

**REVIEW**

# The vertebrate middle and inner ear: A short overview

Cathrin Pfaff<sup>1</sup>  | Julia A. Schultz<sup>2,3</sup>  | Rico Schellhorn<sup>3</sup> <sup>1</sup>University of Vienna, Department of Palaeontology, Vienna, Austria<sup>2</sup>University of Chicago, Department of Organismal Biology and Anatomy, Chicago, Illinois, USA<sup>3</sup>Rheinische Friedrich-Wilhelms-Universität Bonn, Steinmann Institut für Geologie, Mineralogie und Paläontologie, Bonn, Germany**Correspondence**

Cathrin Pfaff, University of Vienna, Department of Palaeontology Geozentrum, UZA II Althanstrasse 14, 1090 Vienna Austria. Email: cathrin.pfaff@univie.ac.at

The evolution of the various hearing adaptations is connected to major structural changes in nearly all groups of vertebrates. Besides hearing, the detection of acceleration and orientation in space are key functions of this mechanosensory system.

The symposium “show me your ear – the inner and middle ear in vertebrates” held at the 11th International Congress of Vertebrate Morphology (ICVM) 2016 in Washington, DC (USA) intended to present current research addressing adaptation and evolution of the vertebrate otic region, auditory ossicles, vestibular system, and hearing physiology. The symposium aimed at an audience with interest in hearing research focusing on morphological, functional, and comparative studies. The presented talks and posters lead to the contributions of this virtual issue highlighting recent advances in the vertebrate balance and hearing system. This article serves as an introduction to the virtual issue contributions and intends to give a short overview of research papers focusing on vertebrate labyrinth and middle ear related structures in past and recent years.

**KEYWORDS**

auditory ossicles, bony labyrinth, otic region, vestibular system

## 1 | INTRODUCTION

The vertebrate ear region, - middle ear structures and labyrinth - is one of the most intricate anatomical systems and has been in the focus of various studies over the centuries. With the increasing application of high resolution and noninvasive computer tomography since the 1980s, 3D visualization and their respective analyses became essential for anatomical studies of the middle and inner ear.

The vertebrate ear combines two main functions: balance and hearing. The vestibular part of the inner ear is the organ of equilibrium detecting head and body movements during locomotion (e.g., swimming, running, and flying). The semicircular canals (SCs) (three in gnathostomes: anterior semicircular canal, posterior semicircular canal, lateral/horizontal semicircular canal) of the vestibular system detect angular acceleration, while utricle and saccule detect linear acceleration (e.g., Breuer, 1903; de Burlet, 1934; Retzius, 1881). Sound conduction and perception in living vertebrates is performed by the stapedial structure and lagenar recess (in nonmammalian tetrapods), or middle ear ossicles and the cochlea (in mammals; e.g., Doran, 1878; Fleischer, 1978). Those ossicles transmit vibrations from the eardrum (except in nonmammalian tetrapods; Clack & Anderson, 2016) to the

fenestra vestibuli/fenestra ovalis of the vestibule (e.g., Fleischer, 1973; Gray, 1907).

This contribution provides a short overview of the history of research related to the vertebrate middle and inner ear, without any claim on completeness. Furthermore, it highlights evolutionary concepts and serves as an introduction to the virtual issue of the Journal of Morphology uniting research papers related to function and morphology of auditory ossicles of the middle ear and membranous as well as bony labyrinth (skeletal labyrinth: prismatic and globular calcified cartilage in chondrichthyan fishes [Mason & Summers, 2006]) in vertebrates, motivated by the symposium. This virtual issue of the Journal of Morphology provides a unique opportunity to collectively present the current state of research as a synopsis of the symposium.

### 1.1 | Middle ear

The evolutionary origin of the vertebrate middle ear related structures is considered to lie in the hyostyl jaw apparatus (composed of mandibular arch, hyomandibular, and ceratohyal bones) of elasmobranchs (Gegenbaur 1872, 1898, Goodrich, 1930, reviewed by Gaupp, 1898). However, form, function, and homology of these middle ear elements

(auditory ossicles) of vertebrates have been contradictorily discussed since the beginning of the 16th century (reviewed by Gitter, 1990).

Étienne Geoffroy Saint-Hilaire (1818) and Lorenz Oken (1825) were among the first who postulated that the mammalian middle ear ossicles are homologous to the opercular bones of teleosts (contradictory views: Rudolphi, 1821; Huschke, 1824; Henson, 1974). But hearing in cartilaginous and bony fishes is different from hearing in tetrapods and is convergently realized by a great variety of anatomical settings (Fay & Popper, 1978; Popper & Fay, 1977; Retzius, 1881; Tavalga, Popper, & Fay, 1981; Wever, 1974).

In sharks, hearing is realized by the two displacement systems (cupulae with sensory hair cells) of the lateral line receptors and the labyrinth (Dijkgraaf, 1963; Harris & van Bergeijk, 1962), whereas in bony fishes several sound transmission systems exist. In the latter, hearing is realized by the close relationship of the swim bladder and ear region (e.g., notopterids, beryciforms) or by small gas-filled vesicles extending from the swim bladder (e.g., clupeids, mormyrids; Platt & Popper, 1981). The size of these vesicles (Alexander, 1959; Blaxter, 1981; Poggendorf, 1952) and the distance to the inner ear influence the hearing ability of the specimens (Coombs & Popper, 1979; Jerkø, Turunen-Rise, Enger, & Sand, 1989). The swim bladder itself plays an important role in the hearing process of fishes like the detection of long-distance frequencies and spatial hearing. In comparison, fishes without an air-filled cavity are not able to hear sounds outside their near-field (Schellart & Popper, 1991; Siler, 1969). A well investigated system for sound transmissions are the Weberian ossicles (tripus, intercalarium, scaphium, and claustrum) of extant and extinct otophysine fishes. A double chain of ossicles connects the inner ear labyrinth with the swim bladder to enhance hearing sensitivity (see Friedman & Giles, 2016). An analogous structure to this mechanic sensory system is also found in Chanidae (Actinopterygii, Gonorynchiformes), which presumably enhances audition (Rosen & Greenwood, 1970). Absolute sensitivity and hearing bandwidth depends on the anatomical relationships of the hearing related structures, but more importantly on the type of connection between the otolith organs and gas-filled spaces (Blaxter, 1981).

Hearing abilities are strongly depending on the acoustic environment (Hawkins, 1981). When the earliest vertebrates left the water to conquer terrestrial habitats, they were still primarily aquatic animals (Clack, 1997, 2002; Coates & Clack, 1991), but were suddenly confronted with airborne sound. The otic region of the earliest tetrapods from the Late Devonian (*Acanthostega gunnii*, *Ichthyostega* spp.) differs anatomically from the derived amniote ear (e.g., in mammals) in showing large and bulky stapedial bones (relative to braincase size) capable of the detection of substrate-borne vibrations (Clack et al., 2003; Clack & Anderson, 2016). They possibly could only hear low-frequency, ground- or water-borne sounds, which are concordant with the supporting-brace function of the stapes connecting the cranium (Manley, 2010).

One of the key innovations of extant sauropsids, mammals, and anurans (except of gymnophiones and caudates) is the tympanum (tympanic membrane) overlying an air-filled middle ear cavity with ossicles transmitting the sound to the oval window of the inner ear (Hetherington, 1992). This type of middle ear for transmitting airborne sound evolved multiple times independently within terrestrial

tetrapods, reflected for example by the position of the tympanum in relation to Meckel's cartilage or the existence of the extrastapes in sauropsids (Gaupp, 1913; Lombard & Bolt, 1979), but also found in ontogenetic sequences of developmental studies (Tucker, Watson, Lettice, Yamada, & Hill, 2004; reviewed by Tucker, 2017).

In anuran amphibians, the stapes runs through connective and muscle tissue to reach the oval window (Jaslow, Hetherington, & Lombard, 1986; Wever, 1985). At its distal end it connects to an extrastapes (Mason & Narins, 2002) that passes medially (Hetherington, 1992). Covered by a tympanum, the convergently evolved opercularis system is found in metamorphous anurans and salamanders (Hetherington, 1992; Hetherington, Jaslow, & Lombard, 1986; Kingsbury & Reed, 1909; Wever, 1985), which does not occur in completely aquatic and neotenic salamanders and gymnophiones (Hetherington, 1992). This system consists of an opercularis muscle originating from the pectoral girdle and inserting on the otic operculum, which rests in the oval window (Hetherington, 1992). Its function is controversially discussed (Eiselt, 1941; Hetherington, 1985, 1992; Kingsbury & Reed, 1909; Lombard & Straughan, 1974; Wever, 1979, 1985), but it has commonly been assumed that the opercularis system represents the reduction and loss of the middle ear covered by a tympanic membrane possibly due to the lack of vocalization of the respective species (Hetherington, 1992; contradictory view: McDiarmid, 1971, Trueb & Alberch, 1985, Jaslow et al., 1986) and is also considered as a nontympanic pathway of sound perception. However, auditory systems for transmitting sound are highly influenced by evolutionary changes of the body size and shape of amphibians and as a result those changes determined the evolution of the mechanisms of the acoustic reception (Hetherington, 1992).

Some sauropsids (e.g., *Ophisaurus apodus*, *Gecko gecko*, *Eublepharis maculatus*) are able to close their external acoustic meatus with a meatal muscle, possibly for protection against mechanical damage or their own sound (Wever, 1978). In sauropsids, the tympanic middle ear consists of the tympanic membrane connecting to the proximal element of the columella. The footplate of the columella sits in the oval window and transmits the detected sound waves to the scala vestibuli of the membranous labyrinth (Wever, 1978). In some nonmammalian amniotes an extracolumella can occur between tympanic membrane and columella (e.g., in archosaurs and turtles). Whereas the columella is an ossified slender rod with an expanded footplate articulating into the oval window, the extracolumella is entirely cartilaginous showing a number of processes for stiffening the tympanic membrane and transmitting the vibrations. The joint between these two middle ear elements are flexible but can also be a solid union strengthened by a layer of connective tissue (Wever, 1978).

The transition from early to advanced nonmammalian amniotes represents one of the major key steps in the evolution of the vertebrate middle ear. Via the "single-ossicle" middle ear (stapes) of nonmammalian amniotes, sounds bouncing off the skin surface are transmitted to the cochlear duct (Manley, 2010).

In the 19th century, Georges Cuvier (1805) described the middle ear bones of amphibians, sauropsids (lepidosaurs, archosaurs), and mammals, in detail without comparing their anatomical differences and evolutionary history. Following these first anatomical descriptions of the middle ear ossicles, Carus (1818) and Reichert (1837) published the

theory that the mammalian stapes is a homologue of the columella auris of nonmammalian amniotes (reviewed by Russell, 1916). Reichert (1837) hypothesized that two of the mammalian middle ear ossicles (malleus, incus) derived from upper (palatoquadrate) and lower jaw elements (Meckel's cartilage) of primitive gnathostomes. This was followed by a series of scientifically important descriptions of the nonmammalian amniote ear (e.g., Hasse, 1871; Kuhn, 1882; Retzius, 1880, 1884). It took additional 75 years to modify and validate Reichert's theory (Gaupp, 1911a, 1911b, 1913). The 'Reichert-Gauppsche Theorie' (Gaupp, 1911a; Reichert, 1837) basically describes the revolutionary view that the primary jaw joint between quadrate and the articular lost its function in mammals, and that a secondary jaw joint situated between the squamosal and dentary bone is developed. During this process, dentary elements detach from the lower jaw and transform into delicate bony elements for sound conduction that are integrated into the middle ear cavity inside the mammalian skull (Anthwal, Joshi, & Tucker, 2013; Takechi & Kuratani, 2010). These works fundamentally contributed to the finding that the stapes of mammals is homologous to the columella of nonmammalian amniotes and the origin of this bone is considered to be the second pharyngeal arch of ancestral gnathostomes. These results from comparative analyses were recently confirmed by genetic labeling experiments (Thompson, Ohazama, Sharpe, & Tucker, 2012).

The middle ear of modern mammals composed of malleus (hammer), incus (anvil), and stapes (stirrup) is laterally restricted by the ectotympanic ring and completely detached from the mandible (Allin, 1975; Allin & Hopson, 1992). Complex bone reorganization of the mandible occurred during detachment of the mammalian middle ear, which is well supported by fossil evidence (e.g., Allin & Hopson, 1992; Kermack, Mussett, & Rigney, 1981; Luo, Schultz, & Ekdale, 2016; Manley & Sienknecht, 2013; Martin & Luo, 2005; Meng, Bi, Zheng, & Wang, 2016; Meng, Wang, & Li, 2011). Clearing and staining techniques using ontogenetic sequences drew an even clearer picture of the evolution of the mammalian middle ear in more recent years (Anthwal et al., 2013; Ramírez-Chaves et al., 2016a; Ramírez-Chaves, Weisbecker, Wroe, & Phillips, 2016b; Rich, Hopson, Musser, Flannery, & Vickers-Rick, 2005; Urban et al., 2017). Developmental genetics and gene patterning of early ontogenetic stages of extant mammalian species helped to identify complex homoplasies (convergences and reversals) in the evolution of the mammalian secondary jaw joint and middle ear (Maier, 1990; Zeller, 1993; Tucker et al., 2004; Luo, 2011; Kitazawa et al., 2015). The functional shift of elements used for feeding into elements used for hearing is impressively traceable in advanced cynodonts (e.g., *Diarthrognathus*), which possess both functional jaw joints (primary and secondary) at the same time (Allin, 1975; Hopson, 1966; Takechi & Kuratani, 2010). The segregation of the middle ear ossicles from the lower jaw and incorporation into the basicranium is also traceable in the ontogeny of marsupials (Maier, 1990). Even if this morphological transition is well understood, the evolutionary chronology is still controversially discussed (e.g., Segall, 1969, 1973). Doran (1878) conducted the most comprehensive anatomical study of the mammalian middle ear ossicles focusing on the evolutionary morphology of auditory ossicles. Special emphasis must be placed on the work of Fleischer (1973) who distinguished distinct types of articulation between malleus and incus (e.g., freely mobile, micro) and discussed the implications for the mammalian phylogeny and evolution. However, both Doran (1878)

and Fleischer (1973) made mistakes in the anatomy of the Processus anterior mallei and ignored its additional processus internus articularis (Maier & Ruf, 2016).

## 1.2 | Inner ear

The inner ear (labyrinth) of vertebrates comprises two main functions: (a) balancing of the individual using the ampullae of the three SCs and the sensory field of utriculus and sacculus, and (b) hearing ability with the sensory hair cells of basilar papilla of the lagena of nonmammalian amniotes (the homologous structure in mammals is the coiled cochlea with the organ of Corti). The inner ear is composed of a membranous system (membranous labyrinth) filled with endolymphatic fluid enclosed inside a bony endocast (bony labyrinth), filled with perilymphatic fluid. Both fluids differ in their concentration of potassium and sodium (e.g., Ferrary, Huy, Roinel, Bernard, & Amiel, 1988; Sterkers, Ferrary, & Amiel, 1988; Thalmann & Thalmann, 1999). The membranous system of the inner ear is separated in pars superior (utricule and three semicircular canals) and pars inferior (sacculle and cochlear duct; de Burlet, 1929).

In all vertebrates, movement of the animal head and body causes movement of the endolymphatic fluid. Physiologically, this initiates mechanical displacement of the hair cells of the sensory fields of the ampullae and maculae in the inner ear and causes nerve stimulation. The ampullae of the SCs filled with fluid detect rotational movement of the organism, whereas the otolithic layer of the maculae of the vestibule detects longitudinal and vertical acceleration during locomotion (e.g., Ekdale, 2013; Steinhausen, 1933; Van Egmond, Groen, & Jongkees, 1949).

In jawless vertebrates, the number of SCs varies (Retzius, 1881; Stensiö, 1927). The vestibular system of hagfishes shows one semicircular canal (Jørgensen, Shichiri, & Geneser, 1998), while lampreys possess two symmetric horizontal ducts in each labyrinth (Maklad, Reed, Johnson, & Fritzsche, 2014). In the teleost ear, the highest anatomical variation is seen in the lagena and the sacculus, whereas the semicircular canals and the utriculus are less variable (Platt & Popper, 1981). In terrestrial vertebrates, the middle ear communicates with the inner ear via the oval window (fenestra vestibuli) by moving the footplate of the stapes. The oval window represents a remnant of the lateral otic fissure in tetrapodomorph fishes (e.g., *Eusthenopteron*) and early tetrapods, which remains unossified during embryogenesis (Clack, 2016). The round window (fenestra cochleae) is covered by the secondary tympanic membrane (Zeller, 1985), which equalizes pressure induced by the movement of the lymphatic liquid within the membranous ducts of the inner ear (de Burlet, 1934).

In the 16th century, Bartholomeus Eustachius discovered the cochlear part of the ear, which was denoted by Gabriel Falloppio as "cochlea" in 1561 (Gitter, 1990). Politzer (1907) and more recently Hachmeister (2003) extensively reviewed the history of studies focusing on the anatomy and physiology of the inner ear. The early studies of the inner ear anatomy are mainly based on observations and descriptions of dissected human corpses. In the 19th and 20th centuries, many comparative studies used dissection techniques, which enable the extraction of the inner ear endocast from the surrounding bone (Gray, 1907; Retzius, 1881, 1884). Hyrtl (1873) provided the

most comprehensive visualization of the mammalian bony labyrinths. He modified his previously established procedure of “Corrosionsanatomie” (see methodology in Hyrtl, 1845), in which metal based or wax-like fluids are filled in the cavity of the bony labyrinth before the bone is removed. In the early 1980s, the investigation of fragile fossil material with destructive methods was increasingly replaced by noninvasive computer tomography scanning (e.g., Conroy & Vannier, 1984; Hoffmann, Schultz, et al., 2014a), which provides a method to virtually reconstruct the internal anatomy of the bony labyrinth. As then, dozens of studies focus on aspects of phylogeny (e.g., Benoit et al., 2015; Lebrun, De León, Tafforeau, & Zollikofer, 2010; Maisey, 2001), physiology (e.g., Armstrong, Bloch, Houde, & Silcox, 2011; Coleman & Colbert, 2007; Kirk & Gosselin-Ildari, 2009; Manoussaki et al., 2008), ontogeny (Billet, de Muizon, et al., 2015; Costeur, Mennecart, Müller, & Schulz, 2017; Ekdale, 2010; Mennecart & Costeur, 2016; Sánchez-Villagra & Schmelzle, 2007), paleobiology (e.g., David et al., 2010; Neenan & Scheyer, 2012; Pfaff Nagel, et al., 2017; Spoor, Bajpai, Hussain, Kumar, & Thewissen, 2002) or functional morphology (e.g., Coutier, Hautier, Cornette, Amson, & Billet, 2017; Grohé, Tseng, Lebrun, Boistel, & Flynn, 2016; Pfaff, Czerny, Nagel, & Kriwet, 2017b; Pfaff, Martin, & Ruf, 2015; Ruf et al., 2016; Schellhorn, 2018a; Schutz, Jamniczky, Hallgrímsson, & Garland, 2014; Spoor et al., 2007) of the labyrinth organ in extant but also extinct taxa. Anatomical correlations between membranous and bony labyrinths seem underrepresented, and precise and detailed descriptions based on histological serial and thin sections are valuable (e.g., Maier, 2013; Maier & van den Heever, 2002; Schultz, Zeller, & Luo, 2017; Starck, 1995; Wever, 1978, 1985).

Even though Hyrtl (1873) doubted any correlation between the structure of the vestibular system and locomotion type, recent functional investigations of the inner ear morphology in a variety of vertebrates based on micro-CT scanning clearly show that shape and locomotion are linked (e.g., Berlin, Kirk, & Rowe, 2013; Billet et al., 2012; Cox & Jeffrey, 2010; David et al., 2010; Malinzak, Kay, & Hullar, 2012; Pfaff et al., 2015; Pfaff, Czerny, et al., 2017b; Ryan et al., 2012; Spoor et al., 2007; Spoor, Wood, & Zonneveld, 1994; Spoor & Zonneveld, 1998). Even though, the results of these studies appear controversial between different orders (e.g., functional-morphological distinction based on size of SCs vs. diameter of SCs), the diameter and arc size of the SCs are positively correlated among vertebrates and are not independent from one another (Muller, 1999). In addition to locomotion modes, also the head posture of the investigated specimens can be reconstructed (e.g., De Beer, 1947, Blanks, Curthoys, & Markham, 1972, Coutier et al., 2017, contradictory view: Spoor, 2003) and, therefore, feeding preferences in their lifestyle (Schellhorn, 2018a). Most of these studies assume that the anatomy of the vestibular system is quite conservative. However, in some mammalian groups (e.g., Xenarthrans) the anatomy of the bony labyrinth is highly diverse (Billet et al., 2012). Besides functional and morphological adaptations, phylogenetic signals can be seen in the anatomy of the vestibular system (e.g., Billet, Hautier, & Lebrun, 2015; Mennecart & Costeur, 2016).

The shape and number of coils of the mammalian cochlea is known to have a strong phylogenetic signal (Ekdale, 2016a). Monotremes and early mammaliaforms show less than 360° (Luo, Ruf, & Martin, 2012; Luo, Ruf, Schultz, & Martin, 2011; Rowe, 1996; Ruf,

Luo, & Martin, 2013; Ruf, Luo, Wible, & Martin, 2009). In monotremes, the cochlear apex containing the lagena is coiled and enlarged (Schultz et al., 2017), while gondwanatherian mammals show a short tapering cochlear canal with a slightly curved apex (Hoffmann, O'Connor, Kirk, Wible, & Krause, 2014). Therian mammals (marsupials and placentals) show at least one full turn but can have more than three turns (e.g., 3.25 in domestic cats [Schellhorn, 2018b], or 3.3 in whales [Ekdale, 2016b]). Furthermore, the shape of the cochlear is phylogenetically informative in whales (toothless: Ekdale, 2016b; toothed: Costeur et al., 2018).

The evolution of the amphibian inner ear on its way to amniotes is controversially discussed (Lombard, 1977; Romer & Price, 1940; Wever, 1974, 1976). The course of the connection between the periotic tube represented in amphibians as the periotic canal and in amniotes as the scala vestibuli, helicotrema and scala tympani, differs substantially, which questions the homology of these structures (Wever, 1976; reviewed by Lombard & Bolt, 1979) and, therefore, disagreement about the homology of the amphibian basilar papilla with the organ of Corti exists. The papilla amphibiorum of anurans was shown not to be homologous to the basilar papilla of nonmammalian amniotes and the organ of Corti of mammals (de Burlet, 1934; but see Fleischer, 1973). However, it is commonly assumed that the amniotic basilar papilla is the positional homolog to the therian organ of Corti although it is histologically distinct (see Fritzsche et al., 2013). Additionally, it is postulated that during the mammalian evolution the sensory basilar papilla of the lagena was integrated into the apex of the organ of Corti at the apex of the cochlear duct. This evolutionary transformation presumably had occurred after the monotreme-therian split, and within the theriomorph evolution (Schultz et al., 2017).

### 1.3 | Future perspectives

Since the expanding availability of noninvasive microcomputed tomography anatomical investigations of the middle and inner ear region of extant and extinct vertebrates are of still growing interest to the scientific community addressing complex questions. For example, the evolution of the huge diversity of the membranous inner ear labyrinth morphology, the function of the vestibular system for detecting acceleration and deceleration of the head and related transmission of sensory signals, the evolution of the mammalian coiled cochlea for enhanced hearing capability, and many more. Recently conducted studies focus on phylogenetic signals to contribute to the tree of life and reveal ecological adaptations. The goal of the symposium held at the 11th ICVM was to exchange newly acquired insights, new technical approaches, and exchange of information addressing anatomical meaning of the bony structure of inner and middle ear related structures in the system of vertebrates.

### ACKNOWLEDGMENTS

The authors thank all participants of the ear symposium at the ICVM Meeting, and furthermore the contributors to this virtual issue, Larry Witmer and colleagues for organizing the ICVM meeting, and J. Matthias Starck for the opportunity to give us a forum for publishing middle and inner anatomy in a broader context with this virtual



issue. We also want to thank the editor and one anonymous reviewer for their helpful comments and suggestions. RS received support via a congress participation grant of the DAAD (Deutscher Akademischer Austauschdienst; German Academic Exchange Service) to participate in the 11th ICVM meeting 2016 in Washington DC (USA). There was no additional funding to support the symposium.

## CONFLICT OF INTERESTS

There are no Conflict of interests.

## AUTHORS' CONTRIBUTIONS

All authors drafted the manuscript, and gave final approval for publication.

## ORCID

Cathrin Pfaff  <https://orcid.org/0000-0001-5539-2097>

Julia A. Schultz  <https://orcid.org/0000-0003-3147-6346>

Rico Schellhorn  <https://orcid.org/0000-0003-4890-3025>

## REFERENCES

- Alexander, R., & Mc, N. (1959). The physical properties of the swimbladders of fish other than Cypriniformes. *Journal of Experimental Biology*, 36, 347–355.
- Allin, E. F. (1975). Evolution of the mammalian ear. *Journal of Morphology*, 147, 403–437.
- Allin, E. F., & Hopson, J. A. (1992). Evolution of the auditory system in Synapsida ("mammal-like reptiles" and primitive mammals) as seen in the fossil record. In D. B. Webster, R. R. Fay, & A. N. Popper (Eds.), *The evolutionary biology of hearing* (pp. 587–614). New York: Springer-Verlag.
- Anthwal, N., Joshi, L., & Tucker, A. S. (2013). Evolution of the mammalian middle ear and jaw: Adaptations and novel structures. *Journal of Anatomy*, 222(1), 147–160.
- Armstrong, S. D., Bloch, J. I., Houde, P., & Silcox, M. T. (2011). Cochlear labyrinth volume in euarchontoglires: Implications for the evolution of hearing in primates. *Anatomical Record*, 294(2), 263–266.
- Benoit, J., Lehmann, T., Vatter, M., Lebrun, R., Merigeaud, S., Costeur, L., & Tabuce, R. (2015). Comparative anatomy and three-dimensional geometric-morphometric study of the bony labyrinth of Bibymalagasia (Mammalia, Afrotheria). *Journal of Vertebrate Paleontology*, 35(3), e930043.
- Berlin, J. C., Kirk, E. C., & Rowe, T. B. (2013). Functional implications of ubiquitous semicircular canal non-orthogonality in mammals. *PLoS One*, 8(11), e79585.
- Billet, G., de Muizon, C., Schellhorn, R., Ruf, I., Ladevèze, S., & Bergqvist, L. (2015). Petrosal and inner ear anatomy and allometry amongst specimens referred to Litopterna (Placentalia). *Zoological Journal of the Linnean Society*, 173(4), 956–987.
- Billet, G., Hautier, L., Asher, R. J., Schwarz, C., Crumpton, N., Martin, T., & Ruf, I. (2012). High morphological variation of vestibular system accompanies slow and infrequent locomotion in three-toed sloths. *Proceedings of the Royal Society B: Biological Sciences*, 279(1744), 3932–3939.
- Billet, G., Hautier, L., & Lebrun, R. (2015). Morphological diversity of the bony labyrinth (inner ear) in extant xenarthrans and its relation to phylogeny. *Journal of Mammalogy*, 96(4), 658–672.
- Blanks, R. H. I., Curthoys, O. S., & Markham, C. H. (1972). Planar relationships of semicircular canals in the cat. *American Journal of Physiology*, 223(1), 55–62.
- Blaxter, J. H. S. (1981). The Swimbladder and hearing. In W. N. Tavolga, A. N. Popper, & R. R. Fay (Eds.), *Hearing and sound communication in fishes* (pp. 61–73). New York: Springer.
- Breuer, J. (1903). Studien über den Vestibularapparat. *Sitzungsberichte der Akademie der Wissenschaft Berlin*. (pp. 80). Vienna: Karl Gerold sen. Report Number: 113.
- Carus, C. G. (1818). *Lehrbuch der Zootomie*. Leipzig: Fleischer.
- Clack, J. A. (1997). The evolution of tetrapod early and the fossil record. *Brain, Behaviour and Evolution*, 50, 198–212.
- Clack, J. A. (2002). Patterns and processes in the early evolution of the tetrapod ear. *Journal of Neurobiology*, 53, 251–264.
- Clack, J. A. (2016). Vertebrate diversity in a sensory system: The fossil record of otic evolution. In J. A. Clack, R. R. Fay, & A. N. Popper (Eds.), *Evolution of the vertebrate ear: Evidence from the fossil record* (pp. 1–16). Cham: Springer International Publishing.
- Clack, J. A., Ahlberg, P. E., Finney, S. M., Dominguez Alonso, P., Robinson, J., & Ketcham, R. A. (2003). A uniquely specialized ear in a very early tetrapod. *Nature*, 425, 65–69.
- Clack, J. A., & Anderson, J. S. (2016). Early tetrapods: Experimenting with form and function. In J. A. Clack, R. R. Fay, & A. N. Popper (Eds.), *Evolution of the vertebrate ear: Evidence from the fossil record* (pp. 71–105). Cham: Springer International Publishing.
- Coates, M. I., & Clack, J. A. (1991). Fish-like gills and breathing in the earliest known tetrapod. *Nature*, 352, 234–236.
- Coleman, M. N., & Colbert, M. W. (2007). Technical note: CT thresholding protocols for taking measurements on three-dimensional models. *American Journal of Physical Anthropology*, 133(1), 723–725.
- Conroy, G. C., & Vannier, M. W. (1984). Noninvasive three-dimensional computer imaging of matrix-filled fossil skulls by high-resolution computed tomography. *Science*, 226(4673), 456–458.
- Coombs, S., & Popper, A. N. (1979). Hearing differences among Hawaiian squirrelfish (Holocentridae) related to differences in the peripheral auditory system. *Journal of Comparative Physiology*, 132, 203–207.
- Costeur, L., Grohé, C., Aguirre-Fernández, G., Ekdale, E., Schulz, G., Müller, B., & Mennecart, B. (2018). The bony labyrinth of toothed whales reflects both phylogeny and habitat preferences. *Scientific Reports*, 8, 7841.
- Costeur, L., Mennecart, B., Müller, B., & Schulz, G. (2017). Prenatal growth stages show the development of the ruminant bony labyrinth and petrosal bone. *Journal of Anatomy*, 230(2), 347–353.
- Coutier, F., Hautier, L., Cornette, R., Amson, E., & Billet, G. (2017). Orientation of the lateral semicircular canal in Xenarthra and its links with head posture and phylogeny. *Journal of Morphology*, 278(5), 704–717.
- Cox, P. G., & Jeffrey, N. (2010). Semicircular canals and agility: The influence of size and shape measures. *Journal of Anatomy*, 216, 37–47.
- Cuvier, G. (1805). *Leçons d'anatomie comparée. Tome II: Les organes des sensations*. Paris: Baudoin.
- David, R., Droulez, J., Allain, R., Berthoz, A., Janvier, P., & Bennequin, D. (2010). Motion from the past. A new method to infer vestibular capacities of extinct species. *Compte Rendu Palevol*, 9, 397–410.
- De Beer, G. R. (1947). How animals hold their heads. *Proceeding of the Linnean Society London*, 159, 125–139.
- de Burlet, H. M. (1929). Zur vergleichenden Anatomie und Physiologie des perilymphatischen Raumes. *Acta Oto-Laryngologica*, XIII, 153–187.
- de Burlet, H. M. (1934). Vergleichende Anatomie des stato-akustischen Organs. In L. Bolk, E. Göppert, E. Kallius, & W. Lubosch (Eds.), *Handbuch der vergleichenden Anatomie der Wirbeltiere* (pp. 1293–1380). Berlin: Urban & Schwarzenberger.
- Dijkgraaf, S. (1963). The functioning and significance of the lateral-line organs. *Biological Reviews*, 38, 51–105.
- Doran, A. H. (1878). XVIII. Morphology of the mammalian ossicula auditūs. *Transactions of the Linnean Society of London. 2nd Series: Zoology*, 1(7), 371–497.
- Eiselt, J. (1941). Der Musculus opercularis und die Mittlere Ohrsphäre der anuren Amphibien. *Archiv für Naturgeschichte*, 10, 179–270.
- Ekdale, E. G. (2010). Ontogenetic variation in the bony labyrinth of *Monodelphis domestica* (Mammalia: Marsupialia) following ossifications of the inner ear cavities. *The Anatomical Record*, 293(11), 1896–1912.
- Ekdale, E. G. (2013). Comparative anatomy of the bony labyrinth (inner ear) of placental mammals. *PLoS One*, 8(6), e66624.

- Ekdale, E. G. (2016a). Form and function of the mammalian inner ear. *Journal of Anatomy*, 228(2), 324–337.
- Ekdale, E. G. (2016b). Morphological variation among the inner ears of extinct and extant baleen whales (Cetacea: Mysticeti). *Journal of Morphology*, 277(12), 1599–1615.
- Fay, R. R., & Popper, A. N. (1978). Structure and function in teleost auditory system. In A. N. Popper & R. R. Fay (Eds.), *Comparative studies of hearing in vertebrates* (pp. 3–42). Berlin: Springer Verlag.
- Ferrary, E., Huy, P. T. B., Roinel, N., Bernard, C., & Amiel, C. (1988). Calcium and the inner ear fluids. *Acta Oto-Laryngologica*, 105(Suppl. 460), 13–17.
- Fleischer, G. (1973). Studien am Skelett des Gehörorgans der Säugetiere, einschließlich des Menschen. *Säugetierkundliche Mitteilungen*, 21, 131–239.
- Fleischer, G. (1978). Evolutionary principles of the mammalian middle ear. *Advances in Anatomy, Embryology and Cell Biology*, 55(5), 1–77.
- Friedman, M., & Giles, S. (2016). Actinopterygians: The ray-finned fishes—An explosion of diversity. In J. A. Clack, R. R. Fay, & A. N. Popper (Eds.), *Evolution of the vertebrate ear: Evidence from the fossil record* (pp. 17–49). Cham: Springer International Publishing.
- Fritsch, B., Pan, N., Jahan, I., Duncan, J. S., Kopecky, B. J., Elliott, K. L., ... Yang, T. (2013). Evolution and development of the tetrapod auditory system: An organ of Corti-centric perspective. *Evolution & Development*, 15, 63–79.
- Gaupp, E. (1898). Ontogenese und Phylogenese des schall-leitenden Apparates bei den Wirbeltieren. *Ergebnisse der Anatomischen Entwicklungsgeschichte*, 8, 990–1149.
- Gaupp, E. (1911a). Beiträge zur Kenntnis des Unterkiefers der Wirbeltiere. I. Der Processus anterior (Folli) des Hammers der Säuger und das Goniale der Nichtsäuger. *Anatomischer Anzeiger*, 39, 97–135.
- Gaupp, E. (1911b). Beiträge zur Kenntnis des Unterkiefers der Wirbeltiere. II. Die Zusammensetzung des Unterkiefers der Quadrupeden. *Anatomischer Anzeiger*, 39, 433–473.
- Gaupp, E. (1913). Das Kopfskelett der Selachier, als Grundlage zur Beurteilung der Genese des Kopfskeletes der Wirbelthiere. *Archiv für Anatomie und Physiologie, Abteilung Anatomische Entwicklungsgeschichte*, Suppl.-Band, A, 1–416.
- Gegenbaur, C. (1872). *Untersuchungen zur Vergleichenden Anatomie der Wirbelthiere. Drittes Heft. Das kopfskelett der selachier, ein beitrag zur erkenntniss der genese des kopfskeletes der wirbelthiere* (p. 316). Leipzig: Engelmann Verlag.
- Gegenbaur, C. (1898). *Vergleichende Anatomie der Wirbelthiere mit Berücksichtigung der Wirbellosen* (Vol. I). Leipzig: Engelmann.
- Gitter, A. H. (1990). Eine kurze Geschichte der Hörforschung - Teil 2: Renaissance. *Laryngo-Rhino-Otologie*, 69(9), 495–500.
- Goodrich, E. S. (1930). *Studies on the structure and development of vertebrates*. London: Macmillan.
- Gray, A. A. (1907). *The labyrinth of animals: Including mammals, birds, reptiles and amphibians: Vol I*. London: Churchill.
- Grohé, C., Tseng, Z. J., Lebrun, R., Boistel, R., & Flynn, J. J. (2016). Bony labyrinth shape variation in extant Carnivora: A case study of Musteloidae. *Journal of Anatomy*, 228(3), 366–383.
- Hachmeister, J. E. (2003). An abbreviated history of the ear: From renaissance to present. *Yale Journal of Biology and Medicine*, 76(2), 81–86.
- Harris, G. G., & van Bergeijk, W. A. (1962). Lateralline organ response to near-field displacements of sound sources in waters. *The Journal of the Acoustical Society of America*, 34, 1831–1841.
- Hasse, C. (1871). Das Gehör der Schildkröten. *Hasse's Anatomische Studien*, 1, 225–299.
- Hawkins, A. D. (1981). The hearing abilities in fishes. In W. N. Tavolga, A. N. Popper, & R. R. Fay (Eds.), *Hearing and sound communication in fishes* (pp. 109–139). New-York: Springer.
- Henson, O. W. (1974). Comparative anatomy of the middle ear. In W. D. Keidel & W. D. Neff (Eds.), *Auditory system: Anatomy physiology (ear)* (pp. 39–110). Berlin, Heidelberg: Springer.
- Hetherington, T. E. (1985). Role of the opercularis muscle in seismic sensitivity in the bullfrog *Rana catesbeiana*. *Journal of Experimental Zoology*, 235, 27–34.
- Hetherington, T. E. (1992). The effects of body size on the evolution of the amphibian middle ear. In Webster, D. B., Fay, R. R. & Popper, A. N. (Eds.), *The evolutionary biology of hearing* (pps. 421–454). New York: Springer.
- Hetherington, T. E., Jaslow, A. P., & Lombard, R. E. (1986). Comparative morphology of the amphibian popercularis muscle. I. General design features and functional interpretation. *Journal of Morphology*, 190, 43–61.
- Hoffmann, R., Schultz, J. A., Schellhorn, R., Rybacki, E., Keupp, H., Gerden, S. R., ... Zachow, S. (2014a). Non-invasive imaging methods applied to neo- and paleo-ontological cephalopod research. *Biogeosciences*, 11(10), 2721–2739.
- Hoffmann, S., O'Connor, P. M., Kirk, E. C., Wible, J. R., & Krause, D. W. (2014). Endocranial and inner ear morphology of *Vintana sertichi* (Mammalia, Gondwanatheria) from the late cretaceous of Madagascar. *Journal of Vertebrate Paleontology*, 34(s1), 110–136.
- Hopson, J. A. (1966). The origin of the mammalian middle ear. *American Zoologist*, 6(3), 437–450.
- Huschke, E. (1824). *Beiträge zur Physiologie und Naturgeschichte. Bd. 1. Über die Sinne*. Weimar: Landes-Industrie Comptoir.
- Hyrtyl, J. (1845). *Vergleichend-anatomische untersuchungen über das innere gehörorgan des menschen und der säugethiere*. Prag: Ehrlich.
- Hyrtyl, J. (1873). *Die corrosions-anatomie und ihre ergebnisse*. Vienna: Braumüller.
- Jaslow, A. P., Hetherington, T. E., & Lombard, R. E. (1986). Comparative morphology of the amphibian opercularis muscle. I. General design features and functional interpretation. *Journal of Morphology*, 190, 43–61.
- Jerkø, H., Turunen-Rise, I., Enger, P. S., & Sand, O. (1989). Hearing in the eel (*Anguilla anguilla*). *Journal of Comparative Physiology A*, 165, 455–495.
- Jørgensen, J. M., Shichiri, M., & Geneser, F. A. (1998). Morphology of the hagfish inner ear. *Acta Zoologica*, 79(3), 251–256.
- Kermack, K. A., Mussett, F., & Rigney, H. W. (1981). The skull of *Morganucodon*. *Zoological Journal of the Linnean Society*, 71, 1–158.
- Kingsbury, B. F., & Reed, H. D. (1909). The columella auris in Amphibia. *Journal of Morphology*, 190, 43–61.
- Kirk, E. C., & Gosselin-Ildari, A. D. (2009). Cochlear labyrinth volume and hearing abilities in primates. *Anatomical Record*, 292(6), 765–776.
- Kitazawa, T., Takechi, M., Hirasawa, T., Adachi, N., Narboux-Nême, N., Kume, H., ... Kurihara, H. (2015). Developmental genetic bases behind the independent origin of the tympanic membrane in mammals and diapsids. *Nature Communications*, 6, 6853.
- Kuhn, D. (1882). Über das häutige Labyrinth der Reptilien. *Archiv für Mikroskopische Anatomie*, 20(3), 271–360.
- Lebrun, R., De León, M. P., Tafforeau, P., & Zollikofer, C. (2010). Deep evolutionary roots of strepsirrhine primate labyrinthine morphology. *Journal of Anatomy*, 216(3), 368–380.
- Lombard, R. E. (1977). Comparative morphology of the inner ear in salamanders (Caudata: Amphibian). In R. E. Lombard, M. K. Hecht, & F. S. Szalay (Eds.), *Contributions to vertebrate evolution* (Vol. 2, pp. 1–143). Basel, New York: Karger.
- Lombard, R. E., & Bolt, J. R. (1979). Evolution of the tetrapod ear: An analysis and reinterpretation. *Biological Journal of Linnean Society*, 11, 19–76.
- Lombard, R. E., & Straughan, I. R. (1974). Functional aspects of anuran middle ear structures. *Journal of Experimental Biology*, 61, 71–93.
- Luo, Z.-X. (2011). Developmental patterns in Mesozoic evolution of mammal ears. *Annual Review of Ecology and Systematics*, 42, 355–380.
- Luo, Z.-X., Ruf, I., & Martin, T. (2012). The petrosal and inner ear of the late Jurassic cladotherian mammal *Dryolestes leirops* and implications for ear evolution in therian mammals. *Zoological Journal of the Linnean Society*, 166(2), 433–463.
- Luo, Z.-X., Ruf, I., Schultz, J. A., & Martin, T. (2011). Fossil evidence on evolution of inner ear cochlea in Jurassic mammals. *Proceedings of the Royal Society B: Biological Sciences*, 278(1702), 28–34.
- Luo, Z.-X., Schultz, J. A., & Ekdale, E. G. (2016). Evolution of the middle and inner ears of mammaliaforms: The approach to mammals. In J. A. Clack, R. R. Fay, & A. N. Popper (Eds.), *Evolution of the vertebrate ear: Evidence from the fossil record* (pp. 139–174). Cham: Springer International Publishing.
- Maier, W. (1990). Phylogeny and ontogeny of mammalian middle ear structures. *Journal of Zoology*, 40(1–2), 55–74.

- Maier, W. (2013). The Entotympanic in late fetal Artiodactyla (Mammalia). *Journal of Morphology*, 274, 926–939.
- Maier, W., & Ruf, I. (2016). The anterior process of the malleus in Certartiodactyla. *Journal of Anatomy*, 228, 313–323.
- Maier, W., & van den Heever, J. (2002). Middle ear structures in the Permian Glanosuchus sp. (Therocephalia, Therapsida), based on thin sections. *Mitteilungen des Naturkundemuseum Berlin, Geowissenschaftliche Reihen*, 5, 309–318.
- Maisey, J. G. (2001). Remarks on the inner ear of elasmobranchs and its interpretation from skeletal labyrinth morphology. *Journal of Morphology*, 250(3), 236–264.
- Maklad, A., Reed, C., Johnson, N. S., & Fritsch, B. (2014). Anatomy of the lamprey ear: Morphological evidence for occurrence of horizontal semicircular ducts in the labyrinth of *Petromyzon marinus*. *Journal of Anatomy*, 224(4), 432–446.
- Malinzak, M. D., Kay, R. F., & Hullar, T. E. (2012). Locomotor head movements and semicircular canal morphology in primates. *Proceedings of the National Academy of Sciences*, 109(44), 17914–17919.
- Manley, G. A. (2010). An evolutionary perspective on middle ears. *Hearing Research*, 263(1), 3–8.
- Manley, G. A., & Sienknecht, U. J. (2013). The evolution and development of the middle ears in land vertebrates. In S. Puria, R. R. Fay, & A. N. Popper (Eds.), *The middle ear: Science, otosurgery and technology* (pp. 7–30). New York: Springer.
- Manoussaki, D., Chadwick, R. S., Ketten, D. R., Arruda, J., Dimitriadis, E. K., & O'Malley, J. T. (2008). The influence of cochlear shape on low-frequency hearing. *Proceedings of the National Academy of Sciences*, 105(16), 6162–6166.
- Martin, T., & Luo, Z.-X. (2005). Homoplasy in the mammalian ear. *Science*, 307(5711), 861–862.
- Mason, M. J., & Narins, P. M. (2002). Vibrometric studies of the middle ear of the bullfrog *Rana catesbeiana* I. The extrastapes. *Journal of Experimental Biology*, 205, 3153–3165.
- Mason, N. D., & Summers, A. P. (2006). Mineralized cartilage in the skeleton of chondrichthyan fishes. *Zoology*, 109, 164–168.
- McDiarmid, R. W. (1971). Comparative morphology and evolution of frogs of the neotropic genera *Atelopus*, *Dendrophryniscus*, *Melanophryniscus*, and *Oreophrynella*. *Bulletin of LA City of the Museum of Natural History of Science*, 12, 1–66.
- Meng, J., Bi, S.-D., Zheng, X.-T., & Wang, X.-L. (2016). Ear ossicle morphology of the Jurassic euharamiyidan *Arboroharamiya* and evolution of mammalian middle ear. *Journal of Morphology*, 279(4), 441–457.
- Meng, J., Wang, Y., & Li, C. (2011). Transitional mammalian middle ear from a new cretaceous Jehol eutriconodont. *Nature*, 472, 181–185.
- Mennecart, B., & Costeur, L. (2016). Shape variation and ontogeny of the ruminant bony labyrinth, an example in Tragulidae. *Journal of Anatomy*, 229(3), 422–435.
- Muller, M. (1999). Size limitations in semicircular duct systems. *Journal of Theoretical Biology*, 134, 473–501.
- Neenan, J. M., & Scheyer, T. M. (2012). The braincase and inner ear of *Placodus gigas* (Sauropterygia, Placodontia) – A new reconstruction based on micro-computed tomographic data. *Journal of Vertebrate Paleontology*, 32(6), 1350–1357.
- Oken, L. (1825). *Bedeutung der Schädelknochen: Ein Programm beim Antritt der Professur an der Gesamt-Universität zu Jena*. Jena: Göbhardt.
- Pfaff, C., Czerny, S., Nagel, D., & Kriwet, J. (2017b). Functional morphological adaptations of the bony labyrinth in marsupials (Mammalia, Theria). *Journal of Morphology*, 278(6), 742–749.
- Pfaff, C., Martin, T., & Ruf, I. (2015). Bony labyrinth morphometry indicates locomotor adaptations in the squirrel-related clade (Rodentia, Mammalia). *Proceedings of the Royal Society B: Biological Sciences*, 282(1809), 20150744.
- Pfaff, C., Nagel, D., Gunnell, G., Weber, G. W., Kriwet, J., Morlo, M., & Bastl, K. (2017). Palaeobiology of *Hyaenodon exiguus* (Hyaenodonta, Mammalia) based on morphometric analysis of the bony labyrinth. *Journal of Anatomy*, 230(2), 282–289.
- Platt, C., & Popper, A. N. (1981). Fine structure and function of the ear. In W. N. Tavolga, A. N. Popper, & R. R. Fay (Eds.), *Hearing and sound communication in fishes* (pp. 3–38). New-York: Springer.
- Poggendorf, D. (1952). Die absoluten Hörschwellen des Zwergwelses (*Amiurus nebulosus*) und Beiträge zur Physik des Weberschen Apparatus der Ostariophysen. *Zeitschrift für Vergleichende Physiologie*, 34, 222–257.
- Politzer, A. (1907). *Geschichte der Ohrenheilkunde (v.1)*. Stuttgart: Enke.
- Popper, A. N., & Fay, R. R. (1977). Structure and function of the elasmobranch auditory system. *American Zoologist*, 17, 448–452.
- Ramirez-Chaves, H. E., Weisbecker, V., Wroe, S., & Phillips, M. J. (2016b). Resolving the evolution of the mammalian middle ear using Bayesian inference. *Frontiers in Zoology*, 13, 39.
- Ramirez-Chaves, H. E., Wroe, S. W., Selwood, L., Hinds, L. A., Leigh, C., Koyabu, D., ... Weisbecker, V. (2016a). Mammalian development does not recapitulate suspected key transformations in the evolutionary detachment of the mammalian middle ear. *Proceedings of the Royal Society B*, 283, 20152606.
- Reichert, C. (1837). Über die Visceralbögen der Wirbeltiere im Allgemeinen und deren Metamorphosen bei den Vögeln und Säugetieren. *Archiv für Anatomie, Physiologie und Wissenschaftliche Medizin*, 1837, 120–222.
- Retzius, G. (1880). Zur Kenntniss des inneren Gehörgans der Wirbelthiere. *Archiv für Anatomie und Physiologie. Anatomische Abteilung, II*, 235–244.
- Retzius, G. (1881). Das Gehörorgan der Fische und Amphibien. In *Das Gehörorgan der Wirbelthiere: Morphologisch-histologische Studien* (Vol. 1). Stockholm: Samson & Wallin.
- Retzius, G. (1884). Das Gehörorgan der Reptilien, der Vögel und der Säugethiere. In *Das Gehörorgan der Wirbelthiere: Morphologisch-histologische Studien* (Vol. 2). Stockholm: Samson & Wallin.
- Rich, T. H., Hopson, J. A., Musser, A. M., Flannery, T. F., & Vickers-Rick, P. (2005). Independent origins of middle ear bones in monotremes and therians. *Science*, 307, 910–914.
- Romer, A. S., & Price, L. I. (1940). Review of the Pelycosauria. *Geological Society of America, Special Papers*, 28, 1–538.
- Rosen, D. E., & Greenwood, P. H. (1970). Origin of the Weberian apparatus and the relationship of the ostariophysan and goniorhynchiform fishes. *American Museum Novitates*, 2428, 1–25.
- Rowe, T. (1996). Brain heterochrony and origin of the mammalian middle ear. *Memoirs of the California Academy of Science*, 20, 71–95.
- Rudolphi, K. A. (1821). *Grundriß der Physiologie*. Berlin: Dümmler.
- Ruf, I., Luo, Z.-X., & Martin, T. (2013). Reinvestigation of the basicranium of *Haldanodon expectatus* (Mammaliaformes, Docodonta). *Journal of Vertebrate Paleontology*, 33(2), 382–400.
- Ruf, I., Luo, Z.-X., Wible, J. R., & Martin, T. (2009). Petrosal anatomy and inner ear structures of the late Jurassic *Henkelotherium* (Mammalia, Cladotheria, Dryolestoidea): Insight into the early evolution of the ear region in cladotherian mammals. *Journal of Anatomy*, 214(5), 679–693.
- Ruf, I., Volpato, V., Rose, K. D., Billet, G., deMuizon, C., & Lehmann, T. (2016). Digital reconstruction of the inner ear of *Leptictidium auderiense* (Leptictida, Mammalia) and north American leptictids reveals new insights into leptictidan locomotor agility. *Paläontologische Zeitschrift*, 90(1), 153–171.
- Russell, E. S. (1916). *Form and function: A contribution to the history of animal morphology*. London: John Murray.
- Ryan, T. M., Silcox, M. T., Walker, A., Mao, X., Begun, D. R., Benefit, B. R., ... Spoor, F. (2012). Evolution of locomotion in Anthrozoidea: The semicircular canal evidence. *Proceedings of the Royal Society B: Biological Sciences*, 279(1742), 3467–3475.
- Saint-Hilaire, É. G. (1818). *Philosophie anatomique (tome premiere)*. Paris: J. B. Baillière.
- Sánchez-Villagra, M., & Schmelzle, T. (2007). Anatomy and development of the bony inner ear in the woolly opossum, *Caluromys philander* (Didelphimorphia, Marsupialia). *Mastozoología Neotropical*, 14(1), 53–60.
- Schellart, N. A. M., & Popper, A. N. (1991). Functional aspects of the evolution of the auditory system in Actinopterygian fishes. In D. B. Webster, R. R. Fay & A. N. Popper (Eds.), *The evolutionary biology of hearing* (pp. 295–323). New York: Springer.
- Schellhorn, R. (2018a). A potential link between lateral semicircular canal orientation, head posture, and dietary habits in extant rhinos (Perissodactyla, Rhinocerotidae). *Journal of Morphology*, 279(1), 50–61.
- Schellhorn, R. (2018b). Intraspecific variation in the domestic cat bony labyrinth revealed by different measurement techniques. *Journal of Morphology*, 279(3), 409–417.
- Schultz, J. A., Zeller, U., & Luo, Z.-X. (2017). Inner ear labyrinth anatomy of monotremes and implications for mammalian inner ear evolution. *Journal of Morphology*, 278(2), 236–263.



- Schutz, H., Jamniczky, H. A., Hallgrímsson, B., & Garland, T. (2014). Shape-shift: Semicircular canal morphology responds to selective breeding for increased locomotor activity. *Evolution*, *68*(11), 3184–3198.
- Segall, W. (1969). The auditory ossicles (malleus, incus) and their relationships to the tympanic: In marsupials. *Acta Anatomica*, *73*(2), 176–191.
- Segall, W. (1973). Characteristics of the ear, especially the middle ear in fossorial mammals, compared with those in the Manidae. *Acta Anatomica*, *86*(1), 96–110.
- Siler, W. (1969). Near- and farfields in a marine environment. *The Journal of the Acoustical Society of America*, *46*, 483–484.
- Spoor, F. (2003). The semicircular canal system and locomotor behaviour, with special reference to hominin evolution. *Courier Forschungsinstitut Senckenberg*, *243*, 93–104.
- Spoor, F., Bajpai, S., Hussain, S. T., Kumar, K., & Thewissen, J. G. M. (2002). Vestibular evidence for the evolution of aquatic behaviour in early cetaceans. *Nature*, *417*, 163–166.
- Spoor, F., Garland, T., Krovitz, G., Ryan, T. M., Silcox, M. T., & Walker, A. (2007). The primate semicircular canal system and locomotion. *Proceedings of the National Academy of Sciences*, *104*(26), 10808–10812.
- Spoor, F., Wood, B., & Zonneveld, F. (1994). Implications of the early hominid labyrinthine morphology for evolution of human bipedal locomotion. *Nature*, *369*, 645–648.
- Spoor, F., & Zonneveld, F. (1998). Comparative review of the human bony labyrinth. *Yearbook of Physical Anthropology*, *4*, 211–251.
- Starck, M. J. (1995). Comparative anatomy of the external and middle ear of Palaeognathous birds. *Advances in Anatomy, Embryology and Cell Biology*, *131*, 1–137.
- Steinhausen, W. (1933). Über die Beobachtungen der Cupula in den Bogen-gangampullen des Labyrinthes des lebenden Hechts. *Plägers Archiv*, *232*, 500–512.
- Stensiö, E. A. (1927). The Downtonian and Devonian vertebrates of Spitzbergen. I. Family Cephalaspidae. *Skrifter Om Svalbard Og Nordishavet*, *12*(2), 1–391.
- Sterkers, O., Ferrary, E., & Amiel, C. (1988). Production of inner ear fluids. *Physiological Reviews*, *68*(4), 1083–1128.
- Takechi, M., & Kuratani, S. (2010). History of studies on mammalian middle ear evolution: A comparative morphological and developmental biology perspective. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, *314B*(6), 417–433.
- Tavolga, W. N., Popper, A. N., & Fay, R. R. (1981). *Hearing and sound communication in fishes*. New York, Heidelberg, Berlin: Springer.
- Thalman, R., & Thalman, I. (1999). Source and role of endolymph macromolecules. *Acta Oto-Laryngologica*, *119*(3), 293–296.
- Thompson, H., Ohazama, A., Sharpe, P. T., & Tucker, A. S. (2012). The origin of the stapes and relationship to the otic capsule and oval window. *Developmental Dynamics*, *241*, 1396–1404.
- Trueb, L., & Alberch, P. (1985). Miniaturization and the anuran skull: A case study of heterochrony. *Fortschritte der Zoologie*, *30*, 113–121.
- Tucker, A. S. (2017). Major evolutionary transitions and innovations: The tympanic middle ear. *Philosophical Transactions B*, *372*, 20150483.
- Tucker, A. S., Watson, R. P., Lettice, L. A., Yamada, G., & Hill, R. E. (2004). Bapx1 regulates patterning in the middle ear: Altered regulatory role in the transition from the proximal jaw during vertebrate evolution. *Development*, *131*, 1235–1245.
- Urban, D. J., Antwhal, N., Luo, Z.-X., Maier, J. A., Safier, A., Tucker, A. S., & Sears, K. E. (2017). A new developmental mechanism for the separation of the mammalian middle ear ossicles from the jaw. *Proceedings of the Royal Society B*, *284*, 20162416.
- Van Egmond, A. A. J., Groen, J. J., & Jongkees, L. B. W. (1949). The mechanics of the semicircular canals. *Journal of Physiology*, *110*, 1–17.
- Wever, E. G. (1974). The evolution of vertebrate hearing. In W. D. Keidel & W. D. Neff (Eds.), *Auditory system: Anatomy physiology (ear)* (pp. 423–454). Berlin, Heidelberg: Springer.
- Wever, E. G. (1976). Origin and evolution of the ear in vertebrates. In R. B. Masterton, M. E. Bitterman, C. B. G. Campbell, & N. Hotton (Eds.), *Evolution of brain and behaviour in vertebrates* (pp. 89–105). New Jersey: Laurence Erlbaum Association.
- Wever, E. G. (1978). *The reptilian ear: Its structure and function*. New Jersey: Princeton University Press.
- Wever, E. G. (1979). Middle ear muscle of the frog. *Proceedings of the National Academy of Sciences*, *76*, 3031–3033.
- Wever, E. G. (1985). *The amphibian ear*. Princeton: Princeton University Press.
- Zeller, U. (1985). Die Ontogenese und Morphologie der Fenestra rotunda und des Aquaeductus cochleae von *Tupaia* und anderen Säugern. *Gegenbaurs Morphologisches Jahrbuch*, *131*, 179–204.
- Zeller, U. (1993). Ontogenetic evidence for cranial homologies in monotremes and therians, with special reference to *Ornithorhynchus*. In F. S. Szalay, M. J. Novacek, & M. C. McKenna (Eds.), *Mammal phylogeny* (pp. 95–107). New York: Springer.

**How to cite this article:** Pfaff C, Schultz JA, Schellhorn R. The vertebrate middle and inner ear: A short overview. *Journal of Morphology*. 2019;280:1098–1105. <https://doi.org/10.1002/jmor.20880>