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THE OSTEOLOGY OF PROTOSTEGA.

By G. R. WIELAND.

The first mention of ancient gigantic marine turtles from America was made by Cope in 1871 in a letter to Professor J. P. Lesley containing an account of a journey in the valley of the Smoky Hill River in Western Kansas. This letter, as subsequently published in the Proceedings of the American Philosophical Society,¹ includes a preliminary notice of the huge Niobrara Cretaceous turtle, *Protostega gigas*. The type specimen was collected by Cope himself on a bluff near Butte Creek in the vicinity of Fort Wallace. It was secured in a more or less fragmentary condition after the manner of the vertebrate collecting of the earlier days of western exploration, for, in the more extended description given in the Cretaceous Vertebrata of the West, Cope says this fossil is made up of more than eight hundred separate fragments.

The various parts of *Protostega gigas* (type), although mostly in situ, were considerably removed from their natural position. The original specimen is now in the collection of the American Museum of Natural History. It includes much crushed cranial elements with portions of the lower jaw, ten nearly free ribs, several vertebrae, various plastral elements, the shoulder girdle, a humerus, radius, and ulna, and several metacarpals and marginals, as well as parts of uncertain position. Owing, however, to the manner in which the ribs lay athwart the rather imperfect plastral plates, the latter were supposed to be dorsal, and to represent a very primitive condition of carapacial development with large fenestrae. The radius and ulna were

¹ Vol. XII., p. 175.

not distinctly recognized as such although clearly figured. Owing also to a palpable numerical error in the measurements of the cranium (".50 M. = 24 $\frac{1}{2}$ in.") the total length of the original animal was estimated at thirteen feet, and is so referred to in text-books! The actual length is far less, as will clearly appear in the present description of a much completer cotype almost exactly the size of the original Cope specimen. This error was, however, in a sense prophetic, as some of the turtles of the related Dakotan genus *Archelon*, discovered by the writer twenty-four years after the first *Protostega*, did actually reach, or possibly exceed, the enormous size of thirteen feet in length.

Protostega remained a very vaguely known turtle until Baur² pointed out that it must in its main characteristics agree with the Cheloniidæ, and that the plates Cope supposed were dorsal must be plastral. That such was the fact was later more definitely shown by Hay,³ who figured the nuchal and hyo- and hypoplastron of another Niobrara specimen.

The next contributions to our knowledge of the osteology of the Protosteginae were made by the writer, after his discovery of gigantic turtles east of the Black Hills in the Fort Pierre Cretaceous in the summer of 1895. In the communications,⁴ which soon followed, the structure of the greater part of the carapace and plastron was made known from remarkably preserved specimens. All the larger limb bones were also determined and figured; for the first time, indeed, in the case of any extinct sea-turtles of America. There immediately followed these papers the important contribution of Case,⁵ which, in addition to a careful discussion of the systematic position of *Protostega*, added more particularly to a knowledge of the cranial characters, as based on the description of various crushed, but otherwise well defined disarticulated elements. The pelvis was also made known.

Further facts concerning the general cranial type in the Protosteginae were next given by the writer⁶ in a paper describing the splendid skull of *Archelon*, now on exhibition in the Yale Museum. Later an attempt was made by Williston⁷ to restore the tarsus and give the organization of the hind flipper of *Protostega*, and by

² (a) "Die Systematische Stellung von *Dermochelys* Blainville," *Biolog. Centralblatt*, IX., 1889. (b) "On the Classification of the Testudinata," *American Naturalist*, XXIV., 1890.

³ "On Certain Portions of the Skeleton of *Protostega gigas*," *Field Columbian Museum Publication*, No. 7, 1895.

⁴ (a) "*Archelon ischyros*, a New Gigantic Cryptodiran Testudinate from the Fort Pierre Cretaceous of South Dakota," *Am. Jour. Science*, December, 1895. (b) "The Protostegan Plastron," *Ibid.*, January, 1898.

⁵ "On the Osteology and Relationships of *Protostega*," *Journal of Morphology*, Vol. XIV. (This publication bears the date 1897, but did not appear until some time in June, 1898, its presumptively true date.)

⁶ "The Skull, Pelvis, and Probable Relationships of the Huge Turtles of the Genus *Archelon* from the Fort Pierre Cretaceous of South Dakota," *Am. Jour. Sci.*, Vol. IX., April, 1900.

⁷ "On the Hind Limb of *Protostega*," *Ibid.*, Vol. XIII., April, 1902.

Wieland⁸ to show the carpal organization of *Archelon*; but, as will be shown below, both these efforts are almost entirely in error. From the foregoing review of the slow progress of our knowledge of the Protosteginae it is seen that the third of a century which has elapsed since Cope's discovery of *Protostega gigas* has not sufficed to bring forth an entirely complete restoration of any single individual of these great sea-turtles. How welcome then has been the discovery during the past two years by Mr. Charles Sternberg in the Niobrara Cretaceous of Western Kansas of the nearly complete specimens of *Protostega gigas* which permit the present description of the organization of the limbs, the most important of the parts yet undescribed, as well as the least likely to be recovered in complete form. For happily the elements of the first-secured and completer of these exceptional specimens, though somewhat crushed, were found altogether, or nearly, in their naturally articulated position, a condition imperatively necessary to a satisfactory description of the flippers.

This rare fossil turtle was first briefly mentioned in *Science* by Professor Osborn⁹ as “* * * a complete skeleton of *Protostega* which lay on its dorsal surface with the fore limbs stretched out at right angles to the median line of the carapace, measuring six feet between the unguis phalanges.” Afterwards it was secured for the Carnegie Museum by Mr. J. B. Hatcher, who, though he crowded the brilliant work, which might well have crowned the efforts of a long life, into a short one, leaves this ripe fruition mixed with a sorrow surely not lessened by the fact that the hardships of the plains of the Northwest and the Patagonian deserts had all too plainly left their mark upon him.

Having expressed in conversation with Mr. Hatcher much interest in these more recent discoveries of *Protostega*, I was invited to make a study of the newly acquired material, this arrangement being concurred in by Dr. W. J. Holland, Director of the Carnegie Museum. But early in July, 1904, when I visited the Carnegie Museum for the purpose of doing this work, to my extreme sorrow I found, that, although I had a brief word from Mr. Hatcher shortly before, he was so seriously ill that there could be but little or no hope of his recovery. And indeed, as everyone feared, it was but a few days before he passed away. However, it was under such circumstances a relief to be busied, and Dr. Holland very kindly arranged for and furthered the initial study of the material on hand.

Furthermore, during the past summer Dr. Holland has added to the collections first obtained much additional material, also collected by Mr. Sternberg, including

⁸“Notes on the Cretaceous Turtles *Toxochelys* and *Archelon*, with a Classification of the Marine Testudines,” *Ibid.*, Vol. XIV., August, 1902.

⁹N. S., Vol. XIX., No. 470, p. 35, January, 1904.

one very important specimen, a large *Protostega*, represented by a quite complete cranium and lower jaw, accompanied by a humerus, radius, ulna, wrist, and palmar bones — all in place on the same slab. The acquisition of this specimen has been as timely as fortunate; for it has removed all doubt as to the carpal and tarsal organization of *Protostega*, and made possible the avoidance of errors in the description of the completer specimen, most of the elements of which had been dissociated from their matrix, and the position of some of them rendered doubtful through the mistaken zeal of their collector. It will hence greatly simplify our description of the limb organization of *Protostega* as based on the free elements of the original and completer specimen, No. 1420, Carnegie Museum Catalogue of Vertebrate Fossils, if the more recently acquired and less complete *Protostega* with its parts in approximately natural position, be considered first.

Protostega gigas Cope (Cotype).

Specimen No. 1421 (Carnegie Museum Catalogue of Vertebrate Fossils). — This fine fossil is from the Niobrara Cretaceous of Hackberry Creek, Gove County, Kansas. The *ex situ* portions of the original skeleton, which had weathered out and were secured in more or less complete condition, include the left humerus, radius, ulna,

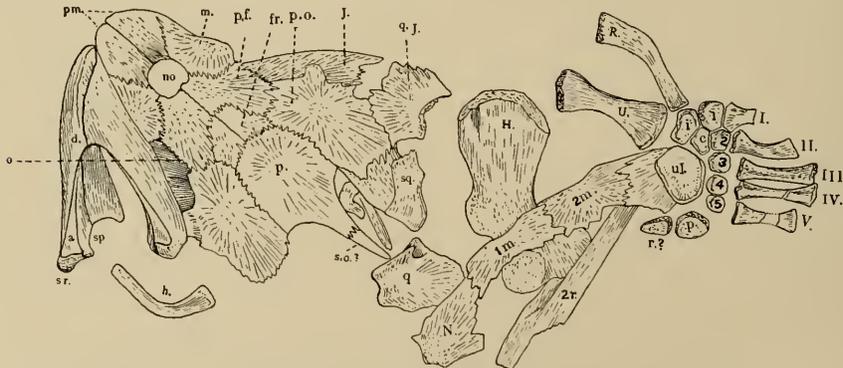


FIG. 1. *Protostega gigas*. Carnegie Museum Specimen, No. 1421, from Niobrara chalk of Hackberry Creek, Gove County, Kansas. Superior view of skull with the lower jaw and a hyoid, the right anterior border of the carapace and most of the right fore flipper, all in nearly natural position and still partially imbedded as collected on a single slab of the chalk matrix. $\times \frac{1}{2}$.

Skull. — *pm.*, premaxillary; *m.*, maxillary; *n.o.*, external nares; *p.f.*, prefrontal; *fr.*, frontal; *o.*, orbital border; *p.*, parietal; *s.o.*, supraoccipital; *j.*, jugal; *q.j.*, quadratojugal; *sq.*, squamosal; *q.*, right quadrate.

Lower Jaw. — *d.*, dentalium; *a.*, angular; *sr.*, surangular; *sp.*, splenial; (*h.*, hyoid).

Carapace. — *N.*, portion of right ala of nuchal; *2r.*, second rib; *1m.*, *2m.*, first and second marginalia.

Flipper. — *H.*, humerus; *R.*, radius; *U.*, ulna; *r.*, radiale (?); *i.*, intermedium; *ul.*, ulnare; *p.*, pisiform; 1-5, first to fifth carpalia respectively; I-V, first to fifth metacarpalia.

ulnare, radiale, and pisiform, with fragmentary phalanges, and many broken pieces of the plastron. The *in situ* portion consists of the right anterior part of the skeleton, and was secured on a single slab of the chalk matrix, in which it still remains intact, as shown in the accompanying drawing, Fig. 1, by Mr. Prentice. It includes the following: the lower jaw in oblique inferior view, with the two larger hyoidal elements; the skull in superior view, less the left squamosal and with the right quadrate disarticulated and its anterior surface up; the right humerus, radius, ulna, wrist, and palmar elements in superior view, and all in place, except the radiale which has slipped across to the posterior border of the wrist; the right ala of the T-shaped nuchal with the first and second marginals, and the distal half of the second rib, all in place and resting over the proximal extremity of the humerus.

Although the various bones are more or less crushed, after the manner of most fossils from the Kansas chalk, the contours are exceedingly good. In the skull, as simply crushed down in the vertical direction with little distortion of parts, there appear in clear preservation and united by distinct sutures the premaxillaries, maxillaries, prefrontals, frontals, postorbitals, and parietals, with the right squamosal, jugal, and quadrato-jugal. The cervicals have in some way been dissociated, but the skull lies in a normal position with respect to the anterior border of the carapace, from under which the right fore-flipper projects in the normal position, the hand being bent back pronately over the position of the third marginal, part of which appears in view.

It will at once be seen what exceedingly satisfactory information is furnished by the present specimen, as compared with all other examples of *Protostega* hitherto found. The more important measurements afforded are the following:

	cm.
Lower jaw : Extreme length of ramus.....	37
Extreme length of median symphysis.....	16
Cranium : Extreme length (as crushed flat) measured from end of beak to posterior extremity of occipital crest.....	58
Median length of narial opening.....	7.5
Greatest width of narial opening.....	5.5
Orbital border of the prefrontal.....	6
Antero-posterior length of orbit.....	12
Humerus : Length across head.....	33
Width of distal end.....	14
Radius : Length.....	19
Ulna : Length.....	18
Carpalia : Width across the five carpalia in place.....	18
Metacarpalia : (Length of 1-5 resp.) ; 7(+ or -), 10.5, 12, 12.5, 10 (+ or -) cm.	

The above cranial and hand measurements have not hitherto been obtained in *Protostega*, whence it is of interest to note, that, allowance being made for the crush-

ing of the specimens of the Niobrara chalk, no wide differences in proportion are evident on comparison with the much larger turtles of the genus *Archelon* from the Fort Pierre Cretaceous. The lack of coössification of the mandibular rami and especially the very low radial crest of the latter form will, however, serve to distinguish it from the fossil before us. But of far greater interest than any question of generic values that may arise is the fact that the bones of the hand are, with the sole exception of the radiale, indisputably in place, the most striking feature being the immense ulnare, and the strong contact of the intermedium with the first carpal. With these remarks we may pass on, basing our main descriptions on the earlier secured and in some respects better specimen with its several elements freed from their matrix.

Specimen No. 1420 (Carnegie Museum Catalogue of Vertebrate Fossils).—The present specimen of *Protostega gigas* is more nearly complete than any other as yet discovered. As originally imbedded in its matrix of chalk, nearly every element was present in an exactly or approximately natural position, and recovered as follows:

1. Portions of the skull, with the crushed lower jaw and two large and well preserved paired hyoids.
2. The 1st, 4th, 5th, 6th, 7th and 8th cervical, the dorsal, sacral, and eight anterior caudal vertebrae.
3. The nearly complete series of ribs, including the anterior pair of sacral ribs, also the neurals, and various marginals.
4. The left shoulder-girdle and proximal half of the humerus, with the right shoulder-girdle and complete front flipper in place, except the unguinal phalanx of the fourth and the second phalanx of the fifth digit.
5. The pelvic girdle and hind limbs complete and in place, less only the fibulare (if ossified), the unguinal phalanges of the right, fourth, and fifth digits and of the left fifth digit.
6. A nearly complete though very much crushed plastron.

Unfortunately the collector of this surprisingly complete fossil, in an attempt to remove and separate the bones from their matrix of chalk, mis-marked some of them, and also made it virtually impossible to either replace more than a very few of the marginals, or to determine the outlines of any of the plastral elements with exactness. Hence it is not worth while, in view of the marked crushing undergone, to give figures of any of these parts now, although they will aid in the restoration. As will be evident to any student of the fossil vertebrates the removal of the fossil from its matrix in the absence of the necessary knowledge, training, and equipment,

was ill advised. Such work is difficult enough in the best equipped laboratories. However none of the bones of the limbs are broken, and Mr. Sternberg redeemed himself by discovering and securing in such excellent condition specimen No. 1421, as just related. The position of the following parts is independently determinable :

1. The fourth to the eighth cervical, the dorsal and sacral centra, with the proximal caudal vertebrae and most of the ribs as shown in part in Fig. 2.

2. The shoulder-girdles and elements of the fore-arm ; in particular (as can be determined by actual close articulation, or by such intervening matrix as the collector permitted in much too small part to remain), the intermedium, first carpale, metacarpale and its phalanges, and also carpalia 3-5.

3. The pelvic girdle and elements of the hind flipper, in particular the *intermedio-centrale* and *tarsalia 1-3, and 4 and 5* (fused), as well as several metatarsals and phalanges.

It should be stated here that it is claimed that, as figured, no element of either flipper is actually misplaced, although the extent of the crushing undergone makes it quite possible that in one or two instances dorsal surfaces have been mistaken for ventral ones, or *vice versa*, and that the ends of several phalanges may have been reversed. Withal it is deemed important to be thus explicit in giving the manner in which the accompanying text-figures and photographs have been obtained, before taking up more detailed description. (Because of the compression undergone it was not thought needful to figure either the lower jaw, cervicals, or caudals. The dorsal view of the carapace can better be given after the restoration now being made.

I. THE CARAPACE. (Fig. 2.)

With the exception of the T-shaped nuchal and the marginals with dactylate interior borders so peculiar to the Protostegine in distinction from all other known marine turtles, the main features of the carapace are very well represented in Fig. 2. The very thin, almost paper-like series of neuralia is present, though much crushed down on the underlying neural arches. The ribs are free through at least the distal two-thirds of their length. The first pair is comparatively slender, it not being clear as to whether, or not, their distal extremities rested on the lateral alæ-like expansions of the nuchal. The shield contour is, instead of elongate as once supposed, relatively broader than in either *Thalassochelys* or *Chelone*, the ratio of the length of the dorso-sacral series to the breadth of the carapace being as three to four.

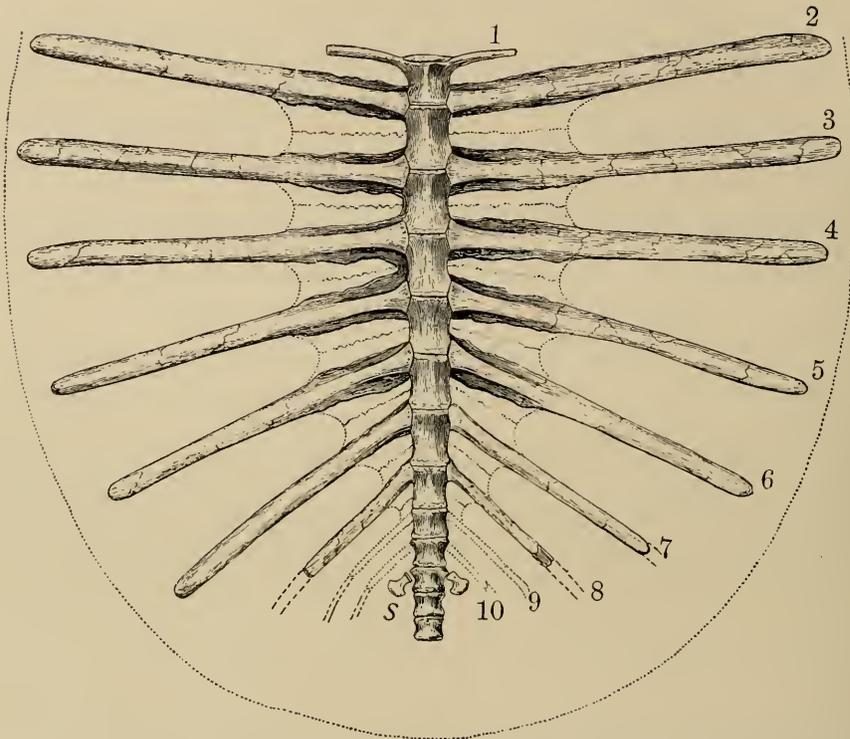


FIG. 2. *Protostega gigas*. Carapace less the nuchal and the marginal series. Inner view. 1-10, the first to tenth ribs respectively; *s*, the first sacral. Ten dorsal, the two sacral, and the first of the caudal centra are shown. (A trial drawing preparatory to mounting of specimen. About one-eighth natural size.)

This greater breadth is quite characteristic of Cretaceous turtles, and a distinct approach to a quite orbicular form like that of *Lytoloma*.¹⁰ It is a form, moreover, that well accords with the powerful and widely expanded flippers now to be described.

II. THE FRONT FLIPPER.

(Plates XXXI. and XXXII., with Figs. 3 and 4.)

The shoulder-girdle of *Protostega* is robust but presents no strongly marked peculiarities, save the elongate coracoid which extended back to the pubis as in *Eretmochelys*, but not either *Chelone* or the long-bodied *Dermochelys*. The

¹⁰ Wieland, "Structure of the Upper Cretaceous Turtles of New Jersey: *Lytoloma*," *Amer. Jour. Sci.*, Vol. XVII.; September, 1904.

features of the humerus are, however, highly characteristic, as is shown more particularly in Figs. 3 and 4, which disclose certain approximations to the humerus of *Dermochelys* not so readily discernible in the figures hitherto pub-

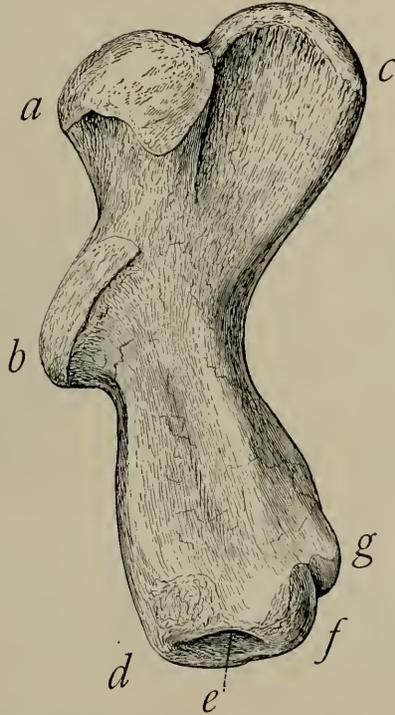


FIG. 3. *Protostega gigas*. Ental view of a large humerus. Actual length, 34 cm. *a*, head; *b*, radial crest; *c*, ulnar condyle; *d*, ectepicondyle; *e*, ectepicondylar foramen; *f*, ectocondyle; *g*, entocondyle.

lished. It must be noted, however, that crushing has been such as to greatly diminish the distal breadth and render it uncertain as to whether there is an ectepicondylar groove. Case speaks of a foramen in describing his specimen,¹¹ though his figure suggests a groove. I suspect that there may be present a true enclosed foramen rather than a deep groove as in *Archelon*. In the latter the groove is much further back from the anterior border and the ectepicondylar process correspondingly larger, while the radial crest is not nearly so prominent as in *Protostega*. (See Fig. 3.)

¹¹ See foot-note 5.

The *carpal* and *finger* organization of *Protostega* has been hitherto wholly unknown, and, in fact, the only fossil marine turtle from America in which these parts have been described is *Toxochelys*.¹² In discussing the carpal organization it is of foremost importance to recall that the *intermedium*, *carpale 1*, and *metacarpale 1*, as well as *carpalia 3-5*, are still naturally articulated as in life, and in all particulars agree precisely with these same elements in specimen No. 1421. Nor is there any

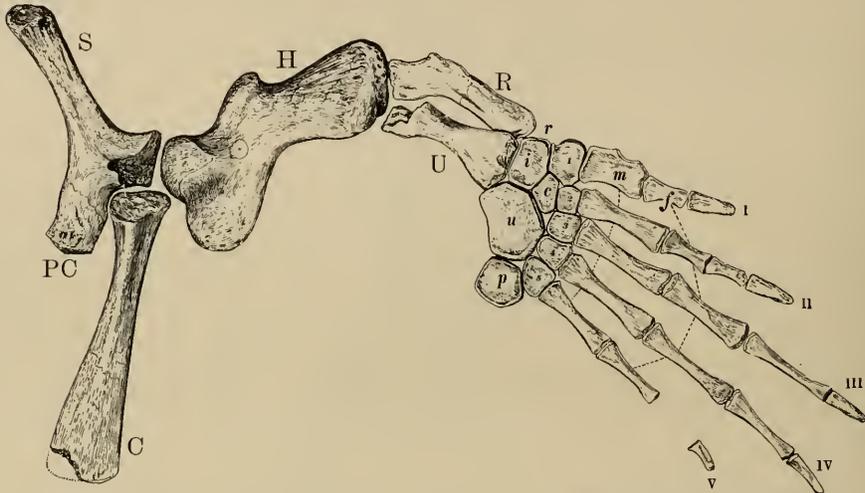


Fig. 4. *Protostega gigas*. Right shoulder girdle and flipper. $\times \frac{1}{2}$. Niobrara Cretaceous. S, scapular; PC, procoraco-scapular; C, coracoid; H, humerus; R, radius; U, ulna; r, position of the radiale; i, intermedium; u, ulnare; c, centrale; 1-5 first to fifth carpalia; p, pisiform; m, metacarpal 1; p, phalanx 1; I-V, first to fifth fingers and ungual phalanges. The view is dorsal with the procoraco-scapular rotated into the plane of the paper.

further doubt concerning the identification of the other elements and agreement *in toto* with that specimen. As so clearly shown in the figures and photographs, the triangular-shaped centrale articulates strongly with carpale 1. I have supposed this was not the condition in *Archelon*,¹³ but must have been in error. No radiale was recovered. Bearing in mind that the several carpal elements are somewhat crushed, no further detailed description of them appears necessary, except that it should be remarked that the ulnare is of sub-hexagonal outline and relatively very large, being of the general form seen in *Thalassochelys*, and especially *Colpochelys*, rather than *Dermochelys*. The ulnare of *Archelon* is of nearly the same relative size,

¹² Wieland, "Notes on the Cretaceous Turtles *Toxochelys* and *Archelon*, with a classification of the Marine Testudinata," *Am. Jour. Sci.*, Vol. XIV., August, 1902.

¹³ *Loc. cit.*, Wieland, "Notes on *Toxochelys* and *Archelon*," etc.

but of rounder and more regular contour. The nearly ovate pisiform is distinctly intermediate in development between that of the existing *Dermochelys* and the Cretaceous congener *Toxochelys* in which the pisiform is smaller than in any other distinctly marine turtle.

The first metacarpal is broad, and the first finger short and robust as in *Toxochelys* (see Fig. 8) and other members of the Cheloniidae. Finger disparity is pronounced, the second finger being little elongate as in *Toxochelys*, with the third and fourth fingers of medium and nearly equal elongation, and the fifth fully as elongate as the second. The first to third fingers bore free claws, but not the fourth and fifth.

In its general features the front flipper of *Protostega* agrees much more closely with that of *Toxochelys* (Fig. 8) than with that of other forms, as one might well expect. The existing Cheloninae do not present so close a likeness, because of the peculiar elongation of the radius and dependent carpal variations, although the boundaries are much the same, the centrale in particular being in contact with carpale 1 in both cases. With *Dermochelys*, in which carpale 1 is small and excluded from contact with the centrale, the points of likeness are more obscure, although there is no distinct suggestion in the carpal organization, that the former belongs to an utterly different race. Pisiform development is also more like that of the primitive forms than in *Dermochelys*.

The relative size of the front flippers as compared with the carapace is great, since they are not only robust, but have a spread equal to about $3\frac{1}{2}$ times the length of the dorso-sacral series of vertebrae. In the existing carnivore *Thalassochelys* this ratio is nearly as great, being equal to about three, but falls to two to one in the algaphagous *Chelone*. In the carnivore *Dermochelys* the ratio is about $2\frac{1}{2}$ to 1, a result of comparison rather unexpected in view of the very great length of fingers in the latter, and accounted for by the great length of the clipper-built Dermochelan body. There is in the comparison just made the very strongest suggestion that *Protostega*, more distinctly than any marine turtle thus far known, hunted prey, which swam actively, and, bearing in mind other features, was perhaps even powerful.

In my description of the front flippers of *Toxochelys*¹⁴ I presented an interesting tabular comparison of the relative percentages of length of the several elements of the front flipper and humerus of various Testudinales, which exhibited the general trend of change since the Jurassic in the development and variation of flippers from a more generalized limb-type. I now include *Protostega* in this comparison. The humerus is in each case considered as having a length of 100, and the finger lengths as reduced to the same ratio, but including arbitrarily for convenience the metacarpals, as follows:

¹⁴See Footnote 8.

	Humerus.	Radius.	Ulna.	First Finger and Metacarpal.	Second Finger and Metacarpal.	Third Finger and Metacarpal.	Fourth Finger and Metacarpal.	Fifth Finger and Metacarpal.	Pisiform.
<i>Dermochelys</i>	100	43	39	127	180	209	173	86	23
<i>Eretmochelys</i>	100	53	44	49	89	128	105	44	12
<i>Colpochelys</i>	100	57	51	56	92	131	107	44	13
<i>Protostega</i>	100	60	50	50	86	128	110	80	17
<i>Archelon</i>	100	54	51	—	—	—	—	—	—
<i>Toxochelys</i>	100	58	50	51	73	100	104	70	11
<i>Chelydra</i>	100	52	53	50	72	73	55	50	small
<i>Acichelys</i> = (<i>Eurysternum</i>).	100	57	51	40	54	63	66	51	17

Inspection of the above table shows :

1. Strongly marked radial and ulnar decrease in length.
2. Marked tendency to radial elongation as compared with the ulna, with considerable variation in the length of the radius and ulna as compared with the humerus.
3. Nearly static length of the first finger in the *Cheloniidae*, with a sharp increase in *Dermochelys*.
4. That elongation of the second finger appeared slowly.
5. Early and persistent increase in the length of fingers three and four.
6. More or less variable tendency to elongation of the fifth finger, with a sharp increase in *Dermochelys*, and a suggestion that this finger may have first elongated in some forms, and then undergone decrease in length.
7. Great and persistent pisiform increase, which began relatively early.
8. Increased finger disparity is mainly coördinated with depression of the radial crest.

III. THE HIND FLIPPER. (Fig. 5.)

The presence of an entire pelvis and the complete hind flippers, save only the unguis phalanges of the right second digit, and of both fifth digits is quite all that the most exacting anatomist could wish. Although as the result of compression in the matrix the bones are of slightly broader outline than in life, their proportions are, as in the front flippers, fairly well retained. Likewise, as is so often and so fortunately the fact in the fossils from the Kansas chalk, most of the articular facets and surface characters are, as in the other parts of this excellent specimen, clearly indicated.

Regarding the pelvis it is only necessary to note that the obturator foramen must have been completely enclosed by the close contact of the ischium and entopubis on the median line as in *Archelon*.¹⁵ The figures given herewith would not of

¹⁵ Wieland, *loc. cit.*, "The Skull and Pelvis, etc., of *Archelon*," p. 247.

themselves be quite clear upon this point were it left unnoticed. The ilia are of course shown in the lateral view; this, as the result of compression, being the only view remaining in fairly exact proportion.

Similarly the left fibula, as shown in Plate II., is turned partly around with a portion of the plastron adhering, the facet for contact with the distal end of the tibia being thus directed upwards. There can be but the barest doubt that the position of all the elements of the hind flippers as assigned in the accompanying Fig. 5 is correct. The presence of paired parts afforded a means of so exactly checking

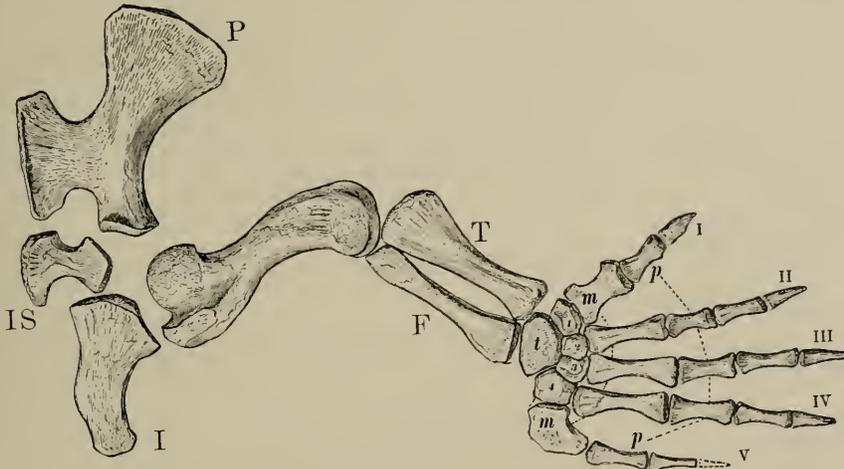


FIG. 5. *Protostega gigas*. Right pelvic girdle and flipper. $\times \frac{1}{2}$. The dorsal or ectal view of flipper with the corresponding ental view of the pelvic elements show in the plane of the paper. P, pubis; F, fibula; T, tibiale intermedium and centrale fused, or calcano-astragalar element; 1-3, first to third tarsalia; 4, fourth and fifth tarsalia fused; m, metatarsal 1; p, phalanx 1; I-V., first to fifth toes and ungnal phalanges.

the determinations as to exclude all possibility of error. Moreover, nearly all the parts, save perhaps the two ulnae, were imbedded in their matrix in a closely articulated natural position. *And it should be noted that the tibiae, all the tarsalia, and the first metatarsal and some of the phalanges of both flippers remain so articulated, the evidence as to their position hence being incontestable.* Also metatarsal V., though not articulated, or otherwise joined by remaining matrix, is of such characteristic form as would testify amply to its position, even though isolated. The same may be said of metatarsal 1. The development is in both cases much the same as in all the marine turtles. Unfortunately, however, no element referable to a fibulare, which appears to have been present, is now determinable. Nor is a

fibulare represented in the drawing, it being difficult to determine what may have been its outline.

The first toe is short, the second, third, and fourth of nearly similar moderate elongation, and the fifth somewhat elongate, as set on the strongly bowed and enlarged metatarsal V., which is similar to that common to all sea turtles.

The first toe bore a heavy and free claw, and I believe the claws of toes II.-IV. were also free and clawed, as indicated by their form and the curvature of the antero-lateral or unguis ridges. Reference may be made to Fig. 6, showing the lateral view of all the unguis phalanges which were all dissociated.

Allusion has been made to Professor Williston's restoration of the hind limb of

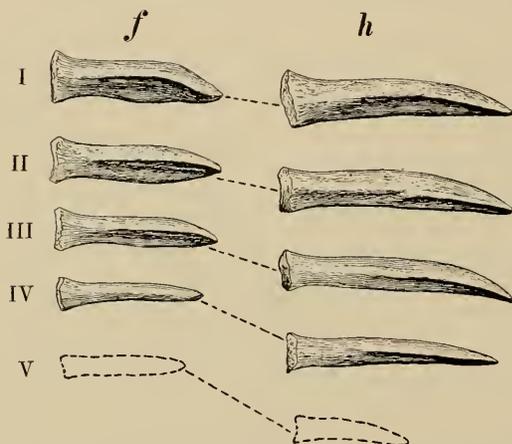


FIG. 6. *Protostega gigas*. Unguis phalanges. *f*, fingers; *h*, toes. Lateral view. $\times \frac{2}{3}$. (Trial series not found to necessarily be the exact finger and toe series.)

Protostega,¹⁶ and, before passing on to a general comparison with other forms, it is necessary to deal with this restoration more specifically. Williston's figure is that of a form so different from *Protostega* and all other turtles, that, if correct, it would indicate the existence of a new and hitherto unknown genus, or even family, of marine turtles. But this cannot be; for the form and proportions of the individual elements is throughout essentially the same as in *Protostega*.

The fact is that the arrangement of elements given by Professor Williston affords no approximation, and no direct hint as to the tarsal organization in *Protostega*. Metatarsal V. is placed in the position of metatarsal I., and the bone supposed to be metatarsal V. is probably from another animal, or else, the metatarsal of the other flipper is much altered by the compression to which nearly all the turtles from the Kansas chalk have been subjected. The other tarsals are difficult to adjust, although it is in particular likely that the element placed in the fibular position is a pisiform; for in both form and proportions it agrees with the pisiform of both of the present specimens, and differs very markedly in these respects from the true tarsal elements. The phalangeal

¹⁶See foot-note 7.

formula of 3, 3, 3, 3, 0, as proposed by Williston, is not that of *Protostega*, in which the true formula is 2, 3, 3, 3, 3.

The strongly marked angular tubercle of the proximal end of the fibula, as figured by Williston, reminds one of the similar and similarly situated process on the femur of the Dinosaur, *Camptosaurus*. It is not present in any of the specimens of *Protostega* known to me, and must at least indicate a new specific form. Should further examination confirm the presence of this feature, the specimen in the collection of the University of Kansas, which shows it, should be known as the type of a new species. And surely its most appropriate name would be one honoring the distinguished paleontologist who first studied it, and who rendered a very distinct ser-

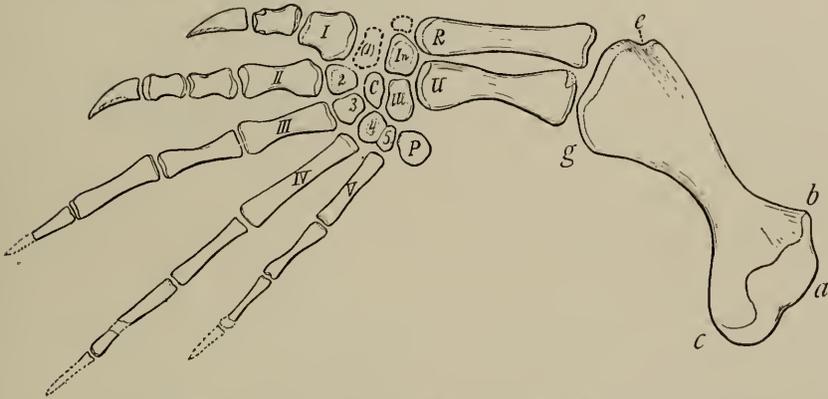


FIG. 7. *Tozochelys latiremis*. Left front flipper. Dorsal view. a, head; b, radial condyle; c, ulnar condyle; e, ectepicondylar groove; g, entocondyle; R, radius; U, ulna; In, intermedium; Ul, ulnare; C, centrale; 1-5, first to fifth carpalia; P, pisiform; I-V, first to fifth metacarpals and fingers.

vice by figuring it as best he could in the absence of further material or means of checking results.

Structurally, aside from the more primitive clawed condition, there is no hiatus between the tarsal and other features of the hind flipper of *Protostega* and the existing sea-turtles, the comparison with *Dermochelys* being quite as close as any other, in some respects closer in fact than with a somewhat aberrant although primitive form like that of *Colpochelys* (Fig. 8). In *Dermochelys* and *Protostega* the relative size and development of all the tarsal elements is suggestively alike. It is indeed increasingly difficult to believe that the former genus belongs to an utterly remote and primitively separated line. But unfortunately there is not yet known amongst the fossil marine turtles a single hind flipper which is sufficiently well preserved to afford

further detailed comparison with *Protostega*. The writer has, however, pointed out the fact that the littoral, or semi-marine, turtles of the Cretaceous of New Jersey, especially *Osteopygis* and *Lytoloma*, present many interesting primitive features, amongst these being relatively longer hind limbs, the inference being a quite clear one, that in the evolution of the limbs of the marine turtles, in correlation with carapacial and other changes, the hind limbs underwent shortening, and the front limbs a compensatory elongation. In fact in *Osteopygis*, a form now known to be very closely related to the ancestors of the Cheloninae, the femur is distinctly longer than

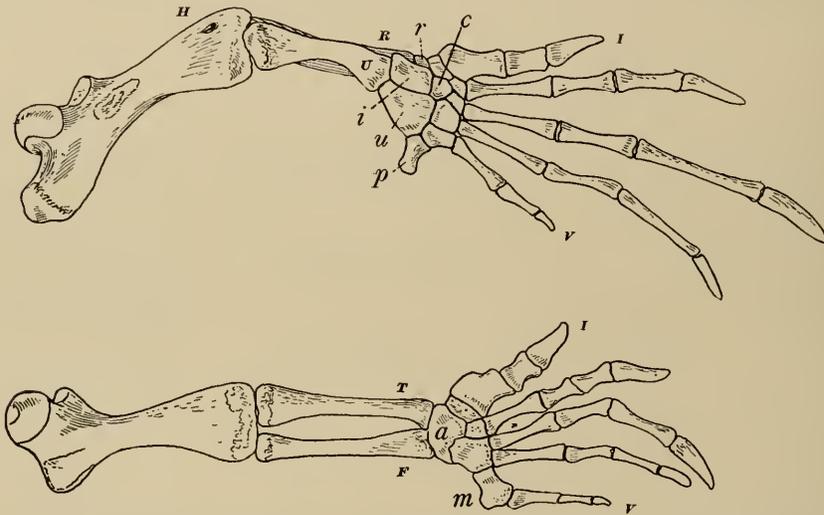


FIG. 8. *Colpochelys Kempi* Garman. $\times \frac{3}{8}$ Fore and hind flipper of a specimen in the United States National Museum (ratio of fore to hind flipper, 1.25).

Fore Flipper. *H*, humerus with ectepicondylar perforation set well in from the anterior border; *R*, radius in natural position revolved somewhat beneath the ulna (*U*); *r*, radiale, bounded by the radius, the intermedium and first carpal; *i*, intermedium, *u*, ulnare; *p*, pisiform; *e*, centrale bounded by the intermedium, ulnare, and first to fourth carpalia; *I*, *V*., first and fifth fingers.

Hind Flipper. *T*, tibia, *F*, fibula; *I*, *V*., first and fifth toes. The tibia and fibula support a single astragalo-calcaneal element, (*a*) theoretically formed by the fusion of four elements corresponding to the radiale, intermedium, ulnare, and centrale. The first toe is borne on tarsale I., the second on tarsale II., and the third to fifth on tarsalia III.-V., fused. Metatarsal 1 (*m*) is the exact equivalent of metacarpal 1, and metatarsal V. has a pisiformoid development.

the humerus, as is also the case in *Chelydra*, a tortoise which is in many respects suggestive of specialization in some direction similar to that doubtless followed by the direct ancestors of the marine turtles. In *Lytoloma*, an upper Cretaceous and lower Eocene genus closely related to *Chelone*, the femur appears to have undergone some

relative shortening. But though a nearly complete carapace has recently been described,¹⁷ in the absence of further description of the Belgian material, now in process of elaboration by M. Dollo, we know very little of the limb development in this form, except by inference. In the case of *Toxochelys*, which is near to *Lytoloma*, we fortunately know the organization of the front flipper within close limits (cf. Fig. 7), while I have but recently described the carapace of a most interesting new species, *T. Bauri*.¹⁸ In *Toxochelys* we find a markedly primitive form of flipper, indeed the most primitive known, although the humeral contour and finger disparity indicate an animal capable of navigating the open seas. Also, the carapace of all the Toxochelyds known has very large fontanelles, suggesting a marine life quite as decidedly as the flipper; for though the laws of carapacial reduction are as yet only surmised, it is only in the marine members of the Cryptodira that prominent pleuro-marginal fontanelles occur.

Because of the facts given it does, however, prove decidedly interesting to find that even in *Protostega* of the Upper Cretaceous, the hind limbs yet remain relatively long, though fully developed as flippers. For in *Eretmochelys* and *Chelone* as well as in *Dermochelys*, the fore flippers vary from about 1.55 to 1.60 times the length of the hind flippers; whilst in the orbicular bodied *Protostega*, with a tremendous spread of front flippers as already pointed out, this ratio falls to 1.30, which is, however, a little in excess of *Colpochelys*. In the latter genus which has in some respects the most primitive flipper organization of any existing Cryptodiran the fore flippers are but 1.25 times the length of the hind flippers. Doubtless there are many further interesting numerical relationships not yet discovered. Though the relatively strong pattern and great size of both fore and hind flippers in *Protostega* and the related *Archelon*, taken with the broad body and shortness of the dorso-sacral series, may not indicate extreme and sustained swiftness, in conjunction with the cranial features these proportions do go far to confirm the opinion already expressed that these turtles, so powerfully equipped for both swimming and attack, may well have hunted actively swimming prey. The Protosteginae plainly included the largest and the most rapacious turtles which ever existed.

¹⁷ Wieland, "Structure of the Upper Cretaceous Turtles of New Jersey; *Lytoloma*," *Am. Jour. Sci.* September, 1904.

¹⁸ Wieland, "A New Niobrara *Toxochelys*," *Am. Jour. Sci.*, November, 1905.

IV. SYSTEMATIC POSITION OF PROTOSTEGA.

CHELONIODEA (Baur).

(Superfamily of the Cryptodira.)

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

(A) DERMOCHELYDIDÆ.

No descending parietal processes; no palatine foramen; other cranial and limb characters not remote from those of the Cheloniidæ; carapace represented by the nuchal only, and body enveloped in a leathery hide with an osteodermal mosaic; no claws. Genera: *Dermochelys*, *Psephophorus*, *Eosphargis*.

(B) CHELONIIDÆ.

Skull with descending processes of parietals, so far as known; palatine foramen sometimes present; vomero-premaxillar union usual but not constant; a normal, though often much reduced carapace and plastron; nuchal with or without articular process on under side; claws one, two, or more.

1. *Protostegina* (Wieland): No free nasals, and no palatine foramina; obturator foramen small and enclosed by ischio-pubic contact on the median line, as in many land forms; nuchal T-shaped; neuralia and pleuralia thin and investing the ribs but slightly; marginalia usually spiniferous on interior borders; plastral elements of medium development with numerous digitations on both outer and inner border of the hyo- and hypoplastron; epiplastron of Trionychoid and Acichelysoid form; body enveloped in a leathery hide (?); claws three or more.

(a) *Protostega* Cope. — Cranial elements nearly as in *Archelon*; mandibular rami coössified; radial process of humerus strong; front flippers very broad and of a more distinctly marine type than those of the Toxochelydinæ (*Toxochelys*); centrale in contact with carpale 1; hind flippers relatively very large, and tarsal region most like that of *Dermochelys*. Species: *P. gigas* Cope from the Niobrara Cretaceous of western Kansas:

Ratio of spread of front flippers to length of the dorso-sacral series. . . . 3.2

Ratio of front to hind flipper. 1.3

First to third fingers free, clawed.

First to fourth toes free, clawed.

V. MEASUREMENTS OF PROTOSTEGA GIGAS.

(All based on the single individual illustrated in Text-figures 2-7 and Plates I. and II. As most of the elements are much flattened lengths only are given, these doubtless remaining much the same as in life.)

(A) *The Lower Jaw.*

Length on median line (estimated, the tip being broken away).....	26	cm.
Length along ramus.....	30	"

(B) *The Carapace, Ribs and Dorso-sacral Centra.*

Total length of the ten dorsal centra.....	68	"
Total length of the three succeeding centra.....	10	"
Length of the dorso-sacral series.....	4.5	"
Extreme width of the carapace (exclusive of marginals) as crushed out flat and measured from tip to tip of the fourth ribs, both of which are complete and are the longest of the rib series.....	106	"
Length of the first to tenth dorsal centra respectively, 5.5, 7.5, 8, 8, 9, 8, 7.5, 6.5, 4, 4		"
Lengths of the first and second sacral and first caudal centra respectively, 3, 3.5, 3.5		"
Lengths of the first rib.....	10 +	"
" " second rib.....	49	"
" " fourth rib.....	51	"
" " fifth rib.....	51	"
" " sixth rib.....	46 (?)	"
" " seventh rib.....	43 (?)	"
Length of first sacral rib (in place)	3.2	"

(C) *The Shoulder Girdle.*

Distance apart of the two distal extremities (the scapular and the precoracoidal) of the procoraco-scapular.....	30	"
Length from interior bow of procoraco-scapular to the glenoid cavity.....	13	"
Length of the coracoid.....	40	"

(D) *The Pelvic Girdle.*

Length of pubis (outer exterior border, on straight line).....	18	"
Length of ischia.....	8.5	"
Length of ilium.....	18	"
Length of pelvis on median line.....	43.5	"
Width across pubis at broadest point.....	48	"

(E) *The Limbs.*

The greatest spread of the front flippers (as based on measurement from the approximate median line of the shoulder girdles to tip of longest finger).....	250	"
Greatest spread of hind flippers	190	"

(1) *The Front Flipper.*

Length from glenoid cavity to tip of finger III.....	106	"
Length of humerus.....	34	"
Length of radius.....	20	"
Length of ulna.....	17	"
Length of intermedium.....	7.5	"
Width of intermedium.....	4.5	"
Length of carpal I.....	6	"
Length laterally across carpalia 3-5, which remains as recovered naturally articulated.	10 6	"

Length of ulnare.....	10	cm.
Greatest width of ulnare.....	7	"
Length of pisiform.....	6.1	"
Length, inclusive of metacarpals, of		
First finger.....	18	"
Second finger.....	29.5	"
Third finger.....	43	"
Fourth finger.....	39	"
Fifth finger.....	30	"
(2) <i>The Hind Flipper.</i>		
Length from acetabulum (or head of femur) to tip of finger III.....	85	"
Length of femur.....	27	"
" " tibia.....	20	"
" " fibula.....	20.5	"
" " tibiale.....	7	"
Greatest length of the first to fourth tarsalia as they yet remain naturally articulated (on line across ankle).....	11	"
Length, inclusive of metatarsals, of		
First toe.....	18	"
Second toe.....	27	"
Third toe.....	30.5	"
Fourth toe.....	31	"
Fifth toe.....	20	"

EXPLANATION OF PLATE XXXI.

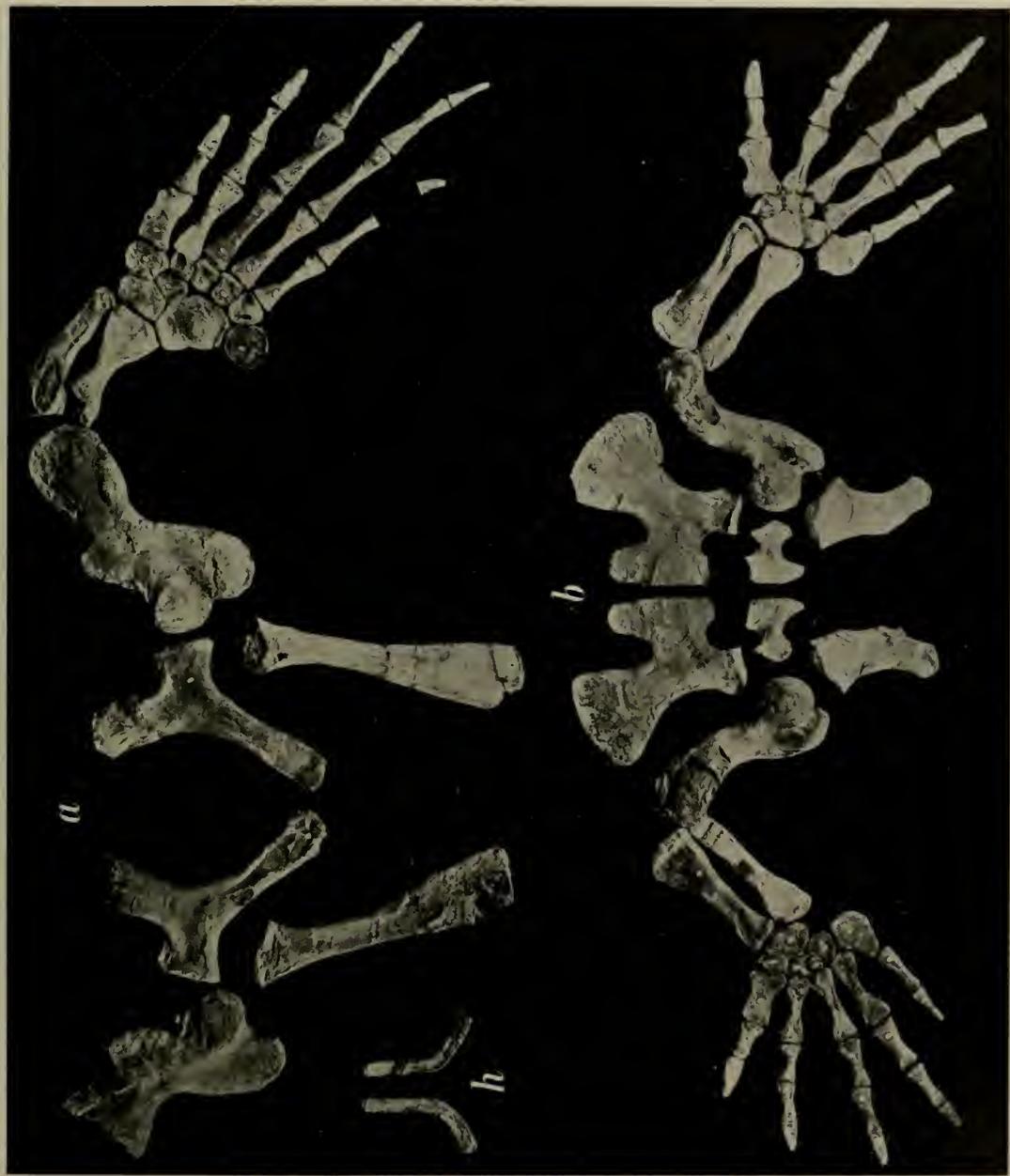
Protostega gigas. (Carnegie Museum. Cat. Vert. Fossils, No. 1420.)

(a) Right and left shoulder girdles, with right front flipper and the proximal half of the left humerus.

(b) Pelvic girdle with both hind flippers.

(h) The accompanying hyoids.

The elements are shown as photographed in superior view in approximately the position in which they were imbedded and crushed out flat in the matrix of chalk. All the elements belong to a single individual from the Niobrara Cretaceous of western Kansas.



Protostega gigas Cope.

EXPLANATION OF PLATE XXXII.

Protostega gigas. (Carnegie Museum. Cat. Vert. Fossils, No. 1420.)

Enlarged views of forearm and hand (upper photograph), and the foot (lower photograph).

Observe in the *upper photograph* that the intermedium, carpal 1, and metacarpal 1, as well as carpal 2-4 are still articulated as in the matrix; and in the *lower photograph* that the tibiae with tarsals 1-5 and metatarsal 1 are likewise articulated as found in their normal position in the matrix.



EXPLANATION OF PLATE XXXIII.

Dermochelys coriacea.

(a) Shoulder girdle with front flipper articulated, and the procoracoscapular thus shown foreshortened.

(b) Hind flipper. Superior view.

I., V., the first and fifth fingers and toes respectively.



