THE VERTEBRATE FAUNA OF THE SELMA FORMATION OF ALABAMA

PART III
THE TURTLES OF THE FAMILY PROTOSTEGIDAE

PART IV
THE TURTLES OF THE FAMILY TOXOCHELYIDAE

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RAINER ZANGERL

CURATOR OF FOSSIL REPTILES

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Turtles of the Family Protostegidae

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INTRODUCTION

The turtles of the family Protostegidae are, for the most part, large, spectacular forms that lived in the oceans of the western hemisphere during Late Cretaceous time. The original discovery of a member of this family dates back to 1871, when Cope, in a letter to Professor Lesley, briefly mentioned the finding of a gigantic turtle in the Cretaceous Chalk beds of Kansas. This formation, now famous for its wealth of vertebrates, has produced many additional finds of protostegid turtles, but complete skeletons in articulation are extremely rare.

In spite of the relative abundance of materials from the Niobrara Chalk of Kansas, detailed knowledge of parts of the organization of these turtles is still wanting. They make such impressive museum pieces that almost all of the better skeletons have been mounted for exhibition, some in such a way that careful study is now difficult. The almost universally defended, golden rule in reconstructing fossils—that added parts should be treated so as to make them unmistakably visible as such—has been violated in some instances.

The historical review (see below) of the gradual increase in our knowledge of the Protostegidae (deterred by misinterpretations of important elements of their organization) illustrates vividly the intrinsic difficulties involved in the study of incomplete fossil materials, increased, in this case, by the (not always wholesome) power of the word of the "eminent authority," and the latter's premature theoretical evaluations of insecurely founded interpretations.

In the following pages, the representatives of the family Protostegidae from the Mooreville Chalk of Alabama will be described, along with hitherto unpublished Niobrara skeletons, the very scanty materials from the Marlbrook Marl of Arkansas, and a form from the Eagle Ford of Texas. Since all of the existing skeletons are more or less incomplete, it was necessary to become acquainted at first hand with the materials that are preserved in many of the major museums of the United States. With the exception of one or two skeletons, I believe that I have had an opportunity to study all of the now existing specimens of protostegid turtles. The amount of material is now vastly greater than at the time when the group was last reviewed by Hay (1908) and by Wieland (1909). Furthermore, neither author studied all the materials available at that time.

I am greatly indebted to the authorities of several institutions for courtesies extended to me during my visits. I wish to express my sincere thanks especially to Dr. E. Raymond Hall, Director, and Dr. Robert W. Wilson and Mr. Edwin C.

Galbreath, of the Museum of Natural History, University of Kansas; Dr. E. H. Sellards, Director, and Mr. Glen L. Evans, Assistant Director, of the Texas Memorial Museum; Dr. John A. Wilson, of the Department of Geology, University of Texas; Dr. C. L. Gazin and Dr. D. H. Dunkle, of the United States National Museum; Dr. Horace G. Richards, of the Philadelphia Academy of Natural Sciences; Dr. G. G. Simpson, Dr. Edwin H. Colbert, and Dr. Bobb Schaeffer, of the American Museum of Natural History; and Dr. Joseph T. Gregory, of the Peabody Museum of Natural History, Yale University.

Since Part I of this series was completed, the following persons have made field trips to the Mooreville Chalk of Alabama and have collected much additional material: autumn, 1946 (Mr. C. M. Barber); spring, 1947 (Mr. C. M. Barber and Mr. William D. Turnbull); spring, 1948 (short visit, Mr. C. M. Barber); autumn, 1948 (Mr. C. M. Barber); spring, 1949 (short visit, Dr. and Mrs. R. Zangerl); spring, 1949 (Mr. C. M. Barber and Mr. J. A. Robbins).

The last field season was conducted under a grant from the Geological Society of America. My sincere thanks are extended to the officers of the Geological Society and to Mr. Watson H. Monroe and Mr. D. Hoye Eagle, of the United States Geological Survey, and to Dr. Walter B. Jones, State Geologist, Alabama State Geological Survey, for their interest in furthering this project.

Mr. Barber was accompanied by Mr. J. A. Robbins, of Flint, Michigan, who greatly contributed to the success of this trip by his interest in the field work and by furnishing transportation in his automobile.

Abbreviations of Institutions

Chicago Natural History Museum: C.N.H.M.

American Museum of Natural History: A.M.N.H.

Museum of Natural History, University of Kansas: K.U. (V.P.)

Peabody Museum, Yale University: Y.P.M.

Carnegie Museum: C.M.

Texas Memorial Museum: T.M.M.

United States National Museum: U.S.N.M.

University of Nebraska State Museum: U.N.S.M.

HISTORICAL REVIEW OF THE DISCOVERY OF THE PROTOSTEGID TURTLES

The first mention of remains of a true protostegid turtle is found in a letter by Cope to Professor Lesley (Cope, 1871), in which he mentioned the discovery of a large chelonian near Butte Creek, south of Wallace, Kansas, in the Cretaceous (Niobrara) Chalk beds. Cope's account of this animal is very brief, but he suggests that it may be called *Protostega gigas*. The proper description of this skeleton, though without illustrations, followed in 1872 (Cope, 1872a). The specimen was a large adult individual, preserved in partial articulation but with considerable portions of the skeleton missing. In the pose in which the partially disarticulated elements of the skeleton were found in the matrix, the inner surfaces of the ribs faced upward, and beneath them there were large, digitated plates. Cope concluded that the plastron was missing and that the

large plates lay over the ribs of the carapace, pointing out that these large plates might be the homologues of what is now referred to as the epithecal armor of ossicles in the Recent *Dermochelys*. The peripheral elements were not in articulation. They were flat bones with a sharp edge on one side and long digitations along the remaining margin. Indeed, there were no "sutures" (in the familiar sense of that word), by means of which a string of peripheral bones might have held together. Therefore, Cope concluded that the marginal elements must have been free from each other and held together by the skin only. Among the materials, Cope had a number of skull bones which he correctly interpreted as such. But, apparently, he did not compare them carefully enough with elements in the skull of, for instance, a Recent sea turtle; nearly all of the bones were misinterpreted, as Hay (1908) has pointed out. Cope's estimate of the size of *Protostega gigas* was excessive. During the same year, Cope (1872b) placed *Protostega* in a new family, Protostegidae, in the suborder Athecae. In 1875, he repeated his description of 1872 with little change, but the text is accompanied by good illustrations of the bones.

Baur (1889) disagreed with Cope regarding the interpretation of the large plates as ossicles of the carapace and suggested that they are regular elements of the plastron.

This view was proved to be correct when Hay (1895) described and figured new materials of *Protostega*. The specimen, now in the University of Chicago collection at Chicago Natural History Museum (UR79), consists of two very large and well-preserved plates that were correctly interpreted as the hyo- and hypoplastra of the left side. There is also a "T"-shaped element whose lateral wings are broken off; this bone was interpreted as the nuchal plate.

A major contribution to the knowledge of the osteology of the protostegid turtles was made by Wieland (1896), who gave a partial description of a complete and articulated skeleton of a very large form from the Pierre Shale of South Dakota. The specimen was enclosed in a hard concretion. As preparation proceeded, Wieland made additional reports from time to time. In his first contribution, he described the carapace without nuchal plate and peripheral bones, save for a fraction of one of them, the pectoral girdle with most of the forelimb, and the larger bones of the hind limb. All of these parts were figured. For this turtle, Wieland proposed a new genus and species, *Archelon ischyros*.

Case (1897) described new materials of *Protostega*. The skeletons at his disposal helped to solve a number of problems. For one thing, he could demonstrate a series of eight articulated peripheral bones, which he interpreted as Nos. 2(?) to 9 of the left side. This is, indeed, their approximate position with regard to the rest of the specimen as found, and Case's illustration of the specimen shows the peripherals in correct order. In the meantime, the specimen must have been remounted, since recent inspection showed that the series is now reversed, the second peripheral being at the posterior end. This specimen shows that the peripheral bones do join in sutural union by means of long interfingering processes. The rest of the specimen consists of the "T"-shaped bone, interpreted

as the nuchal plate (as Hay had done before), the hyoplastra in proper relation-
ship to each other and connected by the "T"-shaped bone whose lateral wings
are firmly attached to the dorsal surfaces of the hyoplastra, the left hypoplastron,
and, in articulation with it, the left xiphiplastron. The latter bone was described
for the first time. The material studied by Case included few carapace elements.
From the peculiarities of the proximal rib ends, he concluded that there was no
space left for a neural series between the ribs. A number of braincase bones
were properly described and figured, as was the lower jaw; but the bones described
by Cope were missing in the specimens studied by Case. The shoulder girdle
and humerus, as well as the pelvis and femur, were described and figured.

Wieland's first report on *Archelon ischyros* (1896) appeared after Case had
completed his manuscript. Case discussed Wieland's report in an "additional
note" in which he admitted having been in error as regards the supposed absence
of a neural series in the carapace. He then discussed briefly the validity of
Wieland's genus and concluded that "*Archelon* must be considered as a synonym
of *Protostega*, and even its specific separation remain an open question."

Hay (1898) published an article entitled "On *Protostega*, the systematic
position of *Dermochelys*, and the morphology of the chelonian carapace and
plastron," which added nothing materially to the understanding of the osteology
of the group, but in which Hay developed what is now being called the duplicity
theory of the chelonian armor. Like Case, Hay pronounced *Archelon* indis-
tinguishable from *Protostega*.

Wieland (1898) published a second contribution to the morphology of
Archelon. He gave an excellent account of the essentially complete plastron.
The front end of it is formed by the "T"-shaped bone, which Wieland correctly
identified as a part of the plastron; he called it entepiplastron or paraplastron,
assuming that the lateral wings of the bone included the epiplastra. At the
same time, he described and figured a bone plate as the nuchal element, com-
paring it to a similar but fragmentary bone figured and tentatively identified
as nuchal by Cope (1875). Wieland illustrated this element in ventral aspect;
it shows medially a conspicuous knob, much as is seen in the Recent sea turtles.
With regard to the status of his new genus, Wieland, no doubt under the influence
of the consensus of opinion, minimized the value of the differences from *Proto-
stega* and referred his material to the latter genus.

The study of the skull (Wieland, 1900), the first articulated skull of a proto-
stegid, clearly revealed that the Pierre material was worthy of distinct generic
status, and Wieland admitted that he had only reversed his opinion in his previous
paper "in deference to high authority." The pelvis of *Archelon* was also described
in this article.

In 1902, Wieland discussed the forelimbs of *Archelon* and *Toxochelys*, and
suggested a classification of the marine turtles. In the same year, Williston
described the hind limb of *Protostega*.

Up to this time, Wieland's descriptions and interpretations were sound and
reliable. But in 1903, he published an unfortunate paper, in which he "rede-

scribed" portions of the carapace of *Archelon*. Here again, Wieland bowed to the opinion of the "authorities," one of whom, Capellini (1898), had stated that Wieland's interpretation of the "T"-shaped bone as an anterior element of the plastron was supported by neither embryological nor paleontological evidence. Case also opposed that interpretation in a manuscript note to Wieland. Thus, in his 1903 contribution, Wieland furnished a reconstruction of the carapace of *Archelon* in which the entoplastron appears as the nuchal bone. This illustration is further inaccurate in that it shows a pair of extraordinarily large first ribs that eventually turned out to be coracoids. It is particularly unfortunate that Hay, in his monograph on the turtles of North America (1908), used this faulty figure rather than the one given in Wieland's first description (1896).

In his article of 1903, Wieland also described the pronounced longitudinal sulci that extend sagittally along the neural plates. Sternberg (1905) described the discovery of two more specimens of *Protostega* from the Niobrara Chalk of Kansas. One of these was illustrated by photograph in a semi-prepared condition. Sternberg corrected some of Cope's initial errors of interpretation in rather harsh terms and criticized Williston's figure of the hind limb of *Protostega*. He spoke forcefully about the "science falsely so-called" as it is often manifested in products of the imagination of paleontologists in the absence of adequate fossil materials. In view of the record, one can hardly fail to agree with the gentleman.

Later, Wieland (1906a) presented another paper dealing with the morphology of the protostegid plastron. Here he returned to his previous interpretation of the "T"-shaped element as a plastral bone, but he now called it the entoplastron. He had meantime discovered a bone that he considered the epiplastron. This element was figured and described, but in the final mount of the type specimen of *Archelon* it was omitted, indicating that the identification was a tentative one, as, indeed, it remains to this day.

The same year, Wieland (1906b) published a memoir in which he described the beautiful specimens in the Carnegie Museum. A great deal of new information was added by the description of the anterior edge of the carapace, that of new skull materials and particularly the girdles and limbs.

Hay (1908) reviewed the osteology and taxonomy of the protostegid turtles, and he then agreed with Wieland in all points that had previously been the subject of argument. The "T"-shaped bone was definitely considered as the entoplastron, and the distinctness of the genus *Archelon* was no longer questioned. Hay also described two additional species of *Protostega*, *P. advena* and *P. potens*, the latter species based on a partially prepared specimen.

In 1909, Wieland published a paper which was primarily a summary of his earlier work on *Archelon*, with photographs of the final mount of the skeleton of *A. ischyros*, and a description of a new species of *Protostega*, *P. copei*.

Wieland's revision of the family marked the close of the early work on these large turtles. In the years that followed, new materials were collected from a number of formations and localities, but with the exception of a semi-popular

article on a find from the Mooreville Chalk of Alabama (Renger, 1935) no further work has been done on members of this family.

It may be of some general interest to note that the controversy that surrounded the gradual increase in the understanding of the skeletal morphology of the protostegid turtles was intimately tied up with the theoretical interpretation of the systematic and phylogenetic position of *Dermochelys* in relation to the rest of the sea turtles, and, in a wider sense, with the question of shell morphology in general. It is almost a matter of certainty that there would have been no argument about the homology of the "T"-shaped bone had the authors not been biased by considerations of a theoretical nature. "T"-shaped entoplastra, almost identical in shape with those of the protostegids, are seen in juvenile individuals of almost all groups of living turtles (except the Trionychidae). In *Dermochelys*, the entoplastron is missing. This is an illustrative example of what may happen when theoretical considerations are permitted to play a part in the recognition of structural relationships, such as homologies, a danger that has repeatedly been pointed out (see, for example, Zangerl, 1948). The following is an outline of what happened in this example: Influenced by the idea that the protostegid turtles are more or less closely related to the Dermochelyidae, in which the entoplastron is missing, the "T"-shaped bone in the Protostegidae was interpreted as the nuchal plate. But in *Dermochelys* and the other living sea turtles, the nuchal bone has on its ventral side a conspicuous knob that articulates with the last cervical vertebra. The "nuchal" bone of the Protostegidae does not have such a knob (the real nuchal plate does, however); consequently, the Protostegidae were depicted as an aberrant side line with merely a possible origin relationship to the Recent sea turtles (Case, 1897, p. 50).

THE MORPHOLOGY OF THE PROTOSTEGID TURTLES

General Discussion

The members of the family Protostegidae represent a group of highly aquatic, marine turtles, confined, so far as known, to the western hemisphere and to the close of the Cretaceous period. Although the earliest member occurs in a formation of Late Turonian age, there can be no doubt that the group had a long phylogenetic history prior to that time. This earliest species belongs to the large and greatly specialized members of the family, whereas the more primitive forms occur, along with the large ones, in later formations. This is unquestionably due to gaps in the record.

The general habitus of the Protostegidae is that of a typical sea turtle, with a relatively large head, a series of stout neck vertebrae that probably did not permit the head to be drawn inside the shell, a flat disk-like shell with large fontanelles, particularly in the carapace, a short tail, and limbs so modified as to serve as powerful paddles, of which the front flippers are the major locomotor organs, as is characteristic only of the Recent sea turtles and their allies. Wieland (1909) assumed that the shell was covered by a leathery hide containing an

osteodermal armature, as in *Dermochelys*, but as will be shown below, there is sufficient evidence that this was not the case. The shell of the Protostegidae was covered, as it is in the majority of turtles, by a system of epidermal shields. This statement applies both to the primitive and to the specialized members of the family.

While it is possible, in the present state of knowledge, to draw a fairly clear picture of the over-all organization of the protostegid turtles, it should be emphasized that many details remain to be ascertained. This situation becomes clear at once if one endeavors to reconstruct the morphotypic organization of any one of the recognized species. Such attempts at reconstruction (fig. 18) reflect no more than our present knowledge of the various forms and should be so understood.

It must be pointed out that there appears to be considerable individual variation among the members of those species of which sufficient material is available, but it is out of the question to formulate such variability in mathematical terms, because the most conspicuous individual differences are largely brought about by post-mortem deformation. In view of this fact, size and minor differences in the shape of individual bones cannot be used to differentiate species. The criteria used in the proposed classification of these forms (p. 128) are consequently very conservative.

The Skull

The skull, as has been pointed out repeatedly, shows many similarities to that of both the Cheloniidae and the Dermochelyidae. The temporal region is roofed over by the parietal, postorbital and squamosal bones, but not as completely as in *Dermochelys*. With the latter form, it agrees in having a primary palate.[1] In other respects, the protostegid skull is intermediate between the cheloniid and dermochelyid conditions. One peculiarity of its own is the relatively large antorbital extent of the beak and, correlated with this, a relatively long symphysis of the lower jaw. In the primitive genera, discrete nasal bones are present.

The Vertebral Column

The cervical region of the vertebral column is relatively short, consisting of vertebral elements that are very robust and about as wide as they are long. Both the centra and the neural arches are stout. In the region of the shell, the vertebral centra, in particular, are very massive, whereas the neurapophyses appear to have been fairly slender arches. According to Wieland (1896, 1906b), there are ten shell vertebrae in *Archelon* and *Protostega*, followed by three sacral elements in *Archelon*. The tail vertebrae of *Archelon* comprise five or more anterior ones with neural arches and ten consisting mainly of the centra.

[1] Wieland's statement (1909) that there are descending processes of the parietals uniting with the pterygoids, as determined by Hay in *Protostega advena*, is probably a mistake, since the skull of that form was represented only by the two isolated postorbital bones. Actually, there is not a single skull that would permit a definite decision in this matter.

The Carapace

The carapace is a relatively short, broad and flat disk. The posterior and lateral edges are broadly rounded, but the anterior margin between the axillae appears shortened. The carapace plates, homologous with the thecal plates of other turtles, are greatly reduced in extent, producing more or less extensive fontanelles between the central and peripheral parts of the shell. None of the plates that constitute the normal turtle carapace are absent, however. The neural plates form a more or less pronounced keel in the sagittal plane. In specimens that were preserved more or less in situ, the neural elements tend to show median, longitudinal sulci. This has been described at length by Wieland (1896, 1903, 1909) as a peculiarity of *Archelon*. As will be demonstrated below, the neural bones have a peculiar, sagittal "cleavage plane" along which they tend to separate into right and left halves. In specimens preserved in situ, the neural plates are often crushed down onto the large and massive vertebral centra, thereby splitting open dorsally along the "cleavage plane." One specimen, U.S.N.M. 11649 (pl. 8), shows plainly that there can be no doubt as to the nature of this dorsal "sulcus." Another matter regarding the neuralia of the protostegids that should be considered with caution is Wieland's assertion that the neurals are very thin and flaky plates that underlie keeled epithecal elements. Wieland was led to this interpretation by the examination of one of his specimens on two cross sections through the concretion containing it. Although there is no possibility now of checking this information (the skeleton being mounted and on exhibition), there is a distinct possibility that his interpretation was wrong, even though his observation suggesting such an interpretation was correct. A transverse break through a neural element in front or in back of the central area of the bone usually shows a condition very similar to that described by Wieland. The thin sheet of bone at the base (usually separated from the bulk of the element by matrix) represents merely the lowest lamella of a very deep, interfingering system of bony lamellae by means of which two adjoining elements meet in suture. The costal plates may be reduced to mere vestiges on the proximal ends of the ribs. The peripherals of the primitive genera are comparatively heavy elements; those of the specialized forms tend to be large, flat plates with sharp outer edges. In the specialized genera, the margins of the dermal bones, where they do not form the outer edge of the carapace, are highly irregular in outline, usually forming long, finger-shaped projections. All of the connections between dermal bones are deeply interfingering sutures. The nuchal plate possesses on its ventral side a strong knob whose homologue is well known in Cheloniidae and Dermochelyidae. The nuchal is connected with the axillary (third) peripheral by two flat and narrow peripherals. The second peripheral is typically attached only to the antero-medial edge of the axillary peripheral, which gives the carapace its characteristic dorsal aspect. Ordinarily there is the normal number of eleven pairs of peripherals, but specimens with twelve pairs are known.

Eight pairs of ribs (Nos. 2 to 9 of the shell ribs) take part in the formation of the carapace in the primitive genera. In the genera *Protostega* and *Archelon*, the number appears to be nine (Nos. 2 to 10) normally.

The Plastron

In contrast to the carapace, which is extremely light, at least in the more specialized protostegid turtles, the plastron consists of large and heavy bone plates. Epiplastra are definitely known only in the primitive members of the family, although Wieland (1906a) tentatively described a small bone as a possible epiplastron in *Archelon*. The entoplastron is a large "T"-shaped plate, whose lateral wings appear to have been in contact with the antero-medial surfaces of the hyoplastra. The hyo- and hypoplastra are large, more or less quadrangular or circular plates whose margins (except for the axillary and inguinal edges) are strongly digitated. The two plates adhere to each other by means of a deeply interfingering suture. The xiphiplastra are wedged into deep "V"-shaped clefts of the hypoplastra and, joining medially in a suture, form a very short posterior lobe of the plastron. The plastral elements enclose one large central fontanelle.

The Girdles and Limbs

The scapula is a stout bone whose processes are relatively short and stand at a wide angle to each other. The coracoid is likewise a massive rod whose distal end is scarcely expanded. Both bones are usually preserved in a crushed condition, in which case they appear considerably flattened. Uncrushed specimens are known, however, and these show that cross sections through the shafts of these bones are nearly circular in outline. The forelimb resembles in many respects that of the Recent sea turtles, particularly *Dermochelys*, as has been noted by Wieland (1906b).

The pelvis is very broad and consists ventrally of greatly expanded pubes and relatively diminutive ischia that enclose between them very small obturator foramina. The ilia are shorter and stouter than those in *Dermochelys*. The hind flipper is relatively much larger than in this genus, and the tarsus is more completely ossified. In both respects, the hind limbs of the Protostegidae resemble those of the Cheloniidae more closely.

Remarks concerning Measurements

Because of the fact that nearly all of the bones of the shell have digitations along their edges (most of which are usually broken off) and that nearly all bones are crushed to a degree not readily determinable, it is virtually useless to give detailed lists of measurements. Since the materials are fairly adequately illustrated, the general size range of the specimens can be obtained from the figures. In *Calcarichelys*, which is represented by well-preserved material, measurements are appended to the descriptions.

NOTES AND DESCRIPTIONS OF PROTOSTEGIDAE FROM FORMATIONS OTHER THAN THE MOOREVILLE CHALK OF ALABAMA

Before describing the protostegid turtles from the Mooreville Chalk of Alabama, it seems advisable to present additional notes on forms from other formations, since much new information can now be added to that already in the literature and some misconceptions corrected. In addition, descriptions of new materials from the Eagle Ford Formation of Texas and the Marlbrook Marl of Arkansas will be given here in order to present as complete an account as is now possible of the turtles of this family.

NIOBRARA FORMATION OF KANSAS

Subfamily **Protosteginae**

Protostega gigas Cope

Discussion.—In spite of the fact that much of the literature on protostegid turtles is based on *P. gigas*, a few important morphological details are still unknown. Some of these gaps can now be filled. One question pertains to the nature of the neural series in the carapace. Case (1897) concluded, on the basis of indirect evidence, that neural plates are absent in *P. gigas*. Wieland (1906b) studied CM1420 and stated that the neuralia are very thin, almost paper-like. Wieland's illustration of this carapace shows it in ventral aspect; hence there is some doubt that he actually saw the dorsal side. At any rate, this statement recalls an earlier observation by Wieland on *Archelon*, when he described the neural series as consisting of a very thin thecal row, covered by a series of keeled epithecal ossicles (see p. 70).

Several skeletons collected subsequently show that both Case and Wieland were wrong. The neural bones are neither absent nor are they thin flakes; they are plates of considerable size and thickness. Moreover, they form a pronounced keel of uneven height along the mid-dorsal line. Sharply keeled neural elements alternate with unkeeled ones. This arrangement corresponds with the epidermal vertebral scale pattern of the carapace. The ridged neurals lie underneath the summits of the vertebral scales. In this regard, *P. gigas* is nearly identical with *P. dixie*, to be described below.

The following description of the neural series of *P. gigas* is based on a partial, unmounted skeleton in the United States National Museum, U.S.N.M. 11652. Four unquestionably adjoining neural elements are preserved. Their deep and complicated sutures leave no doubt that they formed a continuous series (fig. 17). The position of this row of neurals within the entire series can be determined by indirect means. It can be proved that all the protostegid turtles, contrary to earlier statements, possessed epidermal shields. The topographic relationship

between the vertebral shields and the neural plates is fairly constant, particularly in the anterior part of the shell, in the vast majority of turtles. In almost all cases (save abnormally scaled ones) the apex of the second vertebral shield lies above the second neural plate, that of the third vertebral shield above the fourth neural. In the posterior part of the neural series the elements are usually shorter, so that the fourth vertebral shield may span two or more entire neural plates. The four neural elements of U.S.N.M. 11652 consist of two keeled elements alternating with two unkeeled ones. In view of the condition in *Calcarichelys gemma* (fig. 56), it appears reasonable to assume that the shield furrows traversed the unkeeled, saddle-shaped elements of the series. If we consider the slightly smaller size of two of the four plates as an indication of their more posterior position in the shell, there remains only one possible interpretation of the location of the four bones in the entire series of neural elements, namely, Nos. 2, 3, 4,
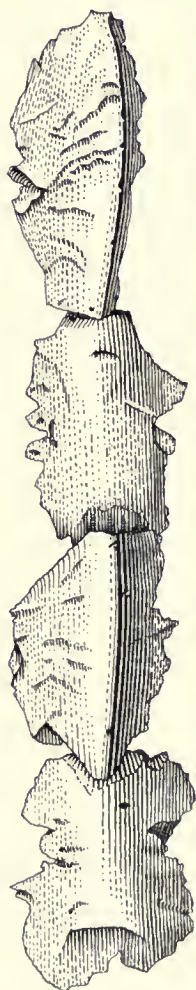

FIG. 17. *Protostega gigas*. U.S.N.M. 11652. Neural plates 2 to 5, dorsal view. Drawn from photograph. About × 0.3.

and 5. This interpretation seems to agree with the condition in two more complete, mounted skeletons.[1]

The shape of the four neural plates of U.S.N.M. 11652 is clearly apparent from the illustration (fig. 17). One peculiarity of these elements, in contrast to those of other turtles, is the absence in some of them of an indication of a

Fig. 18, A. *Protostega gigas.* Reconstruction of carapace. Based on several specimens. About × 0.1.

broken spinal process on their ventral sides, even though the element appears to be complete. This apparent lack seems to be due to the fact that the most ventral parts of the neural bones ossify in the form of thin sheets of bone that

[1] Both of these specimens are reconstructed to a greater or less degree. They should thus only be referred to for confirmation of results obtained by other means, unless the authenticity of a given feature can be ascertained. One of these specimens is the property of the Colorado Museum at Denver. I had an opportunity to see this specimen. Unfortunately, it is now difficult to tell which parts are genuine and which have been recon-

erode quickly when the elements become exposed to weathering. It may be that Wieland saw only these basal sheets of bone when he examined the Carnegie Museum specimen from the ventral side. In U.S.N.M. 11652, the spinal processes are still attached to the neural plates, although much distorted. Careful inspection leaves no doubt that the entire neural is *one* element of thecal origin.

FIG. 18, B. *Protostega gigas.* Reconstruction of plastron. Based on two specimens. About × 0.1.

The nuchal plate of *P. gigas* has not been fully described to date. U.S.N.M. 11651, another unmounted specimen, shows a nuchal similar to that of *P. dixie* structed. According to my notes, the second, third, and fourth neurals agree closely with the corresponding elements in U.S.N.M. 11652. The fifth, however, is keeled in the mount, saddle-shaped in the National Museum specimen.

The second specimen belongs to the Museum of Paleontology, Fort Hays Kansas State College. Unfortunately, I have not seen this mount. Judging from a small photograph, the neural keel conforms in every detail to that of U.S.N.M. 11652. Neurals 2, 4, and 6 are highly ridged, 3 and 5 are saddle-shaped. Behind neural 6, a straight, low keel extends to the suprapygal area.

(fig. 34). The posterior two-thirds of this plate is definitely keeled in the Denver Museum specimen, and even more so in the specimen at Fort Hays, Kansas. In U.S.N.M. 11651, however, there is no definite keel. Apparently, this is a matter of individual variation.

The plastron of *P. gigas* has been figured repeatedly. In U.S.N.M. 11651, the plastron is unusually well preserved. Hyo-, hypo-, and xiphiplastra are in sutural connection, thus showing the proper relationship of the various plates to each other. This is also true in the specimen described by Case (1897), but the sharply bent xiphiplastron in that individual was probably caused by distortion. The reconstruction of the plastron (fig. 18) is based on U.S.N.M. 11651, except for the entoplastron, which is based on an example illustrated by Case (1897) but interpreted by him as the nuchal.

Protostega potens Hay

Discussion.—This species is based on a partial skeleton (A.M.N.H. 180) that was incompletely prepared when it was described. Parts of the specimen are so badly weathered that the prospect of gaining more information by their preparation is doubtful. These parts have been left in their field wrappings, opened for inspection on one side. Dr. Edwin H. Colbert and Dr. Bobb Schaeffer of the American Museum of Natural History kindly supplied me with good photographs of all parts of the skeleton so that the material could be illustrated.

There can be little doubt that this skeleton belongs to a species other than *P. gigas* or *Archelon copei*, even though the features that most clearly characterize these forms are wanting in this skeleton. The bones indicate a turtle of large size, larger, probably, than any known specimen of *P. gigas*, but considerably smaller than the giant type specimen of *A. ischyros*.

The area of the skull posterior to the orbit is present, though not sufficiently well preserved to permit comparison with related forms. Fragments of the carapacial disk indicate that the ribs and costal plates show the same relations as in *P. gigas*.

The plastron merits more detailed discussion. The entoplastron has both of the lateral wings and much of the posterior process missing. The remaining portion of the bone resembles the specimen figured by Hay (1895), C.N.H.M. UR79, except that the plate is relatively thinner and wider at the base of the lateral wings in *P. potens*. The hyoplastron is, indeed, a peculiarly shaped plate (pl. 5). Considering its size, it is very thin, about 20 mm. in the thickest part. The axillary edge is sharp and undamaged. It is much longer than in any other species, in fact about twice as long as in *P. gigas*. The medial edge is broken off, but there is no reliable way of estimating how much might be missing. Judging from the thinness at the broken edge, one is inclined to agree with Hay's (1908) reconstruction, but since the plate does not attain great thickness anywhere, it is conceivable that more than a third of its original area is missing, and that it was a large, thin sheet of bone. I am inclined to favor the latter view, since the hypoplastron does not show any great degree of medial reduction.

The hypoplastron is well preserved, except for the spiny projections. Even though the plate is broken along nearly all of its periphery, a proper reconstruction presents no problems (fig. 19).

The xiphiplastron has a distinctive shape. Its lateral edge forms a rather pronounced angle, which is far more conspicuous than that in the specimen of *P. gigas* described by Case (1897) and here considered to be due to distortion (see p. 76). In A.M.N.H. 180, there is no evidence that the shape of the xiphiplastron was altered by distortion.

Considered as a whole, the plastron of *P. potens* possessed a relatively large anterior lobe and an unusually short posterior lobe. It thus differs decidedly from other members of the genus, in which the posterior lobe is more prominent. In most of its features, the plastron of *P. potens* resembles that of *P. dixie* (see below) more closely than it does that of *P. gigas*.

The left scapula, coracoid, and humerus are preserved. One of the processes of the scapula is broken off near the base, making comparison with other forms difficult. The coracoid has a relatively large proximal end (pl. 6, fig. B) as compared with uncrushed coracoids of other species (fig. 48, *P. dixie*). The humerus is characterized by strong processes and a much expanded distal end. The ulnar
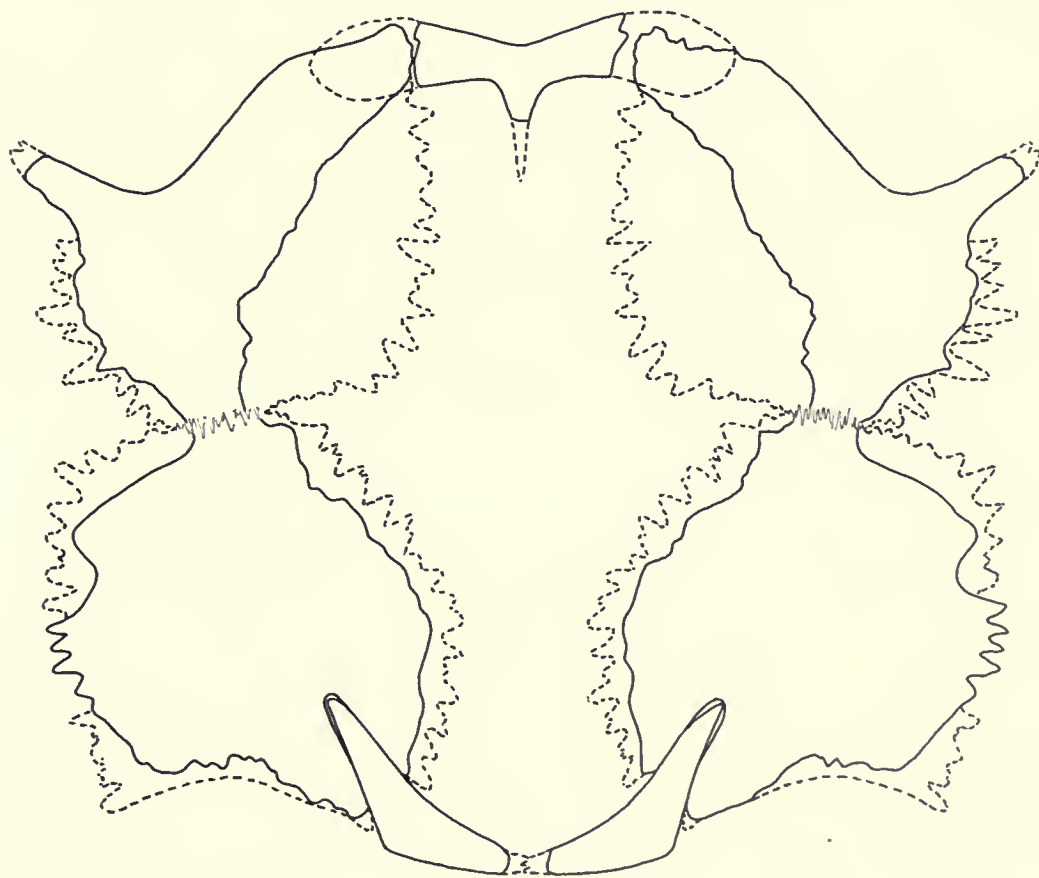

FIG. 19. *Protostega potens.* Reconstruction of plastron. About × 0.1.

process protrudes considerably beyond the caput humeri, and the distal end of the radial protuberance rises abruptly from the shaft. The distal expansion is probably greater than in *P. gigas*, but not as great as in *A. ischyros*. On the whole, the humerus closely resembles that of *P. dixie*.

The ?left femur is shown on plate 6, fig. D. It appears to differ from that of *P. gigas* in being straighter in its distal half, probably because of distortion.

Archelon copei (Wieland)

Protostega copei Wieland, 1909, Amer. Jour. Sci., (4), **27**, p. 104.

Discussion.—This species was based on an originally disarticulated but subsequently mounted skeleton of moderate size, Y.P.M. 1787. The carapace, contrary to what Wieland's illustrations would suggest, is typical for the large and specialized protostegids. One feature that distinguishes this form from *Protostega gigas* is the even keel formed by the neural series. The plastron, according to Wieland, possesses more numerous digitations than that of *P. gigas*, and the hyo- and hypoplastra join in a much broader suture than in that form. The limb bones are said to be relatively short and small.

The skull exhibits a number of differences from that of *P. gigas*, including a more pronounced premaxillary beak area.

There can be no doubt that this species is distinct from *P. gigas*. Since a considerable number of skeletons of *P. gigas* have become known to date, one of the major objectives of my trip to the museums mentioned in the Introduction was to determine whether or not additional materials referable to *A. copei* have accumulated among the undescribed specimens in the collections.

Indeed, a fine skeleton exhibited on a slab in its original burial position in the United States National Museum, U.S.N.M. 11649, is believed to belong to *A. copei* (pl. 8). Careful inspection of the neural series reveals that adjoining elements are uniform in shape and approximate size. Each neural element is longitudinally slit (as in the mounted skeleton of *Archelon ischyros*). There is no doubt whatever, in this specimen, that these slits were made when the neural elements where crushed onto the underlying vertebral centra. In addition to longitudinal cleavage, each neural has a transverse fracture (see pl. 8), which resulted in the raising of the central area. There can be no question but that the neural series of this specimen, before it was altered, formed an even keel, as in the type specimen of *A. copei*. It is also possible to determine that the hyoplastra and hypoplastra are united by a much wider suture than in *P. gigas*, even though the actual sutures are hidden by overlying ribs (pl. 8). The number of digitations on these plastral elements varies greatly from one individual to the next, but Wieland's reconstruction probably included too many digitations.

Besides these similarities, there are differences. The costal plates in U.S.N.M. 11649 do not reach laterad as far as in the type specimen, the supra-pygal plate is relatively longer than in the latter and the last pair of ribs do not appear to have borne costal plates, although it is difficult to make out the exact extent of the sutures in that area.
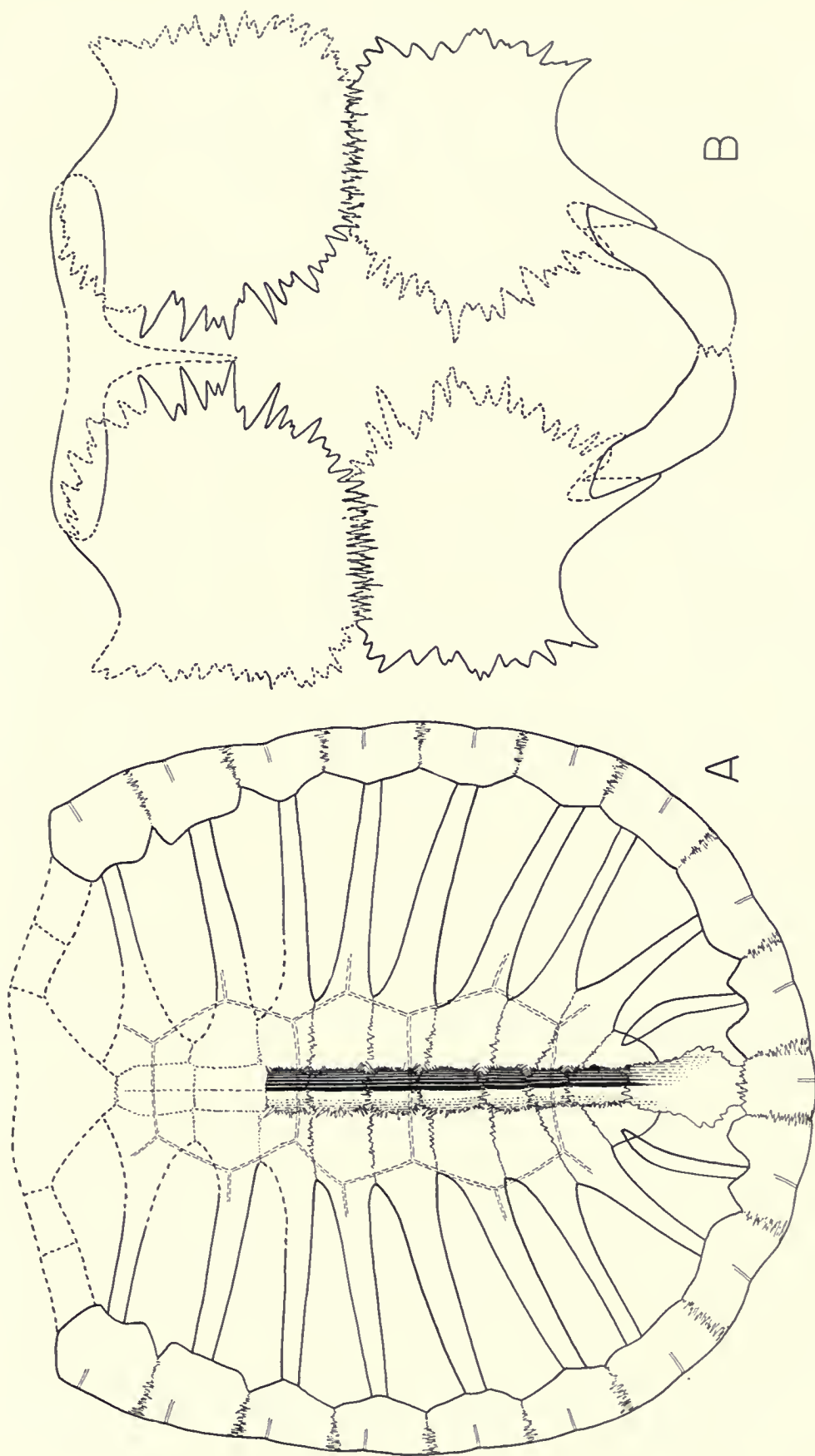
FIG. 20. *Archelon copei.* Reconstruction of carapace (A) and plastron (B). Mostly based on U.S.N.M. 11649 and the type. About × 0.12.

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The reconstruction of the shell of this species is based mostly on U.S.N.M. 11649, with missing parts added from the type specimen (fig. 20).

There appear to be two distinct lines of differentiation of the neural keel in the advanced (as well as among the primitive members; see below, p. 128) Protostegidae, namely, those with an even keel (of which *Archelon ischyros* is an advanced example) and those with an uneven, interrupted one (*Protostega gigas* and *P. dixie*). This distinction affords a far better characterization of the two genera, *Protostega* and *Archelon*, than has hitherto existed. It is consequently proposed that the species *copei* be transferred to the genus *Archelon*.

Subfamily **Chelospharginae**

Chelosphargis gen. nov.

Diagnosis.—Primitive genus of Protosteginae of small or medium size. Skull with blunt, straight premaxillary beak. Frontal bones large and with lateral processes toward the orbital rims. Prefrontals excluded from sagittal contact by nasal bones. Otic and exoccipital area very similar to condition in cheloniid turtles. Lower jaw with long symphysis; rami fused, even in juvenile specimens. A slight, but sharp sagittal crest on triturating surface of lower jaw. Carapace laterally with fontanelles of moderate size in juvenile specimens. Neural bones forming blunt, low keel in midline. Peripheral edge of carapace even. Pygal plate entirely separating eleventh pair of marginals.

Type.—*Protostega advena* Hay (1908).

Chelosphargis advena (Hay)

Protostega advena Hay, 1908, Carnegie Inst. Wash. Publ., **75**, p. 200, figs. 256–259.

Diagnosis.—Same as that of the genus.

Discussion.—The type specimen of this species is preserved at the Museum of Natural History, University of Kansas, and bears the number K.U. (V.P.) 1209. Chicago Natural History Museum recently acquired from Mr. George F. Sternberg a specimen (C.N.H.M. PR121) belonging to this species that is of almost exactly the same size as the type and agrees very closely with it. The exact locality is in doubt; it was collected in the Niobrara Chalk, either from between Bogue and Hill City, or from Gove County, Kansas. Another, larger specimen (C.N.H.M. PR126), consisting of only two peripheral bones, was obtained at the same time; it was found in Gove County, Kansas.

During my recent visit to various collections, I found that this species is not at all rare, but is represented mostly by very young individuals. The following additional specimens, all from the Niobrara Formation, belong to this species:

K.U. (V.P.) 1258.   Martin's Canyon, Kansas. The specimen is a very young individual. The posterior end of the carapace and the middle part of the carapacial disk are preserved (fig. 25).

K.U. (V.P.) 1219. Exact locality unknown. This specimen is of the utmost importance, because it includes a large part of the skull and lower jaw, as well as the rarely preserved anterior end of the plastron (epi- and entoplastra), along with large portions of the carapace and posterior parts of the plastron (fig. 21).

Y.P.M. 3601. Southeast corner of Lane County, Kansas, north of Ira King's ranch, south of Smoky River. Collected by Charles Sternberg, 1906. This is an excellent specimen as regards the state of preservation (fig. 24).

Y.P.M. 3603. Gove County, Kansas. Collected by Charles Sternberg. This specimen consists of the eleventh peripheral in sutural contact with the pygal and the suprapygal; furthermore, there is an interesting small piece belonging to the posterior part of the braincase (fig. 22).

A.M.N.H. 1975. Exact locality unknown. An isolated humerus, tentatively referred to this species by Hay (1908).

C.N.H.M. UR26. Exact locality unknown. An isolated humerus closely resembling A.M.N.H. 1975.

C.N.H.M. UR25. Exact locality unknown. Two peripheral bones of a very small individual.

C.N.H.M. UR84. Exact locality unknown. A fragmentary specimen about the size of the type.

Hay's decision to place this species in the family Protostegidae must have been based on the morphology of the plastron alone, since none of the other bones of the type specimen show unmistakable protostegid affinities. In view of the fact that Hay was as a rule none too conservative in his taxonomic habits, it is rather interesting that he did not propose a new genus in this case.

The morphology of *Chelosphargis advena*—the most primitive member of the known Protostegidae—provides insight into the basic structural organization of the family.

The only element of the shell that is missing in all of the specimens available for study is the nuchal plate. The limbs, most of the girdle elements, and the caudal vertebrae are largely unknown.

Most fortunately, one of the specimens, K.U. (V.P.) 1219, possesses a large part of the skull and lower jaws associated with the shell. The ventral parts of the braincase are either badly distorted or missing, but the area lateral to the foramen magnum is supplied in a small fragment of another individual (Y.P.M. 3603).

The over-all appearance and the major proportions of the skull of this species are very similar to those of the genus *Protostega*. The roof of the cranium includes, besides the regular complement of bones, a pair of distinct nasals. The frontal plates compare closely with those of *Chelonia* in having lateral processes that reach the rims of the orbits. Since the sutures are oblique in relation to the plane of the skull roof, the lateral wings of the frontals clearly separate the prefrontals from the postorbitals on the dorsal side of the orbital rim, whereas, on the ventral side, these two bones are in contact (fig. 21). The great relative length of the orbit, somewhat exaggerated by dorso-ventral crushing, probably reflects the very juvenile condition of this specimen rather than a feature of the organization of the genus or species.

The antorbital region of the skull, as in all known protostegid turtles, is of considerable size. The premaxillae do not form a beak, however. As in the genera *Protostega* and *Archelon* (and in contrast to the Cheloniidae), there is a primary palate whose detailed morphology cannot be made out in this specimen. The posterior part of the braincase and the otic region of specimen Y.P.M. 3603 reveals, in spite of some dorso-ventral crushing, the construction of this area of the skull. On the whole, this fragment compares very well, even in minor detail, with the corresponding region in *Chelonia*, rather than in *Dermochelys*. The stapedial canal of the quadrate is closed, but there is good reason to believe that this is the result of compression and that it was open in life (fig. 22).

There is evidence of the presence of epidermal shields on the skull in the form of a few unmistakable shield furrows. One of these crosses the most anterior part of the parietal bones (fig. 21); the other runs across the bony bridge between the nasal opening and the orbit. The exact pattern of these shields cannot be ascertained, however.

The lower jaw, as in *Protostega* and *Archelon*, has a relatively long symphysis. The rami are completely fused in this young individual. The triturating surface is concave and provided with a sagittal crest (fig. 21).

A few vertebrae belonging to the neck region of the vertebral column are associated with K.U. (V.P.) 1219. Even though these vertebrae are distorted, a characterization of their general structure is possible. The vertebrae are short, about as long as wide, and high. The centra are procoelous, but the state of preservation permits no further characterization of the joint surfaces. A very conspicuous feature of the centrum is the large, thin, hypapophyseal keel. Its dorso-ventral extent amounts to more than a third of the total height of the vertebra. The neurapophyses have very low neural spines and enclose a relatively large neural canal. Both pre- and postzygapophyses are clearly defined processes with the articular facets facing upward and downward, respectively. Strong transverse processes arise from the very base of the prezygapophyses.

The carapace was probably somewhat cordiform in outline, more so in adult than in juvenile individuals. It is made up marginally of a series of peripheral bones, relatively massive, particularly on the sides and in the rear; in front it is bordered by thin and flat peripheral elements, as is typical for all members of the family. One peculiarity lies in the fact that the peripheral bones seem to decrease notably in size from the fourth backward in the type specimen and in C.N.H.M. PR121, both of which are nearly equal in size (see fig. 23), whereas in the smaller specimens such is not the case. Possibly the anterior and posterior peripheral elements have different growth rates.

If the pygal area of the carapace is compared in K.U. (V.P.) 1258 and Y.P.M. 3603 from the ventral side (fig. 25), a number of obvious, though minor differences are noticeable. These are probably individual variations. The third peripheral is particularly characteristic. It is a thin, slightly curved plate whose posterior edge makes contact with the adjoining fourth peripheral by means of a crescent-shaped sutural face. Anteriorly, the plate becomes very narrow where it sutures
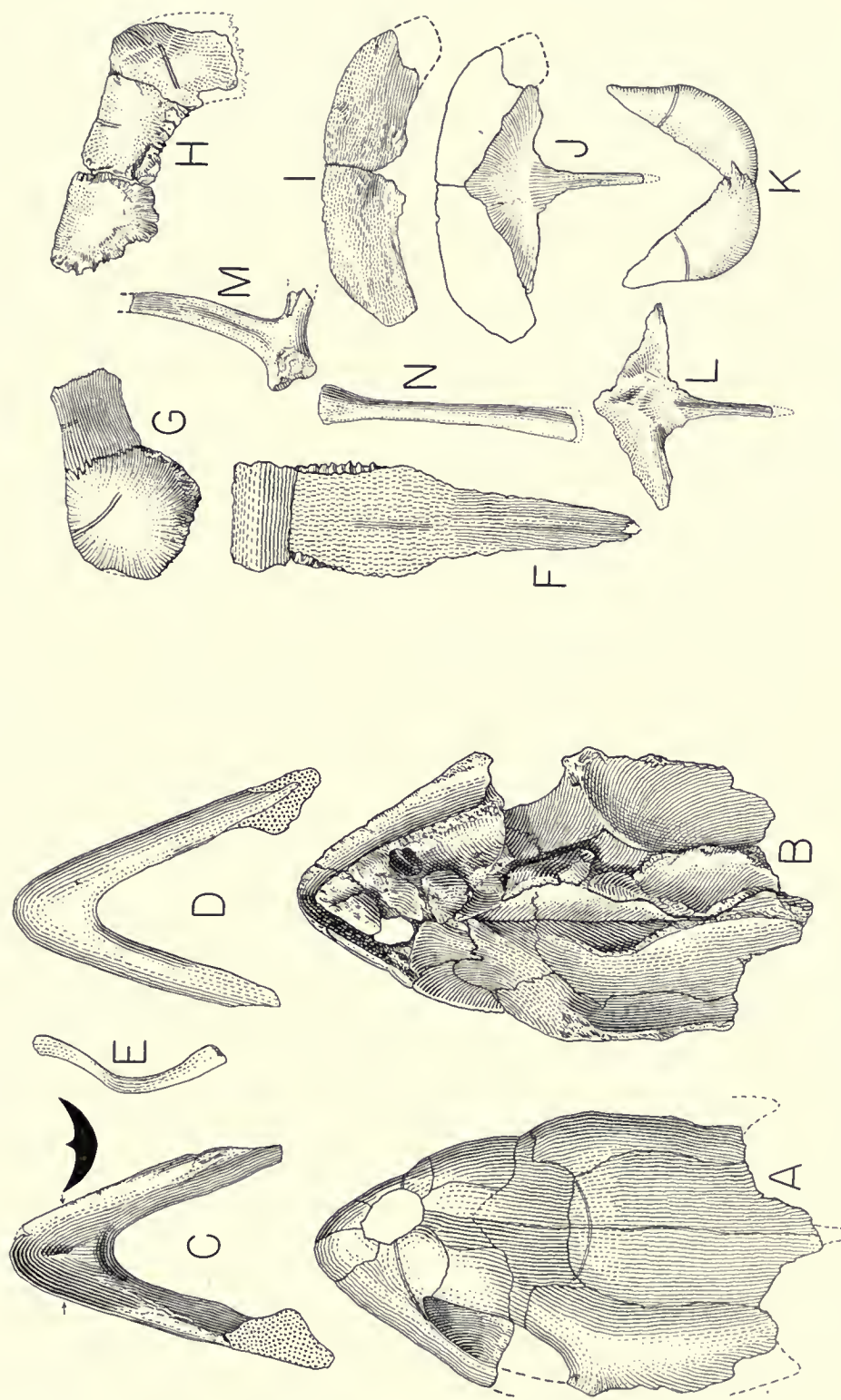
FIG. 21. *Chelosphargis advena.* K.U. (V.P.) 1219. A, skull roof, dorsal view; B, skull roof, ventral view; C and D, mandible; E, hyoid element. A–E, about × 1.14. F, second right costal plate with corresponding neural; G, left second and third peripherals; H, right first, second, and third peripherals; I, epiplastra, ventral view; J, entoplastron, ventral view; K, xiphiplastra, ventral view; L, entoplastron, dorsal view; M, scapular fragment; N, coracoid. F–N, about × 0.81.
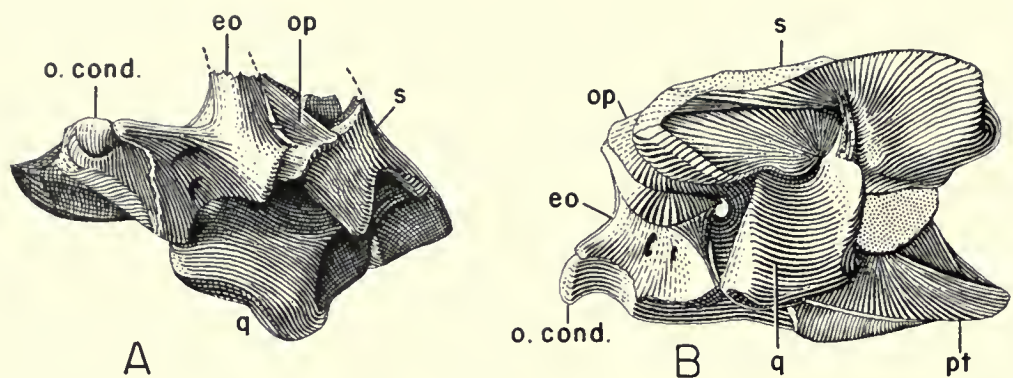
FIG. 22. *Chelosphargis advena*. Y.P.M. 3603. Fragment of occipito-otic region of skull. A, posterior view; B, lateral view. *O. cond.*, occipital condyle; *eo*, exoccipital; *op*, opisthotic; *s*, squamosal; *q*, quadrate; *pt*, pterygoid. About × 0.33.

FIG. 23. *Chelosphargis advena*. C.N.H.M. PR121. This specimen is almost the same size as the type specimen. A, right peripheral plates 4 to 9, ventral view; B, hyo- and hypoplastra, ventral view; C, pygal plate, ventral view. About × 0.51.
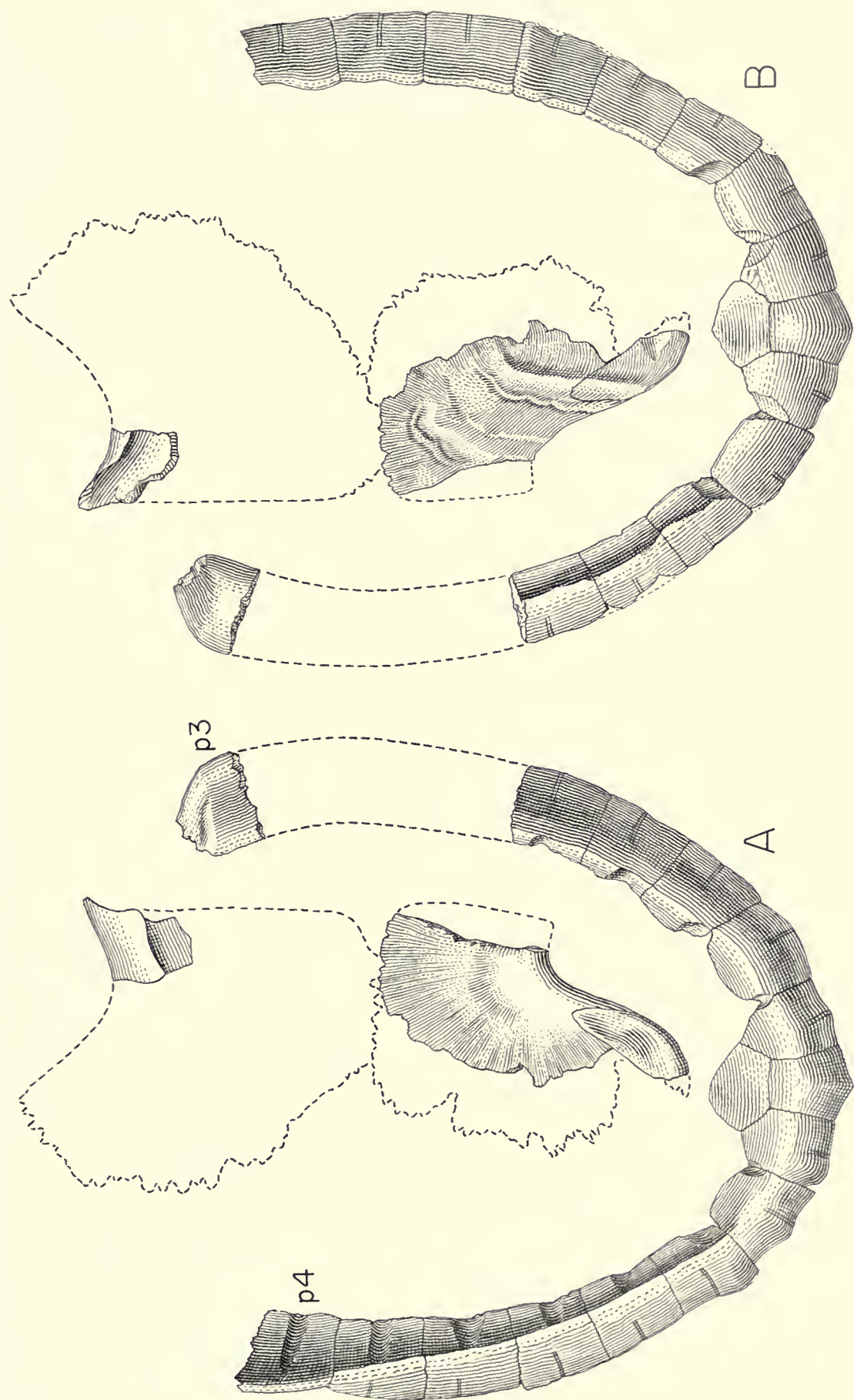
FIG. 24. *Chelosphargis advena.* Y.P.M. 3601. A, ventral view; B, dorsal view. Drawn from photographs. *p3*, third peripheral; *p4*, fourth peripheral. About × 0.79.

onto the second peripheral. In the articulated carapace, the plate stands nearly vertical, so that the contact with the second peripheral is in an antero-dorsal position (see figs. 21 and 26). The third peripheral of *Calcarichelys* (fig. 56) is all but identical with that of *Chelosphargis*. A comparison with the equivalent element in the large species of Protostegidae shows the same basic construction again, except that in the latter forms the edges of the plate are provided with finger-shaped digitations, or pronounced serrations.

In peripherals 4 to 7, the sutural faces are triangular in shape, so that the dorsal surfaces are concave and the ventral ones convex. The medial faces are concave and show distinct rib pits almost exactly as in *Calcarichelys* (see p. 120, fig. 56).
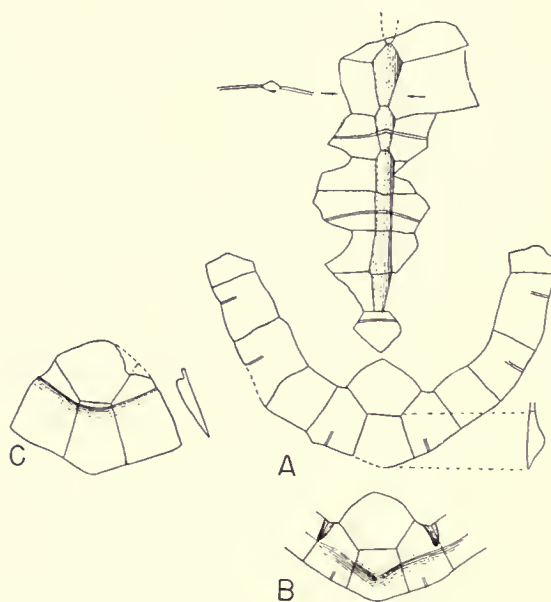

FIG. 25. *Chelosphargis advena.* A and B, sketches of K.U. (V.P.) 1258. A, dorsal view; B, ventral view. C, pygal area of Y.P.M. 3603, dorsal view. About × 0.53.

The sagittal area of the carapace consists of a series of neural bones of normal thickness whose boundaries in dorsal aspect are mostly rectangular in outline. Adjoining elements of the series are of about equal length, and form an even, unbroken keel of little height. This latter statement may have to be modified somewhat when more complete shells of larger specimens become available. In the type specimen, the first and second neurals have a rather sharp crest. In K.U. (V.P.) 1258, the keel is distinct, but low, and is almost perfectly even through six successive neurals that are preserved intact (fig. 25). The same is true in Y.P.M. 3601, except that only five adjoining neurals are preserved. In C.N.H.M. UR84, two neural plates are preserved, neither of which shows a dorsal crest; instead, the dorsal surface is but slightly rounded from side to side. In K.U. (V.P.) 1219, there is only one neural (tentatively identified as the second) whose dorsal face is broadly arched, but not crested.
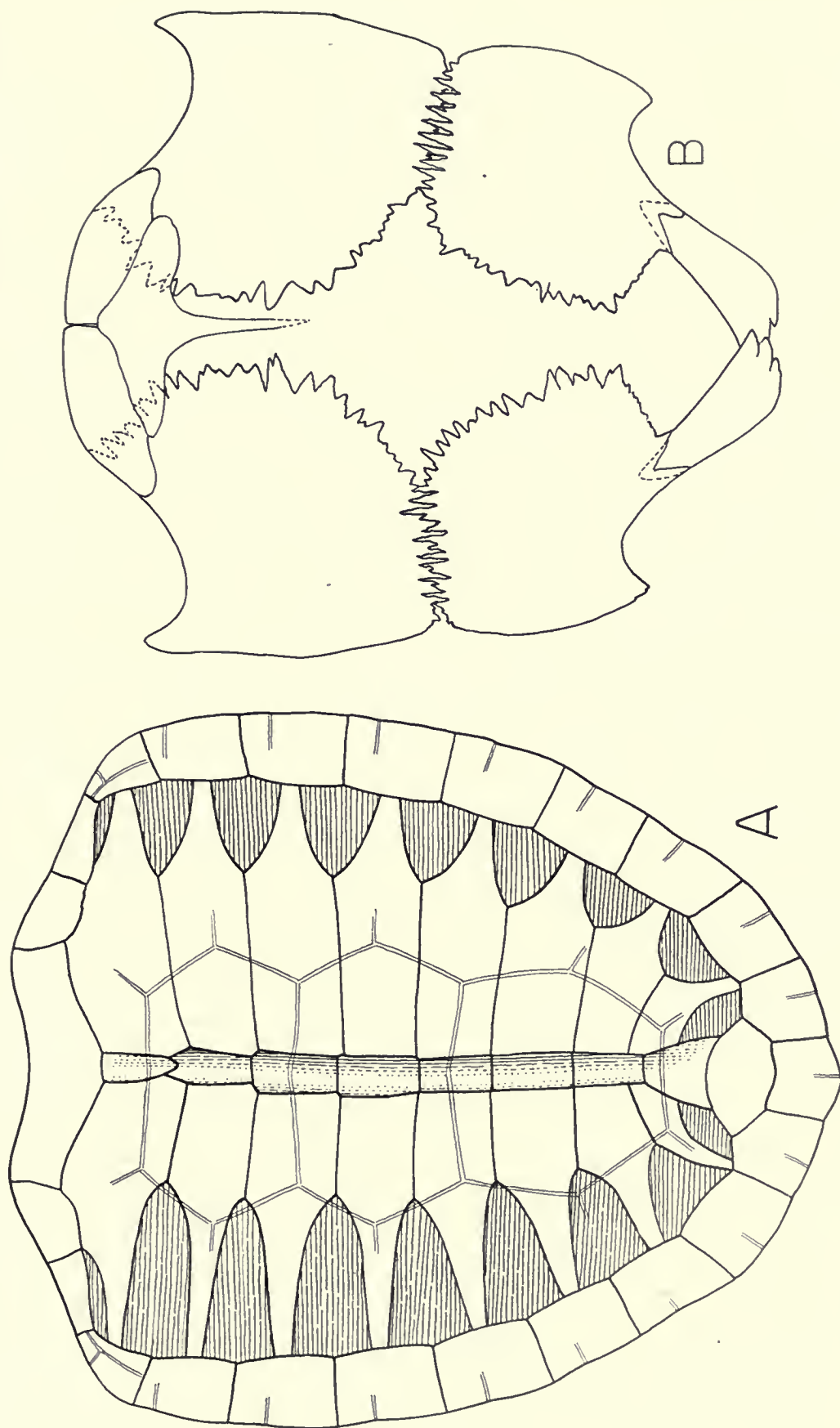
FIG. 26. *Chelosphargis advena.* Reconstruction of carapace (A) and plastron (B) from all available materials. A, left side represents juvenile, right side adult condition.

This difference would indicate that there is a certain amount of variation in these specimens, independent of age.

In very young specimens, large lateral fontanelles lie between the costal plates and the peripherals. Apparently, these fontanelles are reduced to moderate size in the adults (fig. 26, A, right and left). Well-marked scale imprints are visible in all specimens, but only on the carapace.

The plastron of *Chelosphargis advena* is the most primitive known among the Protostegidae. Epiplastra of considerable size are present. They are thin, flat plates whose posterior edges overlie the antero-lateral edges of the T-shaped entoplastron (figs. 21, 26). Hyo- and hypoplastra are large plates, the medial edges of which show numerous digitations; the lateral borders of these plates are but slightly serrated. The xiphiplastra exhibit the typical protostegid shape (fig. 26).

A scapular fragment and a coracoid (fig. 21) are associated with K.U. (V.P.) 1219. The scapula is flattened by compression. It is almost certain that the two scapular processes were nearly circular in cross section, as is the uncrushed shaft of the coracoid. As in *Protostega* and *Archelon,* the distal end of the coracoid is only slightly expanded.

No humeri are associated with any of the shell materials. Hay (1908) mentioned two very similar left humeri (about 65 mm. long)—one in the collection of the American Museum of Natural History (A.M.N.H. 1975) and the other in the University of Chicago collection (UR26)—which he referred to this species. The reason given for this decision is that these bones have the appearance of belonging to adult individuals. Evidence from our material of *P. dixie* tends to confirm Hay's interpretation. The humerus associated with the smallest specimen of *P. dixie* (C.N.H.M. P27319), with a maximum transverse diameter of the hypoplastron of 220 mm., is about 120 mm. long and at least three times as thick as the humeri mentioned by Hay. Furthermore, it has all the earmarks of a juvenile bone.

The reconstruction (fig. 26) presents a composite picture of the organization of the shell, based on all available materials. The left side of the carapace is designed to illustrate the juvenile condition, whereas on the right side the adult condition is depicted. The peculiar decrease in the size of the peripherals, described above, was not included in the reconstruction, because the interpretation, as suggested above, needs confirmation.

Calcarichelys cf. gemma Zangerl

Diagnosis.—See page 119.

Discussion.—Among the turtle material recently acquired from Mr. George F. Sternberg, there is an isolated fifth peripheral of the left side. It compares in every detail but size with the corresponding element in the type specimen of *Calcarichelys gemma* (p. 119). The length of this bone is 34 mm. as against 30 mm. in the corresponding element in the type specimen.

The exact locality of this specimen, C.N.H.M. PR122, is in doubt. The label states that it came from between Bogue and Hill City, or from Gove County, Niobrara Chalk, Kansas.

EAGLE FORD SHALE OF TEXAS

Subfamily **Protosteginae**

Diagnosis.—See page 129.

Protostega eaglefordensis sp. nov.

Diagnosis.—Large protostegid with costal plates less vestigial than in related forms. Ulnar process of humerus scarcely protruding proximally beyond the caput humeri. Radial tuberosity relatively weak. Symphyseal part of pubis very large; prepubic process moderate in size. Ischium relatively long and slender, provided with spur-shaped process on its posterior edge. Foramen puboischiadicum relatively large, and possibly open medially.

Type.—T.M.M. No. 924, partial skeleton, consisting of several ribs and costal plates, a displaced nuchal that lies partly buried under proximal rib ends, one coracoid, both humeri, both zeugopodia of the arm, both carpi and much of the right manus (fig. 28) as well as the left pubis and ischium.

Horizon and locality.—Uppermost part of the lower shale, from six to ten feet below the Flag Member of the Eagle Ford Formation. Lake Waco Dam, McLennan County, Texas.

Discussion.—The specimen was prepared from its ventral side and lies in the original matrix in which it was found. Many of the missing parts were reconstructed at the time it was placed on exhibition.

All parts preserved suggest at once that this is a large protostegid. But the critical elements that would permit a definite generic decision are unfortunately lacking. The limbs and girdles are more primitive than in any known large protostegid, but it is impossible to say whether they are closer to *Protostega* than to *Archelon.* It is possible that a new genus may have to be proposed for this species, but it is desirable to wait until additional materials are discovered before taking this step. The species is tentatively referred to *Protostega.*

Little need be said of the few elements of the carapace that are available. The nuchal plate, in so far as its outline can be made out, agrees closely with that of other large members of the family. On its ventral side, a short distance behind the anterior edge, there is the unpaired articular process characteristic of all living sea turtles and of the Protostegidae as well. The ribs are saber-like and are covered by vestigial costal plates. The latter are, however, relatively greater in extent than in any other large protostegid. The ribs that are preserved are identified (with reservations) as Nos. 2 to 6 and 8.

The humerus shows a number of primitive features (fig. 27). The ulnar condyle is no more conspicuous than the caput humeri and the radial tuberosity
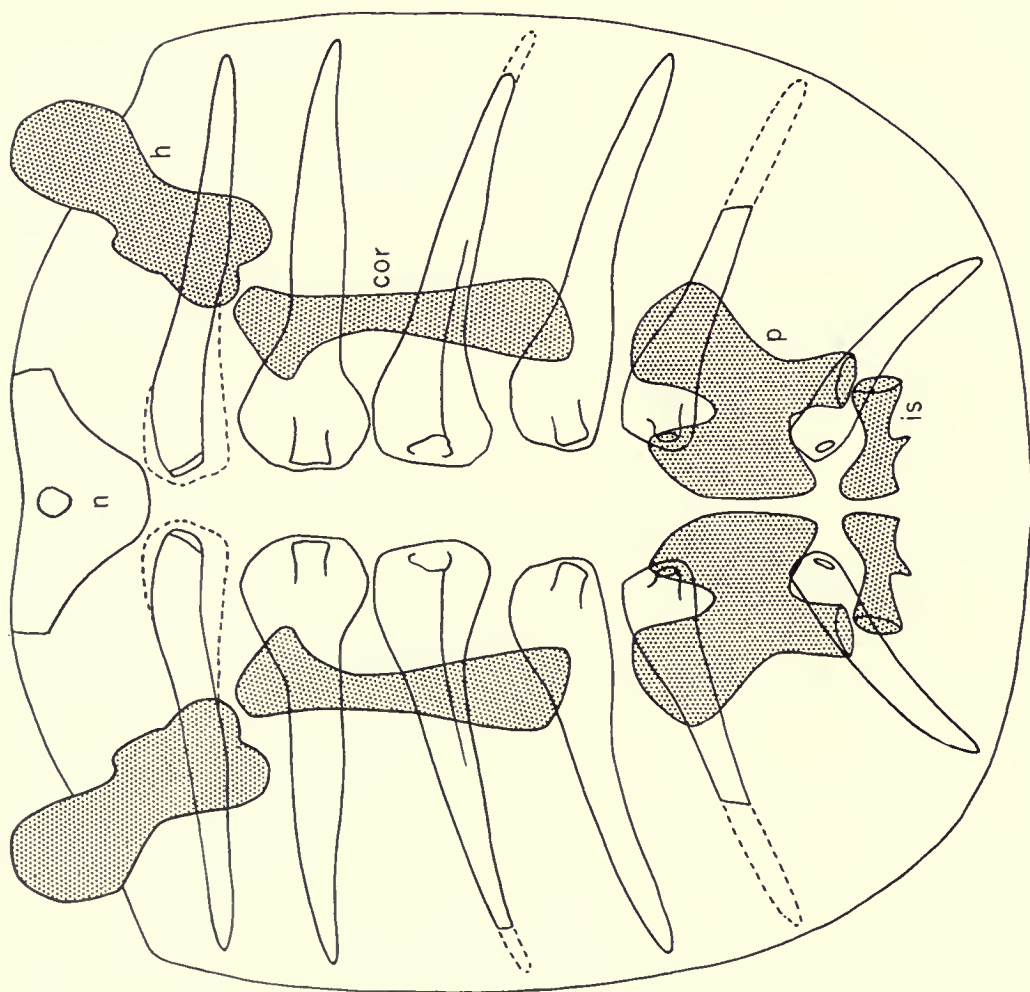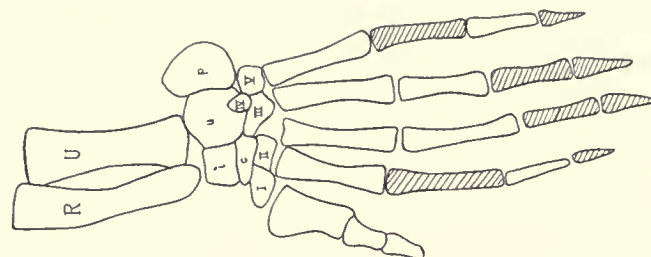
Fig. 28. *Protostega eaglefordensis.* T.M.M. 924. Right forearm, ventral view. *R*, radius; *U*, ulna; *i*, intermedium; *u*, ulnare; *p*, pisiforme; *c*, centrale; I, II, III, IV, V, distal carpal elements. About × 0.11.

Fig. 27. *Protostega eaglefordensis.* Reconstruction of T.M.M. 924. *Cor*, coracoid; *h*, humerus; *is*, ischium; *n*, nuchal; *p*, pubis. About × 0.1.

is likewise less developed than in the geologically younger forms, excepting *Archelon ischyros*, in which it is vestigial. The coracoid exhibits no peculiarities. The relatively great proximal expansion appears to have been caused by crushing.

The pelvis (fig. 27) is significantly more primitive than in any other known protostegid. The pubis is characterized by a large symphyseal process, a prepubic process of normal dimensions and a relatively long acetabular process. The ischium is relatively long and slender, and is provided with a large, spurlike process along its posterior edge. This process faces toward the acetabulum. A homologous process was described and figured by Williston (1898) in *Desmatochelys lowi*, but it is also found among the Toxochelyidae and others. It is possible that the foramen puboischiadicum was open medially (fig. 27).

BROWNSTOWN MARL OF ARKANSAS

Protostega sp.

Discussion.—The anterior part of a large protostegid lower jaw (C.N.H.M. PR2) was collected by Mr. C. M. Barber in a small field gully, about three-quarters of a mile southeast of Ben Lomond, Sevier County, Arkansas. A few skull scraps were also picked up.

The length of the symphysis along the outer face is about 140 mm.; the length of the mouth part of the symphysis that was covered by a horny beak measures about 80 mm., and the height of the jaw at the posterior end of the symphysis is also 80 mm. The specimen is tentatively referred to *Protostega*.

MARLBROOK MARL OF ARKANSAS

Protostega sp.

Discussion.—Among the material collected by Mr. C. M. Barber during September, 1934, in the Marlbrook Marl of Arkansas, there is a large, left, fourth peripheral, 230 mm. long, and a correspondingly large, but undiagnostic fragment of a hyo- or hypoplastron. This lot, C.N.H.M. P27458, was collected on the Charles Townsend Farm, 1½ miles southwest of the junction of the Okolona-Hollywood Road to Arkadelphia, Clark County, Arkansas.

The fourth marginal plate differs from its homologue in the material of *Protostega* that I have available for comparison by the fact that the large rib pit lies considerably farther forward and its limits are not very clearly outlined. In all other respects, the element resembles very closely (save for its much larger size) the corresponding peripheral of C.N.H.M. P27385, a medium-sized specimen of *P. dixie*.

The exact morphology of the peripherals of *Archelon* has never been made out in detail, so that comparison with that genus is impossible. The reconstruction of these elements in the mounted specimen of *A. ischyros* is somewhat idealized (Wieland, 1909). Possibly this specimen belongs to *Archelon*, rather than to *Protostega*.

PIERRE SHALE OF COLORADO

Archelon ischyros Wieland

Discussion.—Apparently, no additional specimens of this species have been found in South Dakota. The remains mentioned below from Colorado add little to our knowledge of this form.

Archelon cf. ischyros Wieland

Discussion.—In the United States National Museum are some large bones, chiefly girdle elements and ribs (U.S.N.M. 13439), that belong beyond doubt to a large protostegid turtle and are tentatively referred to the above species. They were found eight miles east of Trinidad, Los Guimas County, Colorado, by C. W. Gilmore, in 1931.

Most of these bones compare rather closely with those of *Archelon ischyros* of the Pierre Shale of South Dakota, but the ilium is a relatively longer and stouter bone. The length of the ilium measures 250 mm. (300 mm. in *A. ischyros*), the scapula 510 mm. (660 mm. in *A. ischyros*), between the distal ends of the two processes.

DESCRIPTION OF THE ALABAMA MATERIALS

Although Chicago Natural History Museum has now by far the richest known collection of protostegid turtles from the Mooreville Chalk of Alabama, two other institutions have some materials from this formation. Peabody Museum of Yale University possesses a hyoplastron of medium size of *Protostega dixie* that was sent to Professor Marsh by E. R. Schowalter, who claimed, in a letter to Marsh, to have obtained it along Cahaba River, one-half mile south of the railroad bridge. There can be no doubt that the railroad bridge here referred to is the one over which the Southern Railroad crosses Cahaba River east of Harrell Station. The fossil thus came from the large Marion Junction outcrop area, an aerial photograph of which was published in Part I (pl. 3; see also fig. 29).

Some other materials of a protostegid turtle are located in the Museum of Geology of the University of Alabama at Tuscaloosa, Alabama (Renger, 1935). I have not seen these materials, and Renger's account does not state of what they actually consist.

The following description of the protostegid turtles from the Mooreville Chalk of the Selma Formation in Alabama is based on some 40 specimens. A few of these are represented by sufficiently complete skeletons to permit detailed comparison with those from other formations, but none of the specimens were found entirely articulated. As a rule, apparently, the skeletons became completely disarticulated prior to burial. Consequently, remains of protostegid turtles are relatively common finds, whereas major portions of skeletons buried in circumscribed areas seem to be excessively rare. The material at hand is
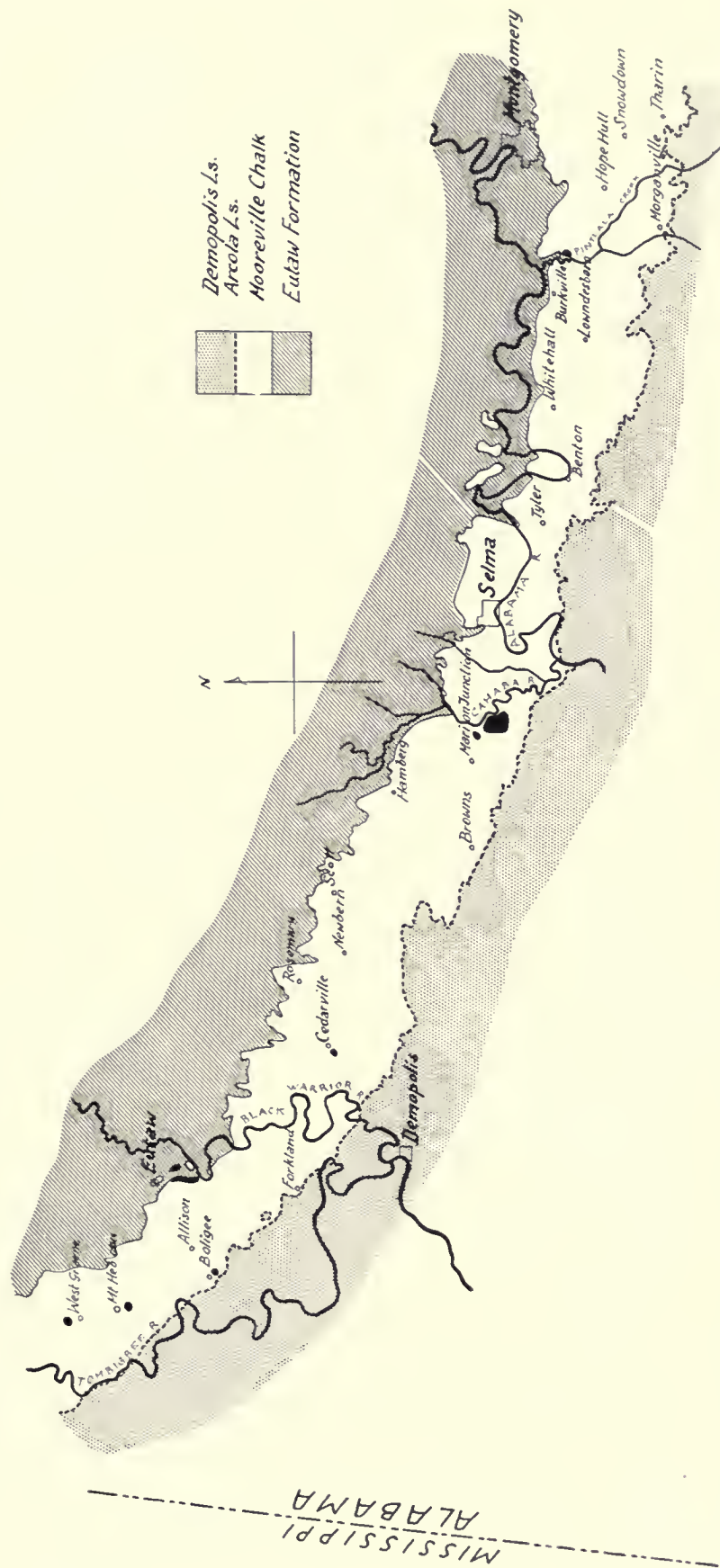
FIG. 29. Map of Mooreville Chalk in Eutaw-Selma-Montgomery area, showing localities (black spots) from which protostegid turtles have been collected.

nevertheless extensive enough to permit an adequate description of nearly every part of the skeleton.

Three protostegid turtles occur in the Mooreville Chalk of Alabama. One of them, by far the most common, is a large form with a calculated carapace width of nearly 1½ meters in the largest specimen. This form is represented in the collection by individuals that show considerable size range. The species is readily determined as a member of the genus *Protostega*. Specifically, however, it is distinct from the Niobrara forms. The remaining two protostegids discovered in the Mooreville Chalk are small (but possibly juvenile) and primitive forms, which, together with *Chelosphargis advena* (Hay) from the Niobrara Chalk of Kansas, represent a most interesting, primitive group within the family.

One of the forms in the Mooreville Chalk collection is, on the basis of the bones preserved, scarcely distinguishable from *C. advena;* the other, however, is so uniquely specialized that it will be described under the genus and species *Calcarichelys gemma*.

Subfamily **Protosteginae**

Diagnosis.—See page 129.

Protostega dixie sp. nov.

Diagnosis.—A large species closely related to *P. gigas* and *P. potens*. Skull nearly as wide as long. Antorbital beak area high, with the curved tip of the premaxilla below the level of the lower rim of the orbit. Plastron with a large central fontanelle reaching posteriorly to the xiphiplastra. Suture between hyo- and hypoplastra very narrow. Antero-lateral edge of hyoplastron about half the distance between axillary notch and hyo-hypoplastral suture.

Type.—C.N.H.M. P27314. A large portion of the skeleton, including the skull, parts of the carapace, a nearly complete plastron, shoulder girdle and elements of the limbs. Collected by C. M. Barber and party during the fall season of 1945. Additional materials belonging to this specimen were collected on subsequent occasions when the locality was revisited.

Horizon and locality.—Lower, marly member of the Selma Formation (Mooreville Chalk), Late Cretaceous. The exact locality is indicated on the aerial map (Part I, pl. 3) of the Harrell Station area, southeast of Marion Junction, Dallas County, Alabama.

REFERRED SPECIMENS LISTED ACCORDING TO LOCALITIES

HARRELL STATION AREA, SOUTHEAST OF MARION JUNCTION, DALLAS COUNTY, ALABAMA

C.N.H.M.

P27315 Skull, jaws, nuchal, neurals, peripherals, plastron, humeri and other limb-bone fragments, ribs. Collected by A. Zangerl.

P27353 Scapula, coracoid. Collected by R. Zangerl and W. D. Turnbull.
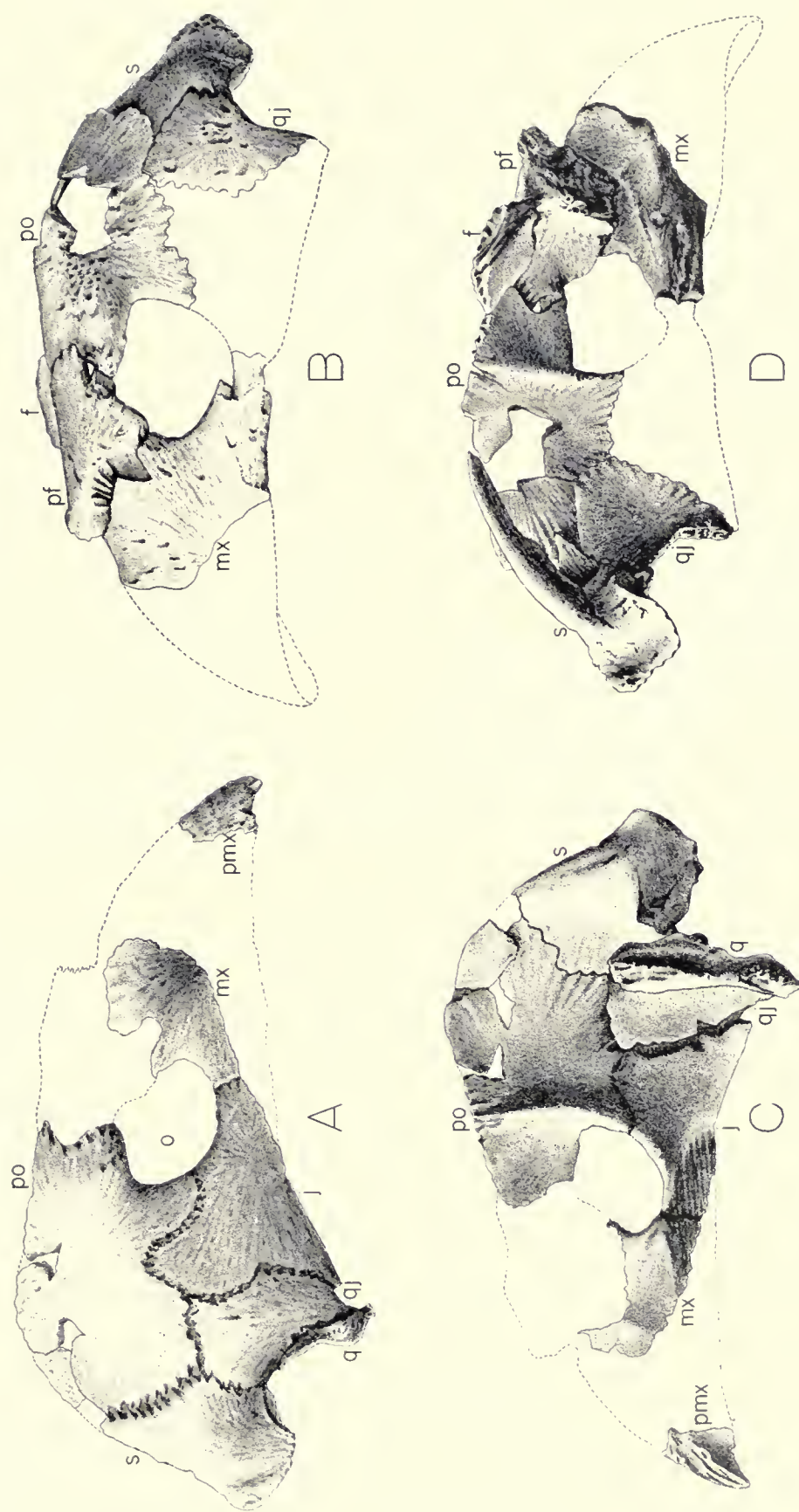
P27368 Rib. Collected by R. Zangerl.

FIG. 30. *Protostega dixie.* C.N.H.M. P27314. A, right side of skull, lateral view; B, left side of skull, lateral view; C, right side of skull, medial view; D, left side of skull, medial view. *pmx*, premaxilla; *mx*, maxilla; *pf*, prefrontal; *f*, frontal; *po*, postorbital; *o*, orbit; *s*, squamosal; *qj*, quadrato-jugal; *j*, jugal; *q*, quadrate. About × 0.19.

95

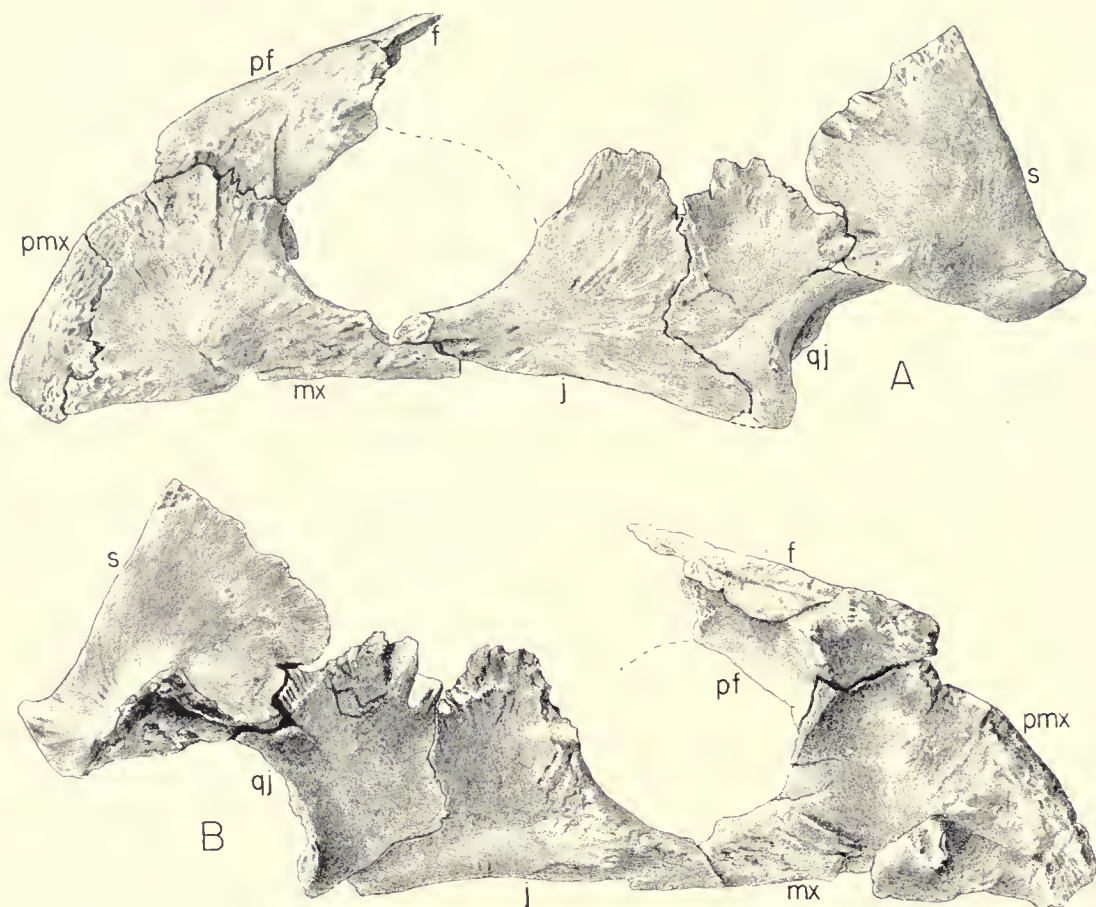FIG. 31. *Protostega dixie.* C.N.H.M. P27315. Skull. A, lateral view; B, medial view. Labels as in Figure 30. About × 0.31.

P27482 Humerus and fifth cervical vertebra. Collected by C. M. Barber.
P27427 Rib fragments. Collected by C. M. Barber.
PR71   Peripheral and rib fragments. Collected by R. Zangerl.
PR70   Two peripherals, vertebra. Collected by R. Zangerl.
PR69   Rib. Collected by A. Zangerl.
PR133   Fragments of carapace, plastron, and skull. Collected by C. M. Barber.
PR190   Peripheral plate. Collected by J. A. Robbins.
PR66   Carapace and plastral fragments. Collected by R. Zangerl.
PR197   Skull bones. Collected by J. A. Robbins.
PR134   Two plastral plates. Collected by C. M. Barber.
PR203   Partial carapace and plastron. Collected by J. A. Robbins.
PR198   Carapace and plastral fragments. Collected by J. A. Robbins.
PR72   Partial plastron. Collected by C. M. Barber.

CEDARVILLE, HALE COUNTY, ALABAMA

Crawford Farm

P27319 Parts of skull, carapace, plastron, humerus, girdle, vertebrae. Collected by R. Zangerl.
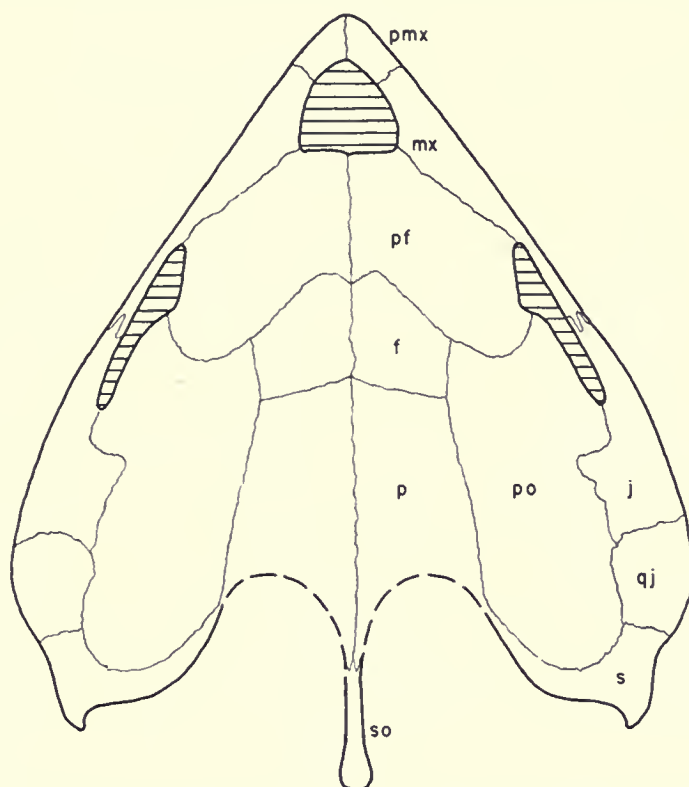PR68   Miscellaneous fragments of shell. Collected by R. Zangerl.

FIG. 32. *Protostega dixie*. Reconstruction of skull in dorsal view, based on all available materials. *pmx*, premaxilla; *mx*, maxilla; *pf*, prefrontal; *f*, frontal; *p*, parietal; *po*, postorbital; *j*, jugal; *qj*, quadrato-jugal; *s*, squamosal; *so*, supraoccipital. About × 0.2.

EUTAW, GREENE COUNTY, ALABAMA
Landis Brown Farm and Banks Farm

P27441 Peripheral. Collected by R. Zangerl.
P27473 Shell fragments. Collected by R. Zangerl.
P27471 Plastron. Collected by R. Zangerl and W. D. Turnbull.
P27452 Limb-bone fragments, carapace and plastron. Collected by C. M. Barber.
P27385 Jaw, nuchal, suprapygal, skull, rib, several peripherals. Collected by R. Zangerl, W. D. Turnbull, and C. M. Barber.
PR67   Carapace fragments. Collected by C. M. Barber.
PR132 Caudal vertebrae, partial carapace, limb bones, skull. Collected by W. D. Turnbull.
PR151 Two neurals, atlas, axis, girdle, costal plate. Collected by J. A. Robbins.
PR147 Humerus. Collected by J. A. Robbins.

BOLIGEE, GREENE COUNTY, ALABAMA
Hewlett Farm

PR58   Three peripherals. Collected by W. D. Turnbull.

MOUNT HEBRON, GREENE COUNTY, ALABAMA
Outcrop Area about 2 1/2 Miles Southeast of Town

PR21   Partial plastron, girdle, rib. Collected by C. M. Barber.
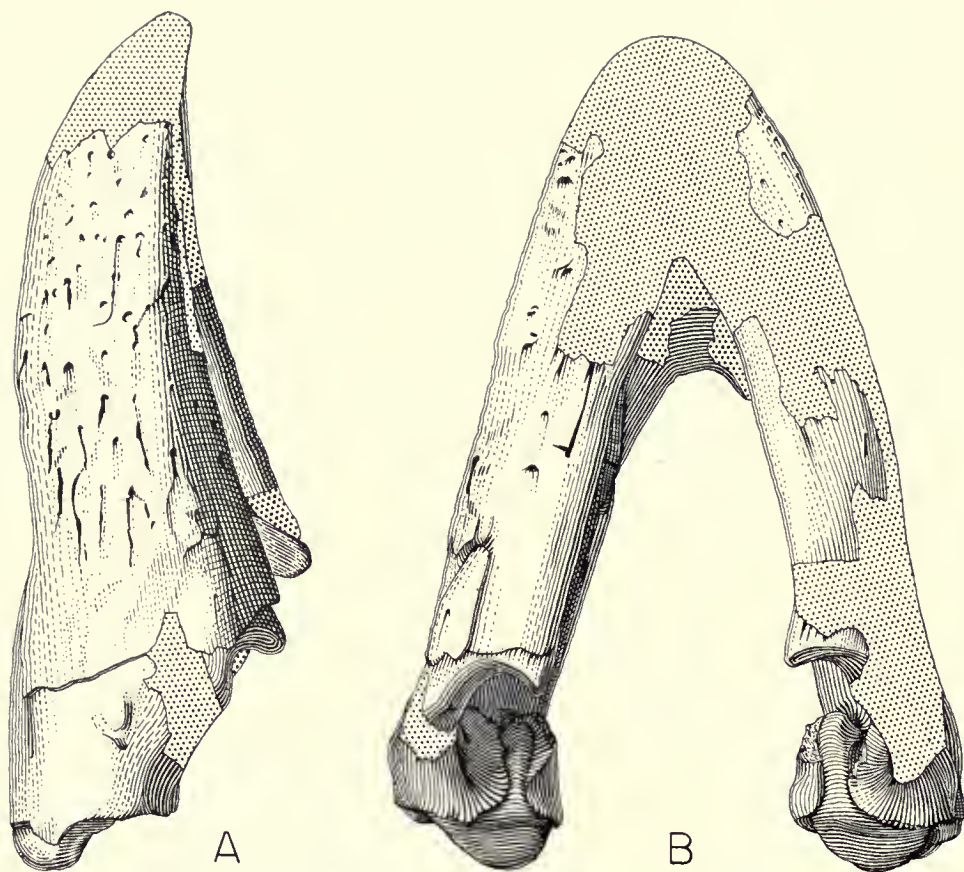PR114 Two costal plates. Collected by C. M. Barber.

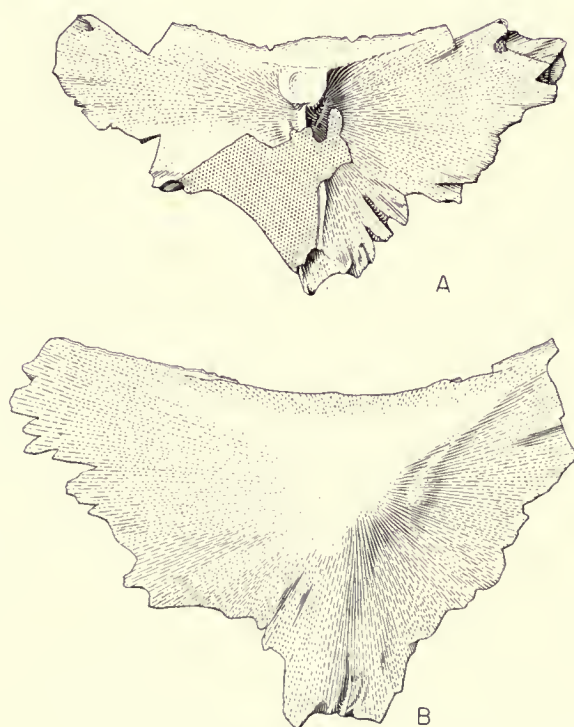FIG. 33. *Protostega dixie.* C.N.H.M. P27385. Mandible. A, lateral view; B, dorsal view. About × 0.5.

FIG. 34. *Protostega dixie.* Nuchal plate. A, ventral view (C.N.H.M. P27385); B, dorsal view (C.N.H.M. P27315). About × 0.33.

PR64   Fragmentary peripherals. Collected by C. M. Barber.
PR65   Skull, jaw and carapace fragments. Collected by W. D. Turnbull.

WEST GREENE, GREENE COUNTY, ALABAMA

Outcrop Area about 3 ¹/₂ Miles Northwest of Town

PR174   Plastral fragments. Collected by C. M. Barber.
PR163   Plastron. Collected by C. M. Barber.
PR159   Incomplete plastron. Collected by J. A. Robbins.
PR170   Incomplete skull. Collected by J. A. Robbins.
PR177   Jaw. Collected by J. A. Robbins.

The geographic distribution of the localities is indicated in figure 29. The Eutaw localities are near the basal contact of the Mooreville Chalk; the locality east of Boligee lies close to the Arcola Limestone, which forms the summit of the Mooreville Chalk.

Skull.—Disarticulated skull bones associated with other skeletal elements are by no means rare. As a rule, however, only the outer roof bones of the skull and the lower jaws are well preserved. The elements forming the braincase and the roof of the mouth cavity are in all cases in such a poor state of preservation that it is usually impossible to determine their identity, to make out their relative positions in the skull, or to attempt close comparison with related forms.

The morphology of the outer shell of the cranium (figs. 30, 31) can be determined beyond doubt. Both the over-all proportions and the shapes of the individual elements are very similar to those of *P. gigas* (see fig. 55). The snout, anterior to the orbits, is long and narrow. The premaxillae form a pointed beak that is curved downward. The external nasal opening is separated from the anterior orbital rim by a wide bridge formed by the maxillae and the prefrontals. There are no nasal bones and the frontals are excluded from lateral contact with the rims of the orbits. The posterior edge of the temporal roof is somewhat excavated on either side of the supraoccipital process; the parietal bones are thus primarily affected by this reduction. An attempt at a reconstruction of the skull in dorsal view (fig. 32), based on all available materials, brings out a peculiarity of the skull of *Protostega* that has not hitherto been noted, namely, the relatively great width across the quadrates compared to the length of the skull. Since none of the materials are entirely free from distortion, it is possible that the reconstruction shows the skull somewhat too wide posteriorly. The possible error can hardly be very significant, however, since, in the reconstruction, the quadrate reaches inward to a point well medial of the postorbital-parietal suture, much as in *Dermochelys* and *Chelonia*. In PR65, the skull roof behind the level of the orbits is complete and shows the great relative width of the structure in this area. It may be noted that this width constitutes a major difference from *Archelon,* whose skull is very narrow relative to its length.
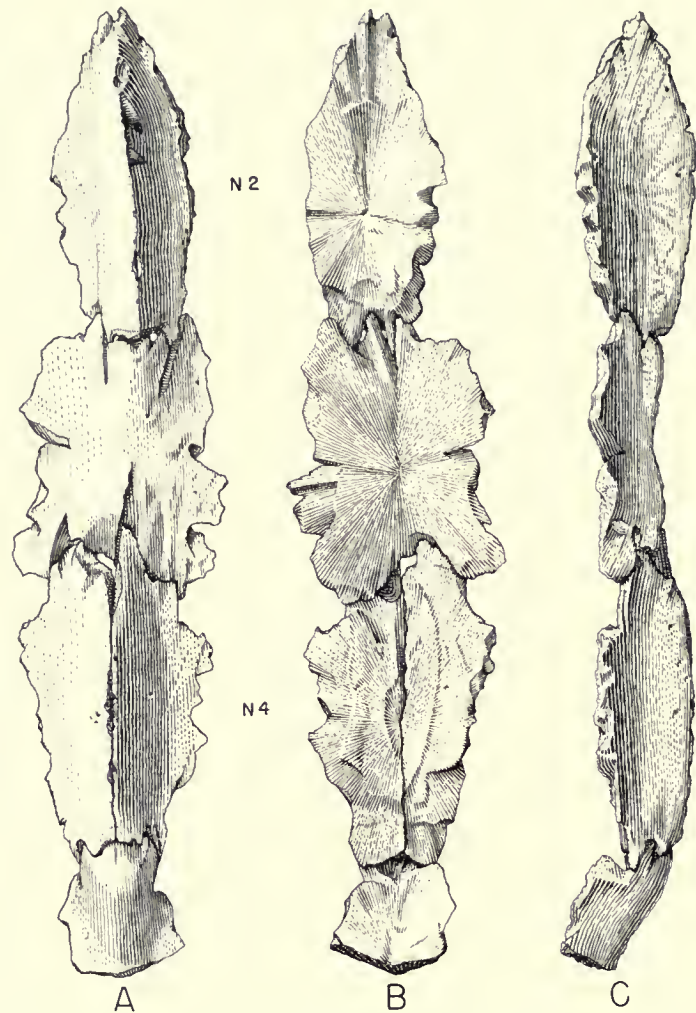
FIG. 35. *Protostega dixie.* C.N.H.M. P27314. Adjoining neural plates 2 to 5. A, dorsal view; B, ventral view; C, lateral view. About × 0.3.

Comparison of the skull of *P. dixie* with that of *P. gigas* shows a few differences that appear to be of specific importance. In the collection of the United States National Museum are two skulls of *P. gigas*, both of which have the lateral walls of the cranium preserved in articulation. One of these (U.S.N.M. 11652) belongs to a skeleton approximately the size of the type specimen of *P. dixie*. The other, smaller skull (U.S.N.M. 11651) compares in size closely with P27315 of *P. dixie*. In figure 55 all four skulls are shown in side view, photographically rendered uniform in over-all size. If the two specimens of *P. gigas* are plotted together, their outlines match fairly well; the same is true of the two specimens of *P. dixie*. A similar difference becomes apparent, however, if the two smaller or the two larger skulls of both species are plotted together. The antorbital area of the skull in *P. gigas* is more pointed and more slender in lateral aspect and the tip of the beak lies at a level about mid-height of the orbit, whereas in *P. dixie* it lies considerably below the lower rim of the orbit. Note also the usual decrease in size of orbit with increase in over-all skull size.

A nearly uncrushed lower jaw (P27385) agrees closely with Case's (1897) description of *P. gigas*. Since most of the bones of the medial sides of the rami are broken away, the presence of a presplenial element cannot be confirmed (fig. 33).

A fragment of a hyoid element is associated with P27315, but shows no unusual features.

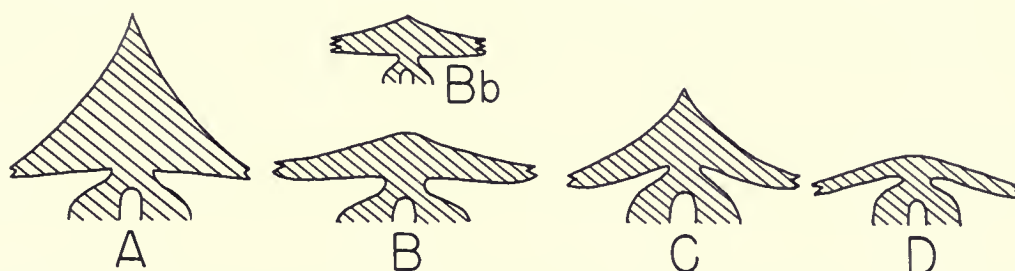*Carapace.*—The detailed morphology of the carapace of *Protostega* is still unsatisfactorily known, for two reasons, (1) the fact that the shell elements are so

FIG. 36. *Protostega dixie.* Semi-diagrammatic cross sections. A, an anterior ridged neural; B, an anterior saddle-shaped neural; Bb, same in a small individual; C, a posterior ridged neural; D, a posterior flat neural. The attachment of the neural plates to the neural arches of the vertebrae is also indicated.

greatly reduced that only the most fortunate burial circumstances could bring about preservation before the shells became disarticulated, and, perhaps even more important (2), the inner construction of the bones. They contain large cavities between delicate trabeculae and are thus almost invariably affected to various degrees by crushing and distortion. This latter point cannot be over-emphasized, since it causes endless difficulties in the comparison of one specimen
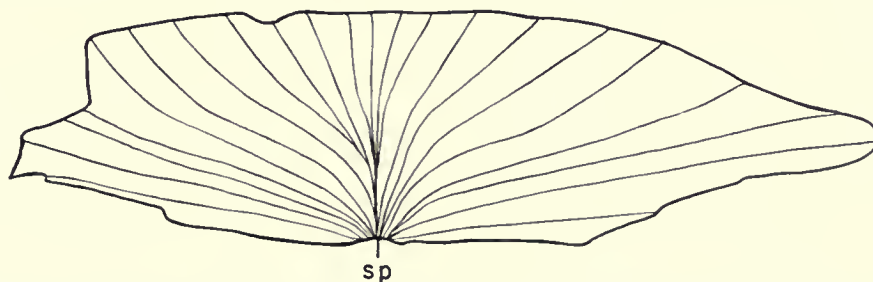

sp

FIG. 37. *Protostega dixie.* C.N.H.M. P27314. Structural pattern in "cleavage" plane of crested neural. *Sp,* attachment area of neural to spinal process of vertebra (see p. 102).

with the next. The differences between a crushed and an uncrushed specimen of the same species may be so great that their original similarity is almost entirely obscured. The large number of specimens from the Mooreville Chalk of Alabama, among which nearly every possible degree of crushing can be observed, has driven home the realization that our idea of the relative thinness of the carapace elements of *Protostega* has been obtained from badly crushed shells;

the carapace was originally far more robust than one is led to believe from the study of the vast majority of the materials. Yet there is no reliable way to estimate the exact degree of post mortem alteration in any given instance. The realization of this matter demands a most cautious appraisal of the differences between compared individuals and species.

The nuchal plate is a subtriangular element whose anterior edge is slightly concave and provided with a shallow groove that runs along this edge. Laterally, the nuchal plate interfingers deeply with the small, flat first peripherals. The postero-lateral edges are serrated and face the first carapace fontanelle. The nuchal is slightly arched from side to side and in its posterior half may be either boldly arched (PR198) or even provided with a low, sharp crest (PR151). A similar variable condition regarding the nuchal crest was observed among specimens of *P. gigas*. The ventral face of the nuchal has a conspicuous unpaired knob with a concave articular surface directly behind the anterior edge (fig. 34). Such an eminence is present in all Recent sea turtles and articulates with the spinal process of the eighth (last) cervical vertebra.

None of the specimens of *P. dixie* reveals a complete set of neural elements. In P27314, four adjoining neurals (fig. 35) show the nature of the neural ridge. Together with many other, isolated, neural plates in different specimens and my comparison with *P. gigas*, it is possible to identify the four neurals of P27314 as Nos. 2, 3, 4, and 5 of the series. Nos. 2 and 4 are sharply ridged, 3 and 5 are broad and saddle-shaped. There is an additional neural fragment of the ridged kind that probably represents No. 6 of the series. The ridged elements attain their greatest heights in their posterior halves, and they are massive and triangular in cross section. Of interest are a crested and a saddle-shaped neural (PR198) that belong to a much smaller specimen. The saddle-shaped element shows a transversal shield imprint; it corresponds in shape with those of P27314, but instead of being broadly arched it is bluntly crested.

Associated with P27315 is one crested neural and two or three broken ones that are not of the saddle-shaped type. These are gently arched and roof-shaped in cross section. The ridged element differs from those of P27314, described above, by being neither triangular nor roof-shaped in cross section; it represents an intermediate condition (fig. 36). These neurals are almost certainly from the posterior part of the series.

The first neural (P27319) is an elongated plate whose posterior half is moderately crested, whereas in front it is but gently arched from side to side. The outline of the broken spinal process of the second shell vertebra is located near the posterior end of the plate.

The neural keel, thus consisting of alternating ridged and saddle-shaped elements, at least in the middle part of the shell, compares closely with that of *P. gigas*.

The ridged elements are often split along a sagittal cleavage plane so that one might be misled into thinking them to be of paired origin. This peculiar cleavage is believed to result from the internal structure of these bones. From a central area beneath the crested neural, where it was attached to the spinal
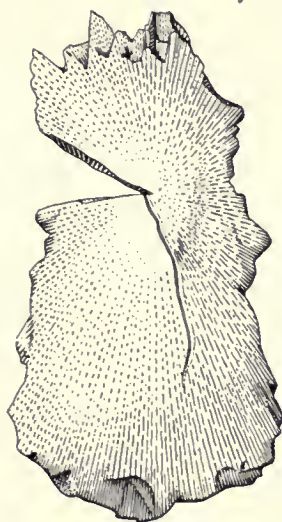
FIG. 38. *Protostega dixie.* C.N.H.M. P27385. Suprapygal plate, dorsal view. About × 0.49.
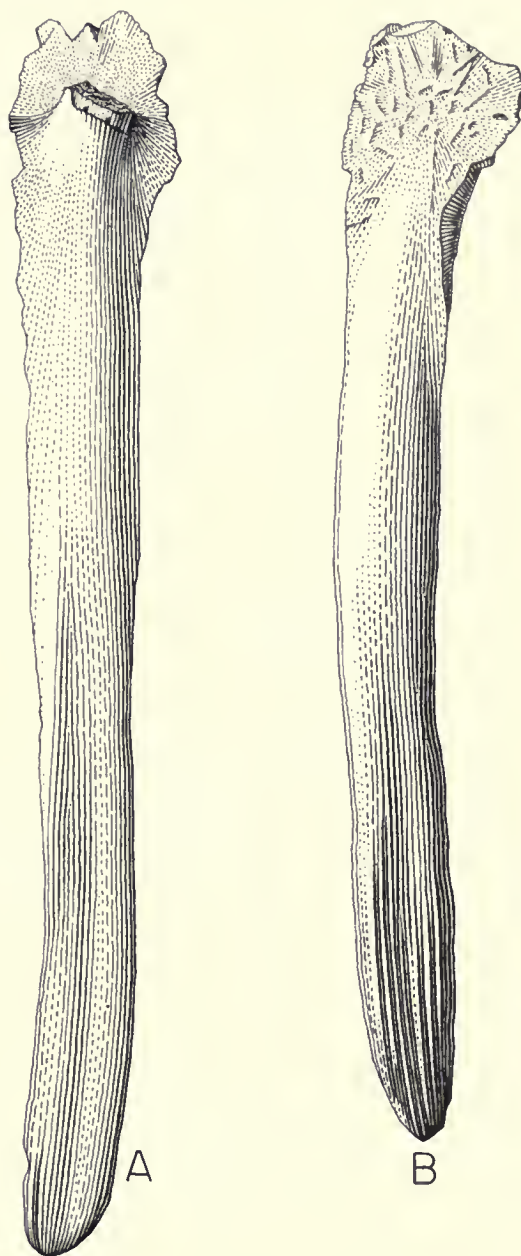
FIG. 39. *Protostega dixie.* C.N.H.M. P27314. Two thoracic ribs, with vestiges of costal plates. A, ventral view; B, dorsal view. About × 0.26.

process of the vertebra, a great many bone canals of different diameter radiate in all directions toward the upper surfaces in a fairly regular pattern. The only place where they lie in one plane throughout the bone is in the sagittal plane (fig. 37). Thus, the two halves of the neural are held together only by the relatively thin walls between canals and are, in consequence, easily separated under pressure in the described fashion (pl. 7). The internal construction of the saddle-shaped elements is much the same as that of the crested plates; they are less massive throughout and thus are apt to break more irregularly.

The suprapygal (P27385) is a flat, elongated, thin plate, whose lateral edges are irregularly serrated (fig. 38). It resembles very closely the corre-
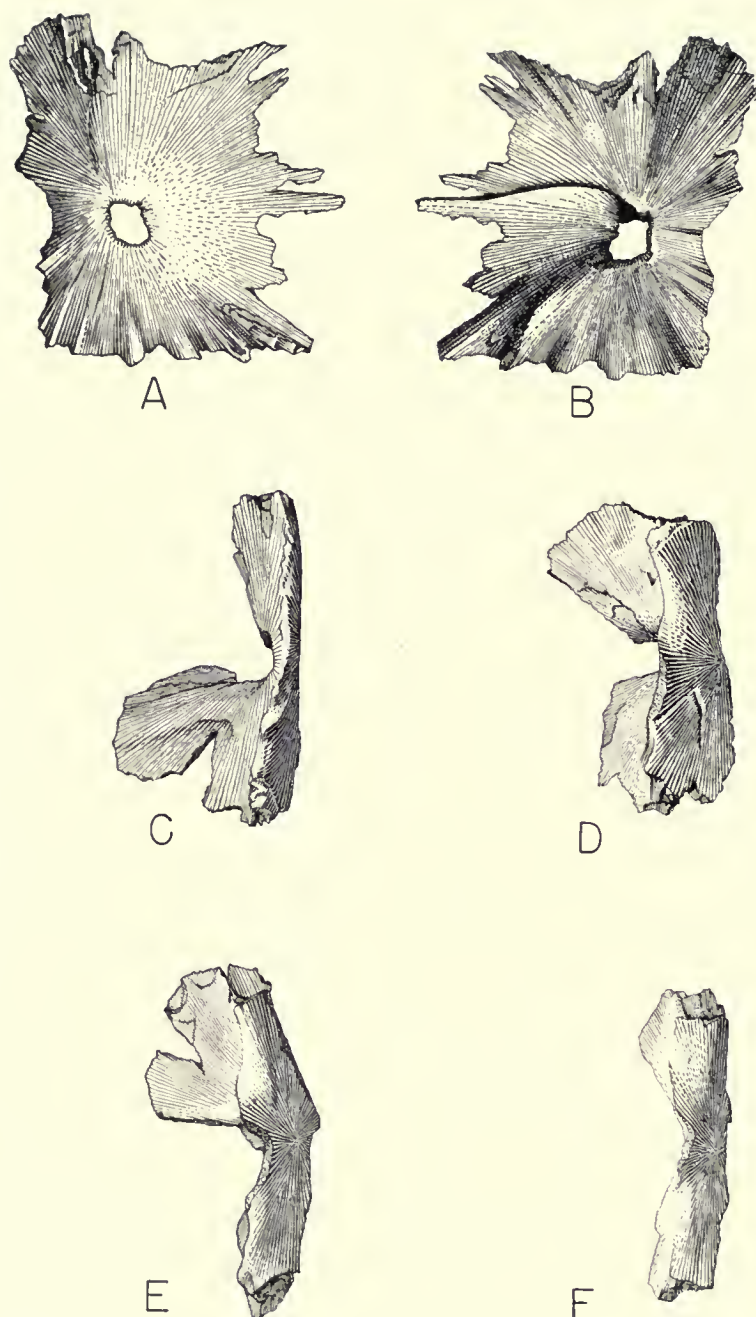
FIG. 40. *Protostega dixie.* C.N.H.M. P27314. Peripheral plates. A, dorsal, and B, ventral view of right third; C, left fourth; D, left fifth; E, left sixth; F, left seventh. C to F in ventral view. About × 0.24.
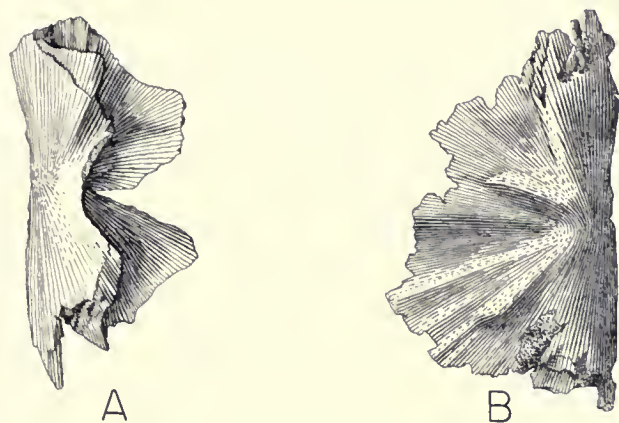
FIG. 41. *Protostega dixie*. C.N. H.M. P27314. Ventral view of peripheral plates. A, right eighth; B, left ninth; C, left tenth; D, right eleventh. About × 0.24.

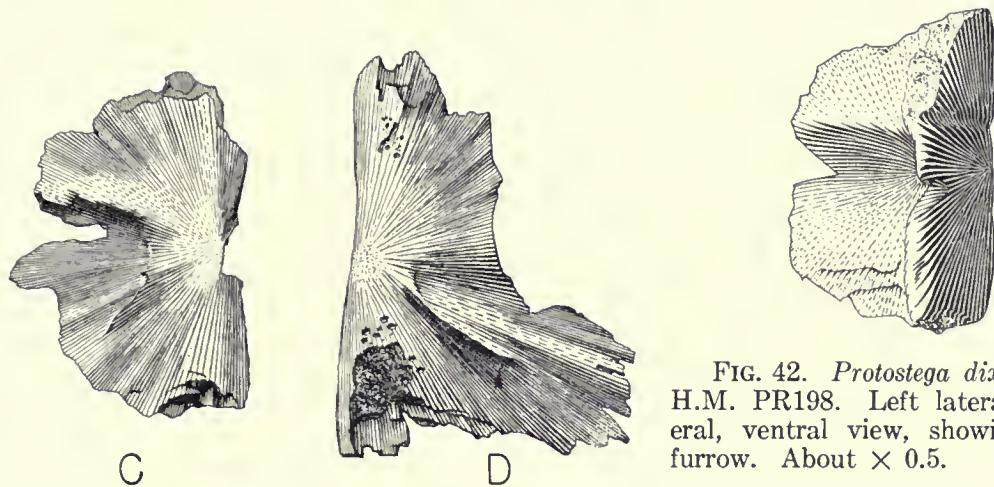FIG. 42. *Protostega dixie*. C.N. H.M. PR198. Left lateral peripheral, ventral view, showing shield furrow. About × 0.5.

sponding plate of *Archelon copei* (U.S.N.M. 11649, pl. 8). The pygal is absent in all specimens of *P. dixie*.

The costal plates are represented by thin flakes of pitted bone at the proximal ends of the ribs (fig. 39). By means of short, deeply interfingering sutures, they are attached to one another and to the neural plates. The degree of reduction of the costal plates is about the same as in *P. gigas*. The ribs are flat and relatively wide, as in other members of the subfamily.

A great number of peripheral bones are among the materials of *P. dixie*. Few of these plates have ever been adequately described or illustrated either for *Protostega* or for *Archelon*, so that no detailed comparison can be made. Considered as a whole, the peripheral fringe is characterized by its extreme weakness in front, the great relative width and thinness of the postero-lateral elements, and the massiveness of those peripherals that belong, morphologically, to the bridge region.

The third peripheral plate is peculiarly modified in all members of the family, and determines the angular outline of the carapace anteriorly. Peripherals 4 to 7 belong to the "bridge" region and possess well-developed dorsal and ventral leaves, whereas, in the remaining elements, the ventral leaves are
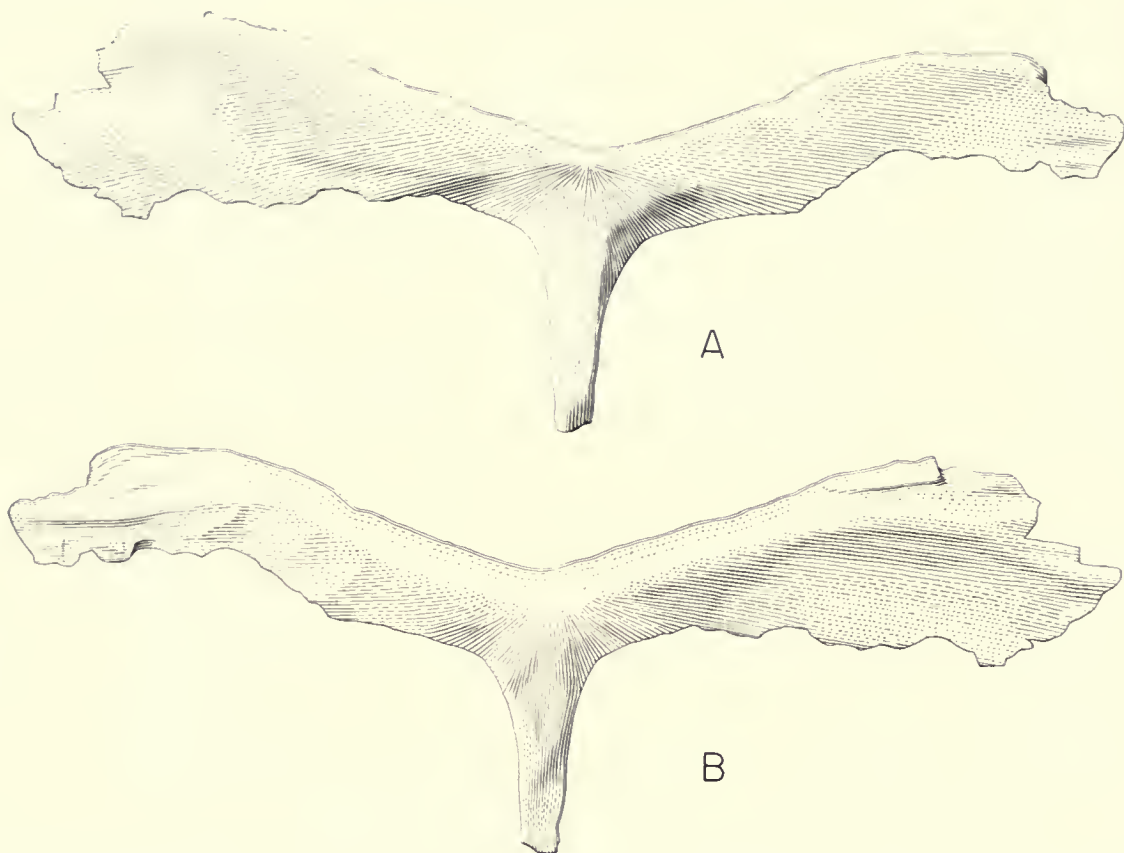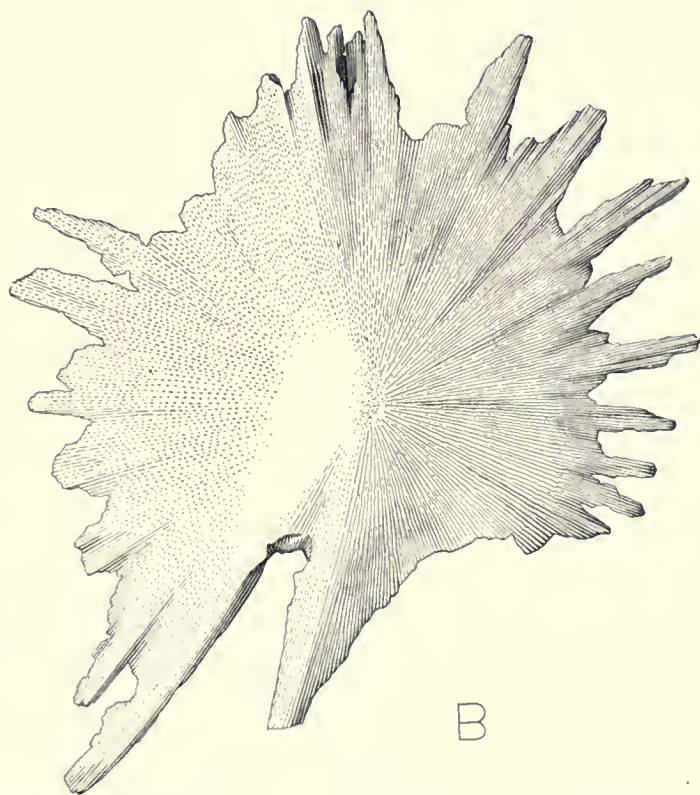
FIG. 43. *Protostega dixie.* C.N.H.M. P27315. Entoplastron. A, dorsal view; B, ventral view. About × 0.32.

greatly or entirely reduced. The dorsal leaves of peripherals 3 to 11 cover the distal rib ends and shallow impressions for their reception are developed. The medial edges of the dorsal leaves end in digital projections. The ventral leaves of the "bridge" peripherals are far shorter and stouter than the dorsal leaves and their ventral margins are irregularly serrated (fig. 40). The lateral edges of peripherals 5 to 11 are sharp, and that of No. 3 is broadly rounded off, the transition taking place in the fourth element.

Only fragments of the first and second peripherals are available. They are small, flat, more or less rectangular plates with blunt anterior and sharp posterior margins. No. 3 can best be described as a "bridge" peripheral whose angle between the dorsal and ventral leaves has reached nearly 180°. The posterior end of the ventral leaf is in the main attached to the fourth peripheral, but the forward connection with the second takes place at the anterior end of the dorsal leaf. This produces the marked angle in the outline of the shell, typical of all protostegid turtles. In the fourth peripheral, the transition from the shape of the third to that of the typical "bridge" peripheral takes place. In the anterior half of the fourth peripheral, the angle between the dorsal and ventral leaves is greater than 90°, in the posterior part smaller than 90°. In the following elements, this angle decreases and the ventral leaves become

FIG. 44. *Protostega dixie*. C.N.H.M. P27314. A, right hyoplastron; B, left hypo-plastron. Ventral views. About × 0.17.

gradually shorter and blunter, until, in the ninth peripheral, the angle is no longer distinguishable as such. Elements 9 to 11 are merely large, thin plates on whose ventral surfaces the rib impressions are indistinctly visible. Discrete rib pits are absent (fig. 41).

The outline of the carapace formed by the articulated peripheral series is slightly lobulated. The lateral edges of peripherals 5 to 11 are very faintly indented anterior to mid-length. In materials with well-preserved surface detail, shield sulci are seen to extend from these points of indentation dorsad and ventrad (fig. 42).

The normal number of peripherals in *P. dixie* is eleven on either side. One (P27385), however, appears to have had twelve, the last pair being more narrow than the eleventh pair and without rib imprints.

Plastron.—Viewed as a whole, the plastron of *P. dixie* (fig. 47) resembles that of *P. potens* (fig. 19) more closely than that of *P. gigas* (fig. 18). The central fontanelle in *P. dixie* is extensive, reaching back to the xiphiplastra, whereas in *P. gigas* it is partially divided by some medial digitations of the hypoplastra. This feature cannot be definitely determined in *P. potens*, but the available material indicates a condition intermediate between *P. dixie* and *P. gigas*. The axillary edge of the hyoplastron of *P. dixie* is longer than in *P. gigas* but shorter than in *P. potens* (fig. 44). The suture between the hyo- and hypoplastra is narrow, more so than in *P. gigas* and probably as narrow as in *P. potens*. The xiphiplastra (figs. 45, 46) resemble those of *P. potens*, except that the postero-lateral edges are rounded rather than forming a marked angle. In both species, the posterior plastral lobe is shorter and broader than in *P. gigas* (figs. 18, 19, 47). The entoplastron (fig. 43) is very much smoother on its dorsal side than it is in either *P. potens* or *P. gigas*, lacking pronounced ridges for muscle attachment.

Girdles and limbs.—As a rule, both girdle and limb bones are preserved in badly crushed, flattened condition. Only P27353, an isolated set of right scapula and coracoid (fig. 48), and the scapula associated with PR151 reveal something of the original shape of these elements.

Both arms of the scapula are slightly oval to round in cross section and so is the shaft of the coracoid except in its distal half, where it is oval. The degree of distal expansion of the coracoid in this specimen probably corresponds very closely to the condition in life. In *Dermochelys* there is no distal expansion in this element, but among Recent cheloniid turtles *Eretmochelys imbricata* shows an expansion similar to that in *P. dixie;* in *Lepidochelys olivacea* the expansion is much more pronounced. It is very difficult to determine whether there are any differences in this respect among the protostegid species because of different degrees of compression. It is virtually certain, however, that the distal expansion of the coracoids is very moderate in all species.

The ventral arm of the scapula is about two-thirds the length of the dorsal process. This proportion is similar to that in *Archelon copei* (U.S.N.M. 11649). In *P. gigas* (C.M. 1420), illustrated by Wieland (1906b), the ventral scapular process is less than half as long as the dorsal. This is, however, not a normal
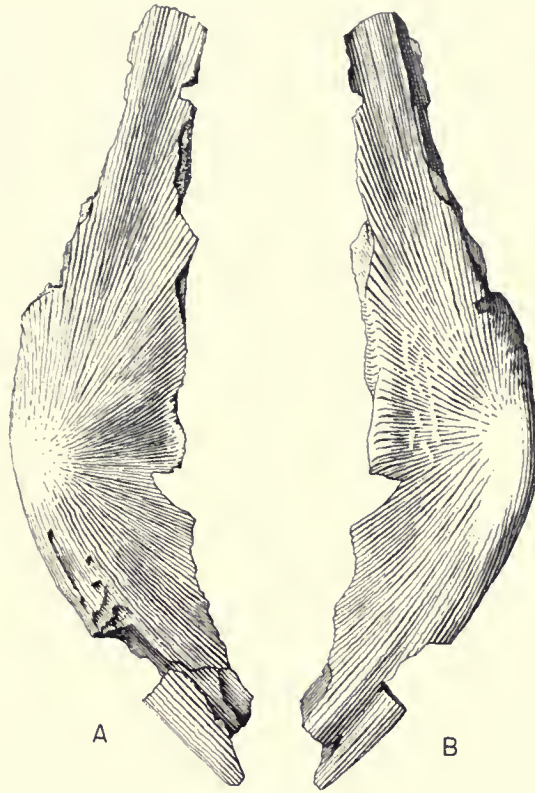
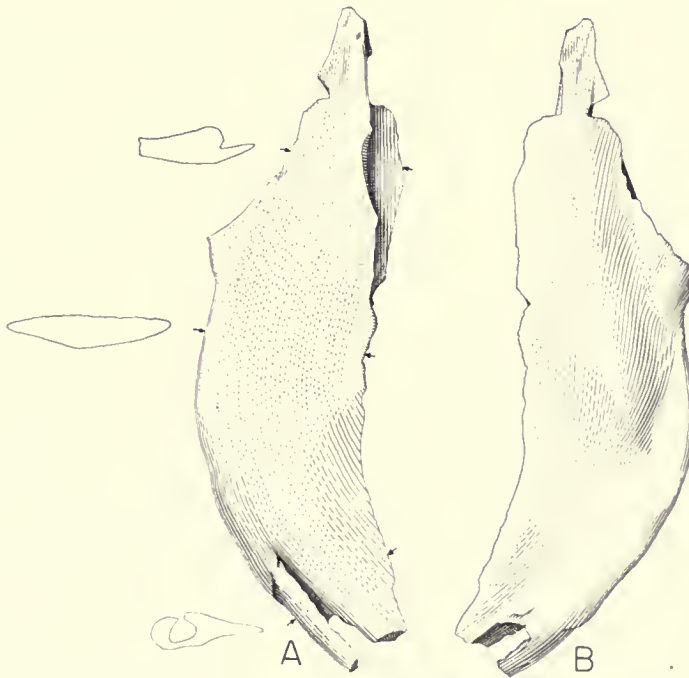FIG. 45. *Protostega dixie.* C.N.H.M. P27314. Xiphiplastron. A, ventral view; B, dorsal view. About × 0.25.

FIG. 46. *Protostega dixie.* C.N.H.M. P27315. Left xiphiplastron. A, ventral view; B, dorsal view. About × 0.34.

condition. All other specimens examined showed more nearly the proportions given for *P. dixie*. In *Archelon ischyros* both arms are of nearly equal length.

The humerus (figs. 49, 50) is provided with a strong ulnar process and a large radial protuberance. Directly distal to the radial tuberosity, the humerus is deeply constricted laterally. The distal end of the bone is considerably expanded.
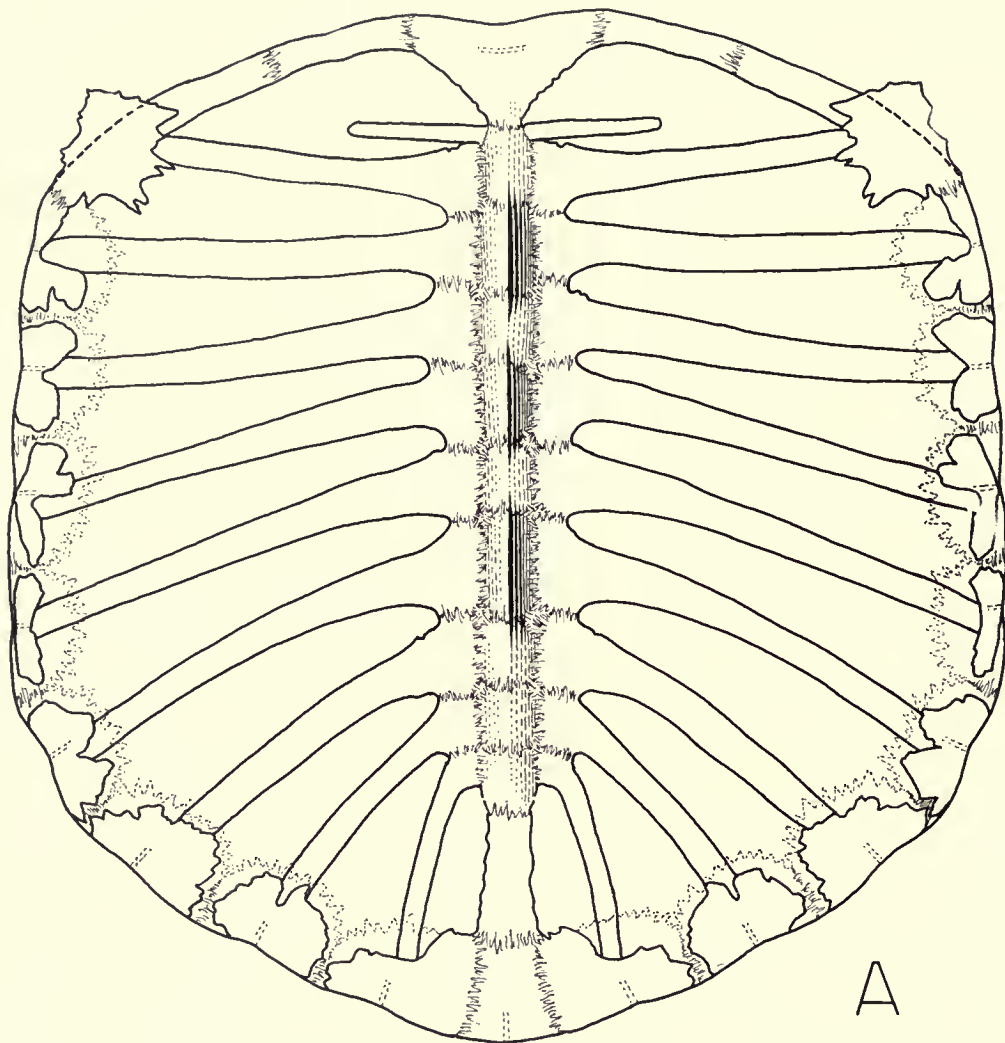

FIG. 47, A. *Protostega dixie*. Reconstruction of carapace. About × 0.09.

Both Case (1897) and Wieland (1906b) stated that the humerus of *P. gigas* possesses an ectepicondylar foramen rather than a groove, and illustrations given by both authors indicate such a condition. In *P. dixie* (P27482 and P27452, fig. 49), there is a groove rather than a foramen, but it appears reasonable to assume that a foramen was present in life and that the roof of the passage was lost by compression and erosion of the very soft bone at the end of the humerus. A humerus of *P. gigas* (UR80) shows a condition similar to that described in *P. dixie*. On the whole, the humerus of *P. dixie* resembles most closely that of *P. potens* (pl. 6, fig. A).

Fragmentary elements of the zeugopodium and autopodium are present in a number of specimens. Both radii and an ulna (P27315) show a fairly close similarity to those of *P. gigas* as illustrated by Wieland (1906b). As in that species, the radius is sharply curved and the zeugopodial bones enclose a large spatium interosseum. Little need be said about the few elements of the manus. So far as can be seen, they agree well with those of *P. gigas*. A
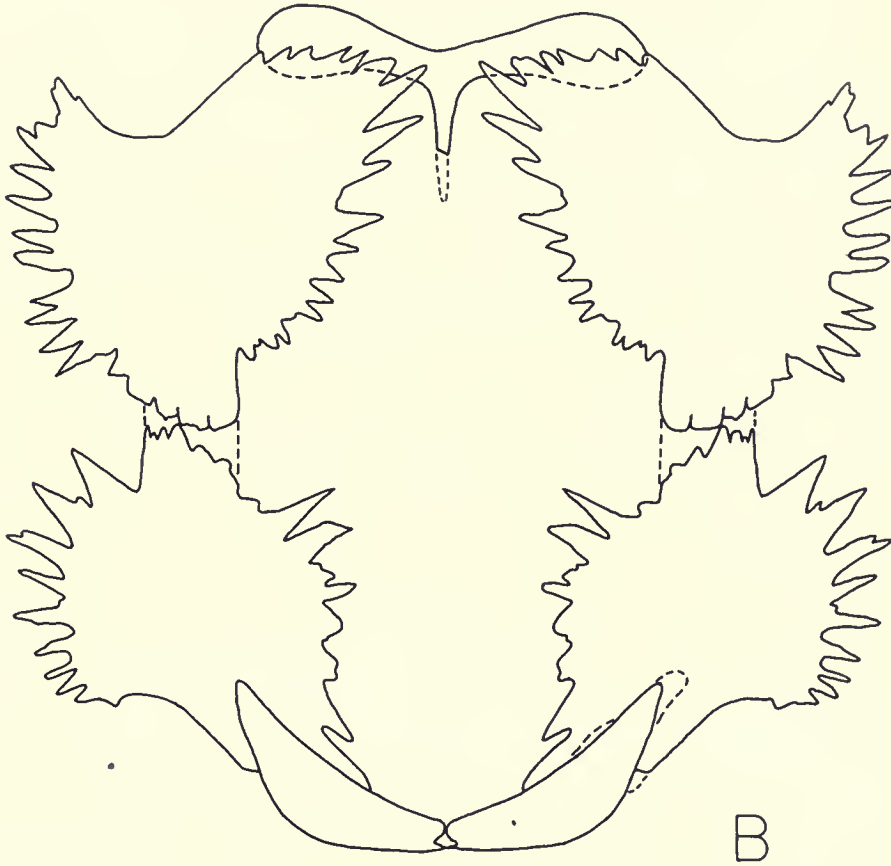
FIG. 47, B. *Protostega dixie*. Reconstruction of plastron. About × 0.09.

number of ossicles of peculiar shape are interpreted as carpal elements. They are not flat platelets, as one might expect in a specialized paddle, but ossifications of somewhat irregular shape, thickest in the centers and tapering towards the edges. Their surface texture indicates that they were enclosed by cartilage in life. An end phalanx (P27385) leaves no doubt that it bore a horny claw.

Of the pelvis and hind limbs of *P. dixie*, very little is preserved in the present material. A badly crushed ilium, scarcely recognizable as such, is associated with the type specimen. There is a partial femur (fig. 51), lacking the proximal end. In so far as it permits comparison, it resembles closely the equivalent part in *P. gigas*. Two phalanges and a metatarsus IV are preserved with specimen PR132. The latter bone has a characteristic shape and can be compared with *P. gigas*. In *P. dixie*, the lateral flange of the bone has the outline of a half
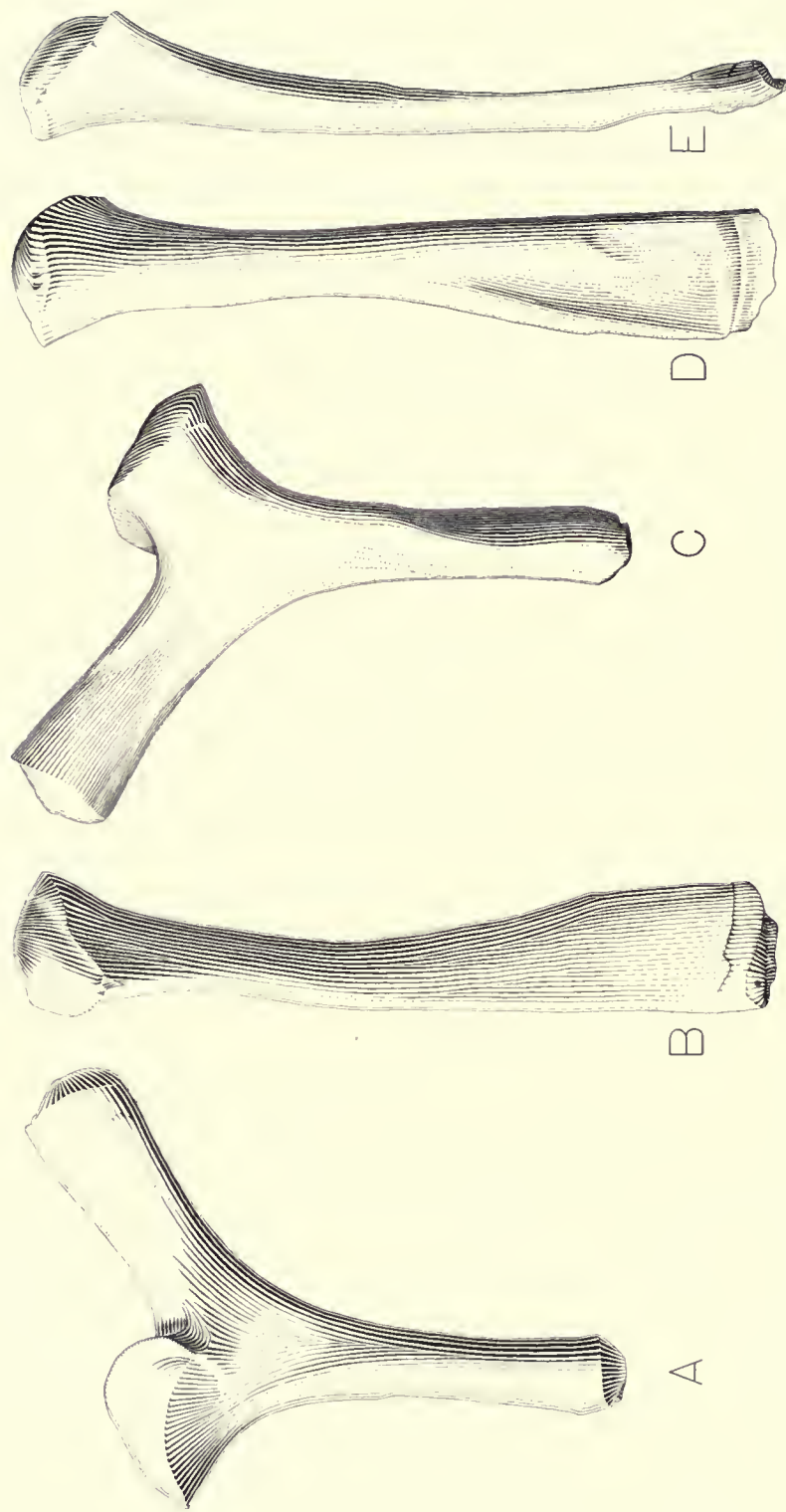
FIG. 48. *Prostostega dixie.* C.N.H.M. P27353. Scapula: A, posterior view; B, anterior view. B, D, and E, coracoid. About × 0.33.
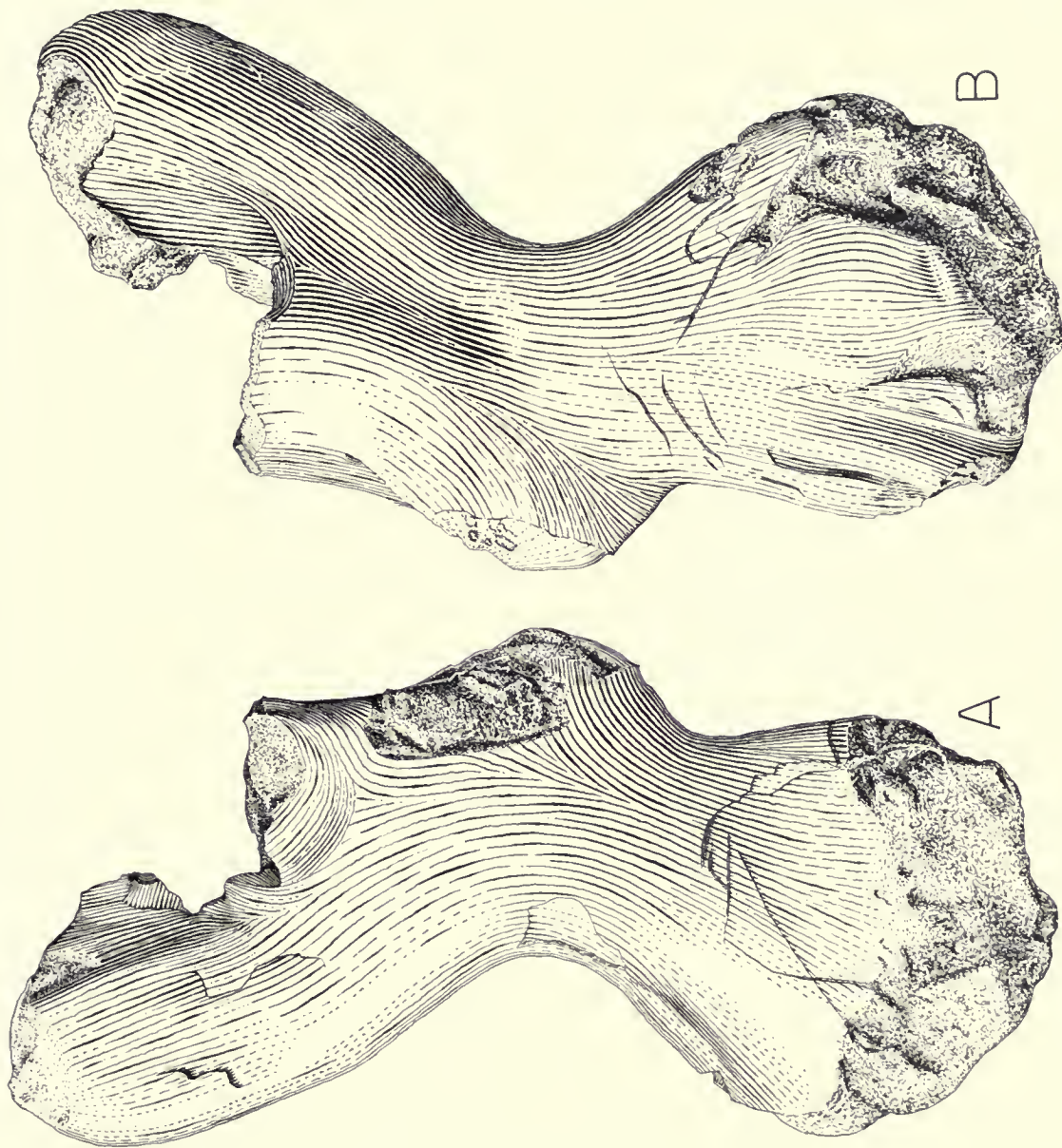
FIG. 49. *Protostega dixie*. C.N.H.M. P27452. Left humerus. A, ventral view; B, dorsal view. About × 0.51.

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circle and is more sharply set off from the main part of the element than in *P. gigas*.

Vertebrae.—The material of *P. dixie* contains enough vertebral fragments from nearly all regions of the column to give an approximate idea of its general construction, but an adequate description of the column as a whole cannot be given.
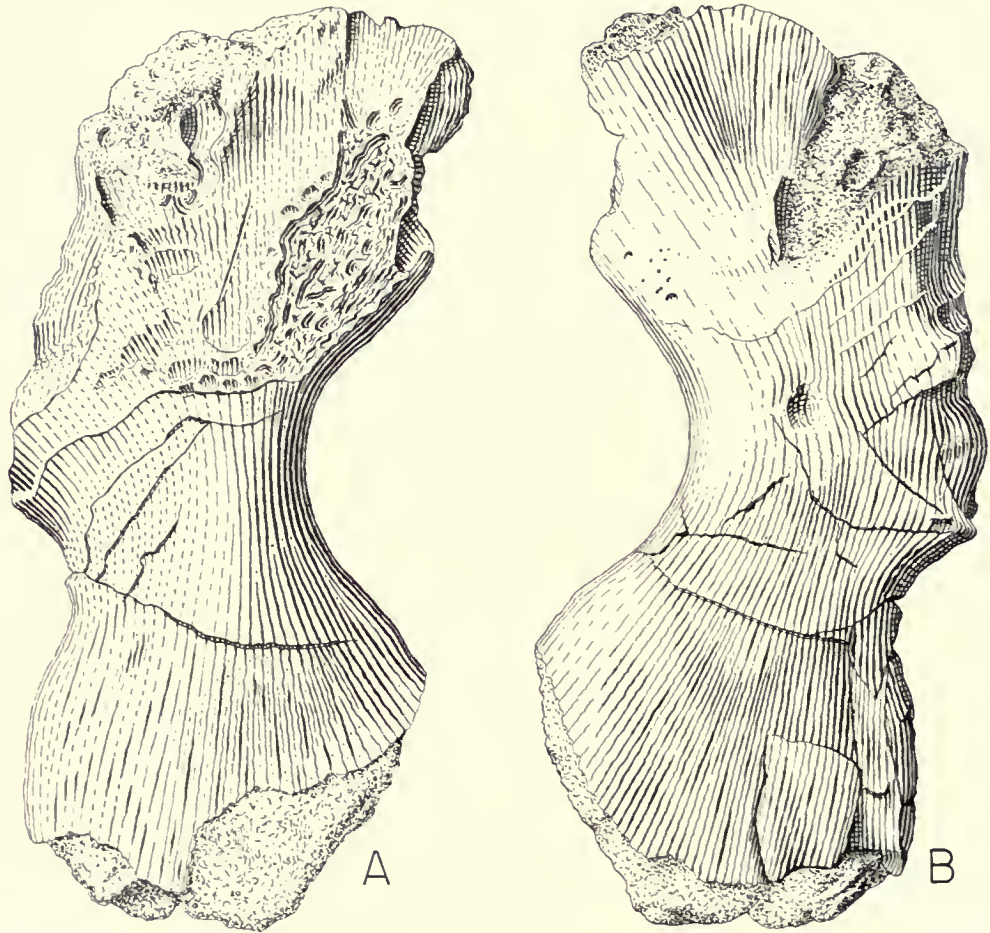

FIG. 50. *Protostega dixie.* C.N.H.M. P27314. Crushed humerus. A, dorsal view; B, ventral view. About × 0.32.

In PR151, two modified vertebral centra probably belong to the atlas-axis complex. The larger element is opisthocoelous and possesses strong, lateral processes on its sides, as well as a hypapophyseal projection that is partly broken off; much of the postero-ventral extent of the centrum proper is missing. The smaller bone lacks the characteristic texture of the surface bone below the periosteal membrane and thus has the appearance of an ossification inside a cartilage element. It has the shape of a disk whose posterior face is concave, approximately corresponding to the convex articular facet of the larger centrum. The anterior face forms a prominent, blunt, centrally located projection. Com-

parison of these two elements with the atlas-axis complex in *Chelonia* suggests that the smaller element is a very short atlas centrum (pleurocentrum of the atlas), the larger bone a likewise foreshortened axis pleurocentrum (fig. 52). A third element of irregular shape might represent an intercentrum, but its relation to the other two bones cannot be determined. Another partial axis centrum, resembling that of PR151 in every detail, is associated with P27452.
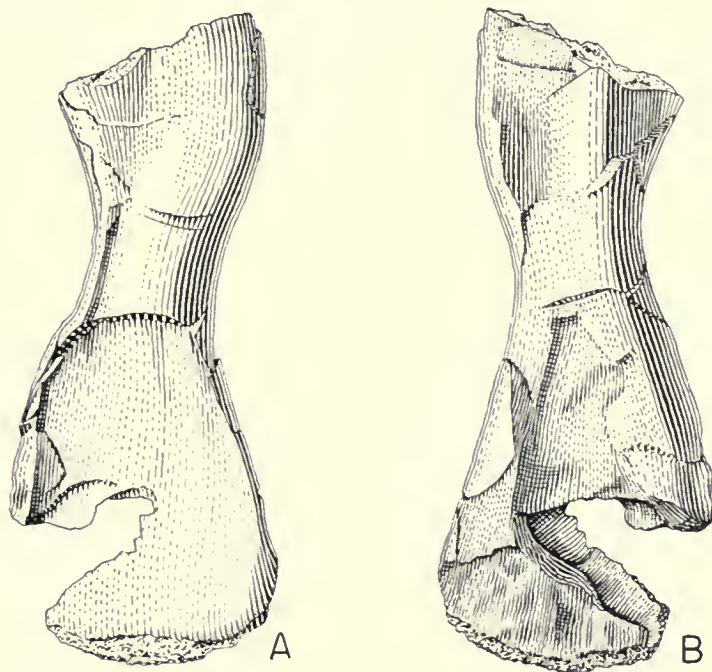

FIG. 51. *Protostega dixie*. C.N.H.M. P27314. Fragment of femur. A, dorsal view; B, ventral view. About × 0.38.

Fragments of neurapophyses and centra of other cervical vertebrae are present in P27315, P27482, P27319 and P27314. In most instances, it is not possible to assign these fragments to a specific vertebra of the cervical region. Their approximate numerical position, however, is rarely in doubt if they are compared with the cervical column of a Recent cheloniid. (The cervical vertebrae of *Dermochelys* are unfortunately not available for comparison.) The probable equivalent of the procoelous fifth vertebra in *Chelonia* is present in fairly good condition in P27482. Its over-all proportions are similar in both species. The transverse processes are located near the anterior end in *Chelonia*, near the middle of the vertebra in *P. dixie* (fig. 53).

The thoracic region of the vertebral column is represented by a number of isolated neurapophyses, a centrum (P27385), and one or two spinal processes of anterior shell vertebrae in PR151. The neurapophyses are conspicuously different from those of *Dermochelys*, but similar to those of cheloniid turtles. The neural canal is high and very narrow in this region. The centrum is intermediate between the condition in *Dermochelys* and that in the cheloniids. The saddle-shaped excavation at mid-length of the centrum, forming the ventral half of the opening
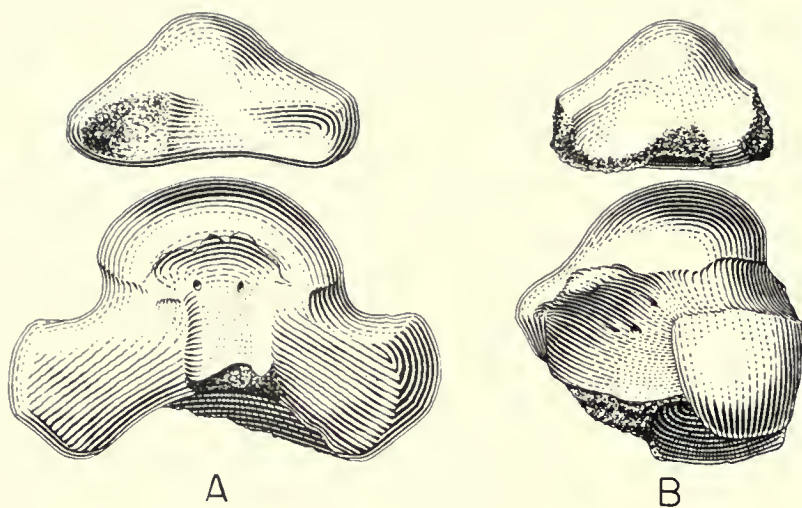
FIG. 52. *Protostega dixie*. C.N.H.M. PR151. Atlas and axis. A, dorsal view; B, lateral view. About × 0.67.

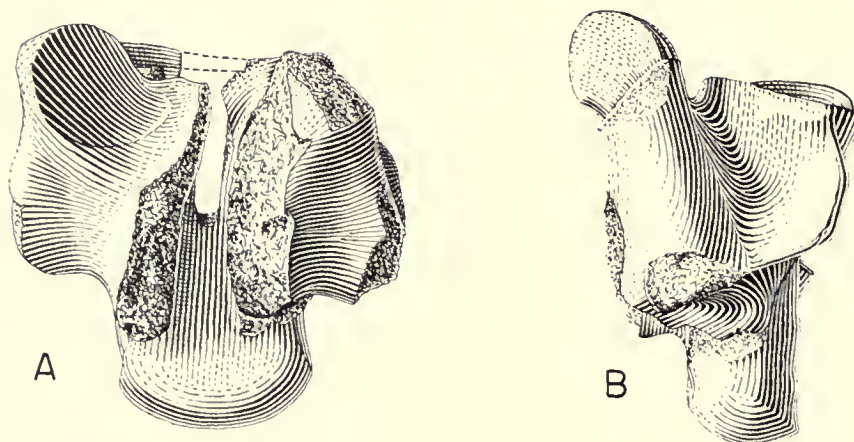FIG. 53. *Protostega dixie*. C.N.H.M. P27482. Fifth cervical vertebra. A, dorsal view; B, lateral view; C, anterior view. About × 0.76.
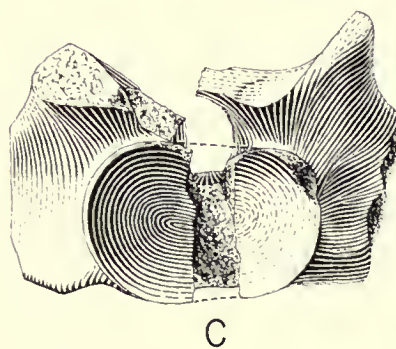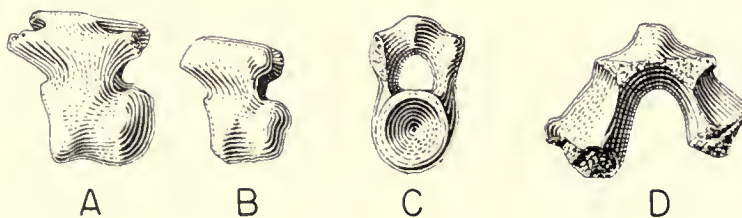
FIG. 54. *Protostega dixie*. C.N.H.M. PR132. Caudal vertebrae. A and C, same vertebra in side and anterior views; B, a more posterior element; D, neurapophysis of a more anterior caudal vertebra. About × 0.76.
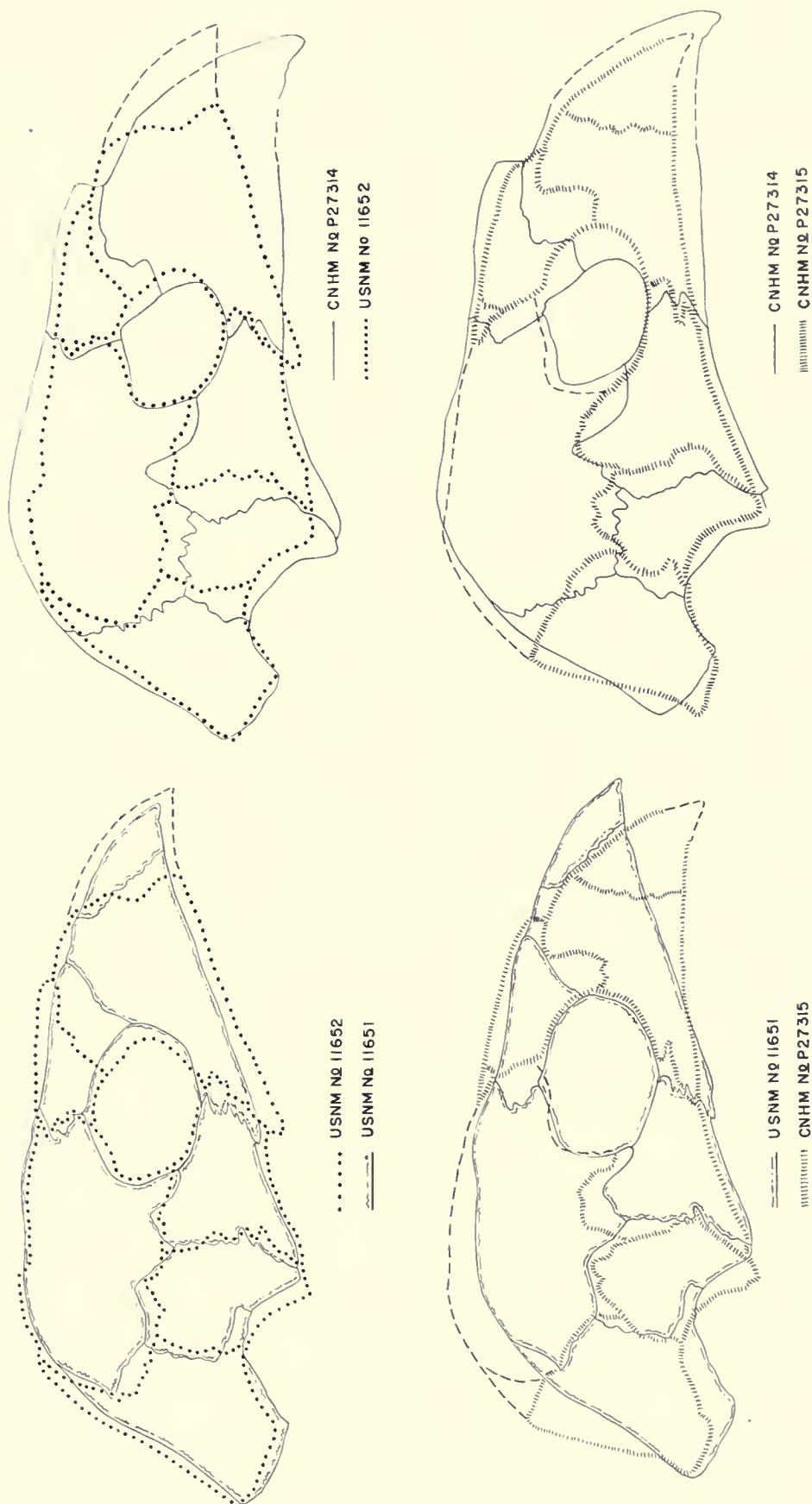

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FIG. 55. Lateral views of skulls of *Protostega dixie* and *P. gigas* superimposed. C.N.H.M. P27314 and P27315, *Protostega dixie*. U.S.N.M. 11651 and 11652, *P. gigas*. C.N.H.M. P27314 and U.S.N.M. 11652 are skulls of comparable size and larger than C.N.H.M. P27315 and U.S.N.M. 11651, also of comparable size.

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that permits the exit for the spinal nerve, is short antero-posteriorly in cheloniids (about 24 per cent of the length of the centrum), intermediate in *P. dixie* (about 45 per cent), but long in *Dermochelys* (about 63 per cent). The spinal process of the first shell vertebra is usually not fused with a neural plate. It forms a dorsal, shoe-shaped expansion, attached by connective tissue to the antero-ventral surface of the first neural plate and, sometimes, also to the postero-ventral surface of the nuchal plate. In *P. dixie* (PR151), a fragment of the nuchal plate and the shoe-shaped dorsal enlargement of the first shell vertebra indicate that, in this species, about half of the length of the process lay under the nuchal plate. Small postzygapophyses, located far dorsad, show fairly well-defined joint facets. This would suggest a certain amount of movability of the first shell vertebra against its posterior neighbors, a contrast to the condition in cheloniid turtles, where the comparable zygapophyseal processes are joined by a suture. The suggestion of a moderate degree of movability of the first shell vertebra in *Protostega* is strengthened by the fact that the vestigial first pair of ribs is free, that is, is not attached to the first costal plate, as is the typical condition.

A few caudal vertebrae are associated with PR132. They consist of well-developed, procoelous centra and relatively massive neurapophyses, forming a large tunnel-shaped neural canal. The spinal processes, as in cheloniids, are either very low or absent. The vertebrae are high and narrow as in *Dermochelys*, rather than low and wide as in the cheloniids. The planes of the zygapophyseal joints stand more nearly vertical than horizontal, thus again resembling the condition in *Dermochelys*, except that both pre- and postzygapophyses are well developed in *P. dixie* (fig. 54).

Subfamily **Chelospharginae**

Diagnosis.—See page 128.

Chelosphargis cf. advena (Hay)

Among the Alabama materials, there are three lots of bones that very closely resemble *Chelosphargis advena* of the Niobrara Chalk. Unfortunately, none of these specimens presents a sufficiently large portion of the skeleton to permit a detailed comparison. Although there are numerous differences between these bones and those of the Niobrara form, I prefer to await the discovery of more complete materials before naming a possible new species.

The bones tentatively referred to *C. advena* are the following:

C.N.H.M.

PR171. West Greene locality, Greene County, Alabama. Mooreville Chalk. Collected by C. M. Barber and J. A. Robbins, May, 1949. Two costal plates, three neurals, and a fragment of a hypoplastron.

P27485. Moore Brothers farm, Harrell locality, Dallas County, Alabama. Mooreville Chalk. Collected by W. D. Turnbull, May, 1946. Left fifth peripheral.

P27397. Central part of large Harrell locality, Dallas County, Alabama. Mooreville Chalk. Collected by C. M. Barber, May, 1946. A number of very poorly preserved fragments, including a peripheral.

The material contained in P27397 is too badly preserved to merit further mention; it was placed in this group because of a peripheral plate that cannot be determined as belonging to any other group of turtles in the Mooreville Chalk.

The bones in the other two lots are well preserved. P27485 is probably a left fifth peripheral plate. It resembles the corresponding bone in the Niobrara form in every detail except for being somewhat less massive and relatively longer. PR171 again differs from the Niobrara form in its thinner plates. This is particularly true as regards the hypoplastron. The process of the latter that holds the xiphiplastron in place laterally appears to be much wider than in the Niobrara form. The neural bones form a gentle ridge much as they do in the small specimens of the Niobrara species. Two complete costal elements indicate that the lateral fontanelles were relatively small; the ribs are wide and flat.

Calcarichelys, gen. nov.

Diagnosis.—A specialized protostegid closely allied to *Chelosphargis*, but with uniquely specialized neural keel and strongly serrate peripheral margin (except in front). Unusually high, sharply pointed neural plates alternate with nearly flat ones. Last keel-thorn located on suprapygal. Pygal plate very narrow. Hypoplastron nearly rectangular.

Type.—*Calcarichelys gemma.*

Calcarichelys[1] gemma[2] sp. nov.

Diagnosis.—Same as that of the genus.

Type.—C.N.H.M. PR129. Three adjoining neural elements, probably the second to the fourth; the left and right third to seventh and the tenth and eleventh peripherals; the pygal and suprapygal in sutural union with the last peripherals on both sides; fragments of costals; essentially complete right hypoplastron and the posterior half of the corresponding xiphiplastron; nearly complete coracoid.

Horizon and locality.—SW. 1/4, NE. 1/4, SW. 1/4, sec. 33, T. 16 N., R. 16 E., Burkville locality, southwest of Montgomery, Montgomery County, Alabama. Mooreville Chalk. Collected by C. M. Barber, 1946. Additional parts were collected by D. H. Eargle, of the United States Geological Survey.

Referred specimen.—C.N.H.M. PR152. Does not add materially to the knowledge of this form. Left third and fourth peripherals; fragments of costal plates. Specimen larger than type. Locality: West Greene locality, Greene County, Alabama. Mooreville Chalk. Collected by C. M. Barber and J. A. Robbins, May, 1949.

Description.—A detailed comparison between the illustrations of *Chelosphargis advena* (figs. 21–26) and those of *Calcarichelys gemma* (figs. 56–58) leaves no doubt that the two genera are closely related. *Calcarichelys*, apparently more

[1] Calcar = spur, thorn; chelys = turtle.

[2] The collector, Mr. C. M. Barber, referred to this specimen as "the gem," because of the superb preservation of the bones and the rarity of the find.

or less contemporaneous with *Chelosphargis*, is very peculiarly specialized, however, in the direction of the development of a bizarre dorsal keel (fig. 58). Alternate neural plates, namely, those located underneath the apices of the vertebral shields, Nos. 2, 4, and presumably 6, have the shape of tall, laterally compressed cones. In front and behind each of these cones are acute ridges that are particularly sharp near the apex. The lateral faces of the cones are somewhat concave, as in a rose thorn. Between two conical neural plates, there is a shorter neural whose dorsal surface is gently arched from side to side and bears a scale impression. The anterior and posterior ends of this neural plate are overlapped by the adjoining conical elements. The pattern of the sutures by which the neural bones are attached to the costal plates is identical with that of *Chelosphargis*, but, since the plates are thicker than in this form, the peculiar sutural pattern is even more clearly developed (fig. 56). The conical neurals in *Calcarichelys* are definitely thecal plates.

The last thorn-like projection of the carapace is formed by the suprapygal element, probably in conjunction with the last neural or another suprapygal. The anterior suture of the element in question reaches dorsad almost to the top of the "thorn," thus indicating participation in the formation of the spine by the anteriorly adjoining plate. The pygal plate is apparently vestigial. It is unusually narrow in dorsal aspect, but ventrally it is even excluded from contact with the suprapygal; the eleventh pair of peripherals is in sutural contact on the ventral side between the pygal and the suprapygal.

The peripheral bones are essentially like those of *Chelosphargis*, but they are much more massive and they form a deeply serrated edge. The dorsal faces of the peripheral elements are slightly concave, the ventral faces are convex, and the medial faces only slightly concave, so that the cross section of peripherals 5 to 8 is subtriangular. In the fourth and particularly in the third, the dorsal and ventral faces tend to become one lateral face, with the result that these bones are no longer triangular in cross section, but slightly curved plates of uniformly even thickness. In peripherals 9 to 11, the ventral and medial faces are no longer distinguishable by a ventral edge, but blend into each other over a broadly rounded, posterior continuation of the latter. One interesting detail is the fact that the thickness of the posterior peripherals is reduced in the area of the ninth peripheral, that is, at the precise point where we can safely assume the limbs to have protruded from beneath the rim of the shell (see figs. 56, 58).

The rib pits in the peripherals are relatively deep and sharply defined. As in all known protostegids, the ribs lay immediately underneath the dorsal faces of the peripherals. In peripherals 3 and 4, the rib pits are located at mid-length of the elements. In all succeeding peripherals, they are located in the posterior half. The last rib pit lies between peripherals 10 and 11.

Shield sulci are clearly visible at the bases of the peripheral projections that form the serrated carapace edge.

The fragmentary costal plates indicate that the extent of the lateral fontanelles was moderate and about as illustrated in the reconstruction (fig. 58).
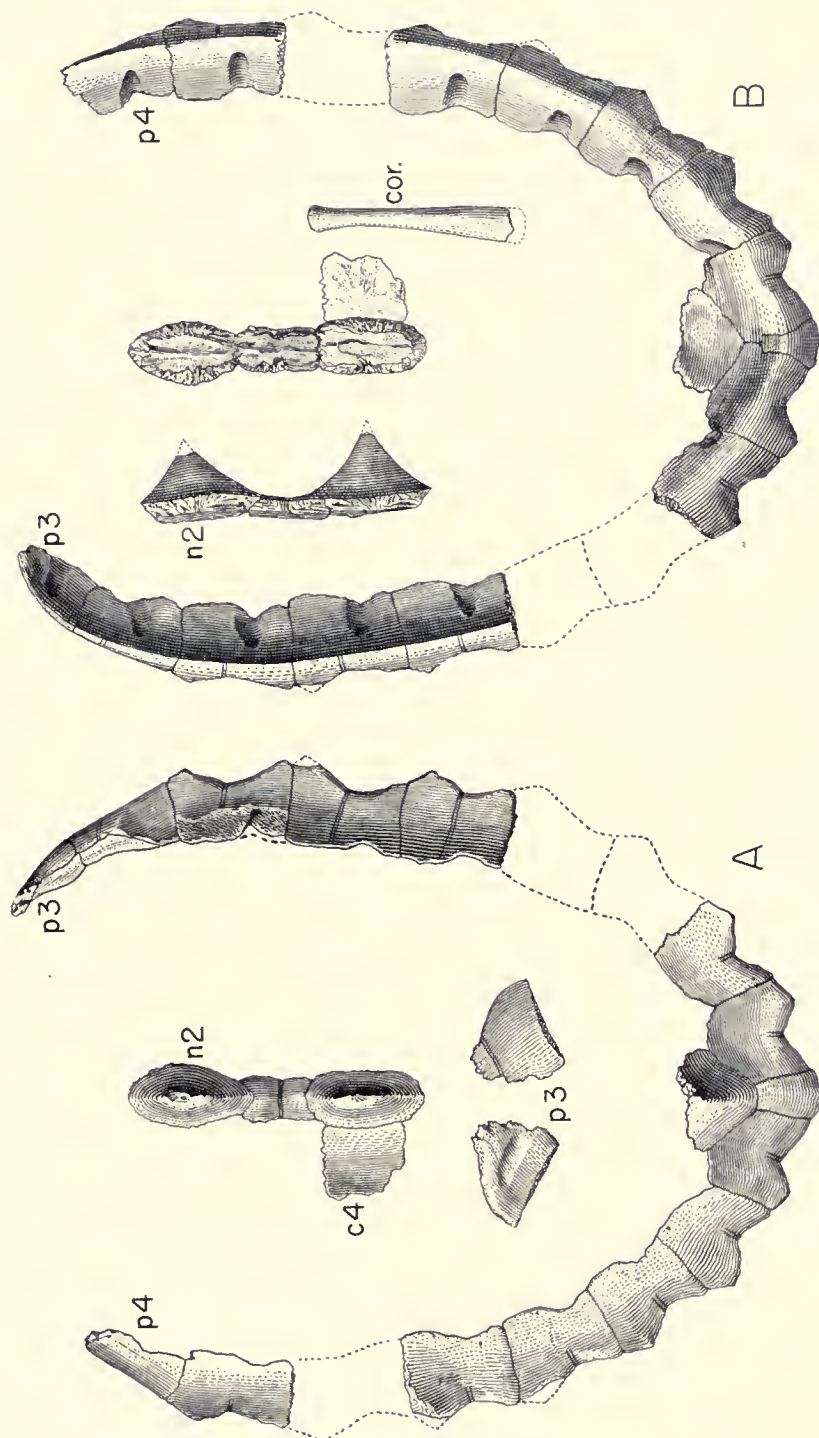
FIG. 56. *Calcarichelys gemma*. C.N.H.M. PR129. A, dorsal view; B, ventral view and neural series in side view. *p3*, *p4*, peripherals 3 and 4; *n2*, second neural; *c4*, fragment of fourth costal plate; *cor*, coracoid. About × 0.53.

The hypoplastron is nearly rectangular in outline. Its medial edge, particularly the posterior part, is provided with finger-shaped projections. The lateral edge is slightly serrate. The entire anterior edge was attached to the hyoplastron by a strong suture. The inguinal edge is sharp and not as deeply excavated as in *Chelosphargis*. The plate is not flat, but is slightly more convex on its ventral face than it is concave on its dorsal surface, with the result that it is thickest at mid-width, particularly just anterior to the notch that receives the xiphiplastron. A shield sulcus appears to traverse the element at about mid-length. The xiphiplastral fragment, representing the posterior half or third of the plate, is identical with the corresponding part in *Chelosphargis*. A faint shield furrow may be observed near its anterior end (fig. 57).

The coracoid belongs probably to the right side. It is nearly circular in cross section, as is typical of all Protostegidae, and the distal end is not flattened. The diameter of the proximal end is but slightly greater than that of the shaft.

MEASUREMENTS
Specimen C.N.H.M. PR129

Bone	Length	Maximum width	Height at mid-length
Third neural	32.5	16.0	18+
Fourth neural	21.0	12.0	5.0
Fifth neural	30.0	14.0	21.0+
Suprapygal	19.0	27.0	10.0+
Pygal	16.5	11.5	9=thickness

	Length	Maximum width between dorsal and ventral edges (posterior end)	Length of dorsal suture
Third peripheral	20.5	26.5	14
Fourth peripheral	28.0	23.0	17
Fifth peripheral	30.0	18+	18
Sixth peripheral	30.0	20.0	18
Seventh peripheral	29.0	18.5	18
Eighth peripheral	28.5	14.5	19.5
Ninth peripheral	24.5	11.0 (=thickness)	18
Tenth peripheral	24.5	13.0	18
Eleventh peripheral	24.0	9.0	16

	Length	Maximum width	Maximum thickness
Hypoplastron	64.0+	57.0+	6.5

	Width at breakline	Length	Maximum diameter of shaft near proximal end
Xiphiplastron	16.0		
Coracoid	....	55.0+	5.5

Specimen C.N.H.M. PR152

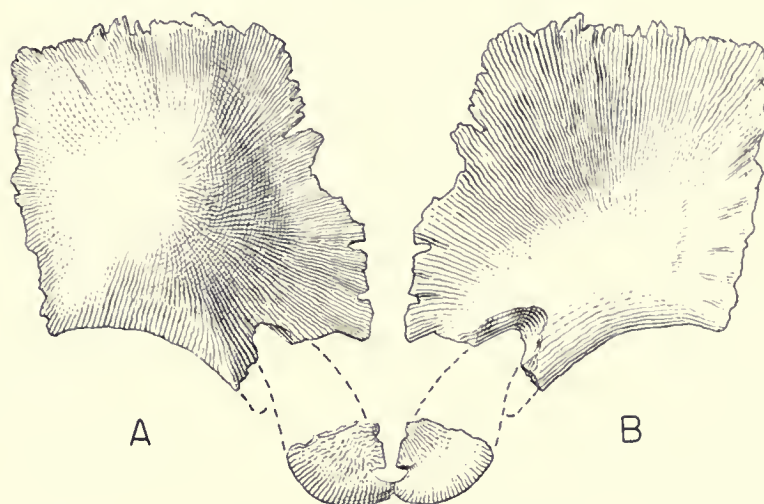|	Length	Maximum width between dorsal and ventral edges	Length of dorsal suture
Third peripheral	26.0	32.0	15.5
Fourth peripheral	29.0	29.0+	17.0+

FIG. 57. *Calcarichelys gemma*. C.N.H.M. PR129. Right hypoplastron and xiphi-plastron. A, ventral view; B, dorsal view. About × 0.78.

THE RELATIONSHIPS OF THE PROTOSTEGIDAE

The protostegid turtles form a well-defined group whose geographical distribution appears to have been limited to the southern shore line area and the inland seas of the North American continent during Late Cretaceous time (fig. 59). None of the materials that have come from the New Jersey Greensand can be assigned to any member of this family, which would indicate that protostegids did not venture into the Atlantic proper, but were confined to the Gulf of Mexico and the extensive northern inland waters that were connected with it. The geographical distribution suggests, however, that members of this family may well be found in Cretaceous Gulf deposits south of the United States.

Species clearly separated in time are easily distinguished morphologically by notable advances in specialization. This is readily shown by comparison of *Protostega eaglefordensis* with the Mooreville and Niobrara species of *Protostega* and *Archelon ischyros*. The differences between the Mooreville assemblage and that of the Niobrara are far less conspicuous. *Chelosphargis* and *Calcarichelys*, probably represented by different species, occur in both formations; *Archelon* has yet to be found in the Mooreville. It is highly probable that the faunal assemblage of the Niobrara is closely paralleled by but is not identical with that of the Mooreville Chalk, a belief that is supported by much additional evidence from other groups of turtles, as will be demonstrated in future contributions. Two possible explanations may be suggested. Either the Mooreville and Niobrara beds were not contemporaneously deposited sediments, though not spaced very far apart in time, or they were laid down simultaneously along a continuous coast line with a geographical barrier, the large Texas peninsula (see fig. 59) partially isolating the populations of the inland basin. Which of these suggestions is the more probable cannot be decided until all the evidence can be evaluated.
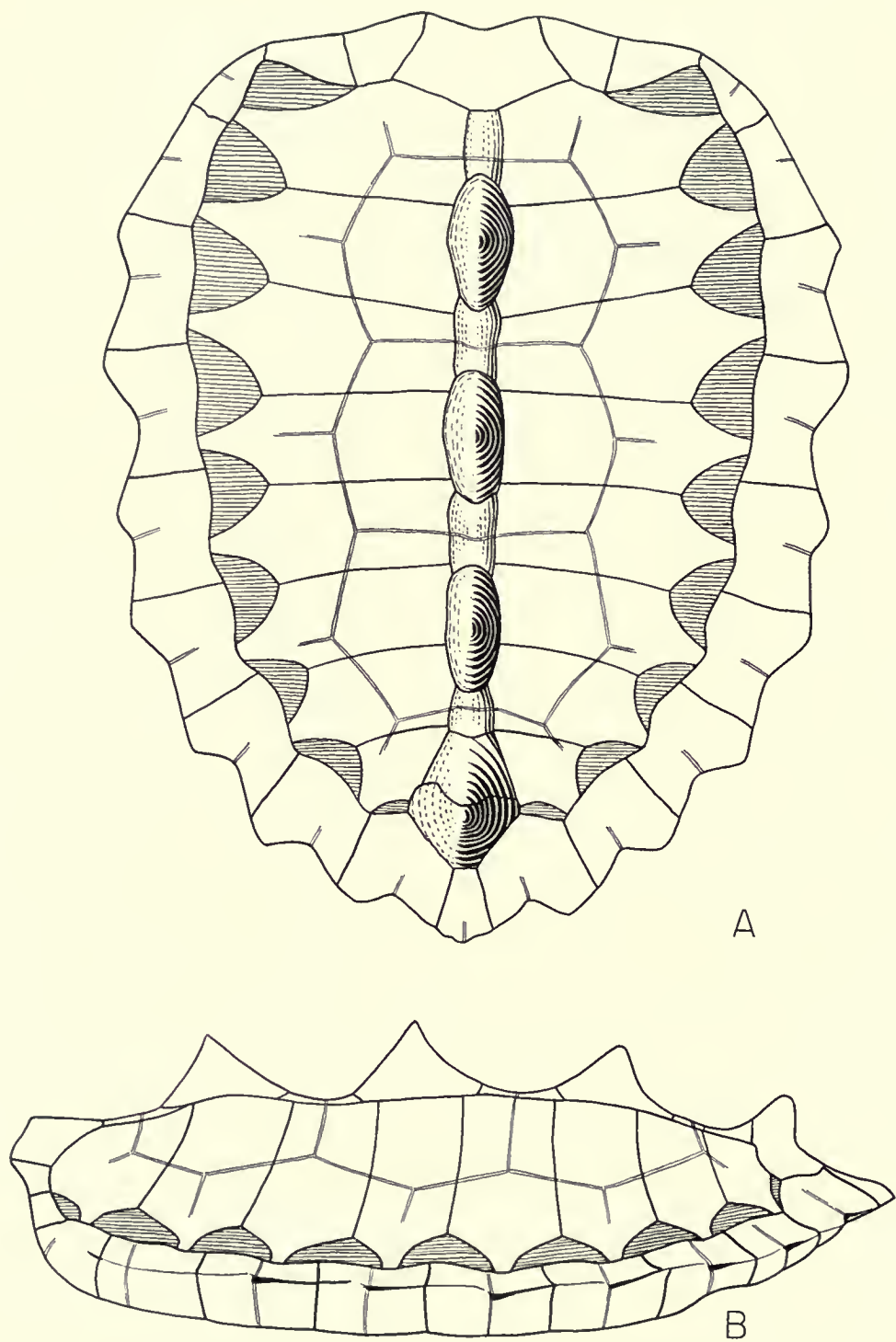
Fig. 58. *Calcarichelys gemma*. Reconstruction of carapace. A, dorsal view; B, lateral view. About × 0.63.

The systematic relations within the family are still rather sketchily known. The number of forms that can definitely be recognized is still small and their distribution, both in time and space, little known. Future work will almost certainly produce protostegid turtles in many more localities and in formations that have not hitherto been systematically searched for vertebrates.

One of the major results of this study is the recognition of two distinct groups of protostegid turtles, one primitive in almost every respect, the other highly specialized and including only large species. The two groups were contemporaneous and their ranges (in part) co-extensive. They represent two levels of organization within the morphotypic pattern of the family, whereby similar specializations developed at both levels. This peculiar phenomenon, which is not at all unique in phylogenetic differentiation, is worthy of further discussion.

The development of keels on the shells of aquatic turtles is frequently observed and is probably correlated with the mode of locomotion in these animals. Morphologically, these keels may be of very different construction. The mid-dorsal keel, for instance, may be formed by thecal neural plates only, by epithecal plates only, or by a combination of both. If it is formed by thecal neurals only, it may be an even sagittal elevation, or it may be interrupted—keeled neural elements alternating with saddle-shaped elements—or the peaks of the keel may be formed by two adjoining elements. The structural variety in the keel formation is even greater in cases where thecal and epithecal elements are combined. Yet, in all these cases, the construction of the neural keel conforms to a mutual morphotypic pattern. It is not, in other words, possible to decide the kind of keel construction that a primitive, unkeeled form could potentially evolve.

In the two groups of Protostegidae, the neural keel construction is basically of the same kind. Since both lines contain forms with very slight keels only (*Chelosphargis advena* in one and *Archelon copei* in the other), it is very likely that the stem group from which the Protostegidae originated was unkeeled.[1]

The basically similar keel constructions in the two groups of protostegid turtles thus arose in both lines independently, a case of parallelism particularly interesting because there is no satisfactory explanation for the fact that other types of keel construction (for example, the kind observed in the Toxochelyidae, which produced a very similar keel in outward appearance and was certainly equal in functional efficiency) are absent in the protostegids. In both the Protostegidae and the Toxochelyidae, there are generalized forms whose neural plates are basically similar. Among the advanced, keeled forms of both families, the protostegids exhibit one type of keel construction and the toxochelyids, without exception, another. The situation represents a good example of a general empirical principle of morphology, namely, that increase in general specialization of a group is accompanied by a decrease in its morphological potential.

[1] Since keel development occurs only in aquatic forms, the assumption that a decrease in keel size is accompanied by an increase in general aquatic adaptation is highly improbable.
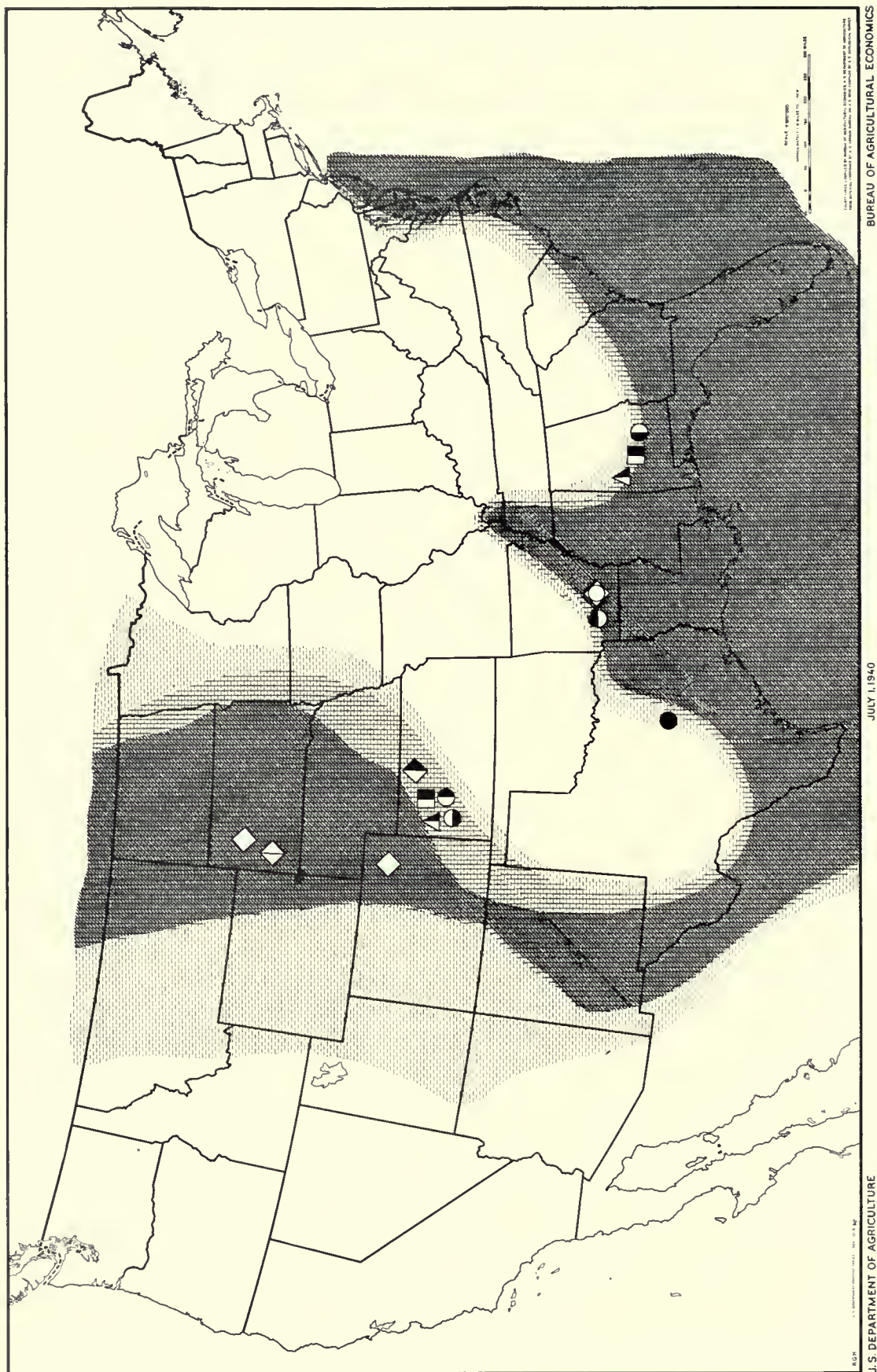
JULY 1, 1940

FIG. 59. Geographic and stratigraphic distribution of protostegid turtles. Lightest shading, approximate extent of Cretaceous Sea during Eagle Ford time; medium dark shading, during Niobrara time; darkest shading, during Pierre time. See also legend, page 127.

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Formation	State	Species
PIERRE SHALE	S. DAKOTA	◇ Archelon ischyros ◇ Archelon marshi
PIERRE SHALE	COLORADO	◇ Archelon cf. ischyros
MARLBROOK MARL	ARKANSAS	◇ protostegid (Archelon or Protostega)
NIOBRARA CHALK	KANSAS	◭ Chelosphargis advena ▣ Calcarichelys cf. gemma ◐ Protostega gigas ◑ Protostega potens ◆ Archelon copei
BROWNSTOWN MARL	ARKANSAS	◑ Protostega sp.
MOOREVILLE CHALK	ALABAMA	◭ Chelosphargis cf. advena ▣ Calcarichelys gemma ◐ Protostega dixie
EAGLEFORD SHALE	TEXAS	● Protostega eaglefordi

THE TAXONOMY OF THE PROTOSTEGIDAE

Emended diagnosis.—Marine turtles with specialized shells covered with epidermal shields. Skull characterized by an unusually large antorbital beak area. Temporal region largely covered by parietals, postorbitals, and squamosal bones. Primary palate. Primitive genera with distinct nasal bones. Symphysis of lower jaw long. Neck short, probably not retractile. Carapace relatively light in construction, plastron consisting of heavy plates. Nuchal plate subtriangular with ventral process for vertebral articulation. First and second peripherals thin, flat plates. Third peripheral much larger, attached to second peripheral by short suture at its antero-dorsal edge only. Sutural contact with fourth peripheral crescent-shaped. Peripherals 4 to 7 more or less triangular in cross section. Posterior peripherals more or less flat. Rib ends impressed and clearly outlined under dorsal leaf of peripherals. Nine or ten carapace ribs with eight or nine costal plates. Costal plates moderately reduced or highly vestigial. Neural plates always thecal, forming a sagittal keel of slight or extreme dimensions. Plastron with or without epiplastra. Entoplastron "T"-shaped, hyo- and hypoplastra large, heavy plates with numerous digitations along edges. Xiphiplastra relatively small, flat, slightly curved plates. Girdle elements large and stout. Coracoid round in cross section, of almost uniformly even diameter proximally and distally, reaching back almost to the anterior border of the pubis. Humerus with pronounced ulnar condyle and radial tuberosity. Paddles of forelimb larger than those of hind limb. Pubis with large prepubic process. Ischium comparatively small. Ilium with short articular process for sacral ribs. Tail short. Late Cretaceous, central and southern United States.

Subfamily **Chelospharginae** nov.

Diagnosis.—Small or medium-sized, primitive protostegid turtles. Skull blunt, straight premaxillary beak. Frontal bones large and with lateral processes toward orbital rims. Prefrontal bones excluded from sagittal contact by nasal bones. Otic and exoccipital area very similar to condition in cheloniid turtles. Symphysis mandibuli long, with rami fused even in juvenile individuals. Slight, but sharp, sagittal crest on triturating surface of lower jaw. Carapace with moderate fontanelles in adults. Lateral and posterior peripherals relatively stout bones without digitations along medial borders. Plastron with epiplastra and "T"-shaped entoplastron. Hyo- and hypoplastra with short digitations.

Chelosphargis, gen. nov.

Diagnosis.—Primitive genus. Neural bones forming blunt, very low keel in mid-line. Peripheral edge of carapace even. Pygal plate entirely separating eleventh pair of peripherals.

Horizon and locality.—Niobrara Chalk, Kansas; Mooreville Chalk, Alabama.

Type species.—*Protostega advena* Hay 1908.

Calcarichelys, gen. nov.

Diagnosis.—Specialized genus probably of small size, closely allied to *Chelosphargis*, but with uniquely specialized neural keel and strongly serrate peripheral margin (except in front). Unusually high, sharply pointed neural elements alternating with nearly flat, saddle-shaped plates. Last mid-dorsal keel-thorn located on suprapygal. Pygal plate very narrow. Hypoplastron nearly rectangular.

Horizon and locality.—Mooreville Chalk, Alabama; Niobrara Chalk, Kansas.

Type species.—*Calcarichelys gemma* Zangerl.

Subfamily **Protosteginae** Wieland

Diagnosis.—Large, highly specialized sea turtles. Skull with pointed, slightly or greatly down-curved premaxillary beak. Frontal bones without lateral processes. Prefrontals meeting in mid-line, no nasal bones. Temporal region excavated on either side of supraoccipital process. No sagittal ridge on triturating surface of lower jaw. Carapace with extremely large fontanelles, costal plates vestigial. Posterior peripherals nearly flat. Peripheral plates with numerous digitations along edges facing fontanelles. Neural bones forming a notable keel in mid-line. Plastron probably without epiplastra.[1] Entoplastron "T"-shaped. Hyo- and hypoplastra very large, more or less oval or circular plates with numerous digitations medially and laterally.

Protostega Cope 1872

Diagnosis.—Skull nearly as wide as long, without or with only slightly down-curved antorbital beak. Neural keel uneven; highly crested neurals alternating with low, saddle-shaped elements. Suture between hyo- and hypoplastra relatively narrow.

Horizon and locality.—Niobrara Chalk, Kansas; Mooreville Chalk, Alabama; Eagle Ford Shale, Texas; Brownstown Marl, Arkansas.

Type species.—*Protostega gigas* Cope.

Protostega gigas Cope 1872

Emended diagnosis.—Skull with low and pointed antorbital beak area; tip of beak nearly straight, and at level of about mid-height of orbit. Central fontanelle of plastron partially subdivided by medial digitations of hypoplastra. Hyo-hypoplastral suture narrow. Antero-lateral edge of hyoplastron slightly more than one third the distance between axial notch and hyo-hypoplastral suture. Xiphiplastra forming narrow, relatively long posterior plastral lobe.

Horizon and locality.—Niobrara Chalk, Kansas.

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[1] An epiplastron was described by Wieland for *Archelon ischyros*, but the matter is still doubtful.

Protostega eaglefordensis sp. nov.

Diagnosis.—Incompletely known. Humerus fairly straight with weak radial tuberosity and relatively small ulnar process. Ischium relatively long and slender, provided with spur-shaped process on posterior edge. Symphyseal part of pubis large, prepubic process moderate in size. Foramen pubo-ischiadicum relatively large and possibly open medially.

Horizon and locality.—Eagle Ford Shale, Texas.

Protostega dixie sp. nov.

Diagnosis.—Closely related to *P. gigas* and *P. potens.* Skull with high antorbital beak area and moderately down-curved premaxillary beak situated on level below ventral rim of orbit. Plastron with large central fontanelle reaching posteriorly to xiphiplastra. Suture between hyo- and hypoplastra very narrow. Antero-lateral edge of hypoplastron about half the distance between axillary notch and hyo-hypoplastral suture. Posterior plastral lobe wide and short.

Horizon and locality.—Mooreville Chalk, Alabama.

Protostega potens Hay 1908

Emended diagnosis.—Incompletely known. Plastron with large central hyo-hypoplastral suture very narrow. Antero-lateral edge of hyoplastron nearly equal to distance between axillary notch and hyo-hypoplastral suture. Postero-lateral edge of xiphiplastron angular.

Horizon and locality.—Niobrara Chalk, Kansas.

Archelon Wieland 1896

Diagnosis.—Skull about 1–1½ times as long as wide, antorbital beak strongly down-curved. Neural keel even, successive neurals similarly crested. Plastron with relatively small central fontanelle.

Type species.—*A. ischyros* Wieland 1896.

Archelon copei (Wieland) 1909

Emended diagnosis.—Smaller than *A. ischyros.* Skull nearly as wide as long. Costal plates in middle of carapace extending distad for one half to one third length of ribs. Hyo- and hypoplastra large plates with numerous relatively short digitations. Suture between hyo- and hypoplastra wide.

Horizon and locality.—Niobrara Chalk, Kansas.

Archelon ischyros Wieland 1896 (?=*A. marshi* Wieland 1909)

Emended diagnosis.—Very large species. Skull about 1½ times as long as wide, with strongly down-curved beak. Costal plates reduced to vestiges. Hyo- and hypoplastra with very long medial digitations; suture between these plates narrow. Humerus with great distal expansion and weak radial tuberosity. Dorsal and ventral processes of scapula of nearly equal length.

Horizon and locality.—Pierre Shale, South Dakota and Colorado.

SUMMARY

1. This study is based on an examination of nearly all available materials of protostegid turtles and describes such new materials as have accumulated since the last revision of the family was published (Wieland, 1909). Two subfamilies can be recognized.

2. Two genera, *Chelosphargis* and *Calcarichelys*, both occurring in the Niobrara Chalk of Kansas and in the Mooreville Chalk of Alabama, are proposed and described as members of the new subfamily Chelospharginae. These represent a generally primitive morphological level of protostegid organization, with specific features of specialization that parallel those in the Protosteginae.

3. The genera *Protostega* and *Archelon* are included in the subfamily Protosteginae. Much new information is added to our knowledge of the genus *Protostega*. Previously named species are redefined or redescribed and two new species are proposed.

4. *Protostega copei* is transferred to the genus *Archelon* as a more primitive species of this genus. Additional material of this form is described.

5. *Protostega gigas* and *P. potens* from the Niobrara Chalk of Kansas and *P. dixie* from the Mooreville Chalk of Alabama are very closely related species. *Chelosphargis advena* and *Calcarichelys gemma* are represented in both formations by the same or, more likely, by similar species. Comparable species in both formations show much the same degree of aquatic specialization. This suggests more or less contemporaneous speciation due to partial or complete geographic isolation rather than speciation in a temporal sequence.

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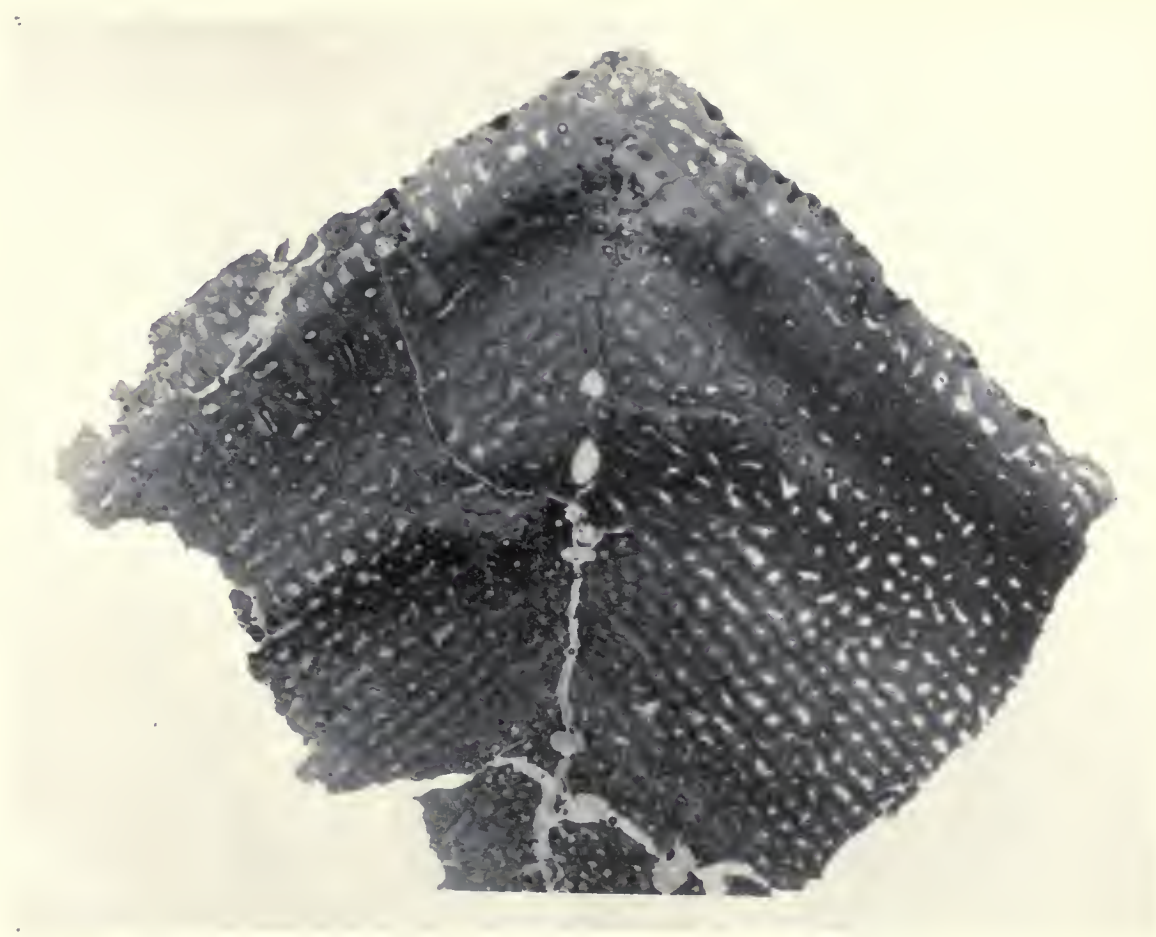
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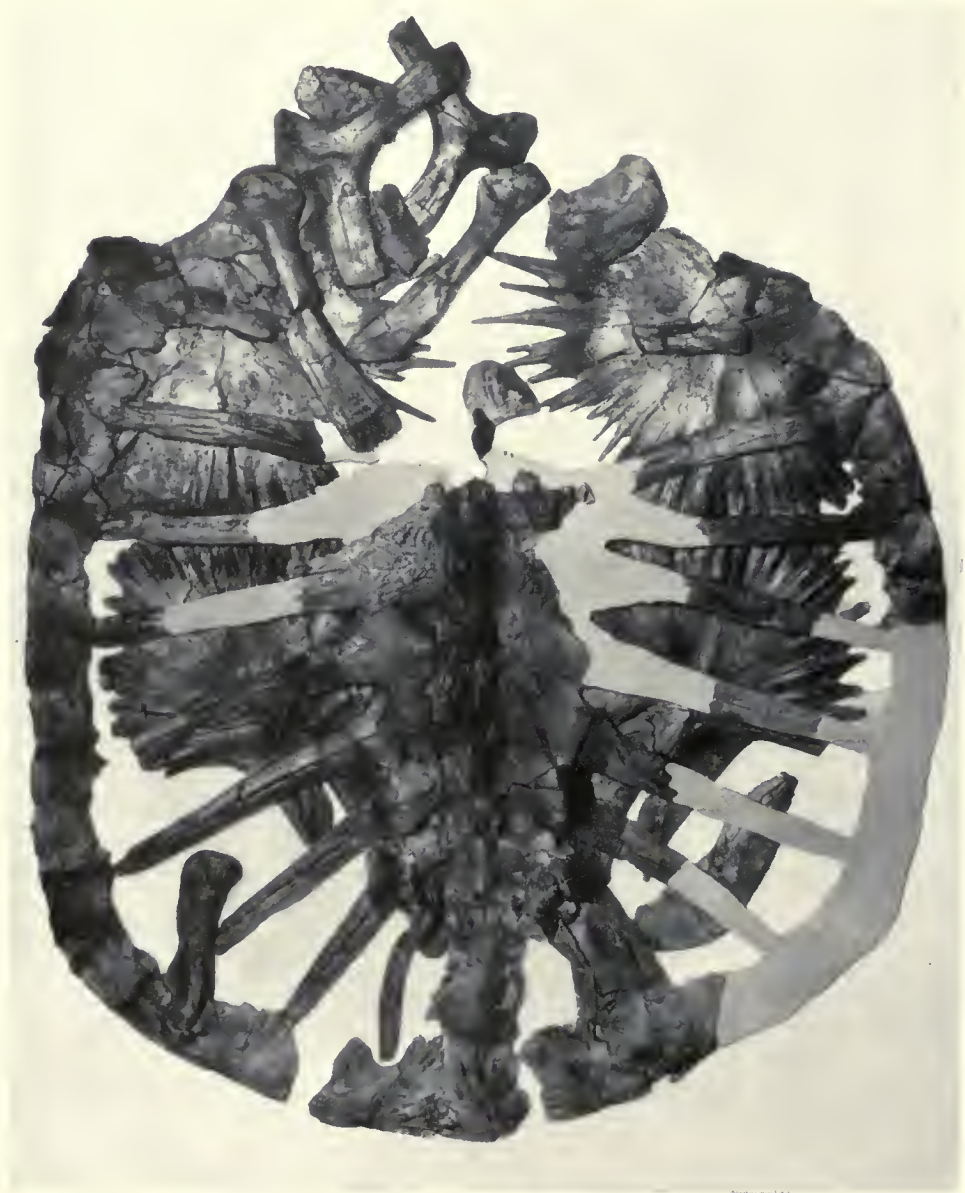
Protostega potens. A.M.N.H. 180. A, entoplastron; B, left hyoplastron; C, left hypo-
plastron; D, left xiphiplastron.

Protostega potens. A.M.N.H. 180. A, left humerus; B, left coracoid; C, left scapular fragment; D, (?)left femur.

Protostega dixie. C.N.H.M. PR133. Cross section through dorsal part of crested neural plate.

Archelon copei.   U.S.N.M. 11649.   About × 0.13.