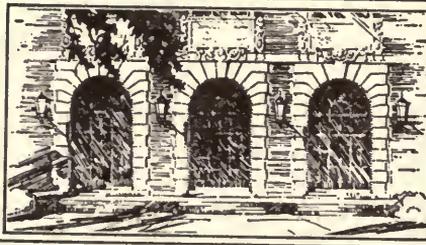


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A New Specimen of *Desmatochelys lowi* Williston A Primitive Cheloniid Sea Turtle From the Cretaceous of South Dakota

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In 1953, in the course of stripping overburden from the Dakota Rose Granite quarry in the Milbank-Ortonville granite district in eastern South Dakota and western Minnesota, a Cretaceous marine vertebrate fauna was found. The quarry is located in Grant County, South Dakota (SW. $\frac{1}{4}$, Sec. 18, T. 120 N., R. 47 W.), and is operated by the Dakota Granite Company, Milbank, South Dakota.

The fossils were found in an arkosic chalky marl that was deposited on top of the early Precambrian Ortonville granite described in detail by E. H. Lund (1956). The depositional environment of the Cretaceous sediment was a marine boulder beach on one of a series of islands in the Milbank-Ortonville area on the west flank of the Sioux Arch. The Cretaceous sediment is thin, not over five feet in thickness, and varies greatly from place to place. The granite surface was deeply weathered prior to the transgression of the Cretaceous sea from the west. Joint cracks were enlarged and widened by weathering to notches 3-4 feet wide and as deep, and were filled with the arkosic sediments as the seas transgressed over the islands, eventually submerging them. Resting directly on the granite is a basal, marine beach boulder conglomerate with the maximum diameter of the boulders about eight feet (average diameter about two feet). The boulders are all well rounded and are composed of the underlying granite. Finer sediments from coarse sands to marls are found between and above the boulders. Large angular fragments of orthoclase feldspar and quartz derived from the underlying granite are common in these sediments, in places amounting to 50 per cent

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of the sediment, particularly in the widened joint cracks. Sharks' teeth and small teleost vertebrae are sufficiently abundant in some places to make up a significant proportion of the rock, up to about 5 per cent. The clay component of the marl seems to be a kaolinitic weathering residuum of the granite similar to that described by Goldich (1938) from the vicinity of Redwood Falls, Minnesota. Thiel (1944) reports similar material to be common, as the basal Cretaceous sediment, where Cretaceous rocks rest on granite in southwestern Minnesota.

The surfaces of the exposures have been glacially scoured and the finer-grained Cretaceous sediments are to be found only on the lee side of the beach boulders, in the widened joint cracks, or in other protected areas.

Similar Cretaceous sediments, most exposures of which contained sharks' teeth and small teleost vertebrae, were found at the Cold Spring Granite Company quarry, one-fourth of a mile west of the Dakota Rose quarry (SE. $\frac{1}{4}$, Sec. 13, T. 120 N., R. 48 W.), in Grant County; the Melrose Granite Company quarry and the D. G. Kaddez and Company quarry (NE. $\frac{1}{4}$, Sec. 17, T. 120 N., R. 47 W.), in Grant County, South Dakota; and in the series of quarries and outcrops 3 miles north of the town of Bellingham in Lac Qui Parle County, Minnesota (fig. 2). Any Cretaceous sediments in the other active quarries in the area or at other outcrops were removed at some time prior to the deposition of the glacial drift.

Five miles west of the granite outcrops, in Milbank, a well reported by the South Dakota Geological Survey (Petsch, 1948) penetrated 41 feet of glacial drift, 188 feet of Carlile shale, 43 feet of Greenhorn limestone and at least 43 feet of Graneros shale. The Milbank-Ortonville granite area was a topographic high during early Cretaceous time, as shown by geophysical studies of the surface of the granite by the South Dakota Geological Survey. In Cretaceous sediments, very slight dips prevail throughout the area of outcrop in southwestern Minnesota, and the only form of deformation recorded is that due to compaction. These facts and the elevations of the outcrops in the Milbank-Ortonville granite district suggest a correlation of the conglomerate and arkosic marl of the latter area with the Carlile shale, the upper formation of the Benton Group.

FAUNA

Teeth of a small species of the shark genus *Isurus* are the most common fossils; next in abundance are the teeth of another shark,

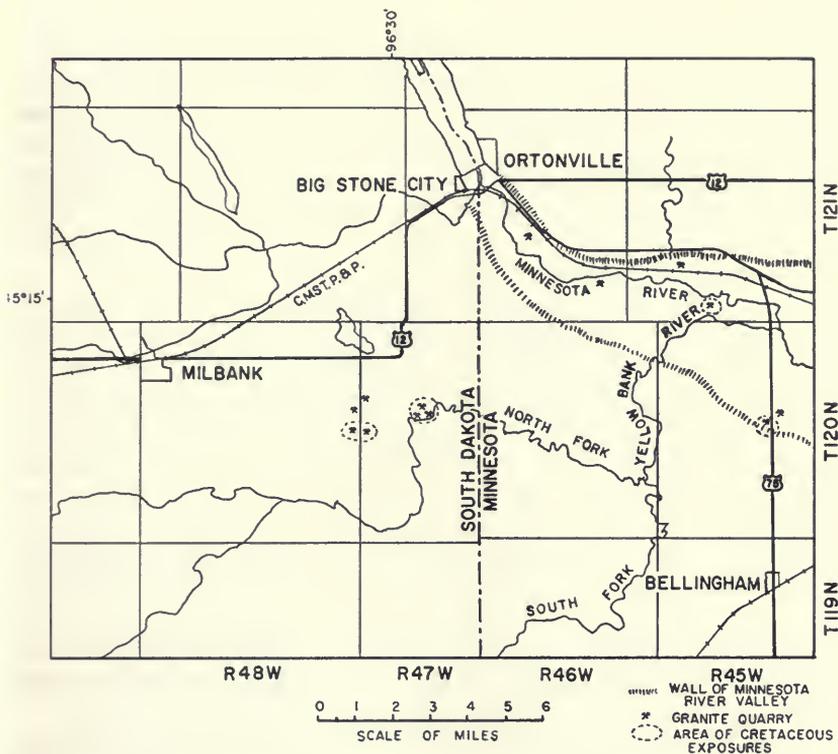


FIG. 2. Map of Milbank-Ortonville granite district in eastern South Dakota and western Minnesota.

Squalicorax. Those of the ptychodont shark *Ptychodus janewayii* are rare. Isolated vertebrae of small clupeoid fishes are very numerous and a species of *Ichthyodectes* is present. Teleost fish scales up to an inch in diameter are fairly common. A few amphiplatyan vertebral centra (possibly plesiosaurian) and isolated reptile teeth have been collected. The most important reptile remains so far discovered is a large portion of the skeleton of a marine turtle, *Desmatochelys lowi* Williston, which will be described below. Pyritized microfossils and carbonized scraps of gymnosperm wood are relatively abundant.

CIRCUMSTANCES OF COLLECTION OF THE TURTLE SKELETON

In the process of stripping the overburden off the top of the granite quarry the turtle skeleton was exposed among rubble loosened by

explosives. Several pieces of sediment containing bones were collected by personnel of the Museum of the South Dakota School of Mines, Rapid City. Another piece found its way into a bar in Ortonville, Minnesota, where it was handed to Dr. Lloyd A. Wilford of the Department of Anthropology, University of Minnesota, who in turn brought it to the attention of the junior author. The late Dr. James D. Bump kindly gave us the pieces in the collection of the South Dakota School of Mines and permitted deposition of the specimen at Chicago Natural History Museum.

The pieces thus reunited fit together perfectly, but part of the skeleton was evidently lost in the blast and some damage has been inflicted on the parts that have been recovered. As preparation of the skeleton neared completion, it became possible to identify the turtle as *Desmatochelys lowi* Williston, originally described from the Benton Group near Fairbury, Nebraska. The bones of the type material of this species are crushed to some extent, whereas the new skeleton is not. For this reason numerous minor differences may be noted between the two specimens, but these reflect, we feel confident, mostly differences in the preservation of the bones. The identification is further strengthened by the similar stratigraphic position of the finds and the fact that the new material cannot be placed in any other group of Cretaceous sea turtles, such as the Protostegidae, the Toxochelyidae or the other members of the Cheloniidae.

Since *Desmatochelys lowi* is inadequately known, the description of the new find substantially increases our knowledge of this form and sheds new light on the question of origin of the sea turtles during Cretaceous time.

Order Chelonia

Suborder Cryptodira

Family Cheloniidae

Desmatochelys lowi Williston

Referred material.—CNHM-PR385, a partial skeleton, lacking most of the skull and the posterior part of the shell.

Locality and horizon.—Cretaceous overburden on top of Dakota Rose Granite quarry (SW. $\frac{1}{4}$, Sec. 18, T. 120 N., R. 47 W.), Grant County, South Dakota. Near top of Benton Group, probably Carlile shale equivalent.

Description.—1. The skull: Only a single skull element, the right postorbital bone, was recovered. It is essentially complete except for

most of the posterior rim (fig. 3), of which only a very small section next to the suture with the parietal was preserved. This, however, shows the position of the posterior edge of the skull roof, very deeply excavated at this point in *Desmatochelys* (Williston, 1894, 1898).

As nearly as can be determined from Williston's illustration, the postorbital bone of the present specimen is virtually identical with

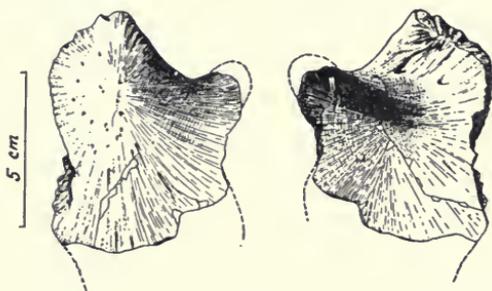


FIG. 3. *Desmatochelys lowi* (CNHM-PR385), postorbital bone in dorsal (left) and ventral (right) views.

that of the type specimen, even including the slight curve in the course of the parieto-postorbital suture.

Williston illustrated both the dorsal and palatal views of the skull; these are correct except for a few details.¹ The lateral aspect of the skull of the type specimen (fig. 4) shows an unusual development of the cheek bones with a very prominent quadratojugal and a jugal restricted in its dorsal extent to the lower margin of the orbit.

¹Dr. Theodore H. Eaton, Jr., has kindly examined the skull of the type specimen of *Desmatochelys lowi* and has rendered drawings (fig. 4). We wish to express our sincere gratitude to Dr. Eaton for his meticulous re-examination; with his kind permission we quote from his account: "The dorsal view is traced over Williston's (1894) pl. II, which is mainly correct except for minor differences in the sutures (esp. prefrontal) and the length of the occipital spine. His palatal view (pl. III) I have not redrawn; it is correct as far as it goes, but there is in addition a median suture separating the pterygoids as well as the palatines, and the vomer comes back to a point almost half the distance between the choanae and the transverse suture. With more preparation the posterior part of the cranium would give many details of value, although a hole $\frac{1}{2}$ inch in diameter has been drilled vertically up into the basicranial region. The actual length of the skull to the point where the occipital spine is broken off is 215 mm., not 205, and its probable length when complete would be about 240. The scale of figs. II and III is approximately $\frac{3}{4}$ rather than $\frac{2}{3}$."

"In lateral view the squamosal, quadratojugal and jugal are plainly visible. The quadratojugal reaches the margin of the orbit on the right side but does not quite do so on the left. In the articular region on both sides there is some doubt, because the quadrate seems to have been pushed up and what was probably an oval tympanic cavity is a narrow slit, as shown. I think the sutures are correct, as given, but possibly one or two of them are cracks."

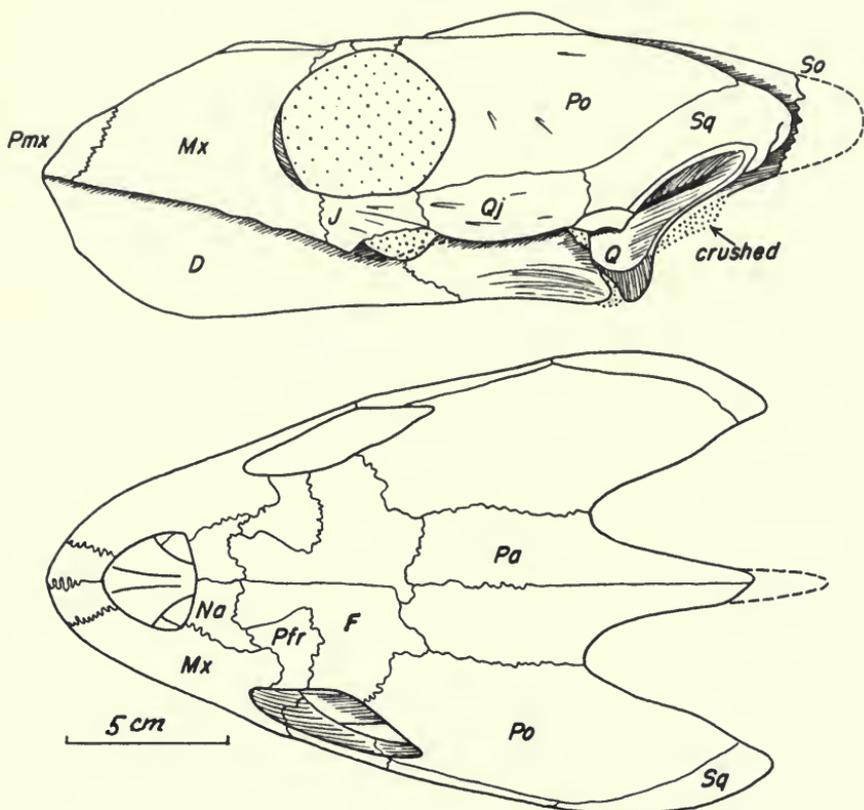


FIG. 4. Sketch of skull of *Desmatochelys lowi*, type specimen, in dorsal and side views (sketch kindly provided by Dr. Theodore H. Eaton, Jr.; see also comments in footnote, p. 11).

2. Vertebral column: Of the neck vertebrae the arches of the atlas and the major portions of the fourth and sixth through the eighth are preserved (pls. 1 and 2). The most striking feature of these cervical vertebrae is their shortness compared to those of all other known sea turtles, with the possible exception of the protostegids (fig. 5). Aside from the fact that vertebrae 6 to 8 were articulated with the shell vertebrae in the matrix prior to preparation, the overall morphology of these elements is sufficiently similar to that of the modern sea turtles to permit the determination of the numerical position within the neck region. In almost every detail, however, there are obvious differences. The articulation pattern of the vertebral centra agrees with the common condition in the Derma-

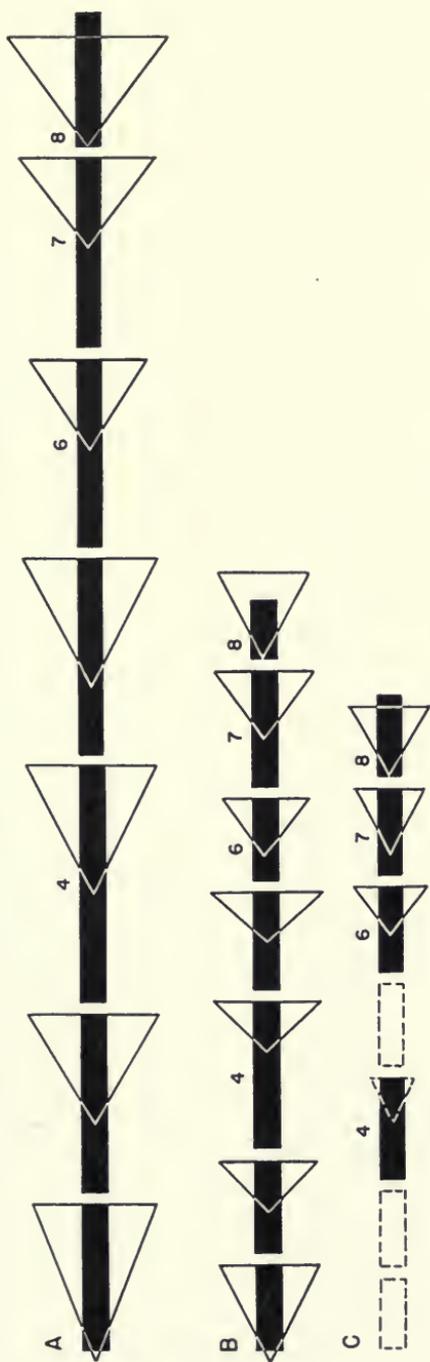


FIG. 5. Relative length and vertebral proportions of cervical column. A, *Chelydra serpentina* (Z 21); B, *Caretta caretta* (CNHM 31023); C, *Desmatocheilus loui* (CNHM-PR385). The measurements were based on the length of the centrum of the third shell vertebra in each form (=100).

temydidæ and the Chelydridæ (Williams, 1950) and the normal condition in the Toxochelyidæ (Zangerl, 1953) as follows:

3 (,4, 5 ,)6,)7,)8)

This condition occurs relatively rarely in modern cheloniine sea turtles.

The atlas arches compare quite well with those of *Caretta* except that the postero-lateral processes are sharply set off from those portions of the arches that are attached to the atlas centrum; in *Caretta* the two areas are connected with a sheet of bone. Furthermore, the antero-dorsal processes are relatively higher than in *Caretta* and the facets of the postzygapophyses are round instead of oval as in the compared genus. The latter difference probably reflects the relative shortness of these elements.

The fourth vertebra is very short and possesses a weak neuropophysis whose suture with the centrum lies above the transverse processes. A pair of low ridges not present in *Caretta* connects the lateral edges of the prezygapophyses with the base of the postzygapophyses. Two shallow pits are located medial to the mentioned ridges and these appear to have served as areas of attachment for muscles or ligaments (pl. 1, fig. d); comparable pits are only vaguely indicated in *Caretta*. Vertebrae 6, 7, and 8 differ notably from those in *Caretta*, but this is largely due, we think, to the fact that the articulation of the centra is of the normal and very probably primitive ball-and-socket type rather than the transversally expanded, flat-jointed (between centra 6 and 7), or double-jointed (between 7 and 8) condition that constitutes the norm in modern sea turtles. The greater range of movability that exists between these vertebrae in *Desmatochelys* (and the shortness of the elements; see above) may be reflected in the details of differentiation of the neural arches as compared with the condition in modern sea turtles. The postzygapophyses of vertebra 6 are separated by a deep, acute, V-shaped notch with near-vertical walls descending to the neural canal. In *Caretta* (see pl. 31, B Zangerl, 1960) this area is flat and the notch is shallow. The postzygapophyseal joint surfaces of vertebra 8 face strongly postero-dorsad and laterad (pl. 1, fig. g).

In *Caretta* the transverse processes of vertebrae 6, 7 and 8 tend to divide into dual processes, the upper, small one being located at the base of the prezygapophyses. These smaller, dorsal processes are absent in *Desmatochelys*.

The major proportions of the neck vertebrae as graphically presented in figure 5 show clearly primitive relations in vertebra 8,

where the centrum is not significantly shortened, as in modern sea turtles, and where the neurapophysis is shorter than the centrum, as in *Chelydra*; in Recent sea turtles and in toxochelyids (Zangerl, 1953) it is longer.

There are other peculiarities in this element. The hypapophysis is not a single ventral sheet of bone as it is in the anterior neck vertebrae and in all the cervicals (save the atlas centrum) of *Caretta*; instead there are two sharp, longitudinal ridges, diverging slightly in posterior direction, along the mid-ventral face of the centrum (pl. 2, fig. *g*). A similar condition of the hypapophysis of the eighth cervical vertebra is present in *Dermochelys* (Völker, 1913, pl. 31). The postzygapophyses, with their characteristic dorsal projection that articulates with a knob on the under side of the nuchal plate in modern and some fossil sea turtles, are less expanded but higher than in *Caretta*. This seems to be correlated with the lack of a nuchal knob in *Desmatochelys*, and with the fact that in this form the eighth vertebra continues the gentle curve formed by the shell vertebrae from the apex of the carapace forward, instead of forming a pronounced angle, in side view, with the first shell vertebra. These features indicate that the neck of *Desmatochelys* was even less retractable than that of modern sea turtles.

The anterior seven shell vertebrae are preserved in articulation with the carapace (fig. 6). The centra are of the normal cheloniine construction, ventrally rounded rather than angular and provided (near mid-length and close to the dorsal border) with small foramina for the exits of the spinal nerves, as in modern cheloniines. The third centrum is the longest. The centrum of the first vertebra resembles, particularly in ventral aspect, the succeeding centra; the anterior, procoelous end faces straight forward, rather than forward and downward as in modern cheloniines (see also discussion of eighth cervical vertebra). The reduced ribs (first pair of shell ribs) are relatively longer than in cheloniines and are only distally attached to the antero-ventral face of the first pair of costal plates; apparently there was no proximal connection with the free ends of the second shell ribs. The neurapophyses form a continuous sagittal ridge along the ventral faces of the neural plates from the second one backward; the neurapophysis of the first shell vertebra is modified and has a long, relatively thick dorsal spine, connected to the anterior end of the first neural plate by connective tissue only. Posteriorly it is suturally connected with the second neurapophysis. The prezygapophyses are strongly developed. The first neural plate is suturally connected to the neurapophysis of the second shell vertebra (figs. 6 and 8). All

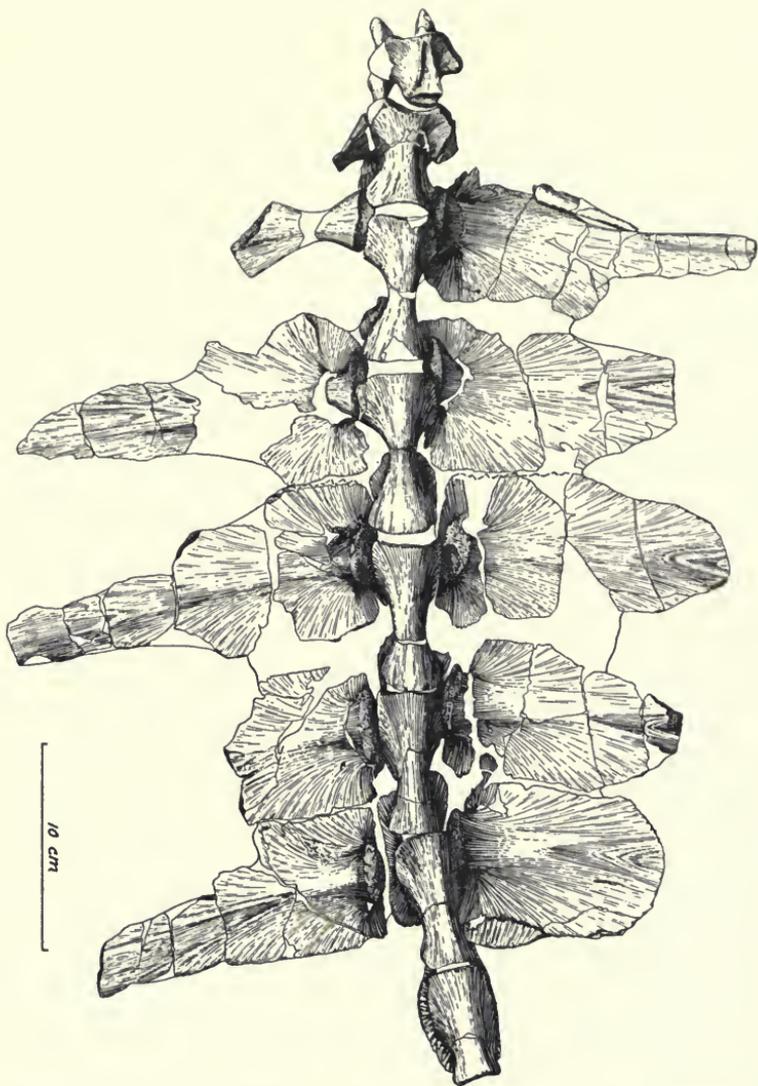


FIG. 6. *Desmatochelys lowi* (CNHM-PR385), last cervical vertebra and under side of articulated part of carapace.

this differs from the situation in modern cheloniid turtles in but minor details.

3. The carapace: The carapace is elongated, but only vaguely cordiform. The antero-lateral margins above the forelimbs are some-

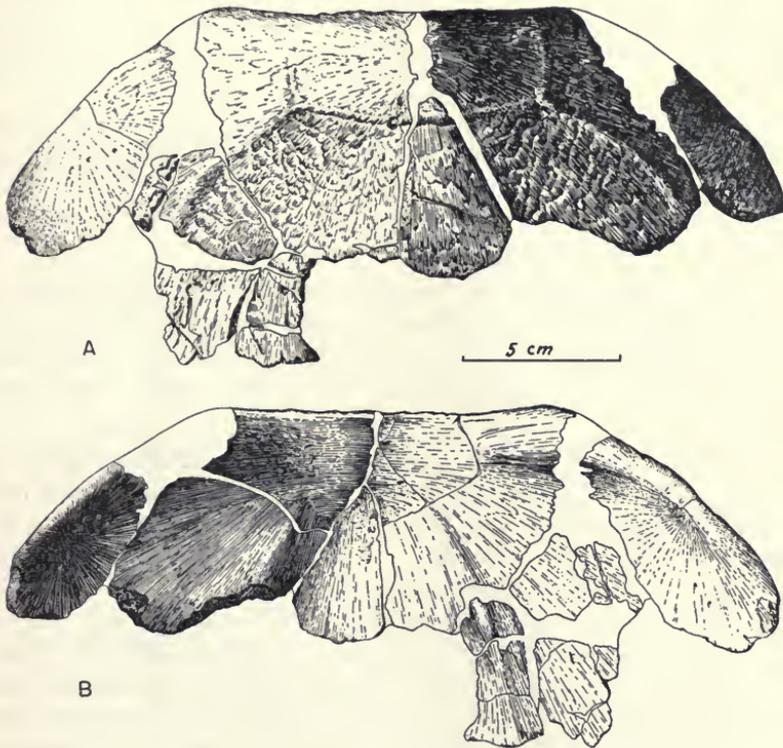


FIG. 7. *Desmatochelys lowi* (CNHM-PR385), nuchal plate and first peripherals. A, dorsal, and B, ventral views.

what excavated in typical sea turtle fashion. The nuchal margin is not incised. There are large lateral fontanelles extending from the peripherals about halfway to the midline and from the nuchal plate to the pygal. Postnuchal fontanelles are present also (fig. 13).

The nuchal plate (fig. 7) forms an obtuse-angled arch from side to side and lacks a mid-ventral boss. Near the midline it is quite thick (13.5 mm.) and gradually becomes thin toward the posterior margin, except for the usual thick ridges that run in the shape of a V back to the suture with the first pair of costal plates. The sutural connection with the first neural is very weak.

The anterior six neural plates (fig. 8) are long, unkeeled and fairly flat in front, and gently arched from side to side farther back. The first and second neurals are narrower than the following four, as sometimes in *Chelonia*. The first neural is broken, and part of its posterior half is crushed down upon the neurapophysis. Its anterolateral edges are extremely thin, which indicates the presence of postnuchal fontanelles. Posteriorly the first neural is about 5 mm. thick.

Five pairs of costal plates are retained in articulation (figs. 6 and 8); in addition there are fragments of the sixth and seventh and nearly the whole eighth (fig. 9) of the left side. The costal plates are flattened and slightly warped so that they could not be mounted in perfect sutural union.

The ribs beneath the costal plates are broad and flat and there is no sharp distal delimitation between costal plates and ribs much as in *Chelosphargis* among the protostegids (Zangerl, 1953) and a number of cheloniids. At the distal ends the ribs are subcircular in cross section.

The only peripherals (figs. 7 and 10) that are definitely determinable as to position in the carapace are the first pair, part of the right second in sutural connection with the third, and the posterior half of the left third. There remain six whole or partial elements whose positions are somewhat open to question. We have interpreted them as the eighth of the right side and 9, 10, and 11 of the left side (because of color differences in the matrix on the right and left sides of the skeleton). Williston (1894, 1898) figured the pygal and the right eleventh peripheral. His description of the latter corresponds generally with our eleventh peripheral except for a notable difference in width; this is almost certainly due to crushing in the type specimen.

The cross sections of the peripherals interpreted as posterior elements have the shape of airfoils, with the thicker edges facing the carapace disc and the blade-like sides forming the peripheral rim of the shell. Two broken elements are certainly bridge peripherals. They are triangular in cross section; the widest faces bear the rib pits.

The pattern of the epidermal shield cover is usually imprinted upon the bones of the shell by sulci formed at the junction of adjacent shields. In the specimen here described there are no sulci; instead, the shield boundaries are indicated by ridges (figs. 7 and 8) and are not equally visible in all parts of the carapace. The significance of this is not presently understood. The cervical shield is large as in modern cheloniines and the pattern as a whole (fig. 13), in so far

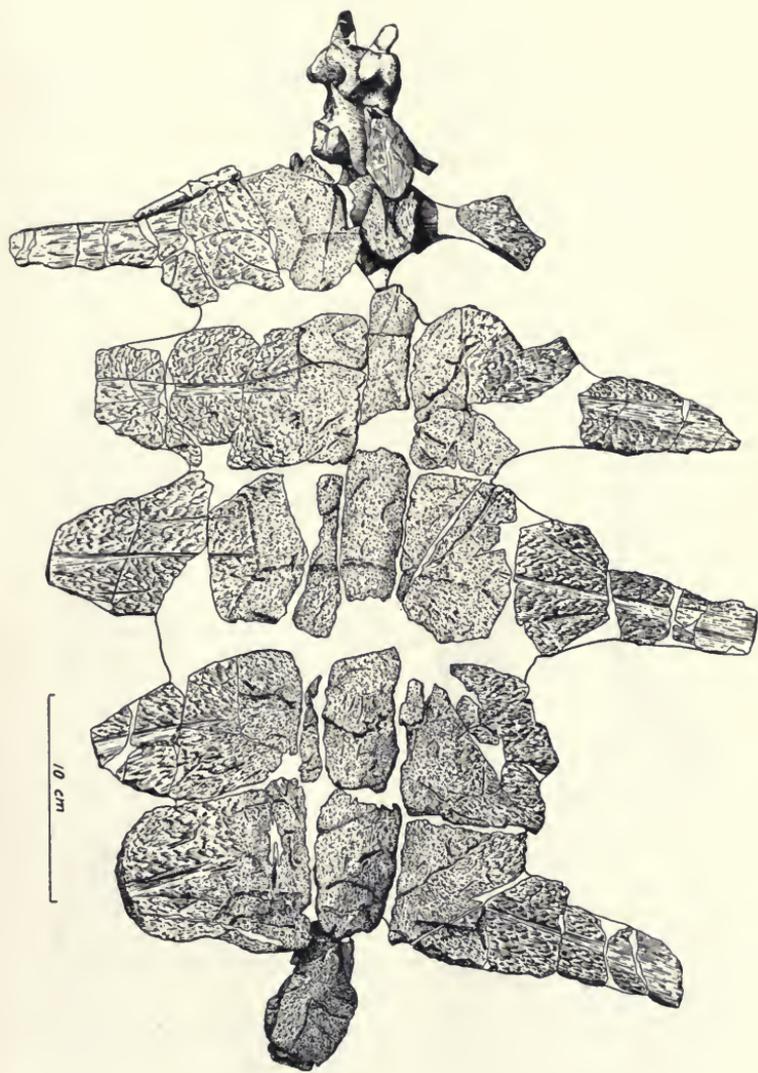


FIG. 8. *Desmatochelys lowi* (CNHM-PR385), last cervical vertebra and dorsal side of articulated part of carapace.

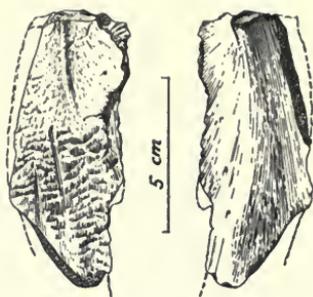


FIG. 9. *Desmatochelys lowi* (CNHM-PR385), eighth left costal plate in dorsal and ventral views.

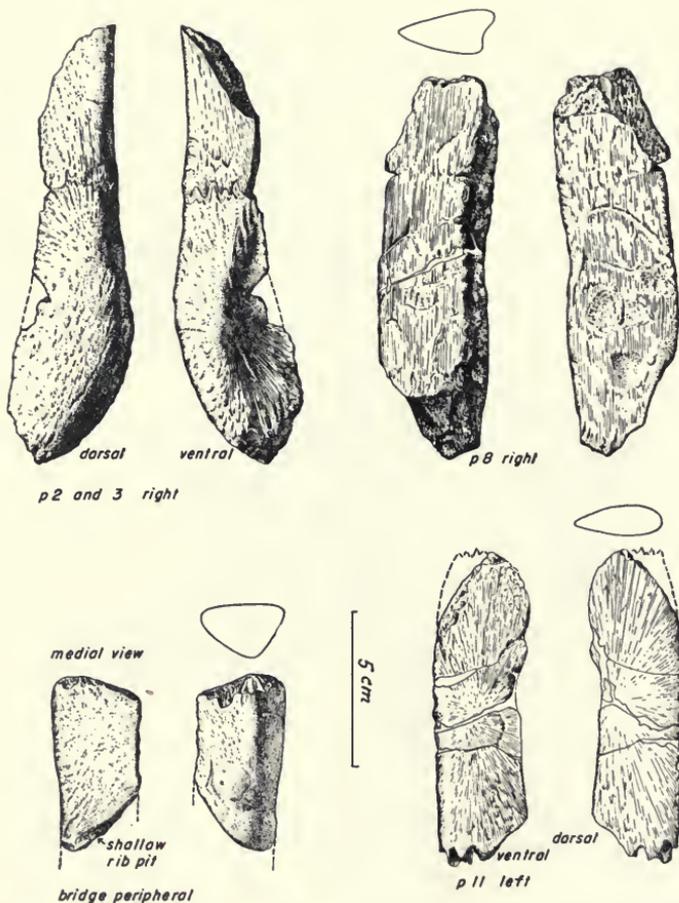


FIG. 10. *Desmatochelys lowi* (CNHM-PR385), isolated peripheral plates in dorsal and ventral views.

as can be determined, shows no unusual features; it conforms to that of the modern Chelonini (Zangerl, 1958) and all of the fossil cheloniids, toxochelyids and protostegids (Zangerl, 1953).

4. The plastron: The bones of the plastron are more fragmentary than those of the carapace. Most of the left epiplastron and part of

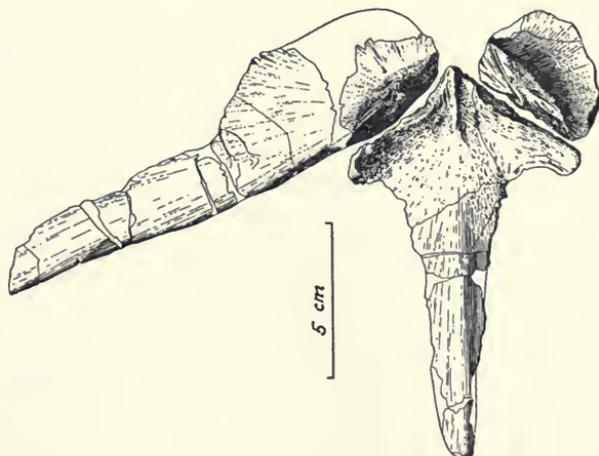


FIG. 11. *Desmatochelys lowi* (CNHM-PR385), epiplastron and entoplastron in dorsal view.

the right one, the entoplastron, and portions of the left hyo- and hypoplastra are preserved. All parts were pressed in more or less natural position onto the ventral side of the carapace, except the lateral fragments of the hyo- and hypoplastra, which were loose and had no matrix contact with the rest of the specimen. The xiphoplastra are missing.

Epi- and entoplastra present no problems (fig. 11). Hyo- and hypoplastra, on the other hand, are quite incompletely preserved, and the reconstruction (fig. 12), while it very probably represents the correct relationships, remains open to some doubt as far as the exact shapes of the plates are concerned. The loose fragment, readily identifiable as the central portion of the hypoplastron, unquestionably belongs to the medial fragment that was left in place. Its dorsal and ventral surfaces are clearly distinguishable and its curvature (ventrally convex from side to side) leaves no doubt that it belongs to the left side; its exact position with regard to the medial fragment, however, cannot actually be determined; figure 12 shows what we believe to be the most likely position.

The fragment here identified as part of the lateral wing of the left hyoplastron obviously presents greater difficulties. The position indicated in figure 12 conforms to the surface characteristics of the fragment, its thickness and its natural edges; apparently it cannot be placed anywhere else, but its exact position in the area indicated remains, of course, doubtful.

The plastron as presently interpreted (fig. 13) is clearly of cheloniid character with a plastral index (Zangerl, 1953 and 1958) estimated at about 105. The anterior plastral lobe is very short and blunt and there are large medial and lateral fontanelles.

The epiplastra are flat, blade-like bones anteriorly expanded and were suturally attached to the antero-lateral edges of the entoplastron. Prominent ridges follow the mentioned sutures along the dorsal faces of the bones (fig. 11). The entoplastron is approximately T-shaped; the lateral processes face outward and backward (fig. 11). The hyoplastron has a broad antero-medial and three clearly separated medial prongs; the preserved fragment is thin except near the center of the plate where it is 9 mm. thick. The lateral fragment measures 13 mm. in thickness along the break facing the center of the plate; its anterior margin is thick and crested; posteriorly its thickness is 7 mm. and the edge is blunt. The hypoplastron has three strong medial and an undeterminable number of smaller postero-medial prongs. The sutural notch for the union with the xiphoplastron is well developed (fig. 12). It reaches its greatest thickness, 13 mm., near the center of ossification.

5. Shoulder girdle: The left half of the shoulder girdle is perfectly preserved in uncrushed condition; on the right side parts of the bones are missing. The scapula (fig. 14) is remarkable in that its dorsal and ventral processes are of nearly equal length as in *Corsochelys* (Zangerl, 1960) and in *Dermochelys coriacea*. The two processes stand at an angle of about 103° to each other, a much wider angle than in the type specimen (88°) (see Williston, 1894, 1898). From Williston's figure it is evident that the type scapula suffered crushing—a process that might well have reduced the value of the angle. The scapula is a relatively heavy bone, not nearly as much flattened in antero-posterior direction as in modern cheloniines. The coracoid (fig. 15) is long, slender and only moderately expanded at its posterior end. There is a very close resemblance between this bone and its homologue in *Eretmochelys*. The bone labeled coracoid by Williston seems to be a badly crushed proximal fragment.

6. Humerus and flipper: The proximal half of the left humerus was articulated with the scapula; the distal end was broken off in

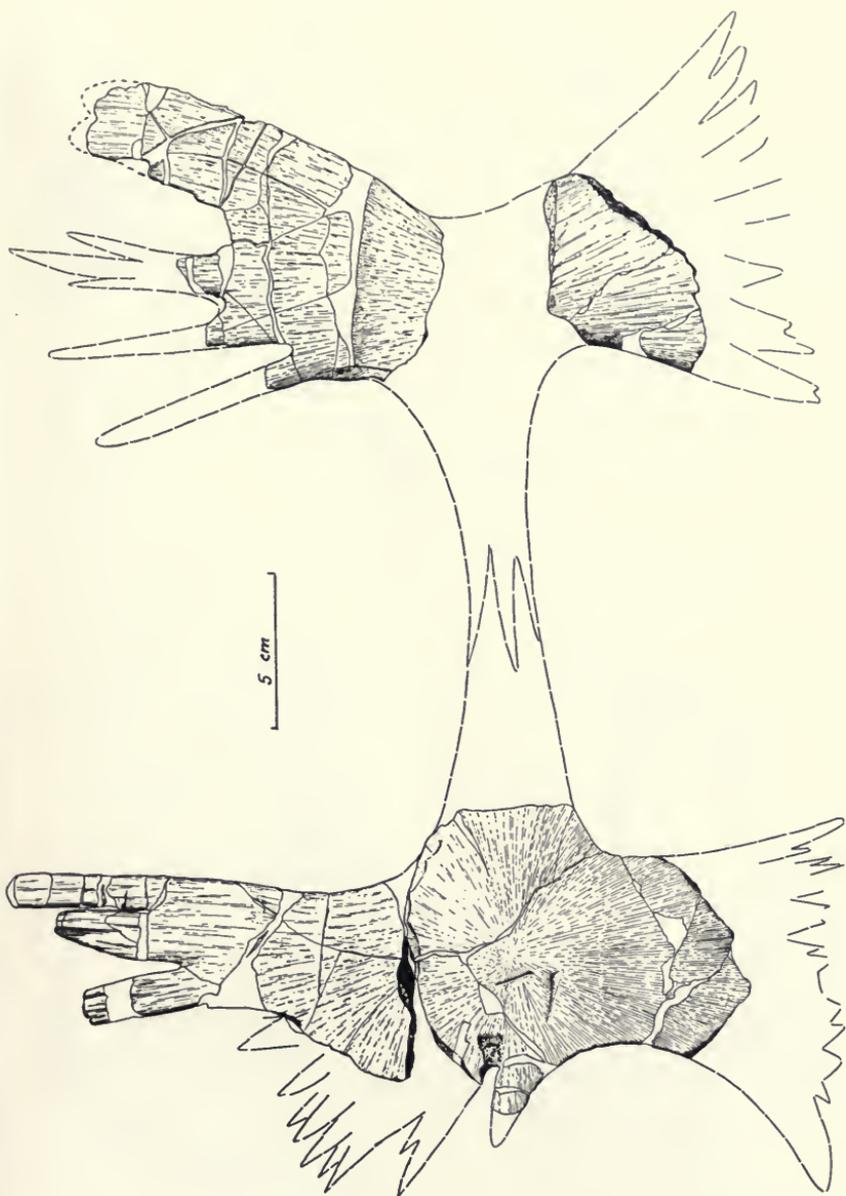


FIG. 12. *Desmatochelys lowi* (CNHM-PR385), parts of hyo- and hypoplastron of left side in ventral view.

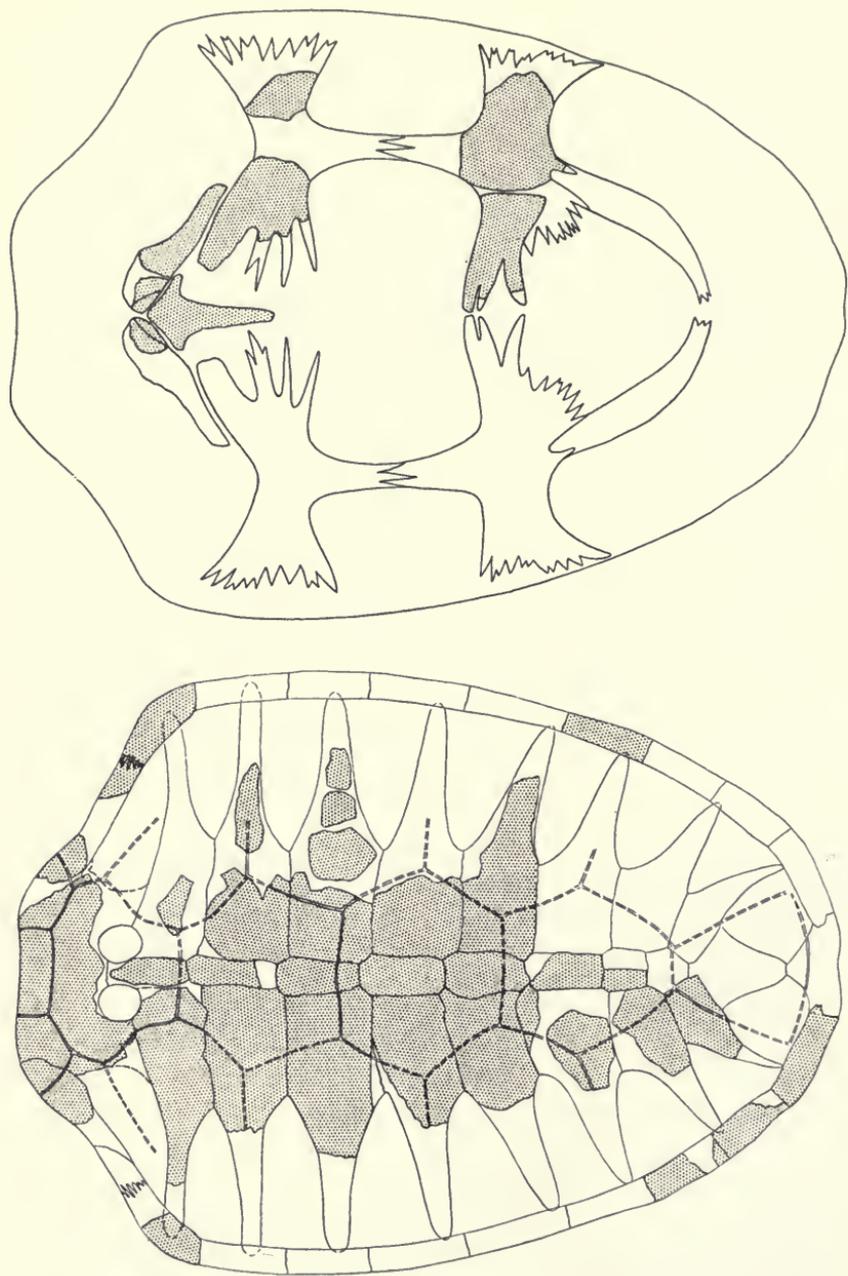


FIG. 13. *Desmatocheilus lovi*, reconstruction of carapace and plastron (based mostly on specimen CNHM-PR385).

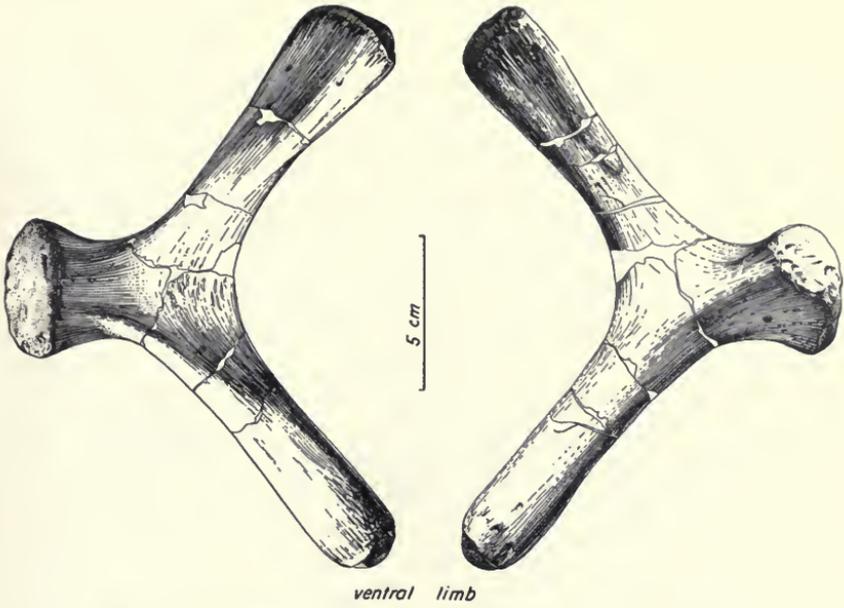


FIG. 14. *Desmatochelys lowi* (CNHM-PR385), left scapula.

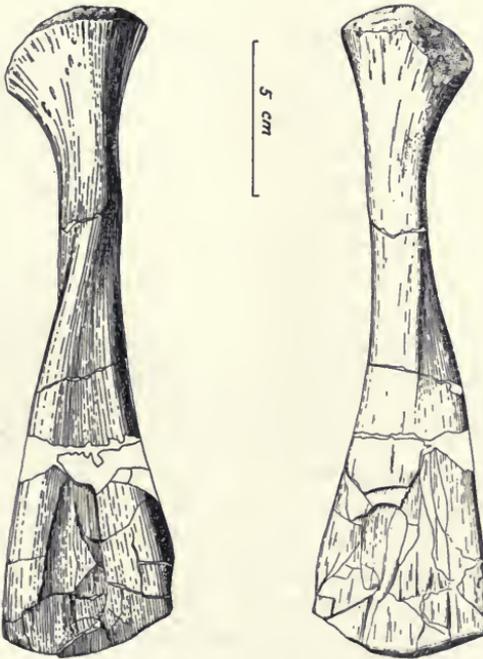


FIG. 15. *Desmatochelys lowi* (CNHM-PR385), left coracoid.

the blasting operation and a small portion of the shaft was lost. In the right humerus a larger portion of the shaft was lost. In the left humerus the two portions were united according to the dimensions of the break surfaces and the surface configuration and we feel confident that the length of the bone and the position of the distal versus the proximal ends are very nearly correct (fig. 16). Comparison of the present material with the type specimen (Williston, 1898, pl. 75) shows very notable differences, which are, however, not necessarily of a systematic nature. The type humerus is obviously flattened by severe crushing, the ends more so than the middle of the shaft, which consists of denser bone. Accordingly, the ends, especially the proximal half of the bone, are spread in the plane in which the bone was preserved and thus give the impression of far greater massiveness than was true in life. Besides differences clearly due to preservation there are others that indicate a difference in the individual ages of the two specimens; these are the same differences that can be observed, for example, in the humeri of mature and very old individuals of modern cheloniines: in the latter we observe full osteogenetic differentiation with very pronounced, rough muscle attachment scars and ridges, a long ulnar process lacking an area occupied by a cartilage cap, an ectepicondylar canal entirely enclosed by bone, and the distal end surface devoid of a cartilage cap except for a thin layer covering the actual joint surface. Accordingly, the new specimen must have been somewhat younger than the type specimen.

Taking these factors into account, we may characterize the humerus as follows: It is massive and stout, provided with a very pronounced ulnar and an unusually big radial tuberosity. This large proximal region is followed by a short, slender shaft and a normally expanded, but unusually thick (32 mm. in the present specimen) distal end (fig. 16; Williston, 1898, pl. 75). The degree of marine specialization (angles α and β , Zangerl, 1953, p. 165) of the humerus falls in the range of modern cheloniine sea turtles. Since the shaft is very short, the radial tuberosity lies close to mid-length between caput humeri and distal joint surface; in its position it is thus intermediate between the condition in modern cheloniines and that in the protostegids. The attachment surface of the radial tuberosity is an equilateral, triangular area (fig. 16); it contains a pit of "finished" bone surface that is located near the dorsal side of the triangle. In cheloniine turtles the radial tuberosity forms a V-shaped attachment ridge with the apex of the V pointing toward the caput. The pit within the triangular area in *Desmatochelys* thus corresponds to the depression between the limbs of the V-shaped ridge in cheloniines. The

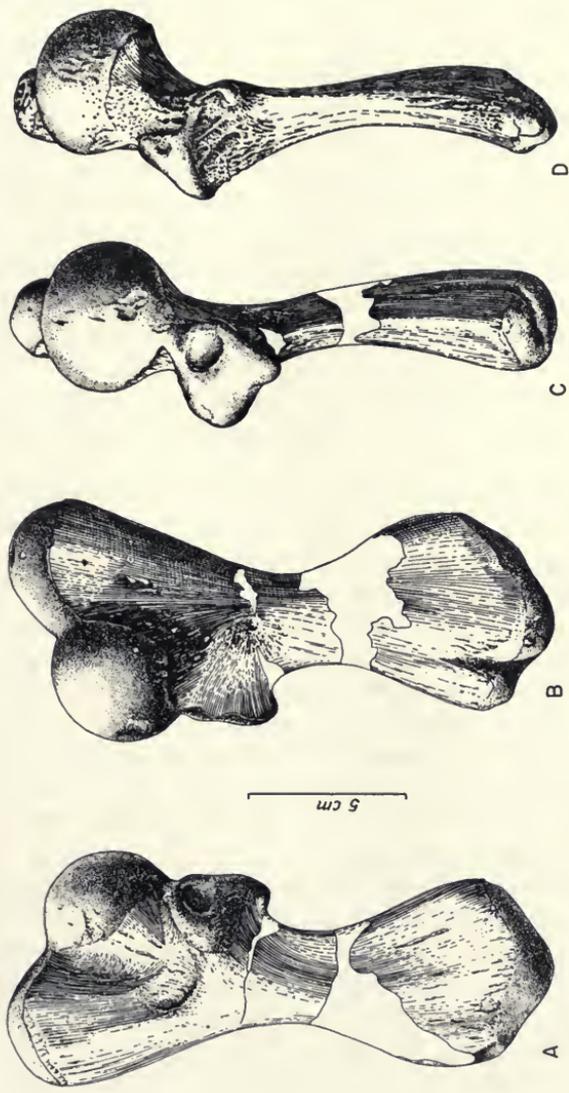


FIG. 16. Views of left humerus of *Desmatochelys lowi* (CNHM-PR385): A, ventral; B, dorsal; C, anterior. D, anterior view of left humerus of *Caretta caretta* (CNHM 31023).

joint surface of the caput humeri is nearly hemispherical, more extensive than in cheloniines, and this indicates, in conjunction with the more pronounced radial tuberosity, that the flipper was capable of greater axial rotation in this form than in modern cheloniines. A steeper forward incline of the flipper surface during the downstroke would result in quicker acceleration.

A fair portion of the right flipper was preserved very nearly in proper articulation (fig. 17). The carpal elements were not entirely freed from matrix because of negative surfaces in the matrix that indicate the position of elements that have been lost, and because it seemed advisable to retain the relative position of the carpal elements as preserved. Part of the shaft of the radius and the distal ends of metacarpals IV and V are missing, but the missing portions were present as negatives in the matrix and could thus be accurately cast in plaster. Of the right ulna only the proximal end is available; the other end is indicated by a matrix imprint on the proximal side of the intermedium. Only the distal portion of the ulnare was preserved.

The radius is relatively long (figs. 17 and 22), notably curved, distally expanded and less angular in cross section than is the case in modern cheloniines. There is, furthermore, no distal contact rugosity by means of which the radius was attached to the ulna in the characteristic fashion of modern cheloniines. The shape of the ulna can only be described in general terms based mostly on indirect evidence. Combination of the right proximal fragment with the left shaft fragment and the matrix imprint of the distal end suggests that the ulna was notably curved and somewhat flattened in dorso-ventral direction. Its distal end was reconstructed (fig. 18) in an unexpected fashion because of the nature of the carpus, which seems to suggest the presence of such a peculiarity.

In the carpus, as preserved (fig. 17), there are two larger proximal elements as in all sea turtles, the intermedium and the ulnare. The intermedium is entirely preserved; the ulnare lacks the proximal end. In modern cheloniines both intermedium and ulnare are notably elongated bones (see Zangerl, 1958, fig. 13). In *Desmatochelys* the intermedium is short, about as long as wide; in shape it agrees fairly closely with the distal half of its homologue in Recent cheloniines. An intermedium of virtually identical shape is present in *Corsochelys* (Zangerl, 1960), and with it a complete, though somewhat flattened ulnare. This element agrees, in so far as comparison is possible, with the ulnare fragment in *Desmatochelys*. For this reason it seems reasonable to assume that intermedium and ulnare had the same

shapes and relationships in the two forms. Since the ulnare in *Corsochelys* is elongated to much the same degree as it is in modern cheloniines we must assume that it extended farther proximad than the intermedium and that the ulna attached itself to both elements

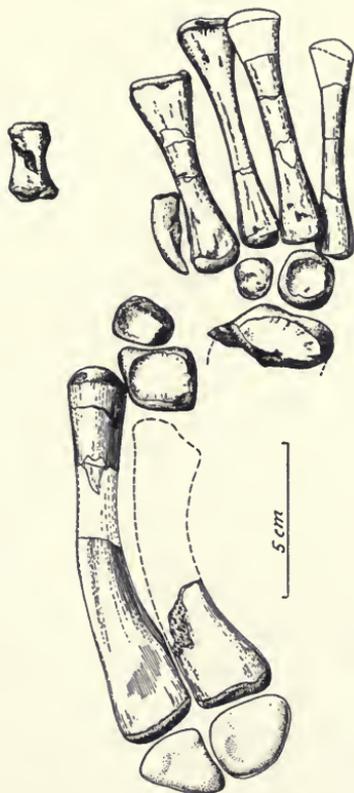


FIG. 17. Part of right flipper of *Desmatochelys lowi* (CNHM-PR385) as preserved; dorsal view and views of proximal ends of radius and ulna.

in the manner suggested in figure 18. Phylogenetically speaking, this condition is thus intermediate between a primitive situation in which intermedium and ulnare are not enlarged and the specialized condition in modern cheloniines where both elements are notably elongated at the expense of the ulna.

Distal to the intermedium in the present specimen there is an element, standing on end, which probably belonged next to the intermedium and which has the shape of the centrale in modern cheloniines. Distal to the ulnare there are a small and a fairly large

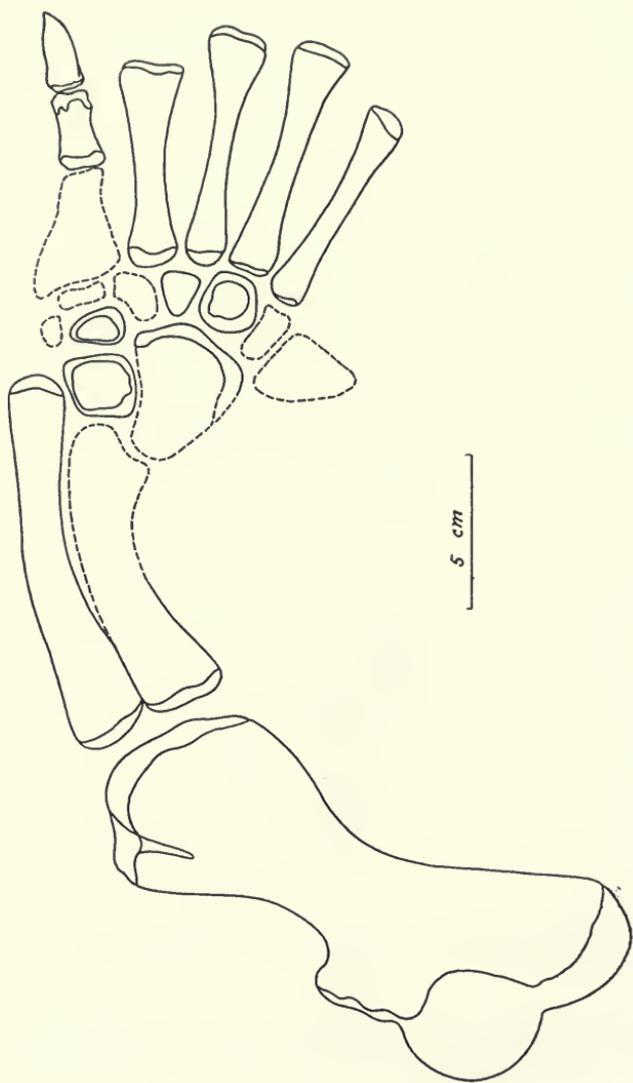


FIG. 18. Outline drawing of flipper of *Desmatochelys lowi* (interpreted on the basis of CNHM-PR385 and another Cretaceous cheloniid; see text).

carpal bone and these can be identified readily as the third and fourth distal carpals. The remaining carpal elements and the pisiforme are missing. Metacarpals II to V are elongated as in modern cheloniids; the fifth one, however, is relatively longer in *Desmatochelys* than in the modern forms. The basal phalanx of the thumb and the claw phalanx differ from those of modern cheloniine sea turtles only in very minor details.

7. Pelvis: Noteworthy portions of the pelvis are known both in the type and in the present specimen (fig. 19). Such areas as are available in both show, we believe, differences in preservation only. The preserved portion of the ilium is more slender and more angular than in cheloniines; in these respects it is intermediate between the toxochelyid condition and that of the cheloniines. The relatively large ischium, well preserved in both known individuals, is provided with a big, posterior spur as in the toxochelyids, chelydrids (and many other fresh-water turtles) and in some protostegids. In the cheloniids, in advanced protostegids, and in dermochelyids this spur is either very much reduced (as in modern cheloniines) or absent. This is clearly a primitive feature probably related to the type of locomotion in fresh-water turtles, and it is therefore to be expected among the more generalized members of all the sea turtle families, as well as among those forms in which the hind limbs are not primarily steering devices. The pubis, although incomplete, shows the essential character of this bone. There was an antero-lateral process of about the same shape and size as in toxochelyids (Zangerl, 1953, fig. 65); the base of the antero-medial process likewise indicates toxochelyid condition.

8. Hind limb: Of the hind limb only the left femur and tibia and a tarsal element are preserved. The femur (fig. 20) was broken and a small section of the shaft was missing; its length as restored is very probably correct; it could not have been shorter than restored because the central parts of the break surfaces are virtually in contact with each other, and it probably was not longer because of the surface configuration of the adjacent break edges. The femur is relatively long compared to the humerus (fig. 22); it is longer than in any of the modern cheloniines, more slender, distally less expanded and the head is more nearly spherical. The trochanters are individual processes as in fresh-water turtles, but they are connected basally by a well-developed ridge, a condition almost perfectly intermediate between the chelydrid turtles and the modern cheloniines. On the distal end of the femur the tibial side of the joint surface is more bulbous than the fibular side, another feature in which *Desmatochelys* resembles the

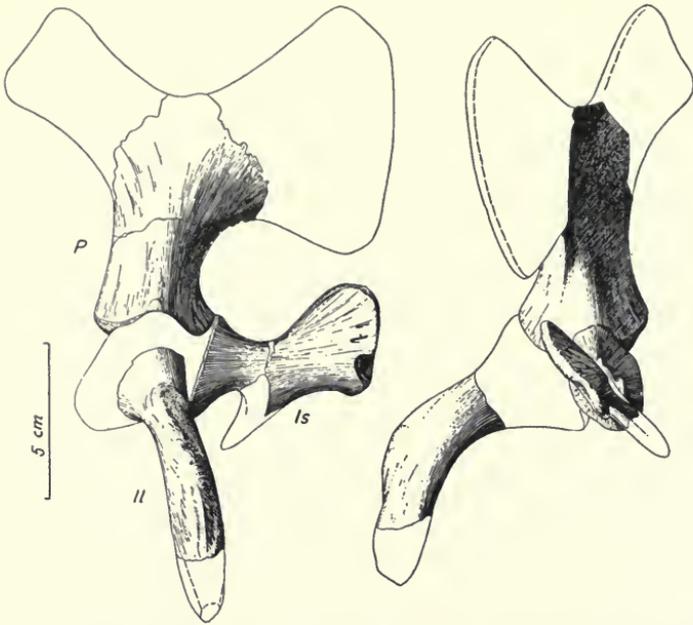


FIG. 19. *Desmatochelys lowi* (CNHM-PR385), pelvic girdle in dorsal and medial views.

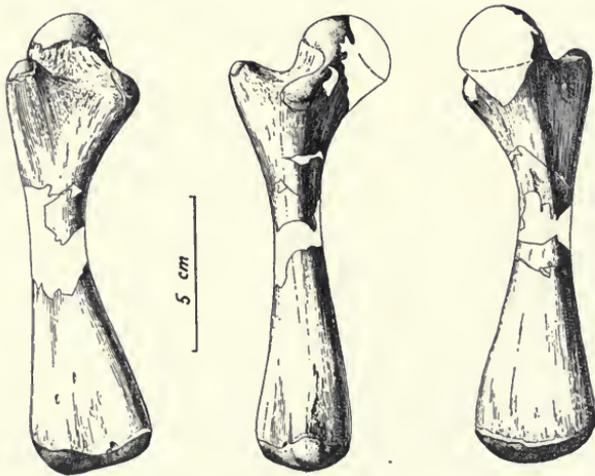


FIG. 20. *Desmatochelys lowi* (CNHM-PR385), left femur.

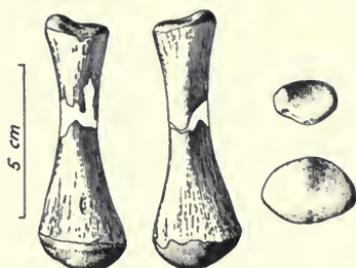


FIG. 21. *Desmatochelys lowi* (CNHM-PR385), left tibia.

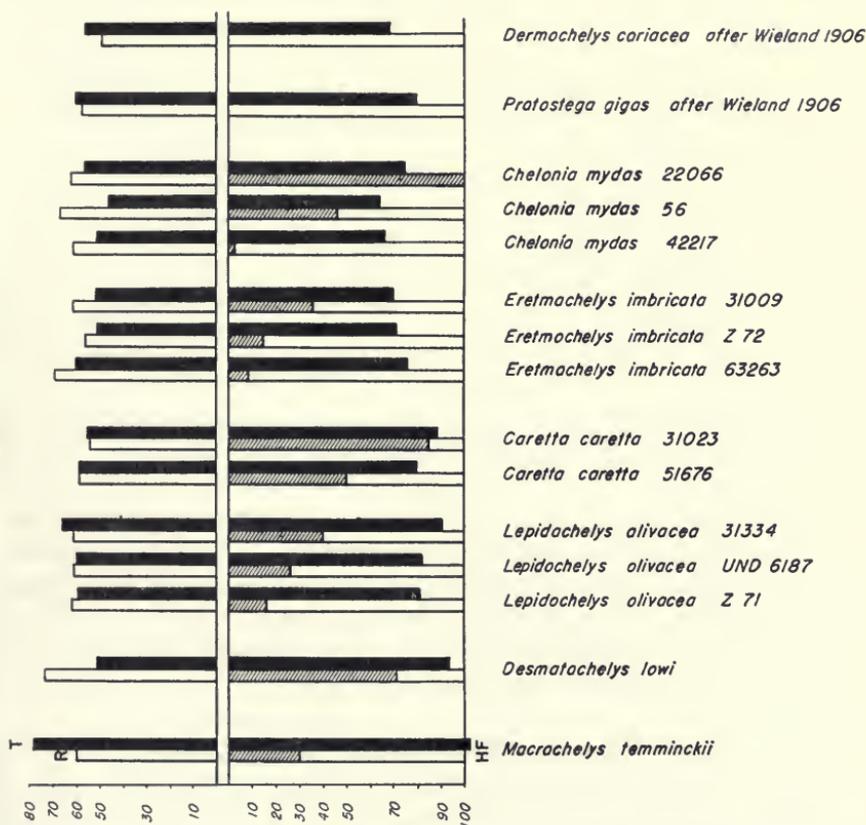


FIG. 22. Bar diagram to show relative sizes of stylopodial and zeugopodial bones in a number of sea turtles and a chelydrid. H (=100), humerus; R, radius; F, femur; T, tibia. The shaded columns within the humerus bars indicate in percentages the absolute size range of the humeri in relation to that of *Chelonia mydas* (CNHM 22066;=100).

fresh-water turtles rather than the cheloniines. The tibia (fig. 21) is relatively short (fig. 22) compared to that of the cheloniines and very much shorter than in the chelydrids. Its proximal end is very bulbous but the distal end compares rather closely with that of the cheloniines.

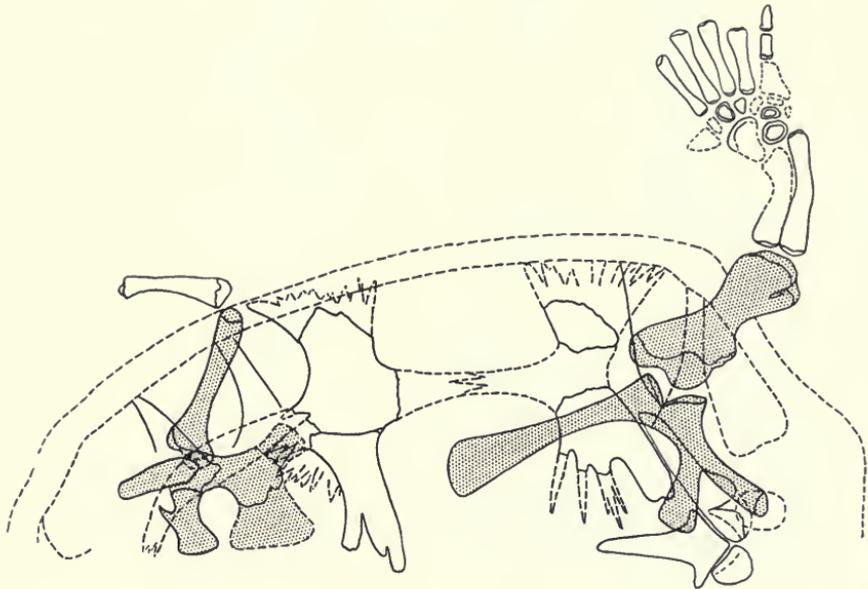


FIG. 23. Semidiagrammatic sketch to illustrate proportions and position of girdles and limbs with respect to those of shell of *Desmatochelys lowi*.

The single tarsal bone is a rather large, fairly flat plate that may best be compared with the tarsale distale IV+V of modern cheloniines. A similar bone is preserved with the type specimen; it does not belong to the carpus and it is not a pisiforme.

The position of the appendicular skeleton with respect to the carapace and plastron is represented in figure 23.

THE PHYLOGENETIC LEVELS OF ORGANIZATION AND THE ADAPTIVE MODIFICATIONS OF THE CHELONOID TURTLES

The foregoing description of a new and better-preserved skeleton of *Desmatochelys lowi* sheds, we believe, fresh light on the phylogenetic history of the sea turtles; since this form was thought to represent a separate family of marine turtles, a general discussion of the phylogenetic levels of organization and the adaptive modifications within the superfamily Chelonoidea seems profitable.

The turtles of the superfamily Chelonoidea have been subdivided into a number of families: the Toxochelyidae, the Protostegidae, the Dermochelyidae and the Cheloniidae. A fifth family, the Desmatochelyidae, was recognized to embrace a number of inadequately known genera of doubtful affinities. The Toxochelyidae and the Protostegidae, recently reviewed (Zangerl, 1953), form clearly circumscribed groups in spite of notable adaptive diversification within each family. The Dermochelyidae present an even more compact group. The Cheloniidae, with the longest known history (from the Cretaceous to the present), have never been studied comprehensively, and many forms, available in collections now, are either not at all or not yet satisfactorily described; a number of finds, furthermore, are very young individuals and cannot be compared profitably with the rest of the material.

What characterizes a chelonoid sea turtle in a most distinctive way and sets it apart from all other turtles (including other sea turtles) is its mode of locomotion: a chelonoid turtle "flies" through the water. The phylogenetic achievement of this mode of propulsion involved profound morphological, functional and behavioristic modifications, which enabled these animals to invade the pelagic realm of the sea (Zangerl, 1953, p. 166).

Until recently it has been rather difficult to characterize the chelonoid locomotor system in a comparative way. Such studies as were made (Wieland, 1900, and Dollo, 1903b) were restricted to the comparison of humeri and femora rather than the apparatus as a whole, and this has led to some conclusions that are no longer acceptable, as will be seen below.

Two principal considerations emerge: (a) the transformation of the locomotor system of a fresh-water turtle into that of a structurally advanced sea turtle; and (b) adaptive modifications affecting the functional efficiency of the locomotor apparatus and the shell construction.

(a) The transformation of the locomotor system of a fresh-water turtle into that of a sea turtle involves the transfer of the function of organs of propulsion from the hind limbs to the forelimbs; the latter become modified into flippers and the plane of their movement changes from horizontal to vertical. The hind limbs become steering rudders. These are profound modifications that have not been fully achieved in all major families of sea turtles.

For functional reasons one would expect an efficient flipper, moving in a vertical plane, to have a certain amount of rigidity, especially

in its proximal and middle regions. A vertebrate limb, however, is constructed of a number of sections that are movably connected to each other by joints. In all vertebrates that have undergone profound secondary adaptation to the marine environment, the modification of their limbs into paddles or flippers has been accompanied by other developments that prevent or reduce the flexibility of the limbs at the joints. Such developments in the sea turtle flipper include:

1. Restriction of the joint surfaces on all limb bones, especially on the carpals.
2. Tough ligaments connecting the limb bones.
3. A firm integument consisting of dense connective tissue covered by large epidermal shields.
4. Staggering of a transversal joint, i.e., division of such a joint into more proximal and more distal joint portions (joint between zeugopodium and autopodium in modern cheloniines).
5. Position of radius and ulna one above the other instead of side by side, and distal adhesion (by contact rugosity) of radius and ulna.

Not all of these features are present in the flippers of all chelonoid turtles. A number of levels of morphological organization of the chelonoid locomotor system may thus be recognized, as follows:

Toxochelyidae: The forelimbs are the major organs of propulsion; their plane of movement was vertical, but the flipper skeleton is notably primitive. The skeleton of the hind limbs is scarcely modified beyond that of the primitive condition in fresh-water turtles.

Protostegidae and Dermochelyidae: The forelimbs are typical flippers, the hind limbs are rudders; the construction of the flipper, however, lacks the elaborate stiffening mechanisms mentioned under points 4 and 5 above. The flipper skeleton of these turtles is thus morphologically relatively primitive although it is not functionally inefficient (see below).

Cheloniidae: The forelimbs are elaborately modified flippers, stiffened by a number of characteristic devices (listed above); the hind limbs are rudders.

(b) Superimposed upon the levels of morphological organization are adaptive modifications that do not change the basic organization of the locomotor system but render it functionally efficient. Such modifications in sea turtles are the streamlining of the shell and the reduction of the dermal bones of carapace and plastron; in the

flippers of protostegid and dermochelyid turtles there is displacement of the radial tuberosity of the humerus toward the distal half of the bone. Both Wieland (1900) and Dollo (1903b) regarded the humerus of these turtles as reflecting the highest degree of pelagic specialization, but it would seem more likely that the functionally advantageous distal position of the radial tuberosity is a compensatory feature in an otherwise relatively primitive and flexible flipper.

The position of *Desmatochelys* in the foregoing discussion of the locomotor apparatus is an interesting one: the forelimb is a flipper, but the hind limbs (to judge from the femur) appear to have reached a stage only half way between the propulsion paddle of a fresh-water turtle and the stiff steering rudder of a sea turtle. In the flipper there appear to be incipient stiffening mechanisms that are typical of only the cheloniid sea turtles, namely, the relationship between radius and ulna and the partial staggering of the joint between zeugopodium and carpus. On the basis of these considerations *Desmatochelys* emerges as a primitive cheloniid.

In the skull there are a number of peculiarities that are not known in any cheloniid turtles—the presence of nasal bones, the great forward extent of the quadrato-jugals to meet the orbital rim, the notable posterior position of the orbits and the primary condition of the palate (though Dollo, 1903a, claims such a condition in *Eochelone brabantica*, a form that requires more detailed description). The primary palate and the presence of nasal bones are primitive features found also in the generalized members of the Protostegidae and Toxochelyidae (Zangerl, 1953) and should be expected among the stem forms of the cheloniids. The forward extension of the quadrato-jugals to the orbital rims is probably related to the backward position of the orbits and although it has not to our knowledge been observed in any other member of this family it does not appear to us as a feature of great systematic weight.

In the foregoing description and comparison of the skeleton of *Desmatochelys* with other chelonoid sea turtles it was repeatedly pointed out that in many details there are definite resemblances to the protostegid, dermochelyid, and toxochelyid turtles, while in most respects (and in our estimation in the most significant respects) the resemblances point toward the cheloniids. *Desmatochelys* is the earliest of the better known chelonoid turtles and as such it is not surprising to find combined in a single form features that have later become characteristics of different families. It is our opinion that *Desmatochelys* may be closer to the stem group of the chelonoid

turtles than any other sufficiently known member of this superfamily. The Toxochelyidae, while primitive in their over-all organization, clearly seem to represent an early offshoot that became specialized in a direction all its own and became extinct without giving rise to any other chelonoids.

Unfortunately, we are not yet in a position to appraise the relationships among the Cretaceous cheloniid sea turtles, because too few forms are sufficiently well known at present. It is startling to note, however, that those few forms that have been described present a picture of surprising variety and often a degree of marine specialization far surpassing that of any of the Tertiary cheloniids, for example, *Desmatochelys*, *Corsochelys* (Zangerl, 1960), *Allopleuron*, *Protosphargis*. It may well be possible, in the future, to group some or all of the Cretaceous cheloniids together in a subfamily characterized by its generally primitive status within the family and by having undergone extensive adaptive radiation during the latter part of the Cretaceous. The formal proposal and definition of such a systematic category at this time would have to be based primarily on *Desmatochelys* and *Corsochelys*, and it seems to us that a definition so narrowly founded could hardly be expected to have more validity than the mere suspicion that the suggested grouping might, indeed, some day emerge as a demonstrable entity.

ECOLOGICAL NOTE

As was stated in the introduction, the locality from which this turtle was recovered was a topographic high during Benton time and the sediment in which the specimen was embedded represents a weathering product of the granite surface. The evidence indicates that these granite mounds were sand-covered islands in the Benton Sea. The occurrence of an articulated sea turtle skeleton embedded in this sand suggests that the turtle was either washed on shore soon after death or ascended it, perhaps for the purpose of laying eggs. Since none of the tail region of the vertebral column was recovered, it is impossible to determine the sex of the individual.

SUMMARY

A second specimen of *Desmatochelys lowi* Williston, herein described, complements the type specimen to a notable extent. Since the present material is uncrushed, a number of peculiar aspects of the type specimen, such as the dermochelyid or protostegid appearance of the humerus, could be explained as due to deformation.

The skeleton of *Desmatochelys* exhibits a number of features that are seen in toxochelyid, protostegid and dermochelyid turtles, but in its over-all morphology it is unmistakably though primitively cheloniid.

An analysis of the locomotor apparatus of *Desmatochelys* indicates primitive cheloniid affinities; the peculiarities of the skull such as the nasal bones and the primary palate are primitive features among chelonoid turtles and are to be expected among early Cheloniidae.

We would like to express our sincere appreciation to Miss Maida Wiebe, staff artist, Department of Geology, for her exact and beautiful art work.

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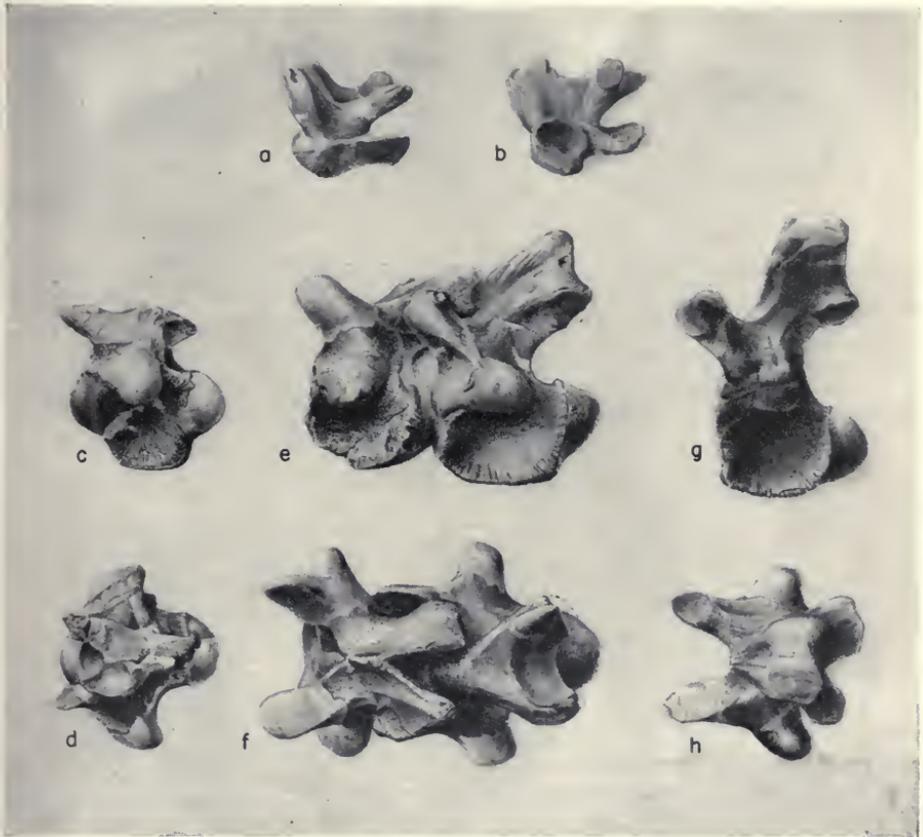
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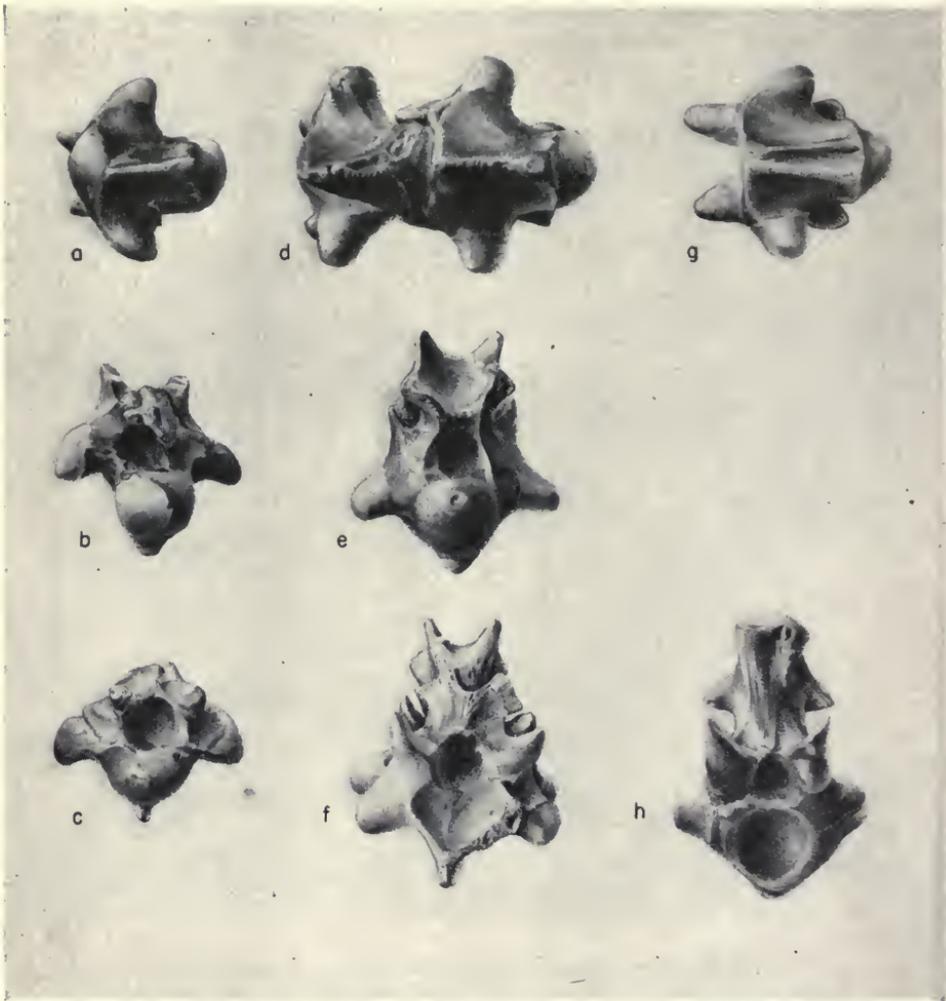
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Desmatochelys lowi (CNHM-PR385), cervical vertebrae
a, b, Lateral and medial views of atlas neurapophysis. *c, d*, Lateral and dorsal views of fourth vertebra. *e, f*, Lateral and dorsal views of sixth and seventh vertebrae. *g, h*, Lateral and dorsal views of eighth vertebra.



Desmatochelys lowi (CNHM-PR385), cervical vertebrae
a, b, c, Ventral, posterior, and anterior views of fourth vertebra. d, e, f, Corresponding views of sixth and seventh vertebrae. g, h, Ventral and anterior views of eighth vertebra.

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