

How a Frog Hears

Andrea Megela Simmons and Darlene R. Ketten

Introduction

Anuran amphibians (frog and toads: see amphibiaweb.org) are key hearing model organisms. Most anurans are highly soniferous, their croaks and calls often heralding the onset of spring in temperate zones and the rainy season in tropical zones (see mister-toad.com/frogcalls.html). During their breeding seasons, males produce prolonged, loud (to humans) advertisement calls to attract females and to announce their location, size, and status to rival males. Acoustic features of advertisement calls are critical for maintaining reproductive isolation between species. Other important calls in the frog's vocal repertoire include aggressive calls, distress calls, and female courtship calls.

In addition to the significant role of hearing for species identification and reproduction, anurans are important bioacoustic models because of what they tell us about the evolution and development of hearing. The middle ear varies considerably across species, related to habitat (aquatic vs. terrestrial) and to evolutionary "age." The frog's inner ear evolved three separate organs that are

sensitive to sounds, making this ear unique among terrestrial vertebrates. The frog's ear is also a model for understanding how genetic and environmental factors may affect hearing (Horowitz et al., 2005). About three-fourths of the approximately 6,000 anuran species undergo metamorphosis, a developmental phenomenon in which the wholly aquatic larval tadpole transforms, in a matter of weeks or months, into a terrestrial frog. For these species, metamorphosis features a switch in sound processing as the ear transforms from adapted to hearing in water to adapted to hearing in air. Understanding metamorphosis is important for understanding the mechanisms regulating growth and development as well as how organisms respond to changing environments (Simmons, 2019).

In this review, we discuss the structure and function of the anuran ear in both its mature form and across larval development.

Frogs Lack External Ears

Anurans do not have pinnae, which are the outer ear "flaps" we commonly think of as ears. Instead, the external

Figure 1. Three-dimensional (3D) reconstructions of microCT images (Zeiss XRadia Versa 520, RadiAnt version 2020.1.1) of an adult female bullfrog. **A:** dorsal view of external surface of the head, showing the two tympana (t). **B:** ventral view of right ear showing extracolumella (ec) extending from the medial surface of the tympanum (t) to the columella (c). **C:** posterior view of right ear middle and inner ear structures showing outer edge of tympanum (t), columella (c), and saccular otoconia (o). Videos of the original scans through the head and a 3D rotating reconstruction in which tissues are "digitally dissected" to gradually reveal tissues from the outer ear through the middle ear can be viewed at acousticstoday/simmonsmedia). Images and multimedia used with permission, copyright © 2020 D. R. Ketten, all rights reserved.

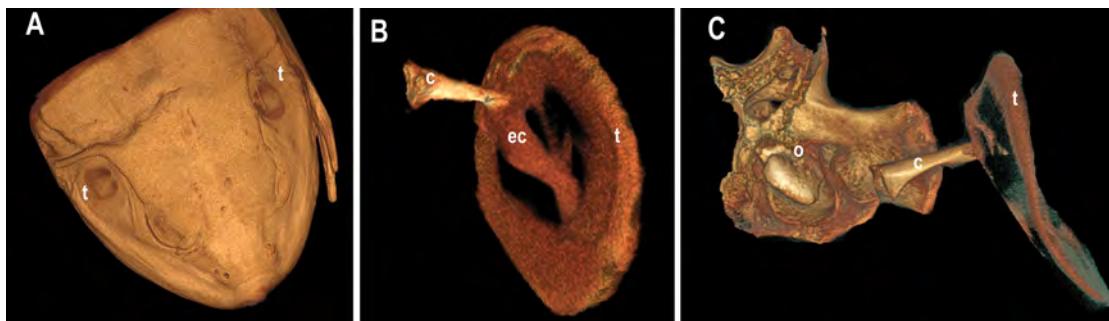
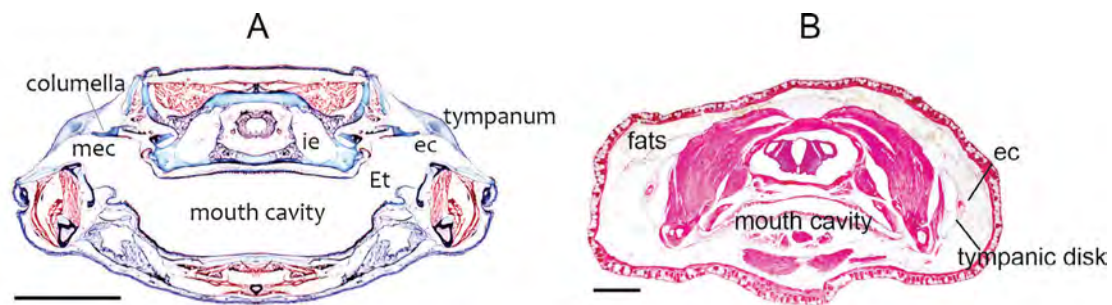


Figure 2. Histological cross (vertical) section through the head of an adult bullfrog (A) and an adult tropical clawed frog *Xenopus tropicalis* (B). In A, shades of red indicate muscle and shades of blue indicate collagen/cartilage. In B, shades of red indicate collagen/cartilage and muscle fibers. Scale bars: 1,000 μm (A); 500 μm (B). Et, Eustachian tube; ec, extracolumella; ie, inner ear; mec, middle ear cavity. Images used with permission, copyright © 2020 A. M. Simmons, all rights reserved.



mark of the ear, if present, is the tympanum (eardrum). A top-down view of the head of a female bullfrog, *Rana catesbeiana*, shows the two external tympana (**Figure 1A** and **2A**). Each tympanum is a thin membrane surrounded by a cartilage ring, the tympanic annulus, that is visible on the skin just behind the eye. In bullfrogs, the male's tympanum is about 50% larger than the female's, even adjusting for body size. The male's tympanum vibrates best at frequencies around 200 Hz, within the range of the low-frequency energy in the bullfrog's advertisement call but also radiates the high-frequency energy in the call. How this might work is discussed by Mason (2007).

Some anuran species, like the fully aquatic adult *Xenopus* frogs, lack a conventional external tympanum (**Figure 2B**), but they do hear and they do vocalize. We discuss the ways by which frogs with and without tympana can detect sounds.

Frogs Have Several Middle Ear Transmission Pathways

Tympanic Pathway

In the anuran's tympanic pathway, similar to the mammal's (Manley et al., 2018; Puria, 2020), vibrations of the external tympanum are transmitted through an air-filled middle ear via a set of linked middle ear structures (see Multimedia 1 and 2 at acousticstoday.org/simmonsmedia). This set of structures in anurans is called the extracolumella and the columella (**Figure 1, B** and **C**). The extracolumella is a rod-shaped piece of cartilage connected to the internal surface of the tympanum (**Figure 1B**) and then joined medially to the bony columella at an angle (**Figures 1C**

and **2A**). The other end of the columella (the footplate) inserts into the bony otic capsule at a membrane called the oval window. The extracolumella and columella function as a lever to increase the acoustic power at the inner ear, analogous to the operation of the three middle ear bones in the mammalian ear (see *Acoustics Today* article by Puria, 2020). Because the extracolumella is cartilaginous rather than bony, it is not very effective in transmitting high-frequency sounds. In most anurans, the high-frequency limit of hearing lies below 8,000 Hz, but there are exceptions.

The middle ear cavity opens into the mouth cavity via the wide Eustachian tubes (**Figure 2A**), which are permanently open in most frogs. This provides a wide path of communication between the two ears, the mouth, and the lungs. The consequence is that incoming sounds can strike both the inside and the outside of the tympanum but with unequal pressures. This is an example of a pressure-gradient receiver (Mason, 2007). Pressure-gradient receivers are inherently directional because of the differences in pressure between the inside and outside of the tympanum. For frogs with their small heads and poor sensitivity to high frequencies, this kind of receiver can improve their ability to localize sounds.

Some unique frogs, such as the concave-eared torrent frog *Odorrana tormota*, produce advertisement calls that include energy extending into the ultrasonic range (Feng et al., 2006). Torrent frogs live in rapidly flowing streams in mountainous areas of southeast Asia in habitats containing considerable

broadband, predominantly low-frequency noise. The use of ultrasound allows these frogs to exploit a relatively silent acoustic niche. Ears of male torrent frogs show some modifications of the tympanic pathway that facilitate detection of high frequencies. These modifications include a very thin and recessed tympanum, a short external ear canal, and a short, low-mass extracolumella and columella (Feng et al., 2006). The tympana of female torrent frogs are larger and thicker than that of males and vibrate best in response to lower frequencies (Shen et al., 2011). These anatomical differences suggest that females are primarily listening for the nonultrasonic frequencies in the male's advertisement calls, whereas males may use ultrasonic frequencies in territorial interactions.

Fully aquatic *Xenopus* frogs detect sounds via a cartilaginous tympanic disk that lies below the fatty tissue and skin behind the eye (Figure 2B). The tympanic disk is larger in males than in females, even correcting

for body size (Mason et al., 2009). The tympanic disk including its extracolumella is coupled to the columella through an air-filled middle ear cavity. As in the bullfrog ear, this middle ear apparatus acts like a lever to increase force on the oval window. In *Xenopus*, vibrations of the tympanic disk produce comparatively larger vibrations of the footplate of the columella than those observed in bullfrogs (Mason et al., 2009). These larger vibrations may be an adaptation for underwater hearing.

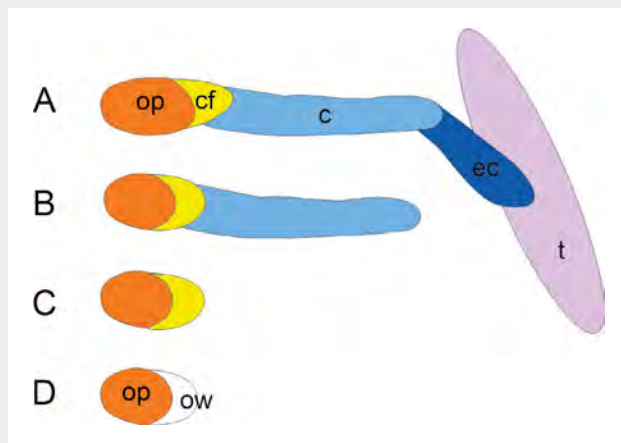
Extratympanic Pathways

Aside from the tympanic pathway, several "extratympanic" (not involving the tympanum) routes to the inner ear have been identified. These include transmission via the operculum (Figure 3), the lungs, the mouth cavity, and through bone conduction via the skull. Extratympanic sources of input do not always act independently from each other or from the tympanic pathway, and how these multiple transmission pathways interact is still being studied.

In evolutionary time, extratympanic pathways are older than the tympanic pathway (Christensen-Dalsgaard and Manley, 2013). Extratympanic pathways are also more enduring, being present in one form or another in all living frogs. These pathways provide good sensitivity to low-frequency sounds and vibrations. On the other hand, many anurans do not have a tympanum or even a middle ear cavity. There are, for example, about 200 species of "earless" toads (Pereyra et al., 2016). Earless and eared toads (Bufonids) have similar hearing sensitivities at low frequencies (<1,000 Hz), but eared toads hear better at high frequencies (Womack et al., 2017). This suggests that the pressure for evolution of the tympanic pathway was to extend the species' audible range.

The operculum (Figure 3) is a structure unique to the anuran ear. It consists a piece of cartilage located at one end of the oval window; the footplate of the columella is located at the other end (Figure 3C). The operculum may have several important functions in hearing (Mason, 2007). In earless species without a columella, the operculum provides an essential route of transmission to the inner ear. In both earless and eared frogs, the operculum may improve detection of low-frequency vibrations via its attachment to the opercularis muscle and then to the shoulder girdle. A frog sitting on the ground or in a tree could pick up seismic vibrations with its forelimbs; these vibrations are transmitted to

Figure 3. Schematics of the middle ear apparatus in an adult terrestrial frog (A) and at progressively earlier stages of development: B: at the end of metamorphosis; both hind and fore limbs are present; C: tadpole with hind limbs but fore limbs still emerging; D: before development of hind limbs. Schematic in A shows all components of the tympanic pathway from the oval window to the external tympanum. op, Operculum; cf, columella footplate; c, columella; ec, extracolumella; t, external tympanum; ow, oval window. Schematic in A redrawn from Christensen-Dalsgaard and Manley, 2013; schematics in B-D based on data from bullfrog tadpoles from Horowitz et al., 2001; Simmons, 2019. Images used with permission, copyright © 2020 A. M. Simmons, all rights reserved.



the shoulder girdle, to the opercularis muscle, to the operculum, and finally to the inner ear. Action of the operculum and opercularis muscle may also protect the ear from damage during respiration and vocalization by shunting vibrations away from the inner ear. Vibrations of the operculum and the footplate are coupled, but how this coupling affects the hypothesized functions of the operculum is not well understood (Mason, 2007).

Frogs can also detect sounds using their lungs in a manner that is analogous to the use of the swim bladder in bony fishes (Popper and Hawkins, 2018). Narins et al. (1988) demonstrated that an area of the lateral body wall overlying the lungs of the Puerto Rican coqui frog *Eleutherodactylus coqui* vibrates in response to airborne sound. When sound waves hit this region, the resulting vibrations are funneled through the lungs and glottis to the mouth cavity, Eustachian tubes, and middle ear cavity to the oval window. Many earless species rely on the lung pathway to detect sounds (Mason, 2007).

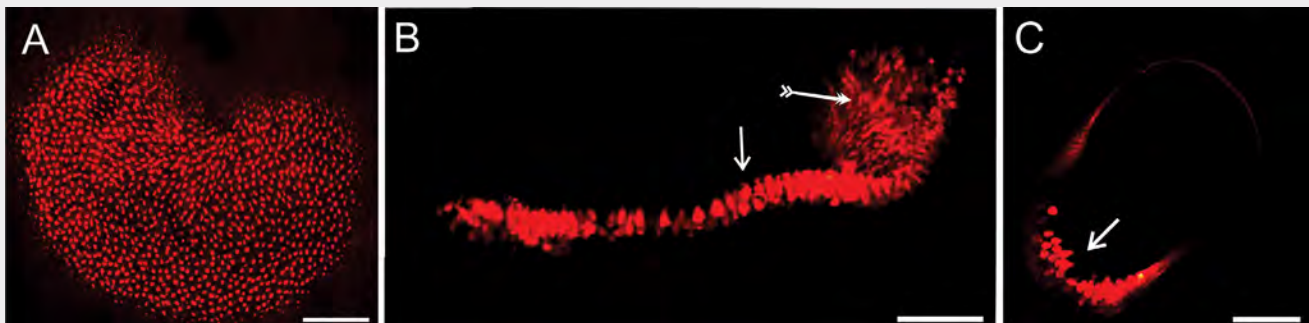
Bone conduction is also an important transmission pathway. Gardiner's Seychelles frog (*Sechellophryne gardineri*) is a small animal lacking a middle ear cavity and a columella. It has poorly developed lungs and an ossified operculum; still, it responds to sounds and it produces advertisement calls (Boistel et al., 2013). The mouth cavity of this frog resonates at around 5,700 Hz, a spectral peak in the male's advertisement call. This resonance is transmitted to the inner ear through bone conduction (Boistel et al., 2013).

The Unique Frog Inner Ear

Unlike mammals (Puria, 2020), the inner ear of frogs does not include a cochlea. Instead, their inner ear contains three organs that respond to sound: the saccule, the amphibian papilla, and the basilar papilla (Figure 4). Each of these organs is located in a separate chamber within the otic capsule and is innervated by separate branches of the eighth cranial nerve (Simmons et al., 2007). The saccule is similar to the hearing organ in bony fishes (Popper and Hawkins, 2018), whereas the joint presence of an amphibian and a basilar papilla is unique to anurans. The relationship between response properties of eighth nerve fibers innervating the two papillae and the frequency composition of vocalizations motivated the proposal that the frog's inner ear is specialized for detecting spectral peaks in the species advertisement call (Capranica and Moffat, 1983).

The saccule detects low-frequency sounds and vibrations. Its location in the otic capsule is shown in Figure 1C. Sensory hair cells in the saccule are arranged along a flat, kidney-shaped area (Figure 4A) covered by otoconia, a gelatinous mass packed with calcium carbonate crystals. This mass is key to the operation of the saccule as an inertial accelerometer, restricting saccular sensitivity to low frequencies (20-300 Hz). In the white-lipped frog (*Leptodactylus albilabris*), some eighth nerve fibers innervating the saccule respond to accelerations as low as 0.001 cm/s² (displacements of 10 Å; Narins and Lewis, 1984). Thus, the saccule is extremely sensitive to seismic cues, which might signal predators or prey.

Figure 4. Fluorescent microscopy images of the three auditory organs in the inner ear of bullfrog tadpoles. Inner ear organs were stained with a marker for sensory hair cells that fluoresce bright red. Images show tadpole organs, but shapes and relative sizes are similar to those in adults. **A:** kidney-shaped saccule; **B:** amphibian papilla, showing the long tail (left arrow), with the shorter club region on the right (right arrow); **C:** cup-shaped basilar papilla; arrow points to hair cells. All scale bars, 100 μm. Images used with permission, copyright © 2020 A. M. Simmons, all rights reserved.



The uniqueness of the amphibian and basilar papillae lies in the absence of a basilar membrane and the largely nonoverlapping range of sound frequencies processed by these two organs. In both papillae, the sensory hair cells lie on a fixed tissue support and extend their hairs toward an overlying tectorial membrane (Simmons et al., 2007). The absence of a basilar membrane means that there is no shearing force generated by differential movement between two flexible membranes as in mammals (Manley et al., 2018); instead, shearing action occurs between the fixed tissue support and the tectorial membrane. This mechanical difference, along with the differences in the tympanic pathway, contributes to the overall weaker sensitivity of the anuran compared with the mammalian ear.

The amphibian papilla (**Figure 4B**) is larger than the basilar papilla (**Figure 4C**), and it varies in size and shape across different anuran species (Lewis, 1981). In the earless Pacific tailed frog (*Ascaphus truei*), the amphibian papilla consists of one club-shaped region of sensory hair cells (**Figure 5**). In eared frogs, the amphibian papilla has two contiguous regions, a club-shaped patch and a longer, curved tail. There is considerable species diversity in the shape and length of the tail (**Figure 5**). Even accounting for body size, species with a longer tail hear a broader range of sound frequencies than those with only the club-shaped region. Lewis (1981) proposed that the tail elongated under selective pressure to extend the range of hearing to higher frequencies.

The amphibian papilla is organized tonotopically. Low frequencies (<300 Hz) are represented in the club-shaped region, and higher frequencies (up to about 2,000 Hz in the bullfrog) are represented progressively further along the tail (Lewis et al., 1982). Thus, this organ is sensitive to a wide range of sound frequencies, those found both in communication calls and in signals from other sources (predators, abiotic sounds).

The basilar papilla (**Figure 4C**) is a small cup-shaped organ with a similar shape in all species. In ultrasound-detecting frogs, it is reduced in size, with a lower mass tectorial membrane and shorter, stiffer hairs on the sensory cells (Arch et al., 2012). In contrast to the amphibian papilla, the basilar papilla is not tonotopically organized. Instead, eighth nerve fibers innervating this organ all respond best to (are tuned to) the same restricted range of high frequencies. Thus, the basilar

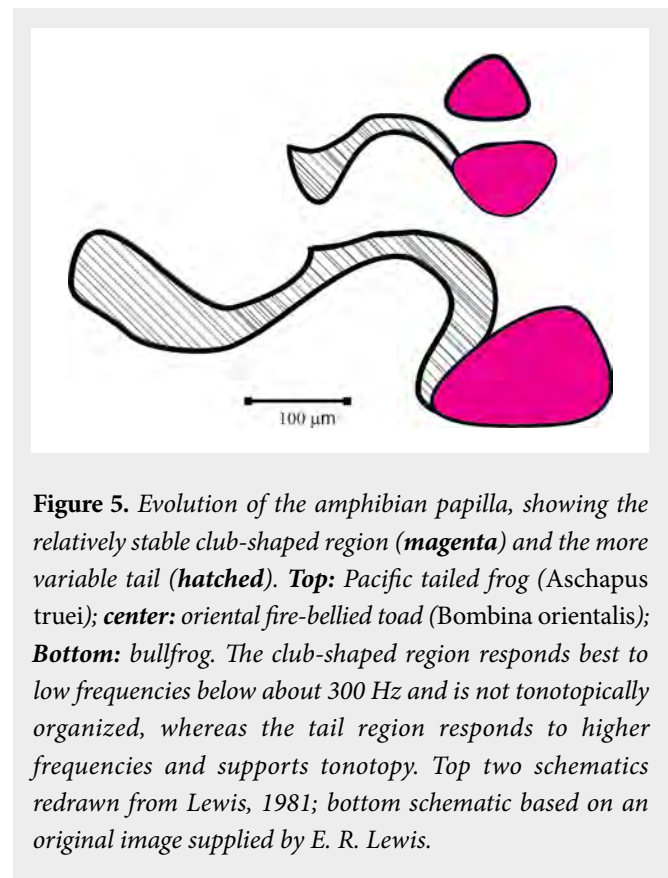


Figure 5. Evolution of the amphibian papilla, showing the relatively stable club-shaped region (magenta) and the more variable tail (hatched). **Top:** Pacific tailed frog (*Ascaphus truei*); **center:** oriental fire-bellied toad (*Bombina orientalis*); **Bottom:** bullfrog. The club-shaped region responds best to low frequencies below about 300 Hz and is not tonotopically organized, whereas the tail region responds to higher frequencies and supports tonotopy. Top two schematics redrawn from Lewis, 1981; bottom schematic based on an original image supplied by E. R. Lewis.

papilla operates as a simple resonator (Simmons et al., 2007). Unlike that of the amphibian papilla, the tuning of the basilar papilla is species specific in a high-frequency range (Capranica and Moffat, 1983). For example, the male bullfrog’s advertisement call contains maximal energy in two frequency ranges, a low-frequency range around 200 Hz and a higher frequency range around 1,400 Hz. The bullfrog’s amphibian papilla is tuned to frequencies between 100 and 1,000 Hz, whereas the basilar papilla is tuned to frequencies around 1,400 Hz (Lewis et al., 1982). The advertisement call of the Puerto Rican coqui frog consists of two tones, a “co” note at 1,100 Hz and a “qui” note with energy between 1,800 and 2,400 Hz. The amphibian papilla and the basilar papilla in this frog are tuned to these two nonoverlapping frequency ranges (Narins and Capranica, 1976).

In some frogs, the frequency sensitivity of the basilar papilla varies with the sex of the animal. In the Puerto Rican coqui frog, nerve fibers innervating the female’s basilar papilla are tightly tuned to the frequencies in the male’s qui note (around 2,100 Hz), whereas the male’s basilar papilla is more broadly tuned between 2,000 and 3,500 Hz, extending

outside the range of the qui note. These sex differences reflect the function of the qui note in attracting females to the male for mating (Narins and Capranica, 1976).

Tadpoles Hear Through Extratympanic Routes

Tadpole metamorphosis features remarkable changes in body morphology: first the hind limbs then the fore limbs emerge, the tail is absorbed into the body, and the small tadpole oral disk transforms into the large frog mouth (see bit.ly/3hrjF8w). In species such as the bullfrog where an aquatic tadpole transforms into a terrestrial frog, the metamorphic transition impacts how sounds are processed because of the different acoustic properties of underwater and terrestrial environments (Popper and Hawkins, 2018). To prepare for the new terrestrial soundscape, the ability to hear airborne sounds should emerge prior to the final emergence to land. Hence, we expect considerable maturation of hearing capabilities before metamorphosis is complete.

Ear development in terrestrial frogs follows an inside-out or medial-to-lateral trajectory (Simmons, 2019; Womack et al., 2016): The inner ear organs develop before the middle ear, and the middle ear develops before the external tympanum (Figure 3).

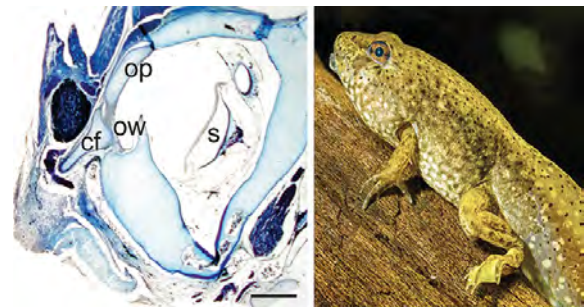
Development of the inner ear organs begins with the formation and differentiation of the saccule, followed by that of the amphibian and basilar papillae (Simmons and Alexander, 2014). These three organs all have the same shape in tadpoles (Figure 4) as they do in adults, but they are smaller and contain fewer hair cells. Developmental changes in hair cell numbers and in numbers of eighth nerve fibers innervating these hair cells have been quantified for the saccule (Simmons and Alexander, 2014), but little is known about these events in the two auditory papillae.

The in-outside developmental trajectory from the inner ear to the external tympanum is illustrated in Figure 3. The oval window is present in the otic capsule early in tadpole life, right after hatching. Around the time of emergence of the hind limbs, the operculum becomes visible at one end of the oval window (Figure 3D; Hetherington, 1987; Horowitz et al., 2001). Later, around the time that the tadpole develops its fore limbs, opercularis muscle fibers can be seen inserting into the operculum (Hetherington, 1987). Thus, the operculum transmission pathway is functional

before metamorphosis is complete. Although tadpoles have lungs, the Eustachian tubes and the large mouth cavity do not appear until after the final transition to land.

The tympanic pathway, in contrast, is not fully developed until sometime after the completion of metamorphosis. In bullfrog tadpoles, the columella footplate begins to differentiate around the time of fore limb development (Figures 3C and 6). The columella is visible at the end of metamorphosis (Figure 3B). But the external tympanum (Figure 3A) does not appear until sometime after the froglet has moved to land. The time course of tympanum development varies between species, from 24 to 48 hours after the end of metamorphosis in bullfrogs (Boatright-Horowitz and Simmons, 1995) to 60 days later in spring peepers *Pseudacris crucifer* (Hetherington, 1987) and even 15 weeks later in the giant toad *Rhinella horribilis* (Womack et al., 2018). These delays in the emergence of the tympanum suggest that froglets in their terrestrial environments have poor sensitivity to airborne sounds (Womack et al., 2016). But we understand little about the role of sounds in the lives of froglets, so the biological

Figure 6. Left: horizontal section through the otic capsule of a bullfrog tadpole immediately before the completion of metamorphosis. The columella has not reached its mature length, the extracolumella has not yet begun to form, and the external tympanum is absent (see Figure 3B). Shades of blue indicate cartilage. cf, Columella footplate; ow, oval window; op, operculum; s, saccule. Medial is to the right and lateral is to the left. Scale bar, 500 μ m. Images used with permission, copyright © 2020 A. M. Simmons, all rights reserved. **Right:** bullfrog tadpole near the completion of metamorphosis. Hind limbs, fore limbs, and tail are present, but no external tympanum is visible. Photo courtesy of Nature Picture Library/Alamy stock photo, used with permission.



consequences of the delayed development of the tympanic pathway are unknown.

Our understanding of sound processing in bullfrog tadpoles is based on inferences from ear structure and on recordings of neural activity from auditory nuclei in the central nervous system. Neural responses to underwater sounds (particle motion) can be recorded in bullfrog tadpoles early in life, even before the appearance of the operculum (Simmons, 2019). These responses may originate from direct activation of saccular hair cells by sound waves passing through the body, in a “fenestral” route (Hetherington, 1987). Once the operculum has developed, all three auditory organs are likely activated by sounds, as shown by the wider range of sound frequencies that evoke good neural activity. With the appearance of the tympanum after the completion of metamorphosis, neural responses to airborne sounds become more similar to those in adults (Simmons, 2019).

“Croaking” Forward

This short review highlighted some general trends in middle and inner ear structure and function in adult and developing frogs, but our picture is incomplete. Frogs are a diverse order, with considerable variation in habitat and in the role of sounds in their lives. Much of our knowledge of frog bioacoustics is based on research on a few key species. The recent discovery of ultrasound-detecting species highlights the surprises that are waiting to be uncovered (Feng et al., 2006). Even in well-studied species, there is more to learn about the function of the operculum and the role of lung transmission. The frog middle ear can show malformations (Horowitz et al., 2005), and understanding their origins can contribute to our knowledge of developmental and environmental factors affecting hearing.

Our current view of ear development across metamorphosis is based on a small number of species. It is not clear if the developmental time course of hearing identified in bullfrog tadpoles is the same as in other species with different ear morphologies. When does the tonotopy of the amphibian papilla develop? When does transmission through the lungs emerge? What is the maturational sequence in totally aquatic frogs? Finally, we know very little about the tadpoles’ acoustic worlds. Frog bioacoustics is a rich line of research that can contribute significantly to our understanding of hearing across the life span and in response to changing environmental demands.

Acknowledgments

Work from Andrea Megela Simmons’ laboratory reviewed here has been funded by the National Institute on Deafness and Communication Disorders, National Institutes of Health, Bethesda, MD. MicroCT images were obtained with the assistance of Aaron Nakasone, Micro-CT and X-ray Microscopy Imaging Facility, Boston University, Boston, MA.

References

- Arch, V. S., Simmons, D. D., Quiñones, P. M., Feng, A. S., Jiang, J., Stuart, B. L., Shen, J.-X., Blair, C., and Narins, P. M. (2012). Inner ear morphological correlates of ultrasonic hearing in frogs. *Hearing Research* 283, 70-79.
- Boatright-Horowitz, S. S., and Simmons, A. M. (1995). Postmetamorphic changes in auditory sensitivity of the bullfrog midbrain. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology* 177, 577-590.
- Boistel, R., Aubin, T., Cloetens, P., Peyrin, F., Scotti, T., Herzog, P., Gerlach, J., Pollet, N., and Aubry, J.-F. (2013). How minute sooglossid frogs hear without a middle ear. *Proceedings of the National Academy of Sciences of the United States of America* 110(38), 15360-15364.
- Capranica, R. R., and Moffat, A. J. M. (1983). Neurobehavioral correlates of sound communication in anurans. In J.-P. Ewert, R. R. Capranica, and D. Ingle (Eds), *Advances in Vertebrate Neuroethology*. Plenum Press, New York, NY, pp. 701-730.
- Christensen-Dalsgaard, J., and Manley, G. A. (2013). The malleable middle ear. In C. Köppl, G. A. Manley, A. N. Popper, and R. R. Fay (Eds.), *Insights from Comparative Hearing Research*. Springer-Verlag, New York, NY, pp. 157-191.
- Feng, A. S., Narins, P. M., Xu, C.-H., Lin, W.-Y., Yu, Z.-L., Qiu, Q., Xu, Z.-M., and Shen, J.-X. (2006). Ultrasonic communication in frogs. *Nature* 440, 333-336.
- Hetherington, T. E. (1987). Timing of development of the middle ear of Anura. *Zoomorphology* 106, 289-300.
- Horowitz, S. S., Chapman, J. A., Kaya, U., and Simmons, A. M. (2001). Metamorphic development of the bronchial columella of the larval bullfrog (*Rana catesbeiana*). *Hearing Research* 154, 12-25.
- Horowitz, S. S., Simmons, A. M., and Ketten, D. R. (2005). Optical and tomographic imaging of a middle ear malformation in the bullfrog (*Rana catesbeiana*). *The Journal of the Acoustical Society of America* 118(2), 1166-1171.
- Lewis, E. R. (1981). Suggested evolution of tonotopic organization in the frog amphibian papilla. *Neuroscience Letters* 21(2), 131-136.
- Lewis, E. R., Baird, R. A., Leverenz, E. L., and Koyama, H. (1982). Inner ear: Dye injection reveals peripheral origins of specific sensitivities. *Science* 215(4540), 1641-1643.
- Manley, G. A., Lukashkin, A. N., Simões, P., Burwood, G. W. S., and Russell, I. J. (2018). The mammalian ear: Physics and the principles of evolution. *Acoustics Today* 14(1), 8-15.
- Mason, M. J. (2007). Pathways for sound transmission to the inner ear in amphibians. In P. M. Narins, A. S. Feng, R. R. Fay, and A. N. Popper (Eds.), *Hearing and Sound Communication in Amphibians*. Springer-Verlag, New York, NY, pp. 147-183.
- Mason, M. J., Wang, M., and Narins, P. M. (2009). Structure and function of the middle ear apparatus of the aquatic frog, *Xenopus laevis*. *Proceedings of the Institute of Acoustics* 31, 13-21.
- Narins, P. M., and Capranica, R. R. (1976). Sexual differences in the auditory system of the tree frog *Eleutherodactylus coqui*. *Science* 192, 378-380.
- Narins, P. M., and Lewis, E. R. (1984). The vertebrate ear as an exquisite seismic sensor. *The Journal of the Acoustical Society of America* 76, 1384-1387.

Narins, P. M., Ehret, G., and Tautz, J. (1988). Accessory pathway for sound transfer in a neotropical frog. *Proceedings of the National Academy of Sciences of the United States of America* 85, 1508-1512.

Pereyra, M. O., Womack, M. C., Barrioneuvo, J. S., Blotto, B. L., Baldo, D., Targino, M., Ospina-Sarria, J. J., Guayasamin, J. M., Coloma, L. A., Hoke, K. L., Grant, T., and Faivovich J. (2016). The complex evolutionary history of the tympanic middle ear in frogs and toads (Anura). *Scientific Reports* 6, 34130. <https://doi.org/10.1038/srep34130>.

Popper, A. N., and Hawkins, A. D. (2018). The importance of particle motion to fishes and invertebrates. *The Journal of the Acoustical Society of America* 143, 470-488.

Puria, S. (2020). Middle ear biomechanics: Smooth sailing. *Acoustics Today* 16(3), 27-35.

Shen, J.-X., Xu, Z. M., Yu, Z. L., Wang, S., Zheng, D. Z., and Fan, S. C. (2011). Ultrasonic frogs show extraordinary sex differences in auditory frequency sensitivity. *Nature Communications* 2, 342. <https://doi.org/10.1038/ncomms1339>.

Simmons, A. M. (2019). Tadpole bioacoustics: Sound processing across metamorphosis. *Behavioral Neuroscience* 133(6), 586-601.

Simmons, A. M., and Alexander, E. E. (2014). Development of the statoacoustic system of amphibians. In R. Romand and I. Varela-Nieto (Eds.), *Development of Auditory and Vestibular Systems*, 4th ed. Elsevier, New York, NY, pp. 370-413.

Simmons, D. D., Meenderink, S. W. F., and Vassilakis, P. N. (2007). Anatomy, physiology, and function of the auditory end-organs in the frog inner ear. In P. M. Narins, A. S. Feng, R. R. Fay, and A. N. Popper (Eds.), *Hearing and Sound Communication in Amphibians*. Springer-Verlag, New York, pp. 184-220.

Womack, M. C., Christensen-Dalsgaard, J., and Hoke, K. L. (2016). Better late than never: Effective air-borne hearing of toads delayed by late maturation of the tympanic middle ear structures. *Journal of Experimental Biology* 219(20), 3246-3252.

Womack, M. C., Christensen-Dalsgaard, J., Coloma, L. A., Chapparo, J. C., and Hoke, K. L. (2017). Earless toads sense low frequencies but miss the high notes. *Proceedings of the Royal Society B Biological Sciences* 284, 20171670. <https://doi.org/10.1098/rspb.2017.1670>.

Womack, M. C., Stynoski, J. L., Voyles, M. K., Coloma, L. A., and Hoke, K. L. (2018). Prolonged middle ear development in *Rhinella horribilis*. *Journal of Morphology* 279, 1518-1523. <https://doi.org/10.1002/jmor.20886>.

About the Authors



Andrea Megela Simmons
 Andrea_Simmons@brown.edu
 Department of Cognitive, Linguistic,
 and Psychological Sciences
 Brown University
 190 Thayer Street
 Providence, Rhode Island 02912, USA

Andrea Megela Simmons is professor of cognitive, linguistic, and psychological sciences (with a secondary appointment in neuroscience) and a member of the Carney Institute for Brain Science at Brown University, Providence, RI. She received her PhD from Harvard University, Cambridge, MA, and pursued postdoctoral work with R. R. Capranica at Cornell University, Ithaca, NY. Her research program investigates auditory physiology and perception in frogs and in echolocating bats, and she teaches courses in animal behavior, brain evolution, and human hearing. Dr. Simmons is a Fellow of the Acoustical Society of America.



Darlene Ketten
 dketten@bu.edu
 Department of
 Biomedical Engineering
 Boston University
 44 Cummington Mall
 Boston, Massachusetts 02215, USA

dketten@whoi.edu
 Biology Department
 Woods Hole Oceanographic Institution
 Woods Hole, Massachusetts 02543, USA

Darlene Ketten is a neuroethologist who employs biomedical imaging techniques to study hearing and hearing loss in terrestrial and aquatic animals. She received a BA from Washington University, St. Louis, MO; MS from MIT, Cambridge, MA; and Ph.D. from the Johns Hopkins Medical Institutions, Baltimore, MD. She is chief scientist of the Woods Hole Oceanographic Institution Computerized Scanning and Imaging Facility, Woods Hole, MA (see csi.whoi.edu) with a joint appointment as senior research scientist in the Hearing Center in Biomedical Engineering at Boston University, Boston, MA. Dr. Ketten is a Fellow of the Acoustical Society of America and the Association for the Advancement of Science.

**YOU CAN MAKE
 A DIFFERENCE**

Support the ASA Foundation:
acousticalsociety.org/acoustical-society-foundation-fund