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THE VERTEBRATE FAUNA OF THE SELMA FORMATION OF ALABAMA

PART V AN ADVANCED CHELONIID SEA TURTLE

RAINER ZANGERL

PART VI THE DINOSAURS

WANN LANGSTON, JR.

FIELDIANA: GEOLOGY MEMOIRS

VOLUME 3, NUMBERS 5 AND 6

Published by

CHICAGO NATURAL HISTORY MUSEUM

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SELMA FORMATION OF ALABAMA

PART V. AN ADVANCED CHELONIID SEA TURTLE

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SELMA FORMATION OF ALABAMA

PART V
AN ADVANCED CHELONIID SEA TURTLE

RAINER ZANGERL
CURATOR OF FOSSIL REPTILES

FIELDIANA: GEOLOGY MEMOIRS
VOLUME 3, NUMBER 5
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CONTENTS

	PAGE
LIST OF ILLUSTRATIONS	283
INTRODUCTION	285
CORSOCHELYS HALINICHES, new genus and species	286
Skull	286
Endocranial Cast	290
Vertebral Column	292
Carapace	293
Plastron	302
Shoulder Girdle	303
Forelimb	303
Pelvis	304
Hind Limb	305
Parasitic Lesions	306
COMPARISON OF CORSOCHELYS WITH OTHER CRETACEOUS SEA TURTLES . .	307
SUMMARY	310
REFERENCES	311

LIST OF ILLUSTRATIONS

PLATES

30. *Chelonia mydas*, *Caretta caretta* and *Corsochelys haliniches*. Dorsal and lateral views of endocranial casts.
31. *Corsochelys haliniches* and *Caretta caretta*. Cervical vertebrae 1 to 4 in dorsal, lateral and ventral views.
32. *Corsochelys haliniches* and *Caretta caretta*. Cervical vertebrae 5 to 8 in dorsal, lateral and ventral views.
33. *Corsochelys haliniches* and *Caretta caretta*. Cervical vertebrae 1 to 8 in posterior and anterior views.

TEXT FIGURES

	PAGE
125. Diagram showing relative sizes of skull and carapace in <i>Caretta caretta</i> , <i>Chelonia mydas</i> , and <i>Corsochelys haliniches</i>	286
126. <i>Corsochelys haliniches</i> . Skull in posterior view, basicranial region in dorsal view, side view of cranium before squamosals were attached, dorsal view of cranium, and ventral view of cranium before squamosals were attached	287
127. <i>Corsochelys haliniches</i> , <i>Chelonia mydas</i> , and <i>Caretta caretta</i> . Ventral aspects of basicranial region	289
128. <i>Corsochelys haliniches</i> . Reconstruction of skull	290
129. <i>Corsochelys haliniches</i> . Nuchal plate and peripherals in dorsal and ventral views	295
130. <i>Corsochelys haliniches</i> . Costal plates 5 to 7 of left side	296
131. <i>Corsochelys haliniches</i> . Dorsal and ventral views of last neural, first and second suprapyrgals, and fragment of right eighth costal . . .	297
132. <i>Corsochelys haliniches</i> . Various neural plates	297
133. Outline sketch of posterior carapace elements of <i>Corsochelys haliniches</i> .	298
134. <i>Corsochelys haliniches</i> . Last presacral rib, first and second sacral ribs, centrum of a shell vertebra, and neurapophysis of a shell vertebra	299
135. <i>Corsochelys haliniches</i> . Epiplastra in ventral and dorsal aspects . . .	300
136. <i>Corsochelys haliniches</i> . Left hyoplastron in ventral view	300

	PAGE
137. <i>Corsochelys haliniches</i> . Fragments of left and right hypoplastra in ventral view	301
138. <i>Corsochelys haliniches</i> . Reconstruction of carapace and plastron . . .	302
139. <i>Corsochelys haliniches</i> . Fragment of left coracoid and anterior and posterior views of right scapula	303
140. <i>Corsochelys haliniches</i> . Right humerus	305
141. <i>Corsochelys haliniches</i> . Proximal end of fibula, distal end of left radius, and ?distal end of fibula	305
142. <i>Corsochelys haliniches</i> . Carpal elements	305
143. <i>Corsochelys haliniches</i> . Metapodials and end phalanges	305
144. <i>Corsochelys haliniches</i> . Left ilium	306
145. <i>Corsochelys haliniches</i> . Left and right tibiae	306

An Advanced Cheloniid Sea Turtle

INTRODUCTION

Among the hundreds of specimens of turtles that have been collected in the Mooreville Chalk of the Selma formation of Alabama (see pts. II–IV of this monograph), there is a single individual, clearly identifiable as a member of the family Cheloniidae. Since good cheloniid material from the Cretaceous is rare anywhere in the world, except possibly in Belgium and Holland, the present specimen is of unusual interest. It was discovered and partially collected in March, 1950, by Mr. R. A. Hard of Tuscaloosa, Alabama, who gave it to the late C. M. Barber of Flint, Michigan. Mr. Barber, in turn, presented the bones to Chicago Natural History Museum. My wife and I revisited the locality later the same year and excavated additional parts of the skeleton. Mr. Hard's generosity and Mr. Barber's untiring interest in the turtles from the Mooreville Chalk are gratefully acknowledged.

My sincere thanks go also to Miss Maidi Wiebe, staff artist in the Department of Geology, who has patiently and carefully prepared the beautiful plates and text figures.

Order CHELONIA

Suborder CRYPTODIRA

Superfamily CHELONOIDEA

Family CHELONIIDAE

Corsochelys, new genus

Diagnosis.—Large, highly specialized sea turtle with relatively small, massive skull, deeply excavated temporal roof, narrow interorbital bridge and tight endocranial cavity; occipital condyle formed by basioccipital alone. Carapace with large costo-peripheral fontanelle and flat neural plates; nuchal plate not incised anteriorly. Plastron highly reduced; hyo-hyoplastral suture short, deeply inter-fingering; plastral index about 106. Centra of cervical vertebrae with thick cartilage discs fore and aft (as in modern *Dermochelys*). Arms of scapula of equal length; coracoid but slightly expanded distally. Flipper (so far as known) primitive cheloniid as in *Desmatochelys*.

Type of genus.—*C. haliniches*.

Corsochelys haliniches,¹ new species

Diagnosis.—Same as for genus.

Type specimen.—CNHM PR249. A notable portion of a skeleton of a large, possibly not fully mature individual.

Horizon and locality.—Collected 2½ miles east of West Greene, Greene County, Alabama; in gully patch, east of old cemetery. Mooreville Chalk, late Cretaceous.

FIG. 125. Diagram showing relative sizes of skull and carapace in *Caretta caretta*, *Chelonia mydas*, and *Corsochelys haliniches*.

Skull.—The skull was completely disarticulated and the component parts were collected loose in the wash. We could not recover many bones, such as the snout region, the quadrates, the basioccipital, the lateral walls of the skull, and the lower jaw. The bones that were collected, however, fit together very well and exhibit a number of most interesting features that were entirely unexpected in a true cheloniid sea turtle. Furthermore, a cast of the brain cavity could be made, and this, likewise, is of notable morphological interest.

The bones of the skull are massive and connected to each other by strong sutural digitations. The skull as a whole is surprisingly small for an animal of such large size (fig. 125). In over-all construction and as regards the differentiation of the braincase this is the skull of a true cheloniid turtle. One of the characters of this group, in contrast to the Dermochelyidae, in so far as they are known, is the presence, on the lower sides of the parietal bones, of descending

¹ κρόταφος, side of head, temple; αλινηχης, swimming in sea.

FIG. 126. *Corsochelys haliniches*, CNHM PR249. A, skull in posterior view; B, basicranial region in dorsal view; C, side view of cranium before squamosals were attached; D, dorsal view of cranium; E, ventral view of cranium before squamosals were attached.

Bsph, basisphenoid; Eo, exoccipital; Fr, frontal; Op, opisthotic; Pa, parietal; Pr, proötic; Pt, pterygoid; So, supraoccipital.

processes that meet corresponding ridges on the dorsal sides of the pterygoids; these processes thus form bony side walls of the braincase anterior to the otic region. In *Corsochelys* these parietal processes are much more extensive than in modern cheloniines (fig. 126, C), and this might reflect a more primitive condition. It is thus all the more surprising that in this form, alone among the known cheloniids, the temporal roof is excavated far forward so as to expose the otic bones to view from above. Another feature that determines the over-all aspect of this skull is the position of the dorsal rims of the orbits, which lie very close to the mid-line and are formed by the frontal bones (fig. 126, D). Bounding of the orbital rim by the frontal bones occurs among very young Recent sea turtles (Zangerl, 1958, fig. 17) and in adult *Chelonia mydas*, where the frontals are broad and the orbits, therefore, not close together.

The right frontal bone is subtriangular in outline; for a distance of 23 mm. it forms the rim of the orbit. No sulci are visible to indicate the shape of the

epidermal shield mosaic. On the ventral side there is, as in modern forms, a longitudinal ridge that separates the orbital cavity from the olfactory trough. This ridge (fig. 126, C and E) is much more massive than in far larger skulls of *Caretta*. The large temporal excavation has reduced the parietals dorsally to less than half the area they occupy in the usual cheloniid skull roof. On the ventral side, however, they form not only the roof of the braincase but to a very notable extent the side walls. These ventral partitions are very thick and form strong sutural attachments with the pterygoids and the proötic bones, as in Recent chelonines, leaving, on both sides, a small fenestra at the junction of the three bones (fig. 126, C). Near the anterior end of each of the ventral projections of the parietals there is a conspicuous thickening which extends laterally to the under side of the parietal roof (fig. 126, C and E). Nothing of the kind is seen in any modern sea turtle. Since this thickened pillar extends outward to the suture with the postorbital bone and since it is located directly behind the orbit, we may safely assume that it connected with the vertical strut of the postorbital bone that is present directly behind the orbit in all chelonoid sea turtles except the dermochelyids. It is thus very probable that the orbital cavities and those containing the adductor musculature were topographically separated from each other by a low, transverse elevation extending from the lateral wall of the braincase across the inner face of the skull roof to the postorbital strut. The parietal surfaces facing the brain cavity will be discussed below.

The supraoccipital bone is much like that in modern cheloniine turtles; its dorsal edge is broken off, but there is no question as to what is missing (figs. 126, A and D; 128). The posterior process is notably shorter than in Recent forms and is bladelike, as in the Carettini. The exoccipitals differ markedly from those of chelonines in a rather important aspect; they do not form part of the occipital condyle (fig. 126, A), as is almost universally true in turtles; in rare cases the basioccipital is not a part of the condyle, for example in *Pelusios* and *Pelomedusa* (Siebenrock, 1897). On the other hand, among primitive turtles, for example the baenids, it is the basioccipital alone that forms the occipital condyle (Hay, 1908, e.g. fig. 78). This may well be the primitive condition in turtles, but the relatively few instances in which this matter can be determined do not yet justify a sweeping generalization. The absence of a similar condition in any modern turtles justifies the contention that this feature is indeed a primitive one in *Corsochelys*. *Allopleuron*, the only other well-known Cretaceous cheloniid turtle in which the skull has been adequately studied, conforms in this regard as well as in many other ways with the modern chelonines (Rüschkamp, 1926). "*Toxochelys gigantea*," in my opinion a doubtful cheloniid, not a toxochelyid, does likewise (Oertel, 1914). In modern cheloniine turtles the exoccipitals contact the pterygoids ventrally to a small extent. In *Corsochelys* such a junction is not effected because of the large size of the fenestra postotica, which is very much expanded mediad in such a way that the wall of the exoccipital, facing the fenestra, is broadly rounded off (fig. 126, A); the two small openings (for the branches of the hypoglossus nerve) next to the condylar process of the exoccipital accord-

ingly face laterad, and the hypoglossal nerve left the skull by way of the fenestra postotica. The opisthotic bones conform in shape and extent fairly closely to those in *Lepidochelys*, but they are much broader dorsally than in the compared form (fig. 126, A, C-E). The right proötic element is present; it differs in shape from those of the modern cheloniines in that its antero-dorsal surface is notably concave in *Corsochelys*, convex (or even crested, e.g., in *Caretta*) in the modern cheloniines (fig. 126, C and D). Since the quadrates are missing, it is possible to

FIG. 127. Ventral aspects of basicranial region, showing differences in topography of ventral surface of pterygoids, and extent of basisphenoid. A, *Corsochelys haliniches*; B, *Chelonia mydas*; C, *Caretta caretta*.

see the course of the canalis carotico-temporalis along the postero-dorsal edge of the proötic (fig. 126, C). The foramen carotico-temporale was very probably formed by the proötic, the opisthotic and the quadratum. The details on the ventral side of the proötic compare quite closely with those in *Lepidochelys*.

The squamosa are essentially complete on both sides. Compared to these bones in modern cheloniines they are much more elongated back of the otic notch (figs. 126, A; 128). The area of origin of the superficial head of the M. depressor mandibulae, directly behind the otic notch, is a very shallow depression that extends to the posterior tip of the squamosal. In *Lepidochelys* it is likewise shallow but is much shorter in antero-posterior direction (Zangerl, 1958). On the medio-ventral side of the posterior process of the squamosal there is a relatively small, narrow and rugose surface that served as area of origin for the deep depressor head. It is likely that in an old individual of *Corsochelys* this area would be delimited medially by a more or less pronounced crest (for a discussion of this region see Zangerl, 1958, p. 12).

The basisphenoid is a very thick bone, measuring 16 mm. (in dorso-ventral direction) at its junction with the basioccipital (fig. 126, A). Its ventrally exposed surface (fig. 126, E), between the pterygoids, is a flat triangle with the sides meeting in front at an angle of about 45°. In modern cheloniines this angle is much wider, 60° and more (depending on how it is measured), and the basisphenoid forms a sharp, very prominent, V-shaped crest (fig. 127); in *Allopleuron*, also, this appears to be the case. The dorsal surface of the basisphenoid, behind the dorsum sellae, is gently concave and very smooth (fig. 126, B). There is no crista basisphenoidalis and no basisphenoidal contribution to the basis tuber-

culi basalis (see Zangerl, 1953, pl. 9). The dorsum sellae is a clearly defined ridge, flanked by relatively strong processus clinoidei, the distal ends of which are broken off. The fossa hypophyseos lies a short distance anterior to the dorsum sellae (fig. 126, B) as in *Chelonia* (Zangerl, 1953, pl. 9) and cheloniines generally. The rostrum basisphenoidale, broken in front of the small dorsal processes

FIG. 128. *Corsochelys haliniches*. Reconstruction of skull.

at the anterior end of the fossa hypophyseos, resembles the typical cheloniine condition in every respect.

The pterygoids are very massive. In ventral aspect they resemble those of *Chelonia* more closely than those of the other cheloniine genera, where the lateral edges of the pterygoids extend downward along the medial edges of the quadrates. In *Chelonia* these edges terminate about mid-length of the pterygoids and in *Corsochelys* they extend, in the form of blunt crests, to the posterior ends of the bones (figs. 126, E, and 127). On the antero-dorsal surfaces of the pterygoids the large ventral "foot plates" of the descending parietal processes are especially striking; their extent is far greater than in any modern cheloniine sea turtle (fig. 126, C).

Endocranial cast.—During the preparation of the skull it was noticed that the endocranial walls of the parietal bones showed well-marked depressions and crests that did not seem to be present in modern cheloniine turtles. Endocranial casts were made for *Chelonia*, *Caretta* and *Corsochelys* (pl. 30). As was demonstrated by Edinger (1929, fig. 9), the endocranial cast of a *Chelonia* skull reflects

the shape of the brain only in a very general way.¹ The two typical flexures of the axis of the endocranial cast (see arrows, pl. 30) correspond well with the principal flexures of the brain axis, one at the forward end of the medulla oblongata, the other at the posterior end of the olfactory region (Edinger, 1929, fig. 9). This permits at least an approximate delimitation of the major parts of the brain. Cerebellum and mid-brain are not differentiated in the casts and lie within the area in front of the posterior arrows and behind the peculiar "riders" immediately in back of the highest points of the braincasts. These "riders" have nothing whatsoever to do with the brain; they represent the fill of the cartilaginous anterior end of the supraoccipital bone that is invariably removed from the skulls during maceration. Anterior to the "riders" lies the space occupied by the cerebrum and in front of it vague indications of the bulbous portion of the olfactory region. In *Chelonia* and *Caretta* (pl. 30, figs. 1 and 2) the cerebral area of the casts is smooth, if one disregards minor irregularities on the bone surfaces. In *Corsochelys* this area is bulbous and subdivided into a pair of larger posterior and a pair of smaller anterior "lobes." Furthermore, the cerebral part of the cast seems sharply set off from the olfactory region, another notable difference compared to the casts of *Chelonia* and *Caretta* (pl. 30, fig. 3).

At first this striking difference between the endocranial casts of modern cheloniines and that of *Corsochelys* seemed difficult to explain and I wish to thank Dr. Tilly Edinger for her kind assistance with the literature and her valued opinion. In order to obtain a first-hand acquaintance with the relationship of the brain to the endocranial cavity, I dissected a head of *Chelonia mydas*; the approximate outline of the brain was entered in dotted lines on the dorsal view of the endocranial cast (pl. 30, fig. 1). This reveals at once that the brain is very much smaller than the endocranial cavity in this form, so that the major divisions of the brain are only vaguely indicated in the cast. It also shows where these brain components lie with regard to the cast of the endocranial cavity.

In the description of the skull of *Corsochelys* the unusual thickness of the bones and the massiveness of the construction of the skull were pointed out. These attributes of the skull bones are the reason why the endocranial cavity was not as roomy in this genus as it is in *Chelonia* and *Caretta*, so that the principal divisions of the brain are reflected in the cast of the cavity—a fact that should guard against generalizations concerning the relationship of the brain to the endocranial cavity.

The anterior arrows in the side views of the casts on plate 30 approximately indicate the position of the sulcus coronalis (de Lange, 1911), which forms the posterior boundary of the olfactory lobes (pl. 30, fig. 1). This permits the definite identification of the anterior pair of "lobes" in the *Corsochelys* cast, mentioned above, as representing the olfactory lobes.

¹ Edinger states (1929, p. 33): "Der Ausguss des *Chelone*-Schädels lässt niemand erkennen, dass das Gehirn dieser Schildkröte gewisse Krümmungen aufweist, dass das Vorderhirn breiter ist, als die übrigen Teile, dabei länglich usw. . . ." It is unfortunate that the endocranial cast available to Edinger was an incomplete one; hence the above statement.

As an aside, it may here be mentioned that the endocranial cast of *Corsochelys*, and any such cast made in a similar manner, will differ considerably from the natural casts of entire turtle skulls, e.g. "*Chelone*" *gastaldi* (Portis, 1879) or the supposed cerebrum of *Polyptychodon* (see Edinger, 1934), especially in the region posterior to the cerebral area. This is because the matrix fills of the temporal cavities (in life filled with adductor musculature) nearly meet in the mid-line, hiding the posterior portion of the endocranial fill that lies beneath. The fill of the anterior, cartilaginous process of the supraoccipital (which forms an elevated, triangular "rider" above the mid-brain region in our casts) is absent in both the natural casts mentioned, and this may indicate that the skulls became filled with matrix soon after burial and before the cartilage was decomposed.

Vertebral column.—The cervical column is well represented, although not all of the vertebrae are complete. The centra of the atlas, the fifth and the eighth and the neurapophysis of the sixth are missing. Neurapophyses 7 and 8 are somewhat incomplete. In spite of these deficiencies the character of the cervical region can be made out in good detail (pls. 31–33). For convenience of comparison the neck vertebrae of a modern *Caretta caretta* are illustrated in all views along with those of the new form.

At a glance one peculiarity of these vertebrae stands out above all others: the centra are slightly amphicoelous throughout. This is a very unusual condition in a cheloniid sea turtle, but the obvious conclusion that comes to mind first, namely, that this is a primitive character (in view of the universally amphicoelous condition of the cervical vertebrae in primitive turtles), is, I believe, erroneous. A closer look at these vertebrae reveals a number of facts that permit a satisfactory explanation of the unexpected condition of the centra. If the second, third and fourth vertebrae, which are perfectly preserved, are placed in normal zygapophyseal articulation, the centra are separated from one another by wide gaps (10 to 12 mm.); the articular surfaces of the centra look superficially like finished bone surfaces, but under magnification they are seen to be merely very thin films of bone with minute pustules and pores that overlie the spongy mass of the centra. Surfaces entirely comparable to these are seen on vertebral centra of *Dermochelys*.

The hypapophyseal keels of vertebrae 2, 3, and 4 are very rugose ventral crests, that supported, beyond doubt, sagittal sheets of cartilage in life as in *Dermochelys*. These observations suggest a picture of the neck region essentially similar to that of *Dermochelys*, as beautifully depicted by Völker (1913, pl. 31). In this modern, very highly specialized sea turtle, the vertebral centra are covered, at both ends, by thick pads of cartilage forming the articular surfaces in a pattern typical of that of the cheloniines (Völker, 1913; Williams, 1950). These numerous resemblances to *Dermochelys* do not indicate phylogenetic affinities of *Corsochelys* to the dermochelyids; they are rather a reflection of the advanced degree of marine specialization in both forms. Aside from these marine specializations, comparison of the vertebrae of *Corsochelys* with those of *Caretta* (pls. 31–33) reveals a high measure of over-all similarity coupled with differences in detail throughout. The vertebrae of *Corsochelys* are relatively narrower and

higher than those of *Caretta* and there are numerous differences in the proportions of the vertebral parts in the two forms; these are quite evident in the illustrations (pls. 31–33). In the posterior half of the cervical region there are, however, some differences that require greater emphasis. The centra of vertebrae 6 and 7 are nearly round in cross section, not at all flattened as in *Caretta*, and instead of a deep hypapophyseal sheath there is a mere crest that did not bear a cartilage extension in *Corsochelys*. In these two vertebrae, furthermore, the neurocentral suture lies notably above the transverse process; in *Caretta* it bisects this process.

One centrum of a shell vertebra (perhaps the fourth or fifth) and two neurapophyses, one from the sacral region, the other attached to a neural plate (figs. 132 and 134), are preserved. The centrum shows the standard cheloniine construction, but the foramen for the exit of the spinal nerve was notably larger than in modern forms (fig. 134). The isolated neurapophysis has a narrow attachment scar for the neural plate and two sharp crests extending from the rib facette forward to the suture with the preceding neurapophysis (fig. 134). The other neurapophysis is connected with a neural plate whose position in the series cannot be determined. At both ends the neurapophysis is broken off; it was connected, in the usual way, with the preceding and the following elements by thin sagittal sheets or bone. The broad central portion of the neurapophysis underlies the anterior half of the neural plate (fig. 132). For indications of neurapophyseal attachments to other neural plates, see description of these elements.

The carapace.—The extent of the preserved parts (except for a few additional neurals) of the carapace is illustrated (fig. 138). Although large portions of the shell are missing, it was possible to identify virtually all parts as to their positions within the shell with adequate confidence. Only some neural plates could not be placed, since none of the medial ends of the anterior costals is present. The carapace was, no doubt, arched in life, but the costal plates are preserved flat so that there are no clues as to the original curvature of the shell. Without a doubt, however, the shell was narrower than shown in figure 138.

When the deficiencies of preservation are taken into account it is probably correct to state that the outline of the carapace was cordiform, with the areas above the forelimbs quite deeply indented; the nuchal plate, on the other hand, was not excavated above the neck as, for example, in *Allopleuron hoffmanni* (Winkler, 1869). Posteriorly, the pygal end of the shell extended notably over the base of the tail (fig. 138).

The nuchal plate is thick (25 mm. along the mid-line, just back of the cervical edge) and subrectangular (fig. 129). On its ventral face there are three broadly rounded ridges that radiate backward from the center of ossification of the plate (located along the mid-line a short distance behind the cervical margin) to effect sutural union with the first costal plates and the first neural. At the posterior ends of the lateral ridges the nuchal is 26 mm. thick, at the medial ridge 17 mm. Between these ridges the nuchal plate is much thinner, about 4 mm.; these are the two areas where the nuchal plate is generally thin in all sea turtles and where in some cases (and often in juveniles) postnuchal fontanelles are located.

The nuchal plate shows an interesting peculiarity. At the anterior right corner of the plate there is a separate ossification (fig. 129) that appears to be a part of the nuchal plate that has ossified separately. This small ossification is homologous (in the sense of Naef and Kälin, see Zangerl, 1948) to the first peripheral plate in the modern *Caretini* (Zangerl, 1958), where the typical set of peripheral plates (eleven pairs) has been increased by one pair at the nuchal end of the series; accordingly, in the *Caretini*, the end of the rib associated with the first costal plate enters a pit in the fourth peripheral instead of the third, as is the usual situation.

In view of the comparative anatomical evidence the asymmetrical ossification in this—the only known specimen of *Corsochelys*—is unquestionably to be regarded as an abnormality; but since it is an element within the pattern of the bony shell mosaic, morphologically corresponding to the pattern norm in the *Caretini*, it may well indicate the presence within the family of early variational trends that have evidently resulted in the differentiation of a new and unique norm of shell pattern in one of the tribes of the subfamily *Cheloniinae*¹ (Zangerl and Turnbull, 1955; Zangerl, 1958).

The first half of the second peripherals is sutureally connected to the first costal plate. From there a large fontanelle extends to the pygal plate and there is no evidence that the right and left fontanelles were separated by the second suprapygal; the latter feathers out to a thin edge posteriorly. The peripherals from the third backward are unusual in that their ventral faces are wider than the dorsal faces, so that the medial sides are visible in dorsal view (fig. 129); as far as I know the reverse condition is the usual one in forms where one of the faces is wider than the other. Both the second and the third peripherals show characteristic features: a groove along the postero-medial face of the second element and the antero-medial face of the third contained the free end of the rib associated with the first costal plate; this rib extended to a shallow pit about mid-length on peripheral 3. The ventral face of the third peripheral at the end of the groove forms a prominent ventral boss; on the ventral margin of this plate immediately behind the boss is a broadly rounded notch and farther back a very sharp edge (fig. 129). Peripherals 4 and 5 are the narrowest; from 6 to 10 there is a gradual increase in the width of the bones (figs. 129 and 138). The medial margins of the ventral faces of peripherals 6 and 7 are irregularly scalloped; rib pits are not clearly defined. Peripherals 9 and 10 are very much wider than thick (fig. 129) and a well-developed rib pit is located near the anterior end of peripheral 10. The dorsal faces of these elements show well-defined extensive "erosions" of the surface bone (fig. 129), which upon closer examination prove to be areas where the surface bone collapsed over insufficiently mineralized spongy bone beneath (a thin section showing crushing of the spongy bone in a turtle peripheral from the Mooreville Chalk is illustrated on plate 1, part I, of this monograph).

¹ A study concerning repetitive individual shield variation in modern turtles and its possible evolutionary significance is currently in preparation. Examples comparable to the phenomenon described above are known in the epidermal shield pattern and evidence in support of the general views expressed above will be presented.

FIG. 129. *Corsochelys haliniches*, CNHM PR249. Nuchal plate and peripherals in dorsal and ventral views.

FIG. 130. *Corsochelys haliniches*, CNHM PR249. Costal plates 5 to 7 of the left side; costal 5 in ventral and dorsal views.

The incomplete eleventh peripheral (fig. 129) shows that the area of the carapace rim covered by the twelfth pair of marginal shields protruded somewhat over the tail region. Impressions of shield boundaries on the peripherals are visible as vague, shallow depressions; sharp furrows do not occur.

Three whole and two partial neural plates that fit together are preserved (fig. 132). Unfortunately only one, the last element of the series (figs. 131 and 132, D), could be definitely identified. For the others there are no contacts and no reliable indications as to their numerical position. The plate illustrated in figure 132, A-C, is almost entirely uninjured except for a matrix-filled break along the dorsal mid-line. Its outline as well as the suture around its posterior

FIG. 131. *Corsochelys haliniches*, CNHM PR249. Dorsal and ventral views of last neural, first and second suprapygals and fragment of right eighth costal.

FIG. 132. *Corsochelys haliniches*, CNHM PR249. Various neural plates of uncertain position in the carapace (except for D, the eighth).

FIG. 133. *Corsochelys haliniches* (CNHM PR249). Outline sketch of posterior carapace elements that fit together in good sutural union.

end indicates a certain amount of asymmetry in the pattern in which neural and costal plates fitted together (for examples of such asymmetry in modern forms see Zangerl, 1958). Anteriorly this neural does not have pronounced suture "teeth" as do the elements in figure 132, E–H. Its posterior suture, at least on the right side, seems to have been attached to the following plate in the manner shown in figure 132, G and H. The element shown in figure 132, E and F, although not entirely complete, shows a complicated anterior suture design in the

form of two antero-lateral suture "teeth" of unequal size. The medial part of the suture is missing. Posteriorly the suture shows a median, V-shaped incision. The two adjacent neural fragments (fig. 132, G and H) are connected by a suture in which large "teeth" laterally frame the posterior end of the preceding plate. The neurapophyseal scars (fig. 132, H) indicate that the broad major parts of the neural arches were located at mid-length, or beneath the posterior half of the

FIG. 134. *Corsochelys haliniches* CNHM PR249. a and b, last presacral rib; c and d, first sacral rib; e and f, second sacral rib; g and h, centrum of a shell vertebra; i and j, neurapophysis of a shell vertebra.

neural plates. The last neural of the series is eight-sided and about as long as wide. It was attached to the last two pairs of costal plates, the preceding neural and the first suprapygial (fig. 133). On the ventral side there is a slight sagittal ridge, and anteriorly there are two shallow depressions on either side of the ridge, indicating that the neurapophysis was not fused with the neural. The first suprapygial is subtriangular and shows ventrally a low sagittal ridge. The second suprapygial is suturally attached only to the first suprapygial; its lateral and posterior margins face the fontanelle. Ventrally it is smooth (fig. 131).

Of the costal plates (figs. 130, 131, 133, and 138) only the numbers 5-7 on the left side and 8 on the right side can be determined with certainty as to position. The other fragments included in figure 138 indicate the most likely places that they might have occupied. The costal plates extend laterad about halfway to the distal rib ends. Their lateral margins are clearly defined as in *Chelonia*. In their distal parts the costal plates are incompletely ossified above the ribs (fig. 130).

On the ventral face of the eighth costal (fig. 131) there is, near the posterior margin, a well-defined notch to which, no doubt, the rib of the presacral vertebra was attached.

Presacral and sacral ribs.—Three ribs, belonging to the last presacral and the sacral vertebrae, were recovered (fig. 134). One of these is greatly expanded distally and may be identified as the right first sacral rib (fig. 134, c, d). The other two elements are very similar in shape but are not equally well preserved. The better-preserved one fits rather well into the notch on the ventral side of the eighth costal plate (see above); its distal end is expanded and flattened and pro-

FIG. 135. *Corsochelys haliniches*, CNHM PR249. Epiplastra in ventral (upper figure) and dorsal aspects.

FIG. 136. *Corsochelys haliniches*, CNHM PR249. Left hyoplastron in ventral view.

FIG. 137. *Corsochelys haliniches*, CNHM PR249. Fragments of left (upper figure) and right hypoplastra in ventral view.

vided with a suture area on the dorsal side of the expansion. Proximally there is a uniform joint end that indicates attachment to the neurapophysis of the vertebra only, rather than to both neurapophysis and centrum. Accordingly this element belongs certainly to the last presacral vertebra (fig. 134, *a, b*). The third element is so similar to the one just described, though its mirror image, that it might indeed be its left mate; unfortunately, the distal end is pyritic and not entirely complete. There may have been a suture area on the dorsal side of the distal end. Proximally the joint surface has two adjacent facettes, indicating attachment to both neurapophysis and centrum; the centrum-facette is somewhat more pronounced than in the first sacral rib. In modern cheloniine turtles the rib attachment to the vertebral column undergoes a transition from neurapophyseal- to centrum-attachment in the region of the sacrum, and for this reason I am inclined to regard the element under consideration as the right second sacral rib (fig. 134, *e, f*).

The plastron.—The recovered parts of the plastron are illustrated on figure 138. It is characterized by a high plastral index of about 106 (Zangerl, 1953 and 1958). Hyo- and hypoplastra are notably reduced and long, finger-shaped projections extend mediad and laterad. The suture between these plates was short but effected by unusually deep interfingering.

The epiplastra (fig. 135) are slender, anteriorly expanded bones; near the symphysis they are thick and are provided on the dorsal side with an area for

FIG. 138. *Corsochelys haliniches*. Reconstruction of carapace and plastron.

the overlapping attachment of the entoplastron. Posteriorly there are longitudinal grooves that lay against the antero-medial prongs of the hyoplastra.

The left hyoplastron (fig. 136) is arched from side to side so that its lateral prongs faced upward in life. The medial prongs, especially the posterior ones, are very long and slender and must have interfingered with corresponding prongs of the right plate. The posterior prongs are strong and are provided with ridges on their lateral sides where they were attached to corresponding grooves along the suture "teeth" of the hypoplastron in the fashion indicated in figure 138. The maximum thickness of the plate is about 20 mm.

The right and left fragments of the hypoplastra complement each other in such a manner that only a small area of the plate (the antero-medial portion) remains unknown. Most of the prongs are missing; their length is in doubt, but not their number or position (fig. 137). The bases of the suture "teeth" show pronounced grooves along their medial sides (fig. 137) so that the suture connection of hyo- and hypoplastra is clear. The maximum thickness of this plate is about 15 mm.

The shoulder girdle.—Both scapulae and large portions of the coracoids are preserved. The right scapula is essentially complete and uncrushed (fig. 139). Its most striking aspect lies in the fact that both the dorsal and ventral processes are very nearly the same length; this is likewise true in *Desmatochelys lowi* Williston (Zangerl and Sloan, in press), *Glarichelys knorri* Gray (Zangerl, 1958), and in *Dermochelys coriacea* (Völker, 1913). The over-all differentiation of the scapula

FIG. 139. *Corsochelys haliniches*, CNHM PR249. Fragment of left coracoid and anterior and posterior views of right scapula.

is typically cheloniid as defined in part IV of this monograph (Zangerl, 1953, pp. 160, 162).

The left coracoid lacks the distal end (fig. 139); it is somewhat crushed and thus appears wider than it was in life. It appears to have been a slender element, only moderately expanded distally much as in *Desmatochelys*.

The forelimb.—The right humerus is virtually complete, but part of the radial tuberosity is broken off (fig. 140). Of the left humerus only the distal end is present. This bone, although massive and about 220 mm. long, looks like the humerus of an immature individual. This individual may not have reached full osteogenetic differentiation at death, but it was most certainly not a juvenile; it seems far more likely that the ends of the humerus were covered by thick pads of cartilage, as is the case in *Dermochelys*. The shape of the bone corresponds very closely to that of the humerus of *Caretta*; the angle, however, between the main axis of the shaft and the principal plane of movement of the humerus (angle β , Zangerl, 1953, fig. 69) is $\pm 40^\circ$ lower than in modern cheloniine forms.¹

¹ Both angles α and β (Zangerl, 1953, figs. 68 and 69) are clearly defined theoretically; the accurate measuring of these angles and the determination of planes and axes depend, however, on the correct posing of the bones and this meets with practical difficulties. Accordingly, in repeated measurements on the same bone, the values tend to differ to some extent (within about 5°). Angle α is much more difficult to determine than angle β . The latter ranges among Recent cheloniines from 50° to 70° .

Only the distal half of the ?left radius is present (fig. 141, b). On the side facing the ulna there is a rough elevation that might indicate a contact with the ulna, but this is by no means certain.

There are three carpal bones (fig. 142, a, b; c, d; e, f) that would be very difficult to interpret, were it not for a nearly articulated flipper of a new specimen of *Desmatochelys* (Zangerl and Sloan, in press) that has recently come to our attention. Comparison of these bones with the carpal elements of *Desmatochelys* leaves no doubt that the construction of the carpus was very similar in these forms.

The largest of the three elements has a characteristic shape (fig. 142, a, b). Along one edge it is slightly concave, and the edge is formed by surface bone; at one end (lower end in the figure) it is fairly thick and provided with a joint facette. A narrow joint surface extends along all the rest of the edge, except for a short distance adjacent to the thick end. The ulnare of *Caretta* is a bone of similar shape and characteristics; in *Desmatochelys* the proximal end of the ulnare is broken off, but the expanded distal portion of the bone is all but identical with the corresponding end of the element here described.

The second largest bone (fig. 142, c, d) has three distinct joint surfaces as indicated in the illustration and a valley (presumably on the dorsal surface) next to the largest joint surface. I fail to discover a carpal (or tarsal) bone closely resembling this element among modern sea turtles, but the intermedium of *Desmatochelys* is virtually identical with it in every respect. There seems to be no reasonable doubt that intermedium and ulnare of *Desmatochelys* and *Corsochelys* were very similar in shape, suggesting a similarity in the construction of the carpus. The adaptive features of the chelonoid flipper have been discussed at some length in connection with *Desmatochelys* (Zangerl and Sloan, in press), where the peculiarities of the *Desmatochelys* flipper led to a somewhat unexpected interpretation of the structure of the carpus, reflecting morphologically and functionally a primitive cheloniid condition. Much the same considerations apply to the carpus of *Corsochelys*, and a diagrammatic sketch (fig. 142) illustrates the relationships between the zeugopodial bones and the proximal carpal elements.

The third bone (fig. 142, e, f) has joint surfaces all around and probably represents a distal carpal element, perhaps the first or the third.

Manus and possibly pes are represented by the bones illustrated in figure 143. There are two massive end phalanges of different size belonging to the right side; the larger one is almost certainly the claw phalanx of the thumb, the smaller one probably the claw phalanx of the first toe; it appears very unlikely that both might belong to the manus. The remainder of the bones in figure 143 belong to manus or pes and show that the elongation of the metacarpals, metatarsals and phalanges had, in principle at least, reached the modern cheloniine condition.

The pelvis.—Only the left ilium was recovered (fig. 144). Its anterior edge is notably more concave than in *Caretta*; otherwise it agrees fairly well with the compared form.

Hind limb.—The bones illustrated in figure 145 were identified as the right and left tibiae; they do not resemble the corresponding bones in *Caretta* and *Che-*

FIG. 140. *Corsochelys haliniches*, CNHM PR249. Right humerus; radial tuberosity is largely broken off.

FIG. 141. *Corsochelys haliniches*, CNHM PR249. *a*, proximal end of fibula; *b*, distal end of ?left radius; *c*, ?distal end of fibula.

FIG. 142. *Corsochelys haliniches*, CNHM PR249. Carpal elements: *a* and *b*, ulnare; *c* and *d*, intermedium; *e* and *f*, probably distal carpal element. An interpretation of the position of ulnare and intermedium with regard to the distal ends of radius and ulna is shown in outline (see text).

FIG. 143. *Corsochelys haliniches*, CNHM PR249. Metapodials and end phalanges.

lonia as well as might be expected (less closely, for example, than does the tibia of *Desmatochelys lowi*; Zangerl and Sloan, in press), but I believe the identification is not doubtful. The characteristic distal end of the sea turtle tibia, with its ventral projection that almost touches metatarsal I, is but vaguely differentiated in *Corsochelys* but may well have been present in the form of a cartilage cap. Two additional fragments of zeugopodial bones (fig. 141, *a*, *c*) are identified as

FIG. 144. *Corsochelys haliniches*, CNHM PR249. Left ilium.

FIG. 145. *Corsochelys haliniches*, CNHM PR249. Left and right tibiae.

proximal (*a*) and ?distal (*c*) ends of the right fibula. This identification is tentative. The only other possibility, however, would be that the fragments are the proximal ends of radius and ulna. The latter bones are quite characteristic in modern forms and readily identifiable in *Desmatochelys*. For this reason it is considered improbable that the elements in question belong to the forearm. The fibula, on the other hand, is a rather nondescript long bone, round in cross section at mid-length and flaring toward both ends. The fossil fragments satisfy these requirements. If our interpretation be correct—and there appears to be no satisfactory alternative—we must assume that the characteristic disparity in thickness of tibia and fibula in modern sea turtles was absent in *Corsochelys* and that these bones were of about equal bulk.

Parasitic lesions.—Between costals 6 and 7 (figs. 130 and 133) there is a large, nearly circular, parasitic lesion, internally walled off by a thin, bulging sheet of bone. Evidently bone was deposited on the internal face of the shell as the lesion grew deeper. Parasitic lesions very similar to the one here described are seen occasionally in other turtles both Recent and fossil, for example, in a juvenile pleurodire (this monograph, part II, fig. 7) and in a shell of *Pelusios sinuatus* (CNHM 12699). A smaller and shallower pit is located on the second suprapygial (fig. 131).

COMPARISON OF CORSOCHELYS WITH OTHER CRETACEOUS SEA TURTLES

The skeleton of *Corsochelys* leaves no doubt as to the family relationships of this turtle; it is clearly a cheloniid sea turtle. For this reason comparison may be restricted to those forms that are either clearly recognized as cheloniids or are tentatively assigned to this family.

Our knowledge of the Cretaceous cheloniid sea turtles is still unsatisfactory. Very few forms are adequately preserved, and much of the descriptive work of the late nineteenth century no longer satisfies present requirements. Furthermore, the outstanding collection of fossil sea turtles in the Musée Royale d'Histoire Naturelle in Belgium, reported upon by Dollo (1909), has not yet been properly described.

The better known late Cretaceous cheloniid sea turtles are *Allopleuron hoffmanni* (Gray), *Glyptochelone suyckerbuyki* (Ubaghs, 1879), *Catapleura arkansaw* Schmidt, *Desmatochelys lowi* Williston, and *Protosphargis veronensis* Capellini.

Corsochelys differs from *Allopleuron* in many respects. The shell is broader relative to its length, and the nuchal plate is not incised as in *Allopleuron*; the neurals are longer than wide, whereas in *Allopleuron* they are as long as wide. The skull of *Allopleuron* (Rüschkamp, 1926; Ubaghs, 1888) differs very notably from that of *Corsochelys* in the relative sizes of the bones and in being essentially roofed over.

Glyptochelone suyckerbuyki (Ubaghs, 1879)¹ shows a remarkable feature in the construction of the bony carapace mosaic in that the neural plates appear fragmented in much the same fashion as in *Procolpochelys grandaeva* (Leidy), "*Euclastes*" *melii* Misuri, and the modern genus *Lepidochelys* (Zangerl and Turnbull, 1955; Zangerl, 1958).²

Since *Corsochelys* has a normal neural series, there can be no confusion with *Glyptochelone*.

Catapleura arkansaw Schmidt is probably a primitive cheloniid turtle; it is known from the shell only. The carapace is not notably elongated and is sub-oval in outline; the plastron resembles that of the Toxochelyidae, except for the plastral index (Zangerl, 1953), which is much higher than would be expected in a toxochelyid of similar shell shape. In all these aspects, *Corsochelys* is clearly distinct from *Catapleura*.

¹ This work has been overlooked by most writers and is missing in the major bibliographic compilations. Dollo (1909) offers a rather casual reference to it and so does Smets, whose numerous descriptions of fossil turtle material have likewise been virtually ignored by contemporary and later students. Ubaghs' work is apparently not available in the United States, and, at this writing, I have seen only a photostat of a small part of the description and two plates pertaining to *Glyptochelone suyckerbuyki*.

² The discovery (in the literature) of a sea turtle of late Cretaceous age with these shell peculiarities was entirely unexpected and some of our recent conclusions, especially those pertaining to the origin of the Caretini, may have to be revised.

Desmatochelys lowi Williston differs from *Corsochelys* in the construction of the skull, which is only slightly excavated in the temporal region and has a broad interorbital bridge. In *Desmatochelys* the nuchal area of the carapace does not protrude as prominently as it does in *Corsochelys* and there are some differences in the shape of the plastron. The basic construction of the flippers of these two forms, however, appears to have been very similar.

Protosphargis (Capellini) has been variously considered as a primitive dermo-chelyid and a highly advanced cheloniid. On the basis of what is known of this animal, namely, most of the shell, it seems impossible to reach a decision. Costal and neural plates have been reduced so that the carapace disc is supported only by the flattened ribs. The peripheral bones are very narrow and evidently not in contact with the rib ends. The plastron is not unlike that of *Corsochelys*, but it is notably more reduced.

Cimochelys benstedii (Mantell) is based on juvenile shell material in fine condition (Owen, 1851; Lydekker, 1889). Renewed study of the originals will be required to determine whether this form is, indeed, a cheloniid. In a number of respects it looks decidedly like a protostegid (there is a notable resemblance to *Chelosphargis* Zangerl, 1953). *Cimochelys* differs from *Corsochelys* by its evidently little reduced plastron and the keeled neural series. The peripherals, especially those of the bridge region, have protostegid rather than cheloniid shape.

Glaucochelone, *Tomochelone* and *Platychelone* are names applied by Dollo (1909) to unpublished materials from the Cretaceous of Belgium.

Toxochelys gigantea Oertel, in my opinion not a toxochelyid, is based on an isolated, rather crushed skull from the Aptian of Hannover. It belongs thus to a notably early sea turtle possibly of cheloniid affinity. The palatal aspect shows a partial undershelving of the choanae composed of a fringe of extremely irregularly deposited bone that gives the impression of a pathological bone growth. The basisphenoid occupies a relatively large triangular area between the pterygoids, much as in *Corsochelys*. Further comparison between these forms is, unfortunately, not possible.

The genus *Rhinochelys* is also based on skulls only. Six species were listed by Lydekker (1889), and a large number of specimens is at hand, virtually all of them from the Cambridge Greensand. The systematic treatment of these specimens reflects the evidently great individual variation in this form. Because of the presence of nasal bones and the sagittal, sutural contact of the palatines Lydekker suggested, tentatively, that they might be pleurodires. The same combination of characters occurs also in *Desmatochelys*, which is quite clearly a cryptodire and moreover a cheloniid. A closer relationship between *Rhinochelys* and *Desmatochelys* has been suspected for some time, and the great variability of *Rhinochelys* may be a reflection of the rapid adaptive radiation, in the late Cretaceous, of the early cheloniid turtles.

Notochelone costata Owen from the Cretaceous of Queensland consists of a partial carapace and plastron and the scapulae. The carapace fragment resembles *Corsochelys* in principle. The neural plates are much narrower relative to

their length than in *Corsochelys*. The plastral elements appear to be less reduced than in *Corsochelys* and the arms of the scapulae are of uneven length. DeVis (1911, pl. 4) has tentatively referred to this species a well-preserved skull¹ showing fairly large temporal excavation of the roof (but not nearly as deep as in *Corsochelys*) and premaxillary bones that meet above the external nasal opening, anterior to the prefrontals. The frontals barely reach the rims of the orbits and the interorbital bridge is wide.

Cratochelone berneyi Longman is known only from a few very incomplete but large fragments of a sea turtle, also from Queensland. The material permits no useful comparison.

The genus *Peritresius* from the late Cretaceous of the east coast of North America is still inadequately known (Hay, 1908). This is a sea turtle with highly ornamented carapace bones and a high neural keel. These features alone separate *Peritresius* clearly from *Corsochelys*.

The genera *Atlantochelys* Agassiz and *Neptunochelys* Wieland are both based on humerus fragments (Hay, 1908). *Atlantochelys* from the Upper Cretaceous of New Jersey comprises a proximal half (or less) of a humerus of enormous size. The proximal position of the strong radial tuberosity coupled with the notable slenderness of the shaft gives this humerus a toxochelyid character. The size would seem to rule out such an assignment at present; but it should be kept in mind that some species of the genus *Prionochelys* Zangerl were rather large animals, and it is at least possible that larger individuals and perhaps larger species may have existed.

Neptunochelys comprises a nearly complete humerus from late Cretaceous deposits at Columbus, Mississippi. It is of interest in the present connection because of its geographic origin and its size, only slightly larger than the humerus of the specimen of *Corsochelys* here described. The humerus of *Neptunochelys* lacks part of the head and the ulnar process; the radial tuberosity lies close to the region of the head and is a large relatively smooth process. In the present specimen of *Corsochelys* the head and the ulnar process are intact, but much of the radial tuberosity is broken away so that comparison of these elements is difficult. The sharp crest extending from the radial tuberosity to the ulnar process stands almost at a right angle to the longitudinal axis of the shaft in *Neptunochelys* and more nearly parallel to it in *Corsochelys*. Furthermore, in this genus the shaft is relatively longer and more slender. These are notable differences that give the humeri a very different aspect in the two forms and I do not believe that they belong to turtles of the same species or even genus.

The above discussion clearly shows that our knowledge of the Cretaceous sea turtles leaves much to be desired. A number of species cannot even be assigned, with confidence, to a family. But if the doubtful forms are disregarded, a very striking fact emerges, namely, that the cheloniid turtles of the late Cretaceous display a great variety of forms and generally a very high degree of marine

¹ The supposed cranium of an immature specimen (op. cit., pl. 3, fig. 1) is a portion of the plastron.

specialization. The picture, as we know it at present, indicates that the cheloniid turtles underwent rapid adaptive radiation during this period and became cosmopolitan in their distribution.

SUMMARY

A new cheloniid sea turtle is described from the Mooreville Chalk (late Cretaceous) of Alabama. Only a single specimen is presently known and this is probably not a fully mature individual, in spite of its large size. In many respects this turtle is greatly advanced in the direction of marine specialization, as is true of most Cretaceous cheloniids. In the differentiation of its locomotor apparatus, however, it appears to be as primitive as is *Desmatochelys*.

The present state of knowledge of the Cretaceous cheloniid sea turtles is very unsatisfactory, and a review based on re-examination of virtually all of the material is clearly indicated.

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Dorsal and lateral views of endocranial casts of three sea turtles ($\times \frac{3}{4}$). 1, *Chelonia mydas*, CNHM 22066; an outline of the brain of another individual is indicated in dotted lines on the dorsal view. 2, *Caretta caretta*, CNHM 31022. 3, *Corsiochelys haliniches*, CNHM PR 249. The arrows indicate the position of the principal flexures of the brain; the anterior arrows also locate the approximate boundary between cerebrum and bulbous olfactorius. *To*, region of tractus olfactorius; *s*, suture between frontal and parietal bones; *so*, fill of the anterior, cartilaginous tip of the supraoccipital bone; *mo*, region of medulla oblongata.

Cervical vertebrae 5 to 8 in dorsal, lateral and ventral views ($\times \frac{1}{2}$). A, *Corsochelys haliniches*, CNHM PR 249. B, *Caretta caretta*, CNHM 31023.

Cervical vertebrae 1 to 4 in dorsal, lateral and ventral views ($\times \frac{1}{2}$). A, *Corsochelys haliniches*, CNHM PR 249. B, *Caretta caretta*, CNHM 31023.

Cervical vertebrae 1 to 8 (from right to left) in posterior view (upper two rows) and anterior view (bottom two rows) ($\times \frac{1}{2}$). A, *Corsochelys halimiches*, CNHM PR 249. B, *Caretta caretta*, CNHM 31023.

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