

Ultrasound Detection in Fishes and Frogs: Discovery and Mechanisms

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1 Introduction

The frequency range of hearing in fishes and frogs historically has been thought to be confined to relatively low frequencies in comparison to mammals (Hawkins, 1981; Fay, 1988). The fishes with the greatest sensitivity and frequency bandwidth, such as the otophysans, a group of species that have a mechanical coupling between the swim bladder and inner ear, have upper frequency sensitivities below 5 kHz (Fay, 1988). Similarly for frogs, audiogram studies typically have tested only up to 4–5 kHz (Fay, 1988).

However, there have been hints of higher frequency sensitivity in some fishes and frogs. In 1982 Boyd Kynard discovered that ultrasonic sonar (about 160 kHz) caused behavioral responses in migrating *Alosa sapidissima* (Kynard & O’Leary, 1990).

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This eventually led Mann et al. (1997) to measure the audiogram of *Alosa sapidissima* and indeed confirmed that the species could detect ultrasound (US). More recently, studies of anurans with a unique canal ear morphology showed that there were ultrasonic components in their vocalizations, and that they could detect these ultrasonic call components (Narins et al., 2004; Feng et al., 2006).

This chapter reviews US detection in fishes and frogs and ultrasonic acoustic communication in frogs. Ultrasonic acoustic communication has not been found in any soniferous fish species to date. Although the evolution of US detection in these species is still a topic of study, both fishes and frogs have faced the challenge of producing very high frequency responses from systems that evolved with low-frequency sensitivity.

2 US Detection in Fish

2.1 Historical Overview of US Detection in Fish

In the early 1990s, several papers were published showing that pulsed high-frequency sounds at 110–140 kHz and with high intensities (180 dB re 1 μ Pa) were effective in deterring at least two fish species belonging to the subfamily of Alosine (shad and menhaden) from power plant intakes: *Alosa aestivalis* (Nestler et al., 1992) and *Alosa pseudoharengus* (Dunning et al., 1992). It was unclear whether the fishes detected the ultrasonic component of the emitted signals or low-frequency byproducts, but still these observations mark the beginning of the study of US detection in fish.

The first audiogram of a member of the Alosinae, the *Alosa sapidissima*, was measured using classical conditioning of heartbeat by Mann et al. (1997), who showed that this species could detect sound in the ultrasonic frequency range up to 180 kHz. The detection threshold was high in comparison to low-frequency thresholds, as the most sensitive ultrasonic frequency of 38 kHz had a threshold of 137 dB re 1 μ Pa (rms) (Mann et al., 1997, 1998) (Fig. 1).

Later behavioral and physiological studies showed that additional species belonging to the Alosinae can detect and respond to US. These include *Brevoortia patronus* (Mann et al., 2001) and two species of European shad, *Alosa fallax fallax* (Gregory et al., 2007) and *Alosa alosa* (Wilson et al., 2008). The ability to detect US appears to be limited to the subfamily of Alosinae, as it has not been found in other clupeiforme fish species in the subfamily Clupeinae, including *Clupea pallasii*, *Anchoa mitchilli*, *Harengula jaguana* (Mann et al., 2001, 2005), *Clupea harengus* (Wilson, unpublished data), or in the subfamily Dorosomatinae, including *Dorosoma petenense* (Casper and Mann, unpublished data).

It also does not appear that other fishes are able to detect US, although very few hearing studies have tested for this ability. One study conditioned *Gadus morhua* to ultrasonic pulses at 38 kHz with a threshold for detection of 204 dB

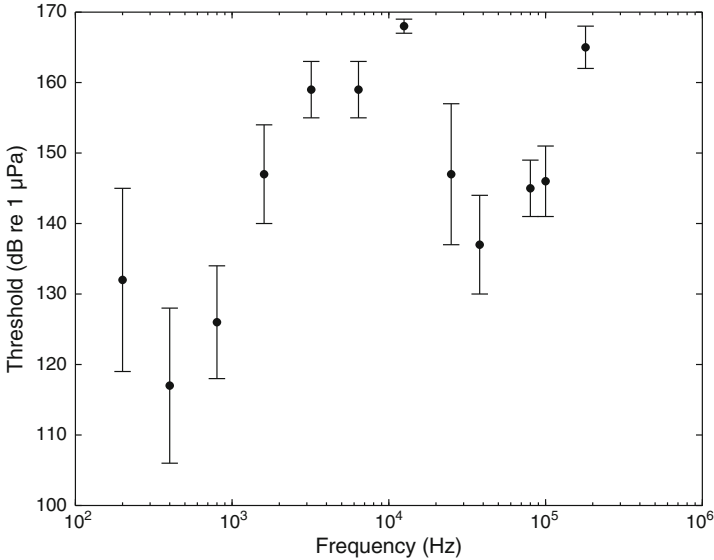


Fig. 1 Audiogram from (*Alosa sapidissima*) obtained by classical conditioning of heartbeat. Means \pm SEM from five American shad. (Modified after Mann et al., 1997, 1998.)

re 1 μ Pa (pp) (Astrup & Møhl, 1993). However, because of the very high thresholds, the authors suggested that the response might be caused by stimulation of cutaneous or other somatosensory receptors. A follow-up study by Schack et al. (2008) found that unconditioned *Gadus morhua* did not show any behavioral or physiological response when exposed to the same type of stimulus generated with the same equipment as used in the study performed by Astrup and Møhl (1993). Thus, there appears to be little evidence favoring US detection by *Gadus morhua*.

2.2 Why Detect US?

No fish species are known to produce communication sounds with ultrasonic frequency components (Bass & Ladich, 2008). Although several clupeid species have been reported to produce sound associated with gas release from the swim bladder (Wahlberg & Westerberg, 2003; Wilson et al., 2004), the frequencies produced are below 20 kHz. One of the obvious questions to ask is, then, why do Alosinae detect ultrasonic signals at all?

One of the natural ultrasonic sound sources in the aquatic environment is the top predatory toothed whales (Odontoceti) that target a broad range of both cephalopod and fish species (Clarke, 1977; Santos et al., 2001). Toothed whales use echolocation to locate and catch prey and to seek information about their surroundings

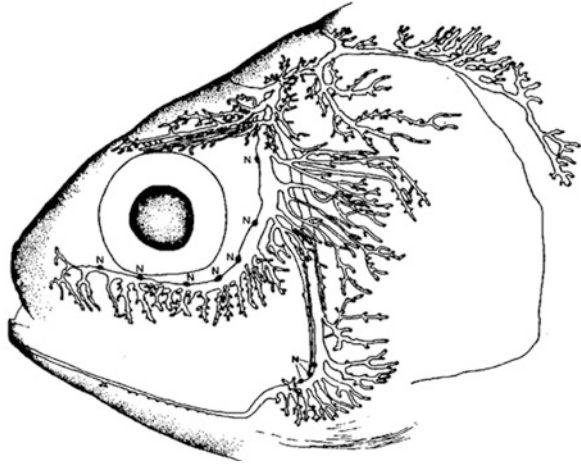
(Au, 1993; Madsen et al., 2005). The source levels of the emitted echolocation clicks can be up to 228 dB re 1 μ Pa (pp) (Au, 1993) and in the case of *Physeter macrocephalus* even up to 240 dB re 1 μ Pa (pp) (Møhl et al., 2003). These clicks travel through the water and reflect off targets, and then are detected by toothed whales (Au, 1993). Because of the very high source levels, the toothed whales loudly announce their presence for a prey that is capable of detecting US. The frequency span with the main energy of the toothed whale echolocation signals coincides with the frequency span within which the Alosinae are sensitive in the ultrasonic frequency range.

The behavioral threshold sensitivity of *Alosa sapidissima* to a simulated dolphin click was 171 dB re 1 μ Pa (pp) (Mann et al., 1998). Assuming spherical spreading and an absorption coefficient of 0.02 dB/m, the predicted detection range is 187 m for a 220 dB re 1 μ Pa (pp) dolphin click (Mann et al., 1998). It is therefore tempting to envision that Alosinae can detect US to potentially avoid or reduce predation by echolocating toothed whales.

This is analogous to a similar acoustic predator–prey interaction between bats and some nocturnal insects (Nestler et al., 1992; Mann et al., 1997; Astrup, 1999). Like toothed whales, the much smaller bats emit intense ultrasonic cries and use the echoes reflected off objects during search and capture of their prey (Griffin, 1958). The heavy predation pressure from echolocating bats is believed to be the main driving force of the parallel evolution of ultrasonic sensitive ears in several distantly related families of moths (Miller & Surlykke, 2001) and in a number of other nocturnal insects (Yack & Fullard, 1993; Hoy & Robert, 1996). When certain moths are exposed to low-intensity ultrasonic bat cries, they turn directly away from the sound source, increasing the distance to the bat (Roeder, 1962). If the bat is close, the moth will exhibit a much stronger and unpredictable flight response pattern that often ends in a power dive or passive fall toward the ground (Roeder, 1998). The different response patterns exhibited by moths indicate that they detect the direction and proximity of the predatory bat by listening to the ultrasonic bat cries.

If US sensitivity of Alosinae is used to serve as a way of detecting and avoiding echolocating toothed whales, one would expect the fish to show behaviors that might resemble those exhibited by moths when exposed to bat cries. This is indeed what playback studies conducted on *Alosa sapidissima* and *Alosa alosa* have shown. When shad are exposed to pure ultrasonic tones played at varying sound pressure levels, they exhibit a graded directional response pattern. If the sound is very intense, the fish exhibit a very strong and panic-like response, but as the sound pressure level is reduced, the response gets weaker (Plachta & Popper, 2003; Wilson et al., 2008). In a following study, *Alosa alosa* were exposed to ultrasonic clicks played at varying repetition rates mimicking toothed whales in different phases of prey capture. Toothed whales generally produce echolocation clicks at a higher repetition rate as they approach prey, and most prey capture attempts are terminated with a buzz phase where the repetition rate can be up to several hundred clicks per second (Madsen et al., 2002, 2005). When the energy for a given time is increased based on a faster click rate (but with a constant sound pressure level), the *Alosa alosa* exhibited an increase in swimming speed and decrease in reaction time.

Fig. 2 The canal lateral line (*Brevoortia tyrannus*) is restricted to the head. N, neuromasts. (From Hoss & Blaxter, 1982. Reproduced with permission.)



It was also found that the response is consistent with a predator avoidance response in that the fish turn away from the sound source (Wilson et al., 2011). Based on these playback studies, it can be concluded that Alosinae behave as if the response to US is used as an antipredatory response against echolocating toothed whales.

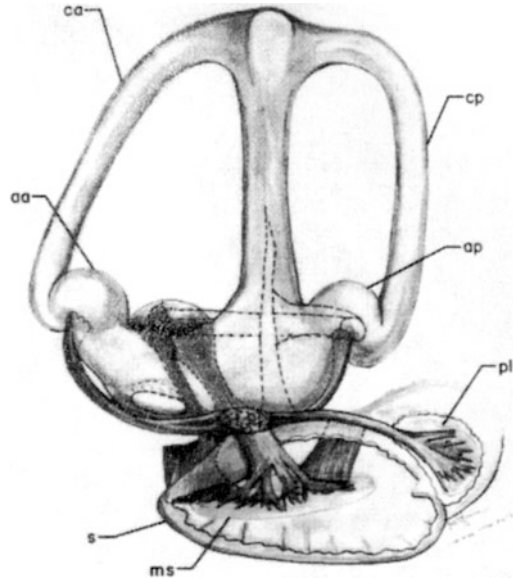
2.3 On the Mechanism of US Detection in Alosinae

During the past 15 years, the mechanism of US detection in Alosinae has been a mystery and there are different hypotheses on how they detect US. It has been suggested that the inner ear is key to US detection (Mann et al., 1998; Higgs et al., 2004; Popper et al., 2004); however, another hypothesis suggests that US detection involves the lateral line (Wilson et al., 2009).

2.3.1 The Fish Lateral Line

Fishes have a lateral line that allows them to detect weak water motions (for reviews see Coombs & Montgomery 1999; Sand & Bleckmann 2008). The sensory receptors are hair cells clustered in groups of varying numbers forming a neuromast. There are two types of neuromasts: superficial neuromasts found on the skin surface and canal neuromasts embedded in canals (Webb et al., 2008). The lateral line can be found on the head, trunk, or tail in varying patterns depending on the species. In Clupeidae, canal neuromasts are restricted to the head (Hoss & Blaxter, 1982; Blaxter et al., 1983) (Fig. 2), whereas the superficial neuromasts are found on the entire body (Higgs & Fuiman, 1996).

Fig. 3 The inner ear (*Clupea harengus*). (From Retzius, 1881.) ca, cp; anterior, and posterior semicircular canals (not shown, horizontal semicircular canal), aa, ap; anterior, and posterior cristae of semicircular canals (not shown; horizontal crista), pl, and ms; lagenar epithelium, and saccular epithelium (not shown; utricular epithelium), s; saccule



The neuromasts are detectors of fluid flow and detect movements between the fish and the surrounding water (Harris & van Bergeijk, 1962; Kalmijn, 1989). The apical parts of the hair cells are embedded in a gelatinous cupula. Stimulation of the neuromasts is by fluid motion that will make the cupula slide over the sensory epithelium, causing a deflection of the hair cell (Kroese & van Netten, 1989). The lateral line is a close-range system sensitive to low-frequency hydrodynamic motion (Sand, 1981; Kalmijn, 1989; Bleckmann, 2008) and is involved in detection of many stimuli, such as larger scale water motions, but also play an important role on a smaller scale, including self-induced motions, swimming motions created by a neighbor in schooling fish species, and predator–prey interactions (Coombs & Montgomery, 1999).

2.3.2 The Fish Inner Ear

Fish have bilateral inner ears (Retzius, 1881). Each ear consists of three semicircular canals and three otolith organs (for a detailed review see Popper et al., 2003). At the base of each canal there is a swelling, the ampulla, containing sensory hair cells on a transverse ridge (crista ampullaris). Ventral to the canals are three fluid-filled otolith organs, the utricle, saccule, and lagena. Each otolith organ contains a dense calcified ear stone, the otolith, located on a gelatinous matrix overlying the sensory epithelium (the macula) containing the hair cells (Fig. 3).

The otolith organs can be modeled as accelerometers with decreasing sensitivity above the resonance frequency of the system (Kalmijn, 1989; Sand & Karlsen, 2000). The fish body itself has almost the same acoustic impedance as water. Thus, fish are effectively acoustically transparent and move with the same phase as the surrounding water particles. However, when a fish is accelerated, hair cells are deflected because of the inertial difference between the denser otolith and the sensory epithelium in the inner ear (De Vries, 1950; Krysl et al., 2012). An unspecialized fish ear is therefore stimulated by the particle motion component of a sound field and is limited to frequencies below a few hundred Hz (Hawkins, 1981). Fish with only this direct pathway of stimulation include those without a swim bladder, such as bottom-dwelling flatfish (Chapman & Sand, 1974), or fish with a swim bladder but without a special connection between the inner ear and the swim bladder, such as salmonids (Hawkins & Johnstone, 1978).

Some fish species have developed more sensitive hearing by mechanically connecting the inner ear and the swim bladder or other gas-filled structures. These specializations make the fish sensitive to the traveling sound pressure wave of a sound field, and fish with this type of specialization can detect sound of frequencies up to 3–5 kHz and with higher sensitivity (Popper et al., 2003).

2.3.3 The Ear of Clupeids

Clupeids have a unique anatomy in which the inner ear, lateral line, and swim bladder are mechanically connected to one another via a hydrodynamic coupling. In all clupeids (both US detecting and non-US detection species), gas-filled tubes on each side of the head extend from the swim bladder and expand to gas-filled bullae that are encapsulated in bone (O'Connell, 1955).

Computed tomography (CT) scans reveal rather elaborate structures of the paired bullae (Wilson et al., 2009) (Fig. 4). All clupeids have one set of paired bullae, the prootic bullae (named after the bone structure surrounding the bullae), which is believed to be an auditory specialization (O'Connell, 1955) because it is connected to the utricle of the inner ear (Fig. 5). The utricle is highly modified in clupeids, unlike in non-clupeid fish, because it is divided into three parts: anterior, middle, and posterior (Fig. 5) (O'Connell, 1955; Popper & Platt, 1979). Each prootic bulla (the auditory bulla) is divided into two halves separated by the elastic prootic membrane (Fig. 5). The lower part is filled with gas from the swim bladder. The upper part of the prootic bulla is filled with perilymph. A slit, the fenestra, connects the upper part of the prootic bulla to the perilymph-filled space under the utricular macula. A small elastic thread passes through the fenestra and links the prootic bulla membrane to the middle part of the utricle (Popper & Platt, 1979; Best & Gray, 1980).

In many clupeids, a second pair of bullae can be found, the pterotic bullae, that are connected to the prootic bullae. They are located within the loop of the horizontal semicircular canal. The function of the pterotic bullae is not known (O'Connell, 1955).

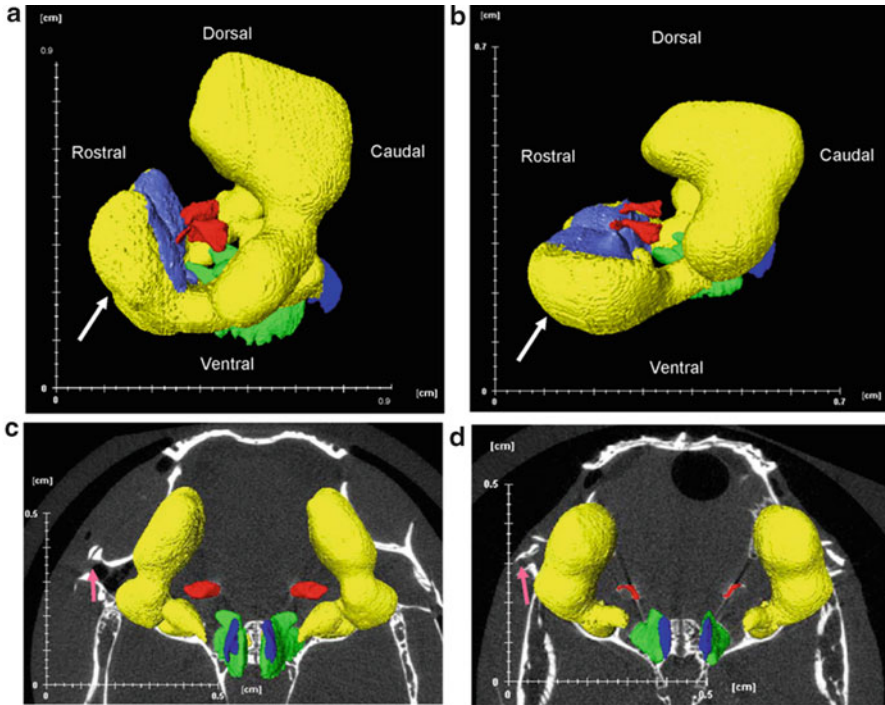


Fig. 4 The bullae complex of (*Brevoortia patronus*) and (*Harengula jaguana*). (a, b) Sagittal views of the 3D reconstructions of the bullae, bullae perilymph, and otoliths in the (a) *Harengula jaguana* and (b) *Brevoortia patronus*. (c, d) Caudal views of the 3D reconstructions in the (c) *Harengula jaguana* and (d) *Brevoortia patronus* with 2D images illustrating the positioning of the bulla and lateral recess relative to the body surface. Bulla, yellow; perilymph of bulla, light blue; utricle, red; sacculle, green; lagena, dark blue; rostral body of bulla, white arrow; approximate location of lateral recess membrane, pink arrow. (From Wilson et al., 2009. Reproduced with permission.)

The bullae are also connected to the lateral line via the lateral recess membrane. The lateral line system of clupeids is heavily branched, with primary branches radiating from the lateral recess (O'Connell, 1955; Denton & Blaxter, 1976; Hoss & Blaxter, 1982) (Fig 2). Sensory neuromasts are found only in the primary lateral line branches. The branches are connected with the surrounding water via numerous pores at the narrowing ends of the branches (Blaxter et al., 1981; Hoss & Blaxter, 1982).

Enger (1967) suggested that each bulla acts as a pressure-to-displacement converter that expands the hearing range, making clupeids able to detecting higher frequencies. When a sound pressure wave impinges on a clupeid fish, the swim bladder and the gas-filled parts of the bullae start to vibrate. Motion of the gas in the bulla presumably generate vibrations of the bulla membrane, which will produce motions of the perilymph and the elastic thread. In that way the sound pressure

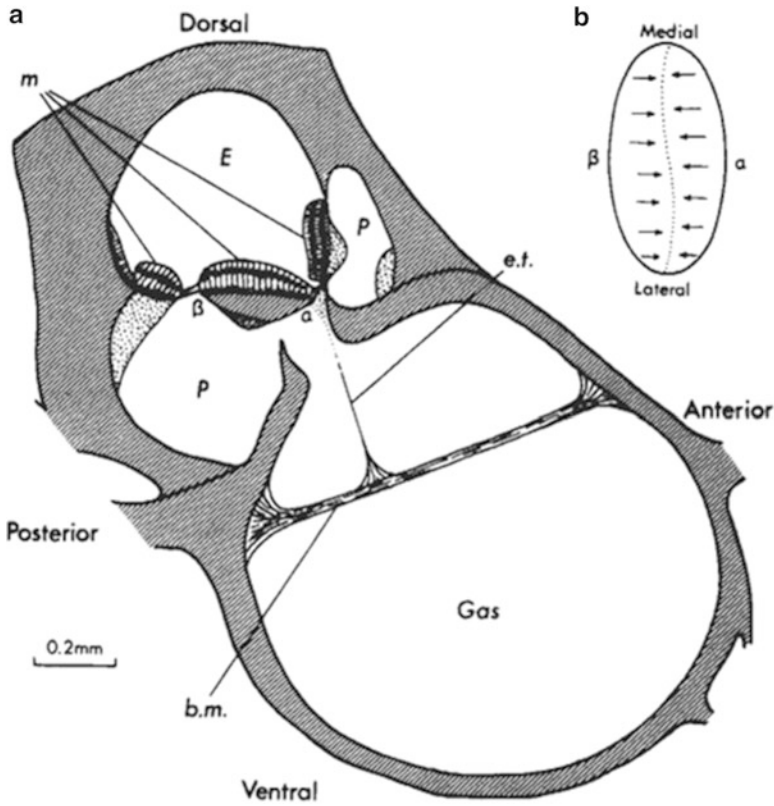


Fig. 5 Model of the prootic bulla and the coupling to the utricular macula (*a*). *bm*; bulla membrane, *et*; elastic thread, *P*; perilymph, *E*; endolymph, *m*; macula. (**b**) The macula of the utricle, showing the division into two areas, where hair cells are orientated in opposite directions. Arrows show the direction of the hair cells. (From Best & Grey 1980. Reproduced with permission.)

wave will be transformed into a local particle motion in the perilymph. This fluid motion and the movement of the elastic thread may stimulate the utricular macula, creating deflection of the hair cells in the utricle (Denton & Blaxter, 1976; Denton et al., 1979). However, the motion of the perilymph generated by the oscillating bullae has been hypothesized to also generate fluid motions in the cephalic lateral line canals because of the very compliant lateral recess membrane (Denton & Blaxter, 1976; Denton & Gray, 1983; Gray, 1984). Clupeids live in schools and the main function of the bullae complex is probably to detect pressure and displacement fluctuations in the water created by the swimming movements of neighboring fish. (Denton & Gray, 1983). It can also be reasonably hypothesized that the US detector of the Alosinae may be associated with the bullae complex.

2.3.4 The Utricle as the US Detector

The prootic bulla and its connection to the utricle has been suggested to be the key to US detection in Alosinae (Mann et al., 1998). Higgs et al. (2004) suggested that a specialization of the utricular macula could be the site for US detection. The connection between the middle part of the utricular macula and the rest of the epithelium differs between the clupeids that detect US and clupeids that do not. In the Alosinae, the support for the middle section of the utricular macula is particularly thin compared to that of other clupeids. Higgs et al. (2004) suggested that the looser connection may allow a higher sensitivity to vibrations of the bullae, leading to the suggestion that this part of the inner ear is the key to US detection in Alosinae. Further, single-unit recordings of US-sensitive neurons were made in regions of the brain typically associated with the auditory system (Plachta et al., 2004). Many of the ultrasonically sensitive neurons did not respond to sonic stimulation, which suggests that the Alosinae have a specialized processing pathway for US detection (Plachta et al., 2004). However, the hypothesis that the utricle mediates US detection has not been verified experimentally.

2.3.5 The Lateral Line as the US Detector

A recent experiment conducted on *Brevoortia patronus* revealed that the gas-filled bullae and lateral line may be involved in US detection in Alosinae (Wilson et al., 2009). Using a laser vibrometer, the authors showed that the gas-filled bulla oscillates when placed in an ultrasonic sound field. They showed that the neural response recorded as evoked potentials to US disappears when gas in the bullae was replaced with a Ringer solution, suggesting that the gas-filled bullae are the transducing element in US detection. Further, mechanical manipulation of a part of the lateral line overlying the lateral recess eliminated the ability of *Brevoortia patronus* to detect US, but did not affect detection of a 600 Hz low-frequency tone. This study showed that the lateral line is somehow involved in US detection, either via the response of sensory cells to US or via its role as a mechanical connection to the inner ear. These results add a new and surprising dimension to the role of the lateral line and the bullae in *Brevoortia patronus*, as the lateral line of fish previously has been believed to detect only low-frequency hydrodynamic stimuli (<100 Hz). Future studies on US detection in Alosinae should focus on neuroanatomy and neural recordings from the lateral line and inner ear to elucidate details of the mechanism of US detection.

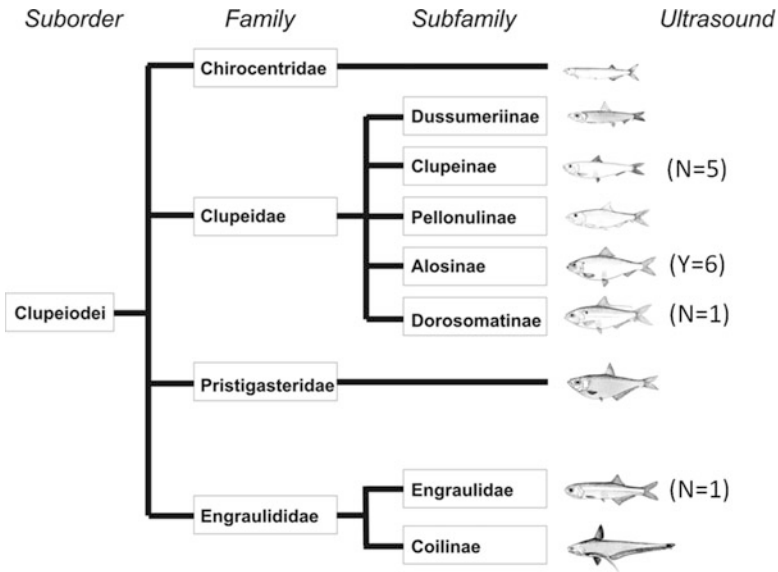


Fig. 6 Hypothesized phylogeny of the suborder Clupeoidei (A). (Modified from Whitehead et al., 1985). Y = number of species with positive responses to US; N, number of species tested that failed to respond to US

2.4 The Evolution of US Detection

Although it is generally accepted that heavy predation pressure from bats on nocturnal insects has led to the evolution of ultrasonic sensitive ears in several species of moths (Miller & Surlykke, 2001), it is less certain what has driven the evolution of US sensitivity in Alosinae. It seems reasonable to assume that the ability to detect US arose in the Alosinae in response to predation by echolocating cetaceans. However, why has it not also arisen in other clupeid fishes that share an evolutionary origin and many of the same specialized ear and lateral line structures?

The Clupeiformes are an ancient lineage and fossils are known from the Lower Cretaceous period (130 million years ago), a long time before the evolution of odontocete cetaceans in the Oligocene (25–38 million years ago). All Clupeiformes share the auditory bullae specializations of the inner ear. So, it is clear that the specialized bullae evolved before the presence of echolocating cetaceans. Because the ability to detect US has been found only in the Alosinae, and not in the closely related Clupeinae, the question becomes: When did the Alosinae evolve? Based on hypothesized phylogeny for Alosinae it was around the same time as the evolution of the echolocating river dolphins (Hamilton et al., 2001; Lavoué et al., 2007) (Fig. 6).

It is therefore tempting to envision that US detection arose in the Alosinae in response to predation from echolocating river dolphins. This hypothesis is based on the following line of reasoning:

- Most of the species in the Alosinae are found in freshwater for all of their lives (e.g., *Gadusia* spp.) or during the freshwater phase of anadromous reproduction (e.g., *Alosa* spp.). A few species, such as the menhaden (*Brevoortia* spp.), can live their entire lives in the marine environment, although juveniles have been found in rivers.
- The Alosinae are likely to be the most recently derived subfamily of the Clupeidae (Lavoué et al., 2007). Given that US detection has been found in every member of this subfamily that has been tested, it is possible that the ability to detect US evolved only once.
- The Platanistidae, river dolphins, are among the oldest lineages of echolocating odontocetes and are thought to have evolved in the early Miocene, about 23 million years ago (Hamilton et al., 2001). The extant members of the Platanistidae are found in the Indus and Ganges River systems, which are also regions of high diversity of Alosinae fishes.
- Rivers are confined areas, and river dolphins could thus present a much greater selection pressure than odontocete cetaceans in the open ocean, where fishes have many more predators that do not echolocate.

3 Ultrasonic Communication in Frogs

3.1 *Historical Overview of the Discovery of Ultra-high-Frequency Sensitivity of Frogs*

Whereas the ability of fish to detect US was discovered by observations of the behavioral responses of migrating American Shad (*Alosa sapidissima*) to ensonification by ultrasonic sonar (Section 2.1), this same capability in frogs was revealed in a completely different manner. It had been known that only two Old World frog species (out of more than 6000 anuran amphibians) possess tympanic membranes that are recessed from the head surface and form the terminus of a chamber or a tube (ear canal) much like the human outer ear: *Huia* (Inger, 1966) and *Amolops* (Zhou & Adler, 1993). It was this unusual ear morphology that sparked a field study to record the vocalizations of *Amolops tormotus* [now *Odorrana tormota* (Frost et al., 2006)] in the animals' riverine habitat in Anhui Province, China. Initial analysis of those vocalizations revealed an extremely high degree of call diversity (Feng et al., 2002), with a call repertoire larger than that of the Madagascar Rhacophoridae frog, *Boophis madagascariensis*, males of which produce 28 different call types, more than any other frog known at the time (Narins et al., 2000). In addition, although the vocalizations appeared to contain multiple

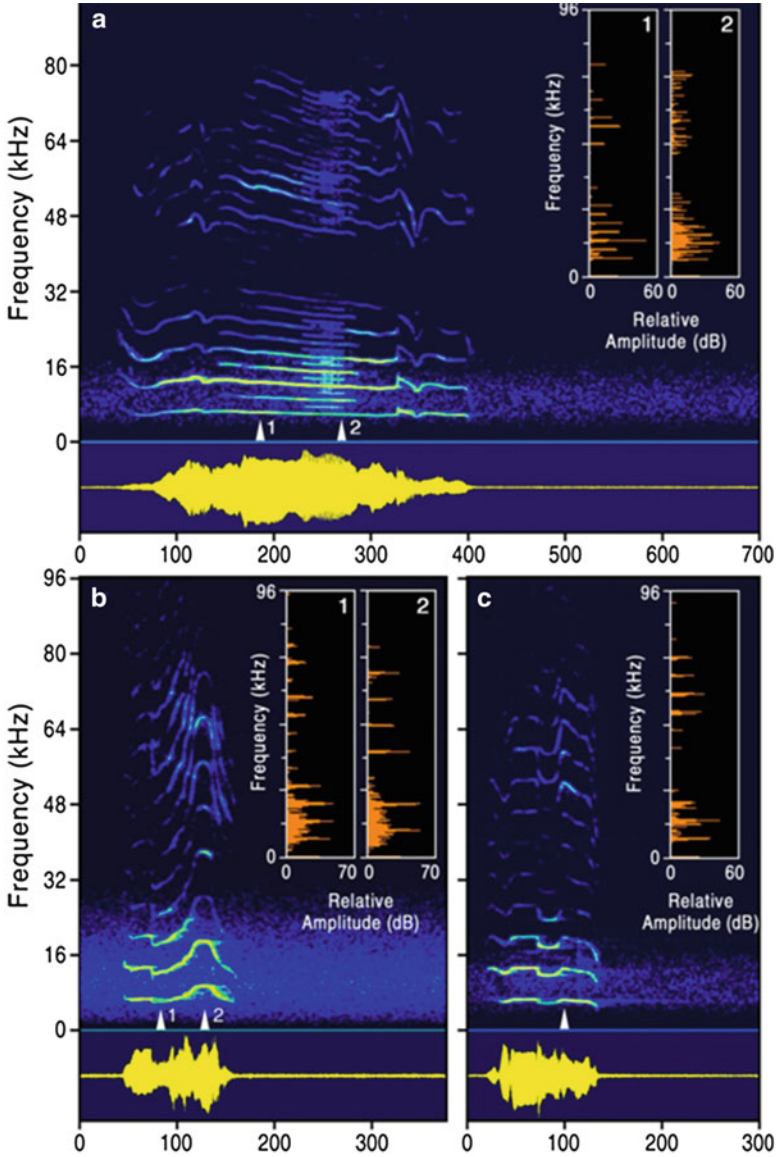


Fig. 7 Sound spectrograms (top section in each panel), waveforms (bottom section in each panel), and instantaneous amplitude spectra [insets taken at indicated points in time (arrowheads)] of vocal signals of the frog, *Odorrana tormota*, in Huangshan Hot Springs, China. **(a)** Long call, and **(b, c)** two short calls showing significant energy in the ultrasonic range and a spectral notch in the range 32–45 kHz. For all plots, dynamic range: 90 dB; temperature range during recordings: 17–18°C. (Permission has been obtained from JASA to reproduce this figure.)

examples of unusually high-frequency call components, frequency response limitations of the recording equipment precluded definitive identification of ultrasonic call components at that time. Subsequent workers, armed with ultrasonic recording gear, were able to establish unambiguously the existence of clear ultrasonic components in *Odorrana* vocalizations as high as 128 kHz (Narins et al., 2004) (Fig. 7).

Acoustic playback experiments in the animal's natural habitat revealed that calling males in the field would vigorously respond to playbacks of (a) their complete advertisement calls, (b) a high-pass filtered version of their advertisement call containing only ultrasonic call components, or (c) a low-pass filtered version of the complete advertisement call containing only audible (to humans) call components. These results, combined with auditory evoked potential (AEP) and single-unit recordings from the torus semicircularis (the amphibian homolog of the mammalian inferior colliculus in the midbrain) of anesthetized males of *O. tormota*, demonstrated the existence of both overall midbrain sensitivity to US as well as the existence of single cells in the inferior colliculus of males of *O. tormota* that reliably and repeatedly increased their spike rate to ultrasonic stimuli (Feng et al., 2006; Narins et al., 2007b). Moreover, the thickness of the tympanic membrane in males of this species is about 3–4 μm , which is about an order of magnitude thinner than that of the American bullfrog, *Rana catesbeiana*. This observation, coupled with the fact that the eardrum is recessed, resulting in a shorter, less massive ossicular chain, are now both viewed as adaptations favoring high-frequency sensitivity (Feng et al., 2006; Narins & Feng, 2007; Narins et al., 2007b).

In a parallel electrophysiological study, males of the sympatric species, *Odorrana livida* (now *Odorrana graminea*), also exhibited responses to US, although with an upper limit of sensitivity of 22 kHz, whereas males of the dark-spotted frog *Pelophylax nigromaculata* living in rice paddies were quite insensitive to frequencies above 4 kHz (Feng et al., 2006).

Subsequent field and lab studies of the Bornean hole-in-the-head frog, *Huia cavitympanum*, revealed that in addition to its recessed tympanic membranes, these animals produce vocalizations containing fundamental frequencies that can exceed the nominal upper limit of human hearing: 20 kHz (Arch et al., 2008, 2009). In other words, *Huia cavitympanum* represents the first known example of a nonmammalian vertebrate that produces a call with frequencies restricted entirely to the ultrasonic range.

3.2 Evolutionary and Environmental Constraints and Selection Pressures on Ultrasonic Signaling

Measurements of the noise energy produced by rushing water in the Tau Hua Creek in Anhui Province, PRC, revealed a high-intensity, broadband sound, with dominant energy in the low frequencies (<5 kHz) and falling off with frequency. Thus, any

frog attempting to communicate acoustically in this environment would gain an advantage by calling using frequencies above 5 kHz. Observations that the torrent frogs *O. tormota* and *O. graminea* are sensitive to US, whereas the *P. nigromaculata* that live in relatively quiet rice paddies are not, gave rise to the idea that these species have increased both their call frequencies and their upper limit of hearing as an evolutionary response to the broadband, principally low-frequency ambient noise (Feng et al., 2006; Gridi-Papp & Narins, 2009). A similar observation was reported for urban populations of Great tits (*Parus major*), which have higher (although not ultrasonic) minimum frequencies in their calls compared to rural populations of the same bird (Slabbekoorn & Peet, 2003). The shifting of echolocation call frequencies by big brown bats (*Eptesicus fuscus*) to avoid noisy echoes in cluttered environments has also been recently reported (Hiryu et al., 2010).

O. tormota exhibits another novel middle ear mechanism that is, so far, unique to this species of frog. Whereas most frogs are believed to have large, permanently open Eustachian tubes (ETs) connecting the mouth cavity to the middle ear (Chung et al., 1981; Jaslow et al., 1988; Jorgensen, 1991), *O. tormota* can actively close its ETs, drastically reducing the volume of air behind the tympanic membranes (TMs; Gridi-Papp et al., 2008). This volume reduction increases the TM stiffness and hence the ear's impedance and shifts the middle ear tuning toward high frequencies. The result is an improvement in the ear's sensitivity to high-frequency (including ultrasonic) signals at the expense of low-frequency sensitivity (Gridi-Papp et al., 2008). This remarkable mechanism is not present in *Rana pipiens*, a frog with advertisement call frequencies confined to <4 kHz (Hall & Feng, 1988), suggesting that it indeed functions as an adaptation for enhancing high-frequency communication (Gridi-Papp et al., 2008).

3.3 Case Studies

3.3.1 *Odorrana tormota* (formerly *Rana tormota* and *Amolops tormotus*)

This species has been the most extensively studied of all ultrasonically communicating amphibians to date. It is an arboreal frog in the family Ranidae restricted in its distribution to Anhui and Zhejiang provinces in central China (Fei et al., 2010). Males of this species call nightly from the low vegetation along the banks of rivers and streams (Narins et al., 2004). Video recordings of vocalizing males in their natural habitat revealed that two pairs of vocal sacs are inflated during calling: a lateral pair and a subgular pair (Narins, *personal observation*). The inflation dynamics for these two pairs of sacs are not known, nor are the delays (if any) between inflations of the two pairs of vocal sacs. Given the extremely wide variety of call notes produced by males of *O. tormota* (Feng et al., 2002; Feng & Narins, 2008), and the nearly ubiquitous presence of nonlinear call features and motifs in this species' calls (Narins et al., 2004; Suthers et al., 2006), we predict that the vocal sac inflation system may exhibit some unusual features worth investigation.

Given the high-frequency call components, it follows that sound localization by *O. tormota* should be highly developed. This is in fact the case—males are able to locate the source of a sound to within 0.7° , rivaling the accuracy of the vertebrates with the highest localization acuity (Shen et al., 2008). In addition, males are able to discriminate individuals by their calls (Feng et al., 2009a) or distinguish neighbors from strangers (Feng et al., 2009b). Moreover, the deeply recessed eardrum is found only in males of *O. tormota*; females exhibit eardrums only slightly recessed from the head surface. Using acoustic playback experiments, AEP recordings from the midbrain, and laser measurements of the TM, Shen and his colleagues recently demonstrated that females of *O. tormota* are insensitive to US; the ultrasonic realm is therefore reserved for males of this species (Shen et al., 2011b).

3.3.2 *Odorrana graminea* (formerly *Odorrana livida*)

O. graminea is a rather common species in the Tau Hua Creek; it is significantly larger than the sympatric and congeneric *O. tormota* (mean SVL male *O. tormota*: 34 mm, female: 60 mm; mean SVL male *O. graminea*: 48 mm, female: 91 mm). Electrophysiological experiments have shown that males of this species are sensitive to tones as high as 22 kHz (Feng et al., 2006). Moreover, broadband recordings of their calls have only recently revealed that the short tonal calls contain frequencies up to 44.1 kHz (Shen et al., 2011a). In summary, males of this species produce ultrasonic vocalizations, they are sensitive to ultrasonic signals (up to 22 kHz), and yet they do not possess a deeply recessed tympanic membrane.

The piebald odorous frog, *Odorrana schmackeri*, is another sympatric, congeneric torrent frog that also inhabits the Tau Hua Creek. It too has nonrecessed tympanic membranes but its auditory sensitivity measured with AEP recordings from the inferior colliculus in the midbrain suggests a high-frequency detection limit of 8.5 kHz, well below US (Yu et al., 2006). Thus, although this species is sympatric with *O. tormota* and *O. graminea*, its calls contain no US components. It appears that there are many and varied responses to high levels of background noise, and future studies will undoubtedly bring many more of these responses to light (Arch & Narins, 2008).

3.3.3 *Huia cavitympanum*

Of the more than 6000 known species of anuran amphibians, there are only two frog species with recessed tympana: *Odorrana tormota* from China and *Huia cavitympanum* from Borneo (Amphibia Web: <http://amphibiaweb.org/>, Inger, 1966). In 2007, an expedition was launched to Gunung Mulu National Park in Sarawak, Malaysian Borneo for the purpose of (1) finding calling males of *H. cavitympanum*, (2) recording their vocalizations *in situ*, (3) obtaining high-quality recordings of the ambient noise in which calling males were found, and (4) initiating the process of capturing and transporting live animals back to the United States for physiological studies. During this first expedition, vocalizations

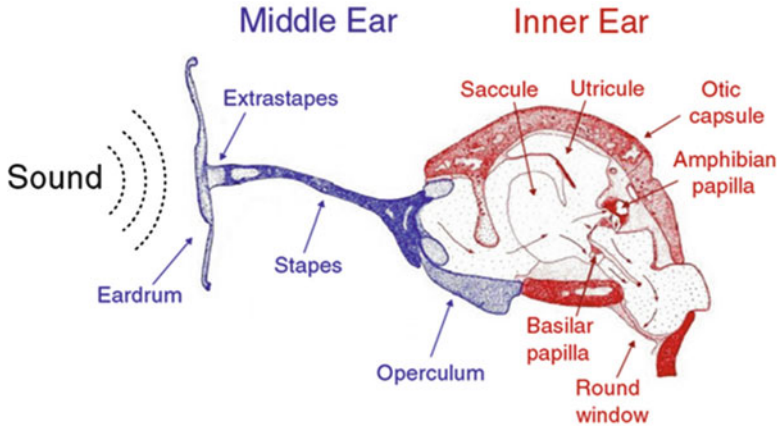


Fig. 8 Schematic diagram of the frog ear. The amphibian papilla and the basilar papilla are the two inner ear organs in the frog that are specialized for detecting airborne sounds. In some frogs, the middle ear and the basilar papilla have undergone a series of morphological changes that facilitate detection of high-frequency sound (see text). (Adapted from Wever, 1973.)

were recorded from 10 males of *H. cavitympanum*. In addition to possessing the recessed tympanic membranes, these animals are capable of producing two classes of vocalizations: (1) those with fundamental frequencies below the nominal upper limit of human hearing (20 kHz), and are therefore audible to humans, and (2) those with fundamental frequencies that exceed the nominal upper limit of human hearing (Arch et al., 2008, 2009). This species represents the first known example of a nonmammalian vertebrate that can produce calls with frequencies restricted entirely to the ultrasonic range. Acoustic playback experiments in this animal's natural habitat showed that vocalizing males change their calling pattern in response to playback of purely ultrasonic signals (Arch et al., 2009), and AEP recordings from the midbrain show robust responses to tones of frequencies as high as 39 kHz, with peak sensitivity *above* 20 kHz, making this amphibian an ultrasonic specialist (Arch et al., 2009).

3.4 Mechanism of US Detection in Frogs—Still Unknown

In a study of the concave-eared torrent frog *Odorrana tormota*, the neural activity patterns in the auditory brain stem were examined in response to a full-spectrum conspecific call, a filtered US-only call, and a control (no sound) stimulus generated by playing back a 30-minute file that does not contain any sound (Arch et al., 2011). To gain insight into the structures responsible for US sensitivity in the frog's brain, brain neural activity was determined by measuring the expression of the immediate

early gene, *egr-1*. *Egr-1* expression was measured in the superior olivary nucleus (SON) in the hindbrain, which is a major source of afferents for the torus semicircularis (TS) in the midbrain, and in the principal (Ptor) and laminar (Ltor) nuclei of the TS. US-only calls elicited robust expression of *egr-1* in the SON and Ptor. Moreover, in the Ptor, *egr-1* expression was greater in response to US-only calls than to the full-spectrum calls, suggesting a pivotal role for this nucleus in US detection in this species (Arch et al., 2011).

Anurans are unique among vertebrates in that their auditory periphery contains two distinct auditory organs (Fig. 8), the amphibian papilla (AP) and basilar papilla (BP) (Wever, 1973; Capranica, 1976; Lewis & Narins, 1999). In the American bullfrog, *Rana catesbeiana*, the BP contains 50–90 hair cells, whereas the AP contains roughly 10 times this number (Geisler et al., 1964; Lewis et al., 1982a). The AP responds to low and middle frequencies and is tonotopically organized, with low-frequency-sensitive hair cells located rostrally and mid-frequency cells located caudally (Lewis et al., 1982a,b). The BP is a simpler organ that acts as a mechanical resonator that responds to a restricted band of higher frequencies (Feng et al., 1975; Ronken, 1990; van Dijk et al., 2011). The BPs of *Rana catesbeiana* and its close relative *Rana pipiens* can detect sounds up to 2 and 4 kHz, respectively—frequencies near the upper frequencies in the species-specific advertisement calls (Capranica, 1976).

The sensory epithelium of the basilar papilla is found at the base of a tubular outpocket of the sacculus, an inner ear organ primarily responsible for detecting substrate vibrations (Narins, 1990; Yu et al., 1991). The BP outpocket is terminated by its contact membrane, which is tuned to the species' BP frequency (Purgue & Narins, 2000a,b). In addition, a tectorial membrane spans the lumen of the BP recess, covering the sensory hair cells that are embedded in the cartilaginous wall of this recess (Wever, 1985). Optical measurements of the mechanical response of the BP tectorial membrane in *R. pipiens* have revealed that it is tuned to a frequency of approximately 2 kHz, corresponding closely to the characteristic frequencies of the species' BP nerve fibers (Schoffelen et al., 2009). Thus, both BP membranes are tuned to the frequency of the organ, consistent with the idea that the BP acts as a mechanical resonator (Feng et al., 1975; Ronken, 1990; van Dijk et al., 2011).

In a recent comparative study, basilar papilla morphologies of six frog species, three known to detect US (*O. tormota*, *O. livida*, and *Huia cavitympanum*), two relatively unstudied frog species from Laos (*O. chloronota* and *Amolops daorum*), and one non-US communicator (*R. pipiens*), were compared (Arch et al., 2012). In this study, immunohistochemistry and confocal microscopy were used to examine several anatomical features of the basilar papillae of the inner ears, including the recess entrance area (REA), epithelium surface area (ESA), number of hair cells or hair cell count (HCC), hair cell soma length (SL), and bundle height (BH). The REA, ESA, and HCC values for all ultrasonic species (US) tested were significantly smaller than those for *R. pipiens*. Moreover, the three US-detecting frogs had values for these metrics that were statistically indistinguishable from one another and from *A. chloronota* (Arch et al., 2012). These data also reveal that *H. cavitympanum*, *O. tormota*, *O. livida*, and *O. chloronota* have significantly smaller BP organs and

sensory epithelia than those of *R. pipiens* and *A. daorum*. In addition, basilar papilla SL, BL, and BH values from the US-sensitive frogs and *O. chloronota* were not significantly different and their SL values were significantly smaller than those of *R. pipiens* and *A. daorum*. Together, these BP morphological data suggest that *O. chloronota* from northeastern Laos be considered a putative US detector, and that future physiological studies of the mechanisms underlying US detection should include this species along with the three known US detectors.

4 Summary and Outlook: Comparative Insights from the Study of High-Frequency Hearing in Fishes and Frogs

The evolutions of US detection in fishes and frogs are clearly independent events with different ecological drivers. These comparative evolutionary stories provide some guide as to where to look for surprises in hearing and communication in fishes and frogs. Frogs with ultrasonic hearing live in unusual environments with high levels of low-frequency noise and also produce sounds at very high frequencies. Thus, communication appears to have been the primary selective force for high-frequency hearing in some frogs (Narins et al., 2007a). No fishes are known to communicate with ultrasonic signals, but it could be interesting to study acoustic communication in fishes with good hearing sensitivity that live in areas of high background noise (see also the chapter by Ladich, this volume). US detection by the Alosinae fishes appears to have resulted from selective pressure from echolocating cetaceans. Some frogs fall prey to echolocating bats, and thus it would be interesting to determine whether they, also, are capable of detecting echolocation signals to avoid bat predation. Likewise, it would be interesting to learn if any of the US-sensing frogs are able to use the ultrasonic components of insect stridulation sounds to locate their prey.

References

- Arch, V. S., & Narins, P. M. (2008). "Silent" signals: Selective forces acting on ultrasonic communication signals in terrestrial vertebrates. *Animal Behavior*, 76, 1423–1428.
- Arch, V. S., Grafe, T. U., & Narins, P. M. (2008). Ultrasonic signaling by a Bornean frog. *Biology Letters*, 4, 19–22.
- Arch, V. S., Grafe, T. U., Gridi-Papp, M., & Narins, P. M. (2009). Pure ultrasonic communication in an endemic Bornean frog. *PLoS ONE* 4(4), e5413.
- Arch, V. S., Burmeister, S. S., Feng, A. S., Shen, J.-X., & Narins, P. M. (2011). Ultrasound-evoked immediate early gene expression in the brainstem of the Chinese torrent frog, *Odorrana tormota*. *Journal of Comparative Physiology*, 197, 667–675.
- Arch, V. S., Simmons, D. D., Quiñones, P. M., Feng, A. S., Jiang, J., Stuart, B., Shen, J.-X., Blair, C., & Narins, P. M. (2012). Inner ear morphological correlates of ultrasonic hearing in frogs. *Hearing Research*, 283, 70–79.

- Astrup, J. (1999). Ultrasound detection in fish—a parallel to the sonar-mediated detection of bats by ultrasound-sensitive insects? *Comparative Biochemistry and Physiology A*, 124, 19–27.
- Astrup, J., & Møhl, B. (1993). Detection of intense ultrasound by the cod, *Gadus morhua*. *Journal of Experimental Biology*, 182, 71–80.
- Au, W. W. L. (1993). *The sonar of dolphins*. New York: Springer-Verlag.
- Bass, A. H., & Ladich, F. (2008). Vocal – acoustic communication: From neurons to behavior. In J. F. Webb, A. N. Popper, & R. Fay (Eds.), *Fish bioacoustics* (pp. 253–278). New York: Springer.
- Best, A. C. G., & Gray, J. A. B. (1980). Morphology of the utricular recess in the sprat. *Journal of the Marine Biological Association of the United Kingdom*, 60(3), 703–715.
- Blaxter, J. H. S., Denton, E. J., & Gray, J. A. B. (1981). Acousticolateralis system in clupeid fishes. In W. N. Tavolga, A. N. Popper, & R. R. Fay (Eds.), *Hearing and sound communication in fishes* (pp. 39–59). New York: Springer-Verlag.
- Blaxter, J. H. S., Gray, J. A. B., & Best, A. C. G. (1983). Structure and development of the free neuromasts and lateral line system of the herring. *Journal of the Marine Biological Association of the United Kingdom*, 63, 247–260.
- Bleckmann, H. (2008). Peripheral and central processing of lateral line information. *Journal of Comparative Physiology A: Neuroethology Sensory Neural and Behavioral Physiology*, 194, 145–158.
- Capranica, R. R. (1976). Auditory system: Morphology and physiology of the auditory system. In R. Llinas & W. Precht (Eds.), *Frog neurobiology* (pp. 551–575). Berlin: Springer-Verlag.
- Chapman, C. J., & Sand, O. (1974). Field studies of hearing in 2 species of flatfish *Pleuronectes-Platessa* (L) and *Limanda-Limanda* (L) (Family Pleuronectidae). *Comparative Biochemistry and Physiology*, 47, 371–385.
- Chung, S. H., Pettigrew, A. G., & Anson, M. (1981). Hearing in the frog: Dynamics of the middle ear. *Proceedings of the Royal Society of London B: Biological Sciences*, 212, 459–485.
- Clarke, M. R. (1977). Beaks, nets and numbers. *Symposia of the Zoological Society of London*, 38, 89–126.
- Coombs, S., & Montgomery, J. C. (1999). The enigmatic lateral line system. In A. N. Popper and R. R. Fay (Eds.), *Comparative hearing: Fishes and amphibians* (pp. 319–362). New York: Springer-Verlag.
- Denton, E. J., & Blaxter, J. H. S. (1976). Mechanical relationships between clupeid swimbladder, inner-ear and lateral line. *Journal of the Marine Biological Association of the United Kingdom*, 56, 787–807.
- Denton, E. J., & Gray, J. (1983). Mechanical factors in the excitation of clupeid lateral lines. *Proceedings of the Royal Society of London B: Biological Sciences*, 218, 1–26.
- Denton, E. J., Gray, J. A. B., & Blaxter, J. H. S. (1979). Mechanics of the clupeid acoustico-lateralis system – frequency responses. *Journal of the Marine Biological Association of the United Kingdom*, 59, 27–47.
- De Vries, H. L. (1950). The mechanics of labyrinth otoliths. *Acta Oto-Laryngologica*, 38, 262–273.
- Dunning, D. J., Ross, Q. E., Geoghegan, P., Reichle, J. J., Menezes, J. K., & Watson, J. K. (1992). Alewives avoid high-frequency sound. *North American Journal of Fisheries Management*, 12, 407–416.
- Enger, P. S. (1967). Hearing in herring. *Comparative Biochemistry and Physiology*, 22(2), 527–530.
- Fay, R. R. (1988). *Hearing in vertebrates: A psychophysics databook*. Winnetka, IL: Hill-Fay Associates, 621 pp.
- Fei, L., Ye, C., & Jiang, J. (2010). Colored atlas of Chinese amphibians. Chengdu, China: Sichuan Publishing House of Science and Technology.
- Feng, A. S., & Narins, P. M. (2008). Ultrasonic communication in concave-eared torrent frogs (*Amolops tormotus*). *Journal of Comparative Physiology*, 194, 159–167.

- Feng, A. S., Narins, P. M., & Capranica, R. R. (1975). Three populations of primary auditory fibers in the bullfrog (*Rana catesbeiana*): Their peripheral origins and frequency sensitivities. *Journal of Comparative Physiology*, 100, 221–229.
- Feng, A. S., Narins, P. M., & Xu, C.-H. (2002). Vocal acrobatics in a Chinese frog, *Amolops tormotus*. *Naturwissenschaften*, 89, 352–356.
- Feng, A. S., Narins, P. M., Xu, C.-H., Lin, W.-Y., Yu, Z.-L., Qiu, Q., Xu, Z.-M., & Shen, J.-X. (2006). Ultrasonic communication in frogs. *Nature*, 440, 333–336.
- Feng, A. S., Riede, T., Arch, V. S., Yu, Z., Xu, Z.-M., Yu, X.-J. & Shen, J.-X. (2009a). Diversity of vocal signals of concave-eared torrent frogs (*Odorrana tormota*): Evidence for individual signatures. *Ethology*, 115, 1015–1028.
- Feng, A. S., Arch, V. S., Yu, Z.-L., Yu, X.-J., Xu, Z.-M., & Shen, J.-X. (2009b). Neighbor-stranger discrimination in concave-eared torrent frogs, *Odorrana tormota*. *Ethology*, 115, 1–6.
- Frost, D. R., Grant, T., Faivovich, J., Bain, R. H., Haas, A., Haddad, C. F. B., De Sá, R. A., Channing, A., Wilkinson, M., Donnellan, S. C., Raxworthy, C. J., Campbell, J. A., Blotto, B. L., Moler, P., Drewes, R. C., Nussbaum, R. A., Lynch, J. D., Green, D. M., & Wheeler, W. C. (2006). The amphibian tree of life. *Bulletin of the American Museum of Natural History*, 297, 1–370.
- Geisler, C. D., van Bergeijk, W. A., & Frishkopf, L. S. (1964). The inner ear of the bullfrog. *Journal of Morphology*, 114, 43–58.
- Gray, J. (1984). Interaction of sound pressure and particle-acceleration in the excitation of the lateral line neuromasts of sprats. *Proceedings of the Royal Society of London B: Biological Sciences*, 220(1220), 299–325.
- Gregory, J., Lewis, M., & Hateley, J. (2007). Are twaite shad able to detect sound at a higher than any other fish? Results from a high resolution imaging sonar. *Proceedings of the Institute of Acoustics, Loughborough University, UK*, p. 29, Part 3.
- Gridi-Papp, M., & Narins, P. M. (2009). Environmental influences in the evolution of tetrapod hearing sensitivity and middle ear tuning. *Integrative and Comparative Biology*, 49, 702–716.
- Gridi-Papp, M., Feng, A. S., Shen, J.-X., Yu, Z.-L., & Narins, P. M. (2008). Active control of ultrasonic hearing in frogs. *Proceedings of the National Academy of Sciences of the USA*, 105, 11013–11018.
- Griffin, D. R. (1958). *Listening in the dark: The acoustic orientation of bats and men*. New Haven, CT: Yale University Press.
- Hall, J. C., & Feng, A. S. (1988). Influence of envelope rise time on neural responses in the auditory system of anurans. *Hearing Research*, 36, 261–276.
- Hamilton, H., Caballero, S., Collins, A. G., & Brownell, R. L., Jr. (2001). Evolution of river dolphins. *Proceedings of the Royal Society of London B: Biological Sciences*, 268, 549–558.
- Harris, G. G., & van Bergeijk, W. A. (1962). Evidence that the lateral-line organ responds to near-field displacements of sound sources in water. *Journal of Acoustical Society of America*, 34, 1831–1841.
- Hawkins, A. D. (1981). The hearing abilities of Fish. In W. N. Tavolga, A. N. Popper, & R. R. Fay (Eds.), *Hearing and sound communication in fishes* (pp. 109–133). New York: Springer-Verlag.
- Hawkins, A. D., & Johnstone, A. D. F. (1978). Hearing of the Atlantic salmon, *Salmo-salar*. *Journal of Fish Biology*, 13(6), 655.
- Higgs, D. M., & Fuiman, L. A. (1996). Ontogeny of visual and mechanosensory structure and function in Atlantic menhaden *Brevoortia tyrannus*. *Journal of Experimental Biology*, 199, 2619–2629.
- Higgs, D. M., Plachta, D. T., Rollo, A. K., Singheiser, M., Hastings, M. C., & Popper, A. N. (2004). Development of ultrasound detection in American shad (*Alosa sapidissima*). *The Journal of Experimental Biology*, 207, 155–163.
- Hiryu, S., Bates, M. E., Simmons, J. A., & Riquimaroux, H. (2010). FM echolocating bats shift frequencies to avoid broadcast-echo ambiguity in clutter. *Proceedings of the National Academy of Sciences of the USA*, 107, 7048–7053.

- Hoss, D. E., & Blaxter, J. H. S. (1982). Development and function of the swimbladder-inner ear-lateral line system in the Atlantic menhaden, *Brevoortia tyrannus* (Latrobe). *Journal of Fish Biology*, 20, 131–142.
- Hoy, R. R., & Robert, D. (1996). Tympanal hearing in insects. *Annual Review of Entomology*, 41, 433–450.
- Inger, R. F. (1966). *The systematics and zoogeography of the amphibia of Borneo*. Chicago: Field Museum of Natural History.
- Jaslow, A. P., Hetherington, T. E., & Lombard, R. E. (1988). Structure and function of the amphibian middle ear. In B. Fritsch, M. J. Ryan, W. Wilczynsk, T. E. Hetherington, & W. Walkowiak (Eds.), *The evolution of the amphibian auditory system* (pp. 69–92). New York: John Wiley & Sons.
- Jorgensen, M. B. (1991). Comparative studies of the biophysics of directional hearing in anurans. *Journal of Comparative Physiology A*, 169, 591–598.
- Kalmijn, J. (1989). Functional evolution of lateral line and inner ear sensory systems. In S. Coombs, P. Görner, & H. Münz (Eds.), *The mechanosensory lateral line* (pp. 187–215). New York: Springer-Verlag.
- Kroese, A. B. A., & van Netten, S. M. (1989). Sensory transduction in lateral line hair cells. In S. Coombs & P. Görner (Eds.), *The mechanosensory lateral line* (pp. 265–284). New York: Springer-Verlag.
- Krysl, P., Hawkins, A. D., Schilt, C., & Cranford, T. W. (2012). Angular oscillation of solid scatterers in response to progressive planar acoustic waves: Do fish otoliths rock? *PLOS One* 7 (8): e42591.
- Kynard, B., & O'Leary J. (1990) Behavioral guidance of adult American shad using underwater AC electrical and acoustic fields. In *Proceedings of the International Symposium on Fishways '90*, Gifu, Japan, October 8–10, 1990, pp. 131–135.
- Lavoué, S., Miya, M., Saitoh, K., Ishiguro, N. B., & Nishida, M. (2007). Phylogenetic relationships among anchovies, sardines, herrings and their relatives (Clupeiformes), inferred from whole mitogenome sequences. *Molecular Phylogenetics and Evolution*, 43, 1096–1105.
- Lewis, E. R., & Narins, P. M. (1999). The acoustic periphery of amphibians: Anatomy and physiology. In R. R. Fay & A. N. Popper (Eds.), *Comparative hearing: Fish and amphibians* (pp. 101–154). New York: Springer.
- Lewis, E. R., Baird, R., Leverenz, E. L., & Koyama, H. (1982a). Inner ear: Dye injection reveals peripheral origins of specific sensitivities. *Science*, 215, 1641–1643.
- Lewis, E. R., Leverenz, E. L., & Koyama, H. (1982b). The tonotopic organization of the bullfrog amphibian papilla, an auditory organ lacking a basilar membrane. *Journal of Comparative Physiology*, 145, 437–455.
- Madsen, P. T., Wahlberg, M., & Møhl, B. (2002). Male sperm whale (*Physeter macrocephalus*) acoustics in a high-latitude habitat: Implications for echolocation and communication. *Behavioral Ecology and Sociobiology*, 53, 31–41.
- Madsen, P. T., Johnson, M., de Soto, N. A., Zimmer, W. M. X., & Tyack, P. (2005). Biosonar performance of foraging beaked whales (*Mesoplodon densirostris*). *Journal of Experimental Biology*, 208(2), 181–194.
- Mann, D. A., Lu, Z., & Popper, A. N. (1997). A clupeid fish can detect ultrasound. *Nature*, 389, 341.
- Mann, D. A., Lu, Z., Hastings, M. C., & Popper, A. N. (1998). Detection of ultrasonic tones and simulated dolphin echolocation clicks by a teleost fish, the American shad (*Alosa sapidissima*). *Journal of Acoustical Society of America*, 104, 562–568.
- Mann, D. A., Higgs, D. M., Tavolga, W. N., Souza, M. J., & Popper, A. N. (2001). Ultrasound detection by clupeiform fishes. *Journal of Acoustical Society of America*, 109, 3048–3054.
- Mann, D. A., Popper, A. N., & Wilson, B. (2005). Pacific herring hearing does not include ultrasound. *Biology Letters*, 1, 158–161.
- Miller, L. A., & Surlykke, A. (2001). How some insects detect and avoid being eaten by bats: Tactics and countertactics of prey and predator. *Bioscience*, 51(7), 570–581.

- Møhl, B., Wahlberg, M., Madsen, P. T., Heerfordt, A., & Lund, A. (2003). The monopulsed nature of sperm whale clicks. *Journal of the Acoustical Society of America*, 114(2), 1143–1154.
- Narins, P. M. (1990). Seismic communication in anuran amphibians. *Bioscience*, 40, 268–274.
- Narins, P. M., & Feng, A. S. (2007). Hearing and sound communication in amphibians: Prologue and prognostication. In P. M. Narins, A. S. Feng, R. R. Fay, & A. N. Popper (Eds.), *Hearing and sound communication in amphibians* (pp. 1–11). Heidelberg: Springer.
- Narins, P. M., Lewis, E. R., & McClelland, B. E. (2000). Hyperextended call repertoire of the endemic Madagascar treefrog, *Boophis madagascariensis* (Rhacophoridae). *Journal of Zoology* (London), 250, 283–298.
- Narins, P. M., Feng, A. S., Schnitzler, H.-U., Denzinger, A., Suthers, R.A., Lin, W., & Xu, C.-H. (2004). Old World frog and bird vocalizations contain prominent ultrasonic harmonics. *Journal of Acoustical Society of America*, 115, 910–913.
- Narins, P. M., Feng, A. S., Fay, R. R., & Popper, A. N. (2007a). *Hearing and sound communication in amphibians*. New York: Springer.
- Narins, P. M., Feng, A. S., & Shen, J.-X. (2007b). Frogs communicate with ultrasound in noisy environments. In B. Kollmeier, G. Klump, V. Hohmann, U. Langemann, M. Mauermann, S. Uppenkamp, & J. Verhey (Eds.), *Hearing – From sensory processing to perception* (pp. 185–190). Heidelberg: Springer.
- Nestler, J. M., Ploskey, G. R., & Pickens, J. (1992). Responses of blueback herring to high-frequency sound and implications for reducing entrainment at hydropower dams. *North American Journal of Fisheries Management*, 12, 667–683.
- O’Connell, C. P. (1955). The gas bladder and its relation to the inner ear in *Sardinops caerulea* and *Engaulis mordax*. *Fishery Bulletin*, 56, 506–532.
- Plachta, D. T., & Popper, A. N. (2003). Evasive responses of American shad (*Alosa sapidissima*). *Acoustic Research Letters Online*, 4, 25–30.
- Plachta, D. T., Song, J. K., Halvorsen, M. B., & Popper, A. N. (2004). Neuronal encoding of ultrasonic sound by a fish. *Journal of Neurophysiology*, 91(6), 2590–2597.
- Popper, A. N., & Platt, C. (1979). The herring ear has a unique receptor pattern. *Nature*, 280, 832–833.
- Popper, A. N., Fay, R. R., Platt, C., & Sand, O. (2003). Sound detection mechanisms and capabilities of teleost fishes. In S. P. Collin & N. J. Marshall (Eds.), *Sensory processing in aquatic environments* (pp. 3–38). New York: Springer.
- Popper, A. N., Plachta, D. T., Mann, D. A., & Higgs, D. M. (2004). Response of clupeid fish to ultrasound: A review. *Journal of Marine Science*, 61, 1057–1061.
- Purgue, A. P., & Narins, P. M. (2000a). Mechanics of the inner ear of the bullfrog (*Rana catesbeiana*): The contact membranes and the periotic canal. *Journal of Comparative Physiology A*, 186, 481–488.
- Purgue, A. P., & Narins, P. M. (2000b). A model for energy flow in the inner ear of the bullfrog (*Rana catesbeiana*). *Journal of Comparative Physiology A*, 186, 489–495.
- Retzius (1881). *Das Gehororgan der Wirbeltiere: I. Das Gehororgan der Fische und Amphien*. Stockholm: Samson and Wallin.
- Roeder, K. D. (1962). The behaviour of free flying moths in the presence of artificial ultrasonic pulses. *Animal Behaviour*, 10, 300–304.
- Roeder, K. D. (1998). Moths and bats. In K. D. Roeder (Ed.), *Nerve cells and insect behavior* (pp. 52–70). Cambridge, MA: Harvard University Press.
- Ronken, D. A. (1990). Basic properties of auditory nerve responses from a “simple” ear: The basilar papilla of the frog. *Hearing Research*, 47, 63–82.
- Sand, O. (1981). The lateral line and sound reception. In W. N. Tavolga, A. N. Popper, & R. Fay (Eds.), *Hearing and sound communication in fishes* (pp. 459–480). New York: Springer-Verlag.
- Sand, O., & Karlsen, H. E. (2000). Detection of infrasound and linear acceleration in fishes. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 355(1401), 1295–1298.
- Sand, O., & Bleckmann, H. (2008). Orientation to auditory and lateral line stimuli. In J. F. Webb, A. N. Popper, & R. Fay (Eds.), *Fish bioacoustics* (pp. 183–232). New York: Springer.

- Santos, M. B., Pierce, G. J., Reid, R. J., Patterson, I. A. P., Ross, H. M., & Mente, E. (2001). Stomach contents of bottlenose dolphins (*Tursiops truncatus*) in Scottish waters. *Journal of the Marine Biological Association of the United Kingdom*, 81(5), 873–878.
- Schack, H. B., Malte, H., & Madsen, P. T. (2008). The response of Atlantic cod (*Gadus morhua*) to ultrasound-emitting predators: Stress, behavioural changes or debilitation? *The Journal of Experimental Biology*, 211, 2079–2086.
- Schoffelen, R., Segenhout, J., & van Dijk, P. (2009). Tuning of the tectorial membrane in the basilar papilla of the Northern Leopard frog. *Journal of Association for Research in Otolaryngology*, 10, 309–320.
- Shen, J.-X., Feng, A. S., Xu, Z.-M., Yu, Z.-L., Arch, V. S., Yu, X.-J., & Narins, P. M. (2008). Ultrasonic frogs show hyperacute phonotaxis to female's courtship calls. *Nature*, 453, 914–916.
- Shen, J.-X., Xu, Z.-M., Feng, A., & Narins, P. M. (2011a). Large odorous frogs (*Odorrana graminea*) produce ultrasonic calls. *Journal of Comparative Physiology*, 197, 1027–1030.
- Shen, J.-X., Xu, Z.-M., Yu, Z.-L., Wang, S., Zheng, D.-Z., & Fan, S.-C. (2011b). Ultrasonic frogs show extraordinary sex differences in auditory frequency sensitivity. *Nature Communications*, 2, 342.
- Slabbekoorn, H., & Peet, M. (2003). Birds sing at a higher pitch in urban noise. *Nature*, 424, 267.
- Suthers, R. A., Narins, P. M., Lin, W., Schnitzler, H.-U., Denzinger, A., Xu, C.-H., & Feng, A. S. (2006). Voices of the dead: Complex nonlinear vocal signals from the larynx of an ultrasonic frog. *Journal of Experimental Biology*, 209, 4984–4993.
- van Dijk, P., Mason, M. J., Schoffelen, R. L. M., Narins, P. M., & Meenderink, S. W. F. (2011). Mechanics of the frog ear. *Hearing Research*, 273, 46–58.
- Wahlberg, M., & Westerberg, H. (2003). Sounds produced by herring (*Clupea harengus*) bubble release. *Aquatic Living Resources*, 16, 271–275.
- Webb, J. F., Montgomery, J. C., & Mogdans, J. (2008). Bioacoustics and the lateral line systems of fishes. In J. F. Webb, A. N. Popper, & R. Fay (Eds.), *Fish bioacoustics* (pp. 145–183). New York: Springer.
- Wever, E. G. (1973). The ear and hearing in the frog, *Rana pipiens*. *Journal of Morphology*, 141, 461–478.
- Wever, E. G. (1985). *The amphibian ear*. Princeton, NJ: Princeton University Press.
- Whitehead, P. J. P., Nelson, G. J., & Wongratana, T. (1985). *FAO species catalogue*, Vol. 7. Clupeoid fishes of the world (Suborder Clupeoidei). FAO Fisheries Synopsis No. 125, 303 pp.
- Wilson, B., Batty, R. S., & Dill, L. M. (2004). Pacific and Atlantic herring produce burst pulse sounds. *Proceedings of the Royal Society of London B: Biological Sciences*, 271 (Supplement), S95–S97.
- Wilson, M., Acolas, M. L., Bégout, M. L., Madsen, P. T., & Wahlberg, M. (2008). Allis shad (*Alosa alosa*) exhibit an intensity-graded behavioural response when exposed to ultrasound. *JASA Express Letters*, 124(4), EL243–EL 247.
- Wilson, M., Montie, E. W., Mann, K. A., & Mann, D. A. (2009). Ultrasound detection in the Gulf menhaden requires gas-filled bullae and an intact lateral line. *Journal of Experimental Biology*, 212, 3422–3427.
- Wilson, M., Schack, H. B., Madsen, P. T., Surlykke, A., & Wahlberg, M. (2011). Directional escape behavior in allis shad (*Alosa alosa*) exposed to ultrasonic clicks mimicking an approaching toothed whale. *Journal of Experimental Biology*, 214(1), 22–29.
- Yack, J. E., & Fullard, J. H. (1993). What is an insect ear? *Annals of the Entomological Society of America*, 86, 677–682.
- Yu, X., Lewis, E. R., & Feld, D. (1991). Seismic and auditory tuning curves from bullfrog saccular and amphibian papillar axons. *Journal of Comparative Physiology*, 169, 241–248.
- Yu, Z.-L., Qiu, Q., Xu, Z.-M., & Shen, J.-X. (2006). Auditory response characteristics of the piebald odorous frog and their implications. *Journal of Comparative Physiology*, 192, 801–806.
- Zhou, E. M., & Adler, K. (1993). *Herpetology of China*. Oxford: Society for the Study of Amphibians and Reptiles.