ART. XXIII.—*The Skull, Pelvis, and Probable Relationships of the Huge Turtles of the Genus Archelon from the Fort Pierre Cretaceous of South Dakota:* by G. R. WIELAND. With Plate II.

THE marine turtles of the Fort Pierre Cretaceous of South Dakota not only represent the most gigantic species known, but also are of much importance as including undoubted descendants of *Protostega* from the underlying Niobrara Cretaceous, in common with which they may be regarded as ancient relatives of *Dermochelys*.

The first of these turtles was discovered and collected by the writer in 1895. The nearly complete carapace, pectoral girdle and limb bones of this specimen were described in this Journal (13)* the year following as those of the new genus and species *Archelon ischyros*. Additional material collected in 1897 and 1898, and in part here described, proves this determination to have been correct, although in describing the fine plastron of the first specimen secured the generic name *Protostega* was needlessly substituted (15). This was done in deference to high authority, but careful comparison made possible by new material of both *Protostega* and *Archelon* places beyond further question the validity of the latter genus.

The Skull of Archelon Ischyros Wieland.

The skull, the description of which is here given, was secured by the writer in the summer of 1897, and belongs to the second specimen discovered, this being nearly complete. Notwithstanding its gigantic size, it represents a turtle only three-fifths as large as specimen I. A fragmentary specimen (III)

* See references on p. 250.

indicates a turtle 4·25 meters long with a cranial length of fully 1 meter.

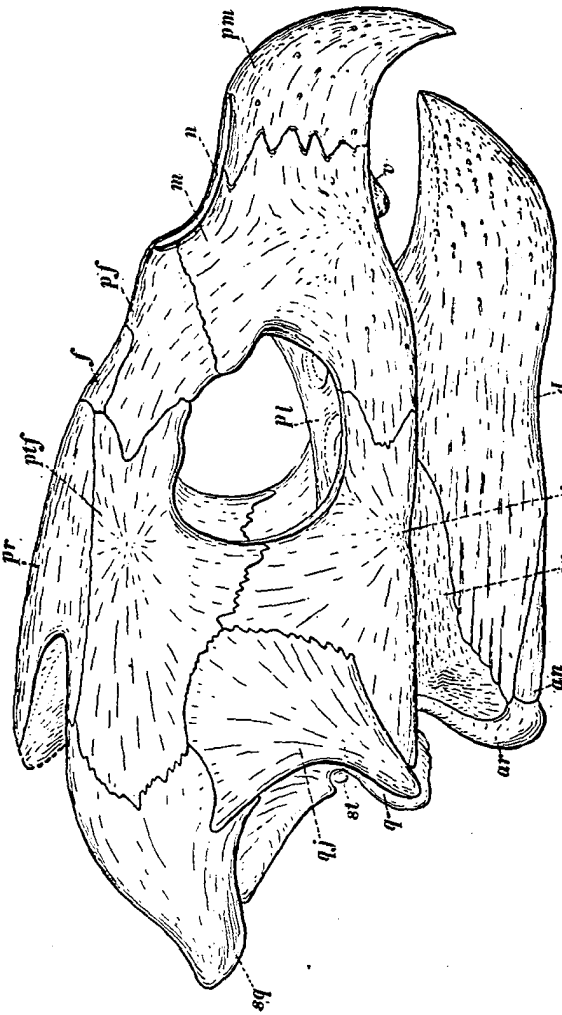

FIGURE 1. Skull of *Archelon ischyros* Wieland, $\times\frac{1}{8}$; *an*, angular; *ar*, articular; *d*, dentalium; *f*, frontal; *j*, jugal; *m*, maxillary; *n*, external nares; *pf*, prefrontal; *pl*, palatal; *pm*, premaxillary; *pr*, parietal; *ptf*, postfrontal; *q*, quadrate; *qj*, quadrato-jugal; *sq*, squamosal; *st*, columella auris in stapedial notch; *sr*, suprangular; *v*, vomer.

The main features of the present skull are well represented in Plate II, based on a photograph of it as excellently mounted

by Mr. Hugh Gibb, and now on exhibition in the Museum of Yale University. The plate is carefully interpreted in fig. 1. Still other features are shown in figs. 2 and 3, which are necessarily somewhat diagrammatic.

Notwithstanding considerable lateral compression of the posterier portions, this skull is an unusually good one, all the main details needed for a restoration being well preserved. It only fails in the region of the brain cavity and the posterior extremity and connections of the vomer. Its description and comparison with its nearest known relative and ancestor *Protostega gigas* from the Kansas chalk has been made all the more exact and satisfactory by the courtesy of Prof. W. M. Wheeler and Dr. E. C. Case, who generously placed in my hands for purposes of comparison the exceptionally fine material so ably investigated by the latter (5). This represents various disarticulated elements of the skull and a fine mandible. Between the two specimens the skull of these important forms of the Cretaceous may now be known with essential completeness. The description of parts follows.

The Premaxillaries.—These elements are strongly coössified and comparatively narrow laterally, but long and massive. The narial border is rounded and horizontal. The dental border is posteriorly less developed into a cutting edge than in other turtles, but anteriorly runs out into the most strongly decurved beak known in any turtle, the aspect being that seen in birds of prey. The surface of the beak especially is deeply pitted, and in life must have been covered by a horn sheath of the relative decurvature and strength of that of the eagle. There is only a shallow excavation for the reception of the mandibular beak.

The great length and other details are the exact antithesis of the short and notched premaxillaries of *Dermochelys* with a persistent suture. The inner features and union with the vomer are shown in fig. 2. The boundaries are, in spite of all disparities, essentially similar to those seen in *Dermochelys*.

The Maxillaries.—The general maxillary outline is that of a broad Y lying on its side, the fork forming the anterior orbital boundary, and the wide base extending forward to an unusual distance. Much of the great cranial length is due to the elongated maxillaries and premaxillaries.

The narial border is only moderately upcurved to aid in the formation of the greatly elongated external nares, which face upwards and but slightly forwards, being much more nearly horizontal than in most turtles.

The dental border is continued by the maxillary as a low cutting edge which soon becomes rounded and continues so to junction with the jugal. It should be noted here that the

entire dental border is peculiar; firstly, because of the decurved premaxillary; secondly, because of the very slight concavity of the vomeral region, and the continuation of the dental border of the jugal as a rounded edge, which instead of ascending is most depressed at its junction with the quadrato-jugal, as will be again noted in the description of the latter elements.

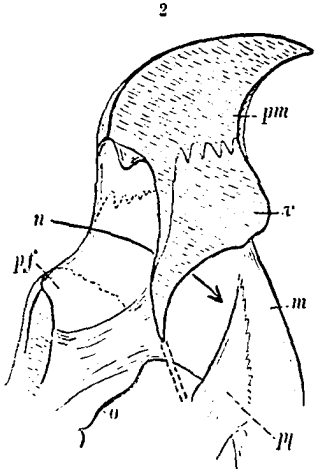

FIGURE 2. *Archelon ischyros* Wieland. Median vertical section through anterior region of skull × ½; *m*, maxillary; *n*, narial opening; *o*, orbital boundary; *pf*. prefronto-nasal; *pl*. palatal; *pm*, premaxillary; *v*. vomer.

The maxillaries do not rise as high relatively to meet the prefrontals as is usual. There is in this conformation a suggestive resemblance to *Lytoloma* (*chelone*) *longiceps* Owen.

The Jugals.—These elements are subtriangular in outline, the basal side being longest, and extending back to the lower extremity of the quadrato-jugal as an un-notched nearly straight, somewhat depressed and rounded border. The depression of the jugal is quite unique and gives great length to the unusual dental border thus formed.

With the postfrontal the jugal forms the posterior two-thirds of the orbit, the orbital border being distinctly flattened and from 2^{cm} broad posteriorly to 3·3^{cm} broad anteriorly. Only the extreme anterior extension articulates with the palatal, making the boundaries those of *Thalassochelys* and not like those of *Dermochelys*.

The Quadrato-jugals (Paraquadrate of Siebenrock 12).—These bones present exteriorly a large gently convex surface of broadly crescentic outline. The concave posterior border stands at a right angle to the outer surface and is 4^{cm} broad, forming a symmetrical surface with the quite similar posterior orbital boundary noted above. See fig. 1.

The quadrate is fortunately present in the specimen of *Protostega gigas* studied by Case, who thus describes it (5, page 27): "The quadrato-jugal of the right side is triangular in general outline. The posterior edge is concave and the whole bone is convex from above downward. The superior edge is narrow, and there is no prolongation of the antero-inferior portion as in *Dermochelys* (5, Pl. V, fig. 7)."

The differences between these two quadrato-jugals are therefore striking. Firstly, the outer area of that of the present specimen, which as just stated is broadly crescentic in outline, is relatively more than double that of *Protostega*, which is isosceles-triangular in outline with the equal sides slightly concave. Secondly, the flat free posterior border just outside the articulation with the quadrate as seen in *Archelon*, is represented in *Protostega* by an oblique surface mostly taken up by the quadrate suture. Lastly, the articulations must be essentially different. Since the outline in *Protostega* is distinctly triangular, the union with the jugal and post-orbital is by two sutural lines making an angle of 60° with each other, instead of by a long curved sutural boundary as in *Archelon*. Now since the upper of these sutural lines is nearly horizontal, and the general outline in *Protostega* that seen in *Dermochelys*, it is probable that the latter and *Protostega* agree in squamoso-jugal union. On the contrary, in *Archelon* there is marked squamoso-jugal separation. For reasons which I have pointed out elsewhere I do not lay great stress upon squamoso-jugal union or non-union alone (13). But the more salient fact to be borne in mind is that the great differences in general conformation compel accompanying variations in the jugal, parietal, and squamosal which are fundamentally generic.

The Squamosal.—This element is also present in both the Kansas material and the present specimen. The anterior portion extends upward to meet the parietal as a long narrow band nearly covered by the post-frontal, and does not expand nearly so much as in *Protostega*. The articular surface for the quadrate is placed well up on the interior side, more as in *Dermochelys* than in either *Protostega* or *Thalassochelys*. The lower border is shallow sigmoidal in outline and the posterior extension instead of ending bluntly as in *Protostega* runs out into a heavy rounded point somewhat as in *Trionyx spinifer*. As in *Protostega*, there is however no posterior inferior grooving of this extension.

The Prefrontals.—These are somewhat rhomboidal in outline. The junction with the postfrontal is long and prominent, and much as in *Dermochelys*. Of the four elements bounding the orbit the prefrontal takes least part. The prefrontals extend much further back from the external nares than in *Dermochelys*, the general resemblances being intermediate to the latter and *Thalassochelys*.

The Frontals.—These bones are narrow and relatively elongate. As the cranial roof underwent some crushing, it is difficult to discern the precise position of the parietal boundary. Resemblances *Thalassochelan*.

The Postfrontal.—The markings and boundaries of this

element are very distinct. It has an especially broad posterior development. Anteriorly it is greatly strengthened by the heavy post-orbital border, which runs up internally as a sharp but heavy buttressing ridge full 2·5^{cm} high in its middle part, and not disappearing wholly until the parietal is reached. No such ridge is present in *Dermochelys*, though a similar one of much less development is seen in *Thalassochelys*. The boundaries are approximately those of the latter form, union with the quadrato-jugal being very distinct.

The Parietals.—These were deeply escalloped posteriorly, nearly as much as in the *Chelydridæ*. As they had been subjected to crushing their outlines were not so distinct as in the case of the other external elements of the skull. Most unfortunately the vexed question as to descending processes of the parietals and parieto-pterygoidal union can not be definitely settled from the present specimen. There certainly was some, if not a strong development of these processes.

Both Baur and Case (1 and 5) have stated that there were strongly developed descending parietal processes uniting with the pterygoids in *Protostega*.

Whether or not the absence of these processes in *Dermochelys* is as important anatomically as convenient in classification, it is to be hoped that future material will determine what the exact condition was in these Dakota descendants of *Protostega*.

The Quadrates.—These are both present in fair condition and but slightly crushed out of their natural articulations. They are short and unusually massive, particularly the posterior border as it extends from the stapedial notch to the squamosal. A portion of the right stapes was still to be seen in the stapedial notch. As implied by the differences between the quadrato-jugal and squamosal of *Archelon* and *Protostega* as pointed out above, the aspect of the quadrate and its boundaries as seen in the present fossil must vary sharply from that of *Protostega*. The quadrates of the latter are illustrated by Case (5), while those of *Archelon* are seen as thrust slightly back in Plate II.

The Vomer.—The vomer is present in place and is remarkably developed. It is illustrated in fig. 2. As in *Protostega* (5) the anterior relations are distinctly *Dermochelan*, the vomer and palatines not roofing the posterior nares. But with these boundaries resemblance to this form ceases. Conforming to the great development of its anterior bounding elements, the vomer is unusually massive. It takes part in the palatal surface as a prominent conical projection in front of the posterior nares 2^{cm} high. Taken in conjunction with the descending premaxillary beak, this is quite the reverse relation to that seen in *Colpochelys Kempii* Garman, which has a flat

palate and no decurvature of the premaxillaries, but an upturned lower jaw with a prominent cone at the inner vertex of the ramial angle.

The superior surface of the vomer forms a distinct saddle contracting as it rises from beneath the overlap of the premaxillaries and passes back to support the inner buttresses of the prefrontals, between which it appears to end. Whether this was the natural condition could not be precisely determined. There is a bare possibility that the vomer did not pass back to form the usual vomero-palatal union. But whether this was the case, or whether the palatals sent a median branch far forward must for the present remain undetermined. The posterior nares however were not bridged by a nether vomero-palatal union, the condition being, owing to the deep gap between the palatals and the prominence of the vomer, intermediate between *Dermochelys* and *Eretmochelys*. Vomero-premaxillar union is stronger than in either the latter genus or *Argillochelys*.

Main Features of the Palatal Aspect.—These are distinctly shown in fig. 3. The only doubtful points are the exact size of the small basisphenoid and the boundaries in the vomero-palatal region just mentioned. Anteriorly the relations are partly *Dermochelan;* posteriorly they are *Thalassochelan*, with the exception of the basal processes of the basioccipital, which are heavy and project downwards and outwards as in *Dermochelys*. They are however much longer antero posteriorly than in this form.

There is a continual reminder that we have here to deal with a remarkable blending of the relations seen in the two genera just mentioned, with certain unusual characters. Especially the great development of the jugal nearly cutting out the quadrato-jugal in the basal view will be noted. Also the girder-like palatals are quite unique, forming a prominent

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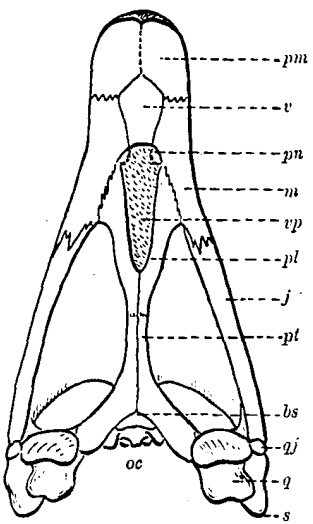

FIGURE 3. *Archelon ischyros* Wieland. palatal view × about $\frac{1}{10}$. *pm*, premaxillary; *v*, vomer; *pn*, posterior narial opening; *m*, maxillary; *vp*, the uncertain vomero-palatal region; *pl*, palatals forming a girder-like structure; *j*, jugal; *pt*, pterygoid; *bs*, basisphenoid; *qj*, quadrato-jugal; *q*, quadrate; *s*, squamosal; *oc*, occipital condyle.

V-shaped bridge, with any vomeral connection very deeply set in the skull. (Compare figs. 3, 4, and 5.)

*The Mandible.**—This was present in position and was quite perfect with the exception of the posterior elements of the left ramus, which were dissociated, only the surangular being recovered. The measurements appended may be taken as quite

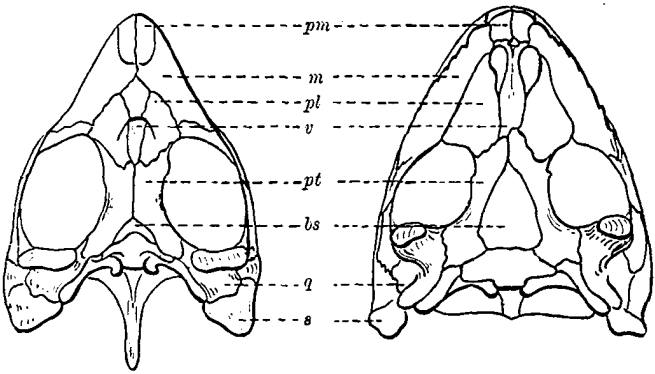

FIGURE 4. *Thalassochelys caretta*, palatal view of skull × 1/5.
FIGURE 5. *Dermochelys coriacea* " " " × 1/5.
pm, premaxillary; *m*, maxillary; *pl*, palatal; *v*, vomer; *pt*, pterygoid; *bs*, basisphenoid; *q*, quadrate; *s*, squamosal.

accurate, the complementary and articular being the only parts much altered by pressure. As the latter is very much flattened and the parts bounding it but little compressed, it may not have been well ossified.

From the apparent shortness of the rami, no less however than in the land turtle *Macrochelys Temminckii*, it may be fairly inferred that both the articular and the articular face of the quadrate were heavily encased in cartilage. This is also suggested by the roughened to spongiose appearance of both these parts. The horn sheath of the beak must also have been very heavy and somewhat upturned.

The general relationship of the present form to *Protostega* is strongly exemplified by the lower jaw. The presplenial of Baur (2) is however apparently less prominent than in that fossil (see Case, 5), the suture between it and the splenial not

*I retain the original nomenclature for the mandibular parts, not being as yet able to reconcile that proposed by Dr. Baur (2) with the conditions found in the Testudinata, and hoping later to present a paper on the homologies of the reptilian lower jaw.

being distinct. The presplenial region has rather the appearance of being a long anterior projection of the splenial (Baur's angular). On the contrary, the angular is a little broader and extends farther forward than in *Protostega*. Again, the narrow but nevertheless robust aspect of the anterior or symphysial portion of the dentary in *Archelon* is notable. Relatively to length the symphysial depth is great, and the weight of this portion of the jaw suggests a hammer-like action against the palatal cone. This would have been very effective in the crushing for food of large mollusca and crustacea, if perchance the Archelones were in any wise similar in feeding habits to existing carnivorous sea turtles.

Another well marked character is the persistent symphysial suture. While in half grown forms of *Protostega* this suture is wholly obliterated, in the present specimen, which may have been from adult to three-fifths grown, the rami readily separated on this line. So pronounced a suture is rare.

The ramial angle, which is 50° in *Thalassochelys* and *Dermochelys*, and 40° in *Protostega*, may not have been more than 25° in *Archelon*. The latter is a very narrow form, and the vertex of the rami forms a nearly sharp instead of rounded angle.

It is scarcely necessary to compare further. There is certainly more resemblance in the mandibulum to *Thalassochelys* than *Dermochelys*, but withal intermediate characters as in other parts of the skull.

General appearance of the skull.—The skull of *A. ischyros* is long in proportion both to the body and to its width, but nevertheless massive. There is in the deeply notched parietals, the decurved beak, and the depressed vicious-looking forehead, a distinct reminder of the features in such carnivorous land turtles as the *Chelydridæ*. Every relation bespeaks a ferocious form. So far as may be inferred from physiognomy it is easy to conceive this turtle with his powerful pinching and clasping beak, as preying not only on crustaceans, but even upon the larger fishes and reptiles of the Cretaceous seas.

The turtle to which this skull belonged was not more than ten feet in length, but had a remarkably broad and robust form. The flippers were short, broad, and of great power.

Measurements of the Cranium of Archelon ischyros Wieland.
(From a cotype approximately three-fifths the size of the type.)

	M.
Greatest length	·72
Width taken across the maxillo-premaxillar suture	·138
Width across middle of vomer	·145

Width through orbits	·22±
Height through center of narial opening	·095
Height directly back of narial opening	·17
Parietal height (greatest)	·28±
Width of narial opening	·07
Length of " "	·12
Greatest length of orbit	·15
" width "	·115
Length of the inferior edge of the premaxillary	·11
Length of inferior edge of the maxillary	·20
Length of inferior edge of jugal	·23
Length from extremity of beak to posterior inferior extremity of the quadrato-jugal	·58
Distance from tip of beak to antorbital border	·24
Least distance from postorbital border to the posterior border of the quadrato-jugal	·166

Measurements of the accompanying Mandible.

Greatest antero-posterior length	·465
Width across articulars	·25±
Antero-posterior length of symphysis	·12
Width at vertex of ramial angle	·155
Depth of symphysis at vertex of the ramial angle	·11
Extreme length of dentalium	·42
Extreme length of angular (lower outer surface)	·14

The Pelvis of Archelon ischyros.

The pelvis here described is entire, and in nearly perfect condition. As collected the parts were imbedded in an indurated marl in their natural position, with the exception of the ilia; which were slightly inclined laterally.

The notable features of the pelvis figured here are the great width, greater than the antero-posterior length, the very broad and symmetrical ectopubic expansion, and the diminutive size of the obturator foramen, which is entirely closed by the entopubis and ischium with the consequent reduction of the interobturator cartilage from a band to a small and solid rhombic area with concave sides. These are quite the reverse of the relations seen in *Thalassochelys*. To the general outline of the pelvis of *Dermochelys* there is strong resemblance, with the important exceptions that in the latter the ilium is longer and slenderer, while the obturator foramen though much reduced in size is not enclosed.

The ectopubis increases quite regularly to its greatest thickness at the heavy anterior border. The entopubis is likewise thickest distally, that is near the median line.

The ischia are short and broad, the middle anterior portion extending inward and forward to meet the pubis.

The ilia are short and robust, and curved into distinct elbows, the dorsal angles of which are very prominent, though ligamental attachment was confined to the distinctly rounded distal ends.

There are few pelves of fossil marine turtles known with sufficient exactness to make a close comparison with the present beautiful specimen wholly satisfactory. It no doubt conforms quite nearly to the pelvis of *Protostega* which has been figured

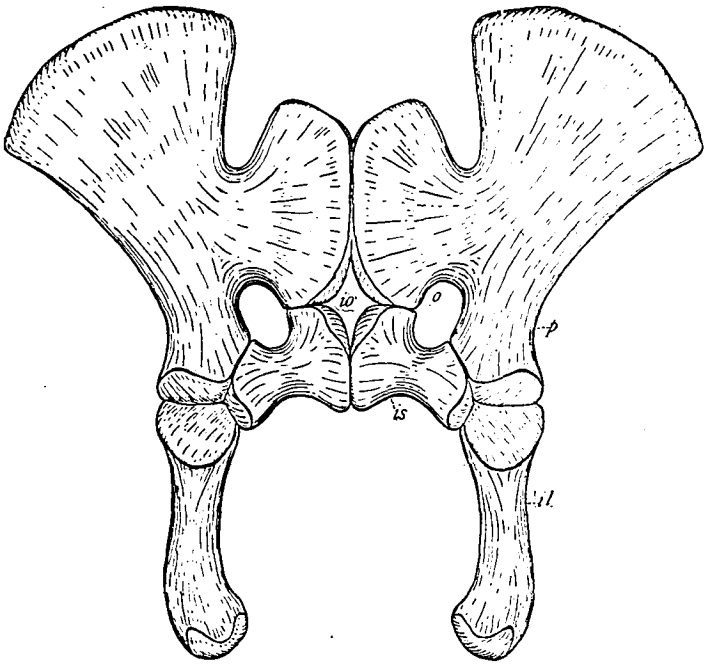

FIGURE 6. *Archelon ischyros* Wieland (type specimen). Ventral view of pelvis of specimen 12 feet in length, $\frac{1}{8}$ natural size; *p*, pubis; *il*, ileum; *is*, ischium; *o*, obturator foramen; *io*, interobturator cartilaginous area.

by Case, though the specimens he examined did not disclose the interesting conformation of the obturator foramen.

The presence of this feature, still seen in certain land turtles, in distinctly marine turtles of the Mesozoic, is certainly interesting, and may be regarded as a persistent character inherited from a land ancestry.

Measurements of the pelvis of Archelon ischyros Weiland (type).

		M.
	Extreme antero posterior length	·79
	Extreme width	·81
	Width taken across the acetabular surfaces	·46
	Shortest diameter of obturator foramen	·05
	Longest diameter of obturator foramen	·08
	Acetabular width	·12
	Acetabular length	·14
Pubis	Antero posterior length	·46
	Width, greatest	·405
	Greatest thickness (acetabular)	·175
	Antero-posterior width of entopubis	·25
	Thickness of entopubis (distal)	·07
	Thickness of ectopubis (distal)	·04
Ischium	Extreme length	·14
	" internal width	·15
	" external "	·10
	Width at middle of shaft	·06
	Thickness of " " "	·033
Ileum	Extreme length	·30
	" width of the acetabular surface	·093
	Thickness (least) at middle of shaft	·046
	Thickness (greatest) at middle of shaft	·105
	Greatest distal diameter	·095
	Least " "	·06

Archelon Marshii, sp. nov.

A second species of the genus *Archelon* is indicated by a specimen collected by the writer on the east side of the Cheyenne River in the Bad Lands proper in August 1898. Like the others, this specimen was found in the uppermost Fort Pierre Cretaceous, just beneath the Miocene or White River formation.

It consists in the plastron, humerus, ribs and a number of marginals indicating a turtle of great size, probably 11 feet in length. The humerus is rather straighter than in *A. ischyros*, and the plastron is relatively more massive, being fully one half thicker than in that species. As a slight token of respect this species is named in honor of Professor O. C. Marsh, to whose interest the Museum of Yale University is indebted for the possession of these gigantic *Testudinates*.

Position of the Genus Archelon.

While the genus *Archelon* presents many intermediate characters and strongly supports the view that *Dermochelys* belongs to the *Crpytodira*, as strenuously insisted upon by

Case in his discussion of the relationships of *Protostega* (5), its exact position may not yet be asserted positively. Bearing in mind that the turtles are an ancient highly specialized and numerous group of great constancy of form, it becomes both convenient and necessary to separate genera and families on less distinct anatomical differences than in the case of more variant orders. Moreover more exact knowledge of the fragmentary material of the Mesozoic is the first requisite; for many forms will be found like the present, disposing of old questions only to raise new ones.

In general I am however inclined to accept Cope's *Protostegidæ* (7) as containing the genera *Protostega* and *Archelon*. It is scarcely necessary to say, however, that there is a vastly greater interval between the *Dermochelyidæ* and *Protostegidæ* as thus constituted, than between the latter and the *Cheloniidæ*. I would lay especial stress upon the necessity of recognizing this general fact.

The position of *Protosphargis Veronensis* Capellini (3) is very doubtful, firstly because its skull, nuchal and fore-arm are unknown, and secondly because of the uncertainty concerning the validity of the *paraplastron*, as I have termed what I suppose represents the fused anterior plastral elements in *Protostega* and *Archelon* (15).

While the latter genera appear to be much too strongly specialized to represent more than a Cretaceous offshoot from the *Dermochelan* line of descent, *Protosphargis* may possibly be exactly in this line. The form of the plastron especially suggests such a position. The center of greatest interest has therefore in large measure shifted to *Protosphargis*. The discovery of further specimens of this genus will be of the first importance.

Attention should here be drawn to the interesting determination of the marginal series of *Protosphargis* by Capellini (4). I may mention too that a single marginal was figured in the first description of *A. ischyros* (13) which is wholly characteristic. The entire marginal series in this form is unusual in the spiny development of both the dorsal and ventral interior marginal borders, which are strongly spine-set after the manner of the plastron. Case has figured a portion of the marginal series in *Protostega* (5), but his material did not bring to light such a full development of spiniferous marginalia as is seen in *A. ischyros* and *Marshii*. That these spines represent the disappearing remnants of a normally developed carapace is a reasonable supposition and nothing more. But whether representing advancing or receding ossification the slender and untoothed marginals of *Protosphargis* indicate a sharp interval in development between these forms. The latter is undoubtedly a well marked genus.

With increasing knowledge of *Protostega* and its allies, that most interesting of questions pertaining to the *Testudinata*, the origin of *Dermochelys*, remains quite as enigmatic as ever. Hence only the following tentative classification can now be presented, the writer hoping to again attack the general subject at a future time.

Family—PROTOSTEGIDÆ Cope.

Genera—*Protostega* and *Archelon*.

{Doubtfully belonging to the *Protostegidæ*, *Protosphargis Veronensis* Capellini (3, 4), and still more doubtfully *Pseudosphargis ingens* von Könen and Dames (8).}

Synopsis of Characters of the Protostegidæ.

Marine turtles with carapace of medium curvature. Neuralia and pleuralia thin and investing the ribs but slightly. Marginalia usually spiniferous on interior borders. Plastral elements of medium development with numerous digitations. Normal epiplastron unknown, the three anterior plastral elements probably uniting into an entepi- or paraplastron. Body enveloped in a leathery hide? Skull intermediate between that of the *Dermochelyidæ* and the *Cheloniidæ*.

Genus Protostega Cope.—Squamoso-jugal union probable. Quadrato-jugal triangular. Mandibular rami coössified. Radial process of humerus strong. Carpals and tarsals unknown. Complete outline of obturator foramen unknown.—Only species *P. gigas* from the Niobrara Cretaceous of Kansas.

Genus Archelon Wieland.—Quadrato-jugal strongly united with the postfrontal, and of crescentic outline. Mandibular symphysis remaining distinct. Radial process of humerus weak, ectepicondyle strong. Carpals and tarsals undescribed. Obturator foramen small elliptical and enclosed.—Type of the genus, *A. ischyros* Wieland. Second species, *A. Marshii* Wieland. Humerus straight and robust. Plastron unusually heavy. Both species from the Upper Fort Pierre Cretaceous of South Dakota.

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