ART. XLII. — *Some Observations on Certain Well-Marked Stages in the Evolution of the Testudinate Humerus;* by G. R. WIELAND.

THE study of the morphology and development of an important skeletal part throughout an order must, as knowledge increases, throw much light on the evolution of the order itself. How far in the definite case here presented, the Testudinate humerus reflects the evolution of the *Testudinata* is a difficult question to answer even in general terms and as yet impossible to deal with finally. Nevertheless its present consideration, as based upon the fundamental principles of evolution, makes possible a clearer discernment of some valuable data.

Obviously if we select a specialized organ in a specialized group we may expect that the factors which have been potent in moulding it will have been on the one hand restricted in their action and on the other more strongly thrown into relief. Such an example is the Testudinate humerus, presenting also many advantages of study. For there is in the turtles to a degree scarcely approached in any other order a graduated change in habitat from dry deserts to the ocean, with varied feeding habits, as well as a wide distribution of both living and extinct forms in latitude and time.

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The two great groups of existing Testudinates, the land and the marine, the clawed and the flippered forms, each possess a characteristic humerus which can never be mistaken the one for the other. But if various intervening fossil types chiefly of Mesozoic age be considered, it at once becomes evident that there has been a steady and well-illustrated transition from whatever was the original form toward the humerus seen in the most highly specialized land turtles in the one direction, and toward that of the most highly specialized or *older* sea turtles in the other. That is, a series may be discerned with well-marked stages easily graduating into each other, at the one end of which stands the humeral form seen in various genera of the *Testudinidæ*, and at the other that of *Dermochelys*, which is either a very ancient, or else the most highly specialized marine turtle known.

Of these stages the attempt is here made to point out and describe six. In doing so it should perhaps be stated at the outset that while variations in humeral outline can scarcely be conceived of except as being chiefly adaptive in character, being so intimately connected with habitat, it will be seen that

quite constantly when dealing with well marked intervals in form there are accompanying generic or family variations. This is indeed so persistently the fact that *presence* of humeral differences must generally be regarded as of distinct diagnostic value, though absence of such may be simply non-determinative.

In the descriptions and notes which follow I shall term the most specialized land humerus as *parachelic*, and the generalized land and freshwater type as *chelic*. It will be seen that there is in general a corresponding humeral distinction between the more specialized and the more generalized land turtles.

Certain Mesozoic turtles regarded as transitional brackish or salt-water forms have intermediate humeri which may be described as *chelicoid* and *thalassoid*, the former resembling more nearly land, the latter oceanic outlines. Finally, the strictly oceanic and the ultra or specialized oceanic humeri will be respectively spoken of as *thalassic* and *parathalassic*.* Here also there is a certain corresponding general development.

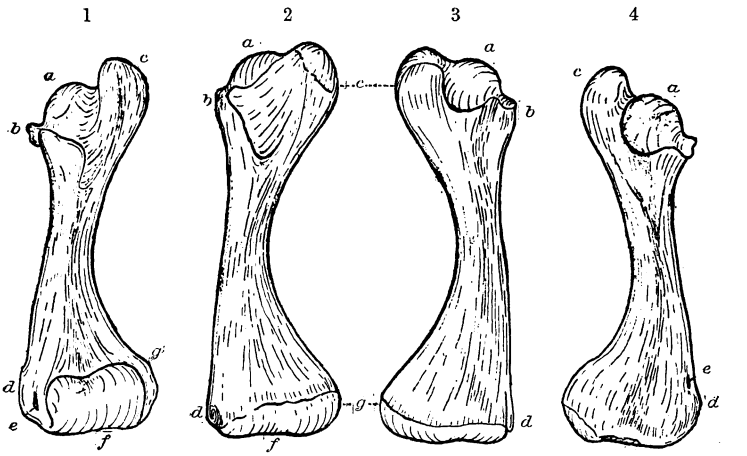
The land forms (Parachelic and Chelic).

The *parachelic* humerus is in general that of short-clawed dry land tortoises, most of the genera of which are rather recent in geological time, and have probably been derived from longer clawed ancestors of more aquatic habit. This humerus is seen in such genera as *Testudo* and *Cinyxis*. Its strongly sigmoidal outline in the dorso-ventral plane with the proximal end upturned and the distal depressed, the reverse of the condition seen in the humerus of running mammals, at once strikes the eye. But with reference to other reptilia a most important feature is the closely proximal position of the radial crest or analogue of the deltoid crest. The ectepicondylar foramen or groove is distinctly ectal, diminutive, and situated well back from the distal end. There is never a very prominent ulnar crest or broad and rounded distal extremity as in *Chelydra*. Instead the distal articular surface forms a roller as in the *Lacertilia*, this being the most important distinguishing feature. (See fig. 12, introduced to show this point as well as the general correspondence of parts in the *Lacertilia* and the *Testudinata*, the same notation having been used for this purpose.)

It may be noted that there is correlated with this form of turtle humerus a tendency to form broad short heavy claws,

* As will be noted, the first three of these adjectives has been derived from the Greek χηλή, *chele*, hoof, claw,—that is humeri bearing clawed feet. It has been thought preferable to derive the second three from *Thalassa*, the sea,—a habitat in which claws are lost, rather than from πτέρυξ, *pteryx*, wing, used once by Nicander for the flipper of a turtle. Some might hold it better to derive the entire series from habitat.

the first step towards an ungulate type of foot. As seen in the accompanying figs. 1–4, the present is a plastic type of humerus which may be well marked in the case of forms only specifically distinct. The humerus of the senile genus *Miolania* Owen (15, 22) would probably fall within the *parachelic* series. *Testudo polyphemus*—with a complex as opposed to a simple carpus, and an innominate pelvis—affords a good example of the distal grooving and other modifications here emphasized.



Parachelic humeri of Galapagos Islands tortoises. Outlined from Günther (9).*

FIGURES 1 and 4.—*Testudo elephantopus* Harlan,—ventral and dorsal view.

FIGURES 2 and 3.—*Testudo ephippium* Günther,†—ventral and dorsal view.

{ *a*, head; *b*, radial crest; *c*, ulnar crest; *d*, ectepicondyle; *e*, ectepicondylar foramen (or groove); *f*, ectocondyle; *g*, entocondyle.

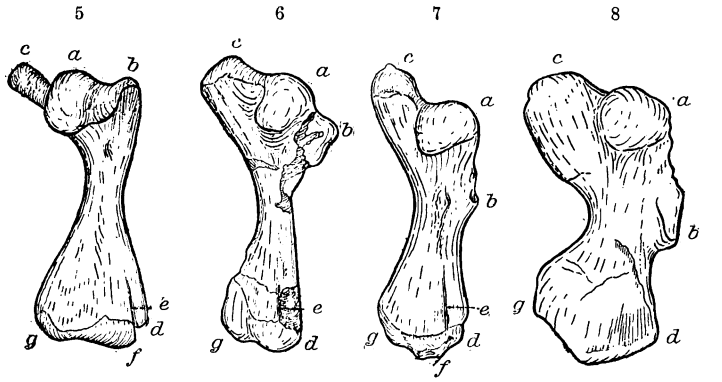
The Chelic humerus.—The fundamental difference between the second or *chelic* type of humerus and the preceding consists in the straightening of the distal extremity into a simple rounded end bearing the articular cartilage, without development into a grooved articular surface. The ulnar crest may be more prominent, and the ectepicondylar foramen oftener seen as a groove more distal in position, but always near the outer edge.

Most distinctly clawed *Testudinates* have this form of humerus, and as these range from land and freshwater to web-toed and partly brackish water species, distinct variations, such as increase or decrease in the angle between and size of the ulnar and radial crests, may be expected, and are present.

* Nos. in parentheses refer to list of references page 423.

† Dr. Baur has proposed to call this tortoise *Testudo Abingdonii* (3), but Rothschild (16) and Günther (11) have shown that *T. ephippium* is to be retained.

Though the uniformity with which this humerus ranges through many genera of the *Cryptodira*, *Pleurodira*, and *Trionychia*, render it as yet of little value to the paleontologist, excepting the *Chelydran* variation here included, although somewhat aberrant and suggestive of natatorial types. Examples of *chelic* humeri are seen in the genera *Emys*, *Chelopus*, *Trionyx*, *Podocnemis*, *Chelydra*, *Chelys*, and others.



Dorsal views of right humeri showing descent of radial process as noted by Dollo (8). Lettering as in figure 1.

FIGURE 5.—*Chelydra serpentina.*
FIGURE 6.—*Lytoloma crassicostatum* Owen (Lower Landenien (Lower Eocene) of Erquellines).
FIGURE 7.—*Chelone mydas* L.
FIGURE 8.—*Protostega gigas* Cope, × about $\frac{1}{7}$. (Niobrara Cretaceous.)
FIGURES 5–7 are outlined from Dollo (8), figure 8 from Cope (6).—Figure 5 is regarded as *Chelic*, 6 *Thalassoid*, and 7 and 8 as *Thalassic.*

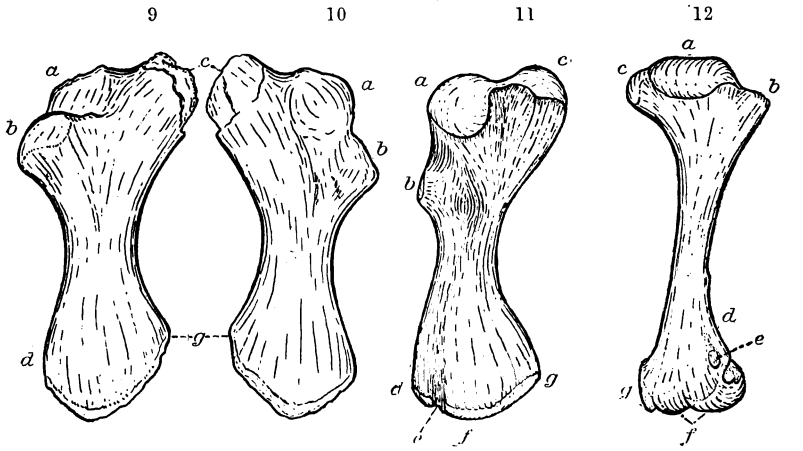
The transitional Water-types of the Mesozoic.

The Chelicoid Form.—General osteological characters in addition to position in time have led to the belief that the straighter shafts noticed in certain Jurassic turtles such as *Acichelys*, are those of primitive oceanic Chelonia. As these humeri yet bear a distinct resemblance to the land forms they may be described as *chelicoid.* They are characterized by an imperfectly developed head, a straightening of the shaft and small ulnar and radial processes, the latter being placed on the level of the head. Examples are seen in the *Acichelyidæ* (14) of the Wealden and Kimmeridge; also in the more chelic humerus of *Acichelys* (Eurysternum) *Wagleri* (22), which has the lateral proximal crests small, but the articular head relatively large with some straightening of the shaft.

It is to be noted that these intermediate forms are the most difficult to place, and that between them and the following

quite distinct early marine, or *thalassoid* humerus there is no very well defined boundary. However, if all the forms were known there would be no hiatus at any point, especially since it would then be possible to determine offshoots from the main line of descent.

The Thalassoid Humerus.—The second transitional form includes humeri of turtles which had probably become wholly marine in habit, but retained certain features of their semi-marine ancestors with *chelicoid* humeri. The conversion into the generalized marine form is however completed by the variations seen in this humerus. The drop of the radial crest so strongly marked in succeeding marine turtles begins, while the angle between this crest and the ulnar crest tends to disappear, the latter becoming very prominent in an ecto-enteral plane. Cf. figs. 6, 9, and 10, also 5–8 in text.



Thalassoid and thalassic turtle humeri (with lizard humerus compared with figures 1–4). Lettering as in figure 1.

FIGURES 9 and 10.—*Neptunochelys* (Protostega) *tuberosa*, × $\frac{1}{6}$. From Cretaceous near Columbus, Mississippi, outlined from Leidy (12). See note p. 418.

FIGURE 11.—*Thalassochelys caretta*. Left outer view.

FIGURE 12.—*Heloderma suspectum* Cope. Right dorsal view.

The humerus of *Lytoloma*, which has been made the subject of a suggestive paper by Dollo (8), may be cited. He holds this form to be essentially "*chelydroid*," a view which is in the main concurred in here. For convenience in the present classification, the term *thalassoid* may as well be used, the resemblance to the humerus of the *Cheloniidæ* being fully as strong. It should be borne in mind that the *chelicoid* humeri of the *Acichelyidæ* intervene, so far as may now be judged,

between such forms as *Lytoloma* and *Toxochelys* on the marine side, and the humerus of *Chelydra*, a *chelic* or land form modified as has been previously noted, in the direction of natatorial types. It is of course possible that the flippered *Cryptodira* represent several lines of descent from land forms, each having distinct, but in the main, parallel characters.

Another very distinct *thalassoid* form which may well be mentioned here is the "turtle-like humerus" from the Cretaceous near Columbus, Mississippi, figured by Leidy and at first referred by him to the *Mosasauria* (12).* As will be seen on comparing figs. 6, 9, and 10, this fossil presents decided approximations to *Lytoloma*, there being however distally more suggestion of distinctly oceanic types.

The humerus of *Toxochelys latiremis* figured by Case (4) is a suggestive *thalassoid* form characteristic of the older *Cheloniidæ* and closely nearing typical oceanic outlines.

With regard to these two transitional forms, the *chelicoid* and *thalassoid*, it may be said that they fairly bridge over the fundamental differences between the humeri of the existing marine and land *Testudinata*. The number of complete skeletons is as yet so meager that the facts can only be presented in a general way.

Turtle humeri of intermediate type are common in the Cretaceous of New Jersey, but there is a dearth of knowledge concerning the forms to which they belong, the collections consisting as yet mainly in hopeless fragments gathered from the surface by untrained collectors, whose efforts usually result in the destruction of the clues to completer specimens.

The Typical Oceanic, or Thalassic and Parathalassic Humeri.

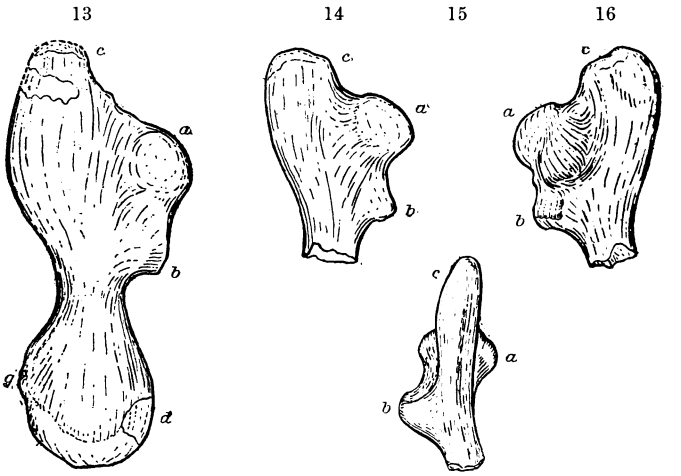
The *thalassic*, or form of humerus seen in the living *Cheloniidæ*, is a widely distributed one and may be considered as the true or generalized ocean type. Variations of this form are seen in the *Protostegidæ* of Cope (6), and the *Desmatochelyidæ* of Williston (19, 20). Cf. figs. 13, 17, 19, and 22 in the present text.

* Leidy has explained in an interesting manner how at a time when the limbs of the *Mosasaurs* were yet unknown, both Cope and himself, as well as Agassiz, had mistakenly concurred in a belief in the Mosasauran character of this fossil (13). Cope was, however, the first to refer to its Testudinate nature under the name *Protostega tuberosa* (6). While the type specimen has not been seen by the writer, there is no suggestion that this humerus is not Testudinate and natatorial in character. Baur has said that it cannot belong to the *Cheloniidæ* (2). Neither can it belong to Cope's *Protostegidæ*, nor to Agassiz's genus *Atlantochelys* as finally proposed by Leidy (13). Cf. figs. 14–16 and 9 and 10 in text. This humerus lacks at the present time a generic name. Necessarily retaining Cope's species, I shall call the turtle to which it belongs *Neptunochelys tuberosa*.

As compared with the preceding or *thalassoid* form the chief variation is seen in the distal retreat of the radial process. No distinct approximations to any of the land forms remain. The entire development is in an ecto-enteral plane. The strong dorso-ventral sigmoid curve, and sharp angle between the radial and ulnar crests as seen in the *parachelic* and *chelic* forms has disappeared.

This type scarcely shows as much constancy of form as the generalized land humerus, but is yet sufficiently uniform to raise any fairly well marked differences to generic value.

Variations of this humerus may very well be illustrated by mentioning certain fossil forms. Of primary interest is the



Fossil *Thalassic* humeri of nearly related genera derived more directly from the *thalassoid* form. Cf. figs. 6, 9 and 10.

FIGURE 13.—*Desmatochelys Lowii* Williston. $\frac{2}{9}$ natural size. From Fort Benton Cretaceous. Outlined from Williston (20).

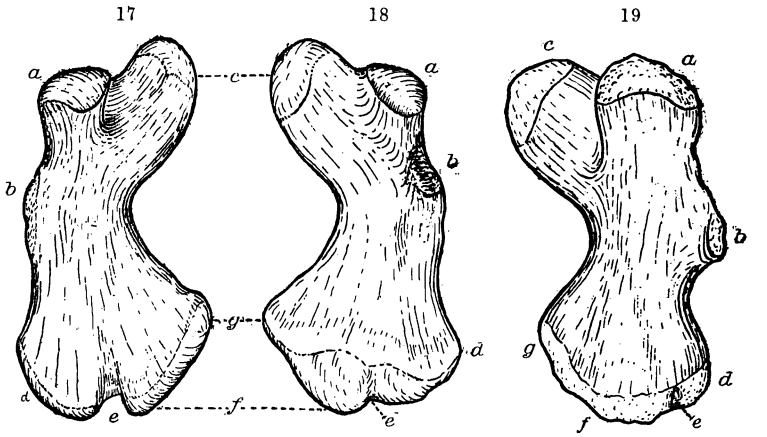
FIGURES 14–16.—*Atlantochelys Mortonii* Agassiz, × about $\frac{1}{5}$. From the Green sand of Burlington County, New Jersey. Outlined from Leidy (12).

historic *Atlantochelys Mortonii* Agassiz described in 1849 (1). Subsequently Leidy referred this fossil humerus, together with that of *Neptunochelys* (Protostega) *tuberosa* mentioned above, to the *Mosasauria* (12). Later Cope referred it to *Protostega* (6). Finally it was validly rehabilitated by Leidy (13). The strongest resemblance of this important form, not before pointed out I believe, is to *Desmatochelys Lowii* Williston (20, 21), the main skeletal characters of which are fortunately known. The resemblance is sufficiently close to suggest allied

genera. Cf. figs. 13 and 14–16. A complete skeleton of *Atlantochelys* should be diligently sought for.

The significance of such variations as may be present in *thalassic* humeri is shown by the well known *Protostega gigas* Cope from the Niobrara Cretaceous of Kansas, and the more recently discovered *Archelon ischyros* (mihi, 17–19) from the overlying Fort Pierre formation of South Dakota. Both these humeri are illustrated in figs. 8 and 17–19 in text.

While the head and ulnar crest are quite similar in both forms, in *A. ischyros* there is a minor development of the radial crest, with a more ental position of the deep ectepicondylar groove. Or conversely it may be said that there is a major development of the ectepicondylar region, obscuring the



A prominent example of generic variation in thalassic humeri approaching the parathalassic type. Cf. figures 20 and 21. Lettering as in figure 1.

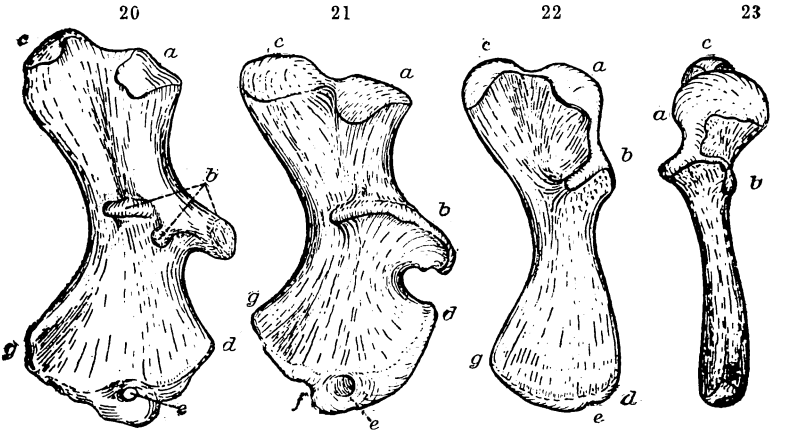
FIGURES 17 and 18.—*Archelon ischyros* Wieland, from the Fort Pierre Cretaceous. Left outer and inner view respectively, × about $\frac{1}{12}$.

FIGURE 19.—*Protostega gigas* Cope from the Niobrara Cretaceous. Left inner view × about $\frac{1}{7}$. Outlined from Case (5).

ala-like projection of the radial process as seen in *Protostega*, and leaving the ectepicondylar groove in a more mesial position. Such a difference is fundamental in the thalassan forms, and the probability that it will be accompanied by marked cranial and other variations is very great. This instance is all the more important because of the direct descent of *A. ischyra* from *P. gigas* (19).

The Parathalassic Humerus.—The final humeral type to be mentioned is the *parathalassic* seen only in a single living example, the most aberrant of sea turtles, *Dermochelys*. In this humerus dorso-ventral curvature of the shaft has wholly

disappeared, and there is an extreme retreat of the radial process. The ectepicondylar groove of the *thalassic* humerus is here deepened into a foramen, it being wholly probable that this change has been correlated with the retreat of the radial crest in this and preceding forms. It will be noticed that the humeri of *Protostega* and *Archelon* are not placed in the same class with this form. There are only vague resemblances with great differences. The peculiarities of the *parathalassic* form may be accentuated by mentioning a most interesting Pliocene example seen in *Psephophorus scaldi*, a turtle which like *Dermochelys* is provided with an external dorsal and ventral bony armor (14). In figs. 20 and 21 it will be noted that anteriorly the radial process of *Psephophorus* is very prominent, while



Views of left humeri showing intermediate or *thalassic* position of the radial crest and ectepicondylar foramen (groove) in figures 22 and 23, and the extreme or *parathalassic* position in figures 20 and 21. Letters as in figure 1.

FIGURE 20.—*Psephophorus scaldi.* From Pliocene of Belgium. Left ventral view × about $\frac{1}{7}$. Outlined from Dollo.

FIGURE 21.—*Dermochelys coriacea.* Recent. Left ventral view × $\frac{1}{6}$.

FIGURES 22 and 23.—*Thalassochelys caretta.* Left ventral and ectal views.

its ventral extension is either disappearing or lacks the strong development seen in *Dermochelys*, only two isolated areas for ligamental attachment being present. Chelonian paleontology awaits complete knowledge of no more interesting forms than the several less known species of *Psephophorus.*

Conclusion.

Whenever it becomes possible to compare an entire series of *Testudinate* humeri and tabulate the results, definite affirmation or negation of causes of development and means of adaptation may be expected. At present only general conclusions can be reached, and these be but briefly stated.

As a modification of mechanical change the instance of responsive variation afforded by the peculiar curvature of the humerus to conform to the presence of the carapace and plastron is impressive. The external armature once developed, the humerus seems to have continuously accommodated itself to it during all the secondary changes subsequently undergone.

Much interest too centers in the transitional forms. That the gap between the *chelic* and *thalassic* humeri must necessarily have been bridged over by primitive straighter shafts cannot be directly affirmed, however strong such an inference at present. For other swimming reptiles with straight humeri scarcely furnish an explanatory analogy. Such have lithe instead of rigid bodies and are provided either with a caudal fin or a powerful swimming tail. There are, however, salient facts bearing on this point.

Those turtles which inhabit dry and especially rocky localities present the most specialized land humerus, while species of intermediate habits like *Chelopus* are marked by the generalized type of land humerus. In passing however from such to the more and more aquatic turtles there is an increasing freedom of leg movement. Footings, or the *fulcra of locomotion*, as used by the animal become more and more equally distributed about the body and undoubtedly furnish a sufficient explanation for humeral straightening in the transitional forms, and the fundamental difference in curvature between the humeri of the existing slow-moving land and swift-moving marine turtles.

Once having entered salt water, a new course of evolution began. The early transitional Testudinates so far as the fossil record indicates were mainly of inconspicuous size. They were yet to undergo development into large and powerful more or less predatory forms invading the high seas. That such an evolution required a constantly increasing differentiation in humeral outline and musculature, is evident. Small creatures of varied feeding habits living in quiet waters, taken together with the fierce turtles of the Cretaceous seas and the huge predaceous *Dermochelys* sweeping the ocean and baffling with its currents and storms, suggest the utmost variation in humeral impacts, stresses, and strains.

The only basis for variant or perfecting leg power is a variant or perfecting musculature, and the only support of this correlated skeletal modification. The nature as well as the extent of such modification in the *Testudinata* will be still better understood after a comparative study of the humeral myology of the order. It is quite obvious at least that the humerus furnishes as readily distinguishable and as important characters as the carpus.

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