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An evolutionary perspective on middle ears

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ABSTRACT

The traditional view that a tympanic middle ear developed only once, when vertebrates made the transition from fish in water to land-living animals, has been shown to be incorrect. Middle ears with a tympanum connected by one or more ossicles to the cochlea developed very much later in evolutionary history and independently in many amniote vertebrate lineages – most now extinct. The mammalian middle ear is unique but it is not simply an "improved" single-ossicle middle ear. It is a radical and fortuitous new development that owes its origin more to changes in feeding patterns than to hearing. It happened to transmit higher-frequency sounds better than single-ossicle middle ears and enabled the evolution of the high upper-frequency hearing limits of most mammals. Parallel to the development of a tympanic middle ear in therian mammals, the brain increased in size and a secondary palate developed, resulting in the ancestral pressure-gradient middle ear being replaced by a purely pressure system. Sound localization then became almost completely dependent on neural computation and this was the most important factor driving up the upper frequency limits of early mammals. This paper presents an historical perspective on these remarkably simple and yet highly effective structures.

1. Introduction

A dedicated hearing epithelium developed as the last of the major sense organs of vertebrates. While eyes and nasal epithelia with basic similarities to those of modern vertebrates can be detected in the earliest fossil material, the earliest otic regions, while bearing obvious similarities to modern vestibular systems, gives no indication of the development of a dedicated hearing epithelium. During their evolution, various lineages of fishes developed an auditory ability through co-opting vestibular epithelia (e.g. sacculus, utriculus, lagena) to also respond to sound. By means of these changes, and in some cases supported by accessory structures which increase sensitivity, some modern fish are quite sensitive to frequencies up to several kHz (Ladich and Popper, 2004). These developments are, however, entirely unrelated to hearing in land vertebrates.

2. Some background

The skull or cranium of vertebrate animals is a unique and highly complex structure (Fig. 1). Seen during its evolution, it is an extremely dynamic set of interlocking structures that have diverse origins and have changed in their relative importance over time. The early cranium is derived from three components: (1) an ancient neurocranium of cartilage that surrounds and protects the brain and sense organs, (2) a viscerocranium below and at the rear that builds the gill-support system, that gave rise to jaws from or near the first gill arches and also partly supports the jaw and (3) in most cases a dermatocranium surrounding everything and derived from bones that develop in the dermis of the complex vertebrate skin. Profound changes in these cranial components contributed to the development of a middle ear.

It is important to note that for much of evolution (and in some vertebrates still today), the upper and lower jaw were and are not tightly fixed to the rest of the skull. Anyone who has seen a shark thrust out its jaws during prey capture will have been impressed as to how incredibly dynamic is the relationship between the jaws and the braincase. These jaws and their supports share their embryonic origins with the gill-slit supports (gill arches) of the viscerocranium (Carroll, 1988). One mechanical strut-stabilizer of these early vertebrate jaws was derived from the upper portion of the second gill arch (hyoid arch) and termed the hyomandibula. The hyomandibula has been traced through vertebrate evolution and is clearly homologous (derived from the same tissues and having the same embryonic origin) to the land-vertebrate columella or stapes. The gill opening between the first and second gill arches was reduced in size and pushed dorsally, forming the so-called spiracle. This connection between the buccal cavity and the outside

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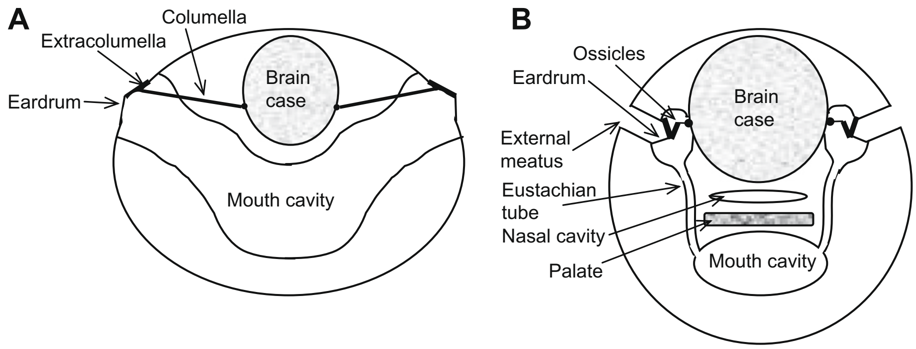

Fig. 1. A highly schematic representation of cross-sections through the ear regions of (A) a non-mammal (here a lizard) and (B) a mammal, to illustrate the constriction of the connection between the ears in mammals. In the lizard in (A), definable middle ear cavities hardly exist, since they open widely and continuously to the mouth cavity. In mammals, growth of the brain and the presence of a secondary palate have led to a restriction of the middle-ear space to a much smaller volume around the ossicles and sometimes the cochlea, with only a narrow, and closeable, connection to the mouth cavity. Of course the nasal cavity connects to the mouth cavity at the rear.

world is still an open canal in most sharks and rays. In other vertebrates, the spiracle is either lost or continues its existence as a small chamber that is usually closed to the outside. It is the basis for the cavity of the middle ear and of the eardrum that arose later in evolution.

In sharks and their relatives, the jaws are cartilaginous structures, but in most vertebrates, these were entirely or mostly replaced by internal ossification (endochondral bone) and covered by dermal bones (of the dermatocranium). Over a long period of time during which jaw mechanics were fundamentally changed, jaw- and jaw-support components became redundant and available for incorporation into middle ears. The redundancy of the columella-stapes (= hyomandibula) in particular can be traced to a better consolidation of the components of the caudal half of the skull and upper jaw that removed the need for the columella-stapes as a supporting strut (Clack, 2002).

3. A traditional view falls

The transition of vertebrate animals from land to water involved changes in many regions of the body, e.g., the loss of medial fins, stronger paired limbs and a firmer connection between the limbs and vertebral column. The senses would also have been affected: eye lenses, for example, that work well in water are not appropriate for land, and air-borne sound would mostly be reflected from the body surface if no impedance-matching system were present. In the 1930s, in *Ichthyostega*, that lived at the time of the water–land transition, a deep notch present in the bones at the rear of the skull was interpreted as supporting the front half of a large eardrum. So arose the concept that a tympanic, or eardrum-carrying, middle ear arose during the transition to land perhaps 360 million years (MY) ago and that all groups derived from these organisms inherited such a middle ear.

As is common in science, first impressions are often not correct and some of the interpretation of these fossils – partly due to new fossil finds – has changed greatly. For example many early land vertebrates did not, as previously assumed, have five digits on their limbs, the ancestral pentadactyl limb is a myth (Coates and Clack, 1990). Similarly, it was discovered that these animals had almost no space for a middle ear and the stapes was far too robust for such an auditory function; thus the "eardrum notch" was reinterpreted as a spiracular notch – the remnant of the spiracle (Brazeau and Ahlberg, 2006; Clack, 1989, 2002). Interestingly, *Ichthyostega* probably used the spiracular space to carry an air bubble that abutted special bony connections to the inner ear (Clack et al., 2003). Such structures belong in the general category of accessory bony structures such as those of some modern fish that clearly improve hearing thresholds through connections to vibrating gas bubbles (e.g. Weberian ossicles to gas bladders). What is significant is that the hyomandibula, which in the earliest land vertebrates was positioned with its inner end contacting the bony surrounds of the inner ear stayed in that position throughout further evolution. Thus there was always the potential for its movements to be transmitted to sensory organs in the inner ear.

The earliest vertebrates possessing a columella small enough to have functioned in a tympanic middle ear was in temnospondyls (one group of "amphibians") of about 300 MY ago, that also possessed a large otic notch. Such animals were known from the mid 19th century and after their study at that time it was assumed – incorrectly, as it turned out – that all tetrapods inherited tympanic ears from animals of that era.

4. The origin of amniote tympanic middle ears

The extensive fossil evidence on vertebrates of the Paleo- and Mesozoic leaves no doubt that over millions of years, land vertebrates radiated into a large number of clades, or lineages, most of which were evolutionary dead ends. It is therefore not surprising that during the evolution of these individual clades, many differences, but also many similarities, can be seen. As noted above, there is clear evidence that a tympanic middle ear arose in the ancestors of modern amphibians. A detailed comparison of amphibian middle ears to the middle ears of other land vertebrates, however, produces a list of important differences that indicate that this type of middle ear arose independently of all others. It is equally clear that the early "stem" (= common ancestral) amniote vertebrates – the ancestors of the later lineages to the archosaurs (birds and crocodilians), lepidosaurs (snakes and lizards) and synapsids (mammal-like "reptiles") – did not possess a tympanic middle ear (Clack, 2002; Manley and Clack, 2004). This fact is one of the centerpieces of this discussion.

The entire structure of the skull region and the generally robust size of the stapes of early stem amniote vertebrates provide no evidence of sensitive hearing to air-borne sounds. The stapes was at that time essential as a strut to support the connection of the neurocranium around the brain to the outer skull (dermatocranium), maintaining the shape of the skull during biting. This condition continued during the era when the above-mentioned lineages leading to living amniotes diverged from one another and began their unique evolutionary trajectories. In each lineage, various new connections between skull components arose, making the posterior end of the skull more rigid and freeing the stapes from its structural role and leading to the development of tympanic middle ears. There may even be an additional, separate lineage