

Chapter 2

The Primate Peripheral Auditory System and the Evolution of Primate Hearing

Sirpa Nummela

Abstract The primate peripheral auditory organ closely resembles that of other terrestrial mammals. Acoustic communication has an important role in primate communities, and hearing characteristics are well-known for several species. In this chapter, morphological variation of the primate outer, middle, and inner ears is reviewed and is related to auditory data known from experimental work. Differences can be discerned among various primate groups, the greatest differences being between small, mainly nocturnal strepsirrhines and larger, mainly diurnal haplorhines. The evolutionary history of primate hearing is discussed in relation to different hypotheses of primate origins with the view that, as in the earliest mammals, the earliest primates were nocturnal and had good high-frequency hearing. Increased sensitivity to lower frequencies evolved later, although relatively early in the history of primates. This was made possible by an elongation of the cochlea and the disappearance of the secondary spiral lamina. The body size and ecology of primates is related to their ear size, and the role of hearing together with other sensory modalities, mainly vision and olfaction, is discussed.

Keywords Acoustics • Allometry • Auditory sensitivity • Cochlea • Eocene • Fossil primates • Haplorhines • Inner ear • Middle ear • Outer ear • Pinna • Primate origins • Sensory ecology • Sound localization • Strepsirrhines

2.1 Introduction

The modern primates (order Primates) are a diverse group of placental mammals (Archibald and Rose 2005) that includes two main groups, the strepsirrhines (Strepsirrhini) and the haplorhines (Haplorhini), inhabiting tropical and subtropical regions of South America, Africa, and Asia, and drier, more open country,

S. Nummela (✉)
Department of Biosciences, University of Helsinki,
POB 65 (Viikinkaari 1), Helsinki 00014, Finland
e-mail: sirpa.nummela@helsinki.fi

particularly in sub-Saharan Africa (Ramsier and Quam, Chap. 1). The living strepsirrhines include two main groups: lemuroids and lorisooids. The lemuroids (Lemuroidea) are endemic to Madagascar, and most species in this group are cathemeral or nocturnal. The lorisooids (Lorisoidea) are found in Africa and Asia, and all are nocturnal (Zimmermann, Chap. 5). The modern haplorhines include three main groups: tarsiers, platyrrhines, and catarrhines. The nocturnal tarsiers (Tarsiiformes) live in SE Asia. The platyrrhines (Platyrrhini, New World monkeys) live in Central and South America, and all but one species are diurnal. Finally, the catarrhines (Catarrhini, Old World monkeys and apes) are diurnal and found in Africa and Asia. The taxonomic diversity of primates is high among mammals, with great morphological and behavioral variety (Fleagle 2013; Henke and Tattersall 2015).

The primate auditory system is much like that in other mammals in general. The peripheral auditory system is situated in the temporal bone. Its three parts, the outer, middle, and inner ears (Fig. 2.1), form a well-functioning sensory system responsible for receiving sound energy from the surrounding environment, transforming this sound energy into mechanical vibrations, and converting this mechanical energy by transduction to nerve impulses (Møller 1974; Rosowski 2003). These nerve impulses are sent forward via the auditory nerve to the brain where they are perceived as sound (Geisler 1998; Ramsier and Rauschecker, Chap. 3). In this chapter, first the peripheral auditory system and its functional morphology in modern primates will be presented separately for the outer, middle, and inner ears (Sects. 2.2–2.4). This is followed by a consideration of the evolutionary history of primate hearing based on data from fossil specimens and modern primates with known audiograms, including the possible role of hearing in the origin of primates (Sect. 2.5). Finally, the sensory ecology of primates is discussed by relating the role of the sense of hearing to other sensory modalities, mainly vision and olfaction (Sect. 2.6).

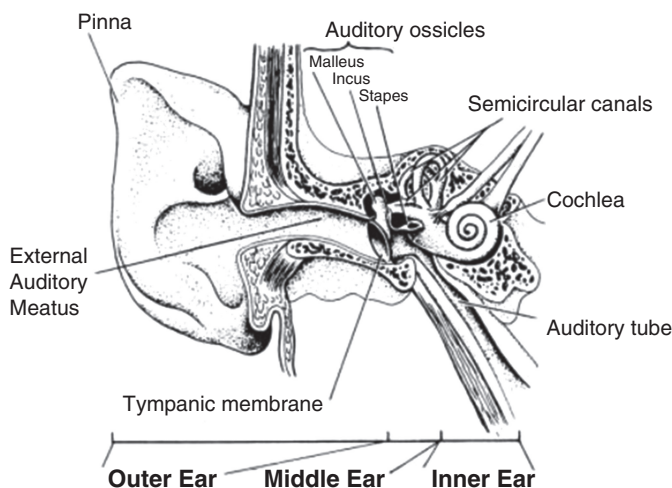


Fig. 2.1 The primate ear. (Reprinted with permission from Fleagle 2013)

Early comparative studies of mammalian/primate auditory anatomy were carried out in the nineteenth century (Hyrtil 1845; Doran 1879) and early twentieth century (van Kampen 1905; van der Klaauw 1931). During the decades since 1960, work by several researchers has moved from pure anatomical descriptions to augmenting the understanding of the functions of mammalian/primate auditory structures. The functional anatomy of the mammalian ear was promoted by Henson (1961, 1974), while Masterton et al. (1969) focused on the evolution of high-frequency hearing among mammals, including primates. Furthermore, Fleischer (1973, 1978) established a basis for future comparative studies in morphology and evolution of the middle and inner ear structures of a wide range of mammalian taxa. Cartmill (1975) and MacPhee (1979, 1981) were early pioneers in the study of the primate auditory region.

Previous reviews have described the diversity among mammalian ears and hearing. Differences in the contribution of each of the temporal bone elements to the construction of the ear region in different mammalian orders were presented in compilations by Novacek (1977, 1993). Research on mammalian hearing and the peripheral auditory system is firmly grounded in the work of Rosowski (1992, 2013). The relationship between the morphological variation of the mammalian ear and hearing characteristics was also studied by Hemilä et al. (1995) and by Nummela (1995). Vertebrate auditory physiology, evolution, and development are presented widely by Manley et al. (2004) and Manley (2014). A comparative view on hearing in the animal kingdom can be found in the review by Köppl et al. (2014). Experimental work on mammalian hearing and on the role of high-frequency hearing in sound localization combined morphological and experimental data (R. S. Heffner and H. E. Heffner 1992a; H. E. Heffner and R. S. Heffner 2014) that expanded the understanding of the significance of the auditory sense in an organism's behavioral ecology.

Primate auditory morphology and its evolution since the Paleocene epoch received detailed attention through the research efforts of Coleman and Ross (2004) and Coleman and Boyer (2012). The primate cochlear labyrinth and its relationship to hearing abilities were studied by Kirk and Gosselin-Ildari (2009) and Armstrong et al. (2011). Auditory capacities in fossil hominins were estimated from the anatomy of the outer and middle ears by Martínez et al. (2004) and Quam et al. (2015). For vertebrates in general, the evolution of the ear and hearing is treated by Clack et al. (2016), and vertebrate sound production and acoustic communication is discussed by Suthers et al. (2016).

The functional approach to sensory research often asks the question: What limits the organism's ability to receive sensory information? Within auditory science, the ultimate goal is to understand how animals hear and how they process information that they receive through their auditory organs (Friedland 2006; Yost et al. 2008). In addition to their auditory physiology, the morphology of auditory structures is useful for revealing ontogenetic changes (Basch et al. 2016; Maier and Ruf 2016), constructing phylogenetic and systematic scenarios (Gunz et al. 2012; Stoessel et al. 2016a, b), studying ecological interactions (Dominy et al. 2001), and discovering possible trade-offs between hearing and other sensory systems (Dominy et al. 2004; Nummela et al. 2013).

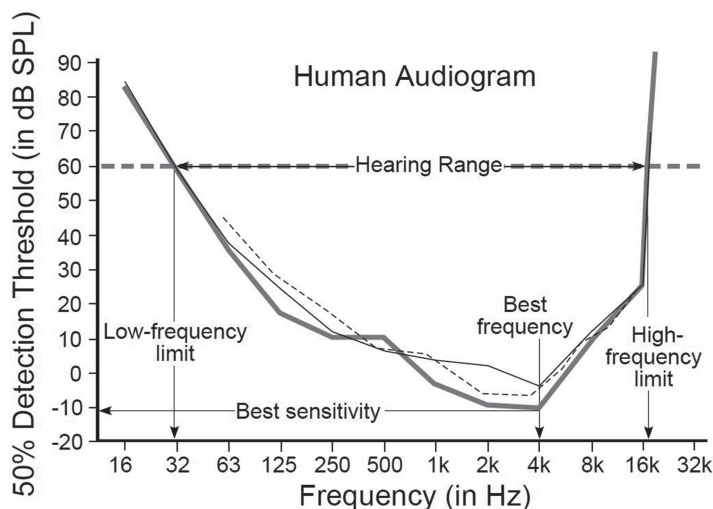


Fig. 2.2 Average human audiograms from three separate studies. The *thick gray line* indicates the audiograms measured with the conditions described by Jackson et al. (1999). Standard audiograms from Sivian and White (1933) (*dashed line*) and from Davis (1960) (*thin line*) are indicated for comparison. Common audiometric parameters used for describing hearing sensitivity are indicated, with the hearing range customarily set between high- and low-frequency limits at 60 dB SPL. (Reprinted with permission from R. S. Heffner 2004)

The two primary methods for measuring the hearing sensitivity of an animal are behavioral testing and auditory brainstem recordings to obtain audiograms, and comparisons of these methods are a matter of discussion (Ramsier and Dominy 2010; Ramsier and Rauschecker, Chap. 3). A comprehensive selection of vertebrate audiograms can be found in Fay (1988). Here, a selection of behavioral audiograms for primates will be presented. A human behavioral audiogram (Fig. 2.2) shows the general characteristics that are often of interest in an animal's hearing. These include the overall hearing range, the low- and high-frequency limits (the lowest and highest frequency heard at 60 dB SPL), the best sensitivity (in dB), and the best frequency (the frequency heard at the best sensitivity). Behavioral audiograms are shown separately for a few strepsirrhines, platyrrhines, and catarrhines (Figs. 2.3, 2.4 and 2.5). The behaviorally measured auditory parameters are often used for finding possible correlations between hearing sensitivity and auditory morphology in primates and determining how different structures affect the hearing characteristics of a species; the outer, middle, and inner ears all are known to contribute to this (Ruggero and Temchin 2002; Vater et al. 2004). This is discussed more in Sects. 2.2, 2.3.3, and 2.4.

Hearing is a particularly important sensory modality since it allows perception of phenomena that might be out of sight. To take advantage of any potential information carried by sound (e.g., vocalizations), an organism has to perform at least one of three basic auditory tasks: sound detection, sound localization, and sound identification (R. S. Heffner 2004; Yost et al. 2008). Although animals are

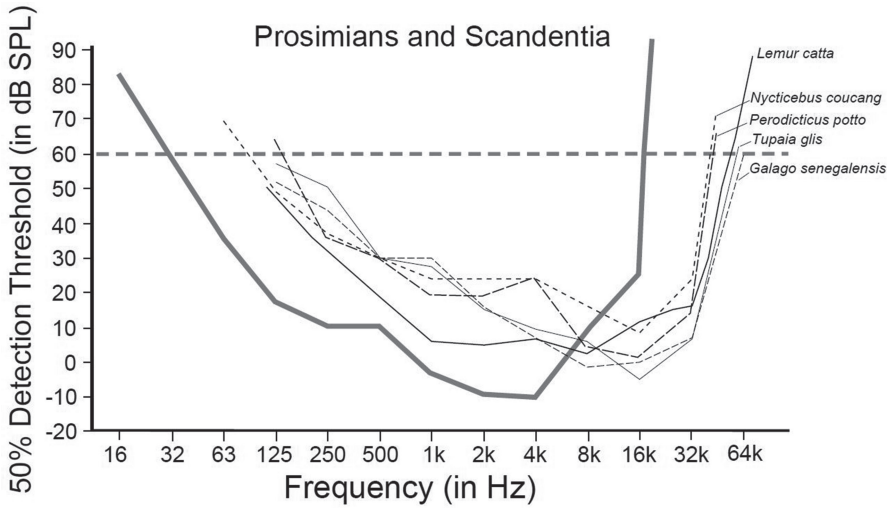


Fig. 2.3 Average audiograms for strepsirrhines (formerly known as prosimians): ring-tailed lemur (*Lemur catta*), lesser bushbaby (*Galago senegalensis*), potto (*Perodicticus potto*), and Sunda slow loris (*Nycticebus coucang*). The audiogram of the tree shrew (*Tupaia glis*; Scandentia), a species closely related to primates, is also shown. The *thick gray line* is the human audiogram. (Modified and reprinted with permission from R. S. Heffner 2004)

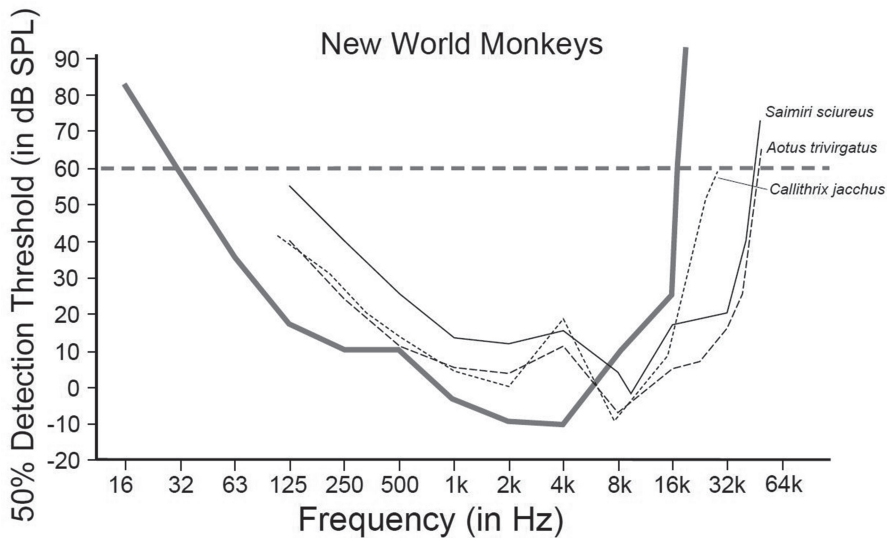


Fig. 2.4 Average audiograms for New World monkeys: squirrel monkey (*Saimiri sciureus*), owl monkey (*Aotus trivirgatus*), and marmoset (*Callithrix jacchus*) with the human audiogram (*thick gray line*) for comparison. (Reprinted with permission from R. S. Heffner 2004)

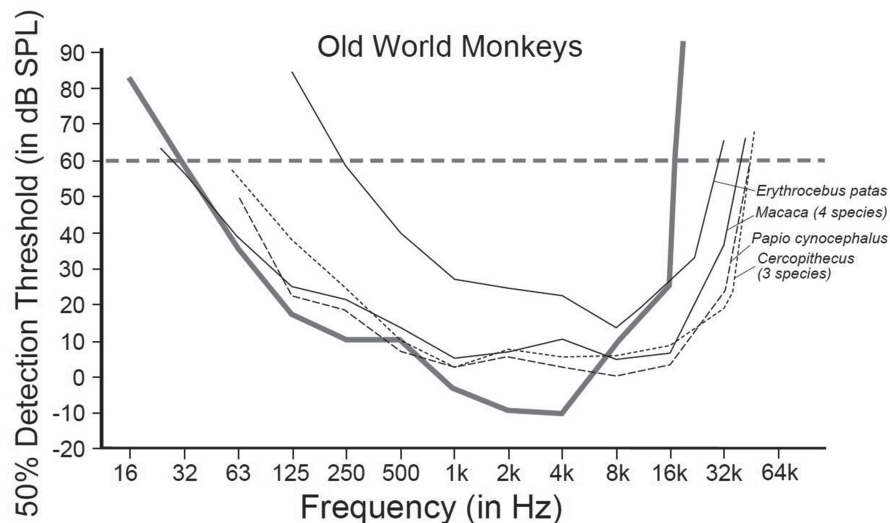


Fig. 2.5 Average audiograms for Old World monkeys: patas monkey (*Erythrocebus patas*), yellow baboon (*Papio cynocephalus*), four macaques (*Macaca fascicularis*, *M. fuscata*, *M. mulatta*, and *M. nemestrina*), and three cercopithecines (*Cercopithecus aethiops*, *C. mitis*, and *C. neglectus*) with the human audiogram (thick gray line) for comparison. (Reprinted with permission from R. S. Heffner 2004)

capable of performing these practically simultaneously, sound detection is still the most basic of these tasks since it underlies the other two. Of the various ways to measure and describe hearing sensitivity, a behavioral audiogram provides insights into what an animal actually hears (see Ramsier and Rauschecker, Chap. 3), and the behavior of an entire organism is generally considered the target for selective pressure (R. S. Heffner 2004).

Primates make use of different sound frequencies (Ramsier and Rauschecker, Chap. 3), they live in different habitats with different acoustics (Brown and Waser, Chap. 4), and they vary in body size (Smith and Jungers 1997; Mattila and Bokma 2008). In general, primate hearing sensitivity follows phylogenetic patterns. Coleman (2009) provided a comprehensive overview of all published nonhuman primate behavioral audiograms, both speaker derived and headphone derived. The best high-frequency hearing among the extant primates tested has been found in strepsirrhines (lemurs and lorises) and tarsiers, whereas low-frequency sensitivity is generally better in haplorhines (monkeys and apes) (R. S. Heffner 2004; Ramsier et al. 2012a). Within haplorhines, the catarrhines are generally more sensitive to lower frequencies than are the platyrrhines, and high-frequency sensitivity is reduced in apes compared with monkeys. Furthermore, monkeys and apes (except humans) often show two peaks of maximum sensitivity, whereas lemurs and lorises, as well as humans, generally have only a single peak in sensitivity in their audiograms (Coleman 2009; Ramsier and Rauschecker, Chap. 3).

2.2 Outer Ear and Interaural Distance

Mammals are the only vertebrates with a distinct outer ear that consists of a pinna and the ear canal (external auditory meatus). Both of these structures show large morphological variation among mammals. The pinna varies in its height and width, location on the head, and size in relation to the head size. The outer ear canal varies in its overall geometry, length, and cross-sectional area. A larger pinna can collect a larger amount of sound energy and is also more suitable for the long wavelengths of low frequencies (R. S. Heffner et al. 1982; Ahlborn 2004). The level of amplification of the incoming sound performed by the outer ear depends directly on the size of the pinna and, especially, on the length of the ear canal (Dallos 1973; Zwislocki 1975).

All primates possess cartilaginous pinnae, which show considerable diversity in prominence, morphology, and mobility (Fig. 2.6). There is also variation in the placement of the pinnae on the head, how much the pinnae protrude above the head, and whether they are covered by fur or not (Packer and Sarmiento 1984). Relative to head size, the pinna is larger in strepsirrhines than in haplorhines, with the largest pinnae found in aye-ayes (*Daubentonia madagascariensis*) (Coleman and Ross 2004) and the smallest ones in orangutans (*Pongo pygmaeus*) (Schultz 1973). In strepsirrhines, the auricular musculature is better developed, and the pinnae are generally more mobile and protrude more above the head than in haplorhines (Coleman and Ross 2004; Fleagle 2013). The large morphological variation of the primate pinna (Fig. 2.6) generally follows phylogeny but also has ecological patterns. Strepsirrhines and tarsiers, both of which include many nocturnal species, have relatively tall and narrow pinnae, whereas platyrrhines and catarrhines, which are mostly diurnal species, have shorter, wider, and more symmetrical pinnae. While no functional significance has been attributed to these shape differences, they may still be useful in primate systematics (Coleman and Ross 2004; Coleman and Colbert 2010).

The length of the bony portion of the outer ear canal was measured on dry skulls by Masali et al. (1992) for small samples of humans, chimpanzee (*Pan troglodytes*), gorilla (*Gorilla gorilla*), and orangutan. The cartilaginous portion of the ear canal was estimated to form one-third of the total length in humans, and the total ear canal length was calculated as one-and-a-half times the length of the bony portion for all the ape species. The fundamental resonance frequency of the outer ear canal (the frequency of maximum dB gain) was estimated from its length and was around 3.0 kHz in humans, while the apes ranged between approximately 1.5–2.0 kHz.

The correspondence between the fundamental resonance frequency of the external auditory meatus and the frequency of best hearing sensitivity can be examined. The best frequency for humans is around 3 kHz (Fig. 2.2) and the fundamental resonance frequency is 3.1 kHz. For the chimpanzee, the best frequency is around 2 kHz (Elder 1934; Masterton et al. 1969) and the fundamental resonance frequency is 2.15 kHz (Masali et al. 1992). A close association between the best-heard frequencies and the central portion of the frequency range of human language is well-known (Shaw 1974), and the fundamental resonance frequency of the ear canal also corresponds to the modal pitch of long-distance calls in the other ape species.

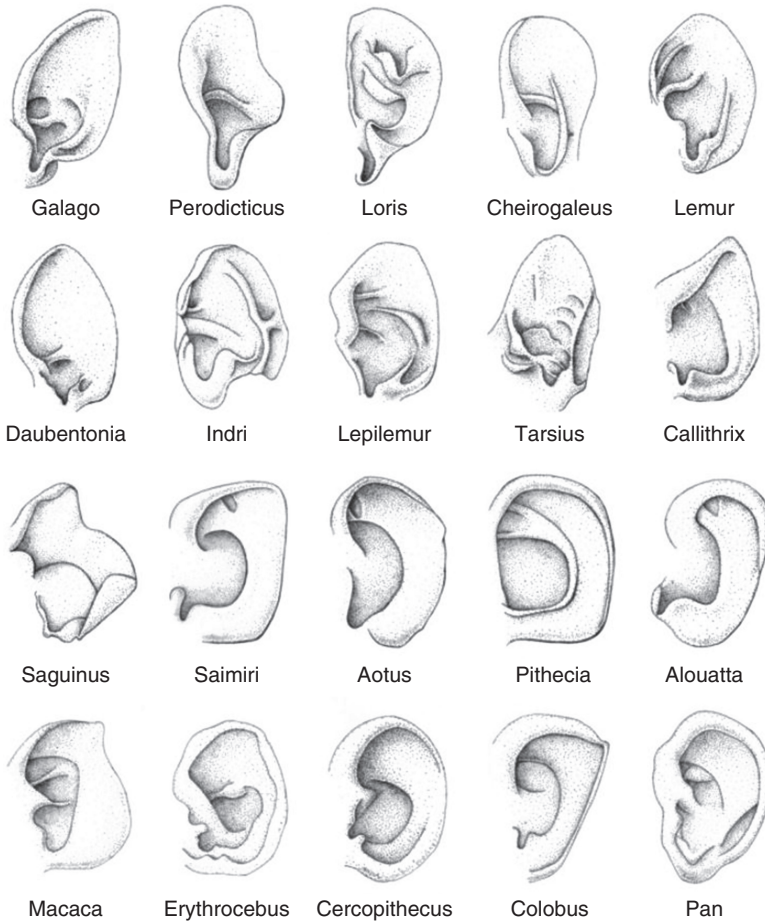


Fig. 2.6 Variation of the primate ear pinna morphology for diverse taxa. The pinnae here are scaled to the same size. Lorisoids: galago (*Galago* sp.), potto (*Perodicticus potto*), and a loris. Lemuroids: dwarf or mouse lemur (*Cheirogaleus* sp.), ring-tailed lemur (*Lemur catta*), aye-aye (*Daubentonia madagascariensis*), indri (*Indri indri*), sportive lemur (*Lepilemur* sp.). Tarsiiformes: tarsier (*Tarsius* sp.). New World monkeys: marmoset (*Callithrix* sp.), tamarin (*Saguinus* sp.), squirrel monkey (*Saimiri* sp.), owl monkey (*Aotus* sp.), saki monkey (*Pithecia* sp.), howling monkey (*Alouatta* sp.). Old World monkeys and apes: a macaque (*Macaca* sp.), patas monkey (*Erythrocebus patas*), guenon (*Cercopithecus* sp.), colobus monkey (*Colobus* sp.), and chimpanzee (*Pan troglodytes*). (Modified and reprinted with permission from Coleman and Ross 2004)

The lower frequencies of best sensitivity in apes (compared with humans) might be advantageous in a forested environment where low frequencies propagate better (Masali et al. 1992; Brown and Waser, Chap. 4).

Sound localization is of vital importance for the survival of an animal and has most likely been under selective pressure during the evolution of mammals (H. E. Heffner and R. S. Heffner 2016). In addition to head movements, mammals can use

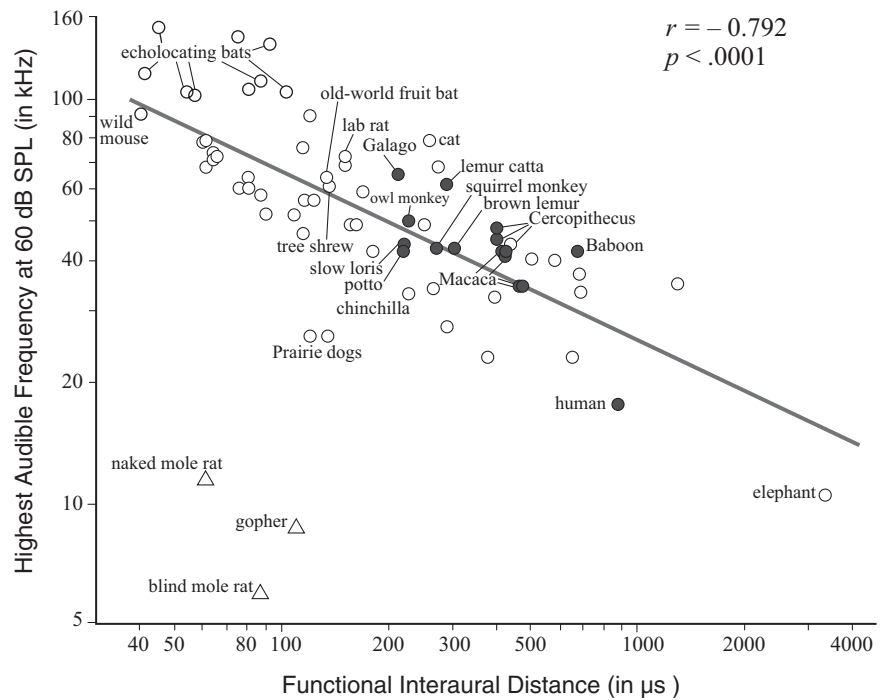


Fig. 2.7 Relationship between maximum functional interaural distance (the time for a sound in air or water to travel from one ear canal to the other) and the high-frequency hearing limit at 60 dB SPL for over sixty mammals. *Filled circles*: primates, with species referenced earlier and the brown lemur (*Eulemur fulvus*), three guenons (*Cercopithecus* sp.), and the yellow baboon; *open circles*: selection of other mammals; *open triangles*: subterranean mammals (not included in the statistical analysis). (Reprinted with permission from R. S. Heffner 2004)

their movable pinnae when locating a sound source and directing the eyes to it, thus enabling the animal to add another sense to the sound localization task (Masterton et al. 1969; R. S. Heffner and H. E Heffner 1992a; also see Sect. 2.6). Large animals with a large interaural distance can use the interaural time difference for sound localization, but for small animals with a small head, including many primate species, the interaural intensity difference is especially useful at higher frequencies.

Figure 2.7 shows how the high-frequency hearing limit is related to the maximum functional interaural distance (interaural distance divided by sound velocity, in microseconds) in over sixty different mammals. The sixteen primate species included do not deviate from the general mammalian pattern in this respect (Masterton et al. 1969; R. S. Heffner and H. E Heffner 1992a). Better high-frequency hearing is correlated with smaller interaural distance. With some exceptions among other vertebrates, only mammals hear frequencies over 10 kHz (Fay 1988).

Indeed, the ability to hear high frequencies gives the advantage of using spectral cues if an animal has a pinna to produce these cues for sound localization (R. S. Heffner 2004).

Coleman and Colbert (2010) studied the relationship between the measured interaural distance and frequency sensitivity (sound pressure level at 32 kHz taken from an animal's audiogram) in a sample of eleven taxonomically diverse primate species. Even with this smaller sample size, they found a similarly strong correlation as found by R. S. Heffner (2004). The few departures were the yellow baboon (*Papio cynocephalus*), which showed relatively good high-frequency hearing, and the Japanese macaque (*Macaca fuscata*) and the Sunda slow loris (*Nycticebus coucang*), which both had somewhat poor high-frequency sensitivity relative to interaural distance. In this particular study, these findings may simply be due to methodological differences. Coleman and Colbert (2010) suggested that in the case of baboons, some other ecological factors related to communication could explain the exceptionally good sensitivity to high frequencies. For the macaque and the loris, other anatomical or ecological factors may be impairing the high-frequency sensitivity that is predicted by the interaural distance.

2.3 Middle Ear

2.3.1 Temporal Bone

The anatomical divisions of the primate temporal bone (squamous, petrous, and tympanic) have large contacts with each other, and the temporal bone articulates with other cranial bones as well (Novacek 1977, 1993). As a result, the ear is not acoustically isolated from the skull, and sound waves can travel through the skull. Primates are the only mammals with an auditory bulla formed solely by the petrous part (petrosal) of the temporal bone (Cartmill et al. 1981; MacPhee 1981). The auditory bulla surrounds the middle ear cavity (Table 2.1; Fig. 2.8). In strepsirrhines, the petrosal is expanded into a balloon-like protrusion and forms a comparatively inflated auditory bulla. Lemurs have a single-chambered middle ear cavity, whereas lorises exhibit a two-chambered middle ear cavity with additional air-filled space in the form of an anterior accessory cavity, but there is no diverticulum (Cartmill 1972, 1975). In tarsiers, which are small nocturnal haplorhines, the auditory bulla is fairly large and located almost in the center of the cranial base, close to the foramen magnum. As a result, the left and right bullae are near one another. As for other haplorhines, in many New World monkeys the petrosal is similar to that in strepsirrhines, whereas in Old World monkeys and apes (including humans), the petrosal has a rough texture on its ventral surface and does not form a balloon-like structure. Haplorhines have a two-chambered middle ear cavity with a posterior accessory cavity with air-filled spaces off of the epitympanic recess and a diverticulum off of the Eustachian tube (Packer and Sarmiento 1984; MacPhee and Cartmill 1986).

Table 2.1 Ear characteristics among different primate groups. For further information, see Sect. 2.3.1

	Strepsirrhines		Haplorhines		
	Lemuroids	Lorisoids	Tarsiers	New World monkeys (platyrrhines)	Old World monkeys and apes (catarrhines)
Petrosal	Forms the auditory bulla in strepsirrhines and haplorhines				
Auditory bulla	Balloon-like and inflated		Enlarged and situated close to the foramen magnum	Balloon-like and inflated (in most species)	Not balloon-like, rough texture ventrally
Middle ear cavity	Single chambered	Two-chambered: anterior accessory cavity with air-filled spaces, but no diverticulum	Two chambered: posterior accessory cavity with air-filled spaces off the epitympanic recess and a diverticulum off the Eustachian tube		
Tympanic	Forms complete bony ring or bony tube in all primates				
Bony ring/ bony tube	Bony ring unfused to the bulla (free floating)	Bony ring fused to the bulla	Bony tube fused to the bulla	Bony ring fused to the bulla	Bony tube fused to the bulla
Outer ear canal	Almost entirely cartilaginous, no bony tube		Elongated tympanic forms the bony part	Almost entirely cartilaginous, no bony tube	Elongated tympanic forms the bony part

In primates, as in moles, many rodents, and elephants, the insertion site for the tympanic membrane takes the form of a complete bony ring (Table 2.1; Fig. 2.9), whereas in some other mammals (e.g., artiodactyls and perissodactyls) the insertion is U-shaped (van der Klaauw 1931; Fleischer 1973). Within strepsirrhines, the tympanic bone consists solely of a bony ring. In lemurs, this ring is unfused (free floating) within the middle ear cavity (Fig. 2.8), but it is still surrounded by the relatively large, single-chambered auditory bulla, whereas in lorises, the tympanic ring is fused to the wall of the bulla (Cartmill 1975). Within haplorhines, New World monkeys resemble lorises in having a laterally fused tympanic ring. In catarrhines, as well as in tarsiers, the tympanic bone is likewise fused to the bulla wall, but instead of forming a single ring, the tympanic forms a bony tube. This elongated bony tube extends laterally toward the external ear opening at the side of the skull and forms the outer ear canal. Strepsirrhines and platyrrhines do not possess this bony tube but have only a tympanic ring, and their external auditory meatus is almost entirely cartilaginous (Table 2.1).

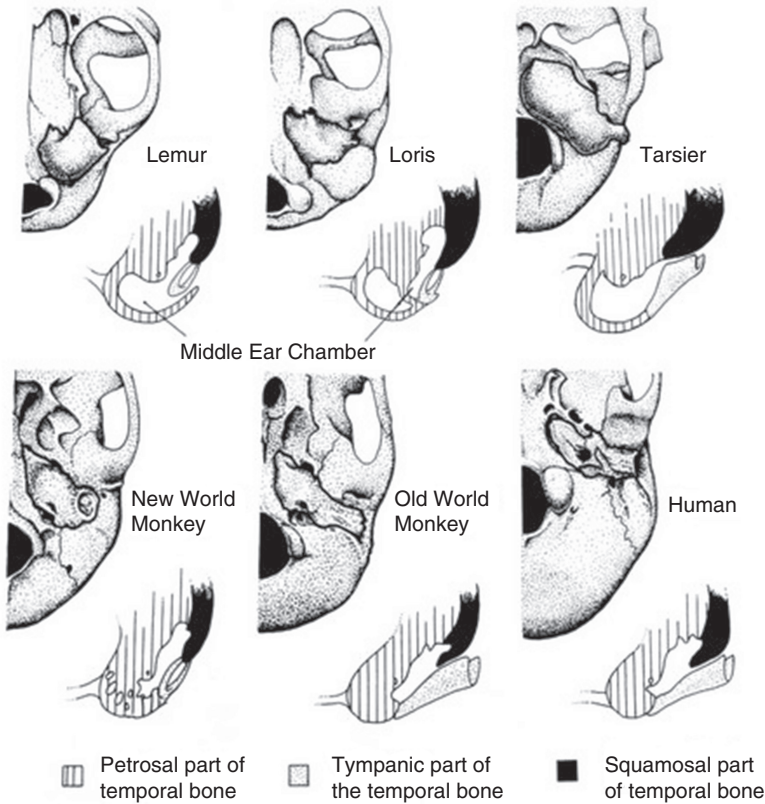


Fig. 2.8 Variations in the temporal bone anatomy of primates: ventral view (*above*) and cross-sectional view of the ear region (*below*). The petrous, the tympanic, and the squamosal portions vary considerably across different taxa (also see Table 2.1). In lemurs, the tympanic (ectotympanic) bone supporting the eardrum is ring-shaped, suspended within the tympanic cavity, and surrounded by the petrous portion. In lorises, the tympanic is connected to the wall of the bulla and the bulla cavity is divided. The tympanic bone is an elongated bony tube on the lateral side of the skull in tarsiers and in Old World monkeys and apes (including humans). In New World monkeys the tympanic forms a tympanic ring that is fused to the auditory bulla laterally. (Modified and reprinted with permission from Fleagle 2013)

2.3.2 Middle Ear Structure and Function

The primate middle ear has the general mammalian anatomy with three middle ear ossicles (malleus, incus, and stapes) forming an ossicular chain in the cavity between the tympanic membrane laterally and the oval window of the cochlea medially (Figs. 2.1 and 2.9). In primates, as in most mammals, the malleus is attached to the tympanic membrane at its lower, slender part called the manubrium. The anterior process of the malleus (also called the gonial or the processus gracilis) makes contact with the tympanic ring anteriorly. The looseness/stiffness of this contact varies

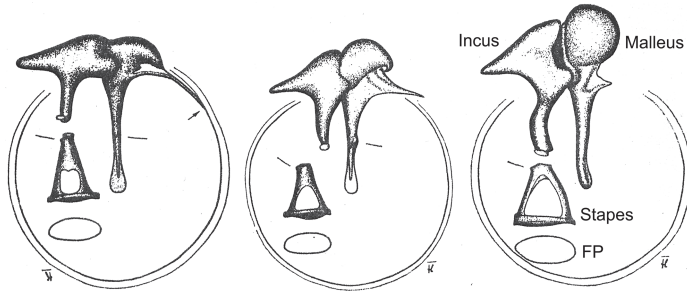


Fig. 2.9 Middle ear ossicles from the left ear of three primate species as viewed from inside the middle ear cavity. *Left*: Greater bushbaby (strepsirrhine, lorissoid); *middle*: macaque (haplorhine, Old World monkey); *right*: chimpanzee (haplorhine, ape). The contours of the tympanic membrane are shown for each as well as the area of the stapes footplate (FP). Tympanic membrane diameters measured perpendicular to the manubrium of the malleus are 5.0 mm, 7.5 mm, and 10.2 mm, respectively. (Reprinted with permission from Fleischer 1973)

among different mammals. In turn, the malleus head and the incus body articulate with one another (incudomalleolar joint). The incus has a small lenticular process at the tip of its long process, and this lenticular process articulates with the stapes head (incudostapedial joint). The medial end of the stapes (the footplate) is attached to the oval window of the cochlea.

In sound transmission, from the lower acoustic impedance of air in the ear canal to the much higher acoustic impedance of the fluid-filled inner ear (Rosowski 1994; Hemilä et al. 1995), the middle ear acts as an acoustic impedance-matching device that compensates for the loss in energy associated with this change in medium. The mass and stiffness of the ossicles are the main factors limiting transmission at higher frequencies; the middle ear cavity volume and the tightness of the connections between the malleus and tympanic membrane and at the joints between the ossicles are the main limiting factors at lower frequencies. Smaller middle ears with smaller tympanic membranes, lighter ossicles, and tighter connections between them are better at transmitting higher frequencies while larger middle ears with larger tympanic membranes, heavier ossicles, and looser connections between them are better suited for transmitting lower frequencies (Møller 1974; Rosowski and Relkin 2001).

This impedance matching in land mammals is accomplished by the *area ratio*, which is the ratio between the tympanic membrane area and the oval window area, and by the *lever ratio*, which is the ratio between the malleus lever arm length and the incus lever arm length (Rosowski 1994; Nummela et al. 2007). The *impedance transformer ratio* is the product of these two ratios: $[(\text{area ratio}) \times (\text{lever ratio})^2]$. Although the middle ear is often seen as a pressure-enhancing mechanism between the surrounding air and the inner ear fluid, it is evident that the earliest land vertebrates did not have such an impedance-matching mechanism in their ears (Manley and Sienknecht 2013). Additionally, the middle ear transmission mechanism is not solely responsible for the hearing sensitivity of mammals. Rather, the outer, middle, and inner ears together are important for determining the overall shape of an animal's audiogram (Ruggero and Temchin 2002; Hemilä et al. 2010).

In an ideal case, the impedance-matching system of the middle ear would offset the loss of sound energy when changing from the air-filled environment to the fluid-filled cochlea. Nevertheless, the theoretical pressure gain based on the ideal impedance transformer ratio of the middle ear does not correspond to empirical results of middle ear pressure gain measured in experimental settings (Rosowski and Relkin 2001).

2.3.3 Middle Ear Morphology and Hearing Sensitivity

Detailed anatomical descriptions on the comparative morphology of mammalian ossicles, including twenty-five primate species from all major taxonomic groups, can be found in Doran (1879), who separated primate ossicles into four groups (as did Hyrtl 1845): (1) humans, (2) apes, (3) Old World monkeys, and (4) New World monkeys and strepsirrhines. Likewise, Masali et al. (1992) identified two grouping for primate ossicles: (1) the Old World primate type, and (2) the New World primate and strepsirrhine type. This grouping mirrors the temporal bone similarities between these two groups (Sect. 2.3.1; Table 2.1).

Based on a wide, systematic survey of the morphology of the mammalian peripheral auditory region, including twenty-five primate species, Fleischer (1973, 1978) studied the evolutionary history of the mammalian middle ear and, particularly, of the malleus-incus complex. Detailed morphological descriptions and quantitative models for ossicular chain function were also presented. Fleischer identified four middle ear types across mammals: the *ancestral ear*, the *microtype ear*, the *transitional ear* (also called the intermediate ear), and the *freely mobile ear*. He suggested that an ancestral middle ear type had given rise to the other three types. A central role in grouping the middle ear types was given to the anterior process of the malleus. This structure varies in size and in strength of attachment to the tympanic ring. Hence, the different ear types deviate from each other by how loose or tight the connections are between different parts.

In the ancestral ear and the microtype ear, the malleus is tightly attached to the tympanic ring with its long anterior process, and the connection between the malleus and the incus is firm (although not ossified) with the joint surfaces being tightly interlocked. These kinds of ears are best suited for transmitting high-frequency sounds and are found in small mammals, such as bats and rodents. The two other types, the transitional ear and the freely mobile ear, are found among primates (Fig. 2.9). In the transitional middle ear (e.g., greater bushbaby, *Otolemur crassicaudatus*, for which the old name *Galago crassicaudatus* was used by Fleischer 1973), the anterior process of the malleus has only a loose contact with the tympanic ring, and the joint between the malleus and incus is not as tight as in the microtype ear. In the freely mobile middle ear (e.g., macaque, *Macaca* sp., and chimpanzee), the anterior process of the malleus has been reduced and is loose from the tympanic ring; the joint between the malleus and incus is also loose with more mobility between the ossicles than in the transitional ear or the microtype ear. The head of the

malleus is larger in the freely mobile ear, and the incus is relatively larger as compared to the malleus than in the other two types (Fig. 2.9).

Based on the sizes of the tympanic membrane and stapes footplate in over fifty mammalian species, including three primates (bushbaby, macaque, and chimpanzee), Fleischer (1973) concluded that the middle ear size is not totally dependent on body size (mass). Nevertheless, strong correlations between both tympanic membrane and stapes footplate area with body mass were found across mammals (Hunt and Korth 1980; Rosowski and Graybeal 1991). The size variation in both the tympanic membrane and the oval window is clearly negatively allometric to body mass in mammals in general, including primates (Rosowski 1994). In addition, a strong correlation was found between ossicular mass and body mass across both placental and marsupial taxa (Nummela 1995; Nummela and Sánchez-Villagra 2006). In contrast, the relationships between different middle ear structures themselves (i.e., tympanic membrane and oval window areas; malleus and incus lever arms and masses) are highly isometric among mammals, including primates (Rosowski 1992; Hemilä et al. 1995). Within primates, Coleman et al. (2010) showed that the areas of the tympanic membrane and stapes footplate are strongly correlated with body mass across a large number of strepsirrhine and catarrhine taxa. They also found a strong correlation between the tympanic membrane and the stapes footplate areas for these same species.

Rosowski (1992) divided twenty mammals, including three primate species, into three groups according to their middle ear type (microtype, transitional, or freely mobile type) *sensu* Fleischer (1973, 1978) and established their low- and high-frequency hearing limits (at 60 dB SPL) and their best frequency on the basis of the behavioral audiogram for each species. These audiometric parameters were then compared with anatomical measurements to establish correlations between ear structure and function. Each mammalian group had a distinct hearing range with only limited overlap. The strongest correlations were found between the best frequency and the tympanic membrane area and for the low- and high-frequency limits with the footplate area. Thus, increases in body size and corresponding increases in the sizes of the tympanic membrane and the stapes footplate lead to a lowering of the best frequency and the low- and high-frequency limits.

It is evident that the middle ear structures and auditory capacities of extant mammals vary widely, and attempts to correlate these two can reveal significant relationships, which in turn can be used to predict the auditory capacities of fossil mammals for which only structural data are available (Nummela et al. 2004; Quam et al. 2013). Plassmann and Brändle (1992) developed a general model to explain auditory function from structural measurements that was applicable to a wide diversity of mammalian species with different ear dimensions, including tympanic membrane radius, the middle ear volume radius, the cross-sectional area and length of the external auditory meatus, and the frequency of best sensitivity. The tympanic membrane area and the middle ear volume have identical resonance frequencies in each species studied, and it is possible to predict the tympanic membrane size on the basis of the frequency range of best sensitivity and vice versa. Similarly, Hemilä et al. (1995) have shown that the behavioral high-frequency limit is inversely related

to the cube root of the combined mass of the malleus and incus across twenty-eight mammalian species, including nine primates. These models can potentially be applied to fossil specimens to predict aspects of their unknown audiograms (see Quam, Martínez, Rosa, and Arsuaga, Chap. 8).

The impedance transformer ratio was studied for thirty-three primate taxa by Coleman and Ross (2004). The area ratio was found not to differ significantly between haplorhines and strepsirrhines, reflecting the largely isometric relationship between these two variables (Sect. 2.3.2). However, clear differences exist in the lever ratio, with strepsirrhines showing a higher lever ratio than haplorhines. These differences are independent of variation in body size but seem to reflect differences in malleus lever arm length, suggesting that differences in the impedance transformer ratio among primates are primarily driven by differences in length of the manubrium of the malleus. Morphological variation of extant hominid (gorilla, chimpanzee, and human) ossicles was studied in detail with a large sample by Quam et al. (2014). The lever ratio was found to be close (gorilla) or equal (chimpanzee) to the mean lever ratio found for haplorhines by Coleman and Ross (2004), whereas in humans the lever ratio turned out to be clearly lower; in fact, humans have the lowest lever ratio among primates (for functional inferences of the hominid lever ratios, see Quam, Martínez, Rosa, and Arsuaga, Chap. 8).

Size variation in middle ear structures in a large number of primate taxa were used to study the relationship between ear morphology and hearing sensitivity (Coleman and Colbert 2010). The sound pressure threshold level at 250 Hz was used as a proxy for low-frequency sensitivity, and the sound pressure threshold level at 32 kHz was used as a proxy for high-frequency sensitivity. Additionally, several other audiometric parameters (taken from behaviorally measured audiograms like those described in Sect. 2.1) were considered. Of the middle ear structures measured, the tympanic membrane area, the oval window area, the ossicular mass, and various middle ear cavity volumes seemed to exert a considerable influence over low-frequency sensitivity. Structures that seemed to play a role in determining high-frequency sensitivity included the ossicular mass and the interaural distance. These findings agree with the studies by Plassmann and Brändle (1992) and Hemilä et al. (1995) and show that primates follow the general pattern between interaural distance and high-frequency hearing (Masterton et al. 1969; R. S. Heffner and H. E. Heffner 1992a).

2.4 Inner Ear

The primate inner ear is a typical mammalian inner ear with the cochlear part and the vestibular part housed within the bony labyrinth of the petrosal portion of the temporal bone. Early quantitative inner ear data on the cochlea and the oval and round windows were presented by Hyrtl (1845) based on cranial and embryological material from several mammalian orders, including a few primate species, together with ideas of sound conduction through the tympanic cavity and hearing ranges of animals related to ear size.

The interspecific variation of the cochlea has raised the natural question of how this variation might correlate with different hearing capacities of mammalian species (West 1985; Echteler et al. 1994). Morphometric studies of the primate cochlea have been accelerated since high-resolution computed tomography was developed to be applied to the bony labyrinth (Spoor and Zonneveld 1995). While it is evident through quantitative data that hearing characteristics of mammals largely depend on the properties of the peripheral auditory system, considerable differences among the outer ears (see Sect. 2.2), the middle ears (Sect. 2.3), and the inner ears have been shown (Vater et al. 2004; Ekdale 2013). Echteler et al. (1994) pointed out that the mammalian cochleae can be divided into generalized and specialized categories, and this should be taken into account when predicting hearing abilities on the basis of cochlear morphology. However, in general, the cochlear labyrinth volume, the number of spiral turns, and the basilar membrane length were found to correlate with the octave range and the high- and low-frequency limits of hearing in several mammalian species. The number of spiral turns in the cochlea is also a good indicator for the hearing range provided that cochlear specializations of the species are known (Echteler et al. 1994; Vater and Kössl 2011).

Manoussaki et al. (2006) suggested that the curvature gradient of the cochlea might be related to low-frequency sensitivity. The radius of curvature of the cochlea decreases toward the apex and is smallest in the region where low-frequency sounds are analyzed, and the cochlea's mechanical response to low frequencies is enhanced. In an analysis with thirteen mammals (including humans), Manoussaki et al. (2008) demonstrated that the ratio between the radii of curvature of the basal turn and the apical turn correlates strongly with low-frequency hearing limits.

Focusing on primates, Kirk and Gosselin-Ildari (2009) measured the cochlear labyrinth volume as a proxy for the basilar membrane length in a taxonomically diverse sample of thirty-three primate species, and they found that the mean cochlear labyrinth volume was strongly negatively allometric when related to body mass. This suggests that cochlear size has increased during the course of primate evolution (Armstrong et al. 2011; also see Sect. 2.5). Three-dimensional virtual reconstructions of the cochlear labyrinth were also published (Fig. 2.10) for ten primate taxa for which audiogram data are available. The high- and low-frequency limits of hearing were strongly negatively correlated with cochlear labyrinth volume in these taxa, independent of body mass or phylogeny (Kirk and Gosselin-Ildari 2009). Thus, the highest and lowest audible frequencies in primates shift downward as cochlear labyrinth volume increases, especially the high-frequency limit of hearing, even when body mass is held constant.

Coleman and Colbert (2010) used cochlear length as a proxy for basilar membrane length, measuring from the edge of the oval window to the apex along the outside of the cochlea. They found a strong positive relationship with body mass for extant primates. Haplorhines had relatively longer cochleae than other primate groups, extant or extinct. The cochlear length also showed a clear correlation with low-frequency sensitivity (Coleman and Colbert 2010), but no relationship between cochlear length and high-frequency sensitivity was found. This seems to indicate that primates have increased their low-frequency hearing by extending the apical

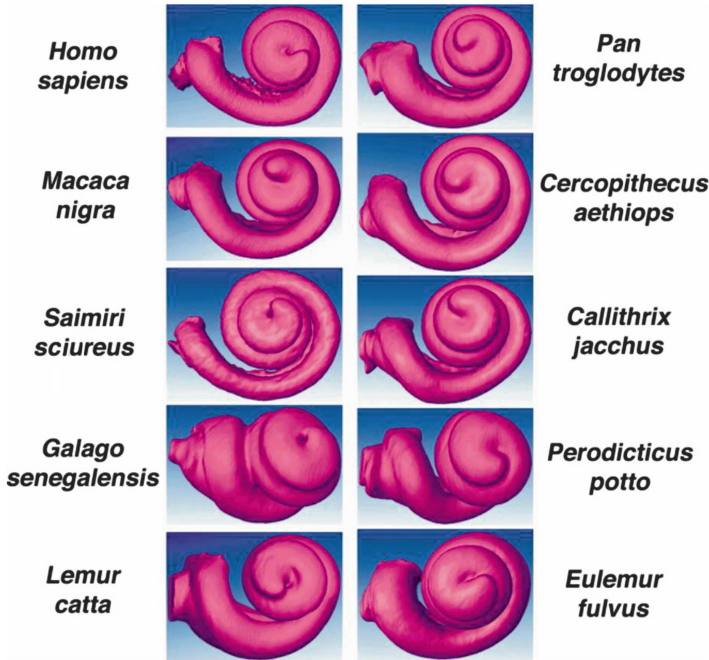


Fig. 2.10 Three-dimensional renderings of the cochlea of ten primate taxa for which audiograms are known. The cochleae are scaled to the same size. The round window for each cochlea faces left. (Modified and reprinted with permission from Kirk and Gosselin-Ildari 2009)

end of the basilar membrane (and presumably the stiffness gradient), which in turn provides space for more hair cells. It is evident that low-frequency sensitivity can be best predicted based on the cochlear length (Coleman and Boyer 2012).

Among living haplorhines, only tarsiers have developed relatively long cochleae while still retaining a well-developed secondary bony lamina that supports the outer edge of the basilar membrane (Fig. 2.11). These features apparently confer both heightened low- and high-frequency sensitivity to this unique genus (Coleman et al. 2010; Ramsier et al. 2012a). The development of secondary laminae does not appear to be directly related to either cochlear length or the number of cochlear spiral turns. Tarsiers show the greatest expression of secondary lamina development, yet they have similar cochlear lengths and a similarly high number of cochlear turns as most monkeys and apes that lack laminae. In some primate groups, the loss of secondary bony laminae may reflect an increase in body size (together with poorer high-frequency sensitivity). However, small-bodied New World monkeys, like tamarins (*Saguinus* sp.) and marmosets (*Callithrix* sp.), apparently lack secondary bony laminae, while similarly sized strepsirrhines, like bushbabies and slender lorises (*Loris* sp.), possess them (Coleman and Boyer 2012), suggesting a phylogenetic component to the expression of this feature as well.

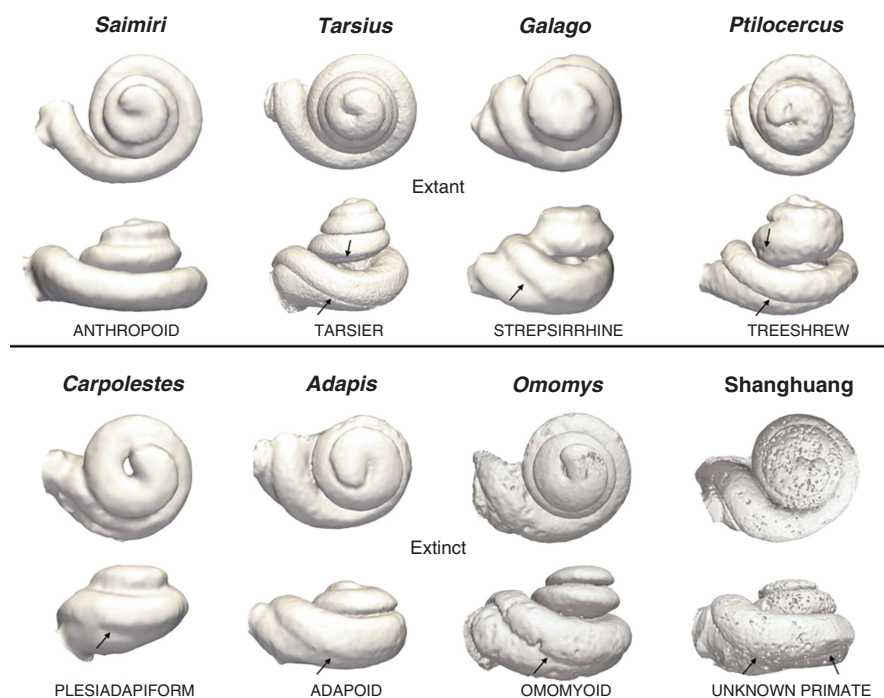


Fig. 2.11 Endcasts based on CT scans of cochleae of mammals, scaled to the same size. From *left to right, upper row*: squirrel monkey, tarsier, bushbaby, and treeshrew; *lower row*: plesiadapiiform, adapoid, omomyoid, and the Shanghuang petrosal. The tarsius cochlea has a higher number of spiral turns than the other taxa shown here. The well-developed secondary bony lamina is shown with *black arrows* in all taxa except in the squirrel monkey, in which there is no evidence of it. (Reprinted with permission from Coleman and Boyer 2012)

2.5 Evolution of Hearing in Primates

The relationships described in Sects. 2.3 and 2.4 between morphological features of the ear, including bony structures, and aspects of the experimentally determined audiogram can be applied to fossil specimens to predict aspects of the hearing abilities in extinct species. This approach provides insights into their lives and makes it possible to understand the evolution of hearing.

2.5.1 Early Mammalian Hearing

An early seminal study into the evolution of mammalian hearing suggested that early mammals were capable of perceiving high frequencies and that ability was related directly to their small head size (Masterton et al. 1969). That idea has been

subsequently corroborated by a large number of behavioral audiograms on diverse mammalian species with a large range in head sizes (H. E. Heffner and R. S. Heffner 2008, 2014). In addition, based on correlations between auditory structures and function, Rosowski and Graybeal (1991) and Rosowski (1992) also concluded that early mammals had good high-frequency hearing. This auditory pattern may represent an adaptation to the nocturnal niches presumably occupied by early mammals (Jerison 1973; Gerkema et al. 2013).

Several studies have revealed more about the hearing abilities and the nocturnal niche of early mammals (Kielan-Jaworowska et al. 2004; Ji et al. 2009). Eutherian (placental) mammals emerged during the Mesozoic era, 160 million years ago (Ma). The earliest mammals were small-bodied animals that fed on insects and occupied nocturnal niches in a low-light environment for most of their history (Allin and Hopson 1992; Luo et al. 2016). Early mammals went through a nocturnal bottleneck that had a tremendous influence on the evolution of mammalian sensory systems, and all extant mammals, including diurnal species, are descendants of these nocturnal precursors. Unlike other terrestrial vertebrates, however, these small and cryptic early mammals de-emphasized vision and, instead, specialized in the senses that could be used in low-light conditions, particularly high-frequency hearing and greatly expanded olfaction (Heesy and Hall 2010; also see Sect. 2.6). Similarly, the likely ancestors of primates show good high-frequency hearing but relatively poor low-frequency sensitivity (Coleman and Boyer 2012). Since high-frequency hearing was present in early mammals, the good high-frequency hearing of modern strepsirrhines would appear to represent a primitive mammalian feature (Coleman and Boyer 2012; H. E. Heffner and R. S. Heffner 2016; Zimmermann, Chap. 5).

2.5.2 Early Primate Hearing

The first primates evolved at the beginning of the Cenozoic era, approximately 60 Ma (Ramsier and Quam, Chap. 1). It is evident that hearing in primates evolved in several stages through the first half of the Cenozoic (60–50 Ma), and the earliest primates are also believed to have been nocturnal (Cartmill 1974; Heesy and Ross 2001). Microcomputerized tomography (μ CT) studies of the cochlea in fossil and living primates have revealed variations in several cochlear structures, including the size of the oval window, the length of the cochlea, and the development of the bony lamina (Fig. 2.11). The low- and high-frequency sensitivities (SPL at 250 Hz and SPL at 32 kHz, respectively) were predicted for many early primate species based on cochlear dimensions and morphology (Coleman et al. 2010; Coleman and Boyer 2012; see Sect. 2.4).

The Plesiadapiforms were small- to medium-sized primates that lived in North America and Europe 60–54 Ma (Silcox et al. 2015). These taxa were characterized by a small oval window and a relatively short cochlea that housed a moderate- to well-developed secondary bony lamina. Those traits suggest good high-frequency sensitivity but relatively poor low-frequency sensitivity, which is somewhat intermediate between primitive extant mammals (e.g., tree shrews and hedgehogs) and

extant strepsirrhines (Coleman and Boyer 2012). The size (volume) of the cochlear labyrinth in early primates and extant mammals closely related to primates was found to be smaller than the cochlear labyrinth size in modern primates, lending support to the idea that the cochlear labyrinth size started to increase first within the Euprimates (strepsirrhines and haplorhines) (Armstrong et al. 2011).

The emergence of the strepsirrhines and haplorhines, representing the major taxonomic division in extant primates today, occurred during the Eocene epoch in North America and Europe between 50 Ma and 35 Ma. These taxa show an increase in cochlear length and a reduction of the secondary bony lamina, indicating that low-frequency sensitivity increased and high-frequency sensitivity decreased modestly and that the strepsirrhine auditory pattern had largely emerged by this time (Coleman and Boyer 2012).

Further lengthening of the cochlea and reduction (or loss) of the secondary bony lamina occurred in haplorhines (except in tarsiers). Evidence from fossil Old World Monkeys from Africa (Oligocene epoch, about 30 Ma) and fossil New World monkeys from South America (Miocene epoch, about 20–16 Ma) suggests that cochlear elongation was completed by the early Miocene. Indeed, three early platyrrhine taxa (*Homunculus*, *Dolichocebus*, and *Tremacebus*) resemble modern platyrrhines in many of their auditory structures (e.g., middle ear area ratio) (Coleman et al. 2010).

Thus, it is evident that some primates had developed low-frequency hearing similar to that of modern species by at least the early Miocene. Low-frequency sensitivity of fossil New World Monkeys was likely very similar to that of their extant counterparts, and they may have had similar high-frequency sensitivity as modern taxa as well. These data are in accordance with the idea that a few characteristics of fossil platyrrhines are still retained in their modern descendants (Fleagle 2013). Given that the fossils studied are most likely not directly ancestral to any specific extant New World taxa (Kay et al. 2008), it is likely that good low-frequency hearing dates back at least 20 Ma.

The good high-frequency hearing in early mammals and the nocturnal bottleneck in the early Cenozoic era (Meng and Fox 1995; Kielan-Jaworowska et al. 2004) suggest that the earliest primates already had good high-frequency hearing (Coleman and Boyer 2012). This ability has presumably been enhanced by increases in social complexity in primates (Ramsier et al. 2012b). However, sensitivity to low frequencies among the earliest primates was likely not as developed as in species that evolved later in the Miocene. The advent of good low-frequency hearing made it possible to take advantage of the fact that low frequencies carry much further than high frequencies (Brown and Waser, Chap. 4). This may indicate something about the acoustic environment and the type of habitat where the Eocene primates lived.

2.5.3 Body Size, Ear Dimensions, and Hearing

Figure 2.12 shows the high- and low-frequency hearing limits for a sample of various mammals ranging in body size and taxonomic diversity. Body size plays an important role in auditory morphology (see Sects. 2.3 and 2.4), and changes in the

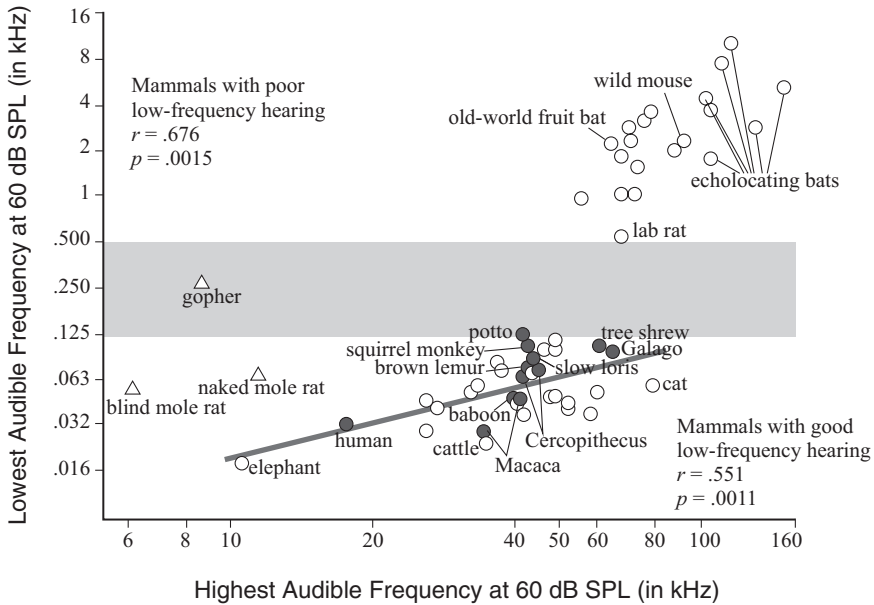


Fig. 2.12 The highest and lowest frequencies detected at 60 dB SPL by various mammalian taxa. Regarding the low-frequency hearing limits, these taxa show a distribution in two groups, with a gap between them (indicated by the *gray shading*). Primates are in the group with good low-frequency hearing, although clearly separated from subterranean species; primates have relatively good high-frequency hearing, though clearly separated from bats and rodents. *Filled circles*: primates and the tree shrew; *open circles*: selection of other mammals; *open triangles*: subterranean mammals (not included in the statistical analysis). (Reprinted with permission from R. S. Heffner 2004)

oval window area and in high-frequency sensitivity throughout primate evolution seem to be largely related to overall increases in body size. Thus, increases in body size (and head size) were likely paralleled by increases in the size of the stapes footplate. In some primate groups, the loss of the secondary bony lamina may also reflect this trend toward larger body size in mammals (together with poorer high-frequency sensitivity). However, here the relationship is less clear; the absence or presence of the secondary lamina is not strictly tied to body size (see Sect. 2.4). All primate fossils older than 30 Ma show some development of a secondary bony lamina, and this structure was already present in ancestral therian mammals (Ruf et al. 2009).

Increases in body size through time have clearly resulted in overall increases in cochlear length, but changes in body size alone cannot explain these patterns. *Plesiadapis cookei*, a fossil primate from the Paleocene, has a cochlear length of 19 mm and a body mass of more than 2 kg, whereas the extant platyrrhine owl monkey (*Aotus* sp.) has a cochlear length of 22.4 mm and a body mass of less than 1 kg. This lack of correlation might suggest that head size is a more important indicator of cochlear length than body mass, at least in some taxa.

Assessing the correlation of cochlear labyrinth volume and low- and high-frequency hearing, it was found that some differences in primate hearing between fossil strepsirrhines and haplorhines were already present by the Eocene, reflecting the differences that characterize living strepsirrhines and haplorhines today (Kirk et al. 2014; Godinot 2015). Changes in the cochlear length also reveal some interesting phylogenetic and temporal patterns in primate auditory morphology, and only the geologically youngest fossils show cochlear length values that approach those found in extant taxa.

2.6 Hearing, Sensory Ecology, and Primate Origins

Coevolution between vision and hearing is well-known among mammals (Seyfarth and Cheney 2009), and one good example of this coevolution involves the ability to localize a sound source (R. S. Heffner 2004; Ramsier and Rauschecker, Chap. 3). Auditory perception frequently initiates visual activity, and the task of localizing a sound source is to inform the visual system where to look (R. S. Heffner and H. E. Heffner 1992b; H. E. Heffner and R. S. Heffner 2016). Cooperation of eyes and ears is crucial for sound localization and shaping the map of auditory space in the brain so that it matches the neural representations of the other sensory modalities (King 1999). Vision and hearing also provide sensory input relevant for locomotion (Ankel-Simons 2007).

Nummela et al. (2013) studied hearing, vision, and olfaction in more than 100 extant mammalian species, including 6 strepsirrhine and 12 haplorhine primates, by measuring functionally relevant structures (tympanic membrane area, vertical eye orbit diameter, and cribriform plate area) and normalizing them to body mass. The primate taxa included show variations in ecological niche, diet, and body mass. The results indicate coevolution between vision and hearing in both arboreal and terrestrial species, corroborating the general mammalian pattern that animals with large eyes (in relation to body size) tend to have large ears, too. For both arboreal and terrestrial groups there seems to be a trade-off between vision and olfaction and, similarly, between hearing and olfaction. In other words, eyes and ears relate to noses in a similar way, although arboreal mammals do tend to have larger eyes and smaller noses than terrestrial mammals. Thus, there is cooperation between vision and hearing in primates, but a trade-off exists between vision and hearing on the one hand and olfaction on the other (Nummela et al. 2013).

This question of trade-offs between different sensory modalities is related to primate origins and phylogeny (Ross and Kay 2004; Silcox et al. 2015), since primate sensory biology forms part of most theories of primate origins (Sayers 2015). The *arboreal hypothesis* of primate origins holds that the grasping abilities, visual adaptation of stereoscopic vision, and brain characteristics arose in response to life in the trees. However, there are animals that show that arboreality clearly predates the rise of primates, including colugos (Dermoptera) and tree shrews (Scandentia), the two closest relatives of primates (Sayers 2015; Silcox et al. 2015).

The *visual predation hypothesis* of primate origins states that certain anatomical features indicate that the initial evolutionary divergence of primates involved a specialization for visual predation on insects (Cartmill 1974). This emphasis was challenged by studies on nocturnal primates that did not support the visual predation theory since many living nocturnal primates are not specialized in feeding on insects (Zimmermann, Chap. 5). The earliest primates most likely did not solely consume insects either, but rather shifted the focus of their diet away from insect predation in favor of flowering plants. Insects are high in protein and fat but are small and thus profitable only when available in large quantities, which most likely had a role in early primate evolution (Rothman et al. 2014).

The evolution and dispersal of angiosperms (flowering plants) approximately coincided with the appearance of primates around the Paleocene-Eocene boundary (Sussman 1991; Sussman et al. 2013). The *angiosperm coevolution hypothesis* of primate origins holds that the grasping and visual adaptations of primates came to be useful when reaching for terminal branches and the flowers, fruits, and seeds found there (Sussman and Raven 1978). It has been suggested that the diversity of angiosperm seed size and fleshy fruits commenced around 80 Ma and peaked in the Eocene around 55–50 Ma (Eriksson 2016). However, terminal branches of the flowering plants were also exploited by plesiadapiforms (a group of fossil primates) and by colugos and tree shrews, the two closest living relatives of primates. It is more likely that the coevolution with angiosperms took place across this larger group, since the increased benefits of seed dispersal would have been significant, and angiosperms also show mutualistic relationships with frugivorous birds, rodents, and bats. Of these three hypotheses of primate origins, only the visual predation hypothesis relies on good hearing, given that sound localization is one component of the ability to locate prey visually (see Sect. 2.2). The characteristics and changes in hearing abilities of primates during their (early) evolution may have provided other advantages than those directly related to feeding, for example, to sound communication within various groups and various habitats.

The multitude of resources available on the newly evolved rain forest trees probably led to the morphological adaptations seen in modern primates, while the prevalence of visual predation in extinct primates has been questioned, since living primates are typically neither specialized visual predators (Silcox et al. 2015) nor insectivores (Sussman 1991). Among extant species, the nocturnal dwarf lemurs (*Cheirogaleus* sp.), whose diet mainly consists of fruits and flowers (e.g., Mittermeier et al. 2010), have been regarded as good living models for the early primates (Sussman et al. 2013). Furthermore, olfaction and hearing are emphasized over vision as methods of capturing prey among many primates, and the lorises, “...the most orbitally convergent primates...” (p. 1057 in Silcox et al. 2015), use scent to detect their slow-moving and often smelly prey (Sussman et al. 2013).

Based on its relatively small orbit size, an early primate from the Eocene in Asia, *Teilhardina asiatica*, was suggested to be diurnal, leading to the argument that the last common ancestor of strepsirrhines and haplorhines would have been a diurnal, visually oriented, insectivorous predator (Ni et al. 2004). While orbit size is a reasonable proxy for visual activity pattern, ancestral primates may have shown only

moderate enlargement of their eye orbits due to the small eyes of their early mammalian ancestors. Some Eocene strepsirrhines did have much smaller orbits than modern diurnal lemurs, but the brain in early primates was also less than half the size of the brains of their modern relatives, suggesting a lower capacity to process sensory information, including visual input (Martin 2004). Furthermore, the markedly larger infraorbital foramen of *T. asiatica* compared to modern primates (large in primitive nocturnal mammals, typically reduced in diurnal mammals) suggests nonvisual orientation by well-developed tactile whiskers.

Based on evidence from other stem primates (Silcox et al. 2009), the increased brain size that is characteristic of living primates (relative to other mammalian orders) evolved within the Euprimates rather than in the basal primate ancestor. This increase in brain size is associated with an increase in the cochlear labyrinth volume (Kirk 2006) along with specializations in other sensory systems, including vision (Hall et al. 2012).

Like brain size, the size of a sensory organ is under conflicting evolutionary pressures. Increases in size of the sensory organs lead to increased sensitivity and improves the signal-to-noise ratio, but a larger sensory organ also necessitates increased metabolic investment from the organism. Body size correlates with many important aspects of biology, and evolutionary changes in body size can have important implications for life style and adaptations, as well as for the accomplishments of the sensory systems of an animal. Primates appear to have undergone a rapid increase in body size early in the evolution of the primate order (Cooper and Purvis 2010). There are also indications of independent evolution of brain size and cerebral organization between Old World monkeys and hominoids (Gonzales et al. 2015). Combining these data with more knowledge from auditory systems will help build an integrated view of the evolution of hearing in mammals, and in primates.

2.7 Conclusions

The primate peripheral auditory organ resembles that of other terrestrial mammals both anatomically and functionally, and hearing sensitivity in primates often follows phylogenetic patterns (Ramsier and Rauschecker, Chap. 3). Low-frequency sensitivity is better in monkeys and apes than in lemurs and lorises, and within the haplorhines, catarrhines (Old World monkeys and apes) are more sensitive to lower frequencies than are platyrrhines (New World monkeys). High-frequency sensitivity is reduced in apes compared with monkeys, and the best high-frequency hearing among the extant primates tested has been found in lemurs and lorises. The audiograms of monkeys and apes (except humans) often show two peaks of maximum sensitivity, whereas lemurs and lorises (and humans) generally have only a single peak sensitivity in their audiograms.

It is evident that hearing in primates evolved through several stages during the first half of the Cenozoic Era (Ramsier and Quam, Chap. 1). The hearing pattern in the ancestors of primates was characterized by good high-frequency hearing but

relatively poor low-frequency sensitivity. The primitive condition for primates is thought to be nocturnality. The morphological variation of the oval window area, the development of the bony lamina of the cochlea, and the cochlear length can be determined from primate species that extend from 60 Ma to recent times using CT. Low-frequency and high-frequency hearing thresholds for fossil primates can be predicted based on comparisons between morphological auditory data from fossil and modern species and experimental data on modern primate hearing.

Plesiadapiforms are fossil stem primates that lived in North America and Europe 60–54 Ma. They were characterized by a small oval window and a relatively short cochlea that housed moderate- to well-developed secondary bony laminae. These traits suggest that plesiadapiforms had good high-frequency hearing but relatively poor low-frequency hearing, perhaps intermediate between extant strepsirrhines and primitive living mammals like tree shrews and hedgehogs (Ravizza et al. 1969).

Indeed, the origin of strepsirrhines and haplorhines, the two major taxonomic groupings in extant primates (appearing 50–35 Ma), is marked by an increase in cochlear length and reduction of the secondary bony lamina. This suggests that low-frequency hearing sensitivity increased and high-frequency sensitivity decreased modestly. Based on a few fossil primate taxa, the strepsirrhine hearing pattern first emerged during the Eocene (about 50 Ma), or perhaps even in the late Cretaceous, based on molecular evidence (Springer et al. 2003; Steiper and Seiffert 2012).

Cochlear elongation and the reduction (or loss) of secondary bony laminae continued in haplorhines. Evidence from early haplorhines in North America and Europe suggests that cochlear elongation might have taken place independently in haplorhines and strepsirrhines relative to the basal primate condition. Unlike other haplorhines, tarsiers retained the secondary bony spiral lamina, an ancestral feature in their inner ear. Evidence from fossil catarrhines (Old World Monkeys) in Africa and fossil platyrrhines (New World Monkeys) in South America suggests that the cochlear elongation process was completed by the early Miocene (about 25 Ma), and fossil platyrrhine taxa share many auditory characteristics with modern species.

It is evident that primates had developed low-frequency hearing, similar to that of modern forms, around this same time, and both the low-frequency and high-frequency sensitivity of fossil platyrrhines was likely very similar to living species. These data are in accordance with the idea that a few characteristics of fossil platyrrhines are retained in their modern descendants. Given that the fossil taxa studied most likely are not directly ancestral to any extant platyrrhine species, good low-frequency hearing, and perhaps good high-frequency hearing, dates back at least 20 Ma.

The potential for good high-frequency hearing in the early mammals and the nocturnal bottleneck in the early Cenozoic together suggest that the earliest primates already had good high-frequency sensitivity. If the earliest primates had good high-frequency hearing, their low-frequency hearing was most likely poorer than later Miocene species. Increased low-frequency hearing may have been advantageous for long-distance communication since low frequencies can travel much longer distances than high frequencies without degrading. This may also reveal something about the acoustic environment and the type of habitat that the earliest Cenozoic primates occupied.

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Compliance with Ethics Requirements

Sirpa Nummela declares that she has no conflict of interest.

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