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Match the membranous labyrinth structures listed in column b

Do you work off campus? Read about our remote access capabilities Volume 228, Edition 2 The inner ear of mammals consists of a cochlea that is involved in hearing loss, and an atrium and three semicircular channels that contribute to the sense of balance. Although different areas of the inner ear contribute to different functions, the bony ventricles and membranous ducts are morphologically continuous. Coarse anatomy of the cochlea, which was related to auditory physiology, includes the total size of the structure, including the volume and total length of the spiral, the development of internal cochlear structures, including primary and secondary bony laminae, the morphology of the spiral nerve ganglion and the nature of the cochlear coil, including the total number of revolutions completed by the cochlear canal and the relative diameters of the basal and apical revolutions. The overall sizes, shapes and orientations of the semicircular channels are related to sensitivity to head rotation and, where appropriate, movement behaviour. Intraspecific variation, especially in the shape and orientation of semicircular ducts, can provide additional clues to help us better understand the form and function of the inner ear. The area of the otis (ear) is part of the special sensory division of the nervous system of vertebrates. The function of the ear is double – hearing in the rechief and balance in the atrium and semicircular channels. The organs of hearing and balance in the inner ear are minute structures that are contained in cavities in volume from 4l; 1 mm3 in swings to more than 1000 mm3 in baleen whales (Ekdale, 2013). The inner ear of a person occupies a space of just over 150 mm3. Although the internal ear organs are small, they are quite strong physiologically. It is amazing that such miniscule structures can cause countless problems frominnitus to motion kinetics to a general lack of balance. This phenomenon has partly caused the ear region to be one of the most studied systems of vertebrate anatomy and physiology. Sense of hearing was the first inner ear function to be recognized by human anatomists and physiologists. The role of the inner ear in hearing was derived in ancient Egypt from the effects of injuries to the time area of the head, but the specific role that Kochlea plays was determined only in the mid-17th century. Feelings of orientation were attributed to the semiciferyary canals and vestibular system at the end of the 19th century. (Retzius, 1884), corrosive casting of bony venturing of the inner ear (Hyrtl, 1845) and extraction of intact membranous inner ear structures as a whole from the surrounding bone (Gray, 1903, 1905, 1907). Only from a functional point of view, auditory and vestibular structures are important substances in vertebrate biology. Hearing certainly played a role in early tetrapod evolution when newly terrestrial animals moved from detecting water transmitted to airborne sounds (Manley, 1972; Clack, 2002). In the case of early mammals likely to be nocturnal animals (Menaker and Col. 1997; Kielan-Jaworwska et al. 2004; Hall et al. 2012; Gerkema et al. 2013), relying on non-invision senses to navigate the mesozoic landscape would be necessary. The auditory abilities of mammals vary and mammals can hear in greater frequency bandwidth than other vertebrates, especially on high pitches (Echtleter and Co. 1994; Heffner & Heffner, 2007). For example, elephants are sensitive to very low frequency sound vibrations (14-24 Hz; Payne et al. 1986; Poole et al. 1988) and whales as a group can be heard in both the infrasonic (below 20 Hz) and ultrasonic (above 20 kHz, up to 180 kHz in some species) ranges (Hall & Johnson, 1972; Ridgway a.m. Ketten & Wartzok, 1990; Ketten, 1997, 2000; Houser and co. Parks and co. 2007). Microchiropteran bats use ultrasonic echolocation during prey detection and capture (Simmons et al. 1973), and ternets and some shrews are known to vocalize in ultrasonic ranges (Coulid, 1965; Tomasi, 1979), in different ranges, which they probably hears. Conversely, most bony and cartilaginous fish are sensitive only to sounds below 1 kHz (Fay, 1988; Myrberg, 2001; Casper a col. Casper & Mann, 2006; Ramcharitar a.m. 2006) and the upper frequency limits are between 1 kHz in amphibians (Mogata-Simmons et al. 1985; Fay, 1988) and 1-1.4 kHz for reptiles including birds (Christensen-Dalsgaard & Manley, 2005, 2008; Manley & Kraus, 2010). Balance was also an important meaning in vertebrate history. When the oldest tetrapods left the aquatic environment for soil, they faced many challenges (Alexander, 2002). An examination of the postcranial skeletons of the first tetrapods reveals adaptations to the new terrestrial lifestyle (Shubin a.g. 2004, 2014; Boisvert, 2005). Equilibrium itself is an integral part of spinal movement, and a wide range of mobility is observed in mammalia (see Spoor et al. 2007). On the other hand, the anatomy of the internal ear departments correlates with the various physical behaviors of mammals (e.g. Malinzak a.m. 2012). The morphology of the inner ear is informative for phylogenetic studies at a more- and less inclusive taxonomic level. For example, the cochlea completes at least one complete 360° transformation of living Therian mammals (marsupials and but less in monomeres and more on the basis of taxa (Gray, 1907, 1908; Rowe, 1988; Ruf et al. 2009, 2013; Luo et al. 2011, 2012). The bony labyrinths of marsupial and placental mammals from the mesozoic era exhibit morphology of ancestors, such as the fusion of posterior and lateral semicircular channels to form secondary common crosses. Secondary common crus is lost in several claws in the crown of Theria, including primates, rodents, some carnivorous mammals, and the posterior and lateral channels are separated along their entire length in the most extant mammals (Meng & Fox, 1995; Schmelzle et al. 2007; Ekdale & Rowe, 2011). The dimensions of the inner ear in primates vary between large apes and other primates (Spoor & Zonneveld, 1998), as well as between humans and subspecies chimpanzees (Gunz et al. 2012). Further phylogenetic information can be found in the inner ears of scything reptiles (Shute & Muller, 1966a, 1968; Maddin & Sherratt, 2014). The generalized ear of mammals is divided into the outer, middle and inner ears. The outer ear contains a pinna, which funnels sound from the environment into the ear area of the head, and extends from the outer surface of the head to the tympanic membrane, or eardrum, through the external acoustic meatus (Fig. 1). The middle ear extends from the tympanic membrane to the lateral surface of the skull and contains three ear ossicles (malleus, incus and stapes) in the tympanic cavity of the middle ear. The tympanic cavity itself is ventrally enclosed by a tympanic (auditory) bull, which often forms an exuberant, bony or cartilaginous structure in most mammalian taxa. The composition of tympanic bullfish differs in a specific bony element or elements contributing to the structure (van der Klauw, 1930, 1931; Novaček, 1977, 1993). The ossicles of the middle ear form a chain connecting the tympanic membrane with the petrosal bone, which contributes to the posterolateral region of the base skull and surrounds the inner ear cavities. The function of the ossicular chain in the middle ear is to transmit airborne sound waves from the tympanic membrane to the liquid-filled chamber of the inner ear. Stapes articulates with a hole in the petrosal known as the fenestral vestibule (oval window) and acts as one of the two main areas of communication between the medial and internal ear cavities (Fig. 1). Another hole, which is usually located posteromedial on the fenestral vestibule, is the fenestral cochleae (round window). The phenestra cochleae is covered with a secondary tympanic membrane that accommodates the expansion of the inner ear space during stapedial vibration. Cross-section over the head of a domestic dog (*Canis familiaris*) showing the structures of the outer, middle and inner ears (modified Blue denotes the structures of the membranous labyrinth, yellow denotes the structures of the bony labyrinth, and red indicates the primary (eardrum) and secondary (including phenestra cochleae) tympanic membranes. The inner ear consists of a set of interconnected spaces in the petrosal bone of mammals known as the bony labyrinth (yellow channels in Figure 1). In the bony labyrinth there are a series of interconnected sacs of soft tissues and ducts known as the membranous labyrinth (blue ventricles in Figure 1). The traditional practice of the ear region reserves the term channel for the structures of the bony labyrinth, while the term canal refers to membranous channels. The membranous labyrinth is divided into a lower division, which includes the cochlear canal and sacculle membranous atrial, and an excellent division that includes a snippet of the atrial and three semicircular channels and associated ampoules. The organ of Corti (the spiral organ of hearing) is hidden in the cyclical canal, and receptors that are sensitive to linear movement are found in the sacculle. Utricle and semicircular channels are involved in the sensation of rotating head movements. The dazzle semicircular ducts and the cochlea of the bony labyrinth reflect the shape of the membranous channels inside, although the bony canals may not accurately reflect the size of the canals (Curthoys et al. 1977). However, the bony labyrinth is often used to study the form and function of the inner ear in the absence of membranous ducts (eg Fleischer, 1976; Geisler & Luo, 1996). Lymphatic fluid both fills and surrounds the membranous labyrinth. The spaces surrounding the membranous labyrinth in the bony labyrinth are filled with perilymph. The composition of the perilymph is similar to extracellular fluid and is rich in sodium, but bad for potassium (Sterkers et al. 1988; Echtleter a.m. 1994). Perilymph originates from the lymphatic system and leaves the inner ear through the membranous perilymphatic duct in the bony cyclical aqueduct into the subarachnoid space surrounding the brain (Fig. 1). The cochlear canal and membranous vestibular devices are filled with endolymph. Unlike perilymphs, endolymph ions are rich in potassium ions but poor for sodium ions with blood plasma-like pH and have a composition similar to intracellular fluid (Bosher & Warren, 1968; Sterkers et al. 1988; Payan et al. 1997). Endolymph is produced by specialized cells in the highly vascular epithelium along the lateral wall of the cochlear canal called stria vascularis (see Echtleter et al. 1994), which maintains the ion composition of the endocochlear endolymph, as well as its unusual electrical potential (Tasaki & Spyropoulos, 1959; Carlisle a.m. Hibino et al. 2010). Endolymph is a resorbated endolymphatic bag that extends from a bony aqueduct and is located in the subdural space around the cerebellum (Fig. 1). There is an apparent heterogeneity of compositions in both endolymph and perilymph in different areas of the inner ear due to irregular forms of membranous structures (Sterkers and co. 1988). Vibrations in the endolymph, either through stapedial vibration or head movements, stimulate auditory receptors in the rechly and motion receptors in the vestibular system. Although the sensory functions of the cochlea (auditory) and atrium (balance) vary, endolymph from one area can flow into another, affecting the function of the other. For example, changes in the pressure and volume of vestibular endolymph affect both vestibular and auditory functions. An increase in the volume of endolymph (known as endolymphatic hydropses) has been associated with Ménière's disease, which manifests itself as a combination of hearing loss and vertigo (Havia a.k.a. 2002; 2005). The semicircular canal of dehiscence, which is the perforation of the bone overlapping the semicircular ducts, reduces pressure in the atrium and affects the hearing and balance of the affected patient (Minor et al. 1998, 2001). Interestingly, the evidence suggests that the atrial sacculle may have some low frequencies of acoustic sensitivity in mammals (Todd et al. 2000; Todd, 2001; 6. Jones et al. 2010) and acoustic waves can trigger a vestibular response (Todd & Cody, 2000; Todd et al. 2003). Functional overlap between systems could be physiological preservation from vestibular origin of the rechilla during mammalian evolution (Todd, 2001). In fact, sacculle falsified hearings in several non-mammalian vertebrates, including some fish (Furukawa & Ishi, 1967; Saidel & Popper, 1983), frogs (Wever, 1973; Moffat & Capranica, 1976) and potential turtles (Wever & Kemp, Vernon, 1956). The bony cochlea is writhed around a central axis known as modiolus in all living mammals except monotremes, in which the canal is bent near its end but has not completed a full bend (Alexander, 1904; Kernack & Mussett, 1983; Jørgenson & Locket, 1995). The center of the modiol is hollow and transmits the cochlear branch of the crate nerve VIII. The tip of the cochlear spiral is known as the apiline, and the basal end arises near the fenestral vestibule for stapedial footplate (Fig. 1). The membranous structure in the bony collet canal is divided into two compartments or scalae, which are scala tympani, which communicate with the phenestra cochleae and scala vestibule, which ends on the fenestral lobby. There is no sesame division between two scalae in monotremes (Alexander, 1904; Zeller, 1989; Luo et al. 2011). However, the two scalae are partially separated in extant therians by a pair of spiral ridges on opposite walls of the rechlear – primary and secondary bony laminae. The primary bony lamina extends for most of the length of the cochlea along the axial (inner) wall, around the modiol cochlear, and it accommodates the spiral ganglion of the auditory nerve (Fig. 2). The secondary bony lamina often extends a short distance along the radial (outer) wall of the cochlear canal opposite the primary bony lamina, but the two laminae never come into contact. Both the bony laminae and the spiral ganglion channel first appear in the fossil record in dryolestids (Therian mammals) and coincide with an increase in neural structures in the brain (Luo et al. 2011, 2012). The development of these structures is likely to indicate the spread of auditory profiles in living mammals. Cross-section through the sea guinea pig cochlea (*Cavia porcellus*; Echtleter, 1994) showing the structures of the primary and secondary bony laminae, basal membrane, cd, cochlear channel (scala media); cm, the cochlear branch of the cran nerve VIII in modiolae; oc, Corti auditory; pl, primary bony lamina; pt, petrosal bone (surrounding cochlea); rm, Reissner membrane; sg, spiral ganglion channel in the root directory of the primary bony lamina; st, scala tympani; st, scala vestibule; tm, tectural membrane. Two bony laminae serve as anchors for a part of the membranous labyrinth known as the basil membrane (Fig. 2). The basil membrane on which the Corti organ sits defines the thympan wall of membranous sochlear channels (often referred to as scala media). The second film of soft tissues known as the vestibular membrane (also known as the Reissner membrane) extends over the entire width of the cochlear canal to define the vestibular wall of the cochlear canal. The cochlear canal separates the scalae tympani and the lobby for most of the length of the cochlear spiral, although the two outer scalae communicate on top through a small hole known as the helicotrema (Fig. 1). In general, the basil membrane is narrow in its base and extends towards the top (Wever et al. 1971; Webster & Webster, 1980). The stiffness and thickness of the membrane decreases longitudinally from the base to the top (Naidu & Muller, Mountain, 2007) and the membrane is much stiffer radially than longitudinally (Echtleter et al. 1994). Vibration steps inside the fenestral vestibule are transmitted to the basilica membrane through endolymphatic and perilymphatic fluids, and are propagated through the basal membrane from the base to the top. Waves reach maximum in specific areas of the cochlea according to vibration frequency (Zhang a. 2007). The spiral organ of Corti sits on the vestibular surface of the basilica membrane in the sochlear canal (Fig. 2). Within the Corti organ, auditory sensations are mixed with cochlear hair cells. The line of internal hair cells in the form of a flask extends lengthwise axial edge of the basilica membrane. Column cells known as outer hair cells occupy a more radial position in the Corti organ. External hair cells contribute more than three-quarters of the sensory cells in the cochlea (Echtleter a.k.a. 1994). Internal and external hair cells differ in morphology and position, but they also have functional differences. Whereas the potential of internal hair cells is positively correlated with the vibration rate of the basilica membrane, the potential of external hair cells correlates with the displacement of the basilica membrane (Dallos et al. 1972; Fettiplace & Hackney, 2006). Between the outer and inner hair cells there are a number of supporting cells that contain the inner and outer cells of the pillar. Pillar cells form the walls of the Corti tunnel. The outer and inner hair cells are innervated branches of the crab nerve VIII, which leaves the crate cavity through the internal acoustic meatus on the endocranial surface of the petrosal. The vestibular branch expands posteriorly to the innervate vestibular end of the form and function of the inner ear in several groups of mammals. As it turns out, there are some extreme differences between species in the cochlea, but some aspects of the cochlea also vary depending on the species. These include the absolute length of the canal and the number of revolutions (coil stage). However, it is unclear how these intraspecific morphological variations are related to intraspecific variations in physiology. For example, the length of the cochlear canal is positively correlated with body weight (Ekdale, 2013), although it is unclear whether larger, more physically larger individuals are more sensitive to wider or narrower frequency bandwidth than smaller physically similar individuals of the same species. Unlike cochlear length, the number of turns completed by the cochlea does not show a strong correlation with body weight, nor does the degree of coil vary widely in most mammals (Ekdale & Rowe, 2011). The exception is the range of almost a quarter of the speed (90°) calculated for the captive population of monodelphis domestica (Ekdale, 2010). Unfortunately, audiograms for persons investigated by Ekdale (2010) have not been recorded. The cochlea of two grey whale individuals of different maturities (juvenile and adult) was compared, and although the number of cochlear rotations, the length of the cochlear canal and the graduated curvature of the cochlea varied slightly between individuals, the low frequency limits estimated for each individual were comparable (Ekdale & Racicot, 2015). Much of the recent attention has been focused on variations within the vestibular system. The connection between channels and rotational sensations is known for almost a century and a half (Dercum, 1879), and the connection between canal anatomy, orientation, sensitivity, behavior, and phylogeny is an active area of investigation in evolutionary biology. Several studies have used the size and shape of semicircular ducts to derive the age, geography and physical abilities of many extinct and extant mammals, such as primates, whales, killer whales and sloths (Spoor et al. 2002, 2007; Silcox a.m. Macrini et al. 2010, 2013; Orlac et al. 2012; 2013). For example, the arc of the ante semicircular canal tends to be more elliptical in marine carnivores, such as pinnipeds, than in terrestrial species such as canids (Fig. 5; Georgi, 2008; Ekdale, 2013). Similar correlations between semicircular morphology and ecology have also been found in other non-mammalian vertebrates (Clack, 2002; Witmer a.m. Clarke, 2005; Georgi & Sipla, 2008; Georgi et al. 2013). However, phylogeny has a strong influence on the evolutionary development of the semicircular canal, so ecological comparisons between distantly related taxa may not be appropriate (Georgi & Sipla, 2008). Line drawings of the form semi-circular channel for terrestrial (A, B) and aquatic (C-F) carnivores. (A) domestic dog (*Canis familiaris*); repainted from Ekdale, 2013); B) Wolf (*Canis lupus*; repainted from Georgia, 2008); C) star sea lion (*Eumetopias jubatus*; repainted from Ekdale, 2013); D) galapagos lion (*Arctocephalus galapagoensis*; repainted from Georgi, 2008); E) Californian sea lion (*Zalophus californianus*; repainted from Georgi, 2008); F) Leopard seal (*Hydrogorga leptonyx*; redrew from Georgi, 2008). There has yet to be a comprehensive and systematic study of variations in the shape of a semicircular canal, as they relate to movement differences in a wide range of mammals representing the spectrum of behaviour. Neither the shape of the semicircular channel arch was connected directly to the sensitivity of the canal. However, neurophysiological data support the link between the size of the semicircular ductor circuit, which is usually expressed as the radius of the arc of the semicircular canal (Jones & Spels, 1963; Spoor & Spels, 1963; Spoor & Zonneveld, 1995; Spoor et al. 2007) and channel sensitivity (Yang & Hullar, 2007). A general pattern is that large semicircular channels are more sensitive to rotation in the universe than small channels. Interestingly, slow-moving animals tend to have smaller channels (relative to body weight) than faster-moving animals, suggesting that there is a link between the size of the semicircular canal, agility and even physical behaviour (Spoor a.k.a. 2007; Silcox a.m. Berlin. The anesthesia semicircular channel tends to have the largest radius of curvature in most mammals, suggesting that most mammals are most sensitive to rotation of the head (front-rear) of the head (Curthoys a. 1977; Calabrese & Hullar, 2006; Spoor et al. 2007; Ekdale, 2013). However, differences in the largest arc of the channel between species may indicate functional differences. For example, the lateral semicircular canal is the most sensitive (largest arc radius of curvature) in some marine mammals, including sea lions, manatees and bottlenose dolphins (Ekdale, 2013), which could indicate that sensitivity to the rotation of seduces (left-right along the horizontal plane) is an adaptation of the secondary aquatic lifestyle in these animals. However, a recent examination of the inner ears of extinct and extinct whales suggests that most whales follow the pattern of terrestrial mammals with large front semicircular channels relative to others (Ekdale & Racicot, 2015), and thus more sensitivity to pitch rotation than bias. An overall reduction in the vestibular system could indicate a completely aquatic lifestyle of marine mammals. For example, it is well known that the semicircular channels of whales are small in terms of cochlea (Yamada & Yoshizaki, 1959; Fleischer, 1976) and this pattern can be traced back to the evolution of whales in the fossil record (Spoor et al. 2002; Ekdale & Racicot, 2015). The reduction of the semicircular canal compared to terrestrial mammals was related to the obliging aquatic lifestyle and, in particular, to the adaptation to rapid rotation of the head in the aquatic environment (Spoor and co. 2002). Two or more cervical vertebrae are wadded in many former whales (Barnes & Kemp, McLLeod, 1984; Geisler & Luo, 1996; Ekdale et al. 2011), which are considered sensitive to low frequency sounds. It is possible that the presence of both functions indicates a further downward shift in the low frequency thresholds of these mysticines in relation to odontocetes and the common ant of the whale crown, but there are no audiograms for all kinds of baleen whales that could be used to test such a hypothesis. Given the apparent plasticity and possible reversal of mammalian morphology, further study of the functional consequences of undivided perilymphatic foramen, as well as its taxonomic distribution, would shed some light on the development of the head. In addition, regression Angle, the velocity sizes and channel pair deviation from 90° (90lar from Malinzak et al. 2012) separate fast jumpers from slow quadruples. There is some indication that these patterns of observed primates may spread to mammals that are not primates. An interesting and potentially important pattern that has recently emerged involves an intraspecific variation of the shapes and orientations of vestibular elements. A study of bony xantran labyrinths found that slow-moving three-layer sloths showed greater intraspecific variation in the orientation of the semicircular channel than faster-moving species such as tamarandus and armadillos (Billet a.c. 2012). In addition, the sizes of the semicircular ducts of mice with different movements and agility (individuals reared for high voluntary operation of wheels vs. an insect control group) do not differ, but channel shapes do (Schutz and co. 2014). As a result, there is intraspecific channel-shape plasticity, which refers to differences in the movement path, but not to the size of the canals themselves. Therefore, changes in the shape of the semicircular canal may indicate changes in sensitivity even among very closely related individuals (within the same species) of very similar body size. The results of both studies highlight the need for increased investigation of intraspecific variations in the morphology of the semicircular canal and orientations in order to fully clarify the link between the form and function of the vestibular system. The inner ear is one of the best studied areas of the nervous system in vertebrates. The general form and function of the inner ear seem simple – the coil of the cochlea is involved in the hearing, and the loops of the semicircular ducts are involved with balance. Differences in coarse morphology between different species almost certainly coincide with the vast diversity of auditory and physical physiologies observed in mammals, and vertebrate morphologists gain a greater understanding of the amount of morphological variations between species. However, further work is needed in the field of intraspecific variation, including the degree and nature of the coil in the cochlear spiral and the shapes and orientations of the semicircular channels. In particular, there may be an

interesting link between how interspecific form-function relationships translate into intraspecific changes in anatomy and physiology. Thank you to M. Mason and A. Tucker (editors), as well as A. Ekdale, Z.-X. Luo and an anonymous reviewer for helpful and constructive comments during the development and review of the handwriting process. A photo of the cochlea in cross-section was taken by N. Zellmer. Alexander G (1904) Entwicklung und Bau des inneren Gehörorgans von Echidna Dekschr Mednaturnwiss Ges Jena 3. 1. Alexander MR (2002) Stability and manoeuvrability of terrestrial vertebrates. *Integr Comp Biol* 42, 158-164. Armstrong SD, Bloch J, Houde P, et al. (2011) Volume of cochlear labyrinth in Euarchontoglires: consequences for the development of hearing in primates. *Anat Rec* 294, 263. Barnes LG, McLeod SA (1984) Fossil record and phyletic relations of gray whales. In: Grey whale: Eschrichtius robustus. (eds ML Jones, SL Swartz, S Leatherwood), p. 3-32. Orlando: Academic Press. 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