

REPTILIAN EPIPHYSES.

BY

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WITH 24 TEXT FIGURES.

It has long been the opinion of anatomists that bony epiphyses are confined exclusively to the skeleton of the Mammalia. Among other features often given as characteristic of the mammals is the one that epiphyses occur on the bones.

Dollo (1) in 1884 first called attention to the fact that real epiphyses are found in the reptiles, although Albrecht (2) had the year before published a short note on epiphysial structures of the vertebral spines of *Sphenodon*. Dollo gave a complete summary of the literature on the subject and a list of epiphyses which he observed in seven families of the lizards and in *Sphenodon*. He promised a more complete description with illustrations but I have not been able to ascertain that his promise has been fulfilled. Parsons (3) writing twenty-two years later, has revived the interest in epiphyses of the reptiles in connection with his studies on the epiphyses of the human skeleton.

At the suggestion of Dr. Williston the study of epiphyses as they occur in the reptiles was taken up in an attempt to solve the problem of the relationship of the Chelonia and Plesiosauria as evidenced in the so-called epiphyses of the two groups. The methods pursued are those referred to in a previous contribution on the lizard sacrum (4) and which are given below in full. These methods of clearing animal tissues were first introduced into America by Dr. Mall and were first fully outlined by him in his study of ossification centers in the human embryo (17). Hill (18) further outlined the methods and gave their application to subjects other than the study of osteology. The method consists principally in the use of KOH as a clearing agent on objects too large for the ordinary clearing agents to act upon. This was the method pursued by Schultze (20) who was its originator, and it is usually known as the Schultze method.

Embryos which have been freshly collected should be placed in 95 per cent alcohol, which acts both as a killing and fixing agent. If the embryos are of large size the alcohol should be changed frequently until the tissues of the specimen are thoroughly shrivelled and hard. For pig embryos of about one-half term, ten days is necessary for proper fixing. Smaller and larger objects can be fixed for a length of time based on the time mentioned. Adult animals are also to be fixed in strong alcohol, 95 per cent serving as well as does absolute alcohol as Hill states. It has been possible to clear quite large animals, both adult and embryonic. I have a cow embryo over five inches in length, the tissues of which are perfectly transparent. I also cleared a small garter snake of nearly two feet in length, and an adult *Heloderma*, so that the method has a wider application than was at first supposed. For objects which have been fixed in any of the acid fixing agents it is best to place them in strong alcohol in which is a strong solution of iodine. This removes the acid and allows the KOH to take effect better. Before using the iodine on such objects it had been found almost impossible to clear satisfactorily, and if cleared at all there still remained a hazy appearance which nothing served to remove. I have just recently received some alligator embryos from Professor Reese, which had been fixed in acetic acid and after several days in the iodine alcohol, they are now beginning to clear nicely. Stains in the tissues are best removed with strong ammonia as Mall and Hill state. Stronger oxidizing agents have been tried but the bubbles formed in the tissues by the more powerful agents are nearly impossible to remove.

Specimens preserved in formalin, I find, clear with uncertain rapidity. Usually it takes a formalin hardened specimen in 10 per cent KOH from three to six weeks to clear but recently I have had some formalin hardened turtle embryos to clear beautifully over night. The embryos had been fixed for at least two months in formalin and were in strong alcohol for about a week before clearing. Just what is the cause of this sudden clearing in objects which have been considered difficult is not apparent.

Objects cleared in KOH should be placed in glycerin diluted with water. Mall suggests the addition of an alkali to kill fungi, but I do not find it necessary. After removing the stains with ammonia the objects are then to be placed in pure glycerin to preserve them permanently. If kept in glass or rubber-stoppered bottles they will keep indefinitely. Cork turns the glycerin brown.

Objects cleared in this way are readily photographed. Sunlight does not serve well for an illuminant on account of the shadows cast. It has been found, after repeated trials, that a strong arc light thrown on the

specimen at an angle of about forty-five degrees with a reflector on the opposite side so as to illuminate the object uniformly gives the best results. The specimens are placed in a broad, shallow glass dish with just enough clear glycerin to cover them. The dish should be raised somewhat on small blocks so as to throw the background out of focus. Two of the half-tones in the present essay were prepared in this way.

For the purpose of determining the presence or absence of epiphyses in the Reptilia the following groups have been investigated and will be discussed in the order named: Chelonia, Plesiosauria, Crocodilia, Lacer-tilia and *Sphenodon*.

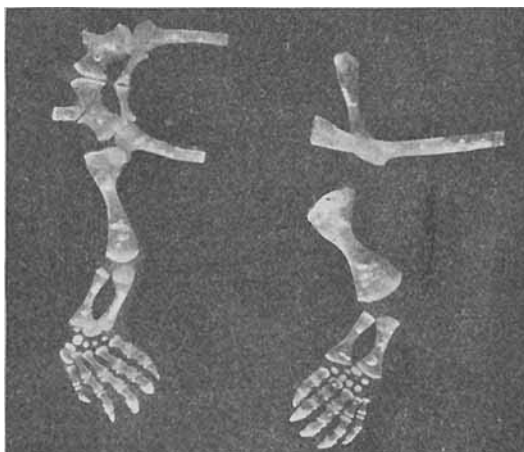


FIG. 1. Limbs and girdles of a young *Chelydra* 44 mm. in length; no epiphyses. $1\frac{1}{4}$ natural size.

The turtles studied consist of embryos of *Chelydra*, *Graptemys*, *Chrysemys*, *Trionyx* and *Aromochelys*, the young of *Chelydra serpentina* Linné and *Chrysemys picta* Hermann, together with adult skeletons of many genera, notably *Chelydra*, *Chrysemys*, *Testudo*, *Chelys*, *Chelone*, *Cistudo* and *Trionyx*.

Very little is to be learned in regard to epiphyses from the embryos of the turtles. In the lizards where epiphyses are found they are not formed until after the time of hatching from the egg. They are seen as minute points in the cartilage at the ends of the limb bones of a young lizard, *Sceloporus*, two days old. The turtle specimens which were investigated particularly for the presence of epiphyses, range from very small embryos in which the carapace is not yet formed to and including the stages of

hatching and subsequent stages. In none of the specimens, although I have examined them with the greatest care, have I been able to find the slightest indication of bony epiphyses on any of the skeletal elements. The embryo turtles, when cleared, show the ossificatory centers of the bones very beautifully, but there is never any separate center for an epiphysis. If epiphyses are to be found in the turtles they should be present in the young animal. In a specimen of *Chelydra serpentina* Linné, 44 mm. in length, the limb bones (Fig. 1) show no differences from the limb bones of an adult *Chelydra* excepting, of course, in size. We should certainly expect epiphyses to be evident at this stage, if ever. They are not present in a slightly younger specimen of *Chelydra*, nor are there any evidences of them in a more advanced *Chrysemys*.

Smith Woodward (5) states: "Other characters, such as the conical epiphyses of certain limb bones, also seem to imply community of origin of the Chelonia with the Sauropterygia and Batrachia"; and Parsons (6) states in parenthesis: "I think that I have found traces of an epiphysial line in the great trochanter of the Chelonia, but am not sure of it." The "conical epiphyses of certain limb bones" were first noted by Seeley (21) in his essay on *Pariasaurus* where he says: "All the long bones of the Nothosauria and Plesiosauria ossify in the same way as the long bones of living frogs, and consist of cylindrical girdles into which long, conical epiphyses penetrate, so as to meet, or nearly meet, in the middle of the shaft, from which they are often easily or naturally separated. I have had no opportunity of determining whether this condition is present in the long bones of Labyrinthodonts, and I only otherwise know it as a rare condition in some of the long bones of Chelonia from the Cambridge Greensand, and in an undescribed epiphysis, which I believe to be Dinosaurian, from the Oxford Clay, and the proximal end of the tibia of *Protorosaurus*." In his essay on *Protorosaurus* Seeley (22) practically repeats the same facts.

From the above quotation it is evident that Seeley had a correct idea of the ossification of the reptilian bones. The term epiphyses was used, it seems to me, inadvertently to express the nature of the elements and not to express the idea of any homology of the reptilian structure with the familiar elements in the mammals. Later authors following Seeley quoted his words but missed the idea and hence has arisen the present discussion. Osborn (23) mentions epiphyses as possible evidences of relationship between the turtles and plesiosaurs. The fact remains, however, that *there is not the slightest evidence either embryologically or anatomically of any bony epiphyses on any of the skeletal elements of the Chelonia that*

I have examined. To be sure there are in the young of the turtles pads of cartilage which form the articular surfaces such as are found on the limb bones of the Amphibia, but in the turtles there is no distinct separation of the cartilage from the diaphysis as in some of the Amphibia, nor is there any trace of any bony structure. The shaft is entirely ossified from its center of ossification and the cartilaginous pad becomes in time fully osseous by such a process. The pad of articular cartilage often makes a distinct line on the bone which becomes evident when the cartilage is macerated. I have noticed such lines on the limb bones of the alli-

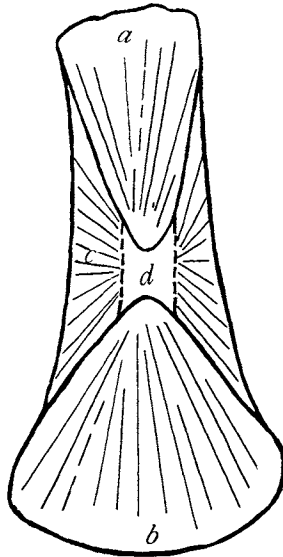


FIG. 2. Longitudinal section of a propodial of a Sauropterygian; from the Kimmeridge Clay of Ely. *a*=Endochondral bone (Proximal epiphysis). *b*=Endochondral bone (Distal epiphysis). *c*=Perichondral bone (Shaft). *d*=Medullary cavity. $\frac{1}{4}$ natural size. After Lydekker. (Lydekker's interpretations in parentheses.)

gator and various turtles. Doubtless the line to which Parsons refers is due to the articular cartilage on the great trochanter.

In the Plesiosaurs there have long been known some propodial bones of young animals which offer very puzzling characters. One of these specimens (Fig. 2) is in the British Museum and was figured diagrammatically by Lydekker in his Catalogue of fossil Reptiles and Amphibia (7). Parsons has also given a diagram of a young propodial, whether of the same bone or not I do not know. Another well known specimen is the

one described and figured by Williston (8). I have studied this propodial and it offers some very peculiar characters. As described by Williston there are two cones of osseous matter whose apices do not quite meet at the center but are separated by a small medullary cavity into which four canals from the outside enter.

The cones of this embryonic propodial (Fig. 3) are represented in the diagram (Fig. 4). Williston says: "The . . . specimen discloses these epiphyses (cones) with a smooth rounded surface . . . the outer

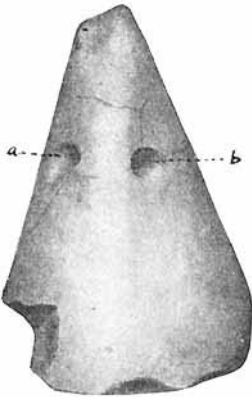


FIG. 3.

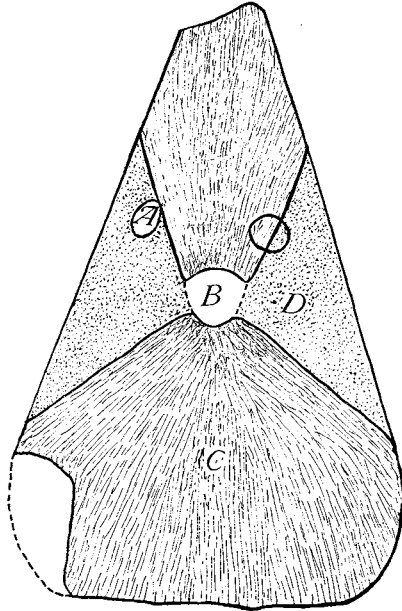


FIG. 4.

FIG. 3. Embryonic plesiosaur propodial. Foramina at *a* and *b*. $\frac{1}{2}$ natural size. After Williston.

FIG. 4. A section through the embryonic propodial shown in Figure 3. *A* = Foramen of the nutrient canal. *B* = Medullary cavity. *C* = Cone of the endochondral bone. *D* = Perichondral bone. $\frac{1}{2}$ natural size.

part peeling away as does the bark from a tree." The structure of this propodial is especially dense and the same has been described for many other bones of young plesiosaurs. The denseness of the tissue is one of the peculiar characters of these cones and persists throughout the life of the individual. I have made sections of several propodials to determine the fate of the cones and find them clearly marked in the propodial of a half-grown individual (Figs. 6 and 8). In this bone there also persists

a remnant of the medullary cavity and a single small canal. On the external surface of the adult propodial (Fig. 7) there is no evidence of the cones or of the canals, but on sectioning an adult humerus (Fig. 9) the cones are seen to be represented by dense areas of tissue at the ends of the bone. The areas are without definite boundaries and merge gradually into the texture of the rest of the bone.

The cavity which lies between the apices of the two cones is the medullary cavity. Its presence in the embryonic bone can be accounted for only

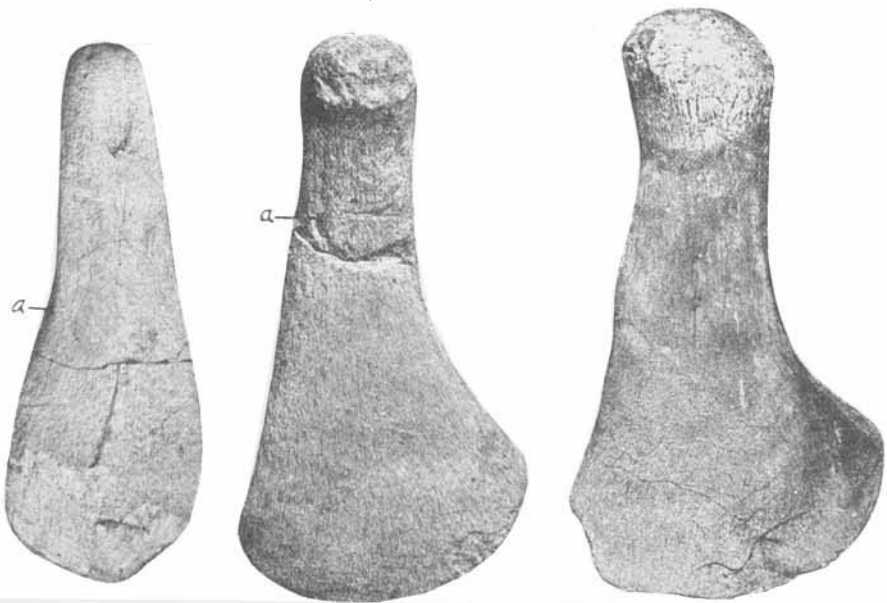


FIG. 5.

FIG. 6.

FIG. 7.

FIG. 5. An immature plesiosaurian propodial showing foramen at *a*. $\frac{7}{10}$ natural size. After Williston.

FIG. 6. Propodial of half-grown plesiosaur showing the foramen at *a*. $\frac{1}{3}$ natural size.

FIG. 7. An adult plesiosaurian humerus seen from the dorsal side. There are no foramina or cones evident. About $\frac{1}{4}$ natural size.

on the presumption that the ancestors of the plesiosaurs had hollow limb bones. The cavity is certainly a vestigial one. It is quite large in the embryonic bone (Fig. 4). There is a small cavity filled with calcite in the propodial of the half-grown individual (Fig. 8). In the adult bone (Fig. 9) the cavity has entirely disappeared. From these facts it is apparent that the cavity is a transitory structure and is on the same plane

as the persistence of the gill clefts in the mammalian embryos. The ancestors of the plesiosaurs are yet to be discovered. When they are brought to light they will probably be found to have hollow limb bones.

The canals and the foramina of the propodials are not so readily accounted for. The presence of canals in the middle of a limb bone is a very remarkable character and is without parallel among the known vertebrates. The canals are probably for the passage of blood vessels, but why

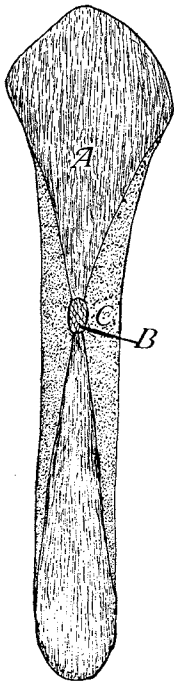


FIG. 8.

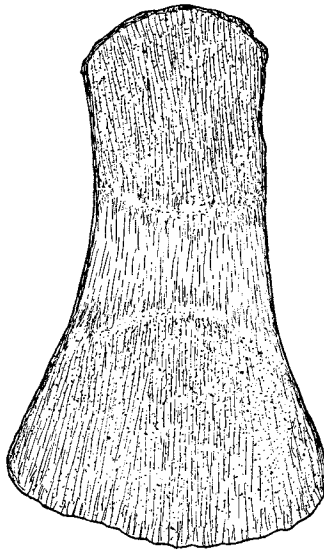


FIG. 9.

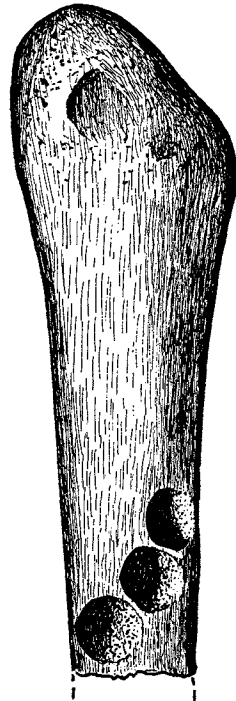


FIG. 10.

FIG. 8. A section through the plesiosaurian propodial shown in Figure 6. A = Endochondral bone. B = Medullary cavity filled with calcite. C = Perichondral bone. $\frac{3}{4}$ natural size.

FIG. 9. A section through the humerus of an adult plesiosaur. $\frac{1}{4}$ natural size.

FIG. 10. Proximal portion of a young plesiosaur propodial showing three foramina. Seen from the edge. $1 \frac{1}{10}$ natural size.

they should be so large and why they should disappear in the adult, is inexplicable. The nutrient foramina, if such they are, have been observed in many specimens. Williston describes four in the embryonic propodial, there are three present in a more mature bone before me (Fig. 10), one

in another, and there is but a single foramen present in the element figured by Williston on Plate XXIII of his *North American Plesiosaurs* (Fig. 5). Kiprijanoff has figured an immature propodial (Figs. 12 and 13) from Russia, in which there is a single foramen present. It is thus evident that the canals and their foramina are very variable in number and there is also a variation in their position on the bone. In the embryonic propodial they open out on both the dorsal and ventral surfaces (Fig. 3). In the propodial shown in the photograph there is a single foramen evident on the dorsal surface (Fig. 6). In all other specimens with which I am acquainted the foramina open out on the edge of the bone (Figs. 5 and 10). From these facts it would appear that the blood

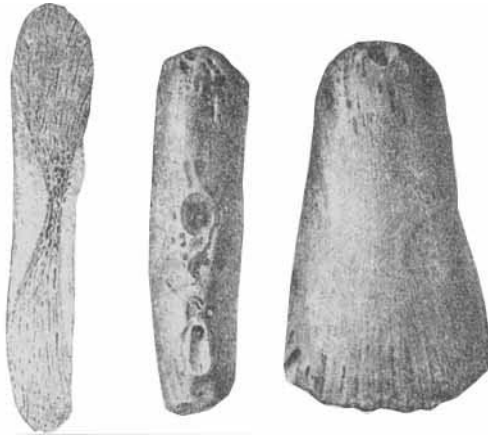


FIG. 11.

FIG. 12.

FIG. 13.

FIG. 11. A longitudinal section through an immature propodial of a plesiosaur showing the cones and the perichondral sheath. $\frac{3}{4}$ natural size. After Kiprijanoff.

FIG. 12. An immature propodial showing foramina. Seen from the edge. $\frac{3}{4}$ natural size. After Kiprijanoff.

FIG. 13. Same bone seen from the dorsal aspect. $\frac{3}{4}$ natural size. After Kiprijanoff.

vessels which the canals contained were veins and not arteries. That arteries are among the more constant structures in the body of the vertebrates is well known among anatomists, and where inconsistencies occur in blood vessels it is usually among the veins. I have made sections of several immature propodials in the hopes of finding some clue to the meaning of the foramina and canals, but nothing can be stated here other than that they are present in the young and absolutely disappear in the adult. The bone fibers around the foramina in one section are seen to have a spiral arrangement (Fig. 14).

Our main interest in these propodials is the fact that the cones of osseous matter (Fig. 11) described above have frequently been called epiphyses. But when these plesiosaurian structures are compared with the true epiphyses of other animals, they are found to be widely different. Epiphyses are always at the ends of the long bones and never go to form any part of the shaft. These cones in the plesiosaurs form part of the diaphysis of the propodial, and are to be compared to the similar

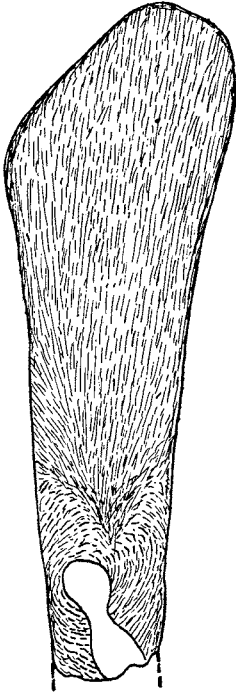


FIG. 14.

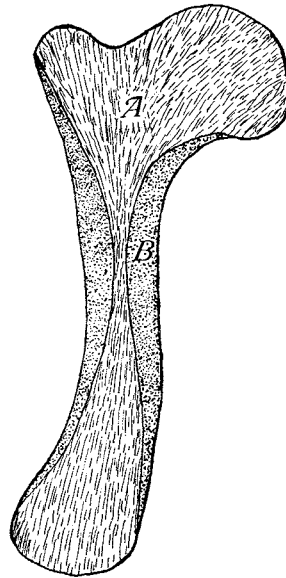


FIG. 15.

FIG. 14. A section through the bone figured in "10" showing the spiral arrangement of the bone fibers. $1 \frac{1}{10}$ natural size.

FIG. 15. Section through the femur of an adult turtle, *Trionyx*. The endochondral bone A is clearly distinct from the perichondral bone B. $1 \frac{1}{2}$ natural size.

structures found in the limb bones of the turtles, lizards and crocodiles (Figs. 15, 16 and 17). The peripheral portion of the plesiosaur bone which is called the shaft by Lydekker, is the periosteal ossification, and goes to form a portion only of the diaphysis. The cones which Lydekker calls epiphyses are the endochondral bone evident in all embryos of the

Sauropsida. The cones are not confined to the long bones, but occur in the ribs and all of the elements of the appendicular skeleton (Fig. 18). Parsons in his last article on epiphyses (10) draws a comparison between the conical ossification at the ends of the plesiosaur bones and the conical cartilaginous ends of the developing long bones of the pigeon. This comparison is a new and interesting one and contains the key to an exact interpretation of these structures in the plesiosaurs. Such an appearance

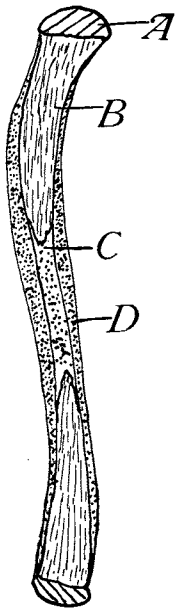


FIG. 16.

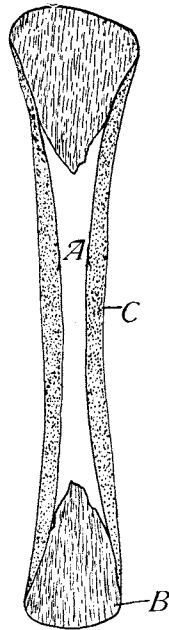


FIG. 17.

FIG. 16. A section through the humerus of *Amblyrhynchus*. A=Bony epiphysis. B=Endochondral bone which is less compact than the perichondrium. C=Medullary cavity partly filled with bone fibers. D=Compact perichondrium. $1\frac{1}{2}$ natural size.

FIG. 17. A section through the tibia of *Alligator*. A=Large medullary cavity. B=Cone of endochondral bone. C=Perichondrium. $\frac{2}{3}$ natural size.

is not confined to the pigeon for I have noticed the cones of cartilage in the developing bones of the lizards, the turtles, and the chick. The cones are due to the mode of ossification in the Sauropsida, which is widely different from the method of ossification in the Mammalia. The formation of the endochondral bone lags far behind the perichondral portions in the Sauropsida. The perichondrium is formed as a sheath around the

entire endochondral part. Brachet gives an account of the development of this cone of cartilage in the chick (11) and I think his account will apply to other Sauropsida. The cone of cartilage is first calcified and the calcified cartilage is subsequently replaced by bone. The formation of the endochondral bone takes place after the formation of the perichondral portion. The perichondral bone is what Lydekker in the plesiosaurs has called the shaft, and the endochondral portion or the cones he has called the epiphyses. Both of these interpretations are incorrect. The cones or endochondral, and the sheath or perichondral portion together, form the diaphysis, and there is no epiphysis on the long bones of the plesiosaurs. The fact that the cones are separate from the perichondrium in the fossilized remains of the plesiosaurs is due, no doubt, to the fact that the



FIG. 18. Photograph of the foot of a chick of sixteen days incubation. The cones of cartilage are clearly evident in the metatarsals and the phalanges. $1\frac{1}{4}$ natural size.

endochondrium forms subsequent to the formation of the perichondrium. The perichondral sheath is almost fully formed before the endochondral cone starts to ossify.

Brachet has fallen into the same misconception of the conical growth at the ends of the bones in the chick as did Lydekker in the case of the plesiosaurs. He calls the endochondral portion an "epiphysis," but it is not epiphysial in any structural sense for epiphysis means a *growth upon* and the structure in this case is certainly not upon, but within, the upper portion of the perichondrium.

The cones or endochondrium in the plesiosaurs have been called epiphyses and have been used as a character on which to base the relationship of the turtles and plesiosaurs. The question of this relationship is an old one and has been discussed by various authors. But the presence of

epiphyses in the two groups cannot be used as a criterion of relationship since neither has these structures. It might be more logically claimed that they are related because of the absence of epiphyses. But the presence or absence of these elements, it seems to me, is of little value. If it is of value, then the lizards and mammals are related, for epiphyses are abundantly present in both groups. That epiphyses are not good diagnostic characters for the distinction of large groups of vertebrates is well shown by the fact that they occur in the lizards and that here they may be abundantly present or almost entirely absent. They may be a good generic or family character, but this point requires further investigation. Some lizards (*Chameleon*, *Heloderma*, *Amblyrhynchus*) have a great number of epiphyses, some (*Phrynosoma*, *Eremias*) have but few. *Draco*, apparently, has none.

I find no epiphyses in the crocodiles. I have examined young specimens of the *Alligator mississippiensis* Daudin, five inches in length from the tip of the snout to the base of the tail, and have seen no indications of any epiphysial growth. I have also examined adult skeletons of the garial, the Florida crocodile, and the Mississippi alligator, but have seen nothing indicative of epiphysis, although there is present a line due to the cap of articular cartilage on the ends of the limb bones.

The lizards offer an interesting field for more extended investigation on this subject. Epiphyses occur abundantly in some forms and principally at both ends of the limb bones, on some of the girdle bones, on some of the carpals and tarsals, on both ends of the metacarpals and metatarsals, at the proximal end of the phalanges, on the spines of the vertebrae, and Dollo has reported them on the skull and ribs in certain forms, although I have not been able to find them on any of the skulls at my disposal, except that epiphysial structures are present on the posterior end of the mandibles of *Amblyrhynchus*.

The epiphyses of the lizards are not always bony. Some are merely calcified cartilage while a few are true bone, as Parsons has shown in *Iguana*. I have made sections of the epiphysial regions of *Amblyrhynchus* and have definitely ascertained that there are Haversian canals and lacunae present in the epiphyses. The fact that some of the epiphyses are not bone is, however, a matter of but slight importance. The important fact is that there are distinct structures present in the lizards which correspond with the similarly placed epiphysial structures in the mammals.

The lizards examined are the same as I have listed in a previous contribution on the lizard sacrum and the reader is referred to that

article for the forms discussed here. In addition to the forms there mentioned I have recently examined the skeletons of two specimens of *Amblyrhynchus cristatus* Gray, of the family Iguanidae, from the Gallapagos Islands; one specimen of *Eremias pulchella* Gray, of the family Lacertidae, from Africa; and a skeleton of a young *Varanus*, of the family Varanidae.

In the embryos of *Cnemidophorus sexlineatus* Linné there are no epiphysial ossifications. In three young specimens of *Sceloporus chrysostictus* Cope, 24 mm. in length from the tip of the snout to the base of the tail, which are two days old, the epiphyses can be detected as minute points in the cartilaginous pads at the upper and lower ends of the humerus and femur, and at the distal ends of the metacarpals and metatarsals. In a slightly older specimen of *Sceloporus* there have appeared at the distal end of the humerus four epiphysial centers. It is not at all unusual for more than one center to appear at the end of a long bone. On the humerus of *Phrynosoma* there are two centers on the distal end, and on the upper and lower ends of the humerus of *Amblyrhynchus* there are four and five centers respectively. In an adult specimen of *Sceloporus* the epiphyses have become almost indistinguishably united with the diaphyses. In this specimen, also, there appears the ununited olecranon, which was not apparent in the young. The olecranon in the lizards is of separate origin from the diaphysis and only unites with it late in life. In his paper on "Traction Epiphyses" Parsons has figured the developing olecranon of *Iguana* and discusses its probable origin and its homologue in the higher vertebrates.

In the young specimen of *Phrynosoma*, 26 mm. in length, there can be detected at the distal end of the humerus two epiphysial centers and one on the proximal end. One epiphysis is present on the distal end of all of the metacarpals. There are no epiphyses either on the radius, ulna, carpals or phalanges. One epiphysis is present on the upper and one on the lower end of the femur. As in the fore limb, there are no epiphyses present on any of the other bones of the leg, but epiphyses are present on the distal end of the metatarsals. In the adult specimen of *Phrynosoma*, 46 mm. in length, the epiphyses are almost indistinguishably united with the diaphyses. The olecranon has not, however, joined the ulna.

In the young specimen of *Iguana*, 73 mm. in length, there is one epiphysial center at each end of the humerus, one on each end of the ulna, none on the radius (Fig. 24). One epiphysis is present on each end of the femur, tibia and fibula, and one at the distal end of all of the metacarpals and metatarsals. There are no apparent epiphysial structures

on the phalanges excepting some very minute points of bone which appear in the articular cartilage of one or two.

So far as can be detected from my single specimen, *Draco volans* Linné, 62 mm. in length, has no epiphyses, but it is possible that they would be evident in the young. The olecranon is free.

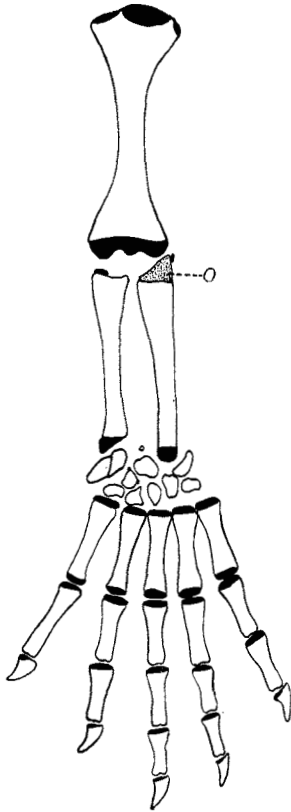


FIG. 19.

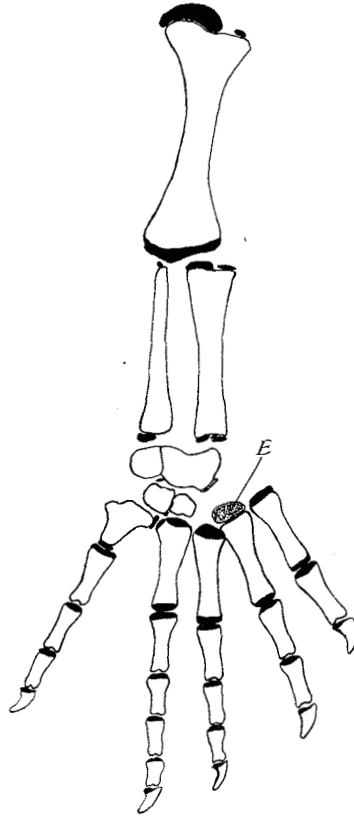


FIG. 20.

FIG. 19. The fore limb of *Heloderma suspectum* Cope. The shaded parts represent the epiphyses. *O* = the olecranon. There are two epiphyses on the os centrale. Twice natural size.

FIG. 20. The right hind limb of *Heloderma suspectum* Cope, seen from above. The epiphysis *E* is probably an element of the tarsus which has become united with the metatarsal. The tibiale has two epiphyses which probably represent atrophied elements of the tarsus. Twice natural size.

In the young specimen of *Chameleon owenii* Gray, 44 mm. in length, there are distinct bony epiphyses on each end of the humerus, radius and

ulna. At this stage there are none apparent on the metacarpals or phalanges. There is a distinct center at each end of the femur, tibia and fibula, but none on the metatarsals or phalanges. In the adult of the same species, 135 mm. in length, the epiphyses are fully as distinct as they are in the young, with the exception of that at the head of the humerus, which appears to be partly fused with the shaft. In the adult form there are epiphyses in the hand and foot.

In the adult specimen of *Heloderma suspectum* Cope, the epiphyses are abundant and in places quite mammalian in appearance. The upper end of the humerus has a small oval epiphysis in the center with a smaller one on each tuberosity. That at the distal extremity of the humerus is quite broad and has a particularly mammalian aspect, being quite long from side to side, entirely covering the lower end of the bone. It is divided into three condyles by two trochlear grooves. The epiphysis at the upper end of the ulna is quite like a mammalian olecranon. The one



FIG. 21. The left mandible of *Amblyrhynchus*. The shaded part *E* represents the epiphysis. *A* = Angular. $1\frac{1}{3}$ natural size.

at the lower end is disc shaped. The radius has small, poorly developed, calcified epiphyses at each end. In the hand the metacarpals have epiphyses at each end and they are present at the base of all of the phalanges (Fig. 19). On the upper and lower end of the femur there are epiphyses, the lower one having a mammalian aspect. The tibia has a small epiphysis on each end and the same condition holds for the fibula. On the tibiale there are two small ones and one also on the fibulare. In the foot, as in the hand, there are epiphysial structures on each end of the metatarsals, with the exception of the first, and one at the base of all of the phalanges (Fig. 20). I have not been able to detect epiphyses on the girdle bones of this form, although Dollo has reported them on some of the forms examined by him. Siebenrock has seen epiphyses on the ilia of *Uroplates*.

There are in many of the epiphyses of *Heloderma* certain resemblances to similarly placed structures of the mammals. This is very remarkable as being the only case in which there is such a resemblance among the

many forms I have examined. I know of no way to account for it save by parallel development. What the causes are which have produced this peculiar development in these lizards is obscure. I know of nothing in their habits of life which could bring about such a development, since they are but slightly different in their mode of life from many other lizards which have the regular reptilian structure.

The epiphyses are more abundant on the skeleton of *Amblyrhynchus cristatus* Gray than on any other form I have examined. There is a small



FIG. 22. Humerus, ulna and radius of *Amblyrhynchus*. $1\frac{1}{2}$ natural size.

one on the proximal end of each mandible, on the angular (Fig. 21), but none can be detected elsewhere on the skull. On the humerus of this form there are four epiphysial centers on the upper end and five on the lower (Fig. 22). The four on the upper end are of unequal size and only one of them is ossified. The other three are calcified cartilage. The ossified epiphysis occupies the head of the humerus, two small ones of calcified cartilage occur on the large tuberosity, and one on the lesser tuberosity. The five at the lower end are also of unequal size and only one of them is ossified. The large central bony one resembles the trochlear epiphysis of a mammal, but the trochlea is itself small. There are three

of calcified cartilage on the external condyle and one on the internal condyle. The upper and lower ends of the radius and ulna have epiphyses. The upper end of the ulna has also an olecranal ossification which, in an older specimen, has become united with the epiphysis. There are no epiphyses on the carpals. On the metacarpals, however, they are found at each end. At the base of the proximal phalanges they are prominent structures, but are not distinguishable at the base of the distal phalanges. The head of the femur has an epiphysis and there is one on the trochanter



FIG. 23. Femur, tibia and fibula of *Amblyrhynchus*. $1\frac{1}{2}$ natural size.

(Fig. 23). On the lower end of the femur there are three epiphyses, none of which appear to be ossified. Each end of the tibia and fibula is provided with a bony epiphysis. There is a small one on the tibiale, two small ones on the fibulare. The condition in the foot is the same as in the hand. There are distinct, bony epiphysial structures on the spines of the posterior cervical and anterior dorsal vertebræ of this form. No epiphyses have been found on the centra of any reptile so far as I am aware. It is of interest to note in this connection that Beddard quotes Parker as an authority for the statement that there are epiphyses on the centra of some of the parrots.

In the skeleton of *Eremias pulchella* Gray which I have recently examined the only epiphyses which can be detected are on the upper end of the humerus and at the distal end of the metacarpals and metatarsals.

The skeleton of *Varanus* shows such close resemblances in the arrangement and position of the epiphyses to the skeletons of *Amblyrhynchus* and *Heloderma* that one is forced to the conclusion that they are closely related members of a natural group of the lizards. This relationship

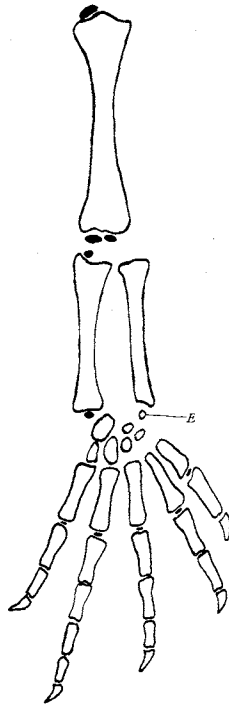


FIG. 24. The right fore limb of a young *Iguana* showing the manner in which epiphyses arise. They are not connected with the diaphyses in the early stages of growth. *E* = Epiphysis? Carpal? $2\frac{5}{7}$ natural size.

has been claimed on other grounds and the arrangement of the epiphyses tends to corroborate this view. As in the two forms mentioned, there are in *Varanus* epiphyses present in abundance on the skeletal elements. Each end of the long bones of the limbs, each end of the metacarpals and metatarsals, the bases of all of the phalanges, including the ungual phalanges as in *Heloderma*, and some of the tarsal and carpal bones, are provided with epiphyses.

It is interesting to note the method of development of the epiphyses in the lizards. As above stated there are no epiphyses present in the embryos of the lizards so far as I am able to determine. In the embryos of *Cnemidophorus* there is not a trace of epiphysial structures in the articular cartilages of the limb bones. In a young *Sceloporus*, the epiphyses are just appearing as minute points. In the adult *Sceloporus* the epiphyses are indistinguishably united with the diaphyses. This seems to be the usual life history of the epiphyses among the Lacertilia. But to this there are some notable exceptions. In the young of *Chameleon owenii* Gray, there are in a young specimen, two inches in length, no epiphyses present in the hand or foot. The epiphyses in the hand and foot of the adult are quite large and do not unite at all with the diaphyses, but remain much more distinct than I have ever seen them in any mammal. I do not possess young stages of the *Heloderma*, but in the young of *Amblyrhynchus* and *Varanus* the epiphyses separate easily from the diaphysis and this is especially true of the *Varanus*. In the adult forms of this genus the epiphyses are closely attached but do not fuse with the shaft.

From the above facts it will be clear that the method of development of the epiphyses in the Lacertilia is not at all uniform. In some lizards the epiphyses are more evident in the young; in others they are more evident in the adult. Whether these facts are of any particular significance or not remains to be determined. At any rate it is clear that the presence of epiphyses in the Lacertilia is a very variable matter and one would be inclined to the opinion that they may occur at any place on the skeleton where there is strain or pressure. Epiphyses are to a certain extent sesamoid, but are not sesamoid bones in the ordinary meaning of that term.

One of the most interesting facts in regard to the epiphyses of the Lacertilia is that they are never found on both ends of the phalanges. In none of my specimens is there the slightest indication of an epiphysis on the distal end. They occur always on the proximal end. In the mammals, with the exception of the Cetacea, the same condition is found. They are present only on the proximal end of the phalanges in both groups. Perhaps this is another case of parallel evolution, but it doubtless has more significance than that. It seems to me that the epiphyses and their arrangement is a matter of some importance in the phylogeny of the vertebrates. Not that they can be of much taxonomic importance, but that they are significant of primitive conditions. It has always been assumed by anatomists that epiphyses were developed first in the mam-

mals, but we now know that they are present in very generalized reptiles. When we come to know the primitive Reptilia better the meaning of the epiphysal structures will be more clearly understood. It is evident that epiphyses are of various origins. Some arise undoubtedly through use, some represent atrophied elements, and some appear to arise from other causes. I am of the opinion that the epiphyses of the Lacertilia are inherited structures which they have obtained from their Rhynchocephalian ancestors and the fact that the arrangement of these structures in the lizards and mammals is the same cannot, it seems to me, be due to like causes. There is some real fundamental cause for such an arrangement. Why epiphyses develop in some forms and not in others is another question and can have no bearing on this suggestion.

Broom (12) has recently called attention to the arrangement of the epiphyses in the human hand and foot where they occur at the base of all of the phalanges, and at the distal end of the metacarpals and metatarsals of digits II, III, IV and V, but at the proximal end of the first metacarpal and metatarsal. He suggests that possibly the first metacarpal and metatarsal have gone into the wrist and ankle and cites for comparison the manus of *Oudenodon*, where the first digit is not reduced. This suggestion as to the fate of the first element of the first digit of the hand and foot is by no means a new one, since the same opinion was held by many of the older anatomists, but it is of interest here because of the bearing it has on the arrangement of the epiphyses, which we should expect to find in the primitive Theriodontia and Therocephalia. If specimens of these animals are ever found well enough preserved to show the epiphyses we should expect to find the arrangement exactly as it is in some lizards. There should be no epiphyses on the proximal end of the metacarpals and metatarsals, but they should be present on the distal end and on the proximal end of the phalanges.

It is to be noted from the foregoing discussion of the epiphyses of the lizards that a great many of them are of calcified cartilage. The presence of an abundance of calcified cartilage in the skeleton appears to be characteristic of the Squamata excepting, perhaps, the snakes. Dr. Williston tells me that there are always abundant evidences of calcified cartilage in the fossilized skeletons of the mosasaurs. In the ear region, on the girdle bones, on the vertebræ and, whenever preserved, the sternum and the sternal ribs, are entirely of calcified cartilage, as are also the tracheal rings. According to the same authority, this condition is never found in the plesiosaurs. There is not the slightest trace of calcified cartilage on the skeleton of these animals.

Howes and Swinnerton (13) make no mention of any epiphyses on the skeleton of the young of *Sphenodon punctatus* Gray, although they figure on Plate VI, Fig. 18, epiphyses on the foot. Albrecht, nowever, in 1883, called attention to certain structures on the neural spines of this form which he thought were bony epiphyses. So far as I am aware his statement has never been corroborated. I am not able to find any indications of epiphysial elements on an adult skeleton of this form, which is the only material available. The only element which might be called epiphysial is the olecranon. This is free as in the Lacertilia. Epiphyses are not wholly absent from the skeleton of the Rhynchocephalians, and it is possible that Albrecht is right. In his large work on fossil vertebrates (16) von Meyer figures a skeleton of *Sapheosaurus* on which there are quite evident epiphyses on the humeri and femora. The epiphyses are especially abundant on the lower end of the left humerus.

Just why epiphyses should develop in some forms of the reptiles and not in others is a very difficult question to answer. They are certainly not essential to the formation of good articular surfaces since they have never been observed in either the pterodactyls or the theropodous dinosaurs. These forms have a perfection of formation of the articular surfaces such as is not excelled among the Sauropsida. In the fowl there is an epiphysis at the upper end of the tibio-tarsus and a larger one on the lower end. There is also an epiphysis at the upper end of the tarsometatarsus. The one at the upper end of the tibio-tarsus is undoubtedly a true epiphysis but the other two are more possibly elements of the tarsus which, in this case, may have an epiphysial appearance but are not true epiphyses (14). The two epiphyses at the ankle joint develop about two weeks after hatching and join with the diaphysis early. The other epiphysis is not formed until more than two months after hatching. In birds the articular surfaces are nearly as well formed as in the groups above mentioned, yet epiphyses are for the most part absent.

It can be well understood how the aquatic and semi-aquatic reptiles, such as the mosasaurs, crocodiles, turtles, plesiosaurs and their allies could have dispensed with epiphyses, but it is rather difficult to understand just why they were not developed in the Pterosauria and Theropoda, and Seeley (25) mentions epiphyses as occurring in the former.

The epiphyses which occur in the reptiles do not all have their origin in the same causes. Those on the ends of limb bones arise, undoubtedly, from different causes than do those which occur on the skull and girdle bones. Parsons calls the epiphyses at the ends of the limb bones "pressure epiphyses." This nomenclature will hold for the higher mammals where

there is a distinct pressure on the limbs but in the case of the majority of lizards, this pressure is not directly transmitted through the axis of the limb since the limbs are set, often, at angles from the body of from ten to sixty-five degrees. In the chameleons, which are to a large extent tree dwellers, the nearest approach to the mammalian attitude is attained and in these the epiphyses may be due to pressure. But in *Amblyrhynchus*, which spends a part of its time in the water, there are more epiphyses than there are in the chameleons and the limbs are set at much wider angles from the body than is the case in the chameleons. I am of the opinion that the epiphyses developed on the limbs in the majority of the Lacertilia are not due to pressure directly but that they arise from other and as yet unknown causes. It is possible that they are developed from both pressure and traction, but we need further evidence on this point.

Some of the epiphyses of the skull can be accounted for by the fact that in certain forms the elements of the skull atrophy and their remnants are left as scales of bone which resemble epiphyses, and in these cases could hardly be distinguished from epiphysial structures. Such a case of an atrophied bone is cited by Baur in the Geckonidae (15). The epiphyses which occur elsewhere on the skull and on the girdle bones may possibly be due to the strain or pull of muscles, but this is doubtful. If they do arise in this way then it must be conceded that the structures which subsequently develop into epiphyses must first be cartilage, then calcified cartilage and then bone. Whether such is the mode of origin of the "traction epiphyses" or not is still to be settled. If this should be claimed to be the case then might we not expect that in time the sternum of the Lacertilia would become osseous. As far back in geological time as we know anything about the sternum of the lizards or their relatives, it has been merely calcified cartilage. Surely the millions of years which have elapsed since the time of the early Lacertilia of the Cretaceous have given ample time for the sternum to become bony, but it is no more bony now than then. For this reason and for others it is to be doubted whether a structure can develop independently from calcified cartilage into bone although calcification is a part of the process of ossification in some forms.

The epiphyses on the carpals and tarsals of the lizards must be the degenerate elements which have become united with their fellows. This is certainly the case in some forms, but in others it is doubtful if this explanation will hold.

What the causes are which have produced epiphyses, I cannot say. It is possible that Parsons' explanation of the pull of muscles and the pressure of the body are the correct ones. So far this is merely a matter of opinion.

We have no direct evidence on these points. In this connection arises the question of the origin of the bone which goes to form any epiphysis. These and many other questions relating to epiphyses still await further investigation.

SUMMARY.

(1) There are no bony epiphyses on any of the skeletal elements of the Chelonia. (2) There are no true epiphyses on the propodials of the plesiosaurs. The conelike structures at the ends of the limb bones are in reality portions of the diaphysis and are homologous with similar elements found in all other existing groups of the Sauropsida. (3) There are no epiphyses on the skeleton of the crocodiles. (4) Epiphyses are variably present on the skeleton of the Lacertilia. (5) Epiphyses are of no importance in the classification of the larger groups of the vertebrates. (6) Parallel characters in the lizards and mammals in the presence and appearance of epiphyses on various parts of the skeleton due not to chance but to some fundamental cause. (7) The arrangement of the epiphyses on the hand and foot of lizards and mammals is of genetic importance. (8) Epiphyses are rarely present in *Sphenodon*. (9) Epiphyses are partially of a sesamoid origin but are not sesamoid bones. (10) Epiphyses are not necessary for the formation of good articular surfaces. (11) Causes of the development of the epiphyses in the Lacertilia various.

I wish in this place to express my hearty appreciation of the interest shown in my work by Drs. S. W. Williston and F. R. Lillie, and my gratitude for the help which I have received from them. The work was done under their direction and advice.

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