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Article IX.—ON THE GROUP OF FOSSIL TURTLES KNOWN AS THE AMPHICHELYDIA; WITH REMARKS ON THE ORIGIN AND RELATIONSHIPS OF THE SUBORDERS, SUPERFAMILIES, AND FAMILIES OF TESTUDINES.

By OLIVER P. HAY.[1]

The group of turtles called the Amphichelydia was established by Mr. R. Lydekker in the year 1889 and made to include, as the author states, a number of generalized later Mesozoic forms which may be regarded as allied to the earlier and at present unknown progenitors of the Pleurodira and Cryptodira. The characters of the group were derived almost wholly from the shell, and this is said to be constructed on the plan of that of the Cryptodira and Pleurodira, in which mesoplastral bones and an intergular shield are developed and the pubis may be articulated without sutural union with the xiphiplastral. The coracoid and humerus, when known, are stated to be of the pleurodiran type. The genera included in this group by Mr. Lydekker are *Pleurosternon*, *Platychelys*, *Helochelys*, *Baëna*, *Archæochelys*, and the very imperfectly known genera *Protochelys* and *Chelytherium*. *Pleurosternon* is to be regarded as the type of the group. The presence of a mesoplastron was regarded as an essential character of the superfamily. Mr. Lydekker's remarks and conclusions on this subject are to be found in the Quarterly Journal of the Geological Society of London, Volume XLV, 1889, pp. 511–518, and in his Catalogue of Fossil Reptilia and Amphibia, pt. iii, p. 204.

In 1890 (Amer. Naturalist, XXIV, pp. 530–536) and again in 1891 (Proc. Acad. Nat. Sci. Phila., 1891, pp. 411–430) Dr. George Baur published the results of his studies on the skeleton of *Compsemys plicatula*, specimens of which had been obtained by Prof. Marsh in the Upper Jurassic of Como, Wyoming. Dr. Baur was enabled to describe almost all parts of the osteology of this ancient turtle. He accepts Lydekker's group Amphichelydia, gives it the rank of a suborder, and assigns to it the following characters:

"Nasals free, a squamoso-parietal arch; descending processes of the prefrontals joining vomer; stapes in an open groove of the quadrate; pterygoids narrow in the middle, without wing-like lateral expansions, separating quadrate and basisphenoid; epipterygoid well developed and free; dentary bones distinct. Cervical vertebræ with well-developed transverse processes, more

[1] For the opportunity of preparing and publishing the following paper the writer is indebted to the Carnegie Institution of Washington.

in front of vertebra, with single articular faces, biconcave; dorsal vertebræ; sacral vertebræ with well-developed ribs; ribs of sacral vertebræ connected with centrum and neuroid. Pelvis not anchylosed to the carapace and plastron. Epiplastra in contact with hyoplastra, entoplastron oval or rhomboidal; a complete series of peripheralia connected with the ribs."

The skull is said to show characters such as we would expect to find in the ancestors of Cryptodira and Pleurodira; yet in specifying the pleurodiran characters this author mentions only the free nasals, the suturally united dentaries, and the "absence of a production of the petrosal."

In his paper of 1891 Dr. Baur discussed the genus *Baëna*, without however having any new materials. He concluded that it is closely related to *Compsemys plicatula*, being probably its direct successor and belonging to the Amphichelydia. Cope had recognized the pleurodiran affinities of *Baëna*, but had arranged it with the Cryptodira.

During the summer of 1903 the writer spent some weeks in the Bridger beds of Wyoming and gave his attention especially to the collecting of turtle remains. It was found that the genus *Baëna* is represented in these deposits by several species and great numbers of individuals. Among the many specimens obtained almost every portion of the osteology is represented. There are three or four quite complete skulls and others which are injured. The result of the investigation of these has been to confirm many of Baur's conclusions, to modify others, and to establish more firmly the validity of Mr. Lydekker's group. Besides the Bridger materials, the writer has had the opportunity of studying a very complete skull of the same genus from the Laramie deposits of Wyoming. This skull belongs to the Marsh collection in Yale University Museum, and has been described by the writer as *Baëna cephalica* (Hay, 1905, p. 263, pl. xii).

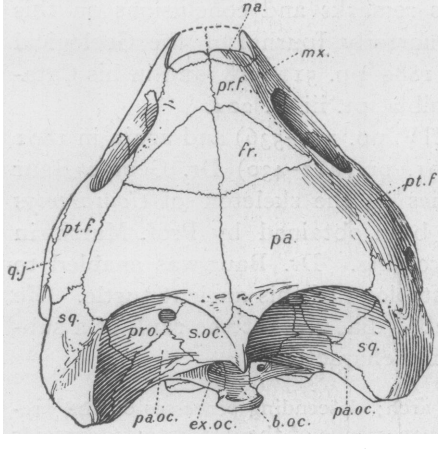

Fig. 1. Skull of *Baëna undata* seen from above. × ⅔.

The skull of *Baëna* is broad and short. The temporal region is extensively roofed over and there are, in the Bridger species, parieto-squamosal arches. In the Laramie

species, called *Baëna cephalica*, the hinder border of the roof has been excavated to the postorbital bone, thus abrogating the union of the parietal and squamosal. Short, broad, nasals are present, and the prefrontals meet the postfrontals, so as to exclude the frontals from the rim of the orbits. There are present distinct lachrymals, elements hitherto, the writer believes, not recognized among the turtles. These occupy the position of those processes of the prefrontals which in other turtles descend to meet the vomer. The choanæ are far forward. The basisphenoid is large, extending forward nearly to the vomer. The pterygoids separate the quadrate from the basisphenoid. The basioccipital enters into the boundary of the foramen magnum. No portion of the exoccipitals enters into the occipital condyle. At the sides of the basisphenoid are foramina for the internal carotid arteries.

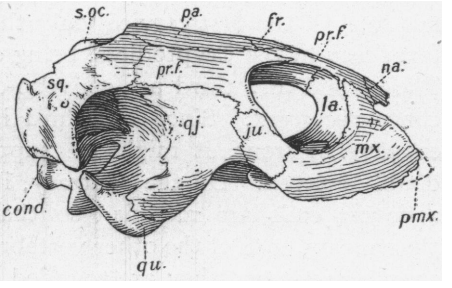

Fig. 2. Skull of *Baëna undata* seen from the side. × ⅔.

An examination of the skulls of *Compsemys* and *Baëna* shows, it seems to the writer, that where the characters are not primitive they are wholly, or almost wholly, cryptodiran. Baur accounted the presence of nasals among the pleurodiran characters; but nasals are absent among the Pelomedusidæ, while they are present in *Desmatochelys* and *Porthochelys*. Cryptodira of the Kansas Cretaceous. The lachrymals must be looked upon as a primitive character. The most distinctive skull character of modern Pleurodira is absent, the expansion of the pterygoids in front and their shortening behind, so as to permit the union of the quadrates and the basisphenoid.

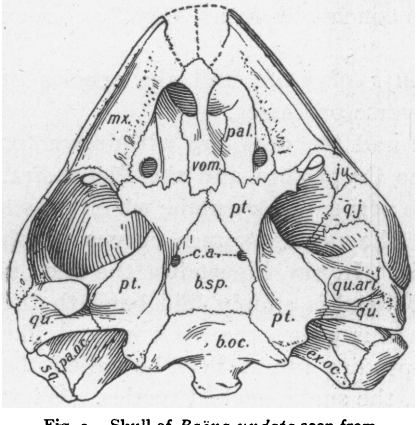

Fig. 3. Skull of *Baëna undata* seen from below. × ⅔.

Baur found that the cervical vertebræ of *Compsemys plicatula* are biconcave, and this observation is confirmed by a quite complete

specimen in the American Museum of Natural History. Baur therefore gives as one of the characters of the Amphichelydia the presence of bicœlous cervicals. The cervicals of *Baëna undata*, however, are not so. Of the first cervical only the odontoid is present; it has the form seen in the Cryptodires, being convex in front, concave behind. The second and third are convexo-concave; the fifth to the eighth concavo-convex. Since the third is concave behind and the fifth concave in front, it might be supposed that the fourth would be doubly convex. On the contrary, it is bicœlous. Nevertheless, the articular ends are modified so that they are quite different from the concave ends of the other vertebræ. Instead of the borders of the cups being sharp, they are rounded off. It seems to the writer that we have here an illustration of the way in which concave articular surfaces have been transformed into convex. The borders surrounding the concavities have grown broader and more convex until the concavities have been abolished. When we come to study more carefully the articular ends of the centra of *Compsemys* we find that they resemble closely those of the fourth cervical of *Baëna*. Hence, even in the Jurassic a beginning had been made toward the development of convex vertebral centra. In a specimen of *Baëna arenosa*, of the Bridger beds, the anterior end of the second cervical is flat, the posterior end concave. The third has the front end slightly convex, with a central depression, the hinder end concave. The fourth is concave in front, flat behind. The fifth, sixth, and seventh are concave in front, flat behind. The eighth is concave in front, slightly convex behind.

The cervicals of both *Compsemys plicatula* and the species of *Baëna* possess well-developed transverse processes.

The manner in which the head and the neck are withdrawn for protection is widely different in the Cryptodira and the Pleurodira. In the former the neck is bent in the perpendicular plane which passes through the axis of the animal. The neck assumes curves which resemble those of the neck of birds. In the Pleurodira the neck is bent in a horizontal plane and the head is simply laid beneath the carapace against the shoulder. In this group the neck is bent like that of a snake. Hence, the Cryptodira might fitly be called the bird-necked turtles; the Pleurodira, the snake-necked turtles. What are the mechanical arrangements which facilitate these different modes of flexure? They may be easily comprehended by comparing the cervicals of *Hydromedusa* with those of a Trionychid. In the former the right and left zygapophysial articular surfaces are near

each other and placed rather high above the centrum. The postzygapophysial surfaces coalesce. The result of these arrangements is to facilitate movements in a horizontal plane and to restrict those in a perpendicular plane. In the Trionychid the right and left zygapophyses are wide apart and placed low down. Thus movements in a horizontal plane are restricted. There is, also, a deep notch between the postzygapophyses, allowing them to ride astride of the next vertebra behind when the neck is strongly flexed. In the various turtles we find gradations in these arrangements here described, but the flexibility of the neck in the one plane or the other depends on them.

What is the condition of the cervicals of *Baëna* and of *Compsemys?* Not that of the Cryptodira, nor yet wholly that of the Pleurodira. The zygapophysial articular surfaces are high above the centra and not far removed from the axial plane, and there is no notch of great depth between the postzygapophyses. On these accounts, motion in a perpendicular plane must have been considerably restricted. On the other hand, the postzygapophyses did not coalesce, and hence motion in a horizontal plane was not so free as in the Pleurodira. It would therefore appear that motion was nearly equally free in all planes, and that possibly the neck and head were partly retracted and partly turned to one side beneath the edge of the shell.

Although all chelonians have in their necks the same number of vertebræ, namely, eight, the length of the neck varies greatly. Taking the length of the dorsal vertebræ as the unit, the length of the neck in five species is as follows:

Hydromedusa tectifera	1.31.
Chelydra serpentina	1.10.
Amyda spinifera	1.08.
Chrysemys elegans	.80.
Thalassochelys caretta	.54.

When the head of the Trionychid is retracted the basal half of the neck is carried far backward beneath the dorsal vertebræ, while the anterior half is carried forward beneath the basal half. When the head of *Hydromedusa* is to be protected, the neck is bent first toward one side, then toward the opposite side. The very short neck of *Thalassochelys* is flexed in a perpendicular plane, but it is so short that the head is not concealed.

Short as is the neck of *Thalassochelys*, that of *Baëna* was still

shorter, forming only .513 of the length of the dorsal part of the vertebral column. It seems, therefore, that this dweller in fresh-water streams was able to protect its head less effectively than our marine turtles. The specimen of *Compsemys* in the American Museum of Natural History presents the hinder half of the neck. An estimate shows that the neck was equal in length to .62 of the dorsal vertebræ. Are we not justified in concluding from *Baëna* and *Compsemys* that the primitive turtles had very short necks?

When we come to compare the cervical vertebræ of *Thalassochelys* with those of *Baëna* we find many resemblances. Those of the modern sea-swimmer are, of course, far more specialized, and this in the direction of the Cryptodira; but it appears certain that they have retained many primitive features, one of which is their shortness.

The first dorsal vertebra has a concave anterior articular surface in both *Compsemys* and *Baëna*. It is to be noted that the ribs of this vertebra have the usual position against the anterior edge of the second ribs; but it is, in *Compsemys*, remarkable for its great length, extending away from the midline at least 65 mm. In *Baëna*, too, the first rib is longer than in modern turtles, except probably that of *Chelydra*.

As stated by Baur, the arrangement of the tenth ribs and the sacral vertebræ is exactly that of the Emydidæ and the Testudinidæ, and therefore cryptodiran and not pleurodiran. These statements apply equally well to *Baëna*. The sacral vertebræ resemble closely those of *Chelydra*. There has apparently been quite free motion between the last dorsal and the first sacral vertebræ. Baur has stated that the posterior articular surface of the last sacral of *Baëna* is concave, and from this has concluded that the caudal vertebræ were opisthocœlous. In the type of *Baëna arenosa* this surface is only slightly concave. In a specimen of another species of *Baëna* from the Bridger this surface is somewhat irregular. The upper half is very slightly concave; the lower half decidedly convex. Notwithstanding this condition, the anterior surface of the first caudal is a shallow concavity, while the posterior surface is deeply concave. The other vertebræ of the tail of this species, and of *B. arenosa*, are convexo-concave, as in *Chelydra*. Chevrons are present in probably all but three or four anterior ones. The transverse processes of the most anterior caudals are long and slender; but they are rapidly reduced; and at about the eighth caudal they disappear.

Baur has described the pelvis of *Compsemys plicatula* and *Baëna arenosa*. The present writer has not seen the *Compsemys* materials

studied by Baur, but has examined the pelvis of the specimen in the American Museum of Natural History. Baur states that the true pubis is a slender element meeting that of the other side in the middle line, and that the ischia do not meet in the midline. The American Museum specimen shows that the pubes are fully as broad anteroposteriorly as in *Chrysemys*. There is a deep notch between them in front for the reception of the epipubic cartilage. It is not certain from the specimen referred to that the ischia joined the pubes between the pubo-ischiadic foramina, but apparently they did. A large species of *Baëna* from the Bridger has furnished a complete pelvis, in which all the bones are thoroughly coössified. The epipubic cartilage also is ossified as a long pointed process in front of the pubes. The pubes and ischia are united along the midline. As stated by Baur, the pelves of *Compsemys* and *Baëna* resemble each other very closely. They differ from the pelves of the Cryptodira and resemble those of the Pleurodira in the presence of backwardly directed ischiadic processes which rest on the xiphiplastra. As is well known, there is no sutural union of the pelvic bones with either the carapace or the plastron in either of the two genera. Scars on the xiphiplastra may mark the points of attachment of the pelvic bones, but there were no sutural articulations.

Mr. Lydekker states that the coracoid of *Pleurosternon* is of the pleurodiran type and much expanded distally. Baur too tells us that the coracoid of *Compsemys* is much expanded distally, as in *Chelys* and some other Pleurodira and in Testudinidæ. So far as can be judged from the somewhat damaged coracoids of the American Museum specimen of *Compsemys* these statements are true. On the other hand, the coracoids of *Baëna arenosa* are not so much expanded distally as are those of *Chrysemys*. At least, it can hardly be affirmed that the coracoids of the Amphichelydia are of the pleurodiran type.

The pedunculated head of the scapula resembles that of *Hydromedusa*.

The limbs of *Compsemys* and of *Baëna* were developed as walking organs; although they were doubtless furnished with webs between the toes, to fit them for swimming. The limbs, both the anterior and the posterior, were longer in proportion to the length of the shell than those of *Chrysemys elegans*, but considerably shorter than those of *Chelydra*. In *Compsemys* the femur is nearly an eighth longer than the humerus; in *Baëna* the two are of the same length. Lydekker regards the humerus as being of the pleurodiran type. Baur, on the

other hand, states that the fore limbs resemble the elements of the Emydidæ, and especially compares the humerus with that of *Terrapene.*

In the year 1903, Dr. E. Fraas, of Stuttgart, published (Fraas, 1903) an extremely valuable and interesting paper in which he described a new species of *Thalassemys.* To this paper he added some general observations on the origin and relationships of the turtles. With many of Dr. Fraas's conclusions the present writer can heartily agree; from others he is compelled to dissent.

In more than one place in this paper Dr. Fraas speaks of the existence of Pleurodira in the Jurassic as definitely determined. More than this, he states (p. 100) that in *Proganochelys* we have a typical land-living Pleurodiran. The same opinion was expressed in his paper on *Proganochelys quenstedtii* (Fraas, 1899). As only the shell of this species is known, the present writer sees no reason why this species may not have been a member of the Amphichelydia; and the probabilities are in favor of this view. Only when the skull shall have been discovered and shown to have possessed pleurodiran characters, or at least when the pelvis shall have been proved to have been articulated suturally with the shell, may we venture to place it among the Pleurodira.

Dr. Fraas refers to a paper by Huene (Huene, 1902) in which are described the cervical vertebræ of two species of turtles from the Muschelkalk, *Chelyzoon latum* and *C. blezingeri.* Huene regarded these turtles as belonging probably to the Cryptodira, on account of the resemblance of the cervicals to those of the Chelydridæ. Dr. Fraas views the discovery as demonstrating the presence of Cryptodires in the Middle Trias. To my mind, there is in these vertebræ no especial resemblance to those of *Chelydra.* They resemble more those of *Baëna;* and there appears to be no good reason why they should not have belonged to some Amphichelydian, possibly to some species of *Proganochelys.*

In his latest paper Dr. Fraas (1903, p. 88) has presented a classified list of the European Jurassic turtles. The two genera *Craspedochelys* and *Plesiochelys* are assigned to the Pleurodira, the genera *Platychelys, Idiochelys, Hydropelta, Chelonides, Parachelys, Eurysternum, Thalassemys,* and *Tropidemys* to the Cryptodira. As to the first two genera, their arrangement with the Pleurodires appears to the present writer as extremely doubtful. At present the only reasons for not placing them definitely among the Amphichelydia are found in the absence of the mesoplastra and the apparent union of the pubis

with the xiphiplastron. It is, however, not at all improbable that there were Amphichelydia which had renounced the mesoplastral bones. With the exception of the absence of these bones, the shell resembles greatly that of *Baëna*. Only the pubis was attached to the xiphiplastron, but even in the Amphichelydia a beginning may have been made toward effecting that union which is so conspicuous in the Pleurodires. The skull of *Plesiochelys* is not certainly known. Rütimeyer has identified with doubt as belonging to this genus a skull which is now in the museum at Solothurn (Rütimeyer, 1873, pp. 98, 183, pl. xiv, figs. 1, 2). Thanks to the liberality of Dr. J. Bloch, now in charge of the collections, I have been permitted to study this skull and the other splendid chelonian materials there. I conclude that there is little about this skull to suggest pleurodiran affinities, as Dr. Rütimeyer himself states. Rütimeyer has indeed represented a suture running from near the fore end of the basisphenoid outward and backward toward the articulation of the lower jaw. If this suture were really present, it would limit the pterygoid posteriorly and permit the basisphenoid to come into contact with the quadrate, a true pleurodiran character; but the writer could not find this suture. If this skull belongs to *Plesiochelys*, as seems probable, this genus belonged to either the Cryptodira or the Amphichelydia. It could be placed among the former only in case future discoveries should demonstrate the presence of ginglymoid articulations in the hinder cervicals.

It appears much more probable that *Chelonides* (name preoccupied, for which **Anaphotidemys** is proposed) is a Pleurodire. If we can rely on Portis's figure (Portis, 1878, pl. xvii, fig. 12) the basisphenoid must have extended behind the pterygoids to the quadrate, and this condition is found only in the Pleurodires. Those who have access to this specimen ought to examine it carefully with reference to this suture.

Dr. Fraas refers *Platychelys* to the Chelydridæ. Now, this genus possesses well-developed mesoplastra, a condition which at once shuts it out of the Chelydridæ, and, according to our present knowledge, out of the Cryptodira. There can be no doubt that Mr. Lydekker was right when he placed this genus among the Amphichelydia. The characters which it possesses in common with the Chelydridæ are those which it and the latter have inherited from common ancestors, of the Mesozoic or Permian. Rütimeyer (1873, p. 183, pl. xiv, fig. 5) has represented a skull, belonging to the museum at Solothurn, which he refers with doubt to *Thalassemys*. This skull closely resembles

that of *Baëna*, and the writer believes that it probably belongs to *Platychelys*. It differs from that of *Baëna* especially in having the frontals enter largely into the rim of the orbit. The writer is convinced that nasal bones are present, having been overlooked by Rütimeyer. Likewise, the suture separating the quadratojugal from the jugal has not been represented. It ought to begin in the drawing just above and in front of the figure 27 and run upward and backward to end apparently below and in front of the figure 8. It is to be noted that this skull is completely roofed over in the temporal region. The supraoccipital spine is broken off posteriorly, but it appears to have been short, as in *Baëna*. The mandibular symphysis is about 12 mm. long.

The writer does not see why *Idiochelys* and *Hydropelta* should not be included among the Thalassemydidæ. If they form a separate family, this must receive the name Idiochelyidæ; for the name "Halmyrachelydæ" violates all modern codes of nomenclature, there being no such genus as *Halmyrachelys*.

Mr. Lydekker assigns *Idiochelys* to the Pleurodira, referring for support to the flexure of the neck, and, as did Rütimeyer, to the transverse processes of the cervicals. The flexure of the neck in these primitive turtles, as shown in the specimens, can indicate nothing with certainty. The ginglymoid articulations of the posterior cervicals, and the other structures controlling the bending of the neck would probably be only feebly developed. The transverse processes might well be yet retained in these primitive Cryptodira. According to the writer's view, the fontanelles found in the carapace and the plastron are indications of its position among the Cryptodira; for, so far as we know them, both the Amphichelydia and the Pleurodira possess well-developed shells. Our knowledge of the skull of *Idiochelys* leaves something to be desired. We know little regarding the structure of the palate and the base of the skull, and no details regarding the cervical vertebræ. The sutures of the skull, as shown in Lortet's figures (Lortet, 1892, pl. ix, fig. 1) are surprisingly distinct and awake the suspicion, perhaps unjust, that they are the sulci which limited the horny shields. Such shields are present in the Chelydridæ (Boulenger, 1889, p. 24, fig. 5) and likewise in *Baëna* (Hay, 1904, p. 264, pl. xii, fig. 1); although indistinct in the species figured in the present paper. The upper surface of an undescribed and undetermined species of Jurassic turtle in the museum at Solothurn shows distinctly the presence of horny scutes. This appears to have been the original condition of the chelonian skull, and has

been inherited by the species of the genus *Chelonia* and some other turtles.

An examination of the figures of *Idiochelys* presented by Rütimeyer and Lortet shows that the neck has been shorter even than in *Baëna*, apparently considerably less than one-half the length of the dorsal portion of the vertebral column. The same condition is displayed by the figure of *Acichelys wagleri*. These add to the evidence that the primitive turtles had very short necks: and we may conclude that *Dermochelys* and the Cheloniidæ have inherited, and not secondarily acquired, their short necks.

A study of the published figures of *Idiochelys*, *Acichelys*, *Plesiochelys*, and other Jurassic turtles, shows that in these primitive forms the nuchal bone was relatively much shorter than in modern forms. That of *Idiochelys* is contained in the length of the carapace 8.5 times; that of *Acichelys*, 13 times; that of *Plesiochelys*, 9 times. In the case of a Bridger species of *Baëna* the length of the nuchal enters the length of the carapace 9 times; in *Compsemys plicatula*, 7.5 times. In *Dermochelys* and the Cheloniidæ the nuchal is short, in *Thalassochelys* about one-eighth of the length of the carapace. As the length of the neck increased and use began to be made of the shell as a protection for the head, the nuchal and the anterior peripherals lengthened to form a projecting roof. In many Emydidæ the nuchal forms from a seventh to a fifth of the length of the upper shell, or even more. In *Hydromedusa* the nuchal forms a fourth of the length of the carapace.

The writer grants as a conclusion probably true that reached by Dr. Fraas (1903, p. 96) that the Thalassemydidæ did not give origin to the land and swamp turtles. Such forms as the Emydidæ probably sprang from Amphichelydia which had retained the completely developed shell, with the plastron suturally united with the carapace. And yet there appears to be no conclusive reason why even Emydidæ might not have had Thalassemydidæ for their ancestors. Are we to suppose that if a group of turtles has had the shell reduced as much as it is in the Cheloniidæ, with the plastron free from the carapace, to adapt the animal to a certain environment, under no conditions can a completely developed shell be recovered? According to such a doctrine, no impairment in the development of an organ under unfavorable conditions could be made good under improved conditions.

Dr. Fraas (1903, p. 96) expresses the conviction that the Thalassemydidæ represent forms of fresh-water turtles which had become adapted to marine life; and as expressing still more distinctly his

meaning he says, "Ich gebe zu und nehme auch an, dass die Thalassemyden die Küste gelegentlich aufsuchten, insbesondere zum Ablegen der Eier." Now, there are no living turtles to which such language can be applied, except *Dermochelys* and the Cheloniidæ. Were the Thalassemydidæ aquatic and marine to any such degree? The writer does not believe that they were. There is not the slightest evidence that they ever left the coast for any considerable distance. They were aquatic perhaps to about the degree that the Chelydridæ are aquatic. Rütimeyer is nearer the truth when he expresses the opinion (1873, p. 171) that the great majority of these fossil turtles did not inhabit the open sea, but the littoral or estuaries and large rivers. An examination of the figures of *Acichelys* (*Eurysternum*) and *Idiochelys* presented by Zittel (1877, pls. xxvii, xxviii) and Lortet (1892, pl. i) demonstrate that the limbs, especially the feet, of these turtles were greatly like those of our more aquatic Emyds; in fact, they were rather feebly developed. The fore and hind limbs were about equally developed, and they had about the same ratio to the length of the shell that they have in *Malacoclemmys geographica*, one of the most aquatic of the North American Emydidæ. The bones of the limbs of *Acichelys* are, however, more stoutly built than those of *Malacoclemmys*, and the fifth finger is longer and has one more phalange; so that it may have been a somewhat bolder swimmer. On the other hand, it may have been accustomed to more vigorous walking, as *Chelydra*. The foot of *Acichelys* is not so much modified for swimming as that of the Trionychidæ. It is not unlikely that the genus under discussion haunted the sea-shores and captured marine prey, much as do our North American salt-water terrapins of the genus *Malacoclemmys*. That such were the habits of these extinct forms is indicated as probable by the occurrence of two species of *Thalassemys* at Solothurn, where are found four species of *Plesiochelys*. Dr. Fraas says that the latter betray themselves by their thick, massive shells as land forms. Three species of *Tropidemys* occur at Solothurn, and these too possess thick heavy shells, and could hardly have been free swimmers in the sea.

In discussing the relationships of the Thalassemydidæ to the Cheloniidæ, Dr. Fraas says that he will not assert that the former were the direct ancestors of the latter, but he holds it as certain that the Thalassemydidæ introduced the course of evolution which led to the Cheloniidæ. He supports his view by arguments drawn from various structures, but the reduced condition of the shell is especially taken to indicate an adaptation to aquatic life, especially to marine

life. We shall then consider the question whether and to what extent reduction of the shell and the freeing of the plastron from the carapace betoken aquatic, and especially marine, habits.

In some of the species of Testudo the shell is thick, especially along the free borders, where a carnivorous animal might fix his jaws; and in some of the species the skin of the legs is furnished with a mosaic of bony plates and nodules, each of which is further strengthened by a layer of horn. When the animal withdraws within the shell these armored legs close all the openings. On the other hand, at least one species of the genus, which inhabited the Galapagos Islands, had a shell of papery thinness, and perforated with holes. There is no probability that aquatic life had anything to do with the reduction of the shell of the latter. In *Terrapene*, a genus almost exclusively terrestrial, the plastron is connected with the carapace by ligaments. On the other hand, many species of Emydidæ spend almost the whole of their lives in the water, and yet they have complete and heavy shells; indeed it is probable that in some cases the shell is thickened for the purpose of increasing the specific gravity of the animal. *Chelydra serpentina* is probably no more aquatic than many of the species of *Chrysemys*, and is accustomed to making marches over land from one body of water to another; yet the shell is as much reduced as that of the Cheloniidæ, which leave the water only to deposit their eggs. The explanation here is probably that the snapper is a vigorous, strong-limbed brute who is ready to use his jaws, and therefore needs less a defensive armor. *Dermochelys* has probably had the advantage of more geological ages in which to get rid of his armor than have the Cheloniidæ; and being a powerful swimmer, getting his sustenance from the surface, he has less need for a strong heavy shell than do the other sea-turtles who must dive to the bottom for their mollusks and sea-weeds. It is not due to the fact that the former is more aquatic than the latter. It may be doubted whether the reduction of the shell in *Protostega* and *Archelon* has reduced the specific gravity of the animal. The plastron of the former is very thick and heavy (Hay, 1895). In the case of *Archelon* (Wieland, 1903) the ribs are club-like, thick, and heavy, and the plastral bones also are thick. It seems to the writer doubtful that this was a pelagic turtle, like *Dermochelys*. That enormous hooked beak (Wieland, 1900A.), that extensive crushing surface between the beak and the choanæ, and the corresponding extensive surface of the lower jaw, together with the obsolete triturating surfaces of the hinder portions of the jaws, indicate an animal which was accustomed

to snapping up and crushing various kinds of mollusks. The beak seems to be admirably adapted to the crushing of the various species of *Nautilus* and related forms which were found associated with the turtle (Wieland, 1903). To obtain such mollusks it would be necessary for the turtle to seek the bottom; and the enormous and heavy head is well fitted for holding the animal in a position favorable for picking up his food.

The points which the writer desires to make are that reduction of the shell and the loosening of the plastron do not necessarily indicate aquatic life; that life in neither fresh nor salt water always leads to reduction of the shell; and that the amount of reduction is not in proportion to the degree of devotion to aquatic life.

The family of Cheloniidæ has within some years, at the hands of various writers, been greatly expanded. Mr. Lydekker (1889B) included in it, besides the living genera, *Argillochelys* and Cope's Propleuridæ. More recently, Dr. Dollo (1903) places in the family, besides the living genera, the following: *Eosphargis*, *Protosphargis*, *Archelon*, *Protostega*, *Allopleuron*, *Toxochelys*, *Desmatochelys*, *Argillochelys*, *Lytoloma*, and *Proëretmochelys*. Dr. G. R. Wieland (1902, 1904A) does not differ essentially from Dr. Dollo, except that in the earlier publication just cited he included *Rhinochelys;* and besides arranged *Eosphargis* with *Dermochelys*. According to these writers, therefore, the family includes a great range of forms and a great variety of structure. The most ancient of the species existed near the beginning of the Upper Cretaceous.

In order to discuss intelligently what genera are to be comprehended in the Cheloniidæ, we ought first to determine what is the essential character or characters of the family.

There can be no question, I think, that in several features the modern Cheloniidæ are very primitive. In the skull we find the stapedial passage forming an open notch, whereas in the higher groups it is wholly closed or nearly so. It is closed even in the Chelydridæ. The roofing of the temporal region is certainly a primitive character. Dr. Fraas (1903, pp. 99, 100) believes that it is a character that has been acquired by the Cheloniidæ, and that even among the Thalassemydidæ it was already developed. It would be very instructive if we could have any Jurassic turtles pointed out which possessed an open temporal region. How are we to explain the slender parieto-squamosal bar of such Pleurodira as *Chelys*, *Rhinemys*, and *Hydraspis* except as the last vestiges of such a roof, which has been eaten away from below and forward? The reduction of the

temporal roof in turtles has probably been correlated with the lengthening of the neck and the ability thereby acquired to retract the head within the shell and thus protect it.

The structure of the carapace and of the plastron have figured largely in determining the assignment of certain fossil genera to the Cheloniidæ. In the living genera there are likely to be persisting fontanelles between the peripheral bones and the costal plates; and there are always fontanelles in the plastron; while the carapace and the plastron are never suturally united. But, as already stated, the reduction of the carapace and plastron and the loosening of the plastro-carapacial articulations are likely to be found in the most widely separated families, in the Cheloniidæ, the Dermatemydidæ, Emydidæ, Dermochelyidæ, Chelydridæ, and Thalassemydidæ; and thus this reduction constitutes no determinative character.

Now, to the writer it appears evident that that character which, joined to the primitive characters mentioned, differentiates the Cheloniidæ from all other Thecophora is the conversion of the fore limbs into flippers, which consist of the elongated fingers bound together beneath the skin and which lack phalangeal condyles. In the living forms this limb has the claws reduced to one or two, the humerus is flattened, and the radial process brought down below the head of the humerus. Unless the family is restricted to forms having such limbs, the bars will be let down for the inclusion of the most heterogeneous materials. Almost any timid testudinate may stick to the coast and never go to sea and still be regarded as a member of the chelonian navy.

The relegation of *Eosphargis* by Dr. Dollo to the Cheloniidæ appears to be wholly unjustifiable; since we have of that genus not only a portion of the shell but the humerus and the skull. These are, as Lydekker has stated, wholly like those of *Dermochelys*, including in the skull the lack of descending parietal plates. Dr. Dollo's reason for removing the genus from the Dermochelyidæ is the absence of mosaic plates: but these appear to be represented, in part at least, by a row of larger median bones. There have probably been different styles of armor among the Athecæ, as elsewhere.

As stated, Dr. Wieland has included *Rhinochelys* among the sea-turtles. Of this Upper Cretaceous genus no part is known but the skull. It has been placed provisionally among the Pleurodira by Lydekker; but there are at least equally good reasons for including it among the Amphichelydia. The skull is certainly a very generalized one.

Osteopygis may now be considered. Dr. Wieland has described this from a fine specimen belonging to the Marsh collection at Yale University (1904A), placing it among the Propleuridæ, but later (1904B, p. 194) referring it definitely to the Cheloniidæ. Nothing is known of this genus except the shell, the humerus, the ulna, femur, tibia, and some phalanges. The humerus is stated to be intermediate between that of *Chelydra* and that of *Testudo*, but the feature recalling the last named genus is the facetted distal end, a feature of various turtles. The other limb bones are said to be comparable feature by feature with those of *Chelydra*.

If now *Osteopygis* with its chelydra-like limbs is to be allowed a place among the Cheloniidæ there appears to be no sufficient reason why the Thalassemydidæ should not be included. In these turtles we have a shell which is admitted by all to be greatly like that of our sea-turtles, the carapace and plastron having suffered various degrees of reduction, and in some at least the plastron being not sutured with the carapace. The skull is well roofed over, the symphysis of the lower jaw is as long as in *Thalassochelys* (Dollo, 1903, p. 813), and the feet were probably fully webbed. Also, the species appear to have lived in the vicinity of salt water. Mr. Lydekker (1889, p. 27) holds that there is considerable probability that our modern sea-turtles have descended from these Thalassemydidæ (Acichelyidæ of Lydekker); Dr. Dollo (1903, p. 840) speaks of the latter family as ancestral forms of the marine Thecophora; and Dr. Fraas (1903, p. 104) concludes that from the Thalassemydidæ the Cheloniidæ might have been evolved. Why, then, should those who admit *Osteopygis* and its allies to a place among the Cheloniidæ refuse to take in also the Thalassemydidæ? Hitherto it has been a want of knowledge of the feet of the "Chelonemydidæ" (Zittel, 1889, p. 528) that has prevented the association of these with the Thalassemydidæ; but now neither that lack of knowledge nor the probability that the feet were chelydra-like prevents various writers from uniting these "Chelonemydidæ" with the Cheloniidæ. The writer regards it as much better to unite the so-called Chelonemydidæ with the Thalassemydidæ as a family distinct from the Cheloniidæ. The former may have sprung from some member of the thus limited Thalassemydidæ; but that furnishes no final reason for comprehending all in one family. Otherwise we might extend the family backward into the Amphichelydia, or even into the Cotylosauria.

It may be permitted at this point to discuss the structure of the humerus of the Testudines. Dr. Wieland (1900B, p. 423) has named

and endeavored to define six forms of the humerus: the parachelic, as exemplified in *Testudo;* the chelic, as presented in *Chelydra;* the chelicoid, as shown in the Thalassemydidæ; the thalassoid, as displayed in *Lytoloma;* the thalassic, the type of which is furnished by our living Cheloniidæ; and the parathalassic, as found in *Dermochelys.* After some study of the subject I believe that only three classes of testudinate humeri can be successfully defended, the chelic, the thalassic, and the parathalassic. The parachelic, chelicoid, and thalassoid humeri are only minor modifications of the chelic. It is doubtful whether a single one of the characteristics of the parachelic form suggested by Wieland will serve to distinguish it from the chelic. The shaft varies in curvature in different species, and it is doubtful whether it is ever as much curved as in *Terrapene* or in some species of Pleurodira. The radial crest of *Testudo radiata,* for example, is lower down on the shaft than it is in *Chelydra* and Trionychidæ. The ectepicondylar foramen is like that of the Emydidæ, and is certainly not higher up than in *Compsemys plicatula.* The feature most conspicuous in the humeri of the Testudos is the small angle between the radial and ulnar tuberosities, both being twisted toward the ventral side of the shaft (Lydekker, 1889, p. 3).

It is difficult to explain the so-called chelicoid form of humerus displayed by some of the Thalassemydidæ, such as the one figured by Mr. Lydekker (1889, p. 2), in which the head of the bone is feebly developed. It has been suggested that this represents the primitive form of the testudinate humerus; but this view can hardly be maintained. Not all of the family had the humeral head so feebly developed. The head appears of normal form in the figure of the humerus of the fore limb of *Acichelys wagleri* (Zittel, 1889, p. 529, fig. 497). In this specimen the ulnar crest is buried yet in the matrix. The head of the humerus has the normal development in the specimen of *A. crassipes,* figured by Dr. Lortet (1892, pl. ii, fig. 7).

Fig. 4. *Compsemys plicatula.* Right humerus seen from above. ×⅔.

The chelic form of humerus appears in the Amphichelydia, the Pleurodira, the Cryptodira, and the Trionychoidea, and must therefore be regarded as more primitive than the apparently abnormal form seen in some of the Thalassemydidæ. The humerus has the true chelic form in *Compsemys plicatula,* of the Upper Jurassic.

Doubtless, the thalassic humerus was derived from the chelic, and there have existed transitional forms which may be described as thalassoid; but probably all known forms will fall into either the chelic or the thalassic. Dr. Dollo was very correct when he affirmed that the humerus of *Lytoloma* was essentially like that of *Chelydra*. This is given by Dr. Wieland as an example of the thalassoid humerus. As a second example, the humerus of *Toxochelys* is suggested (Wieland, 1900B, p. 418, 1902, p. 96), with the statement that this form is characteristic of the older Cheloniidæ and closely approaching typical outlines. Unfortunately, the known humeri of this genus are crushed, so that from them it cannot be definitely determined how much they were curved. Nevertheless, in the view of the writer, this humerus was wholly chelic. From that of *Chelydra* it differs in having a broader shaft, not due to crushing, and the radial process falls slightly below the head; but this process descends quite as low in *Platypeltis*, and still lower in *Hydromedusa tectifera* and especially in *Testudo radiata;* and the latter has not been supposed to be on the way to developing flippers. A humerus of *Toxochelys* in the American Museum of Natural History makes it evident that the shaft possessed a sigmoid curve, that the head rose above the shaft when the latter was held horizontally, and that the tuberosities were separated behind by a broad fossa, as in *Chelydra*.

It is proper to retain the humerus of *Dermochelys* in a distinct class. Here the radial process is extremely prominent, the attachment of the ligaments extends quite across the ventral surface of the shaft, and the ectepicondylar foramen remains within the bone. To the writer it appears probable that these peculiarities have not been developed from Thecophore ancestors, but have been elaborated by an independent line of ancestors.

Returning now to a consideration of some of the other genera which have been thrown into the family Cheloniidæ, I express it as my opinion that *Protostega*, *Archelon*, and *Protosphargis* would better be retained in a family distinct from the Cheloniidæ. It is quite evident that the modern sea-turtles did not originate from the Protostegidæ, as is shown by the greatly reduced carapace of the latter. Not from these, nor from *Osteopygis*, with its probably chelydroid limbs; but from some probably Lower Cretaceous ancestor somewhat like *Toxochelys*, but with probably still better developed flippers, arose the modern Cheloniidæ. The latter and the Protostegidæ may yet be found to constitute subfamilies of one family; but so far as known, their characters are so different, and the times of their cul-

mination so far apart, that it seems better for the present to retain them as distinct families.

We must now consider still further the genus *Toxochelys*. It is regarded by both Dr. Dollo and Dr. Wieland as belonging to the Cheloniidæ. For my part I shall regard the limbs as furnishing a test of the correctness of this disposition of the genus. Dr. Wieland has had the opportunity of studying and describing the best yet known limb of *Toxochelys latiremis* (1902, p. 95, fig. 95). According to Dr. Wieland's description and restoration, the first and second fingers were stout and furnished with strong claws; the other fingers were slender. It seems quite possible that the third finger had a weak claw, but this is not certain. Now, while this limb presents some resemblances to the flippers of the sea-turtles, it had really not yet attained the stage represented by the fore limb of the Trionychidæ. The form of the humerus has already received attention. On page 97 of Dr. Wieland's paper just cited, he has presented a table showing the lengths of the elements of the fore limb of several genera relative to the humerus, this being taken as 100. The reader should consult this table. I here present also the measurements of the limb of *Amyda spinifera*. I add those of *Toxochelys* taken from Wieland:

	Arm.			Fingers.				
	Humerus	Radius	Ulna	1st	2nd	3d	4th	5th
Amyda.	100	53	51	69	90	98	116	98
Toxochelys.	100	58	50	51	73	100±	104±	70±

Here we see that, while there is more difference between the length of the radius and the ulna in *Toxochelys* than there is in *Amyda*, the fingers of *Amyda* are as long as, or longer than, those of *Toxochelys*. The first and second fingers of *Toxochelys* preserve yet the ratios to the humerus which they have in *Chelydra*, while in *Amyda* they are both much lengthened. Moreover, in *Toxochelys* the second finger is still a strong member, but in *Amyda* it is assuming a slenderness seen in *Thalassochelys*. Now, notwithstanding this transformation of the hand of *Amyda* for swimming, the limb must be regarded as essentially a walking leg and not a flipper. Any one who has had experience with these animals while alive knows that they can move over the ground and along the bottom of a stream with surprising rapidity. We can readily grant that the fore limb of *Toxochelys* had entered on the early stages of those modifications which resulted in the production of flippers; but almost certainly this turtle did not navigate the

open seas. It probably passed the greater portion of its life in the salt water, but near the shores.

Therefore, on account of the limbs and the structure of the palate, I would exclude *Toxochelys* and *Porthochelys* from the Cheloniidæ. They are fully as near the Chelydridæ. Neither are they far from *Osteopygis* and *Lytoloma;* but probably the differences in the structure of the palates would keep them apart. Moreover, it is probable that the limbs of *Osteopygis* and *Lytoloma* were not to the same extent modified for swimming. For the writer, for the present the family Toxochelyidæ remains.

A few remarks may be made at this point on the chelonian flipper. As long as the animal habitually employed the limb for locomotion on the land or along the bottoms of streams, the phalanges would retain their condyles, the fingers preserve some degree of freedom of movement, and the humerus would retain its sigmoidal curvature, in order to bring the foot to the ground. When the turtle had once abandoned the land, except for rare visits, the fingers would become bound up together in the skin and muscles, and the condyles would gradually disappear. The humerus would straighten out so as to lift the paddle upward and give it a hold on the water to be thrust backward.

Dr. Dollo (1903, p. 823) has honored me with a notice of my essay on *Toxochelys* (Hay, 1896), and has recorded some differences of opinion. In that paper I expressed the conviction that *Toxochelys* was related both to the Cheloniidæ and to the Chelydridæ. As Dr. Dollo well understood, I did not hold that *Toxochelys* was intermediate in the line of descent. I stated distinctly that "*Toxochelys* is probably an offshoot from the line which led to the Cheloniidæ, an offshoot after the latter had disengaged itself from forms like the Chelydridæ." In this statement the relative "which" refers to "line" and not to "offshoot." The writer still maintains it as probable that the Cheloniidæ, the Chelydridæ, and the Toxochelyidæ sprang from common ancestors which lived in times geologically not long before *Toxochelys*. It is not opposed to this belief that the genus just named has some peculiarities of its own.

Dr. Dollo has mentioned the well-known fact that *Chelydra* possesses opisthocœlous caudal vertebræ, while those of *Toxochelys* are probably procœlous. It is not unlikely that too much importance has been given to this difference. Are we to suppose that the Chelydridæ separated from the other turtles sometime during Jurassic times, while yet the caudal vertebræ of all were bicœlous, and that

the former group developed only opisthocœlous caudals, and the other turtles only procœlous caudals? Rather than accept this view, I would hold Baur's opinion that the opisthocœlous caudals are secondary: but it is more probable still that the procœlous vertebræ are secondary. We cannot believe that the forms of the vertebræ have remained fixed ever since they ceased to be biconvex. In the genus *Testudo* there are specific and doubtless individual variations in the forms of the cervicals. The last paragraph of Leon Vaillant's paper (Vaillant, 1881, p. 102) ought to be read in this connection.

Dr. Dollo places particular emphasis on the fact that the structure of the choanæ of *Toxochelys* is not intermediate between that of the *Chelydra* and that of *Thalassochelys*. In the latter genus the choanæ are removed backward to opposite the middle of the orbits and are bounded externally by the palatines, which join the vomer. In *Chelydra* the choanæ are far forward and are bounded externally partly by the palatines and partly by the maxillæ, which thus intervene between the palatines and the vomer. In *Toxochelys* the choanæ are far forward and are bounded externally by the palatines, which come forward to the vomer.

Dr. Dollo recognizes two types of anteriorly placed choanæ: (1) the primitive, those like the choanæ of *Chelydra;* and (2) the secondary, like those of *Dermochelys* and *Toxochelys*, in which the outer boundary is formed wholly by the palatines. Posteriorly placed choanæ are rightly regarded by Dr. Dollo as an adaptation to a conchifragous diet. In such cases the crushing surfaces of the jaws have become broadened and the choanæ have been pushed backward until the maxillary plate of the palatine has come into contact with the maxillary plate of the vomer. It is Dr. Dollo's contention that, in case a species possessing such a masticatory apparatus should afterwards betake itself to a diet of soft substances, the masticatory surfaces would become reduced and the choanæ would again move forward. They would then belong to the secondary type of anterior choanæ. But, according to Dr. Dollo, the palatine bone, having once been in contact with the vomer, would retain this connection, be carried forward, and thus come to bound outwardly the anteriorly placed choana; for "l'évolution est irréversible."

Now, we have no evidence whatever that *Dermochelys* itself was derived from any form that possessed a broad masticatory apparatus and posterior choanæ: just as little that *Toxochelys* ever came from such a form. It is not necessary to believe that the coast-inhabiting ancestors of *Dermochelys* crushed mollusks or other shell-covered

animals. Even for weak-jawed animals the sea-coasts furnish a living. It is very certain that *Toxochelys* with its inefficient grinding apparatus frequented the shores of the Cretaceous seas. On the other hand, we can readily acknowledge the possibility that the ancestors of *Dermochelys* and *Toxochelys* were crushers of mollusks.

As to the relation of the palatine bone to the choana, we find in many turtles a process of this bone extending itself for some distance along the outer side of the choana. In a specimen of *Chelydra* at hand there is such a process reaching nearly half-way from the hinder border of the choana to the vomer. We could hardly regard it as wonderful that in some species it should attain even to the vomer. Furthermore, even if the ancestors of *Dermochelys* and *Toxochelys* had once possessed posteriorly placed choanæ, with union of palatines and vomer, it is difficult to understand why, if the choanæ had moved forward, the palatine bones should be dragged forward with the vomer. In fact, *Dermochelys* itself furnishes the disproof of Dr. Dollo's hypothesis; for the palatine usually does not join the vomer. He has referred to the figures of the skull furnished by three authors, which figures represent an interval between the palatines and the vomer; but Dr. Dollo is convinced that in the specimens thus represented the slender anterior process of the palatine has been broken off in the preparation of the specimens. However, an examination of materials in the British Museum showed the writer that the process had in no case been broken away, and nevertheless did not reach the vomer. Also, in the American Museum of Natural History there is a skull which displays a short space between the bones on one side and a somewhat greater interval on the other. Without doubt variations in the length of the process in question exist; but the fact that the two bones are usually not in contact is not favorable to the views of Dr. Dollo. The writer maintains that *Toxochelys* broadly considered is intermediate between the Cheloniidæ and the Chelydridæ, although it is not intermediate in all of its structures.

Since the Chelydridæ figure largely in the discussions on the origin and the classification of the turtles, a remark may be allowed here regarding an important structure. As is well known, the nuchal bone of the Chelydridæ is drawn out on each side into a long process, which reaches the end of the first costal plate. Mr. G. R. Boulenger (1889, p. 12) has suggested the possibility that the nuchal, in part at least, represents the modified ribs of the last cervical vertebra. This suggestion has been mentioned approvingly by Dr. J. F. Van Bemmelen (Bemmelen, 1896A, p. 325). Dr. Dollo also (1888, p. 267) adduces

the presence of these supposed nuchal ribs as a reason why the Chelydridæ could not have been derived from the Propleuridæ. Now, if these nuchal processes were originally cervical ribs, we might rightly expect to find them present in some form in the older turtles. On the contrary, they do not appear even as conspicuous processes in the older turtles, much less as ribs. In *Compsemys plicatula* and in the species of *Baëna* there is hardly anything that can be homologized with this process. Apparently it must be looked upon as a secondary development.

It remains to discuss the relationships of *Dermochelys* to the other turtles. Since my former paper on this subject (Hay, 1898), the subject has been further considered by Dr. Dollo (1901, 1903) and Dr. Wieland (1902, p. 105).

Notwithstanding the fact that Dr. Dollo maintains that *Dermochelys* has been derived from some member of the Cheloniidæ, more specifically from *Toxochelys* (1903, p. 826), he regards it as representing one of the two primary divisions, perhaps suborders, of the turtles. These animals he divides into (1) the "Thécophores," turtles having a thecophore armor more or less reduced and no athecate armor; and (2) the "Athèques," those turtles with the thecophore armor extremely reduced, but possessing an athecate armor. Now, while this classification agrees wholly with the present writer's view, the basis of it is not satisfactory. The acquirement of a dermal armor, even by turtles, is of no such importance. Several of the living species of the genus *Testudo* are provided with an armor of bones in the skin of the legs. In some of the fossil species of the genus found in North America the legs are heavily armored, as well as the thighs and the upper surface of the tail. Other species of this genus have no such armor. Dr. Wieland is more consistent, though erring, when he makes the Dermochelyidæ one of the superfamilies of the Cryptodira.

Dr. Dollo is of the opinion that *Dermochelys*, as well as all the sea-turtles, was derived from terrestrial ancestors. He is doubtless correct in this conclusion. This ancestor, he thinks (1901, p. 4), possessed a thecophore, but not an athecate, armor. The next stage in the evolution was probably furnished by a similarly armored turtle which frequented the sea-shore, had broad crushing jaws, and probably lived on mollusks. The successor of this was a littoral turtle, represented by *Toxochelys*, which had changed his habits of life, eating now softer foods, had had the crushing jaws greatly reduced, with the choanæ moved forward, and the thecophore armor also much reduced. The next stage was a pelagic thecophore. It differed from

its predecessor in having the carapace reduced to the nuchal bone, while the plastron formed only a ring, and was without an entoplastron. The next stage was a littoral athecate. The representatives of the line had returned to life along the coasts. They needed an armor of some kind, and were compelled to develop in the skin, one, consisting of a mosaic of small but thick plates. Again, through impulse or necessity, the race was driven to the open sea. Having again less use for an armor, the dermal mosaic of thick plates suffered reduction; and the living representative of the line is our leather-back turtle, which possesses a dermal armor of thin closely joined bony plates, frequents the open sea, and lives on the softest of foods.

As already stated, the reptile which Dr. Dollo has selected for the honor of representing the third stage in these transformations is *Toxochelys* (Dollo, 1903, p. 826). It is an ungracious thing to attempt to divert a distinction from an old friend. I have already given my reasons for thinking that the limbs of *Toxochelys* had not yet advanced beyond the stage seen in the Trionychidæ. It is probable that the shell was not yet reduced so much as has been supposed. The specimen that has been figured by Dr. Case (1898) was probably an immature one, and this will account for the large fontanelles. The carapace of *Porthochelys*, a close relative of *Toxochelys*, has been described by Williston (1901). In this the shell is almost wholly without fontanelles.

Eosphargis of the Lower Eocene London Clay is taken by Dr. Dollo to represent the next stage in the line of development from *Toxochelys* to *Dermochelys*. During the interval between the Niobrara and the London Clay *Toxochelys*, we are to suppose, had to get rid of its carapace, and to transform its chelic humerus into a parathalassic one, its trionychoid feet into dermocheloid flippers, and its chelydra-like head into one like that of *Dermochelys*, wholly devoid of descending parietal plates. If *Eosphargis* had no athecate armor its descendants developed this by the time of the Middle Eocene; for then *Psephophorus* appears with an armor of thick dermal plates. These are very rapid transformations for turtles to accomplish, and some of us may be excused for harboring doubts. It may be proper to call attention to the fact that the supposed reduction of the parietal plates seems to contradict Dr. Dollo's law that "l'évolution est irréversible." It will hardly be contended that the presence of the descending parietal plates is a primitive condition. Through a course of evolution they formed an articulation with the pterygoids. The writer finds it difficult to discover what explanation of the interrup-

tion of this union can be given that would not require the admission that the union of the palatines and the vomer might be abrogated in the production of the secondary type of anterior choanæ.

A second violation of the law referred to seems to be found in the condition of the basisphenoid in *Dermochelys*, if we are to accept Dr. Dollo's genealogy. This basisphenoidal region is quite differently constructed in the Dermochelyidæ and the Cheloniidæ. In the former the basisphenoid is long, and almost entirely separates the pterygoids. In this respect it is like that of *Baëna* and doubtless presents the primitive condition. In the Cheloniidæ, *Thalassochelys*, for example, the pterygoids meet along the midline for a great distance and the basisphenoid has become much shortened. Moreover, in *Dermochelys* the borders of the basisphenoid are overlapped by the pterygoids: whereas, in *Thalassochelys* the borders of the pterygoids pass beneath the basisphenoid. Now, in *Toxochelys* we have the same arrangement of the bones of this part of the skull that we have in *Thalassochelys*. Are we to suppose that in *Dermochelys* there has been a reversion to something greatly like the original condition of the base of the skull?

To some of those who admit the important structural differences that exist between the Dermochelyidæ and the Cheloniidæ the greatest obstacle in the way of accepting *Dermochelys* as the representative of a distinct suborder is the idea that it must then be regarded as the type of a structurally primitive form. So far as I am able to discover, this notion has been most strongly emphasized by the opponents of the early origin of the Athecæ. Dr. A. S. Woodward has, indeed, spoken of the Athecæ as being primitive (1887); but this admission appears to be wholly unnecessary, besides not being wholly justified by our knowledge of the animal. The present writer has already recorded (1898) his view that *Dermochelys* is not in all respects primitive. It is indeed a form highly specialized for life in the open sea. There can be no question that it has been developed from an ancestor which possessed walking limbs. We do not need to deny that the carapace has undergone great reduction, so that now the costals are obsolete and the peripherals wholly wanting and only the nuchal remains; nor that the plastron has suffered conspicuous losses. To undergo such modifications, it is not necessary to suppose that its ancestors belonged to the Cheloniidæ. If a terrestrial member of the Prochelonida (Haeckel, 1895, p. 322), back in Permian times or in the early Trias, had betaken itself to sea-faring life, we can easily imagine that its offspring would have arrived structurally

where we find *Dermochelys* to-day. With such a conception of *Dermochelys* we can, without conceding Dr. Dollo's conclusion regarding its relations (1901, p. 1, par. 3), grant the greater number of his premises, especially those recorded under paragraphs 1, 3, 4, 5, pages 5–7, of the paper just cited. Where the author of that paper employs the term "Thecophore" we may substitute the word "Prochelonida." The primitive turtle from which the leather-back sprang probably possessed a more or less extensively developed system of costal plates, peripheral bones, neurals, and plastral bones, and hence was, in a structural sense, a thecophore; although other characters would have excluded it from the suborder Thecophora.

On Dr. Dollo's paragraph 2, of the paper last referred to, we may remark that the failure hitherto to find pretertiary Athecæ is no certain evidence that they did not exist. One of the attractions of the science of palæontology is the pleasure often enjoyed in discovering members of evolutionary lines in far older deposits than any yet recorded. Is not Dr. Dollo compelled to await the finding of the late Cretaceous and early Tertiary links in his *Toxochelys-Dermochelys* chain? Do we not likewise yet hope for the discovery of the predecessors of *Proganochelys?*

On Dr. Dollo's paragraph 3, the comment may be made that the plan of the plastron of *Dermochelys* and that of the other turtles is the same because the Prochelonida had the plastron built on the same general plan. It probably contained more bones than are now found in the plastron of any turtle; but similar needs have led to the retention of practically the same bones in all the groups of turtles. No doubt, the Prochelonida all possessed mesoplastra and an entoplastron; but the great majority of turtles have dispensed with the mesoplastra; *Dermochelys* and *Kinosternon* no longer possess the entoplastron; and *Dermochelys* and the Trionychidæ have lost the peripheralia. We cannot suppose that the Dermochelyidæ sprang from the Trionychoidea because both groups lack peripherals, nor from the Kinosternidæ because both families lack the entoplastron.

On paragraph 6 of Dr. Dollo's paper it may be said that as regards the loss of nails, the regression of ossification, and various points in the structure of the skull, all these modifications might have been effected in the two groups independently during descent from a common ancestor. Whether or not the primitive turtles possessed the descending plates of the parietals we cannot now be certain. At least, it must have appeared in the primitive Thecophore, for it has been transmitted to all the superfamilies, the Amphichelydia, the

Pleurodira, the Cryptodira, and the Trionychoidea. Dr. E. C. Case is inclined to believe that such plates existed in the Diadectidæ (Case, 1905, p. 140): and if this is true, it is probable that they existed also in the Prochelonida. They have then been lost during the history of the Athecæ: but the utter elimination of elements so completely removed from outside influences, apparently so useful in strengthening the skull and protecting the brain and the cephalic nerves, must, seeing how slowly changes in turtles are effected, have required an immense extent of time.

Dr. Wieland (1902, p. 97) has attempted to show, by measurements taken from *Chelydra*, *Toxochelys*, *Eretmochelys*, and *Dermochelys*, the general trend of the changes which have occurred in the testudinate flipper. In the opinion of the present writer, his results are not especially favorable to the view that the last-named genus has been derived from the Cheloniidæ. He announces that the measurements show "strongly marked radial and ulnar decrease in length." On the contrary, as compared with the radius of *Chelydra*, whose radius is .52 of the length of its humerus, an increase of length is shown in *Toxochelys* to .58; in *Archelon* to .54; in *Eretmochelys* to .53. I find in a specimen of *Thalassochelys* that the radius is .60 of the length of the humerus. Now, if *Dermochelys* is a final term in the series, we might expect to find its radius still longer relatively to the humerus. On the contrary, it is greatly shortened, being only .43 of the humeral length. As to the ulna, it has retained practically its primitive length in *Thalassochelys*, *Toxochelys*, and *Archelon*. In *Eretmochelys* it is considerably shortened, and in *Dermochelys* still more, that of the latter being .39 of the humerus, *Chelydra* being .53. Nevertheless, the ulna of *Dermochelys* is less shortened relatively to the radius than in the other genera, the difference being only .04 of the length of the humerus: whereas, in *Toxochelys* and *Thalassochelys* the difference is .08, and in *Eretmochelys* .09 of the length of the humerus. Hence, we again see a reversal of the changes which are supposed by Dr. Wieland to be going on leading up to *Dermochelys*.

The present writer remains convinced that it is in the mosaic carapace and plastron of *Dermochelys* that we find incontestable evidences that the Athecæ did not have their origin from any of the Cryptodira; but from the Prochelonida. However specialized the limbs and the jaws may be, however much reduced the costal plates and the plastral bones, this mosaic is primitive. It may, indeed, have undergone modifications and reductions. It was thicker in *Psephophorus;* in *Eosphargis* it may, or may not, have been reduced

to a row of median plates. The importance of this dermal armor does not consist merely in its presence; for, as already stated above, such a dermal armor might have arisen secondarily. The significance of the armor of *Dermochelys* is found in the fact that it consists of a number of longitudinal bands of larger plates which correspond in number and position with the rows of horny scutes which must have belonged to the common ancestors of all the turtles. This proposition has already been discussed by the writer (Hay, 1898); but some further consideration of it is here required.

An examination of the dermal armor of *Dermochelys* shows that there are on the upper surface a median longitudinal band, or keel, of bony plates, and on each side of it three lateral keels, the outer one forming the corresponding margin of the body. Although in the adult the surface of the skin is smooth, in the very young the skin is broken up into areas which undoubtedly correspond with the bony plates. The median row of plates then represents the row of vertebral scutes found in most turtles: the first lateral row represents the row of costal scutes; the second lateral keel, or row of plates, occupies the position of the supramarginal scutes of *Macrochelys*, *Platychelys*, and *Proganochelys*. The third keel on each side corresponds to the marginal scutes.

On the ventral surface *Dermochelys* possesses five rows of bony plates, a median and two pairs of lateral ones. It is not certain that the median row is represented in any living turtle; but it is probable that the intergular of some genera corresponds to a portion of it. Mr. Lydekker (1889, p. 218) has described and figured portions of the plastron of *Archæochelys*, from the Wealden, which appears to have possessed a median, azygous row of horny shields. This would correspond exactly with the median plastral keel of *Dermochelys*.

The first lateral keel on the plastron of *Dermochelys* represents the paired horny scutes found on each side of the midline of nearly all turtles. The second lateral keels of *Dermochelys* correspond with the inframarginal scutes of the Cheloniidæ. Dr. Fraas (1903, p. 98) states that the development of inframarginals in the Thalassemydidæ is surprising, inasmuch as thereby the condition of the shell gains a pronounced *Chelonia*-like character. There can, however, be no doubt that the possession of inframarginals is a primitive, not a secondary, character. They are present probably in all of the Amphichelydia, being greatly developed in *Pleurosternon*, *Compsemys plicatula*, and in *Plesiochelys*. They are present in the Dermatemydidæ and in *Kinosternon*. The Emydidæ have retained only the ends

of the series as axillary and inguinal scutes. The inframarginals appear to be wanting in the Pleurodira. Being primitive structures, it is not strange that they appear in *Thalassemys*. We may confidently expect to find them in *Proganochelys*.

In the paper by the present writer (Hay, 1898), he has called attention to the carinæ, or keels, sometimes tuberculated, which are found on the shells of various turtles. Conspicuous among these are the Chelydridæ, in which the areas of nearly all the carapacial scutes are raised into bosses. *Platychelys*, of the European Jurassic, presents another example; and it may be here remarked that, although it belongs to the Amphichelydia, it is not incredible that our Chelydridæ have descended from it. When these keels and rows of bosses are present they occupy positions corresponding to some of the keels of *Dermochelys*.

The writer has further formulated the hypothesis that each scute of the primitive turtles was supported by a distinct bone, as it is in the young of *Dermochelys*. Some of these bones with their scutes expanded at the expense of their neighbors. Among the Thecophora a time came when the bones underwent reduction, but the scutes of some of them remained and became such as we find to-day on the most of our turtles. In that paper the fact was mentioned that in a specimen of *Toxochelys* there were found along the middle of the back, at the rear border of each horny scute, a distinct bone, which was articulated to the underlying neurals. In the collection of vertebrate fossils at the University of Kansas is found another specimen which furnishes nearly the whole median line of the carapace; and here we see a series of these median bones. What can be the significance of this row of bones if it be not that they are remains of an old superficial armor like that of *Dermochelys?* Dr. Fraas (1903, p. 110) has concluded that the supramarginals of *Proganochelys* represent a series of bony plates which lay upon the ends of the ribs. I do not understand from Dr. Fraas's description of this turtle that he actually found such bones; but I have no doubt that his explanation is the correct one.

How are we to explain the coincidences above noted? How happened it that when there are so many rows of enlarged plates in *Dermochelys* this number should agree with the typical number of rows of scutes in other turtles? Is it an accident that in both cases there is a median row above and below, whereas, there might have been in one case or the other only paired rows? If *Dermochelys* originated from some of the Cheloniidæ, its ancestor had, in all probability, lost

at least all traces of the supramarginals and all of the azygous plastral scutes: and yet in the offspring of these turtles there reappear a complete series of both.

All the phenomena involving the relationships of the Athecæ and the Thecophora are easily explained on the supposition that they diverged from each other far back in Triassic or Permian times; that somewhat later the Cheloniidæ arose; and that the latter and the Athecæ have ever since pursued parallel lines of development.

On the following page there is given a phylogenetic table which is intended to exhibit the writer's views on the origin and relationship of the various families, superfamilies, and the suborders of turtles.

It may be allowable to indulge in some reflections on the structure and appearance of one of the Prochelonida, the common ancestor of the Athecæ and the Thecophora. We must suppose that it lived during Permian times. The form of the skull was probably not greatly different from that of *Chelydra* or *Thalassochelys*. The temporal region was extensively roofed over; the supraoccipital was short. Even at that stage there were probably no teeth, and the jaws, as now, were covered with horn, or there may have been feeble teeth in the hinder portions of the maxilla and dentaries. The surface of the head was doubtless invested with horny scutes, some of considerable size. The quadrate bone was feebly notched behind for the passage of the stapedial rod. There were well developed nasal bones and lachrymals. The choanæ were probably well forward. There were posterior palatine foramina. The transverse bone had doubtless already disappeared. The palatines did not reach to the vomers in front of the choanæ, and these bones were separated by the body of the vomer. Doubtless the pterygoids extended backward so far as to exclude the basisphenoid and basioccipital from contact with the quadrate. The vacuity between the pterygoids and the basisphenoid had been partially or wholly closed. It seems probable that the basisphenoid did not come into contact with the vomer, thus permitting the pterygoids to meet anteriorly in the midline.

The neck was short. The vertebræ were eight in number, biconcave, furnished with transverse processes, and possibly with rudimentary ribs.

The trunk of the animal was, as now, short and broad. There were ten ribs in the trunk but the first and last were already reduced in size. There were, overlying the ribs and probably in adult life consolidated with them, a series of eight bony plates, such as existed in the Otocœlidæ and the Diadectidæ, and which did not overlap, but

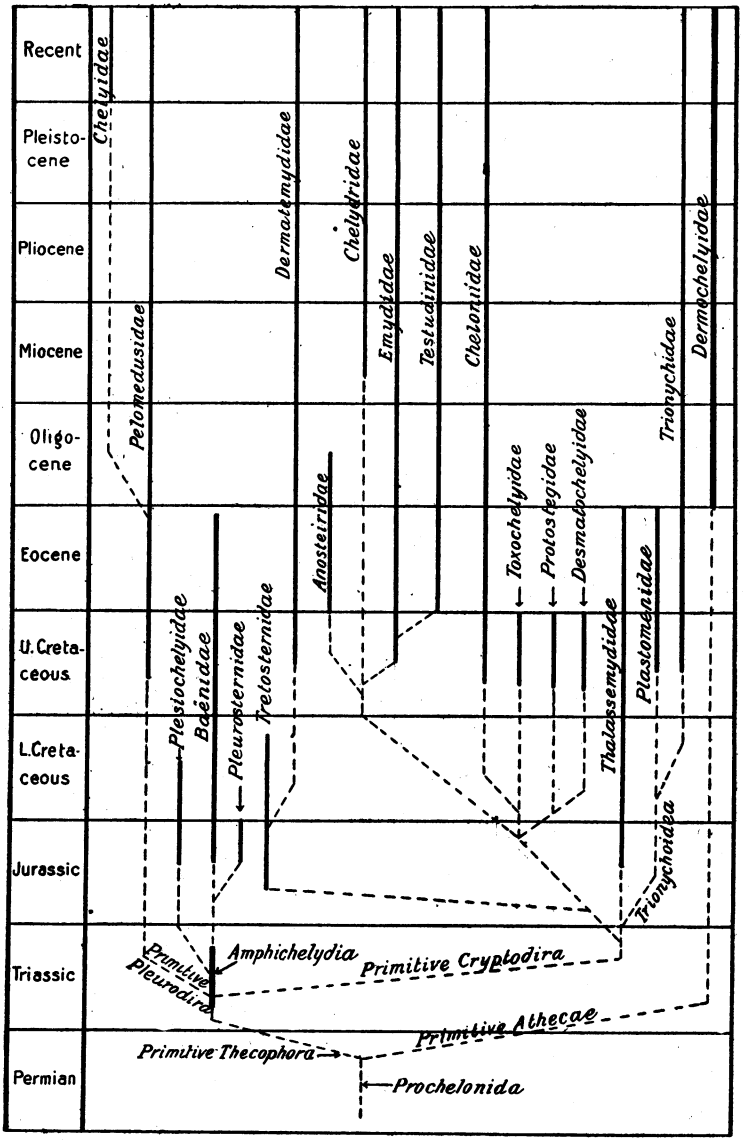

Fig. 5. Phylogenetic Chart showing supposed origin of the suborders, superfamilies, and families of turtles.

joined each other edge to edge, at least at their proximal ends. There were probably a series of median plates, corresponding to the neurals, and another series surrounding the margins of the animal, the peripherals. All these costal plates, these neurals, and peripherals lay beneath the skin. In this skin there were, above, seven longitudinal rows of dermal bones corresponding to those of *Dermochelys*. The spaces between these rows were then probably not occupied by bony plates. Where these bony plates existed they were overlaid by corresponding horny scutes.

The tail was long and thick and furnished below with chevron bones. Along the upper surface was a row of bony nodules, such as are found to-day in *Chelydra*.

The plastron of this animal doubtless possessed, besides the bones found in the Emydidæ, also mesoplastrals. From *Polysternon* it becomes probable that there was also a pair of bones between the hypoplastrals and the xiphiplastrals. At that stage there were, it would seem, extensive fontanelles between the bones of the plastron; and we are hardly compelled to believe that the carapace and plastron were suturally united. All the plastral bones were subdermal, like the abdominal splints of crocodiles. In the skin covering these bones were five longitudinal rows of bony plates, as in *Dermochelys*. The caymans possess bony plates similarly lodged in the skin, superficial to the bony abdominal splints.

As to the shoulder girdle, it is practically the same in all known turtles, and we may conclude that it was similar in the primitive stock. Possibly the precoracoidal process had not yet become so thoroughly consolidated with the scapula as in the known forms of turtles.

While we must regard the primitive turtles as terrestrial, we do not need to suppose that they were such in the sense that the Testudinidæ are terrestrial. Their feet were not constructed for marching over dry rocky plains. The animals were rather denizens of low, perhaps swampy, grounds. The limbs of all the early turtles of which we have knowledge indicate this. In general form and structure the primitive turtle limbs were probably like those of *Chelydra*. The digital formula for all the limbs was doubtless 2, 3, 3, 3, 3. Any deviation from this shown in either fossil or living species has been due to later specializations. It is not improbable that the tarsus possessed three distinct bones in the first row, as well as a centrale.

Of the offspring of the animals thus constituted, some, with need for a strong and unyielding armor, developed more completely the subdermal bones, that is, the costals, the neurals, the peripherals, and

the plastrals. These, if not already in contact, extended their borders and formed sutural unions. As this thecophore skeleton evolved, the overlying skin became thinner, the dermal bones underwent reduction, and some of the horny areas extended themselves at the expense of their neighbors, resulting in the production of the large scutes which break joints with the bones of the thecophore armor. In most of the Thecophora thus produced all traces were lost of the dermal bones, but they were sparingly preserved in a few, as *Toxochelys;* just as to-day we find in *Macrochelys* vestiges of the supramarginals.

Other offspring of the Prochelonida had need for an armor that was more flexible. In these the thecophore skeleton of subdermal bones underwent gradual absorption, so that to-day, in *Dermochelys*, there are only traces of it in the carapace and, on the abdomen, in the ring of plastral bones. On the other hand, the skin thickened and the bands of dermal bones spread until there was a complete athecate armor on both the back and the abdomen. Probably from the first these individuals were the more aquatic and soon betook themselves to the sea. Their limbs then began that series of transformations the result of which we see in *Dermochelys*.

Sometime during the Triassic or early Jurassic the Amphichelydia gave off two vigorous branches, the Pleurodira and the Cryptodira; and not long thereafter the Cryptodira sent off the Trionychoidea. That the latter did not spring from the Pleurodira is manifest. The latter appear never to have had a tendency to become modified for a purely aquatic life. Even the species of *Podocnemis* that swarm in the rivers of South America show no tendency toward a modification of the limbs into flippers. Neither is there in the Pleurodira any pronounced tendency toward a reduction of the shell. Although the pterygoids of the Trionychoidea are broadened somewhat as in the Pleurodira, they have, instead of withdrawing from between the axial bones of the skull and the quadrates, extended themselves still farther backward than in the Cryptodira. The long supraoccipital is more cryptodiran than pleurodiran. The pelvis shows no leanings toward that of the Pleurodires. Whether or not the mode of flexure of the neck indicates relationships is somewhat doubtful. The most natural mode of forming permanent curvatures in the neck is that shown in the Cryptodira, and might have been developed independently in different groups. This, however, is to be said: in the Trionychoidea the neck is never flexed laterally in order to conceal the head.

In the author's opinion, there is no sufficient reason for regarding the Trionychoidea as the primitive Thecophora, as Prof. E. Haeckel has done (Haeckel, 1895, pp. 323, 328). In order to accept Haeckel's opinion, we must conclude either that the original Trionychoidea were so different from what they now are that they were not at all Trionychoidea, or that the course of evolution in the turtles has been just the opposite of what is generally held. For example, either the primitive soft-shells possessed mesoplastra and a pair of bones between the hypoplastra and the xiphiplastra, or these bones developed in some of the turtles which sprang from the Trionychoidea. The latter either possessed horny scutes or these developed later on the delicate skin of the shell of these animals. The peripheral bones must have appeared among the other turtles after they departed from the parent Trionychids. Furthermore, the limbs of the early Trionychids must have been typical walking feet, like those of *Chelydra;* and strange transformations must have affected the entoplastron. We must rather believe that the Trionychoidea originated from some aquatically inclined Cryptodira, possibly from some of the earlier Thalassemydidæ, and suffered still further reductions in the carapace and plastron. Very early they must have assumed their present structure; for *Aspideretes beecheri* (Hay, 1904, p. 274, pl. xvi) of the Laramie, and probably also of the Judith River Cretaceous, is in all known respects like a modern *Amyda.* Practically the whole skeleton of this species, except the skull, is known.

The Pleurodira deviated from the Amphichelydia especially in skull structure and in the pelvis, but likewise in neck structure and in the shell. The pterygoids have become shortened posteriorly, but broadened and uprolled at the anterior borders. There has been a strong tendency toward a reduction of the temporal roof. The neck has developed in an extraordinary way. The limbs appear in no cases to have become transformed into flippers. The mesoplastra have persisted in many genera. The sutural articulation of the pelvis with the shell is one of the characteristic features of the group. There may have been the beginnings of these attachments in the Amphichelydia; but the apparent articulation of the pubis alone will hardly serve to settle decisively the position of any particular genus. Another structure to which the Pleurodira have clung tenaciously is the intergular. So general is the presence of this scute, or scutes, in the superfamily that many cryptodire genera have been referred to the Pleurodira on this character alone.

The Cryptodira have proved to be the most expansive group of

turtles. There have been evolved forms adapted to amphibious life, some for habitation in fresh waters, others for life on dry plains and rocky islands, others for life on the high seas. No form yet discovered was intended for aërial flight. Although the Cryptodira have preserved the general plan of the amphichelydian skull, they present in it a range of modifications unequalled in any of the other superfamilies. Usually the temporal roof is greatly reduced, but in some cases retained intact. In no living species are there nasals. The jaws are variously modified for the preparation of the most different kinds of food. There is also a great range in the modifications which the shell has suffered. The hinge in the plastron of *Emys* and *Terrapene;* the hinges between the plastron and carapace in *Terrapene* and *Ptychogaster;* and that between two portions of the carapace of *Kinyxis* are illustrations of these modifications. Perhaps the most specialized shell among all turtles is found in the genus *Testudo*, with its wedge-shaped costals, its variously shaped neurals, and its plastron posteriorly notched, anteriorly beaked. In this genus, as already stated, several species possess a dermal armor on the limbs, the jaws are modified for a vegetable diet, and the stapedial notch is closed. Taken altogether, it appears to the writer that the Cryptodira rank higher than the Pleurodira; although the contrary opinion is usually held.

The writer wishes to notice briefly a paper published recently by Dr. Carl Rabl, under the title "Ueber einige Probleme der Morphologie" (Rabl, 1903). In this paper Rabl discusses particularly the structure of the carpus and tarsus and that of the temporal region of the skull. His conclusions, reached after a study of the ontogenetic development of the carpus and tarsus of various reptiles, are (1) that the turtles are the most primitive among reptiles; (2) that among the chelonians the sea-turtles, including *Dermochelys*, take the lowest position; (3) that the turtles are to be divided into two groups, the "Eretmopoden," embracing the Cheloniidæ and the Dermochelyidæ, and the "Dromopoden," embracing all the other turtles; and (4) that the former group has given origin to the latter.

The ground for this primary division of the order is found in the different disposition of the second carpale and second tarsale in the two groups. In the "Eretmopoden" these bones preserve the primitive relationships, being in contact with both the first and the second metacarpals and metatarsals respectively; while in the "Dromopoden" the second carpale and second tarsale are in contact with only the second metacarpal and metatarsal respectively.

Whatever may be said regarding the propriety of splitting the order of turtles into suborders on a single, not well-understood, character, it may be remarked that Rabl's conclusions contravene the results of modern inquiry. Leaving out of the account *Dermochelys*, the order is recognized as comprising three groups, the Cryptodira, the Pleurodira, and the Trionychoidea, and this grouping is based on many important structural characters. The Cheloniidæ are recognized as being truly Cryptodira; but Rabl's arrangement would make the Trionychidæ and the Pleurodira more closely related to such forms as *Chelydra*, for example, than are the sea-turtles.

Rabl's belief that the land and swamp turtles have been derived from the sea-turtles involves the necessity of supposing that the great flippers of some ancient marine forms have become enormously modified, that the fingers have become shortened, once more freed from their common envelope of skin and muscles, have recovered the lost claws, and more especially that the humerus has become restored, in such forms as *Chelydra* and *Amyda*, for illustration, to something like the primitive condition. For the proposition that the humerus of the sea-turtles represents the primitive form of this bone is one that can hardly be successfully maintained.

Dr. Rabl finds in the structure of the temporal region of turtles support for his views on the division of these reptiles into two groups, and on the origin of all the others from the sea-turtles. In their possession of a complete temporal roof the latter prove themselves to occupy the lowest position among turtles. But Rabl has not taken into account the fossil forms. *Baëna* and its allies possess the temporal roof fully developed, but they are far from belonging to the "Eretmopoden."

Dr. Rabl emphasizes his conclusion that the temporal arch of the turtles has not resulted from the expansion of persistent fontanelles, but through the deepening of an incision, or excavation, in the occipital border of the temporal roof. This explanation serves well for the condition found in the Cryptodira and the Trionychoidea; but does not explain the presence of a parieto-squamosal arch in such Pleurodira as *Rhinemys*, *Hydraspis*, *Emydura*, and *Elysia*. Evidently in these cases the bone has been eaten away from below in a direction upward and backward.

The forms assumed by the temporal roof were fully explained long ago by Dr. George Baur (Baur, 1889, p. 472).

At the conclusion of this paper, which has already taken a wider range than was originally intended, I may be allowed to make some

further remarks on Dr. Fraas's description of *Proganochelys quenstedtii.*

If I have made no error in counting, Dr. Fraas has mapped off in his restoration of this turtle (Fraas, 1899, p. 409, fig. 1) twenty-two marginal scutes on each side. As this is about double the number usually found in turtles, it seems evident that there is some error. It appears probable that alternate ones of these lines ought to represent the sutures between the peripheral bones.

The hinder peripheral bones of this turtle are extraordinarily drawn out into lobes. It is to be suspected, however, that really two of these lobes belong to a single peripheral, each of these bones being not only separated from its neighbors by a notch, but also notched in the middle of its border. Dr. Fraas thinks that we must suppose that these lobes were imbedded in a dense mass of connective tissue. The present writer sees no necessity for such a supposition. The hinder border of various turtles is notched, although not so deeply as in *Proganochelys;* and yet they are covered with horn as elsewhere.

The inference made by Dr. Fraas that the pelvis of this genus was articulated to the plastron is, I believe, not justified; neither is the conclusion that the ilium was grown fast to the carapace. The plastral attachments, of course, could not be observed, because the xiphiplastrals were not preserved. What is observed in the case of the carapace is that there is an elevation where the ilium came into contact with it; but such a structure is often seen in Cryptodira.

In his excellent description of this interesting turtle, Dr. Fraas has, the writer fears, fallen into another error. On pages 417–419 are figures and a description of the dorsal vertebræ. The first dorsal is represented as possessing on each side a long process, which Dr. Fraas regards as a diapophysis. The rib which articulates with the first and second centra is described as the first, and the succeeding ribs are numbered accordingly. Now, an examination of a modern turtle shows that the rib which articulates between the first and second dorsal centra is the second rib, that which is consolidated with the first costal plate; and where there is a sternal chamber, this rib runs out, as a ridge, on the lower side of the costal. The first rib is usually greatly reduced; starts from the first dorsal centrum exactly where the supposed diapophysis starts, and is applied to the lower side of the first costal plate, usually against the border of the second rib. There can be no doubt whatever that the supposed diapophysis is really the first rib; nor that the succeeding ribs should each have

its number increased by one. As already stated, the writer believes that *Proganochelys* is not a Pleurodire, but an Amphichelydian.

LITERATURE CITED.

Baur, G., 1889. On the morphology of the vertebrate skull. Journal of Morphology, III, pp. 467–474.

Baur, G., 1890. On the classification of the Testudinata. Amer. Naturalist, XXIV, pp. 530–536.

Baur, G., 1891. Notes on some little-known American fossil tortoises. Proc. Acad. Nat. Sci. Philadelphia, 1891, pp. 411–430.

Bemmelen, J. F. Van, 1896. Bemerkungen zur Phylogenie der Schildkröten. Compte-rendu des séances du troisième Congrès Internat. de Zoologie, Leyden, 1895, pp. 322–335.

Boulenger, G. R., 1889. Catalogue of the chelonians, rhynchocephalians, and crocodiles in the British Museum (Natural History). Pp. i–ix; 1–311, with pls. i–v and 73 text-figures.

Case, E. C., 1898. *Toxochelys.* University of Kansas Geological Survey, IV, pp. 370–385, with pls. lxxix–lxxxiv.

Case, E. C., 1905. The osteology of the Diadectidæ and their relation with the Chelydosauria. Journal of Geology, XIII, pp. 126–159.

Dollo, L., 1888. On the humerus of *Euclastes.* Geological Magazine (3), V, pp. 261–267.

Dollo, L., 1901. Sur l'origine de la tortue luth (*Dermochelys coriacea*). Bull. Soc. roy. des sciences médicale et naturelles de Bruxelles, 1901, pp. 1–26.

Dollo, L., 1903. *Eochelone brabantica*, tortue marine nouvelle du Bruxellien (Éocène moyen) de la Belgique et l'évolution des chéloniens marins. Bull. Acad. roy. Belgique, 1903, pp. 792–850 (reprints, pp. 1–62).

Fraas, E., 1899. *Proganochelys quenstedtii* Baur (*Psammochelys keuperina* Qu.). Ein neuer Fund der Keuperschildkröte aus dem Stubensandstein. Jahreshefte Vereins f. vaterl. Naturkunde in Württemberg, LV, pp. 401–424, with pls. v–viii and 5 text-figures.

Fraas, E., 1903. *Thalassemys marina* E. Fraas aus dem oberen weissen Jura von Schnaitheim nebst Bemerkungen über die Stammesgeschichte der Schildkröten. Jahreshefte Vereins f. vaterl. Naturkunde in Württemberg, LIX, pp. 72–104, with pls. i–iii and 3 text-figures.

Haeckel, E., 1895. Systematische Phylogenie der Wirbelthiere (Vertebrata). Dritter Theil des Entwurfs einer systematischen Stammesgeschichte. Pp. i–xx; 1–660.

Hay, O. P., 1895. On certain portions of the skeleton of *Protostega gigas.* Publications Field Columbian Mus., Zoöl., I, pp. 57–62, with pls. iv, v.

Hay, O. P., 1896. On the skeleton of *Toxochelys latiremis.* Publications Field Columbian Mus., Zoöl., I, pp. 101–106, with pls. xiv, xv.

Hay, O. P., 1898. On *Protostega*, the systematic position of *Dermochelys*, and the morphogeny of the chelonian carapace and plastron. Amer. Naturalist, XXXII, pp. 929–948, with 3 text-figures.

Hay, O. P., 1904. On some fossil turtles belonging to the Marsh collection in Yale University Museum. Amer. Jour. Science, XVIII, pp. 261–276, with pls. xi–xvi and 7 text-figures.

Huene, Fred. V., 1902. Uebersicht über die Reptilien der Trias. Geol. und Palaeont. Abhandl., VI (X), pp. 1–84, with pls. i–ix and 78 text-figures.

Lortet, L., 1892. Les reptiles fossils du bassin du Rhone. Archives du Muséum d'histoire naturelle de Lyon, V, pp. 1–139, with pls. i–xii and 10 text-figures.

Lydekker, R., 1889A. On certain chelonian remains from the Wealden and Purbeck. Quart. Jour. Geol. Soc. London, XLV, pp. 511–518.

Lydekker, R., 1889B. Catalogue of the fossil Reptilia and Amphibia in the British Museum. Pt. III, pp. i–xviii; 1–239, with 53 text-figures.

Portis, A., 1878. Ueber fossile Schildkröten aus dem Kimmeridge von Hannover. Palaeontographica, XXV, pp. 125–140, with pls. xv–xvii.

Rabl, Carl, 1903. Ueber einige Probleme der Morphologie Verhandl. Anatom, Gesellsch., xvii, Heidelberg, pp. 154–190, with pls. i, ii, and 22 text-figures.

Rütimeyer, L., 1873. Die fossilen Schildkröten von Solothurn und der übrigen Juraformation. Mit Beiträgen zur Kenntniss von Bau und Geschichte der Schildkröten im Allgemeinen. Neue Denkschr. schweiz. naturf. Gesellsch. Naturwiss., XXV, art. 2, pp. 1–185, with pls. i–xviii.

Vaillant, L., 1881. Mémoire sur la disposition des vertèbres chez les chéloniens. Ann. Sci. Nat. Paris (6), X, art. 7, pp. 1–106, with pls. xxv–xxxi.

Wieland, G. R., 1900A. The skull, pelvis, and probable relationships of the huge turtles of the Fort Pierre Cretaceous of South Dakota. Amer. Jour. Sci., IX, pp. 237–251, with pl. ii, and 6 text-figures.

Wieland, G. R., 1900B. Some observations on certain well-marked stages in the evolution of the testudinate humerus. Amer. Jour. Sci., IX, pp. 413–424, with 23 text-figures.

Wieland, G. R., 1902. Notes on the Cretaceous turtles, *Toxochelys* and *Archelon*, with a classification of the marine Testudinata. Amer. Jour. Sci., XIV, pp. 95–108, with 2 text-figures.

Wieland, G. R., 1903. Notes on the Cretaceous turtle *Archelon*. I. On the structure of the carapace. II. Associated fossils. Amer. Jour. Sci., XV, pp. 211–216, with 1 text-figure.

Wieland, G. R., 1904A. Structure of the Upper Cretaceous turtles of New Jersey: *Adocus*, *Osteopygis*, and *Propleura*. Amer. Jour. Sci., XVII, pp. 112–132, with pls. i–ix and 7 text-figures.

Wieland, G. R., 1904B. Structure of the Upper Cretaceous turtles of New Jersey: *Lytoloma*. Amer. Jour. Sci., XVIII, pp. 183–196, with pls. v–viii, and 6 text-figures.

Williston, S. W., 1901. A new turtle from the Kansas Cretaceous. Trans. Kansas Acad. Sci., XVII, pp. 195–199, with pls. xviii–xx.

Woodward, A. S., 1887. On "leathery turtles," recent and fossil, and their occurrence in British Eocene deposits. Proc. Geologists' Assoc., X, pp. 2–14.

Zittel, K., 1877. Bemerkungen über die Schildkröten des lithographischen Schiefers im Bayern. Palaeontographica, XXIV, pp. 175–184, with pls. xxvii, xxviii.

Zittel, K., 1889. Handbuch der Palaeontologie, III, pp. 437–632, with figures.