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ART. VII.—*Revision of the Protostegidæ;* by G. R. WIELAND. (With Plates II–IV.)

[Contributions from the Paleontological Laboratory of Yale University.]

THERE is no family among all American fossil turtles which, following the discovery of its initial type, has so steadily yielded new forms and additions to our knowledge of the structure and history of marine turtles as the Protostegidæ. True enough, no further members of the family were noted and few specimens were collected for twenty years after Cope's original discovery of *Protostega gigas;* but then came the addition of the related genus *Archelon* from the Pierre Cretaceous in 1895, since which time scarcely a year has passed without yielding new data to the structure, extent and significance of the Protostegidæ.

Indeed, even before the discovery of *Archelon* the attention of the brilliant and incisive Baur had been turned to *Protostega;* and since then Hay, Case, Williston and Wieland have all contributed in turn to the literature of the Protostegidæ,—while in Europe Dollo has published papers of the greatest supplemental interest dealing with the origin of marine turtles.

Furthermore the collection of the splendid cotypes of *Protostega gigas* showing the complete limb structure, now in the Carnegie Museum of Pittsburg, and more recently the mounting for exhibition of the huge type of *Archelon ischyros* in the Yale Museum, have contributed much toward the increasingly accurate picture of the Protostegidæ. With the description of new species, meanwhile, and the appearance of the great volume of Hay—easily the foremost contribution to the literature of the Testudinata yet made—it is already evident that the Protostegidæ include a series of forms of the greatest structural interest, and that further additions to the family are certain to be made. Moreover, to all these newer facts and viewpoints we are enabled to add the description of a new species, calling for analysis of the group.

To these forewords to the present revision I wish to add praise for the painstaking labor bestowed upon the mounting of *Archelon* by the Yale Museum preparator Mr. Hugh Gibb. Likewise we are indebted to the rare skill of the well known scientific illustrator and artist Mr. R. Weber for the illustrations following.

CHELONIOIDEA Baur.

Superfamily of the Cryptodira.

A parieto-squamosal arch; palatine foramen and free nasals sometimes present (Desmatochelyidæ); fourth cervical cyrtean, with the centra of the sixth to eighth less modified in Cretaceous than in recent forms.

The five great marine families, namely, the Cheloniidæ, Protostegidæ, Desmatochelyidæ, Toxochelyidæ, and Dermochelyidæ, all doubtless independently acquired their equipment for life in the sea.[15]

Family *Protostegidæ* Cope.

Turtles with highly specialized thalassic humeri, but with three or more claws. A leathery hide and osteodermal armature evidently present. Carapace usually greatly reduced in later forms, the disk investing less than one-half the rib lengths. Plastron not markedly reduced. Peripherals serrate to strongly digitate on their interior borders; intra-peripheral dermogene ossicles sometimes present (known in *Archelon* only). Plastron very large, dactylosternal, with prominent fontanelles; epiplastra small, out-turned, separate, and wholly supported by the very large T-shaped entoplastron; hyo- and hypoplastra moderately digitate (*Protostega advena*) to strongly digitate (*Archelon*); xiphiplastra short and bowed. Pelvis with obturator foramina enclosed by complete ischio-pubic border. Coracoid extending all the way back to the pre-pubis except possibly in *P. Copei*. Skull large; temporal region broadly roofed over; descending processes of parietals; antorbital projection marked; quadrato-squamosal vertex much depressed; narial aperture more or less upturned; choanæ far forward, opening free behind vomer.

Genus Protostega Cope, 1872.[1]

Premaxillary beak less developed than in *Archelon*; maxilla with rather broad grinding surface, which extends backward to behind front of orbit. Lower jaw with rami early coössified. Neuralia normal so far as yet seen, and without median pits or grooves. Radial process of humerus large and projecting.

Species of Protostega.

A. Niobrara Cretaceous :—

1. A medium-sized to large turtle, with a thin carapace investing one-third the rib lengths, and interior borders of marginals splitting into medium-sized digitations. *P. gigas.*
2. A small turtle, with more than half the rib lengths expanded and with less reduced plastron than the preceding ; the hyo- but not the hypoplastra meeting on the median line ; xiphiplastrals only slightly bowed ; marginalia heavy and without digitation of interior borders. *P. advena.*
3. A medium-sized turtle, with a comparatively thick carapace investing the proximal half of the ribs; plastral form nearly as in *P. gigas* but with more numerous digitations and smaller fontanels; marginal borders serrate rather than smooth ; limb bones relatively short and small. This form has the heaviest shell of any Protostegid. The carapace is little more, and the plastron less reduced than in the Cheloniidæ. *P. Copei.*
4. A large turtle, with xiphiplastra nearly joined on the median line and epiplastral pittings on outer anterior projection of hyoplastra. *P. potens.*

B. Pierre Cretaceous :—

5. An immense turtle, with neuralia like *P. Copei*, but humerus without a markedly strong radial process ; marginalia strongly digitate on interior borders. *P.* (*Archelon*) *Marshii.*

Genus Archelon Wieland, 1896.[6]

Premaxillary beak greatly developed and strongly decurved; crushing surface of upper jaw set far forward and limited to vomero-maxillar region; lower jaw with rami not coössified until old age. Neuralia greatly reduced, to partly absent anteriorly, and replaced by epineuralia with a deep median sulcus nearly continuous to the eighth true [underlying] neural; tenth rib relatively large, free, and extending out to marginalia. Radial process of humerus weak.

Archelon ischyros from the uppermost Pierre Cretaceous of the valley of the South Fork of the Cheyenne River is the only species.

Protostega Copei sp. nov. (Figures 1–4).

A new species, which may be appropriately named for the illustrious discoverer of the Protostegidæ, is indicated by the most complete and best conserved specimen referable to its family, thus far obtained. This splendid fossil is from the Niobrara chalk of the Hackberry Creek Valley, Gove county, Kansas, and was found in the summer of 1905, by the veteran collector and explorer, Mr. Charles H. Sternberg.

Fig. 1.

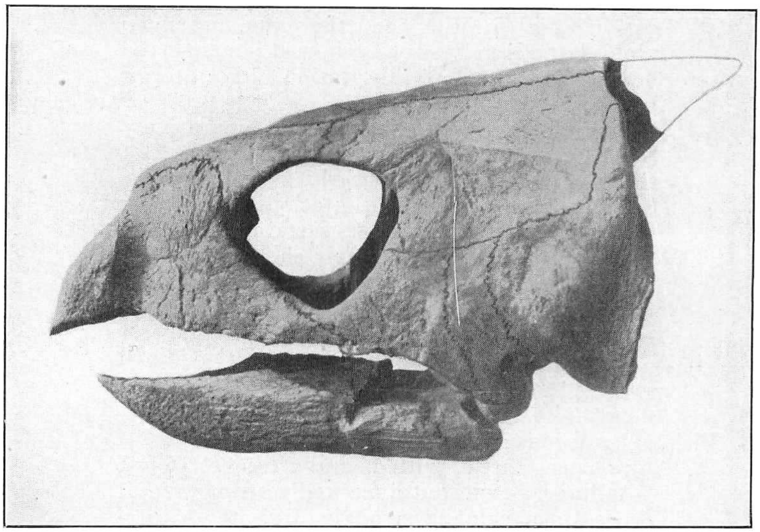

Figure 1.—*Protostega Copei.* Photograph of skull and lower jaw of type as mounted in the Yale University Museum by bringing together the dissociated and for the greater part but little crushed cranial elements. One-fourth the natural size.

Only minor portions of certain boundaries had to be restored. A little attention will at once reveal the limiting sutures of the premaxillary, maxillary, frontal, post-frontal, parietal, jugal, post-frontal and squamosal. Only the boundaries of the quadrato-jugal are generalized. The premaxillary is a little crushed to the left, and the most striking feature is the low-set position of the squamosal, which is but little if at all exaggerated. Cf. figure 6.

Not only is the present type one of the most complete of fossil turtles, but more than any other known specimen of *Protostega*, it permits exact comparison with *Archelon*, being for the most part free from the crushing which so often obscures the characters of the otherwise fine material from the

Kansas chalk. Owing to this freedom from crushing, it has been possible to restore with approximate accuracy the outline of the skull, carapace, and plastron, although all the elements of the entire skeleton were dissociated during erosion from their matrix, those recovered being as follows:

Skull, with lower jaw,—nearly complete, one squamosal and certain minor portions only missing.

Carapace: Nuchal; first to fourth neuralia; pygal; fairly complete series of ribs; first and second marginalia of both sides, with third and fourth of right side.

Plastron: Alæ of the entoplastron; hyoplastron of right side; hypoplastra and xiphiplastra complete.

Shoulder girdle: Both humeri and the procoraco-scapulars, with coracoid of right side only.

Pelvis: Only the right ischium missing.

The chief parts lacking, therefore, are the radius and ulna, the femora, and the bones of the hands and feet.

The dissociated elements of the cranium, as brought together and mounted with the lower jaw, afford the most satisfactory representation of a Protostegan skull thus far seen. In fact, the result displayed by photographic figure 1 must be of nearly the true form, since in addition to the presence of the lower jaw and nearly all the exterior elements, the main outline is further confirmed by the practically complete palatines, pterygoids, and quadrates. Only in the interior of the skull are clear characters lacking; for instance, the descending process of the parietals, noted by Dr. Hay in *Protostega advena*, cannot be observed.

In the main, the present fine cranium merely serves to corroborate the characters of the Protostegan skull, as already determined, and to bring out more clearly the major differences from *Archelon*. Thus, the strongly decurved beak and the upturned nares of the latter genus are absent, the outlines being more like those of other sea-turtles, with the orbits fairly well forward. The low-set squamosal, which certainly sent up a process along the posterior border to meet the parietal, however, is a family characteristic. The general outline reminds one not a little of the skull of *Colpochelys Kempii* Garman. Interiorly, there is no great conelike palatal projection of the vomer, as seen in *Archelon*.

While the present species is here defined as new, there is no very marked character not possessed by *Protostega gigas*, specific differences being mainly exhibited by the smaller limbs and the heavier carapace and plastron now to be described.

Carapace.—Hitherto it has not been possible to gain a satisfactory picture of the shell of any species of *Protostega*. All the specimens known have either lacked a large part of the neuro-pleural series, or they have been so badly crushed as to render the general form and structure more or less doubtful, as in the case of the Carnegie Museum specimen that yielded such clear testimony to all the characters of limb organization; and even in the present instance the evidence is not so convinc-

FIG. 2.

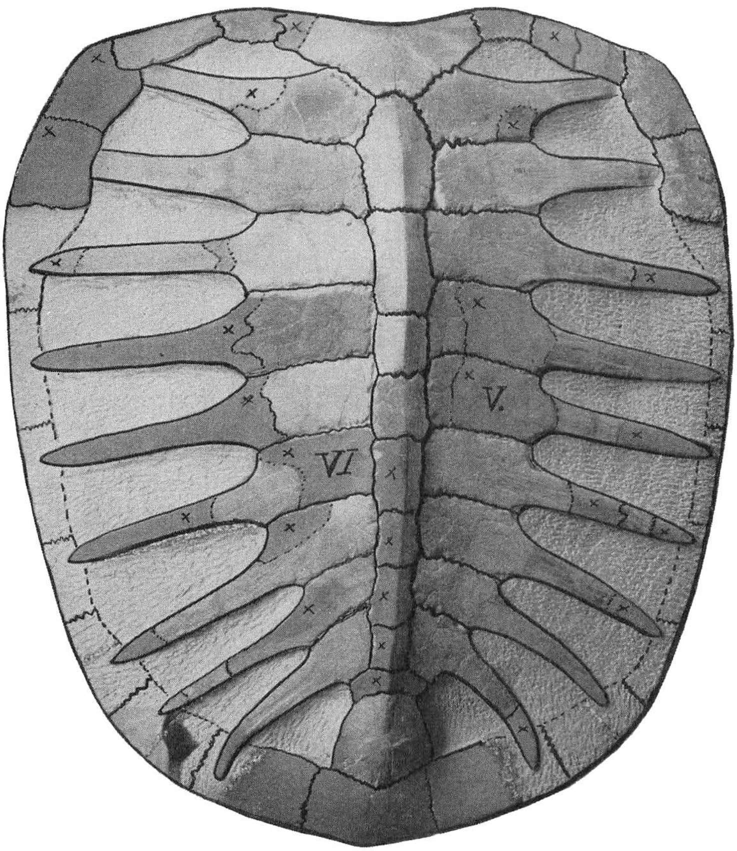

FIGURE 2.—*Protostega Copei*, 1/7 natural size. Carapace of the type as mounted in the Yale University Museum, from little crushed but dissociated elements lacking those portions marked by an (×) or else given in dotted outline. The portions actually present thus include a fine nuchal (with a nether process), the four first neurals and pygal with the three first marginals perfect, together with eight pairs of pleuralia. The disk is then correctly indicated; but concerning doubts as to the existence of a large ninth pair of ribs in contact with the marginals consult the text.

ing and complete as in *Archelon*, where the series of ribs is not only entire, but articulated. Nevertheless, owing to absence from crushing, splendid conservation of all surface features, and the presence of a nearly complete series of ribs, with the nuchal, the anterior neurals. and important marginals completing all the frontal border, the present carapace must be regarded as a magnificent specimen. In fact, the only structural point in the restoration here given, which awaits confirmation or disproval by future discovery, is the degree of development exhibited by the tenth pair of ribs. They are represented free, as in *Archelon* in figure 2, and such ribs extending out to meet the final marginal are regarded as a probable family distinction. It may be, however, that placing the proximal portion of the right fifth pleural as assigned and then restoring a sixth and a seventh pleural on the left side are not warranted. In such a contingency two suppositions are, therefore, open, as follows: (*a*) The pair of ribs shown as the tenth may be really the ninth, and the true tenth pair of ribs may not be present, perhaps being only slightly smaller than those shown in the restoration, but passing out to meet the marginals. Such being the case, the only error made is in placing the pleuralia, from the fifth pair of ribs on, one number too far back; (*b*) An unrecovered tenth pair of ribs may be reduced, as in the Cheloniidæ, and may not have passed out to the final marginal. In this case, the post-fifth pleuralia would not only be one number too far back, but the carapace would be as here represented several centimeters too long. If either error has been made, the former seems by far the more probable.

The neuralia are heavier than in *Protostega gigas*, and form a strong unbroken mid-ridge of normal Testudinate form in sharp distinction to the epineural grooving and anomalous structure of *Archelon*. Though it is to be noted that on the first neural, the second and third, evidently on the fourth and fifth, and probably on the missing eighth and ninth, there is a strong accentuation of the mid-ridge, suggesting the appearance seen in *Toxochelys Bauri*. In the latter form, however, this feature is due to discrete epineural ossicles, while in *Protostega Copei* there is no evidence of osteodermal elements. Nor are there any hornshield groovings; on the contrary, the evidence is always to the effect that the Protostegidæ were enveloped in a leathery hide.

Fortunately, the nuchal is sufficiently complete to show the entire outline as a heavy normal element much as in *Osteopygis*, except that a prominent nether process is present. The first marginals, which are rather short and flat elements, are quite complete, as is also the rather long second marginal of the left side, with the distal half of that of the right side. On the latter may be traced with precision, one after the other, the articular digitations and grooves corresponding to those of the next member of the marginal series, namely, the third, which is also complete and is followed by a fourth in equally good preservation. I am thus explicit, because it is important to note that all the anterior border of the carapace is indicated with certainty, and shows the presence of a peculiar upturning

FIG. 3.

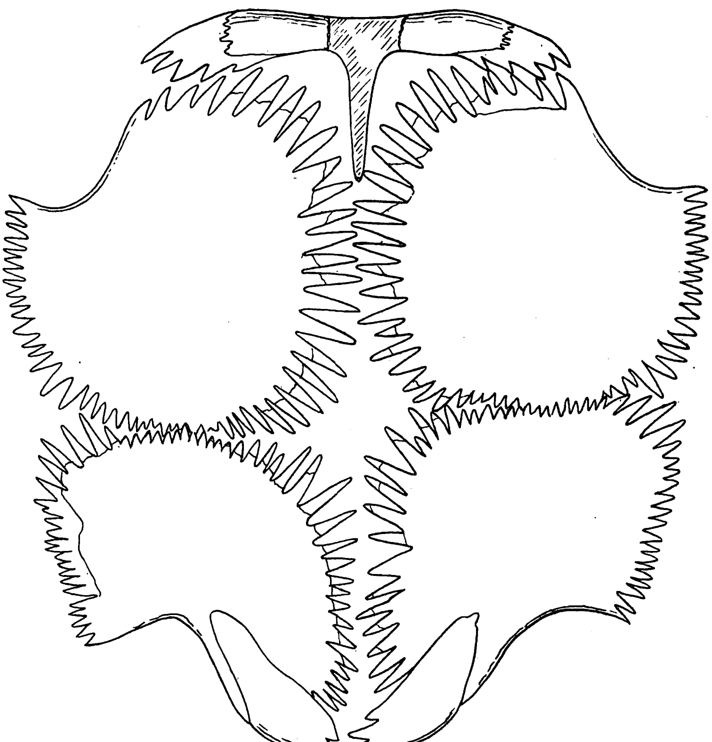

FIGURE 3.—*Protostega Copei.* Plastron of the type × 1/7 nearly. The hypo-xiphilastræ are especially well conserved, and the left hyoplastron in fair condition. The right hyoplastron and portions of the T-shaped epiplastron are not present; and as indicated in the figure, the ends of most of the digitations of all the elements are missing. Nevertheless the plastral form is quite accurately indicated in its entirety by the original specimen as here outlined.

of the portion of the carapacial edge formed by the junction of the third and fourth marginals. Evidence is here furnished that the strong anterior and much upturned prolongation of the third marginal of *Archelon* was an articulating portion rather than a spine; and use has been made of this fact, although it might have remained in doubt but for the exact testimony of the present fine specimen. The interior borders of these marginals, however, do not have the strong digitation seen in *Archelon*, being only slightly serrated.

FIG. 4.

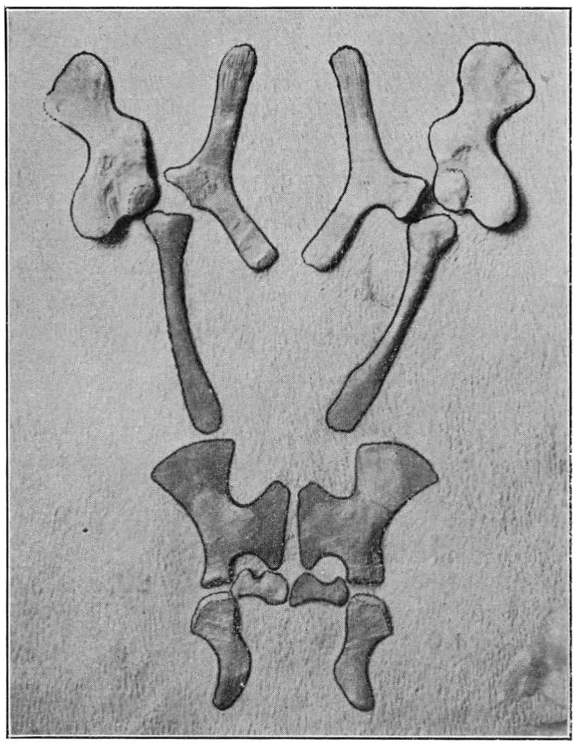

FIGURE 4.—*Protostega Copei.* Shoulder girdle with humeri and the pelvis of the type × 1/7. The only portions restored are the left coracoid and the right ischium. These elements belong to the very same individual as the skull, carapace and plastron shown in figures 1–3. [It is likely that consonant with the heavy carapace the limbs were shorter than in *P. gigas*, and that the coracoids did not actually come into contact with the ecto-pubis.]

Protostega Copei was not so orbicular a form as *Archelon ischyros*, and its plastron was relatively much shorter. As to the elements other than those now described, it appears necessary only to state that the accompanying illustrations sufficiently exhibit not merely their characters, but their chief dimensions. Certain measurements, however, are appended, as follows:

Length of cranium from snout to condyle (accurate)	24·0^{cm}
Greatest width of cranium across the condyles (close)	20·0
Length of lower jaw (on median line)	15·0
Length of carapace (estimated)	80·±
Greatest length of plastron	63·5±
Greatest width of plastron	66·0
Greatest thickness of plastral elements measured through their centers of ossification:	
Entoplastron	15·^{mm}
Hyoplastron	23·
Hypoplastron	20·
Xiphiplastron	13·

FIG. 5.

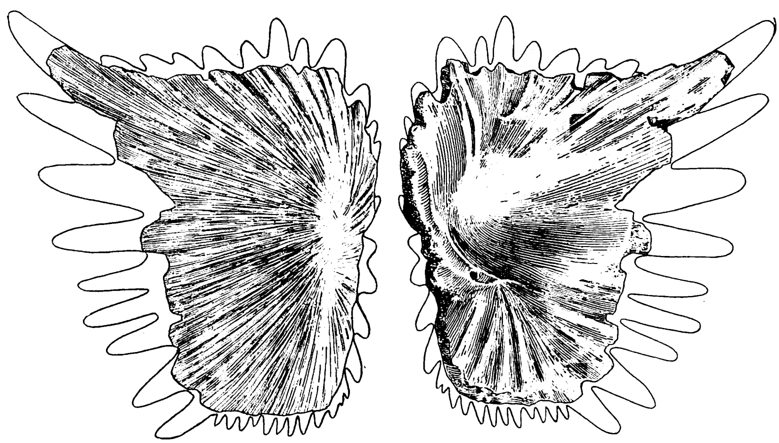

FIGURE 5.—*Protostega (Archelon) Marshii.* Right third marginal x¼. Dorsal view to the left, and ventral view showing large pit for the second rib to the right. [Dactylations should be represented as distinctly acuminate, but not much longer.] Observe, that as proven in *Protostega Copei*, articulation with the second marginal was formed by the long upward and forward projection, resulting in abrupt change in direction of the marginal line at the humeral notch, as revealed further by the figures of the entire skeleton.

Protostega (*Archelon*) *Marshii* Wieland[11] (Figure 5).

In this Journal for April, 1900, I gave a brief description of a new species of *Archelon*, which was based on the portion of a skeleton collected by me in 1898, on the left bank of the Cheyenne River. Until further material is found, as will with certainty transpire, the fragmentary condition of the present remains will scarcely justify much work upon them by a preparator; nevertheless, the species represents an important fossil type.

A reëxamination of the specimen confirms the characters given, namely, a relatively short humerus and great thickness of the plastron, the latter being half as thick again as that of *Archelon*. As it is probable that the present turtle was not quite as large as *A. ischyros*, type (3·4 m.=11 feet long), however, it may be that its plastron was proportionally twice as thick as that of the latter species.

A fine third marginal of the right side shown in figure 5 is also present, and with it are articulated the keels of the more fragmentary fourth and fifth marginals. These elements are of much the same form as in *A. ischyros*, type, and although relatively heavier than in that species do not show the great disparity in weight noted in the plastron. More obvious differences of taxonomic bearing, however, are exhibited by a fragmentary, though otherwise finely conserved neural from near the middle of the neural series. This lacks the groove so highly characteristic of *Archelon*, and has a strong and continuous median ridge precisely like that in *Protostega Copei*. It therefore becomes necessary to transfer the present species from the genus *Archelon* to *Protostega*, where it holds a position of importance, as exhibiting not only the continuation of the latter genus from the Niobrara into the Fort Pierre, with marked increase in size, but, as far as we know, represents the closest structural approach of the genus *Protostega* to *Archelon*, thus far observed.

The Mounted type of Archelon ischyros (with Figures 6–12, and Plates II–IV).

All the material thus far referred to the genus *Archelon* has been discovered and collected by myself during the past fourteen years. The original type of *Archelon ischyros* was found in the brakes of the south fork of the Cheyenne River, about five miles west of the mouth of Rapid Creek, Custer county, South Dakota, in August, 1895. Though a remarkably complete fossil, it lacked the skull, which, however, was supplied by an excellent younger specimen with a fine cranium and the lower jaw in place, obtained in 1897. This is here shown by the photographic drawing, figure 6. In 1898, the related type *Protostega* (*Archelon*) *Marshii* was procured from the same horizon as the specimens of *Archelon*, but on the east bank of the Cheyenne, in the Pine Ridge Indian reservation. Later still, in 1902, a large individual of *A. ischyros*, nearly identical in size with the original type, was collected at a point several miles farther south, on the west bank of the Cheyenne. This specimen has been of considerable value in showing the more important carpals in natural position, and in yielding additional finger bones and the epiplastron. A well-conserved lower jaw with fully coössified rami accompanies it. Like the type, it was completely imbedded in one of the lenticular masses of marl or clayey limestone common in the Pierre, but as this was much checked by cleavage planes there has been considerable shifting of parts. The specimen, while good, is not comparable to the original type, which, barring the lack of the skull (destroyed by erosion), is one of the finest of all great fossil vertebrates. It was but little crushed, and nearly all the parts present were in their normal position.

In addition to the examples mentioned, fragmentary portions of other specimens were obtained at different times, all pertaining to the uppermost one hundred feet of the Pierre, and all from within an area of about eight square miles. The best skeletal conservation was found in the bluish clays of the upper thirty feet of the Pierre, as covered by the Oligocene overlap in the Cheyenne River valley; but most unfortunately a broad Oligocene river, the clearly marked bed of which I definitely located west of the Cheyenne, scooped out of these Pierre strata exactly the portion that must once have contained the most numerous and the best turtles, as indicated by frequency of occurrence as well as fine conservation on both banks of the old Oligocene valley.

The various specimens of *Archelon* have been made the subject of five contributions to this Journal. [6, 8, 11, 12, 14]. These partial descriptions have been repeated in a summarized abstract, with certain additional interpretations and views, in Dr. Hay's great volume on the "Fossil Turtles of North America."[17] It does not therefore seem necessary again to repeat the preliminary descriptions, except in so far as needed to call attention to inaccuracies disclosed by the final mounting of the type specimen, together with the great additions to our knowledge of *Protostega* made during the past half dozen years. It is the present purpose to give in concise form the features of this greatest of marine turtles disclosed by new discoveries and by mounting, which always sheds new light on the characters of a fossil vertebrate; and especially to give the facts of classificatory value, together with a discussion of relationships.

The Skull (figure 6).—It is to be hoped that a second skull may be recovered. Thus far only the type skull and one additional lower jaw have been found; hence, it is not possible to add to the earlier descriptions except in wholly minor points of interpretation. Moreover, abstracts of these descriptions with figures are given in admirable form in Hay's work previously cited, a work which every student of the Testudinata must find indispensable. It may, however, be stated that in the restoration, Plate IV, the skull undoubtedly shows the exact proportions of the supra-occipital, this being an improvement upon the earlier figures.

The Vertebral Column.—The fact that the vertebral column of *Archelon* is so nearly complete and uncrushed, with nearly all the elements in undisturbed natural position, gives to the restoration high value. Only the four proximal cervicals and a few of the smaller caudals from near the tip of the tail are missing, while from the eighth cervical to the fifth caudal,

FIG. 6.

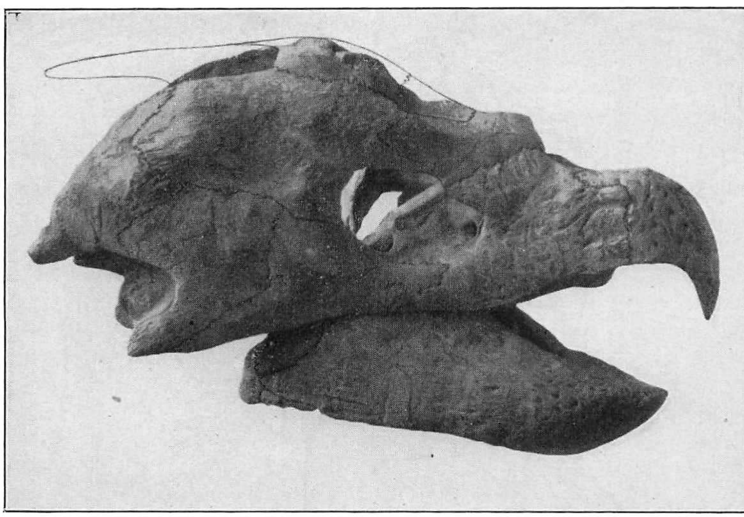

FIGURE 6.—*Archelon ischyros.* Skull of cotype shown about 1/8 natural size. The bounding sutures of all the exterior elements may readily be distinguished. [The restored supra-occipital crest, perhaps, is shown too slender.] The low set squamosal is, in comparison with *P. Copei* and *P. gigas*, seen to be a family character of the Protostegidæ.

inclusive, all the vertebræ are complete and in natural contact. Further, in the large specimen collected in 1902, the fourth cervical is present and of the normal or cyrtean form common to all marine Testudinata.

In *Archelon*, the cervicals succeeding the fourth are cœlo-cyrtean, with the inferior sides of the centra heavily double-keeled. The valley between the keels is broad and shallow. Neither in form nor size is there much variation in the distal cervical centra. Aside from strength and great size, the dorsosacral series presents no marked peculiarity, while the caudal series is rather short. The arches of the first eight to ten caudals are free, but those of the remainder of the series are strongly fused to their centra. It is not likely that the tail could have been so freely moved as might be implied from the over strong curve in the restoration.

FIG. 7.

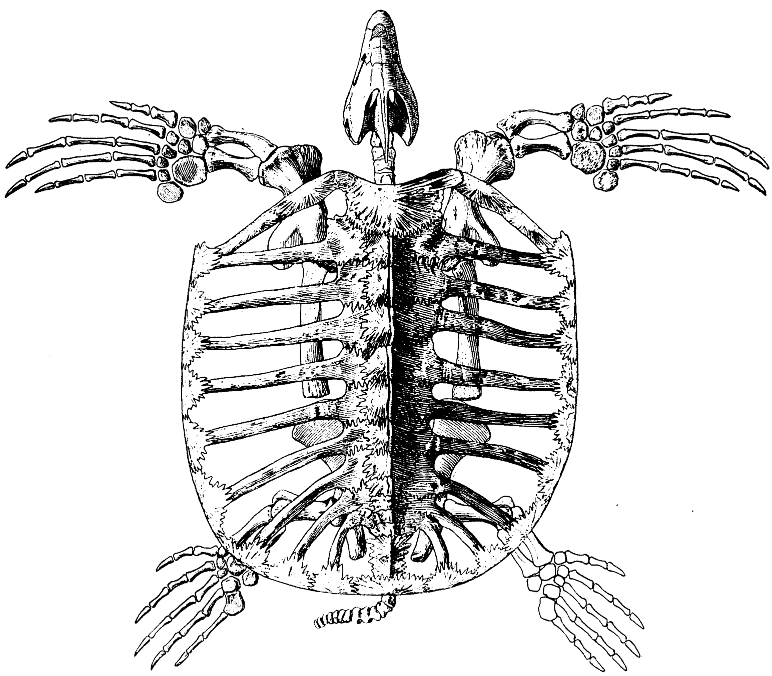

FIGURE 7.—*Archelon ischyros*, × 1/36. Dorsal view of original type. It is not necessary to give in detail the exact outline of the restored portions. The skull is outlined from a cotype, and the right hind flipper shown in the normal outline was not present beyond the proximal half of the tibia and fibula, having, as explained in the text, been bitten away in the early life of the turtle.

Note on the mid-line following the nuchal seven larger plates followed by four smaller ones and then the pygal. All these eleven plates intervening between the nuchal and the pygal are adjudged to be epineurals seated on the greatly reduced neural series which did not, as in all other turtles except *Dermochelys*, normally come into view at all.

Observe the nine pairs of fully developed ribs, of which the first large pair is the second, the small first pair not coming into view. Infra- and supra-peripherals not indicated.

The Carapace.—The nearly orbicular form of the carapace is a striking feature. The *nuchal* is very large and very thin, especially in the lateral portion, indeed so thin as to suggest the necessity for strengthening by overlapping dermal ossifications. The anterior edge is strongly concave, being sharp, not rounded, in the middle region. The nether or cervico-neural articular process is prominent; it takes the form of a heavy trapezoidal ridge, longest in front, with a keel-like buttress radiating from all four corners.

The medial elements of *Archelon* are anomalous and require discussion as well as description. At first sight one would certainly say that there is a series of seven larger neurals following the broad thin nuchal, with four much smaller neurals preceding a single pygal element and making eleven neurals in all. On closer inspection, however, it is found that despite the fact that the neural region of *Protostega* is of simple and normal structure there is in *Archelon* a more complex arrangement of parts than in any turtle thus far discovered—a condition moreover that has a more distinct bearing on the meaning of the Dermochelan anatomy than any other thus far observed in fossil turtles.

In my original description I stated that "The medial plates unite very imperfectly by means of loosely doubled interlocking sutures and overlapping digitations grading into frequent free spines [spine-like projections] posteriorly. These digitations are mostly long, thin and ribbon-like, and produce a junction quite different from the usual suture. In many cases there is an appearance such as would result if the digitations of the one plate had lain upon the surface of the adjoining plate when it was in a plastic condition and thus raised rounded ridging about their edges. The order of the digitations and their size is rather regular." It was also explained that the carapace was very thin on the midline and that at a break exposing the section back of the sixth rib there were thin layerings. And it should now be added that, bearing in mind that in the mounted specimen the dorsal vertebræ remain articulated as originally, I am, perhaps, censurable for not having the carapace sawn through at the line say of the third, sixth and eighth dorsal centra. However this may be it was not done, and, awaiting further specimens, the type specimen in which all details are certainly present must yield as its only quota of new fact the superficial details. Indeed, were it not for the accidental fact that back of the ninth medial element two prepygal median elements are missing, and yet that there is continuity of the carapace, it would likely escape us that two layers of bone are present on the midline. At the point where these elements have become disarticulated one can see that the pleurals expand broadly beneath the median plates, but we cannot tell to what extent they replace or crowd the neurals, which are evidently small posteriorly. Immediately back of the nuchal, however, there does not appear to be an underlying neural, and one may say with certainty that all the anterior neurals at least are very greatly reduced. It is, too, equally clear that these mere thin sheets of underlying bones that can be referred to neurals, so far as they were seen in fracture sections, have had *their function taken over by the*

Fig. 8.

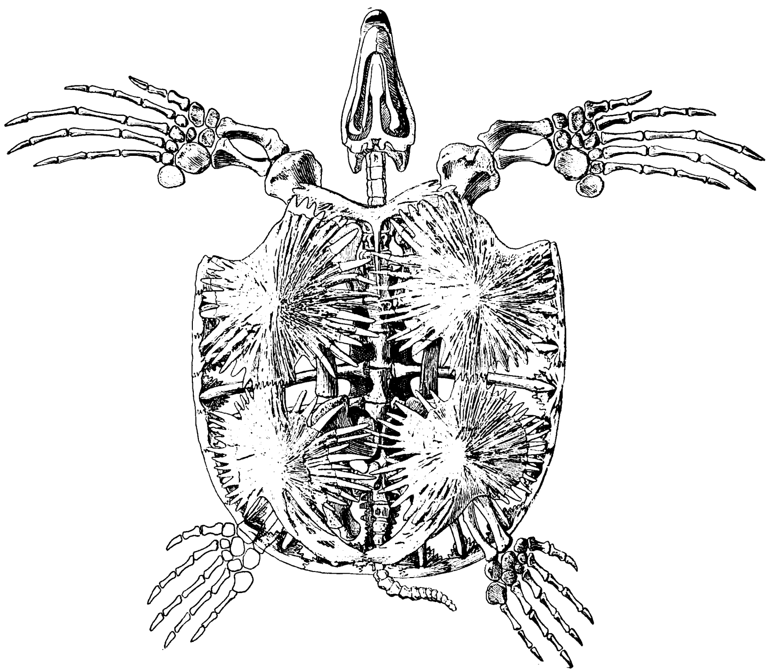

Figure 8.—*Archelon ischyros*, × 1/36. Ventral view of type. Compare legend of the preceding figure. Note that all the elements of the plastron here shown occupied their normal position as originally recovered. Only the doubtful position of the omitted epiplastra prevents final accuracy. Note also the great length of the plastron; it is nearly as long as the carapace. Observe the small size of the femoral notches. The rib pair passing beneath the hyo-hypoplastral suture is the fifth.

outer dermal series, which is continuous from nuchal to pygal and thus corresponds to the neural keel of *Dermochelys*.

On the nuchal itself no additional elements were observed, but, as just stated, one may suppose from the great reduction in thickness such may well have been present. Indeed, it is not impossible that the posterior end of the nuchal extended beneath the first of the median supra-neural elements, and that as a consequence our restoration is thus some ten centimeters too long.

Summarizing then: there are to be seen on the midline apparently overlapping all the neurals and the proximal borders of the laminæ of the nine pairs of normal ribs which pass out to meet the marginals, a series of eleven thin supra-neural elements simulating in size and outline a neural series.

These supra-neurals form a distinct median keel and are of distinctly quadrangular outline all the way back to the eighth and ninth, which are short on the median line, but nearly as broad as the others. The digitate character of the sutures between the successive members, but more particularly of the pleural overlap, has already been commented upon. All the outlines are quite exactly shown in my original figure (reference 6, Plate VI). A dominant feature of the midline is a narrow median groove which extends from the second to the seventh member inclusive and is most pronounced in the second and fifth. In the mid-region of each neural enumerated the groove is somewhat widened and deepened, sending out a radially ranged series of nutrition furrows or striations which form a dominant sculpturing of the mid-region of the carapace. Some further horny or even ossified elements may have occupied the mid-region of these shields. The aspect of the neural keel is thus seen to be different from that of any other turtle.

The supra-neurals of *Archelon*, be it noted, vary distinctly from those of *Toxochelys* in which the series is not continuous and corresponds to a normal series of vertebral hornshields.

In *Archelon*, however, a leathery hide must have been present, with a system of keels of the usual number, as denoted by dermogene ossifications rather than hornshields; these will be treated more fully later on. An ossicle like the supraneurals of *Toxochelys* was found by Hay accompanying *Protostega advena*, but its derivation was left in doubt.

The pleural investment of the *ribs* occupies only the proximal fifth of their length. The free ends of the ribs are thus the dominating feature of the carapace. They are very heavy, in compensation for the light to almost paste-board thickness of the carapacial shield. The first rib is small and more or less curved and flattened. As in *Protostega*, it passed well to the front beyond the expansion of the first pleural, and may have supported either the thin posterior nuchal ala or possibly some osteodermal element.

It is here necessary to note that the type specimen remained packed, partly in the matrix, from 1898 until 1906. Owing primarily, however, to a luckless defect in my field notes, which rendered a lapse of judgment easy, it was thought for a time that the crushed coracoid of the specimen collected in 1902 was a heavy first rib.

As a result of this misconception, together with the uncertainty regarding the carapace that had long existed in the mind of every student of the Testudinata, I published the

Fig. 9.

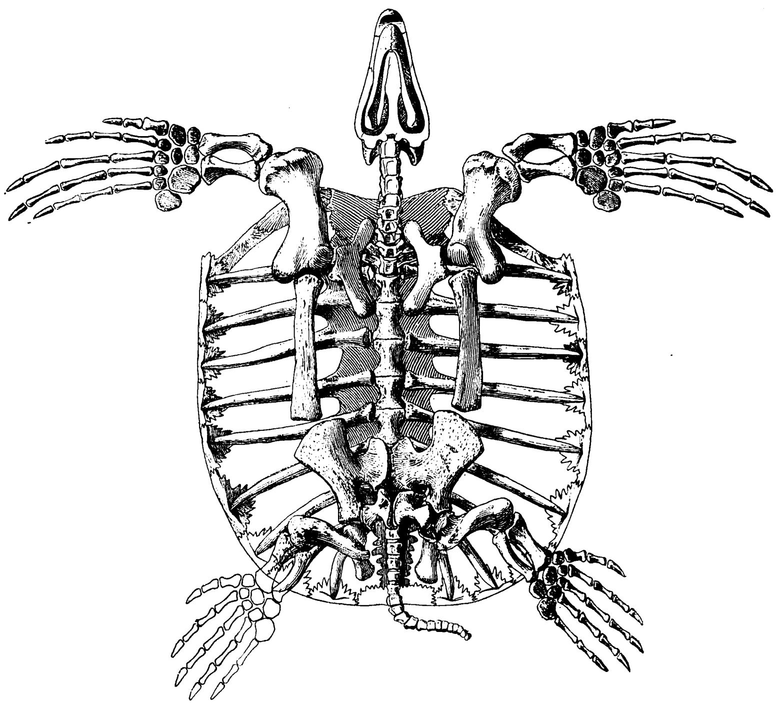

Figure 9.—*Archelon ischyros*, × 1/36. Ventral view of the type with plastron removed. Compare legends of the two preceding figures. Recall that as originally collected the vertebral column from the fourth cervical on was found normally articulated and complete all the way to the smaller caudals, a few of which were missing. Observe that the coracoids pass all the way back to the ectopubes. Note in the hind paddle the large size of the tibiale and fibulare, and the pisiformoid development or functioning of the fifth carpal.

erroneous figure of my paper of 1903.[14] But why Dr. Hay has reproduced this in his volume,[17] I fail to understand, as I specifically declared the figure to be a mistaken one several years ago. I can only regret that the original figure of *A. ischyros*[6] was not used, and still more deplore the fact that the labor of preparation on the type was not sufficiently advanced to permit the offer to Dr. Hay of a photograph of the mounted skeleton in time for use in his volume.

The tenth ribs verify the original and excellent figure of the carapace in an important detail. In that figure, these ribs are both shown as distally restored to a length indicating support of the last marginal, were that element present. This restoration is correct, the right tenth rib having since been found complete, so that the length of the entire series is now absolutely known; and it should here be emphasized that while some of the ribs had disintegrated on one side or the other of the carapace, there is not a pair in the succession, from the first to the tenth inclusive, that lacks either a right or a left member complete to the tip.

This functional development of the tenth rib is unique in the Thecophora. It denotes either a more primitive condition or a restrengthening of this element in compensation for a carapacial shield not only in process of reduction, but probably also of replacement by an external dermal series corresponding to the usual Testudinate keels or lines of longitudinal development.

The Marginals.—The marginal series of *A. ischyros*, type, is considerably restored in the figures given (Plates II–IV), but not hypothetically so. There are present in sufficiently good condition for the determination of all the main features, marginals referred to ribs extending all the way from the second to the eighth or ninth rib. Further, the fine third marginal is present (cf. figure 5), which in *Protostega* (*Archelon*) *Marshii* is suturally united with the fourth to sixth, the latter species having marginals of quite the same form as in *A. ischyros*, type. In the additional specimen of *A. ischyros* obtained in 1902, the seventh (?) marginal is also present, while the first to fourth are positively known in *Protostega Copei* (cf. figure 2). Hence, remembering the functional tenth rib, it may be definitely stated that each rib beginning with the second bore a marginal and that the pygal marginal, the only member of the peripheral series not recovered in any of the larger forms of the Protostegidæ (it is present in *P. advena*), was thin, short, and broad, and must have had the form shown in the restoration (Plate II).

The noteworthy and strange feature of the marginals is the strong digitation of both the superior and inferior plates and also of the anterior elbow formed by the outer border of the third marginal. Were it not for the fact that in *P. Copei* the junction with the second marginal is definitely shown, it would scarcely be suspected that the true articulation of the third marginal with the second in *A. ischyros*, type, takes place by means of its long spinelike extension, which projects upward and forward; for even in that portion of the outer border next to the humeral notch there are blunt spines.

Did the spines of the marginals articulate with one or more carapacial and plastral rows of dermal ossifications, and thus afford the nearest approximation to the osteodermal mosaic of *Dermochelys* yet discovered by adding dermal ossification on all the keel lines, that is the neural keel, the pleural keel, the supra-marginal, and marginal keel? I believe such to be the case, for at least two elements referable to a similar additional series corresponding to the supra-pleural keel of *Dermochelys* have been recovered. Nor is it strange that more have not been obtained. A fine shark's tooth pertaining to a scavenger species related to *Lamna* was found with the type, and clearly indicates that all dermal portions loosely affixed to other elements of the carapace or plastron must have been peculiarly liable to disassociation. In what other than a supra-marginal or infra-marginal position is it possible to place the thin and distinctly asymmetrical element shown in figure 10? It represents an integral part either of the carapace or of the plastron. Further, the likewise unique element shown in connection with the marginal in figure 11 can not be interpreted as in other than a natural position. From the fact that it is digitate all around and slightly asymmetrical, it may be inferred that a series of such elements lay inside of, and articulated with, the superior borders of the marginals, alternating quite regularly with them in about a double number, and that beyond this space a second much thinner supra-marginal series was present. The space between the latter and the midline of the carapace, where, as has been already seen, the presence of a median row of supra-neural or in part osteodermal elements is demonstrated, may or may not have been continuously occupied by ossifications. In any event, there are the seven dorsal keels, as in *Dermochelys*. On the plastral side, direct evidence of

Fig. 10.

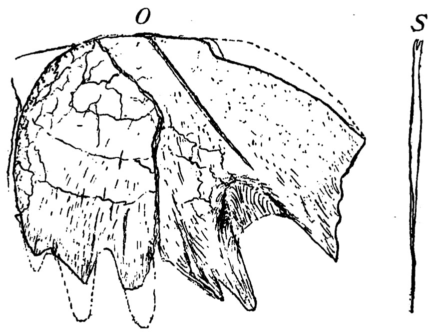

Figure 10.—*Archelon ischyros* × ¼. A large dermal ossicle found in connection with the plastron of the original type, but possibly dorsal. *O*, the outer view; *S*, sectional view showing the extreme thinness of the element. Note that the asymmetry of this element and its dactylate border indicate not only connection with other dermal elements, but the probability of the presence of entire series of such elements.

dermal elements is lacking, although an agreement with the five plastral keels of the leatherback may be conjectured.

The Plastron (figure 8).—The nearly perfect plastron of the type has suffered somewhat during collection, by its removal from an exceedingly hard marl matrix into which the numerous and often interlocking spines of the mid-plastral region penetrated. Nevertheless, as finally mounted, the plastron may be said to be in splendid condition. All the central

FIG. 11.

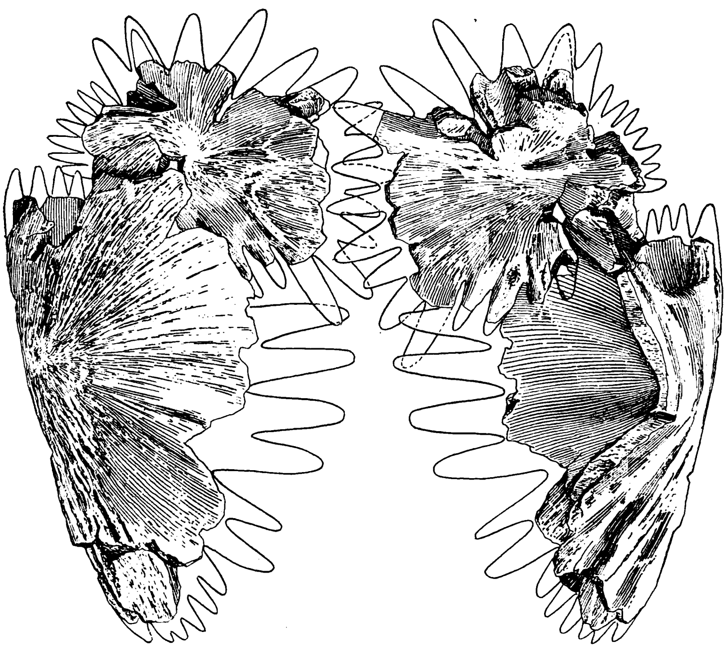

FIGURE 11.—*Archelon ischyros.* Left eighth or ninth marginal as found in conjunction with an additional element in a supra-marginal position. Shown ⅓ natural size. If the anomalous element is not a supra-marginal it must be referred to the supra-neural series just anterior to the pygal. A slight asymmetry does not prevent, although it makes such a position less probable. It is easier to consider this element as having been found in a natural position, and as perforce thus accounting for the supra-marginal keel of the carapace of *Dermochelys.*

portions of the large plates are present, with most of the spines, so that neither their size, form, length, or number, is ever in doubt. More important still, all the elements are but little crushed and, save the epiplastra, are present in their normally articulated position, just as they were figured in 1898.[9] In commenting on this figure, Dr. Hay states that a length of 2100 millimeters is thus indicated for the plastron, making it larger than the carapace, which he considers impossible. Neglecting my measurement of the plastron, which was given as 2000+ millimeters, as well as the fact that the entoplastron is very plainly shown a little anterior to its true position, he also fails to note that the exact length of the carapace with the nuchal in position had not been determined by anyone. His first premise is therefore unfounded and his conclusion a pure assumption.

The important point, however, is that in the restoration, where the length of both carapace and plastron is definitely determined, the two are found to be nearly equal. In the dorsal view, the plastron appears a little shorter than the carapace, while in the ventral view, the enormous expanse of the plastron, greater by far than in *Protostega Copei* and greater than in any other sea-turtle, entirely cuts out the carapace. *Archelon ischyros* was certainly a very singular marine form; with its enormous size, huge plastron, and small femoral notch set far back, it had need of the great humerus, which by reason of form and musculature represents a powerful sea-type.

The unique T-shaped *entoplastron* of the Protostegidæ has had an interesting history. First called a nuchal by Hay in a Kansas specimen, it was left for Wieland[8] to determine conclusively and figure both these elements in *A. ichyros*, although there was uncertainty whether epiplastra were present at all. For reasons that now appear trivial, being merely an imperfectly indicated condition of overlap seen in the field, the excellent point of view developed in the paper just mentioned was abandoned for a time.[14]

Meanwhile the specimen of 1902 was obtained and was found to include still another puzzling bone,—the element that must be regarded as an anomalous epiplastron; and still later the fine type of *Protostega Copei*, here described, was discovered by Sternberg and acquired for the Yale collections. Thus was I enabled to determine finally that the nuchal and entoplastron noted in the paper of 1898[8] were truly such. This correction appeared in the Annals of the Carnegie Museum of Pittsburg for 1906.[15]

That scarcely one of the naturalists interested in the Protostegidæ escaped from wrong conclusions as to the nuchal and entoplastron, is after all not surprising. Both elements are of a form not before observed, this being especially true of the entoplastron, which except in *P. potens* Hay shows no indication of any ordinary type of epiplastral superposition or junction.

The epiplastra are doubtless of the form shown in figure 12. Referring to my first description, however, Dr. Hay thinks that the element figured must be the right, not the left member; superposition would therefore not be of the out-turned Trionychoid type that I have supposed. Dr. Hay saw this element soon after it was collected, and is consequently in a position to judge; nevertheless I think he errs and that the explanation of his opposite opinion is the condition he has observed in the entoplastron of *P. potens*. Moreover, I am not sure that he has correctly determined the hyo- and hypoplastra in that turtle, for the elements he figures as xiphiplastra

FIG. 12.

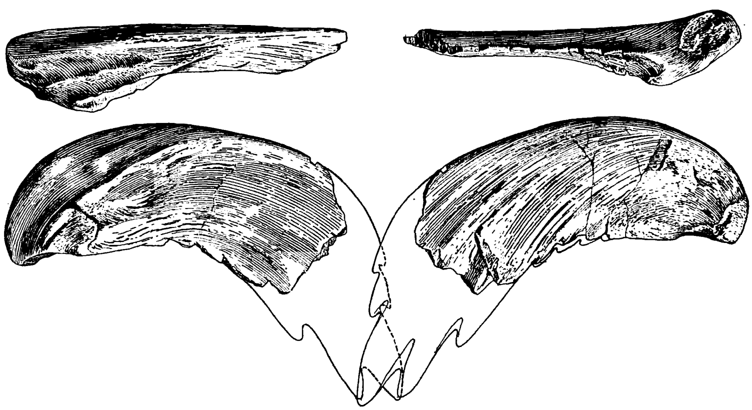

FIGURE 12.—*Archelon ischyros.* Left epiplastron, × ¼. Ectal view on the right below and ental view on the left. On the right above, the anterior, and on the left, the posterior edge views of the recovered portion are shown. (There is no doubt that the restoration of the thin dactylate end is fairly accurate both as to form and size,) This element was not present in the original type, having only been observed once in all the history of the Protostegidæ.

I should certainly have called hyoplastra. In either case, however, *P. potens*, the type of which Dr. Hay was kind enough to show us, is a quite different turtle from any of the foregoing, and the evidence it affords as to the form of the epiplastra is only negative and quite uncertain. It seems much better to accept the positive evidence at hand, which is to the effect that if the element figured is the true epiplastron, it projected beyond the anterior border of the entoplastron and was borne on it quite as in Trionychids. But rather than risk finality in error, it has not been given a place in the restored type of *A. ischyros.*

The *hyo-* and *hypoplastra* exhibit no very unusual features, except a great number of peripheral spines. The curved or somewhat boomerang-shaped *xiphiplastra* are of course more primitive than are the long and straight forms common to the Cheloniidæ.

That the plastral fontanelles appear to be of less area than is shown in figures of *Protostega*, is due more to the fact that the plastron under consideration is the best and most complete example known in the Protostegidæ than to any marked variance in proportions. The plastral resemblance in *Protostega* and *Archelon* is very striking, in view of other differences separating these genera.

The Shoulder Girdle and Manus.—The marked feature of the huge shoulder girdle is the projection of the coracoid all the way back to the pubis, a feature also present in *Protostega* and common to the existing *Eretmochelys.* The most characteristic element in the shoulder girdle of *Archelon* is the humerus because of its distinctly thalassic type.

The testimony as to the organization of the manus is reasonably complete and aside from minor differences exhibits general agreement with that of *Protostega.* The centrale in the latter is, for instance, more distinctly angled. While all the carpal elements of either a right or a left flipper are present, only the principal bones of the carpus have been found in position or approximately so. It is only in the left flipper that bones from another specimen have been introduced, namely, carpale I, the intermedium, and the pisiform, which fortunately were found together in this supplementary specimen. The only element in doubt was the centrale, but this seems to have been of a *rounder* form than in *Protostega.*

Of the metacarpals and phalanges, the majority are present and the proportions of the fingers are essentially those adopted in the restoration, although when a specimen is once found with these elements in place, as in the case of the Pittsburg Museum specimen, some slight modification of the present restoration may prove necessary.

The important anatomical features of the front flipper then are: (a) Agreement with *Protostega;* (b) general agreement with the Cheloniidæ, the centrale exhibiting strong contact with metacarpal I, instead of exclusion from contact with this element by junction of the intermedium and carpale II; (c) the comparatively slight modification and elongation of the phalanges for pelagic life, as contrasted with the much modified thalassic humerus. Although the latter is thus modified, it lacks much of the strength exhibited by the parathalassic Dermochelan humerus; for while the radial crest has shifted toward the middle region of the shaft, it has failed to retain a strong pedestal affording a powerful and firm type of muscular insertion. Curiously enough, the earlier Niobrara *Protostega* was better provided in this respect, since its radial crest forms a distinct ala nearly as prominent as that seen in *Dermochelys.*

This failure of *Archelon* to develop or retain, as the case may be, a prominent crest with stronger type of radial musculature may indeed indicate a certain failure to progress in swimming power and in resultant ability to follow the southward retreat of the great central Pierre sea. In fact, it was at just about this period of culmination in size of the Protostegidæ that the Dermochelan line more successfully accomplished such a change, as shown by the Eocene *Psephophorus,* a turtle nearly approaching *Archelon* in size and having a strongly pronounced and very low-set radial crest. It is on such grounds, as much as by the possible destruction of the eggs of the young by marine or even by newly evolved mammalian enemies, that sufficient cause is surmised for the extinction of these most gigantic of all marine Testudinates.

The Pelvic Girdle and Pes (figure 9).—The very perfect and uncrushed pelvis of the type was accompanied by the left femur, tibia, fibula, tarsals, and nearly all the metatarsals. On the right side, the femur is also present, with the proximal two-thirds of both tibia and fibula, which end in obliquely bitten off but healed surfaces. Both the femur and those mutilated elements are lighter and several centimeters shorter than the corresponding bones of the left side. In short, the evidence is conclusive and unmistakable that this animal had its right flipper bitten off when still young, and that as a result of this injury the remaining portion of the flipper was more or less arrested in growth by disuse. Such accidents are now and then noted in fossils. The type of *Dromocyon vorax* shows a broken lower jaw, subsequently reknitted, which was doubtless received in some raid on the young of *Palæosyops*, while a large percentage of existing marine turtles have had their flippers more or less mutilated by predaceous fishes and sharks.

I need not remind those familiar with the Testudinate osteology that the tarsal region of the sea-turtles is decidedly more variable in its organization than is the carpal region. Owing to this cause and to the failure to identify the excellently conserved tarsals with those of the crushed elements of *Protostega gigas*, it has not proved possible to orient the tarsals except in the most provisional manner. They are all free and heavy bones, and there is little doubt that all were present on the left side, however difficult and uncertain exact orientation may be.

The metatarsals are more readily recognizable, the fifth being much flattened and highly characteristic. Its distal half is largest, not smallest as in *Protostega gigas*. In closing this brief description of the flippers of *A. ischyros*, type, it should be emphasized that while there is marked resemblance to *Protostega*, it is only the resemblance of members of the same family, and that the chief variation is in the humerus and the pes. [The other region of marked variation is on the neural line ; the crania do not differ greatly.]

The more important measurements of *Archelon ischyros*, type, are as follows:—

[Weight of humerus, exactly 75 pounds = 34 kilograms.]

Length of cranium from beak to occipital condyle	60·^{cm}
" four distal cervicals (estimated)	35·
" four proximal cervicals (present)	33·
" ten dorsal centra measured on the ventral face	125·
" two sacral vertebræ	9·5
" eighteen caudal centra (estimated; only a few of the more distal members are absent)	67· ±
Total absolute length from beak to tip of tail, from measurements on ventral face of centra	329·5

(The corresponding total exterior measurement is not so accurately obtained, being slightly affected by pressure, but must have been 3·4^{m} = 11 feet.)

Length of first dorsal centrum			8·^{cm}
"	second	" "	15
"	third	" "	16·5
"	fourth	" "	16·5
"	fifth	" "	16·5
"	sixth	" "	14·5
"	seventh	" "	14·
"	eighth	" "	10·
"	ninth	" "	7·
"	tenth	" "	6·
Total length of ten dorsal centra			124·0

Length of first sacral centrum			5·
"	second	" "	4·5
"	first caudal	"	4·5
"	second	" "	4·5
"	third	" "	4·5
"	fourth	" "	4·0
"	fifth	" "	4·0
"	sixth	" "	3·0

Carapace :—

Greatest length on median line over slight curvature, as mounted	$2{\cdot}00^{m}$
Greatest absolute length	1·93
Greatest width over partial curvature, as mounted	2·18
Width over curvature of second pair of ribs	2·10

Plastron :—

Absolute length on median line	$1{\cdot}87^{m}$
Width on line drawn across the humeral notches	1·83
Greatest width of hyo-hypoplastral fontanelle (that at hyo-hypoplastral suture)	·87
Distance between humeral and femoral notches	1·15

Comparative measurements of the right and left femora, tibiæ, and fibulæ, showing the check on growth due to the loss of the right foot.

Femora :—

	Right	Left
Extreme length	$43{\cdot}5^{cm}$	$49{\cdot}^{cm}$
" distal width	20·0	22·3
Least antero-posterior thickness of shaft	7·2	9·

Tibiæ : —*

Greatest proximal thickness	13·3	15·0

Fibulæ :—

	Right	Left
Greatest proximate thickness	$7{\cdot}2^{cm}$	$8{\cdot}3^{cm}$

Flippers :—

Distance between glenoid cavities	$58{\cdot}\pm^{cm}$
Extreme length of front flipper outstretched in a straight line (measure from glenoid cavity),	$200{\cdot}\pm$
Extreme length from tip to tip of fully outstretched front flippers	$458{\cdot}\pm$
Distance between acetabular foramina	28·
Extreme length of fully outstretched hind flipper	$138{\cdot}\pm$
Extreme length from tip to tip of fully outstretched hind flippers	$304{\cdot}\pm$

A few comparative measurements of *Protostega* and *Archelon*, clearly showing the differences in proportion to be expected in different genera, are the following :—

*The distal ends of right tibia and fibula are cut away by a clean shearing bite ; hence the measurements of the left side are the normal ones.

	A. ischyros (type)	*P. gigas* (cotype)*
Extreme length of coracoid	75·cm	40·cm
Procoraco-scapular length	66·	30·
Median line to tip of second rib	100·	56·
Extreme length of humerus	60·	34·
Length of ten dorsal centra	127·±	68·
Extreme length of femur	49·	27·
" " " tibia	33·	20·
" " " fibula	31·	20·5
" " " radius	30·	20·
" " " ulna	35·	17·

Concluding Remarks.

Not only will future field work reveal new members of the Protostegidæ of the greatest interest, but quite all the skeletal features now in doubt must certainly be clearly observed as one specimen after another is collected. Indeed it can be freely predicted that but a very few years will be required to accumulate the material demanding a second revision.

Meantime it must be left to such further discovery to determine, among various other features, what the exact condition of the neural line of *Protostega gigas* really is, and whether this species and *P. Copei* do not really belong to separate genera; for there is a distinct suspicion that the species of Protostegidæ already known may really include a third genus. Evidently the marked difference in the structure of the carapacial midline between *Archelon* and *Protostega Copei* indicates a condition promising variations of the most striking and interesting character, to say nothing of the possibility of variety in the dermogene elements on the lines of the keels. These should very clearly be named in both *Dermochelys* and other turtles, the neural, pleural, supra-marginal, and marginal keels above, and the infra-marginal, hyo-hypoplastral, and the nether median or epi-xiphiplastral keels below.

It is not presumable that there is any doubt as to the presence of broad generic distinctions between *Protostega gigas* and *Archelon*, although the midline of these two forms may prove to be much more nearly similar than we now suppose. It is, however, a very striking fact that *Protostega Copei* and *P.* (*Archelon*) *Marshii* are both so much more nearly normal in their carapacial structure than is *Archelon*. This is to say, normal when we have in mind the great majority of turtles with normal neuralia such as the early Protostegids are shown to have. One might indeed suspect it possible from the strong

* This is the splendid specimen, No. 1421, of the Carnegie Museum, Pittsburg.

functional value of the epineurals of *Archelon* that there are turtles in which following elimination of a true neural series, an overlying dermogene series like that of *Archelon* has dropped down into the neural position once more.

The possibility of such cycles is, however, only hinted at. Taking the evidence at its face value, the important point is that *Archelon*, without having lost the power to develop an ossicular series, or perhaps in spite of having retained such a series, once had a closed carapace and plastron like that of modern turtles. Moreover, the earlier Niobrara Protostegas include the primitive forms like *P. Copei* and doubtless *P. advena* with well-developed neurals, and with far less of osteodermal development than in the later *Archelon*.

It is thus seen that of the two camps which have attacked the difficult and highly attractive problem of the origin of *Dermochelys*, those favoring the view of a close relationship to other turtles and a comparatively recent origin have rather the best of the argument. We have had on the one side Cope, the earlier Dollo, and Hay advocating an ancient and remote origin of *Dermochelys;* while on the other, Baur, the later Dollo, and Wieland have believed *Dermochelys* a highly specialized descendant of true turtles, and hence of modern or relatively recent derivation. That the latter of these hypotheses more nearly expresses the final truth is now evident; though both contain elements of truth, and are by no means so remote as they at first sight appeared to be.

Thus, just as Dollo deserted the one camp for the other, so Hay has gradually developed, not to say modified, his premises to a point where they adjoin our own. While not absolutely closed, therefore, and still lacking the testimony of many forms yet sure to be discovered, this famous controversy of the biologist as to the origin of the "leatherback" is now nearly eliminated. Nor is it too much to say that it has proved quite as fruitful throughout as the broader but scarcely more profitable question of the origin of the Testudinata.

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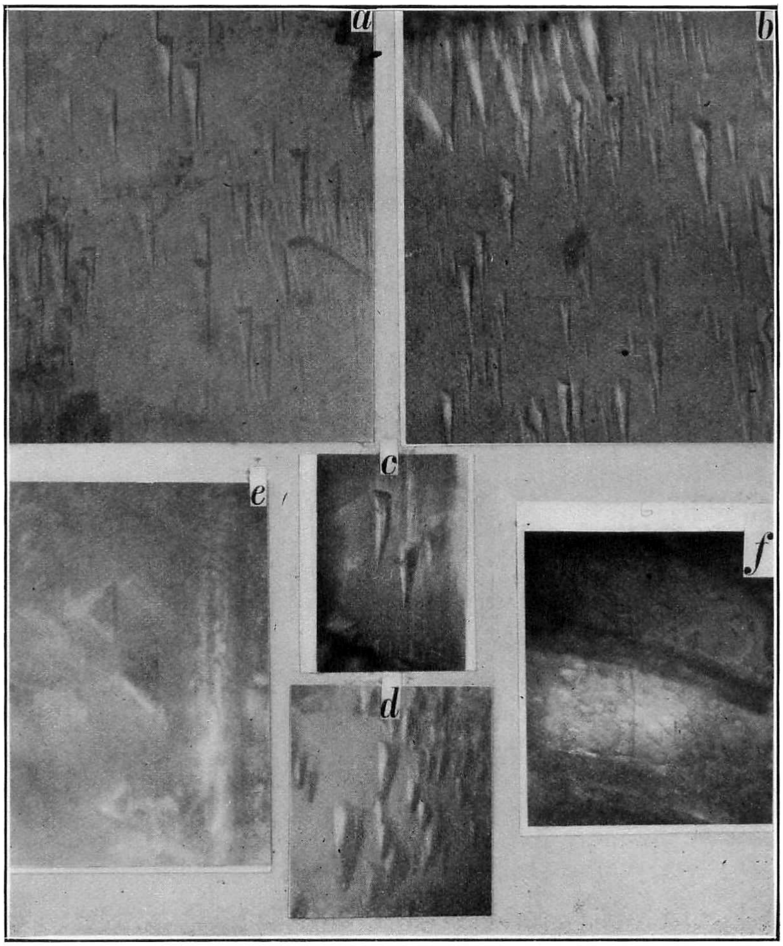


Photomicrographs.

a Artificial diopside. Etch pits on 110 produced by action of hot commercial HF for 40 seconds. Magnification 200 diameters.

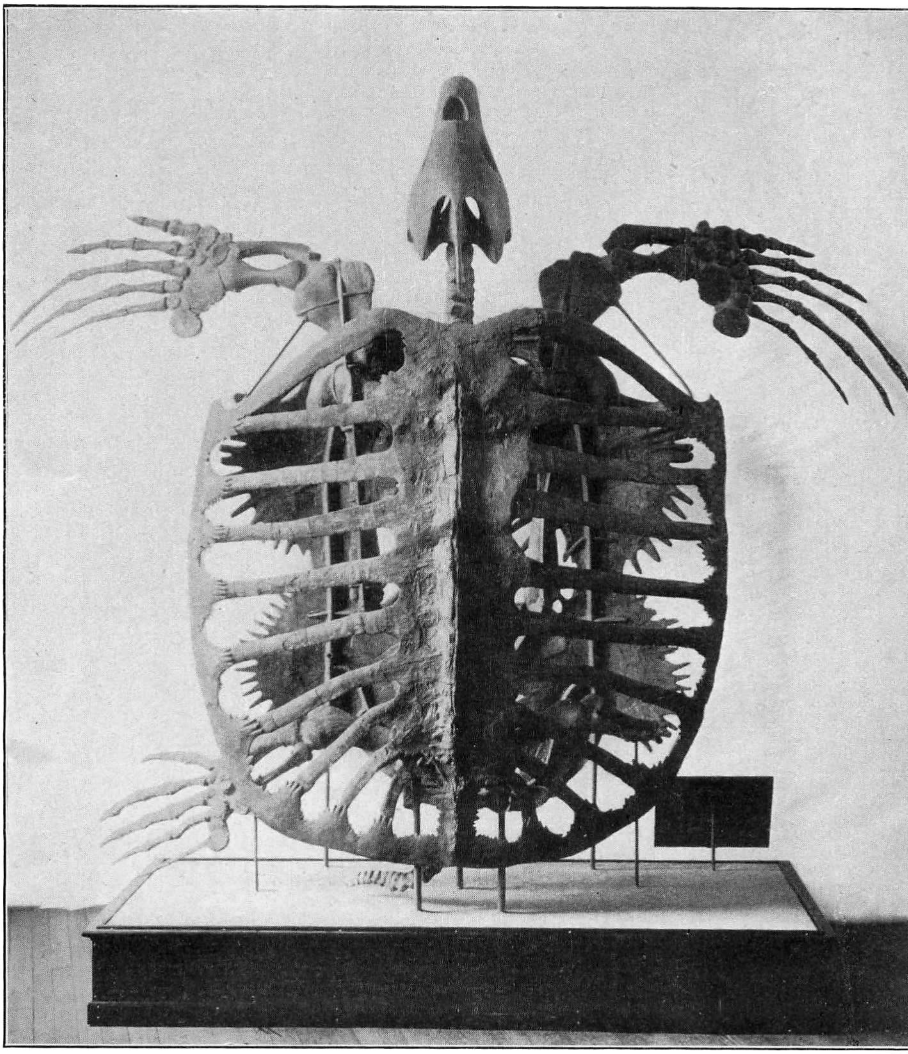
b Artificial diopside. Etch pits on $1\bar{1}0$. Exposed to hot commercial HF 40 seconds. Magnification 230 diameters.

c Etch pits on $1\bar{1}0$ of crystal $MgSiO_3$ 50 per cent, $CaSiO_3$ 50 per cent. Time of exposure 40 seconds in hot commercial HF. Magnification 220 diameters.

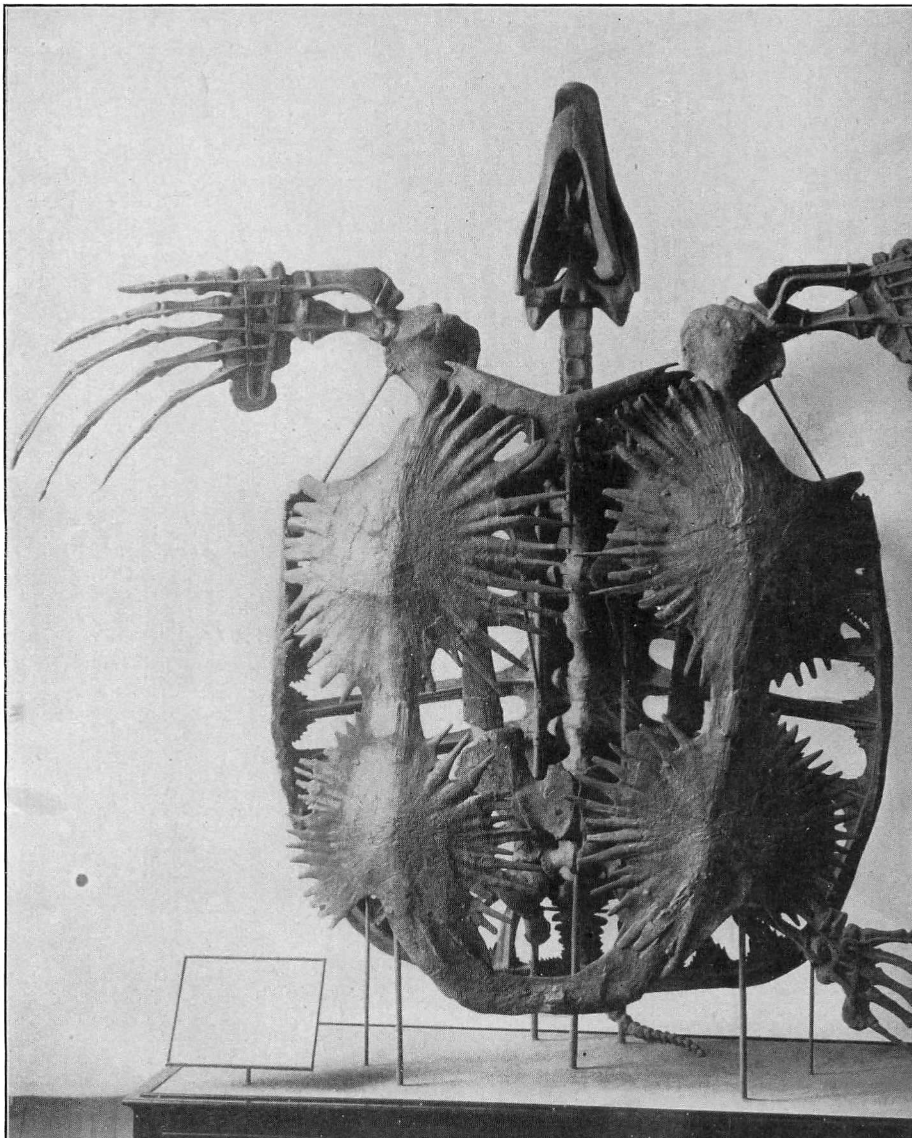
d Etch pits on $1\bar{1}0$ of crystal $MgSiO_3$ 55 per cent, $CaSiO_3$ 45 per cent. Time of exposure in hot commercial HF, 40 seconds. Magnification 440 diameters.

e Etch pits on 110 Mg-pyroxene (β-$MgSiO_3$). Exposed 50 seconds in hot commercial HF. Magnification 1065 diameters.

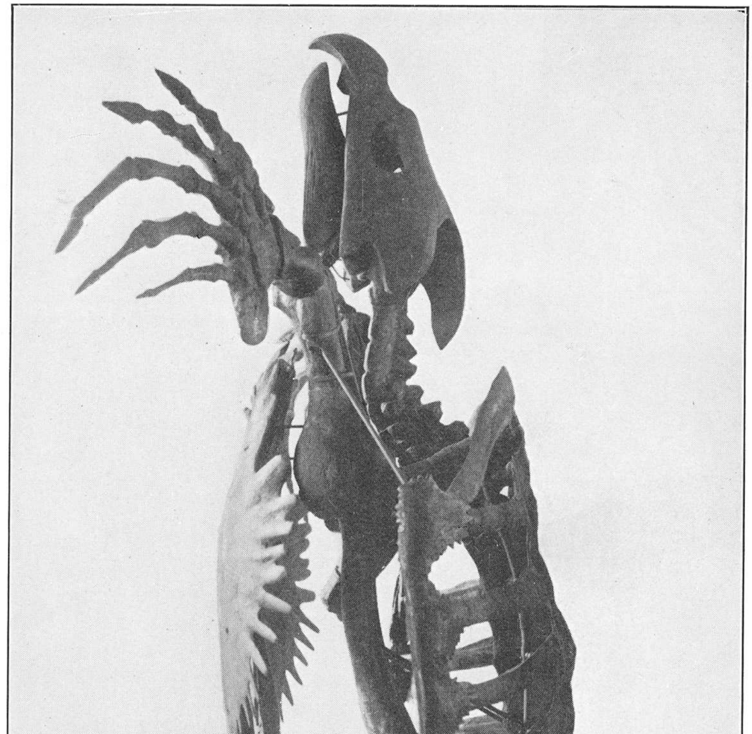
f Etch pits on 110 of crystal $MgSiO_3$ 75 per cent, $CaSiO_3$ 25 per cent. Exposed 40 seconds in hot commercial HF. Magnification 230 diameters.



Archelon ischyros Wieland.—Photograph of dorsal view of the type as mounted in the Yale University Museum. (Compare with text figure 7.—The right flipper was bitten away just above the heel early in life by some predaceous enemy, either a shark, a fish or a mosasaur.)



Archelon ischyros Wieland.—Photograph of ventral view of the type as now on exhibition in the Yale University Museum. (Cf. text figure 8, and compare with the preceding plate.)



Archelon ischyros Wieland.—Photograph of lateral view of the type as now mounted in the Yale University Museum. [Plastron in approximate position.]