Review article

A review of anatomical adaptations in the middle ear of living aquatic Tetrapods

Uma revisão sobre as adaptações anatômicas do ouvido médio dos Tetrápodes aquáticos atuais

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Abstract: Tetrapods have evolved from aquatic vertebrates and have conquered and diversified in the terrestrial habitat. While most species have well adapted to inland forms, some of them have returned to the aquatic environment due to increasing competition on Earth's surface. Studies regarding these species have been focused on hearing anatomy and auditory processes, neglecting the adaptations developed throughout evolution to compensate for pressure in the middle ear during dives. This review compiles the available information of mechanisms employed by tetrapods to prevent middle ear barotrauma underwater and how these processes have changed during evolution. The results show that throughout the evolution process, different lineages have developed distinct, and occasionally shared, mechanisms to avoid middle ear barotrauma underwater. Also, the results evince the lack of information on some Tetrapods lineages regarding middle ear evolution, from unique species, such as the Galápagos marine iguana, to marine mammals.

Keywords: tetrapods; aquatic; pressure; diving.

Resumo: Os tetrápodes evoluíram de vertebrados aquáticos e conquistaram e se diversificaram no ambiente terrestre. Enquanto algumas espécies se adaptaram à vida na terra, alguns táxons retornaram ao ambiente aquático devido à grande competição na superfície terrestre. Estudos realizados com espécies de tetrápodes aquáticos normalmente focam na anatomia e processos auditivos, negligenciando as adaptações desenvolvidas ao longo da evolução para compensar a diferença de pressão no ouvido médio durante mergulhos. Essa revisão compila informações sobre os mecanismos usados pelos tetrápodes para prevenir o barotrauma do ouvido médio e como esses processos se modificaram durante a evolução. Os resultados demonstram que ao longo da evolução, diferentes táxons e linhagens desenvolveram mecanismos diferentes, e ocasionalmente compartilhados, para evitar o barotrauma do ouvido médio no meio aquático. Os resultados também indicam que há falta de informações acerca das adaptações ao hábito de vida aquático em diversas espécies, desde as formas mais únicas, como a iguana marinha de Galápagos, aos mamíferos marinhos.

Palavras-chave: tetrápodes; aquático; pressão, mergulho.

1. INTRODUCTION

Barotrauma is the term ascribed to characterize an injury of the tissue in air cavities, such as the lungs or the middle ear, caused by a change in atmospheric pressure (Collins Dictionary, 2012). The middle ear barotrauma occurs in the absence of an adequate pressure equalization at both sides of the eardrum (external and middle ear), which can be caused by some activities such as diving and lead to permanent hearing loss (Carlson *et al.*, 1992; Melamed *et al.*, 1992; Karahatay *et al.*, 2008). At sea level, all organisms are subjected to 1 atm of pressure, meaning that at normal atmospheric conditions, every inch of our bodies is under 6.6 kg of pressure, which increases by 1 atm at every ten meters of water depth (Beebe, 1951). Pressure equalization has been described for humans to occur in two different paths: one via the Eustachian tube; and the other by transmucosal gas exchange. However, while the first one needs an active maneuver from the organism to happen, the second one is irrelevant in diving situation because the pressure increases quickly underwater (O'Neill *et al.*, 2022).

The middle ear, also known as the tympanic cavity, corresponds to an air-filled space present in the tetrapod's skull, which is limited externally by the eardrum and internally by the inner ear (Haines and Mihailoff, 2018). The tympanic cavity contains one or more bones, which vary among taxa lineages, and is connected to the oral cavity by the Eustachian tube (Zachary, 2016). Its function is related to the hearing process, transmitting the sound vibration that reaches the eardrum to the inner ear through an ossicular chain (Hood, 1977).

Throughout the vertebrate evolution pathway, the middle ear evolved after colonizing the terrestrial environment. The middle ear changed several times in different taxa providing unique features adapted to their environmental conditions for each group (Clack and Allin, 2004). Amphibians possess a single bone in the middle ear, the stapes (columella), wrapped by connective and muscle tissue (Jaslow *et al.*, 1986). The tympanic membrane is present only on terrestrial species, being completely lost on strictly aquatic salamanders and gymnophiones (Hetherington, 1992). However, some studies suggest that, given the anurans wide distribution among habitats, this adaptation may not be exclusively due to the environment where each species lives (Womack *et al.*, 2017; Catenazzi *et al.*, 2014). In sauropsids, a group that includes "reptiles" and birds, the middle ear also contains one bone, the columella, that forms a bridge between the tympanic membrane and the inner ear. Whitin sauropsids, archosaurs, and turtles may yet have another element, the extra columella, a cartilaginous extension of the columella that tensions the tympanic membrane, which can also be seen in some anuran and some lizards (Wever, 1978; Pereya *et al.*, 2016; Sánchez-Martínez *et al.*, 2021). At last, large modifications in mammal skulls significantly changed the arrangement of bones that articulate with the jaw, providing this lineage with three ossicles in the middle ear: the malleus, incus, and stapes (Anthwal *et al.*, 2013; Allin and Hopson, 1992).

While most studies regarding the middle ear in tetrapods have focused on the auditory system and underwater hearing, no study has aimed to understand how pressure-controlled adaptations occurred from land to water, and how they evolved and diversified among taxa. Therefore, the present review aims to compile the available information on the mechanisms employed by tetrapods to prevent underwater middle ear barotrauma, highlighting how these processes have changed due to the increasing complexity of these lineages throughout evolution and the still unexplored gaps in this area of study.

2. MATERIALS AND METHODS

The search for the materials was performed at available scientific databases, such as Google Scholar and the CAPES website, the governmental agency from Ministério de Educação do Brasil. The keywords used were either related to whole taxa: "amphibians middle ear pressure", "reptiles middle ear pressure", "birds middle ear pressure", "marine mammals middle ear pressure"; or to specific orders and/ or families: "phocidae middle ear pressure", "whale middle ear pressure", etc. In the end, a total of 6 studies were selected for Amphibians, 37 for Sauropsids (including reptiles and birds), and 16 for Mammals.

3. RESULTS AND DISCUSSION

Amphibians

Commonly found in adult amphibians, a tympanic middle ear is present in most of the anuran species, but absent in species with strictly aquatic habits, such as salamanders, gymnophiona and some anuran species (Hetherington, 1992). However, studies focusing on the anuran taxa suggest that the loss of the tympanic membrane is not related to a specific type of habitat, since anurans can be found in a wide range of ecological environments and, therefore, having distinct evolutionary pressures acting on their morphological features (Womack *et al*., 2017; Catenazzi *et al.*, 2014).

According to Mason (2006), the pressure balance inside anuran's middle ear might occur by the action of the opercularis system. Once frogs breathe in, the air reaches the middle ear through the Eustachian tube and forces the tympanic membrane outward. Acting like a pressure buffering, the opercularis muscle contracts and relaxes to regulate the pressure by keeping the stapes in place during the breathing process. The same procedure was observed for the African clawed frog *Xenopus laevis* during submerged periods. In these conditions, with their mouths filled with water, the lungs' pulsations push the air into the middle ear cavity, balancing the pressure on both sides of the tympanic membrane (Wever, 1985; Christensen-Dalsgaard and Elepfandt, 1995).

Sauropsids

A shared mechanism among the "reptilian" and bird species is the ability to close their external acoustic meatus, also known as the external ear cavity, with a variety of "mental muscles" (Sade *et al*., 2008; Han and Young, 2016). This contraction isolates and protects the tympanum against mechanical damage caused by the change of pressure between terrestrial and aquatic habitats (Wever, 1978). Apart from this synapomorphy, both "reptiles" and birds developed different mechanisms to deal with their amphibious lifestyle and the constantly changing pressure.

Reptiles

The Squamata order species present a great diversification in their middle ear structures, such as the lack of a tympanic middle ear in sea snakes, represented by the families Elapidae and Hydrophiinae (Hartline and Campbell, 1969), and different levels of development of the tympanic membrane on lizards (Paparella and Caldwell, 2021). The Galápagos marine iguana *Amblyrhynchus cristatus*, the only extant lizard to depend upon the marine habitat to forage, has a reduced tympanic membrane due to a lack of a structure called crista interfenestralis, which, in terrestrial lizards would elongate

the tympanic cavity, and consequently, increase the membrane size (Paparella and Caldwell, 2021). The absence of this structure and reduction of the tympanic membrane is shared among other marine lizards and swimming animals, such as sea turtles (Hetherington, 2008). Although there is not enough data on the tympanic complex of living or extinguished marine lizards to conjecture on the function of this modification, Paparella and Caldwell, (2021) hypothesize that it might be linked to an aquatic habit.

Unlike other reptiles, the tympanic membrane of an amphibious lizard species, the water monitor *Varanus salvator*, remains constantly exposed in both terrestrial and aquatic environments (Han and Young, 2016). Being unable to hide the tympanum to protect it from the changing pressures, the species presents two synchronized processes to balance the pressure in the middle ear during land-water transitions: the expansion of the pharyngeal cavity and the tension applied on the tympanic membrane by the tympanic muscle (Han and Young, 2016). The active and voluntary expansion of the pharyngeal cavity forms a "gular pouch" that changes the pressure in this cavity, which due to the connection between the oral cavity and the middle ear via the Eustachian tube, also changes the internal pressure in the tympanic membrane (Murphy and Lamoreaux, 1978; Owerkowicz *et al.*, 2001). Simultaneously, the tympanic muscles contract to compensate for the shift in pressure in the middle ear, keeping the tympanum stabilized (Han and Young, 2016). This connection between the middle ear and the oral cavity is also described for the Nile Monitor (*Varanus niloticus*), an aquatic species, and the savannah monitor V. exanthematicus, a terrestrial monitor lizard (Dijk and Manley, 2013), suggesting that this process may not be a habitat driven adaptation. Anatomical variations occurred also among monitor lizards, with the semi-aquatic earless monitor lizard *Lanthanotus borneensis* middle ear resembling closely to those of turtles, particularly softshell turtles like Trionychidae and Carettochelyidae, due to the shallowness of the middle ear cavities (McDowell, 1967).

Testudines are a monophyletic group that comprises species adapted for a wide range of habitats, from marine to semi-arid biomes (Guillon *et al.*, 2012). Despite the ecological niche, all turtle species have compartmentalized middle ears as a synapomorphic feature (Gaffney *et al.*, 2006). Although the reason for these divisions or why some portions are filled with air remains unexplained, some authors suggest that it may be related to either improving underwater sound location or preventing the middle ear from collapsing during deep diving (Hetherington, 2008).

A comparison study performed with green sea turtle *Chelonia mydas* and other three terrestrial turtle species demonstrated that sea turtles appear to have yet other two specializations in their middle ears, including the reduced middle ear cavity volume, about 33% smaller than terrestrial turtles and the presence of a considerable amount of fatty tissue inside middle ear cavity, which in terrestrial species is filled with air (Willis *et al.*, 2013; Foth *et al.*, 2019). The differences in the skull are also present

among sea turtle species, with the hawksbill sea turtle, *Eretmochelys imbricata*, possessing a rounded tympanic cavity but an undeveloped antrum postoticum (one of the portions) and the leatherback sea turtle, Dermochelys coriacea, not having neither of those structures (Raselli, 2018). Some theories have been proposed to explain such modifications, many of them suggesting it to be a mechanism to facilitate diving. During deep diving, both air-filled spaces and the fatty tissue are compressed by the increasing pressure inside the middle ear cavity. Therefore, middle ears with smaller or fewer compartments (lacking some portions), with volume reduction and less air-filled space availability, would have better pressure resistance (Foth *et al.*, 2019). Regarding the fatty tissue presence, considering that the skull elements of sea turtles do not differ from the ones observed in other testudines, it's possible that it may be a secondary adaptation to the marine habitat (Willis *et al.*, 2013). It was also hypothesized to be related to pressure equalization in the middle ear cavity, by optimizing air exit through the Eustachian tube (Lenhardt *et al.*, 1985).

The crocodilians are the only group of "reptiles" to possess an external ear, meaning that, unlike other reptiles, a thin canal connects the environment with the tympanic membrane that does not level with the skin and cannot be seen from the outside (O'Malley, 2005). The crocodilians present yet another morphological difference, a specialization of the Eustachian tube, which was already present in Mesozoic Crocodyliformes as thalattosuchians (Colbert, 1946). Contrasting with the other "reptiles" that have only one Eustachian tube, in crocodiles this structure is divided into two branches: the lateral (Le) and the median (Me) tubes. While each lateral branch (left and right) follows up the usual path to each side of the head, the median tube divides into two small portions, an anterior (Mea) and a posterior (Mep), each bifurcating again into left and right branches (**Figure 1**).
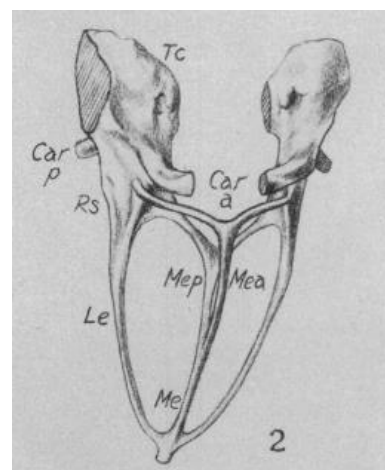

Figure 1. Tympanic cavities and eustachian tubes of the cast, shown in Fig. 1, as seen in an antero-oblique view. Somewhat enlarged. over Fig. 1. Car-a, anterior exit of carotid artery from tympanic cavity (from whence it runs forward to enter the sella turcica); Car-p, posterior entrance of carotid artery into tympanic cavity; Le, lateral eustachian tube; Me, median eustachian tube; Mea, anterior branch of median eustachian tube, bifurcating dorsally to enter the right and left rhomboidal sinuses; Mep, posterior branch of median eustachian tube, bifurcating dorsally to enter the right and left rhomboidal sinuses; Rs, rhomboidal sinus; Tc, tympanic cavity. (Colbert, 1946).

Each pair of branches follows to one side of the head, where it connects to the lateral tube in the middle ear (Colbert, 1946). Although the reason for such a complex tube structure has not been yet fully elucidated, Colbert (1946) suggested that these small branches might provide a faster pressure equalization in each side of the tympanum than a single tube; or even that branched canals would allow a pressure equalization from one ear straight to the other without the necessity of air passing down to the throat by one tube and then up by the other.

Ventrally, both lateral and median tubes merge into one single passage, which is an extension of the median pharyngeal tube (Tahara and Larsson, 2022), and opens in one chamber dorsally to the pharynx by a median pharyngeal valve (Young and Bierman, 2019). This valve isolates the middle ear from the pharynx and opens every two minutes independently from the auditory stimulus, thus suggesting that it may be a structure associated with pressure regulation, leading the air through the tubes to the middle ear cavity (Young and Bierman, 2019).

Birds

Birds belong to the Archosauria branch of the reptile evolution, sharing an ancestor with modern crocodiles and alligators (Brusatte *et al.*, 2010). Apart from the ancestry, birds also inherited the two air-filled pathways that connect the right and left middle ears (from now on referred to as intracranial air cavities and interaural pathway). Under normal conditions, the Eustachian tube remains closed, but when the pressure gradient in the middle ear increases or decreases, the tube opens, venting the air in or out and balancing the pressure inside (Sauders *et al.*, 2000; Larsen *et al.*, 2016).

Plunge-diving bird species, such as gannets, auks, and cormorants may be subjected to high amounts of pressure, up to tens of pressure differentials per second when diving through the air and into the water to fish (Claes *et al.*, 2017). Studies suggested that birds have a sense organ, the paratympanic organ, which detects changes of pressure in the middle ear, would cause a reflexive opening of the Eustachian tube and provides stability and adequate tension on the tympanic membrane (Von Bartheld, 1994; Von Bartheld and Giannessi, 2011). However, a study performed by Claes *et al.*, (2017) with mallards observed that the stimulus to either open the Eustachian tube or increase venting frequency was not influenced by the amount of pressure in the tympanic membrane, thus suggesting that these mechanisms may depend upon other stimulus, such as visual cues, or occur voluntarily, by the action of brain functions. Another morphological feature, the solidified eardrum, previously observed in auks by Kartaschew and Iljitschow (1964) and in some Pelecaniformes and Ciconiiformes by Saiff (1978), was recently described in the great-cormorant *Phalacrocorax carbo* sinensis by Larsen et al, (2020). This feature is supposed to be a mechanism developed to protect the tympanic membrane during the increasing pressure in the middle ear during plunge-diving behaviors (Larsen *et al.*, 2020).

Plunge-diving and deep-diving birds seem to present specializations to reduce the effect of changing pressure in the middle ear and prevent barotrauma. According to Zeyl *et al.*, (2022), underwater pursuit species have: (1) a diverse range of cranial pneumaticity loss in the interaural and/or intracranial cavities, which can be filled with air or tissue; and (2) the reduction of tympanic membrane area. The full closure of the intracranial cavity can be observed in underwater-pursuit species such as penguins, several cormorants, the African-darter (*Anhinga rufa*), the great-northern-diver *Gavia immer*, and the black-guillemot *Cepphus grylle*; while the complete absence of interaural cavities was found only in penguins and in the south-Georgia-shag *Leucocarbo georgianus* (Zeyl *et al.*, 2022).

Deep-diving birds have a large and complex corpus cavernosum underlying their submucosa and filling the space between the mucosa and the skull. During diving activities, as the animal descends into the water column, these vessels are flooded with blood. This causes the middle ear to reduce in volume and increases the pressure within this cavity, balancing it with the surrounding pressure (Sade *et al.*, 2008). Among diving birds, this structure was mostly observed in two species of penguin, in which the existent cranial cavities are only filled with tissue, the king penguin *Aptenodytes patagonicus* and emperor penguin *Aptenodytes forsteri*, (Kooyman *et al.*, 1992; Kooyman and Kooyman, 1995). However, other species, such as the African-penguin (*Spheniscus demersus*), seem to have just remains of this tissue, and the gentoo penguin *Pygoscelis papua*, appears to have lost it completely (Frahnert *et al.*, 2020). While both Aptenodytes species can dive up to 500 meters, *S. demerus* and *P. papua* only reach 130 m and 210 m, respectively (Wilson 1985; Bost *et al.*, 1994). Therefore, the progressive loss of air cavities and the appearance of the corpus cavernosum are associated with the diving capacity and the foraging behavior (e.g. underwater pursuit) (Zeyl *et al.*, 2022).

Similarly to "reptiles, penguins can isolate their tympanic membrane from the outside by contracting muscles in their external ear (Sade *et al.*, 2008). Apart from the corpus cavernosum, air reservoirs in penguins' oral cavity during diving was considered to have a role in equalizing middle ear pressure, but this mechanism has not been clarified (Frahnert *et al.*, 2020).

Regarding the tympanic membrane area, the reduction of 70% of the size of the structure from a terrestrial species would allow thinner cavities (intracranial and interaural) and reduce the amount of air volume subjected to pressure in their skull (Zeyl *et al.*, 2022; Smith, 2011). It would particularly improve the ability to collapse those middle ear canals during diving, as previously observed in cormorants (Larsen *et al.*, 2020) and auks (Kartaschew and Iljitschow, 1964).

Mammals

Mammals have evolved from the order Therapsid in the Permian, over 252 million years ago (Kemp, 2006). Contrary to the Archosaurs and birds, the enlargement of the brain in mammals caused the reduction of the connections between the oral cavity and the middle ear,

restricting the connection only to the Eustachian tube (Manley, 2010). The term 'marine mammals' is designed to describe the mammal species that live or depend upon the aquatic environment to accomplish life history requirements, such as feeding. The living marine mammals are distributed in three orders: Carnivora, which encompasses Phocidae (seals), Otariidae (sea lions) and Odobenidae (walruses), Ursidae (polar bear) and Mustelidae (sea otters); Sirenia (manatees and dugongs), and Artiodactyla (whales and dolphins) (Jefferson *et al*., 2015).

Amongst the most diverse of the orders, Carnivora species present different mechanisms, apomorphies, to deal with changing pressure. The Pinnipeds, composed by the Phocidae, Otariidae and Odobenidae families, possess two plesiomorphic features: (1) the presence of the corpus cavernosum within the middle ear cavity, which floods with blood during diving and blocks the Eustachian tube, isolating the middle ear cavity from its connection, and (2) voluntary muscles in the external meatus that close the external canal when the animal submerge, preventing water from entering and maintaining an air-filled canal in the outer side of the tympanic membrane (Møhl, 1968; Repenning, 1972; Stenfors et al, 2001;). Pinnipeds species also have narrow external canals, which facilitates the closure during deep diving expeditions (Au and Hastings, 2008). Regarding the apomorphy, it relies on the presence of a corpus cavernosum also in the inner portion of the external meatus canal. Therefore, in depths between 70 meters and 100 meters, both outer and middle ear tissue swelling act to stabilize the eardrum and equalize the pressure in the tympanic membrane (Repenning, 1972).

Although adapted for an amphibious lifestyle, both Phocidae and Otariidae have considerable skull structure differences, including middle ear cavity volume, which is larger in seals (Phocidae) than in sea lions (Otariidae) (Graham, 1967; Wannaprasert, 2013). Contrary to what was suggested in sea turtles by Foth *et al*., (2019) (see the Reptiles section), according to Graham (1967), the larger the volume of the middle ear cavity in Pinnipeds, the deeper each species can dive and still have a reasonable ability to receive transossicular vibrations underwater. Thus, as Phocids have larger middle ear cavities, seals should be able to hunt in greater depths than sea lions (Graham, 1967).

Since the sea otter's *Enhydra lutris* and the California sea lion's *Zalophus californianus* hearing physiology appears to have converged to a low-frequency system (Ghoul and Reichmuth, 2014), and the sea lion's ancestors had similar foraging behaviors to the extant aquatic mustelids (Riedman, 1990), inhabiting coastal areas, both may share the same mechanism to regulate pressure within the middle ear cavity (Riedman, 1990). However, no study was found to either agree or disagree with that statement. As for the last of the Carnivora families, the Ursidae, no data was found regarding the mechanisms employed by the polar bear Ursus maritimus to regulate the middle ear pressure during diving. *Polar bears* are the only bear species considered marine mammals, as it is completely dependent on the water habitat to feed (Jefferson et al, 2015, Lone et al, 2018). Although authors often diverge about how deep can a polar bear dive, Stirling and Van Meurs (2015) recorded the longest and deepest dive from a wild polar bear, which dove for 3 minutes straight and reached up to 50 meters underwater during hunting excursions. This, gathered with the poor information on polar bears' aquatic behavior (Lone *et al*., 2018) emphasizes the necessity of more studies to uncover the species' underwater unique adaptations, as the species is facing the risk of extinction due to melting glaciers around the world.

Contrary to the Carnivora order, Cetaceans and Sirenia orders comprise fully aquatic mammals, which spend their whole lives in the water, mainly at the sea (Thewissen *et al*., 2009). The order Cetacea includes two distinct clades, the Odontoceti and the Mysticeti represented by the toothed and baleen whales, respectively (Bianucci and Landini, 2007).

In general, cetaceans external ear canal is narrow and mostly occluded by wax and debris, and ends in the tympanic membrane, which is elongated, hollow, and everted (Ketten, 2000; Tubelli et al, 2018). The middle ear cavity in both groups is filled with a thick corpus cavernosum tissue, and partially filled with air (Ketten, 1994; McCormick *et al*., 1970). Differently from other marine mammals, such as the Pinnipeds, when Cetaceans engage in deep diving, the swelling of the corpus cavernosum does not block the connection between the Eustachian tube and the middle ear cavity, then the tube functions as a continuous air passage from the lungs to the tympanic cavity (Fleischer, 1978). This mechanism of pressure equalization is the same employed by human divers.

Toothed whales (Odontocetti) and baleen whales (Mysticeti) differ, yet, in some morphological features, from physical to structural aspects. Mysticeti species have a unique wax cap covering the tympanic membrane (Purves, 1955) and a tough Eustachian tube wall that avoids tube closure during pressure differentials (Ketten *et al*., 1997). According to Ketten (1997), the tympanic cavity increases with species size, thus making the middle ear cavity in whales larger than dolphins and explaining how diving depths vary between these groups (Graham, 1967).

Ecologically distinct from all other marine mammals, the order Sirenia comprises strictly herbivore species of manatees and dugongs, which inhabit shallow waters in the tropical regions of America, Africa, and the Indo-Pacific Ocean (Wannaprasert, 2013). Sirenians have large middle ears, thick and stiff tympanic membranes like cetaceans, and external meatus canals occluded by fatty tissue (Ketten, 2003; Chapla, 2006). Ventrally, the middle ear cavity is obstructed by the soft tissue of the throat, being dorsally filled with air, and coated with a vascularized fibrous sheet (Ketten, 1993). Contrary to Carnivora and Cetacea, Sirenians lack the corpus cavernosum in the middle ear cavity and the musculature in the external meatus canal is responsible for closing the opening (Chapla, 2006; Nummela and Yamato, 2018). Regarding the mechanism employed by Sirenians to avoid

barotrauma even in shallow waters, the only hypothesis found in the present review suggests that underwater pressure would cause the air inside the middle ear to pulse, bulging the tympanic membrane outward, balancing the pressure at the eardrum (Chapla, 2006; Nummela and Yamato, 2018).

CONCLUSION

Throughout the course of evolution, distinct adaptive pressures led tetrapods to develop a wide range of mechanisms to cope with land-water transitions (**Table 1**), as terrestrial habitats continued to be colonized and environments became even more competitive (Laurin, 2010).

Middle ear morphology evolution is directly related to the complex rearrangement of bone articulation between the jaw and the skull in Tetrapoda (Clack and Allin, 2004). The middle ear is composed of a columella, which prevailed for the longest timescale, being present in the first tetrapods (amphibians and sauropsids) and posteriorly improved to a three-bone middle ear in mammals (Wever, 1978; Anthwal *et al.*, 2013; Allin and Hopson, 1992). Although skull modifications have changed the middle ear bone morphology, the mechanisms employed by aquatic tetrapods did not quite differ among taxa, being shared both directly from common ancestors ("reptiles" to birds), or through evolutive convergence.

The mechanism related to the ability to close the external meatus, although shared with all taxa within the amniotes, is not one example of symplesiomorphy (old and shared feature) since mammals were not originally aquatic organisms. Mammals evolved from Therapsids about 252 million years ago and had its first aquatic representative only about 65 million years ago (Kemp, 2006). The existing marine mammals are lineages from Proboscidea (sirenia), Artiodactyla (cetaceans) and Carnivores (Thewissen *et al.*, 2009; Gatesy and O'Leary, 2001). Therefore, rather than a symplesiomorphy, it is an example of evolutive paralelism, a phenomenon characterized by the sharing of features between species within the same group but not directly related, contrary to convergence

Table 1. Summary of the mechanism and morphological features developed by aquatic Tetrapods related to middle ear barotraumas avoidance, sorted by taxonomic group and orders.

Taxonomic group	Order	Mechanisms /morphological features related to barotrauma avoidance	Reference
Amphibians	Anuran	Opercularis system	Mason, 2006; Wever, 1985; Christensen-Dalsgaard and Elepfandt, 1995
Sauropsids	"Reptiles" and birds	Closure of the external acoustic meatus	Wever, 1978; Sade *et al.*, 2008; Han and Young, 2016.
	Squamata	Loss or reduced tympanic membrane; Expansion of the pharyngeal cavity and tension on the tympanic membrane; Reduced middle ear cavity.	Hartline and Campbell, 1969; Paparella and Caldwell, 2021; Han and Young, 2016. McDowell, 1967
	Testudines	Compartmentalized middle ears and air-filled portions; Reduced middle ear cavity volume; Presence of fatty tissue in the middle ear cavity	Hetherington, 2008; Willis et al, 2013; Foth *et al.*, 2019
	Crocodilia and birds	Eustachian tube divided in two branches	Colbert, 1946
	Charadriformes, Suliformes, Pelecaniformes and Ciconiiformes	Solidified eardrum	Kartaschew and Iljitschow 1964; Saiff 1978; Larsen *et al.*, 2020.
	Suliformes, Gaviiformes, Charadriformes	Different levels of cranial pneumaticity loss; Reduced tympanic membrane	Zeyl *et al.*, 2022.
	Sphenisciformes	Corpus cavernosum; Air reservoirs in the oral cavity	Sade *et al.*, 2008; Kooyman *et al.*, 1992; Kooyman and Kooyman, 1995; Frahnert *et al.*, 2020.
Mammals	Carnivora (Pinnipeds)	Corpus cavernosum in the inner portion of the external meatus canal; Voluntary muscles in the external meatus. Narrow external canal; Middle ear volume	Møhl, 1968; Repenning, 1972; Stenfors *et al.*, 2001; Au and Hastings, 2008; Graham, 1967; Wannaprasert, 2013
	Cetacea (general)	Middle ear cavity with both corpus cavernosum and air-filled spaces; Narrow and occluded external ear canal; Hollow and elongated tympanic membrane;	Ketten, 2000; Tubelli et al, 2018; Ketten, 1994; McCormick *et al.*, 1970;
	Cetacea (Mysticeti)	Wax cap covering the tympanic membrane and tough Eustachian tube wall	Purves, 1955; Ketten *et al.*, 1997
	Sirenia	External meatus occluded by fatty tissue; Middle ear filled with soft tissue, vascularized fibrous sheet and air; Lack of corpus cavernosum	Ketten, 2003; Chapla, 2006; Ketten, 1993; Nummela and Yamato, 2018

which requires a distant relationship between species. The same evolution path can be seen for the presence of the corpus cavernosum in penguins, Pinnipeds and Cetaceans.

The present review, by compiling systematic information from most lineages which possess aquatic species, recognized some knowledge gaps. Although much is discussed about Cetaceans, studies on ear morphology demonstrated some negligence regarding non-Pinnipedia carnivorans, such as sea otters and polar bears.

Finacial support

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