

Article II.—ON THE CLASSIFICATION OF THE REPTILES¹

BY R. BROOM

DEDICATED TO THE MEMORY OF SAMUEL WENDELL WILLISTON

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INTRODUCTION

One of Professor Williston's latest papers, published the year before his death, gives what may be regarded as his final conclusions on the very difficult subject of the "Phylogeny and Classification of Reptiles." No one recognized more fully than Williston the difficulties of making a satisfactory classification when so many of our types are little more than fragments, and he rather discouraged the attempts made by others. He

¹This and the following paper were written in 1919 with the view to their forming part of a proposed memorial volume, which was to be issued in honor of the late Samuel Wendell Williston. For various reasons, the project had to be abandoned, but I trust these papers will, at least, serve as a small wreath offered by one scientist to the memory of another.

From 1903 for ten years, Williston and I corresponded very regularly and threshed out many of the problems of the Permian reptiles and their affinities. I kept him constantly informed of all advances in South African paleontology, and he let me know of all that was being done in America. I met him when he was in London in 1913 and spent a most enjoyable time with him.

During the war our correspondence was interrupted but on my return to South Africa was resumed. Shortly before his death, he wrote me about his illness and, from the symptoms he described, I recognized the case as probably very serious,—more serious than he apparently believed. I wrote with much anxiety as to his condition, but he probably passed away before my letter arrived.

In all branches of science, America has played a very important part, but in paleontology in the past fifty years she has stood preëminent. Leidy, Marsh and Cope made paleontology almost exclusively an American science. Williston has done much to continue this preëminence, and when the history of the science comes to be written, Williston's name will be placed beside those of these other immortals.

says, "It is only hesitatingly that I have ventured, for the first time, to express in tabular form my own views."

Personally I have always considered that something was gained by even a very provisional classification which might contain much error. Professor Osborn's classification of 1903 has a good many things in it to which exception might be taken, and yet the main truth that it emphasized, that most reptiles can be divided into two subclasses, remains well established, and his groups Synapsida and Diapsida are with some slight modifications accepted by most workers including Williston himself, though for a time he objected to them.

Each classification has helped us a little farther on the road and the very free criticism of each has perhaps helped nearly as much; and I am very sure that, were Williston still with us, a very full and frank criticism of his latest classification would be much more pleasing to him than a mere blind acceptance of it as it stands.

In the classification of the reptiles there are only a few important points that remain in doubt, apart from the attempt to place forms that are very imperfectly known, such as *Eunotosaurus* or *Broomia* or *Mesosaurus*, and of these we need consider at length only the lizards, the chelonians and the plesiosaurs.

THE TEMPORAL BONES OF THE LIZARDS

By most scientists the lizards have been regarded as descended from some two-arched reptile somewhat resembling *Sphenodon*, but which lost the lower temporal arch and came to have a loose quadrate. Williston believed that the Squamata have no near relationships with the Diapsida, having sprung quite independently from a different cotylosaurian ancestor, and that they only resemble the rhynchocephaloid forms by convergence. He believed that *Aræoscelis*, with a single upper temporal fossa, had a type of skull from which the lacertilian was derived by "simple emargination of the broad lower temporal arch." Watson, though he does not wholly agree with Williston, also believes that the temporal arch of the lizard does not correspond to the upper arch of the Diapsida, but is really a latero-inferior arch thinned out from below and thus really homologous with the two arches of *Sphenodon*.

The two points in the structure of the lacertilian skull which have given rise to differences of opinion are, the nature of this temporal arch and whether it is homologous with the upper arch of *Sphenodon*, and the nature of two bones which lie above the quadrate in the post-temporal region. And on the solution we find to the latter problem, depend, to a considerable extent, the conclusions we must come to on the former.

In a typical lacertilian, such as *Varanus*, there are two bones, each of which has its posterior and lower end wedged in between the top of the quadrate and the outer end of the paroccipital. The outer bone passes upward and then forward and forms a long articulation with the post-orbital. The inner passes upward and forward and clasps the lower part of the posterior process of the parietal.

In agamids the outer bone articulates in front with both the post-orbital and the jugal and has an inner process which overlaps both the inner bone and the parietal. The inner bone lies mainly underneath the parietal, but it has a fairly large articulation with the paroccipital and also with the quadrate.

In many lizards one of the two bones is missing, but, as two are present in very different suborders or families, it is manifest that two bones in this region is the primitive condition.

It will be unnecessary to consider all the different interpretations that have been given to these two bones. The inner one has been regarded as the squamosal by Gegenbaur, Baur, Gaupp and Watson; the outer has been held to be the squamosal by Huxley, Parker, Cope, Boulenger and Williston. By Owen, Gegenbaur, Baur and Watson the outer bone has been considered to be the quadratojugal. Huxley, Parker, Cope and Boulenger have looked on the inner bone as a supratemporal, while Williston has identified it with the tabular. For many years, I held the opinion of Gaupp that the inner bone was the squamosal and the outer a new element which might be called prosquamosal or paraquadrate, but in 1913, as a result of the study of pythonomorph skulls in the American Museum, I became convinced that the outer bone must be looked upon as the squamosal, and the inner, as held by Williston, the tabular.

As the study of the lizard skull has led to such varied opinions, it is necessary to look to other forms for further help.

Watson thinks that the skull of *Pleurosaurus* in the British Museum specimen supports his conclusion that the outer bone is the quadratojugal and the inner the squamosal. A few years ago, I also examined this specimen but did not think Watson's conclusions were justified. The specimen as preserved is crushed very flat, and, while showing well the top of the skull, it gives no clear idea of the sides. Watson gives a side view restoration and makes the skull very low. In my opinion he makes it very much too flat. The reptilian eye is fairly spherical and the sclerotic plates show that it filled the orbit well. In Watson's restoration, it would be quite impossible to accommodate a spherical eye whose diameter was

about equal to the length of the orbit. Hence Watson's restoration of the temporal region must be in error. Either there was a deep continuous outer temporal wall, or there were two arches as in *Sphenodon*. Boulenger has recently reëxamined the skull of the allied *Saphæosaurus* and satisfied himself that it is undoubtedly a two-arched form, but he points out that it differs from *Sphenodon* in having both a supratemporal and squamosal.

The examination of the skull of *Youngina capensis* confirmed me in my opinion of the lizard temporal bones. In *Youngina* there is a large squamosal with a small quadratojugal below it and a small additional bone above. This upper bone, which I identify as the tabular, as I do the upper bone in the lizard, is the same as the bone which in *Saphæosaurus* Boulenger calls the supratemporal.

For further help I thought it might be well to study carefully the condition of affairs in the primitive, if very aberrant, *Chamæleon*.

In 1880 Kitchen Parker published an account of the structure of the *Chamæleon* skull. While showing the same care and marvelous minute dissection that characterizes all his papers, it unfortunately is marred by his having misunderstood the nature of the parietal region, and his great authority has led to the acceptance of his opinion by others. Methuen and Hewitt have corrected Parker's error.

In the genus *Chamæleon* as represented by *C. vulgaris* and *C. quilensis* we have a parietal which, from a transverse articulation with the frontal and small lateral articulation with the postorbitals, is produced backward as a narrow median crest. All this parietal was held by Parker to be the interparietal. The upper and posterior fourth of the orbital margin is formed by the large postorbital, which also sends a process backward to meet the squamosal and with it forms the temporal arch.

The bone which I hold with most others to be the squamosal is a triradiating bone. The anterior process, besides forming a long articulation with the postorbital, passes downward and meets the upper end of the jugal. The descending process, which is well developed, meets the upper end of the quadrate, while the lower end of the squamosal is supported by the paroccipital process. It is for the most part only indirectly so, as the little bone which I believe to be the tabular is wedged in between the two. There is, however, a small part of the squamosal that directly articulates with the paroccipital. The ascending branch of the squamosal passes right up to meet the parietal median crest almost in the middle line. In some specimens of *C. quilensis* they actually meet over

the top of the parietal, and this seems also to be the case in *C. dilepis*. Instances of squamosals approaching one another near the middle line are met with in many groups, such as Plesiosauria, Chelonina (e.g., *Hydromedusa*) and even Therapsida and Mammalia, but in no known groups do quadratojugals ever approach each other in the middle line. Yet this is the bone which is the undoubted homologue of the one in lizards that is held by Watson to be the quadratojugal.

The small bone which I call the tabular was well figured and described by Parker as the supratemporal. It is entirely on the occipital face of

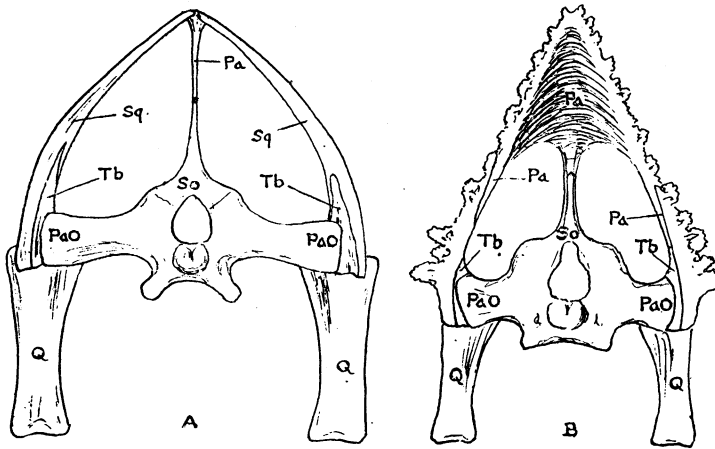


Fig. 1. A. Occiput of *Chamæleon quilensis*.¹

B. Occiput of *Lophosaura* sp., showing the relations of the tabulars to the neighboring bones.

the squamosal, with the lower part wedged between the squamosal and the paroccipital. It has a fairly large articulation with the quadrate. The upper end of the tabular reaches to the level of about the middle of the post-temporal arch.

The small chamæleons have a skull which differs so very greatly from the typical forms that they must be placed in a distinct genus, *Lophosaura* Gray. The typical chamæleons lay eggs; the species of the genus *Lophosaura* are viviparous. The most striking characters of the skull of *Lophosaura* are, that the parietal, instead of forming a narrow median crest, forms a fairly broad casque which sends down lateral

¹References to lettering in figures: A.C., Auditory capsule; Ang., Angular; Art., Articular; Bo., Basioccipital; Co., Coracoid; D., Dentary; D.M., Depressor mandibulæ muscle; E.O., Exoccipital; E.Pt., Epityergoid; F., Fr., Frontal; Ip., Interparietal; Ju., Jugal; L., Lachrymal; M.C., Meckel's cartilage; Mx., Maxilla; Na., Nasal; Pa., Parietal; P.Art., Prearticular; Pa.O., Paroccipital; Pmx., Premaxilla; Po.F., Postfrontal; Po.O., Postorbital; Pr.F., Prefrontal; P.S., Parasphenoid; Pt., Pterygoid; Q., Quadrate; Q.J., Quadratojugal; S.Ang., Surangular; S.O., Supraoccipital; Sp., Splenial; Sq., Squamosal; Tb., Tabular; T.M., Temporal muscle.

processes to become part of the post-temporal arches; that the squamosals have only short ascending processes and merely form part of the post-temporal arches; and that the prefrontals and postorbitals do not meet above the orbits.

The squamosals do not meet the jugals as they do in *Chamæleon*, but in some species they approach pretty close to them. The descending process of the squamosal is so short that it can hardly be looked on as a process at all. It is almost entirely separated from the paroccipital by the interposed tabular. Only for a very small space in front does it touch. In *L. tæniabronchus* the squamosal forms the greater part of the post-temporal arch, meeting and passing to the back of the descending parietal process. In another species of which I have the skull, probably *L. damaranus*, the post-temporal arch is formed almost as much by the parietal as by the squamosal, the parietal forming most of the inner and anterior side by a long, slender descending process.

On one side of this skull the descending process of the parietal nearly meets the tabular and on the other it forms an articulation with it.

The tabular is considerably smaller relatively than in *Chamæleon* and is mainly packed in between the end of the paroccipital and the squamosal. It has a fairly strong articulation with the quadrate.

While the study of the condition in the adult skulls of *Chamæleon* and *Lophosaura* leaves in my mind no doubt that the large bone is the squamosal, some doubt might remain as to whether the small bone is the supratemporal or tabular. The large bone agrees very closely in its relations with the large bone which is believed to be the squamosal in *Sphenodon*. It articulates in front with the postorbital as in *Sphenodon*, it supports the quadrate, and it has an ascending process for articulation with the parietal. There is, further, no doubt that the bone regarded as squamosal in *Sphenodon* is the same as the bone which is called squamosal in the therapsids and which, unquestionably, is the homologue of the mammalian squamosal. That it cannot be the quadratojugal scarcely requires any argument.

The small bone, if the large one is, as seems certain, the squamosal, must be either a supratemporal, a tabular or a neomorph. As the evidence from the adult skull is not as convincing as one would wish, I have examined a number of early developmental stages of the skull of *Lophosaura*, and the relations of the bones when they commence to ossify is very suggestive.

Most of the membrane bones of the temporal region ossify at the same time, but the squamosal and the postorbital ossify a little earlier

than the parietal, the jugal or the tabular. But in an embryo very slightly larger than that which shows the first ossification of the squamosal, we find all the other membrane bones well ossified. The tabular is so early and so well ossified, though it is so small a bone in the adult, that we may safely assume that it is a primitive skull element and not a

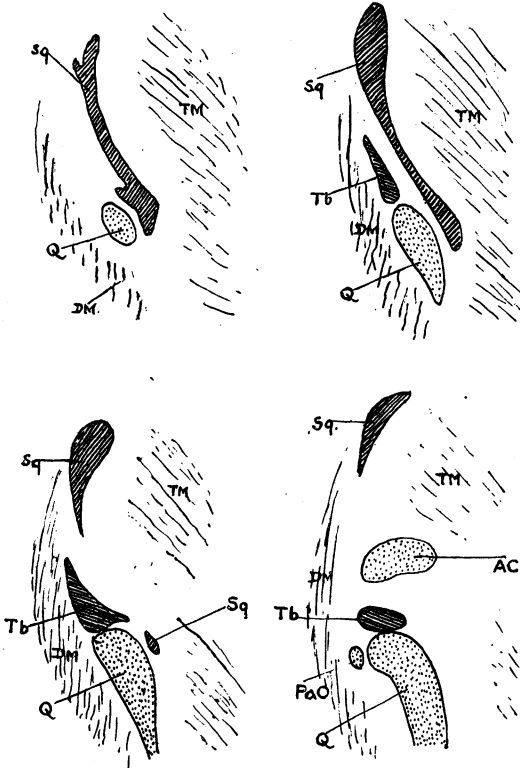


Fig. 2. Tangential sections (1, 4, 7, 10) through the upper end of the quadrate and associated bones of an early embryo of the chamæleon, *Lophosaura tæniabronchus* Smith, showing that, in this form, the supposed tabular is an occipital element practically excluded from the temporal fossa by the squamosal, and that it gives no attachment to any of the fibers of the temporal muscle, though giving attachment behind to part of the depressor mandibulæ.

neomorph. I have given a series of tangential sections of the quadrate region in an embryo *Lophosaura* of head length of 4.5 mm. The four sections given are all equidistant one from the other and may be numbered 1, 4, 7, 10. Section 1 is immediately outside the end of the tabular.

Section 4 shows the tabular supporting the quadrate and entirely behind the squamosal.

It will be observed that no fibers of the temporal muscle can approach the tabular, though, posteriorly, it gives an attachment to the muscle which pulls up the posterior angle of the jaw. Section 7 shows the relations of the muscles even more fully; and, though here the squamosal is no longer in front, there are no fibers of the temporal muscle near it. The next section, which is through the inner corner of the tabular, shows that, though the squamosal is no longer in front, a large part of the auditory capsule is seen in front, and, though the squamosal as ossified is not quite in contact with the paroccipital, we know that it is in contact in the adult and that there are certainly no muscular fibers passing between. So that, in reality, the tabular is practically shut out from the temporal fossa and is entirely a bone of the occiput.

The supratemporal is, really, in the stegocephalians and those cotylosaurs in which it occurs, a roofing bone of the temporal fossa which doubtless gave attachment to a portion of the temporal muscle. The tabular, though it is originally a bone of the top of the skull, in stegocephalians is largely an occipital element, and, in most early reptiles in which it is retained, purely an occipital element. Normally it is situated between the interparietal and parietal above and passes down between the paroccipital and the squamosal below. If the small bone in lizards is one of these two elements, as seems pretty certain, it appears to me that it must be regarded as the tabular.

Watson says, "In the great majority of Therapsids a tabular is present. In all cases it lies entirely behind the parietal and squamosal."

Having considered the question of the homology of the two bones and seen reasons for regarding the upper as the tabular and the outer bone the squamosal, let us consider whether we have good reason for holding that the lizards have lost the lower arch or whether Watson is right in regarding the lizard arch as representing both arches of *Sphenodon* and our supposed squamosal as the quadratojugal.

Many years ago I became convinced of the truth of that part of the recapitulation theory which holds that developing embryos frequently retain ancestral characters which are lost in the adults; and, in dozens of embryos of reptiles, birds and mammals that I sectioned in my hunt for such ancestral features, a good many startling discoveries were made. I found that the early marsupial has a monotreme-like coracoid which articulates with the sternum; that the ostrich embryo has four digits in the manus and five in the pes, and that the human foetus has the central

carpal element. I examined the lizard embryo to see if there were any evidence of a fixed quadrate and found that there was very distinct evidence thereof.

As the paper in which I described my results has been lost sight of, I think it may be well to reproduce some of the figures, which are very striking. I could discover no trace of a quadratojugal bone, but I found

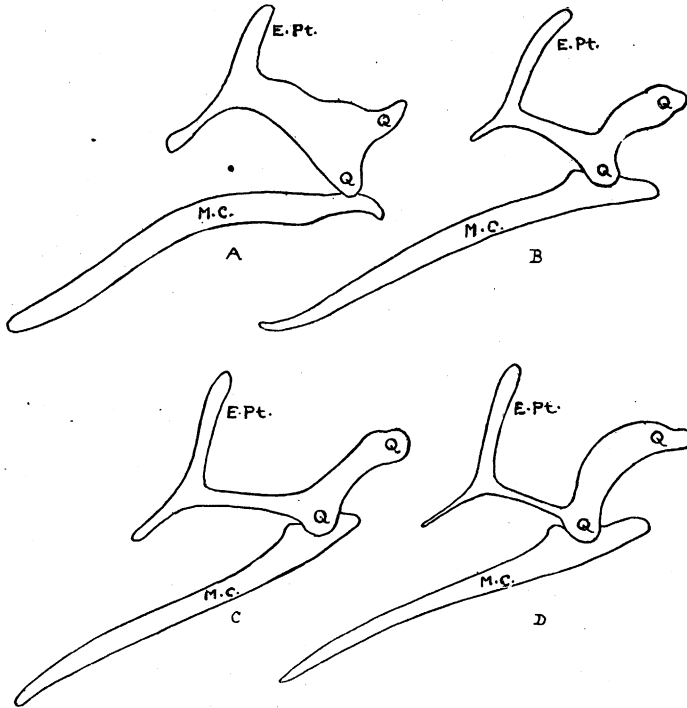


Fig. 3. The lower jaws with quadrate, epipterygoid and connecting cartilaginous bar in embryos of A, *Sphenodon punctatus* Grey (after Howes and Swinnerton); B, *Eremias capensis* Smith; C, *Zonurus polygonus* Smith; D, *Mabuia sulcata* Peters; showing that lizard embryos have a fixed quadrate almost exactly as in *Sphenodon*.

in such different lizards as *Zonurus*, *Eremias* and *Mabuia* a well-developed cartilaginous bar fixing the lower end of the quadrate to the lower end of the epipterygoid almost exactly as in *Sphenodon*, and in *Agama* and *Lophosaura* distinct remains of the bar, though here it is no longer chondrified. The resemblance to *Sphenodon* is so close that we can safely homologize regions, and as in *Sphenodon*, the small quadratojugal is situated at the lower end of the quadrate. We may be certain that the

ancestral lizard quadratojugal was also in this region. In *Youngina* the quadratojugal is also low down in a line with the jugal. The quadratojugal ligament is doubtless the remains of the lower arch in the lizard. If a bony arch is replaced by a ligamentous one, the bones that formed the arch can cease to be ossified, but they cannot wander away.

DERIVATION OF THE LIZARDS

There is nothing in the girdles or feet that does not support the view that the lizards are derived from a form near the ancestor of *Sphenodon*, but from a form which still retained the two bones in the temporal region. *Sauranodon*, *Pleurosaurus* and *Saphæosaurus* give us some indications of what the ancestral condition of the temporal region was like. *Sphenodon* may be regarded as a primitive lizard which still retains the quadratojugal but has lost the tabular, or, as Boulenger would prefer to call it, the supratemporal.

There is one other probably allied group to which reference may be made,—the Thalattosauria of Merriam. Unfortunately, the group is not so well known as one would desire, and no known specimen has the temporal region perfect. If Merriam's restoration of the top of the skull be compared with Lortet's figure of *Sauranodon* or Watson's of *Pleurosaurus*, it will be observed that there is a very considerable resemblance between them, and that all that is missing from the upper part of the temporal region is the tabular. When the tabular is restored, it will be seen that the Thalattosauria are aquatic forms closely allied to the land animals from which branched off the lizard *Sphenodon* and the *Sauranodontidæ*.

RELATIONSHIPS OF THE CHELONIA

The second group of reptiles which has given rise to trouble is the Chelonia, and there is no order of reptiles living or extinct concerning whose affinities greater differences of opinion have been expressed. Had the order been extinct, known only by imperfect specimens, one could easily have understood the uncertainty, but it is an order represented by very many living species inhabiting most parts of the world. The anatomy of typical examples is as well known as that of the frog, and thanks to the lamented Mitsukuri, the embryology is as completely known as that of almost any living vertebrate.

Unfortunately, the members of the order are all extremely specialized and in some respects degenerate, so that the picking out of the ancestral characters amid the more recent specializations is somewhat like the reading of a difficult palimpsest.

The principal views that have been expressed are: (1) that the chelonians are allied to the rhynchocephalians; (2) that the nearest allied forms are the plesiosaurs; (3) that they are allied to the anmodonts, and (4) that they are modified cotylosaurs.

It will be unnecessary to discuss at any length these various views, nor would it be possible for me to do so fully or satisfactorily, writing as I am seven hundred miles from the nearest scientific library. Watson, in his recent paper "*Eunotosaurus africanus* Seeley and the Ancestry of the Chelonia,"¹ has dealt at considerable length with what he considers to have been the characters of the hypothetical ancestor "Archichelone." He considers the skull to have been a completely roofed skull such as is seen in the Cotylosauria and that the girdles were of the "old-fashioned" type,—the shoulder girdle having the primitive two coracoidal elements and the pelvis a plate-like pubis and ischium. Were this so, there could be little doubt that the chelonians sprang directly from some cotylosaurian ancestor and that they are not nearly related to any of the later reptiles. The limbs he also holds are such as might readily be derived from a cotylosaurian type. Versluys had previously, though very guardedly, expressed the opinion that the ancestor of the Chelonia may have been a cotylosaur, and Williston had made the same suggestion as early as 1907.

Watson obtains considerable support for his view from the remarkable South African fossil reptile *Eunotosaurus*. This imperfectly known animal has eight greatly developed broad ribs, which certainly have a considerable resemblance to a chelonian carapace, and the shoulder girdle and pelvis are apparently of the primitive type. He concludes that "so far as the structure is known, *Eunotosaurus* agrees exactly with the hypothetical 'Archichelone'" and that "it is by no means improbable that it is an actual ancestor of the Chelonia." He adds "whether it be or not it does, I think, give us a great many suggestions of the changes which must have taken place during the development of the Chelonian shell and all that it implies."

Eunotosaurus is unfortunately imperfectly known. We know very little of the skull, only a little of the girdles and nothing of the manus and pes. We do not know whether the skull is roofed, and certainly the vertebræ so far as known differ greatly from those of any known cotylosaur. The large ribs do not meet to form any sort of carapace but really overlap and are apparently freely movable. The specimen (B. M. 4054) figured by Watson is, apparently, not much crushed, and it seems to

¹1914. Proc. Zool. Soc., p. 1011.

show that the body of the animal was deeper than broad, and, as the limbs so far as known are relatively very feeble, we seem forced to the conclusion that the animal must have been an aquatic form. But, till a really good specimen of *Eunotosaurus* is discovered, it will be quite impossible to form any definite conclusions as to its affinities.

The chelonian is manifestly an extremely aberrant type, where the ancestral characters are so obscured by their being intermingled with remarkable specializations that it is very difficult to tell which is which, and our idea of the structure of "Archichelone" will entirely depend on which characters we regard as primitive. Those who regard the structure of the temporal region of the skull as the safest guide to affinity will naturally place the chelonians either with the primitive mammal-like reptiles or the cotylosaurs; those who hold that more reliance can be placed on the structure of the girdles and limbs will be more impressed with the affinities to the primitive diapsids such as *Sphenodon*.

Cope, Smith Woodward, Osborn and others have shown how extremely important the structure of the temporal region is as a guide to classification. In the mammal-like reptiles we have a temporal arch formed by the squamosal and jugal which scarcely shows any alteration in structure from the pelycosaurs to such varied groups as the dinocerophalians, the anmodonts, the dromasaurians, the therocephalians, the gorgonopsians, the cynodonts and even on to the mammals. Then again we have a large number of reptilian orders in which we find with little variation two temporal arches,—an upper postorbito-squamosal and a lower quadratojugo-jugal arch. All reptiles whose arches conform to one of these two types we can place with such confidence that there is rarely any difference of opinion. But all those whose arches are anomalous have given rise to the greatest difference of opinion,—lizards, snakes, placodonts, plesiosaurs, ichthyosaurs and chelonians.

While everyone must agree to the extreme importance to be placed on the structure of the temporal arches, it must be admitted, nevertheless, that we do occasionally find most remarkable variations in the structure in even allied forms. We have merely to look at the different suborders or families of the Lacertilia to see how unreliable the structure of the temporal region may become as a guide to classification.

Let us look at three well-marked common lacertilian types such as are lying before me,—a varanid, *Varanus*, an agamid, *Chlamydosaurus*, and a scincid, *Cyclodus*. All will agree that they belong to the Lacertilia, but the arches differ considerably. In the agamid, there is a powerful postorbital arch formed by the jugal and the postorbital, and a large

supratemporal fossa bounded mainly by the parietal and the postorbital. In the varanid, the jugal is rudimentary and there is no complete post-orbital arch, but the supratemporal fossa is bounded essentially as in the agamid. In the scincid, there is a postorbital arch formed mainly by the jugal, but when we look for the supratemporal fossa, we find the top of the skull completely roofed. There is a broad parietal which, laterally, meets the long postorbital and, more posteriorly, the bone which I regard as the squamosal. Here there can be no doubt that the upper temporal fossa has become lost by the parietal and the postorbital coming together.

In other lacertilian types we can see the intermediate stages. If Watson be right that the lacertilian ancestor never had an infratemporal fossa and that the lateral broad bony arch became emarginated from below, then the scincid skull is as much a completely roofed skull as that of the chelonian, and there is exactly the same amount of evidence in favor of the scincid's being descended directly from a cotylosaurian ancestor as there is in the case of the chelonian, and, curiously enough, exactly the same bones form the roof,—a broad parietal with, laterally, the post-orbital and the squamosal. Yet we know beyond all doubt that the scincid is not a direct descendant of a cotylosaur; and thus we see how very misleading the condition of the temporal region may become.

It is only a very few chelonians that have a roofed skull at all. The large majority have an open temporal region. And, if it by no means follows that a roofed temporal region indicates a cotylosaurian ancestry, then there is not a single other scrap of evidence pointing to such affinity, while I hold that there is the very strongest evidence pointing to a quite different ancestry.

Apart from the development of the carapace and plastron, the most remarkable feature of the chelonian structure is the peculiar shoulder girdle. This consists of a long rod-like scapula from whose lower end there passes inward a long rod-like prescapular process and a long slender coracoid. It has been suggested by various authorities that the prescapular process is a precoracoid, but there is not the least doubt that, as held by Baur, it is a true scapular development, and that there are only two cartilage-bone elements in the girdle, the scapula and the coracoid. An anterior scapular development of this sort is met with in only a very few forms, such as the plesiosaurs and the ostrich, and it is evidently a provision of nature for a large ventral muscular attachment, where one of the original coracoidal elements is lost. It could not occur in any form where both coracoid and precoracoid were present, and it is, to me, conclusive proof that the chelonian is not nearly related to the therapsids

but is descended from a lizard-like ancestor which had already lost one of the coracoidal elements.

The pelvis and the tarsus are very like those of *Sphenodon*, and Goodrich considers that the similar specialization of the fifth metatarsal in the two types is evidence of a close affinity, apparently implying that the common ancestor had this character. Though I agree with Goodrich that the Chelonia are much more nearly related to *Sphenodon* than to the mammal-like reptiles or even to the cotylosaurs, I do not consider that the common ancestor had either an open pelvis or a hooked fifth metatarsal. Most early rhynchocephaloid reptiles have a plate-like pelvis, and the earliest known form, *Youngina*, has not only a plate-like pelvis but also a moderately straight, unhooked fifth metatarsal, and it even retains the fifth distal tarsal.

It is much to be regretted that we do not know the skull of *Protorosaurus* thoroughly. There is some reason to believe, however, that it has only a single supratemporal fossa, and, if this be so, it must be pretty near to the lizard-like forms with the single upper opening, from which I believe the Chelonia must have sprung. It is held by Goodrich to have a hooked fifth metatarsal, and there seems to be evidence of a plate-like pelvis opening up. If *Protorosaurus* has only a single temporal opening, and thus is near the chelonian ancestor, then the evidence will be fairly strong in favor of both the hooked fifth metatarsal and the lizard-like pelvis of the Chelonia and the Rhynchocephalia having been independently formed by convergence. And, further, if the lizards and *Sphenodon* are both derived from a *Youngina*-like form, then the striking resemblance in the pelvis and tarsus of these must also have been due to convergence.

It would appear as if any Permian or Triassic reptile with the primitive plate-like pelvis and simple tarsus which took on a lizard-like habit developed independently—apart altogether from the structure of the skull—an open pelvis and a hooked fifth metatarsal. In the light of the paleontological evidence, it is much easier to believe this than that all forms with a hooked fifth metatarsal inherited this from a common ancestor which had this character. If we try to accept this latter view of Goodrich, our difficulties are overwhelming in connection with primitive two-arched forms such as *Youngina*, which is a typical diapsid or sauropsid, yet has not the hooked fifth metatarsal. We cannot admit the possibility of *Youngina*, like most dinosaurs, having lost the character, for the retention of the fifth distal tarsal renders it certain that no ancestor of *Youngina* could ever have had a hooked fifth metatarsal.

All the evidence at present available from comparative anatomy, embryology and paleontology seems to me to point to the chelonians having arisen from an Upper Permian or Lower Triassic somewhat lizard-like reptile which had a skull not unlike that of *Sphenodon*, but with only a supratemporal fossa, a shoulder girdle of the *Sphenodon* type, a plate-like pelvis and an unspecialized fifth metatarsal. Before any chelonian-like specialization took place, a more lizard-like habitus gave rise to a *Sphenodon*-like pelvis and a specialized hook-like fifth metatarsal.

Beyond this point we have no clear light to guide us, but possibly what happened was that the lizard-like ancestor became a semiaquatic, swamp-and-mud-frequenting animal, and, as a result of this change in habit, the body became broad and flat, and protecting dermal ossifications arose. The feeding on soft succulent plants and weeds led to the loss of the teeth and the development of a horny beak. The great development of the temporal muscle for the wide-snapping jaw led to the loss of the post-temporal arch in most types, though in some chelonians (e. g., *Hydromedusa*) this is still retained. The large majority of chelonians are still fresh-water-and-swamp-frequenting animals. Only a few have become dry-land forms, while others are pelagic.

RELATIONSHIPS OF THE PLACODONTIA

There is another group of reptiles which has caused some difficulty, namely, the Placodontia. As, however, we know little of the skeleton except the skull, few have ventured any very definite opinion as to their affinity. In 1861, Owen referred them to the Sauropterygia, but, in later life, thought the affinities were rather with the Anomodontia. Seeley definitely regarded the Placodontia as a suborder of the Anomodontia. Lydekker regarded the ordinal position as quite uncertain. Osborn, in his 1903 classification, followed Seeley's view.

More recently there has been a tendency to revert to Owen's early opinion and place the placodonts somewhere near the sauropterygians. Until we know something of the postcranial skeleton, the problem will remain in doubt, but there are two groups with which the skull seems to show more affinity. At first sight, the skull looks very unlike that of a chelonian, but, on more careful examination, there are seen to be some striking resemblances. The placodontian palate is a very remarkable type. The pterygoids are large flat bones which are firmly sutured to each other in the middle line and from the roof of the mouth to near the back of the skull. Laterally, they are firmly articulated with the large quadrates. This very unusual condition is found

elsewhere only among the chelonians and sauropterygians. The occiput of a placodont such as *Placochelys* is fundamentally so surprisingly similar to that of the chelonian that one is forced to the conclusion that the two types are closely related. For, while the occiput is almost chelonian in type, it is unlike that of any other reptiles except that

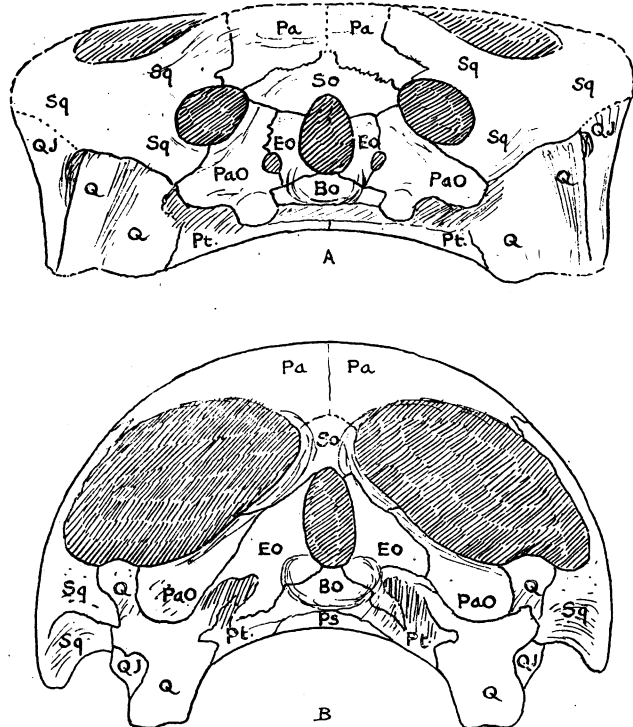


Fig. 4. A. Occiput of *Placochelys placodonta* Jaekel. After Jaekel, with the dermal ossifications omitted.

B. Occiput of *Dermochelys coriacea* Linn. After Nick.

A comparison of the two shows that the types are essentially similar, the chelonian differing from the placodont only in having lost the post-temporal arch, and in sometimes having, as in *Dermochelys*, the temporal fossa secondarily roofed by a posterior extension of the postorbital arch.

of the plesiosaurs and ichthyosaurs, with which it has some affinity, though more remote than with the chelonian. If we compare the side view of the skull of *Placochelys* with that of a chelonian like *Emys*, we again see the striking resemblance.

Of course there are the two great differences which have prevented the affinity from being generally recognized,—the presence of teeth and of a post-temporal arch in the placodont. But some ancestor of the Chelonia must have had teeth, and there is good reason to believe that the early chelonians also had a post-temporal arch. If this be so, then the placodonts may be merely highly specialized proto-chelonians, and the discovery of a very chelonian-like carapace in *Placochelys* strongly confirms this view.¹

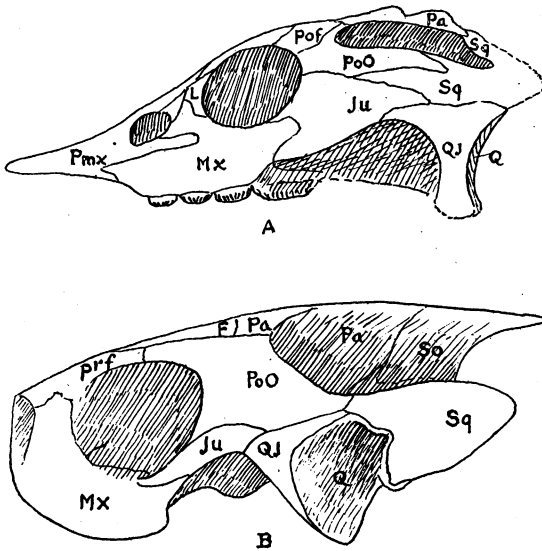


Fig. 5. A. Skull of *Placochelys placodonta* Jaekel. After Jaekel, with the dermal ossifications omitted.

B. Skull of *Emys orbicularis* Linn. After Rabl. Showing the similarity in the structure of the jugal arch in the two types.

RELATIONSHIPS OF THE PLESIOSAURIA

One other group which has given rise to much difference of opinion is the Plesiosauria. Andrews has recently summarized the principal different views that have been expressed, as follows:

Many writers (e.g., Baur and Fürbringer) have considered that there is a close relationship with the Chelonia, but the many objections to this view which have been summed up by Williston and Hay render it untenable. Broom considers that the group sprang from a land ancestor somewhat resembling *Sphenodon*, but with the supra-

¹Or, in other words, the chelonians may be regarded as the descendants of a placodont-like type which became edentulous and ultimately lost the post-temporal arch.

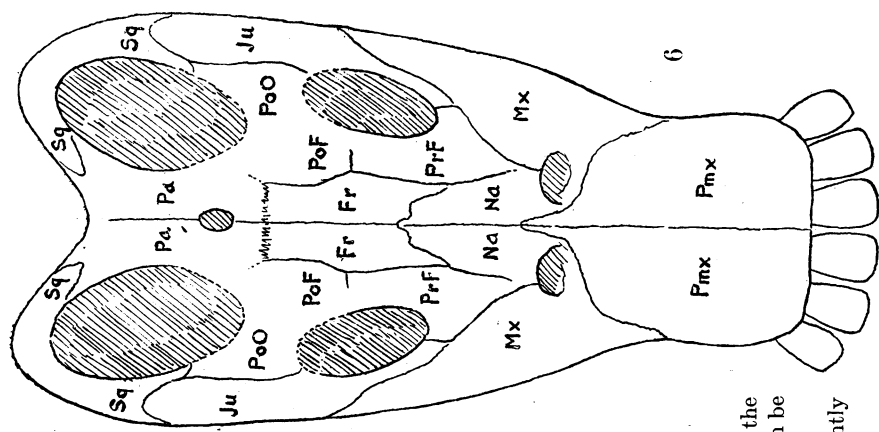
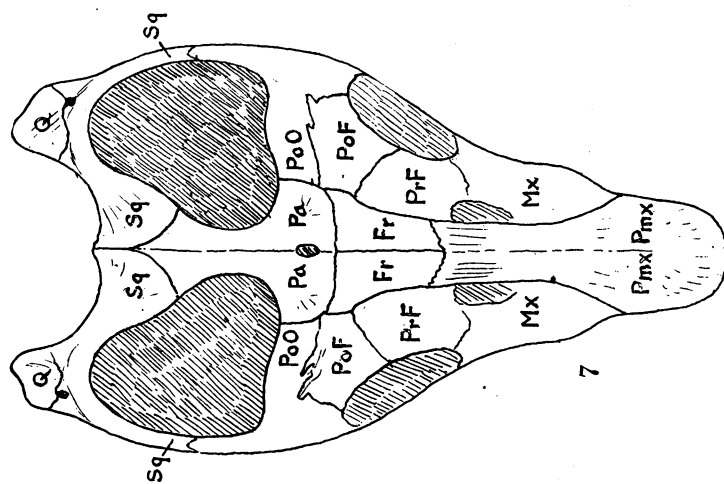


Fig. 6. Skull of *Placodus gigas* Agassiz. From a specimen in the British Museum. The sutures in line are those that I believe can be traced in the specimen.

Fig. 7. Skull of *Plesiosaurus macrocephalus* Buckland. Slightly restored from the very fine skull in the British Museum.

temporal fossa alone developed; Jaekel, on the other hand, considers that both fossæ were developed, but that the lower temporal bar had been lost. The present writer [Andrews] also, chiefly on account of the structure of the palate, once regarded the Sauropterygia as descended from a primitive Rhynchocephalian reptile. Boulenger considers, as Seeley did, that *Mesosaurus* is closely related to the Sauropterygia; but the skull in *Mesosaurus* is too imperfectly known to be certain of its relationships

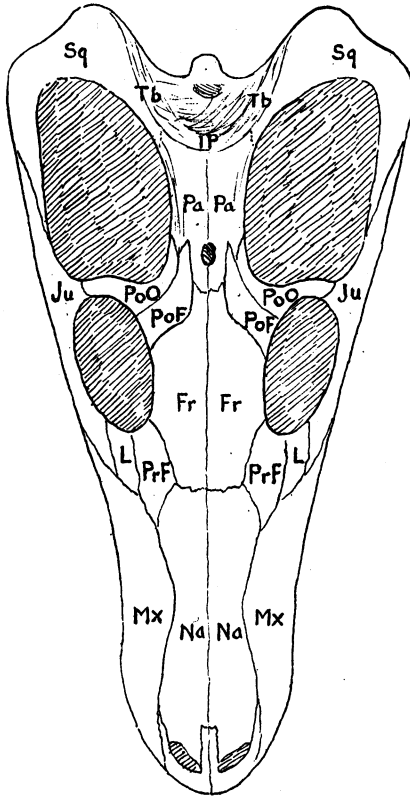


Fig. 8. Skull of a therocephalian, *Scylacosaurus sclateri* Broom, for comparison with the plesiosaurian skull.

either to the Sauropterygia or any other order, though it has been referred by Osborn to the Diaptosauria, a group including the primitive Rhynchocephalian types. A. S. Woodward and Williston, especially the last-named author, consider the group as nearly related to the Theriodontia.

Andrews discusses at considerable length the characters probably found in the ancestral plesiosaurian and concludes that it was related to the Dromasauria or to the primitive therocephalians.

The view which I expressed fifteen years ago, I have never seen any reason to change, and I am to-day more convinced than ever that it is correct.

The plesiosaurian skull is thoroughly well known, though only a very few good specimens have been discovered. The specimen which best shows the structure of the upper side is the skull of *Plesiosaurus macrocephalus*, figured many years ago by Andrews, and of which I give two new drawings differing in a few very minor points from that given by

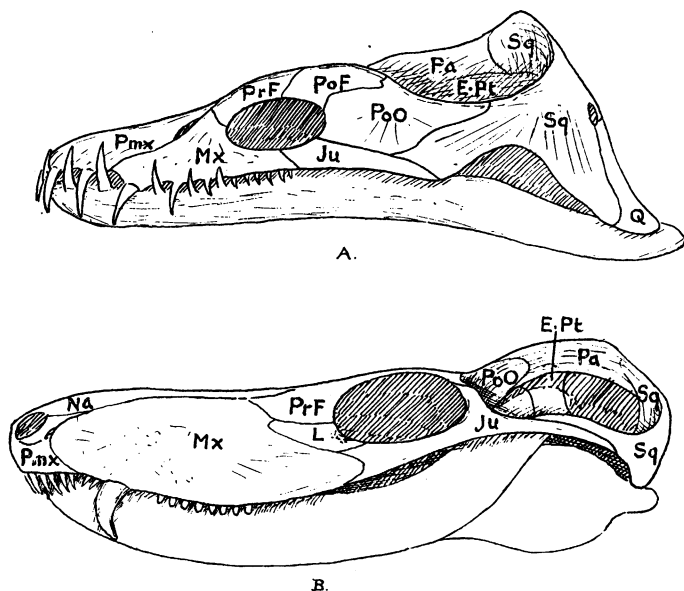


Fig. 9. Skull of *Plesiosaurus macrocephalus* Buckland, A, and skull of *Ictidosuchus longiceps* Broom, B, to show the resemblances and differences between the skull of a plesiosaur and that of a primitive therocephalian. The figure of the plesiosaur skull is slightly restored from the very fine skull in the British Museum; the figure of the *Ictidosuchus* skull is slightly restored from the type specimen.

him. Apart from the specializations seen in the plesiosaurian, it must be admitted that the general resemblance to the therocephalian skull shown is considerable. In each there is a single temporal fossa which, in the former, is bounded by the postorbital, the squamosal and the parietal, and, in the latter, by the postorbital, the jugal, the squamosal and the parietal.

Are the fossæ, however, really homologous? If the therocephalian skull and those of allied forms were unknown, I do not think anyone would

for a moment hesitate in concluding that the fossa in the plesiosaurian is the homologue of the upper fossa of the typical diapsidans. Yet we know from the position of the bones in allied groups that the fossa in the Therocephalia is originally a lower fossa which gradually encroached on the postorbital and squamosal above till it has reached the parietal and looks almost like a union of both the diapsidan fossæ.

But, apart from the resemblance of the fossæ, which I believe to be secondary, and primitive characters, such as the rhynchocephaloid structure of the palate, the two skulls do not greatly resemble each other, and in one or two points differ very fundamentally.

The plesiosaurian occiput is very unlike that of any therapsidan or even of the more primitive American pelycosaurs,—so very unlike that it is difficult even to compare them. Yet it resembles very considerably those of primitive diapsidans.

The mandible has been described by Andrews from a number of good specimens, but one or two new drawings will not be superfluous, considering the importance of the subject, and also as I have been able to discover a prearticular in both *Peloneustes* and *Plesiosaurus* which Andrews had not observed. In all specimens in which the back part of the inner side of the mandible is well preserved, a small prearticular can be seen in the situation indicated in the figures.

The plesiosaurian mandible will be seen to have very little resemblance to that of the therocephalians, though it has undoubtedly some considerable likeness to that of the dinocephalians and pelycosaurs, but not more than it has to that of primitive diapsidans.

The vertebræ and ribs in the plesiosaur are very unlike those of any therapsidans, but considering the great specializations in the former for an aquatic life, one can hardly expect much evidence of affinity from the vertebræ.

When we come to consider the structure of the girdles and limbs, we get evidence of a very clear and positive nature.

The shoulder girdle is fully known in a large number of genera. It consists of a very large coracoid which meets its neighbor in a large median suture, and a curiously twisted scapula which has a short upward and outward process and a large anterior and inward-passing process which, in many genera, also meets its neighbor in the middle line. Fundamentally, the shoulder girdle is strikingly similar to that of the chelonian and it seems probable that the two have a common origin. The type is known in no other reptiles, living or extinct.

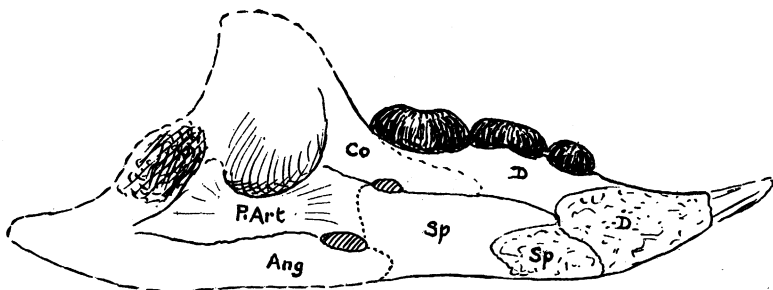


Fig. 10. Inner side of mandible of *Placodus* sp. Much reduced. Slightly restored from specimen in British Museum.

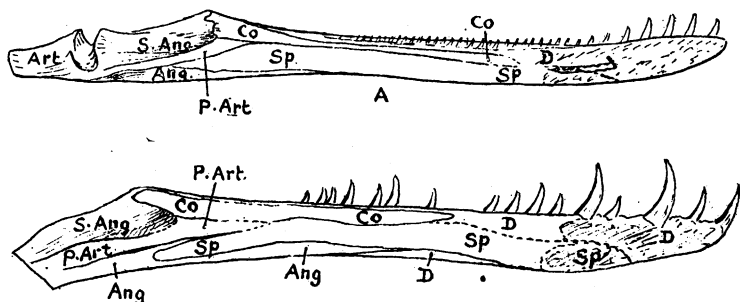


Fig. 11. A. Jaw of *Peloneustes philarchus* Seeley, B. M. 3803. Inner side. Reduced.

B. Imperfect lower jaw of *Plesiosaurus rostratus*, B. M. 38525. Inner side. Reduced.

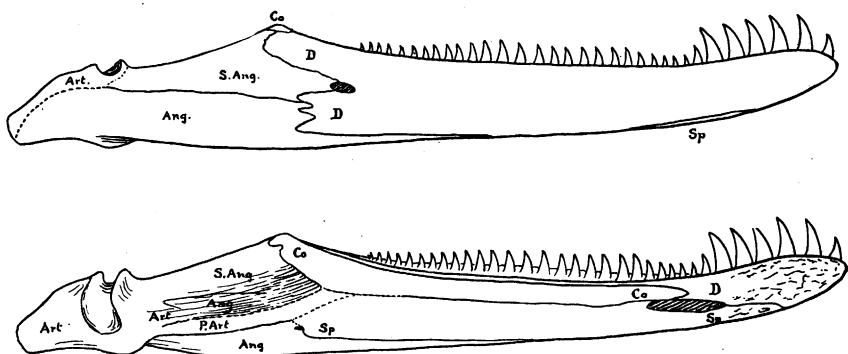


Fig. 12. Lower jaw of *Peloneustes evansi* Seeley.

In the Dromasauria and all other Therapsida and in the pelycosaurs there are always two ventral coracoidal elements, and the plesiosaurs are manifestly animals that require a large ventral support for the shoulder girdle. Had they been evolved from any therapsid, they would have retained the two coracoidal elements. The plesiosaur in its evolution must have come from a land ancestor which had already lost one of the coracoidal elements, and, as a large ventral support was necessary with the change of habit, there must first have been developed an antero-ventral process from the scapula such as we find in the chelonian, and later there was a great increase in size of both this process and of the coracoid. The shoulder girdle condition affords to my mind quite conclusive evidence that the plesiosaur was not derived from any therapsid or theromorph.

The pelvis of the plesiosaur, like the shoulder girdle, gives convincing proof that the ancestor was not a therapsid. All primitive therapsids have what is called a plate-like pelvis, where the ventral elements are a large rectangular pubis with a foramen and completely sutured to a somewhat elongated ischium. The early diapsidans also have a similar pelvis. At first sight, the plesiosaurian pelvis looks very similar but, on more careful examination, it is seen to be entirely different. It has a large rectangular pubis and an elongated ischium, but the pubis has no foramen and it is separated from the ischium by an obturator foramen. Though, by convergence, the pelvis has come to resemble that of the primitive Therapsida, it cannot have been derived directly from such a pelvis nor can it have come even from the plate-like pelvis of a primitive diapsidan. It must have come from a triradiate pelvis of a land ancestor, —a pelvis such as is seen in the chelonians and fairly similar to that seen in *Sphenodon*.

The foot structure shows that there has been a large fifth metacarpal and that the land ancestor must have had a foot like *Sphenodon*, —a type of foot never found in any therapsid or theromorph.

CONCLUSIONS ON THE PHYLOGENY AND CLASSIFICATION OF THE REPTILES

All the lines of evidence from the skull, girdles and feet seem to me to point conclusively to the plesiosaur's having been derived from a land ancestor on the diapsidan line, but a little more primitive than the diapsidan, and which had, by a lizard-like habit, independently evolved a triradiate pelvis.

It is further difficult to avoid the conclusion that the chelonian must also have been evolved from just such an ancestor, and, if this be so, we

must regard the plesiosaurs and the chelonians as nearly related groups, though, each having specialized in different ways, they are so very unlike each other.

Eunotosaurus is too imperfectly known to enable us to say anything definite about its affinities. In having eight pairs of enlarged ribs it looks like a primitive chelonian, yet the ribs overlap and were doubtless movable. *Mesosaurus* and a number of other aquatic forms have enlarged ribs, and I do not think the evidence that *Eunotosaurus* is an ancestral chelonian is at all conclusive.

If we now take (1) the Diapsida, as including all the two-arched orders, together with the Squamata, which I believe to be a modification of the same type, (2) the Synapsida, as including the mammal-like Therapsida and the more primitive theromorphs of America, (3) a third group of primitive reptiles with fully-roofed skulls, i.e., the Cotylosauria, and (4) a fourth group which would include the Sauropterygia and the Chelonia, then it will be seen that only a very few forms are left for consideration and, with the exception of the ichthyosaurs, none of them at all fully known.

The Ichthyosauria form a very isolated, highly specialized group of aquatic animals distinctly more primitive than the plesiosaurs. Concerning their origin and affinities we know very little. Years ago, not knowing where else to place them, I gave them a separate origin from the cotylosaurs, as had previously been done by Cope, though I was not then aware of it. The skull has a very manifest upper temporal fossa; the shoulder girdle has lost one of the coracoidal elements, and the pelvis has been derived from a triradiate type. We are probably, therefore, justified in concluding that the ichthyosaur is derived from a lizard-like land form which had advanced some short distance along the diapsidan line, but not quite so far as the point where the chelonians and plesiosaurs were given off.

One or two forms that may perhaps be allied to the ichthyosaurs are *Mesosaurus*, *Protosaurus*, *Heleosaurus* and *Broomia*. All are primitive long-snouted forms, but in none is the skull fully known. In each the shoulder girdle has only a single ventral element and the pelvis is of the plate-like type. The skull will probably prove to have a single upper temporal fossa.

Having given a little consideration to the more important groups concerning whose affinities there has been some difference of opinion, we may now briefly consider what may have been the main lines of evolution of the reptiles.

The Cotylosauria are held by all to be the most primitive reptilian superorder, or class. They form a rather heterogeneous group, and most of the forms known are too specialized to have been ancestors of any of the later reptilian orders. But there were certainly many small generalized types, and, from one of these, all the later reptiles were derived.

Very early there arose a branch probably of small broad-headed forms which developed a lower temporal fossa for the greater accommodation of the temporal muscle. From these were evolved, first, the theromorph types so well known from the Lower Permian of America, and later the therapsid types of the Upper Permian and Trias of South Africa. These latter, while retaining the two coracoidal elements and for a long time the plate-like pelvis, became further specialized by having the legs developed for walking and running, with the body well off the ground. From some higher therapsid arose the Mammalia.

From another branch of small lizard-like forms arose all the other reptiles. The early forms had probably a skull essentially like that of *Ichthyosaurus* but without the specializations. *Aræoscelis* of Williston is probably very near to these ancestral forms, and *Mesosaurus* is one of the earliest modifications for aquatic life. *Aræoscelis* still retains the ancestral two coracoidal elements, but very early one of these was lost,—I believe the posterior, as is certainly the case in *Varanops*,—and in all later forms only the one element remains, often much enlarged.

The ichthyosaurs are the result of an extreme aquatic specialization of one of the earlier lizard-like members of the group.

The chelonians and plesiosaurs are specializations from a later lizard-like form,—the one becoming a slow-moving, heavily-armored, swamp-frequenting type, and the other adapted for an aquatic life in comparatively shallow water.

For this group of primitive reptiles a new name seems required. Enaliosauria might be retained in an extended sense, but one can hardly expect the tortoises to be considered as enaliosaurs. In harmony with the terms for the other two large groups of reptiles, the Synapsida and the Diapsida, the name Anomapsida might be given.

The Diapsida, the third large group of the later reptiles, arose in Permian times doubtless from an anomapsid ancestor by the formation of a lower temporal fossa in addition to the upper one. The earlier group seems to have been unsuited for an active land life, and, except the chelonians, which took on a most remarkable specialization, the only other types that were successful were those that became long-headed and adapted for a semiaquatic or aquatic life. But, as soon as the lower

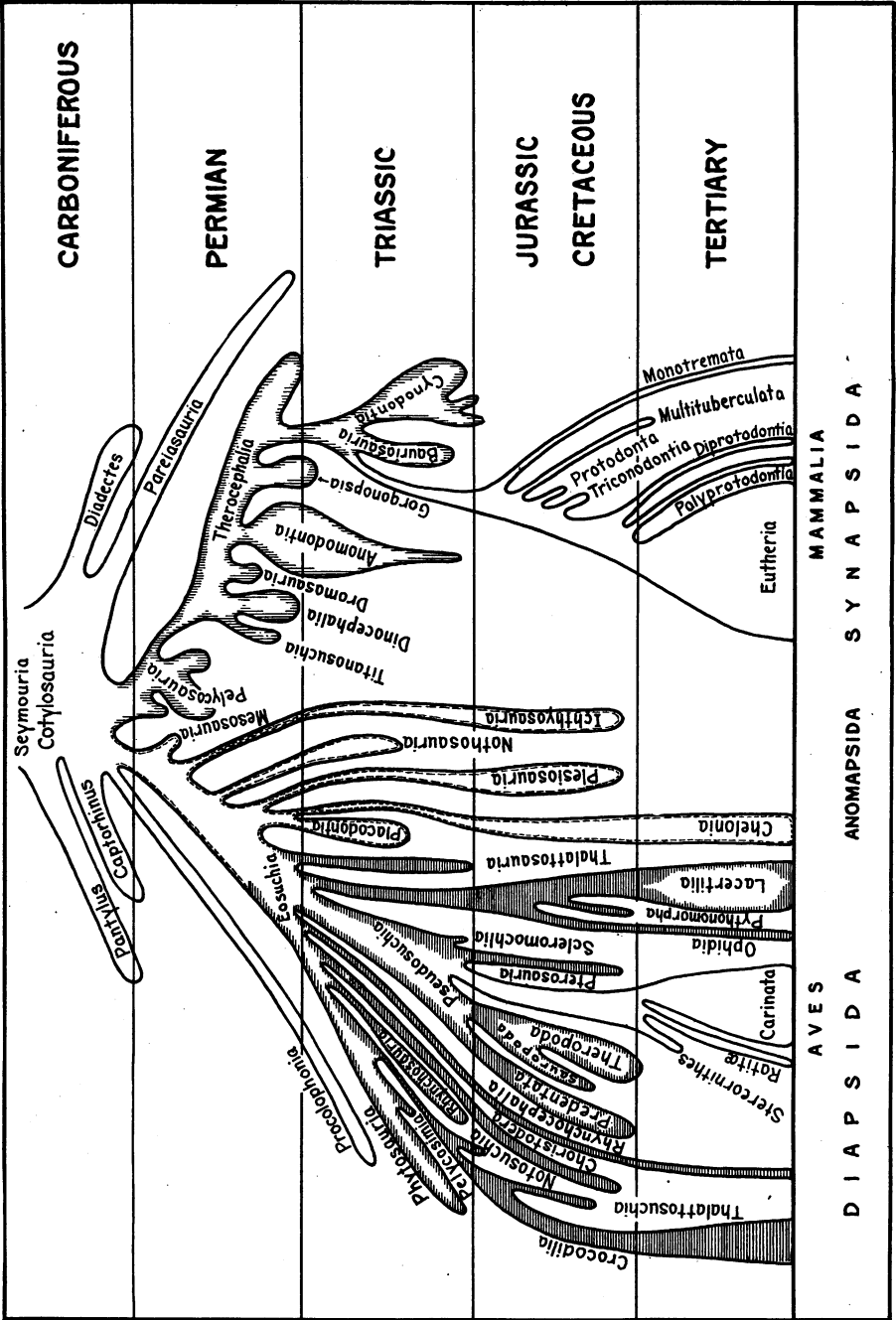


Fig. 13. Evolution and Classification of the Reptilia.

temporal fossa became developed, a large number of varieties of land forms arose, all apparently more or less successful. In fact, so successful did the land forms become that aquatic types became quite exceptional.

The oldest known diapsidan is *Youngina* from the Upper Permian of South Africa. Like the later pseudosuchians it had a long, pointed snout and well-developed running limbs.

Youngina I made the type of an order or suborder, Eosuchia, and from this group arose not only the Pseudosuchia and the primitive crocodiles, the rhynchocephalians and gnathodonts, but also, by the loss of the lower temporal arch and the freeing of the quadrate, the Squamata.

From the pseudosuchians arose the pterodactyls, the dinosaurs and, ultimately, the birds.

In the accompanying diagram, I have indicated what I believe to be the relationships of the principal reptilian orders.

Anyone not very familiar with the subject in reading this paper might readily assume that my views differ very greatly from those of Professor Williston. But this is merely because I have devoted most of my space to the discussion of those few points wherein we disagree and have said practically nothing on the large number of points on which we are in harmony. If the diagram I give be carefully studied and compared with the table given by Williston, it will be seen that, even where we disagree, the disagreement is not so very great. It is merely that he would place a little farther back than I would the origin of the Squamata, the Chelonia and the Ichthyosauria, and that he derives the Plesiosauria from a point near the origin of the Synapsida rather than, as I prefer, from a point some little distance along the line that gave rise to the Diapsida. And, further, on none of the four main points at issue have we any satisfactory paleontological evidence.

