## I. PLASTRON OF THE PROTOSTEGINÆ.

### By G. R. WIELAND.

In all the earlier discovered skeletons of the huge Cretaceous turtles included in the Protosteginæ, the hyoplastra were found in normal position in contact with the peculiar T-shaped entoplastron characterizing this subfamily; while elements definitely referable to the epiplastra were singularly absent. This condition having repeated itself at widely separated localities, and in two genera as represented by fully six specimens approaching completeness, I was led to suppose after the discovery of a median nuchal-like bone in *Archelon* that the T-shaped entoplastron might represent a fusion of the epiplastra with the entoplastron. This idea of fusion was beset by certain doubts



FIG. I. Achelon ischyror Wieland. Left epiplastron. Inner (superior) view.  $\times \frac{1}{6}$ . *c*, anterior limit of entoplastral overlap. Compare with epiplastra of Aspidonectes, etc., in figures 2 and 3. at the time it was discussed in my description of the plastron of the type specimen of Archelon, and has proven incorrect. Dr. E. C. Case and Dr. O. P. Hay also held unpublished odinions on the subject, the one being inclined to accept, the other disagreeing with the idea of a supposable fusion of the anterior plastral elements; although both had mistakenly identified the T-shaped entoplastron as the nuchal of Protostega. However, as presenting one more example of the exigencies attending the uncovering of the fossil record, in spite of the various specimens known and the fact that the question of plastral structure in the Protosteginæ had thus become an open one, no direct evidence was obtained until two years ago.

Then I secured on the west bank of the Cheyenne River where it breaks through the Oligocene Bad Lands of South Dakota, the greater part of a large *Archelon* skeleton including along with the hyo-, hypo-, and xiphiplastra a single epiplastron. This proves of quite unexpected interest, because it is of the out-turned type seen in the Trionychids and

## WIELAND: PLASTRON OF THE PROTOSTEGINÆ.

Dermochelys amongst existing, and amongst extinct forms, only in the several genera of the Thalassemydidæ of the European Jurassic and Cretaceous, together with *Protosphargis* of the scaly clays of Italy.

The epiplastron of *Archelon* as represented in superior view in Fig. 1 is of subcrescentic outline with the anterior limb heavy, and the posterior broadened, flattened, and digitate. The thickness of the heavy anterior end is 4.5 centimeters, and an accompanying humerus is exactly 2 feet in length.

As in the Trionychydæ there is no true sutural union with the entoplastron, the contour showing that the superior face of the epiplastron was overlain by the antero-external border of the entoplastron. Beyond this border the anterior limb of the epiplastron projected about 7 cm. like a broad, short, heavy horn, with its convex side ental. Four



FIG. 2. Aspidonectes spinifer. Nether (ectal) view of plastron.  $\times \frac{1}{3}$ . ep, epiplastron; en, entoplastron; f, f, anterior and mesial foramina. (Cf. epiplastron of Archelon and Dermochelys, also of Thalassemydidæ.)

broad, shallow furrows increasing in depth from the inner to the outer side, mark the contact of as many overlying digitations or ridges which may all have been entoplastral, rather than in part hyoplastral. This lack of sutural union and the boomerang-like shape of the epiplastron show how it must have been the very first bone to be torn out by predaceous fishes and sharks, or by wave action, after the turtle went down, and thus explain the rarity of its recovery and why the explorations of thirty years have hitherto failed to reveal so interesting a skeletal part.

Inasmuch as the adequate mounting and preparation for description of the original type of *Archelon ischyros* has now been begun at the



FIG. 3. Dermochelys coriacea. Plastron with (a) ectal and (b) ental view of nuchal. After Gervais (*cf.* out-turned epiplastra with those of *Archelon*, etc., in subjoined figures).

Yale Museum, there is no present need to attempt further plastral restoration of this largest of seaturtles. Meanwhile, however, a very good idea of the plastral form may be had by comparison, in combination, of the writer's figure of the ento-, hyo-, hypo-, and xiphiplastra of Archelon with the figure of the Jurassic Thalassemyd Hydropelta Meyeri given on page 530 of Vol. III. of Zittel's Hand-The manner in which buch. the epiplastra of Archelon projected anteriorly is quite closely paralleled in Hydropelta, except that in the former it appears that there was no epiplastral abutting on the median line, and that the entoplastron is relatively larger.

The present determination for the first time of the true type of plastron in the Protosteginæ is of far more than casual interest because of the obvious bearing on the most vexed of zoöpaleontological problems, the origin of *Dermochelys*, as well as on the highly interesting question of the mono- and polyphyly of the other existing and the various extinct genera of marine turtles.

The testudinate plastron while undergoing characteristic variations of form within closed groups is fully as conservative a structure as the carapace. Also, since in *Dermochelys* the plastron and nuchal are the only parts left for comparison with the normally developed carapace and plastron of other Testudinates, the paleontologic record has been scanned year after year for true marine turtles with a more or less reduced

# WIELAND: PLASTRON OF THE PROTOSTEGINÆ.

carapace and similar plastral type, which might stand in an ancestral or approximately ancestral relationship. Nevertheless, *Dermochelys* has retained its isolated position; fossil evidence bearing directly on its origin has been singularly lacking, in fact going scarcely further than to indicate that *Psephophorus* of the Belgian Pliocene may have

marked the culmination in size of the . Dermochelydidæ. For a time, however, after Cope's description of Protostega in 1875 this genus, as very imperfectly known, was supposed to largely bridge the gap between Dermochelys and the other marine turtles. mainly on the ground of its considerable carapacial and its doubtless complete hornshield reduction. The discovery, in much better preservation, of the closely related Archelon, as well as the study of better specimens of Protostega, however, developed the presence of far closer relation-



FIG. 4. Ental view of nuchal, of (a) Aspidonectes spinifer  $(\times \frac{1}{2})$ , and (b) the entoplastron of Archelon ischyros  $(\times \frac{1}{20})$ . t, small nether tubercular process articulating with neural arch of cervical vertebra; r, a lateral ridge for muscular attachment. Entoplastral and nuchal similarity are correlated in these forms.

ship to the Cheloniidæ than was at first suspected, the writer finally being led to include these forms in a Chelonidan subfamily, this doubtless being their correct morphologic rather than their exact phyletic position.

Nevertheless it now becomes possible to coördinate several hitherto isolated facts. If we regard *Dermochelys* as the most specialized Testudinate, and the *osteodermal* mosaic as a secondary structure, the plastron has been more persistent than the carapace, only the entoplastron having been lost by reduction, whereas the nuchal is the sole remaining carapacial element. The Protosteginæ also, though structurally speaking members of the Cheloniidæ, are now seen to have with their much reduced carapace the same highly characteristic epiplastral type as *Dermochelys*, as well as other minor resemblances which need not now be enumerated. The same is true of the Thalassemydidæ of the European Jurassic and Cretaceous, as represented by

#### ANNALS OF THE CARNEGIE MUSEUM.

various genera, for the greater part but imperfectly known. Moreover these Thalassemyds compose the group, which has been considered to stand most nearly in an ancestral relationship to the existing marine turtles, previous to my demonstration of the structure of the Propleurinæ of the New Jersey Cretaceous, and proof that this primitive littoral subfamily includes the forms which virtually bridge the gap between primitive land tortoises and the existing genera of the Cheloninæ. On the other hand it is to be emphasized that several other



FIG. 5. Osteopygis gibbi Wieland,  $\times \frac{1}{8}$ . Plastral view. Primitive semi-marine turtle from the New Jersey Cretaceous, showing the elongate and in-turned epiplastra characteristic of the Cheloniidæ. The horn shields are not indicated, but are in approximate agreement with *Thalassochelys*.

Cretaceous subfamilies besides the Protosteginæ are so different from the New Jersey forms, that their ancestry must still be sought for amongst the Thalassemyds. Such are in particular the Desmatochelydinæ. It is hence more and more strongly suggested, as the





#### WIELAND: PLASTRON OF THE PROTOSTEGINÆ.

facts accumulate, that the flippered turtles represent a great complex of forms which have arisen through repeated invasion of the sea in Mesozoic time, it being indeed not improbable that most of the groups most conveniently grouped as marine subfamilies have thus independently arisen from more or less nearly related genera of land tortoises. The tracing of such independent lines is, however, doubtless rendered difficult, as much by subsequent homoplastic adaptations, as by the imperfections of the record as known. But while we are not yet in a position to absolutely prove such a polyphyly of the Cheloniidæ, the general facts in the case of the Protosteginæ, their various ear marks suggesting a certain relationship to *Dermochelys* by way of the Thalassemyds, together with culmination in the Cretaceous, assuredly suggest independent origin from forms other than the New Jersey Propleurinæ as so closely related to the Cheloninæ.

The hypothesis is therefore advanced, in conclusion, that: (a)The marine turtles are distinctly polyphyletic; that is, various more or less distantly related tortoises have from the Jurassic on repeatedly assumed littoral habits, and developed flippers. (b) Five of these distinct lines of marine turtles are exemplified by (I) Dermochelys, (2) the Protosteginæ, (3) the Desmatochelydinæ, (4) the Cheloninæ, (5) Carettochelys insculpta, the Fly River Turtle of New Guinea, a flippered pleurodiran with complete reduction of the horn shields. (c) The Ancestry of Dermochelys and the Protosteginæ falls within the Thalassemyds, or Acichelydidæ, and the plastron and nuchal also suggest certain affinities between the latter and some ancient form near to the original Trionychid line.

As correlative to this hypothesis I may add, though somewhat in repetition, that however one may split hairs about the meager evidence as to the nature of the mutations which have resulted in the osteodermal mosaic of *Dermochelys*, the safe and simple working view is to my mind that his plastron is a turtle plastron, his nuchal a true nuchal, all his other organization likewise testudinate and impossible of homoplastic origin, and that his ancestors were simply more ancient than those of the Cheloninæ, but withal typical tortoises, quite probably falling, as above suggested, within the Thalassemydidæ, and probably without an osteodermal mosaic. The epineural ossicles of *Toxochelys*, and the epimarginals of *Lytoloma*, show well that an osteodermal series corresponding to the hornshield system was once far more conspicuous in the turtles than now ; and the keels of *Dermochelys* are in exact correspondence to such a series.

13

## Annals of the Carnegie Museum.

#### EXPLANATION OF PLATES.

Plate I. *Thalassochelys caretta*, Delaware Bay. Ectal view of plastron.  $\times \frac{1}{2}$ . Plastral type of the Cheloniidæ, except the Protosteginæ, with narrow in-turned epiplastra. The ventral horn-shield, or that imbricating over the hyo-hypoplastral junction, is the only one likely to be clearly indicated in fossil plastra of this type.

Plate II. *Chelone mydas* (var. or sp. nov.). Southern Atlantic coast of the United States. Plastron with marginals (less nuchal) placed in natural position very nearly. More reduced than the preceding.

# ANNALS CARNEGIE MUSEUM, Vol. IV.

Plate I.



Ectal View of Plastron of Thalassochelys caretta,  $\frac{1}{2}$ .



# ANNALS CARNEGIE MUSEUM, Vol. IV.



Chelone Mydas, less than  $\frac{1}{2}$ .

Plate II.



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