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Anatomical influences on internally coupled ears in reptiles

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Abstract Many reptiles, and other vertebrates, have internally coupled ears in which a patent anatomical connection allows pressure waves generated by the displacement of one tympanic membrane to propagate (internally) through the head and, ultimately, influence the displacement of the contralateral tympanic membrane. The pattern of tympanic displacement caused by this internal coupling can give rise to novel sensory cues. The auditory mechanics of reptiles exhibit more anatomical variation than in any other vertebrate group. This variation includes structural features such as diverticula and septa, as well as coverings of the tympanic membrane. Many of these anatomical features would likely influence the functional significance of the internal coupling between the tympanic membranes. Several of the anatomical components of the reptilian internally coupled ear are under active motor control, suggesting that in some reptiles the auditory system may be more dynamic than previously recognized.

Keywords Morphology · Acoustics · Squamates · Frequency

In a “typical” reptilian ear, sound pressure waves cause displacement of the tympanic membrane, which induces displacement of the middle ear ossicle. In reptiles, the middle ear ossicle, the stapes (columella), is generally continued distally by a cartilaginous extrastapes (extracolumella). In squamate reptiles, the extrastapes gives rise to a number of processes that attach to the inner surface of the tympanic membrane, on the adjacent quadrate, or in the soft-tissue margins of the tympanic membrane. The arthrology between the stapes and extrastapes is highly variable and can include multiple synovial joints; interestingly, this linkage seems particularly variable in snakes (e.g., Rieppel 1980; Kley 2006). The displacement of the stapes at the oval window induces particle motion within the perilymphatic fluid. This (indirectly) deflects the stereocilia of the tectorial hair cells, ultimately resulting in action potentials in the auditory nerve fibers. Each component of this system, and each link between successive components, has a specific transfer function; for example, the tympanic membrane undergoes differential displacement to different frequencies presented at the same pressure level (Saunders et al. 2000).

The combined performance of this system is traditionally presented as an auditory (or frequency) response curve. Squamate reptiles (the group composed primarily of lizards and snakes) are frequently described as having both low-frequency and high-frequency auditory ranges (e.g., Manley 1977). Squamates, as well as other reptilian taxa, exhibit a wide range of variation in their frequency response curves. Wever (1978) provided a large compilation of frequency response curves, though the accuracy of his methodology has been questioned (see Manley 1990). Some taxa, including the snakes, have lost the high-frequency portion of their auditory range (Young 2003), while other taxa have a reduced low-frequency response and are specialized for high-frequency audition (Manley and Kraus 2010). In any case, the squamate audiogram rarely demonstrates comparable low-frequency and high-frequency sensitivities (meaning the animal can detect frequencies in these two ranges at equal pressure levels); instead, the low-frequency range has greater sensitivity and the high-frequency range is manifest as a transitory

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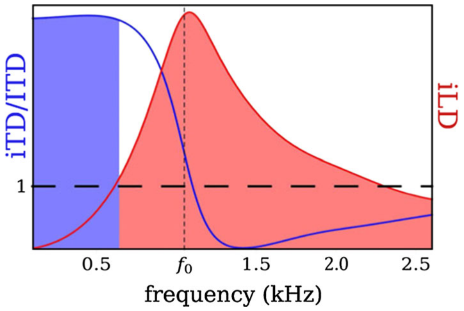

Fig. 1 Two main sensory cues that arise from internally coupled ears, the internal time difference or iTD (here expressed relative to the interaural time difference or ITD) and the internal level difference or iLD differ in relative magnitude (y-axis) depending on the frequency of the sound relative to the fundamental frequency (f_0 *dashed vertical line*) of the tympanic membrane (x-axis). Expressed another way, the fundamental frequency of the tympanic membrane segregates the sensory cues into a temporal domain (*shaded blue*) and an amplitude domain (*shaded red*). Anatomical features that could alter either the fundamental frequency (or tension) of the tympanic membrane, or the frequency profile of the propagating intertympanic pressure wave, could shift the relative intensity of these two sensory cues. Figure reproduced from Vedurmudi et al. (2016a) (color figure online)

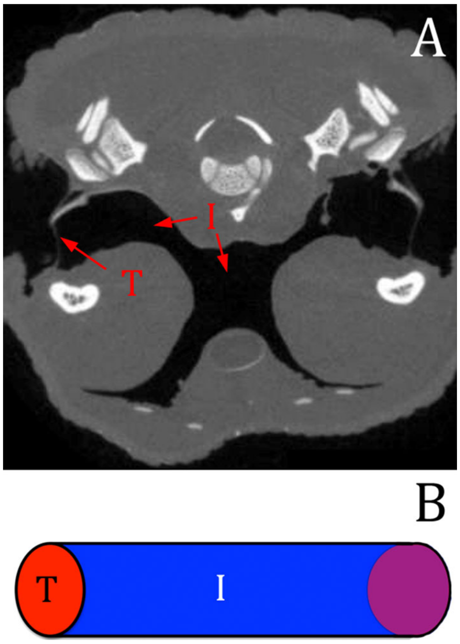

Fig. 2 Depiction of internally coupled ear in which the patent connection through the head linking the contralateral tympanic membranes (T) is modeled as a simple cylinder termed the interaural canal (I). **a** Micro-CT scan through the internally coupled ears of *Varanus exanthematicus*; **b** simple schematic to illustrate the model construct of this system

plateau in the decrease in sensitivity seen with increasing frequency. Specializations in the auditory response of a reptile can be produced at any one of the components of the auditory system (e.g., Saunders et al. 2000; Manley 2002; Ruggero and Temchin 2002; Werner and Igic 2002; Christensen-Dalsgaard and Manley 2014). Ultimately, the auditory action potentials are processed in the cochlear nuclei and higher brain centers (Carr and Code 2000; Willis et al. 2014) to produce information that is used for a wide range of inter- and intraspecific behaviors (Young et al. 2014).

Recent experimental work has shown that some reptiles have an additional auditory pathway, termed internally coupled ears (e.g., Christensen-Dalsgaard and Manley 2008; Bierman et al. 2014). In this auditory system, external pressure waves cause displacement of the tympanic membrane, and this displacement creates a pressure wave within the middle ear cavity. The pressure wave within the middle ear cavity radiates to the contralateral side of the head (by way of the pharynx or other passages) to reach the contralateral middle ear cavity. The displacement of the contralateral tympanic membrane will depend on the difference between the propagated (internal) pressure wave and the external pressure wave. The resulting displacement of the contralateral tympanic membrane is transmitted through the stapedial complex to reach (ultimately) the tectorial hair cells. Internally coupled ears can produce novel temporal (termed internal time difference or iTD) and amplitude (termed internal level difference or iLD) information which is particularly useful for auditory localization (Christensen-Dalsgaard and Manley 2008; Vossen et al. 2010). The biophysics of the tympanic membrane effectively partitions the sensory stimuli (Vedurmudi et al. 2016a); frequencies below the fundamental frequency of the tympanic membrane will generate primarily temporal information (via iTD), while frequencies above the fundamental frequency generate primarily amplitude information (via iLD), Fig. 1.

A recent contribution (Vedurmudi et al. 2016b) presented a universal model for internally coupled ears. This model was built upon an explicit abstraction: the anatomy of the auditory system was modeled as two sectorial membranes (the tympanic membranes) coupled by a cylinder (Fig. 2). In the present composition, the cylinder will be referred to as the interaural canal. The influence of the volume of the interaural canal has been previously addressed (Vedurmudi et al. 2016b). The interaural canal can course inferior or superior to the braincase, and multiple canals may be present (Miall 1878; Witmer and Ridgely 2008).

The anatomy of the interaural coupling in squamates is quite different from the more familiar mammalian system, perhaps primarily because in squamates the Eustachian tube is a poorly demarcated region, rather than a discrete conduit of bone, fibrocartilage, or connective tissue. The middle ear cavity of squamates is not located within a bony cavity, but rather is defined (on all but the medial or deep surface) by soft-tissue structures. When viewed from within the pharynx, the squamate interaural canal is a continuity of gaps between adjacent muscles, rather than a single "tube" (Fig. 3a). The

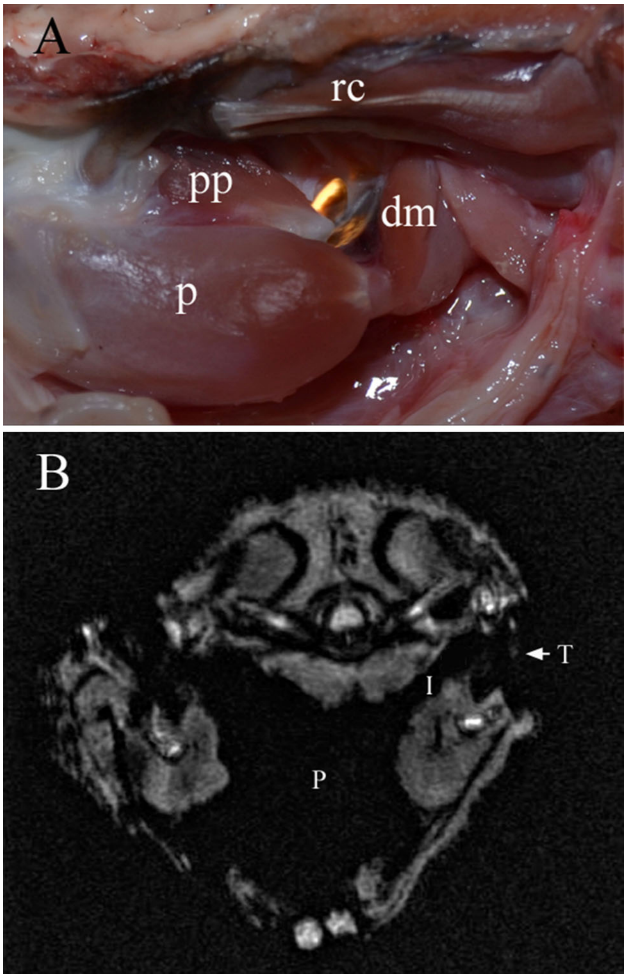

Fig. 3 Anatomy of the internal coupling between the tympana of *Varanus salvator*. **a** The muscular boundaries of the interaural canal are shown in the hemisected head in which the tympanum has been illuminated (*yellow*); *dm* depressor mandibulae, *p* pterygoideus, *pp* protractor pterygoid, *rc* rectus capitis. **b** MRI of the head of *V. salvator* showing the positional relations of the interaural canal (*I*), pharynx (*P*), and tympanic membrane (*T*)

purpose of the present contribution is not the identification of the component parts (e.g., the Eustachian tube) within the interaural canal, as this is not germane to the underlying biophysics of internally coupled ears.

The topographic relationships between adjacent muscles (e.g., the pterygoideus and protractor pterygoid in Fig. 3), can include extensions (or diverticula) off of, as well as projections (or septa) into, the interaural canal. Further, not only will the contractile state of these muscles define the physical size and contour of the interaural canal, but in squamates the underlying bones (e.g., the pterygoid) are generally kinetic, so there is considerable potential for active alteration of this system. Studies of the traditional auditory pathway in reptiles have shown that anatomical variations can be associated with specializations of both the auditory response range and the behavioral ecology of the animals (e.g., Manley and Kraus 2010). The purpose of the present contribution is to explore anatomical variations within reptiles, particularly squamate reptiles, which could be used to either test or expand the biophysical model of internally coupled ears (Vedurmudi et al. 2016b). The focus of this paper will correspond to the conceptual design of the biophysical model, the tympanic membrane and the interaural canal. Owing to the paucity of research in this area, most of the anatomical features described herein have received little or no attention since Wever's (1978) extensive, but hardly complete, survey of the reptilian ear. Some of the anatomical features described below are static, but others are at least potentially dynamic. Such dynamic systems could afford a reptile a means of actively "tuning" either the response of the tympanic membrane, or the biophysical influence of the interaural canal (or both) depending on the stimulus.

1 Variations in the tympanic membrane

There are two general classes of anatomical variation associated with the reptilian tympanic membrane: its superficial covering and the nature of the substance it abuts internally. The tympanic membrane of reptiles (Fig. 4a,b) is a fairly thin, largely avascular sheet of connective tissue and epithelium (Versluys 1898). It may be located at the surface of the animal's head, or slightly recessed, but in either case the basic histological features will largely determine its frequency response. In some squamate reptiles (e.g., *Chamaeleo*, *Draco*, *Phrynosoma*), the superficial surface of the tympanic membrane is covered with skin and/or scalation (Fig. 4c). This superficial covering may have three (not mutually exclusive) effects: (1) the increased mass associated with the covering would increase the impedance of the tympanic membrane (lowering the sensitivity) at higher frequencies. (2) The superficial covering could increase the stiffness of the tympanic membrane which would increase its impedance (again, lowering the sensitivity) at lower frequencies. (3) The fundamental frequency of the tympanic membrane would likely shift due to the influence of the covering which would alter the frequency range of the temporal and amplitude cues (Fig. 1). The potential for increased impedance to both lower and higher frequencies indicates that the surface covering could function as an acoustic filter. If the frequency range of the increased impedance corresponds to the shift in the fundamental frequency of the tympanic membrane, the temporal or amplitude cues could diminish to the point of being ineffectual.

In some reptiles the tympanic membrane is not simply covered by a layer of skin/scalation, it is completely replaced by it such that no anatomically discrete membrane remains (Fig. 4d). In some of these forms (e.g., *Amphisbae-*

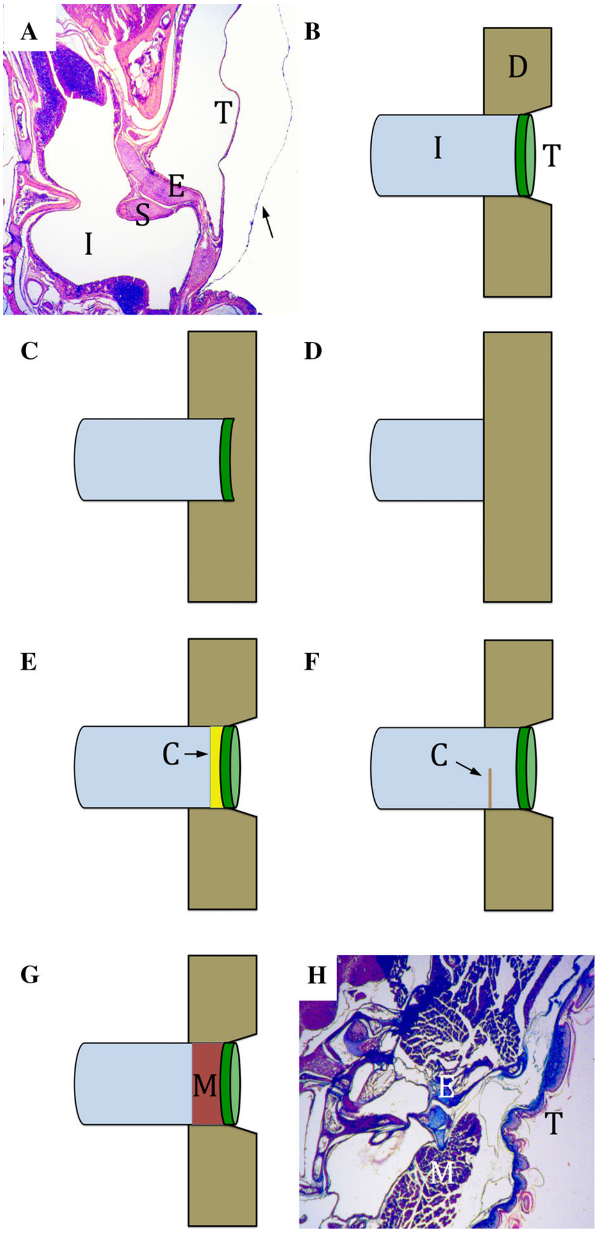

Fig. 4 Variations in the tympanic membrane of squamate reptiles. **a** Frontal section through the tympanic region of *Varanus salvator*, demonstrating the "openness" of this ear and the relatively thin tympanic membrane (there is a desquamation artifact superficial to the membrane, *arrow*); **b** schematic depiction of this ear; **c** schematic depiction of an ear in which the scalation covers the tympanic membrane; **d** schematic depiction of an ear in which the tympanic membrane is completely lost; **e** schematic depiction of an ear in which loose connective tissue abuts the deep (internal) surface of the tympanic membrane; **f** schematic depiction of an ear in which a connective tissue septum is located immediately deep to the tympanic membrane; **g** schematic depiction of an ear in which the inner (deep) surface of the tympanic membrane is covered with skeletal muscle; *h* frontal section through the ear of *Holbrookia maculata*, showing the marked contrast with the condition seen in *Varanus* (**a**). In *Holbrookia*, the tympanic membrane is covered with scalation and the deep surface of the tympanic membrane is covered by an expansion of the depressor mandibulae muscle. *C* connective tissue, *D* dermal covering of the body surface, *E* extrastapes, *I* interaural canal, *M* skeletal muscle, *S* stapes, *T* tympanic membrane

nia, *Xenosaurus*), the stapedial complex attaches to the inner surface of the dermis in the region where the tympanic membrane would normally be found, while in other taxa lacking the tympanic membrane this dermal contact is also lost. Taxa with a stapedial attachment to the dermis probably retain a sensitivity similar to, but slightly less than, taxa in which the tympanic membrane is covered by scalation. If the attachment between the stapedial complex and the dermis is lost, then the sole distal attachment of the stapes is the quadrate bone (Wever 1978).

The quadrate is covered by integument, so routing all reception through the quadrate would increase, not decrease, the mass/inertia and differential frequency response issues described above for the tympanic membrane. It has frequently been postulated that the evolutionary loss of a tympanic membrane is associated with fossoriality (the argument being that moving through the earth would subject the tympanic membrane to too much damage) and that concurrently the restriction of the stapedial complex to the quadrate was associated with a transition from the reception of airborne pressure waves to the reception of vibratory stimuli (see Young 2015). Snakes are the largest group in which the extrastapes attaches solely to the quadrate, and recent experimental work has shown that in *Python regius*, the sensitivity to airborne sound pressure is far lower than that to cephalic vibrations and that, as expected, in both modes of reception the python shows differential sensitivity with a significant loss of higher frequencies (Christensen et al. 2011). Young (2015) argued that the evolution of the jaw suspension and mobility in snakes led to the loss of the tympanic membrane and middle ear cavities and with them the internal coupling of the ears.

In a "typical" reptile, the inner (medial) surface of the tympanic membrane supports an attachment site for the stapedial complex. With the exception of this attachment, which generally involves a small fraction of the membrane surface, the inner surface of the tympanic membrane forms the lateral boundary of the air-filled interaural canal. This is how displacement of the tympanic membrane can result in pressure waves within the interaural canal that, ultimately, form the internal coupling of the tympanic membranes. In some taxa, the lateral margin of the interaural canal is "filled in" with a loose connective tissue and/or adipose tissue. The impact of this connective tissue will depend on three spatial/anatomical features: (1) the degree of direct contact between the connective tissue and the inner (medial) surface of the tympanic membrane, (2) the relative thickness/consistency of the connective tissue, and (3) the relative occlusion or patency of the interaural canal in any parasagittal plane.

If the connective tissue "filling" within the interaural canal abuts the medial surface of the tympanic membrane (as in *Acontias*, Fig. 4e), it may have an acoustical effect similar to that of an integumentary cover over the tympanic membrane.

The lower mass and greater compliance of loose connective tissue would result in lower impedance (when compared to the integumentary covering) and a lesser impact on sound transmission.

If the connective tissue is medial to the tympanic membrane, so that an air-filled space separates them (as is found, for example, in *Cophosaurus* and *Phrynocephalus*), then the acoustical influence will depend on the thickness of the connective tissue layer. A thin connective tissue layer, essentially a membranous septum (Fig. 4f), would have little dampening effect but could hypothetically function like a harmonic coupler, effectively amplifying some frequencies of pressure waves. The biophysics of such a septum could potentially "offset" the influence of a thickened tympanic membrane, thus enhancing the species ability to utilize certain sensory cues. A thicker connective tissue layer, particularly one that was rich in adipose tissue (as is found, for example, in *Anniella* and *Sphenodon*), would practically block any pressure waves created by the tympanic membrane from propagating through the interaural canal. In this configuration, there is no functional coupling between the contralateral tympanic membranes.

Loose or adipose connective tissues are not the only tissues that can extend into the interaural canal. In several squamates (e.g., *Holbrookia*, Fig. 4g, h), skeletal muscle, particularly the depressor mandibulae, expands to cover the inner surface of the tympanic membrane and fill the lateral portion of the interaural canal. The increased mass of skeletal muscle, when compared to loose connective tissue, makes it more likely that the muscle within the interaural canal will have a dampening, rather than a vibratory function. If this skeletal muscle extends throughout the cross-sectional area of the interaural canal, it will likely isolate the displacements of the tympanic membrane, effectively preventing functional coupling between the contralateral ears.

Several aspects of the tympanic portion of internally coupled ears have, at least potentially, a dynamic capacity. In geckos (but not the Sphaerodactylidae), the scalation around the outer surface of the tympanic membrane is mobile and under skeletal muscle control (e.g., Wever 1973). This suggests that the animals could, crudely perhaps, acoustically filter external stimuli by altering the contractile state of these muscles. A skeletal muscle attaching to the middle ear ossicle and/or inner surface of the tympanic membrane has been described in crocodilians and some gekkonid lizards (e.g., Versluys 1898; Baird 1970; Henson 1974; Wever and Werner 1970). Though other functional interpretations have been proffered, Wever (1978) argued (without experimental support) that this muscle would increase tympanic tension, thus changing the distribution between temporal and amplitude cues (Fig. 1). Recently Han and Young (2016) offered the first description of a tympanic muscle in *Varanus* and used a combination of laser Doppler vibrometry and microstimulation to demonstrate that this muscle was capable of altering the tension and vibrational response of the tympanic membrane.

2 Variations in the interaural canal

Vossen et al. (2010) and Vedurmudi et al. (2016a) have shown how the physical dimensions of the interaural canal shape the frequency profile of the pressure waves radiating between the contralateral tympanic membranes. As the volume of the interaural canal decreases, the amplitude cues are lost first (Vedurmudi et al. 2016b), followed by the temporal cues (which become less utile before they are lost). While the influence of varying the size of the interaural canal has been explored mathematically, virtually nothing is known about how the size (or shape) of the interaural canal scales ontogenetically in reptiles—the recent study of *Alligator mississippiensis* by Dufeau and Witmer (2015) is the only clear exception to this paucity of information.

In some reptiles, there are blind-ended expansions, or diverticula, off of the interaural canal. These diverticula are best known in *Chrysemys* which, like all turtles, lacks internally coupled ears (Christensen-Dalsgaard 2011; Carr et al. 2017). Wever (1978) has described diverticula on the interaural canal of other reptiles (Fig. 5a,b). These diverticula could function as resonators; the exact size of the diverticulum and its location along the interaural canal would determine which frequencies were amplified, which were damped, and the fundamental frequency and harmonics that could be produced.

In the Chamaeleonidae, there is a septum near the middle of the interaural canal (Fig. 5c), but this septum is perforated (Wever 1978). A perforated septum should act as a form of acoustic filter, with the exact impact being dependent on the thickness of the septum and the size of the perforation.

The potential impact of these septa and resonators must be evaluated in relation to three considerations: (1) their physical size; (2) the fact that there are two (roughly identical) structures (one on each side of the head) so their influence would be doubled; and (3) the acoustic signature relative to the fundamental frequency of the tympanic membrane, since this will determine how the structures shape the available sensory cues produced by the internal coupling.

In most squamate reptiles, the central portion of the interaural canal is the pharynx. Transverse sections through the interaural canal would demonstrate a considerable amount of morphological variation among reptiles. In some lizards, such as *Gecko*, the interaural canal maintains a relatively similar diameter throughout its length; in others, such as *Varanus*, the pharyngeal portion of the interaural canal is several times "deeper" than the remainder (Figs. 1, 3b, 5d). The pharynx has a greater cranial–caudal extent than the interaural canals in most lizards, but the ratio is certain to vary. In some reptiles,

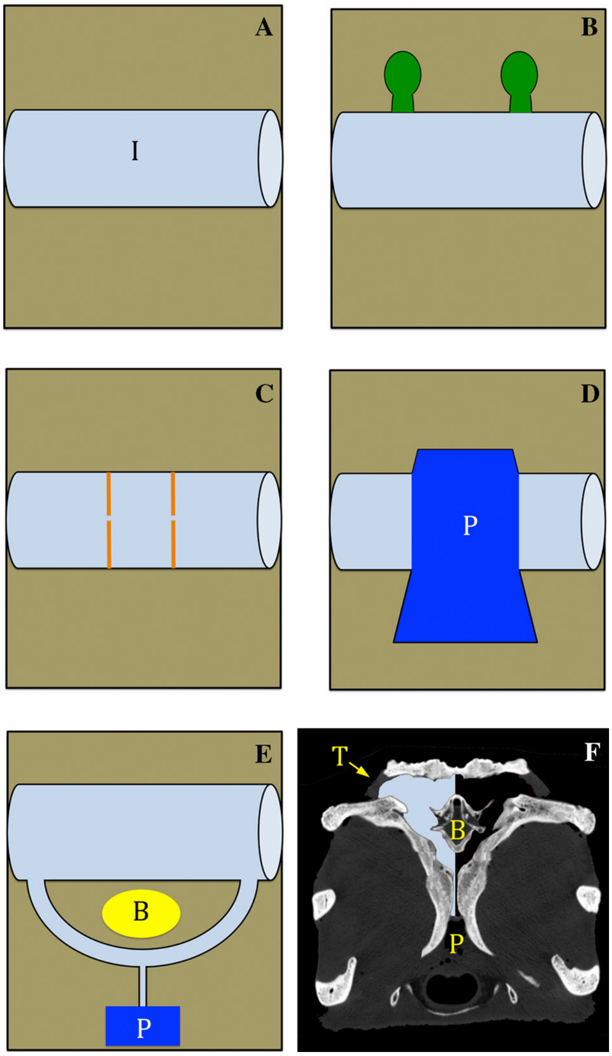

Fig. 5 Variations in the interaural canal in squamate and other reptiles. **a** Schematic of the interaural canal (*I*) coursing through the head; **b** a diverticulate interaural canal; **c** a septate interaural canal; **d** pharyngeal (*P*) expansion relative to the rest of the interaural canal; **e** the condition found in crocodilians in which dorsal and ventral interaural canals course around the braincase (**B**) and a conduit connects the ventral canal to the pharynx (**P**); **f** micro-CT scan through the head of *Alligator mississippiensis* showing the dual interaural canals, the canals on the *left* have been colorized

the pharynx may serve as an inline resonator or acoustic filter. Since the pharynx has the largest volume of any component of the interaural canal, it would confer the least impedance.

In crocodilians, the relationship between the interaural canals and the pharynx is more complicated. A large interaural canal is present superior to the braincase, while a second smaller (and often split) canal courses inferior to the braincase (Witmer and Ridgely 2008). Neither of these canals make direct contact with the pharynx; the inferior interaural canal (or canals) support a short ventrally directed passage which opens to the midline of the pharynx (Fig. 5e). The opening to the pharynx is sealed by a valve of skeletal muscle (Bierman et al. 2014), suggesting that these animals can actively modulate this connection and the acoustic influence on the ear (as suggested by Colbert 1946).

Many reptiles expand their upper throat region (termed the gular pouch) during a variety of behavioral interactions (e.g., Carpenter and Ferguson 1977). The active expansion of this region (which is accomplished by skeletal muscle, Owerkowicz et al. 2001) would increase the size of the pharynx and the pharyngeal portion of the interaural canal. Gular expansion can also be used for ventilatory pumping; the changes in air pressure recorded during gular pumping (Owerkowicz et al. 1999) would also occur during behavioral displays. Given the continuity of these spaces, any pressure change within the gular pouch would also be present on the deep surface of the tympanic membrane. Pressure change on the deep (internal) surface of the tympanic membrane would alter the tension (fundamental frequency) of the membrane, thereby altering the frequency profiles of the temporal and amplitude sensory cues (Fig. 1). Han and Young (2016) used laser Doppler vibrometry to demonstrate that pressurization of the gular pouch of *Varanus* resulted in significant changes in the frequency response of the tympanic membranes.

The internally coupled ears of reptiles have been explored from both theoretical (e.g., Vossen et al. 2010; Christensen-Dalsgaard 2011) and experimental (e.g., Christensen-Dalsgaard and Manley 2005, 2008; Bierman et al. 2014) perspectives. While these studies have clearly demonstrated the bioacoustic significance of this auditory system, they have involved representatives from only a few reptilian clades, and far $<1\,\%$ of the extant reptilian species. As such, little is known about the magnitude of interspecific variation within this auditory system.

A particularly intriguing aspect of the relationship between morphological variation and the function of internally coupled ears is the presence of dynamic components within this system. The mathematical formalizations of this system (Vossen et al. 2010; Vedurmudi et al. 2016a,b) have (somewhat by necessity) treated these systems as static constructs. One common feature of the internally coupled ears of reptiles appears to be the presence of skeletal muscle either along a segment of the interaural canal (squamates) or at the junction between the interaural canal and the pharynx (crocodilians). Previous studies have shown that the concave-eared torrent frog (*Odorrana tormota*) uses skeletal muscle to occlude the interaural canal, functionally isolating the tympanic membranes (Gridi-Papp et al. 2008). While there is no experimental support for a similar system in reptiles, the recent evidence that *Varanus* is capable of actively modulating the biophysical response of its tympanic membrane (Han and Young 2016) suggests that reptilian audition may be more dynamic than previously recognized. Active regulation of the tympanic membrane, or other aspects of internally coupled ears, would enable a reptile to tune its auditory performance to maximize certain sensory cues.

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