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*Editors*

# The Middle Ear
## Science, Otosurgery, and Technology

Springer

Springer Handbook of Auditory Research

Sunil Puria • Richard R. Fay • Arthur N. Popper
Editors

# The Middle Ear

Science, Otosurgery, and Technology

With 60 Illustrations

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Printed on acid-free paper

*This volume is dedicated by
Sunil to his Love, Neshie.*

# Series Preface

The following preface is the one that we published in Volume 1 of the Springer Handbook of Auditory Research (SHAR) back in 1992. Thus, 2012 marks the 20th year of SHAR. As anyone reading the original preface, or the many users of the series, will note, we have far exceeded our original expectation of eight volumes. Indeed, with books published to date and those in the pipeline, we are now set for more than 50 volumes in SHAR, and we are still open to new and exciting ideas for additional books.

We are very proud that there seems to be consensus, at least among our friends and colleagues, that SHAR has become an important and influential part of the auditory literature. While we have worked hard to develop and maintain the quality and value of SHAR, the real value of the books is very much because of the numerous authors who have given their time to write outstanding chapters and to our many coeditors who have provided the intellectual leadership to the individual volumes. We have worked with a remarkable and wonderful group of people, many of whom have become great personal friends of both of us. We also continue to work with a spectacular group of editors at Springer, currently Ann Avouris. Indeed, several of our past editors have moved on in the publishing world to become senior executives. To our delight, this includes the current president of Springer US, Dr. William Curtis.

But the truth is that the series would and could not be possible without the support of our families, and we want to take this opportunity to dedicate all of the SHAR books, past and future, to them. Our wives, Catherine Fay and Helen Popper, and our children, Michelle Popper Levit, Melissa Popper Levinsohn, Christian Fay, and Amanda Fay, have been immensely patient as we developed and worked on this series. We thank them and state, without doubt, that this series could not have happened without them.

**Preface 1992**
The Springer Handbook of Auditory Research presents a series of comprehensive and synthetic reviews of the fundamental topics in modern auditory research. The volumes are aimed at all individuals with interests in hearing research including

advanced graduate students, postdoctoral researchers, and clinical investigators. The volumes are intended to introduce new investigators to important aspects of hearing science and to help established investigators to better understand the fundamental theories and data in fields of hearing that they may not normally follow closely.

Each volume presents a particular topic comprehensively, and each serves as a synthetic overview and guide to the literature. As such, the chapters present neither exhaustive data reviews nor original research that has not yet appeared in peer-reviewed journals. The volumes focus on topics that have developed a solid data and conceptual foundation rather than on those for which a literature is only beginning to develop. New research areas will be covered on a timely basis in the series as they begin to mature.

Each volume in the series consists of a few substantial chapters on a particular topic. In some cases, the topics will be ones of traditional interest for which there is a substantial body of data and theory, such as auditory neuroanatomy (Vol. 1) and neurophysiology (Vol. 2). Other volumes in the series deal with topics that have begun to mature more recently, such as development, plasticity, and computational models of neural processing. In many cases, the series editors are joined by a coeditor having special expertise in the topic of the volume.

Richard R. Fay, Falmouth, MA
Arthur N. Popper, College Park, MD

# Volume Preface

To date, the middle ear has not been the focus of any single SHAR volume despite its importance in auditory function. In this volume, however, we take a broad look at this structure from a wide range of interdisciplinary perspectives, starting with basic science and evolutionary approaches and ending at clinical issues.

In Chap. 2, Manley and Sienknecht discuss the evolution and embryonic development of the middle ear, while in Chap. 3 Rosowski compares the middle ears across diverse vertebrate species.

In Chap. 4, Voss, Nakajima, Huber, and Shera review the overall physiological functioning of normal and diseased middle ears. In Chap. 5, Dirckx, Marcusohn, and Gaihede focus on mechanisms by which the balance of pressure is maintained between the middle ear and the atmosphere, while Stenfelt, in Chap. 6, focuses on mechanisms of bone conduction. In Chap. 7, Funnell, Maftoon, and Decraemer describe the role of computational approaches in helping to further our understanding of middle ear structure and function.

Clinical issues are more specifically discussed starting in Chap. 8, where Popelka and Hunter describe the clinical techniques for measuring and diagnosing the human middle ear. In Chap. 9, Merchant and Rosowski follow this with a description and discussion of the various middle ear pathologies that clinicians are able to repair as well as the surgical procedures they use. Finally, in Chap. 10, Puria describes various types of hearing devices that operate by mechanically vibrating the middle ear.

While the middle ear has not been the focus of past volumes, it has been discussed in chapters throughout the series. These include a chapter on the outer and middle ears by Rosowski in Volume 4, *Comparative Hearing: Mammals* (edited by Fay and Popper, 1993) and a chapter in Volume 6, *Auditory Computation* (edited by Hawkins, McMullen, Popper, and Fay, 1996) on models, also by Rosowski. The middle ear in birds and mammals was discussed in a chapter by Saunders et al. in Volume 13, *Comparative Hearing: Birds and Reptiles* (edited by Dooling, Fay, and

Popper, 2000), and the middle ear in amphibians was covered in a chapter by Mason and Narins in Volume 28, *Hearing and Sound Communication in Amphibians* (edited by Narins, Feng, Fay, and Popper, 2007).

Sunil Puria, Stanford, CA
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Arthur N. Popper, College Park, MD

# Editors' Note

We are saddened by the announcement that co-author of Chapter 9 Saumil N. Merchant, MD passed away on June 27th 2012. He was one of the finest clinicians, researcher scientist, scholar and teacher. To his patients he generously gave the gift of time and used his surgical skills to enable them to hear. We will forever miss his warm and infectious smile and guiding presence in our lives.

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# Chapter 1
# The Middle Ear: Science and Applications

**Sunil Puria**

The clinical and scientific study of the middle ear attracts professionals from disciplines as diverse as evolutionary and developmental biology, biophysics, engineering, otology, and audiology; however, because each of these professions works with its own set of journals and societies, it can be difficult to find a single resource that provides comprehensive overviews of the corresponding wide-ranging literature. This volume aims to provide just such a resource, for newcomers and specialists alike, by compiling knowledge bases and gateways to the literature for the major subfields of middle ear study.

Regardless of whether they concern themselves primarily with promoting scientific, surgical, or technological advancements, each discipline of middle ear study is intimately concerned with the functional implications of middle ear structure. In the chapters of this volume, one can appreciate the evolutionary wonder of the mammalian middle ear and its unique structural suitability for high-frequency hearing, as well as the various avenues by which researchers and engineers continue to leverage their understanding of middle ear structure–function relationships to deliver the practical results of new and improved diagnostic methods, surgical procedures, passive prostheses for repairing the middle ear, and devices for sound amplification through the direct stimulation of the middle ear and cochlea.

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In Chap. 2, Geoffrey A. Manley and Ulrike J. Sienknecht discuss the development of the middle ear, in terms of both its evolutionary history and its growth within a developing embryo. They argue against the idea that the middle ear evolved as a direct result of vertebrates transitioning from water to land, arguing instead that the development of the tympano-ossicular system did not occur until more than 100 million years later. They also argue that each of the three middle ear bones of mammals evolved independently, rather than through the addition of two more bones to the less complex one-bone system of amphibians, birds, and other nonmammals. High-frequency hearing appears to have arisen in small mammals over a very long period of time, and very possibly to the detriment of low-frequency hearing. Sensitivity to low frequencies in larger mammals and more specialized small mammals likely evolved later.

The results of developmental studies are also discussed, which suggest that the primary jaw joint of nonmammals, as well as the columella/stapes and the malleus and incus, all arise from a common developmental foundation that can transform into these diverse structures through processes controlled by gene patterning and cellular interactions. Changes in the number of genes and in their temporal and spatial expression during development can then lead, in turn, to the kinds of morphological transformations that are observed over evolutionary time.

The significant variability in the middle ear anatomies of nonmammals such as amphibians, reptiles, and birds, as well as land and marine mammals, is well known. In Chap. 3, John J. Rosowski summarizes the results from a number of studies comparing the middle ears of these different vertebrates, and argues that the wide variations in hearing capabilities among different mammalian species correlate with the form and size of their middle ear structures, with these in turn correlating with body size. He further argues that the different parts of the middle ear and the inner ear coadapted in parallel with one another to meet the demands required for survival, rather than developing independently of one another.

The approach taken by Susan E. Voss, Hideko Heidi Nakajima, Alex M. Huber, and Chris A. Shera in Chap. 4 is to review the functional differences between a normal middle ear and middle ears with alterations due to the effects of disease or other structural changes (e.g., tympanic-membrane perforations, stapes fixation, stapes disarticulation, middle ear fluid). They also describe techniques for performing accurate in vivo and in vitro physiological measurements (e.g., impedance, eardrum motions, 3D ossicular vibrations, cochlear fluid pressure) of both human and animal ears, which vary relatively smoothly with frequency, and use simple mathematical models to provide a theoretical framework for drawing conclusions from such measurements.

In Chap. 5, Joris J. J. Dirckx, Yael Marcusohn, and Michael L. Gaihede describe the different physiological mechanisms for actively controlling the volume of gas in the middle ear cleft, which is the combined airspace of the middle ear cavity and the mastoid, and thus maintaining a pressure balance between the middle ear cleft and the atmosphere. Changes to the volume of the cleft (e.g., due to a thickening of the mucosa) can alter the pressure balance. Gas can enter or leave the middle ear cavity either through the Eustachian tube during the action of swallowing, or by gas

exchange through the mucosa either by diffusion or by perfusion. The overall regulation of middle ear pressure includes active neural feedback control based possibly on peripheral mechanoreceptors. Various pathologies can occur when the pressure balance is not maintained (particularly in children), causing a disruption of the normal function of the tympano-ossicular system.

Although hearing depends primarily on sound reaching the cochlea after passing through the tympano-ossicular system via air conduction, in Chap. 6, Stefan Stenfelt explains some of the known ways that sound can alternately reach the cochlea via bone conduction. While the measurement of bone-conducted hearing is clinically important, the mechanisms of bone conduction—and their relationship to air-conducted hearing—are still not well understood. Changes to the mass and stiffness of the middle ear can affect bone-conducted hearing, although the middle ear generally has less of an effect on the bone-conduction route of hearing than it does on the air-conduction route. For this and other reasons, a number of implantable (percutaneous and transcutaneous) and nonimplantable hearing devices (such as cross-aids and dental transducers) have been developed that make use of the bone-conduction route to stimulate the cochlea.

In Chap. 7, W. Robert J. Funnell, Nima Maftoon, and Willem F. Decraemer describe how various computational approaches have helped to codify our modern understanding of middle ear structure and function. Finite-element models, which offer realistic representations of anatomic features and material properties but can be computationally expensive, are contrasted with simpler two-port and circuit modeling approaches. Finite-element models have been formulated for the simulation of middle ear prostheses and implants, perforations and pathologies of the eardrum, ventilation tubes, fluid in the middle ear cavity, and bone conduction, as well as reverse transmission to determine the effects of the middle ear on ear-canal measurements of otoacoustic emissions. Finite-element models can also be quite useful for studies of the effects of anatomic variability and changes in material properties. Although a majority of the finite-element models have been formulated for the human ear, others have been formulated and validated for cat and gerbil ears. Most of these models have not incorporated the effects of active control of the middle ear muscles. Another area of research interest discussed in this chapter is the measurement and modeling of the high-frequency behavior of the middle ear.

In Chap. 8, Gerald R. Popelka and Lisa L. Hunter delve into the existing conventional, and upcoming, clinical measures and technologies used to quantify the physical and functional status of the human middle ear in a minimally invasive manner. These include measures based on behavioral voluntary responses, physical attributes, and physiological responses, as well as the use of recent imaging techniques. From the individual and combined results of these methods, assessments of the different components making up the middle ear, including the two middle ear muscles, can be formed. Significant challenges still lie ahead with regard to quantifying conductive and sensorineural hearing impairments at frequencies above 4–6 kHz, which would make it possible to assess and potentially improve surgical outcomes with respect to high-frequency hearing. This requires the

development of clinical techniques for producing and calibrating high-frequency acoustic stimuli, as well as the development of suitable bone-conduction transducers.

When a conductive hearing impairment is diagnosed, an ENT (ear, nose, and throat) physician or a more specialized otologist might recommend surgical repair or reconstruction of the middle ear. In Chap. 9, Saumil N. Merchant and John J. Rosowski outline the different kinds of pathologies that clinicians can repair, as well as the approaches they use. Well-covered surgical procedures include the repair of the tympanic membrane, as well as the reconstruction of eroded or missing middle ear bones resulting from, for example, chronic otitis media. In other cases, a stapedectomy is performed to remove a fixation of the stapes to the surrounding bone. Various passive prostheses can be used to repair the ossicles to alleviate conductive impairment. Outlined areas for future development include better understanding the structure–function correlations for reconstructed eardrums, improving methods of coupling passive prostheses to the stapes, and finding better methods of assessing the effects of tension in ossicular reconstruction.

Although acoustic hearing aids are currently the standard of care in cases of sensorineural hearing impairment, in Chap. 10, Sunil Puria describes various types of middle ear hearing devices (MEHDs) that mechanically vibrate the middle ear. The basic configurations of acoustic hearing aids and MEHDs are very similar, with the primary difference being in the output transducer: acoustic hearing aids use a tiny loudspeaker whereas MEHDs typically use a tiny mechanical actuator. The latter has the potential to overcome limitations of acoustic hearing aids by offering a broad-spectrum output, an increased gain margin due to reduced feedback, and better sound quality. A new classification system for transducers is introduced, which is based on the number of required anatomical connection points and how those points are linked to one another. Surgical devices are discussed, including totally and partially implanted systems, as well as nonsurgical, nonimplanted devices that contact and mechanically vibrate the eardrum. Technologies such as these have the potential to change the standard of care by providing a variety of new treatment options for individuals who are not well served by acoustic hearing aids.

A recurring point of discussion in many of the chapters in this volume is the ability of the middle ear to transmit high frequencies from the outer ear to the inner ear. The range of mammalian hearing varies from up to 10 kHz in elephants, 20 kHz in humans, 100 kHz in mice, and even higher in some marine mammals and bats. At frequencies below a few hundred Hz, the middle ear is reasonably straightforward to characterize because at those frequencies the eardrum surface moves more uniformly and the ossicles are minimally constrained by mass inertia. As the frequency increases, however, the eardrum begins to exhibit more and more complex modes of vibration, and the motions of the ossicles might become more and more constrained due to their mass inertia. A challenge has been to understand how the middle ear is still able to transmit sound to the cochlea smoothly over such a wide range of frequencies in spite of these higher-frequency

effects. An exciting development for the investigation of structure–function topics such as these is the recent availability of genetically engineered varieties of mice that exhibit well-characterized alterations to middle ear structures.

People with vision impairment currently have multiple treatment options, such as eyeglasses, contact lenses, and surgical methods of vision correction. In the treatment of hearing impairment, on the other hand, acoustic hearing aids have long been the standard of care and the only option available in most cases. This appears to be changing, however, as alternate nonsurgical treatments, akin to the contact lens, and surgical treatments are either becoming available now or are well on their way to becoming available in the near future. Owing to their potential for broad-spectrum amplification, these new options could help to overcome limitations of acoustic hearing aids related, for example, to hearing in noise and sound quality.

The ongoing, highly cross-disciplinary efforts to better understand the structural and functional interrelationships of the middle ear will no doubt continue to bring forth compelling scientific insights, while at the same time leading to improved care and treatment options for individuals with hearing impairment.

# Chapter 2
# The Evolution and Development of Middle Ears in Land Vertebrates

**Geoffrey A. Manley and Ulrike J. Sienknecht**

## 2.1 Introduction

This chapter is an attempt to reconcile interpretations of the structures of fossil mammalian middle ears with what is known about the development, anatomy, and physiology of modern mammalian and nonmammalian ears. As Bennett and Ruben (1986) wrote: "It is obviously difficult to ascertain physiological characters from dead animals. It is even more difficult to infer those characters from fossilized animals" (p. 207). In spite of these truisms, it is possible, when taking all known paleontological, developmental, anatomical, and physiological data into account and observing the traditional rules pertaining to the interpretations of each set of data, to come to a consistent view of the changes in structure and function of the hearing of mammals over geological time. Detailed overviews of the structure and physiology of amniote middle ears already exist (see, e.g., Rosowski, Chap. 3 and Rosowski 1994).

The term *middle ear* applies to any structure that improves the transmission of sound energy between a conductive medium outside the body and the inner ear. Strictly speaking, the term could be applied where water or air is the conductive medium, thus also in certain kind of fishes—even though they swim in a medium whose acoustic impedance is essentially the same as that of the inner-ear fluids. In those animals, the presence of a gas-filled swim bladder creates an interface

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within the body where there is a large change in acoustic impedance, and stronger acoustic vibrations occur at that interface. Connecting the inner ear to this interface, as with the Weberian ossicles in certain fish groups, greatly improves sensitivity to water-borne sound (Ladich and Popper 2004) and fulfills the definition of a middle ear. In the present discourse, however, coverage is restricted to the middle ears of land vertebrates.

The emergence of vertebrate animals onto the land was, without doubt, one of the most far-reaching events in evolution. As so often in science, early concepts of this "event" have had to be strongly modified in the face of newer evidence. For example, examination of the first fossils of this period led early to a number of dogmata that have since been shown to be false. One example is the idea that the earliest vertebrates transitional to the amphibians were at least partially land-living and possessed pentadactile, or five-toed, appendages. It has since been shown that limbs, as opposed to fins, in fact developed in water-living animals, limbs that were presumably used to move around more easily among water plants and that these animals possessed more than five toes on their appendages (Coates and Clack 1990; Clack 2009). Another dogma, which is very relevant to our understanding of middle ears, is that vertebrates developed a tympanic (or eardrum-bearing) middle ear at the time of the water-to-land transition and that all subsequent vertebrates inherited this kind of middle ear and modified it accordingly. In fact, the history of hearing in land vertebrates is, at least for the first half of their evolutionary story, much more varied than expected. As described later, most lacked a tympanic middle ear and were presumably "hard-of-hearing."

A second "auditory" dogma has also fallen victim to the clarity that has emerged from newer fossils. The mammalian middle ear did not emerge by the addition of two more ossicles to an existing, one-ossicle middle ear, for the simple reason that mammalian ancestors, like all other vertebrate lineages of those late Permian-early Triassic times, lacked a tympanic middle ear. These and other issues are the topics briefly discussed in the text that follows.

## 2.2  The Water–Land Transition and Early Attempts at Middle Ears

It is not the intention of this chapter to go deeply into paleontological issues, but of course the history of land vertebrate middle ears is being discussed and—besides comparisons between modern lineages—fossils are the main source of information. Older textbooks reiterate the story that developed from the early descriptions in Paleozoic amphibians of a deep notch in the back of the skull that, among the various changes to sensory organs that were necessary when vertebrates emerged on to land, was assumed to be the start of the evolution of a tympanic, impedance-matching middle ear. Air-borne sound reflects strongly from a surface with a higher impedance and this development would have improved hearing sensitivity by at

least 40 dB compared to the absence of such a middle ear (Manley 2011; Puria and Steele 2008). As it turns out, however, although there is evidence of some highly interesting innovations for hearing in air and water in early fish (e.g., Clack et al. 2003; Clack and Allin 2004; Brazeau and Ahlberg 2006), none of these innovations survived very long or they were found only in lineages that themselves died out. Reinterpretation of some early fossils led to the conclusion that at least some of the skull notches interpreted as tympana instead housed a spiracle, an open passage for water between the buccal cavity and the outside world (e.g., Clack 2002). For the best part of 100 million years (Ma) after vertebrates emerged onto land, fossil indications of a tympanic middle ear are scattered and provide no evidence for the early development of a middle ear that was inherited by all later forms.

## 2.3 Middle Ears Developed Late in Evolution and Many Times Independently

Over the course of land vertebrate evolution, several kinds of tympanic middle ears developed, only to be lost again or in lineages that died out. Some forms in the late Carboniferous (310 Ma; e.g., Clack 2002) and late Permian (265 Ma; Müller and Tsuji 2007) show evidence of possessing a middle ear, but died out during, for example, the great extinction event of the Permian-Triassic, at the transition from the Paleozoic to the Mesozoic. Until the beginning of the Triassic (~250 Ma ago) the majority of land vertebrate lineages showed no history of a tympanic middle ear (Clack and Allin 2004). During the Triassic period, probably over a period of tens of millions of years, however, all lineages of tetrapods that survive until today developed a tympanic middle ear—and all independently of each other (Clack and Allin 2004; Manley and Clack 2004). Although the skeletal elements that were used to create these middle ears were common to all groups, the formation of these elements into a functional tympanic middle ear was independent in all cases, as it has been shown that their respective ancestors did not have a middle ear and presumably heard only louder, lower frequencies (e.g., Kemp 2007).

The aforementioned conclusions mean that the middle ear of amphibians, of archosaurs (birds and their crocodilian relatives), of lepidosaurs (tuataras, lizards, and snakes), and of mammals do not have a common ancestry, although their individual components do. The independent emergence of middle ears and the scattered attempts at middle ears in earlier vertebrate history was possible thanks to an amazing flexibility in development provided by a cell type unique to vertebrate animals, the neural crest cells (see Sect. 2.6). A close look at the middle ear of amphibians shows clearly that, among middle ears, it is unusual (Smotherman and Narins 2004). Among other interesting features, there is a unique linkage in the columellar system such that—in contrast to all other middle ear systems—when the eardrum is pushed inwards, the columellar footplate is pulled outwards. In spite of their independent origins, the middle ears of mammals and nonmammals share

important features in individual development or ontogeny (see Sect. 2.6). The mammalian middle ear is, of course, the only one that uses three ossicles to connect the eardrum to the inner ear, and the above discussion makes clear that it developed de novo and was not an "improvement" on a preexisting, single-ossicle middle ear (Manley 2010). In fact, as shown later, it also arose multiply and independently within several related groups of early mammals, some of which did not survive until modern times.

## 2.4 The Single-Ossicle Middle Ear of Archosaurs and Lepidosaurs

In these two groups, as also perhaps in the others, a change in jaw-movement patterns during evolution led to adjustments in the structures bracing the jaws against the rest of the skull. For our purposes, the most important change was that the columella ("stapes") bone lost its most important function. At that time, it was a substantial skeletal element that had until Triassic times braced the rear part of the outer skull (specifically the quadrate bone, later to become the incus in mammals) against the braincase. The columella thinned greatly and changed its orientation, the outer end migrating dorsally, where an eardrum evolved and connected to the columella via a new extension, the extracolumella. This apparatus lay directly behind the skull, above and behind the jaw joint. Thus in these lineages, the changes in skull and head structure necessary to evolve a tympanic middle ear were not very great, as the columella-stapes had always connected on its inner end to the bones surrounding the inner ear at a location that later became the oval window. It has been suggested that the relatively massive columella-stapes bones of the amniote ancestors might have worked as an inertial system (Manley 1973, based on Hotton 1959). Thus head vibration caused by low-frequency sound or ground vibrations might have been accompanied by a delay in the movement of the (large) stapes, which would have vibrated out-of-phase with the rest of the head and thus provided a stimulus to the inner ear.

There has, in the past, been considerable confusion in the literature with regard to the performance of the ears of mammals and nonmammals, also with regard to their middle ears. Earlier, the multiple-ossicle middle ear was considered to be responsible for the fact that mammals heard "better" than nonmammals, "better," however, generally not being clearly defined (Masterton et al. 1969; Taylor 1969). The middle ear of nonmammals was supposed to be inferior to that of mammals, and this idea was based partly on the belief that (supposedly) mammals added two ossicles to a preexisting middle ear and this presumably would not have happened if it had not led to an improvement in performance. We now know that in fact the mammalian three-ossicle middle ear evolved de novo (see later) and thus the relationship between the two types of middle ear must be discussed quite independently of any assumptions of "improvement." All three mechanisms that are used by the three-ossicle middle ear

to match impedances (area ratio between the eardrum and the footplate, lever ratio between the malleus and incus "arms," and the curved-membrane lever system) are also all found in single-ossicle middle ears (Manley 1972; Fig. 2.1). The only difference is that, in contrast to the primary lever system of mammals, the single-ossicle system uses a secondary lever along the extracolumella–columella system (Fig. 2.1a). The "performance" at the level of the eardrum is equivalent (Fig. 2.1c), but above about 4 kHz, the secondary lever system is less efficient at passing along the stimulus, resulting in an increasingly large loss at the footplate for the higher frequencies. This is, however, at least partly due to an increase in inner-ear impedance at higher frequencies (Manley 1972). In the guinea pig, there is also a dramatic decrease in middle ear performance at frequencies exceeding those processed by the inner ear (Manley and Johnstone 1974).

Manley (1973), comparing the inner and middle ears of mammals and nonmammals, came to the conclusion that in general, the mammalian ear was superior to that of nonmammals only with respect to its frequency-hearing range. Generally, but not always, the upper frequency range of hearing in mammals is higher or much higher—leaving aside new evidence for ultrasonic hearing in frogs (Feng et al. 2006) and an upper frequency limit in lizards of 14 kHz (Manley and Kraus 2010). The upper frequency limits of inner and middle ears in all species have apparently coevolved and, despite earlier concepts to the contrary, the upper frequency limit of the middle ear does not alone determine the upper limit of hearing. Instead, middle ear performance also depends on the frequency range "accepted" by the inner ear. Above the highest frequencies of the inner-ear receptor, the impedance of the inner ear rises and this influences the upper limit of the middle ear (Manley 1972). The discussion concerning the relative importance of inner and middle ears regarding the shape of the audiogram has more recently been extended and strengthened by Hemilä et al. (1995) and Ruggero and Temchin (2002). A discussion of the evolution of the mammalian middle and inner ears must be carried out fully free of preconceptions of "better" or "poorer" and concentrated on the status of inner and middle ears during the fascinating evolutionary innovations of the Triassic period.

## 2.5 The Origins of Mammalian Middle Ears

The title of this section is couched in the plural to emphasize that the mammalian type of three-ossicle middle ear originated several times, perhaps indeed many times. Modern (extant) mammals are divided into three groups: the placental (eutherian), marsupial (metatherian), and egg-laying monotreme mammals. Placentals and marsupials together are termed therian mammals. Before the origin of true mammals in the late Triassic (Lucas and Luo 1993), the ancestral synapsid "reptiles" had already developed some features that are considered uniquely mammalian. Indeed, the features that today are considered as mammalian (some of which were present in now-extinct nonmammals) arose over a very long period of time: there was no "big
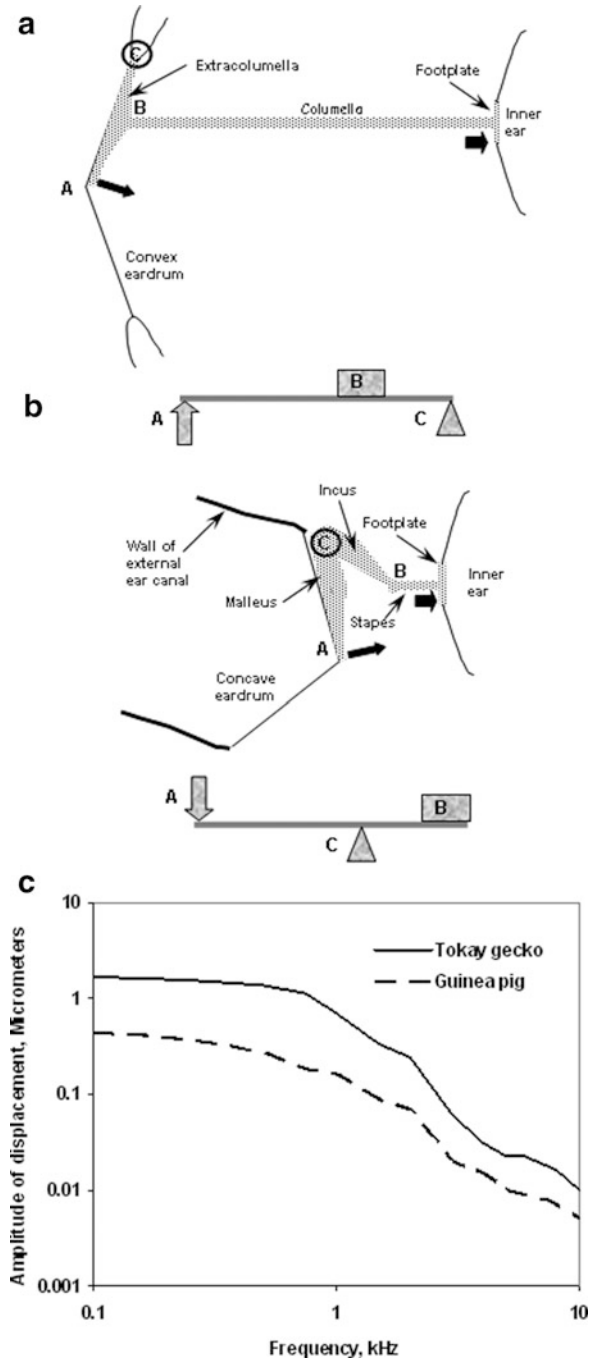
**Fig. 2.1** Schematic representation of middle ear function, comparing (**a**) nonmammalian amniote and (**b**) mammalian middle ears, both in (**c**). In both cases, a diagram of the lever system involved is shown, with the capital letters corresponding to the positions of force application (*A*, idealized to

bang" origin for mammals. One of the first of the features typical of mammals (but that had its origin in the lineage well before true mammals arose) is a heterodont set of teeth, which indicated a substantial change in diet. This change in diet was accompanied by a coordinated series of changes in the muscles that moved the jaws and the bones that made up the lower jaw. The lower jaw progressively became simplified, from originally seven bones to one single bone, the dentary, which was later part of a new, secondary jaw joint. All of the jaw muscles thus became attached to the dentary, a process that involved migration of the muscle–tendon attachments. The final stage brought forth a jaw suitable for chewing, correlated with the processing of food in the mouth cavity, rather than the typical nonmammalian bite-and-swallow technique. Detailed, comparative examination of individual development in nonmammals and mammals strongly supports the ideas generated from paleaontological evidence and indicates that changes in the genetic control of the ontogenetic processes that led to the jaw-joint and middle ear components could gradually re-mold this region of the head (see Sect. 2.6).

A further, parallel, development was the growth of a bony plate, the secondary palate, separating the mouth from the nasal cavity. This structural feature is also—with the exception of its independent evolution in crocodilians—uniquely mammalian and arose more or less parallel to the loss of the primary jaw joint (Carroll, 1988). The secondary palate prevented food particles entering the nasal cavity and thus permitted uninterrupted breathing during chewing. This innovation permitted mammals to begin the masticatory and enzymatic digestive processes in the mouth itself. It has been suggested that this palate—and other changes—would also have played an important role in separating the middle ears of mammals from each other and from the mouth cavity, thus leading to the loss of a previously existing pressure-gradient received system (Christensen-Dalsgaard 2010; Manley 2010). A reinterpretation of the evidence indicates, however, that
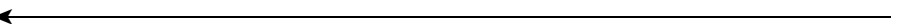
**Fig. 2.1** (continued) the middle of the eardrum), load (*B*), and fulcrum (*C*). The axis of rotation is shown as a circle around the fulcrum. The necessity for transforming a rotation of the extracolumella in the nonmammalian middle ear into a piston-like movement of the columella is enabled by a flexible joint between the extracolumella and the columella. The amplitude and force at the eardrum (*longer black arrow*) is changed by the lever into a smaller amplitude and greater force at the footplate of the columella/stapes (*shorter but wider black arrow*). (**c**) Comparison of the displacement amplitudes of the middle of the eardrum in (*continuous line*) the Tokay gecko and (*dashed line*) the guinea pig over the same frequency range and using the same apparatus for stimuli at 100 dB SPL. In both cases, the outer ear was driven by a closed sound system. Although these are similar measurement conditions, the relative amplitudes may be influenced by the different impedance conditions on the inside of the eardrum (opened mouth floor in the gecko, open bulla condition in the guinea pig) (Partially after Manley 2011; Tokay gecko data from Manley 1972; guinea pig data from Manley and Johnstone 1974)

the immediate ancestors of mammals did not in fact have a tympanic middle ear, and thus had no pressure-gradient receiver that they could lose.

Thus the immediate ancestors of true mammals had changed their jaw construction and eliminated six bones from the lower jaw, making it more stable. During the transition period from a primary to a secondary jaw joint (the latter between the squamosal in the upper jaw and the dentary), species with a double jaw joint existed. The primary jaw joint was gradually eliminated because its lower-jaw component, the articular bone, which connected to the upper-jaw quadrate, was moved medial to and out of the lower jaw. The secondary jaw joint evolved lateral to the primary joint, and contemporary species such as *Diarthrognathus* used both joints simultaneously (Allin and Hopson 1992). With time, the old joint moved deeper and entered the middle ear while retaining a connection to the lower jaw over a long period of time. There is a general consensus that the mammalian middle ear, including its eardrum, evolved at a completely different location from that of the single-ossicle middle ear (e.g., Allin 1986). Instead of directly behind the head, the tympanum originated near the rear end of the lower jaw, over those bones that were in transition out of the jaw and into the middle ear. The angular bone of the lower jaw became known as the ectotympanic, and grew into a circular support for the eardrum; the articular became the incus. The malleus originated from the upper-jaw quadrate. This series of events were, in basic form, elucidated very many years ago, of course, by Reichert (1837) and later Gaupp (1912) and provided an early and very convincing case of evolutionary transformation of function. Since then, this research area has been enormously enriched by new fossil material but has not been free of controversy. Some authors suggested, for example, that early mammals had a double middle ear, with two tympana, or that the early tympana were perhaps also sound-producing, rather than only sound-absorbing organs (see, e.g. Allin 1986). Maier (1990), however, considered it unlikely that early mammals had anything other than a single tympanum behind the lower jaw.

The three ossicles of the mammalian middle ear evolved independently at least three times. In monotremes, for example, the jaw depressor muscles and thus the relative placements of middle ear structures, differ from the therian situation, indicating independent evolutionary acquisition (Rich et al. 2005). In therian mammals, the three ossicles of the middle ear did not suddenly detach from the lower jaw and become freely suspended in a middle ear space. Although middle ear spaces are difficult to find in early mammals, it is obvious that the malleus, in particular, remained attached to the inside of the lower jaw via an ossified Meckel's cartilage (a remnant of the embryonic lower jaw of vertebrates). This condition is considered as an intermediate stage in the evolution of freely suspended ossicles and persisted for a remarkably long time (transitional mammalian middle ear [TMME]; Allin and Hopson 1992; Figs. 2.2 and 2.3). This morphological stage can be seen in a very similar form today in embryonic monotreme (egg-laying) mammals, as the ossicles in modern monotreme mammals separate fully from the lower jaw only around the time of hatching (Luo 2007) but remain very stiff throughout life (Aitkin and Johnstone 1972).