

Chapter 7

The Lepidosaurian Ear

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Abbreviations used in Figures

aam, anterior ampulla; aLRST, apertura lateralis recessus scalae tympani; aMRST, apertura medialis recessus scalae tympani; ar, acoustic recess (entry of CN VIII nerve foramina); art.s, articular surface; asc, anterior semicircular canal; as.ip, articular region of internal process; Bo, basioccipital; CCF, crista circumfenestralis; Cd, cochlear duct; cif, crista interfenestralis; cEs, contact surface on stapedia shaft for extrastapes; CN, cranial nerve; CN VIII, vestibulocochlear nerve; CN IX, glossopharyngeal nerve; CN X, vagus nerve; cp, crista prootica; ctb, crista tuberalis; Cw, compensatory window; Ed, endolymphatic duct; En, endolymphatic sac; Eo, exoccipital; Es, extrastapes; fen, foramen for endolymphatic duct; FP, footplate of stapes; fV, fenestra vestibuli; f5, foramen for CNV; f8, foramen for CN VIII; f9, foramen for glossopharyngeal nerve, CN IX; ham, horizontal ampulla; hsc, horizontal semicircular canal; ip, internal process; isp, infrastapedial process; Jr, jugular recess; JSF, juxtastapedial fossa; la, lagena; mf, Metotic fissure; Mx, maxilla; occ, osseus common crus; O.cp, otic capsule; or, orbit; pam, posterior ampulla; Pc, periotic cistern; Pd, periotic duct; Pf, periotic foramen; Ppr, paroccipital process of opisthotic; Pro, prootic; Ps, periotic sac; psc, posterior semicircular canal; pt.ip, pit for process internus; Qu, quadrate; Qu.co, quadrate conch; Qu.tc, quadrate tympanic crest; Ra, retroarticular process of jaw; rm, rim around stapedia footplate; RST, recessus scalae tympani; sap, suprastapedial process; Sp, sphenoid; sst, statolith; St, stapes; Stm, meatus for stapes; Sts, stapedia shaft; Tm, tympanic membrane; Va, vestibular apparatus; Vc, vestibular chamber; vf, vagus foramen.

Institutional abbreviations

BAD, Badlands National Park collection, South Dakota, USA; BGS GSb, collections of the British Geological Survey, Keyworth, UK; FFHM, Fick Fossil and History Museum, Kansas; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; KUVP, University of Kansas, Museum of Natural History; MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; NHMG, Guangxi Natural History Museum, Zoology collections

7.1 Introduction

Lepidosauria is the reptile group encompassing lizards, snakes and their relatives. Today it comprises two monophyletic sister-clades, Squamata and Rhynchocephalia, that are very disparate in terms of species number and biogeography. Squamata includes more than 9000 species of lizards, snakes (Serpentes), and worm-lizards (Amphisbaenia), and has a global distribution. The group is also morphologically and ecologically diverse. In contrast, Rhynchocephalia is represented by a single living species, *Sphenodon punctatus*, the Tuatara of New Zealand, although the group has a rich Mesozoic history.

Clearly an understanding of lepidosaurian interrelationships is important to our understanding of the polarity (i.e., primitive or advanced) and evolutionary trajectories of different characters, including those of the ear region. Most recent phylogenies (morphological and/or molecular) of squamates recognise the monophyly of the following subgroups: Gekkota (geckos), Dibamidae (rare limbless burrowers), Scincoidea (e.g., skinks, girdled-lizards), Teiioidea (e.g., tegus, whiptails), Lacertidae (e.g., wall lizards), Amphisbaenia (worm lizards), Iguania (e.g., iguanas, chameleons), Anguimorpha (e.g., monitor lizards, slow worms), and Serpentes (snakes). However, there are some major discrepancies in the relative placement of these groups between different researchers. Phylogenetic analyses based solely on morphological characters (e.g., Estes et al., 1988; Conrad, 2008, Gauthier et al., 2012) consistently place Iguania as the sister group to all other squamates. However, analyses based on molecular data (e.g., Townsend et al., 2005; Wiens et al., 2012; Pyron et al., 2013), or a combination of molecular and morphological characters (e.g., Wiens et al., 2010; Reeder et al., 2015) always place Iguania as the sister group of Anguimorpha and/or Serpentes, with Gekkota and/or Dibamidae emerging as the sister taxon to other squamates (Fig. 7.1). These molecular analyses also group Amphisbaenia with Lacertidae and Teiioidea. Snakes are broadly divided between the small-mouthed burrowing Scolecophidia (questionably monophyletic) and Alethinophidia, which encompasses all remaining snakes, most notably the Macrostromata (e.g., boas, pythons, vipers, cobras, sea snakes). For obvious reasons, fossil taxa can only be accommodated within morphology-based or combined evidence analyses, and this can lead to differing opinions as to their precise phylogenetic position.

Note that in this chapter, 'lizard' is used to refer to a squamate that is neither a snake nor an amphisbaenian. In older classifications, the formal name Lacertilia was applied to this grouping, but as lizards do not form a monophyletic group, a formal clade name is inappropriate

7.2 The Fossil Record of Lepidosauria

Recent molecular divergence estimates (e.g., Jones et al., 2013) place the origin of Lepidosauria in the Early Triassic (~240-250 million years ago [Ma]) and that of Squamata in the Early Jurassic (~193 Ma). However, most lepidosaurs are small and this limits both the potential for their skeletons to be preserved after death, and the chances of recovering their fossils. As a result, the earliest stages of lepidosaurian history and diversification are poorly documented. The lepidosaurian stem is represented by a small number of Triassic and Jurassic genera, most of which represent survivors of earlier originating lineages. These stem-taxa are grouped with lepidosaurs into a more inclusive clade, Lepidosauromorpha. The position of the marine Sauropterygia (nothosaurs, plesiosaurs, placodonts, pliosaurs) and Ichthyosauria in relation to Lepidosauromorpha or Archosauromorpha remains unresolved (e.g., Jiang et al., 2014; Motani et al., 2015), and these taxa are covered in Chapter 8 by Reisz, Müller, Sobral, Scheyer & Neenan. Currently, the first recorded crown-group lepidosaurs are all rhynchocephalians, dating from the Middle Triassic onward (Jones et al., 2013). The first uncontentious squamate fossils are from the Middle Jurassic (e.g., Evans, 1994, 1998; Evans & Jones, 2010), but these are both rare and mostly fragmentary. The squamate record improves substantially from the Cretaceous onward, with the first records of specialised marine lizards (Mosasauria) and the first unambiguous snakes in the mid-Cretaceous, and the first amphisbaenians in the Palaeocene.

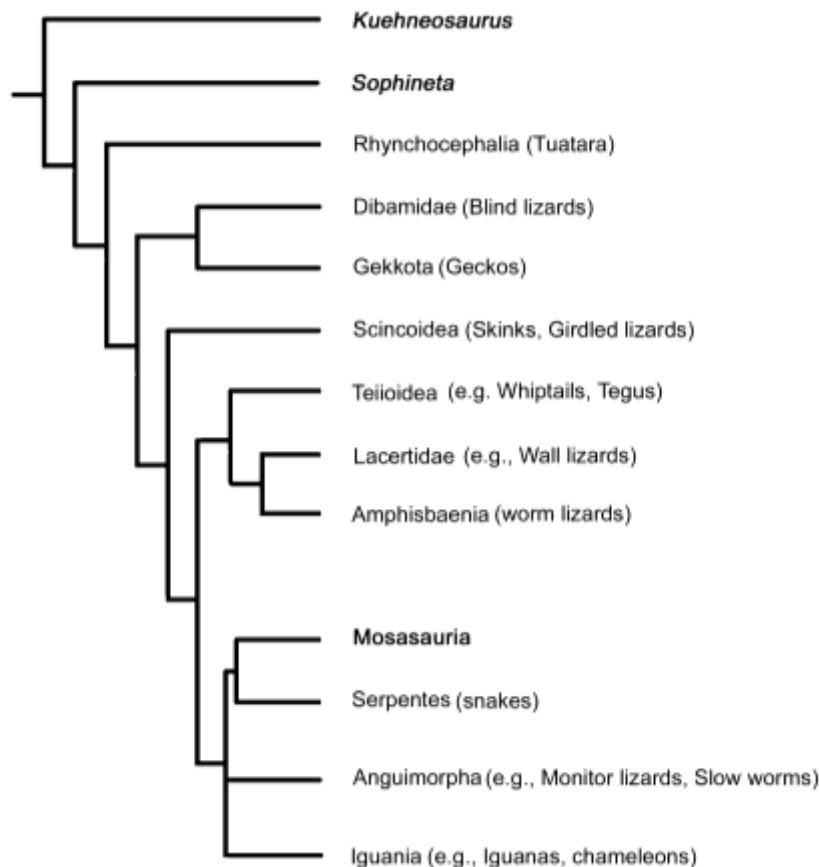


Fig. 7.1 Simplified tree of lepidosaur relationships based mainly on the combined evidence tree of Reeder et al. (2015) with additional data from Evans (2009) and Evans & Borsuk-Bialynicka (2009). Taxa in bold have no living representatives.

Knowledge of lepidosaurian ear evolution is limited because many early fossils come either from microvertebrate localities, where the bones are three-dimensionally preserved but disarticulated, or from fine-grained deposits (e.g., Solnhofen, Germany; the Yixian Formation, China; Las Hoyas, Spain), where the skeletons are articulated but two-dimensionally compressed. Most data on the lepidosaurian ear therefore comes from rare three-dimensionally preserved specimens. High Resolution X-ray Computed Tomography (HRXCT) and Synchrotron CT (SR μ CT) offer ways to access the morphology of the inner ear but, to date, relatively few lepidosaur fossils have been examined in this way.

7.3 The Lepidosaurian Ear

The ear of a typical lizard provides a good basis from which to consider lepidosaurian ear evolution as a whole. The outline presented here is mainly based on the works of Baird (1970) and Wever (1978)(Fig. 7.2).

There is no external ear in the mammalian sense (Fig.7.2A). The tympanic membrane is exposed on the side of the head and is usually free of scales (Fig. 7.3A). However, in some lizards the membrane is recessed more deeply below the surface and may be protected by projecting scales and/or by a meatal closure muscle (geckos). The tympanic membrane is supported dorsally, anteriorly and ventrally by the curved tympanic crest of the quadrate bone and, in part, ventrally by the retroarticular process of the lower jaw (Fig.7.3B). Posteriorly it is attached to soft tissue (fascia and muscle). In striking contrast to mammals, the frame supporting the lizard tympanic membrane is not rigid. Tension in the membrane fluctuates during feeding, partly because of the changing angle between quadrate and lower jaw, and partly because the quadrate of most lizards is streptostylic (capable of independent movement at its dorsal and ventral articulations). Despite this, lizards can apparently still hear while feeding (Wever, 1978).

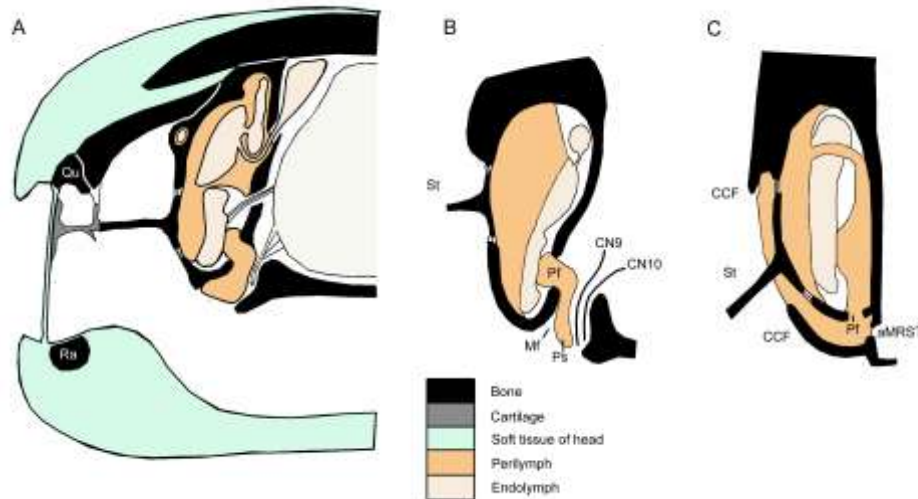


Fig. 7.2 Lepidosaur ear anatomy. A, schematic coronal section through ear region of a generalised lizard showing features of middle and external ear discussed in the text. B, schematic coronal section through otic capsule of *Sphenodon* showing the relationships of the periotic system to the metotic fissure. C, as B, for a generalised snake showing the relationship between the periotic sac and the crista circumfenestralis. In all figure parts, perilymph is coloured in darker orange, endolymph in the lighter shade. (A-C, adapted from Baird, 1970, Figs 2, 25A, 23A).

Medial to the tympanic membrane, the middle ear cavity is an air-filled diverticulum of the pharynx, usually with little distinction between the two regions, unlike the narrow Eustachian (auditory) tube of mammals (Fig. 7.2A). It is bounded medially by the bony otic capsule, dorsally by muscles and braincase structures such as the paroccipital process, and laterally by the quadrate, quadrate process of the pterygoid, and associated muscles. The stapes of most lizards has a small medial footplate and a long slender shaft that is extended laterally by a cartilaginous extrastapes (Fig. 7.2A). The extrastapes typically terminates in one or more anterior processes, as well as a posterior process and an inferior process. The latter two form an oblique bar across part of the tympanic membrane, contributing to its stability and to a lever effect that enhances sound pressure. Close to the junction with the bony stapes, two further processes may help to support the ossicle within the middle ear. These are the internal, or quadrate, process that contacts the quadrate, and the dorsal process that meets the paroccipital process. One or more of these processes may be missing.

The otic capsule is composed of the prootic, opisthotic, and supraoccipital (Fig. 7.3C-D). These enclose the cochlear duct (lagena) ventrally and vestibular apparatus dorsally. The fenestra vestibuli lies at the lateral junction of the prootic and opisthotic (Fig. 7.3C). Early in development, the otic capsule is separate from the basal plate (which will form the sphenoid anteriorly and basioccipital posteriorly) and occipital arch (contributing to the exoccipital). Although the occipital arch subsequently contacts the opisthotic posterodorsally, a gap, the metotic fissure, is left between the posterior surface of the otic capsule and the occipital arch/basal plate. In squamates, this metotic fissure is divided into dorsal and ventral portions by a second, more ventral, contact between the otic capsule and exoccipital. The dorsal passage carries the vagus nerve (Cranial nerve [CN] X). The ventral passage is the recessus scalae tympani (RST) (Rieppel, 1985; =occipital recess of Oelrich, 1956) (Fig. 7.3C). The RST has a medial opening into the cranial cavity, the apertura medialis recessus scalae tympani (aMRST) (Fig. 7.3D) and a lateral opening, the apertura lateralis recessus scalae tympani (aLRST) into the middle ear cavity. In most lizards, the RST also gives passage to the glossopharyngeal nerve (CN IX) (Fig. 7.2A, 7.3C-D), although some taxa (e.g., gekkotans) subdivide the RST again to produce a separate nerve canal. A periotic (=perilymphatic) foramen opens from the otic capsule into the roof of the RST, providing an exit for the periotic sac (Fig. 7.2A). Some authors (e.g., Wu, 1994) have termed this opening the fenestra rotunda (or fenestra cochleae), but this has

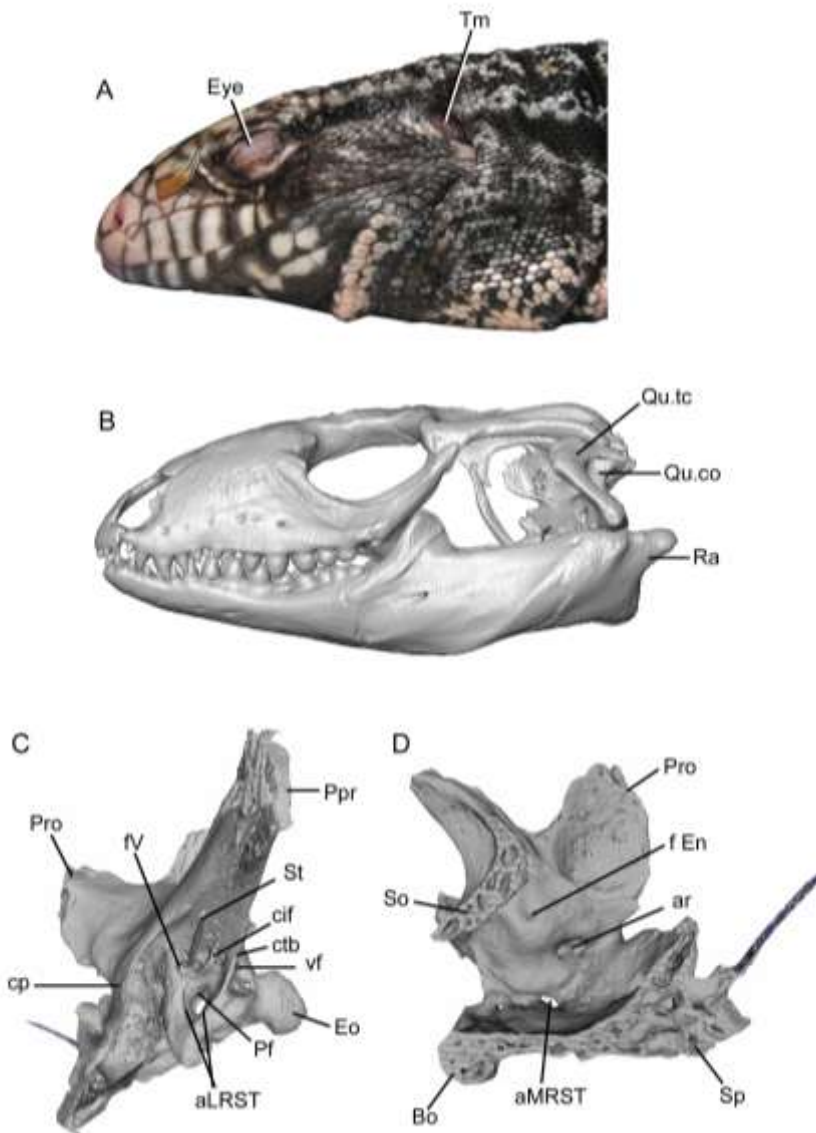


Fig. 7.3 Osteological correlates of ear anatomy in the otic capsule. A, left lateral view of the head of the teiid lizard *Tupinambis meriana* showing the external tympanic membrane. B, lateral view of the skull of *Tupinambis meriana*, based on surface model built from HRXCT data and visualised using Amira 6.3. C-D, braincase of the lacertid lizard *Gallotia sp.*, based on surface models built from HRXCT data and visualised with Meshlab. C) ventrolateral view showing relationship between fenestra vestibuli, apertura lateralis recessus scalae tympani, and surrounding crests. D) medial view showing positions of apertura medialis recessus scalae tympani, acoustic recess with foramina for CN8, and endolymphatic foramen. (All figures original)

homology implications and also causes confusion when the same term is used for the aLRST (e.g., Palci & Caldwell, 2014). Fenestra rotunda is better avoided completely in reptiles. In a typical lizard, the periotic sac extends both medially, where it is blind-ending, and laterally where it attaches to the margins of the aLRST to form a compensatory window (=secondary tympanic membrane) that lies adjacent to the membrane lining the middle ear/pharynx (Fig. 7.2A). This structure is a functional analogue of the mammalian fenestra cochleae (=fenestra rotunda). In many lizards (e.g., *Iguana*, *Gallotia*), the margins of the aLRST, and therefore of the compensatory window, are expanded by the development of two crests, the crista interfenestralis and crista tuberalis (Fig. 7.3C). The former, as its name suggests, lies between the fenestra vestibuli and the aLRST. The crista tuberalis extends down the edge of the exoccipital and separates the aLRST from the vagus foramen. It may combine with a similar crest on the basioccipital to form a more extensive frame. Medially (Fig. 7.3D), the otic capsule is pierced by anterior and posterior foramina for the vestibulocochlear nerve (CN VIII), usually placed within a depression (acoustic recess), and by a more dorsal foramen through which the endolymphatic duct emerges into the cranial cavity from the otic capsule.

The inner ear is enclosed within the otic capsule and comprises a short ventral lagena (=cochlear duct) and the sacs (sacculae, utricle), ampullae and semicircular ducts (anterior, posterior, horizontal) of the vestibular apparatus (Baird, 1970; Wever, 1978). Both the utricle and sacculae contain sense organs (maculae) that respond to changes in body position. These are composed of a gel-like matrix into which are embedded calcareous particles, the whole structure sometimes building into a large statolith that fills the saccular cavity. An endolymphatic duct connects the sacculae to a reservoir, the endolymphatic sac, which lies in the cranial cavity (Fig. 7.2A). The endolymph filled labyrinth is encircled by the perilymph filled periotic system (Fig. 7.2). This is complex in its shape but the key parts are the periotic cistern that lies behind the fenestra vestibuli and the periotic sac that exits the vestibular cavity at the periotic foramen as described above. The two regions (cistern and sac) are connected by a periotic duct of varying length (Baird, 1970; Wever, 1978).

The utricle, sacculae, and ampullae, as well as the associated periotic labyrinth, are accommodated within the central vestibular chamber (=cavum vestibuli), with the semicircular ducts within canals that perforate the more peripheral parts of the capsule. In many lizards there is little separation between the dorsal vestibular portion of the chamber and the ventral cochlear region, but in some taxa (e.g., gekkotans) a variably developed crest (cochlear crest) marks the boundary between the two cavities. The semicircular canals lead off from the vestibular chamber, which also accommodates their ampullae. The cross-sectional diameter of the semicircular ducts varies, as does their angulation in relation both to one another and to the vestibular chamber. The sensitivity of the ducts and their ampullary sense organs is reported to increase with both the diameter and length of the ducts, with the latter expressed in terms of radius of curvature (Sipla & Spoor, 2008). Burrowers also to show a tendency for the semicircular ducts to be more tightly wrapped around the enlarged central chamber than in terrestrial or climbing taxa.

7.4 Osteological Correlates of Ear Function in Lepidosaurs

7.4.1 Middle Ear

Most information on the presence and/or size of the tympanic membrane is derived from the quadrate bone (Fig.7.3B). An expanded lateral quadrate concavity (=conch), bordered by a tympanic crest, is usually taken as evidence of a tympanic ear. In the absence of a tympanic membrane, medial rugosities or pits on the quadrate shaft may provide evidence of stapedial abutment. The stapes itself is only rarely preserved in fossil lepidosaurs, but where it is, the length and diameter of the shaft and the relative size of the footplate are indicative of hearing ability. Lepidosaurs with good tympanic ears tend to have a long slender stapes with a small footplate, whereas loss of the tympanic membrane generally correlates with an enlarged footplate (sometimes forming almost the entire wall of the otic capsule) and a short, robust shaft (e.g., Wever, 1978). Some living squamates that lack the tympanic membrane utilize alternative sound reception surfaces. These include an unossified region at the posterior end of the pterygoid (e.g., some chameleons), and skin on the mandible (e.g., some amphisbaenians). The former would be evident in a fossil, the latter could be interpreted if an mineralised extrastapedial element were associated with it.

7.4.2 Inner Ear

Osteological correlates for the inner ear comprise external features of the otic capsule and internal casts. The former include the size of the fenestra vestibuli, the position and size of the periotic foramen, the presence and size of the RST and of any crests (e.g., crista interfenestralis, crista tuberalis) indicating the extent of a lateral compensatory window. In snakes, these crests usually contribute to the formation of a crista circumfenestralis (CCF), associated with the development of a juxtastapedial recess (Section 7.5.6.1) and a specialised fluid re-entrant system (Fig.7.2C).

Internal casts of the inner ear, now possible through segmentation of the vestibular apparatus from HRXCT or SRμCT scan data, provide an approximation of inner ear anatomy including the size and shape of the

vestibular chamber and lagena, the presence of any statoliths, and the size and orientation of the semicircular canals (note that duct is the preferred term for the soft tissue structure and canal for the bone cavity that contains it, Sipla & Spoor, 2008). In squamates, as in other groups, there is a correlation between the shape of the vestibular apparatus overall and lifestyle (e.g., Boistel et al., 2011). To date, relatively few fossil lepidosaurs have been studied using HRXCT data, partly because of the rarity of suitably preserved specimens and partly due to limited access to scanning facilities (e.g., Kearney et al., 2004; Daza et al., 2013).

7.5 The Fossil Record of Ear Evolution in Lepidosauria

7.5.1 Overview

The lepidosaurian ear is comparatively well-known in extant taxa (e.g., Wever, 1978). The principal questions that can be addressed from an examination of fossil specimens relate to the evolution of the ear in different lineages and ecotypes, notably: the structure of the stem-lepidosaurian and early rhynchocephalian ears; the evolutionary history of the derived squamate ear; and the changes that occurred in ear morphology in response to specialised lifestyles.

7.5.2 Stem-lepidosaurs

The ancestral sauropsid ear was probably not tympanic (Reisz, Müller, Sobral, Scheyer & Neenan, Chapter 8) and an impedance matching middle ear arose independently in descendent lineages (Walsh et al., 2013). The fossil record of stem-lepidosaurs is very limited, but currently includes *Paliguana whitei* (Permo-Triassic, South Africa), kuehneosaurs (Triassic, Europe and North America: Robinson, 1962; Evans, 2009), *Sophineta cracoviensis* (Early Triassic, Poland: Evans & Borsuk-Bialynicka, 2009), and *Marmoretta oxoniensis* (Jurassic, Europe: Evans, 1991). With the exception of the latter species, these stem-lepidosaurian taxa all have a quadrate with a large lateral conch and a tympanic crest (Fig. 7.4A,B), features suggestive of a tympanic ear. However, within the braincase the metotic fissure is undivided (as determined from the exoccipitals). The stem-lepidosaur middle ear may therefore have been a reasonably efficient sound transducer, but with limitations imposed on sound perception by the lack of an efficient compensatory pathway.

7.5.3 Rhynchocephalia

Although *Sphenodon punctatus*, the New Zealand Tuatara, is the sole surviving rhynchocephalian, the group was both geographically and morphologically diverse in the Mesozoic (Jones & Cree, 2012). Rhynchocephalians survived in South America into the Palaeocene (Apesteguia et al., 2014), and the ancestors of *Sphenodon* itself are first recorded in the New Zealand Miocene (Jones et al., 2009).

Sphenodon lacks a functional tympanic membrane (and quadrate conch) and the middle ear cavity is filled with fatty tissue. The stapes has a large footplate and a relatively thin shaft that connects to an expanded extrastapes. Between the extrastapes and the overlying depressor mandibulae muscle is a connective tissue sheet that some authors have interpreted as the original tympanic membrane (Gans & Wever, 1976). The lateral surface of the head may therefore serve as a sound receptor. Medially, the footplate sits in a large fenestra vestibuli. As in stem-lepidosaurs, the metotic fissure is undivided and the periotic sac passes via a posteromedial periotic foramen into the cranial cavity as well as extending laterally to end blindly in the supratharyngeal region (Fig. 7.2B). The compensatory system is therefore fairly rudimentary. Nonetheless, *Sphenodon* is relatively good at perceiving low frequency sound (below 2000Hz) using both aerial and substrate pathways (Gans & Wever, 1976).

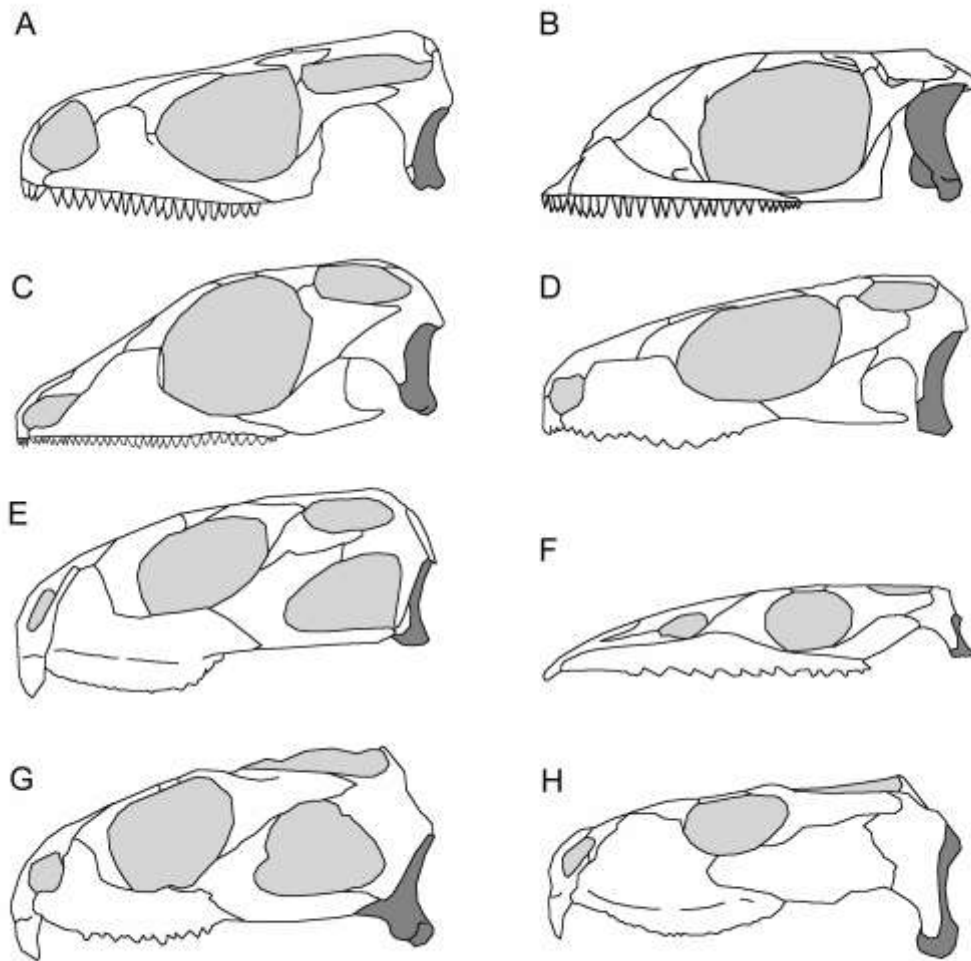


Fig. 7.4 Lateral views of the skull in stem-lepidosaurs (A,B) and rhynchocephalians (C-H) showing differing degrees of quadrate (dark grey) embayment in relation to possession of a tympanic membrane A, *Sophineta cracoviensis* (Early Triassic). B, *Kuehneosaurus latus* (Late Triassic). C, *Gephyrosaurus bridensis* (Early Jurassic). D, *Planocephalosaurus robinsonae* (Late Triassic). E, *Clevosaurus bairdii* (Late Triassic). F, *Pleurosaurus goldfussi* (Late Jurassic/Early Cretaceous). G) *Sphenodon punctatus* (Recent). H, *Priosphenodon avelasi* (Late Cretaceous). (Redrawn from Evans & Borsuk-Białynicka, 2009 [A], Evans, 2009 [B], Evans, 1980 [C], Jones, 2008, Fig.2 [D-F, H] and Fig.3 [G]).

In the past, many researchers regarded *Sphenodon* as a primitive reptile ('a living fossil'), leading to the assumption that it represented the primitive lepidosaurian condition in a majority of its morphological features, including those of the ear (Manley, 2000). However, the fossil record shows this to be wrong in many respects. Basal rhynchocephalians from the Late Triassic and Early Jurassic (e.g., *Gephyrosaurus bridensis*, Evans, 1980; *Diphydontosaurus avonius*, Whiteside, 1986; *Planocephalosaurus robinsonae*, Fraser, 1982), as well as the more derived *Clevosaurus hudsoni* (Robinson, 1973; Fraser, 1988), resemble stem-lepidosaurs and squamates in having a quadrate with a well-developed tympanic crest and lateral conch (Fig. 7.4C-D). They almost certainly had a tympanic middle ear. However the size of the fenestra vestibuli, and therefore of the stapedial footplate, has not been reported in any of these taxa. No fossil rhynchocephalian shows a divided metotic fissure (Jones, 2006; contra Wu, 1994) or a evidence of a compensatory window.

However, if the ears of early rhynchocephalians were tympanic, it raises the question as to why the middle ear degenerated in *Sphenodon*. The quadrate of *Clevosaurus bairdii* (Fig. 7.4E) (Late Triassic, USA) appears less emarginated than that of *C. hudsoni*, and a further reduction is seen in many derived rhynchocephalians from the Jurassic onward (e.g., *Palaeopleurosaurus posidoniae* and *Pleurosaurus goldfussi*, Carroll, 1985; Carroll & Wild, 1994; *Priosphenodon avelasi*, Apesteguia & Novas, 2003) (Fig. 7.4, F-H). Loss of

the tympanic membrane may be related to the refinement of the characteristic fore-aft shearing jaw action of derived rhynchocephalians (e.g., Jones, 2008; Jones et al., 2012). It is difficult to see how a tympanic membrane stretched between lower jaw and quadrate could have accommodated movement of that kind.

7.5.4 General Squamates

Given the morphology of stem-lepidosaurs and rhynchocephalians, it is likely that stem-squamates also inherited a tympanic ear lacking an efficient compensatory mechanism. Development of the latter required the division of the metotic fissure into dorsal and ventral passages as described above. Again, however, the timing of this change is difficult to determine. Although stem-squamates must have existed in the mid-Triassic (due to the presence of their sister clade, Rhynchocephalia), the earliest uncontested squamate fossils are from the Middle Jurassic (Britain, Russia, Central Asia, Evans, 1998, Evans & Jones, 2010). This Middle Jurassic material is mostly composed of isolated skeletal elements but there is currently no braincase material. The squamate record improves in the Late Jurassic but apart from embayed quadrates (e.g., the Solnhofen lizard *Eichstaettisaurus schroederi*, Evans et al., 2004), there is no direct data on the ear in these taxa. However, the anguimorph *Dorsetisaurus* is known from both the Late Jurassic (Portugal, Broschinski, 2001; North America, Prothero & Estes, 1980), and Early Cretaceous. Although the Jurassic material of this genus is fragmentary, that from the Early Cretaceous includes a well-preserved braincase (see below), and it is reasonable to assume that the Jurassic representatives had a similar morphology.

The squamate fossil record improves significantly in the Cretaceous, with well-preserved skulls in many specimens. However, in many cases, the only indicator of ear anatomy is the presence of a quadrate that has a lateral conch and tympanic crest (Fig. 7.5A-C). The earliest known squamate braincases are currently from the Early Cretaceous. They include *Dorsetisaurus purbeckensis* (UK, Hoffstetter, 1967: Fig. 7.5D), and other taxa from South Africa (Ross et al., 1999), Mongolia (Conrad & Norell, 2006; Conrad & Daza, 2015), and Thailand (Fernandez et al., 2015). In all known braincase specimens, the metotic fissure is fully divided, with the aLRST opening defined by flanking crests. Where the braincase is described in detail (Ross et al., 1999; Conrad & Norell, 2006), it is seen to preserve all of the features, internal and external, described above in extant lizards. Taken together with quadrate anatomy, this implies sound perception similar to that of extant lizards. Remarkably, recently described embryonic lizards from the Early Cretaceous of Thailand (Fernandez et al., 2015), imaged in ovo using SR μ CT, have been shown to preserve large calcified endolymphatic sacs in the cranial cavity. Calcified sacs of this kind are typically (though not exclusively) associated with gekkotan lizards that have hard rather than leathery eggshells, and it is interesting that the Thai eggs, though attributed to anguimorphs, also appear to be hard-shelled.

Direct evidence that the concave quadrate supported a tympanum is provided by another Early Cretaceous lizard, *Liushusaurus acanthocaudata* (Yixian Formation, China, Evans & Wang, 2010). One specimen (IVPP V14715: Evans & Wang, 2010) preserves traces of cranial soft tissues. As in most extant lizards, the head scales terminate at the anterior border of the quadrate, leaving the outline of the tympanic membrane above the retroarticular process of the lower jaw. Traces of the cartilaginous extrastapes lie adjacent to the tympanic region. The outline of the tympanic membrane and adjacent scalation are also preserved in a younger (Eocene) lizard specimen preserved in amber, the lacertid *Succinilacerta succinea* (Borsuk-Białynicka et al., 1999: Fig. 7.5E).

Three-dimensionally preserved cranial material is known for many Late Cretaceous lizards, especially from Mongolia and China, but the braincase is only described (often briefly) in a subset of these. They include anguimorphs (e.g., Borsuk-Białynicka, 1984; Norell & Gao, 1997; Conrad et al., 2011); lacertoids (Borsuk-Białynicka, 1988); iguanians (Borsuk-Białynicka & Moody, 1984), and a stem-gekkotan (Borsuk-Białynicka, 1990; Daza et al., 2013 [HRXCT]). Of these, the most complete material is that of the anguimorphs *Estesia*

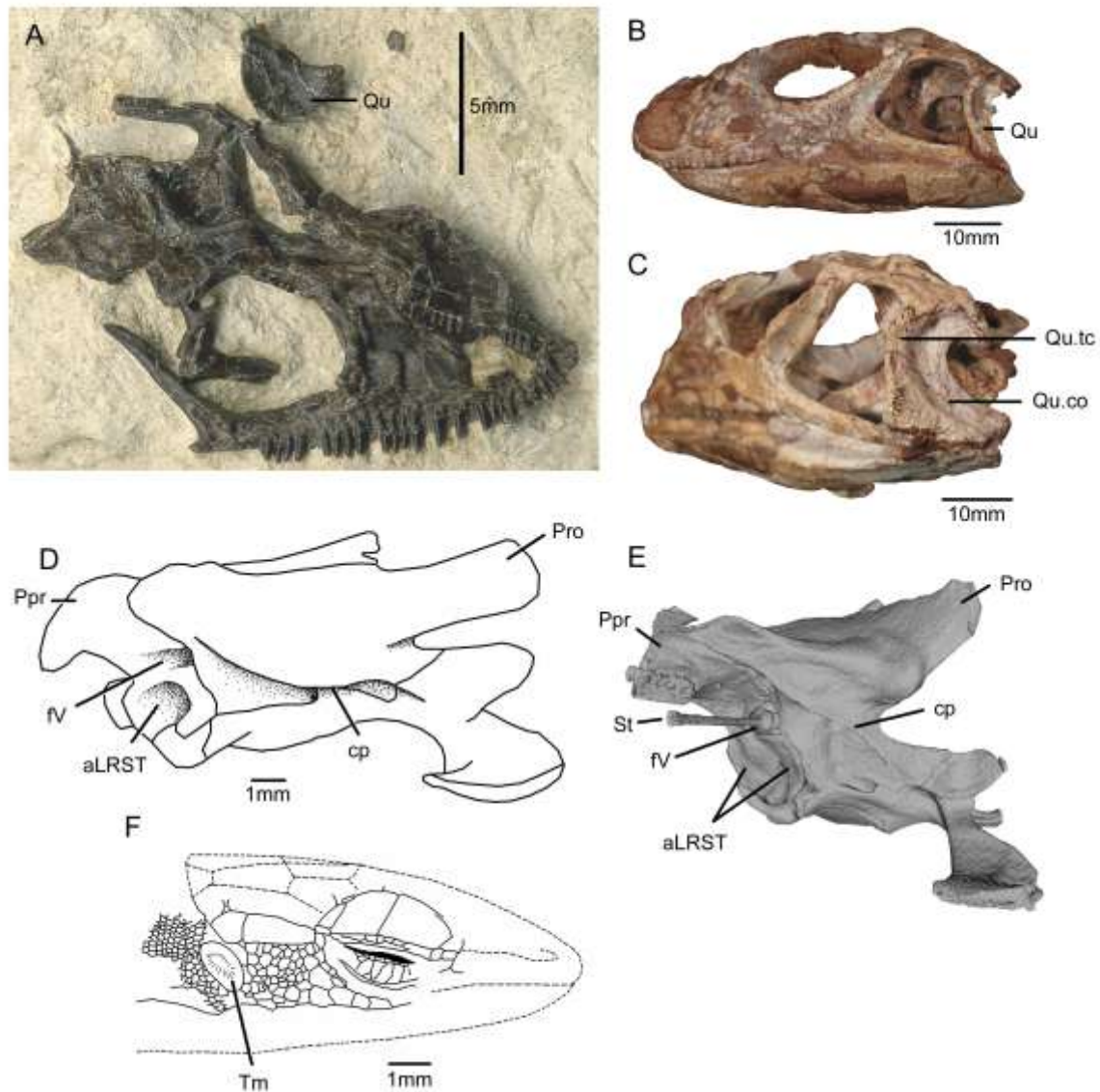


Fig. 7.5 The ear in fossil lizards. A, BGS GSb581, the skull of the Early Cretaceous lacertoid lizard *Purbicella ragei*, Purbeck Limestone Group, UK, with the disarticulated quadrate above it. B-C, skulls of the Late Cretaceous lizard *Tianyusaurus* sp., Nanxiong Formation, China, showing the typically embayed quadrate associated with a tympanic lizard ear. B, lateral view of an immature skull (NHMG 9316). C, posterolateral view of a mature skull (NHMG 9317) showing the quadrate conch and expanded tympanic crest. D, lateral view of the braincase of the Early Cretaceous anguimorph *Dorsetisaurus purbeckensis*, showing earliest recorded subdivision of Meckelian fossa to produce a compensatory window in apertura lateralis recessus scalae tympani. E, lateral view of the braincase of the extant anguimorph lizard *Diploglossus lessonae* for comparison. F, lateral view of the head of the Eocene *Succinilacerta succinea*, a lacertid lizard preserved in amber. (A-C, original; D, redrawn and simplified from Hoffstetter, 1967, Fig.12; E, based on original HRXCT scan, surface, imaged using Meshlab; F, redrawn and adapted from Borsuk-Białynicka et al., 1999, Fig.3).

mongoliensis and *Gobiderma pulchrum*, the braincases of which are described in detail by Norell & Gao (1997) and Conrad et al. (2011) respectively, with *Gobiderma* examined by HRXCT. Conrad and Norell (2008) also described the braincase and ear region of Neogene anguimorph glyptosaurs. However, in none of these taxa does the ear region depart substantively from that of the typical extant lizard pattern described above, and their hearing is likely to have been similar. To date, however, the inner ear of fossil lizards has received little attention.

Squamates show a diversity of lifestyles, but two in particular are associated with ear modifications that can be recognised in the fossil record. These are burrowing and marine swimming.

7.5.5 Burrowing Squamates

Many squamates burrow in loose soil or leaf litter to find food, escape predators, or avoid excessive heat, but a sizeable minority are adapted more obviously to a fossorial or semi-fossorial existence. These include many limbless or limb-reduced lizards, as well as larger groups like the scolecophidian snakes and amphisbaenians. Burrowing imposes constraints on the ear as it needs to be protected from physical damage. In addition, much of the sound reaching the head comes via the substrate rather than in air. Unlike ears that detect airborne sound, and thus pressure changes, those of burrowers are displacement sensitive (*sensu* Lombard & Hetherington, 1993). Sound vibrations shake the otic capsule creating relative motion between it and more loosely attached elements like the stapes. Although the footplate may remain still, the relative motion between it and the otic capsule causes displacements at the fenestra vestibuli similar to those that would be caused by movements of a tympanic membrane. This system is improved by enlargement of the stapes and footplate so that they have greater inertia. Alternatively, incoming sound vibrations actually deform the bone of the otic capsule and thus produce displacement of the perilymph directly (Lombard & Hetherington, 1993).

Burrowing adaptations have evolved independently in several squamate lineages, but their ears show similar adaptations (e.g., Baird, 1970; Wever, 1973). The middle ear is typically lost or reduced, and may become filled with connective tissue or muscle (e.g., depressor mandibulae). The stapes usually increases its mass and has a short robust shaft and an enlarged footplate that forms much of the lateral wall of the otic capsule. In the absence of a tympanic membrane, the stapes abuts the quadrate, allowing some sound vibrations to be transmitted directly from the surface of the head. The aLRST is often reduced in size, with the periotic sac ending blindly rather than expanding into a compensatory window. However, many burrowers develop a re-entrant fluid circuit (Wever, 1973) whereby the periotic sac leaves the vestibular chamber ventrally or medially and finds an alternative pathway to the lateral surface of the stapedial foot plate (Baird, 1970; Wever, 1973).

Burrowing reptiles are poorly represented in the fossil record. *Tamaulipasaurus morenoi* from the Early Jurassic (Pleinsbachian) La Boca Formation of Mexico (Clark & Hernandez, 1994) is an enigmatic little burrower represented by skull and neck vertebrae. Originally placed as either a stem-lepidosaur or stem-squamate (Clark & Hernandez, 1994), its phylogenetic position within reptiles is currently unresolved, but it is included here for completeness. The skull is convergent on extant squamate burrowers like amphisbaenians and differs strikingly from the stem-lepidosaur taxa described above (Section 7.5.2). The quadrate is narrow and there is a large fenestra vestibuli, presumably accommodating a large stapedial footplate (obscured). A short stapedial shaft projects laterally and contacts a second component (possibly an ossified extrastapes or hyoid element) that abuts the quadrate. The occipital surface of the skull bears a large opening (jugular foramen of Clark & Hernandez, 1994) that appears circular in one specimen and ovoid in another. Without visible sutures, the identity of this opening remains uncertain but it presumably represents all or part of the metotic fissure. This material would benefit from re-examination either with HRXCT or SR μ CT.

Other than a few early snakes (Section 7.5.6), the only clear example of a Cretaceous squamate burrower is *Sineoamphisbaena hexatabularis* (Late Cretaceous, China: Wu et al., 1996)(Fig. 7.6). Although it was originally classified as a stem-amphisbaenian, the relationships of this small lizard are unclear (e.g., Reeder et al., 2015). The skull is rounded and robust (Wu et al., 1996; Fig. 7.6A,B)), and the ear anatomy matches that of extant squamate burrowers as outlined above. The short quadrate lacks an embayment for a tympanic membrane. The stapes has a large footplate and short shaft that abutted the quadrate, and the aLRST is reduced to a small foramen for the glossopharyngeal nerve (Fig. 7.6C). The otic capsules appear inflated compared the rest of the skull (Fig. 7.6 B)

Extant amphisbaenians spend most of their lives underground. There is no tympanic membrane, but in many amphisbaenians, the extrastapes forms a cartilage plate or bar that runs along the lower jaw with its tip embedded in the skin - often at a specially enlarged labial scale (Fig. 7.7A). Vibrations pass from the skin to the extrastapes and then along the stapes. The stapedial footplate fits into a fenestra vestibuli that may extend over

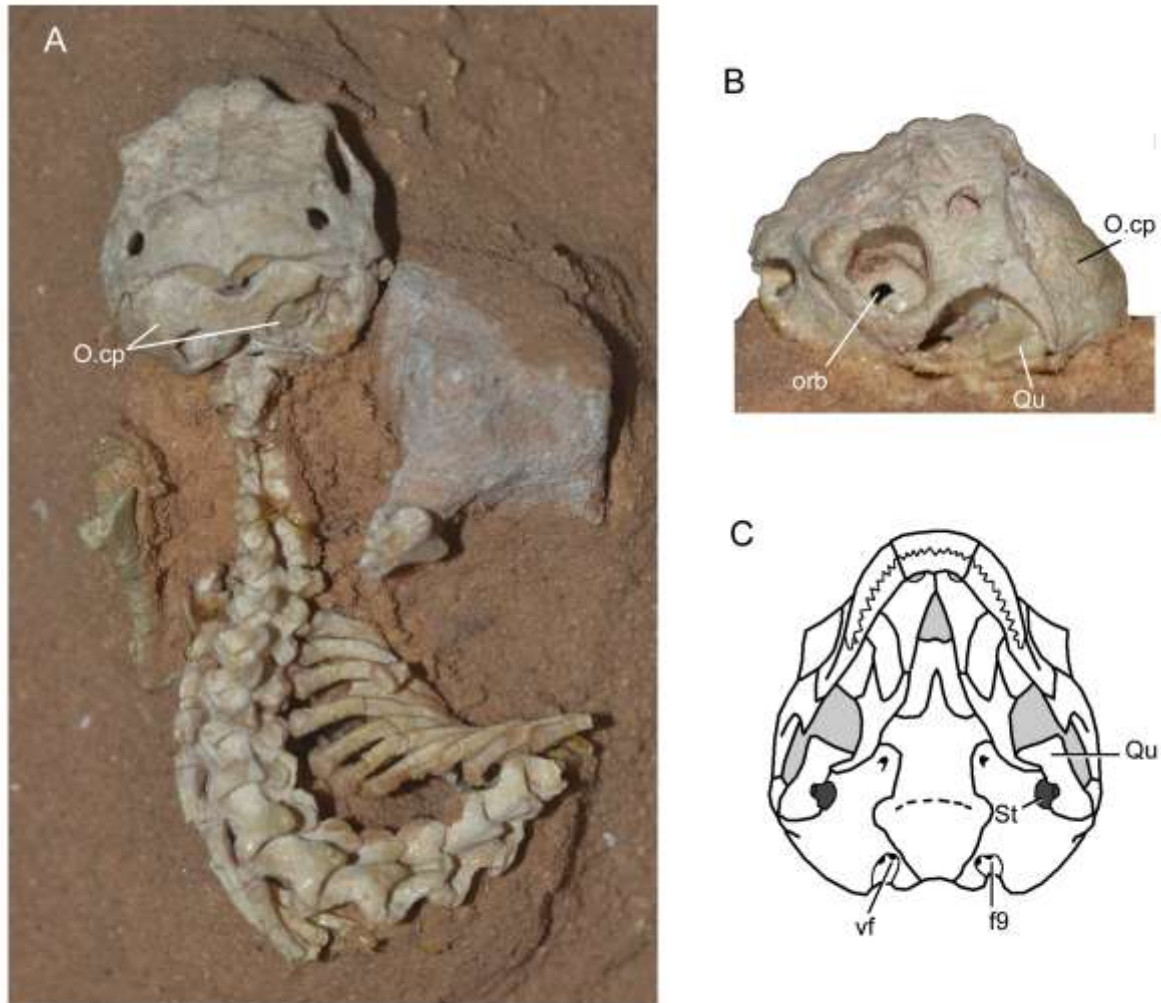


Fig. 7.6 The burrowing squamate ear: *Sineoamphisbaena hexatabularis*. A, dorsal view of the holotype specimen (IVPP V10593). B, left lateral view of the skull of IVPP V10593. C, reconstructed palatal view showing stapes (dark grey) with short shaft and large footplate. (A-B, original; C, redrawn from Wu et al., 1996, Figure 4B).

most of the external surface of the otic capsule (Fig. 7.7C) and is set within a deep jugular recess (Kearney et al., 2004)(Fig. 7.7B, D–G). The stapedia shaft projects laterally to the level of the quadrate where, in most taxa, it abuts the extrastapes (Gans & Wever, 1972; Wever & Gans, 1973). In the inner ear, the large vestibular chamber generally accommodates an extensive statolith (stt, Fig. 7.7E–G), and, as in many burrowers, the semicircular canals are narrow and compacted so there is little separation between them and the central vestibular chamber. As in *Sineoamphisbaena*, the aLRST is restricted to a foramen for the glossopharyngeal nerve and does not accommodate a compensatory window. The periotic cistern fills the space behind the stapedia footplate, but then narrows into a long periotic duct that enters a channel (sometimes fully enclosed, e.g., *Rhineura floridana*) that runs first anteriorly and then turns sharply through 180 degrees to run posteromedially within the walls of the otic capsule to reach the periotic foramen. From there, the periotic sac enters the RST and extends medially where it communicates with fluid filled spaces that run anteromedially through the cranial cavity, before passing via the trigeminal foramen to enter the jugular recess and the lateral surface of the stapedia footplate (Gans, 1978; Wever, 1978). Movements of the stapedia footplate set up a continuous fluid displacement around the circuit (Gans, 1978; Wever, 1978). Amphisbaenians perceive low frequency sound (300-700 Hz) and reportedly have better reception than snakes, but this is dependent on the extrastapedia system. Any interruption results in a major loss of sensitivity (Gans & Wever, 1972).

Molecular phylogenetic analyses group amphisbaenians with lacertid lizards (e.g., Vidal & Hedges, 2005; Pyron et al., 2013) which are predominantly tetrapodal surface-dwellers. *Cryptolacerta hassiaca* (Eocene, Germany: Müller et al., 2011) was described as a potential transitional stem-amphisbaenian, but some subsequent analyses (Longrich et al., 2015; Tañanda, 2015) have placed *Cryptolacerta* with lacertids rather than amphisbaenians. Moreover, the braincase and ear region are crushed. More recently, *Slavoia darevskii* (Late Cretaceous [Campanian], Mongolia) has been proposed as a stem-amphisbaenian (Tañanda, 2015). Although its morphology is plausible for a burrower (short snout, robust build, reduced limbs), the quadrate appears to be large and embayed, suggesting the ear was tympanic. However, the braincase has never been described, although many skulls of this taxon exist in collections. HRXCT scanning could be informative.

The earliest uncontested amphisbaenian records are currently from the Paleocene of Europe and North America (Folie et al., 2013; Longrich et al., 2015), but the first three-dimensionally preserved skulls are those of Eocene rhineurids from North America (Berman, 1973, 1976). *Spathyrhynchus fossorium* (Middle Eocene, North America: Berman, 1973) resembles living amphisbaenians in having a large fenestra vestibuli lying within a deep jugular recess and covered by an ovoid stapedial footplate. The stapedial shaft is directed anteroventrally and ends in a small knob which, by comparison with extant taxa, would have articulated with the extrastapes (a remnant of which may persist). However, the shaft differs from that of extant taxa in being long and slender rather than short and robust. *Dycticonastis* (Oligocene, North America: Berman, 1976) is closely similar, and Berman (1976) correlates the long slender stapedial shaft of these and other early taxa (e.g., *Ototriton* and *Jepsibaena*, Eocene) with the retention of paroccipital processes on the braincase and therefore a wider head. In amphisbaenians with narrow skulls (e.g., *Lophocranium*, Miocene, Kenya: Charig & Gans 1990), the stapedial shaft is shorter and more robust. *Rhineura hatcherii* (Oligocene, North America: Kearney et al., 2005) was HRXCT scanned (Fig. 7.7B,D–F). Its ear closely resembles that of the extant *R. floridana*, including an internal channel for the periotic duct leading to the periotic foramen, a large saccular statolith, a large fenestra vestibuli opening into the roof of the jugular recess, a stapes with a relatively large footplate and a short shaft bearing a terminal articular region for the extrastapes, and narrow semicircular canals packed close to the vestibular chamber (Fig. 7.7B,D–H).

7.5.6 Marine Squamates, the Mosasaurs

Today, the only squamates that are obligate marine swimmers are sea-snakes, although the Galapagos Marine Iguana, *Amblyrhynchus cristatus*, regularly feeds offshore. However, in the Late Cretaceous, a group of lizards (Mosasauria: Marsh, 1880, Camp, 1942) dominated marine ecosystems worldwide for around 30 million years.

Mosasaurs were, until recently, widely considered to be relatives of extant varanid lizards (e.g., Conrad, 2008; Wiens et al., 2010; Conrad et al., 2011), but their position is now contested (e.g., Gauthier et al., 2012 v. Reeder et al., 2015). Figure 7.1 shows one recent hypothesis (Reeder et al., 2015). Within Mosasauria, three morphological grades are typically recognised: 'dolichosaurs', small, often long-bodied Albian-Cenomanian lizards (e.g., *Dolichosaurus longicollis*: Caldwell, 2001; *Pontosaurus lesinensis*: Caldwell & Dal Sasso, 2004; Pierce & Caldwell, 2004); 'aigialosaurs', larger, Cenomanian-Turonian lizards (e.g., *Aigialosaurus dalmaticus*, Carroll & DeBraga, 1992; Dutchak & Caldwell, 2006); and finally the mainly Turonian-Maastrichtian mosasaurids (e.g., Bell, 1997, Fig.7.8A). A variety of different within-clade names have been invoked (e.g., Bell, 1997), but herein Mosasauridae (mosasaurid) is used for the Late Cretaceous crown-clade (Gauthier et al., 2012), Mosasauoidea (mosasauroid) for the group encompassing 'aigialosaurs' and Mosasauridae (e.g., Conrad et al., 2011), and Mosasauria (mosasaur) for the total clade ('dolichosaurs' and Mosasauoidea) (Marsh, 1880, Camp, 1942). However, although Mosasauridae is generally considered as monophyletic (e.g., Gauthier et al., 2012), the other two 'groups' may not be. Understanding these relationships is important in understanding the evolutionary trajectory of their ear morphology, particularly in relation to increasing marine specialization.

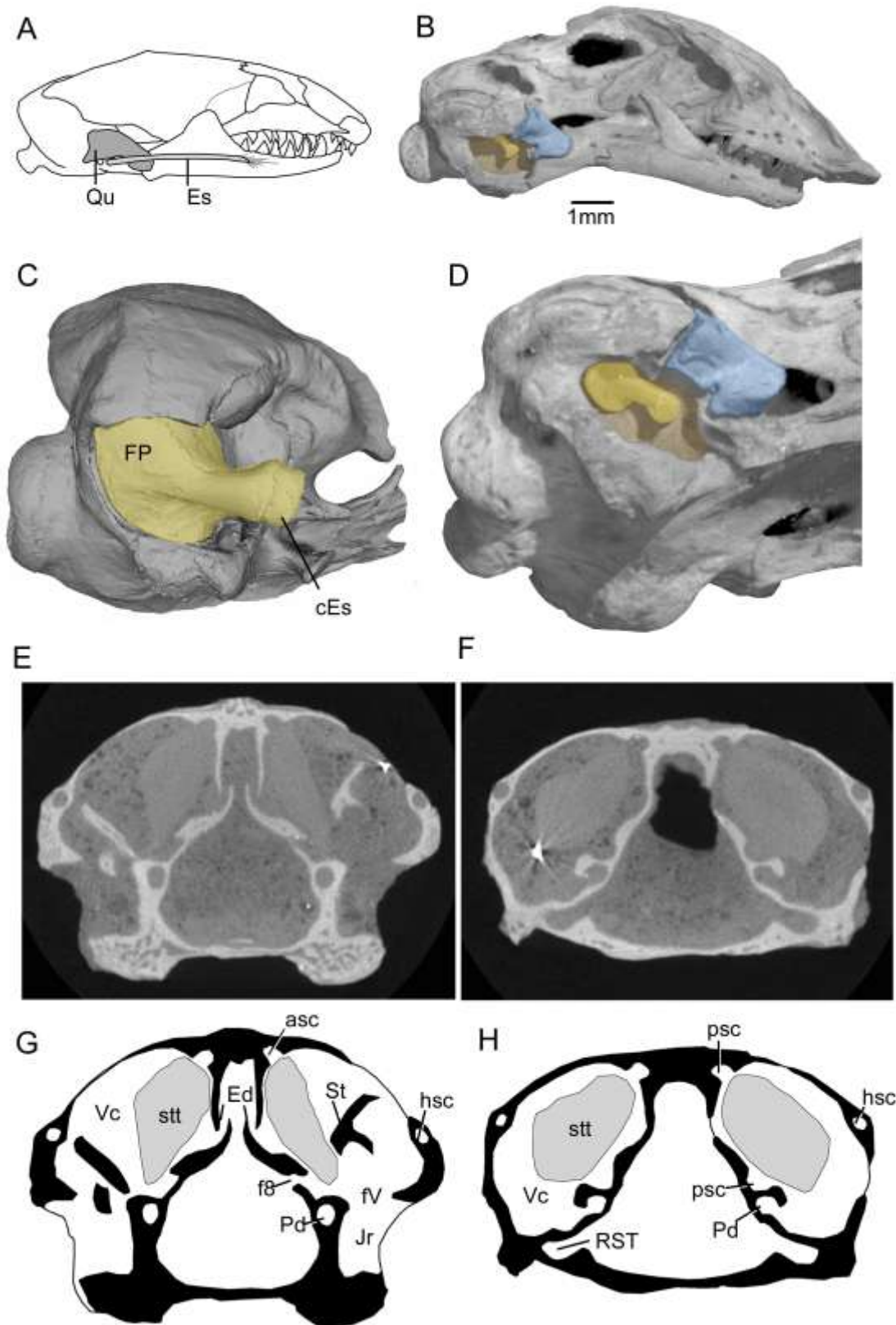


Fig. 7.7 The burrowing squamate ear: amphisbaenians. A, lateral view of the skull of the extant *Amphisbaena alba* showing the relationship of the extrastapes to the quadrate and lower jaw. B, lateral view of the skull of *Rhineura hatcherii* (BAD 18303), Oligocene, USA, surface model created from HRXCT data. C, the braincase of the extant *Diplometopon zarudnyi*, right lateral view, to show the size and robusticity of the stapes and its footplate. D-H, *Rhineura hatcherii* (BAD 18303). D, detail of ear region in ventrolateral view. E, G, coronal section through fenestra vestibuli and jugular recess. F, H, coronal section posterior to E showing recessus scala tympani closed laterally. The same colour scheme is used in B, C, and D: blue, quadrate; yellow, stapes; brown, jugular recess. (A, redrawn from Gans & Wever, 1972, Fig.2; B, D-F, original from HRXCT scan data; C, original based on HRXCT scan, surface visualised with Meshlab).

Dolichosaurs, aigialosaurs, and basal mosasaurids had feet rather than paddles and their pelvis were still firmly in contact with the sacrum, suggesting they were at least facultatively terrestrial (Caldwell & Palci, 2007). More derived mosasaurids developed paddles and lost the sacro-pelvic contact, a change that may also mark a shift from a primarily undulatory (anguilliform) locomotor style, to one that relied to a greater degree on the tail (Lingren et al., 2007, 2011). Mosasaurs mainly colonised epicontinental seas but their global distribution from the Campanian period onward suggests an increasing tendency to move into deeper water as they became more adapted to a pelagic lifestyle (Lindgren et al., 2007, 2011; Houssaye et al., 2013). Based on mosasaur brain endocasts and snout morphology, Polcyn (2010) suggested that the increasing marine specialisation in derived mosasaurids was accompanied by a shift from a reliance on olfactory cues to vestibulocochlear stimuli, as has been reported for whales.

Sound vibrations in water have greater strength than those in air and no impedance matching is required between the water and soft tissues. Swimming animals also live in a more three-dimensional environment than land animals, where the effects of gravity are reduced by the density and viscosity of the water. Living marine tetrapods (e.g., sea turtles, whales) often show specializations in both the middle and inner ear (Lombard & Hetherington, 1993; Hetherington, 2008). Some extant taxa continue to use a tympanic route, with a tympanic membrane or plate underlying the skin of the head but overlying an air-filled chamber so that displacements of skin move the stapes. Other taxa rely on bone conduction as in burrowers, with an enlarged stapes or stapedial footplate acting as an inertial element. Mosasaurs seem to fall into the first category.

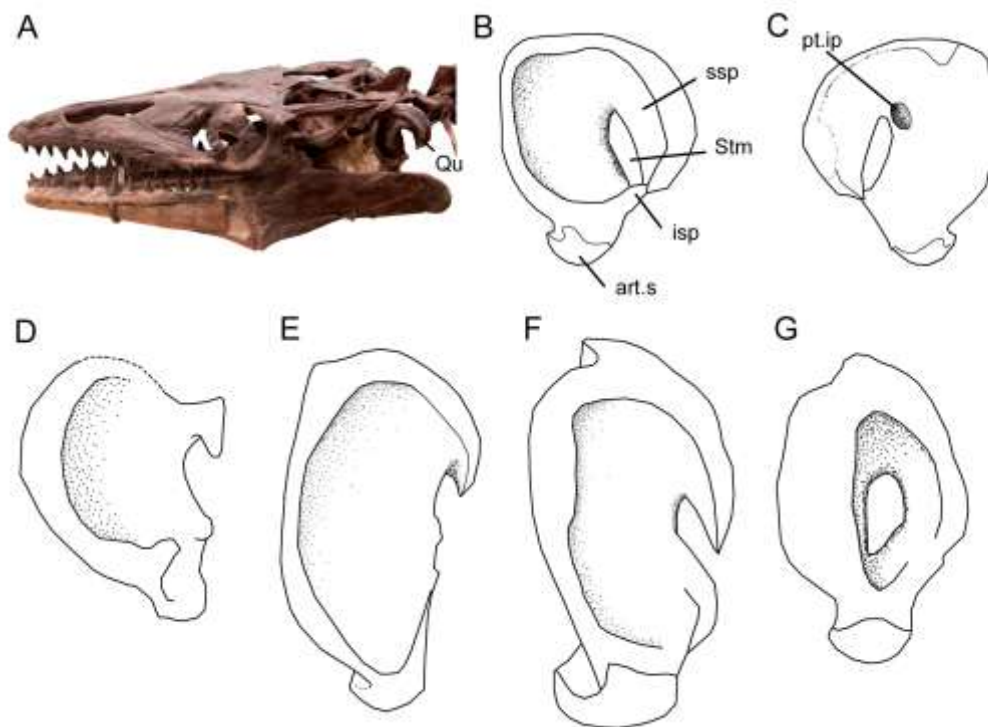


Fig. 7.8 Mosasaur quadrates. A, lateral view of the skull of *Platecarpus tympaniticus* (KUV 1007). B-G, isolated right quadrates. B-C, *Platecarpus tympaniticus*, lateral and medial views. D, *Pontosaurus kornhuberi*. E, *Mosasaurus hoffmannii*. F, *Tylosaurus proriger*. G, *Prognathodon rapax* (not to scale). (All redrawn and simplified from Russell, 1967: A, Fig.90; B-C, Fig.25; E, Fig.80; F, Fig.94; G, Fig.91, except D, redrawn from Caldwell, 2006, Fig.6).

7.5.6.1 Mosasaur Middle Ears

The mosasauroid quadrate has a distinctive shape (Fig. 7.8). The dorsal margin curves posteriorly or posteroventrally to form a suprastapedial process and this is mirrored to a varying degree by an infrastapedial process (Fig.7.8B). Where known, the 'dolichosaur' quadrate (e.g., *Pontosaurus*: Pierce & Caldwell, 2004; Caldwell, 2006: Fig.7.8D) approaches this morphology, but the infrastapedial process is small. Enlargement of

this process in more derived taxa creates a deep notch or, frequently, a fully enclosed meatus when the supra- and infrastapedial processes make contact (Fig. 7.8B-C, F-G). This meatus forms a passage for the stapedial shaft. Posterodorsal and posteroventral expansion of the tympanic crest may then combine to form a circular or ovoid bulla around the stapedial shaft (Fig. 7.8G). Berman and Regal (1967) speculated that this morphology might protect the middle ear cavity from being collapsed by movements of the quadrate or depressor mandibulae, but this does not occur in lizards with highly mobile quadrates. By comparison with sea turtles, the bulla-like quadrate shape is probably associated with aquatic habits. Variation in mosasauroid quadrate morphology (overall shape, size of the infrastapedial process, depth of the conch, development of the tympanic crests, see Fig. 7.8) has been documented (e.g., Camp, 1942; Callison, 1967; Konishi & Caldwell, 2007) and used in phylogenetic analysis (e.g., Bell, 1997). However, there has been little attempt to link the variation to hearing and/or lifestyle, other than Polcyn (2010) who suggested that increased depth of the conch in derived plioplatecarpine mosasaurids might have enhanced spatial sensitivity.

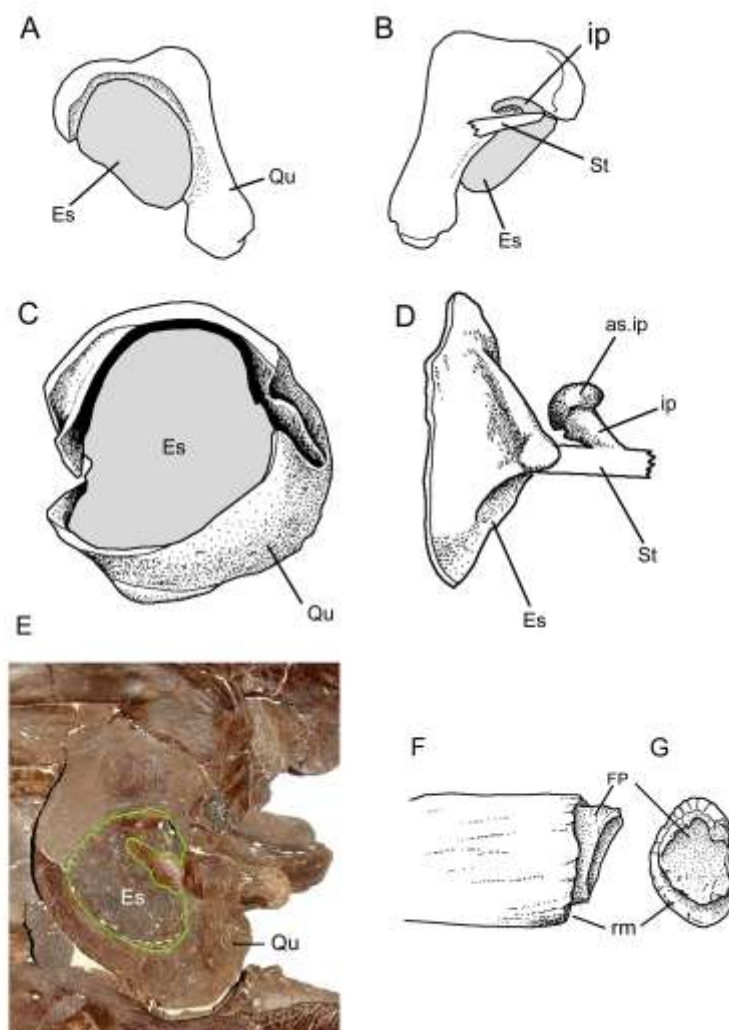


Fig. 7.9 Mosasaur stapes and extrastapes. A-B, lateral and medial views of the quadrate and discoidal extrastapes of the extant lizard *Lanthanotus borneensis*. C-D, *Plioplatecarpus houzeani*, C, lateral view of the right quadrate and mineralised extrastapes, D, reconstruction of the mineralised extrastapes, stapes, and internal process, anterior view. E, left quadrate of *Tylosaurus proriger* (FFHM-1997-10) showing mineralised extrastapes, outlined in green. F-G, posterior and medial views (respectively) of the footplate region of the stapes in *Platecarpus* sp. (A-B, redrawn and simplified from McDowell, 1967, Fig. 3; C-D, redrawn from Camp, 1942, Fig. 22; F-G, redrawn from Callison, 1967, Fig. 8).

A round or ovoid pit in the medial surface of the mosasauroid quadrate (Fig. 7.8C) probably accommodated the equivalent of the internal (=quadrate) process of the extrastapes (McDowell, 1967, Rieppel & Zaher, 2000). In extant squamates, this process is usually cartilaginous but mineralisation has been recorded in some

mosasaurids (*Plioplatecarpus*, McDowell, 1967; *Platecarpus*, Callison, 1967), suggesting a stiffening of the extrastapedial mechanism to provide additional support (Fig. 7.9C-E). The mosasaurid stapes is usually long and relatively slender (e.g., *Plotosaurus* [as *Kolposaurus*], Camp, 1942; *Plioplatecarpus*, McDowell, 1967; *Clidastes*, *Platecarpus* and *Tylosaurus*, Callison, 1967). At its medial end, the stapedial shaft bears a terminal footplate that is smaller in diameter than the shaft itself (Fig. 7.9F-G), creating a margin for a thick cartilaginous or fibrous ring that attached the footplate to the rim of the fenestra vestibuli (*Clidastes*, *Platecarpus*, Callison, 1967). A complementary furrow may be present around the fenestra. This arrangement may have served to resist inward displacement of the footplate due to water pressure (Camp, 1942), aided by a limiting ridge within the fenestra, and the medial restriction of the stapedial shaft to a narrow groove (stapedial canal, Callison, 1967) in the oto-occipital (e.g., in *Platecarpus*, *Plioplatecarpus*).

Discs of bone or thick calcified cartilage have been recorded within the quadrate conch in several mosasaurid specimens (e.g., *Platecarpus* and *Tylosaurus*, Williston, 1914; Callison, 1967; *Plioplatecarpus*, Camp, 1942; *Clidastes*, Callison, 1967; *Ectenosaurus*, Russell, 1967; *Aigialosaurus* Carroll & DeBraga, 1992, but see Dutchak & Caldwell, 2006). These discs were originally interpreted as mineralised tympanic membranes that represented an adaptation to deep diving, the pressure of which might rupture a thinner structure. However, a similar discoid cartilage in the extant Earless Monitor lizard, *Lanthanotus borneensis* (Fig. 7.9A-B), is an extrastapes (McDowell, 1967), and subsequent authors have generally accepted this interpretation of the mosasaurid disc (e.g., Konishi & Caldwell, 2009). Like *Lanthanotus*, these mosasaurids probably lacked a tympanic membrane, at least of the type that would have responded to air-borne sound. Polcyn (2010) proposed that the extrastapes formed a 'stiff but functional tympanum' by expansion and calcification of the cartilage, a not unreasonable explanation given that the disc fills the lateral quadrate cavity (Fig. 7.9C,E) and connects with the relatively slender stapes through the stapedial meatus (Fig. 7.9D).

Extant sea turtles provide a partial analogue for the mosasauroid ear (Lombard & Hetherington, 1993) in that they have a strongly concave quadrate that forms much of the medial wall of the middle ear, enclosure of the stapedial shaft in a bony meatus, and an enlarged disc-like extrastapes (Lombard & Hetherington, 1993; Christensen-Dalsgaard et al., 2012). In sea turtles, a thickened tympanic membrane underlies the skin and scales, and is itself underlain by a layer of fatty connective tissue (Wever & Vernon, 1956; Hetherington, 2008). As in sea turtles, the enclosure of the mosasauroid stapes within a meatus would have limited its movements to a piston-like action with little possibility of rotation or hinging to provide lever action. The relatively slender mosasaurid stapes and small footplate differ strikingly from those of marine ichthyosaurs (Reisz, Müller, Sobral, Scheyer & Neenan, Chapter 8) where a massive stapes acts as an inertial element. The mosasaur ear is likely to have been adapted primarily to receive sound passing through water, mainly by a direct 'tympanic' route through thick skin and the extrastapedial plate to the stapes and then fenestra vestibuli (Hetherington, 2008).

In more basal mosasaurs, where the quadrate is less specialized and the postcranial morphology is suggestive of amphibious habits, the ear may have been able to perceive aerial sounds in a manner similar to that of terrestrial or occasionally amphibious lizards like varanids (e.g., Lombard & Hetherington, 1993; Hetherington, 2008). A reconstruction of the head of the 'dolichosaur' *Pontosaurus* (Caldwell & Dal Sasso, 2004; Caldwell, 2006) clearly made that assumption. However, although this specimen does preserve traces of head scales, they do not extend to the ear region and therefore the restoration of an external tympanum is speculative.

7.5.6.2 The Mosasaur Inner Ear

There are no informative descriptions of the dolichosaur or aigialosaur braincase, but it has been described in several mosasaurids (e.g., Russell, 1967; Rieppel & Zaher, 2000; Cuthbertson et al., 2015). The morphology is generally similar to that of extant lizards. Taking *Platecarpus* as an example (Camp, 1942), the fenestra vestibuli, aLRST, and vagus (=jugular) foramen were described (Rieppel & Zaher, 2000) as more broadly exposed than in the extant *Varanus* due to a weaker development of surrounding bony crests. However,

the aLRST is smaller and forms a rounded aperture or slit. If there was a compensatory window within the aLRST, it would have been small and without an obvious frame.

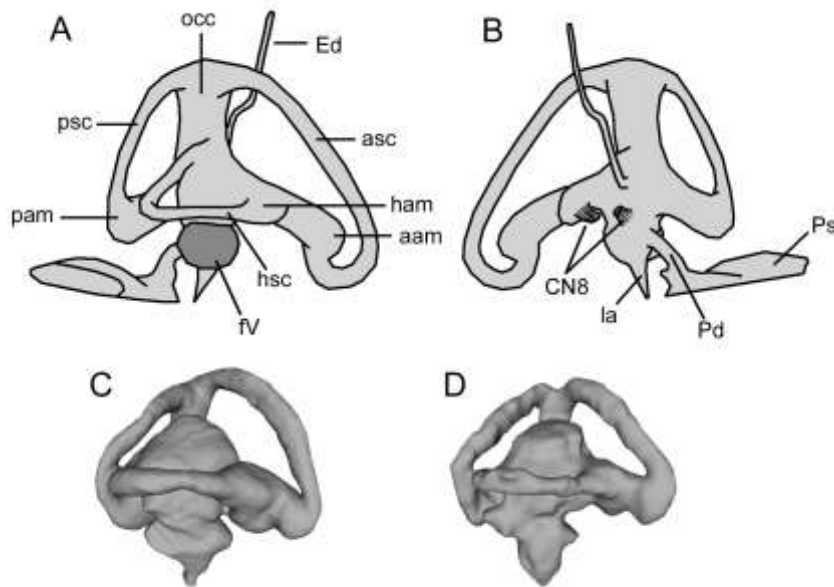


Fig. 7.10 The vestibular apparatus in mosasaurs. A-B, reconstructions of vestibular apparatus of *Platecarpus tympaniticus* in A, lateral and B, medial views. C-D, lateral views of the same region in two extant lizards often used in comparison, C, the Marine Iguana, *Amblyrhynchus cristatus* and D, a Monitor lizard, *Varanus exanthematicus*. (A-B, redrawn and simplified from Camp, 1942; C-D, originals, segmented from HRXCT scans and visualised with Meshlab).

Camp (1942) prepared an internal cast of the ear region of *Platecarpus* by filling the cavities in the braincase with latex, and then removing the surrounding bone on one side (Fig. 7.10A-B). HRXCT permits less destructive access to the inner ear although, to date, there has been relatively little work on mosasaur inner ears and much of that is contained in conference abstracts (Polcyn, 2008, 2010; Yi et al., 2012) rather than peer-reviewed publications. The exceptions, other than Camp (1942), are Georgi & Sipla (2008) on *Platecarpus* and *Tylosaurus*, and Cuthbertson et al. (2015) on *Plioplatecarpus peckensis*. The latter described *Plioplatecarpus* as having a relatively long, conical lagena, with the fenestra vestibuli placed at its posterodorsal limit.

The vestibular apparatus of *Platecarpus* and *Tylosaurus* has been described as broadly similar to that of *Varanus* (Camp, 1942; Georgi & Sipla, 2008; Yi et al., 2012), although the central chamber is relatively larger in the living taxon (Fig. 7.10A,D). In *Platecarpus*, the anterior semicircular canal is longer than the posterior one, and of slightly greater diameter. The horizontal canal is relatively short (Fig. 7.10A-B). In *Plioplatecarpus* (Cuthbertson et al., 2015), the canals are more symmetrical in their cross-sectional diameter (narrow) and radius of curvature (strong), with the anterior and posterior canals arching up above the level of the central vestibular chamber (as in *Platecarpus*). Taking shape and orientation together, Cuthbertson et al. concluded that the vestibular apparatus of *Plioplatecarpus* was most sensitive in the pitch plane. In their analysis, *Plioplatecarpus* fell within the range of extant lizards with respect to semicircular canal diameter, but the radius of curvature was most like that of arboreal and marine iguanians moving in three-dimensional space (e.g., *Amblyrhynchus*, Fig. 7.10C). Given that most mosasaurs probably retained an essentially lizard-like, undulatory swimming mode (Lingren et al., 2007, 2011), it is not surprising that their vestibular apparatus generally resembles that of terrestrial lizards using similar movements. However, some derived mosasaurids may have used locomotor styles more suited to deep water. The mid-Maastrichtian mosasaurid *Plotosaurus* (Lingren et al., 2007) has been interpreted as having a more tuna-like body shape with a stiff, deep body propelled mainly by the tail. Unfortunately its inner ear is undescribed.

7.5.6 Snakes

The debate as to the origins and relationships of snakes is divided between proponents of a terrestrial ancestry (e.g., Zaher & Scanferla, 2012; Hsiang et al., 2015), possibly with a burrowing or semi-burrowing lifestyle (e.g., Camp, 1923; Apesteguia & Zaher, 2006; Reeder et al., 2015), and advocates of a marine ancestry who contend that snakes evolved directly from early dolichosaur-like mosasaurs (e.g., Caldwell & Lee, 1997; Caldwell, 2001). The reduced eyes (Walls, 1940), reinforced skulls, and body proportions (e.g., Wiens & Slingluff, 2001; Wiens et al., 2006) of snakes are consistent with the first hypothesis, as are some features of the ear (Bergman & Regal, 1967). Like burrowing lizards, snakes lack a tympanic membrane and a middle ear cavity, and are sensitive to ground vibration arriving via the lower jaw and quadrate (Friedel et al., 2008; Christensen-Dalgaard et al., 2012). The columnar quadrate lacks a conch and the stapedial footplate is generally larger than that of lizards of equivalent size (Baird, 1970). Laterally, the stapes is continued by a cartilaginous extension, but this may be homologous to the internal process rather than the main body of the extrastapes as in generalized lizards (Rieppel & Zaher, 2000, based on its relationship to the chorda tympani nerve). The process contacts the quadrate (shaft or suprastapedial process) via a hyoid arch derivative (stylohyal) that is fused to the quadrate (Rieppel, 1980; Rieppel & Zaher, 2000).

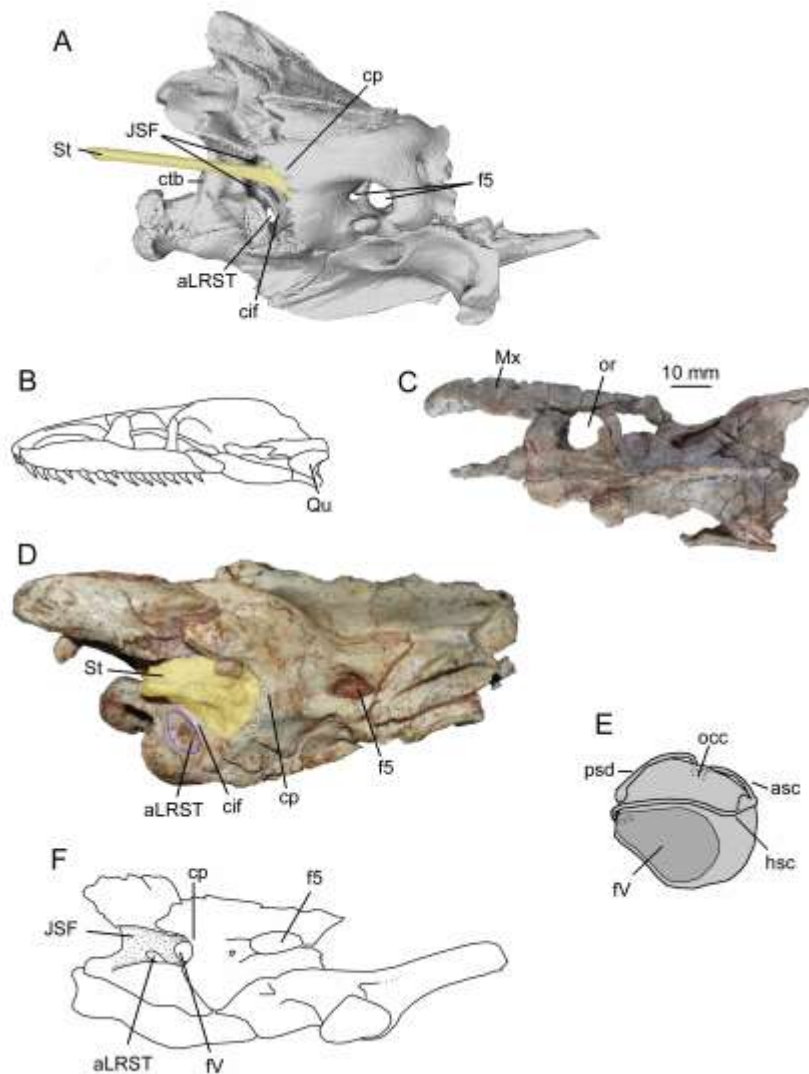


Fig. 7.11 The snake ear. A, right lateral view of the braincase of the extant *Python sp.* to explain terminology used in the text. B-E, the Late Cretaceous snake *Dinilysia patagonica*, in B, left lateral view of skull, C, dorsal view of MACN 1013; D, right lateral view of the braincase, MACN 1014, and E, reconstruction of right side vestibular apparatus of *Dinilysia*. F, the Pleistocene snake *Wonambi*, braincase without stapes in right lateral view. Stapes is coloured yellow in A and D. (A, original from HRXCT scan, visualised in Meshlab; B, E, redrawn and simplified from Zaher & Scanferla, 2012, Figs 23 and 19 respectively; C, D, original; F, redrawn and simplified from Rieppel et al. 2003a, Fig.6).

In snakes, the periotic sac leaves the otic capsule, passes laterally through the aLRST and into a recess (the juxtastapedial recess) (Fig. 7.2C). This recess is created around the aLRST and the fenestra vestibuli (and thus also around the stapedial footplate) by the development of an encircling crista circumfenestralis (CCF) (Figs 7.2C, 7.11A). Laterally, the periotic sac attaches to the free edges of the CCF so that the juxtastapedial recess is closed off by a thick periotic membrane that is perforated by the stapedial shaft (Fig. 7.2C). The CCF is formed by an amalgamation of the otic crests present in lizards (Rieppel & Zaher, 2000): crista prootica, crista interfenestralis, and crista tuberalis (Fig. 7.11A). However, there is variation in the development of component parts of the CCF, leading to disagreement as to the precise definition and homologies (e.g., Rieppel & Zaher, 2000; Rieppel et al., 2003a; Palci & Caldwell, 2014). This debate is largely beyond the scope of this chapter, except that it affects interpretations of the ear region in early fossil snakes.

The Mesozoic fossil record of snakes is dominated by isolated vertebrae and there is relatively limited information on the early snake skull. Although snakes probably separated from their closest lizard ancestors in the Jurassic (Jones et al., 2013), the earliest informative articulated specimens are from the Late Cretaceous, with one possible exception. *Tetrapodophis amplexus* is a remarkable snake-like fossil recently described from the Lower Cretaceous of Brazil (Martill et al., 2015). As its name suggests, it retains both fore- and hind limbs, but the skull is poorly preserved.

7.5.6.1 Terrestrial Fossil Snakes

The Late Cretaceous (Coniacian) snake *Dinilysia patagonica* (Fig. 7.11B-E) is represented by several skull specimens and has been the subject of numerous anatomical (e.g., Estes et al., 1970; McDowell, 2008; Zaher & Scanferla, 2012), and phylogenetic studies. It has been considered a stem snake (e.g., Scanlon, 2006; Gauthier et al., 2012, Maximum Parsimony tree; Longrich et al., 2012), a stem-alethinophidian (e.g., Zaher & Rieppel, 2002; Wiens et al., 2010), or a crown-group alethinophidian (e.g., Gauthier et al., 2012, Bayesian tree; Zaher & Scanferla, 2012). Zaher & Scanferla (2012) provided the most detailed description and illustrations of this taxon. The quadrate is large and somewhat resembles the quadrate of some tympanic lizards (Estes et al., 1970). However, the stapes has an exceptionally large footplate and a slender shaft directed posterodorsally toward the suprastapedial process of the quadrate (Fig. 7.11D). A small articular facet on the posterodorsal edge of the fenestra vestibuli suggests there may have been a rocking movement of the stapedial footplate about that point (Estes et al., 1970). The aLRST is large, opens ventrolaterally into the juxtastapedial space (sensu Palci & Caldwell, 2014: the region adjacent to the stapes irrespective as to whether a recess and CCF are fully developed) posterior to the crista interfenestralis (Fig. 7.11D). Estes et al. (1970) refer to the aLRST as the fenestra rotunda, but see comment above re terminology. There is disagreement as to the definition of the CCF, and therefore as to whether or not a CCF is present in *Dinilysia* (Estes et al., 1970; Zaher & Scanferla, 2012; Palci & Caldwell, 2014), but regardless of the semantics, *Dinilysia* does not appear to have a functional juxtastapedial recess that could contain an expanded periotic sinus.

Najash rionegrina is a second terrestrial stem-snake from the early Late Cretaceous of Argentina (Apesteguía & Zaher, 2006; Zaher et al., 2009). It is represented by both cranial and postcranial material, the latter showing the presence of small hind-limbs. The ear region is represented by an attributed partial braincase and a small quadrate that lacks a conch (Apesteguía & Zaher, 2006; Zaher et al., 2009). The stapedial shaft is broken but, as in *Dinilysia*, a large footplate is preserved in situ within the fenestra vestibuli. Again as in *Dinilysia*, there is a lack of consensus on the presence of a CCF in *Najash* (e.g., Zaher et al., 2009 v. Caldwell & Calvo, 2008). The aLRST is smaller than that of *Dinilysia* and opens posteroventrally into a shallow juxtastapedial space.

Thus both *Najash* and *Dinilysia* have large stapedial footplates, as found in extant burrowing snakes and lizards, but they lack a deep juxtastapedial recess and it seems unlikely that they had a functional re-entrant fluid system like that of derived snakes. The vestibular apparatus, reconstructed for *Dinilysia* by Zaher et al. (2009),

also resembles that of burrowing squamates in the large size of the central chamber compared to the closely packed semicircular canals (Fig. 7.11E).

Madtsoiids are a group of, mostly, large snakes known from Gondwana and southern Europe (Rage et al., 2014). They are known primarily from late Cretaceous to Eocene deposits, but they survived into the Pleistocene in Australia. Their phylogenetic position is, again, controversial. Some authors (Scanlon & Lee, 2000; Longrich et al., 2012; Palci et al., 2013a) have argued for a basal position, close to *Dinilysia*, whereas others (e.g., Rieppel et al., 2003a; Wiens et al., 2010; Wilson et al., 2010) place madtsoiids within Alethinophidia, either within or on the stem of Macrostromata. The ear region certainly seems more derived than that of *Dinilysia*. Three madtsoiids have well-preserved braincases - the Australian *Wonambi naracortensis* (Scanlon & Lee, 2000; Rieppel et al., 2003a; Scanlon, 2005) and *Yurlunggar camfieldensis* (Scanlon, 2006), and the Indian *Sanajeh indicus* (Wilson et al., 2010). The latter species, from the Indian Late Cretaceous, is the oldest representative with a braincase preserved. Unlike *Najash* and *Dinilysia*, all three madtsoiids possess a distinct juxtastapedial recess framed by a CCF (e.g., *Wonambi*, Fig. 7.11F), although this is relatively low and directed laterally so that the footplate of the stapes, where preserved, is largely visible in lateral view. The aLRST opens posterior to the fenestra vestibuli and is separated from it by a crista interfenestralis that extends ventrally to contribute to the CCF. In *Wonambi*, a slit-like aLRST (=foramen pseudorotunda of Scanlon & Lee, 2000) opens into the juxtastapedial recess just behind the crista interfenestralis, but the aMRST is very small. Further details are provided by Scanlon (2005). Individual braincase elements are well illustrated and show the periotic foramen (Scanlon's 'foramen cochleae') opening into the RST. The semicircular canals are very small in diameter relative to the large vestibular chamber. The anatomy of *Yurlunggur* appears very similar (Scanlon, 2006).

7.5.6.2 Marine Limbed Snakes

Several genera of marine snakes have been described, mostly from Cenomanian deposits in the western Mediterranean region. Again, their phylogenetic placement varies from basal (e.g., Scanlon & Lee, 2000; Scanlon, 2006; Palci et al., 2013b) to alethinophidian (e.g., Zaher & Rieppel, 2002; Wiens et al., 2010; Gauthier et al., 2012). Although several of these snakes preserve articulated skeletons, none has an uncrushed braincase. *Pachyrhachis* was described as having a large plate-like quadrate (Lee & Caldwell, 1998), suggesting ear specialisation, but Polcyn et al. (2005), working with HRXCT data, showed that this shape was an artefact of crushing. The only other relevant element is a slender stapedial shaft (Polcyn et al., 2005), but the size of the footplate is unknown. *Haasiophis* also has a slender quadrate but the stapes is not preserved (Tchernov et al., 2000; Rieppel et al., 2003b). It is therefore not possible to determine whether the ear of early marine snakes resembled that of *Najash* and *Dinilysia*.

7.6 Discussion

The combination of an external tympanic membrane held in a supportive quadrate conch/tympanic crest, a gracile stapes, and a compensatory window in the aLRST permits terrestrial lizards to have acute hearing over a range of frequencies. The middle ear of the iguanian *Crotaphytus collaris* was found to increase the reception of aerial sound by around 35dB over the frequency range of 300-4000Hz (Wever & Werner, 1970), compared to a cat where the increase was 30dB over the same range (although the shorter lagena obviously limits the discriminatory ability of the squamate ear). Until recently, the vestibular apparatus had received less attention than the rest of the ear but this is beginning to change as HRXCT and SRμCT scanning allow access internal structures (e.g., Boistel et al., 2011).

The body of work that exists on extant lepidosaurs permits a degree of confidence in interpretations of fossil taxa. The tympanic crest and lateral conch on the quadrate of stem-lepidosaurs and early rhynchocephalians provide compelling evidence that early lepidosaurs had a tympanic middle ear, but this was coupled with a suboptimal compensatory mechanism that probably reduced overall acuity. By subdividing the

metotic fissure and expanding the lateral aperture of the recessus scalae tympani (aLRST), squamates developed a more efficient compensatory system and an extended hearing range. On current evidence, rhynchocephalians never developed an equivalent mechanism and derived members of the group subsequently lost the tympanic ear, perhaps in conjunction with the evolution of an efficient horizontal (pro-oral) jaw action that allowed shearing (Jones, 2008; Jones et al., 2012).

The squamate ear was also adapted in response to specialist lifestyles, although the fossil record of each of the key changes is missing. Arboreal climbers like chameleons appear to have sacrificed efficient hearing for a better visual system and feeding strategy, but the earliest known fossil chameleon skulls (e.g., Rieppel et al., 1992) are referable to living genera and already had an atympanic columnar quadrate. The same problem exists for amphisbaenians where the first known skulls can be assigned to living genera (or their close relatives). Burrowers and derived marine lizards independently lost the tympanic membrane and were presumably reliant mainly on substrate borne/water borne sound. Nonetheless, they responded in different ways - burrowers by enlarging the stapes and its footplate to form an inertial element, and mosasaurs by expanding the quadrate into a bulla and constraining a slender stapes (by the stapedia meatus, soft tissue, fenestral ridge, and stapedia groove) so as to resist inward displacement due to pressure changes during diving.

Understanding how the squamate ear has responded to burrowing versus marine swimming impacts on current arguments as to the ancestral lifestyle of snakes. What may be called the traditional view hypothesises that snakes arose from terrestrial lizards (e.g., Zaher & Scanferla, 2012; Hsiang et al., 2015) with a secretive (burrowing or semi-burrowing lifestyle) (e.g., Camp, 1923; Apesteguía & Zaher, 2006; Reeder et al., 2015), is consistent with their reduced eyes (Walls, 1940, but see Simões et al., 2015), reinforced skulls, and trunk-tail proportions (e.g., Wiens & Slingluff, 2001; Wiens et al., 2006). Berman and Regal (1967) also considered the ear of living snakes to reflect a burrowing ancestry. A second hypothesis, originally proposed by Cope (1869) but more recently championed by Lee, Caldwell and collaborators (e.g., Lee, 1997; Caldwell & Lee, 1997; Caldwell, 2001), proposes that snakes evolved directly from early marine mosasaurs ('dolichosaurs'). The 'dolichosaur' quadrate, as exemplified by *Pontosaurus*, suggests these lizards may still have had a tympanic middle ear, although confirmation of that would require data on the rest of the ear, which remains unknown. In contrast, where described (*Najash*, *Dinilysia*), the ear of stem-snakes (or stem-alethinophidians) had the large stapedia footplate of lizard burrowers, although probably not the re-entrant fluid system that characterises the ear of extant snakes. However, the ear of early marine snakes is also unknown.

To a large degree, a fuller understanding of lepidosaurian ear evolution is dependent on the recovery of new and more complete material of stem-lepidosaurs, early rhynchocephalians, stem-squamates, stem- and basal snakes, stem-amphisbaenians, and early mosasaurs. However, in the interim, there exists a considerable amount of three-dimensional skull material of many of these groups in museum collections. These would benefit from ear-focused (rather than character-scoring) re-study, especially if HRXCT or SR μ CT scanning is employed. Moreover, given the large amount of mosasaurid material in collections world-wide, there is clearly scope for a detailed comparative study of the mosasaur ear region (quadrate, braincase, inner ear) in relation to ear function and lifestyle.

7.7 Summary

Fossil evidence provides compelling evidence that stem-lepidosaurs had a tympanic ear, and that this ear was inherited by both early rhynchocephalians and early squamates. The tympanic membrane appears to have been lost in more derived rhynchocephalian lineages, perhaps in association with the evolution of a pro-oral shearing bite. In squamates, subdivision of the metotic fissure and the addition of a compensatory window in the apertura lateralis of the recessus scalae tympani would have improved sound perception and extended the frequency range.

The efficient tympanic ear of squamates was modified in burrowing lizards and amphisbaenians on the one hand, and in aquatic mosasaurs on the other, to allow for perception of either substrate- or water-borne sound. Although these two strikingly different lifestyles show some similarities (e.g., loss of the tympanic membrane and air-filled middle ear), burrowers and swimmers differ in the size of the stapedial footplate and the shape of the quadrate. The ear of snakes more closely resembles that of burrowers than that of swimmers, but the ear of early snakes remains incompletely known.

Reconstruction of the early history of the lepidosaurian ear (stem-taxa, extinct rhynchocephalians, early lizards) remains limited by a lack of three-dimensional early fossils, and by a tendency to focus descriptions of existing specimens on characters of phylogenetic rather than functional significance. Where three-dimensional fossils exist (e.g. stem-lepidosaurs, rhynchocephalians, early lizards and snakes), greater use HRXCT and SR μ CT imaging, as available, could provide valuable new data on middle and inner ear anatomy. The mosasaur ear would benefit from a focused study that links ear anatomy (quadrate, stapes, braincase foramina, vestibular apparatus) to postcranial specialisations in a more rigorous way.

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