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THE EAR IN MAMMAL-LIKE REPTILES AND EARLY MAMMALS

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The early members of the Theropsida lacked a tympanic membrane. In the later theropsids, the Therapsida, a tympanic membrane developed from the skin on the lateral side of the lower jaw. The tympanum is not homologous in the Therapsida and the Sauropsida. The therapsid ear was a poor receiver of airborne sound, both in high frequency response and in the range of frequencies encompassed. With the radiation of the Sauropsida in the Triassic the large therapsids became extinct, the small therapsids evolved into the mammals and became nocturnal. High frequency hearing was essential for the nocturnal mode of life; quadrate and articular became dissociated from the jaw hinge to become the mammalian auditory ossicles. In the Theria the cochlea became coiled. The spiral cochlea could not have existed until there was a middle ear with the necessary high frequency response. This may not have been until the Cretaceous.

Key words: Theropsida, Therapsida, *Morganucodon*, *Kuehneotherium*, monotremes, Theria, Mesozoic, ear, hearing.

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Reichert suggested in 1837 that two of the mammalian auditory ossicles (incus and malleus) equated with the reptilian quadrate and articular. This was confirmed by the work of Palmer (1913) on the development of the pouch young of *Perameles* (figs. 1, 2). Thus, for the last sixty eight years, there has been no doubt that the bones, which in a mammal-like reptile form the hinge of the jaw, in a typical mammal transmit sound from the tympanic membrane to the inner ear. Equally it is certain that the bone which supports the tympanic membrane in a mammal is represented in mammal-like reptiles by another bone of the lower jaw — the angular.

The problems which remained quite intractable were the location of the tympanum in the mammal-like reptiles, and the manner in which

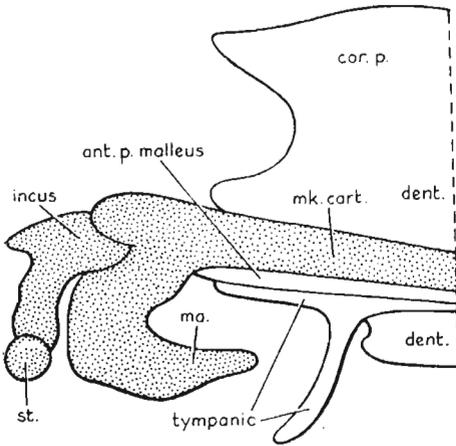


Fig. 1. *Perameles*: diagrammatic medial view of the posterior end of the lower jaw and the ear bones of a fetus (after Palmer 1913).

See page 157 for abbreviations

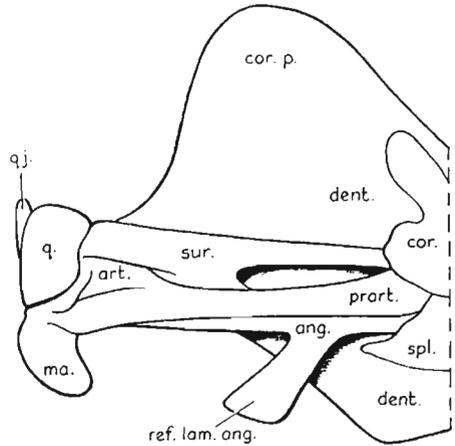


Fig. 2. *Diademodon*: diagrammatic medial view of the jaw articulation and the posterior end of the lower jaw.

the ear functioned as a receptor of sound. The solution of these problems was long delayed because they were studied by palaeontologists entirely from the point of view of evolution and not at all from the point of view of acoustics. Whether the ears postulated by the palaeontologists would actually have functioned as receivers of sound seems not to have bothered them overmuch. On the other hand, those physiologists who were interested in the problem did not put their criticisms in terms understood by the palaeontologists.

There were two schools on how the ears of mammal-like reptiles were constructed. The leader of one was Watson (1953). His studies had convinced him that the early mammal-like reptiles, along with their close relatives the captorhinomorph cotylosaurs, completely lacked a tympanic membrane. These animals heard by bone conduction. In the later mammal-like reptiles, he considered that a tympanum existed supported by the reflected lamina of the angular, which is the homologue of the mammalian tympanic bone. In both cases we have no doubt at all that he was right. Unfortunately Watson was influenced by the theory put forward by Gregory (1910), that a groove in the therapsid squamosal housed the external auditory meatus. This groove terminates just posterior to the quadrate. Hence it would place the eardrum in therapsids in exactly the same place as it occupies in primitive sauropsid reptiles — directly posterior to the quadrate, with the leading edge of the membrane attached to the quadrate bone. Watson, therefore, extended the tympanic membrane back to this position. Having done this, he then felt impelled to connect the stapes to the tympanic membrane by a purely hypothetical extra-stapes (fig. 3).

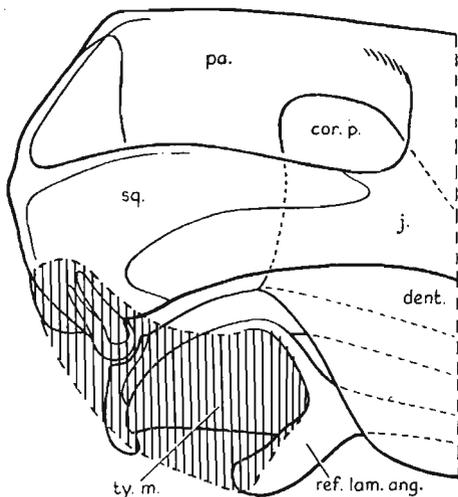


Fig. 3. *Thrinaxodon*: diagrammatic lateral view of the posterior part of the skull to show the tympanic membrane as restored after Watson (1953).

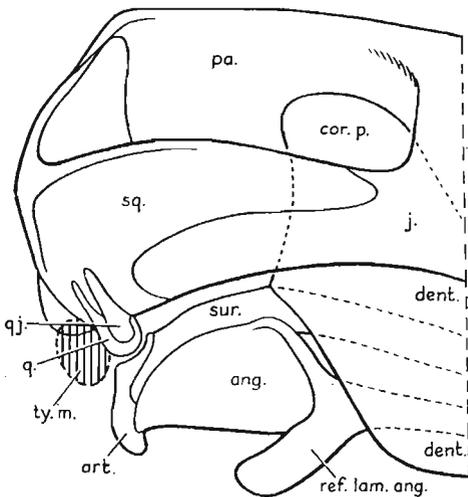


Fig. 4. *Thrinaxodon*: similar view to figure 3 but showing the position of the tympanic membrane as restored after Parrington (1949). He accepted Broom's theory.

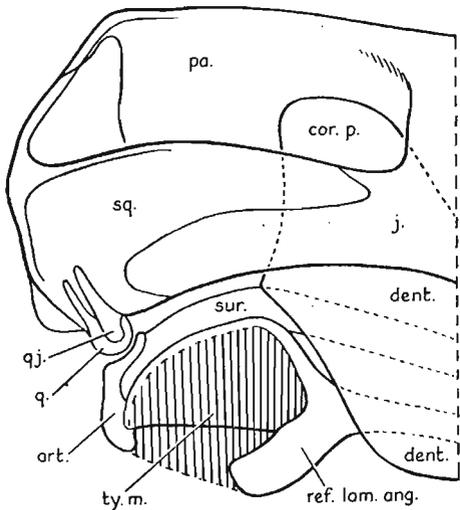


Fig. 5. *Thrinaxodon*: similar to figure 3 but showing the position of the tympanic membrane as restored after Allin (1975).

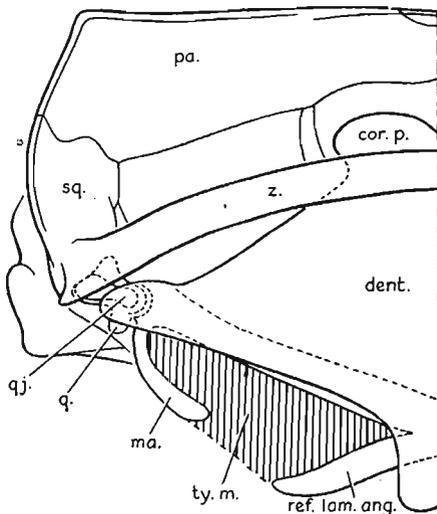


Fig. 6. *Morganucodon*: similar view to figure 3 showing the position of the tympanic membrane as restored by Kermack *et al.* (1981).

See page 157 for abbreviations

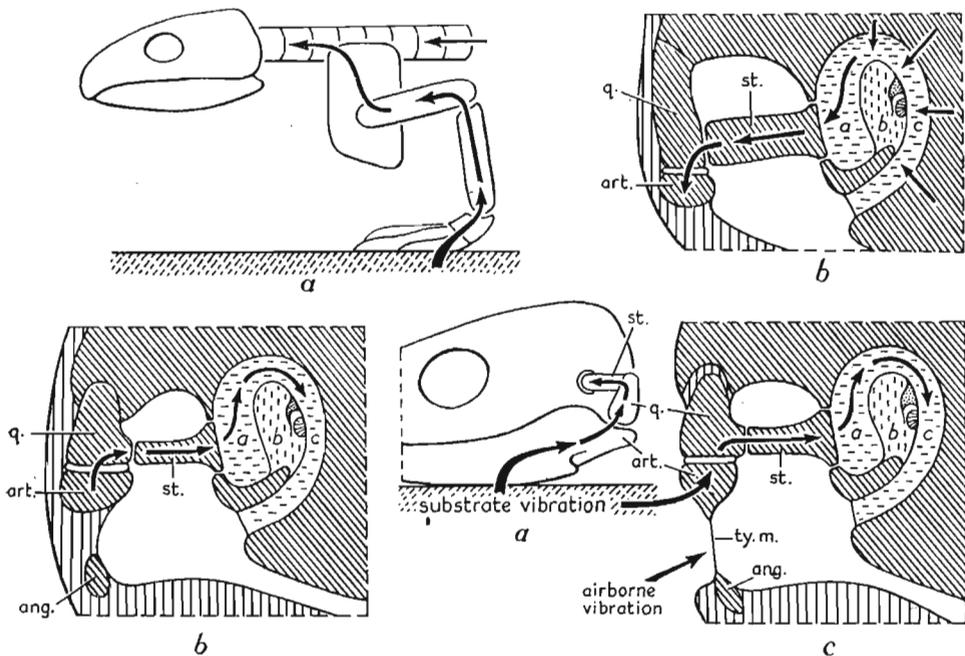


Fig. 7. (Top). To illustrate the *indirect* route of conduction of sound from the ground to the inner ear: *a* diagram showing path of sound waves through the body to the ear; *b* diagrammatic vertical section of the ear showing the passage of the sound waves through it.

Fig. 8. (Bottom). To illustrate the *direct* route of sound conduction: diagrams *a* and *b* show the reception, by an ear without a tympanic membrane, of sound waves transmitted through the ground; *c* is a diagrammatic vertical section of an ear with a tympanic membrane receiving airborne sound.

See page 157 for abbreviations

The second school was led by Broom (1912, 1936). He simply postulated that the ear in therapsids was the same as the ear in sauropsids; the tympanum being entirely posterior to the quadrate and supported by it (fig. 4). Again the tympanum would have been contacted by an entirely hypothetical extrastapes. We shall see later that this ear could not possibly have functioned as a receptor of airborne sound.

Tumarkin (1968) stated quite categorically that in mammal-like reptiles there was no tympanum and hearing was entirely by bone conduction. He distinguished two routes by which sound waves in the ground reached the inner ear. In what he called the "direct route" the acoustic energy passed *via* the lower jaw, assumed to be resting on the ground, the quadrate and the stapes to the endolymph (fig. 8). In the "reverse route" (Indirect route of Kermack *et al.* 1981) the sound reached the inner ear *via* the legs, the vertebral column and the bones of the skull (fig. 7). Tumarkin commented that the cells of the cochlea are only receptive to the movement of the endolymph. They are not sensitive to changes in

pressure. For this movement of the endolymph to take place, there must be in the system a fixed reference point. In the direct route the stapes moves and the periotic bones remain stationary; in the indirect route it is the skull bones which vibrate and the stapes forms the fixed reference point. Clearly, the greater the mass of the stapes the more efficiently it will form this fixed reference point. Nor would a massive stapes, as in a pelycosaur, be a disadvantage in direct route conduction. The stapes did not vibrate as an entity (Watson 1953), as it does when a tympanum is present; but sound waves were propagated along it.

Tumarkin's theory explained two remarkable facts: the invariable contact of the stapes and the quadrate in the Theropsida, and the great mass of the stapes in all early theropsids. Neither of the palaeontological theories explained these crucial facts. Despite this, the work of Tumarkin attracted little support.

Without a tympanum the efficient reception of airborne sound is impossible. This is due to the wide difference between the specific acoustic impedance of air ($414 \text{ kg/m}^2/\text{s}$), and that of the endolymph (taken here as the same as that of sea-water: $1.5 \times 10^6 \text{ kg/m}^2/\text{s}$). When a wave impinges on the interface between two media, some of the energy is transmitted into the second medium, and some reflected back from the interface. The proportion of each depends upon the ratio of the impedances of the two media. For sound waves; if R_1 is the impedance of the first medium, R_2 that of the second and β the transmission constant ($\beta = \text{transmitted sound energy/incident sound energy}$), then:

$$\beta = \frac{4R_1R_2}{(R_1 + R_2)^2}$$

For transmission between air and the endolymph:

$$R_1 = 414 \text{ kg/m}^2/\text{s}, R_2 = 1.5 \times 10^6 \text{ kg/m}^2/\text{s}; \text{ consequently } \beta = 0.001.$$

No more than 0.1% of the energy is transmitted. In acoustic terms the loss is 30dB, and a loss of 30dB is associated in man with severe deafness. Hence for the reception of airborne sound some form of transformer is necessary, and it is the function of the tympanum and auditory ossicles to act in this way. The concept of a transformer is perfectly familiar. For example, the antireflection coating on a lens matches the impedances of the air and the glass, so reducing the loss of light and contrast by reflection; and in an electrical circuit a transformer is used to match two circuits of different impedance. In the latter case, the ratio of the input and output voltages must equal the square root of the ratio of the input and output impedances. The pressure in a sound wave is analogous to the voltage in an electrical circuit. Therefore, the auditory transformer needs to increase the pressure at the fenestra ovalis over that at the tympanum by the ratio:

$$\sqrt{(R_1/R_2)} = \sqrt{(1.5 \times 10^6/414)} = 60.$$

The domestic cat actually achieves this ratio; man can do no better than a ratio of 18 (Wever and Lawrence 1954). Despite this, in man more than a third of the energy incident on the tympanum reaches the inner ear. This is perfectly adequate.

The transformer formed by the tympanic membrane and the middle ear obtains the necessary pressure multiplication in two quite distinct ways (Wever and Lawrence 1954). The first of these is a simple hydrostatic multiplication due to the area of the tympanum being greater than that of the footplate of the stapes.

Then:

$$\frac{\text{Pressure at fenestra ovalis}}{\text{Pressure at tympanum}} = \frac{\text{Effective area of tympanum.}}{\text{Area of footplate.}}$$

Wever and Lawrence (1954) state that the effective area of the tympanum is two thirds of its actual area.

This hydrostatic transformer action is always the most important and, in many tetrapods, is the only one present (fig. 9). We shall call this the "Primary transformer". For example, *Gekko gekko* manages an acoustic transformer ratio of 40, simply by using this mechanism and no other (Wever 1978). In some tetrapods — mammals with their three auditory ossicles, or some lizards where the stapes and extrastapes are capable of relative movement — there can be a second amplification. This amplification of pressure is due to the lever action produced by the relative movement of the ossicles on each other, in a mammal; or by the relative movement of the stapes and extrastapes, in a lizard. This secondary transformer, however, only produces a small magnification of the order of two or three times.

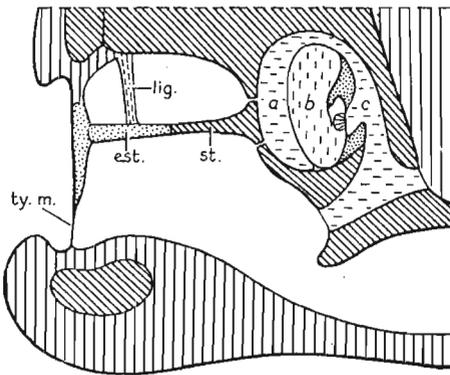


Fig. 9. Vertical section of ear of lizard: simplified after Goodrich. Many reptiles and birds have similar ears.

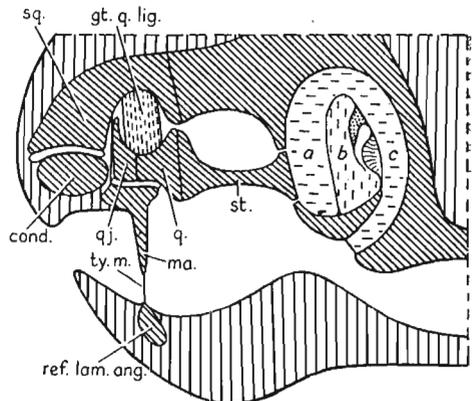


Fig. 10. *Morganucodon*: diagrammatic oblique horizontal section of the ear through the dentary condyle and the manubrium (infra-articular process of articular bone).

The therapsid ear as reconstructed, following Broom, by Parrington (1949) would have been hopeless as an acoustic transformer (fig. 4). The tympanic membrane was about the same area as the footplate of the stapes, always relatively enormous in therapsids. So the primary transformer ratio would have been close to unity. The stapes in therapsids being in articulation distally with the quadrate, it is difficult to see how there could have been any significant lever action; and the whole system would have been ludicrously inefficient at matching the impedances of the air and the inner ear. So much is this so, that Manley (1973), accepting Parrington's reconstruction, suggested that the stapes-tympanum mechanism functioned as a pressure release mechanism in indirect route hearing.

Allin (1975), in a brilliant paper, stated that the therapsid ear as reconstructed by Parrington was impossible. Allin located the eardrum in the lower jaw, supported by the reflected lamina of the angular (fig. 5). In this he agreed with Watson (1953). There was, however, a most significant difference between the two reconstructions. Allin did not extend the tympanum to the quadrate, but contained the eardrum entirely within the lower jaw. Airborne sound was then transmitted to the inner ear *via* the angular, articular, quadrate and stapes. There is ample room in the lower jaw for a tympanic membrane of adequate size; and, as suggested by Hopson (1966), some secondary transformer action was possible due to the rocking of the quadrate. We were studying the ear of *Morganucodon* when Allin's paper appeared, and we decided to try his theory on our material.

If the tympanum of *Morganucodon* be located posterior to the quadrate, in the position suggested by Parrington, the maximum area of membrane that can be fitted in is 1 sq.mm. The effective area is two thirds of this (0.67 sq.mm.). The area of the footplate of the stapes is 0.28 sq.mm. (Kermack *et al.* 1981). So:

$$\text{Primary transformer ratio} = 0.67/0.28 = 2.4,$$

giving a value of β of 0.006. This is a loss of 22dB; less than 1% of the energy in the incoming wave is transmitted to the endolymph. This confirms the conclusions of Manley (1973) and Allin (1975) that such an ear would be hopelessly inefficient as a receiver of airborne sound.

If the tympanic membrane is located entirely within the lower jaw, as suggested by Allin, then a different picture emerges (figs. 6, 10). A tympanic membrane of 4.5 sq.mm. can be fitted in without difficulty, and the primary transformer ratio becomes 10.7. There is a secondary transformer action due to the rocking of the quadrate. In *Morganucodon* this gives a ratio of 2.7. The final transformer ratio is the product of these two quantities, or 28.9. This is well within the range for modern mammals, and gives a functional ear with a value of β of 0.58. The loss is 2.4dB and 58% of the energy in the incoming wave is transmitted to

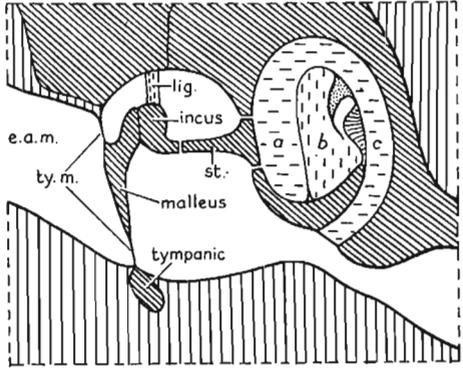
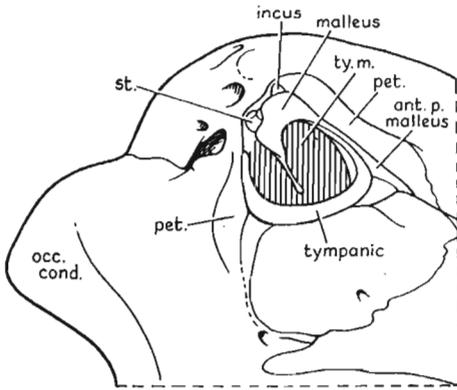


Fig. 11. *Tachyglossus*; ventral view of the posterior right side of the skull.

Fig. 12. Diagrammatic vertical section through the ear of a modern mammal.

See page 157 for abbreviations

the inner ear. The relevant parts of the lower jaw of *Morganucodon* are closely similar to those of the later therapsids (Kermack *et al.* 1973) and these later animals must also have had an highly efficient transformer in the middle ear.

Amongst living mammals the monotremes have the closest approach to the pattern of ear in *Morganucodon*. Although the articular and quadrate have ceased to form part of the jaw joint—becoming the malleus and incus—the auditory ossicles are much larger, relative to the size of the animal, than in the Theria (figs. 11, 12). The ossicles are also much more constrained in the monotremes, the malleus being firmly bound to the tympanic. Aitkin and Johnstone (1972) comment on the inefficiency of the ear of *Tachyglossus*, both as to the sensitivity (at 250 Hz there is 80 times the displacement of the footplate in the guinea pig than there is in *Tachyglossus*), and in the high frequency response. Inefficiency at the low frequencies is due to stiffness in the middle ear system, at high frequencies due to the mass of the middle ear bones. Despite all this, the overall transformer ratio of the ear is perfectly respectable. Aitkin and Johnstone estimate the secondary transformer ratio as 2. By measuring the area of the tympanic membrane in a museum specimen we have been able to estimate the overall transformer ratio as 30—better than in man. A good transformer ratio is not everything.

All the factors which reduce the efficiency of the ear of *Tachyglossus* would apply with even greater force to that of *Morganucodon*. Here the transmitting elements are still more firmly bound together and have relatively still greater mass. The ear of *Morganucodon* was vastly inferior to that of the modern Theria in two respects: high frequency response and sensitivity. The amphisbaenids are a modern group of squamates in which the skin on the lateral side of the lower jaw functions as a tympanum. The efficiency of their ears is almost always low for frequencies above

2 kHz (Wever 1978). In the same way the cut-off frequency in the therapsids and in those early mammals in which the ear was similar to *Morganucodon* must have been not much above 2 kHz. We must picture for *Morganucodon*, a rather insensitive ear with a high frequency cut-off not much above 2 kHz. The same will apply to the other early mammals with ears similar to those of *Morganucodon* — for example *Kuehneotherium* — and to the Therapsida.

But when we consider the modern Theria the position is utterly different. These mammals differ from all other tetrapods in the remarkably high cut-off frequency (better than 100 kHz in bats). No sauropsid can reach values anything like this. Small passerine birds can reach 8 kHz, but the highest limit amongst the Sauropsida is probably achieved by some owls. The Barn Owl (*Tyto alba*) can range up to 12 kHz (Knudsen 1980). Man is a rather poor performer at the high frequency end of the spectrum, but even he can manage 20 kHz, the domestic cat can better 50 kHz. To perceive these high frequencies the auditory ossicles need to be light and free from restraint. In man the natural frequency of the eardrum-auditory ossicle system is above 40 kHz (Hartridge 1947), so that it can respond without distortion to the frequencies concerned in hearing.

Equally dramatic is the wide spectrum which therian mammals can encompass. Man can cover 16 Hz to 20,000 Hz, a range of ten octaves. Other Theria have a comparable range. To perceive this great range a long basilar membrane and organ of Corti is necessary, since each of the hair cells responds only to a narrow range of frequencies. In man, the cochlea is about 30 mm. in length. To fit this length in the space available, the cochlea is coiled. This is the functional reason for the spiral cochlea found in marsupials and placentals.

The fully adapted therian middle ear and the spiral cochlea are correlated absolutely; one is useless without the other. The earliest known member of the Theria is *Kuehneotherium*, from the Early Jurassic of South Wales. *Kuehneotherium* had a double jaw-articulation essentially similar to that of *Morganucodon* (Kermack *et al.* 1968). The arrangement of the tympanum and middle ear in both must have been identical. In material from the South Wales fissures there is never any evidence of anything but a straight cochlea, even if *Kuehneotherium* is the most abundant mammal in the particular sample under consideration. This is reasonable and quite to be expected: a spiral cochlea along with the middle ear of *Kuehneotherium* would be a patent absurdity. The spiral cochlea could only evolve along with a middle ear capable of transmitting the high frequencies efficiently. This may not have happened until the Lower Cretaceous.

The modern monotremes are functionally, although clearly not phylogenetically, intermediate between *Kuehneotherium* and the modern

Theria. The quadrate and the articular have become free from the jaw articulation, and the auditory ossicles have become lighter and less constrained. The cochlea turns through 180 degrees in *Tachyglossus* and 270 degrees in *Ornithorhynchus*.

In other Atheria in which the cochlea is known — *Trioracodon ferox* (Kermack 1963) and *Ptilodus* (Broom 1914) — it is straight. The malleus and incus, however, had lost all connection with the jaw articulation and must have been fully transformed into the auditory ossicles. The ear in these forms would have been more sensitive than that of *Morganucodon* or *Kuehneotherium*, and it would have cut-off at an higher frequency, possibly something like 5 kHz. It has been suggested that the multituberculate middle ear lacked malleus and incus, having only a stapes which directly connected the tympanum. This is quite impossible. In no known theropsid does it happen; and no mechanism is conceivable by which the stapes could lose its invariable and long established contact with the quadrate and contact the tympanic membrane directly.

We should now give a summary of our ideas. The earliest theropsids lacked a tympanic membrane. These early members of the Theropsida, captorhinomorphs and pelycosaur, could hear only sounds transmitted through the ground. These sounds reached the inner ear by two routes: the direct route *via* the lower jaw, assumed to be in contact with the ground, quadrate and stapes; or by the indirect route of the limbs and skull bones. In both cases a massive stapes would have been advantageous: in the first case as a conductor of sound, and in the second case as a fixed reference point. The later mammal-like reptiles, the Therapsida, had evolved a tympanum but as modification of the skin on the lateral side of the lower jaw. Lombard and Bolt (1979), on different evidence, have concluded that the tympanum in the Therapsida is not homologous with that in the Sauropsida. Although the Therapsida had an ear which was capable of receiving airborne sounds, it had both a poor sensitivity and a poor high frequency response. This was due to the mass and constraint of the moving parts.

By the Middle Trias the mammal-like reptiles were coming under severe and increasing pressure from the Sauropsida. The large therapsids failed to compete and became extinct. The dinosaurs replaced them. The small mammal-like reptiles were in direct competition with the lepidosaurs, which had already evolved a highly efficient middle ear. The small mammal-like reptiles survived by becoming nocturnal. A number of fundamental changes in the sense organs became necessary. The retina, which primitively consisted predominantly of cones, came to consist mainly of rods. The senses of smell and hearing are both much more important in a nocturnal environment. For the accurate location of sources of sound by small animals high frequencies and a wide frequency range are advantageous (Knudsen 1980). There also seems to be some evidence

that sonar was employed by primitive mammals (Kermack *et al.* 1981). High frequencies are clearly advantageous here also.

To obtain the desired high frequency response the bones of the middle ear had to lose all connection with the jaw-articulation and become solely concerned with the transmission of sound from the tympanum to the stapes. The cochlea had to become modified to respond to a great range of frequencies. These changes occurred over a considerable period of time. The first known therian mammal (*Kuehneotherium*) of the Early Jurassic had an essentially therapsid ear. By the Middle Jurassic, mammals are known in which the quadrate and articular play no part in the jaw-articulation and consequently the mammalian middle ear had evolved. The modern monotremes are at this stage of evolution. With the evolution of mammalian middle ear the spiral cochlea could evolve, but possibly this did not occur until the Lower Cretaceous.

ABBREVIATIONS FOR LABELS TO FIGURES

a.	scala vestibuli
ang.	angular
ant. p. malleus.	anterior process of malleus
art.	articular
b.	cochlear duct
c.	scala tympani
cond.	condyle of dentary
cor.	coronoid bone
cor. p.	coronoid process of dentary
dent.	dentary
e.a.m.	external auditory meatus
e.st.	extrastapes
gt.q.lig.	great quadrate ligament
j.	jugal
lig.	ligament
ma.	manubrium
mk.cart.	Meckel's cartilage
occ. cond.	occipital condyle
pa.	parietal
pet.	petrosal
prart.	prearticular
q.	quadrate
qj.	quadratojugal
ref.lam.ang.	reflected lamina of the angular
spl.	splénial
sq.	squamosal
st.	stapes
sur.	surangular
ty.m.	tympanic membrane
z.	zygoma

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