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Dinosaur Stapes

By Edwin H. Colbert and John H. Ostrom

INTRODUCTION

In recent months individual investigations by each of the authors have resulted in the discovery of well-preserved stapes (columella auris) in two dinosaur specimens in the collections of the American Museum of Natural History. Because preservation of the stapes is rare in fossil archosaurians and indeed has been noted only once previously in a member of either the Saurischia or the Ornithischia (when it was described by von Huene in 1926 in the prosauropod *Plateosaurus fraasianus* from the Triassic of Germany), these discoveries are considered to be of rather unusual significance.[1] They are described in the present paper.

The senior author was astonished, several months ago, when reëxamining the type skull of *Dromaeosaurus albertensis* (A.M.N.H. No. 5356) to see both stapes exposed and in position on each side of the skull. This specimen is a much better fossil than would seem apparent from the type description and the figure published by Matthew and Brown in 1922. Indeed, it merits a new study, as the original brief description and the rather diagrammatic figure are the only sources in the literature at the present time for an appreciation of the fossil. The senior author of the present contribution intends to bring out such a new study of the skull in the not too distant future.

[1] Von Huene, in his paper of 1926 on *Plateosaurus,* did not designate the species to which might be assigned No. 13200 in the Tübingen Museum (the specimen in which the stapes are preserved.) In his monograph of 1932 he created a new species, *Plateosaurus fraasianus,* and included within it this particular specimen.

In the meantime an account of the stapes in this dinosaur is given. As mentioned above, the discovery of the stapes was something of a surprise, as Matthew and Brown made no mention of the bone in their original description of the genus and species. Here was evidence, not new but rather neglected, to supplement our knowledge of dinosaurian stapes, based, until now, on von Huene's description of the bone in *Plateosaurus.*

Not long after the discovery of the stapes in *Dromaeosaurus,* the junior author, while engaged in a study of hadrosaurian cranial morphology, discovered a left stapes preserved in the plesiotype of *Corythosaurus casuarius* (A.M.N.H. No. 5338) described by Brown in 1916, which is on exhibit in the Tyrannosaur Hall of the American Museum. Unfortunately for the purposes of the present study the specimen is mounted with the right side displayed and the left side of the skull close against the plaque against which the skeleton is exposed, thus making a thorough examination of the element impossible.

The junior author was able, however, to explore the stapes and the area around it with sharp awls and other fine tools, and to study it by the use of mirrors. The photograph of the *Corythosaurus* stapes used as one of the illustrations in this paper was obtained by placing a mirror at such an angle that the reflection of the bone could be caught on the plate of the camera. Naturally such roundabout methods are not so completely satisfactory as having the specimen freely at hand, but under the circumstances we feel that they have given us reasonably accurate knowledge as to the form of the stapes in this dinosaur.

The drawings used as illustrations in this paper were made by Mr. Michael Insinna.

The abbreviations used with catalogued specimens are as follows:

A.M.N.H., the American Museum of Natural History, Department of Geology and Paleontology
A.M.N.H.:A.R., the American Museum of Natural History, Department of Amphibians and Reptiles
U.T.M., University of Tübingen Museum

DESCRIPTION

The Stapes in *Dromaeosaurus*

Evidence as to the presence and the location of a functional ear in the Saurischia, and among the dinosaurs in general, has hitherto rested on the single specimen of *Plateosaurus* mentioned above. Von Huene shows in his description of 1926 that the stapes in this dinosaur is a thin rod proximally, but expands in a horizontal plane distally so that

at its outer end it is a flattened bar with a vertical diameter of 4 mm. and a horizontal dimension of 6 mm. Its total length is 40 mm. The stapes extends from the fenestra ovalis in a posterolateral direction, descending slightly to its distal end at a point immediately behind the quadrate and beneath the paroccipital process. Although the stapes is directed slightly down, its distal end is none the less located at a fairly high position on the skull, so that a high position may be assumed for a tympanic membrane.

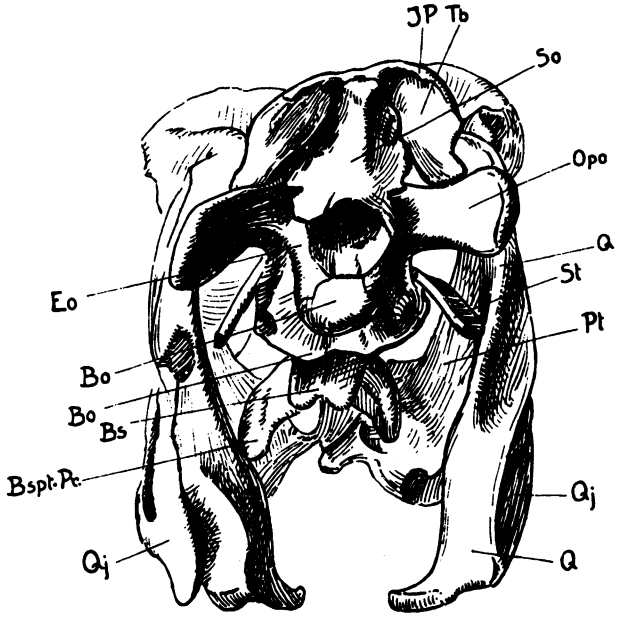

FIG. 1. *Plateosaurus fraasianus* von Huene (U.T.M. No. 13200). Occipital view of skull. Of the abbreviations, st is the stapes. From von Huene (1926). One-half natural size.

Both stapes are present in the type skull of *Dromaeosaurus albertensis*, but the stapes on the right side is much more completely preserved than the one on the left. Consequently the following description is based, for the most part, on this particular bone. Although it is remarkably well preserved, when it is considered what a small, thin bone it is, the stapes of *Dromaeosaurus* nevertheless lacks some of the proximal end, including a presumed foot plate, and perhaps a small fraction of the distal end.

Even with both ends missing, the stapes in this dinosaur is very long and rod-like. Not very much bone has been lost from either end of the

element, so that, when allowances are made for the missing portions, the estimated length of the bone is only slightly greater than the preserved length. The measurements of the stapes in *Dromaeosaurus albertensis* (A.M.N.H. No. 5356) are: length as preserved, 24.4 mm.; estimated total length, 27.5 mm.; diameter at mid-section, 1.3 mm.

The stapes in *Dromaeosaurus*, which is almost straight, runs from the fenestra ovalis laterally and posteriorly so that its outer end terminates near the upper end of the quadrate. Whereas the stapes in *Plateosaurus* takes a course slightly downward from its inner to its outer end, the bone in *Dromaeosaurus* is directed upward to some extent. This naturally results in a very high position for the outer portion of the middle-ear apparatus and correlatively for the presumed tympanic membrane.

Throughout most of its length the stapes in *Dromaeosaurus* is a cylindrical bone, but near its distal end it flares to a somewhat flattened termination, the long axis of which is horizontal. Quite possibly the shaft of the bone also flared near the foot plate, as is common in many archosaurian stapes, but of this there is unfortunately no evidence. There is no foramen for a stapedial artery.

As mentioned above, there probably is very little missing from the distal end of the stapes. Because this end of the bone rests against the posterior surface of the quadrate there is good reason for thinking that the cartilaginous extracolumella, if present, must have been comparatively short—certainly no more than half of the length of the bony stapes. These relative proportions of a long stapes, or columella, and a much shorter extrastapedial element, or extracolumella, are in accord with the conditions found in other archosaurians; in the crocodiles, for example.

Throughout its length, from the fenestra ovalis to the quadrate, the stapes in *Dromaeosaurus* is partially enclosed and protected within a groove, formed for the most part in the anterior surface of the paroccipital process of the opisthotic, but including in its anteromedial section the posterior part of the prootic. Even though open ventrally, this long groove forms a solid roof for the cavity of the middle ear. The containment of the middle ear was probably completed ventrally by a cartilaginous floor.

In summary, it may be said that the stapes of *Dromaeosaurus* is of the type that would be expected from our previous knowledge of the stapes in *Plateosaurus*, as well as from the structure of this bone in modern diapsid reptiles. It clearly indicates the probable existence of an extracolumella and a well-developed tympanic membrane, located at a high position on the back of the head.

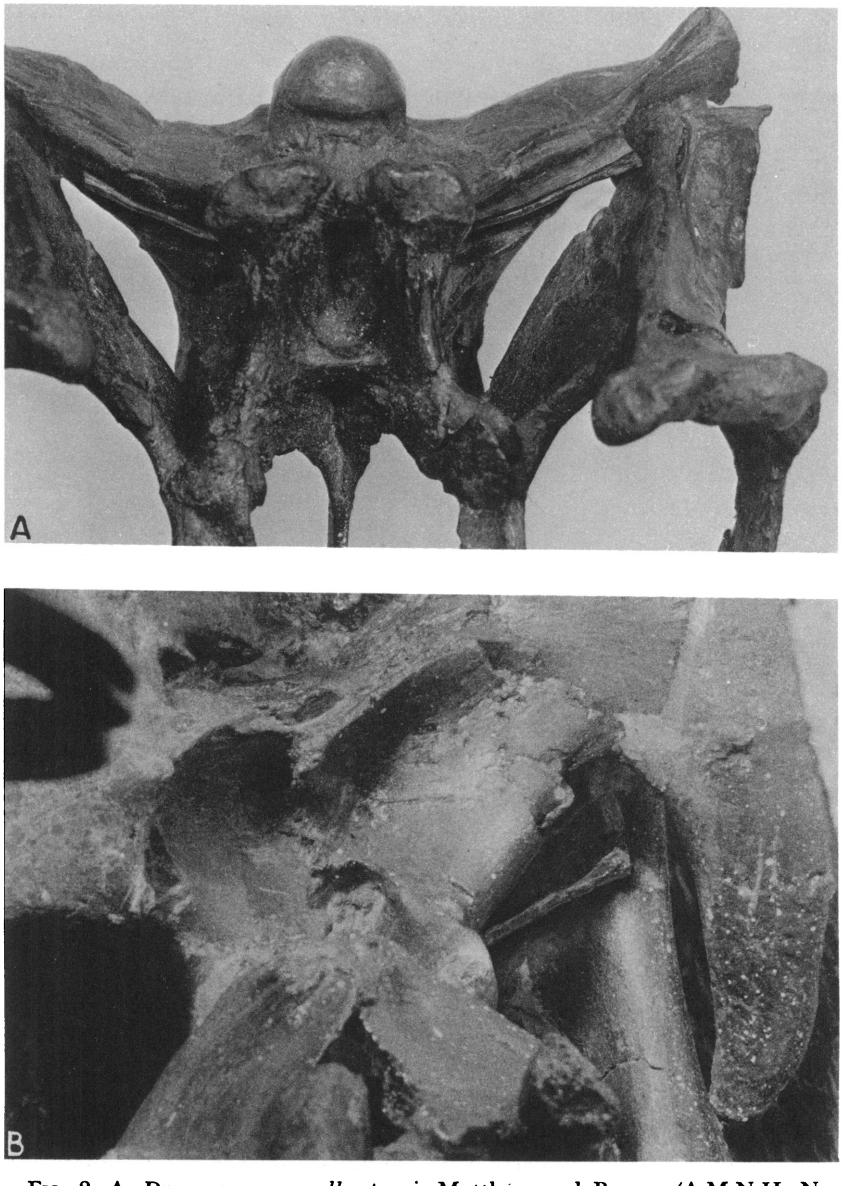

FIG. 2. A. *Dromaeosaurus albertensis* Matthew and Brown (A.M.N.H. No. 5356), type. Ventral view of posterior portion of skull, showing the two stapes in position. B. *Corythosaurus casuarius* Brown (A.M.N.H. No. 5338), plesiotype. Occipital view of posterior portion of skull, showing left stapes (here reversed, because photograph was made with aid of a mirror) in position. Both approximately natural size.

THE STAPES IN *Corythosaurus*

The presence and location of the external ear and tympanic membrane in the Ornithischia have long been debated, but never definitely established. General agreement placed the external ear posterior to the upper part of the quadrate on the lateral surface of the head. This position is now verified, at least for the Hadrosauridae, and most probably for the Ornithischia in general.

The plesiotype of *Corythosaurus casuarius* (A.M.N.H. No. 5338) was collected in 1914 by Brown and Kaisen from the Belly River beds near

FIG. 3. *Dromaeosaurus albertensis* (A.M.N.H. No. 5356). Posterior oblique view of skull showing stapes in approximate position. Note the well-defined stapedial groove, partially enclosing the stapes. Not to scale.

Steveville, Alberta. Although the specimen is incomplete, the preservation is very fine, for, in addition to the stapes, the delicate sclerotic plates are preserved, and a portion of the hyoid apparatus was found associated with the skull.

The stapes is located posterior to the dorsal fourth of the quadrate, extending from the braincase laterally to the opening between the quadrate and the paroccipital process of the opisthotic. It is a nearly cylindrical rod measuring approximately 50 mm. in length and having a maximum diameter of about 2.5 mm. at its distal end. The dorsal and anterior surfaces are not visible, but the other exposed surfaces are

FIG. 4. *Corythosaurus casuarius* (A.M.N.H. No. 5338). Posterior oblique view of skull showing stapes in position. The stapes in this dinosaur is quite free from any bony protection, a distinct contrast to the condition characteristic of *Dromaeosaurus*. Not to scale.

smooth, cylindrical surfaces which suggest a simple, rod-like shape for the main shaft. A foramen for the stapedial artery is not evident.

The proximal end is firmly fitted into the left fenestra ovalis located at the anterior margin of the opisthotic that forms the lateral wall of the posterior third of the braincase. No expanded foot plate was detected at the proximal end, but this may be present within the foramen. The fenestra ovalis penetrates the wall of the braincase at a point just medial to the anterior margin of the dorsal end of the quadrate. As a

FIG. 5. *Sphenodon punctatum* (A.M.N.H.:A.R. No. 74776). Posterior oblique view of skull showing stapes in position. The stapes is partially enclosed within a stapedial groove, a condition similar to that seen in *Dromaeosaurus*. Not to scale.

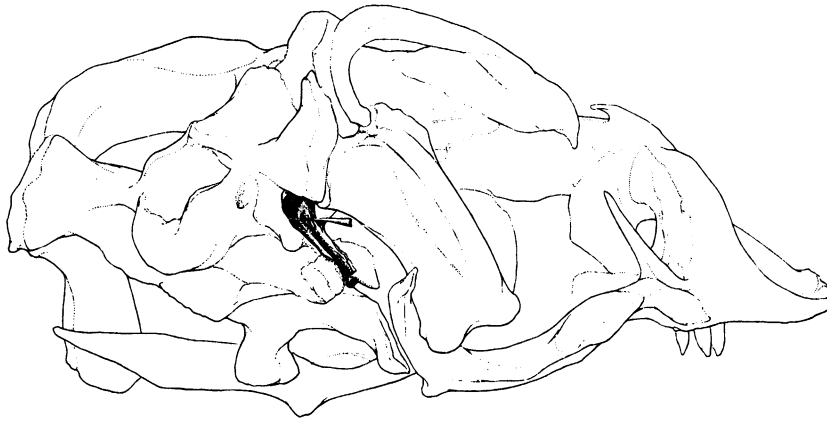

FIG. 6. *Varanus bengalensis* (A.M.N.H.:A.R. No. 71195). Posterior oblique view of skull showing stapes in position. In this lizard the stapes is free from any bony protection and in life was enclosed within a membranous middle ear. The condition here may be compared with that characteristic of *Corythosaurus*. Not to scale.

result, the stapes passes as a thin, straight rod posterolaterally from the fenestra ovalis to the lateral opening immediately posterior to the quadrate and anterior to the paroccipital process. The distal end of the stapes lies close behind the quadrate but is not in contact with this bone. This distal end does not extend laterally to the external surface of the quadrate but ends abruptly in a slight swelling approximately 10 mm. medial to this surface. Except at its distal end, the stapes is not

FIG. 7. *Crocodylus acutus* (A.M.N.H.:A.R. No. 15175). Posterior oblique view of skull showing stapes in position. In the crocodilians the stapes is completely enclosed within a tube formed by the quadrate, squamosal, opisthotic, and exoccipital. This is a highly specialized condition, probably an adaptation to aquatic habits. Not to scale.

paralleled or enclosed by other skull elements. This lack of contribution by adjacent skull elements to the formation of the tympanic or middle-ear cavity suggests that this cavity was largely membranous or cartilaginous in *Corythosaurus* and lacked bony walls.

THE STAPES IN SOME RECENT REPTILES

At this point let us consider briefly the conditions that occur in several modern reptiles: *Sphenodon, Varanus,* and *Crocodylus.*

In *Sphenodon,* the tympanic membrane has been lost. In spite of

this, a well-ossified stapes and a short, cartilaginous extracolumella are both retained. The long, rod-like stapes expands proximally into a broad, circular foot plate which fits closely into the fenestra ovalis. From this foramen, in the posterolateral wall of the cranium, the stapes passes laterally and caudally to its distal end behind the quadrate, immediately below the junction of the quadrate with the squamosal and the opisthotic. Throughout its entire length, the stapes occupies a shallow, ventrally open groove formed by the paroccipital process above and behind and the quadrate and pterygoid "wings" anteriorly.

The short extracolumella articulates with the distal end of the stapes. Although the tympanic membrane is absent, the distal end of the extracolumella is attached to an incomplete, secondary membrane. This secondary membrane is formed by a strong aponeurotic expansion extending from the posterior surface of the quadrate and the angle of the mandible to the anterior cornu of the hyoid.

Although *Sphenodon* lacks a tympanum, there are basic similarities between the ear structure of this diapsid reptile and that of some of the dinosaurs. The stapes of *Dromaeosaurus* and *Sphenodon* are strikingly similar, not only in shape, but in position as well. In both cases this element is shielded in front, above, and behind by adjacent bony elements of the skull, principally the opisthotic, prootic, and to a lesser extent the quadrate and pterygoid.

The stapes in *Varanus* is much longer and thinner than that of *Sphenodon*. For most of its length it is a simple cylindrical rod. The proximal end is expanded in a horizontal plane to form an oval foot plate embedded in the membrane that closes the fenestra ovalis. The distal end is also slightly expanded in a vertical plane, forming an oval articular surface for the more distal extracolumella. The stapes passes from the fenestra ovalis laterally and caudally and slightly downward to end just behind the quadrate. The short, cartilaginous extracolumella passes nearly the full width of the quadrate to its attachment in the exposed tympanic membrane.

Unlike that of *Sphenodon*, the stapes in *Varanus* is not protected by a bony sheath. The middle-ear cavity is entirely membranous except proximally where the fenestra ovalis is recessed between two wings of the prootic and opisthotic. This is similar to the condition found in *Corythosaurus*, in which the stapes is not enclosed or paralleled by any adjacent skull elements.

The Crocodilia possess a third arrangement quite unlike that of either *Sphenodon* or *Varanus*. The stapes in *Crocodylus* lies completely within a bony passage which extends upward and outward from the

otic capsule. This bony passage is formed almost entirely by the quadrate and only slightly by the squamosal above, and the opisthotic and exoccipital medially. The crocodilian stapes is a very thin, long bone with a large circular foot plate proximally and a slightly enlarged distal extremity. A short, cartilaginous extracolumella articulates with this distal end and completes the connection with the tympanic membrane.

The tympanum in the Crocodilia is a taut, externally concave membrane located beneath the squamosal and recessed within the large external auditory meatus. It is firmly attached to the quadrate and the overlying squamosal by the thickened fibers of the peripheral annulus tympanicus at the slight constriction of the bony middle-ear cavity at its lateral extremity. In addition to its recessed position, the tympanic membrane is further protected by a superficial, valve-like flap of epidermis above, which may be closed tightly against a fold of skin below the external opening. This protects the tympanum from damage which might result from water pressure.

Thus the tympanic cavity of the Crocodilia is quite different from that of the Lacertilia, the Rhynchocephalia, or the dinosaurs. In brief, the crocodilian cavity is a bony passage lined with membrane, while the cavity of the other forms is partly or completely membranous, with incomplete bony walls.

GENERAL DISCUSSION

It is stated that the stapes of *Dromaeosaurus* and *Corythosaurus* are simple rod-like elements. In both cases the form of the proximal end is unknown, but at the distal end there is a slight over-all expansion. The stapes of *Plateosaurus*, on the other hand, is not uniform for all of its length but expands gradually into a broad, flat bar distally. In all three fossil stapes the distal end is noticeably enlarged, as it is in modern reptiles. As this distal expansion in modern reptiles provides an enlarged surface for the articulation of the cartilaginous extrastapedial element, the presence of such an expansion in the dinosaurian stapes is interpreted as a similar adaptation, thus indicating that an extrastapedial element existed in the dinosaurs.

Additional evidence that suggests the presence of an extracolumella in the dinosaurs is the length of these fossil stapes. Although the *Corythosaurus* skull has been deformed somewhat (which appears to be true of von Huene's *Plateosaurus* specimen also), the *Dromaeosaurus* skull is almost completely uncrushed. In the latter, the stapes fail to extend the entire distance between the fenestra ovalis and the external surface of the quadrate; the distal end of the stapes terminates about

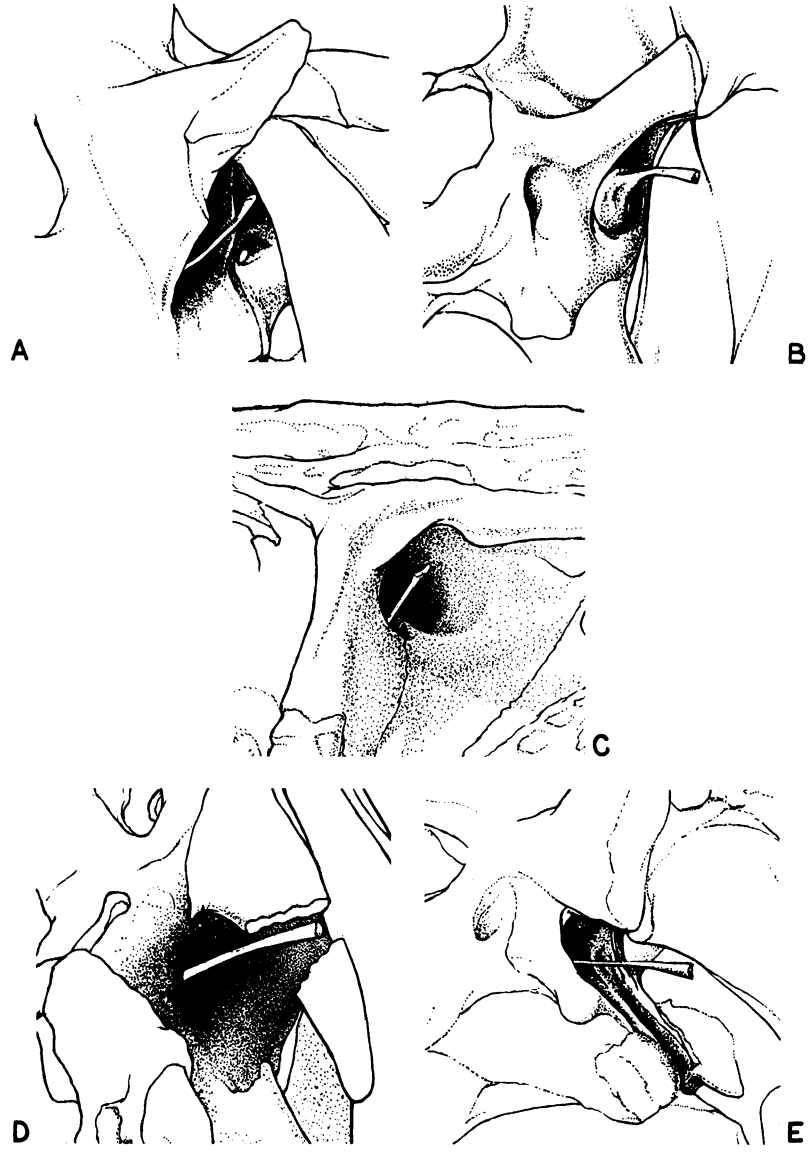

FIG. 8. The middle-ear regions of the five skulls shown in figures 3–7. A. *Dromaeosaurus albertensis*. B. *Sphenodon punctatum*. C. *Crocodylus acutus*. D. *Corythosaurus casuarius*. E. *Varanus bengalensis*. This figure shows in detail the position of the stapes within a stapedial groove in *Dromaeosaurus* and *Sphenodon*, as contrasted with the "free" stapes in *Corythosaurus* and *Varanus*, and also the highly specialized middle ear of *Crocodylus*. Not to scale.

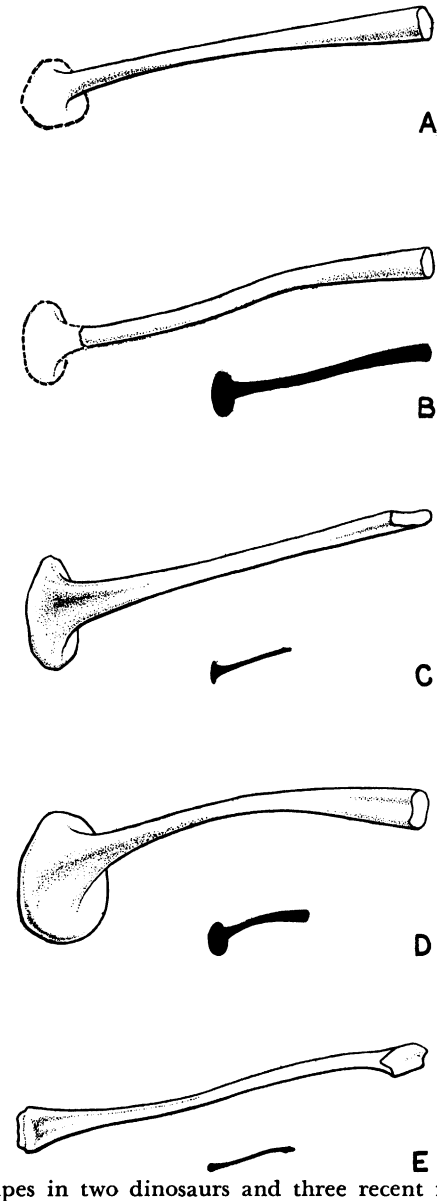

FIG. 9. The stapes in two dinosaurs and three recent reptiles, all in posterior view. A. *Corythosaurus casuarius* (A.M.N.H. No. 5338). B. *Dromaeosaurus albertensis* (A.M.N.H. No. 5356). C. *Crocodylus acutus* (A.M.N.H.:A.R. No. 15175). D. *Sphenodon punctatum* (A.M.N.H.:A.R. No. 74776). E. *Varanus bengalensis* (A.M.N.H.:A.R. No. 71195). Drawn to unit length. A. Natural size. B–E. Black silhouettes are natural size.

4 mm. medial to this surface. The same situation occurs in *Corythosaurus*, in which the stapes falls short of the lateral surface by 10 mm., and apparently also in *Plateosaurus*. The failure of the stapes to reach the outer surface of the quadrate in these last two cases may have been even more pronounced in life, as these two skulls are both somewhat crushed laterally.

Because the tympanic membrane in most living reptiles occupies an exposed superficial position slightly lateral to the outer surface of the quadrate, a similar position is inferred for the dinosaurs. The distance between the distal end of the stapes and the probable position of the tympanum requires the presence of a cartilaginous extrastapedial element distal to the stapes to complete the connection between the external tympanic membrane and the inner ear. It is possible that the tympanum was slightly depressed into the space behind the dinosaurian quadrate (the crocodilian tympanum is deeply recessed), in which case the extracolumella might have been very short indeed.

Of course the assumption that a tympanic membrane was present in the dinosaurs may be questioned, because, on the basis of *Sphenodon*, it can be shown that the presence of a stapes does not guarantee the presence of a tympanum. Other recent forms that have lost the tympanum are specialized burrowing lizards and snakes, in which the hearing is effected by bone conduction. But in non-burrowing, terrestrial lizards the tympanum is usually present. It therefore seems quite logical that the dinosaurs, being non-burrowers, possessed a superficial tympanic membrane located immediately behind the quadrate.

The considerable bony protection of the stapes in *Dromaeosaurus*, and the almost complete absence of any bony protection for this element of the middle ear in *Corythosaurus*, raise the question of the structure of the middle ear among all the dinosaurs. As the stapes is known in only three forms (*Dromaeosaurus*, *Plateosaurus*, and *Corythosaurus*), conclusions as to the relationship of this bone and adjacent skull elements in other dinosaurs must of necessity be based on inferences. But knowing the relationships of the stapes to skull elements in those genera in which the stapes are preserved and having before us in other dinosaurian skulls the form of the paroccipital process and the position of the fenestra ovalis with regard to the paroccipital, we believe it is justifiable to make inferences concerning the middle ear in the various dinosaurs.

If the coelurosaurian theropods are considered as the most generalized of the saurischians, a point on which there is general agreement, and if these dinosaurs are considered as more primitive than any of the

ornithischians, as is usually considered to be the case, then the condition of the middle ear in such forms can be taken as a starting point from which the otic structure in other dinosaurs may be derived. In turn, the middle ear of the coelurosaurs may be compared with, and possibly derived from, that in the Triassic thecodonts, the basic archosaurians.

In Camp's monograph on the phytosaurs (Camp, 1930, fig. 37) there are some excellent figures showing the details of cranial structure and the otic region in these thecodonts. Camp demonstrates quite clearly that in the phytosaurs the stapes extended from the fenestra ovalis to the region of the tympanum within a groove formed on the lower surface of the paroccipital process. His description is as follows: "The stapedial groove continues postero-laterally beneath the ventral margin of the paroccipital as far as the narrowest part of its shaft. Here it gradually dies out. Its direct projection would indicate that the outer end of the *stapes* lay in the groove, formed by the quadrate, beneath the squamosal expansion of the paroccipital, and that the tip of the stapes on the external tympanum lay in the center of the notch just behind the quadrate foramen.

". . . The stapes . . . in a large animal would have been about 200 mm. in length and much flattened in cross-section at its outer end, becoming more rounded near the foot plate" (Camp, 1930, p. 112).

This description applies very nicely in its essential details to the relationships of stapes and paroccipital process in *Dromaeosaurus*. Whether it can be applied with equal facility to the stapes and paroccipital process in other theropods, especially the earliest forms from upper Triassic sediments, cannot at this time be determined definitely on the basis of materials at hand. It seems significant, however, that such close resemblances should characterize the middle ear in a thecodont, such as a phytosaur, and a theropod, such as *Dromaeosaurus*. The resemblances point to the possibility that the condition of the middle ear in these forms is a basic one among the archosaurs.

Much the same relationship of stapes to paroccipital seems to have held over into the giant carnosaurs, except that among these dinosaurs the stapedial groove is perhaps less pronounced than is the case in *Dromaeosaurus*.

One might expect this structure of the middle ear to be continued in the sauropod dinosaurs, but such is not the case. In these dinosaurs the paroccipital process is commonly curved and bent downward. Along with this development there seemingly has been a flattening out or even an elimination of the stapedial groove. Perhaps one might envis-

age the evolutionary process here as being a sort of arching of the paroccipital away from the stapes. Thus it seems likely that the stapes in the sauropods might commonly have been largely unprotected by bone; perhaps it was enclosed within a membranous middle-ear cavity, similar in a general way to the middle ear as described above for the lizards (Janensch, 1935, fig. 2). Perhaps a foreshadowing of this condition is to be seen in *Plateosaurus*, in which the stapes is not intimately associated with the paroccipital process, even though the latter is not modified as to shape as it has been in many of the sauropods.

The middle ear of *Corythosaurus*, as described above, illustrates the condition that is typical of the ornithopods. In these dinosaurs there

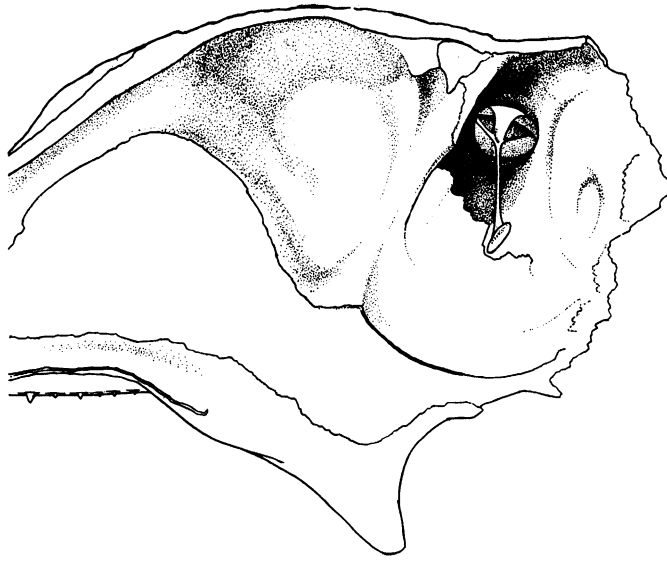

FIG. 10. *Alligator mississippiensis*, from a dissection, showing stapes and extrastapedial elements in place, as seen from within the cranial cavity. Note the elongated foot plate of the stapes and the trifid structure of the cartilaginous extracolumella, attaching to the tympanic membrane. Four times natural size.

has been a marked arching of the paroccipital process, so much so indeed that the long axis of the bone follows a semicircular course, as seen in occipital aspect. Thus the stapes is left as an "exposed" bone, which in life must have been enclosed by membrane. This development represents among the dinosaurs the extreme departure from the primitive condition as seen in the theropods.

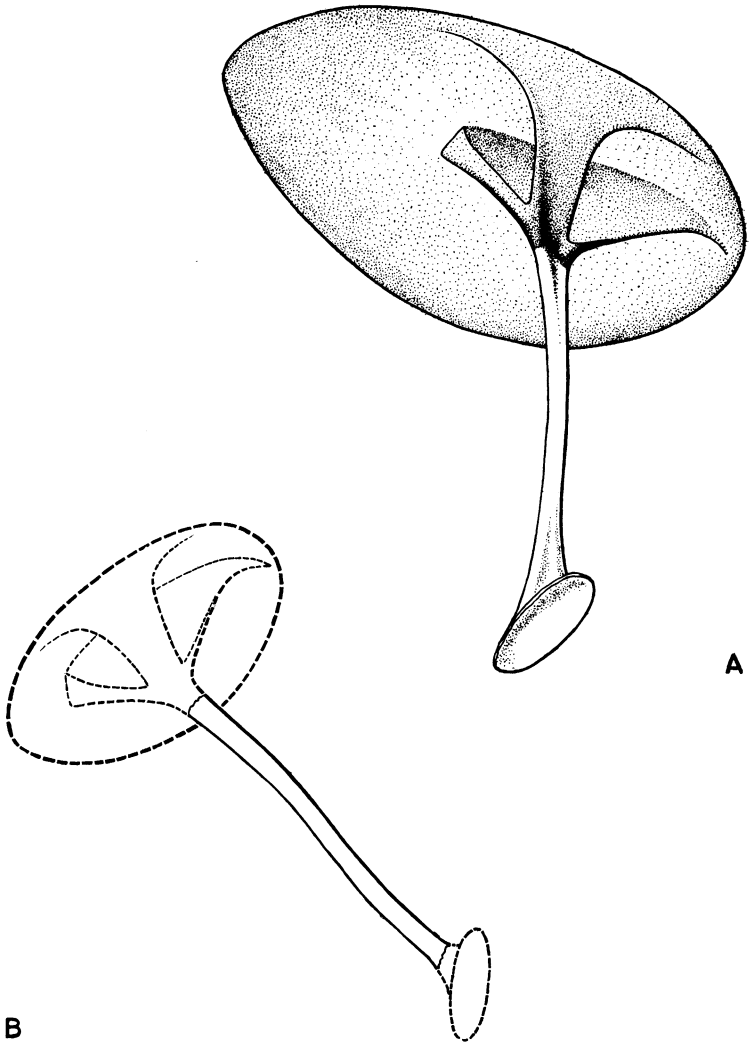

FIG. 11. A. *Alligator mississippiensis*, from a dissection, showing the stapes as seen from approximately the same position as in figure 10. The extracolumella and the tympanic membrane are stippled. Ten times natural size. B. *Dromaeosaurus albertensis* (A.M.N.H. No. 5356), showing the stapes as viewed from approximately the same position as in figure 10, with the foot plate, extracolumella, and tympanic membrane restored; the restoration is based on the shape of the homologous parts in the crocodilians. Twice natural size.

In the ceratopsians, on the other hand, the structure of the middle ear appears to approximate rather closely the condition found in the primitive theropods (Brown and Schlaikjer, 1940, fig. 15). Thus the paroccipital is elongated, extending out as a flat, straight bone on each side of the occiput. On the lower portion of its anterior surface there is a distinct groove that fades laterally, and this groove, as its inner and deepest portion leads to the fenestra ovalis, must be regarded as a stapedial groove, similar to the one seen in the thecodonts and in the primitive theropods. It is unfortunate that no stapes has as yet been recognized among the known remains of ceratopsians; it must have been a very long bone.

The middle ear in the stegosaurs is rather similar to that in the ceratopsians, except that the paroccipital process is a comparatively short bone (Gilmore, 1914, fig. 10). But as in the ceratopsians, it has a stapedial groove on the lower part of its anterior surface, and this groove must have accommodated a well-developed stapes.

Among the ankylosaurs there have been modifications of the paroccipital, with correlative effects on the structure of the middle ear. The paroccipital process in these dinosaurs is a flattened bone, with a smooth anterior surface. Its lower border is arched (Sternberg, 1929, pl. 18, fig. 1). Therefore it would seem probable that the stapes in the ankylosaurs was not closely associated with the paroccipital process and that it ran from the fenestra ovalis to the general area of junction between the paroccipital and the quadrate, with most of its length enclosed within a membranous sheath.

To review these remarks, it may be said that the primitive middle ear among the dinosaurs is exemplified by the middle ear of *Dromaeosaurus*, in which there is a well-defined stapedial groove along much of the course of the paroccipital process. It is probable that this condition is a heritage character derived from the Triassic thecodonts. This type of middle ear is continued with variations in the theropods, and also among the ceratopsians and the stegosaurs. There have been departures from this "basic archosaurian" middle ear in the sauropods, the ornithopods, and the ankylosaurs, all probably independently achieved. Such departures, all of which involve significant changes in the shape and the structure of the paroccipital process, probably have been a result of evolutionary changes in the structure and the proportions of the skull as a whole among these particular archosaurian groups. Finally, this review leads to the conclusion that the middle ear was well developed among all the dinosaurs and that the stapes was

regularly present among the several groups and the various genera that constitute these two reptilian orders.

Our discussion of the external and middle ear in the dinosaurs ultimately leads to the question of whether or not the dinosaurs could hear. Because the presence of a stapes in three genera of dinosaurs, while not conclusive in itself, suggests that an external membrane was present, we certainly have good reason to think that they possessed a sense of hearing. Hearing is a distinctly advantageous faculty in terrestrial animals, serving two functions that are quite necessary for survival of the species. First, it enables the individual to detect and recognize the presence of members of its own species (in those forms that are capable of making audible sounds). Second, in most modern forms it is a protective sense which warns the individual of the approach of its natural enemies.

Whether the dinosaurs had a voice or not is a debatable point, as this can never be established one way or the other on the evidence of the fossils. It may be significant that crocodiles, the nearest living relatives of the dinosaurs, are notoriously noisy reptiles, especially during the breeding season. Therefore it seems reasonable to suppose that the dinosaurs, the large archosaurian cousins of the crocodilians, also were reptiles with strong voices.

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