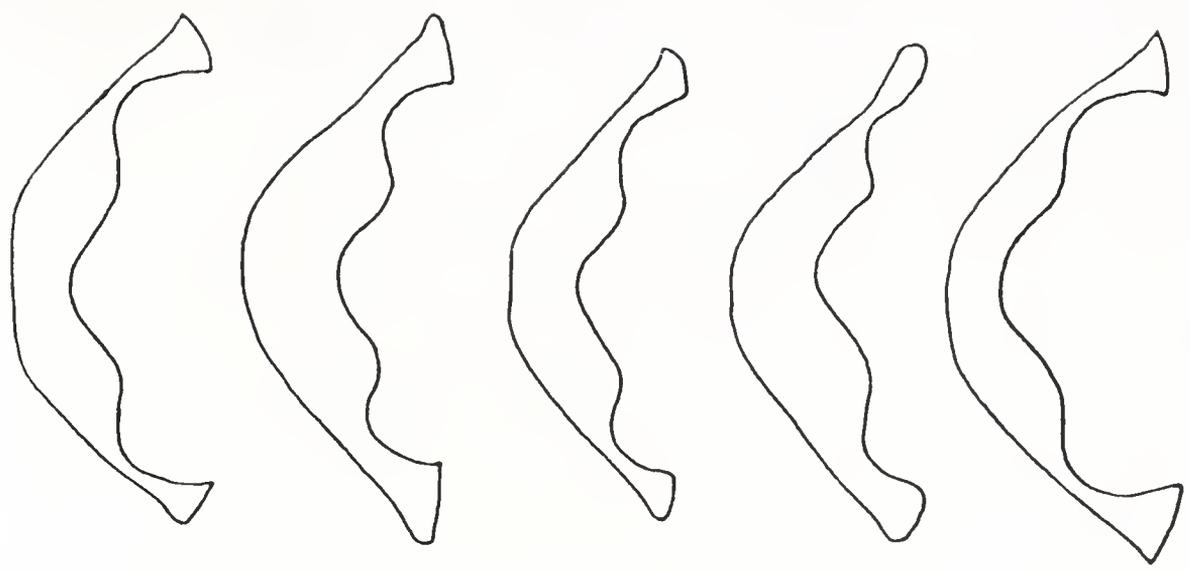


Figure 18. (left) anterior carapace profiles of L.kempi
from Rancho Nuevo

(middle) same for L.olivacea from Guyana and
Surinam

(right) same for L.olivacea from Pacific
Mexico



Carapace Osteology

No detailed comparative studies of the osteology of the carapace of Lepidochelys were undertaken.

The bony carapace of Lepidochelys consists of a large proneural, twelve (rarely thirteen) pairs of peripherals, eight pairs of pleurals, two (or occasionally three) suprapygals, the anterior of which has a characteristic crescentic shape, the postero-lateral rami enclosing the second suprapygal (in adult specimens) and frequently coming in contact with the penultimate peripherals, and a single pygal.

Great variability is shown by the neural series. The basic chelonian number of nine neurals has been increased by transverse (and occasionally longitudinal) division of most of these elements, so that they now number between eleven and fifteen. The most frequent type of division occurs when a curved suture, with the convex side directed anteriorly, splits an elongated, hexagonal neural bone into a nearly regular hexagon and a smaller bone, subovate or almost square in shape.

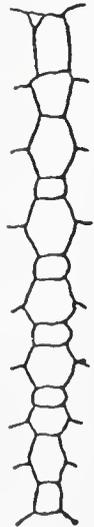
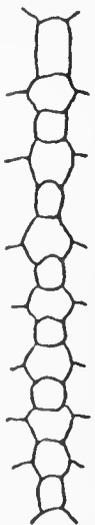
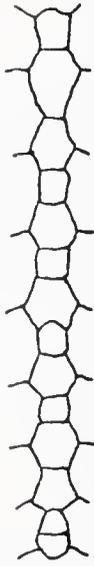
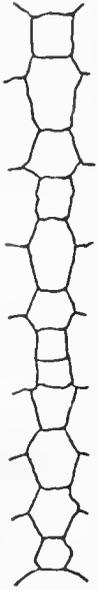
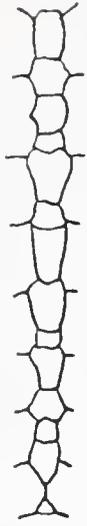
Figure 19 shows the neural bones of three mature Lepidochelys olivacea from Bahia Banderas, Nayarit, Mexico; of two mature and one nearly mature L. olivacea from Ceylon (redrawn from Deraniyagala, 1939a); and of three L. kempi (two mature specimens from Veracruz, Mexico, and one nearly mature from Cedar Key, Florida).

These series are of course far too small for any statistical conclusions to be drawn from them. Nevertheless it is interesting to note that fragmentation of the neural bones

Figure 19. (above) neural bones of L.kempi
from Veracruz, Mexico and Cedar Key, Florida

(middle) same for L.olivacea
from Pacific Mexico

(below) same for L.olivacea from
Ceylon (after Deraniyagala, 1939a)



takes place in both Lepidochelys kempi and L.olivacea, even though fragmentation of the laminae of the carapace only occurs in L.olivacea.

Likewise, no detailed studies of the osteology of the plastron were undertaken. However, one abnormal specimen was found in Guyana (Shell Beach) in which an extra pair of bones was present, which showed a close morphological correspondence to the mesoplastra of extinct amphichelid turtles (Pritchard, 1966). One is tempted to postulate an atavistic interpretation of this condition, but, considering the great length of time since a Lepidochelys ancestor had mesoplastra, it is perhaps more likely that the present specimen merely shows a casual division of embryonic ossification centers.

Skull Characters

Comparison of Size of Skulls of Mature Females

The basicranial lengths (measured from the tip of the snout to the occipital condyle) of eleven skulls of mature female Lepidochelys kempi from Rancho Nuevo; of 19 skulls of mature female L.olivacea from Shell Beach, Guyana; and of 18 skulls of mature female L.olivacea from San Luis de la Loma, Guerrero, Mexico, were as follows (cm):

L.kempi: 13.2; 13.65; 13.75; 14.0; 14.0; 14.1; 14.1;
14.4; 14.2; 14.5 (mean = 13.95; n = 10; S.D. =
 ± 0.21 ; 95% confidence interval for mean = 13.95
 ± 0.1311)

L.olivacea (Guyana): 13.1; 13.2; 13.3; 13.3; 13.4; 13.5;
13.5; 13.7; 13.8; 13.8; 14.0; 14.0; 14.0; 14.1; 14.1;
14.1; 14.2; 15.0 (mean = 13.80; n = 18; S.D. =
 ± 0.47 ; 95% confidence interval for mean = 13.80
 ± 0.2150)

L.olivacea (Guerrero): 12.75; 12.9; 13.0; 13.1; 13.1;
13.2; 13.2; 13.5; 13.5; 13.5; 13.6; 13.8; 14.0; 14.0;
14.0; 14.1; 14.15; 14.3 (mean = 13.54; n = 18;
S.D. = ± 0.48 ; 95% confidence interval for mean =
13.54 ± 0.2216)

The difference in average length between the L.kempi and the Guerrero L.olivacea skulls, though slight (0.41 cm), is significant at the 95 percent level. Moreover, the difference in bulk between random kempi and Guerrero olivacea skulls

is very striking (figure 20); the supraoccipital process, in particular, shows marked differences in the two species, being long, thick, and with a strong ventral flange in kempi, and being shorter and thinner, and with only a slight ventral thickening in olivacea (figure 21).

In the course of preparation it was noticed that the skulls of kempi remained intact, while those of olivacea from Guerrero frequently fell apart at the sutures, as did a few of those from Guyana. It is doubtful if human predation has had any differential effect in altering the structure of the three populations; in the three cases there is some predation on both adults and eggs, so there is no particular reason why one population should have a marked preponderance of very old or very young individuals. The differences in degree of suture-closing may mean that olivacea alone reaches sexual maturity while still growing quite rapidly. Another possibility is that it is more important for kempi to have a tightly sutured shell in view of its diet of hard-shelled crabs and molluscs.

Comparison of Relative Widths of Skulls of Mature Females

Figure 23 shows the relative width of the skulls of eight L.kempi from Rancho Nuevo, of fifteen L.olivacea from Guyana and fifteen of L.olivacea from Guerrero. The width of each skull was measured at the widest point (at the back of the tympanum), and was divided by the basicranial length, measured as above.

Figure 20. Dorsal view of skulls of mature female L.olivacea (left) and L.kempi (right)

Figure 21. Ventral view of skulls of mature female L.olivacea (left) and L.kempi (right)

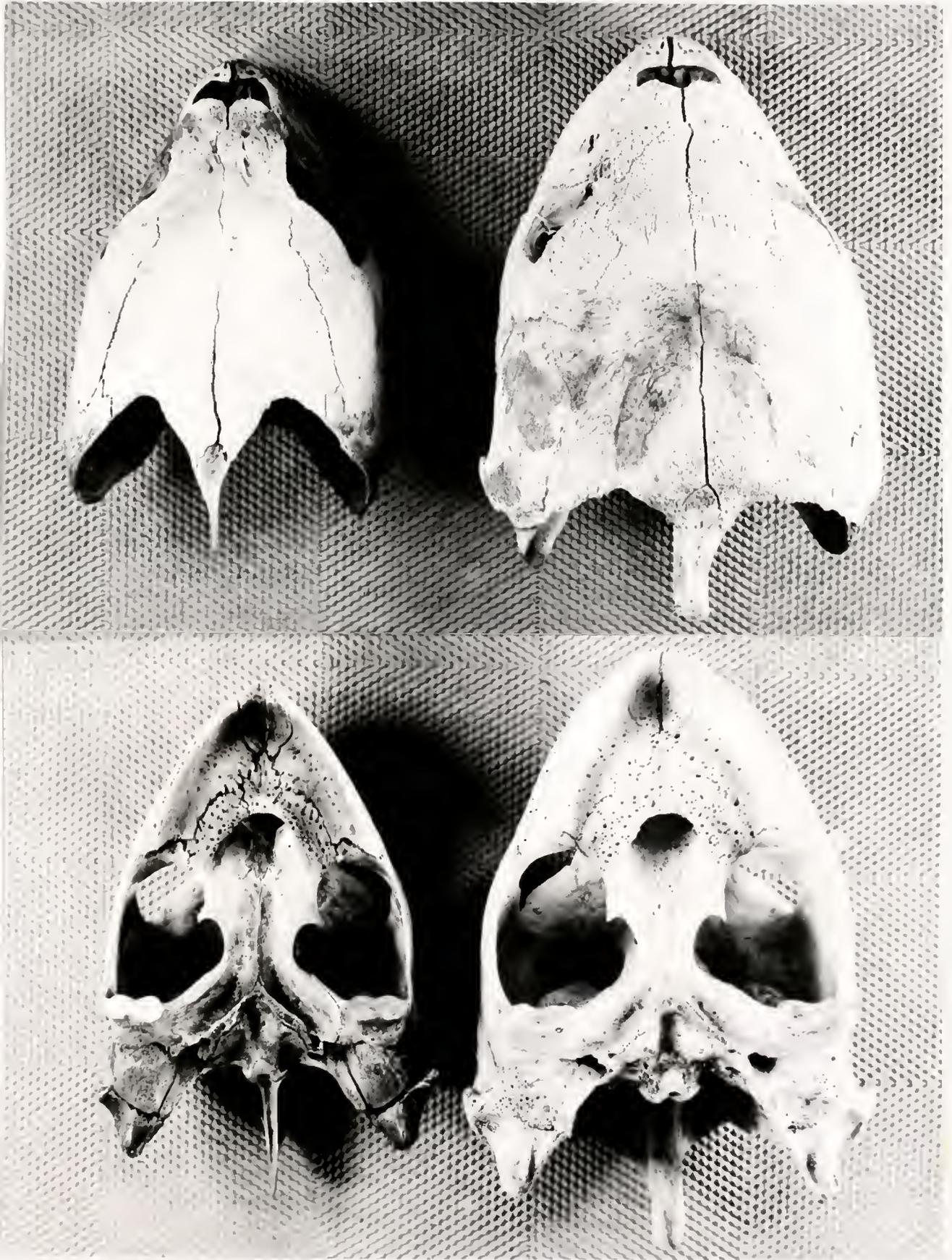


Figure 22. Width/basicranial length of skulls of mature female L.kempi and L.olivacea from Guyana and Guerrero, Mexico

L. kempli N = 8

L. olivacea (Guyana) N = 15

L. olivacea (Guerrero) N = 15

.87 .88 .89 .90 .91 .92 .93 .94 .95 .96 .97 .98 .99 1.00

It may be seen that the average relative width of kempi skulls (0.938) is distinctly greater than the average relative width of skulls from the two olivacea populations (0.914 and 0.909 respectively). Moreover, although our samples are not large, since all eight kempi skulls had a relative width greater than 0.95, while all the olivacea skulls had a relative width of less than 0.95, there is clearly no need for statistical confirmation of the different relative widths of the skulls of the two species.

It is difficult to interpret the statistical significance of the averages and ranges of values of the relative skull width in the two populations of L. olivacea. The minimum and maximum relative widths of Guerrero olivacea are both greater than the corresponding figures for Guyana olivacea, but the mean is less. Expressing this somewhat differently, Guerrero specimens tend to have narrow heads, but an occasional one is very wide, while Guyana specimens tend to have somewhat wider heads, but an occasional one is very narrow.

Relative Height of Orbit

Superficial examination of a series of skulls of L. kempi and L. olivacea gives the impression that the orbit of kempi is relatively smaller (figure 23). Measurements of the maximum vertical height of the orbit were taken for 11 L. kempi, 23 L. olivacea from Guyana and 18 L. olivacea from Guerrero. These values were expressed relative to the height of the maxillary bone below the orbit, this height being taken at its

Figure 23. Lateral views of skulls of
mature female L.kempi (above) and L.
olivacea (below)



lowest point, directly below the orbit and close to the jugo-maxillary suture. The results are plotted in figure 24. The separation of values for L.kempi and L.olivacea is very striking, while it can be seen that the relative size of the orbit in the two populations of L.olivacea is virtually identical.

The most obvious interpretation of the smaller orbit of kempi is simply that this animal is a diurnal nester and does not require the large, presumably nocturnally adapted eyes of L.olivacea (and the other species of sea turtle, all of which nest by night and have conspicuously large orbits). On the other hand, relatively small orbits may be a result of relatively deep maxillaries, and this deepening may simply be a manifestation of the generally heavier construction and stronger jaws of kempi. However, it is doubtful if the necessity for stronger jaws would affect so critical a structure as the eye. The upper jaw could be strengthened simply by extra buttressing rather than by diminishing the size of the eye, and since the eye is a highly vulnerable organ in an otherwise well-armored head, it would seem reasonable that both species would have evolved an orbit as small as possible while retaining the necessary perfection of vision.

Relative Width of Pterygoid Bridge

On casual inspection the minimum width across the pterygoid bones is less in kempi than in olivacea. Values for this measurement, expressed relative to the basiscranial length, are plotted in figure 25.

Figure 24. Vertical height of orbit (relative to minimum vertical height of maxilla below orbit) for skulls of three populations of Lepidocheilys

Lepidocheelys
kempi _____ N = 11

Lepidocheelys olivacea (Guyana) _____ N = 23

Lepidocheelys olivacea (Guerrero) _____ N = 18

1.1 1.2 1.3 1.4 1.5 1.6 1.7 1.8 1.9 2.0 2.1

Figure 25. Width of pterygoid bridge (as fraction of basicranial length) for three populations of Lepidochelys



Lepidochelys kempi



Lepidochelys
olivacea
(Guyana)



Lepido-
chelys
olivacea
(Guerrero)



The figure shows an almost perfect separation of the values of pterygoid bridge width of the two species; only one skull of kempi had a wider pterygoid bridge than the single specimen of L.olivacea that was narrowest in this respect. The narrow pterygoid bridge of kempi may well be simply an accommodation for more massive temporal muscles on either side of it - yet another manifestation of the generally stronger, more massive head of this species.

Structure of the Alveolar Surface

Both L.kempi and L.olivacea have a well-defined ridge on each side of the upper rhamphotheca, running parallel to the tomium. These ridges are, however, different in the two species; those of kempi are heavily constructed and very blunt; those of olivacea are of lighter construction and have an angular cutting edge (figure 26). Moreover the bone beneath the rhamphotheca of L.kempi shows a blunt ridge on each side, coinciding approximately with the maxillary-palatine suture. The bony alveolar surface of L.olivacea shows no such ridges, indicating that the rhamphothecal ridges in this species have no bony core (figure 27).

Characters of the Lower Jaw

Five lower jaws of adult female Lenidocheilys kempi from Rancho Nuevo, Mexico; 27 of adult female L.olivacea from San Luis de la Loma, Guerrero, Mexico; and 13 of adult female L.olivacea from Shell Beach, Guyana were available for study. All



Figure 26. Upper rhamphothecae of mature female Lepidochelys kempi (left) and L. olivacea (right)

were obtained from nesting turtles killed by local people for meat and skins.

The five lower jaws of kempi show little variation in size or in width of the alveolar surface. However the larger series of jaws of L. olivacea from Guerrero shows marked variation both in absolute size and also in width of the alveolar surface. Figure 28 shows the extremes in width of alveolar surface for the Guerrero series and the Guyana series. It may be seen that in both cases the jaw with the relatively wider surface is slightly larger, which suggests that the increase in width of the surface of the jaw is allometric. This was demonstrated by measurement of symphyseal lengths against measurements of the greatest total width of the jaws, taken between the lateral expansions of the angular bones,

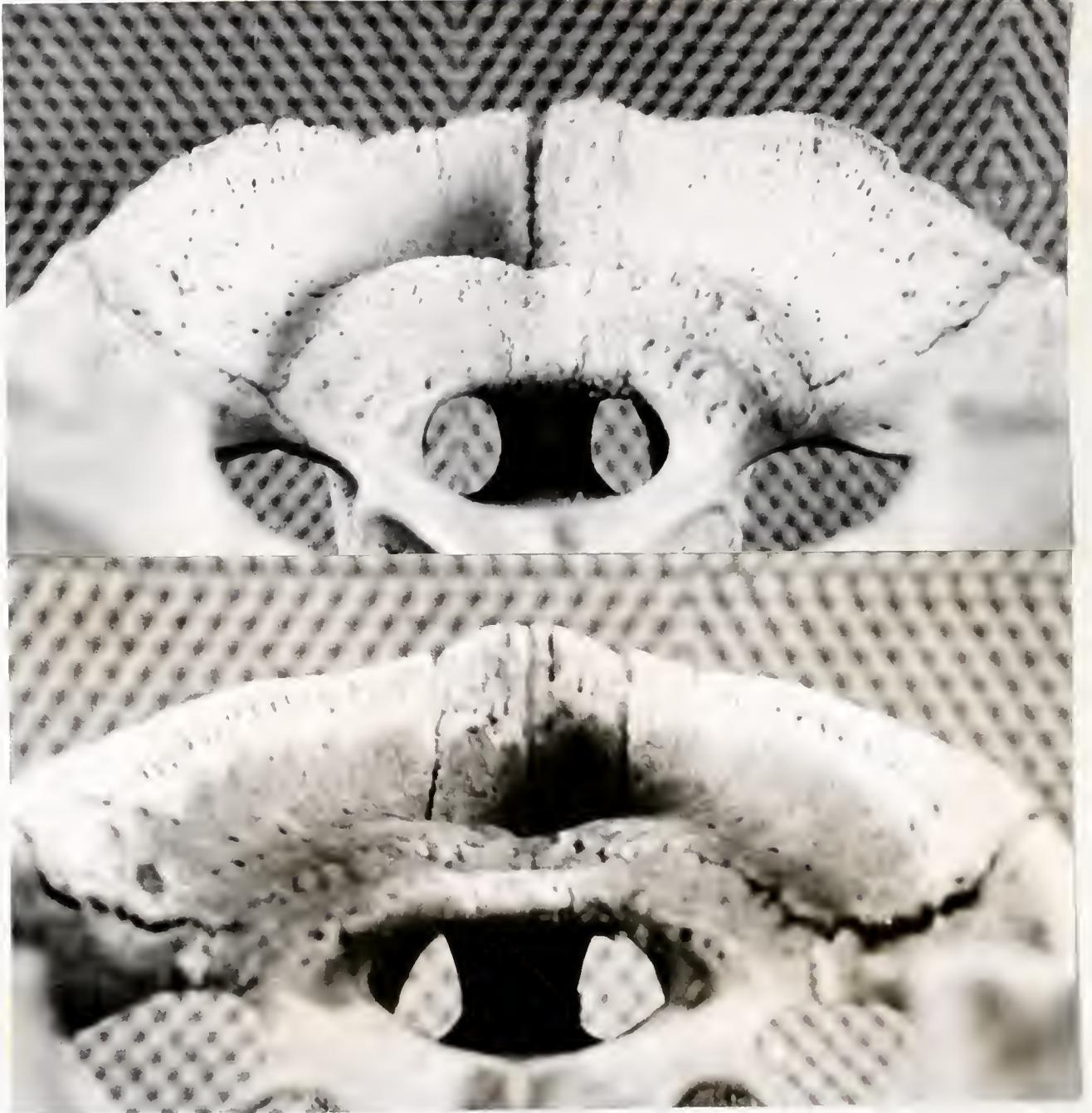


Figure 27. Posterior views of skulls of L.kempi (above) and L.olivacea (below), showing presence of strong bony alveolar ridge in kempi only

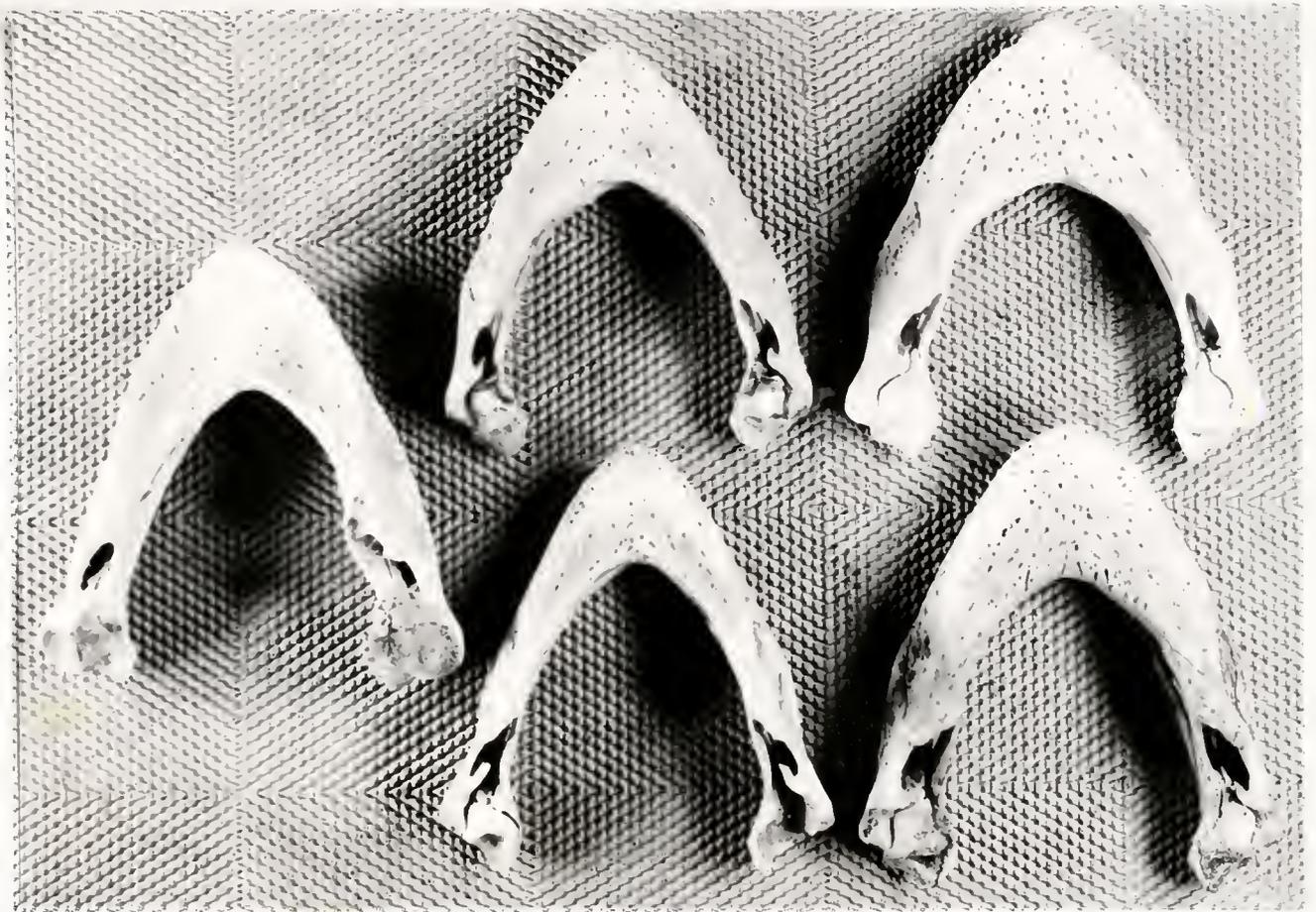
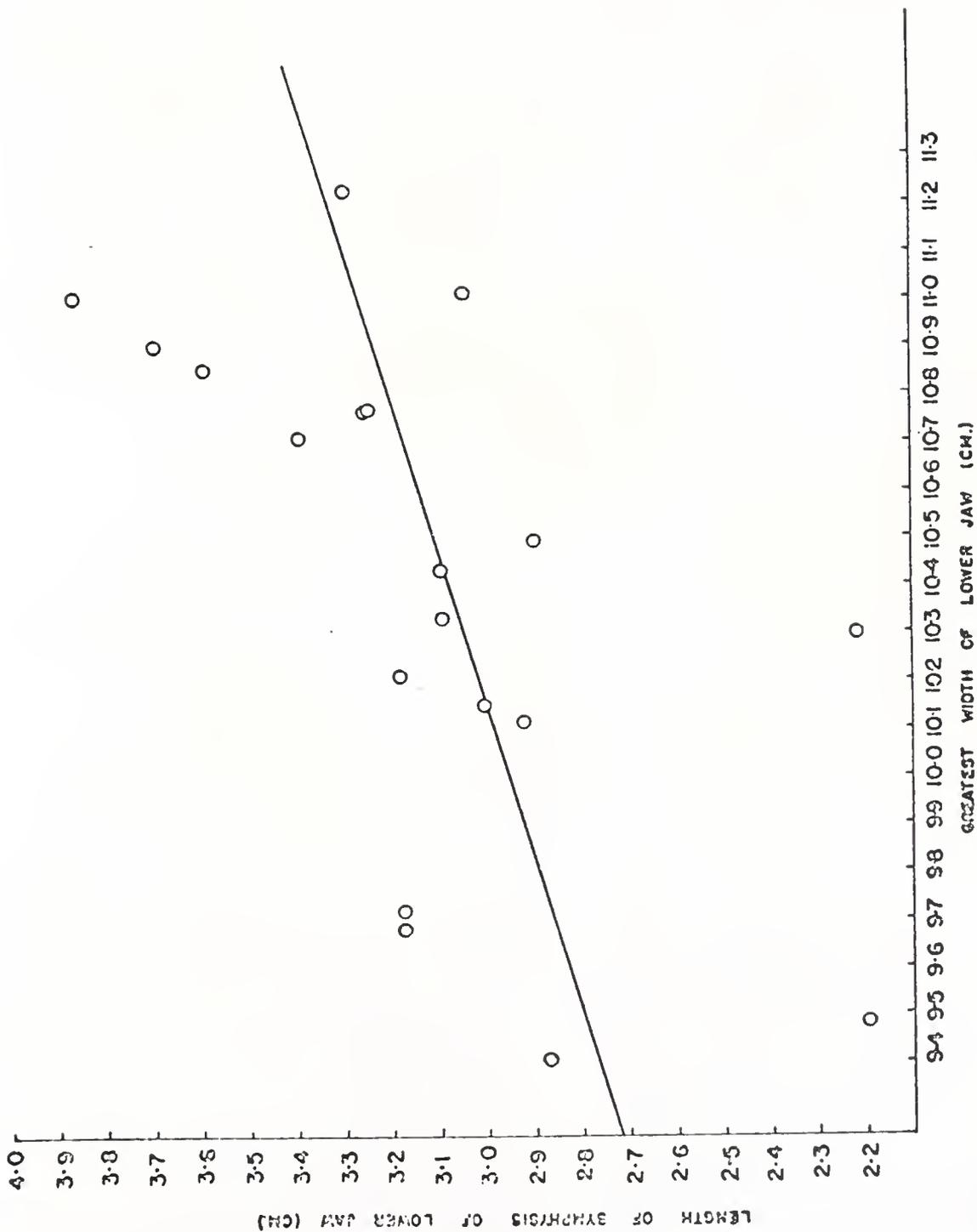


Figure 28. Lower jaws of L.kempi (left); of L.olivacea from Guerrero (above center and right); and of L.olivacea from Guyana (below center and right)

for the 19 intact olivacea jaws (figure 29). A straight line corresponding to direct proportionality and passing through the visual mean of the jaws of intermediate size has been superimposed on the graph; it may be seen that in most cases jaws slightly larger than average size have disproportionately wide alveolar surfaces.

Several minor differences between the lower jaws of L.kempi and L.olivacea were noted. The most obvious was the universal presence in kempi jaws of a bony point situated at

Figure 29. Plot of symphyseal length against
total width for 19 lower jaws of mature female
Lepidochelys olivacea from Guerrero



the rear of the symphysis (figure 28); this was always absent in olivacea, although frequently a barely discernible median bony ridge extends along the entire symphysis of the lower jaw of olivacea. Lower rhamphothecae of both species show ridges along the posterior margin (figure 30), but only that of kembi has a strong median projection with a bony core.



Figure 30. Lower rhamphothecae of L. kembi (right) and L. olivacea (left)

Other differences between the lower jaws of kembi and olivacea are as follows:

i) The entire bony alveolar surface of kembi is rather strongly concave, while that of olivacea is flat.

ii) The overall depth of the jaw of kembi is somewhat greater than that of olivacea (figure 31).

iii) The tip of the coronoid bone, which provides

attachment for the temporal muscle closing the jaw, is bluntly pointed in kempi and more or less rounded-off in olivacea (figure 31).

iv) The dorsal mandibular vacuity is relatively smaller



Figure 31. Lateral view of lower jaw of L. kempi (above) and L. olivacea (below)

is kempi than in olivacea, the bones bordering the vacuity (the prearticular, coronoid and angular) being distinctly stouter in kempi (figure 32).

v) The articular facets of kempi tend to face backward more than those of olivacea, which tend to face somewhat upward (figure 31).



Figure 32. Posterior views of lower jaws of L.kempi (left) and L.olivacea (right)

vi) The bones comprising the articular facets (the articular, prearticular and angular) tend to be well fused together in kempi, while in olivacea these bones are loosely sutured, and tend to be separated at the antero-dorsal end (figure 32).

Significance of Skull Differences

Nearly all of the differences between the skulls and lower jaws of L.kempi and L.olivacea that have been described may be correlated with one overall adaptation - that

of extra biting and crushing power in the jaws of kempi, presumably associated with the necessity of handling the predominantly hard-shelled organisms which make up the diet of this species. The differences in skull structure between L.kempi and L.olivacea, however, are not nearly as pronounced as those between the males and females of several freshwater turtle species - for example Graptemys barbouri, in which the female alone has a huge, wide head with greatly expanded alveolar surfaces and very strong flanges on the supraoccipital process. Such features in the females are all adaptations towards a diet of large, hard-shelled organisms; the much smaller males of the species eat small, soft-bodied creatures only.

It is certainly no objection to the full specific status of the two forms of Lepidochelys that the degree of difference is less than that found between the sexes of other species; no one argues that Graptemys barbouri is conspecific with Graptemys geographica because the males of the two species are more similar than are the two sexes of one of the species. Nevertheless it could be argued that the skull and jaw differences between kempi and olivacea are not genetic but are merely responses that are developed anew with each generation according to the diet which is available. I consider this unlikely, partly because there are excellent shrimp grounds in the Gulf of Mexico, at least at the present time; there is no necessity for a young, weak-jawed kempi to try to crack up molluscs and large crabs when there is an abundance

of shrimp available. However if kempi is genetically predisposed to having stronger jaws, it would experience no trouble changing over from whatever the juvenile diet might be to one of hard-shelled organisms. Perhaps when kempi first reached the Gulf of Mexico crabs and molluscs were much more abundant than shrimp, and the species gradually adapted to this diet, which it retained even after the establishment of good shrimping grounds in the Gulf. However, the question must await the raising of hatchling kempi and olivacea to maturity on identical diets before a definite answer can be given. Nevertheless, as we have mentioned before, some of the observed differences, such as the differences in orbital diameter, are independent of the overall strengthening of the jaws in kempi, and are almost certainly genetic in nature.

Scalation of the Head

Each of the three species of the Subfamily Cheloniini (Chelonia mydas, Chelonia depressa and Eretmochelys imbricata) has a 'standard' pattern of scales on the dorsal surface of the head, shown by a majority of individuals; deviants from this standard pattern are frequently asymmetrical, although in some cases a secondary standard pattern, symmetrical and similarly expressed in a minority of individuals, may exist.

Dorsal head scales of twelve hatchling Chelonia mydas from Tortuguero, Costa Rica, are shown in figure 33. The standard pattern is that on the extreme left, shown by six individuals; it consists of a large, median scale, the frontoparietal, preceded by a smaller frontal and the paired prefrontals. On each side of the frontal is a supraocular, and behind each of these a temporal. A pair of parietals is situated behind the frontoparietal, with an additional temporal on the outer margin of each parietal. Deviations from the standard pattern include absence or splitting of the frontal, extra temporals, or divided parietals.

The standard pattern of Chelonia depressa (figure 33), based on a series of fourteen young from Northern Territory, Australia, differs from that of mydas only in the inclusion of a median scale between the paired parietals of mydas. The parietal region of depressa is somewhat variable, however,

Figure 33. Dorsal head scales for:

- A: Chelonia mydas
- B: Chelonia depressa
- C: Wretmochelys imbricata
- D: Caretta caretta

six deviants being present in the series of fourteen. Nevertheless none of the deviants had the median interparietal seam typical of C.mydas.

Eretmochelys imbricata (figure 33) differs from Chelonia mydas in having two pairs of prefrontals but only one pair of temporals in the standard condition (shown by nine out of fifteen hatchlings from Tortuguero). There is also a frequent tendency for a median seam to enter the anterior part of the frontoparietal and thus partially divide that scale. Deviants from the standard condition showed increases in the number of temporals (to two pairs in four cases; to one pair and one extra scale in one case), and in one case the median interparietal seam was displaced laterally.

No species of the Subfamily Carettini shows a standard pattern of head scales; in all three cases a considerable, and variable, amount of scale fragmentation occurs. Nevertheless it is possible to discern some common features.

Caretta caretta has a large frontoparietal scale, preceded by a smaller frontal as in the Chelonini. The frontal may, however, be longitudinally split. There are two pairs of prefrontals, as in Eretmochelys; sometimes these four scales enclose a small, diamond-shaped element. The parietal, temporal and supraocular scales are extensively and usually asymmetrically fragmented; it is not possible to designate a standard configuration. The dorsal head scales of seven random Caretta caretta hatchlings from Fort Pierce, Florida, are shown in figure 33.

The two species of Lepidochelys have dorsal head scales somewhat similar to those of Caretta, but the fragmentation is even more extensive and variable, while frequently individual scales are split by irregular, wandering seams which fail to divide the scale completely and which make it virtually impossible to quantitate the scalation for comparative purposes. Figure 34 shows the dorsal head scales of six individuals (three hatchlings and three mature females) of each of the three populations of Lepidochelys which were studied: Lepidochelys kempfi from Rancho Nuevo, Tamaulipas, Mexico; Lepidochelys olivacea from the Gulf of Fonseca, Honduras; and Lepidochelys olivacea from Eilanti, Surinam. The enlarged frontoparietal scale is constant, though decreasing in relative size with maturity; the frontal is also constant. It is possible to perceive a standard arrangement of two pairs of prefrontal scales, but these may enclose a smaller extra scale, as in some specimens of Caretta, and in other cases their arrangement is completely chaotic. In nearly all cases there is one pair of enlarged parietals, though these may be asymmetrical and separated or partially separated by smaller scales. No pattern to the arrangement of the supraoculars and the temporals is discernible; the supraocular-temporal area is divided randomly by transverse, diagonal and longitudinal seams, while frequently the scales in this region are penetrated by partial, irregular lines of division, which also on occasion may infringe upon the frontoparietal.

It may be seen that the arrangement of the dorsal head

Figure 34. Dorsal head scale arrangements for:

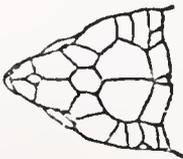
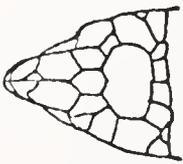
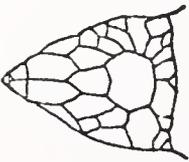
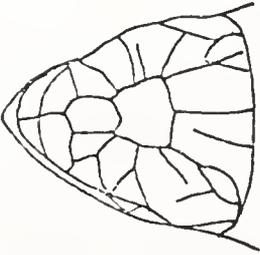
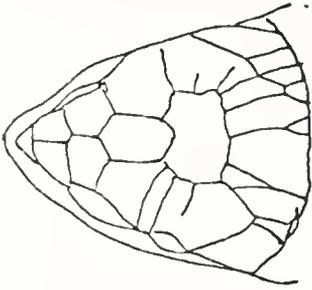
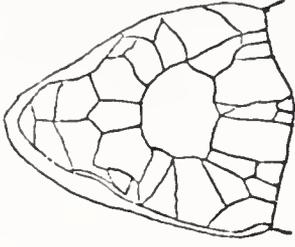
A. Lepidocheilys kempfi

B. L. olivacea from Honduras

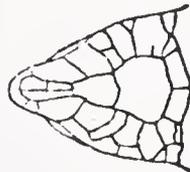
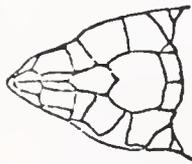
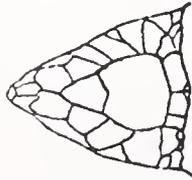
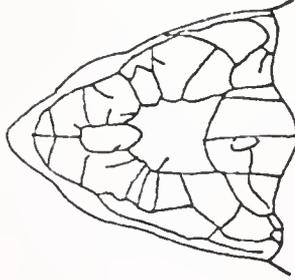
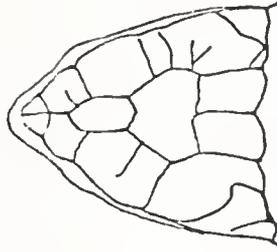
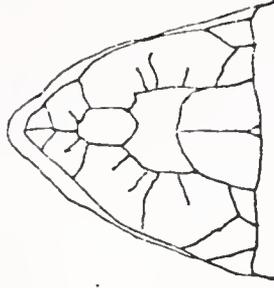
C. L. olivacea from Surinam

(three hatchlings and three adults in each case)

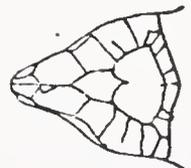
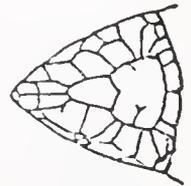
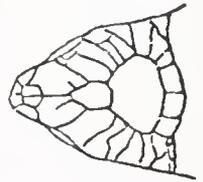
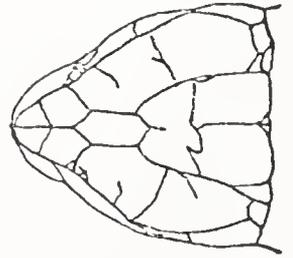
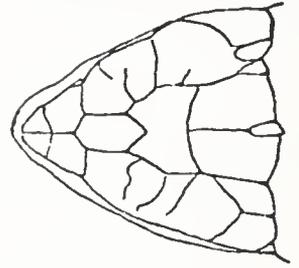
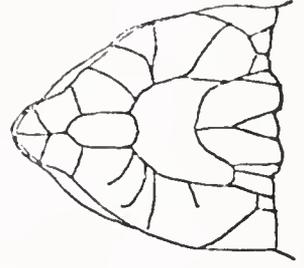
A



B



C



scales of Lepidochelys is too variable and apparently random to be of taxonomic value.

Brongersma (1967:1) illustrates the enlarged scales behind the rhamphotheca in Caretta caretta and Lepidochelys kempfi; the drawings show a single elongate scale on each side in Lepidochelys and a series of three scales of approximately equal size in Caretta. The character is, however, of less than 100 percent value in separating the genera; most specimens of both species of Lepidochelys do have an elongate scale here, but an appreciable percentage have the scale divided, sometimes very close to one end, but in other cases into two or three fragments of comparable size. The scale is certainly of no value in separating the two species of Lepidochelys.

Color

The supposedly different colors of the two species of Lepidochelys have frequently been cited in the literature; L.kempi, according to most accounts, is gray while olivacea is olive-green. However, such comparisons were made using immature kempi and mature olivacea. Large numbers of mature kempi have now been seen, and it is now known that both species when mature are dorsally gray-green to olive-green, and ventrally a uniform pale yellow (figure 35). This pale yellow extends to the soft skin of the shoulder region, to the jaws, and to the margins of the scales behind the eye and on the pre-frontal and frontal regions of the head. However, mature kempi are usually somewhat lighter in color than mature olivacea.

Hatchlings of both species are very dark gray-black when wet, pale or mid-gray when dry. Circumscribed white areas are also frequently present; these occur on the projections of the plastral ridges, on the hind half of the umbilical prominence, on the corners of the jaws, on the throat, and as a very narrow line along the carapace margin and the trailing edge of the flippers. The intensity of pigmentation is a little greater on the carapace and other dorsal surfaces than on the ventral surface. After prolonged preservation in alcohol hatchling ridleys often acquire a rich, deep-brown color, but this is never found in living specimens. I can

Figure 35. Color of ridley turtles:
A: adult female Lepidochelys kempi
B: young L. kempi
C: adult female L. olivacea from Surinam
D: adult female L. olivacea from Honduras

B



D

A



C

detect no variation in intensity or disposition of pigment between hatchlings of olivacea and kempi.

Half-grown L.kempi, in the 25-35 cm range, have the gray-black coloration of the hatchlings, but the disposition of pigment is similar to that of the adults. The plastron becomes progressively paler between the hatchling stage and a length of about 20 cm or less. The plastra of turtles which have grown 2 or 3 cm after hatching are already noticeably paler. I have not had the opportunity to examine half-grown specimens of olivacea; however Deraniyagala (1939a: 159) described the coloration of a 17 cm, 210-day-old captive-raised L.olivacea from Ceylon as follows:

The dorsal colour is dark grey which forms diffuse radiating streaks on each scute. The carapace possesses a broad yellow margin, while dirty white patches appear on the plastron. The pores on the inframarginal scutes are clearly visible and pink in color.

Habitat and Diet of Adult Turtles

The ridley turtles, like other sea turtles, have rarely been positively identified in the open sea, long distances from land. While this may in part reflect the relative paucity of fishermen and other potential observers in the open sea, it probably also reflects a genuine tendency for ridleys to remain in coastal waters, where food is abundant, throughout their lives. The only known exception to this generalization is that immature Atlantic ridleys are occasionally caught in the Gulf Stream and swept passively across the North Atlantic to the British Isles and Europe. Although strongly migratory, at least in some parts of the range, no known migration of Lenidochelys involves a necessary departure from coastal waters. The genus is also conspicuously absent from oceanic islands, in sharp contrast to the green turtle and hawksbill, and even to the loggerhead and leatherback, which are known to nest at least sporadically on islands some hundreds of miles from the nearest continental landmass. However, ridleys may breed abundantly on very large islands lying close to each other or to the mainland, such as Borneo, Sumatra, Ceylon and Japan (Kyushu and Shikoku).

Deraniyagala (1939a: 162) writes as follows about the habitat of L. olivacea in Ceylon:

The commonest chelonian in Ceylon waters. Its eggs are brought to market more frequently than those of the other turtles and its remains are the most numerous around fishing camps. Although so abundant, the author has not seen a single specimen out at sea throughout his eleven years of marine work upon the pearl banks and trawling surveys. This is remarkable as the other three chelonians have been noticed on various occasions. A possible explanation for this scarcity, at the surface, of so common a turtle is suggested by its corselet shape which is more depressed than in these others. Lepidochelys is probably more of a bottom dweller and less given to floating at the surface. It inhabits the shallow water between the reef and shore and is by no means uncommon in the larger bays and lagoons, where it appears to frequent certain restricted areas. In the Gulf of Manaar it is commonly captured in nets set for green turtles across underwater channels in the coral and is not infrequently liberated by the fishermen.

Oliver (1946: 103) recorded the following observations of Lepidochelys olivacea off the Pacific coast of Mexico.

While I was enroute by ship from San Diego, California, to the Panama Canal Zone an unusually large number of marine turtles was encountered throughout the day on November 28, 1945. The species was subsequently identified as Lepidochelys olivacea (Eschscholtz). On this date our location was approximately 50 miles off the Mexican State of Guerrero. Our course was southerly at a speed of 15 knots. The sea was exceedingly calm with virtually no wind or swells. The turtles were first called to my attention at 9.30 A.M., but I was not able to observe them personally until after 11 A.M. At this time 24 individuals were in sight. The turtles were floating idly at the surface with the upper one-third of the carapace, and rarely the head, protruding above the surface. Individuals were usually at least 500 yards from the nearest neighbor so that there was no close aggregation. All seemed to be adult or subadult, ranging in estimated carapace length from 18 to 30 inches. A large bird, probably the masked booby, was utilizing the turtles as a place of rest; birds were standing on approximately half of the turtles. The number within sight at any one time was fairly constant until after 3 P.M., when progressively fewer were seen. Several schools of porpoises and about 15 sea-snakes, Polamis platurus, were observed during the same period of time.

Carr (1961: 9) and Eder (1969: 12) also testify to the frequent occurrence of ridleys floating at the surface on the Pacific coast of Mexico. The direct contrast between the situation here and in Ceylon is most interesting.

Ridleys in Ceylon and in the East Pacific also show differences in diet. Deraniyagala (1939a: 154) writes that:

This species is usually vegetarian, its stomach often full of algae, but it also devours the flat sea-urchin, Clypeaster humilis, as well as young pearl oysters whenever available.

On the other hand Carr (1961: 9) writes:

Two Mazatlan turtles taken respectively 10 and 14 miles offshore had eaten nothing but tiny shrimp which packed the gut to distension. The average body length of the shrimp was only about an inch, and when I expressed surprise that a big-jawed Ridley should be able to feed itself on such tiny, agile prey, the fishermen told me that the turtles eat, not shrimp, but lama (moss - filamentous algae?) in which the shrimp are thickly entangled. I doubt that. Except for a few brown filaments that seemed to me only broken-off shrimp antennae, there was nothing plant-like in the stomachs at all - only hundreds of the little shrimp, all of which had been swallowed whole.

Márquez (in press) found jellyfish and crabs in most of twenty adult female ridleys from Zihuatenejo, Guerrero, while one of the stomachs contained a single Carangid fish. Five other specimens dissected by Waller contained nothing but crustaceans (Márquez, in press).

I have not had the opportunity to examine the stomach contents of ridleys from the Guianas. It is possible that the shrimp which abound in these waters provide a substantial

part of the diet, but this is unconfirmed. Caldwell et al., 1969: 23, list the stomach contents of a single female ridley, 70 cm in length, caught in 10-12 fathoms off the coast of Surinam on 31 October 1967 as follows: "2 small fresh unidentified catfish each about 9 cm in length, 10 small unidentified and broken snail shells, three small unidentified crab carapaces, about two liters of yellow-green slimy fluid (jellyfish remains it was postulated) and some sand and mud massed near the anus." However, the diet of this individual may well have been atypical since one of its front flippers had been severed and its swimming (and food-catching) abilities were presumably seriously impaired.

Sexual Dimorphism

I have not personally seen mature male Lepidochelys of either species, except in photographs.

Deraniyagala (1939a: 154) summarizes the external differences between the sexes of Ceylonese L. olivacea as follows:

The profile of the male is often concave, the plastron concave, and the tail-tip extends as far back as the tips of the hind limbs when placed edge to edge. In the female, the plastron is convex or flat and the tail tip does not extend beyond the margin of the carapace. Its dorsal pigmentation is not as intense as in the male.

Márquez (in press) also mentions the strongly curved "grappling-hook" claws on the fore flippers (and also on the hind flippers) of the adult male; these are used for holding on to the carapace of the female during copulation; also he considers the head of the adult male to be slightly larger than that of the female. Waller, quoted by Márquez, identified mature females by the notches in the anterior part of the carapace, caused by the claws of the male during copulation; he also noticed that females have more humped carapaces than males.

It is probable that the sexes of Lepidochelys kempi may be differentiated by the same characters, though since the carapace is not humped even in the female, the carapace profile may be of no sexual significance. Carr and Caldwell (1958: 249) furnish photographs of mature individuals of both sexes.

Copulation

Lepidochelys kempi apparently copulates during the nesting season and in the general vicinity of the nesting beach. Chávez et al. (1967: 21) record a copulating pair being watched for 15 minutes offshore from Barra del Ostional several miles north of Rancho Nuevo on 21 May 1966; the turtles were not disturbed by a boat passing about five meters away.

Márquez (in press) records that copulating pairs are first seen at the beginning of April, and that couples may stay embraced for several hours. The film of the arribada of 18 June 1947 at Rancho Nuevo shows an over-zealous male actually coming ashore and attempting to mount a nesting female. Chávez et al. (1967: 21) mention the frequent occurrence of obviously recent scars on the second central lamina of nesting female ridleys, indicating that copulation often occurs shortly before nesting.

I have never seen paired or even single individuals of L. olivacea at sea off the Guianas. Many nesting female turtles in Surinam, however, were found with the laminae on the entire rear third of the carapace rubbed off, the shell in this region being no longer horny but having the color and consistency of black, vulcanized rubber. This may well represent an area of friction with the plastron of the male during copulation.

Deraniyagala (1939a) makes no mention of having witnessed copulation of the species in the Indian Ocean. However mated pairs of L. olivacea have frequently been observed in the East

Pacific.

One such instance was recorded by Dr. Carl L. Hubbs on 29 June 1965 at 3.40 P.M., 50 miles WSW of Cabo San Lucas, Baja California Sur; two individuals out of a total of 22 observed between 1 June and 3 July were seen copulating on this date (Márquez, in press). Carr (1961: 9) received a report during early August 1960 that large numbers of mated pairs of sea turtles were being seen by commercial and sports fishermen off Guaymas, Sonora and Mazatlan, Sinaloa, Mexico, while on 22 August he observed three pairs of ridleys and many single specimens between 8 and 15 miles off Mazatlan. However four days later none of more than 60 turtles in the same area was paired.

Carr (1952: 407) is very likely correct in postulating that the mating season of the Pacific ridley coincides with the nesting season. However copulation may occur long distances from the nesting beaches; for example the record above mentions mated pairs of sea turtles offshore from Guaymas, although the nearest known nesting by sea turtles of any kind is by ridleys at Topolobampo, 200 miles down the coast, and even there nesting is diffuse and sporadic (Márquez, in press).

According to Márquez (in press) copulation tends to occur during the middle hours of the day, when the female turtles are prone to float quietly on the surface of the water. Copulation often takes several hours and the female, completely submerged by the weight of the male, has to raise her head from time to time to breathe.

Choice of Nesting Beaches

Deraniyagala (1939a: 154) reports that L.olivacea, which breeds freely on the coasts of Ceylon, tends to choose nesting sites close to river mouths; he suggested that the selection is due either to a preference for the fine river sand washed on to the beach, or to the low salinity of the water, since sea water rapidly coagulates the yolk of turtle eggs. However Hendrickson and Balasingam (1966: 70) conclude that Lepidochelys olivacea in Malaya shows no tendency to congregate in particular areas for nesting; they had not found it possible to define any particular area on the east coast of Malaya where this species nests in predictable numbers. A wide variety of beach types is utilized in Malaya, even the very broad, flat beaches not used by the heavier turtles (presumably because of the difficulty such animals experience in making long overland crawls before reaching a nesting site above the high-tide mark).

In the Guianas, diffuse nesting by L.olivacea probably occurs on most beaches in Guyana and Surinam. The only known concentration of nesting individuals in the area occurs at Eilanti Beach, Surinam, a half-mile strand which may well be the nesting place for the majority of ridleys in South American Atlantic waters. Eilanti is set off from other turtle beaches in the Guianas by two features: it is close to the mouth of a large river (the Marowijne), which has caused a marked depression in salinity of the sea throughout the area (cf.

Deraniyagala's observations in Ceylon); and until a few decades ago Eilanti was completely separated from the mainland by an arm of the sea. This may well have served as a deterrent to terrestrial potential predators. Eilanti Beach is subject to a complex cycle of erosion and deposition, incompletely understood at present; former beaches are discernible in the forested area behind the beach, while even during the last few years an offshore sandbank has increased markedly in size and may well be completely exposed during all stages of the tide at some time in the future. The cycle may well consist of the regular establishment of offshore islands of sand, which gradually become connected to the mainland by further deposition of sand and mud.

In direct competition with turtles of other species on crowded beaches, Lepidochelys is clearly at a disadvantage; it is so small that it cannot dig as deep a nest as the other species. Consequently its nests will be liable to destruction if a larger turtle comes later and nests on the same site. On the other hand construction of its own nest is unlikely to disturb the much deeper nests of other species. However, in the Guianas at least, Lepidochelys tends to avoid this type of competition by nesting later in the year than the other species. Numerous green turtles do in fact nest at Eilanti during the earlier months of the year, while nesting by Lepidochelys does not become frequent until June.

In the East Pacific I have observed nesting ridleys only on the shore of the Gulf of Fonseca, Honduras. Here I noticed

a definite tendency for ridleys to choose nesting sites on or near headlands and projecting tongues of beach rather than on the long, gently curved stretches of beach between such points. The most concentrated nesting witnessed took place on a sandbar offshore from Isla de Ratonés; on occasions over a dozen turtles were nesting simultaneously on this bar, although at such times on the mainland beach the density would be less than one turtle per mile. This sandbar could be reached by wading through shallow water at low tide but was inaccessible by high tide. Although its estimated diameter at low tide was perhaps half a mile, it shrank to less than 80 yards across at high tide; nevertheless no turtles were seen nesting below the high tide mark.

Throughout the remainder of the East Pacific nesting range, published records do not indicate any preference for a particular type of beach. It would be interesting to know if there is any physical characteristic common to the four Mexican beaches on which aggregated nesting by this species is known to occur.

Nesting by Lepidochelys kempi is virtually restricted to a stretch of beach in southern Tamaulipas, Mexico, where nesting is almost entirely by large diurnal aggregations. Except that it is remote from human habitation the shore here has no evident unusual features. However, nesting does frequently take place on sections of the beach which are backed up either by extensive swampy areas or by moderately large, open bodies of water which have seasonal narrow connections to the ocean.

Possibly this nesting site preference reflects an adaptation to avoid terrestrial predators, particularly coyotes. As such, it has not worked very well, but it probably does mean that prowling coyotes have to walk somewhat further than otherwise to find a turtle nest. Other adaptations that might minimize such predation are discussed in a later section.

Nesting Process

I have observed the entire nesting process of Lepidochelys kempi only once, while parts of the process of several other individuals were watched; on the other hand many hundreds of L. olivacea were watched nesting, many of them throughout the entire process. The account for kempi below therefore describes the precise behavior of a single individual, while that for olivacea, although initially based on one individual also, was expanded and qualified after intensive or casual observations of hundreds of others.

Lepidochelys kempi

In the following account the nesting of a single Lepidochelys kempi is described; the turtle left the sea near Rancho Nuevo, Tamaulipas, at 12:30 P.M. on 16 May 1968.

- 0 mins. The turtle emerged from the sea and started walking straight across the beach, perpendicular to the shoreline. The mode of progression involved alternating, 'walking' movements of the four flippers, similar to the gait of a hawksbill, and contrasting with the 'breast-stroke' land movement of the larger green turtle and leatherback.
- 5 mins. Still walking across beach, resting intermittently. The course had now shifted from due west to west with a slight southerly component.

- 8 mins. Now climbing with some difficulty over driftwood and litter on upper part of beach. At this point she started pushing her snout about violently in loose sand with strong thrusting movements of the neck.
- 12 mins. Started walking in a northerly direction; moved only a few yards, thrusting snout strongly down into the sand.
- 14 mins. With front flippers anchored and head pointing slightly to the north of straight inland, the turtle started excavating her nest cavity with her hind flippers, the hind part of her shell moving through a large angle between insertions of alternate hind flippers in the growing cavity.
- 17 mins. Digging still proceeding without interruption; front part of the animal was now being raised high up with each digging movement in order to allow the tips of the hind flippers to reach as deep into the cavity as possible. The nuchal tendons were tense and prominent throughout the excavation. Insertion of each hind flipper into the nest cavity was preceded by a sharp forward flick of the same flipper, which threw the excavated sand about six feet in front of the turtle's head. Throughout the excavation the eyes were open; sand adhered to the moist area around the eye but the 'tears' were not nearly as copious as in nesting green turtles or leatherbacks.
- 29 mins. Nest cavity now completed; the turtle stopped digging

and, with hind flippers splayed out flat and far apart, she started laying. Actual oviposition lasted about twelve minutes and was accompanied by deep, noisy breathing. The eyes were now closed; there was considerable buccal action and some partial opening of the mouth. Periodically the head and shoulders were withdrawn slightly. From observations of other turtles these contractions of the foreparts immediately precede the actual dropping of a batch of one to three or four eggs.

41 mins. Oviposition completed; the turtle started filling in the nest cavity with curling-round movements of her hind flippers. Each flipper came into light contact with the tail and opposite thigh while drawing sand into the cavity.

41½ mins. With eyes open and distal parts of her foreflippers still anchored in the sand, the turtle flattened the sand beneath her by means of vigorous thumps of alternating sides of her shell. The hind flippers patted the sand flat with movements in almost perfect synchrony with the rocking shell movements. In between bursts of four or five thumps the turtle pulled sand towards the tail with the hind flippers.

44 mins. Front flippers moved for the first time since the onset of excavation of the nest cavity; they made sluggish movements throwing sand backward between bursts of shell rocking.

45½ mins. Thumping with shell ceased and the turtle started throwing sand backwards with simultaneous movements of one front flipper and the hind flipper on the opposite side. Several movements with such a combination of flippers would take place, then the opposing pair would come into action. Such series of movements were occasionally interrupted by simultaneous sand-flinging movements of the two front flippers. These movements carried the turtle away from the nest site with a twisting motion. After a few yards the turtle turned round to the right, so as to face towards the sea, and rested briefly.

49 mins. Turtle returned to the sea.

The process described above showed virtually no variation in the eight or nine individuals whose nesting process was at least partially witnessed. Even the unwavering march direct from the sea to the dry sand of the nesting site seemed to be invariable, while oviposition in all cases witnessed took place with the turtle's head pointing more or less directly inland. Local people as well as other visitors confirmed that the total time from emergence to return to the sea took within a few minutes of 50 minutes in all cases they had witnessed. However, Chávez et al. (1967: 22) found that most turtles turned to the left after nesting in order to regain a seaward orientation.

I have not personally seen an arribada of L. kerpi; however

from films, photographs and the account of Carr (1963) I cannot find any indication that nesting behavior of individual turtles is in any way affected by the close proximity of hundreds or thousands of other nesting turtles.

Lepidochelys olivacea

The following composite account describes the nesting process of Lepidochelys olivacea at Eilanti, Surinam.

Emergence from Sea

This phase, which almost always occurs during the hours of darkness, appears to be relatively uncomplicated. The turtle usually rests for a few seconds at the edge of the surf, then proceeds to walk perpendicularly up the slope of the beach. The walking movement is carried out with the front flippers working alternately, each moving simultaneously with the opposite hind flipper. When the turtle is actually walking, the head is carried low, almost touching the sand, but every few yards the turtle stops, raises her head, and may look around to either or both sides and breathe loudly. Even at this early stage it is difficult to distract the turtle with a flashlight, and sometimes it can be tagged at this stage, showing only a brief flinching before proceeding. Within two or three minutes after emergence the turtle has climbed up the shelf of the beach, and in most cases preparation of the nest site proceeds with little or no further wandering.

Preparation of Nest

When the turtle has reached the chosen nest site, the walking movement is altered to a sand-swiping movement, which excavates a shallow body pit. The first few swipes are carried out with alternating movements of the front flippers, but very soon this becomes a simultaneous movement, the head of the turtle pushing into the ground and the flippers being drawn forward until their back surfaces lie alongside the side of the head. The sand is then thrown back with a vigorous 'breast-stroke' movement. During this time the hind flippers are not working in any highly organized fashion, but are carrying out a desultory alternating flicking-back of sand. Within a minute or two this becomes the dominant action, and the front flippers become anchored in the sand. The front part of the shell is now fixed, but the back part is switching left and right as each hind flipper is engaged in the sand. The movement grades into a digging movement which continues virtually unchanged until the nest cavity is completed; the turtle thrusts each hind flipper, with the palm surface upward, into the sand immediately under the tail, lifts it out, revolves the flipper, and then either pats the sand down or throws it gently backwards. Just before the flipper is thrust into the growing cavity to remove more sand, it is brought sharply forward, sometimes with such vigor that it slaps on the underside of the shell. The movement throws sand forward, much of it settling on the slightly upturned side margins of the shell, where it may pile up to a depth of two inches, but much of it also

being propelled well in front of the turtle's head. The digging movement is rapid and jerky, and the shell bounces up and down slightly. The distal halves of the front flippers are now anchored in the sand, but as the hind feet are alternately engaged in the hole, the rear part of the shell moves sideways through a distance of about a foot. The maximum depth of the cavity is reached quite quickly, but the enlargement of the lower part to a flask-shape takes more time. The movement becomes a little slower as digging proceeds, and the rear part of the shell, having reached its lowest point when the flipper reaches the bottom of the cavity, is raised a little and re-lowered before it is raised fully and the flipper removed from the cavity; earlier the rear part of the shell had described a simple down-up movement. The turtle may also rest between strokes at this stage, with one of the flippers dangling in the hole. The turtle lowers the hind part of the shell in the movement described above by a slight straightening of the proximal joints of the front flippers, which raises the front part of the shell and thus tilts the back part down. A little sand is now present around the jaws of the turtle, where the secretion of the eye has caused it to stick. Buccal pulsations are evident as the head is raised with the front part of the body. The side-to-side movement of the shell, which originally describes a foot-wide arc, now describes a span of only about two inches.

Laying of Eggs

When the turtle has completed the nest cavity -- i.e. when the flippers can no longer reach to bring up more sand -- the laying position is assumed, with the hind flippers resting limply on the sand, well apart. This position may be assumed immediately, or the digging movements may become slower and slower until one flipper moves towards the cavity, hesitates, and then returns to a lateral position without being inserted in the hole. On other occasions there may be four or five cyclical movements, in which the foot, instead of being inserted into the cavity, is contracted at all joints and drawn under the shell, each movement being preceded by a forward flick. The position during laying, however, appears to be invariable. The head and elbow joint rest on undisturbed sand, but the hind part has been lowered several inches by the movements of the hind flippers. As the eggs are laid, there is a barely perceptible raising and lowering movement of the shell; there is a general contraction of the muscular upper surface of the hind flippers, and the hind margins of these members are raised slightly, the head is raised a little, and the turtle breathes with a hoarse, throaty sound. During each deposition the cloaca is protruded, then retracted just before the eggs are dropped. Usually one or two, but sometimes three or four, eggs are laid at a time. No dents are visible in most of the eggs at this stage.

Finishing Off Nest

When all the eggs have been laid, the hind flippers pull sand into the cavity with an initially very slow movement; the flippers work alternately, and the action becomes progressively more vigorous, soon involving a side-to-side movement of the hind part of the turtle's shell, the flippers reaching out sideways to pull in sand. Only 90 seconds or so after the initiation of this movement, the turtle commences the thumping action which impacts the sand over the nest site. The movement is generated by the shoulders, and the shell is tilted rapidly from side to side, producing a sound audible at some distance. A fraction of a second after one side of the shell has hit the sand, the hind flipper on the same side pats the sand down. In between these series of thumps, the hind part of the shell is moved to one side and the hind flipper on that side reaches out as far as possible to pull in sand over the nest cavity with several sweeping movements. Before long the thumping action stops and the hind flipper movement is accompanied by sand-sweeping movements of the front flipper on the opposite side. This movement of one front flipper and the hind flipper on the opposite side has the effect of moving the turtle away from the nest and twisting it round; the action of the other two flippers continues the movement away from the nest and reverses the change in orientation. This movement may carry the turtle as much as eight or ten yards away from the nest before a walking movement is established. The turtle rests little on the walk back to the sea, and its speed becomes

greater as it gets closer to the water. It may halt momentarily at the very edge of the sea, but contact with the next wave causes it to continue walking until its weight is supported by the water, when a swimming movement is established.

Duration of Nesting Stages

The duration and timing of each of the above stages is shown by the following schedule of a typical turtle, which emerged from the sea at 1:24 A.M. on 12 July 1966 at Eilanti Beach, Surinam.

- 0 mins. Turtle emerged from sea.
- 2 mins. Selected nest site and started body pit.
- 6 mins. Started excavating nest cavity.
- 21 mins. Changed digging movement to flipper-curling movement
(see above).
- 22 mins. Started laying.
- 31 mins. Began to fill nest cavity.
- 32 mins. Commenced sand pounding with sides of shell.
- 36 mins. First front flipper movement.
- 45 mins. Started moving towards sea.
- 46 mins. Turtle reached sea.

Apart from my own (Pritchard, 1969: 106), no published account of the nesting process of Lepidochelys olivacea is based on more than one or two observations. The only divergence from the nesting process described above that has been recorded for olivacea from other parts of the world is that of Carr

(1947: 53), who wrote that a Honduras ridley whose nesting process he witnessed carried out part of the sand-pounding process by raising itself on all four flippers and letting itself drop. I have not seen this in over 100 ridleys nesting at the same place, and Carr informs me that he was probably mistaken.

Geographical Differences in Nesting Process

The nesting of Lepidochelys kempi and L. olivacea thus differ most strikingly in timing; the former species is almost entirely diurnal and the latter in nearly all areas almost entirely nocturnal. The earliest emergence of L. kempi at Rancho Nuevo observed by Chávez et al. (1967: 21) was at 8:25 A.M.; the latest at 6:25 P.M. However Chávez was informed that three individuals had nested by night on 11 May 1966, preceding an arribada on the following day, and he himself saw an ancient, mutilated female lay eleven eggs in a shallow depression in the sand shortly before midnight on 1 June 1966.

Lepidochelys olivacea almost always nests by night in the Guianas. One exception was a specimen which emerged from the sea at 5:00 P.M. on 10 May 1966 at Bigi Santi, Surinam. Also the first one or two individuals in an arribada at Eilanti Beach frequently emerge by daylight, at around 5:30 or 6:00 P.M.

I know of no diurnal emergence record for the Indian Ocean or the Indonesian area. In the East Pacific nesting is almost always nocturnal, but in several recorded cases

arribadas on the Pacific coast of Mexico have occupied more than 24 consecutive hours.

At Eilanti Beach, Surinam, the time of emergence is under strong tidal control, since a huge mud bank, about half a mile wide, is exposed by low tide, making an approach to the beach impossible. To a lesser but still marked extent, turtle nesting in the Gulf of Fonseca, Honduras, is also tide controlled, nearly all turtles nesting by high tide.

The nesting of the two species also differs in that olivacea spends several minutes in construction of a body pit before beginning work on the nest cavity. L.kempi makes no, or almost no, attempt to dig a body pit; having reached the chosen site, there may be, at most, one or two swipes with the front flippers, then the hind flippers settle down to systematic excavation of the nest cavity. Also a nesting olivacea may face in any direction with equal probability; a nesting kempi is usually pointing straight inland. A further point of difference is that not all nesting olivacea thrust the head into the sand ('sand smelling'; see Carr, 1963: 300), and those that do were only seen doing so on the wet, lower part of the beach. L.kempi, on the other hand, frequently if not invariably thrusts the snout vigorously into the dry sand around the actual nest site. Another minor difference is that none of the few specimens of kempi watched were seen to curl the hind flippers alternately under the shell, in between sharp forward sand-flicks, between the completion of excavation of the nest cavity and the onset of oviposition. Chávez et al.

(1967) also make no mention of this mannerism in kempi, which was frequently, though not invariably, observed with olivacea in Surinam.

Clutch Size and Egg Dimensions

The mean number of eggs per clutch for Lenidochelys olivacea at Eilanti, Surinam, is 116.07, based on 928 clutches from the beginning, middle and end of the nesting season. The smallest clutch found contained 30 eggs and the largest 168, but only four clutches contained less than 70 eggs, and only four more than 155. The standard deviation was approximately ± 13 .

It is unfortunate that no comparable series of clutches from the Indian Ocean region has been counted. Deraniyagala (1939a: 155) states that nests of L. olivacea in Ceylon contain from 90 to 135 eggs, without mentioning the number of clutches examined. This range would exclude only about 14 percent of Surinam nests, and considering the likelihood that Deraniyagala's sample was much smaller than mine, it is quite possible that the distribution of clutches of different sizes is similar in the two areas.

Fifty-five clutches from the Pacific coast of Honduras ranged from 48 to 151 in number of eggs; a further ten nests contained a total of 1076 eggs, giving an overall average (for 65 nests) of 106.00; standard deviation approximately ± 23 .

Nineteen nests of L. kempi found freshly made at Rancho Nuevo in early and mid-May 1968 contained the following numbers of eggs: 93, 100, 101, 101, 103, 106, 110, 115, 115,

118, 121, 121, 121, 125, 128, 129, 130, 132, 135 (mean 116.00; S.D. \pm 12.5). This mean is virtually identical to that for clutches of L. olivacea in Surinam. However, Chávez et al. (1967: 28) found that the average number of eggs in 271 L. kempi clutches from Rancho Nuevo ranged in number from 54 to 185, the mean being 110 and with 62 percent of individuals laying between 100 and 129 eggs (which suggests a standard deviation of approximately \pm 11).

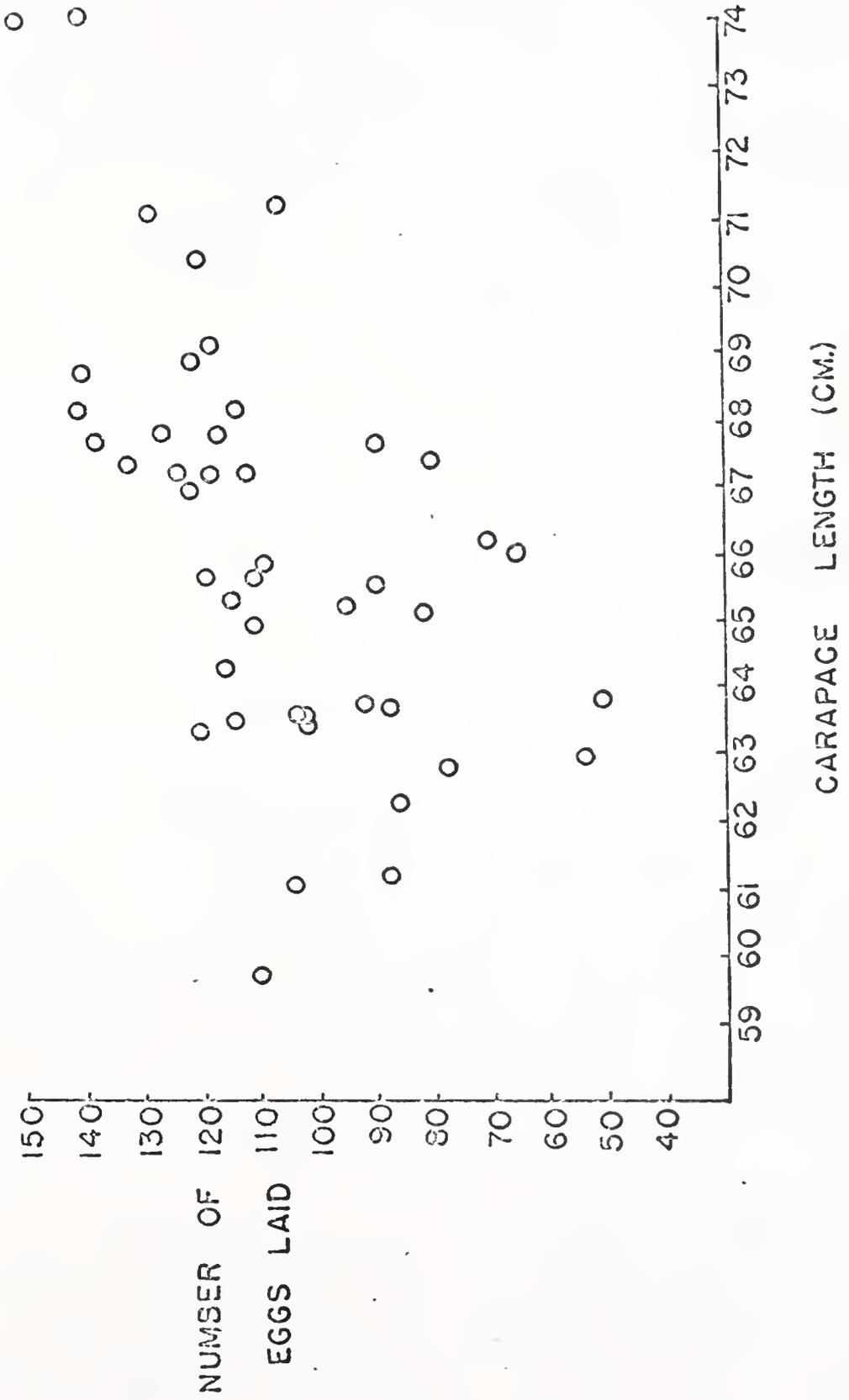
The difference between my average (116) and that of Chávez (110) is significant at the 95 percent level, by Student's t. However, my series was collected entirely during the beginning of the nesting season (early and mid-May), while that of Chávez et al. may well have embraced the entire nesting season (though this is not specifically stated). Caldwell et al. (1959: 33) lends substance to the widespread belief that average clutch sizes of the loggerhead turtle decrease as the season progresses, and Carr informs me that the same phenomenon occurs with green turtles at Tortuguero, Costa Rica, so it seems very possible that the same holds true for the ridley. Indeed, Hildebrand (1963: 111) quotes information he received from local people in Tamaulipas to the effect that, on their first nesting of the season, ridleys lay 120 to 130 eggs, on the second about 100 and on the third 60 to 70. Chávez' series, including these small, late-season clutches, would thus give a lower average than a series taken entirely in May.

The difference in mean clutch size in Honduras (106.00; n = 65, S.D. \pm 23) and in Surinam (116.07; n = 981, S.D. = \pm 13)

is statistically significant at the 95 percent level. However the same argument applies; Surinam nests were taken throughout the season, while those in Honduras were taken towards the end of the season, in October and November, and in fact it was noticed that increasing numbers of very small clutches were laid as the season progressed. To give this generalization some quantitative support, fifteen clutches were recorded on 20 and 21 October, of which only two contained fewer than 100 eggs (84 and 86 respectively). However, twenty clutches laid on 11 and 16 November included twelve with fewer than 100 eggs (48, 51, 53, 66, 78, 78, 80, 82, 88, 88, 90, 90), although some very large clutches (132, 138, 151) were also laid in this period.

It is also possible that part of this difference is attributable simply to the fact that turtles in Honduras, being on the average smaller in size, lay fewer eggs than those in Surinam. No data from which clutch size might be correlated with the length of the nesting turtle are available for Surinam turtles, but figure 36 shows a plot of number of eggs laid against carapace length for 45 L.olivacea from Honduras (all clutches laid October-November 1967). It may be seen that there is a definite trend for smaller turtles to lay fewer eggs; indeed the 25 smallest turtles laid, on average, 95.9 eggs each, while the 20 largest laid, on average, 123.8 each, considerably more than the overall mean in Surinam.

Figure 36. Plot of clutch size against carapace
length for 45 mature female Lepidochelys olivacea
from Honduras



Egg Dimensions

Table 8 shows maximum and minimum diameters (in cm) for 45 eggs (five from each of nine clutches) measured when freshly dug up, 18 hours after laying by L.olivacea at Eilanti, Surinam.

TABLE 8

DIAMETERS OF RANDOM EGGS LAID BY LEPIDO-
CHELYS OLIVACEA AT EILANTI, SURINAM

3.84 X 3.84	4.04 X 3.95	4.13 X 4.04
3.86 X 3.85	4.05 X 3.97	4.13 X 4.04
3.87 X 3.73	4.06 X 3.93	4.14 X 3.95
3.88 X 3.87	4.06 X 4.02	4.14 X 4.05
3.90 X 3.84	4.08 X 4.08	4.18 X 3.80
3.94 X 3.83	4.09 X 3.97	4.18 X 3.99
3.94 X 3.85	4.09 X 4.00	4.19 X 3.73
3.94 X 3.90	4.09 X 4.09	4.20 X 4.02
3.95 X 3.92	4.10 X 3.98	4.21 X 3.99
3.98 X 3.88	4.10 X 4.03	4.21 X 4.01
3.99 X 3.89	4.10 X 4.05	4.22 X 4.08
4.00 X 3.90	4.11 X 4.02	4.22 X 4.19
4.02 X 3.96	4.12 X 3.88	4.26 X 4.12
4.03 X 3.97	4.12 X 4.02	4.03 X 3.87
4.04 X 3.93	4.13 X 4.00	4.10 X 3.92

The mean of the maximum diameters is 4.07 cm, and of the minimum diameters, 3.94 cm.

No measurements of a comparable series of eggs from the Indian Ocean area have been made. However, according to Deraniyagala (1939a: 155), the eggs in Ceylon Lepidochelys range from 38 to 43 mm in diameter. There is no mention of sample size, but the average maximum diameter of the 14 eggs whose dimensions he gives in full is 4.075 cm, so we are probably safe in assuming that both the mean diameter

and range of diameters of L.olivacea eggs in Surinam and in Ceylon are the same.

Carr (1952: 410) measured 50 eggs (ten from each of five nests) for L.olivacea from Honduras. Diameters ranged from 3.21 cm to 4.54 cm, the mean being 3.75 cm. It thus appears that in this part of the range the species lays, on average, eggs of lesser diameter, but the overall range of diameters is much greater (1.33 cm between largest and smallest on 50 eggs; cf 0.42 cm between largest and smallest of 45 eggs from Surinam). Unfortunately, lacking standard deviation data for Honduras eggs, we can make no more than this crude comparison.

Chávez et al. (1967: 27) found that the range of diameters of 221 eggs from 30 clutches of L.kempi at Rancho Nuevo was 3.50 to 4.45 cm, with a mean of 3.89. However, a number of eggs smaller than 3.50 cm were considered abnormal and were not counted with the above. For example, one turtle laid seven undersized eggs, ranging in diameter from 2.22 to 3.29 cm. Inclusion of such small eggs would both extend the range and lower the mean diameter of eggs from this area, and thus would probably give figures for both range and mean that would be closely comparable to those of L.olivacea from Pacific Honduras.

Taking the above data at face value, we would conclude that the eggs of Lepidochelys from the South Atlantic and Indian Oceans are larger and less variable in size than those from the East Pacific and the Gulf of Mexico. However, it is possible that eggs from the end of the season are more variable and smaller than those from mid-season, and that the observed

differences are merely seasonal effects of this kind. The Surinam clutches were all collected in mid-season (26 June 1968). The Honduras clutches were collected on 11 October 1947, probably somewhat after the mid-point of the season. It was not stated in the original texts if the Ceylon and Gulf of Mexico samples included end-of-season clutches, so the data are not really comparable.

Intervals Between Nesting Emergences

All species of sea turtle (with the exception of Chelonia depressa, which has not yet been studied) are now known to nest, or at least to be capable of nesting, twice or more in a season. Green turtles frequently nest three or four times in a season, and on occasion as many as seven times (Hendrickson, 1958); the nesting interval is usually about 12-14 days, showing slight variation in different parts of the world. The loggerhead in Natal is known to nest at intervals of 16-17 days, and probably three or four times in a season (Hughes et al., 1967: 23). In the same area the leatherback is known to nest up to four times in a season, at around ten-day intervals. The hawksbill has not yet been demonstrated to nest more than twice in a season; Carr et al. (1966: 9) record interesting intervals for the hawksbill at Tortuguero of 17, 18 and 30 days. Hornell (1927) cited "various trustworthy observers" in the Seychelles as having found that females marked while nesting came back to nest again after 13 to 15 days.

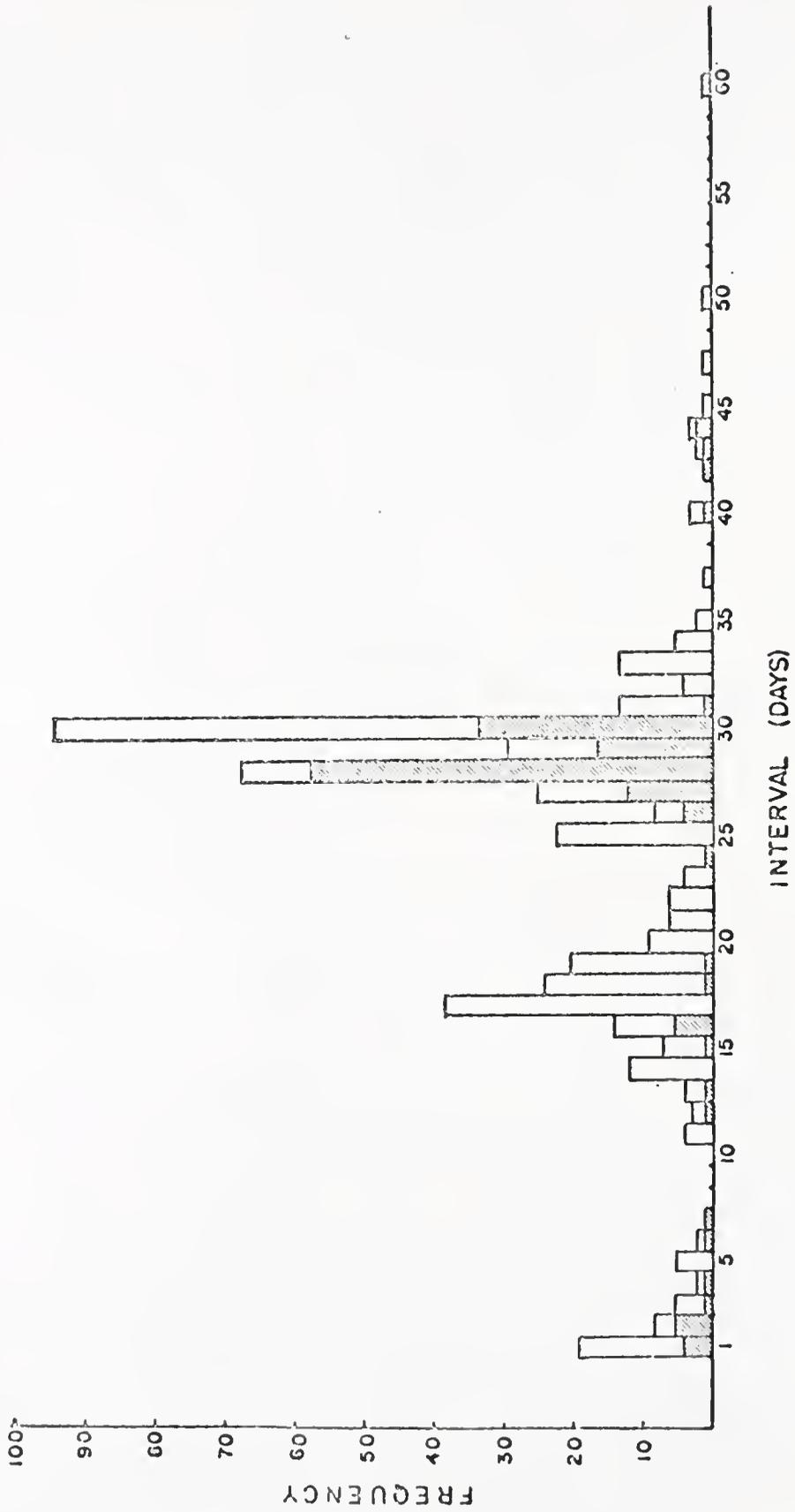
Internesting intervals for Lepidochelys kempi have been recorded only a few times. Chávez et al. (1967: 26) recorded the following intervals (in days) for individuals found nesting twice at Rancho Nuevo in 1966: 20, 24, 24, 28, 28, 28, 28, 49; intervals between nesting emergences for two individuals found three times were: 27 and 26 days; 28 and 23 days. Supplementary

data for the 1967 season are: one individual re-appeared the following day; three between 20 and 24 days; one after 42 days (Chávez, 1968: 9).

No interesting intervals for Lepidochelys olivacea from the Indian Ocean or the West Pacific have been recorded, while from the East Pacific the only records available seem to be those of two individuals out of 100 I tagged on the Pacific coast of Honduras. One was tagged on 30 October and returned 16 November (17 days); another, tagged 31 October, returned 15 November (15 days). The latter laid 102 eggs the first time, 104 the second. Also, three individuals which returned the night after they were tagged were presumed to have failed to nest on the first occasion.

In Surinam tagged turtles were found nesting later the same season on 492 occasions. The interesting intervals are plotted in histogram form in figure 37. This histogram shows a polymodal pattern similar in superficial appearance to those supplied by Hughes et al. (1967: 23) and Hendrickson (1958: 498) for loggerheads and green turtles respectively. Nevertheless there are certain differences which suggest that the polymodal pattern is caused by very different factors. Both Hughes et al. and Hendrickson conclude (probably quite rightly) that a small peak around one day is made up by turtles which were disturbed before nesting on the first occasion, and which attempted to lay their eggs a day or two later, while the peaks around 16-17 days and 10-11 days respectively refer to turtles which were seen re-nesting for the first time after tagging. Subsequent

Figure 37. Histogram showing frequency of intervals (in days) between nesting emergences of Lepidochelys olivacea at Eilanti, Surinam in 1967 (shaded) and 1968 (unshaded)



peaks, of rapidly decreasing height, are supposedly made up by turtles whose second, or second and third, appearances on the beach were not witnessed.

One anomaly in applying this interpretation to the Lepidochelys data is that both Hughes et al. and Hendrickson found the mean value for the second and third peaks to be almost perfect multiples of the mean value for the first peak. Thus, Hendrickson found that the first peak corresponded to a mean interval of 10.5 days; the second to a mean interval of 20.9 days, and the third (based on a much smaller sample) to 32.5 days. Hughes et al. found the first peak for loggerheads to correspond to an interval of 16 to 17 days, the second to 32-33 days, and the third to 48-50 days, with two possible peaks at 64 and 82 days. My histogram for Lepidochelys olivacea, however, has the first peak (not counting the small peak corresponding to presumably disturbed turtles) at around 17.5 days, and the second at around 29.3 days - scarcely even a rough approximation to 2×17.5 . There is a suggestion of a third peak at 44-45 days. It is hard to see why the second peak should not be closer to twice the value of the first peak if the second peak merely represented individuals which had been missed on their first return to the beach.

Another anomaly is the relative heights of the peaks. In both the loggerhead and the green turtle histograms the first peak was by far the highest, as would be expected if relatively few nesting turtles were missed. In the Lepidochelys histogram the second peak is easily the highest. Even if we take into

account the fact that a critical mid-season arribada night (26 June 1967) was missed the first year, the second peak is too high to be explained simply as reflecting the turtles which were missed on their second nesting. In 1968 no nights were missed, and since the beach on which all nesting took place was only about half a mile long, it was theoretically possible to tag every turtle that nested and record every previously tagged turtle that returned. In practice probably at least 75 percent of turtles that nested were seen, though on really busy nights it was hard work for two or three people to keep up with the large numbers of turtles on the beach. Yet the second peak for 1968 alone is as high as the first peak.

A third point which suggests that the second-peak nesters were not, at least for the most part, ones which had been missed on their first return, is that extremely few turtles were seen nesting three times in a season. Altogether 1060 turtles were tagged, and 492 cases of re-nesting the same season were recorded, yet in only 27 cases were turtles recorded on the beach more than twice in a season. Moreover in many of these 27 cases one of the intervals was suspiciously short, suggesting that the turtle had been disturbed before nesting on the earlier emergence. The actual intervals recorded (in days) between the first and second and between the second and third emergences were as follows: 12 & 17; 20 & 11; 18 & 16; 17, 3 & 28; 18 & 19; 11 & 19; 17 & 16; 17 & 16; 18 & 16; 12 & 30; 14 & 16; 28 & 1; 17 & 1; 11 & 5; 7, 32 & 1; 3 & 14; 25 & 5; 2 & 20; 1, 1 & 16; 14 & 1; 1 & 17; 17 & 1; 25 & 5; 25 & 5; 5 & 3;

1 & 18; 1, 1, 15 & 1. In all cases except the first eleven it is very likely that the turtle nested only twice and was disturbed before nesting on the other occasion(s).

We may conclude that Lepidochelys olivacea at Eilanti, Surinam, frequently nests twice in a season, but very rarely nests three times, and very possibly some individuals nest only once.

The situation may well be different in other areas, however. It was noted above that two individuals of L. kempi were recorded nesting three times at Rancho Nuevo, even though only eight were recorded twice. Moreover a female slaughtered on the beach at Rancho Nuevo after depositing 118 eggs contained in the oviducts 258 eggs of diameter 26.0 - 31.5 mm, presumably representing two or more clutches to be laid that season (Chávez et al., 1967: 29)

We have still to explain the strongly polymodal inter-nesting interval histogram for L. olivacea at Eilanti, Surinam. As is discussed in the next section, nesting of Lepidochelys on this beach is strongly cyclical, there being three brief periods of intensive, aggregated nesting during the season, with relatively few turtles nesting in between. The very fact that turtles emerge from the sea to nest in great numbers only on certain nights either forces us to the unlikely conclusion that the eggs ripen within the female turtle in such perfect synchrony that the urge to lay comes upon the whole local population simultaneously, or to the conclusion that the eggs ripen in approximate, but not perfect, synchrony, and that the female

can hold the shelled eggs for a reasonably long period until the right combination of tide, moon and wind brings about an independent urge to lay in all the local turtles simultaneously. This theory must be viewed in the light of the common observation that a turtle frightened back to the sea before it nests will usually try to nest again either the same night or the following night. It seems likely that, once a turtle comes voluntarily from the sea to nest, the eggs start moving towards the cloaca and produce a pressure which can be relieved only by laying the entire clutch. If the turtle has not yet tried to leave the sea, however, it seems that the eggs may be held much longer. We may conclude provisionally, then, that the ideal combination of nesting conditions recurs at approximately fortnightly intervals, and turtles which for one reason or another fail to deposit their first clutch during the first 'ideal period', or their second clutch during the second period, will simply hold their eggs another two weeks or so until another ideal period occurs. The fact that the average interval for 'second-peak' nesters is less than twice the average for 'first-peak' nesters may be explained as follows: those turtles which have deposited a clutch of eggs two weeks before will deposit their next clutch at leisure during the first, middle or last day(s) of the second ideal period. However those turtles which miss this period altogether will feel some urgency to lay them during the third period, and they will tend to exploit the very first ideal or near-ideal days of this period; thus their average internesting interval will not be

quite double that of the turtles which nested during the first and second periods.

This theory assumes, then, that ridleys are motivated to nest by external factors or wind, tide, etc., in sharp contrast to all the other genera of sea turtles, whose interesting intervals seem to be under the control of intrinsic internal rhythms.

Reproductive Cycles

A surprising discovery was that of frequent nesting by Lepidochelys olivacea at Eilanti in successive years. In 1966, 130 turtles were tagged on 7 June. Thirty-nine of these were found back on the nesting beach in 1967, and 59 in 1968; 28 were found nesting in all three years. Of 445 nesting turtles tagged in 1967, 214 were found renesting in 1968 -- many of them twice, and several twice in both years.

Chávez (1968: 11) lists nine records of females of Lepidochelys kempi nesting at Rancho Nuevo in both 1966 and 1967; also Hughes et al. (1967: 59) record that two out of 82 nesting female loggerheads tagged in the 1963-64 season at Natal were found nesting again the following year, while four out of 221 tagged during 1964-65 renested the following year, and two out of 187 tagged during the 1965-66 season renested in 1966-67. These appear to be the only published records of sea turtles of any species nesting in successive years; abundant data for green turtles from several areas and sparse data for leatherbacks and hawksbills show no record of these species having nesting seasons more frequently than every two years.

ARRIBADA FORMATION

The word arribada (Spanish for arrival) has entered the language of herpetology for a behavioral trait peculiar among turtles to the genus Lepidochelys - the formation of nesting aggregations, numbering from a few hundreds to many thousands of individuals, emerging simultaneously on limited stretches of shoreline. Despite the fact that arribadas constitute perhaps the most spectacular manifestation of reptile life in the world, and are now known to occur on a least six points on the shores of the Americas, they were, amazingly, unrecorded and unknown to the world at large until 1961, although presumably all have been known to the people inhabiting the remote areas close to where they occur for many generations.

Nesting of the Atlantic ridley (Lepidochelys kempi) is not only virtually limited to a single stretch of beach in the world, that near Rancho Nuevo in southern Tamaulipas, Mexico, but also takes place almost entirely by means of arribadas, with the result that throughout the entire year except for a few days in May and June even the beach at Rancho Nuevo appears innocent of ridley nesting activity. It was for reasons such as these that Dr. Archie Carr spent nearly twenty frustrating years attempting to find the nesting place, or even a single record of nesting, of this by no means rare turtle.

The arribada of the Atlantic ridley in Tamaulipas was first filmed by Andres Herrera, a Mexican engineer, on 18 June

1947. Herrera, following up local rumors of massed turtle nesting, conducted an aerial reconnaissance of the beach from Soto la Marina to Tampico for 26 consecutive days in May and June 1947. It was on the last day that the arribada was found, after 25 days without seeing a single turtle. Herrera's film lay unknown in a desk drawer for 14 years before it reached the hands of Henry Hildebrand who showed it at the A.S.I.H. meetings in Austin, Texas in 1961. Since 1966 a division of the Mexican Departamento de Herpetología has been stationed on the beach at Rancho Nuevo throughout the ridley nesting season, in order to carry out research and protection of the turtles.

The salient facts revealed by the Herrera film and the subsequent work of Mexican biologists (principally Humberto Chávez and René Márquez) are as follows:

Arribadas of Lepidochelys kempi are invariably diurnal, and take place in May and June close to (usually a little to the north of) Rancho Nuevo, a small township about two miles from the Tamaulipas coast. A strong wind from the sea, generally from the north-east, precedes and accompanies each arribada.

The arribada of 18 June 1947 was estimated by Hildebrand to involve about 40,000 nesting turtles, a maximum of about 10,000 being on the beach at one time. Carr (1963: 103) repeats hearsay information that the emergence occurs three times each season, at ten-day intervals. On the other hand, Hildebrand (1963: 103) reports that the above arribada was preceded by one on 26 April 1947, though from the context this

may be a misprint for 1949.

World population numbers of L.kempi were severely cut down in the 1950's when the lagoons behind the beach at Rancho Nuevo dried up, and the fishermen who usually fish in these areas turned to collecting turtle eggs. Not being content to wait for the turtles to nest, they pulled great numbers of ridleys out of the sea and cut them open for their eggs. Following this slaughter no arribadas were seen for several years; Carr (1967: 157) could find no report of an arribada later than the latter part of the 1950's. However Mexican biologists and conservationists, working at Rancho Nuevo throughout the 1966 season and patrolling the entire part of the beach on which arribadas have been found, recorded nesting aggregations as shown in Table 9.

TABLE 9

OBSERVED NESTING AGGREGATIONS OF LEPIDOCHELYS
KEMPI IN 1966 (fide Montoya, pers. comm.)

Date	Estimated number of turtles	Location
3-4 May	200	Spread along 7.5 km. of beach, from a point 600 metres S of Cachimba to a little S of Barra Coma; nesting densest at southern end.
11 May	150-200	Between Boca San Vicente and Barra Coma
28 May	98	From 4 km S of Barra Coma to Boca San Vicente
31 May	1317	785 turtles nested between Barra Calabazas and a point 2 km to the S; 532 others on the rest of the beach between Boca San Vicente and Barra Coma

TABLE 9 (continued)

4 June	20	From 1 km N of Barra Coma to 200 metres S of Barra Calabazas
16 June	200	Between Cachimba and Barra Coma
23 June	25	Between Cachimba and Barra Coma

Barra Coma is about 1 km south of the nearest part of the beach to Rancho Nuevo, being about 23° 11' N. Barra Calabazas is about 6 km to the north, Cachimba about 2 km north of Calabazas, and Boca San Vicente is about 2 km north of Cachimba. When I was at Rancho Nuevo in May 1968, Boca San Vicente was merely a dry sand bar similar to Barra Coma and Calabazas. These bars are differentiated from the beach proper by the lack of the *médano*, or raised dune area, which backs up all the rest of the beach.

Cachimba is the name given to a single wooden shack, a useful landmark since it is the only building anywhere on the beach.

It is difficult to detect any pattern to these dates, especially considering the very variable numbers of turtles that nested on each of them. Perhaps the most likely explanation is that the turtles grouped together offshore and nested as soon as a suitable wind sprang up. It may be significant that one *arribada* (that of 31 May) included more than six times as many turtles as any other that season. In 1967 also only one

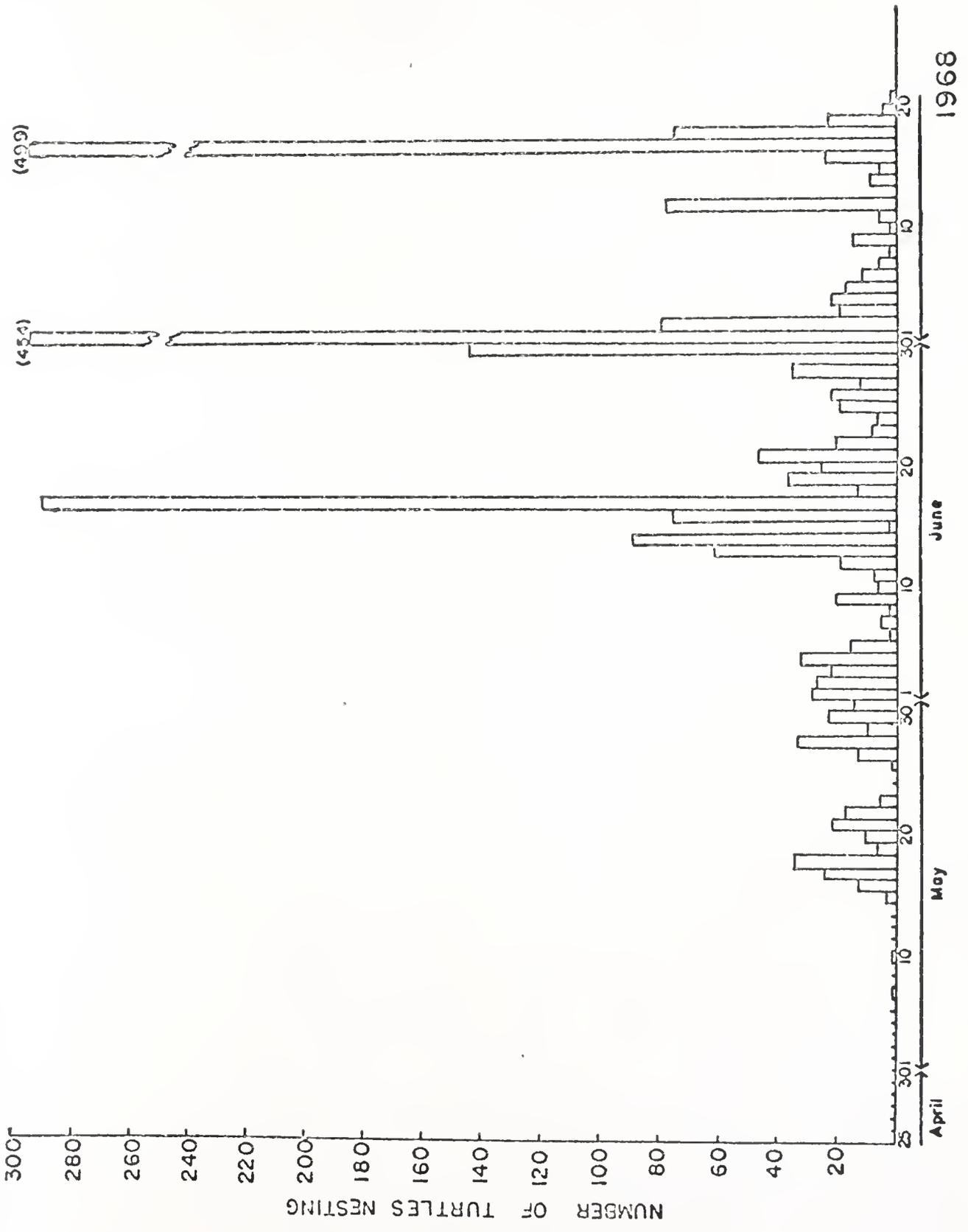
large arribada (numbering an estimated 3,000 turtles) was seen, and again in 1968 an arribada estimated at 5,000 was seen on 23 May, while no other group seen that season even approached that number. Moreover aerial reconnaissances of a stretch of beach much longer than that actually patrolled were carried out, without any indication that turtles were nesting in more than ones and twos outside the patrolled area. If this is true it would suggest that a considerable proportion of ridleys in the population nest only once in the season, though we do know that double and even triple nesting can occur (see above).

For several years after its discovery, the arribada at Rancho Nuevo was considered to be a phenomenon unique in the world. I was very surprised therefore, on my first visit to Surinam in 1966, to be told by Mr. G. Plak (the chief game warden in Surinam) that warana turtles (i.e. Lepidochelys olivacea) nested in aggregations of several hundreds on certain nights in June and July at Eilanti Beach in the mouth of the Marowijne River. My studies on the turtles on that beach during a 4-day period in 1966 and throughout the 1967 and 1968 nesting seasons comprise much of the work reported in this paper.

The numbers of turtles found nesting each night at Eilanti during the 1967 and 1968 seasons are shown in histogram form in figures 38 and 39. The numbers recorded even on nights of aggregated nesting may be considered fairly accurate since every nest made was claimed by one of the local Carib Indians, who sold us the eggs for transplantation in a hatchery the following morning.

Figure 38. Numbers of turtles nesting each night at Tilanti, Surinam, in the 1967 season

Figure 39. Numbers of turtles nesting each night at Eilanti, Surinam, in the 1968 season



The nesting of L. olivacea at Eilanti shows a cyclical regularity contrasting with the haphazard-seeming arribadas of L. kempi at Rancho Nuevo. The pattern revealed is one of intensive nesting at approximately two-week intervals. Each year there were three such periods, while in 1967 a much smaller peak preceded the first major peak by about two weeks, and in 1968 there were two such peaks at about fortnightly intervals before the first major peak.

Analysis of the data for 1967 reveals a remarkable circumstance. If we define a phase of intensive nesting as a series of nights on each of which more than twenty turtles nested, we find a first phase lasting from 11 to 15 June, a second from 24 June to 1 July, and a third from 9 to 12 July. The total numbers of turtles nesting during the three phases are then 654, 650 and 653. The extreme similarity of these numbers, together with the abundantly confirmed observation that sea turtles of other species often nest at fortnightly intervals three or more times in a season, leads us to suspect that the same turtles are nesting during each phase, and that those turtles which nest on intervening nights constitute an out-of-phase minority.

This theory is refuted, however, as we argued before, by the extreme scarcity of records of individual turtles nesting three times in the season, even though, in 1963 at least, almost every turtle nesting during the first phase was tagged, while virtually every turtle nesting during the second and third phases was seen.

Careful, though qualitative, studies of the external environmental factors obtaining during each of the arribadas at Eilanti were undertaken. Whether the night was clear or clouded, whether it was raining or whether the moon was visible, had no observable effect on the emergence of nesting aggregations. It would be expected, considering the apparently fixed periodicity of nesting, that the state of the tide, an entirely predictable and regular variable, might have some bearing on nesting; and indeed it seems to, even beyond the mere preference to nest by high tide that we have discussed earlier. Arribadas at Eilanti take place when high tide occurs in the early part of the night; that is, when the tide is rising at dusk and falling at midnight. Since the tidal cycle drops back about 50 minutes each day, the observed inter-phase period of around fourteen days agrees nicely with the time required for the tide to have dropped back by a full twelve hours, so that it was again high during the early part of the night.

The reason for the correlation may be as follows: at Eilanti, turtles can nest only by moderately high tide, as we have mentioned before, since the enormous mud flats off the beach exposed by low tide are almost impossible for a turtle to traverse. Moreover the turtles at Eilanti follow the nearly universal turtle custom of nesting during the hours of darkness or near-darkness. With these two restrictions, if a turtle were to nest by a high tide at, say, 3 A.M., there would be some chance (as there always is) of the turtle being

stranded by the receding tide and having to await the next high tide to lift it off the mud bank. This would entail a long wait beneath the unshaded tropical sun, which might well cause the turtle to overheat fatally. On the other hand, a turtle nesting by high tide soon after dusk, even if it gets stranded on the mudbank, will be able to swim off by the next high tide before the sun is up. Since the actual risk of an individual turtle being stranded on the mud bank is slight, however, small numbers of turtles nest on intervening nights with probably only the very occasional fatality from this cause. Nevertheless it is curious that during nights of aggregated nesting the majority of turtles nest while the tide is falling rather than rising. It may be that the turtles can simply not get to the beach any quicker, since they have to remain several miles away from the beach during low tide in order to be in water deep enough to swim. Once the incoming tide floods the mud flats, their navigation (by means still unknown) to the small nesting beach may well involve an indirect, time-consuming route.

Another environmental factor found to be essential for an arribada is an onshore wind of at least moderate strength. Even when an arribada is 'due' in terms of tide and interval since the previous massed emergence, few turtles will nest unless there is a reasonably strong breeze from the sea. This happened for example during all three phases in 1968. A group of 61 turtles on 13 June and 83 on 14 June gave the impression of a build-up towards a major arribada. However on 15 June the air

was absolutely still, and only two turtles nested. A slight wind the following night brought 75 turtles on shore, while on the night of 17 June, when the wind was reasonably strong, 289 turtles nested. Similar events occurred during the second and third phases respectively; on 29 June and 13 July arribadas were 'due' in terms of tide, interval since the last major group, and a build-up of more turtles than usual the previous night. On both nights, however, there was no wind, and not a single turtle nested; the large groups - over 400 turtles in both cases - had to wait two and four more nights respectively for a suitable wind.

The ridley populations of the East Pacific were until recently thought always to nest singly or in small groups. Carr (1961a: 9) was the first to notice an odd disparity between the large numbers of sexually mature ridleys seen offshore from the Pacific coast of Mexico and the small number of turtles actually found nesting, even in the middle of the breeding season; the obvious implication was that the turtles were nesting in high concentrations on inaccessible parts of the coast. This observation was expounded in somewhat more detail by Caldwell (1966: 12), who predicted that a mass nesting ground for the species would be found on the coast of Mexico between the mouth of the Gulf of California and the State of Guerrero. He also mentioned unconfirmed reports of large numbers of sea turtles nesting on the coast of Jalisco, south of Bahia Banderas.

Caldwell was correct in his predictions. Studies by

personnel of the Mexican Instituto Nacional de Investigaciones Biológico-Pesqueras have revealed arribadas at four localities on the Pacific coast of Mexico:

i) At el Playon de Mismaloya, between Cabo Corrientes and the mouth of the Rio Tomatlán, Jalisco

ii) Near the Rio Apiza on the Colima-Michoacan State Line

iii) Near la Piedra de Tlacoyunque, near San Luis de la Loma, Guerrero

iv) At Playa la Escobilla, near Puerto Escondido, Oaxaca.

Moreover the arribadas on the west coast of Mexico are made up of enormous numbers of turtles. Two arribadas near San Luis de la Loma in August 1967 were estimated to involve 30,000 and 15,000 turtles respectively; the former lasted for 18 hours, the latter for 24.

Table 10 gives the estimated numbers of turtles in each of the major arribadas witnessed in 1968 by Mexican conservation personnel.

Unlike arribadas at Rancho Nuevo or Eilanti, which last for four or five hours and take place by day and by night respectively, arribadas on the Mexican Pacific coast may last for two days or more, and thus turtles nest both by day and by night. As with the Rancho Nuevo situation, however, it is difficult to discern a pattern to the nesting. Only one arribada was seen at Playon de Mismaloya, for example, even though the beach was kept under observation

TABLE 10

ESTIMATED NUMBERS OF TURTLES IN NINE
ARRIBADAS OF LEPIDOCHELYS OLIVACEA
 RECORDED IN 1968 (fide Montoya, pers.
 comm.)

Locality	Date	Number
Playon de Mismaloya	9-11 July	20,000
Playa la Escobilla	7-10 August	80,000
"	28 August	20,000
"	19 September	30,000
"	6-7 October	15,000
"	20-21 November	8,000
Piedra de Tlacoyunque	26 August	10,000
"	2-4 September	40,000
"	30 September	5,000

from 9 July until 20 November. On the other hand five major aggregations were seen at Playa la Escobilla, ranging in size from an estimated 80,000 turtles (the largest arribada on record) down to 8,000. Intervals between arribadas were 18, 22, 17 and 46 days. The three arribadas at Piedra de Tlacoyunque, of which the middle one included more than twice as many turtles as the other two together, took place at intervals of 6 and 26 days.

The single environmental characteristic common to all recorded arribadas at Rancho Nuevo, at Eilanti, and on the

Mexican Pacific beaches is that of a moderate to strong offshore wind, without which the turtles do not come ashore in large numbers. Even in Honduras, where arribada formation has yet to be demonstrated, more turtles nest on windy nights than on calm ones. It has been suggested that strong winds may in some way help the turtles to "ride the waves" and thus be speeded on the beach. Much more likely is the theory of Hildebrand (1963) that a strong wind will help cover up the tracks and nests of the turtles and thus render them less conspicuous. Little short of a tornado will obliterate the tracks of a green turtle or leatherback, but the track of a ridley is so shallow that wind-blown sand can erase it quite quickly. William Greenhood has suggested that a strong wind helps to dislodge the mosquitoes that descend in clouds upon ridleys nesting, in Surinam at least. This reason too may have some substance, though it is hard to see how mosquitoes act as anything more than an uncomfortable inconvenience to the nesting turtles; it is unlikely that they would actually contribute to their early death, and thus exert some selective pressure upon the behavior of the population as a whole (unless they carry some disease to which reptiles are liable).

The advantage of massed nesting is not immediately obvious; some benefit must be gained, as arribada-formation is a highly 'organized' trait, and must require constant selective pressure to maintain. Since the beach situations are considerably different at Eilanti and on the coasts of Mexico, we will be wise to consider the two situations separately.

Eilanti, as we have mentioned before, undergoes an erosional cycle which makes it a true island for much of the time, and at such times it is the only island close to shore in the area. Turtles nesting at Eilanti will therefore enjoy a comparative freedom from terrestrial predators such as jaguars, which are still found close to shore along the Surinam coast (a ridley was killed by a jaguar at Bigi Santi on 20 June 1968). Jaguars, of course, can swim perfectly well, but they would probably be reluctant to embark on a swim which entailed a preliminary wade through deep mud unless they had some certainty of food on the other side. Given the small size of the island, the relative freedom from predators and the excellence of the surrounding feeding grounds, it is easy to see how a large nesting population could be built up, while the marked periodicity of that population as I have mentioned earlier is caused by the offshore mud flat which forces the turtles to nest by the high tide that occurs early in the night on an approximately fortnightly basis. We thus have all the ingredients for an arribada.

It is clear that the situation in Mexico is not the same. Nesting here takes place, not on a small island, but on a variable point on a long mainland beach. The turtles here cannot escape predation by island nesting, as there are no suitable islands in the area. Thus, since some predation, especially on the eggs, is unavoidable, the turtles have evolved so that, rather than furnishing predators

with a regular supply of eggs throughout the nesting season, they emerge from the sea in huge numbers in closely circumscribed and not accurately predictable places, so that the few predators which happen to be around will be swamped with such an abundance of food at one time that, even though they eat all the eggs they can, many will be left over. When the predators are hungry again, rain and wind will have done their work and they will no longer be able to find the nests. In similar fashion, when the eggs hatch, thousands or millions of young turtles will emerge at around the same time, and it will be impossible for the gulls and other predatory birds in the area to get all of them.

The theory of swamping of predators with an overabundance of prey for a very short time would certainly seem to hold in the case of Lepidochelys kempi at Rancho Nuevo. The menace here is the coyotes, which abound in the area behind the beach, and which come out by night to search for ridley eggs. The nesting ridleys have evolved several adaptive responses to this predation. They nest by day, so that the eggs will at least be in the ground, rather than in the process of being laid, when the coyotes come searching for them. Moreover since the ridley is a small turtle, it cannot bury its eggs very deep in the sand, so it flattens the sand over the nest site by tamping it down with the specially expanded sides of the shell; the more compact the sand over the eggs, presumably the less likely it is that odor from the new-laid eggs will attract

coyotes. However, these devices are inadequate as nests made by straggling turtles which have missed an arribada are almost invariably robbed by coyotes the following night.

A possible theory to account for the synchronization of nesting by ridleys has been advanced earlier. However, although we have postulated a possible advantage to the practice, we have not yet put forward a possible mechanism whereby large numbers of turtles manage to nest at the same point on an apparently uniform stretch of beach. In this case it seems that the turtles are not merely reacting in similar fashion to a common stimulus; they are in some way taking note of each others' presence. In the Surinam arribadas I observed that the turtles do not emerge from the sea at random, but rather in bunches; within a few seconds many turtles may emerge on a particular ten yards of shore, then no more will emerge there for several minutes. I have also seen the same thing in films of arribadas of both species in Mexico. It is very possible that the turtles group together offshore, possibly being mutually attracted by a pheromonal secretion of the inframarginal glands (if there indeed are secretory glands under the inframarginal pores, which has not yet been proven).

EVIDENCE FOR LONG DISTANCE MIGRATION

Whether the genus is migratory in all parts of its range is not known; it is quite possible that in those areas where nesting appears to be entirely diffuse (for example in Indonesia) the turtles do not undergo long migrations. However, where aggregated nesting occurs, the conclusion is inescapable that the turtles are recruited from at least a moderately wide range, since no small area could provide sufficient food for the large numbers of turtles involved.

Long distance movement of some *Leidochelys kempi* has been demonstrated by the tagging experiments of Chávez (1968). A total of 285 nesting females was tagged near Rancho Nuevo in 1966, 17 of which have been recaptured to date. Six individuals were recovered from the coast of Campeche, one from Tabasco, one from Veracruz, three from Texas, five from Louisiana and one from Key West, Florida. Most of the recoveries were made in July and August (2-3 months after tagging), possibly because this is the time when the greatest number of fishing boats is abroad. The recovery data suggest that the feeding grounds of mature ridleys are concentrated throughout the western half of the Gulf of Mexico, with smaller numbers travelling to the opposite end of the Gulf.

It is also possible that immature *L. kempi* may travel

in groups along the Atlantic shore of the United States.

Carr (1957: 53) writes:

With respect to the Atlantic form, the only positive evidence is an astonishing observation disinterred by Mr. William Schevill of the Woods Hole Oceanographic Institute, and communicated to me by letter. A few months ago, Mr. Schevill examined some 20-year-old sea-turtle specimens in the collection of the Marine Biological Laboratory and found that they were all ridleys. In making inquiries about the origin of these he learned that Mr. James McInnis of HBL had picked them up, all at the same time, from among dozens of carcasses left stranded on Woods Hole beaches after "a whole fleet of such turtles" had travelled from Buzzards Bay into Vineyard Sound and then headed out to sea. This is the only authentic case of a mass migration in kempi. The implications of its taking place outward from a New England bay are unsettlingly unclear, but of obvious relevance to the inquiry at hand.

Table 11 summarizes data for recoveries of female L. olivacea tagged on the nesting beach at Eilanti, Surinam.

TABLE 11

RECOVERY DATA FOR FEMALE LEPIDOCHELYS
OLIVACEA TAGGED AT EILANTI, SURINAM

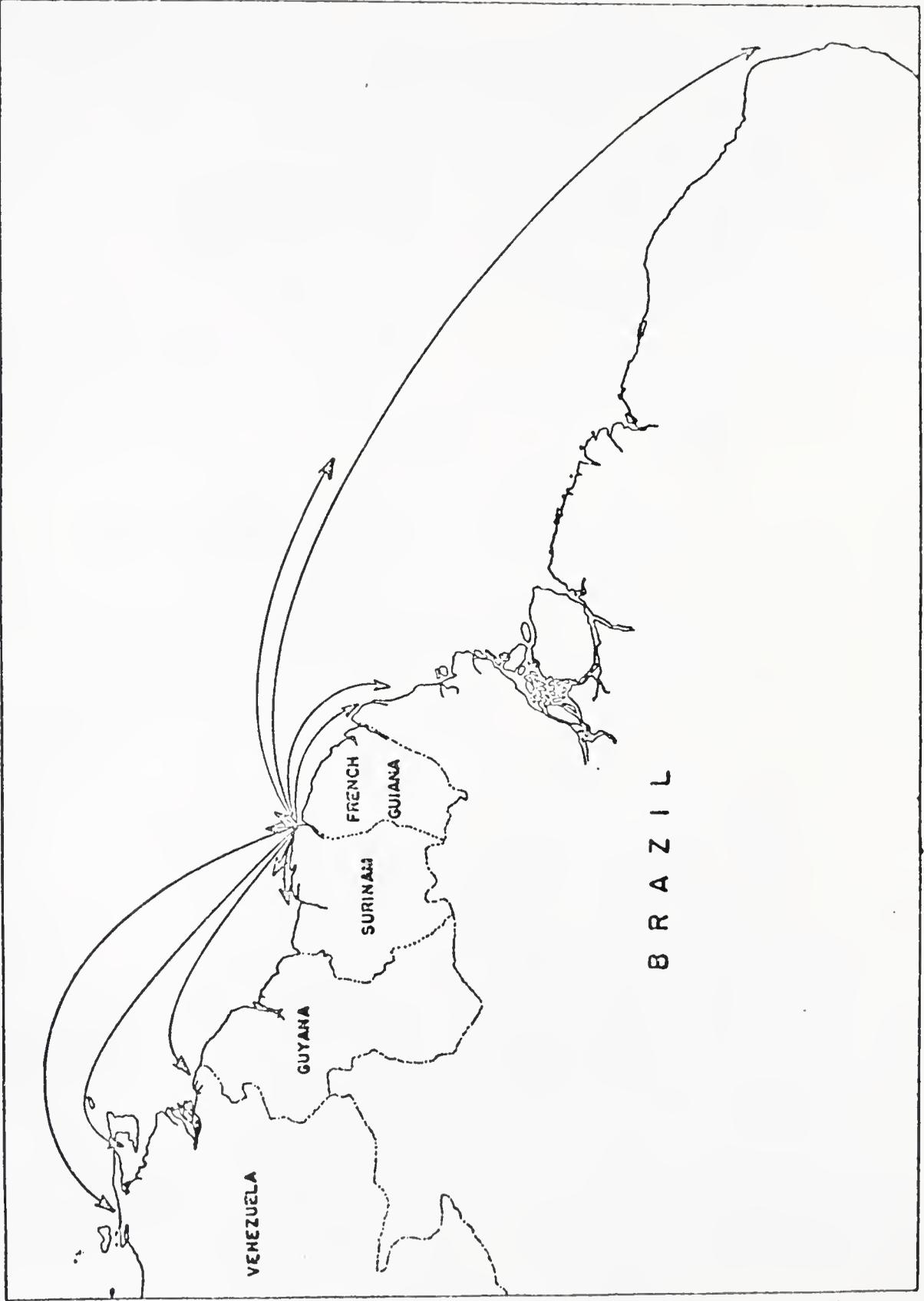
Tag Number	Date tagged	Date recovered	Locality of recovery
E142	7 June 1966	Nov. 1967	"Off Surinam"
E277	30 May 1967	Jan. 1968	Maracajau, Municipio de Touros, near Natal, Brazil
E300	31 May 1967	1 Aug. 1967	8° 15' N, 60° 20' W (Punta Barima, Venezuela)
E307	31 May 1967	1 Feb. 1968	Between Amazon and Oyapoke mouths, Brazil
E423	11 June 1967	1 Dec 1968	6° 15' N, 53° 20' W (off the coast of French Guiana).

Table 11 (continued)

E459	11 June 1967	18 Sept. 1968	4°45'N, 45°35'W (open sea 400 miles from mouth of Ama- zon)
E545	13 June 1967 (renested 18 May 1968)	29 Dec. 1968	Off mouth of Maro- wijn River, Surinam (water 160-180 ft. deep)
E582	13 June 1967 (renested 11 July 1967)	26 July 1967	6°15'N, 55°30'W (off Surinam coast)
E594	13 June 1967	4 Feb. 1969	2 miles from Sol- dado Rock, off W coast of Trinidad
E648	13 June 1967 (renested 17 July 1968)	4 Jan. 1969	"off the shores of Dutch Guiana"
E936	17 June 1968 (renested 17 July 1968)	13 Feb. 1969	25 miles N of Trini- dad
E1054	20 June 1968	2 July 1968	4°2'N, 50°50'W (off the coast of Brazil between Amazon and Oyapoke mouths)
E1120	25 June 1968	18 Sept 1968	1½ miles N of Carú- pano, Venezuela

These recovery locations are shown on the map in figure 40. It is interesting to note that four out of the 13 recoveries were made in Surinam waters, and three of them at a time of year almost diametrically opposed to the nesting season, even though the coast of Surinam occupies only about a tenth of the entire spread of coastline between the extreme records. This suggests that ridley

Figure 40. Recovery locations for female Lepido-
chelys olivacea tagged at Eilanti, Surinam;
arrows do not show routes actually travelled



populations are denser in Surinam waters than elsewhere along the coast of Northern South America, since the entire area is fished by shrimp trawlers and other vessels. However, those turtles which leave Surinam waters after nesting may move east or west with comparable frequency.

Three individual records are of the greatest interest. Turtle 1120 was recovered 18 September 1968, 85 days after nesting, about 800 miles to the west, near Carúpano, Venezuela. To quote the letter accompanying the tag return:

The fishermen informed me that, while they were fishing big anchovies, they saw a shoal of turtles passing by. One of them caught itself with a hook that passed its back foot. When they brought it on board they noticed the information tag that I'm sending to you as required.

This record not only shows that ridleys actually enter the Caribbean Sea, but also that at least one individual of a "shoal of turtles" can be positively identified. Records of aggregations of turtles at sea for which the species is definitely known are all too few.

Turtle E459 was picked up, by coincidence also on 18 Sept. 1968, at an unusual distance from land (about 400 miles). It is possible that the turtle was deflected from its normal course by the huge output of water from the Amazon. However it is also possible that those turtles which do migrate to feeding grounds beyond the Amazon tend to skirt the mouth of that river by hundreds of miles.

Turtle E277 was caught near Maracajau in the Município de Touros, Brazil, along with two tagged green turtles from

Ascension Island. This location is hundreds of miles east of the previous easternmost record for the species in South America. The precise date of capture was not stated in the letter accompanying the return (which was dated 25 January 1968), and since the letter was not written by the man who caught the turtle (who was illiterate), it was unfortunately not possible to get confirmation of the accuracy of the stated locality of recapture.

There are no published records of tagged turtles from the Mexican Pacific population being recovered in other areas. This may be due to the large size of the population there, and the difficulty of tagging more than an insignificant fraction of individuals. A single turtle (H73) tagged 12 November 1967 at Isla de Ratonés was recovered around September 1968 near Corinto, Nicaragua, on the opposite side of Consiquina Volcano. However, considering the huge numbers of turtles involved in arribadas on the Pacific coast of Mexico, it is likely that the species is also strongly migratory in this area, a large arribada being recruited from many miles of coastline.

HORIZONTAL AND VERTICAL RELATIONSHIPS OF LEPIDOCHELYS;
FOSSIL CONSIDERATIONS

i) Relationships Within the Family Cheloniidae

There is some disagreement among modern writers as to whether or not the modern sea turtle genera distribute themselves naturally into two or more subgroups. Carr (1942: 6) listed 25 characters by which at least some of the genera could be separated from each other. An analysis of this tabulation forced him to the conclusion that, for the time being, no subdivision could be made; but if such a subdivision were to be made, the most natural one would be to restrict the Cheloniidae to the single genus Chelonia, and to place Eretmochelys, Caretta, and Lepidochelys in a separate family, the Carettidae. Zangerl and Turnbull (1955) criticized Carr's choice of characters, and argued that the various characters used cannot reasonably be accorded equal importance, while some of the more "trivial" characters used, especially those of the skull, were correlated and should not be considered as three or four, but as one, when computing the total numbers of similarities and differences. Zangerl and Turnbull argued that Caretta and Lepidochelys formed a natural grouping, distinguished from Chelonia and Eretmochelys by the inclusion of a small extra costal lamina and a tendency to fragment various bone and scale elements in the carapace and head - a tendency which begins in Caretta and is well advanced in Lepidochelys. In

addition, both Lepidochelys and Caretta have a bridge index (shortest width of bridge X 100 / half width of plastron) of 55-80, while that of Chelonia and Eretmochelys is 80-100. Their conclusion was that Caretta and Lepidochelys formed a natural grouping, the Carottini, the other two modern sea turtle genera comprising the Chelonini.

If we accept Zangerl and Turnbull's definition of the Carottini, we find relatively few fossils which fit naturally into it. However the form Euclastes nelii Hisuri from the Miocene of Europe is considered by Zangerl to represent a possible ancestor to the Carottine line. It agrees with the Chelonini in showing no increase in the laminae of the carapace or head or in the peripheral bones, but three of the neurals (5-7) are laterally doubled, a definite Carottine character.

Another fossil sea turtle with some Carottine characters is Procolpochelys grandaeva (Leidy) from the Miocene of New Jersey. The species was first called Chelonia grandaeva by Leidy (1851), but was transferred to the genus Procolpochelys by Hay (1908b) who reviewed the previously described specimens and found further material in the collections of Rutgers College and Princeton University. The material is very fragmentary, but much later was carefully reconstructed (Zangerl and Turnbull, 1955), showing that parts of either three or four turtles were present. It became possible to interpolate most of the carapacial characters, but plastra were exceedingly fragmentary and incomplete and skulls were not represented in the material.

The reconstructions show that Procolpocheilus was a large turtle with the normal Chelonine number of carapace laminae and peripheral bones; the neurals however are divided both laterally and longitudinally. The turtle is most closely comparable to Caretta among living forms, but the carapace is narrower and the intercostal fontanelles are persistent even in very large specimens; both of these are probably adaptations to a pelagic existence, and suggest that the form was too specialized in that direction to have been a likely direct ancestor of modern Carettini.

One more fossil Carettine turtle has been described: Carolinochelys wilsoni Hay, based on a well-preserved skull and a single humerus, from the Ashley Marl of Charleston, South Carolina. Cooke (1936) considers it to be of Miocene age; Zangerl (1958) places it in the Oligocene. Lacking both geological training and first-hand knowledge of the material, I shall withhold judgement on the relative merits of these opposing views. Carr (1942: 8) writes:

A comparison of this specimen with skulls of existing Cheloniidae shows an apparently close affinity between Carolinochelys and Lepidochelys, so close, in fact, that it appears reasonable to regard the former as a direct ancestor of the latter. Although differences between the two are certainly of generic value, the similarities which exist suggest that most of the evolution of the thecophoran sea turtles took place at a very early date, and that Lepidochelys was probably fully differentiated from the other genera during Miocene time.

According to Zangerl (1958), the secondary palate of Carolinochelys differs from that of Lepidochelys in showing

two parallel bony ridges which run approximately parallel to the alveolar edges, and in having a humerus which differs in many respects from the humeri of all modern Cheloniids. While it is true that Lepidochelys olivacea lacks ridges on the secondary palate, these are well defined in the present-day Eastern North American species, Lepidochelys kempi, especially in large, old specimens.

Despite the fact that Procolobochelys and Carolinochelys were both found in mid-Tertiary deposits of the central part of the Atlantic coastal plain of the United States, the suggestion that Carolinochelys may represent the unknown skull of Procolobochelys has apparently not been entertained in the literature.

ii) Relationships with Other Sea Turtle Families

Five families of sea turtles are currently recognized: the Cheloniidae, the Dermochelidae, the Toxochelidae, the Thalassemyidae and the Protostegidae. All but the first two are now extinct. The consensus of modern opinion is that these five families were monophyletically derived from the amphichelid family Plesiochelidae in the early or mid-Mesozoic; all the families include at least some specialized members which were clearly not ancestral to any other family. The point at which the scuteless, highly divergent Dermochelidae separated from the main line of chelonoid evolution is unknown, although recognizable but incomplete dermochelid fossils are found in the Eocene and Miocene of Europe.

I think it is most likely that the family shares a marine ancestor with the Cheloniidae, but shall avoid further discussion of this fascinating, but for the moment irrelevant, question.

Williams (1950: 555-556) places the Thalassemyidae in the Amphichelydia, and the Toxochelidae, Protostegidae, and Cheloniidae in the Cryptodira, superfamily Cheloniioidea. This disposition, though defensible, does emphasize the arbitrary nature of the classification of modern sea turtles with the Cryptodira. The non-retractile neck would link the Cheloniioidea with the Amphichelydia rather than with the Cryptodira, as would the completely roofed-over temporal region of the skull. The complete skull roof of modern sea turtles has presumably been retained as a protection for the non-retractile head. It has been argued by many authors that this condition is secondary. However the skull is completely roofed-over in Permian cotylosaurs, in Triassic ancestral turtles (Triassocheilyidae) and in sea turtles from the Jurassic onwards; it seems an unnecessary complication to postulate hypothetical links between these stages in which the skull roof was emarginated. This again is a common amphichelid character which is retained by only one modern non-marine Cryptodiran genus (Platysternum).

The absence of mesoplastra in the Cheloniioidea does not necessarily imply relationship to the Cryptodira; all possible mesoplastral conditions (two pairs, one pair, or

none) are well represented among the Amphichelydia; while at least one plastron of Lepidochelys has been found with a well-defined pair of contiguous mesoplastra (Pritchard, 1966). Yet another frequently cited cryptodire character, the lack of fusion of the pelvis and the plastron, while certainly universal among Chelonioida, is also found in several amphichelyd families, even as far back as the Triassic (Triassochelyidae, Subfamily Triassochelyinae).

A character which would seem to link the Chelonioida more definitely with the Cryptodira is the frequent doubling of the most proximal cervical joint. Nevertheless this doubling not only involves several vertebrae in most other Cryptodira, but also it is not always found even at the proximal cervical joint in Chelonioida (Williams, 1950: 525), this joint being sometimes single (though broadened), and sometimes cylindrical. It is very possible that the alteration of this joint represents an independent improvement on the somewhat wobbly amphicoelous cervical joints of the amphichelyd ancestors.

Retention of the Chelonioida within the Cryptodira, then, would require that the latter group be polyphyletically derived from the Amphichelydia, and would necessitate a complex and highly artificial definition of the Cryptodira which would seriously weaken our argument for the separation of the two suborders.

Although one is probably justified in distributing the 'theopheran' sea turtles among the four families Thalassomyidae

Toxochelidae, Protostegidae, and Cheloniidae, it is nevertheless true that the points which separate the families are for the most part rather trivial. For example, Zangerl (1953: 267) cites the following characters to separate the Thalassemyidae and the Toxochelidae.

Thalassemyidae	Toxochelidae
Carapace	
Vertebral shields always much wider than pleural shields	Vertebral shields always much narrower than pleural shields
Neural series tend to be suppressed	Neural series always normal
Usually one suprapygals	Two suprapygals
Plastron	
Distance between axillary and inguinal notches 90 percent or more of half the width of plastron	Distance between axillary and inguinal notches 60 percent or less than half the width of plastron

The relative width of the vertebral shields (=central laminae) relative to the width of the pleural shields (=costal laminae) is known to vary with age in modern sea turtles; for example hatchling Lepidochelys have centrals almost as wide as the costals, while in the adults the centrals are $\frac{1}{4}$ or less the width of the costals. The neural series is also highly variable in at least two modern sea turtle genera (Lepidochelys and Caretta), while within a single family of turtles (Chelidae) all conditions, from a complete neural series to no neurals at all, are found.

The suprapygai character is not absolutely constant, while the difference in bridge index of the two families is almost exactly that which separates the two existing subfamilies of the Cheloniidae. An additional character, not tabulated above, is that the forelimbs of the Toxochelidae are better adapted for aquatic life than those of the Thalassemyidae; but this, though important, is not a qualitative character.

I am not arguing that the separation of the two families is indefensible; but I do believe that they are closely related and that their inclusion in different suborders is unnatural.

The Toxochelidae, Protostegidae, and Cheloniidae are separated by characters of the humerus, which in the Protostegidae and Cheloniidae is better adapted for wielding a flipper than a foot than it is in the Toxochelidae. Also, the presence or absence of a secondary palate is considered important. However the secondary palate is an obvious adaptation to protect the internal nares from damage caused by crushing hard-shelled organisms, and is simply a narrow shelf projecting from the rear of the upper alveolar surface; moreover in one family (the Toxochelidae) the secondary palate is absent in one subfamily (the Toxochelinae) and present in the other (the Osteopyginae). Otherwise the families show some differences in the pattern of articulation of the cervical vertebrae (most turtle species are polymorphic in this respect), and differences in average carapace

and plastral proportions. The plastron is in fact more generalized in the Cheloniidae than in the other two families; the Toxochelidae show a reduction of the anterior lobe, and the Protostegidae a reduction in the posterior lobe.

My point, then, is that the concept of the superfamily Chelonioidea is a natural one, and that it is meaningful to speak of Lepidochelys, not only as a morphologically (though not behaviorally) primitive member of the family Cheloniidae, but also as a relatively primitive representative of the Chelonioidea. The carapace outline of Lepidochelys is more like that of the round or broadly cordiform Toxochelidae than like the elongate-cordiform shells of 'advanced' Cheloniids (Chelonia and Eretmochelys). The low bridge index, too, allies Lepidochelys with the toxochelids rather than with the subfamily Chelonini. The lack of shell fenestration in mature individuals of Lepidochelys is also a primitive character, as may be the small overall size. Nasal bones are admittedly absent in Lepidochelys, as in all cheloniids, but they are very small in the Toxochelidae and give the impression of undergoing elimination. Lepidochelys has the typical tetrapod mode of progression on land, which may be a primitive character, but it may well merely be a function of the small size of the animal. The same argument applies to flipper size; these are relatively much shorter in Lepidochelys than in, say, Chelonia.

DISCUSSION

I have gone to some length in the preceding section to reason that Lepidochelys is a morphologically primitive member, not only of the Cheloniidae, but of the inclusive sea turtle superfamily, the Chelonioidae. Let us assume, then, that the gens, even if not the genus, Lepidochelys was established before the end of the Mesozoic. Another assumption that we shall make - a major one, perhaps - is that several of the continents of the world were fused into a hypothetical supercontinent, "Gondwanaland", at the beginning of the Mesozoic, and that a gradual process of continental drift separated what are now India, Africa, South America, Antarctica, and Australia during the second half of that era. This theory was first proposed by Wegener (1915), and after a long period of relative disfavor (the zoogeographer Darlington, 1957, for example, did not subscribe to it, though he does now; nor did most geologists and geophysicists at that time) is now receiving increasing support from such eminent paleontologists as Alfred S. Romer as more and more geological and paleontological evidence is accumulated. (It is also worth pointing out that, without continental drift gradually widening the South Atlantic, it is extremely difficult to visualize how the Chelonia mydas population that nests on Ascension Island and feeds on the coast of Brazil might have evolved its migration habits.)

With these two assumptions, the gens or genus Lepidochelys may well have evolved in the Pacific Ocean, for the simple reason that the Indian and South Atlantic Oceans did not exist at the time. This does not eliminate the North Atlantic, but the genus does not nest there today and there is no evidence that it ever did. One could postulate that the ancestral form was Lepidochelys kemp in the Gulf of Mexico, but I doubt that this is so for the reasons given below.

The only published discussion of the possible means whereby the genus Lepidochelys spread throughout its known range, that of Deraniyagala (1943), is rendered almost useless by several misapprehensions, for example that kemp "is most abundant in the Caribbean Sea," that "the only known breeding grounds are the shores of Georgia in North America," and also the author's ignorance of the existence of a breeding population of L.olivacea in the West Atlantic. Nevertheless his conclusion that Lepidochelys kemp is a product of isolation of Lepidochelys olivacea in the Gulf of Mexico is probably correct, as I shall discuss below.

Let us postulate that Lepidochelys originated on the west coast of Mexico in the late Mesozoic. The genus is today much more numerous there than anywhere else, and this locality also will provide at least a feasible basis for the later distribution of the genus throughout the world. B&S (1905, 1906), and in particular Durham et al. (1955) have marshalled very cogent evidence showing that the last

marine connection across the Isthmus of Tehuantepec was during the Cretaceous. These authors effectively refute many other writers (e.g. Maldonado-Koerdell, 1950; Eardley, 1951: 587; von Engeln and Carter, 1952, fig. 326), who assumed that there was a marine connection across the Isthmus during the Tertiary. Such a late Mesozoic marine connection would accord well with my theory: a population of Lepidochelys crossing the then-submerged isthmus in the Cretaceous, would since then have been isolated from the main Pacific stock of the genus. Lepidochelys is even today very abundant on the Pacific side of the isthmus, while the corresponding point on the coast of the Gulf of Mexico is quite close to the southernmost point of the nesting range of kempi. Ridleys picked up by the clockwise current in the Gulf might well nest in scattered fashion along the coasts of Veracruz and Tamaulipas. The significance and possible evolution of the large concentration of nesting turtles at Rancho Nuevo, Tamaulipas, has been discussed earlier.

There were, of course, marine connections across the Central American Isthmus for much of the Tertiary, but these connect with the Caribbean, not with the Gulf of Mexico. Despite this possibility of repeated colonization of the Caribbean by East Pacific ridleys, the genus is now (and may always have been) absent from the Caribbean, for reasons guessed at below.

This theory is not without weaknesses. For one thing, the general current trends in the Gulf of Mexico may well

have been very different when there was a marine connection across the Isthmus of Tehuantepec. Also, it is difficult to see how a local population derived from Lepidochelys olivacea, and presumably well-endowed, as is olivacea, with the genes, or at least the capacity, to develop extensive polymorphism with respect to the carapace laminae, should be subjected to sufficient selective pressure to eliminate this seemingly harmless polymorphism. One possibility is that olivacea developed its curious multilaminar carapace after kempi was isolated by the closing of the Tehuantepec Strait; and that olivacea invaded the Indian and South Atlantic Oceans, bringing with it its mutant multilaminar carapace, at some later date.

The carapacial multilamination of Lepidochelys olivacea is only an extreme aspect of a phenomenon found in all Carettini. Caretta caretta has fragmented dorsal head scales; Lepidochelys kempi has fragmented head scales and neural bones; L. olivacea has fragmented head scales, neural bones and carapacial laminae. The phenomenon is probably non-adaptive, as I have argued earlier; it is probable simply that the Carettini lineage is so ancient that the genes controlling head and shell elements, being under no particular selective pressure either way, have allowed this harmless trait to drift unchecked; and over many millions of years the drift has been considerable. However, the possibility of some pleiotropic effect should also be borne in mind.

It is arguable that the Gulf population was founded by just a few ridleys that crossed the Tehuantepec Strait in the late Mesozoic, and that these were all recruited from that small percentage (10-20 percent) of Pacific olivacea which have the pentocostal kempi carapace pattern. This is argued against by some inconclusive experiments of mine on Surinam olivacea which suggest that the costal count of the mother turtle has little or no bearing on those of the offspring; but here of course eggs of the mother could have been fertilized by several males carrying genes which could affect the costal counts of the offspring in a completely unpredictable fashion.

The spread of L.olivacea from the north-east Pacific throughout its present Indo-Pacific range is not hard to visualize. The species gradually extended its breeding range south until it came in contact with the cold waters of the Humboldt Current in Ecuador. The species today seems to take to the open sea relatively rarely, but over millions of years it would be surprising if some colonization of the West Pacific had not occurred. The Indonesian islands - a fertile breeding ground today - provided no barrier at certain geological periods, and once in the Indian Ocean the Cape of Good Hope would provide access, at least during the summer months, to turtles entering the South Atlantic.

The above process probably took the greater part of the Cenozoic Era for completion. The colonization of the

West Atlantic gives one the impression of being a geologically recent phenomenon, considering the small number of points along the South American coast where the ridley is known to breed, and the absence of the species from all but the extreme south-east corner of the Caribbean. The mechanism of such a colonization is not hard to postulate: the species is well established on the west coast of Africa as a breeding animal, and the Equatorial Current moves in a steady westward direction. In the course of long periods of time the chance of an ovigerous West African ridley being swept off course and laying its eggs on a South American beach become appreciable; and one successful laying and hatching could, under suitable conditions, establish a colony. The absence of the species from the Caribbean may well reflect that it has not yet penetrated this far; there are no historical records of its occurrence there, and it would be surprising if the Caribbean environment would be fatally hostile to this, elsewhere, successful species.

However, there there may be complex reasons for the absence of either species in the Caribbean. If Lepidochelys originated in western Mexico, the colonization of the Pacific coast of Central America would surely have been an early step. Much evidence suggests that, until the uppermost Cenozoic, Central America was not continuous but was a series of large islands. Under these circumstances it is hard to see why the Caribbean was not invaded.

The answer may lie in the diet of the ridleys. On the Pacific coast of the Americas, ridleys subsist mostly on shrimp, and to a lesser extent on other crustaceans. In the Atlantic area the best shrimp grounds are associated with the estuaries of large rivers; brackish water is necessary for certain stages of the development of young shrimp. In the Atlantic the distribution of olivacea closely follows the distribution of good estuarine situations. The rain forests of West Africa are drained by many large rivers, and ridleys feed and nest in large numbers along the tropical West African coast. The predominantly savanna and scrub country of East Africa on the other hand does not contribute to large estuarine situations, and the genus Lepidochelys is represented by precisely four recorded specimens in East African waters. On the other hand, across the Indian Ocean, the huge delta of the Irrawady is frequented by large numbers of ridleys; Smith (1931) mentions an annual harvest of 1,500,000 olivacea eggs in this area.

In the West Atlantic, feeding and nesting grounds of the ridley are associated with the estuaries of the giant rivers - the Amazon, the Oyapoque, the Marowijne, the Corantijn, and the Essequibo, and with those of a host of lesser ones. In the Caribbean there are no ridleys at all - except in the extreme south-east, where they are possibly quite abundant, and where there is a huge estuarine situation, the mouth of the Orinoco. The Caribbean Islands, and most of

the mainland, have numerous small rivers, but no really big ones that create the extensive brackish water areas suitable for shrimp development.

In the Gulf of Mexico large brackish water situations are again encountered - for example the Mississippi mouth and Florida Bay; and again we find ridleys. Here, however, they are the big-jawed kempi species, which has apparently developed many head and jaw specializations towards a hard-shelled diet. Shrimp are present in large numbers in the Gulf of Mexico at present, but perhaps this was not always so, as crabs and molluscs make up the greater part of the diet of L.kempi.

Sea turtles of other genera, notably Chelonia, make migrations from good feeding grounds to suitable nesting beaches, which may be thousands of miles away and in an area entirely without supplies of their normal food. The reason for this is that green turtles are vegetarian, and graze on the extensive submarine pastures of "turtle-grass" that grow mainly in shallow, protected waters. Good nesting beaches, however, have a steep shelf a little above the high tide mark, so that the turtle can reach a point well above the reach of the highest tide without having to move too far from the sea. Such beaches are associated with moderately strong wave action, and thus tend to be distant from the calm-water feeding grounds. Consequently green turtles frequently have to make a deliberate migration from point A to point B, rather than a mere convergence towards

a good nesting beach somewhere in the middle of the feeding range.

The ridleys, however, can exploit a greater variety of beach types than the green turtles; being small, a long overland walk does not exhaust them, and because they dig shallow nests, they do not have to nest as far above high tide as green turtles. Moreover, their crustacean food is often extremely abundant in the general vicinity of the nesting beaches. On the other hand, I have postulated above a possible advantage to ridley populations that undergo extensive predation from terrestrial animals on the nesting beaches in forming huge nesting aggregations (arribadas) to overwhelm predators with a temporary overabundance of food. Consequently movements will occur; but they will be more in the nature of a convergence from extremes of the feeding range towards a suitable beach within those extremes, rather than a uni-directional shift from the feeding ground at point A to the breeding ground at point B. The only two sites of aggregated nesting from which some tagged females have been recovered (Bilanti and Rancho Nuevo) do reveal just such a pattern; turtles swim to the left or to the right on reaching the sea after nesting, with comparable frequency.

I have suggested above that the isolated population in the Gulf of Mexico was derived from the East Pacific L. olivacea population by a trans-Tehuantepec migration towards the end of the Mesozoic. If this were so kermi would be

expected to show greater similarity to the East Pacific olivacea population than to the zoogeographically more remote olivacea populations in the South Atlantic. It has been shown above that this holds true for the numbers of carapace laminae. The plots of numbers of left and right costal laminae and of central laminae given earlier show that the East Pacific population is almost exactly intermediate between the Gulf of Mexico and the South Atlantic populations in these respects. Another point of agreement is the sharing of the peculiar habit of forming huge, partially or completely diurnal arribadas by the Gulf and East Pacific populations of Lepidochelys (though the Eilanti, Surinam population does form small, entirely nocturnal arribadas).

For completeness, three other logical possibilities for the establishment of the two species of Lepidochelys should be mentioned:

i) The original population was that of L.kempi in the Gulf of Mexico, and that the East Pacific was colonized by turtles passing south through the Tehuantepec Strait in the late Mesozoic.

ii) The Gulf population (kempi) was derived from the South Atlantic olivacea population by trans-Caribbean migration.

iii) The South Atlantic, and later the Indo-Pacific, olivacea populations were derived from kempi by an eastward trans-Caribbean migration.

I consider the first of these unlikely, partly because of the present nesting range of kempi; if the species could cross Tehuantepec, why has it not extended beyond Tehuantepec on the Gulf side? Also kempi appears to be a more specialized species than olivacea, in particular in the structure of the head and the sides of the carapace.

I reject the second possibility, partly because, as has been shown, the Gulf and South Atlantic populations represent the extremes of variation in certain characters (e.g. carapace lamina counts), partly because there is no reason to assume that the Caribbean was once a more suitable habitat for ridleys than it is now; and if it had been, the alteration would probably have been gradual enough for the turtles to adapt to a different food source, or to whatever other different conditions that developed to make the area anathematic to modern ridleys.

The third possibility has both of these weaknesses, with the added defect that the prevailing current would oppose such a migration.

Finally, I should make some statement as to whether my morphological studies of Lepidochelys alter or confirm the present taxonomic status of the forms included in that genus.

My conclusion is that L.kempi and L.olivacea should be considered full species, while there is no evidence to suggest that either species has valid subspecies. Owing

to the peculiar reproductive isolation of even neighboring populations of sea turtles, we have to rely on rather subjective morphological criteria for deciding what constitutes a species, and what a subspecies. I feel that kempi should be maintained as a full species because several of its characters show no overlap with those of olivacea, within the limitations of our sample size, while others show only slight overlap. In the first category we include relative vertical height of the orbit, relative width of the skull, and presence of bony ridges on the alveolar surfaces. In the latter category we include relative width of the pterygoid bridge, relative width of the carapace, numbers of central and costal laminae, and shape of the mid-marginal and supracaudal laminae.

On the other hand, the statistical differences between even the extreme olivacea populations do not justify even subspecific recognition. The South Atlantic and Indian Ocean populations are certainly more similar to each other than to that of the East Pacific, but even the latter is differentiated by little more than a slightly lower average hatchling and adult size, and slightly lower average costal and central lamina counts. While it would probably be possible to allocate correctly a series of ten adults from either population, if the series were truly random, no individual turtle could be conclusively allocated on morphological grounds alone to any of the Lepidochelys olivacea populations studied.

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This dissertation was prepared under the direction of the chairman of the candidate's supervisory committee and has been approved by all members of that committee. It was submitted to the Dean of the College of Arts and Sciences and to the Graduate Council, and was approved as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

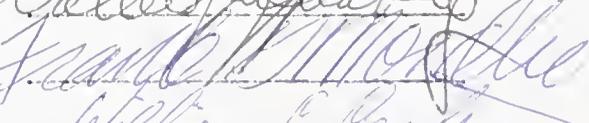
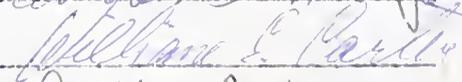
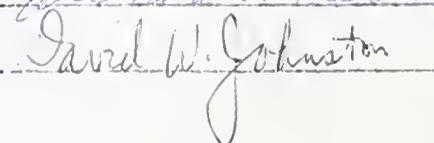
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