The Extracolumella and Tympanic Cavity of the "Earless" Monitor Lizard, *Lanthanotus borneensis*

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*Lanthanotus borneensis* lacks a tympanic membrane, but has a transversely shallow tympanic cavity, walled medially by the quadrate and laterally by the extracolumella. The ossified part of the stapes barely enters the cavity, but is bound to the quadrate. The extracolumella is discoidal and very similar to the structure generally identified as an “ossified tympanic membrane” in some Mosasauridae. The similarity of *Lanthanotus* to the Mosasauridae in ear structure confirms the close relationship between the families. The snake ear can be easily derived from that of the *Lanthanotus*-mosasaur group through loss of extracolumella and tympanic cavity. The nodule intervening between the quadrate and the stapes in snakes, identified as the intercalary by most recent authors, is identified as the processus internus plus the most proximal part of the extracolumella. Some misstatements and important over-sights in the literature are corrected.

**INTRODUCTION**

THE earless monitor of Sarawak, *Lanthanotus borneensis* Steindachner, is a surviving relative of the Cretaceous lizards of the families Dolichosauridae, Aigialosauridae, and Mosasauridae (McDowell and Bogert, 1954) without an external tympanic membrane. The soft anatomy, aside from the form of the tongue, has not been described, but the snake-like features of its skull suggest it is morphologically annecant between the snakes and the lizards of the superfamily Varanoidea or Platy nota (op. cit.; contrary opinion expressed by Underwood, 1957a and 1957b).

I have recently been able to dissect the right middle ear of an adult female *L. borneensis* in the American Museum of Natural History (AMNH 87575), received from the New York Zoological Society in 1961. (This specimen is preserved with the mouth open, and the quadrate thrust forward.) There is no tympanic membrane, but rather the thick skin of the head continues over the middle ear without differentiation. Beneath this skin is found the extracolumella (Fig. 1), which is cartilaginous and roughly oval in form. A narrow fissure separates the extracolumella from a tough connective tissue rim on the edge of the external concha of the quadrate bone. The outer surface of the extracolumella is smooth and convexly curved, and the extracolumella is both the lateral and the posterior wall for the tympanic chamber. The depressor mandibulae muscle lies immediately behind the middle ear and slightly overlaps the rear of the extracolumella (it is drawn pulled slightly caudal in the figure, to expose the extracolumella fully).

The plate-like extracolumella is not of uniform thickness, but has a thick nucleus on its posterior edge, continued forward and downward across the disc by an L-shaped thickening. When viewed from outside (upper drawing in Fig. 1) this shows as a paler and more opaque area on the extracolumella; when the extracolumella is reflected (lower
McDowell—Earless Lizard Extracolumella

drawing), this thickening shows as a ridge on the inner side of the disc. The thickening perhaps represents the pars inferior of the extracolumella (terminology of Oelrich, 1956) of such unspecialized lizards as Ctenosaura. A band of connective tissue forming a juncture between the extracolumella and the tip of the paroccipital process on the posteroventral wall of the tympanic chamber probably represents the extracolumella ligament, but there is no intercalary cartilage or bone.

The junction between the extracolumella and bony stapes is firmly bound to the body of the quadrate in the apex of the arch-like postero-ventral profile of that bone, and the bony stapes is in contact with the quadrate, as figured by McDowell and Bogert (1954). The photograph published by them was misinterpreted by Underwood (1957b) to indicate that the stapes was isolated from the quadrate, in spite of a note in the text of the contact. (Unfortunately, it seems Underwood was unable to examine the skull figured until too late for retraction of the erroneous implications of his published statement.)

The tympanic cavity, which is remarkably shallow, does not extend medial to the level of the stapes-quadrate contact, and the quadrate bone forms both the medial wall and the roof of the cavity. The Eustachian tube has a large and circular orifice just ventral to the stapes-quadrate contact. Because of the slight medial extent of the tympanic cavity, the chorda tympani nerve does not lie in its wall but lies medial to the cavity.

The middle ear structures that lie medial to the tympanic cavity were examined through a ventral incision, as illustrated in Fig. 2. The stapes has a cartilaginous processus internus, narrow and tongue-like in form, that runs forward along the inner surface of the posterior crest of the quadrate (Oelrich's terminology). Because of the direct stapes-quadrate contact, the entire length of the processus internus is applied against the quadrate bone, rather than just the tip as usual in lizards. The chorda tympani nerve is just lateral to the base of the processus internus and runs along the inner surface of the posterior crest of the quadrate.

The Eustachian tube (which here represents both the Eustachian tube and the medial part of the tympanic cavity of normal lizards) runs almost parallel to the stapes and dips ventrally to open into the pharynx. It does not become closely applied to the scala tympani, and hence there is no secondary tympanic membrane. (The secondary tympanic membrane of lizards is discussed by Baird, 1960.)

Discussion

The expanded and disc-like extracolumella and the medial limitation of the tympanic cavity by the quadrate, along with absence of a secondary tympanic membrane, make the middle ear of Lanthanotus a surprisingly close analogue to that of turtles, and in the lack of differentiation of the skin to form a tympanic membrane and the shallowness of the cavity there is a particularly close analogy to the thoroughly aquatic softshell turtles (Trionychidae and Carettochelyidae).
Lanthanotus is now known to be both a superficial burrower and a highly aquatic form (Harrison and Haile, 1961) with extreme dorsal displacement of the nostrils as an adaptation to life in water (Mertens, 1964).

McDowell and Bogert argued from its lower jaw structure, shortened limbs, and other details that Lanthanotus is most closely related to the Cretaceous lizards of the families Aigialosauridae, Mosasauridae, and (particularly) Dolichosauridae. All of these lizards are from marine deposits and seem to have been at least partially aquatic; the limb modifications of the Mosasauridae indicate that family was thoroughly aquatic. The stapes and quadrate of the Dolichosauridae are essentially unknown, but the ear skeleton of Mosasauridae has been described by numerous authors (reviewed by R. Hoffstetter in Piveteau, 1955:630-637) and the quadrate of the aigialosaurids Opetiosaurus (Kornhuber, 1901) and Aigialosaurus (Kramberger, 1892) indicate virtual identity of that group with the mosasaur in ear structure.

In some of the mosasaurs, such as Plioplatecarpus, the middle ear chamber of the quadrate was completely covered by an ovoid lid. This lid is usually identified as an ossified tympanic membrane, but in not overlapping the edge of the quadrate and in being a much flattened cone with an inner ridge it more closely resembles the discoid extracolumella of Lanthanotus (Fig. 3). The other mosasaurs probably had a similar ear, to judge from the quadrate, but lacked ossification of the extracolumellar disc. In mosasaurs, the quadrate surrounds the middle ear chamber essentially completely on the medial side, leaving only a small meatus or narrow notch for the stapes-extracolumella; so closely does the quadrate impinge on the stapes that the bones would have to be called “in contact” unless one is also prepared to quibble with the statement, “the hip-bone’s connected to the thigh-bone,” because there is an intervening joint apparatus. On the inner face of the quadrate, just anterior to the meatus, the mosasaurs have a pit for the processus internus of the stapes, a part of the stapedial apparatus that is ossified as a small bone in Plioplatecarpus. The processus internus of Lanthanotus is not received in a pit, but the position of the processus in Lanthanotus is as in mosasaurs. In the extreme shallowness of the tympanic cavity, as indicated by the form of the quadrate, the mosasaurs and aigialosaurs strongly resemble Lanthanotus.

It is worth noting that the middle ear of Plioplatecarpus would yield a remarkably snake-like structure if the tympanic cavity and extracolumella disc were to disappear and their space (essentially the entire rear aspect of the quadrate) be taken over by a quadrate head of the depressor mandibulae muscle; the little ossecle representing the processus internus would correspond closely to the position of the ossecle on the inner surface of the upper end of the quadrate of snakes, an ossecle connected to the tip of the stapedial shaft. Although Bellairs and Underwood (1951) discussed the contact of the stapes with the quadrate as a snake-like character in some burrowing lizards, they omitted all mention of the stapes-quadrate contact of mosasaurs. This oversight is unfortunate, because the mosasaur condition is decidedly more snake-like in detail than is the condition in the burrowing lizards with such contact that I have examined (Dibamus novaeguineae, Anelytropus papillosus, Felinia currori, and Annifella pulchra). In mosasaurs the stapedial shaft is snake-like in being slender and directed backward to
connect (in Plioplatecarpus, at least) with an ossicle on the inner face of the quadrate; but in the burrowing lizards the stapes has a very short and thick shaft (perforated in the first three genera) that extends forward to meet the rear surface of the quadrate (indirectly, through a reduced extracolumella, in Annia). The nodule or ossicle in mosasaurs is placed in the same position as that of snakes, and is also similar to the position of the processus internus of other lizards.

In snakes, the nodule is identified by de Beer (1957) as an intercalary, although he noted (p. 247), "The relation to the facial nerve would be the same in the case of a processus internus [as in the case of an intercalary]. . . . . . . ."

The nodule in both snakes and mosasaurs is attached to the inner surface of the dorsal end of the quadrate, the usual attachment of a processus internus, rather than to the paroccipital process (the usual site of an intercalary in lizards). If the nodule in snakes is indeed an intercalary, in spite of appearances in the adult to the contrary, then it would seem equally reasonable to consider the nodule in mosasaurs as an intercalary, in spite of all appearances to the contrary. Simplicity is best served by considering it the processus internus in both groups.

Kamal and Hammouda (1965) discussed the homologies of the nodule on the inner face of the quadrate in snakes, and reached conclusions essentially identical with those of de Beer. But while the relations of this nodule to the chorda tympani and to the embryonic remnants of a middle ear cavity (points discussed by Kamal and Hammouda) demonstrate clearly that the nodule is not the tympanic portion of the extracolumella, there are no such points to show the nodule is an intercalary (part of the processus dorsalis) rather than the processus internus. Lanthanotus and Varanus, as well as some geckos and skinks, are unusual among lizards in lacking an intercalary. This latter represents the tip of the processus dorsalis of the stapes, a process that extends dorsally to meet the paroccipital process just behind the contact of the latter with the cephalic condyle of the quadrate. The tip of the processus dorsalis usually is not directly connected with the stapes in the adult, but is represented by a nodule, the "intercalary" on the paroccipital process connected with the stapedial apparatus by ligament. Study of de Beer's and Kamal and Hammouda's arguments shows their only reason for believing the nodule on the ophidian quadrate to be an intercalary, rather than a processus internus, is that there is ample precedent among lizards for dissociation of the processus dorsalis from the stapes, but no precedent among living lizards for dissociation of the processus internus. The ear of the mosasaur Plioplatecarpus is precedent for the isolation,
at least so far as ossification is concerned, of the processus internus.

In most snakes, the parocipital process is vestigial or absent and is remote from the quadrate. It is not altogether farfetched, therefore, to argue that the processus dorsalis has been shifted from its usual dorsal direction to an horizontal direction, and from a connection with the parocipital process to a connection with the quadrate. (I take this to be de Beer's argument.) In some snakes, however, the quadrate is still in association with the parocipital process; examples are Cylindrophis and uropeltids. In these snakes the nodule is attached to the quadrate as in other snakes, rather than to the parocipital process, and it is very difficult to see why this should be so unless the nodule represents the processus internus, which normally connects with the quadrate in lizards. Baumeister (1908) has described the nodule between stapes and quadrate in the uropeltid Rhinophis, and Smith (1943) noted that in Cylindrophis the stapedial region is as in Xenopeltis (that is, with a nodule intervening between the shaft of the stapes and the quadrate).

The nodule, here identified as the processus internus, is connected to the stapes only by elastic tissue in snakes, although Kamal and Hamouda (1965) have demonstrated that it arises in continuity with the stapedial shaft. Although many authors consider the processus internus part of the "otostapes" because it lies medial to the chorda tympani, the processus is functionally part of the extracolumella ("hyostapes") in many lizards, including Varanus and Lanthanotus, because it lies distal to a flexible joint between the shaft of the stapes and the extracolumellar apparatus. If the extreme base of the extracolumella of Varanus or of Lanthanotus (i.e., the part medial to the chorda tympani and articulating with the stapedial shaft) were retained, along with the attached processus internus, and the rest of the extracolumellar apparatus lost, then the joint between the stapedial shaft and extracolumellar remnant would be in precisely the same position as the elastic connection between stapedial shaft and nodule in snakes. Thus, the dissociation as a nodule of the processus internus of snakes can be interpreted as the result of the loosening of a joint already developed in lizards. By this interpretation, the nodule in snakes would correspond, to be precise, not to the processus internus, but to the processus internus plus the section of the extracolumella medial to the chorda tympani and lateral to the joint.

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