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Review article

The mammalian Cretaceous cochlear revolution

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A B S T R A C T

The hearing organs of amniote vertebrates show large differences in their size and structure between the species' groups. In spite of this, their performance in terms of hearing sensitivity and the frequency selectivity of auditory-nerve units shows unexpectedly small differences. The only substantial difference is that therian, defined as live-bearing, mammalian groups are able to hear ultrasonic frequencies (above 15–20 kHz), whereas in contrast monotreme (egg laying) mammals and all non-mammalian amniotes cannot. This review compares the structure and physiology of the cochleae of the main groups and asks the question as to why the many structural differences seen in therian mammals arose, yet did not result in greater differences in physiology. The likely answers to this question are found in the history of the mammals during the Cretaceous period that ended 65 million years ago. During that period, the therian cochlea lost its lagenar macula, leading to a fall in endolymph calcium levels. This likely resulted in a small revolution and an auditory crisis that was compensated for by a subsequent series of structural and physiological adaptations. The end result was a system of equivalent performance to that independently evolved in other amniotes but with the additional – and of course "unforeseen" - advantage that ultrasonic-frequency responses became an available option. That option was not always availed of, but in most groups of therian mammals it did evolve and is used for communication and orientation based on improved sound localization, with micro-bats and toothed whales relying on it for prey capture.

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1. Introduction

This review discusses the ears of amniotes with an emphasis on the unique features of the mammalian – and specifically the

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therian - cochlea. What is it that makes the therian cochlea so very different in structure even though its performance in comparison to many non-mammals is in most respects not exceptional (Manley, 2016)? What are the proximate (e.g. body structure) und ultimate reasons (e.g., evolutionary selection pressures) underlying the profound change in cochlear structure that mammals evolved during the Cretaceous?

Modern amniotes are the descendents of ancient "reptilian" groups and thus of egg-laying ancestors (Carroll, 1988). More than 320 million years ago, during the Carboniferous era, the ancestors of all mammalian groups separated from the ancestral "reptiles" (a diverse conglomeration) that continued in their own lineages. About 70 million years later, near the beginning of the Mesozoic, the latter group again split up, this time into not two, but three groups that survived to modern times (plus many that went extinct). These three groups were: One lineage (the Lepidosauria) leading to modern squamates (mostly lizards and snakes), another to chelonians (tortoises and turtles) and the third to Archosauria (birds and crocodilians). These three groups, together with the mammals, are the survivors of the ancient "reptiles"; all other lineages went extinct (Carroll, 1988; Manley and Köppl, 1998; Manley, 2000). Lepidosaurs, archosaurs and mammals together constitute the amniotes, since all are descended from a group that laid amniotic eggs (i.e. eggs in which the embryos have extraembryonic membranes, such as the amnion).

At the time when the amniote groups split apart, their hearing systems could hardly have been described as such. None of the earliest representatives of all the above modern amniote groups possessed a middle ear (Manley, 2010). It is also likely that, at best, they had an auditory epithelium that was very small, about 1 mm in length, with a few hundred sensory hair cells (Manley and Köppl, 1998) perhaps similar to that of modern turtles (Manley, 1990) or of the rhynchocephalian *Sphenodon* (the Tuatara; Gans and Wever, 1976). Due to the lack of a middle-ear system, this organ would have been rather insensitive to airborne sound, responding instead mainly to sounds entering the tissues directly, either ground-borne vibrations or body sounds such as those produced by the jaws. Apparently these signals were important enough to maintain the epithelium (feedback information on sounds from the mouth could be important), although in comparison to the hearing of modern forms, it seems woefully inadequate. This was to change during the subsequent period – the Triassic – during which all of these lineages, independently of each other, evolved middle ears. These events, which produced the three-ossicle middle ear of all mammalian groups and the single-ossicle middle ears of all other groups, have already been reviewed (Manley, 2010).

2. New middle ears catalyzed changes to cochleae

Remarkably, we still have no clear idea which selection pressures acted almost simultaneously (on a geological time scale) across all lineages and resulted in the two kinds of middle ears. While there is no question that the resulting increase in hearing sensitivity (of >40 dB) to airborne sound would have offered a range of advantages, there are no indications of a common driving selection pressure behind these events and this remains one of the great unexplained mysteries of the fossil record. Of course a middle ear could have arisen first in one lineage and, due to the increased competition caused by its success, itself become a selection pressure working on the other lineages. Nonetheless in that case also, the selection pressures driving the origin of the "first" middle ear remain unclear.

One avenue worth exploring is the possibility that in fact mammals were the first group to make this step. If the early inner ear was largely exposed to stimuli that also originated in the jaws (e.g. acoustic control of biting force), then mammal ancestors may have experienced a change when they went through a period during which the coupling of the jaws changed. This event initiated the origin of the 3-ossicle middle ear and defines the evolutionary transition to mammals. The gradual change to the secondary jaw joint of mammals made two bones from the primary jaw joint redundant; later these would be known as the malleus and incus. These bones would have been on the outside – the skin side - of the jaw joint and thus more exposed to stimuli impinging on the skin than previously. The significance of these stimuli might then have influenced selective pressures on the building of a middle ear. Mammals also evolved a secondary palate, which enabled the processing of food in the mouth without disturbing ventilation of the lungs – enabling breathing and eating at the same time. Thus – uniquely - mammals can spend time chewing their food and possess several kinds of teeth for slicing, grinding, etc. of the food and secrete enzymes in the saliva that initiate digestion in the mouth. It is possible that the acoustic information concerning these processes passed through the tissues of the head to the ear and was important enough to delay the evolution of the definitive mammalian middle ear (in which the ossicular chain is free from connections to other bones; Meng et al., 2003). It may thus have prolonged the use of the transitional mammalian middle ear - in which the malleus maintained a connection to the lower jaw (Ji et al., 2009) – during the Mesozoic era for many millions of years (Luo, 2011, Fig. 1).

As reviewed elsewhere (Manley, 2010, 2016), the middle ears of mammals and non-mammals are of equivalent efficiency in terms of the optima of their transfer functions, except that in the mammalian middle ear, these optima extend to higher – sometimes much higher - frequencies. The upper frequency limits are of course in each case also a reflection of the upper frequency limit of the inner ear (Manley and Johnstone, 1974; Ruggero and Temchin,

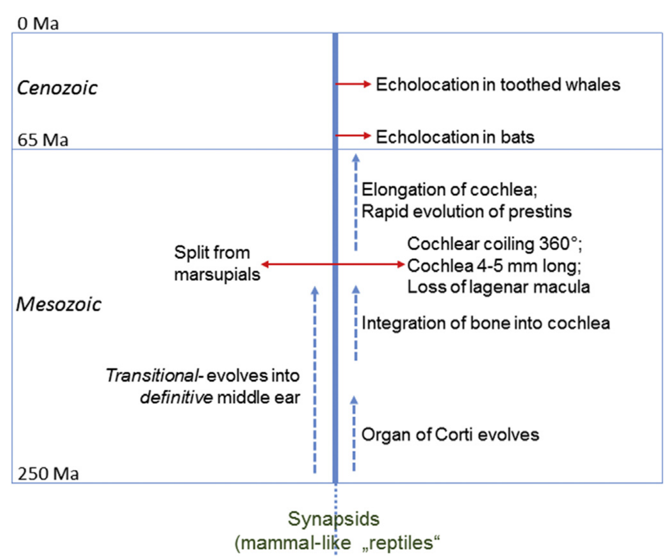

Fig. 1. Time line of the evolution of the eutherian mammalian ear. In the Paleozoic (>250 million years ago) the synapsids split off the stem "reptiles" and formed the ancestors of mammals. Most major events concerning the evolution of the eutherian ear took place during the Mesozoic era. Early in the Mesozoic, this group had a "transitional" middle ear that was still connected to the lower jaw. The loss of this connection marks the origin of a "definitive" middle ear. During this period, mammalian ancestors adopted the characteristic structure of the organ of Corti. The integration of bone into the cochlea occurred only in therian mammals and preceded both cochlear coiling and the split of placentals (Eutheria) from the marsupials (Metatheria). Cochlear coiling resulted in the loss of the lagenar macula and its consequences, with subsequent important biochemical changes, such as the rapid and parallel evolution of prestins in the different sub-groups.